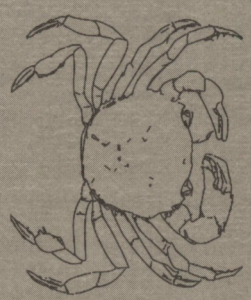
THE FRESHWATER CRABS OF AMERICA

Family Trichodactylidae and Supplement to the Family Pseudothelphusidae



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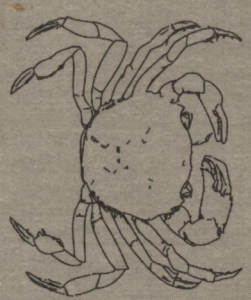

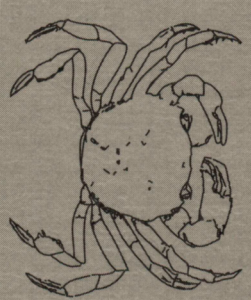

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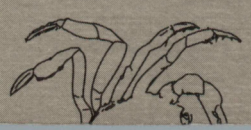

FAUNE TROPICALE XXXI

THE FRESHWATER CRABS OF AMERICA

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Légende de couverture / *legend for the crab represented in the cover : Sylviocarcinus piriformis* (Pretzmann, 1968), young male from the Maracaibo Lake basin, carapace breadth 36 mm

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THE FRESHWATER CRABS OF AMERICA

Family
Trichodactylidae
and Supplement
to the Family
Pseudothelphusidae

GILBERTO
RODRÍGUEZ

Editions de l'Orstom

INSTITUT FRANÇAIS DE RECHERCHE POUR LE
DÉVELOPPEMENT EN COOPÉRATION

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CONTENTS

PRÉFACE

En présentant, en 1982, le mémoire du Dr Gilberto RODRÍGUEZ *sur les Pseudothelphusidae, je soulignais l'intérêt, l'utilité et la qualité de cet ouvrage traitant de l'une des deux familles de crabes propres aux eaux douces néotropicales et largement distribuées dans ce milieu. Offrant, comme beaucoup de Décapodes d'eau douce, une forte variabilité morphologique, ces crustacés étaient d'une identification souvent malaisée : si de nombreux genres, sous-genres, espèces et sous-espèces en avaient été décrits, le groupe n'avait jamais fait l'objet d'une étude systématique d'ensemble comportant une recherche sérieuse des synonymies et l'énoncé des caractères propres à chaque taxon reconnu comme valide.*

Ce premier mémoire constituait une excellente remise en ordre de la famille des Pseudothelphusidae. Fondé sur l'examen d'un matériel considérable, incluant en particulier les collections du Muséum national d'Histoire naturelle étudiées par Mary RATHBUN *dans sa grande monographie parue en 1904-1905 sous le titre «Les crabes d'eaux douce», il est apparu à l'usage comme un instrument d'identification désormais indispensable dans toute recherche portant sur cette famille.*

Le Dr G. RODRÍGUEZ *complète ici son oeuvre en nous proposant une révision des Trichodactylidae, dont la distribution et l'écologie diffèrent notablement de celles des Pseudothelphusidae. En effet, alors que ceux-ci sont cantonnés dans les régions montagneuses au nord de l'Amazone, avec une large extension à travers l'Amérique centrale, jusqu'au nord du Mexique, les Trichodactylidae habitent principalement les plaines côtières et les grands bassins fluviaux sud-américains, jusqu'à l'Uruguay au sud, toujours à basse altitude. Moins diversifiée, comptant moins de formes décrites, mais posant les mêmes problèmes d'identification, cette seconde famille est ici traitée comme la première, avec, outre des remarques générales sur le choix et la signification des caractères morphologiques retenus, une révision taxonomique complète et détaillée, incluant la description de plusieurs espèces nouvelles. On trouvera ainsi dans le présent ouvrage, et pour chaque taxon reconnu, une liste des synonymies et des principales références, une diagnose ou une description substantielle, en même temps que des remarques sur les variations, les affinités et la distribution. Pour chaque espèce, la liste du matériel examiné et les données relatives aux types sont également fournies. Enfin, aux différents niveaux taxonomiques, les identifications sont facilitées par des clefs dichotomiques bien construites et par une excellente illustration, l'utilisateur étant de surcroît aidé par une importante bibliographie et par l'index.*

Si la systématique des Pseudothelphusidae repose en grande partie sur la conformation des appendices sexuels mâles, les gonopodes, celle des Trichodactylidae fait aussi appel à d'autres caractères somatiques,

nombreux, à valeur diagnostique. G. RODRÍGUEZ a pu, de ce fait, recourir à une analyse cladistique qui l'a orienté vers une classification originale, laquelle s'écarte sensiblement de celles, elles-mêmes diverses, proposées dans le passé. Sur le plan pratique, ce nouvel arrangement a l'avantage de la simplicité, puisque les sous-genres et sous-espèces se trouvent, soit élevés respectivement aux rangs de genres et d'espèces, soit placés en synonymie. La nomenclature du groupe, devenue tri-ou quadrinominale par l'action de certains spécialistes des crabes d'eau douce, reprend ainsi une forme strictement binominale.

On notera encore que, en dehors de son utilisation taxonomique, l'analyse cladistique conduit l'auteur à séparer très nettement les Trichodactylidae des Pseudothelphusidae sur le plan phylétique et à les rapprocher au contraire d'une famille de crabes marins, celle des Portunidae. De même, après avoir distingué plusieurs groupements géographiques, c'est encore à la lumière des relations cladistiques qu'il interprète les particularités et l'origine de la distribution actuelle des différents genres et espèces.

Au cours des dix dernières années, beaucoup de chercheurs se sont intéressés aux crabes d'eau douce américains. En ce qui concerne les Pseudothelphusidae, de nombreuses espèces et plusieurs genres ont été décrits comme nouveaux et se sont ajoutés à ceux recensés en 1982. Aussi, dans un souci d'actualisation, G. RODRÍGUEZ a-t-il rassemblé l'essentiel des données récemment acquises sur cette famille en un supplément inséré à la fin du volume qu'il publie aujourd'hui.

Pour sa nouvelle et importante contribution à la connaissance des eaux douces du Nouveau Continent, le Dr G. RODRÍGUEZ a droit à nos félicitations et à nos remerciements. Mais il convient en même temps de rendre hommage à l'organisme qui assure l'édition du mémoire : en l'accueillant dans la série Faune tropicale, *l'Institut français de recherche pour le développement en coopération (Orstom) manifeste une fois de plus son intérêt pour des travaux d'ordre systématique, conscient que leur réalisation est un préalable au développement des recherches biologiques, tout spécialement dans le domaine de l'écologie.*

Jacques FOREST
Professeur au Muséum national d'Histoire naturelle de Paris

RÉSUMÉ

Les crabes d'eau douce d'Amérique : famille des Trichodactylidae, et supplément à la famille des Pseudothelphusidae

Les crabes de la famille des Trichodactylidae sont un élément important de la faune des grandes rivières et lacs de basse plaine dans les plus grands bassins continentaux à l'est des Andes, c'est-à-dire ceux de l'Amazone, de l'Orénoque, du Magdalena, et du Paraguay-Paranà. On trouve aussi deux genres, isolés de cette région principale, au Mexique, près de l'isthme de Tehuantepec ; parmi les cinq espèces mexicaines, trois sont cavernicoles, une est épigée, et la dernière se rencontre dans les deux milieux.

Ces crabes, comme toutes les autres espèces d'eau douce groupées auparavant dans la famille des Potamidae Ortmann, 1896, appartiennent à la section des Heterotremata Guinot, 1977, regroupant les brachyoures chez lesquels l'orifice génital de la femelle est sternal, l'orifice du mâle pouvant être coxal ou coxo-sternal. Chez toutes les espèces d'eau douce, l'orifice est coxal, mais le pénis est logé dans une gaine péniale de position variable selon la famille. Chez les Pseudothelphusidae la gaine péniale se situe entre le bord postérieur du 7e épisternite et le bord antérieur du 8e sternite, suggérant une étape primitive, conduisant aux types d'orifices localisés dans la suture 7/8 des Ocypodidae et Pinnoteridae.

Chez les Trichodactylidae et quelques crabes d'eau douce asiatiques, la gaine péniale se situe au milieu du 8e sternite, entourée par le 7e épisternite et un lobe sternal rudimentaire. Une localisation similaire, et les mêmes structures auxiliaires, s'observent chez les crabes de la famille des Portunidae. Les deux familles partagent aussi les caractères suivants dans leur carapace et leurs appendices : présence d'un «lobe portunien» sur l'angle interne de l'endopodite du premier maxillipède qui, chez les Trichodactylidae, forme une expansion latérale ou s'enroule pour former une projection ovale ; présence d'une suture orbitaire ; orbites entières ; antennules pliées transversalement ; carpe du troisième maxillipède articulé près de l'angle antéro-latéral du mérus ; pattes ambulatoires comprimées, dépourvues d'épines, avec le propode et le dactyle frangés de soies. On peut ajouter aussi la forme du premier gonopode mâle de quelques Trichodactylidae, qui est simple, allongé, avec la portion distale s'amincissant régulièrement jusqu'à une fine pointe couverte de fortes épines coniques et avec l'orifice apical (gonopore) en forme de V, similaire au gonopode de *Carcinus maenas* et d'autres Carcininae.

La sous-famille des Carcininae est utilisée comme groupe externe (*out-group*) pour la polarisation des caractères dans l'analyse cladistique parce que c'est, parmi les Portunoidea, celle qui présente le plus d'affinité avec les Trichodactylidae. Cette analyse s'appuie sur les caractères de la carapace et du plastron, les structures respiratoires annexes (orifice supérieur des canaux respiratoires, l'endopodite du premier maxillipède, le troisième maxillipède, les épines péristomiales, les orbites et l'article basal de l'antenne), les structures reproductrices (gaine péniale, abdomen du mâle, premier et second gonopodes), et les péréiopodes.

Le cladogramme résultant de l'analyse cladistique est à la base de la classification adoptée dans cet ouvrage. Deux groupes sont séparés au niveau des sous-familles : les Trichodactylinae H. Milne Edwards, 1853 (genres *Trichodactylus* Latreille, 1828, *Mikrotrichodactylus* Pretzmann, 1968, *Rodriguezia* Bott, 1969, *Avotrichodactylus* Pretzmann, 1968), et les Dilocarcininae Pretzmann, 1978. Cette dernière sous-famille est divisée en tribus : Holthuisiini Pretzmann, 1978 (genre *Sylviocarcinus* H. Milne Edwards, 1853), Valdiviini Pretzmann, 1978 (genres *Valdivia* White, 1847, et *Forsteria* Bott, 1969), Dilocarcinini Pretzmann, 1978 (genres *Zilchiopsis* Bott, 1969, *Fredilocarcinus* Pretzmann, 1978, et *Dilocarcinus* H. Milne Edwards, 1853). Cette classification diverge cependant du cladogramme par la validation du genre *Zilchiopsis* bien que les espèces du genre soient partagées entre les tribus des Holthuisiini et des Dilocarcinini dans le cladogramme.

Dans cet arrangement taxonomique, lequel diffère des classifications employées par d'autres auteurs, tels que RATHBUN (1906), PRETZMANN (1968b) et BOTT (1969) (Appendice 1), 41 espèces sont reconnues dans la famille, parmi lesquelles 5 sont nouvelles pour la science : *Trichodactylus kensleyi, Avotrichodactylus oaxensis, Dilocarcinus truncatus, D. bulbifer* et une espèce de *Sylviocarcinus* classifiée au niveau générique seulement. La partie systématique comprend des descriptions détaillées et des illustrations de toutes les espèces de la famille, aussi bien que les données morphométriques pour chacune. Les distributions géographiques détaillées sont enregistrées, avec un répertoire de localités à l'appui.

Les aires de répartition des espèces sudaméricaines correspondent à 3 types : (1) deux espèces, *Valdivia serrata* et *Sylviocarcinus devillei*, possèdent de larges aires centrées dans l'Amazone, (2) trois espèces couvrent de larges aires comprenant les bassins de l'Amazone, du Madeira et du Paraná, (3) quelques espèces sont restreintes à de petits territoires dans le cours supérieur de l'Amazone et ses tributaires, (4) un dernier groupe est endémique des bassins périphériques à l'Amazone et à l'Orénoque.

Toutes les espèces des cours inférieur et moyen de l'Amazone, de l'Orénoque, et du Paraná ne vivent qu'à de basses altitudes, mais un petit groupe atteint des hauteurs modérées, 350-550 m, dans les Guyanes, les flancs des Andes, la vallée du Magdalena et quelques autres bassins intérieurs. Il y a peu de barrières effectives pour les crabes de ces basses altitudes. En outre, dans le cas de plusieurs rivières de basses terres, une nappe d'eau couvre les plaines pendant la saison pluvieuse. Dans ces conditions, la haute «porosité» des barrières est responsable des aires du type (1) et (2) déjà mentionnées, et même des aires les plus grandes des espèces endémiques des bassins périphériques. Cependant, les espèces du type (3) n'ont pas été capables d'étendre leur distribution aux cours moyen et inférieur de ces rivières.

A une échelle plus grande, l'Amazone et d'autres bassins majeurs communiquent entre eux par un labyrinthe de canaux et de plaines d'inondation. Ainsi, l'Amazone communique avec l'Orénoque par la bifurcation du Cassiquiare, avec les bassins guyanais par le Rio Branco, et avec le système des rivières Paraguay-Paraná par la plaine marécageuse du Madeira supérieur. Ainsi la distribution des espèces de type (2) déjà mentionnées corres-

pond à la communication entre l'Amazone et le Paraná. Au nord, la distribution de *Valdivia serrata* depuis l'Amazone jusqu'aux plaines du sud de l'Orénoque et le plateau guyanais est le produit de la bifurcation du Cassiquiare et de la zone inondée du Rupununi.

La distribution géographique montre quelques disjonctions de «sister groups» du cladogramme entre le Mexique et l'Amérique du Sud, et entre groupes de bassins de l'Amérique du Sud. Les deux disjonctions Mexique-Amérique du Sud concernent les trois clades formés par les espèces d'*Avotrichodactylus* et les autres Trichodactylinae, et les genres *Rodriguezia* et *Trichodactylus*. L'explication de ces disjonctions par une hypothèse dispersaliste comporte l'établissement d'une voie de migration théorique à travers l'Amérique Centrale après le Pliocène (3,1 millions d'années). L'absence d'espèces intermédiaires dans cette région, le long intervalle de temps géologique nécessaire à l'évolution et à la dispersion d'espèces cavernicoles, et l'origine polyphylétique des deux genres mexicains, sont les objections principales à cette hypothèse dispersaliste. D'un autre côté, le postulat d'une hypothèse vicariante demande la continuité des aires de distribution entre le Mexique et l'Amérique du Sud pendant l'époque pré-crétacée, quand l'Amérique du Sud faisait partie du continent gondwanien ; ce contact de plaques aurait permis la première expansion des Trichodactylidae avant 125 millions d'années, dans le crétacé inférieur.

Les disjonctions sudaméricaines intéressent les paires d'espèces («sister species») *Sylviocarcinus devillei-S. piriformis* dans les vallées de l' Amazone et du Maracaibo, respectivement, et les deux groupes *Trichodactylus kensleyi-T. quinquedentatus* et *Sylviocarcinus devillei-S. piriformis* dans les vallées de l'Amazone et du Magdalena. Selon une hypothèse de Rod (1981), le fleuve Orénoque s'ouvre dans le bassin du Maracaibo à l'Eocène inférieur ; l'isolement des deux bassins date de l'Oligocène inférieur, et par conséquent la date de colonisation du bassin de Maracaibo par *Sylviocarcinus* doit être fixée avant cette époque. Une communication directe de la vallée du Magdalena avec l'Orénoque ou l'Amazone jusqu'à l'époque miocène ne peut être exclue. La différentiation allopatrique des paires d'espèces formées par *Trichodactylus kensleyi-T. quinquedentatus* et *Sylviocarcinus devillei-S. piriformis* doit être postérieure à cette époque, quand la vallée inférieure de la Magdalena s'isole des autres bassins.

Le postulat d'une hypothèse vicariante dans le cas des disjonctions mexicaines-sudaméricaines, comme les explications tectoniques pour les disjonctions sudaméricaines, requiert une longue durée de temps pendant laquelle l'évolution des Trichodactylidae a pu avoir lieu. Cette famille se présente en effet comme un groupe très ancien par sa grande diversité morphologique et ses mécanismes respiratoires primitifs ; on ne connaît cependant pas de formes fossiles qui permettraient de préciser son ancienneté. Les premiers restes fossiles connus des Portunoidea, ancêtres potentiels des Trichodactylidae, datent du crétacé inférieur. Les genres de la sous-famille des Trichodactylinae présentent les caractères les plus primitifs de la famille ; ils sont dispersés sur un vaste territoire, avec leurs espèces séparées par des distances considérables. Ce groupe, tel que le montre le cladogramme, constitue une première branche qui a évolué indépendamment pendant une très longue période de temps. D'un autre côté, les espèces de Trichodactylinae mexicaines, avec leur mode de vie troglobie et leurs aires de distribution réduites et isolées, doivent représenter les restes d'une faune très ancienne.

INTRODUCTION

The freshwater crabs are an important faunal element in the inland waters of tropical America. These crabs belong to two different families: (1) the Pseudothelphusidae are found, with few exceptions, in mountainous streams up to an altitude of 3,000 meters, within a geographical range which extends from the State of Sonora in Northern Mexico, to Central Peru. With three exceptions, they do not extend south of the Amazon River. (2) The Trichodactylidae inhabit the large rivers and lakes of the low lands in the major continental basins of South America east of the Andes, that is, the Amazonas, Orinoco, Magdalena, Paraguay-Paranà and the smaller basins of the Guianese and Brazilian coastal plains. Isolated from this main area, there are also 5 species in the states of Tabasco, Veracruz, Chiapas and Oaxaca in southern Mexico. With the exception of one Colombian species reported from Nicaragua, and of one mainland species which extends into Trinidad, the Trichodactylidae are absent from Central America and the Antilles.

The present monograph deals with the cladistics, systematics and biogeography of the family Trichodactylidae as part of a revision of the freshwater crabs of America, published under the auspices of the Orstom (Institut français de recherche scientifique pour le développement en coopération); the Pseudothelphusidae were already treated in a previous monograph of the series *Faune tropicale* (RODRÍGUEZ, 1982).

The taxonomic structure of the family

The first description of a species of Trichodactylidae, *Cancer orbicularis*, was published by MEUSCHEN (1781). But since his *Index Zoophylacium Gronovianum* is not accepted as a precedent in binomial nomenclature, its junior synonym, *Cancer septemdentatus* Herbst, 1783, is considered the first valid name proposed for a species of this family. From 1825 to 1901, LATREILLE, Henri MILNE EDWARDS, RANDALL, EYDOUX & SOULEYET, GERSTÄKER, WHITE, Alphonse MILNE EDWARDS, VON MARTENS, KINGSLEY, GÖLDI, STIMPSON, RATHBUN, ORTMANN, NOBILI, and MOREIRA, added 26 new species. RATHBUN's monograph of 1906 included 29 species, 9 of which were new species. During the first half of the twentieth century only three new species were described by PEARSE (1911), MOREIRA (1912) and PARISI (1923), respectively, but from 1966 there have been a relatively copious literature. Thirteen new species have been published in the contributions by BOTT, COTTARELLI and ARGANO, PRETZMANN, PRETZMANN and SCHMITT, PRETZMANN and MAYTA, RODRÍGUEZ and MANRIQUE, and SMALLEY and RODRÍGUEZ, bringing the total number of published specific names to 52.

From this large number of taxa, probably no more than 41 are good species. As a result, and notwithstanding the relatively modest dimensions of the family, its systematic is encumbered with a large

remnant of synonyms. In addition, BOTT and PRETZMANN have described 7 and 15 subspecies each. At least two of PRETZMANN's subspecies are in fact distinct species, but others cannot be differentiated from the typical forms. This situation is further complicated by the existence of different competing systems of genera.

The taxonomic arrangement used by RATHBUN (1906) for the family reflected the work done by previous workers during the nineteenth century. LATREILLE (1828), WHITE (1847a) and H. MILNE EDWARDS (1853), respectively, had erected *Trichodactylus, Valdivia, Sylviocarcinus*, and *Dilocarcinus* as separate genera. RATHBUN (1906) gave generic status only to *Trichodactylus*, reduced *Valdivia* and *Dilocarcinus* to subgenera of the first, and discarded *Sylviocarcinus*. This simple arrangement was used by all latter authors until PRETZMANN (1968b) and BOTT (1969) proposed two alternative systems, with little in common with RATHBUN's and between themselves (Appendix 1).

The differences in rank between these systems imply also considerable differences in the grouping of the species. For example, the species *Sylviocarcinus pictus* H. Milne Edwards, 1853, is placed by RATHBUN (1906) in the genus *Dilocarcinus*, by BOTT (1969) in the genus *Sylviocarcinus* and by PRETZMANN (1968b) as the type species for his new genus *Holthuisisia*.

List of species

The list that follows indicates the classification employed herein, based on the cladistic analysis presented in the following section, and shows the species numbers refered to in the appendices.

Family TRICHODACTYLIDAE H. Milne Edwards, 1853
Subfamily TRICHODACTYLINAE H. Milne Edwards, 1853

Genus ***Trichodactylus*** Latreille, 1828
1. *Trichodactylus fluviatilis* Latreille, 1828
2. *Trichodactylus maytai* Pretzmann, 1978
3. *Trichodactylus kensleyi*, new species
4. *Trichodactylus petropolitanus* (Göldi, 1886)
5. *Trichodactylus quinquedentatus* Rathbun, 1893
6. *Trichodactylus ehrhardti* (Bott, 1969)

Genus ***Mikrotrichodactylus*** Pretzmann 1968
7. *Mikrotrichodactylus borellianus* Nobili, 1896
8. *Mikrotrichodactylus panoplus* (von Martens, 1869)

Genus ***Rodriguezia*** Bott, 1969
9. *Rodriguezia mensabak* (Cottarelli & Argano, 1977)
10. *Rodriguezia villalobosi* (Rodríguez & Manrique, 1967)

Genus ***Avotrichodactylus*** Pretzmann, 1968
11. *Avotrichodactylus bidens* (Bott, 1969)
12. *Avotrichodactylus constrictus* (Pearse, 1911)
13. *Avotrichodactylus oaxensis*, new species

Subfamily DILOCARCININAE Pretzmann, 1978
Tribe HOLTHUISIINI Pretzmann, 1978

Genus ***Sylviocarcinus*** H. Milne Edwards, 1853
14. *Sylviocarcinus devillei* H. Milne Edwards, 1853
15. *Sylviocarcinus maldonadoensis* (Pretzmann, 1978)
16. *Sylviocarcinus pictus* (H. Milne Edwards, 1853)
17. *Sylviocarcinus piriformis* (Pretzmann, 1968)
18. *Sylviocarcinus* sp.

Tribe VALDIVIINI Pretzmann, 1978

Genus ***Valdivia*** White, 1847
19. *Valdivia camerani* (Nobili, 1896)
20. *Valdivia gila* Pretzmann, 1978
21. *Valdivia harttii* (Rathbun, 1906)
22. *Valdivia latidens* (A. Milne Edwards, 1869)
23. *Valdivia serrata* White, 1847

Genus ***Forsteria*** Bott, 1969
24. *Forsteria venezuelensis* (Rathbun, 1906)

Tribe DILOCARCININI Pretzmann, 1978

Genus ***Zilchiopsis*** Bott, 1969
25. *Zilchiopsis chacei* (Pretzmann, 1968)
26. *Zilchiopsis cryptodus* (Ortmann, 1893)
27. *Zilchiopsis emarginatus* (H. Milne Edwards, 1853)
28. *Zilchiopsis sattleri* Bott, 1969

Genus ***Dilocarcinus*** H. Milne Edwards, 1853
29. *Dilocarcinus argentinianus* (Rathbun, 1906)
30. *Dilocarcinus truncatus*, new species
31. *Dilocarcinus bulbifer*, new species
32. *Dilocarcinus castelnaui* H. Milne Edwards, 1853

33. *Dilocarcinus dentatus* (Randall, 1839)

34. *Dilocarcinus laevifrons* Moreira, 1901

35. *Dilocarcinus medemi* Smalley & Rodriguez, 1972

36. *Dilocarcinus niceforei* (Schmitt & Pretzmann, 1968)

37. *Dilocarcinus pagei* Stimpson, 1861

38. *Dilocarcinus septemdentatus* (Herbst, 1783)

39. *Dilocarcinus spinifer* H. Milne Edwards, 1853

Genus ***Fredilocarcinus*** Pretzmann, 1978

40. *Fredilocarcinus raddai* (Pretzmann, 1978)

41. *Fredilocarcinus musmuschiae* (Pretzmann & Mayta, 1980)

species *incertae sedis*

42. *Trichodactylus (Dilocarcinus) gurupensis* Rathbun, 1906

43. *Trichodactylus petropolitanus paranensis* Bott, 1969

44. *Trichodactylus (Valdivia) faxoni* Rathbun, 1906

Collecting localities

The exact location of collecting places is indispensable for the delimitation of the ranges of the species. This task, however, is fraught with difficulties in such a vast area as the plains of South America, overall when the collector only gives the name of a small village, a stream or even the nearest farm. For these reasons I have appended a gazetteer (Appendix 2) of all the localities mentioned in the text or found in the literature, compiled with the help of many sources, too numerous to be listed. The Columbia Limpicott Gazetteer of the World (1951) was used in many instances. The location of several collecting stations recorded by BOTT (1969) was provided by Dr Harald SIOLI through the courtesy of Dr Hans KLINGE.

Repositories and abbreviations

The materials reported herein are deposited in the following institutions: Instituto Venezolano de Investigaciones Cientificas, Caracas (Ivic); Museo de Biologia, Universidad Central de Venezuela, Caracas (MB); Museo de la Sociedad de Ciencias Naturales La Salle, Caracas (LS) ; Museo de Historia Natural De La Salle, Bogota (LSB); Museo de Historia Natural, Universidad Nacional de Bogota (ICN-MHN); Museo de Historia Natural, Universidad Nacional de San Marcos, Lima (ML); Museo de la Universidad de Santa Ursula, Recife (Usu); Museo de Biologia, Universidad Nacional Autonoma, Mexico (Unam); Muséum national d'histoire naturelle, Paris (MP); US National Museum, Washington (USNM); Zoologisches Museum, Hamburg (MH); Zoologische Staatssammlung, Munich (ZSM); Rijksmuseum van Naturlijke Historie, Leiden (RNH). Other abbreviations employed are: Disca = Division de Investigaciones Sobre Contaminacion Ambiental, Venezuela; cl = carapace length; cb = carapace breadth; alt = altitude of collecting localities.

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I - CLADISTIC ANALYSIS OF THE FAMILY TRICHODACTYLIDAE

The systematic position of the TRICHODACTYLIDAE

As has being pointed out by GUINOT (1978), the position of the sexual openings is a character of fundamental phylogenetical significance in the Brachyura. All the freshwater crabs formerly grouped in the family Potamidae belong in the section Heterotremata Guinot, 1977, i.e. brachyuran crabs in which the female opening is sternal, but the male opening could be coxal or coxo-sternal. The heterotrematous condition suggests an evolutionary process begining with the location of the penis in the coxa of the fifth pereiopod; in successive stages the penis is lodged in a sternal groove which latter forms a channel due to the disposition of the sternites in this area; finally 7th and 8th sternites completely cover the channel and the penis is implanted in the sternum, although the male duct still reaches the coxa.

In the Trichodactylidae, as well as in some Asiatic freshwater crabs like *Sommaniathelphusa sexpunctata* (Fig. 11C), the penial groove is located along the 8th sternite; this disposition suggests a primitive condition which could have led to the situation found in the Grapsidae. In some species of this latter family the penis is implanted near the lateral margin of the 8th sternite (Fig. 11D, E), while in others it is located away from the margin, but leaving a slight furrow which suggests a progressive migration of the appendage along the mid-line of the sternite (Fig. 11F). From this point of view, the penial groove of the Grapsidae could be considered as the apomorphic state in relation to the one found in the Trichodactylidae and thus unavailable as an out-group for the present cladistic analysis.

The development of the penial groove followed a different path in other freshwater crabs. Thus, in the Pseudothelphusidae, the penial groove is located between the posterior margin of the 7th episternite and the anterior margin of the 8th sternite (Fig. 11G). This is probably a primitive stage in the process leading to the orifices located near the 7/8 sutures in the Ocypodidae and Pinnotheridae, as illustrated by GUINOT (1978, Fig. 3H). Consequently, any close relationship between the two families of neotropical freshwater crabs should be ruled out.

According to the heterotrematous condition of the Trichodactylidae, their closest phylogenetic affinities should be looked for in other members of the Section in which the penial groove is not only rudimentary, but also centrally located along the 8th sternite. Some members of the superfamily Portunoidea satisfy both conditions (Fig.11A) since their penial grooves form a very shallow depression along the 8th sternite. The primitive condition of this groove is reflected also in the 7th episternite which do not overlap the 5th coxa. On

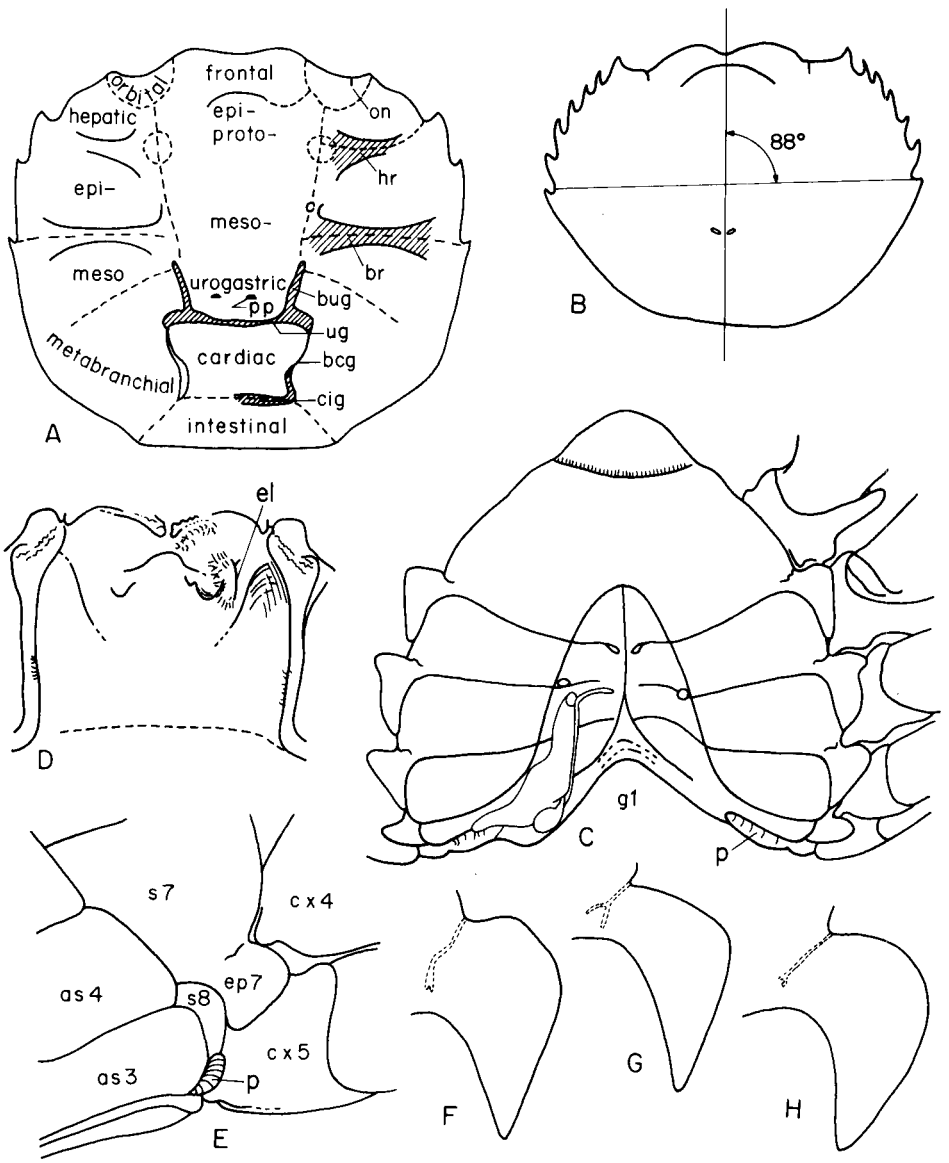

FIGURE 1

A, Carapace of a Trichodactylidae; B, carapace of *Dilocarcinus pagei* with horizontal and vertical axes of symetry; C, plastron of *Trichodactylus quinquedentatus*, male, with abdomen and left gonopods removed; D, buccal frame and endostome in *Trichodactylus fluviatilis*; E, left posterior corner of plastron in *T. fluviatilis*; F-H, fourth epipodites (between 1st and 2nd pereiopods) in *Valdivia serrata*, *Forsteria venezuelensis*, and *Dilocarcinus dentatus*. as3, 3rd abdominal segment; as4, 4th abdominal segment; bcg, branchio-cardiac groove; br, branchial ridge; bug, branchio-urogastric groove; cig, cardio-intestinal groove; cx4, 4th coxa; cx5, 5th coxa; el, elevated line; ep7, 7th episternite; g1, first male gonopod; hr, hepatic ridge; on, orbital notch; p, penis; pp, postgastric pits; s7, 7th sternite; s8, 8th sternite.

the other hand, in some members of the Portunoidea the penial groove is supplemented by a rudimentary sternal lobe (Fig. 11A; r), which is also present and more developed in the Trichodactylidae (Fig. 11B, C; r). This sternal lobe should be considered as an autapomorphy shared by both groups.

Another possible autapomorphy shared by the Trichodactylidae and Portunoidea is the small lobe on the inner angle of the endopodite of the 1st maxilliped ("portunid lobe", Fig. 5A). In the Trichodactylidae it forms a lateral expansion (Fig. 5G-I) or rolls over to form an oval-shaped projection located on the cephalic surface of the endopodite (Fig. 5B-F, K-N).

Finally, the reduced orbital suture present in the Trichodactylidae could be considered the apomorphic state of the well developed suture found at least in some species of Portunidae.

Other characters shared by both groups are the following: (1) orbits complete, (2) antennules folding slantwise or transversely, (3) carpus of third maxilliped articulating at or near the antero-lateral angle of the merus, (4) walking legs compressed, without spines, propodus and dactylus with upper and lower rows of setae.

Most species of Trichodactylidae fit into the definition of the subfamily Carcininae given by STEPHENSON & CAMPBELL (1960): "*legs stout and long, at least one pair as long as chelipeds, last pair with lanceolate dactylus, but otherwise similar to the 3 other pairs. Carapace not broad, antero-lateral borders cut into 4 or 5 teeth. Basal joint of second antenna fixed, longer than broad, lying in longitudinal axis of carapace*". Further, the first male gonopod in many Trichodactylidae is simple, long, with the neck tapering evenly to a fine tip, with the apex provided with stout spines and the apical opening (gonopore) V-shaped. A similar morphology is found in *Carcinus maenas* (see STEPHENSON & CAMPBELL, 1960, Fig. 1A, 2A) and other Carcininae.

According to the preceeding considerations, the Carcininae can be considered as the most likely sister group of the Trichodactylidae and will be used as an out-group for the polarization of characters in the cladistic analysis discussed below.

Characters examined

CARAPACE

The outline of carapace in the Trichodactylidae could be either hexagonal or suborbicular, but always it is slightly wider than long. The hexagonal outline is related to the outline found in some Carcininae, like *Carcinus maenas*, and thus should be considered as the plesiomorphic state of the character. The relative position of the widest part of carapace on the longitudinal axis varies in different species from 36 % of the carapace length in *Zilchiopsis emarginatus* to 57 % in *Mikrotrichodactylus borellianus*. The values show a normal unimodal distribution around a mean of 43.0, with a strong skewness to the left (0.65). The slight bilateral asymetry found in some specimens (Fig. 1B) is associated with a strong development of the left cheliped.

The progressive smoothness of the upper surface is a character often accompanied by the progressive convexity from front to back and in frontal view.

In figure 1A is presented the nomenclature for the regions, grooves, etc., of carapace, used in the description of the species. A more pronounced delimitation of the regions and the presence of ridges and grooves is closer to the condition found in the Carcininae. This is the case of the transbranchial ridge present in several species, the crescent shaped triangular prominence on each side of the mesogastric region in the species of *Valdivia*, and

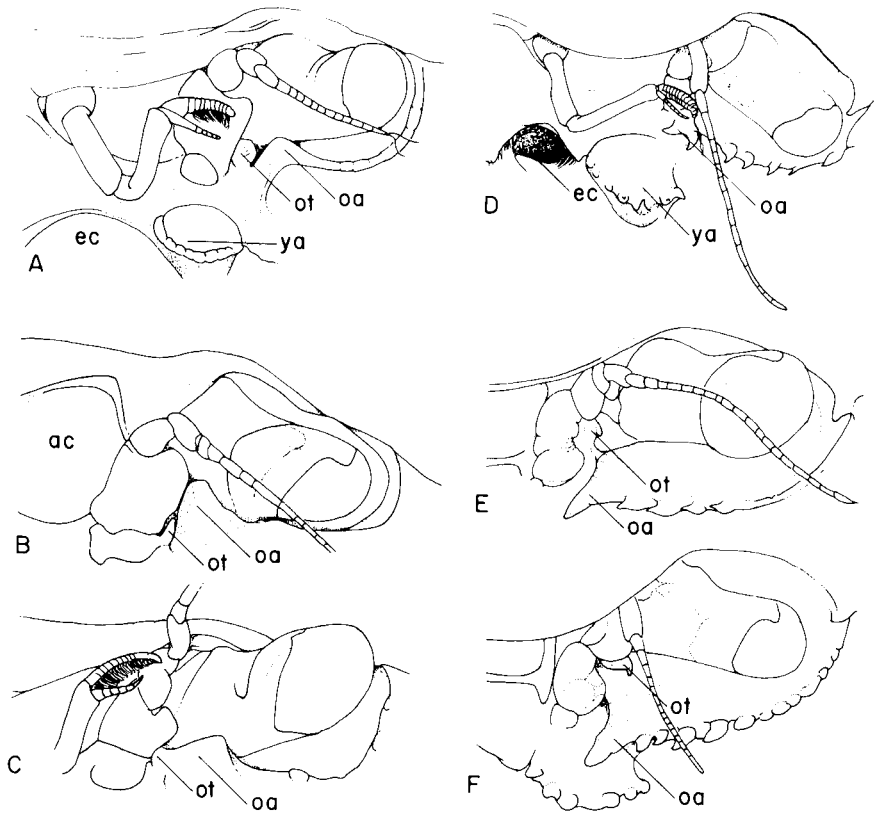

FIGURE 2

Orbital area: A, *Avotrichodactylus constrictus*; B, *Mikrotrichodactylus borellianus*; C, *Valdivia camerani*; D, *Dilocarcinus dentatus*; E, *D. bulbifer*; F, *Fredilocarcinus musmuschiae*. ac, antennal cavity; ec, endostomial cavity; oa, internal orbital angle; ot, occlusive tooth; ya, buccal angle.

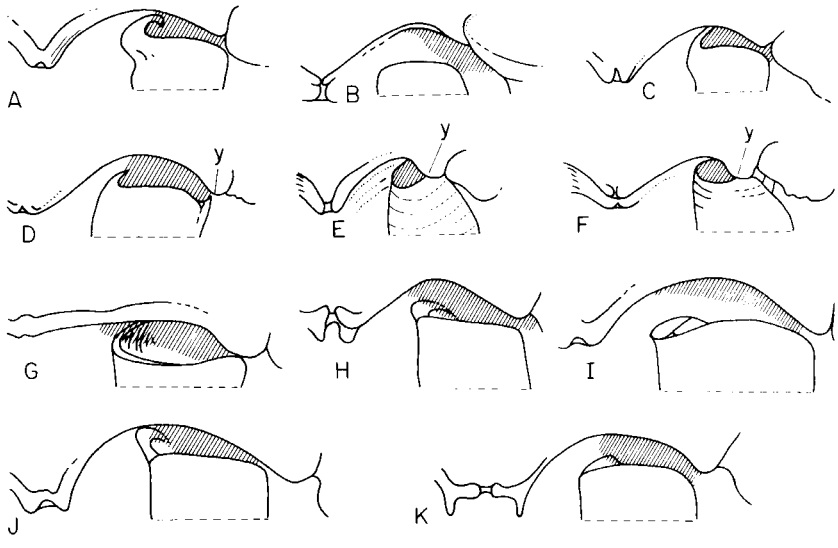

FIGURE 3

Aperture of left efferent channel: A, *Trichodactylus fluviatilis*; B, *T. quinquedentatus*; C, *Avotrichodactylus oaxensis*; D, *T. kensleyi*; E, *Mikrotrichodactylus borellianus*; F, *M. panoplus*; G, *Zilchiopsis emarginatus*; H, *Valdivia serrata*; I, *Sylviocarcinus piriformis*; J, *Z. sattleri*; K, *Dilocarcinus truncatus*. y, lateral yugal lobe.

the transverse cervical groove of *Z. emarginatus*. A similar plesiomorphic state can be assigned to the angulation of the lateral margins, forming a thin ridge directed laterad, versus the margin regularly rounded. The presence or 4-5 large lateral teeth (versus the presence of 6 to 10) is also closer to the number found in the Carcininae.

The front is wider in the Trichodactylidae than in Carcininae. In this subfamily most species have the front cut into teeth, but there are also a few, like *Nectocarcinus integrifrons*, which have the anterior margin entire, similar to the shape of the front in some Trichodactylinae, *Valdivia* and *Sylviocarcinus*. The strong bilobation of the front in other species, particularly in *Dilocarcinus*, is related to the forward projection of the epistome discussed below as a respiratory adaptation. The depth of the frontal sinus was determined as a percentage of the total length of the front (Fig. 17E; a/bx100). In those cases where the sinus was larger than 10%, the front was considered as bilobed (table III).

The postgastric pits, which mark the position of the internal pillars for the insertion of the gastric muscles, are present in the majority of species; their obsolescence in the Trichodactylinae is indeed an apomorphic condition.

The plastron in this family is considerably wide (Fig. 1C). The first and 2nd+3d tergites of male in some species, like *Valdivia serrata*, have deep depressions on both sides, and their surface is conspicuously eroded. The episternites, inserted as supplementary plates between the coxae of successive pereiopods, are delimited from the nearest sternal plate by a suture sometimes reduced to a translucent dendritic pattern reminiscent of the respective suture in the Portunidae.

STRUCTURES RELATED TO RESPIRATION

The environmental constrictions imposed by the freshwater habitat are manifested in the freshwater crabs by adaptations in the respiratory structures (RODRÍGUEZ, 1986). The main adaptations found in the Trichodactylidae concern (1) the reduction of the opening of efferent channels, achieved by transformations in the endostome, folding of the endopodite of 1st maxilliped, prolongation of external angle in the ischium of 3d maxilliped, projection of the two channel arches, and relative projection of the epistome, and (2) the reorganization of the external currents of water by means of the perioral spinulation and the closing of the orbit.

Mouth

The buccal frame is square, bounded distally by the two strong arches of the efferent channels (Fig. 1D). There are no conspicuous endostomial ridges, characteristic of the more advanced portunids, but at least in some *Trichodactylus* a thin elevated line is present on each side (Fig. 1D; el). The function of the endostomial ridges is taken in the trichodactylids by a row of long hairs which restrict the efferent channels to the sides of the endostome.

Aperture of efferent channels

The upper arch of the efferent channels shows a variable degree of curvature in different species of the family. *Zilchiopsis emarginatus* shows the lowest arch (Fig. 3G), whereas *Forsteria venezuelensis* shows one of the higher; the other species are arranged between these extremes. The endopodite of 1st maxilliped restricts the aperture of the channel to a segment of this arch. In *Valdivia* and *Sylviocarcinus* this segment is located at the center, but in *Trichodactylus* it is usually restricted to the lateral corner; in *T. kensleyi, Mikrotrichodactylus borellianus* and *M. panoplus* the aperture is restricted to a small orifice formed by the rolling of the exopodite, a portion of the arch and a lateral yugal lobe (Fig. 3D, E, F; y).

The variability of the arches of efferent channels is reflected in the middle of the epistome where both channels meet to form a mid-gutter. This gutter consists of a single point in *Sylviocarcinus devillei, S. piriformis*, and in the young of *Zilchiopsis emarginatus* (Fig. 4H, K, O); in the other species there are two distinct points, which are farthest apart in *Dilocarcinus dentatus*.

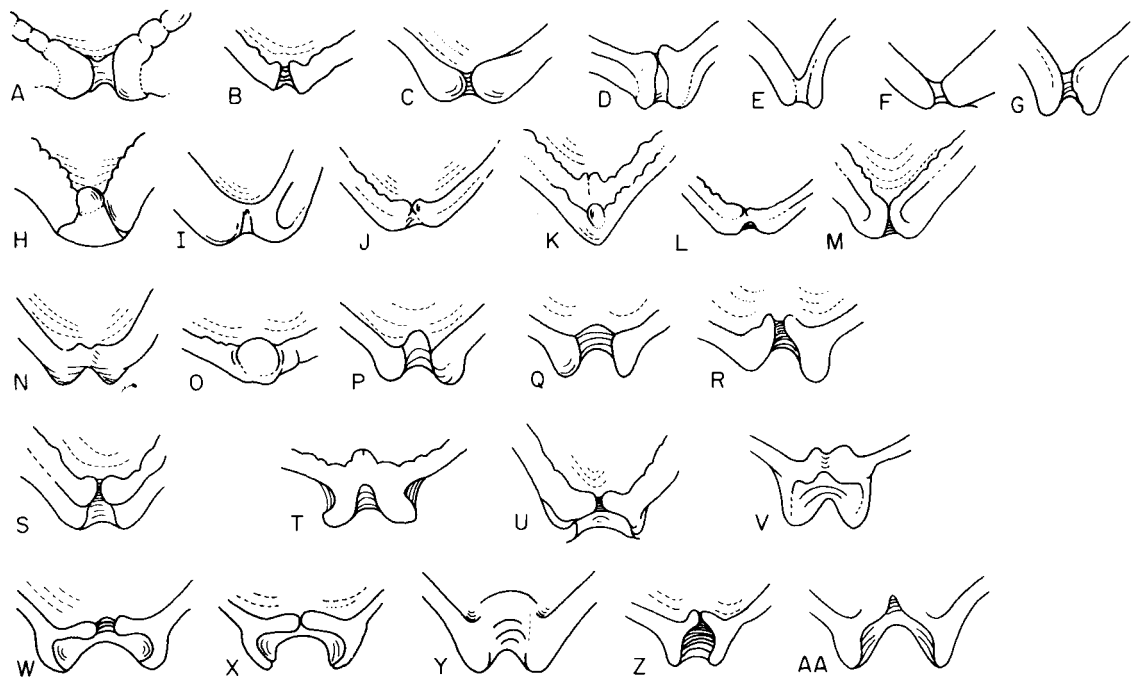

FIGURE 4

Middle gutter of epistome: A, *Trichodactylus fluviatilis*; B, *T. kensleyi*; C, *T. petropolitanus*; D, *T. quinquedentatus*; E, *Mikrotrichodactylus borellianus*; F, *M. panoplus*; G, *Avotrichodactylus oaxensis*; H, *Sylviocarcinus devillei*; I, *S. maldonadoensis*; J, *S. pictus*; K, *S. piriformis* (Maracaibo basin); L, *S.* sp.; M, *S. piriformis* (Magdalena Valley); N, *Valdivia camerani*; O, *Zilchiopsis emarginatus*, young; P, *V. gila;* Q, *V. harttii*; R, *V. serrata*; S, *Forsteria venezuelensis*; T, *Z. emarginatus*; U, *Z. sattleri*; V, *Fredilocarcinus musmuschiae*; W, *Dilocarcinus truncatus*; X, *D. bulbifer*; Y, *D. dentatus*; Z, *D. niceforei*; AA, *D. pagei*.

Endopod of first maxillipeds

The distal margin of the endopod of first maxillipeds forms the lower boundary for the efferent respiratory channels; the portunid lobe, present in the Portunidae and Trichodactylidae, constitutes an accessory structure for the delimitation of the channels on the mesial side. In many portunids, the lobe is separated from the main blade of the endopodite by a deep incision (Fig. 5A). In the Trichodactylidae the mesial side of the blade is separated from the rest of the blade by a prominent hairy ridge which runs longitudinally along the inner (cephalic) surface of the appendage; in all species, except in *Sylviocarcinus piriformis*, the blade is bent over this ridge to form a mesial boundary to the efferent channel (Fig. 2D). In *Mikrotrichodactylus* the portunid lobe is retracted to a lateral position, restricting the channel openings to circular orifices located close to the external buccal angle (Fig. 3E, F).

Third maxillipeds

The general morphology of the third maxillipeds in this family is characterized by (1) the palp articulated at the antero-mesial angle of ischium, (2) the antero-lateral angle of this segment produced into a long, curved spine which forms part of the lower boundary of the efferent channels, and (3) the merus with a longitudinal or oblique depression also present in species of the family Portunidae. For the rest the group displays considerable

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

Peristomial spinulation, orbits and basal antennal articles

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

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

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

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

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

REPRODUCTIVE STRUCTURES

Penial groove

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

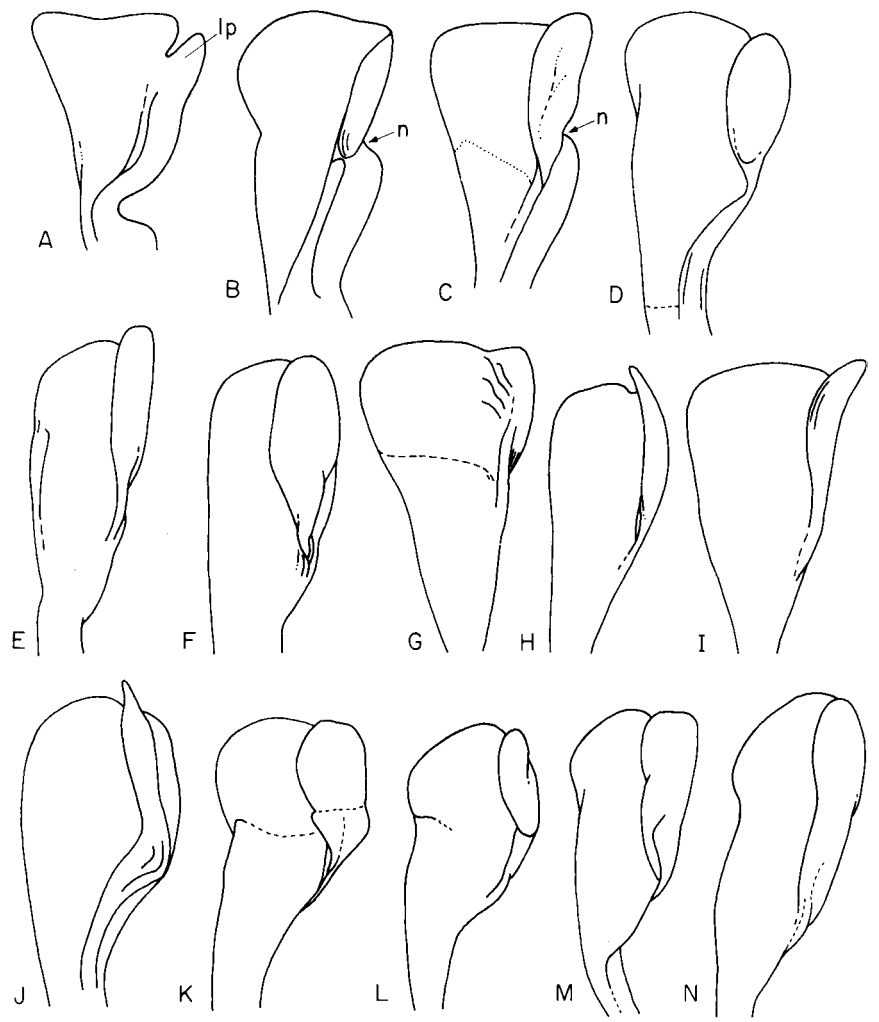

FIGURE 5

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

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

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

Male abdomen

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

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

First male gonopod

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

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

Second male gonopod

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

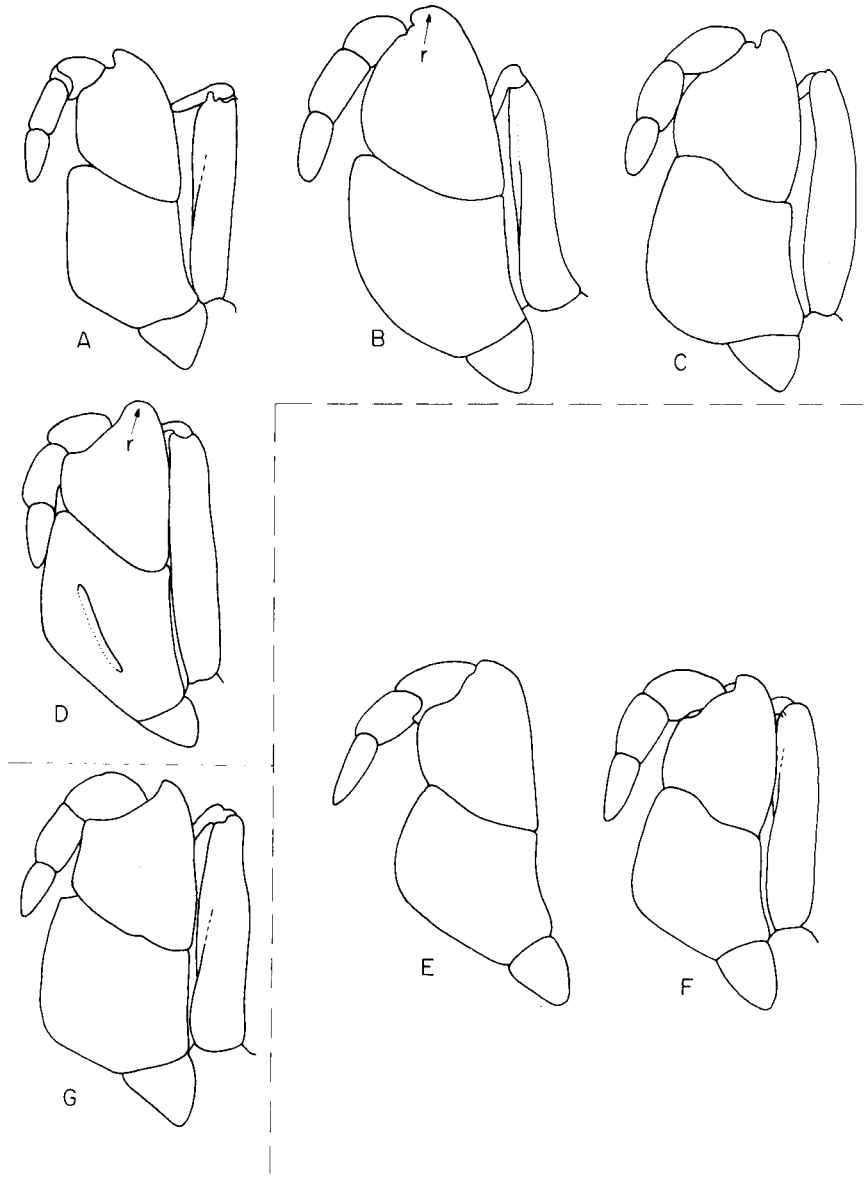

FIGURE 6
Left third maxilliped in Trichodactylidae: A, *Trichodactylus fluviatilis*; B, *T. petropolitanus*; C, *T. kensleyi*; D, *T. quinquedentatus*; E, *Mikrotrichodactylus borellianus*; F, *M. panoplus*; G, *Avotrichodactylus oaxensis*. r, distal external spine.

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

PEREIOPODS

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

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

Data Analysis

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

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

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

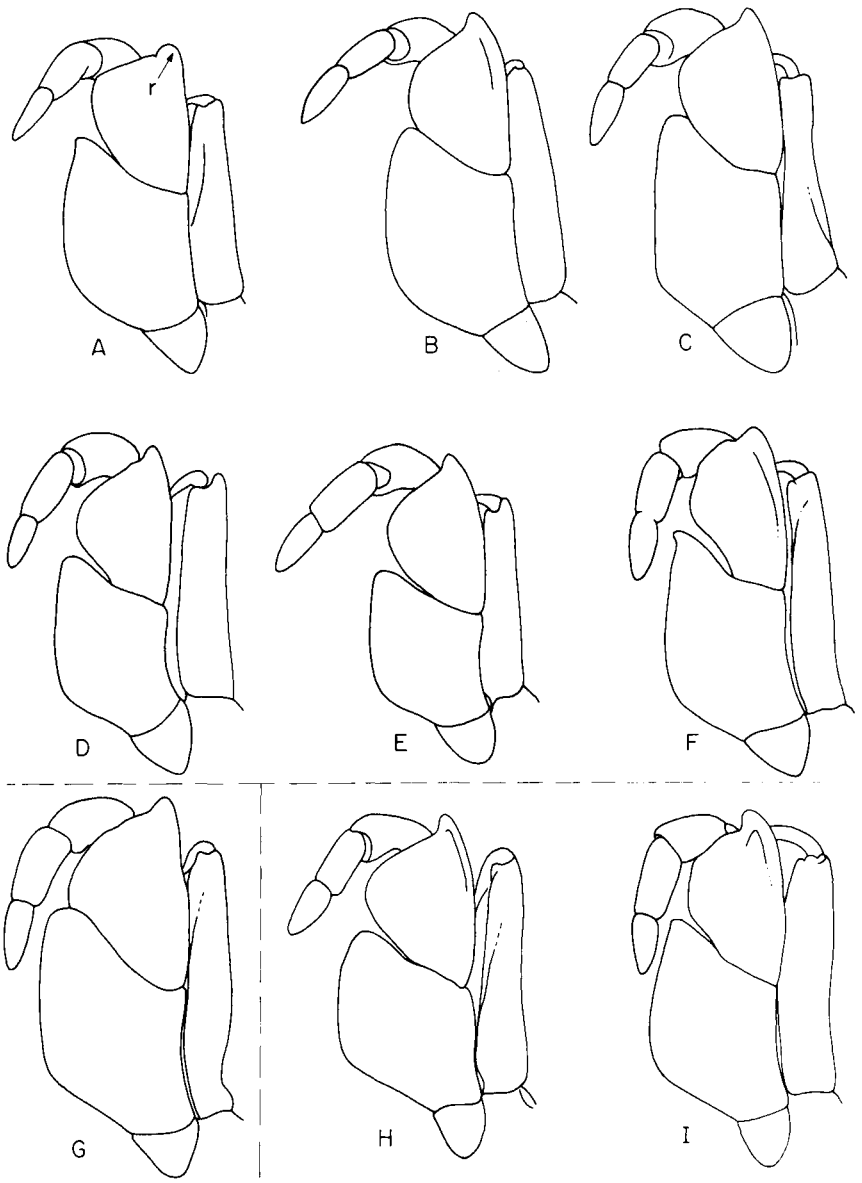

FIGURE 7

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

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

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

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

Subfamily TRICHODACTYLINAE H. Milne Edwards, 1853
- Genus *Trichodactylus* Latreille, 1828
- Genus *Mikrotrichodactylus* Pretzmann, 1968
- Genus *Rodriguezia* Bott, 1969
- Genus *Avotrichodactylus* Pretzmann, 1968

Subfamily DILOCARCININAE Pretzmann, 1978

Tribe HOLTHUISIINI Pretzmann, 1978
- Genus *Sylviocarcinus* H. Milne Edwards, 1853

Tribe VALDIVIINI Pretzmann, 1978
- Genus *Valdivia* White, 1847
- Genus *Forsteria* Bott, 1969

Tribe DILOCARCININI Pretzmann, 1978
- Genus *Zilchiopsis* Bott, 1969
- Genus *Fredilocarcinus* Pretzmann, 1978
- Genus *Dilocarcinus* H. Milne Edwards, 1853

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

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

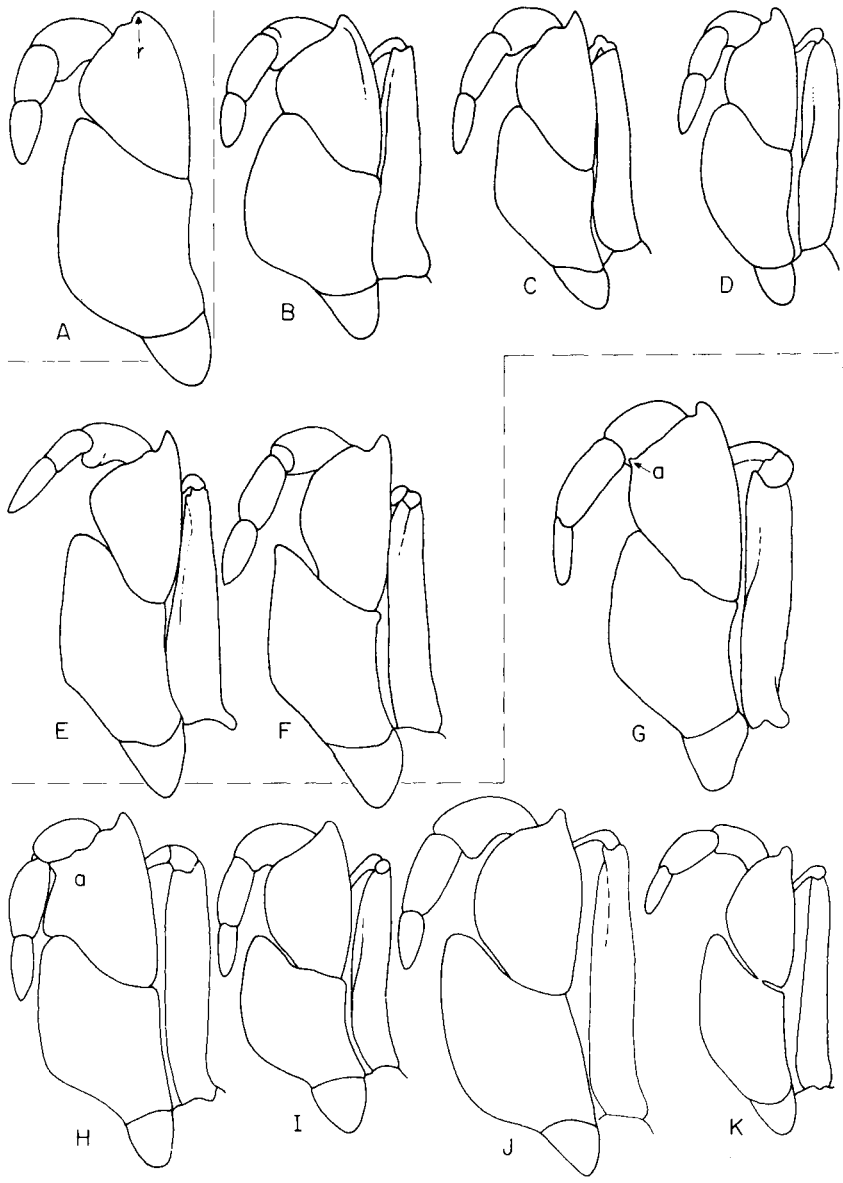

FIGURE 8

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

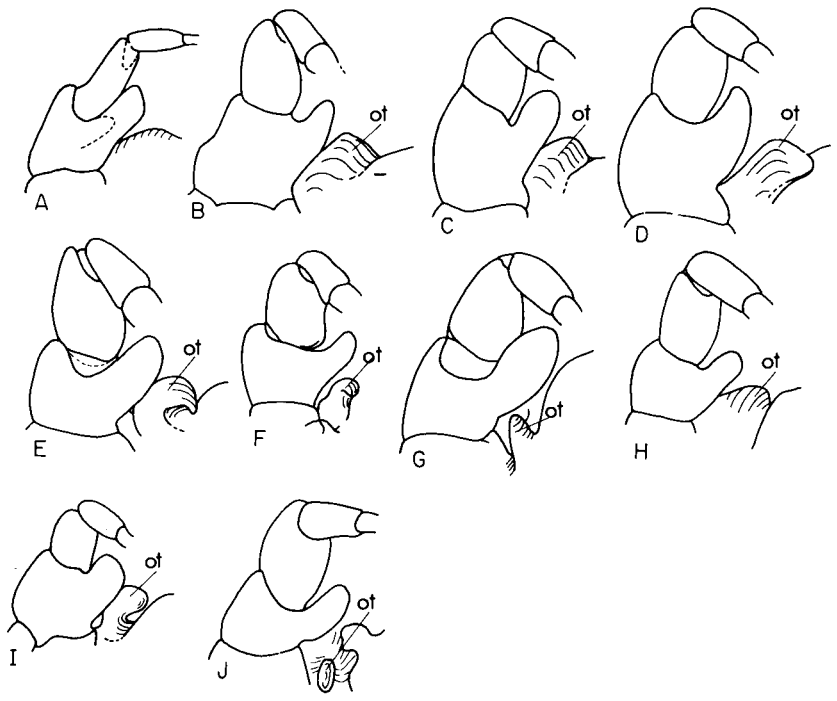

FIGURE 9

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

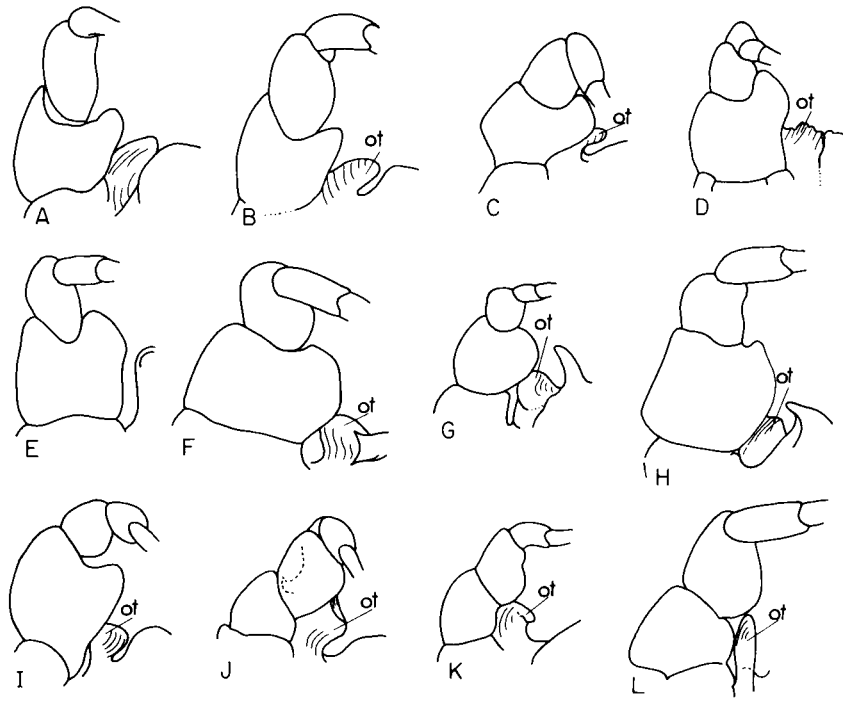

FIGURE 10

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

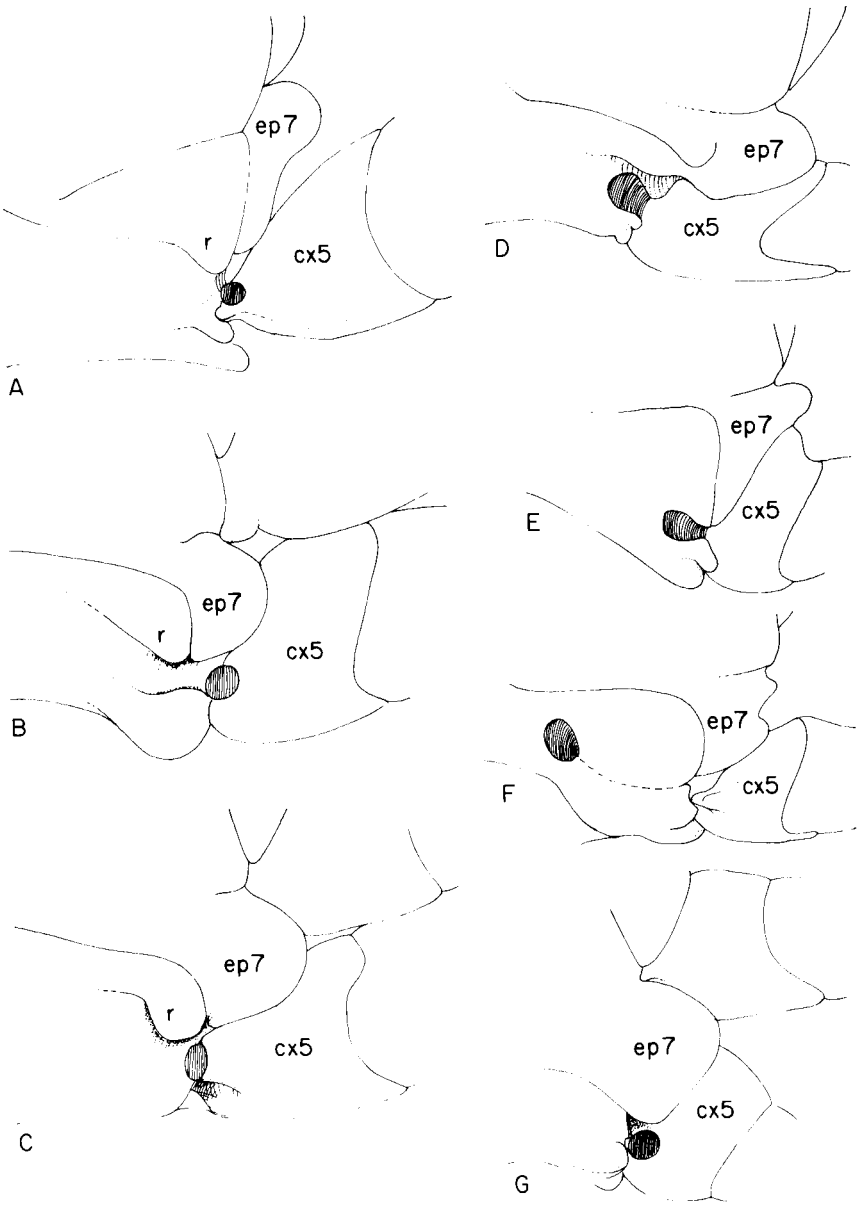

FIGURE 11

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

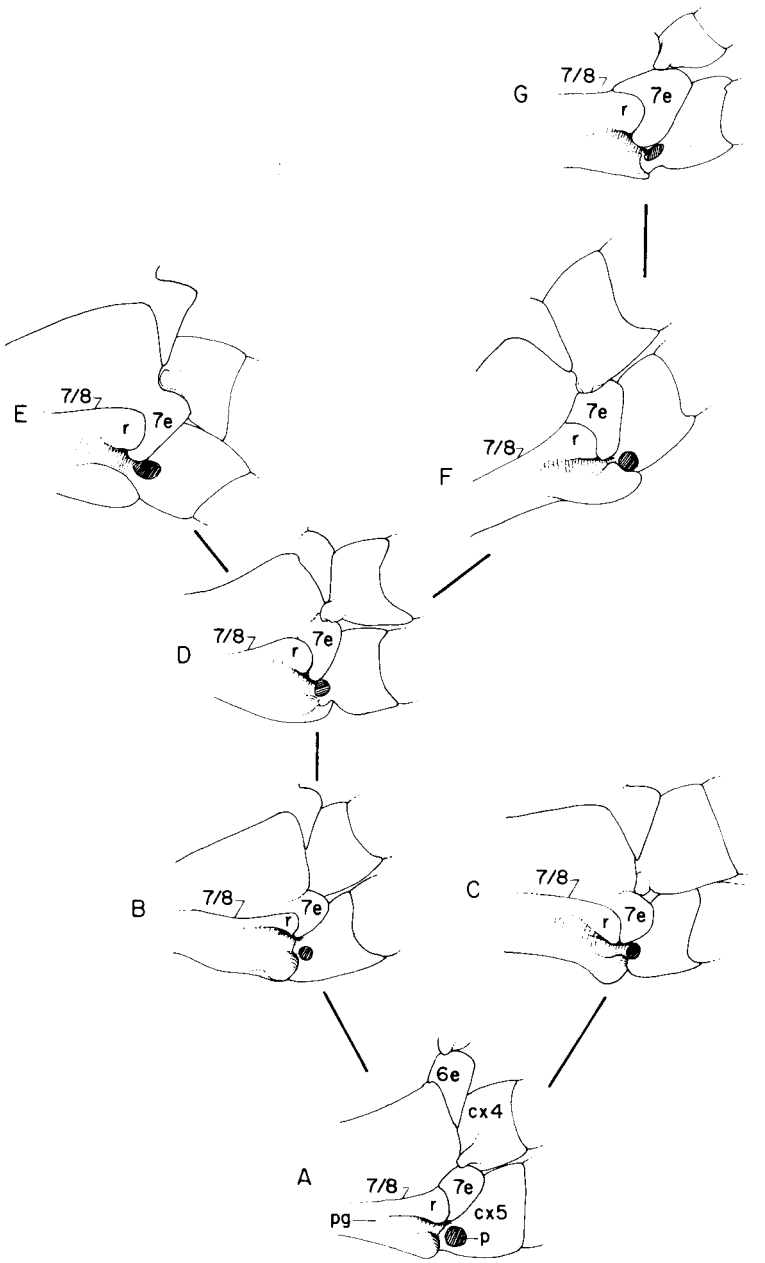

FIGURE 12

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

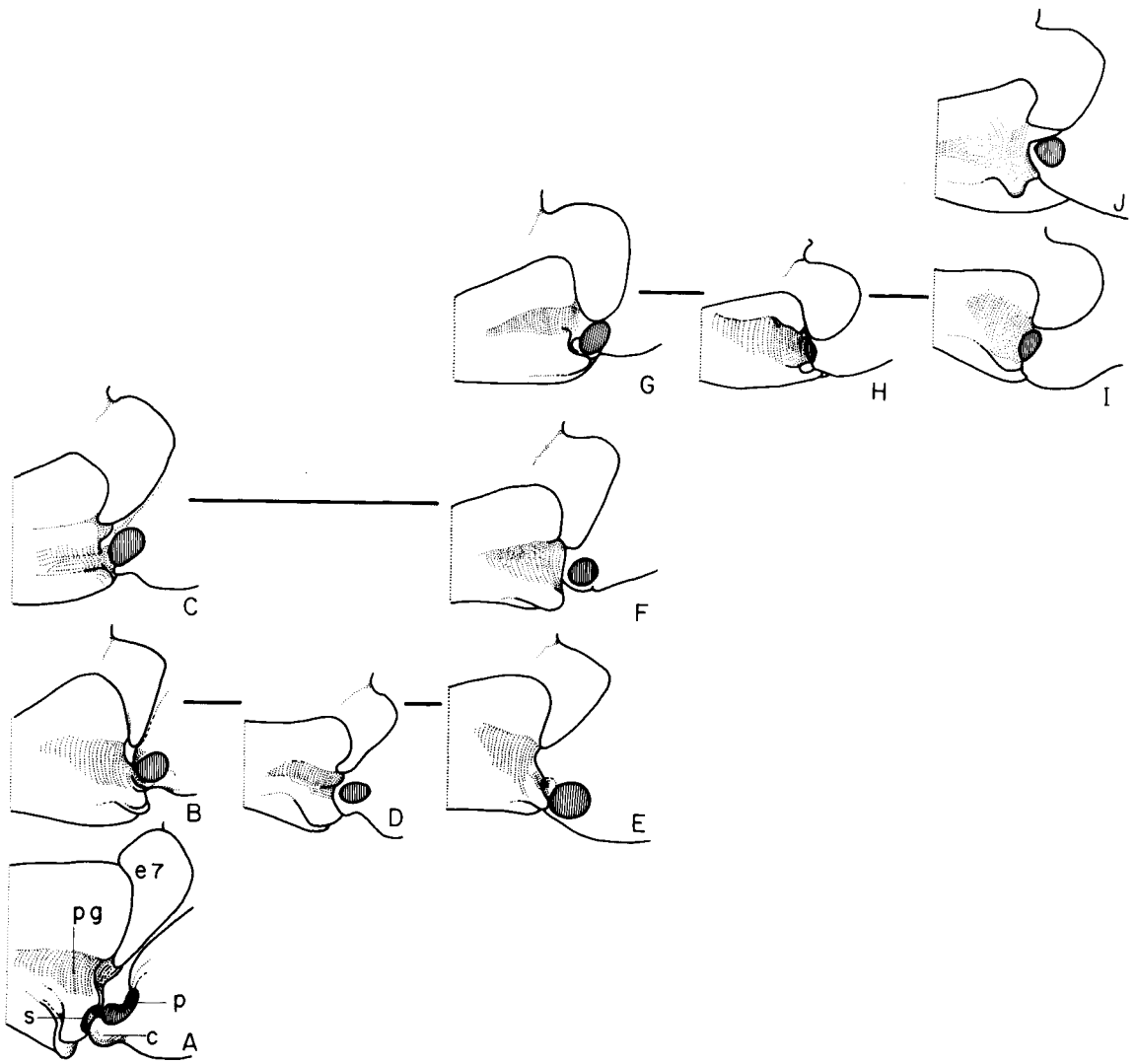

FIGURE 13

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

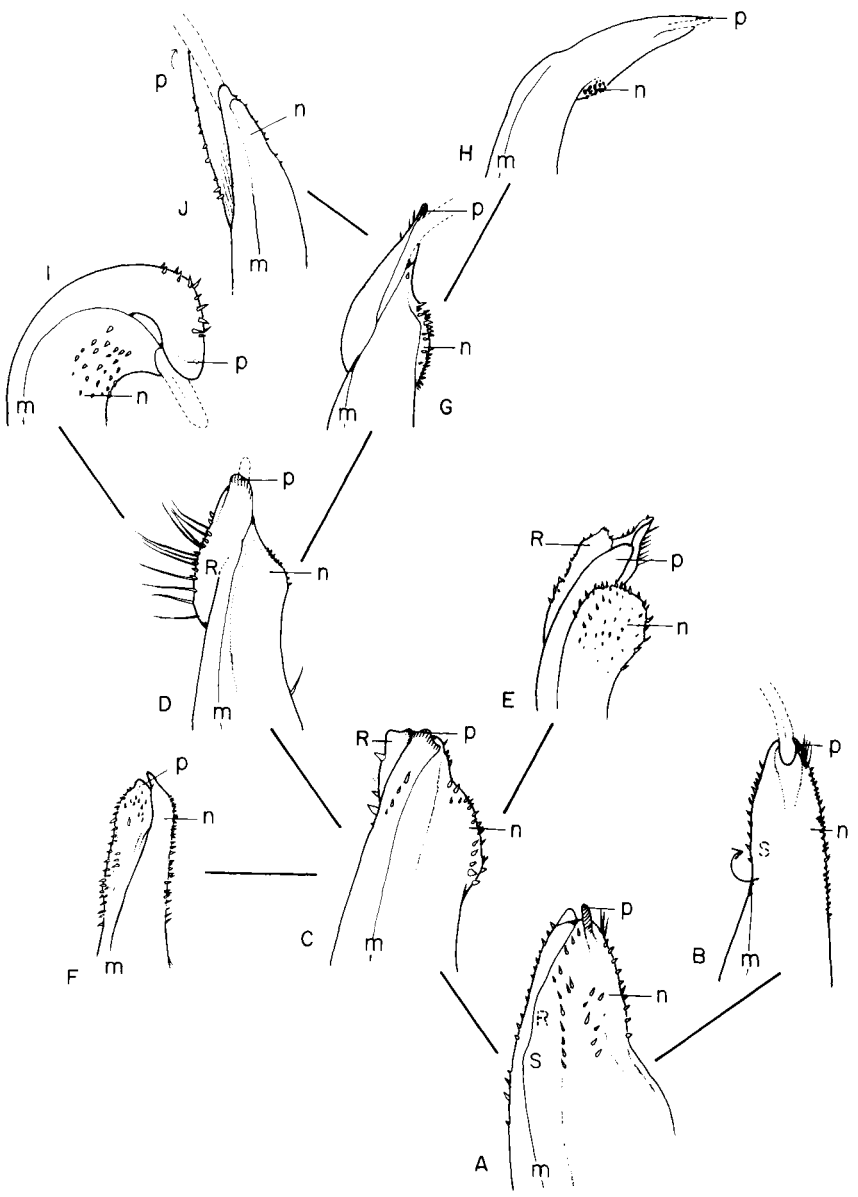

FIGURE 14

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

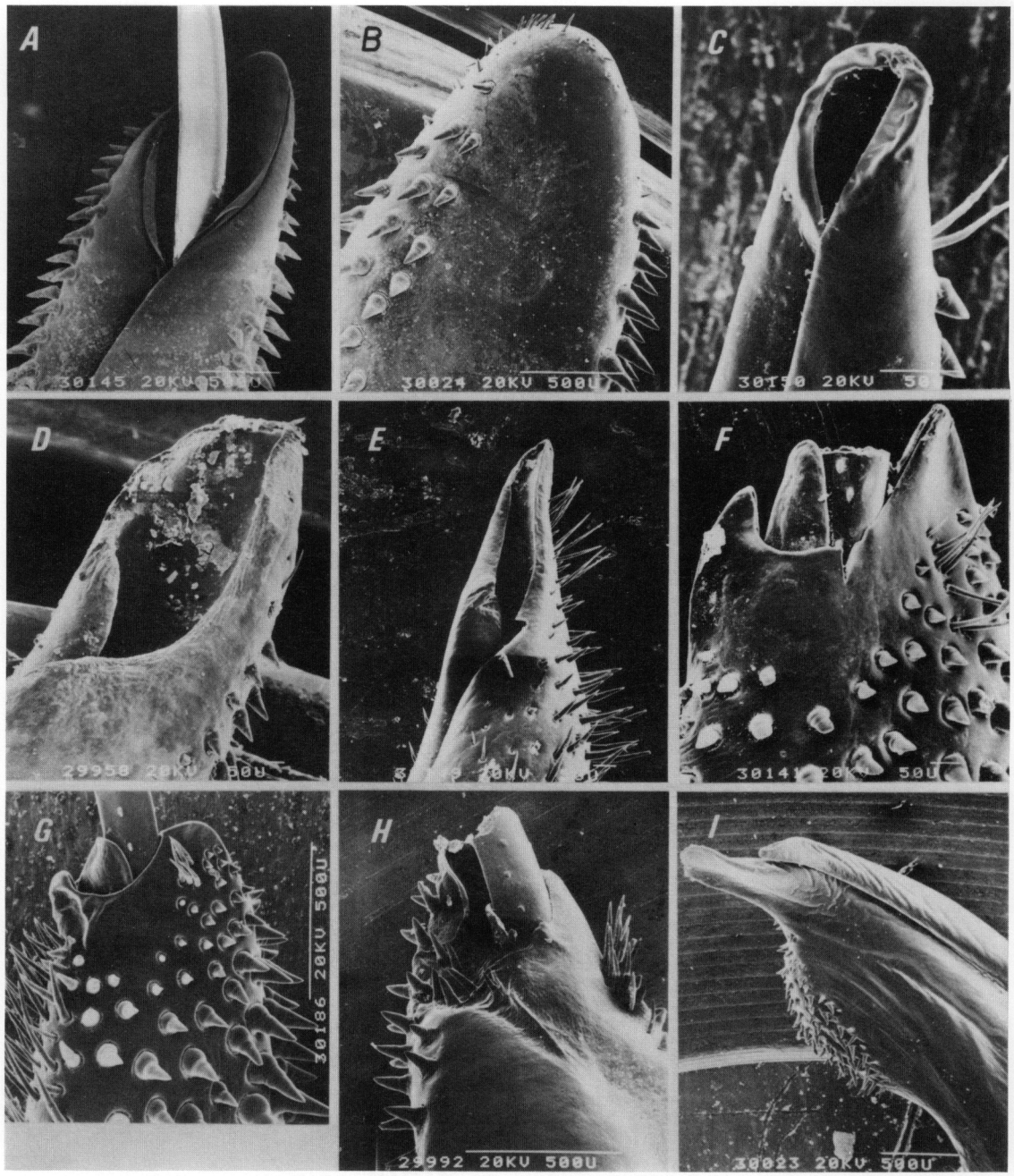

FIGURE 15

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

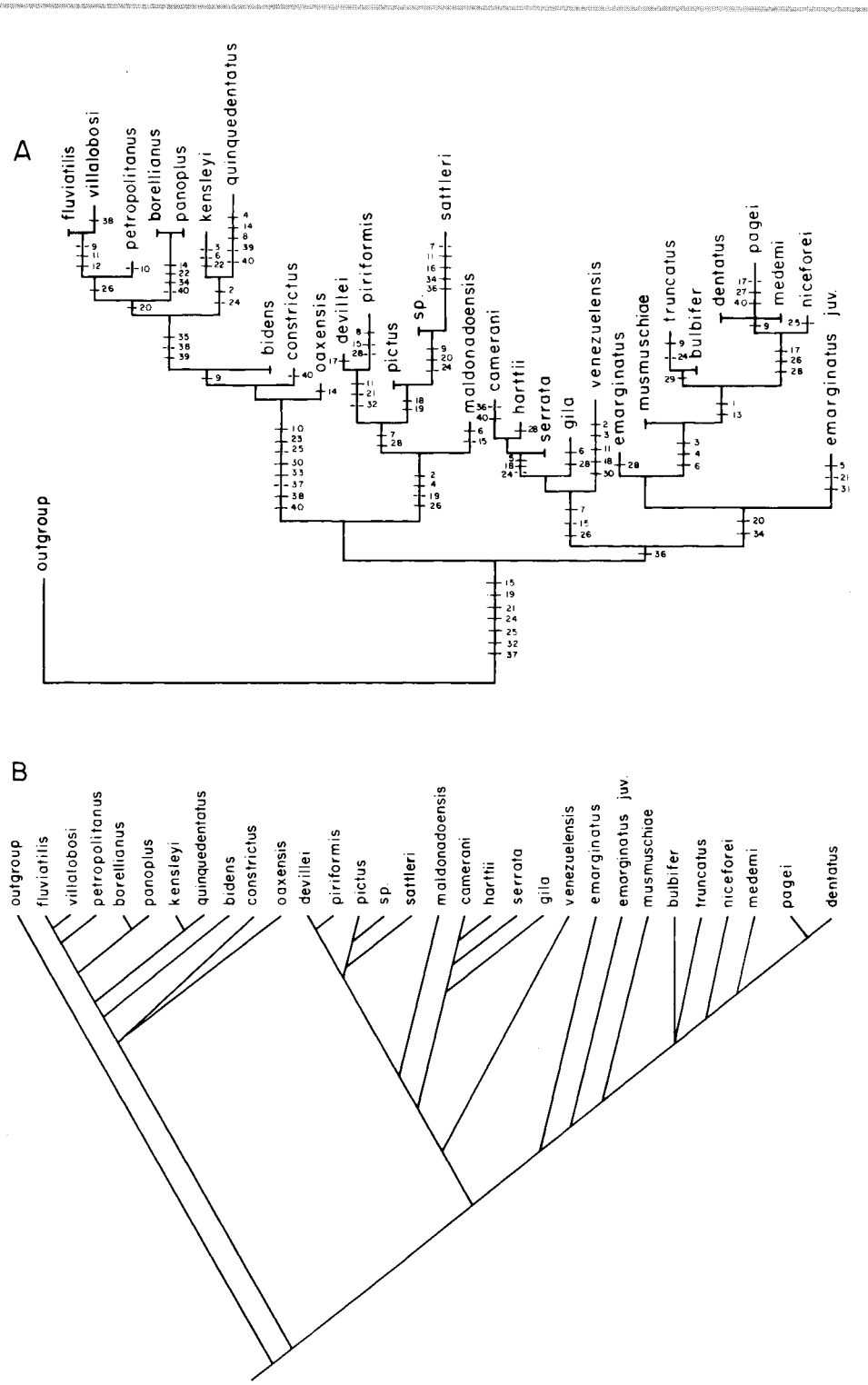

FIGURE 16

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

TABLE I

Characters used to compare the Trichodactilidae species

The first alternative listed for each character is considered to be plesiomorphic

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

TABLE II
Data matrix of 40 characters of the Trichodactylidae

Trichodactylus fluviatilis	1010000001110010001110110100010110100011
T. kensleyi	1100010011000010001011100000010110100011
T. petropolitanus	1010000010000010001110110100010110100011
T. quinquedentatus	1111000011000110011010100000010110100000
Mikrotrichodactylus borellianus	1010000011000110001111110000010111100010
M. panoplus	1010000011000110001111110000010111100010
Rodriguezia villalobosi	1010000001110010001110110100010110100111
Avotrichodactylus bidens	1010000011000010001010110000010110000101
A. constrictus	1010000001000010001010110000010110000100
A. oaxensis	1010000001000110001010110000000110000101
Sylviocarcinus devillei	1111001000100010100000011101000000001000
S. maldonadoensis	1111010000000000000010011100000100001000
S. pictus	1111001000000010011010011101000100001000
S. piriformis	1111001100100000000000011100000000001000
S. sp.	1111001010000010011110001101000100001000
Valdivia camerani	0000010100000000001101000110000010000 1001
V. gila	0000011100000000000101001110100010001 1000
V. harttii	0000010100000000001101000110100010001 1000
V. serrata	0000010100000000000101000110000010001 1000
Forsteria venezuelensis	0110001000100000011010011100010100011000
Zilchiopsis emarginatus	0100000000000011001110011001000101011000
Z. emarginatus, juvenile	0000100000000010001100011000001101011000
Z. sattleri	1111000010100011011110001101000101011001
Dilocarcinus truncatus	1111010010001011001110001000100101011000
D. bulbifer	1111010000001011001110011000100101011000
D. dentatus	1111010010001011011100111010001010 11000
D. medemi	1111010010001011011100111010001010 11000
D. niceforei	1111010000001011011100101010001010 11000
D. pagei	1111010010001011001110011111000101011001
Fredilocarcarcinus musmuschiae	0111010000000011001110011000000101011000

II - SYSTEMATIC STUDY

Family TRICHODACTYLIDAE H. Milne Edwards, 1853

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

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

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

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

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

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

Type genus.- *Trichodactylus* Latreille, 1828.

Key to the subfamilies and tribes of TRICHODACTYLIDAE

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

– Postgastric pits present, abdominal segments with sutures 3-5 obsolete, penial groove not overlaped by 8th tergite and sternal lobe, first gonopod conical, elongate (Subfamily DILOCARCININAE) 2

2. Carapace hexagonal, upper surface moderately arched, (exceptionally strongly arched), with regions well marked, 2-6 lateral teeth, first gonopod with a strong lateral lobe on proximal half, gonopore terminal ..... Tribe VALDIVIINI

– Carapace suborbicular, strongly arched, surface smooth, 3-11 lateral teeth 3

3. Front advanced, epistome not visible in dorsal view, gonopore V-shaped, open caudal, second gonopod much longer than first, rolled-over ..... Tribe HOLTHUISIINI

– Front bilobed, partially or completely retracted, exposing the epistome, gonopore terminal, apical, second gonopod moderately longer than first ..... Tribe DILOCARCININI

Subfamily TRICHODACTYLINAE H. Milne Edwards, 1853

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

Key to the genera of Trichodactylinae

1. Gonopod flask-shaped 2

– Gonopod conical, progressively tapering to a narrow tip ..... ***Avotrichodactylus***

2. Second male gonopod considerably shorter than first (approximately 1/2), the terminal article considerably shorter (approximately 1/2) than first, acuminate ..... ***Rodriguezia***

– Second male gonopod considerably longer than first, sinuous or sickle-shaped; terminal article slightly longer (1.2-1.5) than first 3

3. First male gonopods in normal position placed along longitudinal axis of body; apex not bent mesiad ..... ***Trichodactylus***

– First male gonopods in normal position folded diagonally under abdomen; apex bent mesiad ..... ***Mikrotrichodactylus***

Type genus.- ***Trichodactylus*** Latreille, 1828.

Trichodactylus Latreille, 1828

Trichodactylus Latreille, 1828, p. 705.

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

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

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

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

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

Key to the species of Trichodactylus

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

Trichodactylus fluviatilis Latreille, 1828

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

Trichodactylus fluviatilis Latreille, 1828, p. 705.- White, 1847a, p. 31.- Lucas, 1857, p. 8.- Ortmann, 1897, p. 325.- Nobili, 1899a, p. 2. - Moreira, 1901, p. 45, 107.- Pretzmann, 1968b, p. 70.- Rodríguez, 1981, p. 48.

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

Trichodactylus (Trichodactylus) fluviatilis fluviatilis, Bott, 1969, p. 15, pl. 1, fig. 1a, b, pl. 18, fig. 33.- Bott, 1970, p. 333.- Manning & Hobbs, 1977, p. 159.

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

Trichodactylus quadrata, H. Milne Edwards, 1837, p. 16.

Trichodactylus quadratus, H. Milne Edwards, 1839, p. 60, pl. xv, fig. 2 (see H. Milne Edwards, 1836-1844).- H. Milne Edwards, 1853, p. 214.- Heller, 1865, p. 171.- von Martens, 1869a, p. 2.- von Martens 1869b, p. 515.- Smith, 1869, p. 36 (part.).- Göldi, 1885, p. 662.- Göldi, 1886, p. 25, pl. ii, fig. 2.- Thallwitz, 1891, p. 53.- Young, 1900, p. 228 - 229.

Trichodactylus punctatus Eydoux & Souleyet, 1842, p. 237, pl. iii, fig. 1, 2.- (?)Dana, 1852, p. 294.- H. Milne Edwards, 1853, p. 214.- Smith, 1869, p. 36.- Rathbun, 1893, p. 660.

Trichodactylus dentatus H. Milne Edwards,1853, p. 214.- Lucas, 1857, p. 8.- A. Milne Edwards, 1869, p. 173.- Ortmann, 1897,

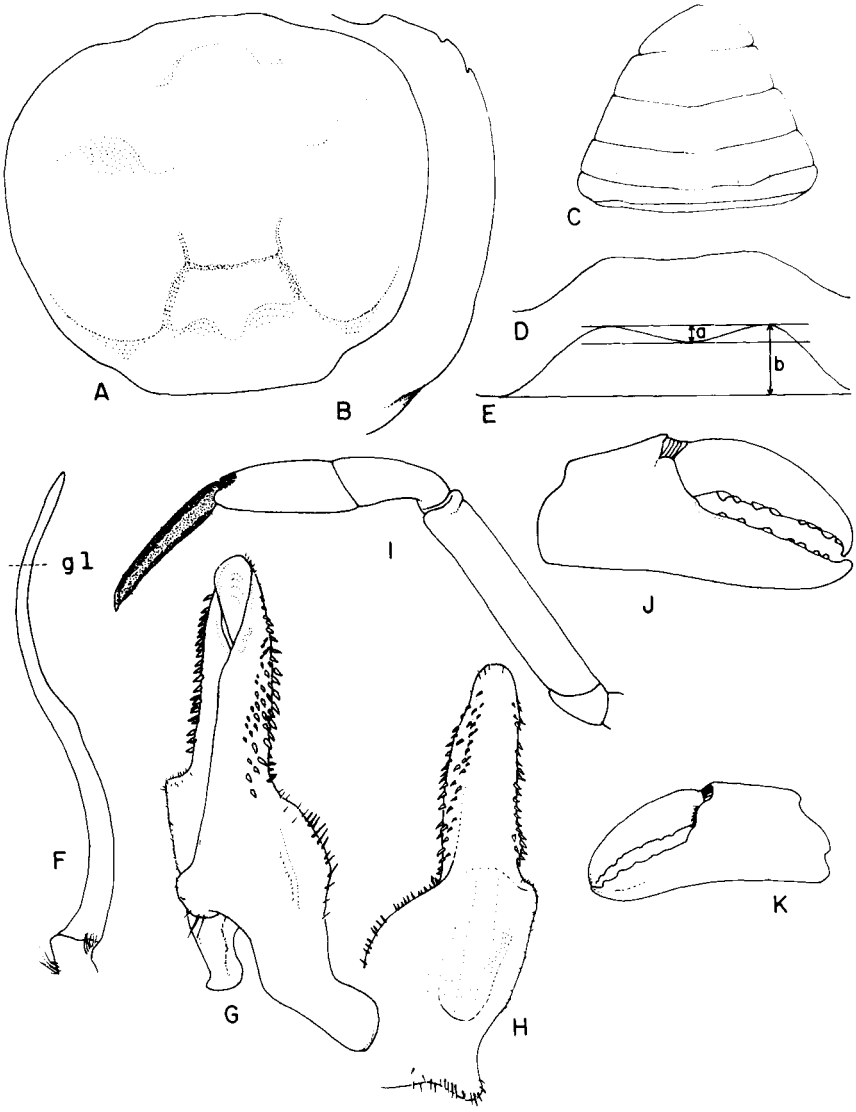

FIGURE 17

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

p. 325, 326.- NOBILI, 1899a, p. 2.- YOUNG, 1900, p. 228, 229.- MOREIRA, 1901, p. 46, 108.

Trichodactylus (Trichodactylus) fluviatilis dentatus, BOTT, 1969, p. 18, pl. 24, fig. 64.- MANNING & HOBBS, 1977, p. 159.

Trichodactylus (Trichodactylus) edwardsi Rathbun, 1906, p. 40, pl. xix, fig. 3 [*nomen novum pro Trichodactylus dentatus* H. Milne Edwards, 1853, *non Orthostoma dentata* Randall, 1839 = *Dilocarcinus dentatus* (Randall, 1839)].- PRETZMANN, 1968b, p. 70.

Uca cunninghami Bate, 1868, p. 447, pl. xxi, fig 3.- VON MARTENS 1869b, p. 515.- *Trichodactylus cunninghami*, A. MILNE EDWARDS, 1869, p. 172.- (?)SMITH, 1869, p. 36.

Trichodactylus dentatus var. *cunninghami*, NOBILI, 1899a, p. 1.- NOBILI, 1897, p. 3.

Trichodactylus crassus A. Milne Edwards, 1869, p. 172.- ORTMANN, 1897, p. 325.- MOREIRA, 1901, p. 45, 107.

Trichodactylus (Trichodactylus) crassus, RATHBUN,1906, p. 41, pl. xv, fig. 9, 10.- PRETZMANN, 1968b, p. 70.

Trichodactylus (Trichodactylus) fluviatilis crassus, BOTT, 1969, p. 17, pl. 18, fig. 34.

Trichodactylus (Trichodactylus) fluviatilis rionovoensis Bott, 1969, p. 17, pl. 1, fig. 2a, b, pl. 18, fig. 35.- MANNING & HOBBS, 1977, p. 159.

Description

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

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

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

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

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

Material examined

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

Type and distribution

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

Remarks

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

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

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

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

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

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

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

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

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

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

Trichodactylus maytai Pretzmann, 1978

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

Description

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

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

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

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

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

Type and distribution

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

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

Description

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

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

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

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

Material examined

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

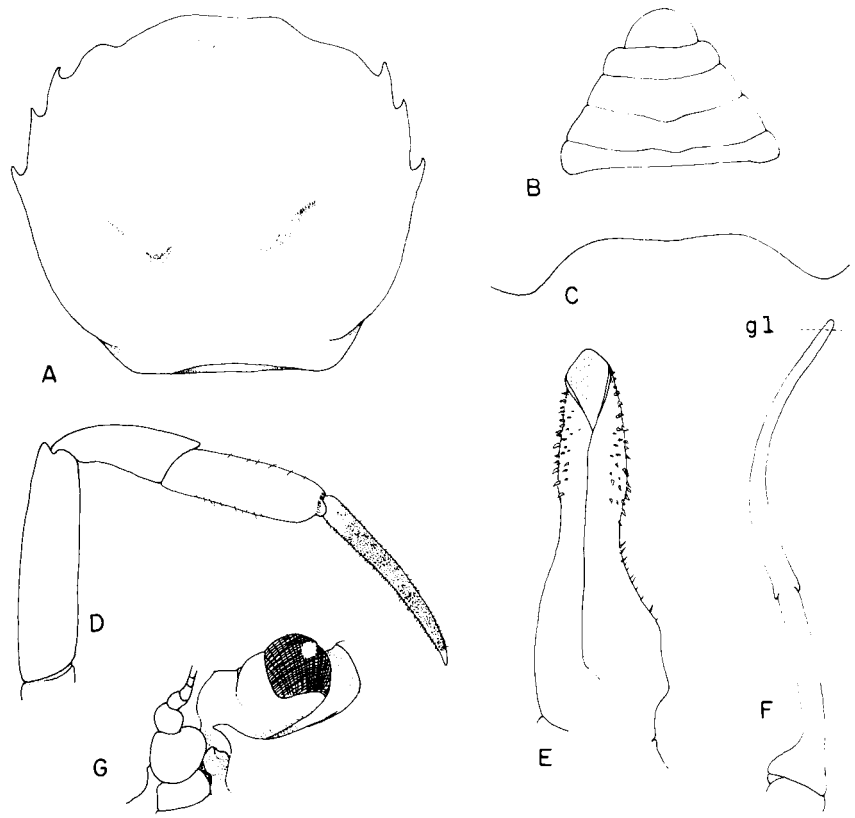

FIGURE 18

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

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

Remarks

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

Etymology

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

Trichodactylus petropolitanus (Göldi, 1886)

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

Sylviocarcinus petropolitanus Göldi, 1885, p. 663 (*nomen nudum*).- GÖLDI, 1886, p. 33, pl. 3, fig. 18-23.
Trichodactylus petropolitanus, MOREIRA 1901, p. 46, 108.- RODRÍGUEZ, 1981, p. 48.
Trichodactylus (Trichodactylus) petropolitanus, PRETZMANN, 1968b, p. 70.
Trichodactylus (Valdivia) petropolitanus, RATHBUN, 1906, p. 46.
Trichodactylus (Trichodactylus) petropolitanus petropolitanus, BOTT, 1969, p. 19, pl. 2, fig. 3a, b, pl. 18, fig. 36.- BOTT, 1970, p. 335.- MANNING & HOBBS, 1977, p. 160.
Trichodactylus (Valdivia) thayeri Rathbun, 1906, p. 45, pl. 16, fig. 11.
Trichodactylus (Valdivia) thayeri glaber Pretzmann, 1968a, p. 4.
Trichodactylus (Trichodactylus) thayeri, PRETZMANN, 1968b, p.70.
Trichodactylus (Valdivia) tifucanus Rathbun, 1906, p. 47, pl. 17, fig. 3.
Trichodactylus (Valdivia) tifucanus acutidens Pretzmann 1968a, p. 4.
Trichodactylus (Trichodactylus) tifucanus, PRETZMANN, 1968b, p. 70.
Trichodactylus (Trichodactylus) tifucanus theresiopoliensis Pretzmann, 1968b, p. 70.

Description

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

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

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

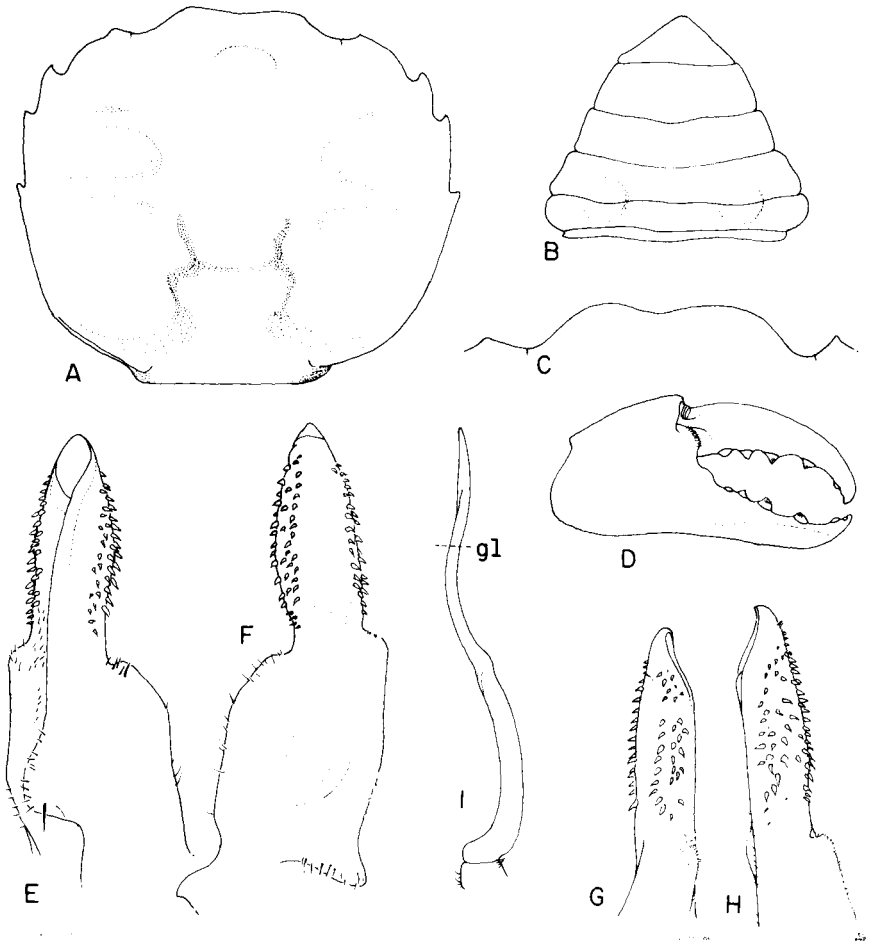

FIGURE 19

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

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

Material examined

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

Type and distribution

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

Trichodactylus quinquedentatus Rathbun, 1893

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

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

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

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

Description

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

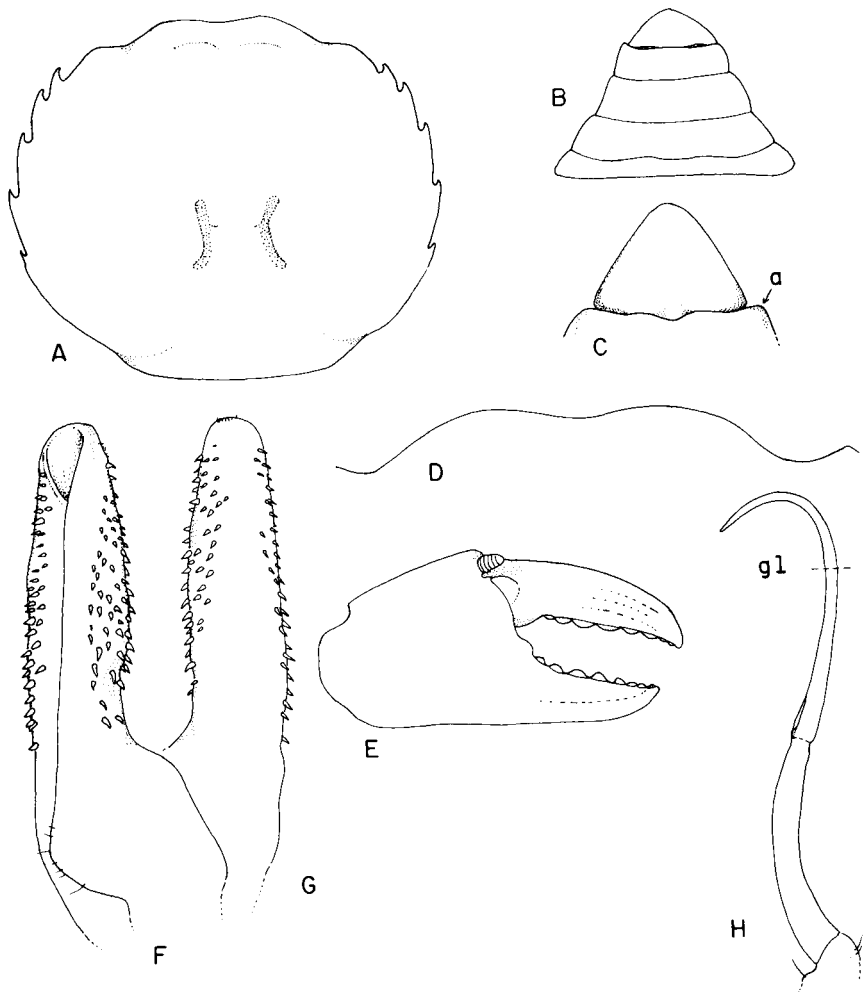

FIGURE 20

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

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

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

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

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

Material examined

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

Type and distribution

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

Trichodactylus ehrhardti (Bott, 1969)

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

Type and distribution

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

Remarks

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

Mikrotrichodactylus Pretzmann, 1968

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

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

Type species.- *Trichodactylus borellianus* Nobili, 1896

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

Key to the species of *Mikrotrichodactylus*

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

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

Mikrotrichodactylus borellianus (Nobili, 1896)

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

Trichodactylus borellianus Nobili, 1896, p. 2.- Nobili, 1898, p. 12.- Nobili, 1899a, p. 3.- Nobili, 1901, p. 11.- Rodríguez, 1981, p. 48.
Trichodactylus (Valdivia) borellianus, Rathbun, 1906, p. 5, pl. 17, fig. 6, text-fig. 115.
Trichodactylus (Dilocarcinus) borellianus, Ringuelet, 1949, p. 104, pl. 8, fig. 2.
Trichodactylus (Trichodactylus) borellianus, Bott,1969, p. 23, pl. 5, fig. 8a, b, pl. 18, fig. 39.- Lopretto, 1976, p. 74, fig. 6-9.- Manning & Hobbs, 1977, p. 159.
Trichodactylus (Mikrotrichodactylus) borellianus brasiliensis Pretzmann, 1968b, p. 71.
?*Trichodactylus (Trichodactylus) parvus* Moreira, 1912, p. 151, pl. 6, fig. 12, 13, text-fig. 2, 3.

Description

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

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

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

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

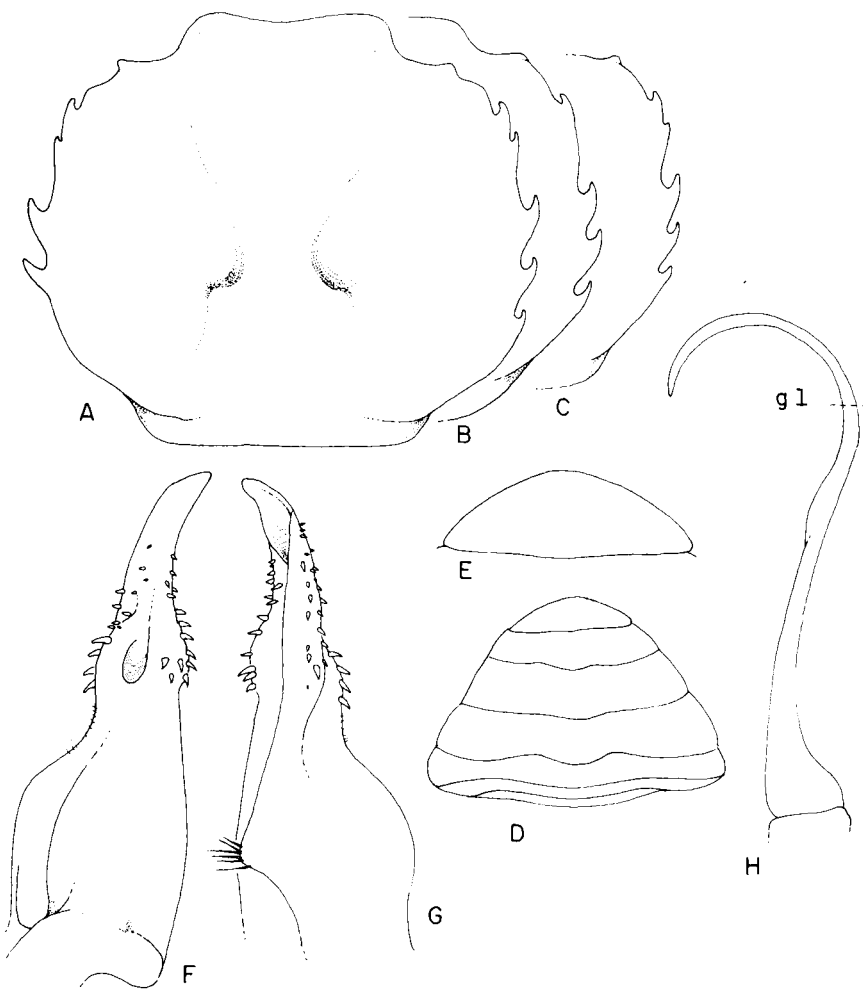

FIGURE 21

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

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

Material examined

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

Type and distribution

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

Remarks

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

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

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

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

Mikrotrichodactylus panoplus (von Martens, 1869)

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

Sylviocarcinus panoplus von Martens, 1869a, p. 3, pl. 1, fig. 1.- GÖLDI, 1886, p. 34.- NOBILI, 1896, p. 3.
Orthostoma panoplus, NOBILI, 1898, p. 12 (part.).- ORTMANN, 1897, p. 326.
Dilocarcinus panoplus, ORTMANN, 1893, p. 492.- NOBILI, 1899a, p. 3.- ORTMANN, 1903, p. 311.
Trichodactylus (Valdivia) panoplus, RATHBUN, 1906, p. 52, pl. 17, fig. 5, text-fig. 114.- RINGUELET, 1949, p. 103, pl. 8, fig. 3, pl. 9, fig. 1.
Trichodactylus (Trichodactylus) panoplus, GARCIA, 1973, p. 97, fig. 1-5.- LOPRETTO, 1976, p. 79, fig. 10-13.
Dilocarcinus panoplus var. *marmorata* Nobili, 1901, p. 11.
Trichodactylus (Trichodactylus) panoplus panoplus, BOTT, 1969, p. 21, pl. 4, fig. 6a, b, pl. 18, fig. 37.- MANNING & HOBBS, 1977, p. 160.
Trichodactylus panoplus, RODRÍGUEZ, 1981, p. 48.
Dilocarcinus armatus A. Milne Edwards, 1869, p. 177.
Trichodactylus (Valdivia) spec. [*aberratio Trichodactylus (V.) panoplus* (von Martens, 1869)], RINGUELET, 1949, p. 103, pl. 8, fig. 3, pl. 9, fig. 1.

Description

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

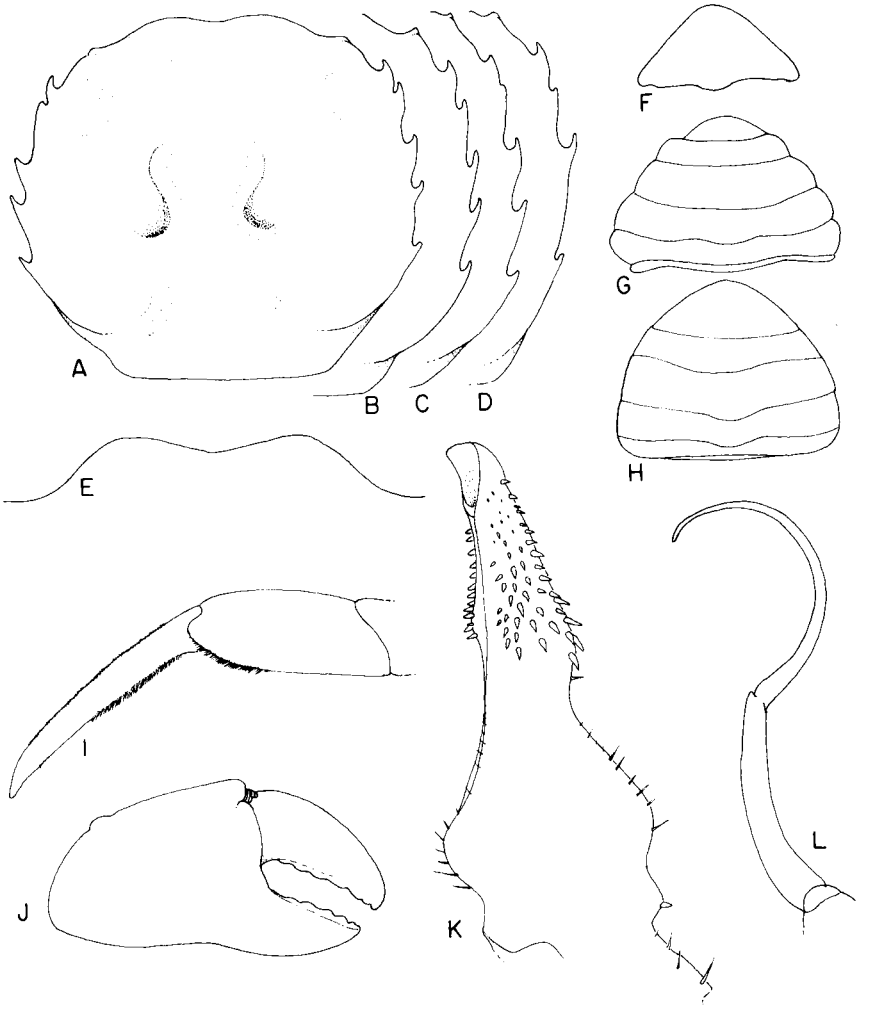

FIGURE 22

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

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

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

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

Material examined

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

Type and distribution

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

Remarks

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

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

Rodriguezia Bott, 1969

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

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

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

Key to the species of *Rodriguezia*

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

Distribution

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

Rodriguezia mensabak (Cottarelli & Argano, 1977)

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

Description

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

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

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

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

terminal article considerably shorter (approximately 1/2) than first, slightly recurved, subtriangular and acuminate, with few denticles.

Type and distribution

Mexico, Chiapas State: Tila (COTTARELLI & ARGANO, 1977, holotype).

Rodriguezia villalobosi (Rodríguez & Manrique, 1967)

Fig. 23G-H.

Trichodactylus villalobosi Rodríguez & Manrique, 1967, p. 183, fig. 1, Pl. 1.

Description

Carapace suborbicular; upper surface with pores and small granules, not visible to naked eye, rest smooth and polished; gastric region more prominent than rest, hepatic slightly elevated; frontal region concave, progressively sloping downwards to margin of front; postfrontal lobes inconspicuous; cardiac, branchio-urogastric and urogastric grooves wide and shallow; oval metagastric region defined by these grooves. Lateral margins angled, devoided of teeth; postero-lateral ridge of carapace bent mesially in posterior end, continuing in thinner ridge parallel to posterior margin. Front moderately bilobed.

All abdominal segments distinct in male and female; male abdomen subtriangular, wide, outer margin slightly concave, last segment triangular, pointed.

Chelipeds strongly unequal, largest with palm swollen, inferior margin sinuous; fingers gaping, with rows of dark points on external surface; merus with strong distal spine on the upper border. Legs not slender, dactylus covered by felt-like pubescence, with longer hairs over internal margin; propodus with similar pubescence over distal external portion.

First gonopod straight, wider in basal portion, constricted at middle, slightly expanded distal half, with strong conical spines over distal portion; gonopore long, suboval. Second gonopod considerably shorter than first (approximately 1/2), terminal article considerably shorter (approximately 1/2) than first, proximally wide, long acuminate distally.

Type and distribution

Mexico. Chiapas State: Rancho La Esperanza (type) and San Juan Bosque (RODRÍGUEZ & MANRIQUE, 1967).

Avotrichodactylus Pretzmann, 1968

Trichodactylus (Avotrichodactylus) Pretzmann, 1968b, p. 71.
Avotrichodactylus Pretzmann, 1978b, p. 54.- PRETZMANN, 1980, p. 661.

Carapace with 2-5 lateral teeth behind external orbital angle; front slightly bilobed; postgastric pits absent; abdominal segments with sutures 3-5 partially obsolete; third maxilliped with merus trapezoidal, not conspicuously narrow, distal external spine not reduced; first gonopod conical, progressively tapering to very narrow opening; gonopore very small, subcircular, open disto-caudally; second gonopod considerably shorter (0.6) than first, distal article shorter (0.25) than first.

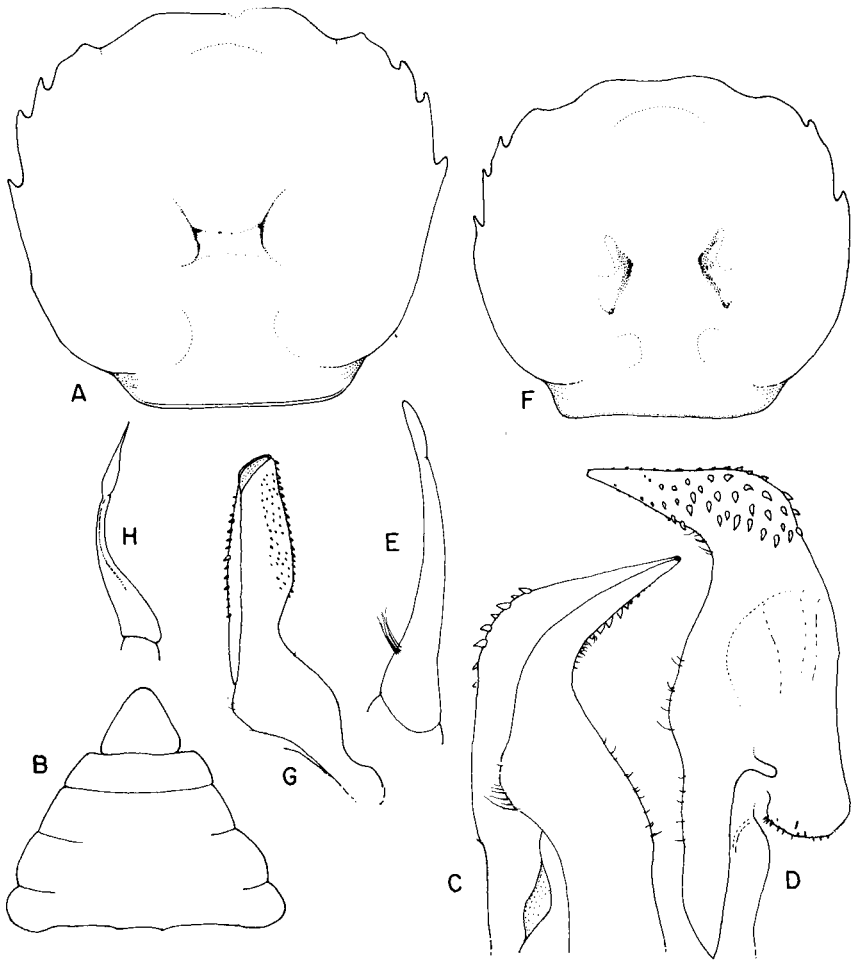

FIGURE 23

Avotrichodactylus constrictus (Pearse), A-E, male specimen, cl 20.2 mm, from Lago Catemaco: A, outline of carapace; B, abdomen; C, first male gonopod, left, caudal; D, same, cephalic; E, second male gonopod; *Avotrichodactylus bidens* (Bott), F, female specimen cl 14.2 mm from Cueva del Azufre: outline of carapace; *Rodriguezia villalobosi* (Rodríguez & Manrique), G, H, male holotype, cl 14.5 mm: G, first male gonopod, left, caudal; H, second male gonopod.

Type species.- *Trichodactylus constrictus* Pearse, 1911.

Distribution

Southern Mexico, rivers in the States of Veracruz, Oaxaca, Tabasco and Chiapas draining into the Gulf of Mexico.

Key to the species of *Avotrichodactylus*

1. First male gonopod sinuous, only slightly bent caudo-laterad; gonopore caudal; 4-5 spines on lateral side ..... *oaxensis*
– First male gonopod with distal half bill-like, strongly bent laterad and forming a "knee" covered by short, stout spines; gonopore terminal 2
2. Antero-lateral margin with 3 spines ..... *constrictus*
– Antero-lateral margin with 2 spines ..... *bidens*

Avotrichodactylus bidens (Bott, 1969)

Fig. 23F

Trichodactylus bidens Bott.1969, p. 25, pl. 24, fig. 68, 69.- COTTARELLI & ARGANO, 1977, p. 207, fig. 3, 4.

Description

Carapace suborbicular; upper surface moderately irregular; in frontal view regularly arched; frontal and orbital regions excavated; lobes distinct, not prominent; branchio-urogastric and anterior portion of branchio-cardiac grooves deep, well marked, urogastric and posterior part of branchio-cardiac groove indicated by flat depressions. Postgastric pits absent. Antero-lateral margin with 2 small, spiniform teeth of approximately equal size behind external orbital angle; interdental space approximately twice space between outer orbital angle and 1st tooth; postero-lateral ridge of carapace, not bent mesially in posterior end as in other species, but parallel to lower ridge located over 5th coxa, ends away from postero-lateral angles of carapace. Margin of front slightly concave. Orbits suborbicular; orbital suture absent or represented by small depression; lower orbital margin papillated; inner orbital angle blunt; occlusive orbital tooth rounded, small, located close to inner orbital angle, but not continuous with it; outer orbital not prominent, its border in contact with orbital margin; margin between outer orbital angle and first tooth of carapace forms rounded lobe; buccal angle smooth. Front advanced, hiding epistome in dorsal view; anterior surface of front sunk, low in middle, thin on sides; margin over each antennular fossa more or less straight; antennular septum sunken; epistome moderately high, inclined forwards.

Third to fifth abdominal segments fused in both male and female.

Basal article of antenna with outer lobe prominent and narrow; ischium of third maxilliped with deep groove. Chelipeds strongly unequal; larger chela of male with upper border of hand strongly arched and lower sinuous, fingers with elongated gap between them, teeth small, regularly placed along cutting edges; carpus with inner margin produced in sharp hooked spine; merus with apical spine on upper border, another at distal angle of latero-inferior margin and another at inner margin. Legs with long coarse hairs on lower margin of dactylus; similar hairs cover all the lower margin of propodus in 5th, 3/4 in 2nd, 1/2 in third and only distal angle in 4th pereiopod; upper margin of propodus and dactylus with shorter sparse hairs, rest of surface covered by felt-like pubescence; claws of dactyli very short, with indistinct longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First and second gonopods, as illustrated by COTTARELLI & ARGANO (1977), similar to those of *Avotrichodactylus constrictus*.

Material examined

Mexico. Cueva del Azufre, 100 m above sea level, Tapijulapa, Teapa, Tabasco State; 1 February 1982; M. W. WILKENS; 1 female, cl 14.3 mm, cb 15.5 mm (MH). Cuevita de la Cascada Azufre,3 km of Tapijulapa, Tabasco State; 15 June 1975; A. GRUBBS; 1 juvenile male (USNM 230083).-

Type and distribution

BOTT (1969) designated as holotype a male from "Arroyo del Solfo" near Tapijulapa, Tabasco, which is almost certainly the same as, or an extension of, the "Cueva del Azufre" where the specimens mentioned above were collected. COTTARELLI & ARGANO (1977) call this species troglophile. It certainly seems restricted to this cave and has not been collected elsewhere.

Remarks

The species is closely related to *Avotrichodactylus constrictus* and their gonopods are identical. The female specimen recorded above (Fig. 23F), has a supplementary tooth intercalated in the left side, and a rounded lobe intercalated on the right side, thus suggesting a continuity of characters with *A. constrictus*. However, the teeth in *A. bidens* are smaller and less prominent. The specimens always are pale colored, a character obviously associated with cave dwelling, whereas all specimens of *A. constrictus* which I have examined, even those associated with caves, are brown-black.

Avotrichodactylus constrictus (Pearse, 1911)

Fig. 2A; 10I; 12F; 23A-E

Trichodactylus constrictus Pearse, 1911, p. 111, fig.4.- RODRÍGUEZ & MANRIQUE, 1967, p. 183.

Trichodactylus (Trichodactylus) constrictus, COIFMANN, 1939, p. 111.

Trichodactylus (Avotrichodactylus) constrictus, PRETZMANN, 1968b, p. 71.

Trichodactylus (Rodriguezia) constrictus, BOTT, 1969, p. 26.- COTTARELLI & ARGANO, 1977, p. 210.

Avotrichodactylus constrictus, PRETZMANN, 1980, p. 661, pl. 14, fig. 61-63.- RODRÍGUEZ & HOBBS, 1989, p. 399.

Description

Carapace suborbicular; upper surface moderately irregular; regularly arched in frontal view; frontal and orbital regions strongly excavated, and consequently epigastric lobes well delimited; branchio-urogastric and anterior portion of branchio-cardiac grooves deep and well marked, urogastric and posterior part of branchio-cardiac groove indicated by flat depressions. Postgastric pits barely visible. Antero-lateral margin with 3 teeth behind external orbital angle, subequal in size, with wide base, directed laterally; 1st and 2nd teeth nearer than 2nd and 3rd; postero-lateral ridge of carapace not bent mesially in posterior end as in other species, but parallel to lower ridge located over 5th coxa, ends away from postero-lateral angles of carapace. Margin of front slightly concave. Orbits suborbicular; orbital suture absent or represented by small depression; lower orbital margin smooth, continuous; inner orbital angle prominent, pyramidal; occlusive orbital tooth rounded, small, located close to inner orbital angle, but not continuous with it; outer orbital angle forming triangular tooth, border in contact with orbital margin; margin between outer orbital angle and first carapace tooth forms sinuous lobe; buccal angle smooth. Front advanced, hiding epistome in dorsal view; anterior surface of front sunk and low in middle, thin on sides, with 2 distinct middle pillars separated by U-shaped sinus which forms deep recess; margin over each antennular fossa sinuous and slightly projected; antennular septum sunken; epistome moderately high, inclined forwards.

First abdominal tergite of male separated from tergite 2 + 3 by straight ridge; tergites 2 + 3 with depression on both sides. Third to 5th abdominal segments fused in both male and female; male abdomen subtriangular, wide at base, outer margin almost straight; last segment with sides slightly concave, approximately 0.7 as long as broad.

Basal article of antenna with outer lobe prominent, narrow; ischium of third maxilliped with deep groove. Chelipeds strongly unequal, smaller chela unusually small; larger chela of male with upper border of hand strongly arched and lower sinuous, fingers with elongated gap between them, teeth small, regularly placed along cutting edges; carpus with inner margin produced in sharp hooked spine; merus with apical spine on upper border, another in distal angle of the latero-inferior margin and another in inner margin. Legs with lower margin of dactylus thickly clothed with long coarse hairs; similar hairs cover all lower margin of propodus in 5th, 3/4 in 2nd, 1/2 in 3rd, and only distal angle in 4th pereiopod; upper margin of propodus and dactylus thickly clothed by shorter hairs evenly distributed, not arranged in parallel longitudinal rows, rest of surface covered by felt-like pubescence; claws of dactyli very short, with indistinct longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First gonopod conical, base expanded, distal half bill-like, strongly bent laterally and forming "knee" covered by short, stout spines; gonopore very small, terminal. Second gonopod very short, flagellum reduced to short stump.

Material examined

Mexico. Playa Hermosa, Lago Catemaco, Veracruz State; 3 August 1966; L. B. HOLTHUIS, J. CABRERA & F. MANRIQUE; 1 male, 1 female (IB-UNAM). 1 km N of Palenque, Chiapas State; 25 July 1973; J. REDDELL, N. KAWAKATSU, D. DENTON & S. R. MITCHELL; 2 males, cl 19.8 and 12.5 mm, cb 17.9 and 12.9 mm (USNM 230085).

Type and distribution

Mexico.Veracruz State: Lago Catemaco (PEARSE, 1911, holotype; RODRÍGUEZ & MANRIQUE, 1967); Rio Tepalapan, Santiago Tuxtla; Arroyo del Pital, Ciudad Alemán (RODRÍGUEZ & MANRIQUE, 1967).- Chiapas State: Rio Michol, S of Palenque (RODRÍGUEZ & MANRIQUE, 1967). The species is sometimes associated with caves (RODRÍGUEZ & HOBBS, 1989).

Avotrichodactylus oaxensis new species

Fig. 3C; 4G; 6G; 12G; 15C; 24A-H

Description

Carapace suborbicular; upper surface moderately irregular; regularly arched in frontal view; frontal and orbital regions strongly excavated, and consequently epigastric lobes well delimited; branchio-urogastric and anterior portion of branchio-cardiac grooves deep and well marked, urogastric and posterior part of branchio-cardiac groove indicated by flat depressions. Postgastric pits not distinguishable from other irregularities of carapace. Antero-lateral margin with 4-5 teeth of approximately equal size behind other orbital angle, with narrow base and directed transversely upwards; third interdental space smaller than other, and thus the 3rd and 4th teeth closer to each than others; first three teeth subequal, fourth tooth is smaller than other 3, 5th when present very small, usually replaced by small papilla or indentation; postero-lateral ridge of carapace not bent mesially in posterior end as in other species, but parallel to lower ridge located over 5th coxa, ends away from the postero-lateral angles of carapace. Margin of front slightly concave. Orbits suborbicular; orbital suture absent or represented by small depression; lower orbital margin with 4-5 acute, triangular teeth on proximal half,

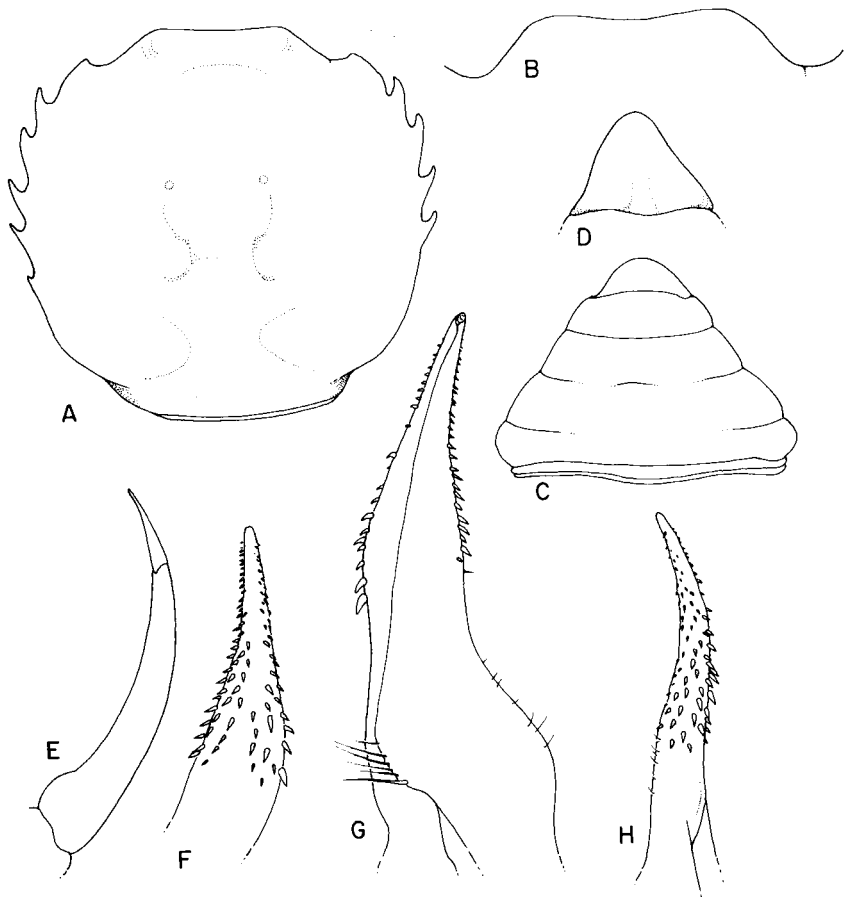

FIGURE 24

Avotrichodactylus oaxensis, new species, male holotype, cl 21.2 mm: A, outline of carapace; B, front; C, male abdomen; D, 7th abdominal segment; E, second male gonopod; F, first male gonopod, left, cephalic; G, same, caudal; H, same, lateral.

smooth on distal half; inner orbital angle with acute and prominent spine; occlusive orbital tooth rounded, small, located close to inner orbital angle, but not continuous with it; outer orbital angle obtuse, not projected as spine, its border in contact with orbital margin, or discontinuous in some small specimens; margin between outer orbital angle and first tooth of carapace forms a rounded lobe; buccal angle smooth. Front advanced, hiding epistome in dorsal view; anterior surface of front sunk and very high in middle, lower on sides, with middle pillars not distinct and without U-shaped middle sinus; margin over each antennular fossa forms rounded lobe; antennular septum sunken; epistome moderately high, inclined forwards.

First abdominal tergite of male separated from tergite 2 + 3 by straight ridge; tergites 2 + 3 with depression on both sides. Third to 5th abdominal segments fused in both male and female; male abdomen subtriangular, wide at base, outer margin slightly concave; last segment with sides slightly sinuous, approximately 0.7 as long as broad.

Basal article of antenna with outer lobe prominent and narrow; ischium of 3rd maxilliped with deep groove. Chelipeds strongly unequal, smaller chela unusually small; larger chela of male with upper border of hand strongly arched, lower sinuous; teeth small, regularly placed along cutting edges; carpus with inner margin produced in sharp hooked spine; merus with apical spine on upper border, another at distal angle of latero-inferior margin and another at inner margin. Legs with lower margin of dactylus thickly clothed with long coarse hairs; similar hairs cover all lower margin of propodus in 5th, 3/4 in 2nd, 1/2 in 3rd and only distal angle in 4th; upper margin of propodus and dactylus thickly clothed by shorter hairs evenly distributed, not arranged in parallel longitudinal rows; rest of surface of dactylus and propodus covered by felt-like pubescence; claw of dactylus very short, with indistinct longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First gonopod slender, progressively tapering to very narrow tip; distal part moderately bent cephalo-laterad; in caudal view narrow triangular, slightly widened at middle; in lateral view narrow and sinuous; distal third of cephalic surface covered by spines which strongly diminish in size distally and tend to form four rows proximally, leaving naked band over mid-line of appendage; gonopore very small, open on caudal surface. Second gonopod very short, flagellum reduced to short, acute stump.

Material examined

Mexico. Cañada Acatlan, Rio San Antonio, Oaxaca State; 2 February 1988; H. WILKENS; 1 male holotype, cl 21.2 mm, cb 22.8 mm, 5 males paratypes, cl 18.0, 16.8, 16.5, 11.9, 11.3 mm, cb 19.0, 17.2, 18.3, 12.3 and 12.0 mm, 1 immature female paratype, cl 11.4 mm, cb 12.4 mm (MP).

Subfamily DILOCARCININAE Pretzmann, 1978

Postgastric pits present; abdominal segments with sutures 3-5 obsolete; penial groove not overlapped by 8th tergite and sternal lobe; first gonopod conical, elongate, apical setae long, conspicuous; second gonopod moderately or considerably longer than first.

Tribe HOLTHUISIINI

Carapace suborbicular, strongly arched, surface smooth, 3-5 lateral teeth behind external orbital angle (sometimes obsolescent in large males), median grooves usually deep; abdomen trapezoidal; first gonopod with basal portion expanded laterally, or with middle lateral lobe provided with conical spines; gonopore V-shaped, open caudal; second gonopod much longer than first, rolled-over.

Type and only genus.- *Sylviocarcinus* H. Milne Edwards, 1853

Sylviocarcinus H. Milne Edwards, 1853

Sylviocarcinus H. Milne Edwards, 1853, p. 215.
Holthuisisia Pretzmann, 1968b, p. 74.
Holthuisia Pretzmann, 1968b, p. 74; PRETZMANN, 1983b, p. 321.

Carapace suborbicular, strongly arched, surface smooth, with the regions ill-defined and the grooves shallow or obsolescent, but median grooves usually deep; 3-5 lateral spines (sometimes obsolescent in large males), in addition to spiniform external orbital angle; front bilobed; buccal area usually with yugal and orbital prominences as blunt teeth, exceptionally spiniform; first gonopod with the basal portion expanded laterally, or with a middle lateral lobe provided with conical spines; gonopore V-shaped, open caudal; second male gonopod considerably longer than first, usually twisted as a question mark (except in *Sylviocarcinus* sp.).

Type species.- *Sylviocarcinus devillei* H. Milne Edwards, 1853.

PRETZMANN (1968b, p.74) erected the genus *Holthuisisia*, which in the same page of that publication and in PRETZMANN (1983b) he spelled *Holthuisia*, with *Dilocarcinus pictus* H. Milne Edwards, 1853, as the type species. Later (PRETZMANN, 1983b) he gave as his reason to discard the genus *Sylviocarcinus* and replace it with *Holthuisia* (=*Holthuisisia*) the fact that the type species of the former genus, *S. devillei*, is a female specimen. However, *S. devillei* is easily recognized by the somatic characters, without recourse to male gonopods (see Remarks under *S. devillei*).

Distribution

The genus *Sylviocarcinus* is widely distributed in the Amazon River and its Andean affluents, Magdalena River basin, Lake Maracaibo basin and Paraguay River basin. It is occasionally present in the Guiana basins, but absent from the Orinoco and the Atlantic basins of Brazil, except for the record of *S. pictus* from the Poty river (RATHBUN, 1906). As here understood it is divided into 6 taxa, well defined geographically as follows. (1) *S. pictus* (H. Milne Edwards, 1853) (syn. *pardalinus* Gerstäcker, 1856), widely distributed in the Amazon basin and its tributaries, as well as in the nearby basin of the Paraguay, is easily distinguished from the other species by the acute spines surrounding the mouth area. (2) *S. maldonadoensis*, known only from Puerto Maldonado, Perú, is almost identical with *S. pictus*, except for the absence of the 2 buccal spines. (3) *S. piriformis* Pretzmann, 1968, with a disjunct distribution in the Maracaibo basin and the Magdalena valley, show a characteristic growth pattern, with a progressive obsolescence of the lateral spines and an increase in width of the posterior section of carapace. Another species, (4) *S. devillei* H. Milne Edwards, 1853, characterized by the spinulation of the rostral lobes, is distributed in the Amazon and its affluents of Colombia and northern Perú. The species has been recorded in the literature under several synonyms, the most recent of them *S. gigas* Smalley & Rodríguez, 1972. (5) *S.* sp. superficially resembles *S. pictus*, but in fact differs from all other species of the genus in its short second gonopod. The records of this species include specimens from the Amazon and northern Argentina.

Key to the species of *Sylviocarcinus*

1. Two acute hooked spines on buccal angle, 1 on inner orbital angle and 2 or 3 similar one on the lower orbital margin ..... *pictus*

- Buccal angle with a large spine or tubercle, followed by several smaller tubercles or papillae. Inner orbital angle formed by a pyramidal prominence, followed on the lower orbital margin by a series of papillae 2
2. Second male gonopod slightly longer than first, S-shaped ..... sp.
- Second male gonopod considerably longer than first, usually twisted as a question mark 3
3. First gonopod not wide basally, without a well developed lateral lobe on the proximal half 4
- First gonopod very wide basally, with a conspicuous lateral lobe on the proximal half. Margin of front without large granules ..... *piriformis*
4. Gonopod with a conspicuous lateral "hump" on distal quarter. Margin of front often with large granules or spines ..... *devillei*
- Gonopod without a conspicuous lateral "hump" on distal quarter. Margin of front without large granules or spines ..... *maldonadoensis*

Sylviocarcinus devillei H. Milne Edwards, 1853

Fig. 4H; 5C; 7F; 9B; 13A; 25A-F

Sylviocarcinus devillei H. Milne Edwards, 1853, p. 215.- H. Milne Edwards, 1854, p. 176, pl. 14, fig. 1a-2.- Lucas, 1857, p. 6, pl. 2, fig. 1.- Smith, 1869, p. 36.- A. Milne Edwards, 1869, p. 174.- Göldi, 1886, p. 33.- Nobili, 1896, p. 2.- Young, 1900, p. 231.- Bott, 1969, p. 28 (part.).- Rodríguez, 1981, p. 48.

Trichodactylus (Valdivia) devillei, Rathbun, 1906, p. 51, pl. 17, fig. 2.

Sylviocarcinus peruvianus A. Milne Edwards, 1869, p. 174.-Nobili, 1896, p. 3.- Moreira, 1901, p. 44.

Trichodactylus (Valdivia) peruvianus, Rathbun, 1906, p. 51, pl. 17, fig. 1.- Del Solar *et al.*, 1970, p. 31.

Orthostoma peruvianum, Ortmann, 1897, p. 327.

Holthuisia peruviana peruviana, Pretzmann, 1983b, p. 323, pl. 4, fig. 7, 8, pl. 5, fig. 9, 10, 11.

Dilocarcinus spinifrons Kingsley, 1880, p. 35.

Dilocarcinus margaritifrons Ortmann, 1893, p. 492, pl. 17, fig. 11.- Young, 1900, p. 231.

Orthostoma margaritifrons, Ortmann, 1897, p. 327.

Trichodactylus (Valdivia) margaritifrons, Rathbun, 1906, p. 44.- Pretzmann, 1968b, p. 71.- Del Solar *et al.*, 1970, p. 31.

Holthuisia peruviana margaritifrons, Pretzmann & Mayta, 1980, p. 141, fig. 9, 10.

Sylviocarcinus gigas Smalley & Rodríguez, 1972, p. 48, fig. 6-7, 21-22.-Rodríguez, 1981, p. 48.- Campos, 1985, p. 270.

Description

Carapace suborbicular; upper surface slightly irregular; in frontal view forms irregular arch; gastric region slightly more prominent than adjacent epibranchial regions; metabranchial region slightly more prominent than adjacent cardiac and intestinal; epigastric lobes very prominent and well delimited anteriorly; frontal region strongly concave in frontal view; branchio-urogastric and urogastric grooves wide and shallow, branchio-cardiac groove almost absent. Postgastric pits lunulate, placed across urogastric groove. Lateral margins angled and directed obliquely upwards, except in large males where they become rounded; postero-lateral ridge of carapace bent mesially in posterior end, ending in elongated swelling over postero-lateral angles of carapace; antero-lateral margin with 3-4 prominent, evenly spaced, acute spines; last spines smaller; lateral teeth becomes obsolescent in large males. Margin of front bilobed, with 13 to 19 spines which become papilliform and obsolescent with age. Orbits oblong, orbital suture absent or indicated by inconspicuous depression; lower orbital margin with 7-9 papillae; inner orbital angle prominent, pyramidal, topped by prominent and acute spine or rounded tubercle; occlusive orbital tooth rounded, small, fused to inner orbital angle; outer orbital angle spiniform, prominent particularly in females and young specimens, represented by stump in old males; buccal angle with large acute spine followed laterally by smaller one, or large tubercle followed by one or two smaller ones. Front advanced, hiding epistome in dorsal view; anterior surface of front inclined backwards, moderately high in the middle, lower on sides, middle pillars short and thick, widely separated, sometimes not distinct,

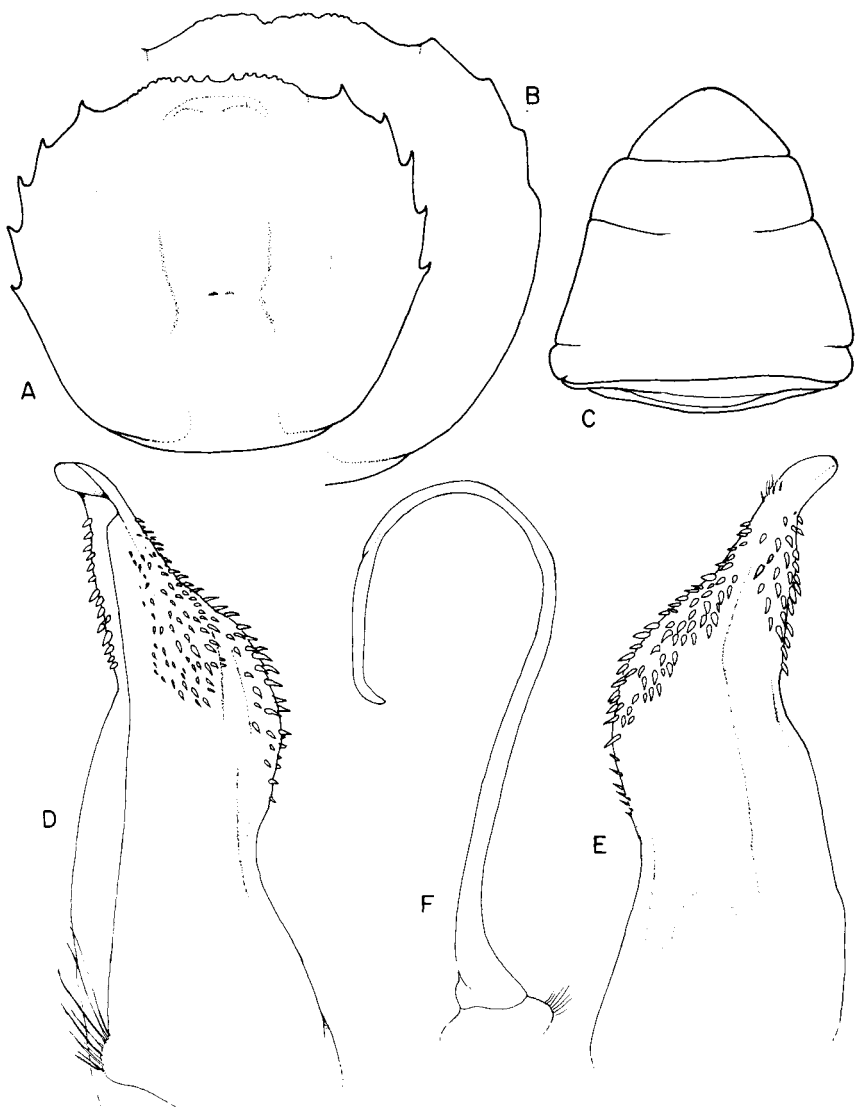

FIGURE 25

Sylviocarcinus devillei (H. Milne Edwards), specimens from Caquetá, Colombia: A, B, outline of carapace; C, abdomen; D, first male gonopod, left, caudal; E, same, cephalic view; F, second male gonopod. A, female, cl 45.5 mm, B-F, male, cl 55.7 mm.

margin over each antennular fossa slightly thickened, but not projected, antennular septum sunken; epistome high, inclined forwards; mid-point of epistome acute, in ventral view appearing as a triangular spine.

First abdominal tergite of male separated from tergite 2 + 3 by suture or deep depression, tergite 2 + 3 with very shallow depression on both sides. Third to 5th abdominal segments fused in both male and female; suture 5/6 very well marked, suture 4/5 only as a thin line and suture 3/4 visible only near lateral margins and on mid-line; 7th segment freely movable; male abdomen elongated, narrow at base, outer margin almost straight, last segment with sides straight, approximately 0.5 as long as broad.

Basal article of antenna with outer lobe prominent and narrow; ischium with shallow longitudinal depression. Chelipeds unequal; upper border of chela strongly arched, lower almost straight or slightly concave; teeth alternatively large and small; acute spine on upper distal angle of hand, above articulation of finger; inner margin of carpus produced in sharp hooked spine; apical spines on upper border and latero-inferior margin of merus. Legs with lower margin of dactylus and lower margin of propodus of 5th pereiopod thickly clothed with band of coarse hairs; these pubescence absent from other pereiopods, except for inferior distal angle of 2nd; upper margin of propodus and dactylus thickly clothed with shorter hairs arranged more or less in 2 parallel longitudinal rows, more extensive in 2nd and 3rd; claws of dactyli with 5 longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First gonopod sinuous, tapering strongly to narrow apex, which is directed mesiad; lateral margin of appendage with strong constriction at middle and conspicuous "hump" on distal half; lateral lobe undivided; field of terminal spines extends proximally along posterior margin, lateral margin ("hump") and cephalo-mesial surface, forming 3 distinct patches; brush of long setae on lateral side of apex; gonopore slit-like, open on caudal side. Second gonopod considerably longer than first, bent mesially in form of question mark.

Color

The carapace is mottled with red specks, which in some specimens are restricted to the distal half, the anterior portion being uniformly reddish.

Size

The largest male on record of this species, cl 88.2 mm (SMALLEY & RODRIGUEZ, 1972) is also the largest known specimen of Trichodactylidae.

Material examined

Colombia. Florencia, Caquetá Department; H. NICEFORO MARIA; 1 male, 1 female (Ivic).- Perú. Upper Rio Marañon, between Jaen and San Ignacio; 15 November 1979; Ministry of Fisheries of Perú;1 male (Ivic). Puerto Maldonado; 7 November 1972; E. DEL SOLAR; 1 male (MHNL).

Type and distribution

The type is a small (cl 32.8 mm) female (MP), collected by the count Francis de CASTELNAU and Mr Emile DEVILLE, this last an employee of the Paris Museum, at Salinas, on the Rio Crixas Açu, affluent of the Rio Araguaia, where they stayed from May 14 to June 10, 1844, during their expedition across South America (PAPAVERO, 1971).

The other records of the species in the literature are the following. Brazil. Amazonas State: Lago Manacapuru near Manaus (BOTT, 1969); ?Rio Madeira (MOREIRA, 1901). Colombia. Caqueta Department: Rio Orteguaza, near Venecia (type *S. gigas*). Putumayo Department: Rio Putumayo, Puerto Asis (SMALLEY & RODRÍGUEZ, 1972). Ecuador. Rio Bobonaza-Pastaza (PRETZMANN, 1983b, as *Holthuisia peruviana peruviana*). Peru. Rio Ucayali (type of *Dilocarcinus margaritifrons* Ortmann, 1893). Guyallaga (type of *S. peruvianus* A. Milne Edwards, 1869). Upper Rio Marañon (present record).

Remarks

There is considerable confusion in the literature concerning the specific status of the specimens of *Sylviocarcinus* with spinous fronts, but it is almost sure that all of them could be grouped under *Sylviocarcinus devillei*. The female holotype (cl 32.8 mm) of *S. devillei* was satisfactorily described by LUCAS (1857) and supplemented by RATHBUN (1906); illustrations were provided by H. MILNE EDWARDS (1854), LUCAS (1857) and RATHBUN (1906). The diagnostic characters of the species are the carapace suborbicular; the front almost horizontal, advanced, with the margin of front bilobed and armed with tubercles; the antero-lateral margin with 5 teeth which do not stand out and have a wide base, the last spiniform; an elevated line over the postero-lateral margin; the lower orbital margin tuberculated, with an obtuse spine over the internal orbital angle; buccal angle with a large acute spine followed laterally by smaller one; abdominal segments incompletely fused in the female.

S. peruvianus, described by A. MILNE EDWARDS (1869) from a female holotype (cl 59 mm) agrees in all characters with the holotype of *devillei*, except that the margin of the front has blunt spines rather than tubercles. *Dilocarcinus spinifrons* described by KINGSLEY (1880) from a young specimen (cl 18 mm), only differs from the holotype of *S. devillei* in that the internal spine of the buccal angle is long and acute and the external is rudimentary, a character undoubtly connected with the immaturity of the specimen.

Dilocarcinus margaritifrons Ortmann, 1893 is known from the type locality only, Rio Ucayali, Perú, where REISS collected the holotype, a male with cl approximately 40 mm, in 1874. RATHBUN (1906) and PRETZMANN (1968b) considered this a valid species, but BOTT (1969) synonymized it with *Sylviocarcinus pictus*. However, the moderately bilobed front, bordered with large tubercles, the spinulation of the lower orbital margin and the stump-like lateral spines are characteristics of *S. devillei*. Furthermore, the specimen of *S. devillei* from Rio Marañon recorded above approaches the area of distribution of this species to the type locality of *Dilocarcinus margaritifrons*.

The large male (cl 76 mm) of *S. devillei* described and illustrated by MOREIRA (1901) agrees in all characters with the female holotype, (except that the lateral spines are reduced), as do the specimens from Manaus and Santarem recorded by BOTT (1969). More recently, SMALLEY & RODRÍGUEZ (1972) described a large species, *S. gigas* whose characters coincide with those of the specimens mentioned above, including its relative large size.

Sylviocarcinus maldonadoensis (Pretzmann, 1978)

Fig. 4I; 7B; 9D; 26A-F

Holthuisia picta maldonadoensis Pretzmann, 1978a, p. 7.- PRETZMANN, 1983b, p. 322, pl. 3, fig. 6, 7, 8.

Description

Carapace suborbicular; upper surface slightly irregular, in frontal view forms an irregular arch, flattened on top; gastric region more prominent than adjacent epibranchial regions and metabranchial region, not more prominent than adjacent cardiac and intestinal; epigastric lobes well delimited anteriorly; frontal region concave in frontal view; oblique elevation runs over anterior region, from level of 2nd lateral tooth to mid-line of carapace; mesogastric, branchio-urogastric and branchio-cardiac groove almost obsolete, represented only by shallow depression; urogastric groove absent. Front, orbits and lateral margins of carapace, including lateral spines, bordered by flat, elongated papillae arranged in single line; upper surface of carapace covered by small, rounded, closely set papillae, particularly over anterior and lateral regions. Postgastric pits slit-like, placed in

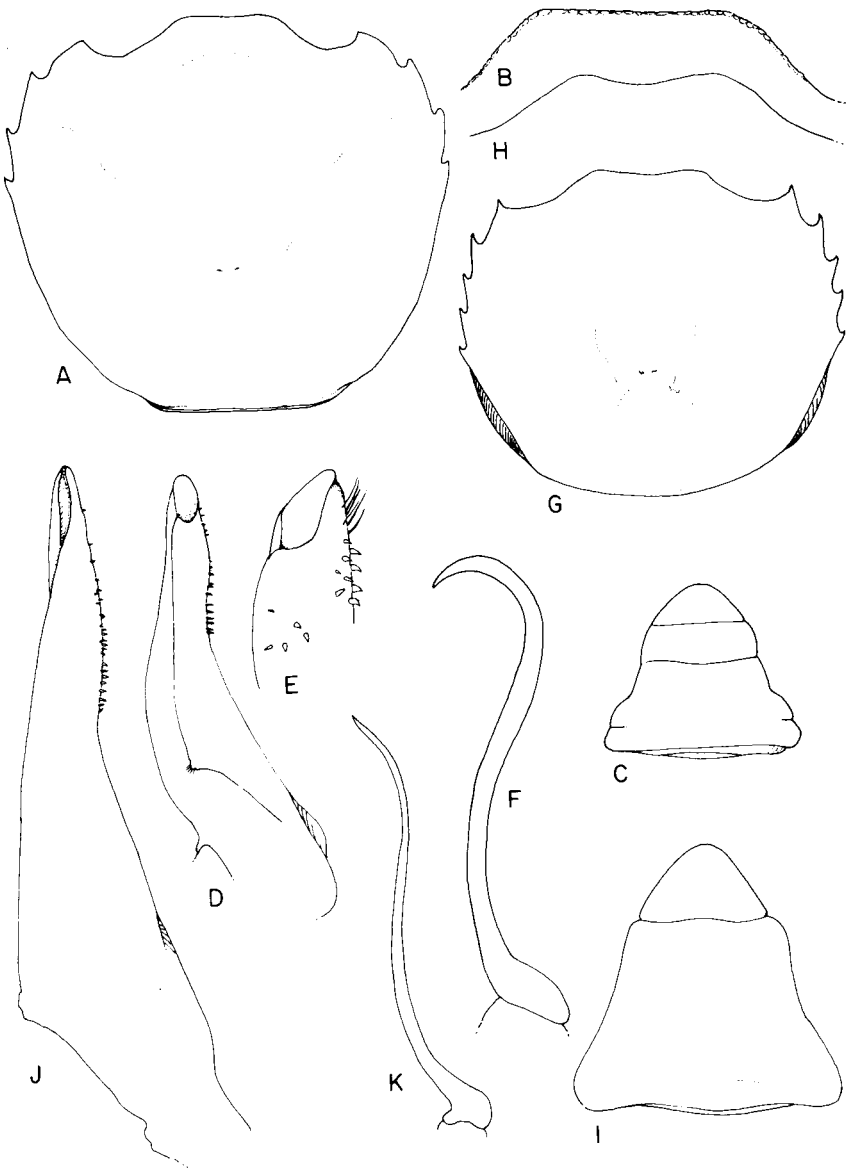

FIGURE 26

Sylviocarcinus maldonadoensis (Pretzmann), A-F, male specimen from Puerto Maldonado, Perú, cl 20.4 mm: A, outline of carapace; B, front; C, abdomen; D, first male gonopod, left, caudal; E, same, detail of apex, latero-caudal; F, second male gonopod. *Sylviocarcinus* sp., G-K, specimen from Lago Grande de Santarem, Brazil, cl 25.5 mm: G, outline of carapace; H, front; I, abdomen; J, first male gonopod, left, caudal; K, second male gonopod.

front of urogastric sulcus. Lateral margins angled and directed obliquely upwards; postero-lateral ridge of carapace bent mesially at posterior end; antero-lateral margin with 3 broad based teeth behind external orbital angle, directed forward and slightly upwards; first interdental space longer than second. Margin of front almost straight. Orbits oblong, orbital suture represented by shallow depression; lower orbital margin with 8 papillae; inner orbital angle pyramidal, obtuse. Occlusive orbital tooth rounded, small, located close to inner orbital angle; outer orbital angle triangular, blunt; buccal angle with 5-6 ill-defined papillae. Front advanced, hiding epistome in dorsal view; anterior surface of front inclined backwards, moderately high in middle, lower on sides, middle pillars short and thick, widely separated, not distinct, margin over each antennular fossa thickened, not projected, antennular septum sunken; epistome high, inclined forwards.

Third to 5th abdominal segments fused in male and female; male abdomen elongated, narrow at base, outer margin sinuous, last segment with sides slightly convex, approximately 0.6 as long as broad.

Basal article of antenna with outer lobe narrow, projected forward; ischium of third maxilliped with very shallow longitudinal depression. Chelipeds unequal; largest chela slender, with upper border arched, lower almost straight or slightly convex; fingers slightly gaping, with well marked carinae; inner margin of carpus produced in sharp hooked spine; merus with terminal spines on upper margin. Lower margin of dactylus of legs thickly clothed with patches of long coarse hairs; these patches cover all lower margin of propodus in 5th, 3/4 in 2nd,1/2 in 3rd and only distal angle in 4th pereiopod; upper margin of propodus and dactylus thickly clothed by shorter hairs arranged more or less in 2 parallel longitudinal rows, more extensive in 2nd and 3rd; claws of dactyli with 5 longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First male gonopod slender, with straight margin; single patch of heavy spines extending proximally on lateral edge; brush of long setae on lateral side of apex. Gonopore open on caudal side. Second gonopod considerably longer than first, bent mesially in form of question mark.

Material examined

Perú. Puerto Maldonado, Laguna Valencia, Rio Madre de Dios; 7 November 1972; 1 male, 1 mature female, 1 ovigerous female with 125 eggs under the abdomen (MHL).

Type and distribution

The holotype specimen, a female, lc 28 mm (Naturhistorisches Museum Wien No 4179), was collected by Dr Enrique M. DEL SOLAR, at Puerto Maldonado. The specimens recorded above under Material examined belong to the same lot used by PRETZMANN (1978a, 1983b) for his original description. The species is known from the type locality only.

Remarks

Although *Sylviocarcinus maldonadoensis* resembles *S. pictus*, its is not conspecific with it, since it lacks some of the distinctive characters of this latter species, among others, the spinulation of the buccal and suborbital ridges, the deeply bilobed front and the spiniform outer orbital angle. The specimens preserved in alcohol do not show the characteristic pattern of coloration of *S. pictus*. PRETZMANN's (1978a, 1983b) holotype is a female, but in the male examined by me (cl 20.4 mm), although not fully mature, the gonopod resembles the appendage of *S. pictus*.

Sylviocarcinus pictus (H. Milne Edwards, 1853)

Fig. 4J; 5D; 7E; 9F; 13C; 27A-H

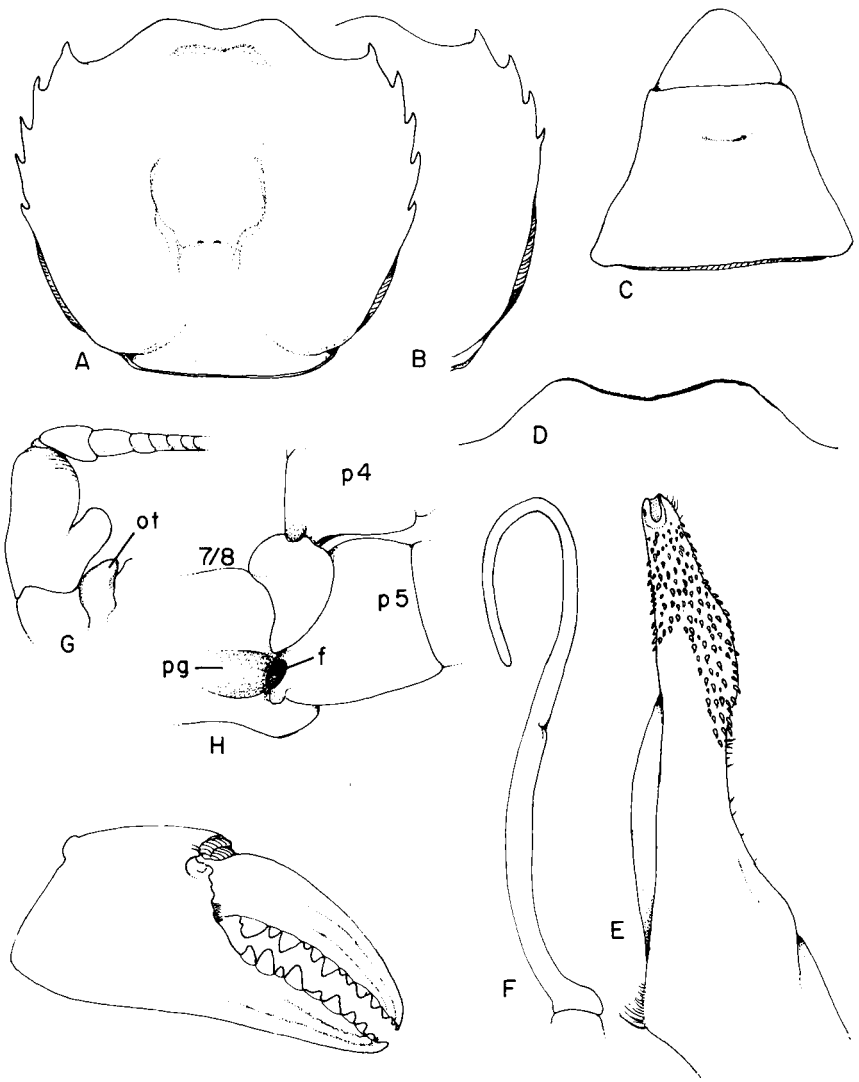

FIGURE 27

Sylviocarcinus pictus (H. Milne Edwards). Specimens from Manaus, Brazil: A,B, carapace; C, abdomen; D, frontal lobes; E, first male gonopod, left, caudal; F, second male gonopod; G, antennal peduncle and occlusive tooth; H, fifth coxa and left side of 8th abdominal tergite showing penial groove. A, C-H, male, cl 19.0 mm, B, female, cl 19.2 mm. f, foramen; ot, occlusive tooth; pg, penial groove; p4, fourth coxa; p5, fifth coxa; 7/8, suture between 7th and 8th sternites.

Dilocarcinus pictus H. Milne Edwards, 1853, p. 216.- H. MILNE EDWARDS, 1854, p. 181, pl. 14, fig. 2.- GERSTÄCKER, 1856, p. 148.- LUCAS, 1857, p. 7, pl.2, fig. 3.- A. MILNE EDWARDS, 1869, p.177.- SMITH, 1870, p. 36.- NOBILI, 1896, p. 1.- YOUNG, 1900, p. 231.- MOREIRA, 1901, p. 44.- MOREIRA, 1913, p. 19, pl. 6, fig. 1-3.- COLOSI, 1920, p. 16.- RINGUELET, 1949, p. 102, pl. 7.

Dilocarcinus picta, STIMPSON, 1861, p. 373.

Trichodactylus (Dilocarcinus) pictus, RATHBUN, 1906, p. 62, pl. 19, fig. 9.- MOREIRA, 1912, p. 150, pl. 6, fig. 9-11.- RINGUELET, 1949, p. 102, pl. 7.

Orthostoma pictum, ORTMANN 1897, p. 327.- NOBILI, 1898, p. 11.

Sylviocarcinus pictus pictus, BOTT, 1969, p. 31, pl. 12, fig. 22a, b, pl. 21, fig. 53.

Sylviocarcinus pictus, SMALLEY & RODRÍGUEZ, 1972, p. 48, fig. 8.- RODRÍGUEZ, 1981, p. 48.- CAMPOS, 1985, p. 270.

Holthuisia picta picta, PRETZMANN, 1983b, p. 321, pl. 1, fig. 1, 2, pl. 2, fig. 3-5.

Holthuisia picta rionegrensis Pretzmann, 1968b, p. 74.

Holthuisia picta collastinensis Pretzmann, 1968b, p. 74.

Dilocarcinus pardalinus Gerstäcker, 1856, p. 148.- A. MILNE EDWARDS, 1869, p. 177.- KINGSLEY, 1880, p. 35.- NOBILI, 1896, p. 1.- MOREIRA, 1901, p. 44.- RODRÍGUEZ, 1981, p. 48.

Orthostoma pardalinus, ORTMANN, 1897, p. 327.

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

Sylviocarcinus pictus pardalinus, BOTT, 1969, p. 13, p. 32, fig. 23a, b, pl. 21, fig. 54.

Description

Carapace suborbicular; upper surface slightly irregular, in frontal view forms irregular arch, flattened on top; gastric region not more prominent than adjacent epibranchial regions, and metabranchial region slightly more prominent than adjacent cardiac and intestinal; epigastric lobes well delimited anteriorly; frontal region slightly concave in frontal view; branchio-urogastric and branchio-cardiac grooves very shallow, urogastric groove almost absent. Postgastric pits slit-like, placed in front of urogastric sulcus. Lateral margins angled and directed obliquely upwards; postero-lateral ridge of carapace bent mesially in posterior end; antero-lateral margin with 4 equally spaced prominent acute teeth behind external orbital angle (see below under Remarks), directed forward and slightly upwards, and sometimes fifth smaller one placed farthest from rest. Margin of front deeply bilobed covered with minute papillae. Orbits oblong, orbital suture absent; lower orbital margin with 2-3 spines directed mesially and decreasing in size laterally, followed by 3-4 papillae; inner orbital angle has sharp, hooked well-developed spine directed ventrally. Occlusive orbital tooth rounded, small, fused to inner orbital angle; outer orbital angle spiniform; buccal angle with 2 well-developed hooked spines. Front advanced, but leaving exposed the lower angle of epistome in dorsal view; anterior surface of front vertical, moderately high in middle, lower on sides, middle pillars short and triangular, widely separated, sometimes not distinct, margin over each antennular fossa thickened, not projected, antennular septum sunken; epistome high, inclined forward.

First abdominal tergite of male separated from tergite 2 + 3 by shallow depression, tergite 2 + 3 with very shallow depression on both sides. Third to 6th abdominal segments fused in both male and female; male abdomen elongated, narrow at base, outer margin concave, last segment with sides straight or slightly convex, approximately 0.6 as long as broad.

Basal article of antenna with outer lobe prominent and narrow; ischium of third maxilliped with very shallow longitudinal depression. Chelipeds unequal; largest chela slender, with upper border arched, lower almost straight or slightly convex; fingers not gaping, with well marked carinae at least in young specimens, teeth alternating large and small; inner margin of carpus produced in sharp hooked spine; merus with terminal spines on upper and inner margins; spine on the latero-inferior margin of this segment in largest chela and two in smaller one. Lower margin of dactylus of legs thickly clothed with patches of long coarse hairs; these patches cover all lower margin of propodus in 5th, 3/4 in 2nd, 1/2 in 3rd and only distal angle in 4th; upper margin of propodus and dactylus thickly clothed by shorter hairs arranged more or less in 2 parallel longitudinal rows, more extensive in 2nd and 3rd; claws of dactyli with 5 longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First male gonopod slender, with straight margin; lateral edge in caudal view has curve at 4/5 length of gonopod from base, forming slight constriction, followed by strong outward curve, and ending in slender tip; single patch of heavy spines, extending proximally on lateral edge; brush of long setae on lateral side of apex. Gonopore slit-like and open on caudal side. Second gonopod considerably longer than first, bent mesially in form of question mark.

Colour

Carapace light brown, with scattered red spots persistent in alcohol.

Material examined

Colombia. Leticia, on the Amazon River, Department of Amazonas; H. NICEFORO MARIA; 1 male (LSB).- Brazil. Sistema Janavaca, South of Manaus, Amazon River; July 1978; 2 males, 2 females (Ivic).- Venezuela. Caño Sin Nombre, left bank of Rio Cuyuni, near Isla Jacobo, Bolivar State; 26 January 1977; F. MAGO; 1 soft shell male (Ivic).- Paraguay. Concepcion, Rio Ipare at ferry crossing, approximately 2.0 km S by dirt road of Belen (which is 18 km ESE of Concepcion); Rio Paraguay drainage; 9 October 1979; J. N. TAYLOR, B. SMITH, E. KOON & R.MYERS; Lat/Long: 23º 27' 18" S - 57º 27' W; Field Number P79-110 (USNM Accession No 341275); 1 specimen. Canendiyu, Rio Jejui-Guazú, bridge approximately 14 km S of Ygatimi on dirt road and approximately 29.5 km N of Curuguaty; Rio Paraguay drainage; 7 July 1979; R.M. BAILEY, J. N. TAYLOR & T. W. GRIMSHAW; Lat/Long: 24º 14' 12" S - 55º 37' 30" W; Field Number P79-43 (USNM Accession No 341275); 1 specimen. Amambay Department, Rio Apaca approximately 0.5 km upstream (=E) of bridge between Brazil & Paraguay in Bella Vista, Paraguay; Rio Paraguay drainage; 27 July 1979; J. N. TAYLOR, T. W. GRIMSHAW & R. MYERS; Lat/Long: 22º 6' 30" S - 56º 30' 36" W; Field Number P79-65A (USNM Accession No 341275); 1 specimen.

Type and distribution

The types are two females (MP) collected by the count Francis de CASTELNAU and Mr Emile DEVILLE at Loreto, Colombia, where they stayed from December 25 to 28, 1846, on their way back from their expedition across South America (PAPAVERO, 1971). The other records of the species in the literature are the following. Perú. Nauta (RATHBUN, 1906); Rio Siamiria (BOTT,1969); 25 km W of Iquitos (PRETZMANN, 1983b). Colombia. Rio Arara, Leticia, on the Amazon River (SMALLEY & RODRÍGUEZ, 1972). Brazil. Manaus; Villa Bella, 600 km upriver Amazonas; Poty, Piauhy State (RATHBUN, 1906); Solimoes, Fonte Boa; Rio Negro, Ponta Arara; Rio Tapajos; Rio Mulata (BOTT, 1969). Bolivia. Rio Chimpire, Rio Chapare (BOTT, 1969). Paraguay. Rio Paraguay, near Puerto Max, North Paraguay (BOTT, 1969); Colonia Risso, Rio Apa (RATHBUN, 1906). Argentina. Buenos Aires (probably Buenos Aires Province); Candelaria, Misiones (RATHBUN, 1906). French Guiana. Rivière Camopi; Haut Carsevenne (RATHBUN, 1906). The specimens from Rio Parana Mini, in front of La Invernada island, Reconquista Department, Santa Fe Province, Argentina reported by RINGUELET (1949) probably belong to the *Sylviocarcinus* sp., described below. As *Sylviocarcinus pictus pardalinus*, it has been recorded from the following localities in Brazil. Peixe Boi near Para; entrance of the Igarape into the Rio Tapajos; Ducke Reserve; Rio Guamá at Ourem; Rio Aripuana at Beneficiente; Rio Cupari at Goiabal; Rio Irapiri; Rio Marauia at Cachoeira; all these records by BOTT (1969) come from the lower Amazon and its affluents. As *Dilocarcinus pardalinus* it has been recorded from Paraguay, Rio Apa (NOBILI, 1896).

Remarks

As shown in Fig. 48, the area of distribution of the species covers a very large territory comprising the basins of the Amazon and its tributaries, the Parana-Paraguay basin, and the Atlantic basins of the Guianas. This wide,

scattered distribution rises doubts about the cohesion of the species and have led BOTT (1969) and PRETZMANN (1968b, 1977a) to segregate some specimens into distinct subspecies.

The type specimen of *Dilocarcinus pardalinus* is a female from an unknown locality. The species was later recorded from Rio Apa, Upper Paraguay by NOBILI (1896). BOTT (1969) considered this a subspecies of *Sylviocarcinus pictus* and recorded it as such from the lower Amazon. The only character with diagnostic value given by BOTT (1969) to separate it from the typical form *S. pictus,* besides the form of the red dots of the carapace concentrated "as in the leopard" (GERSTÄCKER, 1856), is the presence of 3 lateral teeth instead of 4, behind the spiniform external orbital angle. This character, however, is variable as shown by specimens collected in the same locality. Thus, in 4 specimens from Manaus, 3 males had 4 lateral teeth and 1 female had 3 (Fig. 27a, b); in three females from Paraguay River, 1 specimen had 3 teeth on each side, 1 had 3 teeth on each side and an indentation on the right side, and 1 specimen 4 teeth on each side. On the other hand the specimens from the Paraguay River also present some variability in the characteristic pair of buccal spines which in this case could be present or replaced by a large and a smaller one, or even by a single spine.

PRETZMANN (1968b, 1978a) described three subspecies of *Sylviocarcinus pictus* as follows.

(1) *Holthuisia picta rionegrensis* Pretzmann, 1968, based on an immature male (cl 20.2 mm), from the mouth of Rio Negro (i. e. near Manaus). The specimens I have examined from Manaus (see above), cannot be differentiated from typical *S. pictus.*

(2) *Holthuisia picta collastinensis* Pretzmann, 1968, from Collastine, based on a female from Santa Fe. SMALLEY & RODRÍGUEZ (1972), suggest that *collastinensis* refers to the city of Clatine, formerly called Collatina, 50 km north of Vitoria, Spirito Santo State, Brazil, but this locality lies outside the area of distribution of *S. pictus.* Another possibility is that Santa Fe refers to the Santa Fe Province in Argentina where RINGUELET (1949) has recorded *S. pictus.*

(3) *Holthuisia picta maldonadoensis* Pretzmann, 1978. As stated before, the characters displayed by this taxon are enough to give it specific rank.

Sylviocarcinus piriformis (Pretzmann, 1968)

Fig. 3I; 4K, M; 5B; 7A, C; 9C, G; 13B; 15D; 28A-G; 29A-F

Valdivia (Valdivia) piriformis Pretzmann, 1968b, p. 73.- SCHMITT, 1969, p. 98, fig. 3, a-e, f-i.
Sylviocarcinus piriformis, SMALLEY & RODRÍGUEZ, 1972, p. 45, fig. 5.- RODRÍGUEZ, 1980, p. 340, fig. 97.- RODRÍGUEZ, 1981, p. 48.- VON PRAHL, 1982, p. 23, fig. 1.- VON PRAHL, 1988, p. 13.
Valdivia (Valdivia) torresi Pretzmann, 1968b, p. 72.
Sylviocarcinus torresi, SMALLEY & RODRÍGUEZ, 1972, p. 44, fig. 3, 4.- RODRÍGUEZ, 1981, p. 48.

Description

Carapace suborbicular in smaller specimens, widest between fourth lateral teeth; in larger specimens becoming subquadrate to piriform, widest behind 4th lateral teeth due to swelling of lateral wall of branchial chamber; finally in largest specimens becoming orbicular with posterior lateral walls considerably swollen. Upper surface slightly irregular, in frontal view forms irregular arch, gastric region slightly more prominent than adjacent epibranchial regions; metabranchial region slightly more prominent than adjacent cardiac and intestinal; epigastric lobes well delimited anteriorly; frontal region concave in frontal view; branchio-urogastric and branchio-cardiac grooves wide and shallow, urogastric groove almost absent. Postgastric pits lunulate, placed in front of urogastric sulcus. Lateral margins angled and directed obliquely upwards, except in large

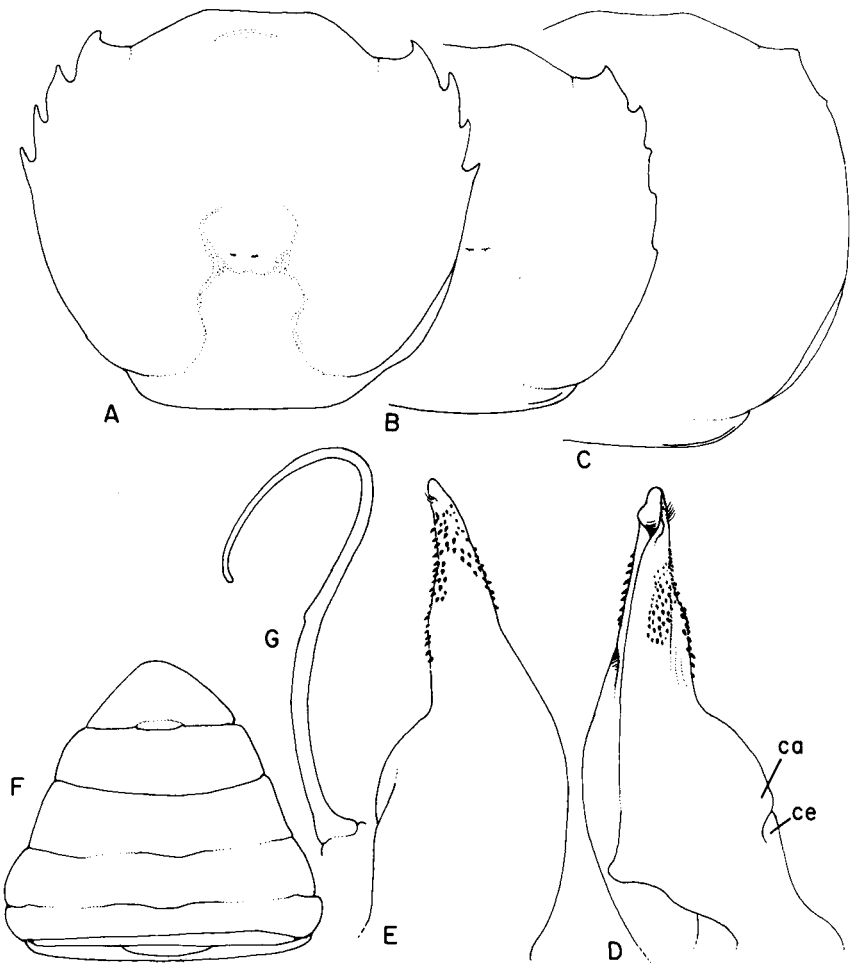

FIGURE 28

Sylviocarcinus piriformis (Pretzmann). Specimens from several localities in the Maracaibo basin: A, B, C, carapace; D, first male gonopod, left, caudal; E, same, cephalic; F, male abdomen; G, second male gonopod. A, female from Mene Grande, cl 25.0 mm; B, F, male from Caño Chamiras, cl 47.3 mm; C, male from Rio Curarigua, cl 52.6 mm; D, E, G, male from Rio Guasare, cl 74.7 mm. ca, lateral lobe, caudal segment; ce, lateral lobe, cephalic segment.

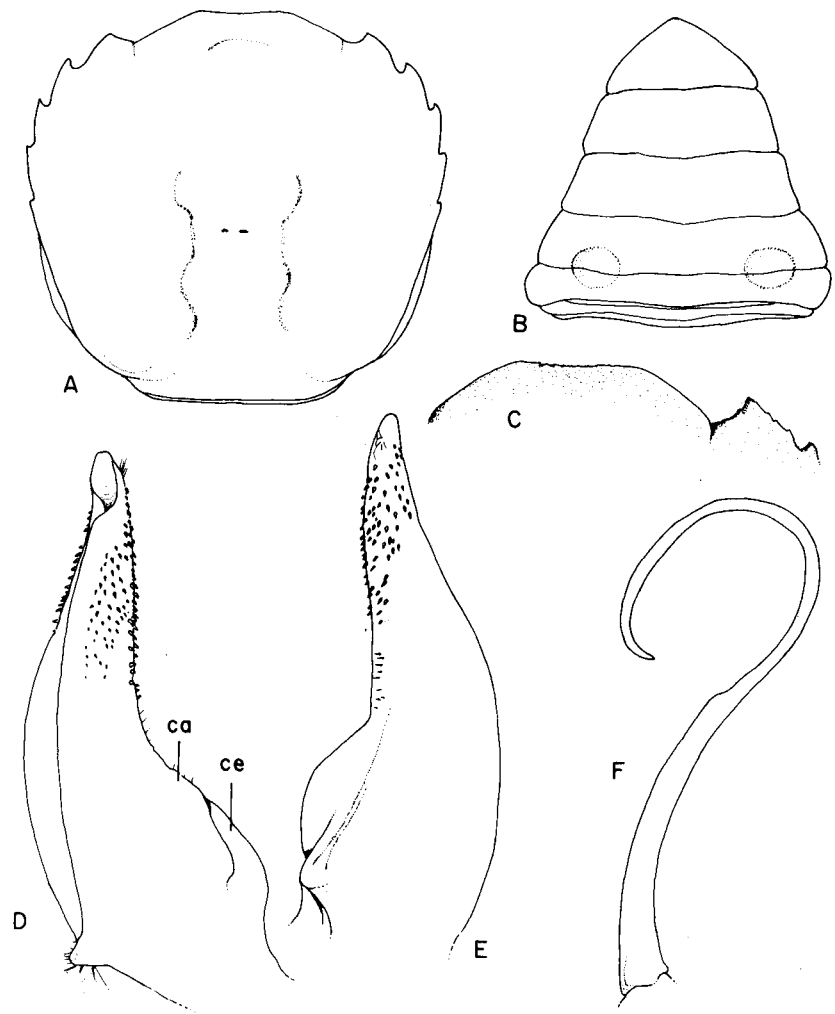

FIGURE 29

Sylviocarcinus piriformis (Pretzmann). Specimens from the Magdalena Valley, Colombia: A, carapace; B, abdomen; C, right margin of orbit and front; D, first male gonopod, left, caudal; E, same, cephalic; F, second male gonopod. A, B, D-F, male from Rio Fundación, cl 53.7 mm; C, male from Rio Gualanday, cl 51.5 mm. ca, lateral lobe, caudal segment; ce, lateral lobe, cephalic segment.

males where become rounded; postero-lateral ridge of carapace bent mesially in posterior end, ending in elongated swelling over postero-lateral angles of carapace; antero-lateral margin with 4 prominent acute teeth behind external orbital angle, the last smaller and placed farthest from the rest; in large males (cb > 45 mm) lateral teeth become obsolescent. Margin of front slightly concave, covered with minute papillae. Orbits oblong, orbital suture absent or indicated by inconspicuous groove; lower orbital margin with 6-8 papillae which decrease in size laterally; inner orbital angle prominent, pyramidal; occlusive orbital tooth rounded, small, located close to inner orbital angle; outer orbital angle spiniform, prominent in females and young specimens, represented by stump in old males; buccal angle with large triangular tooth followed laterally by 4-5 denticles or papillae. Front advanced, hiding epistome in dorsal view; anterior surface of front inclined backwards, moderately high in middle, lower on sides, middle pillars short and thick, widely separated, sometimes not distinct, margin over each antennular fossa thickened, slightly projected, antennular septum sunken; epistome high, inclined forward.

First abdominal tergite of male separated from tergite 2 + 3 by suture or deep depression, tergite 2 + 3 with very shallow depression on both sides. Third to 5th abdominal segments fused in both male and female; male abdomen elongated, narrow at base, outer margin slightly concave, last segment with sides straight, approximately 0.6 as long as broad.

Basal article of antenna with outer lobe prominent and narrow; ischium of third maxilliped devoided of grooves or depressions. Chelipeds strongly unequal; upper border of chela strongly arched, lower almost straight or slightly concave; teeth alternatively large and small; young specimens with inner margin of carpus produced in sharp hooked spine; apical spines on upper border and latero-inferior margin of merus; in old males larger chela becomes enormously developed, hand > 1.5 as long as carapace, the spines of carpus and merus become obsolescent and fingers often, but not always, have large gap between them. Lower margin of dactylus of legs thickly clothed with patches of long coarse hairs; these patches cover all lower margin of propodus in 5th, 3/4 in 2nd, 1/2 in 3rd and only distal angle in 4th pereiopod; upper margin of propodus and dactylus thickly clothed by shorter hairs arranged more or less in 2 parallel longitudinal rows, more extensive in 2nd and 3rd; claws of dactyli with 5 longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First male gonopod very wide basally, tapering strongly to narrow apex; basal expansion regularly convex mesially; laterally more irregular, with accessory elongated lobe on caudal surface; field of terminal spines extends proximally along posterior margin, lateral margin and cephalo-mesial surface, forming 3 distinct patches; brush of long setae on lateral side of apex; gonopore slit-like and open on caudal side. Second gonopod considerably longer than first, bent mesially in form of question mark.

Material examined

Venezuela. River between San Pedro and San Juan, 10 km of Mene Grande, Zulia State; 2 February 1968; G. RODRÍGUEZ; 3 males, 3 females (IVIC). Caño Chamiras, Zulia State; 11 September 1968; DISCA; 1 male, 1 female (MB XI 1539). Rio Guasare, Zulia State; 1 September 1957; 1 male (Ivic). Rio Curarigua, affluent of Rio Tocuyo, near Curarigua, Lara State; 21 May 1978; L. AGUANA & F. MAGO; 3 males (MB). Quebrada Chipuen, 1 km from Chimpire, between Pampanito and Valera, Trujillo State; 14 February 1966; G. RODRÍGUEZ; 3 males, 1 female (Ivic). Rio Buena Vista, near town of Buena Vista, 150 m alt, Trujillo State; 14 February 1964; G. RODRÍGUEZ; 1 female (Ivic). Rio Onia, tributary Rio Escalante, 5 km from the highway El Vigia-San Cristobal, Merida State; 23 April 1964; F. MAGO & J. MOSCO; 1 male (MB). Represa El Isiro, Falcón State; F. AGUIRRE; 2 males (Ivic).- Colombia. Rio Fundación, Santa Marta, Magdalena Department; 18 November

1967; A. ZAMORA; 1 male (Ivic). Rio Gualanday, Tolima Department; M. CAMPOS; 1 male (Ivic). Quebrada Lumbi, Mariquita, Tolima Department, 550 m alt; 20 September 1983; M. CAMPOS; 1 male (ICN-MHN-CR 451).

Type and distribution

Colombia. Norte de Santander Department: Cúcuta (PRETZMANN, 1968b, type; SMALLEY & RODRÍGUEZ, 1972); Rio Sardinata; Puerto Santander (SMALLEY & RODRÍGUEZ, 1972). Bolivar Department: La Regla (PRETZMANN, 1968b, type of *Valdivia (Valdivia) torresi* Pretzmann, 1968). Magdalena Department: Rio Fundación, Rio Aracataca, and Rio Sevilla, near Santa Marta; Rio Cesar, 10 km south of Valledupar (SMALLEY & RODRÍGUEZ, 1972). Venezuela. Zulia State: Mene Grande; Rio Negro, south and west of Machiques (SMALLEY & RODRÍGUEZ, 1972). Falcón State: Represa El Isiro (SMALLEY & RODRÍGUEZ, 1972). Merida State: Rio Onia, near El Vigia (SMALLEY & RODRÍGUEZ, 1972). Trujillo State: Quebrada Chipuen, near Valera; Rio Buena Vista, near Buena Vista (SMALLEY & RODRÍGUEZ, 1972). Lara State: see above.

Remarks

Originally *Sylviocarcinus torresi* and *S. piriformis* were described as two distinct species, occupying respectively the Magdalena and the Maracaibo basins. The distinction between both species, according to SMALLEY & RODRÍGUEZ (1972), was based on the fact that the carapace in the older specimens of *Sylviocarcinus piriformis* is always wider in the posterior portion, the lateral wall becoming swollen with age and producing a pear-shaped appearance; juvenile specimens are almost impossible to separate. However, VON PRAHL (1982, 1988) has recorded the presence of *Sylviocarcinus piriformis* in the middle Magdalena Valley, and consequently the disjuntion of the areas cannot be used as an argument for the specific separation of the populations in both basins.

In the specimen from Rio Gualanday recorded above, the posterior orbital margin is bent at the orbital suture, and the margin from this place to the external angle of front is somewhat produced.

Sylviocarcinus sp.

Fig. 4L; 7D; 9E; 13C; 26G-K

Sylviocarcinus devillei, BOTT, 1969, p. 28 (part.).
Sylviocarcinus pictus, LOPRETTO, 1976, p. 81.

The first and second gonopods of Argentinian specimens illustrated and reported by LOPRETTO (1976) under *Sylviocarcinus pictus* do not belong to this species, but to a new, undescribed form to which belong also a male specimen reported by BOTT (1969, p. 29) under *Sylviocarcinus devillei*, from Lago Grande de Santarem, Brazil.

This form closely resembles *S. pictus*, even in the colour of the carapace and pereiopods, which are brown-reddish, with faint scattered red spots persistent in alcohol. However, it can be clearly distinguished from this species by the following characters: (1) the front is less strongly bilobed and consequently more of the oral area is exposed in dorsal view, (2) the first male gonopod is more slender, it has only a very slight lateral lobe, and the terminal spines are very small, very few, and scattered, (3) the second gonopod is only slightly longer than the first gonopod and S-shaped.

Material examined

Brazil. Lago Grande de Santarem; January 1957; A. MESCHKAT; 1 male, cl 25.5 mm, cb 28.5 mm (Hamburg Museum K27047).

Tribe VALDIVIINI Pretzmann, 1978

Carapace hexagonal, upper surface moderately arched, exceptionally strongly arched, transbranchial ridge on each side, 2-6 lateral teeth behind external orbital angle; median grooves usually deep; first gonopod with strong lateral lobe on proximal half, bordered with setae; gonopore terminal, slit-like; second gonopod moderately longer than first, sinuous (except in *Valdivia camerani*).

Type genus.- *Valdivia* White, 1847.

Key to the genera of VALDIVIINI

1. Carapace not regularly arched in frontal view, but orbital, frontal, hepatic and epibranchial regions excavated; distal half of gonopod ending in straight-sided narrow tube ..... *Valdivia*
– Carapace forms regular arch and antero-lateral regions are only slightly excavated; distal half of gonopod forming conspicuous bulb and directed laterad ..... *Forsteria*

Valdivia White, 1847

Valdivia White, 1847a, p.31 (*nomen nudum*).- WHITE, 1847b, p. 206.- DANA, 1852b, p. 292.- H. MILNE EDWARDS, 1853, p. 214.- PRETZMANN, 1968b, p. 71 (part.).- BOTT, 1969, p. 36 (part.).
Trichodactylus (Valdivia) Rathbun, 1906, p. 43 (part.).
Valdivia (Rotundovaldivia) Pretzmann, 1968b, p. 73 (part.).- PRETZMANN, 1983b, p. 326.
Rotundovaldivia Pretzmann, 1978a, p. 168; 1983b, p. 325 (part.).

Carapace hexagonal, upper surface moderately arched, very uneven, with frontal, orbital, hepatic and epibranchial regions conspicuously excavated and antero-lateral margin forming thin edge directed transversely upwards, epigastric lobes crossed by transverse granular striae visible under microscope, 2 lobes on protogastric region delimited anteriorly by thin, lunular ridges, transverse ridge in front of mesogastric region and extending laterally for short distance across metabranchial regions, usually continued on cardiac region by another transverse ridge, median grooves deep, lateral margin armed with 4 or 5 teeth behind external orbital angle, equally spaced, decreasing in size posteriorly; front straight, or slightly concave; first gonopod wide at base, with well developed lateral lobe with long setae on margin; exceptionally, in *V. camerani*, first gonopod tapers gradually and has poorly developed lateral lobe.

Type species.- *Valdivia serrata* White, 1847.

Distribution

The Amazon seems to be a dividing line for the species of *Valdivia*, with *V. serrata* restricted to the north, and *V. gila* and *V. camerani* to the south. The localities of *V. harttii* are nested within the area of *V. serrata*.

Key to the species of *Valdivia*

1. Carapace with 4 small spiniform teeth, last two usually obsolescent or absent. Larger chela unusually developed in adult males ..... *gila*

– Carapace with 4-6 well developed lateral teeth. Chelae moderately unequal in adult males 2
2. First gonopod slender, tapering regularly to point. Second gonopod much longer, crosier shaped ..... *camerani*
– First gonopod not very wide proximally, strangled near distal part. Second gonopod slightly longer 3
3. First gonopod sickle-shaped, strongly curved outwards ..... *latidens*
– First gonopod bottle-shaped, not strongly curved outwards 4
4. Distal part of first gonopod short tube with parallel sides; proximal lateral lobe wide ..... *harttii*
– Distal part of gonopod slender tube with convergent sides; proximal lateral lobe elongated ..... *serrata*

Valdivia camerani (Nobili, 1896)

Fig. 2C; 4N; 5F; 8D; 13F; 15E; 30A-H

Sylviocarcinus camerani Nobili, 1896, p. 2.- Moreira, 1901, p. 44.- Colosi, 1920, p. 17.
Orthostoma camerani, Nobili, 1898, p. 15.
Dilocarcinus camerani, Nobili 1899, p. 3.
Trichodactylus (Valdivia) camerani, Rathbun, 1906, p. 54, pl. 15, fig. 2, text-fig. 116.- Ringuelet, 1949, p. 105, pl. 9, fig. 3, pl. 10.
Trichodactylus (Trichodactylus) camerani, Bott, 1969, p. 24, pl. 17, fig. 32a, b.- Manning & Hobbs, 1977, p. 159.
Trichodactylus camerani, Rodríguez, 1981, p. 48.
Valdivia (Rotundovaldivia) camerani, Pretzmann, 1968b, p. 73.
Trichodactylus (Trichodactylus) cameranoi, Lopretto, 1976, p. 68.

Description

Carapace hexagonal; upper surface very irregular; high papillated ridge across mesogastric region extending transversely backwards between meso- and metagastric regions; less conspicuous transverse ridge across epibranchial regions; protogastric region with two lobes almost as elevated as mesogastric ridge; metabranchial region moderately convex; surface between these ridges excavated; frontal region flat; urogastric, branchio-cardiac and branchio-urogastric grooves thin but well defined. Postgastric pits lunulated, placed in front of urogastric groove. Lateral margins angled, armed with 5 acute, prominent teeth behind external orbital angle, 1-4 very large, last one very small; interdental spaces approximately equal; small lobe between outer orbital angle and first tooth; postero-lateral ridge of carapace bent mesially in posterior end, ending in elongated swelling over postero-lateral angles of carapace; posterior margin delimited by high carina which hides first abdominal segment. Frontal margin almost straight, sinus very shallow. Orbits suboval; orbital suture thin, but long and well defined; lower orbital margin with acute tooth on inner angle, followed laterally by gap and few large tubercles; occlusive orbital tooth absent; outer orbital angle dentiform; buccal angle smooth. Front advanced, hiding epistome in dorsal view; anterior surface of front vertical, moderately high in middle, lower on sides, middle pillars not distinct, slightly elongated elevation over middle of each antennular fossa; antennular septum slightly sunken; epistome high, vertical or slightly bent backwards. Eyes of normal size, eyestalk not reduced.

Abdominal tergites of male densely covered by pits largest in tergites 1-3, given them eroded aspect under microscope; when closed, abdomen is sunk and tergite in front forms ridge; abdominal tergites 1-3 has excavation anteriorly and 2 on sides, and consequently space between them forms conspicuous Y-shaped ridge in front of last abdominal segment. First abdominal segment hidden behind posterior margin of carapace; 3rd to 5th fused, sutures barely visible; male abdomen narrow, lateral margins conspicuously concave; last segment broadly triangular, apex evenly rounded, approximately 0.6 as long as broad.

Chelipeds moderately unequal, conspicuously rugous or even eroded; middle surface of palm with long longitudinal rugosities; acute, hooked spine on upper distal margin; upper surface of carpus eroded and with

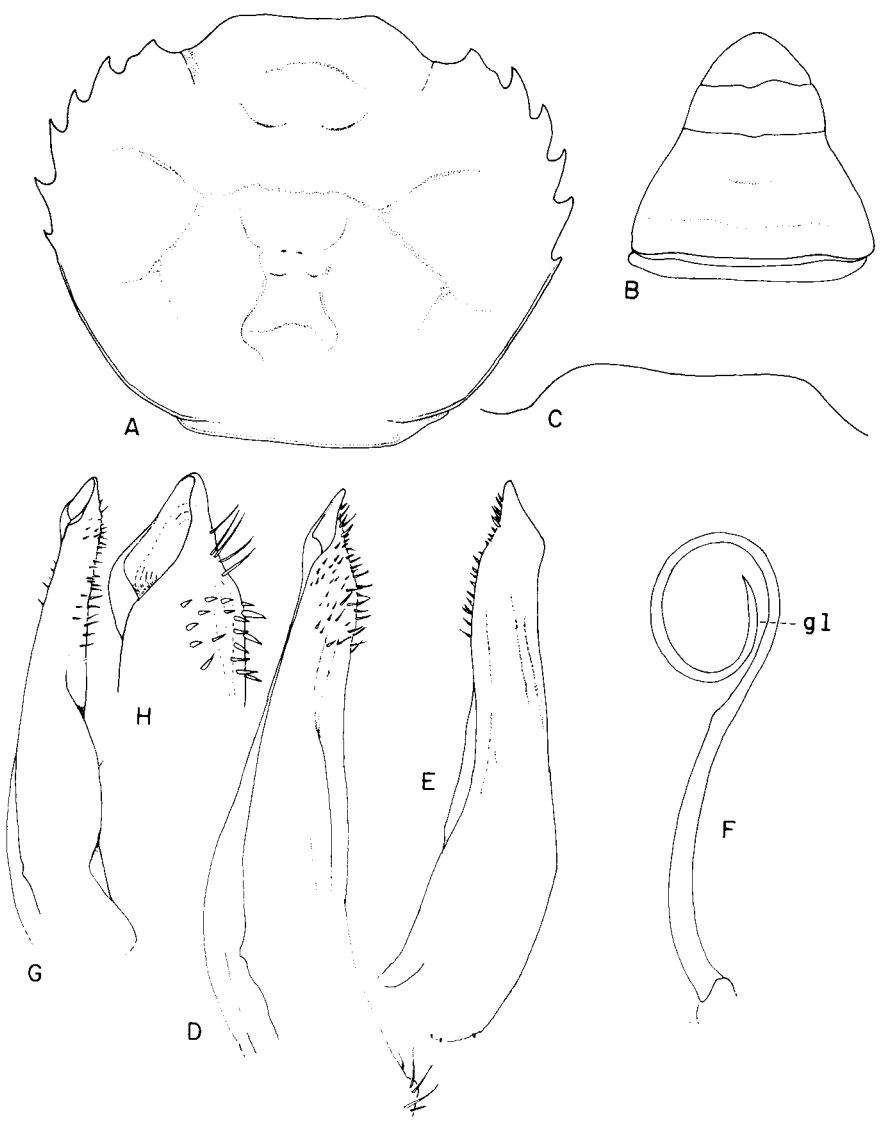

FIGURE 30

Valdivia camerani (Nobili), A-F, male specimen from Rio Beni, Bolivia, cl 22.8 mm: A, outline of carapace; B, abdomen; C, front; D, first male gonopod, left, caudal; E, same, cephalic; F, second male gonopod. G-H, specimen from Rio Paraguay, Paraguay, cl 19.9 mm: G, first male gonopod, caudal; H, detail of apex, caudal. gl, level of gonopore of first gonopod.

long hooked spine on distal margin; merus with upper subterminal spine and a smaller one on lateral distal angle. Legs long and slender; merus of 3rd pereiopod 4 times as long as broad; propodus of 5th widened, 2 times as long as broad (measured on the anterior border); dactylus 1.5 - 1.75 times as long as propodus; two rows of long hairs on lower margin of dactyli.

First gonopod long and slender, tapering regularly to point, with few longitudinal ridges, particularly on cephalic side; apex acuminate; gonopore long and narrow, directed mesially; patch of setae on distal quarter of appendage arranged irregularly on lateral side and extending to margin and tip of appendage; setae long, not spiniform as in other species. Second gonopod considerably longer than first, crosier-shaped, apex long and acuminate.

Material examined

Bolivia. Trinidad, Rio Mamoré, Beni Province; 1 male (MNHNP B.19121).- Paraguay. Concepcion Department, Rio Aquidaban at Paso Horqueta, approximately 24 km NNW of Loreto; Rio Paraguay drainage; 9 May 1979; J. N. TAYLOR, T. W. GRIMSHAW, B. SMITH, E. KOON & R. MYERS; Lat/Long: 23º 03' 48" S - 57º 23' 24" W; Field Number P79-107 (USNM Accession No 341275); 1 specimen.

Type and distribution

The type material is from Paraguay, Rio Apa, near the Brazilian border. This species is fairly rare: I detected only one specimen in a sample of more than 50 specimens of Trichodactylidae from Trinidad, Bolivia, and another specimen in more than 64 specimens of Trichodactylidae collected in Rio Paraguay. Aside from the type locality, it is known from 2 more localities only, covering a vast area: Argentina, Reconquista, Rio Parana Mini, Santa Fe Province (RINGUELET, 1949); Bolivia (see under material examined).

Remarks

The gonopore of this species is intermediate between that of Trichodactylinae and *Sylviocarcinus*, and the more typical *Valdivia*; it opens distally, but in a diagonal plane and the proximal part is V-shaped. The gonopods of my specimen of *V. camerani* from rio Mamoré, a tributary of the rio Madeira and the Amazon, differ from those of Argentinian specimens illustrated by LOPRETTO (1976): the first has fewer apical spines and the second has a double row rather than a single one.

Valdivia gila Pretzmann, 1978

Fig. 4P; 8F; 10A; 13F; 15G; 31A-I

Rotundovaldivia hartii (sic) gila Pretzmann, 1978a, p. 168, fig. 11.- PRETZMANN, 1983b, p. 318, 326 (by implication).
Valdivia (Rotundovaldivia) hartti (sic) gila, PRETZMANN, 1983a, p. 309, pl. 1, fig. 4, pl. 2, fig. 6, pl. 3, fig. 9, pl. 4, fig. 16, pl. 5, fig. 18.- PRETZMANN, 1983b, p. 319.
Valdivia (V.) hartti (sic) gila, PRETZMANN, 1983b, p. 319.
Valdivia (Valdivia) hartii (sic) gila, PRETZMANN, 1983b, p. 326.
Valdivia (Rotundovaldivia) hartii (sic) gila, PRETZMANN, 1983b, p. 326.

Description

Carapace hexagonal; upper surface very uneven; frontal, orbital, hepatic and epibranchial regions conspicuously excavated; epigastric region consists of 2 transverse lobes not clearly delimited, which under microscope appear crossed by transverse granular striae; protogastric region also bilobular, each lobe delimited anteriorly by thin, lunular ridge; branchio-cardiac and branchio-urogastric grooves wide and shallow,

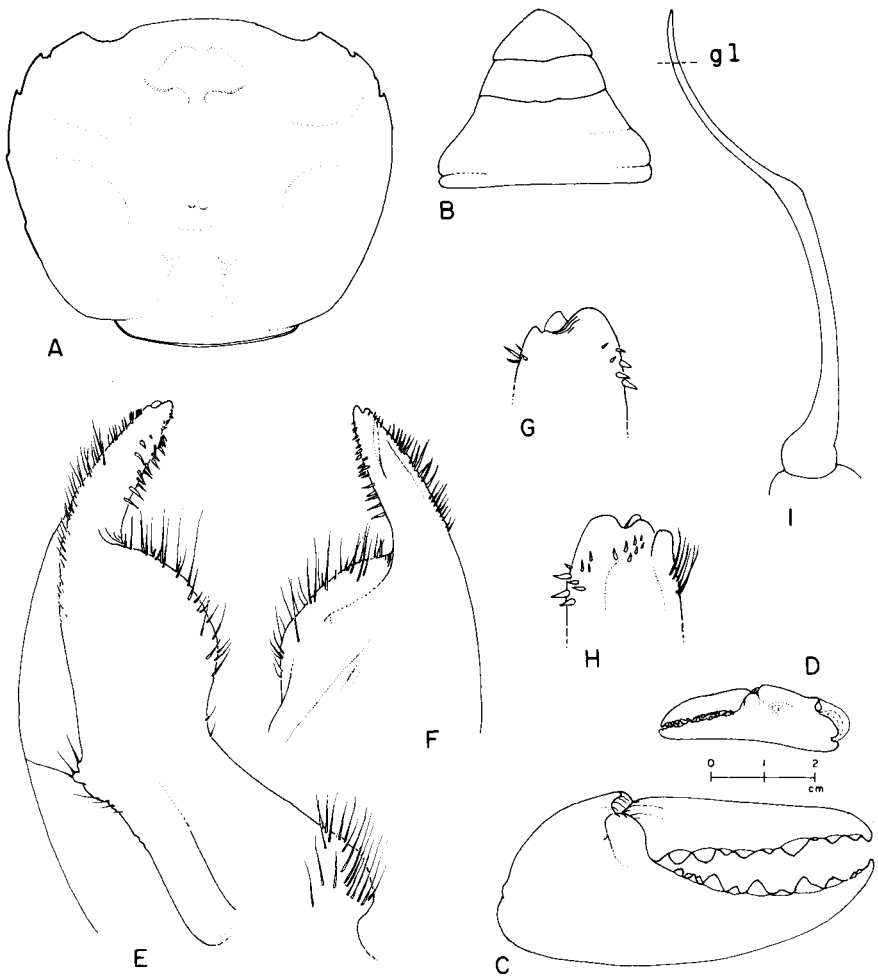

FIGURE 31

Valdivia gila Pretzmann, male specimen from Pakitza, Perú, cl 40.6 mm: A, outline of carapace; B, abdomen; C, larger chela; D, smaller chela; E, first male gonopod, left, caudal; F, same, cephalic; G, same, detail of apex, caudal; H, same, cephalic; I, second male gonopod. gl, level of gonopore of first gonopod.

obsolescent; other grooves of mesial regions not present; wide and elevated ridge separates epi- and mesogastric regions; cardiac region rhomboidal, with transverse ridge across; intestinal region slightly convex. Posterior gastric pits present. Lateral margin armed with 2 small, widely spaced spines, placed on antero-lateral portion of margin and usually followed by 2 wide lobes or indentations (2 small spines in holotype); margin between external orbital angle and first tooth forms a convex, or more generally concave lobe; postero-lateral ridge of carapace bent mesially in posterior end, ending in elongated swelling over postero-lateral angles of carapace; posterior margin delimited by high ridge. Surface of carapace smooth and shiny to naked eye. Frontal margin straight, incurved upwards; orbits more or less rounded, small, eyes completely fill orbital cavity; orbital fissure indicated only by inconspicuous notch or shallow groove in small specimens; lower orbital margin entire or with a small tooth followed by crenulations; inner orbital angle pyramidal, not prominent, topped by a tubercle; conspicuous wide recess between this angle and rest of lower orbital margin; occlusive orbital tooth small, not dentiform, but forming rounded ridge by external side of basal portion of antenna and not concealed by it; outer orbital angle blunt, triangular; buccal angle entire or crenulated. Front advanced, hiding epistome in dorsal view; anterior surface of front sunk, high particularly in middle, with 2 distinct middle pillars separated by U-shaped sinus which forms deep recess, thin ridge over middle of antennular fossae; antennular septum slightly sunk; epistome high, slightly bent backwards.

The abdominal tergites of male covered by pits and rugae which are largest in tergites 1-3 (but not so conspicuously as in *harttii*); abdomen sunk when closed, tergite in front of it forms ridge; abdominal tergites 1-3 only slightly excavated. First abdominal segment of male and female partly hidden by posterior margin of carapace; segments 3-5 fused in male and female; segments 6 and 7 mobile in male, ankylosed in female; male abdomen relatively wide basally, not bulging strongly on each side of segments 2 and 3; outer margin concave, last segment widely triangular, approximately 0.65 as long as broad.

Chelipeds strongly unequal in mature males; when fully developed largest chela unusually large (length of hand/cb=1.5), very deep, particularly at base of fingers (depth/length at this point = 0.4); narrow in dorsal view (breadth/depth = 0.5) and strongly curved; fingers moderately gaping, teeth alternately large and small; cutting edge of finger with 4 small proximal teeth forming square; surface of chela smooth, without longitudinal grooves, excavated on both sides at base of fixed finger and on upper portion of palm; smaller chela considerably smaller, length of palm 0.45 length of larger. Upper surface of carpus excavated, irregular, with pattern of thin ridges clearly visible under the microscope; carpus with strong spine on inner margin; merus with acute apical spine on upper border and tubercle on inner margin. Lower margin of dactylus of legs thickly clothed with long coarse hairs; similar patches of hairs cover lower border of propodus in approximately 68% of 2nd, 38% of 3rd, 24% of 4th, and 95% of 5th pereiopod; upper margin of propodus and dactylus thickly clothed by shorter hairs arranged more or less in 2 parallel longitudinal rows, more extensive in 2nd and 3rd; sides of dactylus covered with felt-like pubescence.

Gonopod forms regular curve directed laterad; very wide in meso-lateral plane in proximal 3/4 and then narrows to short tube with parallel sides; mesial border regularly curved; lateral border with conspicuous rounded lobe; gonopod conspicuously spinuous and hairy; row of long spines arranged in row on distal half of margin, patch of stout distal spines on lateral surface, which increase in length proximally, and long, irregularly placed setae over lateral lobe. Second gonopod moderately longer than first, with basal portion more or less straight and distal portion bracket-shaped.

Color

Pereiopods and dorsal side of carapace light brown; pereiopods with small red spots which forms amottled pattern; these spots form a reticle over the carpus of chelipeds and are less visible on the upper surface of carapace.

Material examined

Perú. Pakitza, Madre de Dios Department, Manabi Province; 17 October 1987-22 September 1988; 5 males, 4 females (MHN Lima).

Type and distribution

The species was previously known from the single type specimen collected in a hole near the University of Pucallpa (PRETZMANN, 1978a; PRETZMANN, 1983a). PRETZMANN, 1983b, mentions that "*the largest chela known ... is from Bobonaza (=Rio Bobonaza) and is 12.9 cm long*", but he does not precisely states whether this belongs to *V. gila*. These previous records are from the Ucayali-Maranon basin; our specimens are from the Madre de Dios-Madeira system. These basins are widely separated at their junctions with the Amazon, but their headstreams (Rio Urubamba and Rio Piedras, respectively) are very close, particularly in the southernmost end of the Loreto Department.

Remarks

PRETZMANN (1978a, 1983a, b) considered this taxon a subspecies of *Valdivia harttii*. However, *V. gila* differs from other species of the genus in the reduction in size and number of the lateral teeth. The strong chelar dimorphism of the male and the shape and armature of the first gonopod are unique to this species within the genus.

Valdivia harttii Rathbun, 1906

Fig. 4Q; 5H; 8E; 13E; 32A-J

Trichodactylus (Valdivia) harttii Rathbun, 1906, p. 55, pl. 17, fig. 9 .- BOTT, 1969, p. 42 .- RODRÍGUEZ, 1981, p. 42.

Description

Carapace hexagonal; upper surface very uneven; frontal, orbital, hepatic and epibranchial regions conspicuously excavated; epigastric region consists of 2 transverse low lobes, not clearly delimited, which under microscope appear crossed by transverse granular striae; protogastric region also bilobular, each lobe delimited anteriorly by U-shaped, irregular, eroded ridge; branchio-cardiac and branchio-urogastric grooves wide and well marked; other grooves of mesial regions not present; inconspicuous ridge between hepatic and epibranchial regions, and similar one between epi- and mesobranchial regions; conspicuous transverse elevation across metabranchial regions; cardiac region rhomboidal, with transverse ridge across it; intestinal region slightly convex. Posterior gastric pits present. Lateral margin with postorbital lobe or small tooth followed by 4-5 equally spaced spines, 1st and 2nd interdental spaces half length of others; last spine considerably smaller, but acute and well defined, followed by 4 or 5 large squamiform tubercles; postero-lateral ridge of carapace bent mesially at posterior end, followed by elongated swelling over postero-lateral angles of carapace; posterior margin delimited by high carina. Surface of carapace eroded, with small warts and pits visible to naked eye. Frontal margin straight or slightly concave, incurved upwards, orbits oblong, orbital fissure indicated by notch and thin transversal ridge; lower orbital margin with 4 or 5 hooked (at least 1st) spines, which decreases in size laterally, inner orbital angle with hooked spine or long cylindrical tubercle; conspicuous U-shaped recess between this angle and lower orbital margin; occlusive orbital tooth small, not dentiform, forming rounded ridge by external side of basal portion of antenna and not concealed by it; outer orbital angle triangular, prominent; buccal angle with small acute spine followed laterally by crenulated ridge. Front advanced, hiding epistome in dorsal view; anterior surface of front vertical, covered by small papillae, high particularly in middle, with 2

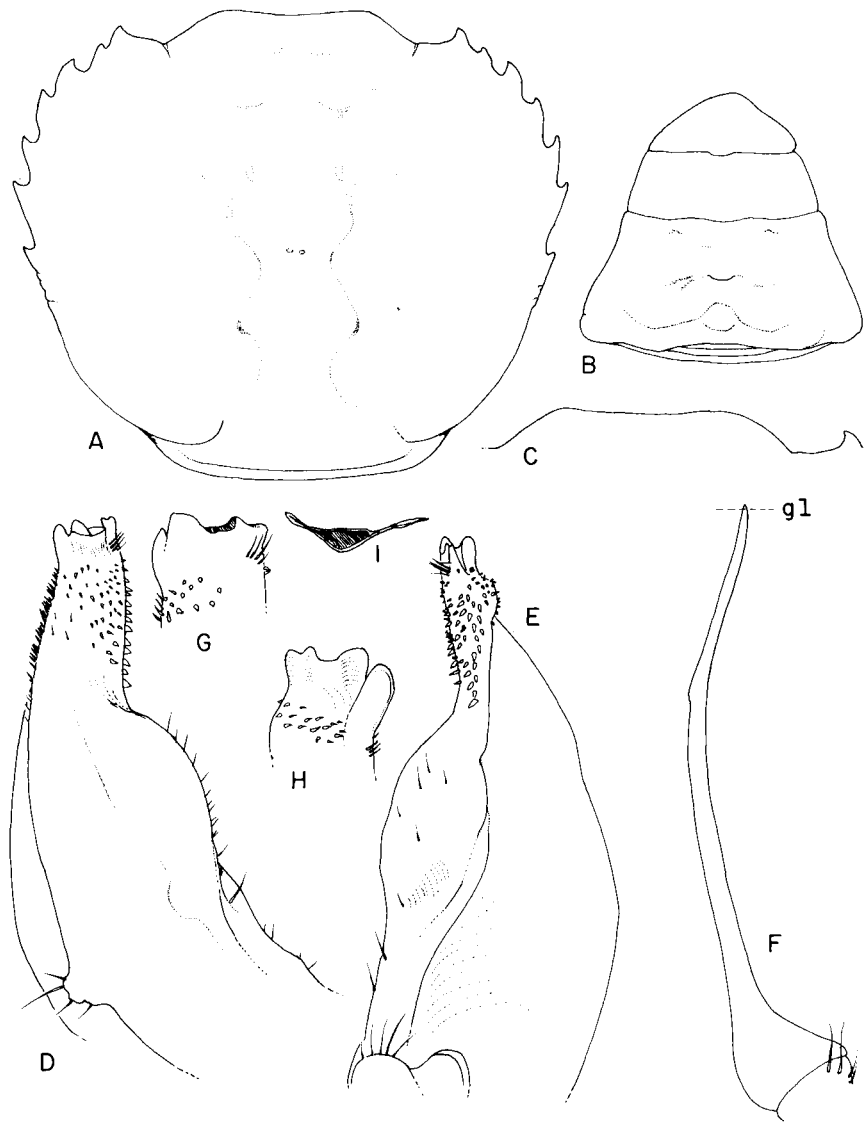

FIGURE 32

Valdivia harttii Rathbun, male from San Carlos de Rio Negro, Venezuela, cl 39.8 mm: A, outline of carapace; B, abdomen; C, outline of front; D, first male gonopod, left, caudal; E, same, cephalic; G, same, detail of apex, caudal; H, same, cephalic; I, same, distal; F, second male gonopod. gl, level of gonopore of first gonopod.

distinct middle pillars separated by U-shaped sinus which forms deep recess, and dentiform ridge over middle of antennular fossae; these ridges partially visible in dorsal view; antennular septum not sunk; epistome high, vertical or slightly bent backwards.

Abdominal tergites of male densely covered by pits, largest in tergites 1-3, which give them eroded aspect under microscope; abdomen sunk when closed, tergite in front of it forms ridge; abdominal tergites 1-3 with one excavation in front, one excavation on each side; space between excavations forms conspicuous Y-shaped ridge. First abdominal segment of male and female partly hidden by posterior margin of carapace; segments 3-5 fused in male and female; segments 6 and 7 mobile in male, ankylosed in female; male abdomen elongated, bulging strongly on each side of segments 2 and 3; outer margin concave, last segment widely rounded, approximately 0.5 as long as broad.

Chelipeds unequal, smallest very small, but largest not extraordinarily developed; hand of largest cheliped with tiny acute teeth on upper margin near articulation of dactylus, large, low tubercle covered by red spot, on side near articulation of fingers; fingers slightly gaping, teeth subequal in size; upper surface of carpus eroded; strong hooked spine on inner margin; merus with acute apical spines on upper border and on distal angle of latero-inferior margin. Lower margin of dactylus of legs thickly clothed with long coarse hairs; these patches cover all lower margin of propodus in 5th, 3/4 in 2nd, 1/2 in 3rd and only distal angle in 4th pereiopod; upper margin of propodus and dactylus thickly clothed with shorter hairs arranged more or less in 2 parallel longitudinal rows, more extensive in 2nd and 3rd; sides of dactylus with felt-like pubescence.

First gonopod very wide at base in latero-mesial direction, very narrow in caudo-cephalic direction, regularly tapering to apex, more evident in caudo-lateral view; base with wide lateral lobe; terminal half narrow, with parallel sides in caudal and cephalic views; apical margin truncate, gonopore terminal, narrow and slit-like in outline, flanked on lateral, mesial and caudal sides by 3 corneous projections; patch of corneous spines on caudal and lateral sides, long band of short translucent setae on mesial side and brush of long slender setae on lateral side near gonopore. Second gonopod longer than first, basal portion more or less straight, distal portion bracket-shaped.

Material examined

Venezuela. San Carlos de Rio Negro, Amazonas Federal Territory; 8 September 1976; 2 males (Ivic). San Carlos de Rio Negro, Amazonas Federal Territory; 9 April 1979; K. CLARK; 1 spent female (Ivic). Rio Siapa, Amazonas Federal Territory; 27 March 1988; R. ROYERO; 1 male, 1 female with marsupial youngs (Ivic).

Type and distribution

Brazil. Tefé; Rio Tapajos (RATHBUN 1906, type); Rio Negro (BOTT, 1969). Venezuela. Rio Negro (present records).

Valdivia latidens (A. Milne Edwards, 1869)

Sylviocarcinus latidens A. Milne Edwards, 1869, p. 175.- NOBILI, 1896, p. 3.- MOREIRA, 1901, p. 44.
Orthostoma latidens, ORTMANN, 1897, p. 326, 328.
Trichodactylus (Valdivia) latidens, RATHBUN, 1906, p. 49, pl. 17, fig. 4, text-fig. 112.
Rotundovaldivia latidens, PRETZMANN 1983b, p. 326, pl. 8, fig.18, 19, pl. 9, fig. 20-22.
?*Trichodactylus (Valdivia) bourgeti* Rathbun, 1906, p. 56, pl. 16, fig. 4, text-fig. 118.
Trichodactylus (Valdivia) bourgeti falcipenis Pretzmann, 1968a, p. 5.
Rotundovaldivia falcipenis, PRETZMANN, 1983b, p. 326, pl. 10, fig. 23, 24.

Type and distribution

The holotype, a male deposited at the Museum of Natural History in Paris, came from an undetermined locality in the upper Amazon. PRETZMANN's material of the species and the holotype of his *Rotundovaldivia falcipenis* are from the Ucayali River, Perú.

Remarks

The first gonopod of this species is very characteristic, and for this reason PRETZMANN (1968b) separated it into the subgenus *Rotundovaldivia* (genus in PRETZMANN, 1983b). However, the first gonopod of *Valdivia gila* (fig. 31E), although not so strongly falcate, is intermediate between this species and the more typical *Valdivia*. Notwithstanding slight differences in gonopod morphology and in the number of lateral teeth, *Rotundovaldivia falcipenis* is conspecific with *Valdivia latidens*. Very possibly, *Trichodactylus (Valdivia) bourgeti*, described from a small (cl 21 mm) female holotype from Tabatinga, Brazil, also belongs here.

Valdivia serrata White, 1847

Fig. 1F; 3H; 4R; 5E; 8C; 10B; 13F; 15F; 33A-L

Valdivia serrata White, 1847a, p.31 (*nomen nudum*).- WHITE, 1847b, p. 200.- H. MILNE EDWARDS, 1853, p. 214.- SMALLEY & RODRÍGUEZ, 1972, p. 50, fig. 11, 12.- RODRÍGUEZ, 1980, p. 342.- RODRÍGUEZ, 1981, p. 48.

Trichodactylus (Valdivia) serratus, RATHBUN, 1906, p. 47, pl. 17, fig. 7, 8, text-fig. 111.- COIFMANN, 1939, p. 94.- HOLTHUIS, 1959, p. 210, fig. 49, 50a.

Valdivia (Valdivia) serrata serrata, PRETZMANN, 1968b, p. 71 (by implication).- BOTT, 1969, p. 39.

Valdivia (Valdivia) serrata, SCHMITT, 1969, p. 98.

Valdivia (Valdivia) serrata surinamensis Pretzmann, 1968b, p. 72.

?*Valdivia (Valdivia) serrata haraldi* Bott, 1969, p. 40, pl. 7, fig. 12a, b, pl. 19, fig. 42.

Valdivia (Valdivia) serrata cururuensis Bott, 1969, p. 41, pl. 7, fig. 13a, b, pl. 19, fig.43.

Trichodactylus (Valdivia) bourgeti novemdentatus Pretzmann, 1968a, p. 5.

Description

Carapace hexagonal; upper surface very uneven; frontal, orbital, hepatic and epibranchial regions conspicuously excavated; epigastric region consists of 2 low lobes, not clearly delimited, which under microscope appear crossed by transverse granular striae; protogastric region also bilobular, each lobe delimited anteriorly by thin, lunular ridge; branchio-cardiac and branchio-urogastric grooves wide, well marked; other grooves of mesial regions not present; transversal ridge runs in front of the mesogastric region and extends laterally for short distance across metabranchial regions, usually continued laterally by low branchial ridge; cardiac region rhomboidal, with a transverse ridge across; intestinal region slightly convex. Posterior gastric pits present. Lateral margin armed with 4 or 5 teeth behind external orbital angle, equally spaced, decreasing in size posteriorly; last, when present, small spine or minute squamiform tooth, in some specimens only a notch in this place, followed in some cases by 4 or 5 squamiform tubercles; postero-lateral ridge of carapace bent mesially in its posterior end, followed by elongated swelling over postero-lateral angles of carapace; posterior margin delimited by high carina. Frontal margin straight, incurved upwards; orbits more or less rounded, small, eyes completely fill orbital cavity; orbital fissure indicated by inconspicuous notch; lower orbital margin with 7 or 8 acute tubercles which decrease in size laterally, inner orbital angle pyramidal, prominent, acute; conspicuous U-shaped recess between this angle and lower orbital margin; occlusive orbital tooth small, not dentiform, forming a rounded ridge by external side of basal portion of antenna, not concealed by it; outer orbital angle triangular, projected, followed posteriorly by prominent sinuous lobe which leaves semicircular recess in front of first

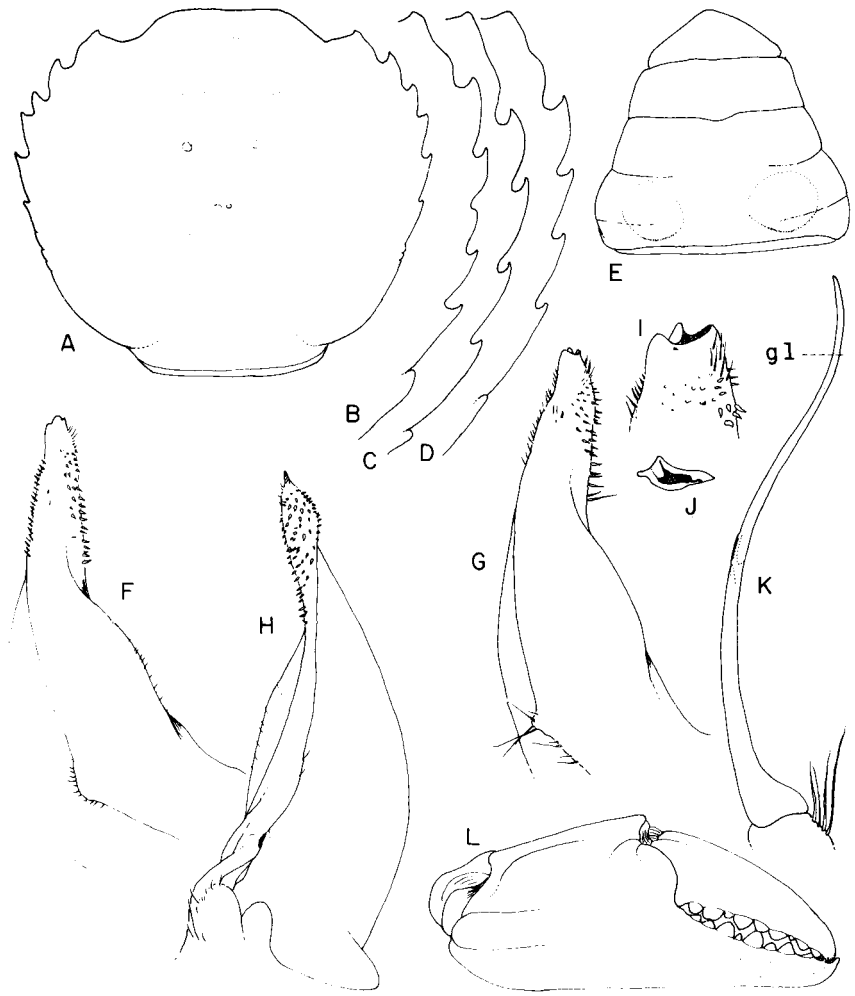

FIGURE 33

Valdivia serrata White: A, outline of carapace; B-D, detail of lateral spines; E, male abdomen; F, G, first male gonopod, left, caudal; H, same, cephalic; I, detail of apex, caudal; J, same, distal; K, second male gonopod; L, largest cheliped. A, E, F, H, male from Alto Caño Rueda, Venezuela, cl 31.8 mm; B, G, I, J, K, male from La Esmeralda, Venezuela, cl 36.3mm; C, L, male from Leticia, Colombia, cl 41.0 mm; D, male from Loreto, Ecuador, cl 39.1 mm. gl, level of gonopore of first gonopod.

lateral tooth; buccal angle crenulated or with 4 ill-defined tubercles. Front advanced, hiding epistome in dorsal view; anterior surface of front vertical, high particularly in middle, with 2 distinct middle pillars separated by U-shaped sinus which forms deep recess, and dentiform ridge over middle of antennular fossae; antennular septum not sunk; epistome high, vertical or slightly bent backwards.

Abdominal tergites of male densely covered by pits, largest in tergites 1-3, giving them eroded aspect under microscope; abdomen sunk when closed, tergite in front of it forms ridge; abdominal tergites 1-3 with one excavation in front, one excavation on each side; space between excavations forms conspicuous Y-shaped ridge. First abdominal segment of male and female partly hidden by posterior margin of carapace; segments 3-5 fused in male and female; segments 6 and 7 mobile in male, ankylosed in female; male abdomen elongated, bulging strongly on each side of segments 2 and 3; outer margin concave, last segment widely rounded, approximately 0.5 as long as broad.

Chelipeds unequal, smallest very small, largest not extraordinarily developed; hand with longitudinal carina in middle of external surface, surface between this carina and upper margin excavated, particularly in smaller chela; acute teeth on upper margin near articulation of dactylus (absent or reduced in some large specimens), and large low tubercle often covered by red spots, on external side near articulation of fingers; fingers slightly gaping, teeth large, subequal, interspaced with smaller ones; upper surface of carpus eroded, with pattern of thin ridges clearly visible under microscope; strong hooked spine on inner margin; merus with acute apical spine on upper border and another on distal angle of latero-inferior margin. Lower margin of dactylus in legs thickly clothed with long coarse hairs; these patches cover all lower margin of propodus in 5th, 3/4 in 2nd, 1/2 in 3rd and only the distal angle in 4th pereiopod; upper margin of propodus and dactylus thickly clothed by shorter hairs arranged more or less in 2 parallel longitudinal rows, more extensive in 2nd and 3rd; sides of dactylus with felt-like pubescence.

First gonopod very wide at base in latero-mesial direction, very narrow in caudo-cephalic direction, regularly tapering to apex, more evident in caudo-lateral view; base with elongated lateral lobe; terminal half narrow, with convergent sides in caudal and cephalic views, bulbiform in latero-cephalic view; apical margin truncate, gonopore terminal, narrow and slit-like in outline, flanked on lateral, mesial and caudal sides by 3 corneous projections; patch of corneous spines on caudal and lateral sides, long band of short translucent setae on mesial side and brush of long slender setae on lateral side near gonopore. Second gonopod longer than first, basal portion more or less straight, distal portion bracket-shaped.

Color

Pereiopods and dorsal side of carapace covered with red spots, which sometimes are elongated and thin, forming a symmetrical pattern; these spots form a reticle over the carpus of cheliped. The background color varies from light to dark brown, reddish or even black.

Material examined

Venezuela. Alto Caño Rueda, Atures, 22 km from Puerto Ayacucho, Amazonas Federal Territory; 30 October 1965; P. ANDUZE; 1 male (Ivic). Carinagua, Puerto Ayacucho, Amazonas Federal Territory; 5 December 1977; 2 juvenile females (Ivic). Id.; 29 November 1978; 3 immature females, 1 juvenile male (Ivic). La Esmeralda, Caño Iguapo, Amazonas Federal Territory; 19 February 1966; J. PULIDO & L. DUQUE; 5 males, 2 females (MB XI-0671). Id.; 450 m alt; 1 March 1968; J. A. RIVERO; 1 female (Ivic). San Pedro de Cataniapo, 100 m alt, Amazonas Federal Territory; 23 August 1981; O. PACHANO; 1 female (LS 1120). Same locality; 25 August 1981; R. FEO; 1 male (LS 1045). Rio Tucuragua, affluent of the Orinoco, between Cuchivero and Caura rivers, Bolivar State; 7 April 1981; G. RODRÍGUEZ; 1 juvenile male (Ivic). Rio Tauca, affluent of the Rio

Caura, Bolivar State; 7 May 1981; G. RODRÍGUEZ; 1 juvenile male (Ivic). Caño Chorro de Agua, Las Bateas, Los Pijiguaos, Bolivar State; 27 April 1988; C. LASSO & G. COLONNELLO; 1 male (LS 1143). Quebrada Trapichote, road to El Jobal, Los Pijiguaos, Bolivar State; 28 April 1988; C. LASSO & G. COLONNELLO; 2 immature females (LS 1137). La Solanera, Los Pijiguaos, Bolivar State; 26 April 1988; C. LASSO & G. COLONNELLO; 1 female (LS 1136).- Colombia. Leticia, Amazonas Department; 1 April 1957; H. NICEFORO MARIA; 1 male (Ivic). Rio Hacha, Florencia, Caquetá Department; 4 January 1954; H. NICEFORO MARIA; 1 male (Ivic). Quebrada La Yuca, Florencia, Caquetá Department, 10 March 1954; H. NICEFORO MARIA; 1 female (Ivic). San Juan de Arama, Meta Department, 500 m alt; 20 September 1987; M. R. CAMPOS; 1 male (ICN-MHN-CR 808).- Ecuador. Loreto, slopes of Monte Sumaco, 450 m alt, Napo Province; 1 June 1968; M. OLALLA; 2 males (Ivic).

Type and distribution

The type specimen is a female and the type locality is unknown. The species occupies an extensive area between the Orinoco and the Amazon, but it does not extend north of the first river neither south of the second. The records in the literature are the following: Brazil. Tabatinga; Tefé (RATHBUN, 1906); Brazilian Guiana, Serra de Tumucumaque, Rio Parú and Rio Parú Superior; Quatipuru, near Rio Toboa; Rio Parú do Oeste; Rio Marauia, Cachoeira San Antonio, type of *Valdivia (Valdivia) serrata haraldi* Bott, 1969, and near Tupuruquara, at the junction of Rio Marauia and Rio Negro; at the junction of the Rio Kenebiit-Tabiri and the Rio Cururú, type of *Valdivia (Valdivia) serrata cururuensis* Bott, 1969. Venezuela. See records above. Colombia. Caquetá Department: Rio Orteguaza, near Venecia; Putumayo Department: Puerto Limon, Rio Caquetá (SMALLEY & RODRÍGUEZ, 1972); Puerto Asis (SCHMITT, 1969); Amazonas Department: Rio Arara. See other records above. Ecuador. Napo Province: Loreto, foothills of Mount Sumaco, 450 m alt (SMALLEY & RODRÍGUEZ, 1972). Suriname. Paramaribo; near Republiek; Zanderdij; Sectie O, 70 km S of Paramaribo; Litani River, upper reaches of the Marowijne River basin (HOLTHUIS, 1959); Paramaribo, type of *Valdivia (Valdivia) serrata surinamensis* Pretzmann, 1968.- Guyana. Demerara River (COIFMANN, 1939).

Remarks

The species displays considerable variations in the number and development of the lateral teeth of carapace, as can be observed in specimens from Venezuela, Colombia and Ecuador (fig. 33A, B, C, D). The gonopod also presents variations in the shape of the lateral lobe, thickness of the distal tube and convexity of the mesial outline, which can be observed even in specimens from localities close to each other (fig. 33G, H). Most of the subspecies of *Valdivia serrata* described by PRETZMANN (1968a, b) and BOTT (1969) are based on these characters of the carapace and gonopod. *Valdivia (Valdivia) serrata surinamensis* Pretzmann, 1968, and *Valdivia (Valdivia) serrata cururuensis* Bott, 1969 cannot be distinguished from the more typical *Valdivia serrata*. On the other hand the inclusion of *Valdivia (Valdivia) serrata haraldi* under this species is doubtful. In this subspecies the lateral teeth of carapace are identical to those of *V. serrata*, but the first gonopod is more recurved laterad, resembling more that of *Valdivia gila* than the one of *V. serrata*.

Trichodactylus (Valdivia) bourgeti novemdentatus Pretzmann, 1968, from the Rio Negro, probably should be grouped under *Valdivia serrata* and not under *V. bourgeti (=V. latidens)*, since the dentition of the carapace falls within the variation displayed by the former species.

Valdivia (Valdivia) serrata oronensis Pretzmann, 1968 (see PRETZMANN, 1968b, p. 72), described from male and female types from Rio Paraguay, R. d. Oro [Rio de Oro, Chaco province, Argentina], according to his diagnosis (front deeply bilobed, carapace strongly arched, without sculpturing, gonopod without lateral lobe), does not belong to the genus *Valdivia* but to the genus *Zilchiopsis*.

Forsteria Bott, 1969

Valdivia (Forsteria) Bott, 1969, p. 37.

Carapace hexagonal, upper surface strongly arched, smooth, frontal and orbital regions excavated, but regions not delimited, antero-lateral margin angled, exceptionally rounded in all males, median grooves not deeply marked, 3 lateral teeth behind external orbital angle, obsolescent in old males, front straight; first gonopod widened at base, with long setae on lateral margin, distal half strongly bent laterad, apex bulbous.

Forsteria venezuelensis (Rathbun, 1906)

Fig. 1G; 4S; 5G; 8A; 9H; 13D; 15I; 34A-H

Trichodactylus (Valdivia) venezuelensis Rathbun, 1906, p. 47, pl. 17, fig. 10.- COIFMANN, 1939, p. 112.
Valdivia venezuelensis, SMALLEY and RODRÍGUEZ, 1972, p. 50, fig. 13, 14.- RODRÍGUEZ, 1980, p. 343, fig. 99.- RODRÍGUEZ, 1981, p. 48.
Valdivia (Forsteria) venezuelensis venezuelensis, BOTT, 1969, p. 37, pl. 5, fig. 9a, b.
Valdivia (Forsteria) venezuelensis edentata Bott, 1969, p. 38, pl. 6, fig. 10a, b, pl. 19, fig. 40.
Holthuisisia venezuelensis, PRETZMANN, 1968b, p. 74.
Trichodactylus (Valdivia) ornatifrons Pretzmann, 1968a, p. 3.
Valdivia (Valdivia) ornatifrons, PRETZMANN, 1968b, p. 71.

Description

Carapace hexagonal; upper surface slightly irregular, in frontal view forms regular arch, only metabranchial region slightly more prominent than adjacent cardiac and intestinal regions; frontal and orbital regions excavated, epigastric lobes well delimited; branchio-urogastric groove weakly marked, urogastric groove almost absent, branchio-cardiac groove indicated by flat depressions. Lateral margins angled, except in largest males where it becomes rounded; postero-lateral ridge of carapace bent mesially in posterior end, followed by elongated swelling over postero-lateral angles of carapace; antero-lateral margin with 3 teeth behind external orbital angle which decrease in size posteriorly; 2nd and 3rd teeth nearer than 1st and 2nd; in the largest males (cb=>40 mm) lateral teeth become obsolete, or only first remains, represented by small tubercle. Margin of front straight, covered with small tubercles. Orbits suborbicular; orbital suture absent, although position sometimes indicated by small depression; lower orbital margin with blunt teeth or papillated tubercles; inner orbital angle prominent, pyramidal; occlusive orbital tooth rounded, small; outer orbital angle forming triangular tooth, border in contact with orbital margin; buccal angle papillated, not armed. Front advanced, hiding epistome in dorsal view; anterior surface of front vertical, moderately high in middle, lower on sides, middle pillars not distinct, margin over each antennular fossae sinuous, slightly projected; antennular septum slightly sunk; epistome high, vertical or slightly bent backwards.

First abdominal tergite of male separated from tergite 2 + 3 by suture or deep depression; tergites 2 + 3 with very shallow depression on both sides. Third to 5th abdominal segments fused in both male and female; male abdomen elongated, narrow at base, outer margin slightly concave; last segment with sides concave, approximately 0.5 as long as broad.

Basal article of antenna with outer lobe prominent and narrow; ischium of third maxilliped devoided of grooves or depressions. Chelipeds strongly unequal in both male and female; upper border of chela strongly arched and lower almost straight, fingers do not gap; teeth small, regularly placed along cutting edges and

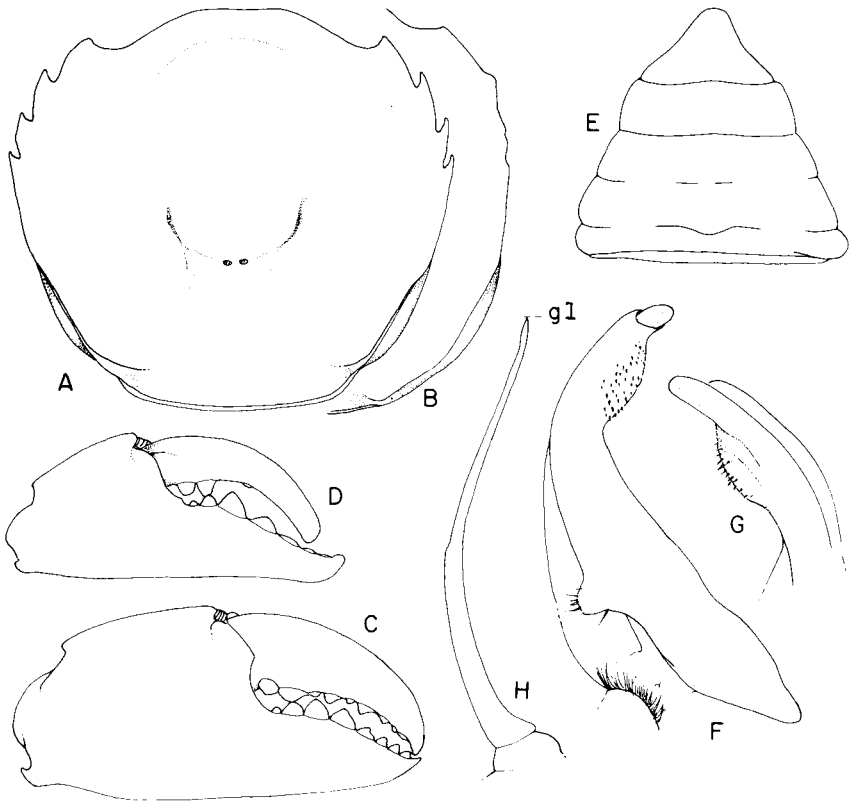

FIGURE 34

Forsteria venezuelensis (Rathbun) : A, B, outline of carapace; C, D, larger chela; E, abdomen; F, first male gonopod, left, caudal; G, same, apex, cephalic; H, second male gonopod. A, C, E-H, male specimen from Rio Taguay, cl 34.4 mm; B, D, male specimen from Rio Guarapiche, cl 41.4 mm. gl, level of gonopore of first gonopod.

regularly diminishing in size distally; carpus with inner margin produced in sharp hooked spine; merus of young specimens with or without apical spine on upper border and another at distal angle of latero-inferior margin; in oldest males largest chela becomes enormously developed, hand > 1.5 as long as carapace, fingers strongly unequal, with dactylus considerably shorter than fixed finger and devoided of teeth in its distal part, and spines of merus obsolete or represented by small tubercles. Lower margin of dactylus of legs thickly clothed with long coarse hairs; these patches cover all lower margin of propodus in 5th, 3/4 in 2nd, 1/2 in 3rd and only the distal

angle in 4th pereiopod; upper margin of propodus and dactylus thickly clothed by shorter hairs arranged more or less in 2 parallel longitudinal rows, more extensive in 2nd and 3rd; claws of dactylus with 5 longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First gonopod with proximal half conical, strongly widened at base and directed mesially; distal half strongly bent laterad, lateral globular expansion covered by short thick setae, arranged in several parallel rows; gonopore overreached by distal corneous expansion. Second gonopod of equal length than first, bracket-shaped, apex flat, lanceolate.

Material examined

Venezuela. Rio Taguay, Aragua State; 12 December 1967; J. PULIDO; 3 males, 2 females (Ivic). Paraima, Guárico State; 31 March 1950; 1 female (Ivic). Caicara, Rio Guarapiche, Monagas State; 8 September 1968; 1 male, 1 female (Ivic). Rio Chiviripa, between La Urbana and Caicara, Bolivar State; 1 April 1958; G. MEDINA; 1 female (Ivic).- Venezuela, without data; 1 female (Ivic).

Type and distribution

Type specimens are 2 females from the Orinoco River (MHNP). The species has been recorded from the Orinoco and many of the rivers draining to it: Ciudad Bolivar (BOTT, 1969); Rio Orinoco (SMALLEY & RODRÍGUEZ, 1972); affluent of the Rio Apure (RATHBUN, 1906); Rio Cura and Rio Taguay, both affluents of Rio Guárico (SMALLEY & RODRÍGUEZ, 1972); Rio Chiviripa, draining on the right margin of the Orinoco, near Caicara (SMALLEY & RODRÍGUEZ,1972); Rio Guarapiche, draining to Rio San Juan and the Gulf of Paria (SMALLEY & RODRÍGUEZ, 1972).

Remarks

The species have been described under several synonyms in the literature (SMALLEY & RODRÍGUEZ, 1972). The characters given for *Trichodactylus (Valdivia) meekei* Pretzmann, 1968, and moreover the illustrations of the carapace, chela, pereiopods and first gonopod given in PRETZMANN (1983a), closely correspond with the characters of *Forsteria venezuelensis,* but I have not examined the holotype of the first species.

Tribe DILOCARCININI

Carapace suborbicular, wider anteriorly, upper surface strongly arched, smooth, front bilobed, partially or completely retracted, exposing epistome; first gonopod expanded laterally at base, with long plumose setae on lateral margin, apex bulbiform; gonopore slit-like, apical; second gonopod moderately longer than first, sinuous, exceptionally much longer and bent as question mark.

Type genus.- *Dilocarcinus* H. Milne Edwards, 1853

Key to the genera of Dilocarcinini

1. 3-4 teeth on lateral margin ..... *Zilchiopsis*
– 6-10 teeth on lateral margin 2
2. Distal part of first gonopod rounded or bulbiform ..... *Dilocarcinus*
– Distal part of first gonopod strongly twisted sinistrally, apex with very few small conical spines ..... *Fredilocarcinus*

Zilchiopsis Bott, 1969

Carapace hexagonal or suborbicular, upper surface strongly arched, median grooves deeply marked, front bilobed, advanced, exposing epistome in dorsal view, lower orbital margin directed downwards at inner orbital angle, 3-4 teeth on lateral margin, often minute or obsolescent; abdomen triangular-rounded or trapezoidal, third maxilliped with merus conspicuously narrow; first gonopod wide basally, strongly reduced in distal half.

Type species.- *Zilchiopsis sattleri* Bott, 1969.

Distribution

The four species of the genus are distributed in the tributaries of the Amazon, in four successive and non-overlapping areas, through an extensive territory on the west and south sides of South America: (a) Venezuela, Colombia and Ecuador (*Z. emarginatus*); (b) Ecuador (*Z. chacei*); (c) Perú (*Z. cryptodus*); and (d) Bolivia (*Z. sattleri*). An exception to this distribution is the record of *Z. sattleri* in the Rio Paraguay (BOTT, 1969), which is not an affluent of the Amazon.

Remarks

The carapace morphology of the species grouped under this genus, although transitional between the Valdiviini and the Dilocarcinini, displays the same basic characters in all the species. On the other hand, there is considerable variability in gonopodal morphology. The simple first gonopod of *Z. chacei* resembles that appendage in some *Sylviocarcinus*, particularly *S. pictus* and *S.* sp., whereas in *Z. emarginatus* it is more akin to *Valdivia*. The morphology of this appendage in *Z. sattleri* and *Z. cryptodus* departs from any of the types found in other genera. However, to avoid an excessive generic splitting, the four species are kept in one genus inside the Tribe Dilocarcinini. To this genus probably belongs also *Trichodactylus (Valdivia) boliviensis* a species from Misiones Molletones, Bolivia, not examined by me.

Key to the species of *Zilchiopsis*

1. First gonopod almost straight, regularly tapering to apex ..... *chacei*
– First gonopod regularly bent laterad, strongly constricted at middle 2
2. A well defined basal lobe on mesial side of first gonopod; apical tube relatively wide ..... *emarginatus*
– Basal portion of first gonopod widened but not forming defined lateral lobe; apical tube narrow 3
3. Apical tube regularly tapering to terminal gonopore ..... *cryptodus*
– Distal portion of apical tube reduced to a filament ..... *sattleri*

Zilchiopsis chacei (Pretzmann, 1968)

Trichodactylus (Trichodactylus) chacei Pretzmann, 1968a, p. 3.

Zilchiopsis chacei, PRETZMANN, 1983b, p. 327, pl. 11, fig. 25, 26, pl. 12, fig. 27, 28.

Zilchiopsis chacei ecuadoroides Pretzmann, 1978b, p. 7.-PRETZMANN, 1983a, p. 310, pl. 6, fig. 21-24.- PRETZMANN 1983b, p. 327, not pl. 6, fig. 21, 22.

As described and illustrated by PRETZMANN (1968a, 1983b), this species has in common with the other three members of the genus the strongly convex carapace, with rounded lateral margins provided with small, obsolescent teeth, and the bilobed front, but it is well differentiated from them by its simple almost smooth gonopod, moderately widened at base and regularly tapering from the middle, with its lateral side slightly sinuous.

BOTT (1969) synonymized this species with *Zilchiopsis cryptodus*. The carapace of both are almost identical, except for the front less deeply bilobed in *Z. chacei*. However the gonopod of both species are different.

Type and distribution

The holotype of *Trichodactylus (Trichodactylus) chacei* is a male specimen, cl 30.4 mm, from Chichirota, Pastaza Province, east Ecuador, and the holotype of *Zilchiopsis chacei ecuadoroides* a male, cl 30.1 mm, from Sevilla del Oro, between Mendez and Paute, Ecuador. Thus the two taxa come from different drainage basins: Bobonaza-Pastaza rivers and Santiago-Marañon rivers; these two localities are approximately 230 km apart (Appendix 2).

Zilchiopsis cryptodus (Ortmann, 1893)

Dilocarcinus cryptodus Ortmann, 1893, p. 493.
Zilchiopsis cryptodus, BOTT, 1969, p. 35, pl. 25a, b, pl. 22, fig. 75.- RODRÍGUEZ, 1981, p. 48.- PRETZMANN, 1983b, p. 327.-
Trichodactylus (Dilocarcinus) emarginatus, RATHBUN, 1906, p. 69 (part.).-

This species, as redescribed and illustrated from the holotype specimen in the Strassburg Museum by BOTT (1969), is well characterized by the suborbicular strongly convex carapace, with the upper surface smooth, the lateral margin with 2-3 minute, blunt teeth behind external orbital angle, and the triangular gonopod densely covered by long setae on the lateral margin, with the apex very thin and directed laterad.

Type and distribution

Zilchiopsis cryptodus was described from 1 male specimen, cl 27 mm, from Rio Ucayali, Perú (ORTMANN, 1893; BOTT, 1969).

Zilchiopsis emarginatus (H. Milne Edwards, 1853)

Fig. 3G; 40 T; 5M; 7H; 8B; 9I; 10C; 13G, H; 35A-E; 36A-H

Dilocarcinus emarginatus H. Milne Edwards, 1853, p. 216.- H. MILNE EDWARDS, 1854, p. 181, pl. 14, fig. 4.- LUCAS, 1857, p. 7, pl. 2, fig. 3.- A. MILNE EDWARDS, 1869, p. 176, 178.- SMITH, 1869, p. 36.- YOUNG, 1900, p. 231, 232.- MOREIRA, 1901, p. 44.
Trichodactylus (Dilocarcinus) emarginatus, RATHBUN, 1906, p. 64, pl. 18, fig. 2.
Orthostoma emarginatus, ORTMANN, 1897, p. 326, 328.
Zilchiopsis emarginatus, BOTT, 1969, p. 35, pl. 21, fig. 56.
Valdivia ecuadoriensis Pretzmann, 1968a, p. 3.
Valdivia ecuadorensis (sic), PRETZMANN, 1968b, p. 71.
Zilchiopsis ecuadoriensis, SMALLEY & RODRÍGUEZ, 1972, p. 49, fig. 9, 10.-PRETZMANN, 1983b, p. 328, pl. 13, fig. 29, 30, pl. 14, fig. 31, 32.
Zilchiopsis ecuadorensis (sic), RODRÍGUEZ, 1981, p. 48.

Description

Carapace hexagonal at least in larger specimens (cl > 30 mm); upper surface irregular; strongly convex from front to back, almost flat in frontal view; mesogastric region less prominent than epibranchial; hepatic region excavated; frontal region flat on middle, convex laterally; triangular prominence on each side, in area of contact of epi-, mesobranchial and mesogastric regions, with transverse cervical groove in front of each prominence; metabranchial regions flattened, not more prominent than cardiac and intestinal; branchio-urogastric and

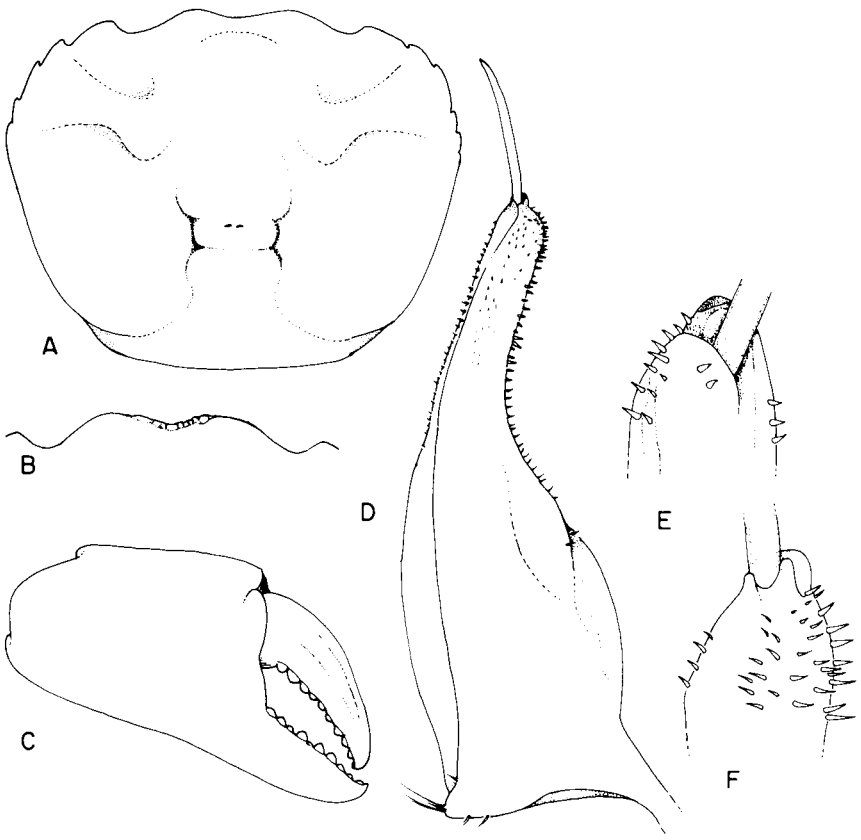

FIGURE 35

Zilchiopsis emarginatus (H. Milne Edwards), male specimen, cl 31.0, from Villavicencio: A, outline of carapace; B, front; C, larger cheliped; D, first male gonopod, left, caudal, with second gonopod in position; E, same, apex, medial; F, same, apex, caudal.

branchio-cardiac grooves thin, well marked, urogastric groove indistinct; postgastric pits triangular, small, close to each other or confluent. Carapace in smaller specimens with upper surface almost smooth, strongly convex from front to back, regularly arched in frontal view, all regions equally elevated, not delimited, carapace grooves not well marked. Lateral margins angled, forming thin ridge directed laterad; postero-lateral ridge of carapace bent mesially in posterior end near postero-lateral margin of carapace, then continued meso-proximally by arched ridge bordering metabranchial region; antero-lateral margin armed with 4, rarely 5, teeth behind external orbital angle, 1st and 2nd well spaced, spiniform or blunt, not projected outside outline of carapace, 3rd and 4th very close, papilliform. Front strongly bilobed with margin of middle sinus papillated and upturned. Orbits subquadrate, very large in vertical direction, eyes very small, disproportionate to orbital cavity; orbital suture absent; mesial end of lower orbital margin directed downwards rather than upwards as in other species, consequently lower portion of orbit very large, expanded, and inner orbital angle absent; this lower margin divided into 10-12 triangular or bead-like tubercles which diminish in size laterally; behind first two, floor of

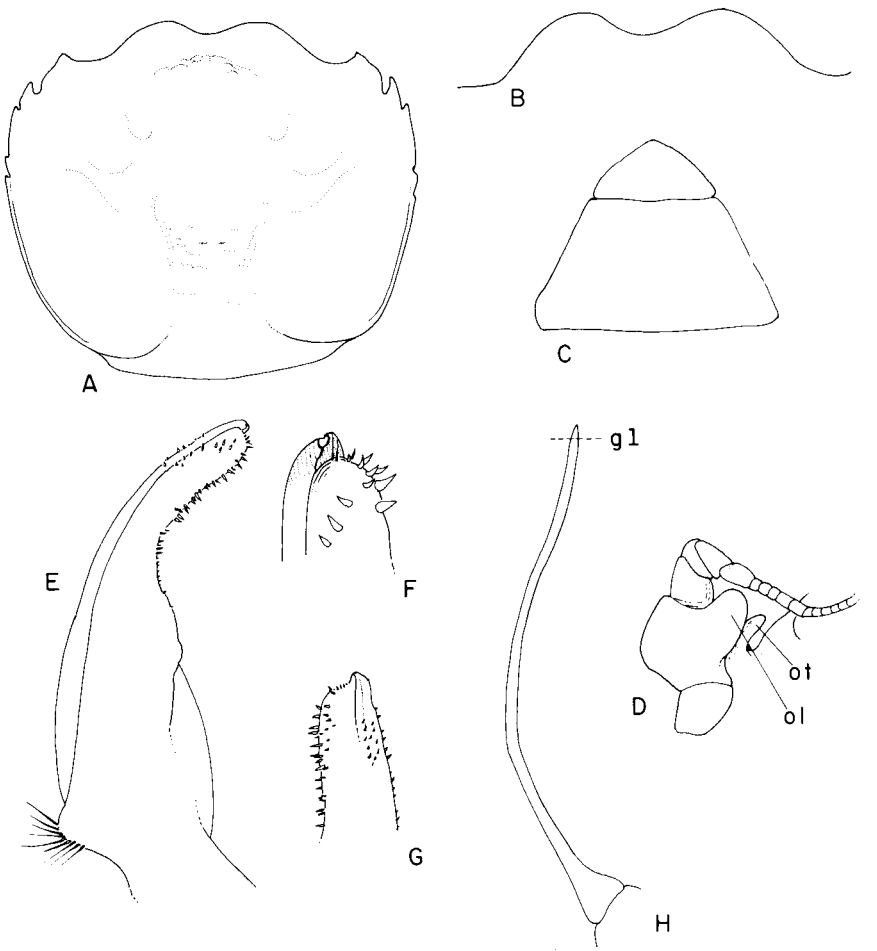

FIGURE 36

Zilchiopsis emarginatus (H. Milne Edwards), young male specimen from Loreto, Ecuador, cl 19.9 mm: A, outline of carapace; B, outline of front; C, abdomen; D, antenna; E, first male gonopod, left, caudal; F, same, detail of apex, caudal; G, same, caudal; H, second male gonopod. gl, level of gonopore of first gonopod; ol, lateral lobe of basal antennal article; ot, occlusive orbital tooth.

orbital cavity has strong tuberculated ridge; occlusive orbital tooth small, spiniform or bead-like; outer orbital angle triangular, blunt; buccal angle entire or faintly papillated. Frontal lobes slightly advanced, but middle sinus retracted, leaving exposed middle portion of epistome; anterior surface of front almost vertical or slightly

inclined forward, moderately high in middle, lower on sides, middle pillars short and thick, widely separated, margin over each antennular fossa slightly thickened, not projected, antennular septum not sunk; epistome high, divided by transverse middle suture into larger upper portion, almost vertical, and lower small portion, projected forward and ending in single mid-point, this continued into buccal cavity by 2 divergent ridges.

First and 2nd + 3d abdominal tergites of male without deep depressions. Third to 6th abdominal segments fused in both male and female; male abdomen very wide, outer margin convex, last segment with sides rounded, approximately 0.57 as long as broad.

Basal article of antenna with outer lobe prominent and narrow; ischium of third maxilliped broad. Chelipeds unequal; larger male cheliped with fingers short, narrow, widely gaping, with small, closely set teeth, fingers with longitudinal ridges and upper distal angle of palm projected or with spine, more conspicuous in smaller male chela and in both female chelae; inner margin of carpus with sharp, hooked spine; merus of male without spines; merus of female with sharp spines on distal angle of upper and inner borders, 2-4 smaller spines on lower margin. Lower margin of dactylus of legs thickly clothed with rows of long hairs, on lower margin of propodus these patches cover 84% of 2nd, 62% of 3rd, 60% of 4th, and 45% of 5th pereiopod; upper margin of dactylus, propodus and carpus with a thick row of short hairs.

First male gonopod slender, small as compared to size of species, wide basally, very narrow distally after middle constriction; basal expansion regularly convex mesially, laterally more irregular, with accessory elongated lobe on cephalic surface; distal portion with subparallel sides, strongly bent laterad; terminal spines small, arranged as thick band on lateral side and diminishing in thickness proximally, forming a single row on mesial side; apical portion rounded on lateral side, straight on mesial side where forms thin lamella which surpasses gonopore; gonopore terminal, small, slit-like. Second male gonopod sinuous, moderately longer than first.

Material examined

Colombia. Tres Esquinas, Rio Orteguaza, Caquetá Department; May 1954; H. NICEFORO MARIA; 1 male, 1 female (LSB 44-45). Vereda Vanguardia, Villavicencio, 500m alt, Meta Department; 29 March 1984; M. CAMPOS; 1 male (ICN-MHN-CR0566).- Venezuela. Caño Carinagua, near Puerto Ayacucho, Amazonas Federal Territory; 29 November 1978; 2 females (Ivic). Alto Rio Cuao, Amazonas Federal Territory; November 1986; S. ZENDT; 1 male, 2 females (Ivic). Las Pavas, Rio Cataniapo, Amazonas Federal Territory; 28 September 1981; R. ROYERO; 2 females (MB XI-1640).- Ecuador. Loreto, in the foothills of mount Sumaco, Napo Province, 450 m alt; June 1968; M. OLALLA; 2 males, 1 spent female (Ivic).

Type and distribution

Colombia. Loreto, upper Amazon (H. MILNE EDWARDS, 1853, type). Perú. Rio Ucayali (ORTMANN, 1893). Ecuador. Napo Province (PRETZMANN, 1968a, type of *Valdivia ecuadoriensis*). The present records extend the distribution of the species towards the north to the Colombian llanos, towards the west to the foothills of the Andes (Loreto, in Napo Province, not Loreto in Colombia, see Appendix), and towards the east to the Venezuelan Guiana.

Remarks

The species presents considerable variability in relation to the sculpturing and convexity of the upper surface of the carapace. In the young specimen from Ecuador (Fig. 36) and Colombia it is more flattened, excavated near the margins, with the grooves well marked, thus resembling the species of *Valdivia*. In the young specimens of the Venezuelan Guiana, it is smooth and more evenly arched, approaching the characters of *Dilocarcinus*.

Fig. 3J; 4U; 5I; 7I; 9J; 13H; 37A-H

Zilchiopsis sattleri Bott, 1969, p. 34, pl. 13, fig. 24a, b, pl. 21, fig. 55.- MANNING & HOBBS, 1977, p. 160.- RODRÍGUEZ, 1981, p. 48.

Description

Carapace suborbicular, wider than long; upper surface slightly irregular; in frontal view forms an irregular arch; gastric region slightly more prominent than adjacent epibranchial regions; metabranchial region slightly more prominent than adjacent cardiac and intestinal; epigastric lobes very prominent, well delimited anteriorly; frontal region slightly concave or almost flat in frontal view; branchio-urogastric, branchio-cardiac and branchio-intestinal grooves wide and deep, urogastric groove may be absent or present. Postgastric pits slit-like, placed in front of urogastric groove. Lateral margins angled and directed obliquely upwards, except in large males where become rounded; postero-lateral ridge of carapace bent mesially in posterior end, ending in elongated swelling over postero-lateral angles of carapace; antero-lateral margin with 4 spines behind external orbital angle, prominent, evenly spaced, acute; last spines smaller; in large males lateral teeth becomes obsolescent. Margin of front bilobed. Orbits oblong, orbital suture absent or indicated by inconspicuous depression; eyes completely fill orbits; lower orbital margin in young specimens with 3 acute, widely spaced spines (including the one at inner orbital angle), followed laterally by approximately 7 small papillae; inner orbital angle prominent, pyramidal, topped by prominent and acute spine or rounded tubercle; occlusive orbital tooth rounded, small, located close to inner orbital angle; outer orbital angle spiniform, prominent in females and young specimens, represented by stump in old males; buccal angle with large acute spine followed laterally by smaller one, or large tubercle followed by one or two smaller ones. Front advanced, hiding epistome in dorsal view; anterior surface of front inclined almost vertical or slightly inclined forward, moderately high in middle, lower on sides, middle pillars short and thick, widely separated, margin over each antennular fossa slightly thickened, but not projected, antennular septum not sunk; epistome high, inclined forward.

First abdominal tergite of male separated from tergite 2 + 3 by deep depression, tergite 2 + 3 with similar depression on both sides. Third to 6th abdominal segments fused in both male and female; male abdomen elongated, narrow at base, outer margin concave, last segment with sides concave, approximately 0.65 as long as broad.

Basal article of antenna with outer lobe prominent and narrow; ischium of third maxilliped with shallow longitudinal depression. Chelipeds unequal; upper border of chela strongly arched, lower almost straight or slightly concave; teeth alternatively large and small; acute spine on upper distal angle of hand, above articulation of finger; inner margin of carpus produced in sharp hooked spine, apical spines on upper border and latero-inferior margin of merus. Lower margin of dactylus of legs thickly clothed with patches of long coarse hairs; these patches cover all lower margin of propodus in 5th, 3/4 in 2nd, 1/2 in 3rd and only distal angle in 4th; upper margin of propodus and dactylus thickly clothed by shorter hairs arranged in 2 parallel longitudinal rows, more extensive in 2nd and 3rd; claws of dactylus with 5 longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First gonopod very wide basally on latero-mesial plane, strongly constricted on distal third, tapering to very thin apex directed slightly cephalad; well developed elongated lobe on latero-cephalic surface on proximal 3/4 of appendage; lateral and mesial surfaces of apex covered by very small spines, forming 2 distinct patches; gonopore slit-like and open distally, major axis directed along cephalo-caudal plane. Second gonopod slightly longer than first, strongly arched, but terminal portion straight.

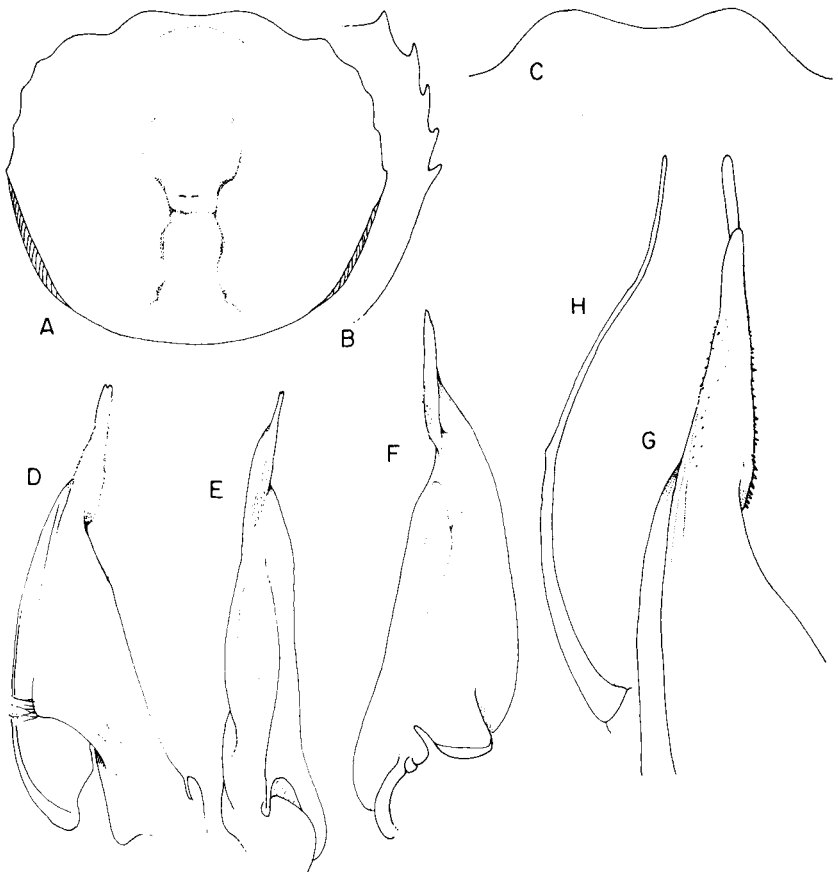

FIGURE 37

Zilchiopsis sattleri Bott, specimens from Trinidad, Beni: A, B, outline of carapace; C, front; D, first male gonopod, left, caudal; E, same, lateral; F, same, cephalic; G, same, apex, caudal; H, second male gonopod. A, C-H, male, cl 41.2 mm; B, female, cl 18.6 mm.

Material examined

Bolivia. Trinidad, Beni Department; G. LOUBENS; 2 males, 1 immature female (MNHNP B.12815); 1 male, 6 juveniles (MNHNP B.19122). This locality is approximately 100 km north from the type locality and on the same river system.

Type and distribution

Bolivia. Rio Chapare, affluent of Rio Grande (type, BOTT, 1969). Paraguay. Chaco, Rio Paraguay (BOTT, 1969).

Dilocarcinus H. Milne Edwards, 1853

Dilocarcinus H. Milne Edwards, 1853, p. 215.

Carapace suborbicular, upper surface strongly arched, smooth, regions not delimited and median grooves shallow or obsolete, bearing 6 to 10 lateral spines behind spiniform external orbital angle, first or second interdental space longer, forming conspicuous U-shaped sinus, lower orbital margin directed downwards at inner orbital angle, front strongly bilobed and retracted, epistome advanced, ending in two well spaced points of mid-guter; openings of efferent channels strongly arched, forming two well defined spouts: as consequence all buccal area, including yugal and suborbital margins, visible in dorsal view; yugal and orbital prominences spiniform; abdomen triangular-rounded or trapezoidal; basal article of antenna without outer lobe; 3rd maxilliped with merus conspicuously narrow, or wide, with antero-mesial angle produced into triangular tooth located near articulation of palp; first gonopod expanded laterally at base, moderately reduced on distal half, with long plumose setae on lateral margin, apex bulbiform; gonopore slit-like, apical, flanked by corneous expansion; second gonopod slightly longer than first, sinuous, or much longer and bent as a question mark.

Type species.- *Dilocarcinus spinifer* H. Milne Edwards, 1853.

Distribution

According to its distribution and apparent abundance, the species of *Dilocarcinus* can be separated into two distinct groups: 1. a first group comprises *Dilocarcinus pagei*, widely distributed and abundant from the Amazon to Bolivia and northern Argentina, and *niceforei, dentatus*, *spinifer*, and *argentinianus*, locally abundant in the basins of Maracaibo, Orinoco-Guianas, Surinam, and Paraná-Paraguay respectively; 2. a second group of species, widely scattered over South America, seems to be rather scarce, since only the type material or a few specimens are known. This is the case of *Dilocarcinus medemi*, *D. septemdentatus*, *D. bulbifer*, *D. truncatus*, *D. castelnaui*, and *D. laevifrons*, collected at isolated localities in the rivers Sinu, lower Amazon, Madre de Dios, Beni, upper Parana, and Cuieiras, respectively.

Key to the species of *Dilocarcinus*

1. Front armed with spines or blunt tubercles 2
– Front unarmed 4
2. Front armed with approximately 4 spines restricted to interlobular sinus ..... *niceforei*
– Front armed with approximately 16 spines covering both frontal lobes 3
3. Gonopod curves and diminishes in size gradually ..... *dentatus*
– Gonopod curving slightly laterad, narrowing abruptly at about midpoint of distal segment of gonopod ..... *medemi*
4. Distal margin of 3rd abdominal segment in both sexes bears strong acute ridge directed forward, which covers suture 3/4 ..... *pagei*
– Distal margin of the 3rd abdominal segment without strong acute ridge 5
5. Lateral margin of carapace with 8-9 lateral teeth, not including orbital ..... *laevifrons*
– Lateral margin with 7 or less lateral teeth, not including orbital 6
6. Gonopod apex slender 7
– Gonopod apex robust, conical, with or without lateral lobe 9
7. Gonopod apex not bulbiform, caudal surface twisted cephalad ..... *castelnaui*
– Gonopod apex with small lateral bulbiform lobe; caudal surface not twisted cephalad 8
8. Gonopod apex directed laterad following main axis of appendage ..... *spinifer*

– Gonopod apex geniculate due to strong laterad bent ..... *septemdentatus*

9. Gonopod apex simple, without conspicuous lateral lobe ..... *argentinianus*

– Gonopod apex with strong rounded lateral lobe 11

10. Outline of apical lobe continuous with gonopore ..... *truncatus*

– Outline of apical lobe separated from gonopore by deep cleft or U-shaped sinus ..... *bulbifer*

Dilocarcinus argentinianus Rathbun, 1906

Fig. 14D; 38A-F

Trichodactylus (Trichodactylus) argentinianus Rathbun, 1906, p. 60, pl. 18, fig. 5, 6, text-fig. 120.
Dilocarcinus argentinianus apaluensis Pretzmann, 1968b, p. 75.
Poppiana argentinianus, BOTT, 1969, p. 52 (part.), pl. 12, fig. 21a, b, pl. 21, fig. 52.- RODRÍGUEZ, 1981, p. 48.
Poppiana argentiniana, MANNING & HOBBS, 1977, p. 159.- PRETZMANN, 1979, p. 592, pl. 3, fig. 6-10.
Dilocarcinus (Poppiana) argentinianus, LOPRETTO, 1976, p. 88, fig. 30-33.
Dilocarcinus septemdentatus, NOBILI, 1896, p. 1 (part.).
Trichodactylus (Dilocarcinus) bachmayeri Pretzmann, 1968a, p. 4.
Dilocarcinus bachmayeri, PRETZMANN, 1968b, p. 75.
Poppiana bachmayeri, PRETZMANN 1979, p.591, pl. 1, fig. 1, 2, pl.2, fig. 3-5.

Description

Carapace suborbicular; upper surface very convex, the convexity more pronounced along antero-posterior axis, forming regular arch; regions not differentiated; epigastric lobes obsolescent, delimited anteriorly only by depression of frontal surface; front bilobed, inclined downwards; urogastric, branchio-urogastric, branchio-cardiac and branchio-intestinal grooves faintly indicated; dorsal surface of carapace smooth, polished, covered by small papillae barely visible to naked eye. Postgastric pits lunulated, well marked. Anterolateral margin with 6 subtriangular teeth or acute spines behind external orbital angle, directed anteriorly, approximately of equal size, last spine smaller; interdental spaces of equal length except first which is longer, sinuous; ridge in postero-lateral margin starts at lateral side of last lateral spine, curves inwards at middle and ends at some distance of ridge on the postero-lateral angle of carapace. Orbits subquadrate in frontal view, large, and eyes relatively small, leaving ample empty space in orbital cavity; orbital suture obsolete or indicated by slight groove. Lower orbital margin with 5 acute spines curved inwards followed by 5 low papillae, innermost spine larger and forming inner orbital angle. Occlusive orbital tooth rounded and small, implanted inside orbit, away from inner orbital angle and partially concealed by basal antennal article; floor of orbit is elevated behind outer orbital angle, forming, with basal antennal article and occlusive tooth, a shallow channel; outer orbital angle with subtriangular spine directed forward, similar to other on antero-lateral margin of carapace; buccal angle armed with approximately 5 conical small spines or low papillae. Front retracted leaving epistome completely exposed in dorsal view; anterior margin of frontal lobes lamellar, not forming distinct surface; epistome strongly advanced, points of the mid-gutter well spaced; opening of efferent channels strongly arched.

Abdominal segments 3-6 fused in both sexes, but suture 3/4 still slightly visible in males; male abdomen triangular, wide at base; outer margins straight; last segment widely triangular with outer margin straight, approximately 0.5 as long as broad, proximal margin slightly shorter than distal margin of penultimate segment.

Basal article of antenna without outer lobe. Shallow depression along ischium of 3rd maxilliped. Chelipeds strongly unequal in male, subequal in female; larger chela of male high and short, with upper border strongly arched, lower border almost straight, with conspicuous swelling on external surface at base of fingers; fingers very high and thick, strongly gaping; larger teeth of cutting edges interspaced by 1 or 2 smaller; carpus with

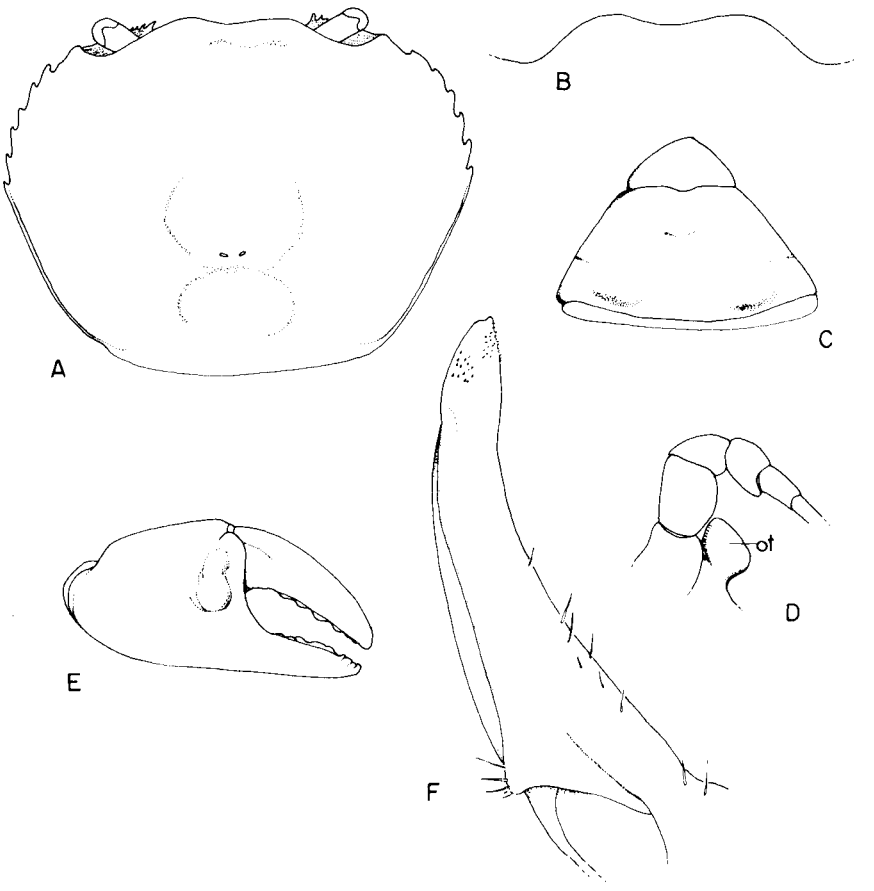

FIGURE 38

Dilocarcinus argentinianus (Rathbun), male specimen, cl 20.0 mm, from Rio Paraguay: A, outline of carapace; B, front; C, abdomen; D, basal article of antenna; E, larger chela; F, first male gonopod, left, caudal. ot, occlusive tooth.

large hooked spine on inner margin, merus with indistinct large tubercles on lateral distal, upper border and middle of latero-inferior margins. Propodus and dactylus of legs devoided of long hairs on lower and upper margins; claws of dactylus with 5 longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First gonopod simple, conical, regularly tapering to apex in caudal view, bracket-shaped, bent laterad; apex with slight caudo-lateral swelling, with few short conical spines, but no conspicuous lateral lobe. Second gonopod slightly longer than first, sinuous, terminal article incurved mesiad.

Material examined

Paraguay. Rio Paraguay; 1 male, cl 20.0 mm, cb 24.8 mm (ZSM 1091/1).

Type and distribution

Argentina. Las Garzas, 25 km from Ocampo, Santa Fe (type). Chaco: Resistencia (RATHBUN, 1906). Buenos Aires. Paraguay. Puerto Max (BOTT, 1969). The type locality of *Trichodactylus (Dilocarcinus) bachmayeri* PRETZMANN, 1968, Ignavi (=Ingavi), is uncertain, since PRETZMANN (1968a) located it in the Chaco, but latter changed its position to 11ºS - 67ºW, (PRETZMANN, 1979). These coordinates correspond to Ignavi, in the Pando Province, Bolivia, on the Rio Orton, affluent of the Rio Beni, but there is, however, an homonymous locality (Fortin Ingavi) in northern Paraguay (19º 55' 00' S - 61º 45'00' W), in the Rio Paraguay basin.

Remarks

The first gonopods from the Paraguayan specimens closely correspond with those of Argentinian specimens illustrated by LOPRETTO (1976). The spinulation of the suborbital border resembles that of *Dilocarcinus bulbifer* and *Fredilocarcinus musmuschiae*, but the spines are conspicuously smaller (Fig. 2E, F)

Dilocarcinus truncatus, new species

Fig. 3K; 8G; 13I; 14C; 39A-E

Poppiana argentinianus, BOTT, 1969, p. 52 (part.).

Description

Carapace suborbicular; upper surface moderately convex, convexity more pronounced along antero-posterior axis, forming an arch slightly flattened on top, with regions not differentiated, epigastric lobes slightly indicated; frontal region flattened; front strongly bilobed inclined downwards; hepato-epibranchial, branchio-urogastric, branchio-cardiac and branchio-intestinal grooves indicated by faint depressions; urogastric groove absent. Dorsal surface of carapace smooth and polished, covered by small papillae not visible to naked eye. Postgastric pits confluent in middle. Anterolateral margin with 6 acute spines behind external orbital angle, directed anteriorly, except first two closer, other equally spaced; last spine smaller; postero-lateral margin marked by well defined ridge throughout, which begins at lateral side of last lateral spine, straight in middle and parallel to ridge on postero-lateral angle of carapace. Orbits subquadrate in frontal view; orbital suture indicated by very faint line; orbits large and eyes relatively small, leaving ample empty space in orbital cavity. Lower orbital margin with 3 or 4 acute spines curved inwards, followed by 8-10 papillae or crenulations; innermost spine fused at base with spine of inner orbital angle. Occlusive orbital tooth reduced to small triangular projection directed laterad, implanted inside orbit, away from inner orbital angle, partially concealed by basal antennal article; notwithstanding reduction of inner orbital angle, a slight elevation behind it forms deep channel with basal antennal article; outer orbital angle with hooked spine directed forward, similar to other on antero-lateral margin of carapace; rounded lobe between outer orbital angle and first lateral angle; buccal angle armed with 4 small spines. Front retracted leaving epistome completely exposed in dorsal view; the anterior margin of the front does not form distinct surface, but rather rounded-off regularly, with the exception of the semicircular middle pillars; epistome strongly advanced, points of the mid-gutter well separated; opening of efferent channels strongly arched, forming two well defined spouts delimited below by second maxillipeds; surface delimiting the

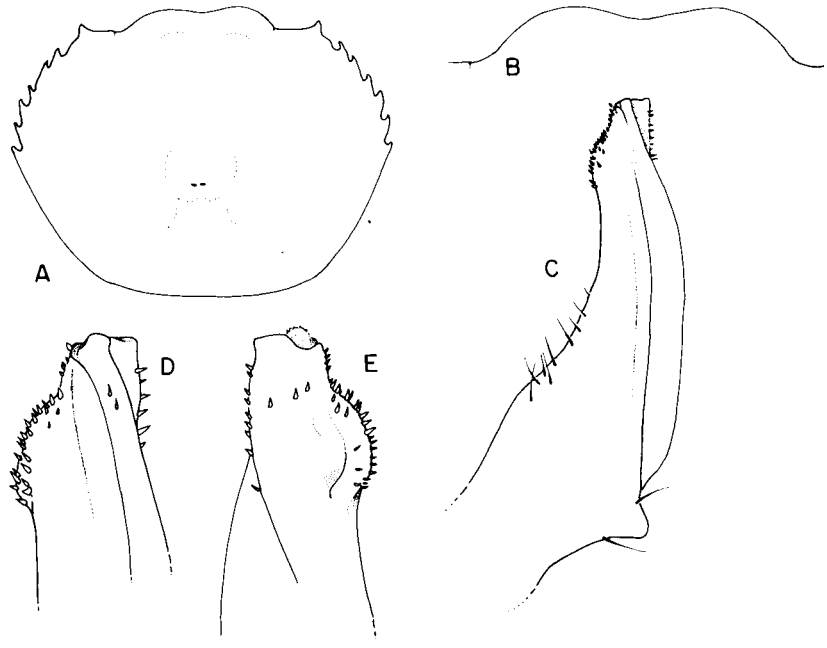

FIGURE 39
Dilocarcinus truncatus, new species, male holotype, cl 23.7 mm: A, outline of carapace; B, front; C, first male gonopod, right, caudal; D, same, apex, caudal; E, same, apex, cephalic.

channels laterally rounded and separated from buccal crest. All buccal area, including yugal and suborbital spines, visible in dorsal view; spines at each side of the epistome define two external respiratory channels, one between yugal spines and suborbital spines, another inside orbits and delimited below by suborbital spines and facilitated by relative reduction of eyes.

Male abdomen triangular, wide at base, outer margins slightly sinuous; last segment with outer margins slightly sinuous, approximately 0.55 as long as broad, proximal margin of approximately same length as distal margin of penultimate segment; segments 3-6 fused, articulation between 6 and 7 segments, although well marked, not movable.

Basal article of antenna without outer lobe. Shallow depression along ischium of 3rd maxilliped. Chelipeds moderately unequal in male, larger with fingers slender, not gaping, swelling on external side of palm near base of fixed fingers; tubercle on upper distal angle; fingers with longitudinal grooves on both chelipeds, more conspicuous on smaller chela; carpus with large conical spine on inner margin; lateral distal margin of merus with spine, latero-inferior margin of same with tubercle in middle and small acute spine on distal angle. Dactylus of legs with row of long hairs on lower margin and 2 rows on upper margin, claws with 5 longitudinal carinae, 1 upper, 2 lateral and 2 inferior; propodus covered with a row of long hairs on upper margin and similar row covering the following proportions of lower margin: 2nd, 95%; 3rd, 40%; 4th, 37%; 5th 90%.

First gonopod strong and stocky, wide at base, gently decreasing distally, mesial border almost straight, lateral border concave; distal part has conspicuous lateral rounded lobe, excavated on caudal surface, covered laterally with short spines, and mesial side slightly convex, also covered with short spines ending distally in thin translucent lamella; terminal portion of margin forms prominent dorsal longitudinal ridge, which reaches gonopore, with transverse row of 4 short dorsal spines; gonopore directed cephalad. Second gonopod longer than first (distal part missing in holotype).

Material examined

Bolivia. Riberalta, Rio Beni, 11º S; 27 August 1909; A. WINKELMANNN; 1 male holotype, cl 23.6 mm, cb 28.1 mm (MH 3682).

Remarks

The type specimen was determined by BOTT (1969) as *Poppiana argentinianus*, but it can be easily distinguished from this species, and all other within the genus, by the characters of the first gonopod, particularly the rounded distal lobe on the lateral side. *Dilocarcinus truncatus* resembles *Dilocarcinus pagei* in most characters, but it lacks the strong abdominal carina characteristic of this species.

Dilocarcinus bulbifer, new species

Fig. 2E; 4X; 8H; 10K; 13I; 14E; 40A-H

Description

Carapace suborbicular; upper surface convex along antero-posterior axis, moderately convex and forming regular arch in frontal view, regions not differentiated, except for semicircular epigastric lobes and slight depressions between protogastric and epibranchial regions; frontal region flat, over antero-posterior axis, concave behind inner orbital angle; front strongly bilobed, inclined downwards; branchio-urogastric, branchio-cardiac and branchio-intestinal grooves shallow and wide, urogastric groove absent. Dorsal surface of carapace smooth and polished, covered by small papillae barely visible to naked eye. Postgastric pits lunulated, well marked. Antero-lateral margin with 6 acute spines behind orbital angle, directed anteriorly and slightly inwards, 2nd with base wider, last smaller; postero-lateral margin with well defined ridge which begins at lateral side of last spine, curves inwards at middle and stops at some distance of ridge on postero-lateral angle of carapace. Orbits subquadrate in frontal view; orbital suture absent; orbits large and eyes relatively small, leaving ample empty space in orbital cavity. Lower orbital margin with 5 or 6 acute spines conspicuously curved inwards, innermost, also curved downwards, forms inner orbital angle. Occlusive orbital tooth reduced to small triangular projection, implanted inside orbit away from inner orbital angle and partially concealed by basal antennal article; notwithstanding reduction of inner orbital angle, strong ridge behind it forms deep channel limited by basal antennal article; outer orbital angle with hooked spine directed forward, similar to other on antero-lateral margin of carapace; buccal angle armed with 5 or 6 small spines or acute papillae. Front moderately retracted, leaving epistome partially exposed in dorsal view; anterior margin of front does not form distinct surface, but rather rounded-off regularly, except for semicircular middle pillars; epistome strongly advanced, points of mid-guter well separated; opening of efferent channels strongly arched, forming two well defined spouts delimited below by second maxillipeds; the surface delimiting the channels laterally forms a triangular tooth which is separated from, and more advanced that, buccal crest; buccal area, including yugal and suborbital spines, visible in dorsal view, but not as projected as in other species of genus; spines at each side of epistome define 2 external

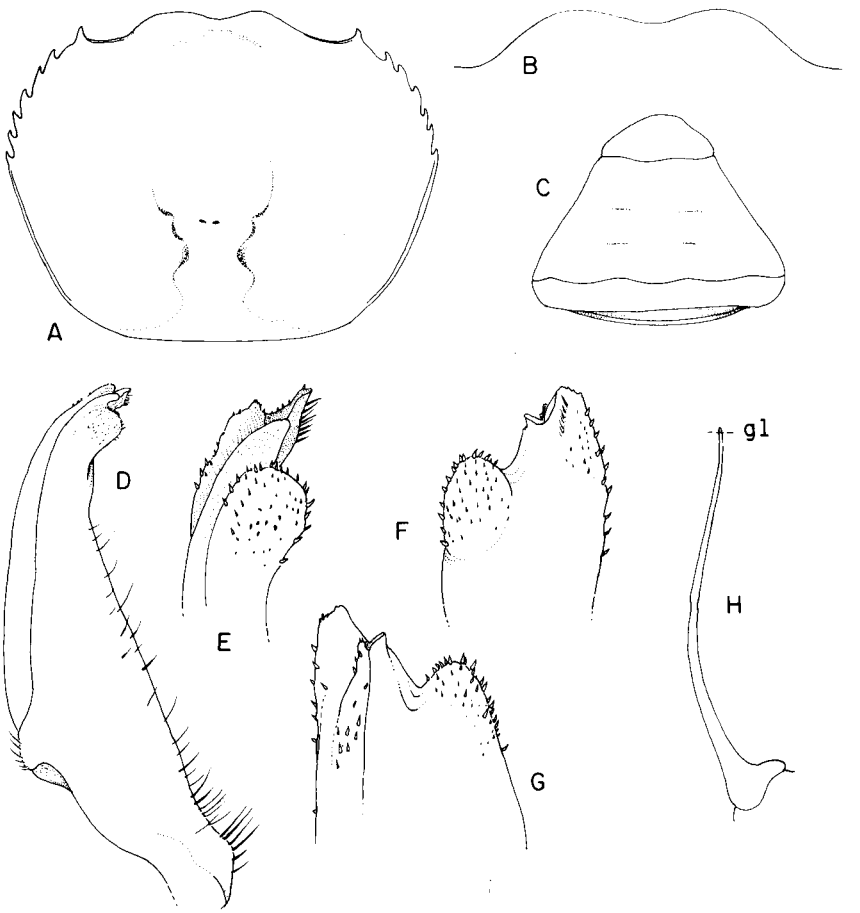

FIGURE 40

Dilocarcinus bulbifer, new species, male holotype, cl 22.7 mm: A, outline of carapace; B, front; C, abdomen; D, first male gonopod, caudal; E, same, apex, caudal; F, same, apex, latero-cephalic; G, same, apex, caudo-mesial; H, second male gonopod. gl, level of gonopore of first gonopod.

respiratory channels, one between yugal spines and suborbital spines, another inside orbits delimited below by suborbital spines.

Male abdomen with segments 3-6 fused, suture 3/4, and partially suture 4/5, still visible, triangular, wide at base; outer margins sinuous; last segment with outer margins sinuous, approximately 0.5 as long as broad, basal border of approximately same length as distal border of penultimate segment. Basal article of antenna without outer lobe. Shallow depression along ischium of 3rd maxilliped. Lower margin of dactylus of legs with row of long hairs; similar hairs cover 72% of 2nd, 39% of 3rd, 39% of 4th and 93% of 5th; dactylus and propodus with rows of smaller hairs on upper margin; claws of dactylus with upper and lower carinae.

First male gonopod wide at base, strongly narrowing distally, apex incurved laterad, mesial border straight, lateral border transverse, provided with row of long plumose setae along proximal 3/4; apical portion consists of conspicuous bulb covered by rows of small conical spinules, marginal process with spinules irregularly arranged on its surface, and corneous awl shaped lamella overreaching other apical processes, provided with row of long setae on caudal surface and small conical spinules on mesial border. Second male gonopod slightly sinuous, of equal length, or slightly longer than first.

Material examined

Perú. Aguajal, Manú Province, Madre de Dios Department; 9 September 1988; H. ORTEGA; 1 male holotype, cl 22.7 mm, cb 26.8 mm, 1 male paratype, cl 20.0 mm, cb 23.5 mm (MHN Lima).

Remarks

Dilocarcinus bulbifer is well characterized by the shape of the gonopod, and in particular by the conspicuous subapical bulb. The dilocarcinian characters are not well developed in this species: the carapace is only moderately convex, the front not strongly retracted, the epistome not completely exposed. The abdomen is wider than in other species of the genus. Our type specimens lacks both chelipeds.

Etymology

The specific name is from the Latin *bulbus* (bulb) and *fero* (I bear) in reference to the conspicuous apical lobe.

Dilocarcinus castelnaui H. Milne Edwards, 1853

Fig. 40A-J

Dilocarcinus castelnaui H. Milne Edwards, 1853, p. 216.- H. MILNE EDWARDS, 1854, p. 182, pl. XIV, fig. 5, (not fig. 4, fide BOTT, 1969).- LUCAS, 1857, p. 8, pl. 11, fig. 4.- A. MILNE EDWARDS, 1869, p. 176, 178.- SMITH, 1869, p. 36.
Dilocarcinus septemdentatus, GERSTÄCKER, 1856, p. 148 (part.).- GOLDI, 1886, p. 28, (part.).- MOREIRA, 1901, p. 44, 49, 109 (part.).
Orthostoma septemdentatum, ORTMANN, 1897, p. 326, 327 (part.).- NOBILI, 1898, p. 9 (part.).
Trichodactylus (Dilocarcinus) castelnaui, RATHBUN, 1906, p. 61, pl. 18, fig. 9, 10.
Dilocarcinus (Goyazana) castelnaui, BOTT, 1969, p. 48, pl. 10, fig. 18a, b, c, pl. 20, fig. 49.
Dilocarcinus castelmani (sic), YOUNG, 1900, p. 231, 233.

Description

Carapace suborbicular; upper surface very convex, more pronounced along the antero-posterior axis, regularly arched; regions not differentiated; epigastric lobes forming semicircular raised surface, delimited anteriorly by conspicuous step; surface of frontal region flat, continuous with surface of protogastric region; front strongly bilobed, inclined downwards; branchio-urogastric, branchio-cardiac and branchio-intestinal grooves defined by few discontinuous depressions; branchio-intestinal grooves indicated in larger specimens by discontinuous line of punctae; urogastric groove absent; dorsal surface of carapace covered by small papillae barely visible to naked eye, and large punctae which form reticular pattern at middle of carapace. Postgastric pits lunulated, well marked. Antero-lateral margin with 6 acute spines behind external orbital angle, directed anteriorly and approximately of equal size, last spine smaller; these spines replaced by blunt large tubercles in old males; interdental spaces approximately equal, first one forming sinuous or angled lobe; postero-lateral ridge from side of last lateral spine, curves inwards at middle, ends at some distance of ridge on the postero-lateral

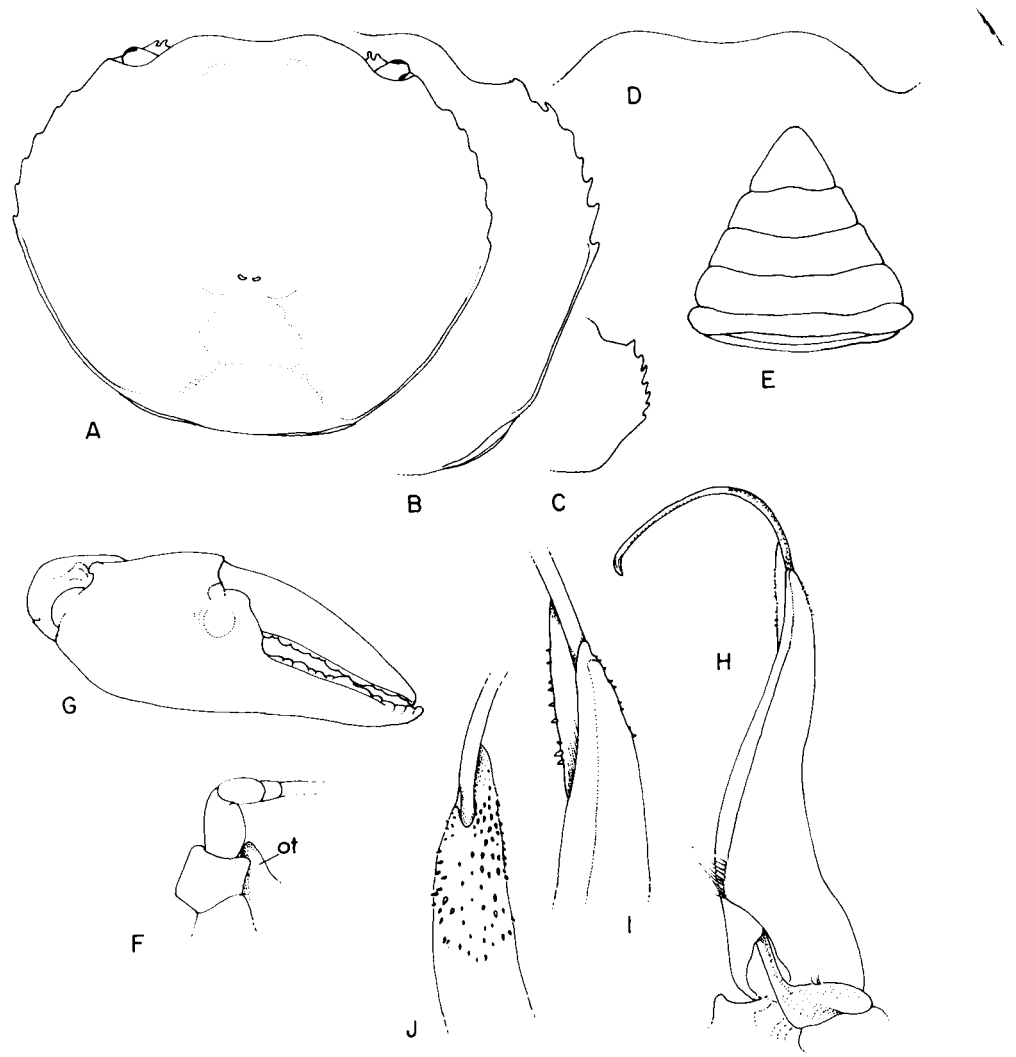

FIGURE 41

Dilocarcinus castelnaui H. Milne Edwards, specimens from Rio Parana, Brazil: A-C, outline of carapace; D, front; E, abdomen; F, basal article of antenna; G, larger chela; H, first and second male gonopods, left, caudal; I, same, apex, caudal; J, same, apex, cephalic. A, D-J, male specimen, cl 40.9 mm; B, female; C, juvenile. ot, occlusive tooth.

angle of carapace. Orbits subquadrate in frontal view, very large in vertical direction, eyes small, leaving ample space in orbital cavity; orbital suture obsolete or indicated by slight groove. Lower orbital margin with 9 acute spines directed inwards and downwards, diminishing in size laterally; innermost long, forms inner orbital angle; last three of series papilliform. Occlusive orbital tooth consists of large ovoid blade, extending anteriorly beyond distal margin of basal antennal article. Orbital floor elevated behind outer orbital angle, forming shallow channel with basal antennal article and occlusive tooth; outer orbital angle with acute spine directed forward, similar to other on antero-lateral margin of carapace, often broken and worn out; buccal angle armed with 4-5 hooked spines. Front retracted leaving epistome completely exposed in dorsal view; anterior margin of frontal lobes lamellar, not forming distinct surface; epistome strongly advanced, points of the mid-gutter well spaced; opening of efferent channels strongly arched, forming 2 well defined spouts delimited below by 2nd maxillipeds; surface delimiting channels laterally forms rounded lobe; all buccal area, including yugal and suborbital spines, visible in dorsal view; spines at each side of epistome define 2 external respiratory channels, one between yugal spines and suborbital spines, another inside orbits, delimited below by suborbital spines.

Sutures betwen abdominal segments 3-6 clearly visible in both sexes; male abdomen triangular, lateral margins of 3rd and 4th segments rounded and expanded, general outline of the abdomen straight or slightly concave; last segment with outer margin slightly concave, approximately 0.6 as long as broad, proximal margin shorter than distal margin of penultimate segment.

Basal article of antenna without outer lobe. Shallow depression along ischium of 3rd maxilliped.Chelipeds moderately unequal; larger chela elongated with upper border moderately convex, lower border almost straight; a large flat tubercle on external surface, at base of fingers; fingers slightly gaping; lower margin of merus of female and small males with 3 median and 1 terminal spine; internal margin with median spine; upper margin with distal spine; carpus with large spine on internal margin; smaller spines on external and upper margins near articulation of palm; legs with row of long hairs on lower margin of propodus and dactylus, and inner and outer distal margin of carpus; two rows of smaller hairs on upper margin of dactylus and similar internal row on propodus; claws of dactylus with 5 longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First gonopod simple, slender, slightly sinuous, progressively tapering to apex, devoided of distal lateral lobe; distal portion of margin bent laterad, shorter than cephalic surface; gonopore large, opening laterad; apical spines very small, forming continuous patch over lateral, cephalic and mesial surfaces. Second gonopod considerable longer than first, bent mesially in form of question mark.

Material examined

Brazil. Paraná River, lagoon near Fundao, 32 km upriver from Puerto Tiberica [Pôrto Tibiriça]; December 1938; SCHINDLER; 1 male, cl 40.9 mm, cb 46.5 mm, 1 female, cl 37.7 mm, cb 41.5 mm, with 180 marsupial youngs (ZSM 1088-1). Highlands of Goias, near Brasilia; 10 August 1965; SCHULTZ; 1 young male, cl 10.8 mm, cb 18.7 mm (ZSM 1088-2).

Type and distribution

The types are two small males (largest cl 16.8 mm) and 1 female (MP), collected by the count Francis de CASTELNAU and Mr Emile DEVILLE, at Salinas, on the Rio Crixas Açu, affluent of the Rio Araguaia, where they stayed from May 14 to June 10, 1844, during their expedition across South America (PAPAVERO, 1971). RATHBUN (1906) excluded from the type material the smallest male, which she placed under *D. spinifer*, but BOTT (1969) kept all the type specimens under *D. castelnaui*. BOTT (1969) recorded 3 males and 3 females from the Xingu river basin, and 1 male and 1 female from the Paraná River (see above under material examined). Thus the area of distribution of the species is located on both sides of the South American water divide formed by the Serra das Divisoes.

Fig. 1H; 2D; 4Y; 5N; 8J; 10L; 13J; 14B; 15H; 42A-I

Orthostoma dentata Randall, 1839, p. 122, pl.5, fig. 1-3.- H. MILNE EDWARDS, 1853, p. 215.- ORTMANN, 1897, p. 326.
Dilocarcinus dentatus, YOUNG, 1900, p. 231, pl. 5, 6.- MOREIRA, 1901, p. 44.- PRETZMANN, 1968b, p. 75.- SMALLEY & RODRÍGUEZ, 1972, p.52, fig. 17, 18.- RODRÍGUEZ, 1980, p. 344, fig. 100.- RODRÍGUEZ, 1981, p. 48.
Trichodactylus (Dilocarcinus) dentatus, RATHBUN 1906, p. 65, pl. 18, fig. 4.- HOLTHUIS, 1959, p. 214, fig. 50b, 51.- CHACE & HOBBS, 1969, p. 152, fig. 44.
Poppiana dentata, BOTT, 1969, p. 50, pl. 11, fig. 19a, b, pl. 20, fig. 50, text-fig. 2.
Dilocarcinus dentatus cayennensis Pretzmann, 1968b, p. 75.
Dilocarcinus dentatus trinidadensis Pretzmann, 1968b, p. 76.
Dilocarcinus multidentatus von Martens, 1869a, p. 5, pl. 1, fig. 2.

Description

Carapace suborbicular; upper surface very convex, the convexity more pronounced along antero-posterior axis, forming regular arch; regions not differentiated; epigastric lobes semicircular, not well delimited; surface of frontal region continuous with surface of protogastric region; front moderately bilobed, inclined downwards, with 16 to 21 acute triangular spines on its margin; branchio-urogastric, branchio-cardiac and branchio-intestinal grooves faintly indicated; urogastric groove absent; dorsal surface of carapace smooth, polished, covered by small papillae barely visible to naked eye. Postgastric pits lunulated, well marked. Antero-lateral margin with 8-10 acute spines behind external orbital angle, directed anteriorly, approximately of equal size, last spine smaller; teeth replaced by semicircular lobes in some specimens; interdental spaces slightly increase posteriorly, 2nd longest, forming conspicuous U-shaped sinus; ridge in postero-lateral margin starts at lateral side of last lateral spine, curves inwards at middle and ends at some distance of ridge on postero-lateral angle of carapace. Orbits subquadrate in frontal view; orbital suture obsolete or indicated by slight groove. Lower orbital margin with 7 to 11, usually 9, acute spines, innermost forming inner orbital angle. Occlusive orbital tooth reduced to slender spine implanted inside orbit, away from inner orbital angle; floor of orbit elevated behind outer orbital angle, forming with basal antennal article and occlusive tooth a shallow channel; outer orbital angle with hooked spine directed forward, similar to other on antero-lateral margin of carapace; buccal angle armed with 5 to 8, usually 6, small spines. Front retracted leaving epistome completely exposed in dorsalview; anterior margin of frontal lobes lamellar, not forming distinct surface; epistome strongly advanced, points of mid-gutter well spaced; opening of efferent channels strongly arched, forming 2 well defined spouts limited below by 2nd maxillipeds; all buccal area, including yugal and suborbital spines, visible in dorsal view; spines at each side of epistome define 2 external respiratory channels, one between yugal spines and suborbital spines, another inside orbits, delimited below by suborbital spines.

Abdominal segments 3-6 fused in both sexes, but suture 3/4 still visible in males; male abdomen triangular, wide at base; outer margins slightly concave; last segment with outer margin sinuous, approximately 0.6 as long as broad, margin of approximately same length as distal margin of penultimate segment.

Basal article of antenna without outer lobe. Shallow depression along ischium of 3rd maxilliped. Chelipeds strongly unequal in male, subequal in female; chela of male with upper border strongly arched, lower border slightly sinuous; fingers very high and thick, not gaping; larger teeth of cutting edges interspaced by 1 or 2 smaller; chelae in both sexes with swelling on external surface at base of fingers; carpus with large conical spine on inner margin, merus with spine on latero-distal margin, another on distal half of upper border and sometimes in middle of latero-inferior margin; female chelae and smaller chela of male with small acute spine on distal upper angle of palm, distal angle of carpus and infero-distal margin of ischium, respectively; 2- 4 spines on the

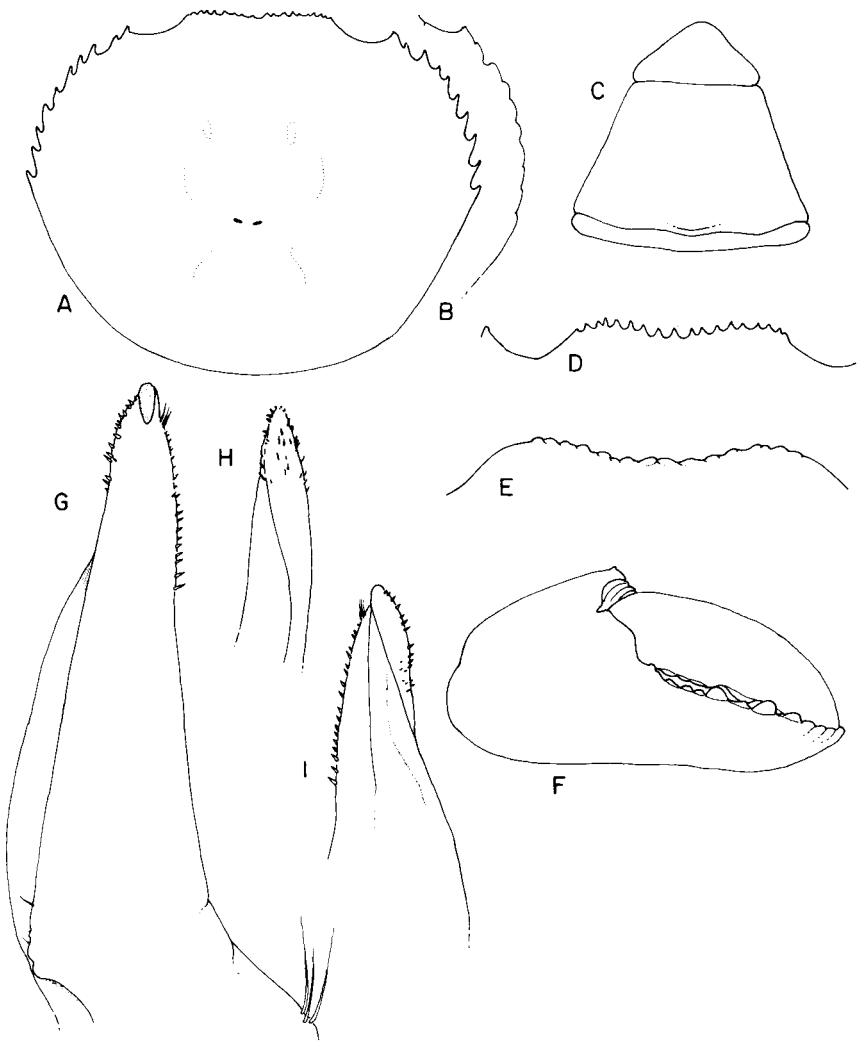

FIGURE 42

Dilocarcinus dentatus (Randall) : A, B, outline of carapace; C, abdomen; D, E, front; F, larger chela; G, first male gonopod, left, caudal; H, same, apex, mesial; I, same, apex, cephalic. A, C, D, F-I, male specimen, cl 39.4 mm, from Agua Negra; B, E, male specimen, cl 33.8 mm, from El Callao.

lower margin of merus. Propodus and dactylus of legs with row of long hairs on lower margin, upper margin with 2 rows of shorter hairs on dactylus and similar internal row on propodus; claws of dactylus with 5 longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First gonopod curved, directed laterad, progressively tapering to apex; distal portion of margin is bent mesially, emerging on anterior surface; basal lateral prominence poorly developed, with long, conspicuous lateral surface, implanted in small pit; gonopore U-shaped, open distally, with thin corneous ridge on lateral side. Second gonopod longer than first, curved mesiad as incomplete semicircle.

Color

In life the color appears to be brown or cream colored (SMALLEY and RODRÍGUEZ, 1972). Specimens preserved in alcohol are very variable, more commonly reddish brown, but sometimes grey or pale brown.

Material examined

Venezuela. Agua Negra, 80 m alt, Yaracuy State; 3 January 1971; O. CHACON; 3 males, 2 females (LS 1044). Agua Negra, Yaracuy State; 23 February 1971; B. ROMAN, 2 males, 3 females (LS 1037). Laguna de Tacarigua, Falcón State; 26 June 1967; E. VALLADARES (LS). Hato La Marrereña, Las Mercedes, Guárico State, 220 m alt; 15 January 1971; D. LOUEIRO (LS). Finca Vuelta Larga, 100 km by road SE of Guaraúnos, Sucre State; 14 August 1987; H. CASTELLANOS, 1 female (LS 1039). Parque Cachamay, Puerto Ordaz, Rio Caroní, Bolivar State; 4 March 1978; J. CLINE, 1 male (Ivic). Caño Onoto, El Callao, Bolivar State; 1 male (Ivic). Hato Terecay, near El Manteco, Bolivar State; 7 June 1977; S. GORZULA; 1 male, 2 females (females captured while walking on gravel road under heavy rain) (Ivic). 70 km SSE from El Manteco, Bolivar State, 250 m alt; 1 female (Ivic). Lago de Guri, Bolivar State; June 1985; 1 male (LS 1043). Quebrada Trapichote, at railway crossing, Los Pijiguaos, Bolivar State; 3 May 1988; C. LASSO & G. COLONNELLO; 1 ovigerous female (LS 1140). Road to El Dorado, Santa Elena, km 88, Bolivar State; 25 February 1988; M. LENTINO; 1 female, 3 males, 3 juveniles (LS 871).- Colombia. Between Cartagena and Bayunca, Bolivar Department; 1 September 1972; P. CALA; 1 male, 1 female (ICN MHN CR 50). Confluence of the Rio Merguia and Rio Cobugón, southern extremity of the Norte de Santander Department; October 1968; B. NICEFORO MARIA; 1 female (LSB).- Trinidad. Mitan; 27 March 1980; A. E. ESTEVES; 28 males, 1 female (Ivic).- Other specimens from Venezuela examined by me are recorded in SMALLEY & RODRÍGUEZ (1972).

Type and distribution

Suriname. Paramaribo (type locality by designation, HOLTHUIS, 1959); Corantijn and Coppename Rivers (HOLTHUIS, 1959). Guyana. Berbice (YOUNG, 1900). French Guiana (RATHBUN, 1906). Venezuela. Very common in the llanos, in rivers discharging into the Orinoco, in the states of Portuguesa, Cojedes, Calabozo, Apure, Guárico, Aragua, Monagas, Bolivar and Delta Amacuro (SMALLEY & RODRÍGUEZ 1972). Trinidad (HOLTHUIS, 1959).

Remarks

PRETZMANN, 1968b, p. 75-76 described two subspecies, *Dilocarcinus dentatus trinidadensis* based on a male cl 35.6 mm, from Trinidad and *D. dentatus cayennensis* on a male specimen cl 44.3, from French Guiana. The characters given for the first subspecies (carapace narrower, flatter, 10 blunt lateral teeth, finger of larger chela gaping, with shorter dactylus, gonopod wider, more recurved, color dark brown) are all very variable in the large series of specimens examined by me from Trinidad, and are also very variable in the specimens which I have examined from the continental part of the range of the species. A similar situation occurs with the second subspecies.

The specimen from Cartagena reported above is completely isolated from the area of distribution of the species. However, it coincides in all characters with those from the Orinoco basin.

Dilocarcinus laevifrons Moreira, 1901

Dilocarcinus laevifrons Moreira, 1901, p. 48, pl. 1, fig. 2.
Trichodactylus (Dilocarcinus) laevifrons, Rathbun, 1906, p.66.
Poppiana laevifrons, Bott, 1969, p. 51, pl. 11, fig. 20a, b, pl. 21, fig. 51.- Rodríguez, 1981, p. 48.

Type and distribution

This species was described from a single female specimen whose typical locality is not well established ("*we found it in a jar with several crustaceans coming from Pernambuco; we believe accordingly that this species lives in the rivers of that state*", Moreira, 1901, p. 49). Bott (1969) assigned to this species one small male (cl 17 mm) from Rio Cuieiras.

Dilocarcinus medemi Smalley & Rodríguez, 1972

Fig. 43A-F

Dilocarcinus medemi Smalley & Rodríguez, 1972, p. 53, fig. 19, 20, 23.- Rodríguez, 1981, p. 48.

Description

Carapace suborbicular; upper surface very convex, convexity more pronounced along antero-posterior axis, forming regular arch; regions not differentiated; semicircular epigastric lobes not well delimited; frontal and postorbital regions depressed; front moderately bilobed, inclined downwards, with 13 acute triangular spines on its margin; branchio-urogastric, branchio-cardiac and branchio-intestinal grooves faintly indicated; urogastric groove absent; dorsal surface of carapace smooth and polished, covered by small papillae barely visible to naked eye. Postgastric pits lunulated, well marked. Anterolateral margin with 7 spines behind external orbital margin, sharp, conical, directed anteriorly and approximately of equal size; 1st interdental space longest, forming conspicuous U-shaped sinus; postero-lateral margin, with well defined ridge from lateral side of last lateral spine, curves inwards at middle and stops at some distance of ridge on postero-lateral angle of carapace. Orbits subquadrate in frontal view; orbital suture obsolete or indicated by slight groove. Lower orbital margin with 6 or 7 acute spines of unequal size, innermost forming inner orbital angle. Occlusive orbital tooth reduced to rounded lobe implanted inside orbit, away from inner orbital angle; orbital floor elevated behind outer orbital angle, forming shallow channel with basal antennal article and occlusive tooth; outer orbital angle with hooked spine directed forward, similar to other on antero-lateral margin of carapace; buccal angle armed with 5 small spines. Front retracted leaving epistome completely exposed in dorsal view; anterior margin of frontal lobes lamellar, not forming distinct surface; epistome strongly advanced, points of mid-gutter well spaced; opening of efferent channels strongly arched, forming well defined spouts delimited below by 2nd maxillipeds; surface delimiting channels laterally forming rounded lobe; all buccal area, including yugal and suborbital spines, visible in dorsal view; spines at each side of epistome define 2 external respiratory channels, one between yugal spines and suborbital spines, another inside orbits and delimited below by suborbital spines.

Abdominal segments with all sutures distinct at least in males; male abdomen trapezoidal, wide at base; outer margins concave; last segment with outer margin conspicuously concave.

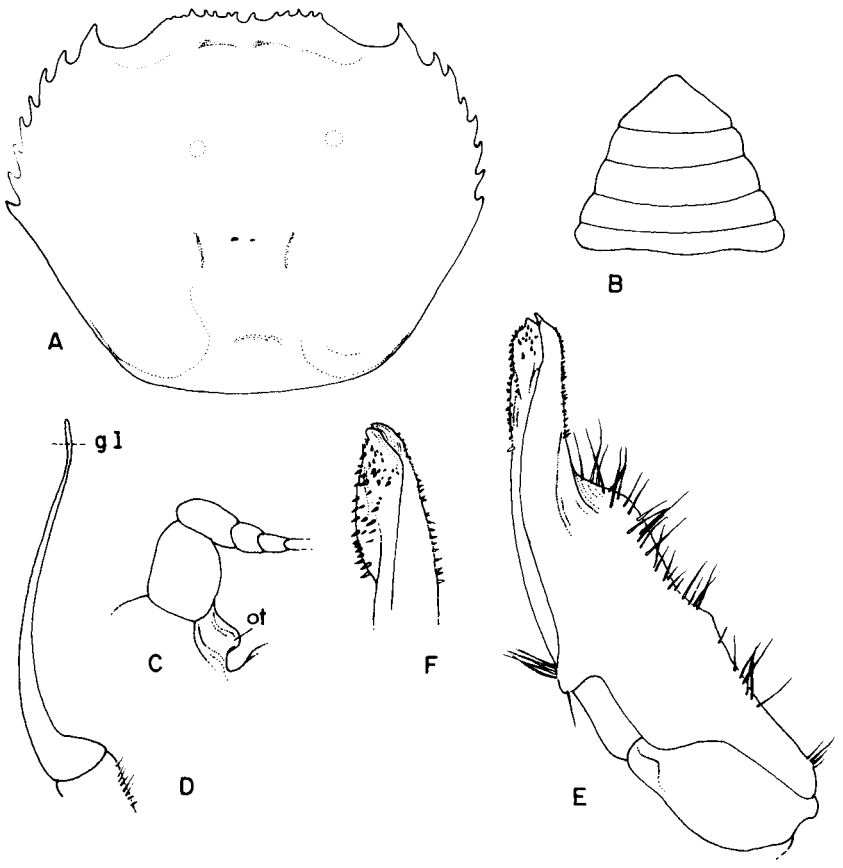

FIGURE 43
Dilocarcinus medemi Smalley and Rodríguez, male paratype, cl 31.7 mm: A, outline of carapace; B, abdomen; C, basal article of antenna; D, second male gonopod; E, first male gonopod, left, caudal; F, same, apex, lateral. gl, level of gonopore of first gonopod; ot, occlusive tooth.

Basal article of antenna without outer lobe. Shallow depression along ischium of 3rd maxilliped. Chelipeds unequal in male, larger chela of male with upper border arched, lower border slightly sinuous; fingers moderately gaping, with large and small tooth alternating on cutting edges, proximal tooth of fixed finger large, small tooth on innerside of large terminaltooth; small acute spine on distal upper angle of palm; distal part of carpus with 3 dorsal spines, median and outer spines small, inner spine very long, curved outwards; merus with long, slender curved dorsal spine, outer margin with 2-3 small, sharp spines, small tubercles grouped near center of merus; inner ventral angle with large spine at center, small spine at anterior corner. Lower margin of propodus and dactylus of legs with row of long hairs, upper margin with 2 rows of shorter hairs on dactylus and a similar internal row on propodus; claws of dactylus with 5 longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First gonopod with proximal half wide in meso-caudal view, mesial border curved laterad, lateral border forming sinuous, lamelliform lobe provided with long, stiff setae; basal lobe prominent, subtriangular, bearing long stiff marginal setae; at distal quarter gonopod becomes abruptly narrowed and bent laterad; sides of distal part nearly parallel, with slight expansion at tip; lateral process hook-shaped at tip, slightly exceeding mesial process; distal part of gonopod bears lateral and mesial patches of small conical spines; no apical tuft of setae. Second gonopod sinuous, slightly longer than first.

Material examined

Colombia. Quebrada Tinajón, Rio Sinú drainage, near Montería, Córdoba Department; April 1962; C. A. VELÁZQUEZ and R. CAMACHO; 1 male paratype, cl 31.7 mm, cb 38.7 mm (USNM 139123, ex Tulane University Collections 4870).

Type and distribution

The species is known only from the two type specimens (SMALLEY and RODRÍGUEZ, 1972).

Remarks

The species closely resembles *Dilocarcinus dentatus*, but could be clearly differentiated from it by the shape of the gonopod.

Dilocarcinus niceforei (Schmitt & Pretzmann, 1968)

Fig. 4Z; 8K; 13I; 14I; 44A-C

Trichodactylus (Valdivia) niceforei Schmitt and Pretzmann, 1968, p. 6.
Valdivia (Rotundovaldivia) niceforei, PRETZMANN, 1968b, p. 73.- SCHMITT, 1969, p. 93, fig. 1.
Valdivia (Rotundovaldivia) niceforei cucutensis Pretzmann, 1968b, p. 73.
Dilocarcinus (Dilocarcinus) niceforei, SMALLEY & RODRÍGUEZ, 1972, p. 51, fig. 15, 16.
Dilocarcinus niceforei, RODRÍGUEZ, 1981, p. 48.

Description

Carapace suborbicular; upper surface very convex, more pronounced along the antero-posterior axis, regularly arched; regions not differentiated; semicircular epigastric lobes not well delimited; surface of frontal region continuous with surface of protogastric region; front strongly bilobed, inclined downwards, with interlobular space bearing 2 to 5 teeth (8 in *cucutensis*) with additional tubercles or papillae; branchio-urogastric, branchio-cardiac and branchio-intestinal grooves defined by thin continuous line, partially obsolescent in small specimens; branchio-intestinal groove indicated in larger specimens by 2 parallel sulci; urogastric groove absent; dorsal surface of carapace covered by small papillae barely visible to naked eye, also large punctae. Postgastric pits lunulated, well marked. Antero-lateral margin with 7 acute spines behind external orbital angle, directed anteriorly and approximately of equal size, last spine smaller; interdental spaces approximately equal, first one longer, forming conspicuous U-shaped sinus; postero-lateral ridge, from side of last lateral spine, curves inwards at middle, ends at some distance of ridge on the postero-lateral angle of carapace. Orbits subquadrate in frontal view; orbital suture obsolete or indicated by slight groove. Lower orbital margin with 5 to 8 acute spines which diminish in size laterally, innermost forming inner orbital angle. Occlusive orbital tooth reduced to low lobe implanted inside orbit, away from inner orbital angle; orbital floor

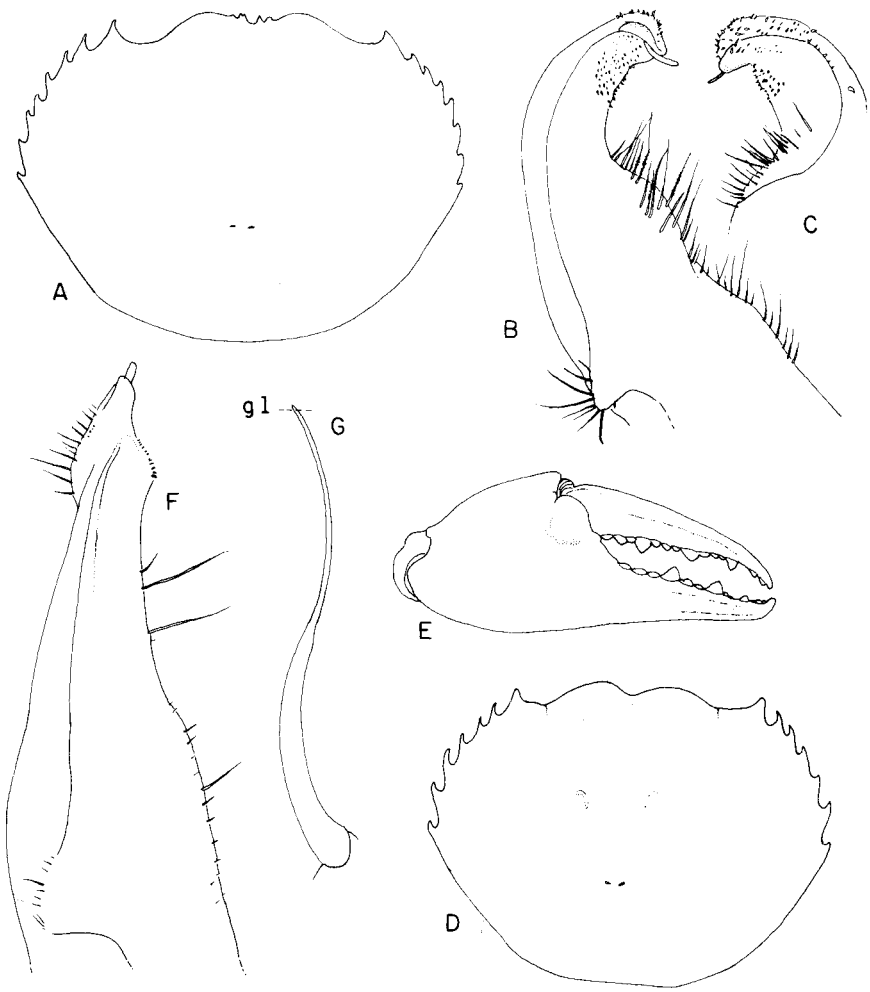

FIGURE 44

Dilocarcinus niceforei (Schmitt & Pretzmann), A-C, male specimen, cl 34.8 mm, from Rio Apon: A, outline of carapace; B, first male gonopod, left, caudal; C, same, apex, cephalic; *Dilocarcinus pagei* Stimpson, D-G, male specimen, cl 44.7 mm, from Trinidad, Beni: D, outline of carapace; E, larger chela; F, first male gonopod, left, caudal; G, second male gonopod. gl, level of gonopore of first gonopod.

elevated behind outer orbital angle, forming shallow channel with basal antennal article and occlusive tooth; outer orbital angle with acute spine directed forward, similar to other on antero-lateral margin of carapace; outer margin of this spine concave or with notch in middle; buccal angle armed with 5 or 6 small spines. Front retracted leaving epistome completely exposed in dorsal view; anterior margin of frontal lobes lamellar, not forming distinct surface; epistome strongly advanced, points of mid-gutter well spaced; opening of efferent channels strongly arched, forming 2 well defined spouts delimited below by 2nd maxillipeds; surface delimiting

channels laterally forms rounded lobe; all buccal area, including yugal and suborbital spines, visible in dorsal view; spines at each side of epistome define 2 external respiratory channels, one between yugal spines and suborbital spines, another inside orbits, delimited below by suborbital spines.

Sutures betwen abdominal segments 3-6 clearly visible in both sexes; male abdomen triangular, lateral margins of 3rd and 4th segments rounded and expanded, general outline of abdomen conspicuously concave; last segment with outer margin concave, approximately 0.6 as long as broad, margin of approximately same length as distal margin of penultimate segment.

Basal article of antenna without outer lobe. Shallow depression along ischium of 3rd maxilliped. Chelipeds moderately unequal; lower margin of merus with 3 median and 1 terminal spine; internal margin with median spine; upper margin with distal spine; carpus with large spine on internal margin; smaller spines on external and upper margins near articulation of palm; lower margin of propodus and dactylus of legs with row of long hairs, upper margin with 2 rows of smaller hairs on dactylus and similar internal row on propodus; claws of dactylus with 5 longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First gonopod with proximal 3/4 wide in meso-caudal view, mesial border slightly curved laterad, lateral border sinuous, provided with long, stiff setae, at least some plumose, projected in lateral view as a sinuous ridge; prominent basal lobe bearing long stiff marginal setae, subtriangular; gonopod becomes abruptly narrowed and strongly bent laterad at distal quarter; apical portion strongly recurved, margin twisted to proximal position and mesial border to distal position, forming two rounded lobes with gonopore in between, directed laterad; distal part of gonopod bears lateral and mesial patches of prominent spines, recurved at different angles, irregular in appearance; apical tuft of setae absent. Second gonopod slightly longer than first, extruded from gonopore as small tongue-like appendage.

Material examined

Venezuela. Rio El Quebradón, near Aguas Calientes, Zulia State; 7 May 1965; captured with Pronox-Fish, bottom sand-gravel, water temperature 28.6º C; F. MAGO; 1 male (MB). Swamp near Bobures, Zulia State; captured with Pronox-Fish, bottom mud with decomposing organic matter, water temperature 30.8º C; 6 June 1965; F. MAGO; 1 male, 1 immature female (MB).- Rio Apon, near Machiques, Zulia State, 90 m alt; 17 August 1978; L. GAMBA; 1 male (Ivic).

Type and distribution

The holotype is a male from Pamplona, Colombia (SCHMITT and PRETZMANN, 1968), collected by H. NICEFORO MARIA; SCHMITT (1969) fixed the holotype designation to a male, cl 34 mm, in the USNM 112117. The holotype and only specimen of *Valdivia (Rotundovaldivia) niceforei cucutensis* is a male from Cúcuta, Colombia, in the Basel Museum, Nº 763-b (PRETZMANN, 1968b). Both localities are 50 km apart, in the same river basin (SMALLEY & RODRÍGUEZ, 1972). In addition to the type material, the species have been reported by SMALLEY & RODRÍGUEZ (1972), RODRÍGUEZ (1980) & CAMPOS (1985) from many localities in the rivers of the Lago Maracaibo drainage in Venezuela and Colombia.

Dilocarcinus pagei Stimpson, 1861

Fig. 1B; 4AA; 8I; 13J; 14D; 44D-G

Dilocarcinus pagei Stimpson, 1861, p. 373.- RODRÍGUEZ, 1981, p. 48.

Dilocarcinus (Dilocarcinus) pagei, LOPRETTO, 1981, p. 23.

Dilocarcinus (Dilocarcinus) pagei pagei, BOTT, 1969. p.46, pl. 9, fig. 16a, b, pl. 20, fig. 47.- LOPRETTO, 1976, p. 84, fig. 26-29.-

MANNING & HOBBS, 1977, p. 159.- LOPRETTO, 1981, p. 22.

Dilocarcinus pagei cristatus Bott, 1969, p. 47, pl. 9, fig. 17a, b, pl. 20, fig. 48 .- LOPRETTO, 1976, p. 86, fig. 14, 17.- LOPRETTO, 1981, p. 22.

Dilocarcinus (Dilocarcinus) pagei enriquei Pretzmann, 1978a, p. 168; PRETZMANN, 1983b, p. 324.

Dilocarcinus (Dilocarcinus) pagei enricei [sic], PRETZMANN, 1983b, p. 318.

Trichodactylus (Dilocarcinus) orbicularis, RATHBUN, 1906, p. 58, pl. 18, fig. 6, text-fig. 119 (part.).- MOREIRA, 1913, p. 19, pl. 7, fig. 1, 2 .- BALSS, 1914, p. 409 .- RINGUELET, 1949, p. 101, pl. 9, fig. 2.

Trichodactylus (Dilocarcinus) septemdentatus, HOLTHUIS, 1959, p. 218 (part.).

Orthostoma septemdentatum, NOBILI, 1898, p. 9 (part.).

Description

Carapace suborbicular; upper surface very convex, convexity more pronounced along antero-posterior axis, regularly arched, with regions not differentiated, except for semicircular epigastric lobes and slight depressions between protogastric and epibranchial regions; frontal region slightly convex over antero-posterior axis, concave behind inner orbital angle; front strongly bilobed, inclined downwards; hepato-epibranchial, branchio-urogastric, branchio-cardiac and branchio-intestinal grooves indicated by thin, obsolescent lines; urogastric groove absent; a short incision in middle of epigastric lobes. Dorsal surface of carapace smooth and polished, covered by small papillae barely visible to naked eye. Postgastric pits lunulated, well marked. Anterolateral margin with 6 acute spines behind external orbital angle, directed anteriorly and slightly inwards; interdental spaces slightly increasing posteriorly; last spine smaller; postero-lateral margin marked by well defined ridge throughout, which begins at lateral side of last lateral spine, curves slightly inwards in middle and stops at some distance of ridge on postero-lateral angle of carapace in female, running parallel to it in male. Orbits subquadrate in frontal view; orbital suture indicated by well marked groove; orbits large and eyes relatively small,leaving ample empty space in orbital cavity. Lower orbital margin with 6 or 7 acute spines curved inwards, innermost pair fused at base to form inner orbital angle. Occlusive orbital tooth reduced to small triangular projection, implanted inside orbit away from inner orbital angle, partially concealed by basal antennal article; strong ridge behind inner orbital angle forms deep channel limited by basal antennal article; outer orbital angle with hooked spine directed forward, similar to other on antero-lateral margin of carapace; buccal angle armed with 5 or 6 small spines or acute papillae. Front retracted leaving epistome completely exposed in dorsal view; anterior margin of front not forming distinct surface, regularly rounded-off; epistome strongly advanced, points of the mid-gutter well separated; opening of efferent channels strongly arched, forming two well defined spouts delimited below by 2nd maxillipeds; surface delimiting channels laterally forms triangular tooth separated from, and more advanced that, buccal crest; yugal and suborbital spines visible in dorsal view; spines at each side of epistome define 2 external respiratory channels, one between yugal spines and suborbital spines, another inside orbits, limited below by suborbital spines.

Abdominal segments 3-6 fused in both sexes; distal margin of 3rd abdominal segment with strong acute ridge directed forward and covering suture 3/4; male abdomen triangular, wide at base; outer margins slightly concave; last segment with outer margin sinuous, approximately 0.6 as long as broad, margin of same length as distal margin of penultimate segment.

Basal article of antenna without outer lobe. Shallow depression along ischium of 3rd maxilliped. Chelipeds strongly unequal in male, subequal in female; chela of male with upper border strongly arched, lower border slightly sinuous; fingers strongly gaping, each cutting edge with approximately 3 larger teeth interspaced by groups of 3 smaller; both chelae in both sexes with large, flat tubercle or swelling on external surface, at base of fingers; carpus with large conical spine on inner margin, merus with spines on distal margin, distal half of upper border and middle of latero-inferior margin; female chelae and smaller chela of male with small acute spine on distal upper angle, distal angle of carpus, infero-distal margin of ischium, respectively; 4 spines on lower margin of merus forming continuous row with ischial and infero-distal spine of merus. Propodus of legs with row of

long hairs on lower margin except on proximal quart, another row on upper margin, dactylus with row on lower margin and 2 rows on upper margin; claws of dactylus with 5 longitudinal carinae, 1 upper, 2 lateral and 2 inferior.

First gonopod with basal portion flattened and expanded on meso-lateral plane; apex directed cephalad, with mesial margin rounded and provided with long hairs, lateral side oblique, with short spines; awl-shaped terminal portion bearing dorsal longitudinal carina, overreaching gonopore; gonopore directed cephalad. Second gonopod slightly longer than first, curved in proximal half, straight or more or less sinuous in distal half.

Material examined

Brazil. Sistema de Janavaca, Amazonas; 19 males, 1 female (Ivic). San Luis de Caceres, Mato Grosso; 27 June 1947; J. JANSEN; 3 males, 1 female (USU 203). Fazenda Nhumirim, Nhecolandia, Pantanal do Mato Grosso; 24 July1948; F. FERREIRA LOURIVAL; 1 male, 1 female (USU 201). Rio Cuiba, Varzea Grande, Mato Grosso; 15 July 1982; M. CATARINO; 1 male (USU 160).- Perú. Rio Tombopata, Madre de Dios Department; 27 October 1972; H. ORTEGA; 1 male (MHNL).-Bolivia. Trinidad, Beni Department; March 1982 - July 1984; G. LOUBENS; 32 specimens (MNHNP B.12813, 12813, 12814, 12816, 12817, 19119, 19120). Arroyo San Juan, Trinidad; 9 January 1982; collected by Orstom (MP B-19116). Laguna Suarez, near the University, Trinidad; 19 October 1981; collected by Orstom (MP B-19118).- Paraguay. Bridge over stream 7 km E of Luque on dirt road to Areguá; Lago Ypacaraí; 17 May 1979; J. N. TAYLOR, T. W. GRIMSHAW & J. K. CREIGHTON; Lat/Long: 25º 18' 30" S - 57º 22' 48" W; Field Number P79-1 (USNM Accession No 341275); 3 females. Overflow inlet along E shore of Rio Paraguay approximately 1 km (=down stream) from Puente Remanso bridge; Rio La Plata drainage; 21 May 1979; J. N. TAYLOR, T. W. GRIMSHAW & J. K. CREIGHTON; Lat/Long: 25º 12' 30" S - 57º 33' W; Field Number P79-4 (USNM Accession No 341275); 1 female. Flooded pastures and river banks along E shore of Rio Paraguay approximately 1 km S of Puente Remanso bridge; La Plata drainage; 6 November 1979; R. BAILEY & J. N. TAYLOR; Lat/Long: 25º 12' 30" S - 57º 33' 00' W; Field Number P79-19B & P79-19C (USNM Accession No 341275); 1 male, 1 female, 1 juvenile. Overflow areas adjacent to Rio Salado (near mouth) at bridges 5.4 and 5.85 km N of Limpio via dirt road, Rio Paraguay; 16 June 1979; R. BAILEY & J. N. TAYLOR; Lat/Long: 25º 08' 42" S - 57º 25' 12" W; Field Number P79-22B (USNM Accession No 341275); 3 females and 2 juveniles. 32.4 km W of turn off to Curuguaty; 21 July 1979; J. N. TAYLOR & T. W. GRIMSHAW; Lat/Long: 24º 22' 54" S - 55º 56' 24" W; Field Number P79-55 (USNM Accession No 341275); 2 females and 2 juveniles. Caaguazu, Arroyo Tobatiry at bridge on dirt highway approximately 22 km N of junction with route 2 in Coronel Oviedo; Rio Manduvira drainage; 29 July 1979; J. N. TAYLOR & T. W. GRIMSHAW; Lat/Long: 25º 16' 54" S - 56º 24' 00' W; Field Number P79-69 (USNM Accession No 341275). Presidente Hayes department; large lagoon above dam (and adjacent small pools below dam) approximately 34.8 km NW toll booth at Puente Remanso bridge; 8 July 1979; G. R. SMITH & J. N. TAYLOR; Lat/Long: 25º 04' 54" S - 57º 36' 00' W; Field Number P79-77A (USNM Accession No 341275); 1 male.- Presidente Hayes Department , Rio Pilcomayo and adjacent overflow pools at bridges (=Puerto Falcon) to Argentina, approximately 12 km WSW Chaco-i; Rio Paraguay; 29 August 1979; J. N. TAYLOR, T. W. GRIMSHAW & B. SMITH; Lat/Long: 25º 15' 48" S - 57º 42' 36" W; Field Number P79-98 (USNM Accession No.341275).

Type and distribution

The holotype is a female collected by Captain PAGE in Paraguay (USNM), Rio Paraguay (STIMPSON, 1861, type; BOTT, 1969). The species have been frequently reported from Brazil, Bolivia, Paraguay and Argentina (RATHBUN,1906; BOTT, 1969; LOPRETTO, 1981; RINGUELET, 1949). To this species probably belong the specimens recorded under *Orthostoma septemdentatum* by NOBILI (1898) from Beni, Bolivia and Alto Rio Paraguay, under *Trichodactylus (Dilocarcinus) orbicularis* by RATHBUN (1906) from Paraguay, and Moreira

(1913) from Rio Paraguay, Mato Grosso, Brazil and the male specimen recorded under *Trichodactylus (Dilocarcinus) septemdentatus* by HOLTHUIS (1959), from Rio Yacuma, Near Espiritu Santo, Bolivia.

The status of the subspecies of *pagei* are highly dubious. LOPRETTO (1981) has convincingly shown that the characters used by BOTT (1969) to diagnose his subspecies *Dilocarcinus pagei cristatus* (type Careiro, near Manaus, Brazil; and other specimens from the lower Amazon, Brazil, and the Beni Department in Bolivia, BOTT, 1969) and those of the typical subspecies, are shared by sympatric specimens from a locality in northern Argentina, possibly due to polyphenic variation of the species. *Dilocarcinus (Dilocarcinus) pagei enriquei*, described by PRETZMANN (1978a) from a single male specimen from Rio Ucayali, Pucallpa, Perú, is also separated from the typical form on highly variable characters: chelae longer,slender; carapace shorter; front narrower, strongly bilobed. Commenting on this subspecies, PRETZMANN (1983b) adds: "*pagei perhaps is only a subspecies of septemdentatus. This question could only be resolved with more study material*". If this is true, *enriquei* would be a subspecies of a subspecies.

Dilocarcinus septemdentatus (Herbst, 1783)

Cancer orbicularis Meuschen,1781, p. 957 (name not available according to Opinion 260-261, International Commission of Zoological Nomenclature, 5: 265-269, 1954).
Cancer septemdentatus Herbst, 1783, p. 155.
Dilocarcinus septemdentatus, GERSTÄCKER, 1856, p. 148 (part.).- GÖLDI, 1885, p. 662.- GÖLDI, 1886, p. 28, pl. 2, fig. 3-17.- NOBILI, 1896, p. 1.- NOBILI, 1899a, p. 5 (part.).- MOREIRA, 1901, p. 44 (part.).
Dilocarcinus (Dilocarcinus) septemdentatus, BOTT, 1969, p. 44, pl. 8, fig. 14a, b, pl. 20, fig. 45.
Trichodactylus (Dilocarcinus) septemdentatus, HOLTHUIS, 1959, p. 218 (part.).
Orthostoma septemdentatum, ORTMANN, 1897, p. 326.- NOBILI, 1898, p. 9 (part.).

Type and distribution

According to HERBST (1783) the type specimen of *Cancer septemdentatus* came from the "American shores"; the type specimen is not extant. All subsequent authors, with the exception of GÖLDI (1886) and BOTT (1969), mentioned the species but did not recorded any specimens. GÖLDI (1886) recorded and illustrated a female from the Island of Marajo. RATHBUN (1906) revived MEUSCHEN name for the species, but the specimens she described and illustrated belonged to *Dilocarcinus pagei*. BOTT (1969) assigned and properly described a male from territory Quatipuru, Campo Cumaru in the road to Santarem, Brazil, which he considered conspecific with HERBST's and GÖLDI's specimens. BOTT's specimen (1969) clearly differs from other species of *Dilocarcinus*: the carapace is wider (cb/cl = 1.30); the first gonopod has the apex slender, slightly bulbiform, strongly bent laterad, the dorsal surface extending over the spinuous ventral surface.

Dilocarcinus spinifer H. Milne Edwards, 1853

Fig. 45A-I

Dilocarcinus spinifer H. Milne Edwards, 1853, p. 215.- H. MILNE EDWARDS, 1854, p. 178, pl.14, fig. 3-3e.- A. MILNE EDWARDS, 1869, p.178.- YOUNG, 1900, p. 234.- MOREIRA, 1901, p. 49.- RODRÍGUEZ, 1981, p. 48.
Trichodactylus (Dilocarcinus) spinifer, RATHBUN, 1906, p. 60 (part.), pl. 18, fig. 1 (not fig. 121).- HOLTHUIS, 1959, p. 210, fig. 50c, 52.
Dilocarcinus (Dilocarcinus) spinifer, BOTT, 1969, p. 45, pl. 8, fig. 15a, b, pl. 20, fig. 46.
Orthostoma spiniferum, ORTMANN, 1897, p. 327.

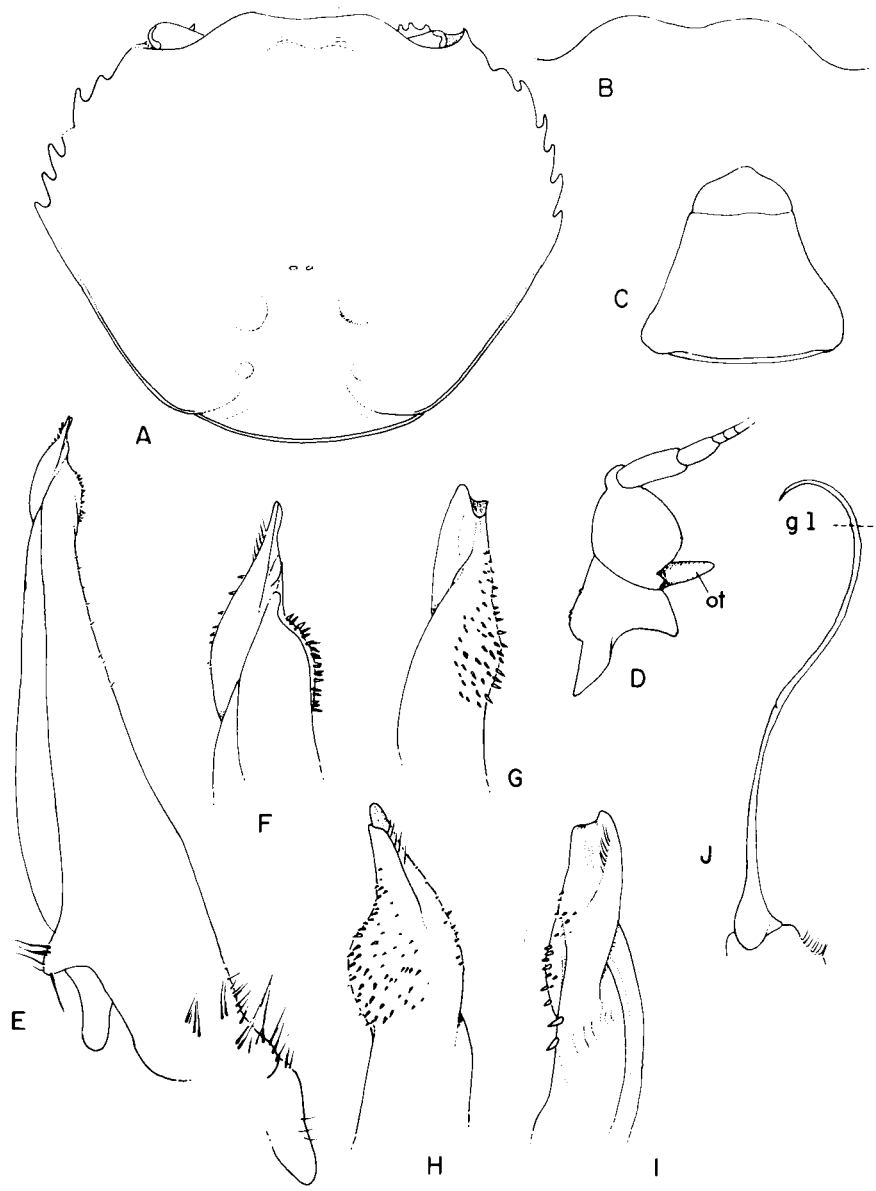

FIGURE 45

Dilocarcinus spinifer H. Milne Edwards, male specimen, cl 34.0 mm, from Compagnie Kreek, Suriname: A, outline of carapace; B, front; C, abdomen; D, basal article of antenna; E, first male gonopod, left, caudal; F, same, apex, caudal; G, same, apex, mesial; H, same, apex, lateral; I, same, apex, caudal; J, second male gonopod. gl, level of gonopore of first gonopod; ot, occlusive tooth.

Description

Carapace suborbicular; upper surface very convex, convexity more pronounced along antero-posterior axis, regularly arched, with regions not differentiated, except for elongated depression on intestinal region; postorbital area depressed; postfrontal lobes obsolescent, only indicated by eroded surface in this area; frontal region slightly concave; front strongly bilobed, inclined downwards; dorsal grooves of carapace absent. Dorsal surface of carapace smooth and polished, covered by small papillae barely visible to naked eye. Postgastric pits lunulated, well marked. Antero-lateral margin with 6 acute spines behind external orbital angle, directed anteriorly and slightly inwards; last spine smaller; third interdental space longest, other subequal in length; rounded lobe behind external orbital angle; postero-lateral margin marked by well defined ridge throughout, which begins at lateral side of last lateral spine, runs parallel to and bends inwards on postero-lateral angle of carapace. Orbits large, subquadrate in frontal view; orbital suture absent or indicated by slight depression. Lower orbital margin with 4 large acute spines curved inwards, followed by 4 smaller. Occlusive orbital tooth reduced to small finger-like spine, implanted perpendicular to basal antennal article; strong ridge behind inner orbital angle forms deep channel limited by basal antennal article; outer orbital angle with hooked spine directed forward, similar to other on antero-lateral margin of carapace; buccal angle armed with 5 acute recurved spines. Front retracted leaving epistome completely exposed in dorsal view; anterior margin of front not forming distinct surface, regularly rounded-off; epistome strongly advanced, points of the mid-gutter well separated; opening of efferent channels strongly arched, forming two well defined spouts delimited below by 2nd maxillipeds; surface delimiting channels laterally forms rounded lobe tooth separated from, and more advanced that buccal crest; yugal and suborbital spines visible in dorsal view; spines at each side of epistome define 2 external respiratory channels, one between yugal spines and suborbital spines, another inside orbits, limited below by suborbital spines.

Abdominal segments 3-6 fused in both sexes; male abdomen trapezoidal, wide at base; outer margins slightly concave; last segment with its outer margin concave, approximately 0.5 as long as broad, margin of same length as distal margin of penultimate segment.

Basal article of antenna without outer lobe. Shallow depression along ischium of 3rd maxilliped. Chelipeds moderately unequal in both male and female; chela of male with upper border strongly arched, lower border slightly sinuous; fingers not gaping, each cutting edge with each larger tooth interspaced by 1 or 2 smaller; external surface of palm with small papillae forming obscure reticulated pattern; carpus with large hooked spine on inner margin, merus with hooked spine on distal margin, distal half of upper border and middle of latero-inferior margin, but no conspicuous row of spines on lower margin of merus. Propodus of legs with row of long hairs on lower margin except on proximal quarter, and 2 rows on upper margin, dactylus with row on lower margin and 2 rows on upper margin; rest of propodus and dactylus covered by felt-like pubescence forming reticulated pattern.

First gonopod slender, curved outwards, with small bulbiform apex ending in acute point directed laterad. Second gonopod sinuous, moderately longer than first.

Material examined

Compagnie Kreek, left bank of Suriname River, near Brokopondo, Suriname; 13 April 1965; G. F. MEES; 4 males, 2 females (RNH 21247).

Type and distribution

This species was described from 2 males collected in Cayenne (French Guiana). HOLTHUIS (1959) and BOTT (1969) give numerous records from Suriname. So far, the species is restricted to these two countries.

Fredilocarcinus PRETZMANN, 1978

Dilocarcinus (Fredilocarcinus) Pretzmann, 1978a, p. 168.

Carapace hexagonal, constricted on posterior half, upper surface strongly arched, smooth, front bilobed, advanced, exposing epistome in dorsal view, lower orbital margin directed downwards at inner orbital angle, 6-8 lateral teeth behind external orbital angle; abdomen triangular-rounded; merus of third maxilliped trapezoidal; first male gonopod moderately widened at base, with irregular mesial lobe and long setae on lateral margin; apex flattened, strongly twisted sinistrally, forming flattened projection which overreaches bulbous expansion; gonopore opening on caudal surface of apex; apex with very few small conical spines and conspicuous row of stiff setae on mesial side of apex; second gonopod of equal length than first.

Type species

Dilocarcinus (Fredilocarcinus) raddai Pretzmann, 1978.

Distribution

The two species of the genus have been collected only in the Ucayali River and the nearby Amazon, from Pucallpa to Iquitos.

Key to the species of *Fredilocarcinus*

1. Subapical bulbous expansion of first gonopod small, simple; contour of apex awl-shaped in caudal view; mesial lobe geniculate ..... *raddai*
– Subapical bulbous expansion large (1/4 of gonopod total length), with longitudinal folds and ridges; contour of apex subtriangular, pointed in caudal view; mesial lobe depressed ..... *musmuschiae*

Fredilocarcinus raddai (Pretzmann, 1978)

Dilocarcinus (Fredilocarcinus) raddai Pretzmann, 1978a, p. 168, fig. 9.- PRETZMANN, 1983a, p. 308, pl. 1. fig. 2, pl. 2, fig. 5, pl. 3, fig.10, pl.4, fig. 13, pl. 5, fig. 17.- PRETZMANN, 1983b, p. 319, 324.

As described and illustrated by PRETZMANN (1978a, 1983a), the first gonopod of the species is clearly related to that of *F. musmuschiae*, but can be distinguish from it by the shape of the apical processes and the lateral lobe. Both species resemble the species of *Dilocarcinus* in carapace morphology, however the gonopod departs considerably from the general type found in this later genus.

Type and distribution

The species was originally described from a single male specimen, without indication of type locality (PRETZMANN, 1978a). Afterwards the locality was given as Iquitos, in a brook near the Rio Nanay (Perú), and 5 juveniles paratypes from this locality and a female paratype from Pucallpa (Perú) were added (PRETZMANN, 1983a). These are the only records known for the species.

Fredilocarcinus musmuschiae (Pretzmann & Mayta), 1980

Fig. 2F; 4V; 5L; 7G; 10J; 13H; 46A-H

Dilocarcinus (Fredilocarcinus) musmuschiae Pretzmann & Mayta, 1980, p. 143, fig. 11, 12.

Description

Carapace hexagonal, antero-lateral sides strongly arched, very narrow posteriorly; moderately convex, in frontal view forms regular arch, with protogastric region prominent but not delimited; protogastric lobes wide, inconspicuous; frontal region slightly convex in frontal view, hepatic region slightly excavated, branchial regions not prominent, slight prominence between epi-, mesobranchial and mesogastric regions; branchio-urogastric groove thin, shallow, cardio-urogastric groove thin, defining 2 small lobes, branchio-cardiac grooves obsolete; shallow wide depression between intestinal and each metabranchial region. Front moderately bilobed, inclined downwards. Surface of carapace rough, densely covered with gross papillae and small wrinkles. Postgastric pits present. Antero-lateral margin with 7 acute spines directed anteriorly which diminishes in size posteriorly, interdental spaces approximately equal throughout; triangular lobe behind outer orbital angle followed by conspicuous U-shaped sinus in front of first lateral tooth; postero-lateral margin marked by well defined ridge throughout, which begins at lateral side of last lateral spine, curves slightly inwards in middle and stops at some distance of ridge on postero-lateral angle of carapace. Orbits circular in frontal view, mesial end of lower orbital margin directed downwards rather than upwards as in other species, consequently lower portion of orbit very large, expanded; orbits large and deep, eyes small, disproportionate to orbital cavity; orbital suture indicated by thin groove. Lower orbital margin with spine implanted on inner orbital angle, considerably longer than others on margin, strongly curved inwards, with 2 spinules on outer margin, followed by 3 similar but smaller spines also directed inwards, and by crenulated ridge. Occlusive orbital tooth is a slender spine implanted inside orbit, away from inner orbital angle; behind outer orbital angle, floor of orbit elevated, forming with basal antennal article and occlusive tooth a shallow channel which runs into orbit; outer orbital angle with hooked spine directed forward, similar to other on antero-lateral margin of carapace; buccal angle armed with 6 large tubercles. Front retracted but epistome not exposed in dorsal view; anterior margin of frontal lobes, lamellar, does not form distinct surface; epistome moderately advanced, points of mid-gutter well spaced; spines at each side of epistome define 2 external respiratory channels, one between yugal spines and suborbital spines, another inside orbits delimited below by suborbital spines and facilitated by relative reduction of eyes.

Abdominal segments 3-6 fused in both sexes, but in males all sutures still visible [unknown in females]; male abdomen triangular, wide at base; outer margins slightly sinuous; last segment with outer margin concave, approximately 0.6 as long as broad, margin of approximately same length as distal margin of penultimate segment.

Basal article of antenna with outer margin expanded but not forming separate lobe. Shallow depression along ischium of 3rd maxilliped. Chelipeds moderately unequal in male, chela with lower border concave; fingers long and slender, not gaping, with well marked longitudinal ridges; larger teeth of cutting edges interspaced by 1 or 2

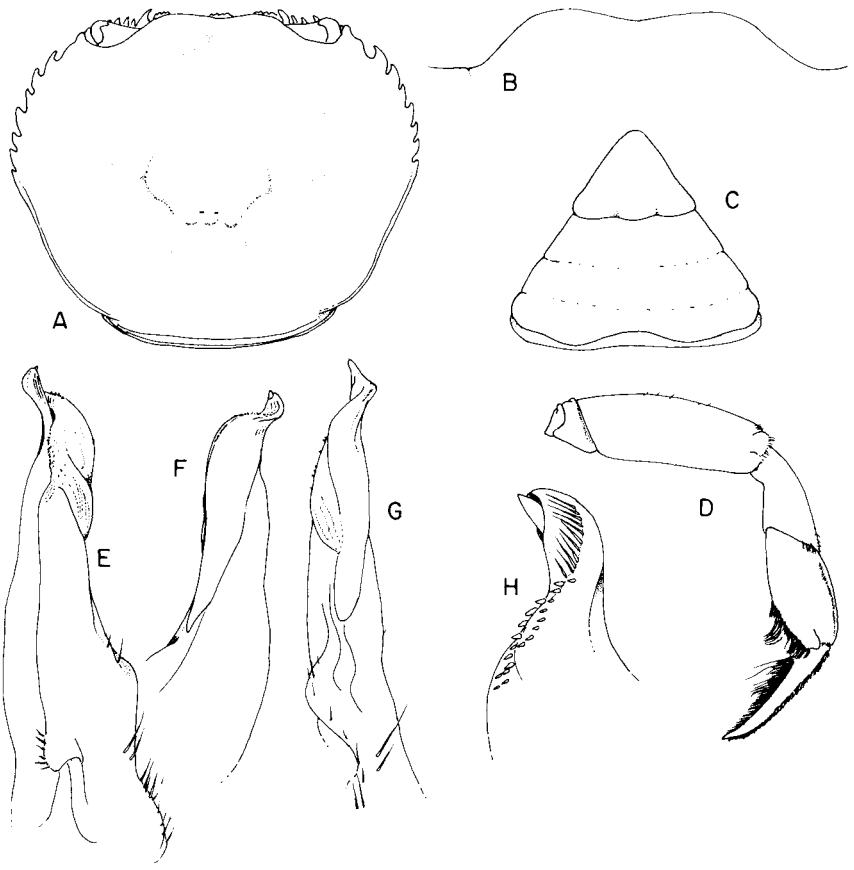

FIGURE 46
Fredilocarcinus musmuschiae (Pretzmann & Mayta), male specimen from Rio Ucayali, cl 30.5 mm: A, outline of carapace; B, front; C, abdomen; D, 5th pereiopod; E, first male gonopod, left, caudal; F, same, caudal; G, same, lateral; H, same, mesial.

smaller; outer surface of chela rugose due to presence of small closely set papillae; depression on external surface of hand; carpus with large conical spine on inner margin, merus with distal hooked spine on upper margin; similar one, but larger, on upper and distal half of inner margin, 2 tubercles on lower margin. Lower margin of dactylus of legs with row of long hairs; similar hairs cover 28% of 2nd, 48% of 3rd, 51% of 4th and 98% of 5th pereiopod; dactylus and propodus with rows of smaller hairs on upper margin; claws of dactylus with upper and lower carinae.

First male gonopod moderately widened on proximal half, with lateral narrow lobe bordered by long setae, progressively narrowing to point; distal half strongly twisted sinistrally; this spiralling defines 2 transverse lobes, one shorter, crossed by longitudinal striae and bearing band of spinules on distal margin, other larger,

surrounding first, extending into apex, provided with lateral row of tiny spinules; apex awl-shaped, strongly twisted mesially, with lateral row of long setae on caudal surface, ending in corneous lamella which overreaches slit-like gonopore. First and second male gonopods of equal length.

Material examined

Perú. Ucayali, Pucallpa, Aguaitia, Rio Huacamayo, km 155, road to Basadre; 24 November 1983; H. ORTEGA & G. CONTRERAS; 1 male (MHN Lima).

Type and distribution

The type and only specimen previously known is a male from the Rio Aguaitia, in the basin of the Rio Ucayali. The specimen recorded above also come from the Rio Aguaitia.

Species *incertae sedis*

1. *Trichodactylus (Dilocarcinus) gurupensis* Rathbun, 1906, p. 64, pl. 18, fig. 7.

The holotype of this species was collected by Louis AGASSIZ in Gurupa, which he visited on the 22 August 1865 and again on the 31 January 1866, during his trip up the Amazon and back to Rio de Janeiro, respectively. Mrs AGASSIZ states on the first occasion: "*In the afternoon we stopped at Gurupa and went on shore; but just as we landed a violent thunderstorm burst upon us...and we saw little of the town...Mr Agassiz obtained a most valuable collection of 'forest fishes'*". On the second occasion she wrote: "*This little town stands on a low cliff some thirty feet above the river* [Amazon]*...Here we received some valuable specimens, collected, since our previous visit by the subdelegado and one or two other residents*" (AGASSIZ & AGASSIZ, 1868). The holotype, deposited at the Museum of Comparative Zoology, No 4950, is a small (cl 21 mm) but adult female. RATHBUN (1906) considered it close to *Sylviocarcinus pictus*, and BOTT (1969) as a synonym of *S. devillei*. The external characters do not permit its allocation to either of these species, or its separation as a valid one.

2. *Trichodactylus petropolitanus paranensis* Bott, 1969, p. 20, pl. 2, fig 4a, b.

Described after several female types deposited in the Museum d'Histoire naturelle de Paris, "from the shores of the Paraná, Seyn, Cuare". The spinulation of the antero-lateral margins corresponds rather with that of *Trichodactylus fluviatilis*, whereas other characters, like the tuberculation of the front and the setation of the pereiopods, point to a species different from both *T. fluviatilis* and *T. petropolitanus*. However, the absence of males in the type material does not even allow a precise generic allocation.

3. *Trichodactylus (Valdivia) faxoni* Rathbun, 1906, p. 49, pl. 16, fig. 10.

Described from 1 male and 5 females collected in Tabatinga, Brazil, by the Thayer Expedition in 1865, and originally deposited in the Museum of Comparative Zoology. According to the characters given in the original description, this species resembles *Trichodactylus ehrhardti* (Bott, 1969) in the possession of five lateral teeth on each side of carapace, the last two very small, difficult to distinguish.

III - MORPHOMETRIC RELATIONSHIPS

The available data on the maximum size attained by each species, the proportions of the carapace, the relative position of its widest part, the relative depth of the frontal sinus, and the proportions of merus of the third pereiopods and propodus of the fifth pereiopods, are presented in table III.

The measurements taken in the carapace, with the respective abbreviations used in table III, are as follows. Length of carapace (cl) from the frontal sinus to the articulation of the abdomen, breadth (cb) in its widest part and including the lateral spines, the depth of the frontal sinus and the total depth of the front measured from a tangent to the frontal lobes, to the dorsal margin of the orbits. From these measurements, the relationship carapace breadth/carapace length (cb/cl), the percentage depth of the frontal sinus (s %) (Fig. 17E) and the position of the widest part of the carapace (w %), were calculated. The first column of the table (cl max.) indicates the maximum carapace length known for each species. These values have been taken from the largest specimen recorded under "Material examined", except in those cases where the record of a larger specimen is available in the literature. According to the information available, 39 % of the species are among the smallest (cl < 25 mm) in the family. This group includes *Trichodactylus maytai, T. kensleyi*, the species of *Avotrichodactylus* and *Rodriguezia*, and *Valdivia camerani*. The largest species belong in the genus *Sylviocarcinus*. The absolute record is the male specimen of *Sylviocarcinus devillei* mentioned by SMALLEY & RODRÍGUEZ (1972) (cl 88.2 mm).

The overall mean of the ratio cb/cl for all species of Trichodactylidae is 1.15 +/- 0.06 SD, with values ranging from 1.05 to 1.30. A clear increase in carapace breadth is found in *Dilocarcinus*, where the species with the widest carapace, *Dilocarcinus septemdentatus*, is found. On the other hand, the species of *Sylviocarcinus* possess a relatively narrow carapace (cb/cl 1.05-1.14).

In table III are also presented the relationship length/width in the merus of the third pair of pereiopods (m3), and the relationship length/width in the propodous of the fifth pair (p5).

TABLE III
Morphometric relationships

	cl max mm	cb/cl	w %	m3	p5	s %	N
Trichodactylus fluviatilis	42.8	1.16	42	4.37	2.21	18	28
T. maytai	16.1*						
T. kensleyi	19.8	1.11	45	3.90	3.18	11	3
T. petropolitanus	31.5	1.13	50	3.42	2.68	15	2
T. quinquedentatus	20.4	1.16	47	4.13	1.60	21	19
Mikrotrichodactylus borellianus	16.7	1.13	57	3.28	1.67	17	4
M. panoplus	16.0	1.14	47	3.28	1.67	20	3
Rodriguezia mensabak	15.0*	1.08*					
R. villalobosi	14.5*	1.17*					
Avotrichodactylus bidens	15.0	1.08	51			12	1
A. constrictus	20.5	1.11	38	3.26	1.45	14	2
A. oaxensis	21.2	1.07	44	5.18	2.00	12	7
Sylviocarcinus devillei	88.2	1.14	40	3.19	1.58	31	4
S. maldonadoensis	29.3	1.10	40	3.45	1.46	2	3
S. pictus	39.0	1.05	37	3.39	1.38	27	7
S. piriformis	78.8	1.05	39	3.39	1.38	1	37
S. sp.	25.5	1.12	50	3.66	1.63	16	1
Valdivia camerani	19.9	1.16	42	4.07	2.00	8	2
V. gila	50.2	1.16	40	3.38	1.75	1	9
V. harttii	39.8	1.18	37			6	3
V. serrata	44.4	1.15	43	4.10	1.83	1	24
Forsteria venezuelensis	45.4	1.11	37	3.46	1.51	1	10
Zilchiopsis cryptodus	27.0*						
Z. emarginatus	34.2	1.20	35	3.15	1.35	30	8
Z. emarginatus, juvenile	21.0	1.08	42	2.72	1.22	35	1
Z. sattleri	49.0	1.16	48	3.32	2.00	20	6
Dilocarcinus argentinianus	24.9	1.24	43	2.00	1.44	21	1
D. bulbifer	22.3	1.19	42	2.29	1.49	25	2
D. castelnaui	40.9	1.19	41	3.14	1.80	21	3
D. dentatus	45.8	1.22	45	2.67	1.64	26	
D. laevifrons	27.0*						
D. medemi	31.0*	1.26*					
D. niceforei	34.8	1.28	40	3.29	1.57	45	2
D. pagei	44.7	1.21	47	2.86	2.08	44	22
D. septemdentatus	40.0*	1.30*					
D. spinifer	38.0	1.16	49	3.16	1.50	40	2
D. truncatus	23.7	1.18	46	2.89	1.33	24	1
Fredilocarcinus musmuschiae	30.5	1.15	40	2.75	1.20	20	1

Abbreviations for the measurements taken are given in Chapter 3.
* indicates records from the literature, N = number of specimens measured.

IV - BIOGEOGRAPHY

Areal distribution of the species

The areas of distribution of the Trichodactylidae in South America are located in the coastal plains of the Guianas and Brazil, the great fluvial plains of the Amazon, Orinoco, Paraguay and Paraná, and the isolated basins of the Magdalena and Lake Maracaibo. Outside South America, two genera of this family are found in a restricted territory of southern Mexico, in the states of Veracruz, Chiapas, Oaxaca and Tabasco, around the Isthmus of Tehuantepec (Fig. 51); of the 5 species inhabiting this area, 3 are strictly cavernicolous, 1 is epigean and another is found in both environments.

Most of the South American species have their vertical range at low altitudes. *Dilocarcinus spinifer*, for instance, is found in the coastal regions of Suriname from quite close to the sea to the anterior mountain range (HOLTHUIS, 1959). All the species found in the lower and middle course of the Amazon are located at very low altitudes since the level of this river is only 60 m above sea level at Iquitos, in Perú. Similarly, the Paraná is only 52 m near its junction with the Paraguay at Resistencia, and the Venezuelan llanos rises from 0 to 42 m above sea level between the mouth of the Orinoco and San Fernando de Apure, 730 km inland. A few species reach some moderate altitudes in the Guianas, the Andean piedmont, the Magdalena valley, and some inland basins: *Valdivia serrata* and *Zilchiopsis emarginatus*, 500 m, *S. piriformis*, 550 m, and *Dilocarcinus niceforei*, probably 500 m.

The areas of distribution of the South American species (Fig. 47-50), correspond to different distributional patterns as follows.

1. Two species possess large areas of distribution centered in the Amazon: *Valdivia serrata* in the extensive hydrological network north of the Amazon, and *Sylviocarcinus devillei* along the main axis of the river.

2. Three species show large areas of distribution which covers the Amazon, Madeira and Paraná basins: *Mikrotrichodactylus borellianus*, *Valdivia camerani*, *Dilocarcinus pagei*.

3. Several species, with small areas, are localized in the headstreams of the Amazon and its tributaries, *Trichodactylus maytai*, *Valdivia gila*, *Dilocarcinus truncatus*, *D. bulbifer*, *Fredilocarcinus musmuschiae*.

4. A last group of species is endemic to peripheral basins. Orinoco basin: *Forsteria venezuelensis*, *Dilocarcinus dentatus*; Maracaibo basin: *D.niceforei*; Magdalena valley: *Trichodactylus quinquedentatus*; Maracaibo and Magdalena basins: *Silviocarcinus piriformis*; Guiana basin: *D. dentatus*, *D. spinifer*; Brazilian

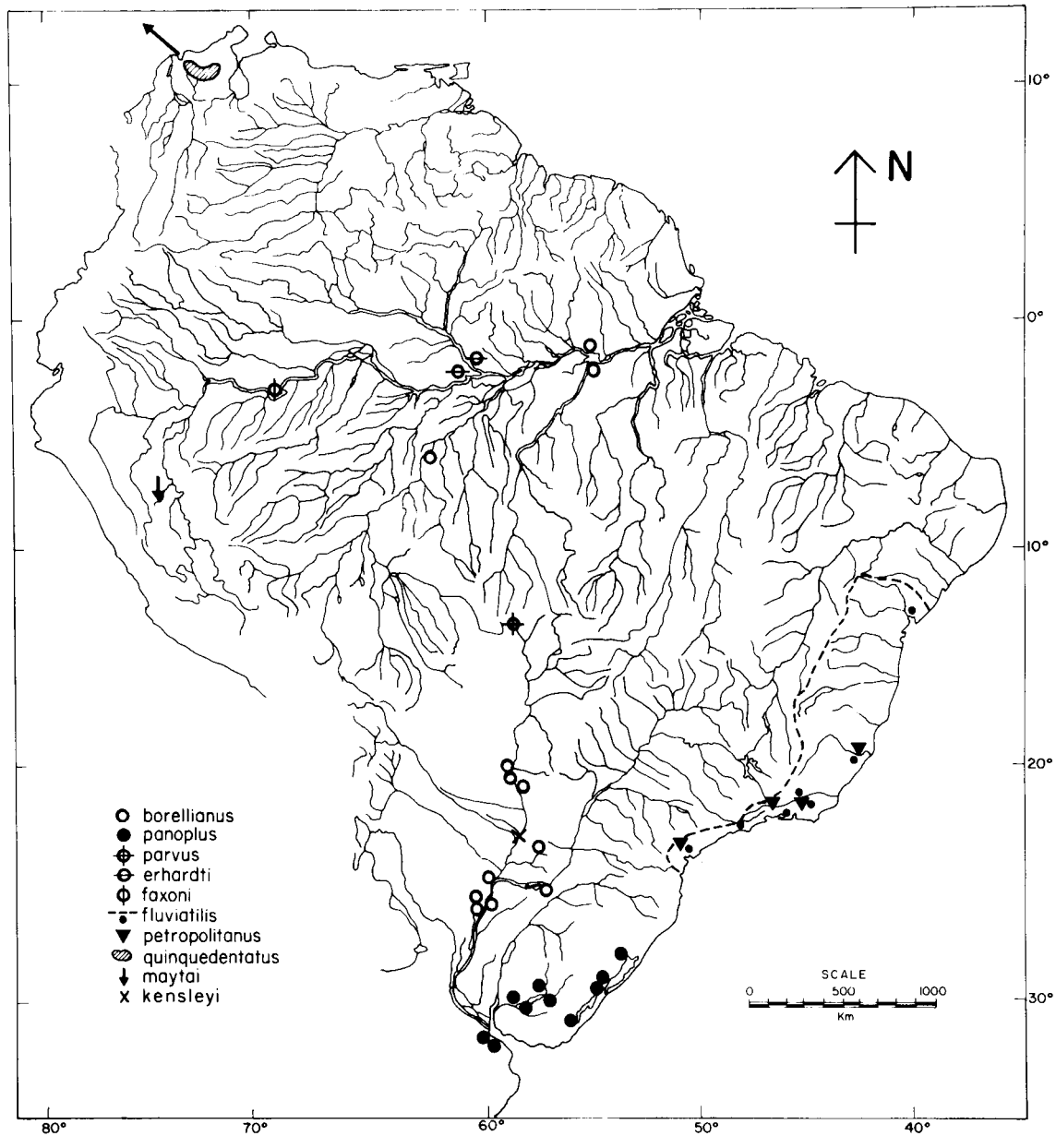

FIGURE 47

Distribution of the species of Trichodactylinae in South America. *Trichodactylus parvus* (?=*Mikrotrichodactylus panoplus*) and *T. faxoni* may be conspecific.

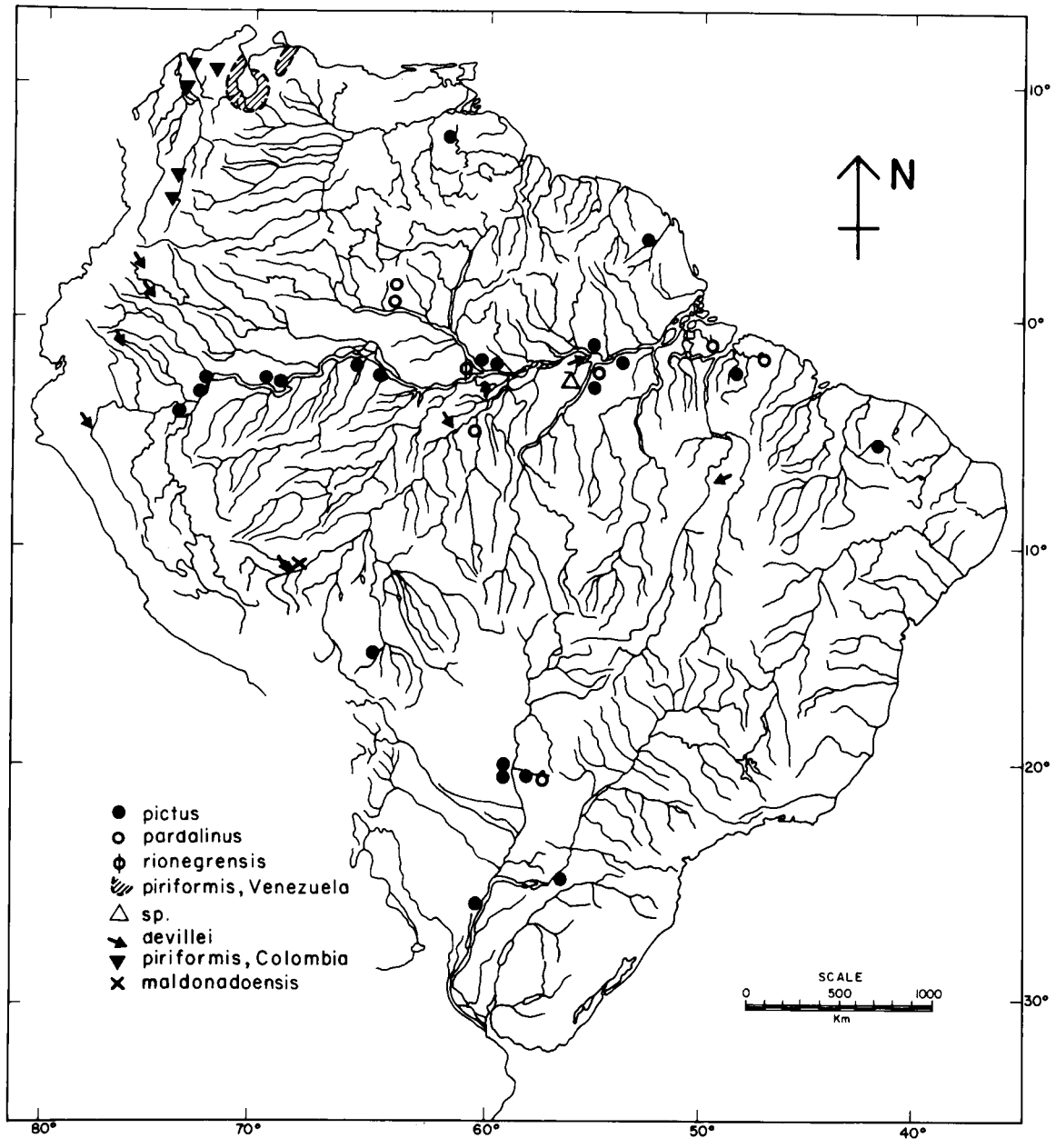

FIGURE 48

Distribution of the species of *Sylviocarcinus* in South America. *Dilocarcinus pardalinus* and *Holthuisia picta rionegrensis* are synonyms of *Sylviocarcinus pictus*.

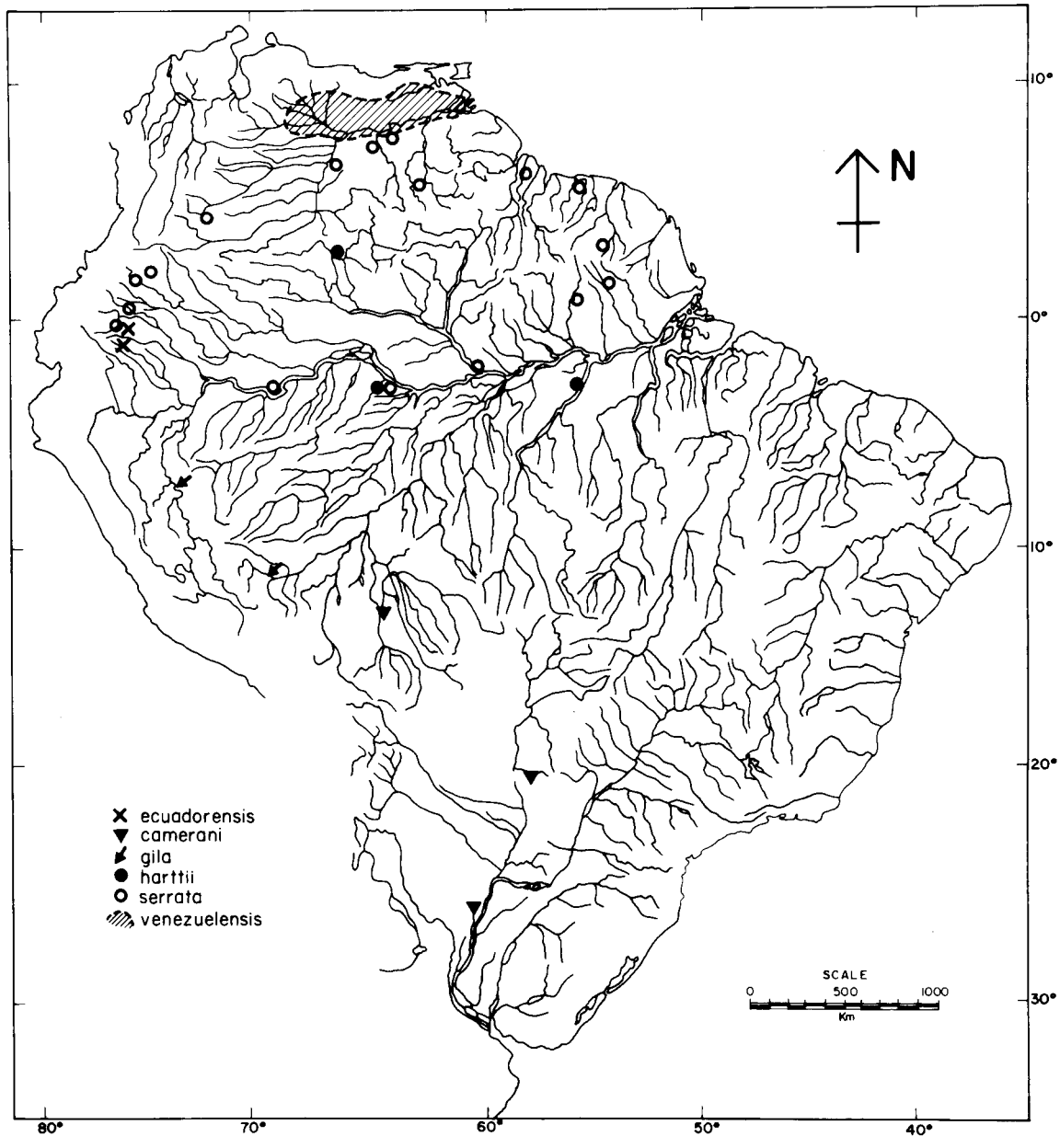

FIGURE 49
Distribution of the species of Valdiviini in South America.

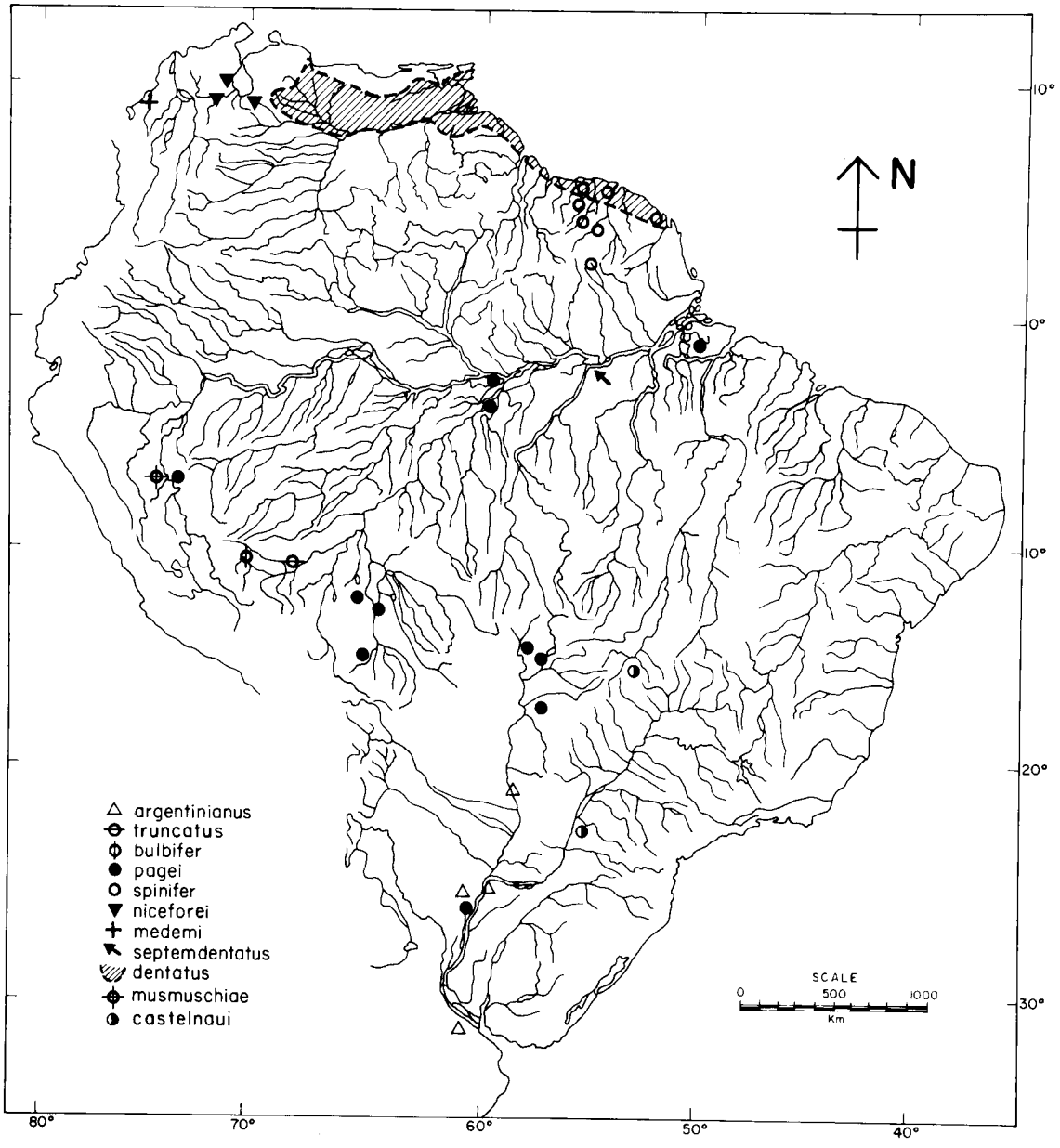

FIGURE 50

Distribution of the species of *Dilocarcinus* and *Fredilocarcinus* in South America.

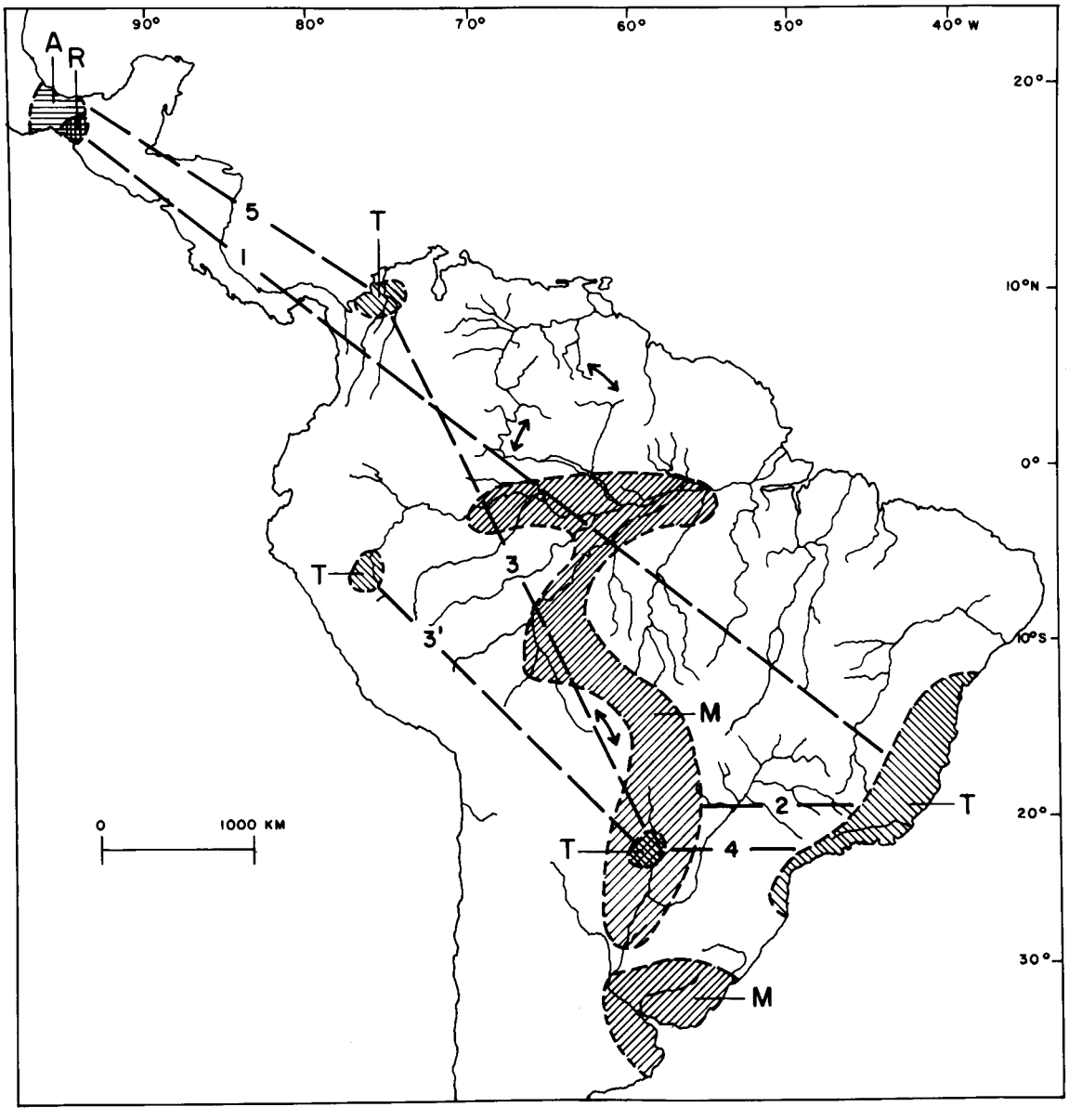

FIGURE 51
Areas of distribution of the Trichodactylinae. A, *Avotrichodactylus*; M, *Mikrotrichodactylus*; R, *Rodriguezia*; T, *Trichodactylus*; 1-5, disjunctions of sister groups; double-headed arrows indicate connections of the Amazon through the Casiquiare channel, Rupunini swamps, and upper Madeira River.

coastal basins: *T. fluviatilis, T. petropolitanus* ; Paraguay-Paraná basin: *T. kensleyi, Mikrotrichodactylus panoplus, D. argentinianus.*

The trichodactylid crabs are restricted by their mode of respiration to live submerged in water (DÍAZ & RODRÍGUEZ, 1977), but there is evidence that, like the Pseudothelphusidae, they are able to migrate overland during heavy rains (see Material examined of *Dilocarcinus dentatus*). On the other hand, as in all freshwater crabs, migration is facilitated by the direct development, since any gravid female is able to transport a propagule with her to a newly colonized territory. Then, aside from paleogeographic considerations, which will be dealt with further, the differences in size and extension of the areas of distribution largely depend on the existence of barriers for the dispersion. From this point of view, at the low elevations covered by these areas of distribution, there are few effective geographical barriers for these crabs inside each drainage basin. In many flatland rivers, flooding of the riverine plains during the rainy season covers the main trunk channel and tributary channels with a continuous sheet of water. Even under dry season conditions, in various basins water drains from the land not in distinct streams and rivers, but in interlaced channels; an example of this geomorphologic setting is the Caroní River in Venezuela, studied by GARNER (1966). Under these conditions, the high "porosity" of the barriers (RAPOPORT, 1985) is responsible for the types of areas 1 and 2 described above, and even for the large areas of the species endemic to peripheral basins (type 4). At the other extreme, the species of type 3 are restricted to the upper tributaries and the headstreams of the Amazon and have not being able to extend their areas of distribution to the middle and lower reaches of this river.

On a larger scale, the water divides between the Amazon and other major drainage basins are bridged in certain areas by an interconnected labyrinth of waterways and flood spillways. This situation is attributed (GARNER, 1975) to desert erosion that occurred in the tropics during Quaternary, in synchrony with the glacial-interglacial fluctuations at higher latitudes, that deposited gravels in areas now occupied by rain forest and savannah ecosystems. The disruption involved deposition of alluvium in stream channels and valleys, sometimes to the point of actual alluvial burial of these depressions. Resumption of humid conditions in more recent times has led to chaotic channel networks due to alluvial clogged flow routes and to diversions plus inland "deltas' where relict riverine deposits impede flow at tributary junctures now situated along former desert margins. Major rivers affected in this manner in South America include the Amazon, Orinoco, and Paraguay. Thus, the Amazon (Fig. 51) communicates with the Orinoco through the Casiquiare channel between the Orinoco and the Rio Negro (GRABEN, 1977), with the Guianas basin through the Rio Branco (LOWE-MCCONNEL, 1964) and with the Paru-Paraguay system through the swamp areas of the upper Rio Madeira (GARNER, 1975).

The distribution of the species mentioned above for the second type of area responds to the communication between the Amazon and Paraná. In the North, the distribution of *Valdivia serrata* from the Amazon to the southern Orinoco llanos and the Guianas plateau has being achieved through the Casiquiare channel and the Rupununi swamps.

Disjunctions

The geographical distribution, together with the cladogram of relationships presented in figure 16A, show several disjunctions of sister groups between Mexico and South America, and between different drainage basins in South America.

The Mexico-South America disjunctions concern (Fig. 51) (a) the three clades formed by the species *Avotrichodactylus* with respect to the rest of the Trichodactylinae, and (b) *Rodriguezia villalobosi* (and presumably the other 2 species of the genus) with respect to its sister species, *Trichodactylus fluviatilis*.

The solution of these disjunctions by means of a dispersalist hypothesis involves the postulation of a theoretical path across Central America after the isthmian bridge was established in the Pliocene, an event dated at 3.1 million years ago by KEIGWIN (1978) on foraminiferal biogeography and paleoceanographic evidence. The absence of intervening species in this area (except for the very problematic record of *Trichodactylus quinquedentatus* in Nicaragua (SMALLEY & RODRÍGUEZ, 1972), the short geological time involved for the evolution of these relatively complex troglobic species, and the polyphyletic origin of the two Mexican genera, are the main objections to this hypothesis.

The establishment of a vicariant hypothesis concerns the continuity of the areas of distribution in the respective parts of South America and Mexico to account for the disjunct distribution of these species, and the synchronization of the paleogeographic evidence available with the branching events postulated in the cladogram.

The only time in which a continuity of the areas can be established is in pre-Cretaceous time when South America was part of Gondwana, together with the other two circum-Atlantic continents of Africa and North America. In the contact zone between North and South America (PINDELL & DEWEY, 1982; PINDELL, 1985) the Caribbean did not exist and the Yucatan block, comprising the northern part of the present Yucatan Peninsula, completely closed the space between North and South America; the Chortis block, comprising the present territories of Honduras and Nicaragua, formed a southern extension of Mexico and was attached to the western side of South America. This configuration existed up to middle Jurassic time, with little tectonic activity or relative motions between the individual constituents. The eastward migration of the Mexican block and the rotation of Yucatan by 140 Ma, led to the juxtaposition of Yucatan and southern Mexico in the Tehuantepec area. By about 125 Ma the continued spreading between North America and Gondwana produced an oceanic seaway, isolating South America from North America. Thus, within a vicariant hypothesis a first radiation of the Trichodactylidae before 125 Ma, in early Cretaceous times, should be postulated. The possible synchrony of these events with the development of the Portunoidea, potential relatives of the Trichodactylidae, have been recently reinforced by BISHOP's (1991) postulation of the species of *Xanthosia* as the possible ancestral roots of the Portunoidea, since the fossil record of *Xanthosia* goes back to early Cretaceous times (Aptian).

The South American disjunctions concern the sister species *Sylviocarcinus devillei-S. piriformis*, in the Amazon and Maracaibo basins, *Trichodactylus kensleyi-T. quinquedentatus*, and *S. devillei-S. piriformis*, in the Amazon, Maracaibo and Magdalena basins. The isolation of these basins from the adjacent Amazon and Orinoco began in Tertiary times. According to an hypothesis (ROD, 1981), in early Eocene times the Merida Andes has not yet emerged so that the Orinoco River was flowing to the northwest into the area of the Maracaibo basin of today. But during the late Eocene the Merida Andes started to rise and caused the gradual migration of the channels of the Orinoco into a depression parallel to the emerging Cordillera; further orogenic activities forced the waters to flow towards east into the Atlantic. Thus isolation of the Maracaibo basin was completed during early Oligocene time by low ridges building a barrier to the northwest, and consequently the colonization by *Sylviocarcinus* (which nearest species *S. devillei* is in the Amazon) could not have occurred after this time.

Regarding the Magdalena valley, WELLMANN (1970) has shown, by the study of paleocurrents during the deposition of Miocene sediments, that the rivers flowed to the east in lower and middle reaches of this valley, and consequently a direct communication with the Orinoco or the Amazon up to this time cannot be ruled out. The allopatric events leading to the disjunct distribution of the sister pairs *Trichodactylus kensleyi-*

T. quinquedentatus and *Sylviocarcinus devillei-S. piriformis* could be dated after this time when the isolation of the lower Magdalena valley was completed, but at least in the first case, the long distances involved point to a much earlier date(1).

Thus, the temporal congruence of the cladogram of relationships with the paleogeographic events discussed above requires a first radiation of the Trichodactylinae at an unknown date, and speciation events within the South American genera, dating back to early Tertiary time.

The Trichodactylidae appear as a very old group, due to (a) the high morphological diversity, which is reflected in the multiplicity of sister groups above species level present in the cladogram, and (b) the relatively primitive respiratory adaptations, which constrast with the highly developed efferent channels and pseudolungs of other freshwater crabs (DÍAZ & RODRÍGUEZ, 1977; RODRÍGUEZ, 1986). Within the family, the Trichodactylinae is perhaps the most ancient group. This subfamily is divided into several genera, with their areas of distribution fragmented over a vast territory (Fig. 51), and the species separated from each other by long distances. For this reason, and notwithstanding the presence of several apomorphic characters, they should be considered as a first branching of the family, which evolved independently for a long period of time. This postulate is supported also by the cladogram. Within the Trichodactylinae, the troglobious habit (HOLSINGER, 1988), isolation, reduced areas of distribution and scarcity of the Mexican species, suggest that these are relicts of an antique fauna. The presumed permanence of these old forms is supported by the stasis observed in some species of Portunoidea. *Carcinus maenas*, for instance, is known since Eocene times (GLAESSNER, 1969).

(1) *Sylviocarcinus piriformis* has been recently recorded from Miocene fossiliferous outcrops of the Honda Group in the Upper Magdalena Valley; Age of these sediments is 13.0 ± 0.88 Ma by fission track (RODRÍGUEZ, *in press*).

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APPENDIX

I - Generic groupings by BOTT (1969)* and PRETZMANN (1968 b)**

The original subgeneric allocation by RATHBUN (1906) is indicated after the respective specific names as follows : T = *Trichodactylus*; V = *Valdivia*; D = *Dilocarcinus*.

*	**
Trichodactylus (Rodriguezia)	***Trichodactylus (Avotrichodactylus)***
constrictus	*constrictus*
villalobosi	
bidens	
	Trichodactylus (Trichodactylus)
quinquedentatus T	*quinquedentatus*
Trichodactylus (Trichodactylus)	
fluviatilis T	*fluviatilis*
edwardsi T	
fluviatilis crassus T	*crassus*
parvus	
petropolitanus V	*petropolitanus*
	thayeri V
	tifucanus V
	faxoni V
	chacei
	Trichodactylus (Mikrotrichodactylus)
panoplus V	*panoplus*
borellianus V	*borellianus*
	Valdivia (Rotundovaldivia)
camerani V	*camerani*
Valdivia (Valdivia)	
harttii V	*harttii*

	latidens
	bourgeti
	niceforei
	gurupensis D
	Valdivia (Valdivia)
serratus V	*serratus*
	torresi
	piriformis
	meekei
	ecuadoriensis
	devillei
	margaritifrons V
Valvidia (Foresteria)	***Holthuisia***
venezuelensis V	*venezuelensis*
Sylviocarcinus	
pardalinus V	*pardalinus*
devillei V	
	peruvianus
pictus D	*pictus*
Dilocarcinus (Dilocarcinus)	***Dilocarcinus***
septemdentatus D	*septemdentatus*
spinifer D	*spinifer*
pagei	
Dilocarcinus (Goyazana)	
castelnaui D	*castelnaui*
Zilchiopsis	
emarginatus D	*emarginatus*
sattleri	
cryptodus	
Poppianus	
argentinianus D	*argentinianus*
dentatus D	*dentatus*
laevifrons D	
	bachmayeri

II - A gazetteer of collection localities

Under every heading are given the localities name, the country, the political division (province, state, etc.), a short description and the approximate coordinates (degrees, minutes) of the localities. The number given in parentheses at the end refers to the order assigned to each species in the list presented in the introduction.

The political division of each country are named as follows:
México, Venezuela, Brazil: states
Bolivia, Colombia, Paraguay, Perú, Uruguay: departments
Argentina, Ecuador: provinces
Suriname, Guyana: districts

- Aguaitia, Perú, Loreto, see San Juan (41).
- Aguajal, Perú, Madre de Dios, locality on Rio Manú, approximately 12º N - 71º W (31).
- Agua Negra, Venezuela, Yaracuy, small village in Rio Yaracuy basin, 10º 25' N - 68º 30' W (33).
- Aguas Calientes, Venezuela, Zulia, unidentified locality in Lago Maracaibo basin (36).
- Alto Caño Rueda, see Atures (23).
- Amazonas, Brazil, name of a state.
- Amazonas, Colombia, name of a department.
- Amambay, Paraguay, name of a department.
- Ansina, Uruguay, Tucuarembo, not identified (8).
- Aparición, Venezuela, Portuguesa, town on Rio Aro, 9º 30' N - 69º 20' W (33).
- Apartaderos, Venezuela, Cojedes, town, 9º 40' N - 68º 55' W (33)
- Apure, Venezuela, name of a state.
- Aracruz, Brazil, Espirito Santo, city on Atlantic, 50 km NNE of Vitoria (1).
- Aragua, Venezuela, name of a state.
- Aregua, Paraguay Central, town on Lago Ypacarai 25º 18' S - 57º 22' W (37).
- Arroyo Caanabe, Paraguay, Paraguari, stream near town of Paraguari, 25º 45' S - 57º 11' W (7).
- Arroyo del Pital, México, Veracruz, creek near Ciudad Alemán, 18º 10' N - 96º 08' W (11).
- Arroyo del Solfo, México, Tabasco, same as, or an extension of, Cueva del Azufre (10).
- Arroyo Gaguaresau, Paraguay, San Pedro, stream near town of Caacupe, 25º 22' S - 57º 15' W (7).
- Arroyo Pindo, Paraguay, stream on San Pedro-Caaguazú Departments border, 24º 52' N - 56º 19' W (7).
- Arroyo Postillón, see Puerto Max (7).
- Arroyo Salsipuedes Grande, Uruguay, Rio Negro, stream joining left side of Rio Uruguay, approximately 32º 30' S - 58º W (8).
- Arroyo San Juan, Beni, Bolivia, stream in the vicinity of the city of Trinidad (37).
- Arroyo Tobatiry, Paraguay, Caaguazú, stream near town of Caaguazú, 25º 16' S - 56º 24' W (7, 37).
- Arroyo Yaguarón, Uruguay, Tucuarembo, small river joining Rio Negro through mouth of Rio Tucuarembo at 32º 25' 30' S - 55º 50' W (8).
- Asunción, Paraguay, Central, capital city on Rio Paraguay, 25º 16' S - 57º 41' W (7).
- Atlántico, Colombia, name of a department.
- Atures, Venezuela, Amazonas Federal Territory, rapids of Rio Orinoco, 22 km S of Puerto Ayacucho (23).
- Azuay, Ecuador, name of a province.

- Bahia, see Salvador (1).
- Barao de Vassouras, see Vassouras (4).
- Barranquilla, Colombia, Atlántico, port on Caribbean Sea, on left bank of Rio Magdalena, 10º 58' N - 74º 46' W (5).
- Basadre, see Pucallpa (41).
- Bayunca, Colombia, Bolivar, town 20 km NE of Cartagena (33).
- Belén, Paraguay, Concepción, town 18 km ESE of Concepción (16).
- Bella Vista, Paraguay, Amambay, at Paraguay-Brazil border, 22º 10' S - 36º 25' W (16).
- Beneficiente, Brazil, Amazonas, town on Rio Aripuana (16).
- Beni, Bolivia, name of a department.
- Berbice, Guyana, a county bounded by Suriname (E) and Brazil (S), drained by Berbice and Corantijn rivers (33).
- Bluefields, Nicaragua, city near Caribbean Sea, at mouth of Rio Escondido, 12º 01' N - 83º 46' W (5).
- Bobures, Venezuela, Zulia, town on SE shore of Lago Maracaibo, 9º 13' N - 71º 10' W (36).
- Boquerón, Paraguay, name of a department.
- Bolivar, Colombia, name of a department.
- Bolivar, Venezuela, name of a state.
- Brokopondo, Suriname, town on Suriname River, 5º 01' N - 56º 02' W (39).
- Buena Vista, see Rio Buena Vista (17).
- Buenos Aires, Argentina (probably Buenos Aires province) (7, 16, 29).
- Caacupe, locality of Paraguay, see Arroyo Gaguaresau (7).
- Caaguazú, Paraguay, name of a department
- Caaguazú, see Arroyo Tobatiri (7)
- Cacaual Grande, unidentified locality in Brazil (37).
- Cachoeira, Brazil, Amazonas, unidentified locality on Rio Marauia (16).
- Cachoeira San Antonio, Brazil, Amazonas, unidentified locality on Rio Marauia (23).
- Caicara, Venezuela, Bolivar, city on right bank of Rio Orinoco 7º 40' N - 66º 10' W (24).
- Caicara, Venezuela, Monagas, town on Rio Guarapiche, 9º 45' N - 63º 40' W (24, 33).
- Cajamarca, Peru, name of a department.
- Calabozo, Venezuela, Guárico, a city on Rio Guárico, 8º 56' N - 67º 26' (33).
- Candelaria, Argentina, Misiones, small town on left bank of Rio Paraná, 27º 30' S - 57º 50' W (16).
- Canendiyu, Paraguay, Caaguazú, town on Rio Jejui-Guazú 24º 14' S - 55º 37' W (3, 16).
- Cañada Acatlán, México, Oaxaca, creek of Rio San Antonio 18º 30' N - 96º 30' W (13).
- Caño Carinagua, Venezuela, Amazonas Federal Territory, creek S of Puerto Ayacucho (27).
- Caño Chamiras, Venezuela, Zulia, unidentified locality (17).
- Caño Chorro de Agua, see Los Pijiguaos (23).
- Caño Iguapo, Venezuela, Amazonas Federal Territory, small river draining E slopes of Mount Duida and S slopes of Mountain Marahuaca, joins Rio Orinoco at 3º 05' N - 65º 28' W; collecting locality at 450 m alt (23).
- Caño Onoto, see El Callao (33).
- Caño Sin Nombre, Venezuela, Bolivar, creek on left bank of Rio Cuyuni, near Isla Jacobo, 6º 45' N - 61º 05' W (16).
- Caquetá, Colombia, name of a department.
- Carabobo, Venezuela, name of a state.

- Careiro (or Carrero), Brazil, Amazonas, town on island in Rio Amazonas, 50 km ESE of Manaus (37).
- Carinagua, Venezuela, Amazonas Federal Territory, locality near Puerto Ayacucho, 5º 40' N - 67º 38' W (23).
- Cartagena, Colombia, Bolivar, port on Caribbean Sea, connected by natural waterway to Rio Magdalena, 10º 25' N - 75º 31' W (5, 33).
- Cayenne, French Guiana, capital city, 4º 56' N - 52º 20' W (39).
- Central, Paraguay, name of a department.
- Cesar, Colombia, name of a department.
- Chaco, Argentina, name of a province.
- Chaco, extensive lowland plain of S Central South America, divided among Bolivia, Paraguay and Argentina (7, 28).
- Chaco-i, Paraguay, President Hayes, undetermined locality, near Puerto Falcón (7).
- Chiapas, México, name of a state.
- Chichirota, Ecuador, Pastaza, locality on Rio Bobonaza, left affluent of Rio Pastaza, 2º 48' S - 76º 32' W (25).
- Chimpire, Venezuela, Trujillo, locality on road between Valera and Pampanito (17).
- Ciudad Alemán, México, Veracruz, town, 18º 12' N - 95º 15' W (12).
- Ciudad Bolivar, Venezuela, Bolivar, city on S bank of Rio Orinoco, 8º 09' N - 63º 33' W (24, 37).
- Clatine, see Collastine (16).
- Cojedes, Venezuela, name of a state.
- Collatina, see Collastine (16).
- Collastine, Santa Fe. RODRÍGUEZ & SMALLEY (1972), suggest that this refers to the city of Clatine, formerly called Collatina, 50 km N of Victoria, Espirito Santo State, Brazil. Another possibility is that Santa Fe refers to Santa Fe Province in Argentina (16).
- Colonia Risso, Paraguay, Concepción, locality on Rio Apa (7, 16).
- Compagnie Kreek, see Brokopondo (39).
- Conception, Paraguay, name of a department.
- Concepción, Paraguay, Concepción, port on Rio Paraguay, 23º 24' S - 57º 28' W (7).
- Coppename River, Suriname, rises in Wilhelmina mountains at about 3º 45' N and flows 400 km to Atlantic just SW of the Saramacca River mouth at 5º 50' N - 56º W (33).
- Corantijn River, Suriname, river along Guyana-Surinam border, rises in Serra Acarai on Brazil border, flows about 700 km to the Atlantic, 8 km of Nieuw Nickerie (33).
- Coronel Oviedo, Paraguay, Caaguazú, town, 25º 25' S - 56º 28' W (7).
- Corrientes, Argentina, name of a province.
- Covanca, Brazil, Rio de Janeiro. Locality in Tijuca (1).
- Cuare, unidentified locality on Rio Paraná (43).
- Cúcuta, Colombia, Norte de Santander, city 4 km from Venezuelan border; drainage of waters is towards Lago Maracaibo, 7º 53' N - 72º 30' W (17, 36).
- Cueva del Azufre, México, Tabasco, cave about 100 m alt, 3 km of Tapijulapa, about 21 km SE of Teapa, 17º 25' N - 92º 45' W (10).
- Cuevita de la Cascada Azufre, see Cueva del Azufre (10).
- Curarigua, Venezuela, Lara, town, 9º 58' N - 69º 35' W (17).
- Curuguaty, Paraguay, Caaguazú, town 24º 22' N - 55º 56' W (16, 37).
- Demerara River, Guyana, rises at 4º 42' N - 58º 21' W and flows generally N to Atlantic at Georgetown (23).

- Delta Amacuro, Venezuela, name of a territory.
- Ducke Reserve, Brazil, Amazonas, forestry reserve approximately 60 km NW of Manaus (16).
- Durazno, Uruguay, name of a department.
- El Callao, Venezuela, Bolivar, town, 7º 20' N - 61º 50' W (33).
- El Dorado, Venezuela, Bolivar, town on headwaters of Rio Cuyuni 6º 33 N - 61º 38' W (33).
- El Jobal, see Los Pijiguaos (23).
- El Manteco, Venezuela, Bolivar, town, 7º 20' N - 62º 30' W (33).
- El Vigia, Venezuela, Mérida, city, 8º 38' N - 71º 39' W (17).
- Ensenada, Argentina, Buenos Aires, suburban port of La Plata (10 km N), on Rio La Plata, 34º 55' S- 57º 58' W (8).
- Espino, Venezuela, Guárico, village in llanos 125 km N of Rio Orinoco, 8º 30' N - 66º W (33).
- Espirito Santo, Brazil, name of a state.
- Espiritu, Bolivia, Beni, unidentified locality, not Espiritu Santo in Cochabamba Department (37).
- Falcón, Venezuela, name of a state.
- Fazenda Nhumirim, see Nhecolandia (37).
- Finca Vuelta Larga, Venezuela, Sucre, ranch 100 km SE of Los Guaraunos (33).
- Florencia, Colombia, Caquetá, city on Rio Orteguaza, upper Rio Caquetá, 450 m alt, 1º 36' N - 73º 37' W (14, 23).
- Floresta do Horto (Horto Florestal), Brazil, Rio de Janeiro, locality S of Rio de Janeiro city, part of Botanical Garden (1).
- Fonte Boa, Amazonas, Brazil, town on right bank of Rio Solimoes, approximately 3º S - 66º W (16).
- Fortin Ingavi, Paraguay, Boquerón, town, 19º 55' S - 61º W (29).
- Fundao, Brazil, Sao Paulo, locality 32 km from Puerto Tiberica (32).
- Goiabal, Brazil, Pará, locality on Rio Cupari (16).
- Goias, Brazil, name of a state.
- Goya, Argentina, Corrientes, town on Rio Paraná, 29º 10' S - 59º 15' W (7).
- Guahyba (Guaiba), Brazil, Rio Grande do Sul, city on right bank of Rio Guahyba, inlet of Lagoa dos Patos, diagonally opposite Porto Alegre, 30º 01' S - 51º 11'W (8).
- Guaira, Paraguay, name of a department.
- Guaraunos, Venezuela, Sucre, village, 10º 33' N - 63º 07' W (33).
- Guárico, Venezuela, name of a state.
- Gulf of Paria, inlet of Caribbean, between Venezuela and Trinidad (24).
- Gurupá, Brazil, Pará, town on the head of Rio Amazonas delta, NE of Porto do Moz (42).
- Guyallaga, Perú, unidentified locality, perhaps a misspelling of Rio Huallaga, a main left affluent of Rio Marañón (14).
- Hato La Marrereña, see Las Mercedes (33).
- Hato Terecay, see El Manteco (33).
- Haut Carsevenne, French Guiana, not identified (16).
- Huanuco, Perú, name of a department.
- Igarapé Agua Preta, undetermined locality in Brazil (7).
- Igarapé das Tres Casas, Brazil, Amazonas, natural channel linking right bank of Rio Madeira with small lake, between Humaita and Borba (H. SIOLI, in litt.), approximately 7º S - 62º 30'W (7, 37).
- Ignavi (Ingavi), Bolivia, Pando, town on Rio Orton, 19º 55' S - 61º 45' W (29).
- Ilha do Puzios, Brazil, Sao Paulo, Buzios Island in Atlantic, 23º 40' S - 45º 05' W (1).

- Iquitos, Perú, Loreto, port on left bank of upper Rio Amazonas, at Rio Nanay mouth, 3º 45' S - 72º 15' W (16, 40).
- Isla Chivera, Venezuela, Delta Amacuro, undetermined island in Rio Orinoco Delta (33).
- Isla Jacobo, Venezuela, Bolivar, small island in Rio Cuyuni, near Caño sin Nombre (16).
- Jaen, Perú, Cajamarca, town in western Cordillera, at 800 m alt, 5º 21' S - 78º 28' W. Collecting station is on Rio Marañón, at approximately 400 m alt, between this town and San Ignacio (14).
- Jaraguá, (Jaraguá do Sul), Brazil, Santa Catarina, city 30 km SW of Joinville (1).
- Jg. Takana, Pará, Brazil, possibly near Tomé-assú, on Rio Acará Miri, 150 km S of Belém, approximately 3º S - 48º 30' (16).
- Joinville, Brazil, Santa Catarina, city, 26º 10' S - 48º 55' W (1, 4).
- La Esmeralda, Venezuela, Amazonas Federal Territory, airstrip and village at base of Mount Duida, 3º 08' N - 65º 32' W (23).
- Laginho, Brazil, Amazonas, locality near Santarem (37).
- Lago Catemaco, México, Veracruz, lake 13 km long, 8 km wide, at SE foot of Tuxtla Volcano, 13 km of San Andres Tuxtla, 18º 25' N - 95º 05' W (11).
- Lago de Guri (Represa Raul Leoni), Venezuela, Bolivar, hydroelectric dam on Rio Caroní, 7º 30'N - 62º 40' W (33).
- Lago do Tostao, Brazil, Pará, "varzea" lake, on left bank of lower Rio Amazonas, N of mouth of Rio Tapajós, between Obidos and Alenquer (H. SIOLI, in lit.) 1º 55' N - 55º W (7).
- Lago Grande de Santarem, Brazil, Amazonas, a large embayment of Rio Tapajos, at its connection with the Rio Amazonas, near the city of Santarem (18).
- Lago Manacapurú (or Lago Grande de Manacapurú), Brazil, Amazonas, formed by small affluent of left bank of Rio Amazonas which joins it in town of Manacapurú, 60 km E of Manaus (6, 14).
- Lago Maracaibo, E Venezuela, large brackish lake, 12000 km2, in free communication with the sea in the N (36).
- Lago Ypacarai, see Aregua (37).
- Laguna de Tacarigua, Venezuela, Falcón, small lagoon near coast, 11º N - 68º 25' W, not to be confused with the larger coastal lagoon in E Venezuela (33).
- Laguna Merin, Uruguay, Treinta y Tres, lake near littoral, Atlantic watershed, at Brazilian border (8).
- Laguna Suárez, Beni, Bolivia, pool in the vicinity of the city of Trinidad (37).
- Laguna Valencia, Perú, Madre de Dios, an inlet of Rio Madre de Dios, near Puerto Maldonado (15).
- La Invernada, Argentina, Santa Fe, small island on Rio Paraná Mini (16).
- La Plata, Argentina and Uruguay, great estuary of combined Rio Paraná and Rio Uruguay (37).
- Lara, Venezuela, name of a state.
- La Regla, Colombia, Bolivar, unidentified locality (19).
- Las Bateas, see Los Pijiguaos (23).
- Las Garzas, Argentina, Santa Fe, town 25 km S from Ocampo (Villa Ocampo), 50 km NNE from Resistencia, near Rio Amores, stream parallel to Rio Paraná Mini and affluent of right side of Paraná, 28º 50' S - 58º 32' W (7, 29).
- Las Mercedes, Venezuela, Guárico, town, 9º 08' N - 66º 25' W (33).
- La Solanera, see Los Pijiguaos (23).
- Las Pavas (Pava), Venezuela, Amazonas Federal Territory, village on creek draining to Rio Cataniapo, right affluent of Rio Orinoco, 5º 35' N - 67º 25' W (27).
- La Urbana, Venezuela, Bolivar, town on left bank of Rio Orinoco, 7º 08' N - 66º 55' W (24).

- Leticia, Colombia, Amazonas, town on upper Rio Amazonas, at Perú and Brazil borders, 4º 10' S - 69º 55' W (23, 16).
- Limpio, Paraguay, Central, town 19 km NE of Asunción (37).
- Litani River, Surinam, Marowijne, one of the headstreams of Marowijne River, joining it at 3º 10' N - 54º 10' W (23).
- Loreto, Colombia, Amazonas, town on left bank of upper Rio Amazonas, 80 km NW from Leticia, 40º 30' S - 70º 30' W (16, 27).
- Loreto, Ecuador, Napo, locality at 450 m alt on E foothills of Mount Sumaco, on Rio Suno, small affluent of Rio Napo (23, 27).
- Loreto, Paraguay, Concepción, town 50 km NE of Concepción (19).
- Loreto, Perú, name of a department.
- Los Guaraunos, Venezuela, Sucre, locality.
- Los Pijiguaos, Venezuela, Estado Bolivar, town SE of Rio Orinoco, 6º 35' N - 66º 15 W (24, 34).
- Luque, Paraguay, Central, city 12 km E of Asunción, 25º 15' S - 57º 40' W (37).
- Macacos, see Rio dos Macacos (4).
- Machiques, Venezuela, Zulia, town near upper reaches of Rio Apon, 10º 05' N - 72º 30' W (36).
- Madre de Dios, Perú, name of a department.
- Magdalena, Colombia, name of a department.
- Manabí, Perú, province in Madre de Dios department.
- Manaus, Brazil, Amazonas, town in confluence of Rio Negro and Rio Amazonas, 3º 05' S - 60º W (16).
- Manú, Perú, a province of Madre de Dios department.
- Maracaibo, Venezuela, Zulia, city on Lago Maracaibo, 10º 40' N - 71º 36' W (17).
- Maracay, Venezuela, Aragua, city, 10º 15' N - 67º 36' N (33).
- Marajó, Brazil, Pará, large island near mouth of Rio Amazonas, 2º S - 49º 30' W (38).
- Mariquita, Colombia, Tolima, city on Magdalena Valley, 5º 12' N - 74º 54' W (19).
- Marowijne River (Maroni River), Surinam and French Guiana, rises in the mountains of French Guiana and flows 720 km N along French Guiana-Surinam border to Atlantic at Galibi Point (23).
- Mato Grosso, Brazil, name of a state.
- Mbutuy, see Arroyo Pindo (7).
- Méndez, Ecuador, Morona Santiago, town, 2º 43' N - 78º 15' W (25).
- Mene Grande, Venezuela, Zulia, city on E coast of Lago Maracaibo, 9º 40' N - 69º 50' W (17).
- Mérida, Venezuela, name of a state.
- Meta, Colombia, name of a department.
- Minas Geraes, Brazil, name of a state.
- Misiones, Argentina, name of a province.
- Mitan, Trinidad, village in central-eastern part of island, near Nariva swamp, 10º 25' N - 61º W (33).
- Monagas, Venezuela, name of a state.
- Montería, Colombia, Córdoba, inland port on Rio Sinú, 8º 40' N - 75º 50' W (35).
- Monte Sumaco, Ecuador, Napo, mountain 3900 m alt, approximately 0º 35' S - 77º 40 W. Nearby localities are Loreto and Payamino (24, 28).
- Morona Santiago, Ecuador, name of a province.
- Mount Tifuca, see Tijuca (1, 4).
- Naguanagua, Venezuela, Carabobo, town in suburbs of Valencia, 10º 20' N - 68º 05' W (33).
- Napo, Ecuador, name of a province.

- Nauta, Perú, Loreto, town on Rio Marañón near its confluence with Rio Ucayali, 4º 37' S - 73º 34' W (16).
- Nhecolandia, Mato Grosso, Brazil, town in Pantanal do Rio Negro, 19º S - 57º W (37).
- Norte de Santander, Colombia, name of a department.
- Nova Friburgo, Brazil, Rio de Janeiro, city in Serra dos Orgaos, 840 m alt, 22º 25' S - 42º 30' W (1).
- Oaxaca, México, name of a state.
- Ocampo (Villa Ocampo), see Las Garzas (7).
- Ourém, Brazil, see Rio Guamá (16).
- Pakitza, Perú, Madre de Dios, undetermined locality in Rio Madre de Dios basin (20).
- Palenque, México, Chiapas, town, near important archeological site, 16º 30' N - 1º 58' W (11).
- Pampanito, Venezuela, Trujillo, town, 9º 24' N - 70º 29' W (17).
- Pamplona, Colombia, Norte de Santander, town on W bank of Rio Pamplonita, 7º 25' N - 72º 40' W (36).
- Pando, Bolivia, name of a department.
- Pantanal do Mato Grosso, Brazil, swampy area in the headwaters of Rio Paraguay, near Bolivia-Paraguay-Brazil borders (37).
- Pará, Brazil, name of a state and also old name for the city of Belém in Rio Amazonas delta, 1º 27' S - 48º 30' W (16).
- Paraguari, Paraguay, name of a department.
- Paraguari, see Arroyo Caanabe (7).
- Paraima, Venezuela, Guárico, unidentified locality (24).
- Paramaribo, capital city of Surinam, on left bank of Suriname River, 24 km upstream from its mouth on Atlantic, 5º 50'N - 55º 13' W (23, 33).
- Paraná, Brazil, name of a state.
- Pardillal, Venezuela, Guárico, undetermined locality (33).
- Parque Cachamay, Venezuela, Bolivar, National Park near Puerto Ordaz (Ciudad Guayana), in rapids of Rio Caroní, 7º 20' N - 62º 40' W (33).
- Paso de la Cruz, Uruguay, Durazno, locality on left bank of Rio Negro (8).
- Paso Horqueta, Paraguay, Concepción, locality on Rio Aquidaban (19).
- Pastaza, Ecuador, name of a province.
- Paute, Ecuador, Azuay, town, 2º 45' N - 78º 45 W (25).
- Payamino (San José de Payamino), Ecuador, Napo, town on foothills of Monte Sumaco, on Rio Payamino, small affluent on left side of Rio Napo, 0º 30' S - 77º 18' W (27).
- Paysandu, Uruguay, name of a department.
- Peixe Boi, Brazil, Pará, locality near Pará, S coast of Isla Marajó, 2º S - 49º 30' W (16).
- Pernambuco, Brazil, name of a state.
- Petrópolis, Brazil, Rio de Janeiro, city on N slope of Serra da Estrela, 22º 30' N - 42º 50' W (4).
- Piauhy, Brazil, name of a state.
- Pindobal, Brazil, Pará, port for Belterra (old Ford Plantations) on right bank of Rio Tapajós, 40 km from Santarem. River here is about 15 km wide (Baía de Boca) and flow is very slow (H. SIOLI, in lit.), 2º 35' S - 55º 30' W (7).
- Playa Hermosa, México, Tabasco, locality in Lago Catemaco (12).
- Ponta Arara, Brazil, Amazonas, a "ponta" on left bank of lower Rio Negro, before Manaus, 3º 05' S - 60º W (16).
- Porto Alegre, Brazil, Rio Grande do Sul, on N end of Lagoa dos Patos, 30º 01' S - 51º 11' (8).
- Porto Espiridiao, Brazil, Mato Grosso, port on Rio Jaurús, 16º S - 58º 50' W (7).

- Portuguesa, Venezuela, name of a state.
- Posadas, Argentina, Misiones, city on upper Rio Paraná, 27º 27' S - 55º 54' W (7).
- Poty, Brazil, Piauhy, possibly Rio Poti, S of Teresina and affluent of Rio Itapecuru; this last river drains into Atlantic independently of Rio Amazonas, 4º 30' S - 42º 25' W (16).
- President Hayes, Paraguay, name of a department.
- Pucallpa, Perú, Loreto, town on Rio Ucayali, 8º 25' S - 74º 35' W (20, 37, 40).
- Puente Remanso, Paraguay, President Hayes, locality on Rio Confuso, on E shore of Rio Paraguay, 25º 40' S - 57º 36' W (7, 37).
- Puerto Asis, Colombia, Putumayo, on upper Rio Putumayo, near boundary with Ecuador, 0º 30' N - 75º 20' W (23, 14).
- Puerto Ayacucho, Venezuela, Amazonas Federal Territory, city on left bank of Rio Orinoco, 5º 35' N - 67º 41' W (23, 27).
- Puerto Casado, Paraguay, Boquerón, port on Rio Paraguay 20 km S of mouth of Rio Apa, 22º 35' S - 57º 40' W (7).
- Puerto Falcón, Paraguay, President Hayes, port on Rio Pilcomayo at Argentina-Paraguay border (7, 37).
- Puerto Limón, Colombia, Putumayo, town on upper Rio Caquetá, 1º 00" N - 76º 35' W (23).
- Puerto Maldonado, Perú, Madre de Dios, small town on S bank of Rio Madre de Dios, 12º 30' S - 73º 30' W (14).
- Puerto Max, Paraguay, Concepción, village on Rio Paraguay, near Puerto Pinasco, 100 km NW of Concepción; collection locality for (7) is on nearby Arroyo Postillón, 21º 12' S - 57º 50' W (7, 15, 28).
- Puerto Ordaz, Venezuela, Bolivar, city, 8º 28' N - 62º 43' W (33).
- Puerto Santander, Colombia, Norte de Santander, village near Venezuelan border, on Rio Sardinata, this last draining to Lago Maracaibo through Rio Catatumbo, 8º 20' N - 72º 30' W (17).
- Puerto Sastre, Paraguay, Boquerón, port on Rio Paraguay, near mouth of Rio Apa; collection locality of (16) is between this port and Puerto Casado, 35 km S, 22º S - 53º W (7, 15).
- Puerto Tiberica (Pôrto Tibiriça), Brazil, Sao Paulo, boat landing on Rio Paraná 5 km NE of Presidente Epitacio, 21º 42' S - 52º 12' W (32).
- Punta do Pharol, Brazil, Santa Catarina. Locality near Sao Francisco do Sul (1).
- Putumayo, Colombia, name of a department.
- Quatipuru, Brazil, Pará, town 180 km NE of Belém, near Atlantic coast, on Rio Toboa basin, 0º 55' N - 47º 30' W (22, 38).
- Quebrada Barbacoas, Venezuela, Aragua, creek near town of same name, 9º 25' N - 67º 00' 34).
- Quebrada Chipuen, Venezuela, Trujillo, creek 1 km from Chimpire, between Pampanito and Valera (17).
- Quebrada La Yuca, creek near Florencia (23).
- Quebrada Lumbi, see Mariquita (19).
- Quebrada Tinajón, see Montería (35).
- Quebrada Trapichote, see Los Pijiguaos (23).
- Rancho La Esperanza, México, Chiapas, undetermined locality (10).
- R. d. O., see Rio de Oro (23).
- Reconquista, Argentina, Santa Fe, town 40 km W of Goya across Rio Paraná, 29º 10' S - 59º 40' W (7, 16, 19, 37).
- Represa El Isiro, Venezuela, Falcón, dam providing water for nearby city of Coro, 11º 20' N - 69º 40' W (17).
- Republiek, Suriname, city 30 km S of Paramaribo, 5º 35' N - 55º 15' W (23).
- Resistencia, Argentina, Chaco, city on Rio Paraná, 27º 28' S - 58º 58' W (7, 28).

- Riberalta, Bolivia, Beni, city at confluence of Rio Beni and Rio Madre de Dios, 11º 30' S - 66º 10' W (30).
- Rio Aguaitia, Perú, Loreto, left affluent of Rio Ucayali, with headwaters in Tingo Maria (41).
- Rio Angu, Brazil, Minas Geraes, left tributary of lower Rio Parahiba do Sul (1).
- Rio Apa, Paraguay, river draining into Rio Paraguay, at Paraguay-Brazil border, 22º 30' S - 58º 30' W (7, 16, 19).
- Rio Apaca, Paraguay, Amambay, small river near Bella Vista (16).
- Rio Apón, see Machiques (36).
- Rio Apure, Venezuela, formed by headstreams rising in Andean Cordillera Oriental of Colombia, flows NE and E for 560 km through Venezuelan llanos to Rio Orinoco, 120 km ESE of San Fernando (24).
- Rio Aquidaban, N Paraguay, rises near Brazil border and flows 240 km SW and W to join Rio Paraguay at Concepción (19).
- Rio Aracataca, Colombia, Magdalena, river draining W slopes of Sierra Nevada de Santa Marta, joining Cienega Grande 62 km S of Santa Marta, 10º 35' N - 74º 10 W (5, 18).
- Rio Araguaia, Brazil, rises on interior plateau near 18º S - 53º W, flows NNW for 2400 km to Rio Tocantins (14, 32).
- Rio Arara, Colombia, Amazonas, small river near Leticia, joins Rio Amazonas at approximately 4º S - 70º W (22, 15).
- Rio Aripuana, Brazil, affluent on right bank of lower Rio Madeira, 5º 35' S - 60º 30' W (16).
- Rio Beni, NW Bolivia, formed at Huachi, flows 96 km past Puerto Pando, Concepción and Riberalta, joining Rio Mamoré at Villa Bella to form Rio Madeira (29, 30).
- Rio Bobonaza, Ecuador, Napo-Pastaza, rises at E slopes of Andes, E of Puyo, flows 180 km SE to Rio Pastaza at Perú border (21, 13).
- Rio Buena Vista, Venezuela, Trujillo, stream draining into S shores of Lago Maracaibo, 10º 20' N - 71º 30' W (17).
- Rio Cadea, Brazil, Rio Grande do sul, stream draining to Lago dos Patos, near Guahyba (8).
- Rio Caquetá, S Colombia, rises in Andes in Cauca Department and flows ESE to Brazilian border where it becomes Rio Japura (23).
- Rio Carapa, Paraguay, Alto Paraná, small affluent of Rio Paraná, near Salto del Guaira (3).
- Rio Caroní, Venezuela, Bolivar, rises at Monte Roraima in Guiana highlands, flows 690 km W and N to Rio Orinoco near Puerto Ordaz (33).
- Rio Cataniapo, Venezuela, Amazonas Federal Territory, rigth affluent of Rio Orinoco, S of Puerto Ayacucho, joining it at 10º 20' N - 67º 10' W (27).
- Rio Caura, Venezuela, Bolivar, rises in Guiana Highlands near Brazil border and flows 740 km NNW to Rio Orinoco at 7º 38' N - 64º 53' W (23).
- Rio Cesar, Colombia, Cesar, runs SW in valley between Sierra Nevada de Santa Marta and Sierra de Perijá; joins Rio Magdalena through system of swamps at 9º N - 75º 50 W; altitude at Valledupar is 138 m (5, 19).
- Rio Chapare, Cochabamba, Bolivia, joins Rio Mamoré 130 km S of Trinidad (28).
- Rio Chimpire, Bolivia, Cochabamba, a lesser affluent of Rio Chapare, 16º 30' S - 65º 35' W (16, 37).
- Rio Chiviripa, Venezuela, Bolivar, small right affluent of Rio Orinoco, 42 km SW of Caicara (24).
- Rio Cobugón, see Rio Merguia (34).
- Rio Confuso, Paraguay, President Hayes, runs parallel to Rio Pilcomayo and joins Rio Paraná at town of Villa Hayes (7).
- Rio Crixas Açu, Brazil, Goias, a minor (approximately 200 km long) rigth affluent of upper Rio Araguaia, at 12º 50' N - 50º 30' W (14, 32).

- Rio Cuao, Venezuela, Amazonas Federal Territory, right affluent of Rio Orinoco, joining it at 5º N - 67º 50' W (27).
- Rio Cuchivero, Venezuela, Bolivar, right affluent of Rio Orinoco, 20 km E of Caicara (23).
- Rio Cuiba (Varzea Grande), Brazil, Mato Grosso, main river in Pantanal de San Lourenço, joins Rio Paraguay at 18º 35' S - 57º 30' W (37).
- Rio Cuieiras, Brazil, Amazonas, left affluent of Rio Negro, joining it 60 km NW of Manaus (34).
- Rio Cupari, Brazil, right affluent of Rio Tapajós, 3º 30' S - 55º 30' W (16).
- Rio Cura, Venezuela, Aragua, one of upper affluents of Rio Guárico, 10º 05' N - 67º 30' W (24).
- Rio Curarigua, Venezuela, Lara, left affluent of upper Rio Tocuyo, 10º 30'N - 70º 50' W (17).
- Rio Cururú, see Rio Kenebiit-Tabiri (23).
- Rio Cuyuni, Guyana and Venezuela, rises in Venezuela in Guianas Highland near 6º N - 61º 30' W and flows along border and into Guyana, to Mazaruni River just before it joins Essequibo River (16).
- Rio de Janeiro, Brazil, Rio de Janeiro, main city, 22º 55' S - 43º 10' W (1, 8).
- Rio de Oro, Argentina, Chaco, river running parallel to Rio Bermejo and joining Rio Paraguay at approximately 40 km N of Resistencia, 27º S - 56º 30' W (23).
- Rio dos Macacos (Macacu), Brazil, Rio de Janeiro, rises in Serra dos Orgaos S of Nova Friburgo and flows 100 km SW to Baía de Guanabara, 22º 45' S - 43º 30' W (1, 4).
- Rio El Quebradón, Venezuela, Zulia, unidentified stream draining to Lago Maracaibo (36).
- Rio Escalante, Venezuela, Zulia, flows 110 km N through upper Maracaibo basin, to Lago Maracaibo, 16 km S of Rio Catatumbo mouth (17).
- Rio Escondido, Nicaragua, flows 100 km to Bluefields Bay on Caribbean Sea (5).
- Rio Fundación, Colombia, Magdalena, river draining W slopes of Sierra Nevada de Santa Marta, joining Cienega Grande 75 km S of Santa Marta, 10º 30' N - 74º 10' W (5, 19).
- Rio Gaira, Colombia, Magdalena, river draining W slopes of Sierra Nevada de Santa Marta, joining Caribbean Sea 10 km S of Santa Marta (5).
- Rio Grande, Bolivia, Santa Cruz, joins Rio Chapare to form Rio Mamoré, at 15º 48' S - 64º 18' W (28).
- Rio Grande do Sul, Brazil, name of a state.
- Rio Grande do Sul, Brazil, Rio Grande do Sul, city on outlet of Lagoa dos Patos, 32º 31' S - 52º 06' W (7).
- Rio Gualanday, Colombia, Tolima, small left affluent of upper Rio Magdalena, joining it 20 km from Girardot, 4º 20' N - 75º W (19).
- Rio Guamá, Brazil, discharges near Belém do Pará; Ourém is a city in banks of this river, approximately 100 km from Belém, 1º 30' S - 47º 35' W (16).
- Rio Guarapiche, Venezuela, Monagas, rises in coastal range SW of San Antonio, flows 160 km generally in a E semicircle, joins Rio San Juan near its mouth on Gulf of Paria (24).
- Rio Guárico, N and Central Venezuela, rises in coastal range N of Rio Orinoco and flows 300 km through llanos to Rio Apure (24, 33).
- Rio Guasare, Venezuela, Zulia, affluent on NE corner of Lago Maracaibo, approximately 11º N - 72º W (17).
- Rio Hacha, small river near Florencia (23).
- Rio Huacamayo, see Pucallpa (41).
- Rio Humboldt, Brazil, Santa Catarina, near Joinville (1)
- Rio Iguassú, Brazil, Paraná, Rigth tributary of Rio Paraná, at Argentina-Brazil-Paraguay border (1).
- Rio Ipare, Paraguay, Concepción, small left tributary of Rio Paraguay, joining this river near Concepción (16).
- Rio Irapiri, Brazil, affluent on left side of Rio Marauia (16).

- Rio Itapoca, Brazil, Santa Catarina, small river near Jaraguá do Sul, 30 km SW of Joinville (1).
- Rio Jaurús, Brazil, Mato Grosso, rises in Serra dos Parecis and flows 280 km to join upper Rio Paraguay at Cáceres, 16º 10' S - 57º 35' W (7).
- Rio Jejui-Guazú, Paraguay, left tributary of Rio Paraguay, near 24º 20' S - 57º 10' W (16).
- Rio Kenebiit-Tabiri, Brazil, Pará, affluent of Rio Cururú, right affluent of Rio Tapajós (23).
- Rio Madeira, Brazil, most important affluent of Rio Amazonas, formed by Rio Mamoré and Rio Beni at Villa Bella (Bolivia); flows N 100 km along Brazil-Bolivia border, then NE through Guaporé territory and Amazonas, past Porto Velho, Humaita and Borba to Rio Amazonas 140 km E of Manaus (14).
- Rio Madre de Dios, Perú and Bolivia, rises in Cuzco Department, S Perú, flows 1100 km to Beni, at Riberalta (15).
- Rio Magdalena, Colombia, rises in the Andes, near 2º N - 76º 30' W and flows N for 1600 km to Caribbean, near Barranquilla (19).
- Rio Mamoré, N Central Bolivia, formed by confluence of Rio Chapare and Rio Ichilo, flows 1920 km to Villa Bella, where it is joined by Rio Beni to form Rio Madeira (19).
- Rio Manduvira, Paraguay, Caaguazú, left tributary of Rio Paraguay, 50 km N of Asunción (37).
- Rio Marañón, one of Rio Amazonas main headstreams in Perú, rises in the Andes from a series of small lakes, flows NNE along high Andean ranges, turns NE to break through Pongo de Manseriche gorge into Rio Amazonas basin, flowing E past Nauta, joins Rio Ucayali to form Rio Amazonas 90 km SSW of Iquitos at 4º 30' S - 73º 27' W (14).
- Rio Marauia, Brazil, Amazonas, left affluent of middle Rio Negro, entering near Tapurucuara (23, 16).
- Rio Merguia, Colombia, river joining Rio Cobugón at 7º 05' N - 72º 05' W, in S extremity of Department Norte de Santander, in upper reaches of Rio Arauca (33).
- Rio Michol, México, Chiapas, small river S of Palenque (11).
- Rio Mulata, Pará, Brazil, small river in N bank of lower Rio Amazonas, near Monte Alegre, approximately 2º S - 54º W (16).
- Rio Nanay, Perú, Loreto, rises near 2º 45' S - 75º W, flows 320 km to Rio Amazonas at Iquitos (40).
- Rio Negro, Brazil, Venezuela, left tributary of Rio Amazonas, known as Guainia from its sources in Vaupés (Colombia) to junction with Casiquiare on Colombia-Venezuela border; enters Brazil at Cocuy and flows generally SE to join Rio Amazonas 20 km below Manaus; communicates with Rio Orinoco system via Brazo Casiquiare (7, 16, 21).
- Rio Negro, Brazil, Santa Catarina, rises in Sierra do Mar, near Curitiba and flows W to Rio Iguazú (1).
- Rio Negro, Uruguay, rises just over the border with Brazil (Rio Grande do Sul State), flows WSW through center of Uruguay to Rio Uruguay, forming main inland watershed (7).
- Rio Negro, Venezuela, Zulia, affluent on western shores of Lago Maracaibo, 10º 35' N - 72º 30' W (17).
- Rio Novo basin, Brazil, Santa Catarina, near Joinville (1, 4).
- Rio Olimar, Uruguay, Treinta y Tres, small river near town of Santa Clara del Olimar, drains to Rio Negro at 32º 05' S - 54º 58' W (8).
- Rio Onia, Mérida, Venezuela, affluent of Rio Escalante, 10º 30' N - 71º 50' W (17).
- Rio Orinoco, Venezuela, rises in Guiana Highlands on Brazil border at 2º 18' N - 63º 15' W, winds in large semicircle along Colombia border, then through center of Venezuela, running NNE to mouth of Rio Apure, and finally E to Atlantic in wide delta S of Trinidad (24).
- Rio Orteguaza, Colombia, Caquetá, see Venecia (23, 25).
- Rio Orton, see Ignavi (29).
- Rio Paraguay, rises in Brazil in central Mato Grosso, on SE slopes of Serra dos Parecis, and flows S past

Caceres (Sao Luiz de Caceres), Corumba and Coimbra; between Caceres and Paraguay border it crosses over marshy flood plain, locally called "Pantanal", inundated November-April; forms Brazil-Bolivia line for 40 km, then Brazil-Paraguay line; enters Paraguay at influx of Rio Apa, divides that country into Chaco and E Paraguay, flows past Concepción and Asunción, then forms Paraguay-Argentina border until its influx into Rio Paraná just above Corrientes (Argentina); collecting locality for (37) is at Puente Remanso, bridge on Trans-Chaco highway, approximately 20 km NE of Asunción (3, 14, 28, 37).

- Rio Parahiba do Sul, Brazil, Rio de Janeiro, chief stream of Rio de Janeiro State, rises at Serra da Bocaina (Sao Paulo), flows SW to Guararema (64 km from Sao Paulo), then turns sharply NE between Serra da Mantequeira (N) and Serra do Mar (S) to narrow rocky gorge below Tres Rios; lower valley begins below influx of Rio Pomba; enters Atlantic below Campos, 21º 40'S - 41º 30' W (1, 4).
- Rio Paraná, Brazil, Goias, rises near Formosa, flows 400 km NNW to Rio Tocantins below Paraná city (32).
-Rio Paraná Mini, Argentina, Santa Fe, river W of Rio Paraná, joining Rio Correntoso at 29º S - 59º 30' (7, 19, 16).
- Rio Parú, Brazil, Pará, rises on S slopes of Serra de Tumucumaque and flows SSE to Rio Trombetas and Rio Amazonas left bank at 1º 35' S - 56º 30' W (23).
- Rio Parú do Oeste, see Rio Parú (23).
- Rio Pardo, Brazil, Rio Grande do Sul, city, 100 km W of Porto Alegre (8).
- Rio Pastaza, see Rio Bobonaza (25).
- Rio Piedras, Perú, headstream of Rio Madre de Dios (20).
- Rio Pilcomayo, Paraguay, President Hayes, chief right affluent of Rio Paraguay, 1100 km long. Its lower course forms Argentina-Paraguay border (7, 37).
- Rio Pindo (Pindoyacu), Ecuador, Pastaza, headstream of Rio Tigre joining this at 2º 10' S - 76º 5' W (27).
- Rio Putumayo, called Icá in its lower course in Brazil; rises in Colombian Andes E of Pasto, flows SE along Ecuador-Colombia and Colombia-Perú borders into Brazil, to left bank of Rio Amazonas (14).
- Rio Salado, Paraguay, Central, left affluent of Rio Paraguay, 25 km NE of Asunción (37).
- Rio San Antonio, see Cañada Acatlán (13).
- Rio San Juan, NE Venezuela, rises in coastal range and flows 120 km SE to Gulf of Paria (24).
- Rio Santiago, Ecuador-Perú, formed by Rios Paute and Zamora near 3º S, flows 240 km to Rio Marañón (25).
- Rio Sardinata, Colombia, Norte de Santander, one of the headstreams of Rio Catatumbo, near Sardinata, 8º 05' N - 72º 45' W (17).
- Rio Sevilla, Colombia, Magdalena, river draining W slopes of Sierra Nevada de Santa Marta, joining Cienega Grande 45 km S of Santa Marta, 10º 50' N- 74º 10' W (5, 18).
- Rio Siamiria, Perú, Loreto, small right affluent of Rio Marañon, approximately 100 km before its union with Rio Ucayali, 5º S - 74º 30' W (16).
- Rio Siapa, Venezuela, Territorio Amazonas, right affluent of Rio Orinoco and Rio Negro through Brazo Casiquiare, near Venezuela-Brazil border (21).
- Rio Sinú, Colombia, Bolivar, rises at N foot of Cordillera Occidental and flows 400 km N to Gulf of Morrosquillo in Caribbean Sea (35).
- Rio Solimoes, Brazil, Amazonas, a sector of Rio Amazonas between Tabatinga and Manaus (16).
- Rio Taguay, Venezuela, Aragua, one of the upper affluents of Rio Guárico, 9º 45' N - 66º 35' W (24).
- Rio Tapajós, Brazil, Pará, right tributary of Rio Amazonas at 2º 30' S - 55º 35' W, just above Santarem (7, 21, 16).
- Rio Tauca, Venezuela, Bolivar, small right affluent of Rio Caura, 7º 33' N - 64º 58' W (23).

- Rio Tepalapan, México, Veracruz, small river near Santiago Tuxtla, 18º 28' N - 95º 22' W (11).
- Rio Tocuyo, NW Venezuela, rises in Andean locality of Humocaro Alto and flows for 3200 km to Caribbean (17).
- Rio Tombopata, Perú, Madre de Dios, right affluent of Rio Madre de Dios, joining it at Puerto Maldonado (37).
- Rio Tucuragua, Venezuela, Bolivar, right affluent of Rio Orinoco, between Rio Cuchivero and Rio Caura, 7º 50' N - 65º 20' W (23).
- Rio Ucayali, Perú, one of Rio Amazonas main headstreams, formed by union of Rio Tambo (Apurimac) and Rio Urubamba at 11º 17' S - 73º 47' W, flows 1600 km joining Rio Marañón to form Rio Amazonas 90 km SW of Iquitos at 4º 30' S - 73º 27' W (14, 22, 26, 37).
- Rio Urubamba, Perú, headstream of Rio Ucayali (20).
- Rio Xingú, N Central Brazil, large right tributary of Rio Amazonas, rises in Mato Grosso and flows N into Pará, entering Rio Amazonas at head of its delta (32).
- Rio Yacuma (written Yacoma by BOTT, 1969, p. 47), Bolivia, Beni, left affluent of Rio Mamoré, joining it at 13º 30' S - 65º 30' W (37).
- Rivière Camopi, French Guiana, river draining into left side of Oyapock River, 3º 30' N - 53º 25' W (16).
- Romallo, unidentified locality on Rio Paraná, perhaps Romang, Argentina, Santa Fe, 12 km inland from right bank of Rio Paraná, 40 km S of Reconquista, 29º 35' S - 59º 45' W (7).
- Sacutenga (probably Santa Rita do Jacutinga), Brazil, Minas Geraes, town on a left affluent of Rio Parahiba do Sul, 40 km NW of Valença, 22º 18' S - 44º 15' W; not to confused with nearby Jacutinga, on Rio Grande watershed, 22º 20'S - 46º 35' W (1).
- Salinas, Brazil, Goias, a locality W of Crixas, on Rio Crixas Açu, tributary of Rio Araguaia, 14º 20' S - 49º 45' W (14, 32).
- Salto del Guaira (Guaira Falls), Paraguay, Alto Paraná, cataract on Rio Paraná, at Brazil-Paraguay border (3).
- Salvador (formerly Bahia or Sao Salvador), Brazil, Bahia, city, 13º S - 38º 31' W (1).
- San Carlos de Rio Negro, Venezuela, Amazonas Federal Territory, town, 1º 55' N - 67º 02' W (21).
- San Cristobal, Venezuela, Tachira, city, 7º 46' N - 72º 14' W (17).
- San Fernando de Apure, Venezuela, Apure, city in Venezuelan llanos, 7º 53' N - 67º 28' W (33).
- San Ignacio, see Jaen (14).
- San Isidro, Paraguay, Central. Shipyard NW of Asunción (7).
- San Juan, Perú, Loreto, locality near town of Aguaitia, 9º 10' S - 76º 20' W (41).
- San Juan, Venezuela, Zulia, town, 15 km SE of Mene Grande (17).
- San Juan Bosque, México, Chiapas, undetermined locality (10).
- San Juan de Arama, Colombia, Meta, town, 500 m alt. 3º 25' N - 73º 55' W (23).
- San Pedro, Paraguay, name of a department.
- San Pedro, Venezuela, Zulia, town, 5 km SE of Mene Grande (17).
- San Pedro de Cataniapo, Venezuela, Amazonas Federal Territory, town on Rio Cataniapo (23).
- Santa Catarina, Brazil, name of a state.
- Santa Cruz (=Aracruz), Brazil, Espirito Santo, town 50 km NNE of Vitoria, 20º S - 40º 55' W (1, 4).
- Santa Cruz (do Sul), Brazil, Rio Grande do Sul, town 30 km N of Rio Pará (8).
- Santa Elena, Venezuela, Bolivar, town in Gran Sabana Plateau, 4º 40' N - 61º 05' W (33).
- Santa Fe, Argentina, name of a province.
- Santa Marta, Colombia, Magdalena, port on Caribbean Sea, 11º 15' N - 74º 13' W (5).
- Santa Rita, Uruguay, Paysandú, unidentified locality between Rio Daymon and Rio Negro (8).

- Santiago Tuxtla, México, Veracruz, town, 18º 28' N - 95º 20' N (12).
- Sao Francisco do Sul, Brazil, Santa Catarina, city and Atlantic port, 20 km ENE from Joinville (1).
- Sao Luiz de Caceres (since 1939 called Caceres), Brazil, Mato Grosso, port on upper reaches of Rio Paraguay, 16º 10' S - 57º 30' W (37).
- Sao Lourenço (do Sul), Brazil, Rio Grande do Sul, city on W shore of Lagoa dos Patos, 31º 28' S - 50º W (8).
- Sao Sebastian, Brazil, Sao Paulo, city 100 km ENE of Santos, 23º 40' S - 45º 20' W (1).
- Sectie 0, Suriname, locality 70 km S of Paramaribo, on railway, 5º 16' N - 55º 17' W (23).
- Serra da Bisca (Bicas?), Brazil, Minas Geraes, Bicas is a town near other localities reported by GÖLDI (1886), 30 km E of Juiz de Fora, 21º 40' S - 44º 55' W (1).
- Serra da Carioca, Brazil, Rio de Janeiro, a part of Serra do Mar, a great scarpment overlooking Guanabara Bay (1).
- Serra das Divisoes, S and Central Brazil, a part of South American water divide which separate Rio Amazonas basin from Paraguay-Paraná basin (32).
- Serra de Tumucumaque, Brazil, Pará and Amapa, montanous range of Brazilian Guiana, near Suriname and French Guiana borders, dividing Guianas Atlantic basins from Rio Amazonas basin (23).
- Sevilla del Oro, Ecuador, Azuay, locality 12 km E of Paute, on headstreams of Rio Santiago, 2º 48' S - 78º 32' W (25).
- Seyn, unidentified locality on Rio Paraná (43).
- Sistema de Janavaca, Brazil, Amazonas, S of Manaus, Rio Amazonas (16, 37).
- Sucre, Venezuela, name of a state.
- Suriname River, Suriname, rises in Guiana Highlands at about 3º 20' N - 56º 10' W, flows 480 km past Paramaribo to Atlantic (39).
- Tabasco, México, name of a state.
- Tabatinga (also Sapurara), Brazil, Amazonas, village on right bank of Rio Amazonas at Perú-Colombia border, 5 km SSE of Leticia, 4º 20' S - 69º 55' W (7, 22, 44).
- Tachira, Venezuela, name of a state.
- Tapijulapa, México, Tabasco, town, 17º 29' N - 92º 47' W (11).
- Teapa, México, Tabasco, city, 17º 35' N - 92º 57' W (11).
- Tefé, Brazil, Amazonas, city on Rio Tefé, just above its influx into Rio Amazonas (also name of a nearby lake) 3º 30' S - 64º 30' W (21).
- Teresópolis, Brazil, Rio de Janeiro, city near crest of Serra dos Orgaos, 880 m alt, 22º 30' S - 43º 35' W (1).
- Tijuca (Pico da Tijuca), Brazil, Rio de Janeiro, mountain 1000 m alt, 12 km WSW of center of Rio de Janeiro (1, 4).
- Tigre, Argentina, Buenos Aires, city at confluence of Rio Las Conchas and Rio Luján, affluents of Paraná delta, 30 km NW of Buenos Aires, 34º 26' S- 58º 35' W (8).
- Tila, México, Chiapas, small village in N foothills of Chiapas plateau, 17º 27' N - 92º 30' W (9).
- Tingo Maria, Perú, Huanuco, town at confluence of Rio Monzón and Rio Huallaga, headstream of Rio Aguaitia, 9º 05' S - 76º W (2).
- Tolima, Colombia, name of a department.
- Treinta y tres, Uruguay, name of a department.
- Tres Esquinas, Colombia, Caquetá, village on junction of Rio Orteguaza and Rio Caquetá, 0º 40' N - 75º 15' W (27).
- Trinidad, Bolivia, Beni, city near Rio Mamoré, 14º 47' S - 64º 38' W (19, 28, 37).
- Trujillo, Venezuela, name of a state.

- Tucuarembo, Uruguay, name of a department.
- Tupuranga, Brazil, Amazonas, small river joining Rio Negro, near Tupurucuara, 0º 25' S - 65º W (23).
- Tupurucuara, see Tupuranga (23).
- Valença (Marques de Valença), Brazil, Rio de Janeiro, city 80 km NW of Rio de Janeiro on Rio Parahiba do Sul, 22º 30' S - 43º 40' W (1).
- Valera, Venezuela, Trujillo, city, 9º 19' N - 70º 36' W (17).
- Valledupar, Colombia, Cesar, town on foothills of Sierra Nevada de Santa Marta, on affluent of Rio Cesar, 10º 25' N - 73º 20' W (5).
- Vanguardia, locality near Villavicencio (27).
- Varzea Grande, see Rio Cuiba (37).
- Vassouras, Brazil, Rio de Janeiro, city near Rio Parahiba do Sul, 22º 25' S - 43º 40' W (4).
- Venecia, Colombia, Caquetá, town on Rio Orteguaza, 20 km NE of Florencia, 0º 30' N - 75º 38' W (23, 14).
- Veracruz, México, name of a state.
- Vereda Vanguardia, see Villavicencio (27).
- Villa Bella, Brazil, Pará, a locality 600 miles up Rio Amazonas (16).
- Villarrica, Paraguay, Guaira, city, 25º 44' S - 56º 27' W (7).
- Villavicencio, Colombia, Meta, town on Rio Guiquitia, 4º 08' N - 73º 37' W (27).
- Vitoria, Brazil, Espirito Santo, city, 20º 18' S - 40º 20' W (16).
- Yaracuy, Venezuela, name of a state.
- Ygatimi, Paraguay, Caaguazú, town 24º N - 55º 30' W (16).
- Zanderdij, Surinam, city 40 km from Paramaribo, 5º 25' N - 55º 15' W (23).
- Zulia, Venezuela, name of a state.

INDEX

The names used in the systematic part for the species are printed in bold-face. Numbers in bold-face denote the pages where an illustration is given.

SUPPLEMENT TO THE FAMILY PSEUDOTHELPHUSIDAE
(G. RODRÍGUEZ, 1982)

Since the publication of the first part of this monograph on the freshwater crabs of America, concerning the family Pseudothelphusidae, in 1982, a number of additional species have been added to the family list and new information published regarding several others. It therefore seemed desirable to prepare a supplement to that work to cover the additional species, correct errors and omissions, record changes in nomenclature, and update the bibliography on different aspects of pseudothelphusid biology, including works omitted in 1982. This article is to be regarded as purely supplementary to my work of 1982 named above. Bibliographic references already given in that work are omitted from the literature below.

New taxa described after 1982

Since 1982, 37 new species have been described and 5 new genera have been erected. These new taxa are listed below, arranged in a systematic order. The list includes also *Ptychophallus costaricensis* Villalobos, 1974, omitted in the first part.

Tribe STRENGERIANINI Rodríguez, 1982

Chaceus Pretzmann, 1965

Chaceus caecus Rodríguez &Bosque. 1989. Venezuela.

Chaceus davidi Campos & Rodríguez, 1984. Colombia.

Chaceus cesarensis Rodríguez & Vilosia, 1992. Colombia

Strengeriana Pretzmann, 1971

Strengeriana antioquensis Prahl, 1987. Colombia.

Strengeriana bolivarensis Rodríguez & Campos, 1989. Colombia.

Strengeriana chaparralensis Campos & Rodríguez, 1984. Colombia.

Strengeriana huilensis Rodríguez & Campos, 1989. Colombia.

Strengeriana risaraldensis Rodríguez & Campos, 1989. Colombia.

Strengeriana taironae Rodríguez & Campos, 1989. Colombia.

Tribe HYPOLOBOCERINI Pretzmann, 1971

Hypolobocera Ortmann, 1897

Hypolobocera alata Campos, 1989. Colombia.

Hypolobocera cajambrensis Prahl, 1988. Colombia.

Hypolobocera dentata Prahl, 1987. Colombia.

Hypolobocera gorgonensis Prahl, 1983. Colombia.

Hypolobocera lloroensis Campos, 1989. Colombia.

Hypolobocera malagueña Prahl, 1988. Colombia.

Hypolobocera meineli Prahl, 1988. Colombia.

Hypolobocera merenbergersis Prahl & Giraldo, 1985. Colombia.

Hypolobocera mutisi Prahl, 1988. Colombia.

Moritschus Pretzmann, 1965

Moritschus narinnensis Campos & Rodríguez, 1988. Colombia.

Neostrengeria Pretzmann, 1965

Neostrengeria charalensis Campos & Rodríguez, 1985. Colombia.

Neostrengeria sketi Rodríguez, 1985. Colombia.

Tribe POTAMOCARCININI Ortmann, 1897

Odontothelphusa Rodríguez, 1982

Odontothelphusa monodontis Rodríguez & Hobbs, 1989. Mexico.

Odontothelphusa toninae Alvarez & Villalobos, 1991. Mexico.

Potamocarcinus H. Milne Edwards, 1853

Potamocarcinus colombiensis Prahl & Ramos, 1987. Colombia.

Potamocarcinus leptomelus Rodríguez & Hobbs, 1989. Colombia.

Ptychophallus Smalley, 1964

Ptychophallus costaricensis Villalobos, 1974. Costa Rica.

Stygothelphusa Alvarez & Villalobos, 1991

Stygothelphusa lopezformenti Alvarez & Villobos, 1991. Mexico (type species).

Typhlopseudothelphusa Rioja, 1952

Typhlopseudothelphusa acanthochela Hobbs, 1986. Belize.

Typhlopseudothelphusa hyba Rodríguez & Hobbs, 1989. Mexico.

Zilchia Pretzmann 1968

Zilchia falcata Rodríguez & Hobbs, 1989. Guatemala.

Tribe PSEUDOTHELPHUSINI Ortmann, 1897

Disparithelphusa Smalley & Adkinson, 1984

Disparithelphusa pecki Smalley & Adkinson, 1984. Mexico (type species).

Eidocamptophallus Rodríguez & Hobbs, 1989

Potamocarcinus (Potamocarcinus) chacei Pretzmann, 1967 (type species).

Pseudothelphusa de Saussure, 1857

Pseudothelphusa galloi Alvarez & Villalobos, 1990. Mexico.

Pseudothelphusa mexicana Alvarez-Noguera, 1987. Mexico.

Pseudothelphusa parabelliana Alvarez, 1989. Mexico.

Pseudothelphusa puntarenas Hobbs, 1991. Costa Rica.

Smalleyus *Alvarez, 1989*

Smalleyus tricristatus Alvarez, 1989. Mexico (type species).

Tribe KINGSLEYINI Bott, 1970

Brasiliothelphusa Magalhaes & Türkay, 1986.

Brasiliothelphusa tapajoense Magalhaes & Türkay, 1986. Brazil (type species).

Kingsleya Ortmann, 1897

Kingsleya besti Magalhaes, 1990. Brazil.

Kingsleya ytupora Magalhaes, 1986. Brazil.

Fredius Pretzmann, 1967

Fredius adpressus Rodríguez & Pereira, 1992. Venezuela.

Fredius adpressus piaroensis Rodríguez & Pereira, 1992. Venezuela.

Fredius platyacanthus Rodríguez & Pereira, 1992. Venezuela.

Fredius estevisi siapensis Rodríguez & Pereira, 1992. Venezuela.

Faunistic lists and taxonomic modifications

RODRÍGUEZ (1981) gave a general listing of the South American species and CAMPOS (1985) included several new records of Pseudothelphusidae in his list of freshwater decapods of Colombia.

PRETZMANN (1983a, 1983b, 1983c) amplified and illustrated the species he had already described from Ecuador and Perú (PRETZMANN 1977b, 1978a) (see Addendum to RODRÍGUEZ, 1982); PRETZMANN & MAYTA (1980) also insist on these species.

The species of *Hypolobocera* and *Potamocarcinus* of the Pacific drainage of Colombia, have been reviewed and adequately illustrated by VON PRAHL (1988). This author (VON PRAHL 1987d, 1988) also redescribed *Hypolobocera buenaventurensis*, previously included in my list of species *incertae sedis*.

Based on the possible homologies found in the gonopods of the species of Potamocarcinini,

RODRÍGUEZ & HOBBS (1989b) have reviewed the structure of this Tribe, giving new diagnosis of the genera, erecting the new genus *Eidocamptophallus* to receive *Potamocarcinus chacei* Pretzmann, 1967, and excluding *Pseudothelphusa pittieri* Rathbun, 1898, and *Potamocarcinus garthi* Pretzmann, 1971 from this Tribe.

SMALLEY & ADKINSON (1984) have reviewed the gonopod terminology and the use of female genital openings as a taxonomic character. Through the use of scanning electron microscope these authors have determined that the setae at the distal terminus of the sperm channel of the male gonopod of their new species *Disparithelphusa pecki* and other pseudothelphusids, are not pointed, but have a large terminal pore; they have called these peculiar setae "terminal pore setae".

SMALLEY & ADKINSON (1984) have also determined that terminal pore setae are present on the inner surface of the merus of the third maxilliped in the Tribes Pseudothelphusini, Potamocarcinini (sensu Pretzmann, 1972) and Kingsleyini, but neither in the Tribe Hypolobocerini (sensu Pretzmann, 1972), nor in the subfamily Epilobocerinae. In view of these results (as well as other criteria based on gonopod morphology), it would be advisable to keep PRETZMANN (1972) arrangement of genera for the Potamocarcinini and Hypolobocerini rather than which I proposed in 1982.

Biogeography and phylogenetics

Many of the taxonomic studies published since 1982 have materially added to a more detailed knowledge of the distribution of the family. An important contribution have been that of MAGALHAES (1986) who have shown an extensive distribution of the Pseudothelphusidae, represented by the species of *Fredius*, troughout the Amazon basin, particularly south of this river. The origin of the species of *Fredius* have been studied by RODRÍGUEZ & PEREIRA (1992) using area cladograms.

The increase in our knowledge of the taxonomy and distribution of the species has also affected our ideas on the biogeography and possible evolution of this family, and have considerably altered my tentative scheme of 1982 for the origin and radiation of the family. Concerning the origin of the Pseudothelphusidae, RODRÍGUEZ (1986) have shown that an analysis of the synapomorphies found in the respiratory structures of the Old- and New World freshwater crabs, suggests a monophyletic origin for the species with reduced exognaths in America, Africa and India. This distribution is evidence of a former Gondwanan distribution and shows at the same time that the transformation of buccal appendages had already began in Mid-cretaceous times in basic groups whose modern representatives are the American Pseudothelphusidae and the African Gecarcinucidae. The Trichodactylidae, in which this buccal reaccomodation does not appear, derive from a separate basic group and are related to the Eupotamonea of Western Africa.

Regarding the separation of the two subfamilies of Pseudothelphusidae, and through the analysis of chorological series and other criteria, RODRÍGUEZ (1986), to explain the disjunct distribution of both groups in the Antilles and South America, postulates the origin of the main phyletic trunks of Pseudothelphusinae of Middle and South America, from a common ancestor in northern South America, represented today by the Strengerianini. Concerning the phylogenetics of this last Tribe, RODRÍGUEZ & CAMPOS (1989) have postulated by means of a cladistic analysis, that this group was widespread in the area of north-western South America in Miocene times. Later the uplifting and displacement of the Santa Marta Massif led to disruption of the ancestral Strengerianini stock to form the actual pattern of distribution and diversification.

Cavernicolous species

The adaptation of some pseudothelphusid crabs to cave life is a well known fact ever since RIOJA (1955) described the strictly stygobiont

Potamocarcinus (Typhlopseudothelphusa) mocinoi from a cave in Mexico. However, the assignment of other species found in subterranean waters to the categories stygobionts, stygophiles and stygoxenes is not an easy task. HOBBS *et al.* (1977) list as troglobitic only RIOJA's species, but added 5 species from Mexico and Central America, and 3 species from the Greater Antilles as associated with caves. REDDELL (1981) cited as troglobious RIOJA's species and the two other *Typhlopseudothelphusa* described by DELAMARE-DEBOUTEVILLE (1976), and include six others that are probably troglophile from Mexico, Guatemala and Belize. HOLTHUIS' list (1986) included the 3 troglobious cited by REDDELL, and as stygophiles or stygoxenes 4 species from the Antilles, 5 from Mexico and Central America and 1 from Venezuela. All the species listed by these authors are also included my 1982 work. GUINOT (1988) have given a useful discussion of these species, and three other recorded by RODRÍGUEZ (1985).

The following troglobious species were described after 1982.

Chaceus caecus Rodríguez & Bosque, 1989. Cueva Punto Fijo, Rio Guasare, Zulia, Venezuela. Pereiopods very slender, corneae absent, carapace depigmented.

Neostrengeria sketi Rodríguez, 1985. Hoyo del Aire, La Paz, Santander, Colombia. Pereiopods very slender, corneae reduced, carapace partly depigmented.

Potamocarcinus leptomelus Rodríguez & Hobbs, 1989. Cueva del Tunel, Veracruz, Mexico. Eyes small, but distinctly faceted and pigmented, walking legs very long.

Zilchia falcata Rodríguez & Hobbs, 1989. Alta Verapaz, Guatemala. Slender pereiopods, but eyes normal.

Stygothelphusa lopezformenti Alvarez & Villalobos, 1991. Cueva de los brujos, Valle Nacional, Oaxaca, Mexico. Elongated pereiopods and carapace not pigmented, but eyes normal.

Typhlopseudothelphusa acanthochela Hobbs, 1986. Blind crab cave, Cayo District, Belize. Degenerate eyes, elongated pereiopods and carapace not pigmented.

Typhlopseudothelphusa hyba Rodríguez & Hobbs, 1989. Cueva de Los Llanos, Chiapas, Mexico. Degenerate eyes, elongated pereiopods and carapace not pigmented.

Odontothelphusa monodontis Rodríguez & Hobbs, 1989. Grutas del Cocona, Tabasco, Mexico. Dorsal surface of carapace pale and walking legs moderately slender; the eyes however, are well pigmented.

Pseudothelphusa mexicana Alvarez-Noguera, 1987. La Jolla Cave, Guerrero State, Mexico. The species exhibits no obvious adaptations to cave environment, but seems restricted to the deeper part of the cave, in complete darkness.

Pseudothelphusa puntarenas Villalobos, 1991. Emus Cave, Costa Rica. This crab lacks any obvious external troglomorphic modifications, but is not yet known from epigean waters.

Additionally, *Neostrengeria charalensis* Campos and Rodríguez 1985, and *Neostrengeria niceforoi* (Schmitt, 1969) were reported as troglophile from the Cueva de Los Indios and the nearby Cueva del Páramo, respectively, La Paz, Santander Department, Colombia (RODRÍGUEZ, 1985).

Corrections

Several errors have been detected after publication of the first part of this monograph. The following were kindly pointed out to me by Dr Alfred SMALLEY: (a) The species *Ptychophallus costaricensis* Villalobos (1974) was not included. (b) In Figure 26d the apical view of *Hypolobocera orientalis* is not referenced in the caption text. (c) The specific name of *Potamocarcinus aspoeckorum* should be spelled with a "c", as in PRETZMANN's original description, since it is derived from the name of Ulrike and Horst ASPOCK; the author subsequently omitted the "c" in other papers, but on pages 16-19 of his monograph (PRETZMANN, 1972) he spelled *Aspoeckia* correctly. (d) On page 44, in the key just before *Phrygiopilus*, "Costa Rica" should be "Guatemala". (e) In Figure 2, VII should be VIb.

Additionally, the caption text and illustrations under Figure 39 should be interchanged with the caption text and illustrations under figure 71.

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Cet ouvrage fait le point sur la seconde grande famille de crabes propres aux eaux douces tropicales d'Amérique, les Trichodactylidae. Ces crabes appartiennent essentiellement à la faune des grandes rivières et lacs de basse plaine dans les bassins continentaux à l'est des Andes. Par leur distribution et leur écologie, les Trichodactylidae s'opposent aux Pseudothelphusidae dont les espèces sont plus nombreuses mais sont cantonnées aux régions montagneuses, au nord de l'Amazone, avec une large extension à travers l'Amérique Centrale, jusqu'au nord du Mexique.

Une fois les caractères morphologiques de la famille bien définis, clefs et descriptions, complétées par une excellente illustration, permettent l'identification des 41 espèces considérées, réparties en 10 genres. Les variations, les affinités et la distribution sont précisées. Les résultats d'une analyse cladistique qui s'appuie sur des critères somatiques nombreux, à valeur diagnostique, ont conduit l'auteur à proposer une classification originale et simple où la nomenclature de la famille retrouve une forme strictement binominale. L'analyse met aussi en lumière les particularités et l'origine de la distribution actuelle des différents genres et espèces, dispersés sur un vaste territoire. Sa grande diversité morphologique et le caractère primitif de ses mécanismes respiratoires montrent que cette famille représente certainement un groupe de crabes très ancien.

Dr Gilberto RODRÍGUEZ is a member of the Instituto Venezolano de Investigationes Cientificas. He first worked on American freshwater crabs in the 1960s and is considered as a leading specialist on the subject today. He has both described new species and worked in simplifying classification within families and has also published interesting discussion of the phylogeny and biogeography of these crustaceans.

The work reviews knowledge of the Trichodactylidae, the second largest family of American tropical freshwater crabs. They belong mainly to the fauna of the large rivers and lakes in the lower plains east of the Andes. Their distribution and ecology is contrasted with the Pseudothelphusidae, of which there are more species but which are limited to the mountain regions north of the Amazon and widely distributed throughout Central America as far as northern Mexico.

Definition of the morphological characters of the family is followed by keys, descriptions and excellent illustrations to identify 41 species belonging to 10 genera. Details of variations, relationships and distribution are provided. The results of cladistic analysis based on numerous somatic criteria of diagnostic value lead to proposing a simple, original classification in which the nomenclature of the family is in strictly binominal form. The analysis also shows the features and origin of the present distribution of the various genera and species which are scattered throughout a vast area. The great morphological diversity and primitive respiratory mechanisms show that the family is certainly a very ancient crab group.

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Le Docteur Gilberto RODRÍGUEZ
est membre de l'Instituto Venezolano
de Investigationes Cientificas.
Ses premiers travaux
sur les crabes d'eau douce d'Amérique
datent des années soixante.
Actuellement considéré comme
l'un des meilleurs spécialiste de ce groupe,
il s'est attaché, tout en enrichissant
l'inventaire par la description
de nouvelles espèces, à simplifier
la classification à l'intérieur des familles.
On lui doit aussi d'intéressantes réflexions
sur la phylogénie et la biogéographie
de ces crustacés.

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