

(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 record 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.- RODRIGUEZ, 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.

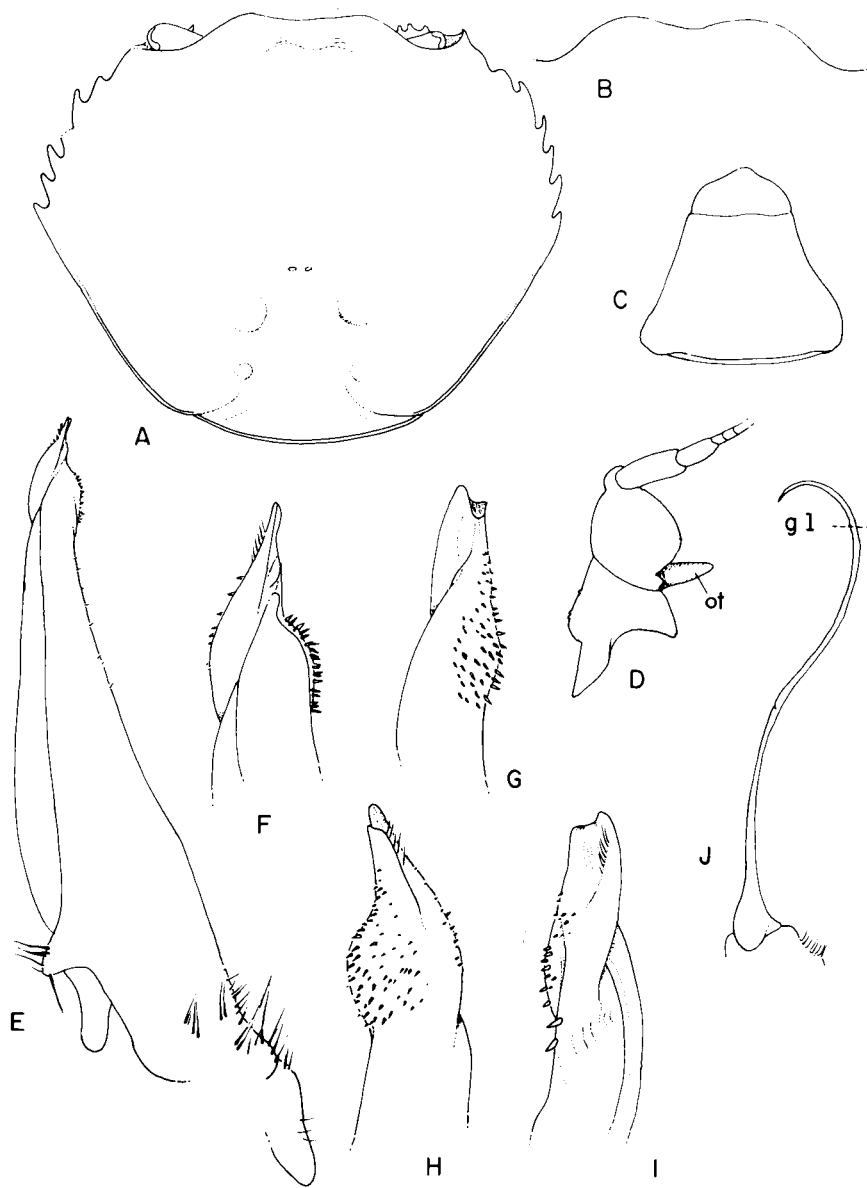


FIGURE 45

*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 than 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

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*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)

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*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

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

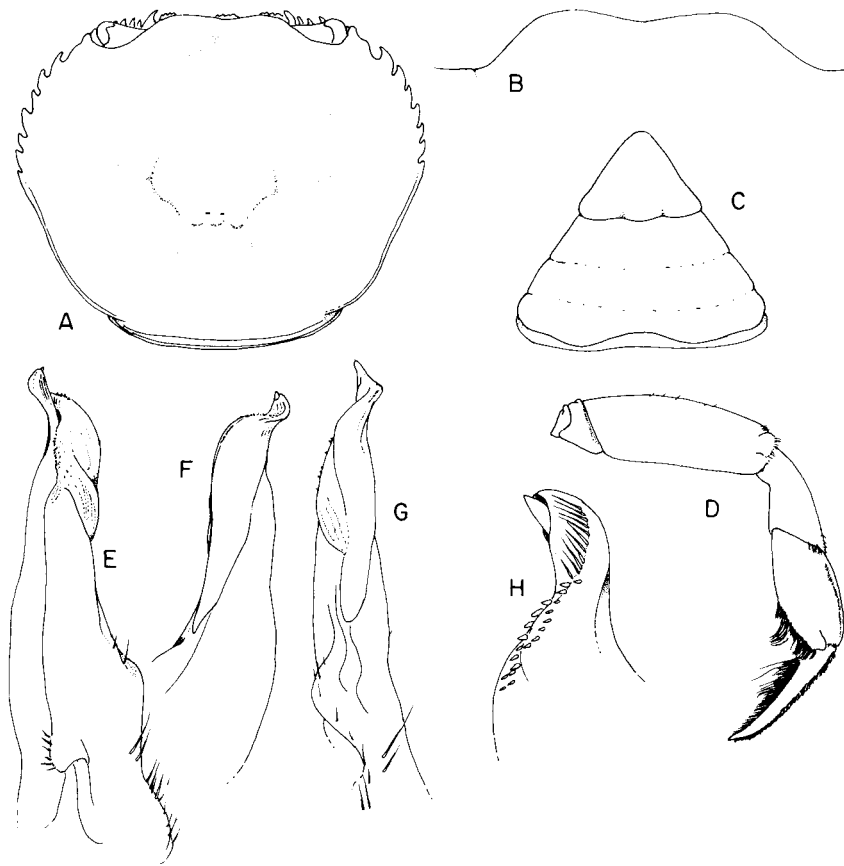
*Dilocarcinus* (*Fredilocarcinus*) *musmuschiae* Pretzmann & Mayta, 1980, p. 143, fig. 11, 12.

### 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 musmuschia* (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*

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##### 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 pereopods, 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

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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 pereopods and propodus of the fifth pereopods, 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 pereopods (m3), and the relationship length/width in the propodus of the fifth pair (p5).



TABLE III  
Morphometric relationships

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

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### Areal distribution of the species

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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: *Sylviocarcinus piriformis*; Guiana basin: *D. dentatus*, *D. spinifer*; Brazilian

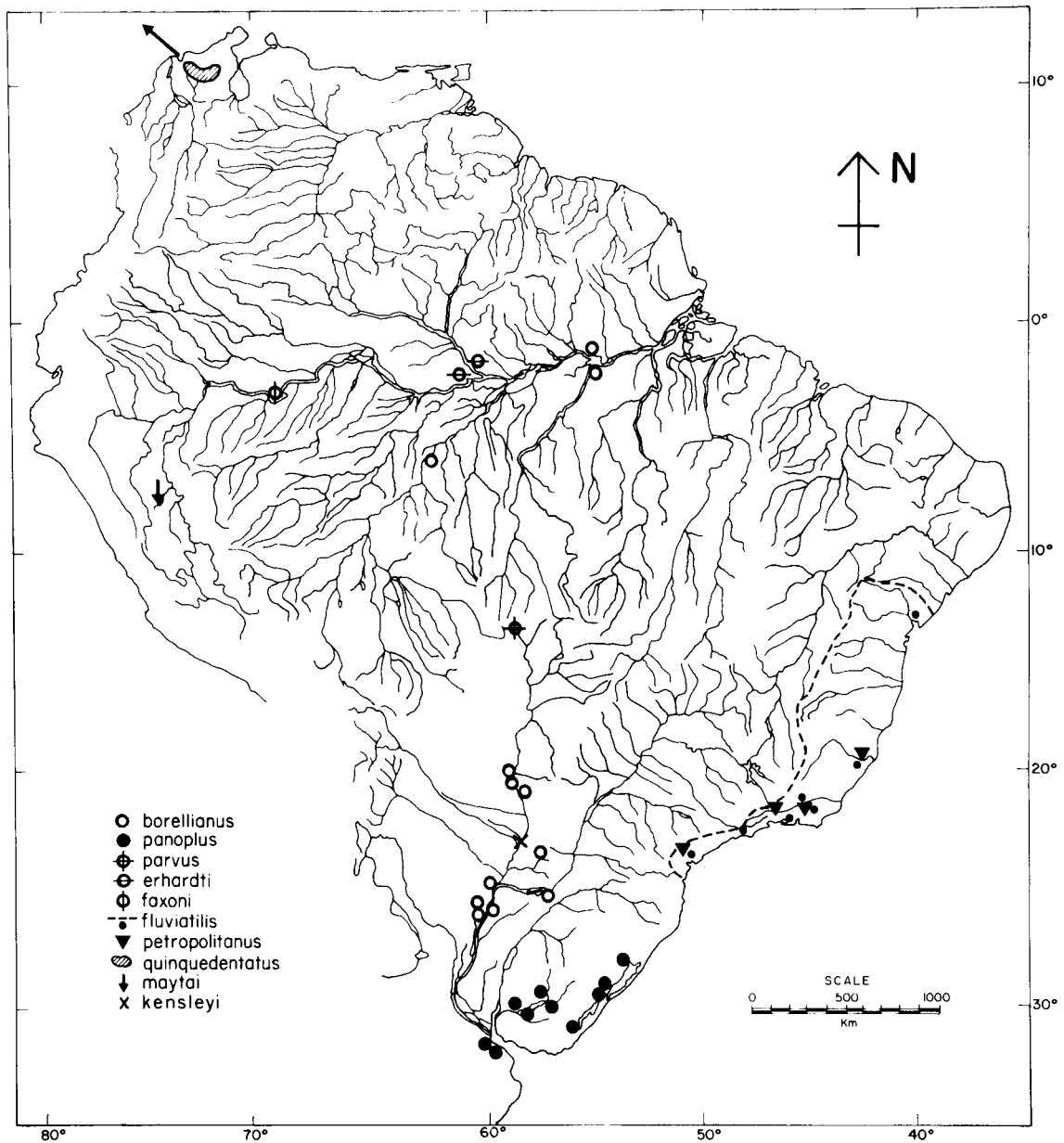


FIGURE 47

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

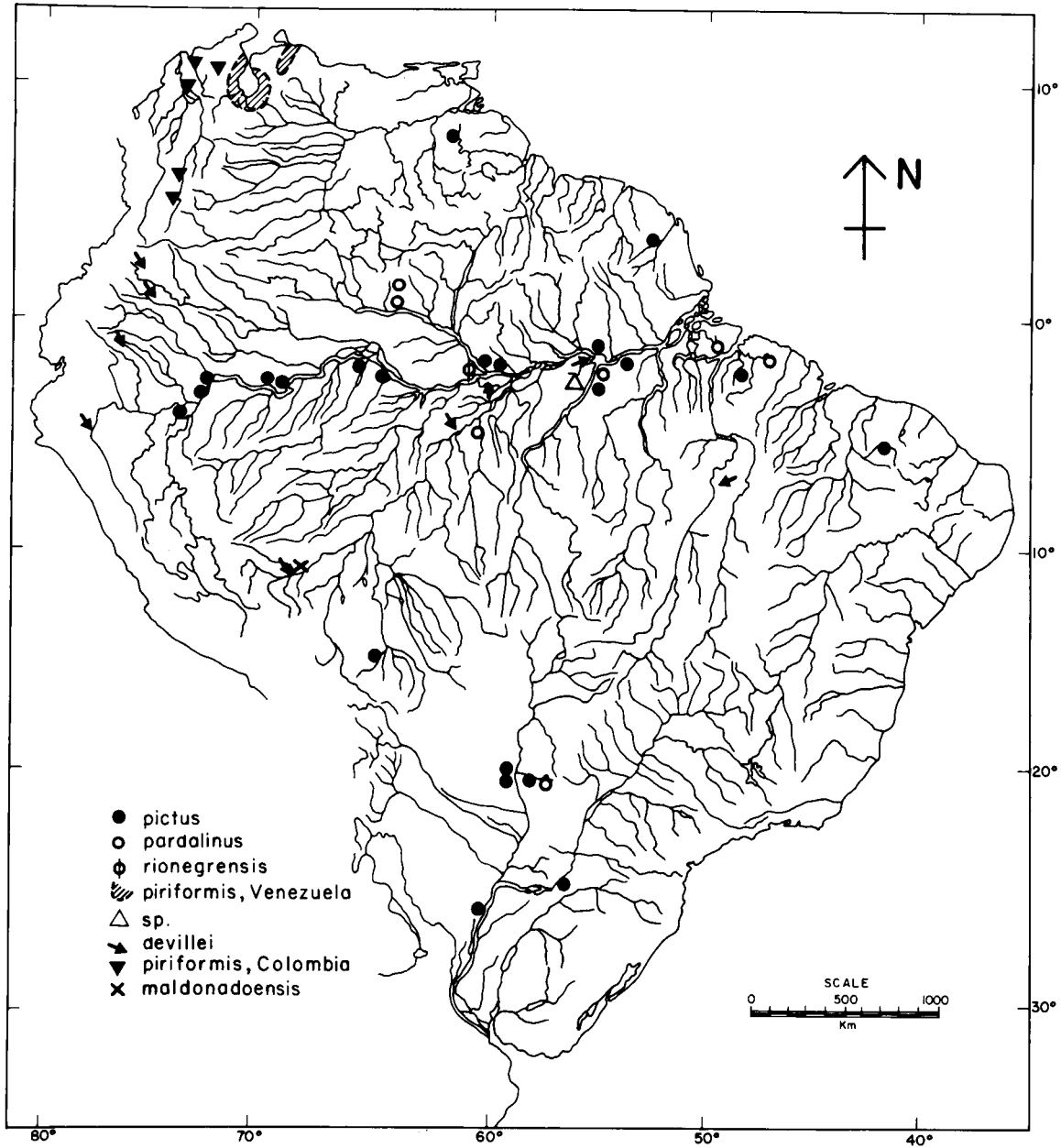


FIGURE 48

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

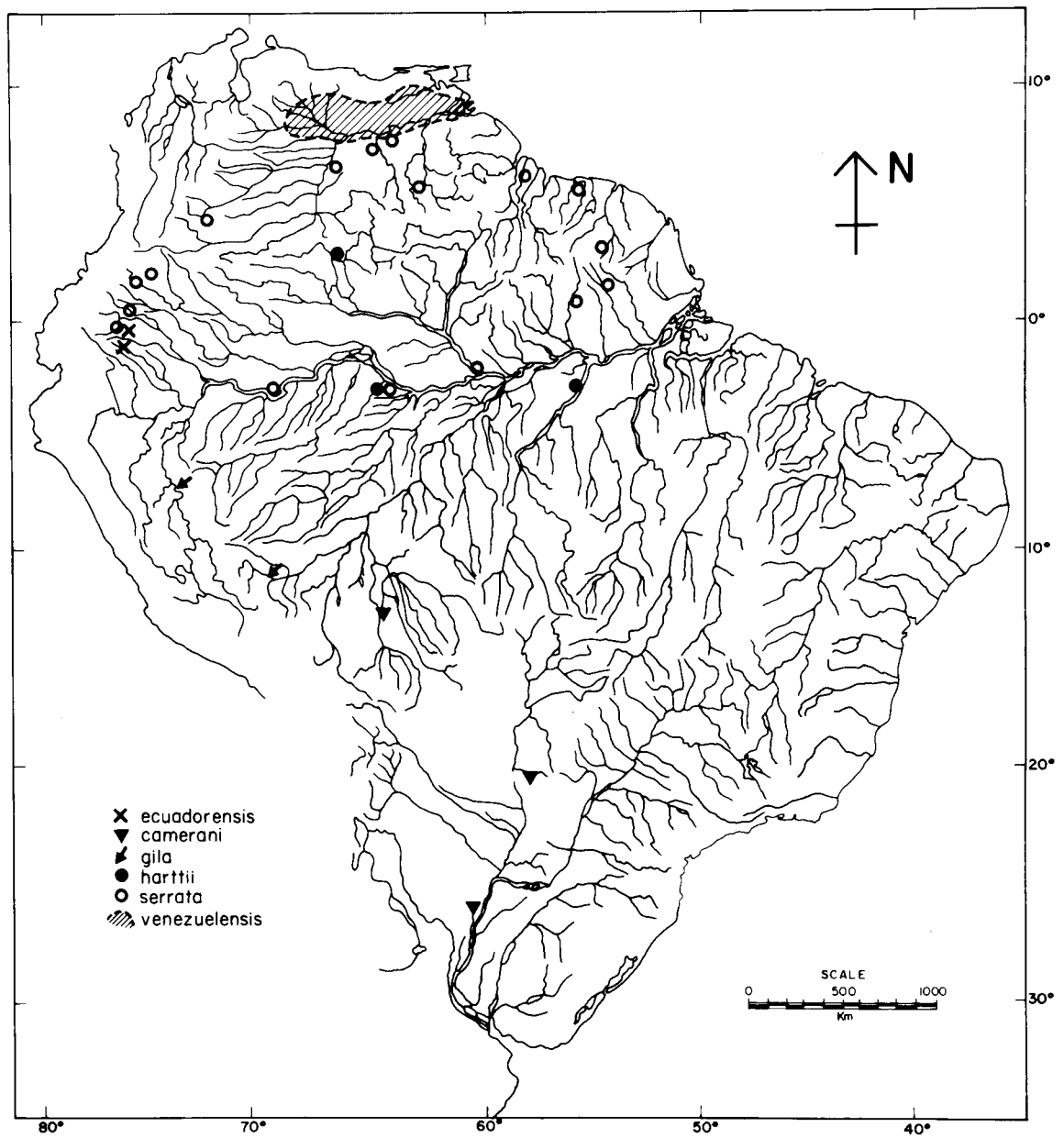


FIGURE 49  
Distribution of the species of Valdiviini in South America.

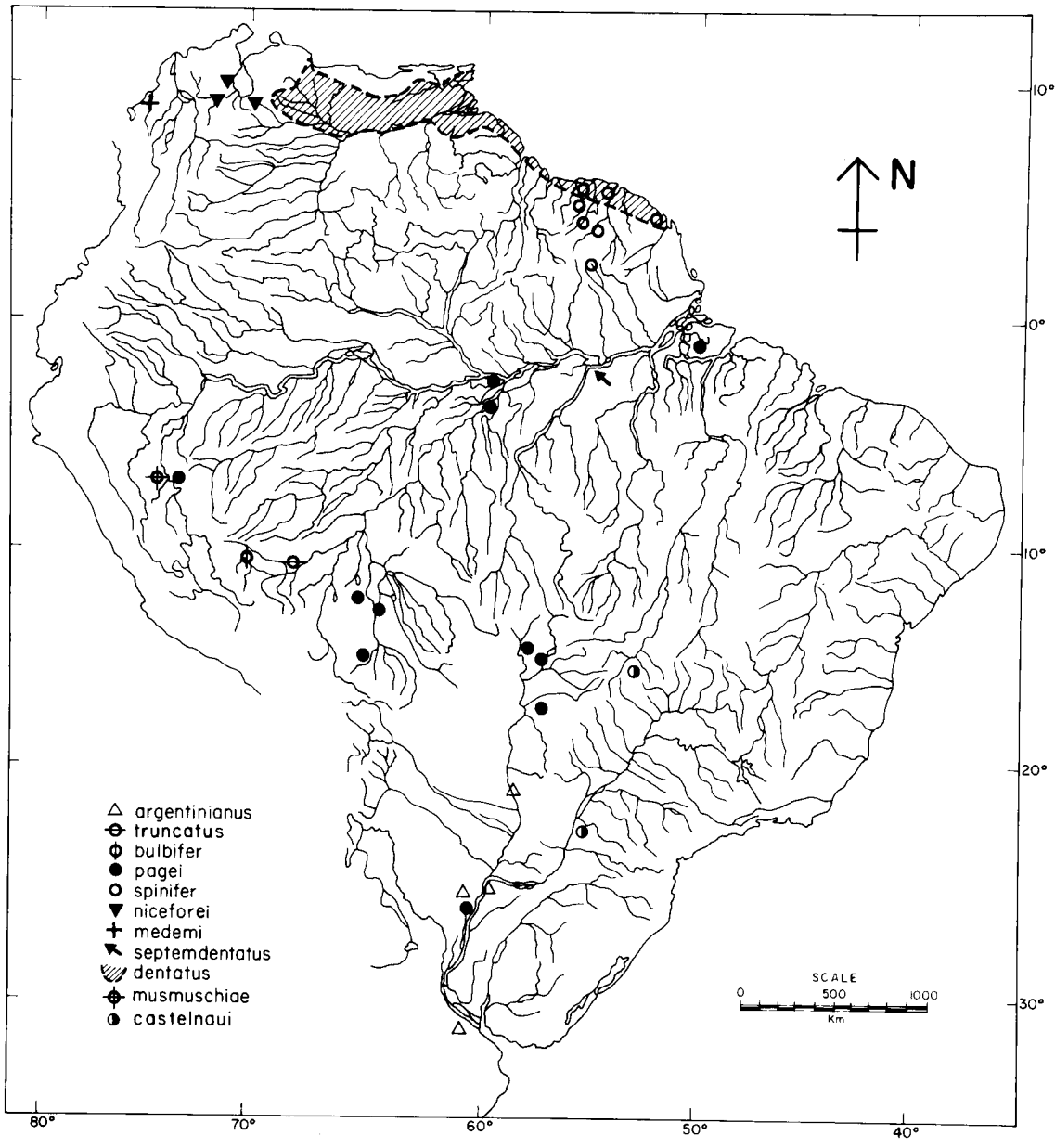


FIGURE 50  
Distribution of the species of *Dilocarcinus* and *Fredilocarcinus* in South America.

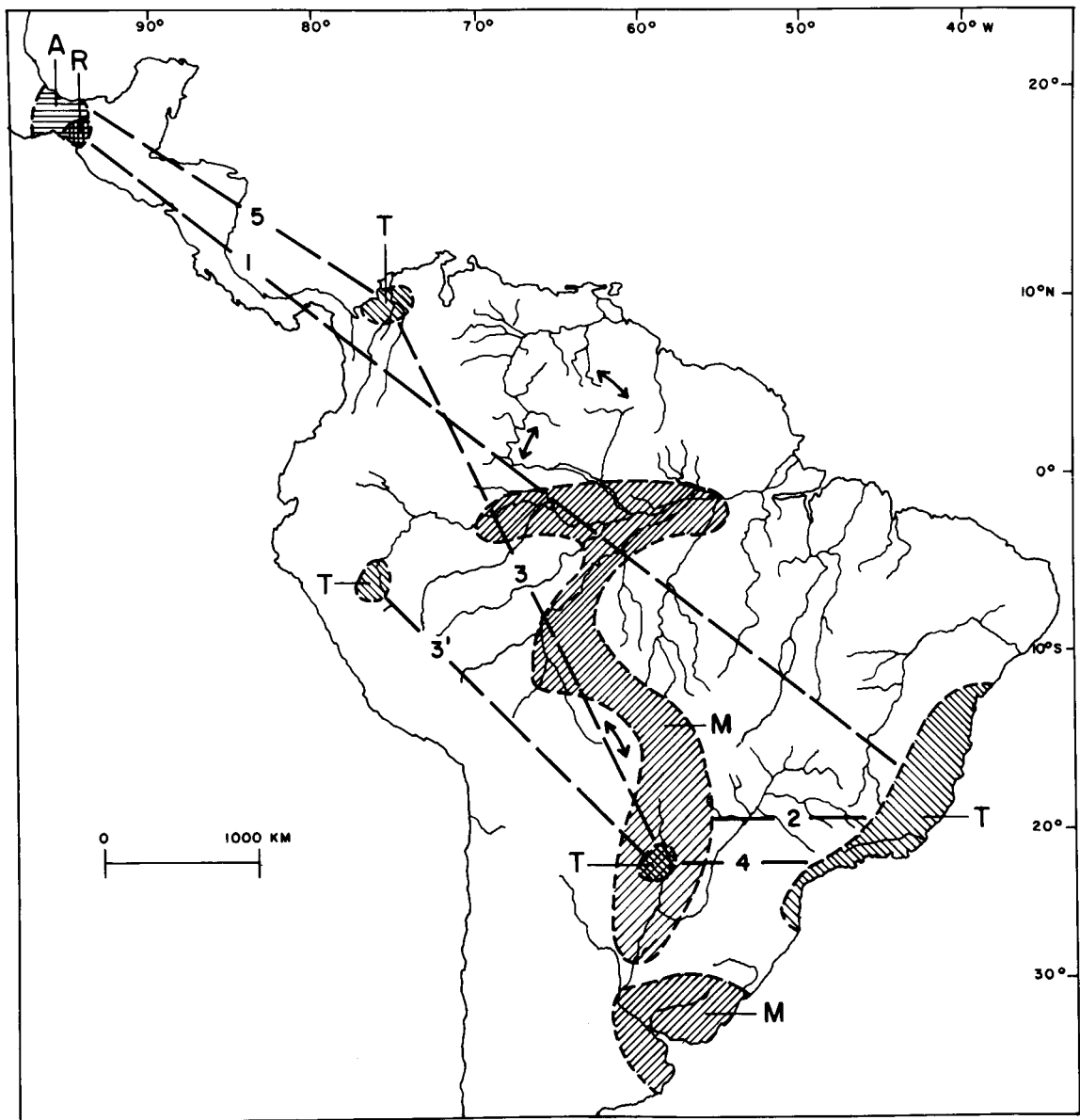


FIGURE 51  
 Areas of distribution of the Trichodactylinae. A, *Avotrichodactylus*; M, *Mikrotrichodactylus*; R, *Rodriguezia*; T, *Trichodactylus*; 1-5, disjunctions of sister groups; double-headed arrows indicate connections of the Amazon through the Casiquiare channel, Rupunini swamps, and upper Madeira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

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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 troglitic 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* (whose 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 contrast 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).

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(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  $13.0 \pm 0.88$  Ma by fission track (RODRÍGUEZ, *in press*).



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# APPENDIX

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

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

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

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

## II - A gazetteer of collection localities

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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 12° N - 71° W (31).
- Agua Negra, Venezuela, Yaracuy, small village in Rio Yaracuy basin, 10° 25' N - 68° 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, Tucuarembó, not identified (8).
- Aparición, Venezuela, Portuguesa, town on Rio Aro, 9° 30' N - 69° 20' W (33).
- Apartaderos, Venezuela, Cojedes, town, 9° 40' N - 68° 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 25° 18' S - 57° 22' W (37).
- Arroyo Caanabe, Paraguay, Paraguari, stream near town of Paraguari, 25° 45' S - 57° 11' W (7).
- Arroyo del Pital, México, Veracruz, creek near Ciudad Alemán, 18° 10' N - 96° 08' W (11).
- Arroyo del Solfo, México, Tabasco, same as, or an extension of, Cueva del Azufre (10).
- Arroyo Gaguarebau, Paraguay, San Pedro, stream near town of Caacupe, 25° 22' S - 57° 15' W (7).
- Arroyo Pindo, Paraguay, stream on San Pedro-Caaguazú Departments border, 24° 52' N - 56° 19' W (7).
- Arroyo Postillón, see Puerto Max (7).
- Arroyo Salsipuedes Grande, Uruguay, Rio Negro, stream joining left side of Rio Uruguay, approximately 32° 30' S - 58° 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, 25° 16' S - 56° 24' W (7, 37).
- Arroyo Yaguarón, Uruguay, Tucuarembó, small river joining Rio Negro through mouth of Rio Tucuarembó at 32° 25' 30' S - 55° 50' W (8).
- Asunción, Paraguay, Central, capital city on Rio Paraguay, 25° 16' S - 57° 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, 10° 58' N - 74° 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, 22° 10' S - 36° 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, 12° 01' N - 83° 46' W (5).
- Bobures, Venezuela, Zulia, town on SE shore of Lago Maracaibo, 9° 13' N - 71° 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, 5° 01' N - 56° 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 Gaguairesau (7).
- Caaguazú, Paraguay, name of a department
- Caaguazú, see Arroyo Tobatiri (7)
- Cacau 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 7° 40' N - 66° 10' W (24).
- Caicara, Venezuela, Monagas, town on Rio Guarapiche, 9° 45' N - 63° 40' W (24, 33).
- Cajamarca, Peru, name of a department.
- Calabozo, Venezuela, Guárico, a city on Rio Guárico, 8° 56' N - 67° 26' (33).
- Candelaria, Argentina, Misiones, small town on left bank of Rio Paraná, 27° 30' S - 57° 50' W (16).
- Canendiyu, Paraguay, Caaguazú, town on Rio Jejui-Guazú 24° 14' S - 55° 37' W (3, 16).
- Cañada Acatlán, México, Oaxaca, creek of Rio San Antonio 18° 30' N - 96° 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 3° 05' N - 65° 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, 6° 45' N - 61° 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, 5° 40' N - 67° 38' W (23).
- Cartagena, Colombia, Bolivar, port on Caribbean Sea, connected by natural waterway to Rio Magdalena, 10° 25' N - 75° 31' W (5, 33).
- Cayenne, French Guiana, capital city, 4° 56' N - 52° 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, 2° 48' S - 76° 32' W (25).
- Chimpire, Venezuela, Trujillo, locality on road between Valera and Pampanito (17).
- Ciudad Alemán, México, Veracruz, town, 18° 12' N - 95° 15' W (12).
- Ciudad Bolivar, Venezuela, Bolivar, city on S bank of Rio Orinoco, 8° 09' N - 63° 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, 23° 24' S - 57° 28' W (7).
- Coppename River, Suriname, rises in Wilhelmina mountains at about 3° 45' N and flows 400 km to Atlantic just SW of the Saramacca River mouth at 5° 50' N - 56° 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, 25° 25' S - 56° 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, 7° 53' N - 72° 30' W (17, 36).
- Cueva del Azufre, México, Tabasco, cave about 100 m alt, 3 km of Tapijulapa, about 21 km SE of Teapa, 17° 25' N - 92° 45' W (10).
- Cueva de la Cascada Azufre, see Cueva del Azufre (10).
- Curarigua, Venezuela, Lara, town, 9° 58' N - 69° 35' W (17).
- Curuguaty, Paraguay, Caaguazú, town 24° 22' N - 55° 56' W (16, 37).
- Demerara River, Guyana, rises at 4° 42' N - 58° 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, 7° 20' N - 61° 50' W (33).
- El Dorado, Venezuela, Bolivar, town on headwaters of Rio Cuyuni 6° 33' N - 61° 38' W (33).
- El Jobal, see Los Pijiguaos (23).
- El Manteco, Venezuela, Bolivar, town, 7° 20' N - 62° 30' W (33).
- El Vigia, Venezuela, Mérida, city, 8° 38' N - 71° 39' W (17).
- Ensenada, Argentina, Buenos Aires, suburban port of La Plata (10 km N), on Rio La Plata, 34° 55' S - 57° 58' W (8).
- Espino, Venezuela, Guárico, village in llanos 125 km N of Rio Orinoco, 8° 30' N - 66° 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 Orteguzaza, upper Rio Caquetá, 450 m alt, 1° 36' N - 73° 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 3° S - 66° W (16).
- Fortin Ingavi, Paraguay, Boquerón, town, 19° 55' S - 61° 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, 29° 10' S - 59° 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, 30° 01' S - 51° 11' W (8).
- Guaira, Paraguay, name of a department.
- Guaraunos, Venezuela, Sucre, village, 10° 33' N - 63° 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 7° S - 62° 30' W (7, 37).
- Ignavi (Ingavi), Bolivia, Pando, town on Rio Orton, 19° 55' S - 61° 45' W (29).
- Ilha do Puzios, Brazil, Sao Paulo, Buzios Island in Atlantic, 23° 40' S - 45° 05' W (1).

- Iquitos, Perú, Loreto, port on left bank of upper Rio Amazonas, at Rio Nanay mouth, 3° 45' S - 72° 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, 5° 21' S - 78° 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 3° S - 48° 30' (16).
- Joinville, Brazil, Santa Catarina, city, 26° 10' S - 48° 55' W (1, 4).
- La Esmeralda, Venezuela, Amazonas Federal Territory, airstrip and village at base of Mount Duida, 3° 08' N - 65° 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, 18° 25' N - 95° 05' W (11).
- Lago de Guri (Represa Raul Leoni), Venezuela, Bolivar, hydroelectric dam on Rio Caroní, 7° 30' N - 62° 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.) 1° 55' N - 55° 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 km<sup>2</sup>, in free communication with the sea in the N (36).
- Lago Ypacarai, see Aregua (37).
- Laguna de Tacarigua, Venezuela, Falcón, small lagoon near coast, 11° N - 68° 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, 28° 50' S - 58° 32' W (7, 29).
- Las Mercedes, Venezuela, Guárico, town, 9° 08' N - 66° 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, 5° 35' N - 67° 25' W (27).
- La Urbana, Venezuela, Bolivar, town on left bank of Rio Orinoco, 7° 08' N - 66° 55' W (24).



- Leticia, Colombia, Amazonas, town on upper Rio Amazonas, at Perú and Brazil borders, 4° 10' S - 69° 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 3° 10' N - 54° 10' W (23).
- Loreto, Colombia, Amazonas, town on left bank of upper Rio Amazonas, 80 km NW from Leticia, 40° 30' S - 70° 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, 6° 35' N - 66° 15' W (24, 34).
- Luque, Paraguay, Central, city 12 km E of Asunción, 25° 15' S - 57° 40' W (37).
- Macacos, see Rio dos Macacos (4).
- Machiques, Venezuela, Zulia, town near upper reaches of Rio Apon, 10° 05' N - 72° 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, 3° 05' S - 60° W (16).
- Manú, Perú, a province of Madre de Dios department.
- Maracaibo, Venezuela, Zulia, city on Lago Maracaibo, 10° 40' N - 71° 36' W (17).
- Maracay, Venezuela, Aragua, city, 10° 15' N - 67° 36' W (33).
- Marajó, Brazil, Pará, large island near mouth of Rio Amazonas, 2° S - 49° 30' W (38).
- Mariquita, Colombia, Tolima, city on Magdalena Valley, 5° 12' N - 74° 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, 2° 43' N - 78° 15' W (25).
- Mene Grande, Venezuela, Zulia, city on E coast of Lago Maracaibo, 9° 40' N - 69° 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, 10° 25' N - 61° W (33).
- Monagas, Venezuela, name of a state.
- Montería, Colombia, Córdoba, inland port on Rio Sinú, 8° 40' N - 75° 50' W (35).
- Monte Sumaco, Ecuador, Napo, mountain 3900 m alt, approximately 0° 35' S - 77° 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, 10° 20' N - 68° 05' W (33).
- Napo, Ecuador, name of a province.

- Nauta, Perú, Loreto, town on Rio Marañón near its confluence with Rio Ucayali, 4° 37' S - 73° 34' W (16).
- Nhecolândia, Mato Grosso, Brazil, town in Pantanal do Rio Negro, 19° S - 57° W (37).
- Norte de Santander, Colombia, name of a department.
- Nova Friburgo, Brazil, Rio de Janeiro, city in Serra dos Orgaos, 840 m alt, 22° 25' S - 42° 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, 16° 30' N - 1° 58' W (11).
- Pampanito, Venezuela, Trujillo, town, 9° 24' N - 70° 29' W (17).
- Pamplona, Colombia, Norte de Santander, town on W bank of Rio Pamplonita, 7° 25' N - 72° 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, 1° 27' S - 48° 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, 5° 50' N - 55° 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, 7° 20' N - 62° 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, 2° 45' N - 78° 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, 0° 30' S - 77° 18' W (27).
- Paysandu, Uruguay, name of a department.
- Peixe Boi, Brazil, Pará, locality near Pará, S coast of Isla Marajó, 2° S - 49° 30' W (16).
- Pernambuco, Brazil, name of a state.
- Petrópolis, Brazil, Rio de Janeiro, city on N slope of Serra da Estrela, 22° 30' N - 42° 50' W (4).
- Piauí, 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. STOLI, in lit.), 2° 35' S - 55° 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, 3° 05' S - 60° S (16).
- Porto Alegre, Brazil, Rio Grande do Sul, on N end of Lagoa dos Patos, 30° 01' S - 51° 11' (8).
- Porto Espiridiao, Brazil, Mato Grosso, port on Rio Jaurús, 16° S - 58° 50' W (7).

- Portuguesa, Venezuela, name of a state.
- Posadas, Argentina, Misiones, city on upper Rio Paraná, 27° 27' S - 55° 54' W (7).
- Poty, Brazil, Piahy, possibly Rio Poti, S of Teresina and affluent of Rio Itapecuru; this last river drains into Atlantic independently of Rio Amazonas, 4° 30' S - 42° 25' W (16).
- President Hayes, Paraguay, name of a department.
- Pucallpa, Perú, Loreto, town on Rio Ucayali, 8° 25' S - 74° 35' W (20, 37, 40).
- Puente Remanso, Paraguay, President Hayes, locality on Rio Confuso, on E shore of Rio Paraguay, 25° 40' S - 57° 36' W (7, 37).
- Puerto Asis, Colombia, Putumayo, on upper Rio Putumayo, near boundary with Ecuador, 0° 30' N - 75° 20' W (23, 14).
- Puerto Ayacucho, Venezuela, Amazonas Federal Territory, city on left bank of Rio Orinoco, 5° 35' N - 67° 41' W (23, 27).
- Puerto Casado, Paraguay, Boquerón, port on Rio Paraguay 20 km S of mouth of Rio Apa, 22° 35' S - 57° 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, 1° 00' N - 76° 35' W (23).
- Puerto Maldonado, Perú, Madre de Dios, small town on S bank of Rio Madre de Dios, 12° 30' S - 73° 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, 21° 12' S - 57° 50' W (7, 15, 28).
- Puerto Ordaz, Venezuela, Bolivar, city, 8° 28' N - 62° 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, 8° 20' N - 72° 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, 22° S - 53° W (7, 15).
- Puerto Tiberica (Pôrto Tibiriça), Brazil, Sao Paulo, boat landing on Rio Paraná 5 km NE of Presidente Epitacio, 21° 42' S - 52° 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, 0° 55' N - 47° 30' W (22, 38).
- Quebrada Barbacoas, Venezuela, Aragua, creek near town of same name, 9° 25' N - 67° 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, 29° 10' S - 59° 40' W (7, 16, 19, 37).
- Represa El Isiro, Venezuela, Falcón, dam providing water for nearby city of Coro, 11° 20' N - 69° 40' W (17).
- Republiek, Suriname, city 30 km S of Paramaribo, 5° 35' N - 55° 15' W (23).
- Resistencia, Argentina, Chaco, city on Rio Paraná, 27° 28' S - 58° 58' W (7, 28).

- Riberalta, Bolivia, Beni, city at confluence of Rio Beni and Rio Madre de Dios, 11° 30' S - 66° 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, 22° 30' S - 58° 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 Ciénega Grande 62 km S of Santa Marta, 10° 35' N - 74° 10' W (5, 18).
- Rio Araguaia, Brazil, rises on interior plateau near 18° S - 53° W, flows NNW for 2400 km to Rio Tocantins (14, 32).
- Rio Arara, Colombia, Amazonas, small river near Leticia, joins Rio Amazonas at approximately 4° S - 70° W (22, 15).
- Rio Aripuana, Brazil, affluent on right bank of lower Rio Madeira, 5° 35' S - 60° 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, 10° 20' N - 71° 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, right affluent of Rio Orinoco, S of Puerto Ayacucho, joining it at 10° 20' N - 67° 10' W (27).
- Rio Caura, Venezuela, Bolivar, rises in Guiana Highlands near Brazil border and flows 740 km NNW to Rio Orinoco at 7° 38' N - 64° 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 9° N - 75° 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, 16° 30' S - 65° 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, Presidente 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) right affluent of upper Rio Araguaia, at 12° 50' N - 50° 30' W (14, 32).

- Rio Cuao, Venezuela, Amazonas Federal Territory, right affluent of Rio Orinoco, joining it at 5° N - 67° 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 18° 35' S - 57° 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, 3° 30' S - 55° 30' W (16).
- Rio Cura, Venezuela, Aragua, one of upper affluents of Rio Guárico, 10° 05' N - 67° 30' W (24).
- Rio Curarigua, Venezuela, Lara, left affluent of upper Rio Tocuyo, 10° 30' N - 70° 50' W (17).
- Rio Cururú, see Rio Kenebiit-Tabiri (23).
- Rio Cuyuni, Guyana and Venezuela, rises in Venezuela in Guianas Highland near 6° N - 61° 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, 22° 55' S - 43° 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, 27° S - 56° 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, 22° 45' S - 43° 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 Ciénega Grande 75 km S of Santa Marta, 10° 30' N - 74° 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 15° 48' S - 64° 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, 32° 31' S - 52° 06' W (7).
- Rio Gualanday, Colombia, Tolima, small left affluent of upper Rio Magdalena, joining it 20 km from Girardot, 4° 20' N - 75° W (19).
- Rio Guamá, Brazil, discharges near Belém do Pará; Ourém is a city in banks of this river, approximately 100 km from Belém, 1° 30' S - 47° 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 11° N - 72° 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, Righth tributary of Rio Paraná, at Argentina-Brazil-Paraguay border (1).
- Rio Ipore, Paraguay, Concepción, small left tributary of Rio Paraguay, joining this river near Concepción (16).
- Rio Iraperi, 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, 16° 10' S - 57° 35' W (7).
- Rio Jejui-Guazú, Paraguay, left tributary of Rio Paraguay, near 24° 20' S - 57° 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 2° N - 76° 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 4° 30' S - 73° 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 7° 05' N - 72° 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 2° S - 54° W (16).
- Rio Nanay, Perú, Loreto, rises near 2° 45' S - 75° 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, 10° 35' N - 72° 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 32° 05' S - 54° 58' W (8).
- Rio Onia, Mérida, Venezuela, affluent of Rio Escalante, 10° 30' N - 71° 50' W (17).
- Rio Orinoco, Venezuela, rises in Guiana Highlands on Brazil border at 2° 18' N - 63° 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 Ortegua, 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 Mantiqueira (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, 21° 40' S - 41° 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 29° S - 59° 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 1° 35' S - 56° 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 2° 10' S - 76° 5' W (27).

- Rio Putumayo, called Ica 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 3° S, flows 240 km to Rio Marañón (25).

- Rio Sardinata, Colombia, Norte de Santander, one of the headstreams of Rio Catatumbo, near Sardinata, 8° 05' N - 72° 45' W (17).

- Rio Sevilla, Colombia, Magdalena, river draining W slopes of Sierra Nevada de Santa Marta, joining Ciénega Grande 45 km S of Santa Marta, 10° 50' N - 74° 10' W (5, 18).

- Rio Siamiria, Perú, Loreto, small right affluent of Rio Marañón, approximately 100 km before its union with Rio Ucayali, 5° S - 74° 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, 9° 45' N - 66° 35' W (24).

- Rio Tapajós, Brazil, Pará, right tributary of Rio Amazonas at 2° 30' S - 55° 35' W, just above Santarem (7, 21, 16).

- Rio Tauca, Venezuela, Bolivar, small right affluent of Rio Caura, 7° 33' N - 64° 58' W (23).

- Rio Tepalapan, México, Veracruz, small river near Santiago Tuxtla, 18° 28' N - 95° 22' W (11).
- Rio Tocuyo, NW Venezuela, rises in Andean locality of Humocaró 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, Bolívar, right affluent of Rio Orinoco, between Rio Cuchivero and Rio Caura, 7° 50' N - 65° 20' W (23).
- Rio Ucayali, Perú, one of Rio Amazonas main headstreams, formed by union of Rio Tambo (Apurímac) and Rio Urubamba at 11° 17' S - 73° 47' W, flows 1600 km joining Rio Marañón to form Rio Amazonas 90 km SW of Iquitos at 4° 30' S - 73° 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 13° 30' S - 65° 30' W (37).
- Rivière Camopi, French Guiana, river draining into left side of Oyapock River, 3° 30' N - 53° 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, 29° 35' S - 59° 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, 22° 18' S - 44° 15' W; not to be confused with nearby Jacutinga, on Rio Grande watershed, 22° 20' S - 46° 35' W (1).
- Salinas, Brazil, Goiás, a locality W of Crixas, on Rio Crixas Açu, tributary of Rio Araguaia, 14° 20' S - 49° 45' W (14, 32).
- Salto del Guairá (Guairá Falls), Paraguay, Alto Paraná, cataract on Rio Paraná, at Brazil-Paraguay border (3).
- Salvador (formerly Bahia or São Salvador), Brazil, Bahia, city, 13° S - 38° 31' W (1).
- San Carlos de Rio Negro, Venezuela, Amazonas Federal Territory, town, 1° 55' N - 67° 02' W (21).
- San Cristóbal, Venezuela, Táchira, city, 7° 46' N - 72° 14' W (17).
- San Fernando de Apure, Venezuela, Apure, city in Venezuelan llanos, 7° 53' N - 67° 28' W (33).
- San Ignacio, see Jaén (14).
- San Isidro, Paraguay, Central. Shipyard NW of Asunción (7).
- San Juan, Perú, Loreto, locality near town of Aguaitia, 9° 10' S - 76° 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. 3° 25' N - 73° 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, Espírito Santo, town 50 km NNE of Vitória, 20° S - 40° 55' W (1, 4).
- Santa Cruz (do Sul), Brazil, Rio Grande do Sul, town 30 km N of Rio Pará (8).
- Santa Elena, Venezuela, Bolívar, town in Gran Sabana Plateau, 4° 40' N - 61° 05' W (33).
- Santa Fe, Argentina, name of a province.
- Santa Marta, Colombia, Magdalena, port on Caribbean Sea, 11° 15' N - 74° 13' W (5).
- Santa Rita, Uruguay, Paysandú, unidentified locality between Rio Daymon and Rio Negro (8).



- Santiago Tuxtla, México, Veracruz, town, 18° 28' N - 95° 20' W (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, 16° 10' S - 57° 30' W (37).
- Sao Lourenço (do Sul), Brazil, Rio Grande do Sul, city on W shore of Lagoa dos Patos, 31° 28' S - 50° W (8).
- Sao Sebastian, Brazil, Sao Paulo, city 100 km ENE of Santos, 23° 40' S - 45° 20' W (1).
- Sectie 0, Suriname, locality 70 km S of Paramaribo, on railway, 5° 16' N - 55° 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, 21° 40' S - 44° 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 Divisoies, 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, 2° 48' S - 78° 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 3° 20' N - 56° 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, 4° 20' S - 69° 55' W (7, 22, 44).
- Tachira, Venezuela, name of a state.
- Tapijulapa, México, Tabasco, town, 17° 29' N - 92° 47' W (11).
- Teapa, México, Tabasco, city, 17° 35' N - 92° 57' W (11).
- Tefé, Brazil, Amazonas, city on Rio Tefé, just above its influx into Rio Amazonas (also name of a nearby lake) 3° 30' S - 64° 30' W (21).
- Teresópolis, Brazil, Rio de Janeiro, city near crest of Serra dos Orgaos, 880 m alt, 22° 30' S - 43° 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, 34° 26' S - 58° 35' W (8).
- Tila, México, Chiapas, small village in N foothills of Chiapas plateau, 17° 27' N - 92° 30' W (9).
- Tingo Maria, Perú, Huanuco, town at confluence of Rio Monzón and Rio Huallaga, headstream of Rio Aguaitia, 9° 05' S - 76° 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 Orteguzza and Rio Caquetá, 0° 40' N - 75° 15' W (27).
- Trinidad, Bolivia, Beni, city near Rio Mamoré, 14° 47' S - 64° 38' W (19, 28, 37).
- Trujillo, Venezuela, name of a state.

- Tucuaembo, Uruguay, name of a department.
- Tupuranga, Brazil, Amazonas, small river joining Rio Negro, near Tupurucuara, 0° 25' S - 65° 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, 22° 30' S - 43° 40' W (1).
- Valera, Venezuela, Trujillo, city, 9° 19' N - 70° 36' W (17).
- Valledupar, Colombia, Cesar, town on foothills of Sierra Nevada de Santa Marta, on affluent of Rio Cesar, 10° 25' N - 73° 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, 22° 25' S - 43° 40' W (4).
- Venecia, Colombia, Caquetá, town on Rio Orteguzaza, 20 km NE of Florencia, 0° 30' N - 75° 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, 25° 44' S - 56° 27' W (7).
- Villavicencio, Colombia, Meta, town on Rio Guiquitia, 4° 08' N - 73° 37' W (27).
- Vitoria, Brazil, Espirito Santo, city, 20° 18' S - 40° 20' W (16).
- Yaracuy, Venezuela, name of a state.
- Ygatimi, Paraguay, Caaguazú, town 24° N - 55° 30' W (16).
- Zanderdij, Surinam, city 40 km from Paramaribo, 5° 25' N - 55° 15' W (23).
- Zulia, Venezuela, name of a state.



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# 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* Prael, 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 HYPOBOCERINI Pretzmann, 1971

### ***Hypobocera* Ortmann, 1897**

- Hypobocera alata* Campos, 1989. Colombia.  
*Hypobocera cajambrensis* Prael, 1988. Colombia.  
*Hypobocera dentata* Prael, 1987. Colombia.  
*Hypobocera gorgonensis* Prael, 1983. Colombia.  
*Hypobocera llorensensis* Campos, 1989. Colombia.  
*Hypobocera malagueña* Prael, 1988. Colombia.  
*Hypobocera meinelii* Prael, 1988. Colombia.  
*Hypobocera merenbergensis* Prael & Giraldo, 1985. Colombia.  
*Hypobocera mutisi* Prael, 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* Prah & 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 & Villalobos, 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 parbelliana* 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*, throughout 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-DEBOUDEVILLE (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.

*Odonthelphusa 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 epigeal 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 aspoecorum* 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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