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NEW SPECIES, CLADISTIC RELATIONSHIPS, AND BIOGEOGRAPHY OF THE GENUS *FREDIUS* (DECAPODA: BRACHYURA: PSEUDOTHELPHUSIDAE) FROM SOUTH AMERICA

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ABSTRACT

The taxonomy of the genus *Fredius* Pretzmann, 1967, is reviewed, and new taxa are described: *Fredius adpressus, F. adpressus piaroensis, F. platyacanthus,* and *F. estevisi siapensis.* The 8 species of this genus inhabit 4 major basins of different geological age in northern South America. The Orinoco basin is the oldest, followed by the Essequibo-Cuyuni basin. The lower Amazon basin, formed from Tertiary to Holocene by alluvionic deposition, is younger than these two. The Atlantic area, formed mainly by marine regressions, is the youngest. The phylogenetic relationships within *Fredius,* studied by means of a cladistic analysis, were compared with the relationships of these areas using Brooks parsimony analysis. The phylogenetic data fully agree with the area cladogram. The position of the ancestors within the area cladogram shows that most of them were present in a hypothetical major basin comprising the present Orinoco, Essequibo, and Cuyuni rivers, and that much of the evolution of the group occurred there. There is some ambiguity about the possible origin of 2 widespread species. The most parsimonious explanation for one of them is that it originated in the Atlantic drainage and then dispersed into the lower Amazon basin.

The genus *Fredius* Pretzmann, 1967, comprises five species of large fresh-water crabs restricted to the Guianas and the Amazon basin, where they inhabit, with one exception, the lowland rivers. The phylogenetic relationships of these species are not well understood at present because of difficulties encountered in the establishment of homologies in the gonopods. In other groups of Pseudothelphusidae, these homologies have been discovered through the arrangement of anatomical characters of these appendages in ordered morphoclines (Rodriguez, 1986; Rodriguez and Campos, 1989; Rodriguez and Hobbs, 1989).

The discovery of two undescribed species and two subspecies in material collected during surveys of the fauna of the Venezuelan Guiana carried out since 1984 has provided new evidence on the relationships of the different types of first gonopods found in this genus. With this new evidence, it has been possible to establish several homologies in all the species of *Fredius* and to propose a phylogeny for the genus on the basis of a cladistic analysis.

MATERIAL AND METHODS

The material studied came from the following areas (Fig. 6): (1) The middle course of the Orinoco River, near Puerto Ayacucho; (2) The Cuao River, a minor tributary of the Orinoco, near Puerto Ayacucho; (3) The Parguaza River, another minor tributary of the Orinoco, north of the Cuao River; (4) The Cunucunuma River, an affluent of the Orinoco, with its headwaters in the Cerro Duida; (5) The Siapa River, a small river which flows near the Orinoco, but drains to the Amazon through Brazo Casiquiare and the Rio Negro; (6) The Gran Sabana plateau, a highland savannah drained by the headwaters of the Caroni River, and the southern slopes of Mount Roraima; and (7) The Icabaru River, a tributary of the Caroni River, with its headwaters in the Sierra Pacaraima.

The material is deposited in the Instituto Venezolano de Investigaciones Cientificas, Caracas (IVIC), the Museum of the La Salle Foundation (LS), Caracas, the Museo de Biologia, Universidad Central de Venezuela (MBUCV), Caracas, and the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH). Other abbreviations used in this paper are CL for carapace length and CB for carapace breadth.

Species Examined.—The autapomorphy that defines all the species of *Fredius* is the possession of an open, flattened, ear-shaped field of apical spines directed cephalad (see below under "Homologies in the gonopodal processes," and Fig. 4), which is substantially different from the narrow field of spines, frequently slitlike and lodged between 2 partially or completely fused lamellae, characteristic of other species of the Tribe Kingsleyini. This character can be considered the primitive condition, since it is present in *Strengeriana fuhrmanni* (Zimmer, 1912), which is regarded as a primitive member of the family (see Rodriguez, 1982a: 32 and fig. 10). The cladistic analysis presented below covers all the known species of *Fredius* (Table 1), including those described in this paper and others examined by Rodriguez (1982a).

Table 1. *Vertical distribution of the species and subspecies of Fredius.*

Species	Meters above sea level
Fredius adpressus adpressus, new species	100
F. adpressus piaroensis, new subspecies	400
F. beccarii (Coifmann, 1939)	50–200
F. chaffanjoni (Rathbun, 1905)	110–300
F. denticulatus (H. Milne Edwards, 1853)	70–400
F. estevisi estevisi Rodriguez, 1966	800–1,250
F. estevisi siapensis, new subspecies	518
F. platyacanthus, new species	500
F. reflexifrons (Ortmann, 1897)	65–200

Table 2. Characters of *Fredius* compared. The first comparison listed for each character is considered to be plesiomorphic.

1 Anterolateral margin (0) continuous with external orbital angle, (1) recurved above this angle.
2 Gonopodal field of apical spines (0) slitlike, (1) open, flat.
3 Apical processes of first gonopod (0) not lyrate, (1) forming lyrate structure with mesial process and accessory spine.
4 Margin of cephalic lobe (0) not expanded, (1) expanded mesiad.
5 Cephalic lobe with caudal surface (0) not spinose, (1) with 1–3 spinules.
6 Cephalic lobe (0) without an accessory lobe, (1) with an accessory lobe.
7 Cephalic spine (0) absent or reduced, (1) extraordinarily developed.
8 Mesial lobe (0) lamelliform, (1) spiniform.
9 Mesial lobe tip (0) single, (1) bifid.
10 Mesial lobe (0) forming angle with back surface of cephalic lobe, (1) attached to back of auricular lobe.
11 Basal denticle of mesial lobe (0) absent, (1) present.
12 Mesial lobe (0) developed, (1) rudimentary.
13 Lateral margin of cephalic lobe (0) not projected, (1) projected laterad.
14 Subapical bulge (0) reduced, (1) well developed.
15 Marginal lobe (0) straight, (1) bent cephalically.
16 Mesial lobe (0) directed laterally, (1) twisted caudally.
17 Gonopod (0) not bent, (1) moderately bent or (2) strongly bent.

Characters Examined.—The strategy used in the cladistic analysis of the species of *Fredius* is the same as the one employed in Rodriguez and Campos (1989), except for the number of somatic characters included. The morphology of the carapace and appendages of *Fredius* is almost completely uniform. Some characters, like the thickness of the chelae, which might appear distinctive in a single specimen or a small group of specimens, may display a considerable variation when a large series is examined. For this reason, the present cladistic analysis is based almost exclusively on the morphology of the first gonopod. The only somatic character retained for the analysis is the postorbital notch (character 1 in Table 2), whose morphology is subjected to little intraspecific variation in the Pseudothelphusidae.

Homologies in the Gonopodal Processes.—The first gonopod of *Fredius* possesses a subapical bulge which covers the lateral and cephalic sides, but with a different degree of development in the different species. It is poorly developed in *F. platyacanthus*, new species, *F. estevisi* Rodriguez, 1966, and *F. chaffanjoni* (Rathbun, 1905); more conspicuous in *F. adpressus*, new species and *F. beccarii* (Coifmann, 1939); and extraordinarily developed as a subapical knob (Fig. 4, sb) in *F. reflexifrons* (Ortmann, 1897) and *F. denticulatus* (H. Milne Edwards, 1853) (character 14).

Distally to the subapical bulge, all species of *Fredius* bear a simple marginal lobe (Fig. 4, a), which ends in an inverted cup-shaped elongation at the base of the field of apical spines. On the other hand, the cephalic and mesial lobes display considerable specific differences in shape, spinulation, and position. The possible homologies found in these 2 lobes, postulated on the basis of similarity of morphology, either directly or through an intermediate form, and topographical position within the first gonopod apex, are the following (Fig. 4). *Fredius platyacanthus* (Fig. 4A, B) shows the generalized condition found in most Kingsleyini, consisting of a wide mesial lobe (ml), ending in an acuminate tip and a cephalic lobe (cl) with a transverse distal margin directed mesiad (character 8). In *F. estevisi siapensis*, new subspecies (Fig. 4C), the mesial lobe is still considerably wide, but in *F. estevisi estevisi* (Fig. 4D) it becomes narrowed into a conical spine directed mesiad; in *F. chaffanjoni* and *F. adpressus* the conical shape is preserved, but the process is directed distally in *F. chaffanjoni* (Fig. 4G), and becomes attached to the back of the cephalic lobe in *F. adpressus* (Fig. 4H) (character 10). The cephalic spine (Fig. 4, cs) also adopts different shapes in this group of species; it is small in *F. platyacanthus* (Fig. 4B) and *F. estevisi* (Fig. 4E), strong in *F. adpressus* (Fig. 4I), particularly in the subspecies *piaroensis* (Fig. 4J), and enormously developed in *F. chaffanjoni* (Fig. 4F, G), producing, with the mesial lobe, a lyrate aspect to the apical processes when seen in caudal view (character 3). In *F. reflexifrons* (Fig. 4K, L) there is also a strong development of the cephalic spine, compensated for by a reduction of the mesial lobe which becomes spiniform (character 12). This last process shows a small basal spine (b) which is also present in *F. adpressus* (Fig. 4H) and *F. chaffanjoni* (Fig. 4F) (character 11). This group of species shows an auxiliary lobe (al) on the lateral side of the field of apical spines (character 6) which is spatulate and strong in the first four species, but reduced in *F. reflexifrons* (Fig. 4K).

The gonopodal morphologies of *F. beccarii* (Fig. 4M, N) and *F. denticulatus* (Fig. 4O, P) differ considerably from those of other members of the genus. The cephalic spine and the accessory lobe are absent (characters 6 and 7, respectively); the mesial lobe (ml) is lamelliform (character 8); the cephalic lobe bears 1 or several denticles (s) on its distal margin (character 5). In *F. den-*

ticulatus (Fig. 4O) this morphology becomes further distorted by the lateral elongation (e) of the margin of the field of spines (character 13).

Out-group Selection.—In recent treatments of the family Pseudothelphusidae (Rodriguez, 1982a), the genus *Fredius* is grouped with eight other genera in the tribe Kingsleyini. The apomorphies which define this tribe are the following: (1) Reduction of the exognath of the third maxilliped to less than half the length of the ischium of the endognath; this trend is already present in all Pseudothelphusidae, but it is more accentuated in the Kingsleyini. In *Eudaniela pestai* Pretzmann, 1965, and *Fredius* spp., the exognath is less reduced than in other members of the tribe. (2) Presence of a spiniform mesial lobe and a hoodlike cephalic lobe in the distal segment of the first gonopod. As theorized by Rodriguez (1982a), the cephalic lobe originated from an ancestral type of gonopod with three independent apical plates, by apposition of the mesial and lateral plates, and reduction of the marginal plate. In *Eudaniela pestai,* the cephalic lobe is still formed by two separate plates, but in other species, only an apical notch remains as a vestige of the recess between both plates. For this reason *Eudaniela pestai* can be considered as approaching the ancestral pseudothelphusid condition and will be used as an out-group for the polarization of the characters of *Fredius.*

The gonopod of *Brasiliothelphusa tapajoense* Magalhaes and Türkay, 1986, has been proposed by these authors as the most primitive type among the Kingsleyini. However, the gonopod of this species resembles that of *Prionothelphusa eliasi* Rodriguez, 1980, in the crested mesial blade and the marginal process; the characteristic narrow high field of spines of *P. eliasi* is bent into a U-shaped lobe in *B. tapajoensis.* The relationships of *Prionothelphusa eliasi* with other Pseudothelphusidae are obscure, but the vestigial apical notch in the field of spines indicates a relationship with the most evolved forms of the Kingsleyini.

Data Analysis.—The phylogenetic programs used were Phylip 3.0 (Felsenstein, 1984) routings MIX and METRO, and PAUP version 2.4 (Swofford, 1985) option ALLTREES.

SYSTEMATICS

Family Pseudothelphusidae Rathbun, 1893
Tribe Kingsleyini Bott, 1970
Genus *Fredius* Pretzmann, 1967
***Fredius adpressus*,** new species

Fig. 1A–E

Material.—Quebrada El Garzon, 18 km from Rio Parguaza, Estado Bolivar, 100 m above sea level; 15 August 1985; B. Bustos; 1 ♂ holotype, CL 46.9 mm, CB 79.6 mm (LS).

Description.—Surface of carapace smooth, with small pores and papillae not visible to naked eye. Cervical groove deep and narrow, sinuous, ending near lateral margin. Anterolateral margin with depression behind antero-external angle, followed by 4 or 5 papillae; rest of margin behind cervical groove with approximately 20 subtriangular teeth, reduced to small papillae at beginning and end of series. Postfrontal lobes low, small, continued laterally by faint ridge; median groove thin and shallow, but well impressed. Surface of carapace in front of postfrontal lobes flat in frontal view and inclined anteriorly. Upper border of front straight in dorsal view, with deep median notch, carinate, marked with row of small tubercles. Lower margin strongly sinuous in frontal view. Surface of front between upper and lower borders high, retracted backwards.

Palm of largest chela moderately inflated; fingers not gaping; brown-black coloration over distal half of mobile finger and tip of fixed finger. Exopod of third maxilliped 0.45 length of ischium of endognath.

First gonopod robust at base, strongly tapering to subapical bulge, with marginal, cephalic, and mesial lobes well developed. Marginal lobe rounded, reduced, not extending over field of apical spines. Cephalic lobe auricular in caudal view, with mesial border sinuous, spinulose proximally, and lateral border with spatulate accessory lobe and strong curved cephalic spine; field of apical spines wide, directed cephalad. Mesial lobe short, conical, bent laterad over back of cephalic lobe, with small spinule on distal border; mesial lobe and caudal spine forming 2 divergent hooks of unequal length in caudal view. Marginal setae arranged in dense row over proximal half of gonopod; lateral surface with numerous long plumose setae.

Etymology.—The specific name is from the Latin *adprimere,* to lie flat against, and refers to the relative positions of the mesial process and the auricular lobe of the first gonopod.

***Fredius adpressus piaroensis*,** new subspecies

Fig. 1F, G

Material.—Venezuela, San José del Cuao, Territorio Federal Amazonas; 28 August 1987; Stanford Zent; 1 ♂ holotype, No. 88, CL 54.9 mm, CB 89.1 mm, 1 ♂ paratype, No. 60, CL 31.1 mm, CB 49.7 mm, 1 immature ♀ paratype, No. 72, CL 49.3 mm, CB 79.1 mm (IVIC).—Alto Rio Cuao, Territorio Federal Amazonas, 400 m above sea level; November 1986; Stanford Zent; 1 mature ♀ CL 62.4 mm, CB 103.5 mm, 1 juvenile ♂, No. 180, CL 30.7 mm, CB 47.5 mm (IVIC).

Differential Diagnosis.—The present subspecies differs from the nominotypical subspecies in the cephalic spine of the first gon-

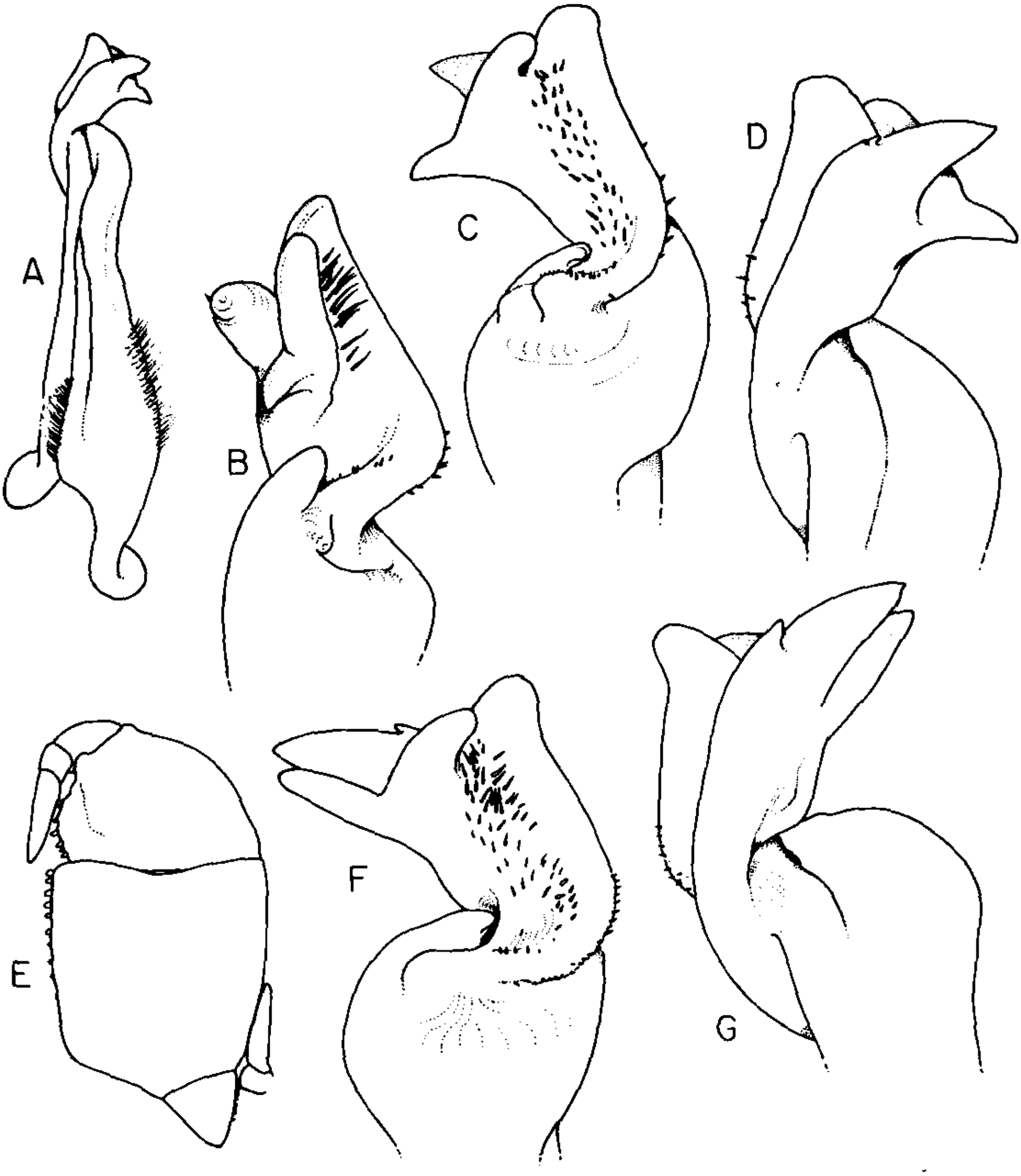

Fig. 1. A–E, *Fredius adpressus*, new species, holotype male from Rio Parguaza: A, left first gonopod, caudal view; B, apex, lateral caudal view; C, apex, cephalic view; D, apex, mesial view; E, third maxilliped. F, G, *Fredius adpressus piaroensis*, new subspecies, male holotype from Rio Cuao: F, left first gonopod, apex, cephalic view; G, apex, mesial view.

opod, which is larger and directed upwards, and the mesial lobe, which is longer, directed upwards, and bears a large spinule over its distal surface. The cephalic spine and the mesial lobe form two parallel hooks of equal length in caudal view.

Etymology.—The subspecific name refers to the Piaroa ethnic group, in whose lands this subspecies lives.

Remarks.—According to Stanford Zent (personal communication), these crabs are commonly eaten by the Piaroa Indians that inhabit the basin of the Cuao River. These crabs are called "uuse" (crab, generic) and "buo uuse" (large crab) in the Piaroa language. Specimen No. 60 recorded above was described as "ithi" (very young). Zent recorded the following observations about the holotype specimen from an Indian informer: "ahena ku" (lives in the channel), "poæ ote kuu" (eats the fruit of the "poæ" palm, *Socratea exorhiza*), "ïbo" (this individual is a male). The Piaroas distinguish this crab from the trichodactylid *Zilchlopsis emarginatus* (Milne Edwards, 1853) which also inhabits this area and is called "awañu'ma uuse." This last species is, however, stated to live in the ground, near the caño, in muddy or swampy soil ("renæwana ahe' hayoto ku") and to eat the "nañari" (*Gymnophiona* sp.) ("nañari kwæni kika").

Fredius chaffanjoni (Rathbun, 1905)

Potamocarcinus chaffanjoni Rathbun, 1905, p. 311, pl. 2, fig. 2. For synonymy see Rodriguez, 1982a.

Material.—Culebra, Rio Cunucunuma, Territorio Federal Amazonas, 175 m altitude; 26 March 1983; G. Colonello; 1 ♂, CL 19.1 mm, CB 28.5 mm (LS).—Carinagua, Puerto Ayacucho, Territorio Federal Amazonas; 6 February 1979; 1 ♂, CL 22.5 m, CB 32.4 mm, 1 immature ♀, CL 24.5 mm, CB 36.5 mm, 1 juvenile, CL 13.8 mm, CB 18.5 mm (IVIC).

Remarks.—The present records extend the known area of distribution of the species from the upper Orinoco and Rio Ventuari basin, to the middle course of the Orinoco.

Fredius estevisi estevisi (Rodriguez, 1966)

Fig. 2A–D

Pseudothelphusa estevisi Rodriguez, 1966, p. 265, fig. 4, pl. 3. For synonymy see Rodriguez, 1982a.

MATERIAL.—Venezuela, without other data, 1 ♂ holotype, CL 55.6 mm, CB 90.0 mm (MBUCV XI-0845), 1 ♂ paratype, CL 43.2 mm, CB 71.3 mm (RMNH), 1 juvenile, CL 12.0 mm, CB 17.8 mm (MBUCV XI-0846).—Quebrada El Jaspe, Gran Sabana, Estado Bolivar; 25 May 1989; P. Lau; 1 ♂, CL 40.2 mm, CB 64.8 mm (LS 1217).—Rio Kama, Gran Sabana, Estado Bolivar; 8 June 1982; L. Perez and A. Guilarte: 1 ♂, CL 41.7 mm, CB 66.0 mm (LS).—Rio Kama, road to San Ignacio de Yuruani, Estado Bolivar, 900 m altitude; 20 September 1987; C. Lasso and G. Colonello: 1 ♂, CL 34.2 mm, CB 61.4 mm, 2 immature ♀♀, CL 32.8 and 26.5 mm, CB 51.3 and 40.3 mm (LS 1055).—5.2 km from San Ignacio de Yuruani, road to La Toma, Estado Bolivar; 1987; H. G. Castellanos: 1 ♂ CL 35.4 mm, CB 55.3 mm, 1 ♀, CL 47.8 mm, CB 78.8 mm (LS 1040).—Creek approximately 10 km from Rio Yuruani, road Yuruani-Santa Elena de Uairen, Estado Bolivar, 800 m altitude; 19 September 1987, C. Lasso and G. Colonello; 1 immature ♀, CL 30.0 mm, CB 47.2 mm (LS 1053).—Tarota Creek, approximately 8 km from Rio Aponguao, road Luepa-Parupa, Estado Bolivar, 1,150 m altitude; 15 September 1987; C. Lasso and G. Colonello; 1 ♂ CL 34.1 mm, CB 53.7 mm (LS 1051).—Caño Urue, south of San Ignacio de Yuruani, Gran Sabana, Estado Bolivar; 10 March 1988; S. Flores; 4 ♀♀, CL 47.5, 48.8, 36.4, and 20.6 mm, CB 76.3, 79.8, 57.5, and 29.8 mm (IVIC).—Rio Ananaiac, near Kama, Estado Bolivar, 10 March 1988; S. Flores; 1 ♀, CL 35.4 mm, CB 55.6 mm (IVIC).—Rio Kukenaam, in the southern slopes of Mount Roraima, approximately 900 m altitude; 27 May to 4 June 1989; C. Lasso and H. Piñango; 1 ♂, CL 44.3 mm, CB 81.4 mm (LS 1218), 2 immature ♀♀ (LS 1219, 1221).

Differential Diagnosis.—The nominotypical subspecies differs from the subspecies described here in the mesial lobe of the first gonopod which has its proximal and distal margins more or less straight, giving this spine a conical shape.

Color.—Most specimens have a marbled pattern of coloration over the dorsal surface of the carapace. This pattern, however, is not apparent in the holotype, perhaps due to discoloration by the preservative.

Distribution.—The holotype is from an undetermined locality in the Venezuelan Guiana (Rodriguez, 1966). Other specimens of the nominate subspecies come from tributaries of the upper Caroni River which drain the Gran Sabana plateau and the southern slopes of Mount Roraima.

Fredius estevisi siapensis, new subspecies

Fig. 2E–G

Material.—Rio Siapa, Territorio Federal Amazonas; 27 March 1988; R. Royero; 518 m altitude; 15 ♂♂, largest (designated as holotype of subspecies) CL 37.5 mm, CB 57.8 mm, 10 immature ♀♀, largest CL 32.8 mm, CB 50.4 mm, 6 juveniles (IVIC).—Guanucuru, Culebra, Rio Cunucunuma, Territorio Federal Amazonas; Martha Granier; 1 ♂, CL 32.5 mm, CB 51.2 mm, 1 immature ♀, CL 39.5 mm, CB 62.5 mm (IVIC).

Differential Diagnosis.—The present subspecies differs from the nominotypical subspecies in that the mesial lobe of the first gonopod has the proximal margin concave and distal margin regularly arched, giving a thumblike appearance to this spine; the cephalic spine being well developed, rudimentary or absent.

Remarks.—These crabs are called "matherimi" in the Yanomami language (Ramiro Royero, personal communication), and are commonly eaten by the Yanomami of the Siapa river, a subgroup of the Yanomami

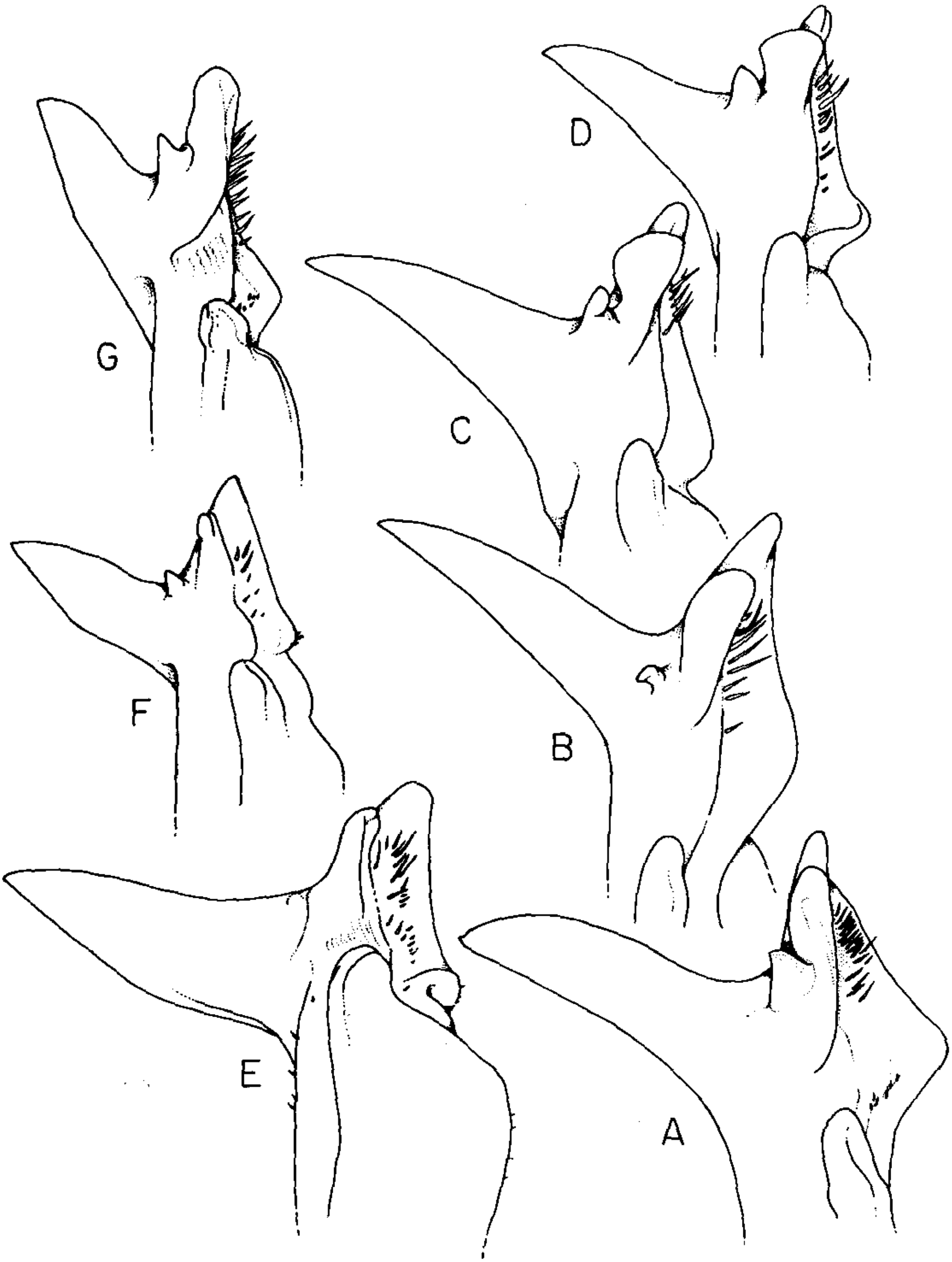

Fig. 2. A–D, *Fredius estevisi estevisi* Rodriguez, 1966, left first gonopod, apex, caudal view: A, holotype, CL 55.6 mm; B, specimen from Rio Kama, CL 32.8 mm; C, specimen from same locality, CL 26.5 mm; D, specimen from Tarota Creek, CL 34.1 mm. E–G, *Fredius estevisi siapensis*, new subspecies, left first gonopod, apex, caudal view; E, holotype from Rio Siapa, CL 37.5 mm; F, specimen from same locality, CL 27.1 mm; G, specimen from Rio Cunucunuma, CL 32.5 mm.

ethnic group that inhabits the basin of this river (Finkers, 1986).

Color.—In the majority of the specimens, a mottled pattern is visible over the upper surface of the carapace and pereiopods, sometimes more conspicuous over the gastric and cardiac regions, where it consists of a light brown reticulation over a chocolate brown or reddish background.

Distribution.—Rio Siapa basin and upper Orinoco River in the Territorio Federal Amazonas, Venezuela.

Etymology.—The subspecific name refers to the type locality in the Rio Siapa.

Fredius platyacanthus,
new species

Fig. 3A–F

Material.—El Abismo, Cantarrana, Rio Icabaru, Estado Bolivar, 500 m altitude, August 1984; J. Ayazaguena and H. Castellanos; 1 ♂ holotype, CL 58.5 mm, CB 96.5 mm (LS 899).

Description.—Surface of carapace smooth, with small pores and papillae not visible to naked eye. Cervical groove deep and narrow, almost straight, ending near lateral margin. Anterolateral margin with depression behind antero-external angle, followed by 3 or 4 papillae; rest of margin behind cervical groove with approximately 18 blunt teeth, decreasing in size posteriorly. Postfrontal lobes low, wide, continued laterally by faint ridge; median groove wide and shallow between postfrontal lobes, narrow and inconspicuous near frontal margin. Surface of carapace in front of postfrontal lobes slightly excavated in frontal view and inclined anteriorly. Upper border of front straight in dorsal view, with small median notch, carinate, marked with row of indistinct papillae. Lower margin thin and sinuous in frontal view. Surface of front between upper and lower borders high, excavated, retracted backwards.

Palm of largest chela elongated, not conspicuously inflated; fingers moderately gaping. Exopod of third maxilliped 0.35 length of ischium of endognath.

First gonopod robust at base, strongly tapering to subapical bulge, with marginal, cephalic, and mesial lobes well developed. Marginal lobe rounded, reduced, not extending over field of apical spines. Cephalic lobe auricular in caudal view, with mesial border rounded, and lateral border with long spatulate accessory lobe and small conical cephalic spine; field of apical spines wide, directed cephalad. Mesial lobe wide triangular, directed transversely backwards, with bifid apex; marginal setae arranged in dense row over proximal half of gonopod; lateral surface with numerous long plumose setae.

Etymology.—The specific name is from the Greek *platys*, broad, and *akantha*, a thorn, and refers to the shape of the mesial process of the first gonopod.

The different taxa of the genus *Fredius* can be distinguished by the following key to characters of the first gonopod.

1\. Mesial lobe wide, ending in bifid tip 2
– Mesial lobe spiniform and ending in single tip or reduced 4
2\. Cephalic spine located on caudal border of cephalic lobe 3
– Cephalic spine located on distal margin of mesial lobe .... *Fredius beccarii*
3\. Cephalic spine small .... *Fredius platyacanthus*
– Cephalic spine forming long spur .... *Fredius chaffanjoni*
4\. Mesial lobe more developed than cephalic spine 5
– Mesial lobe rudimentary 8
5\. Mesial lobe well developed, forming right angle with back surface of cephalic lobe 6
– Mesial lobe reduced, not forming right angle with back surface of cephalic lobe 7
6\. Mesial lobe conical .... *Fredius estevisi estevisi*
– Mesial lobe with distal border concave, proximal border convex .... *Fredius estevisi siapensis*
7\. Cephalic spine shorter than accessory lobe. Mesial lobe with rudimentary spine on distal surface. Cephalic spine and mesial lobe divergent, directed mesially .... *Fredius adpressus adpressus*
– Cephalic spine and auxiliary lobe of equal length. Mesial lobe with well-developed spine on distal surface. Cephalic spine and mesial lobe parallel, directed transversely upwards .... *Fredius adpressus piaroensis*
8\. No spinules on distal border of mesial lobe .... *Fredius reflexifrons*
– Two or more spinules on distal border of mesial lobe .... *Fredius denticulatus*

CLADISTICS

Two most parsimonious trees were found, with 23 steps and CI = 0.78 (Fig. 5A, B). The only difference between both trees is in the position of the clusters *Fredius estevisi–F. platyacanthus* and *F. beccarii–F. denticulatus* which is switched. In tree B (Fig. 5B),

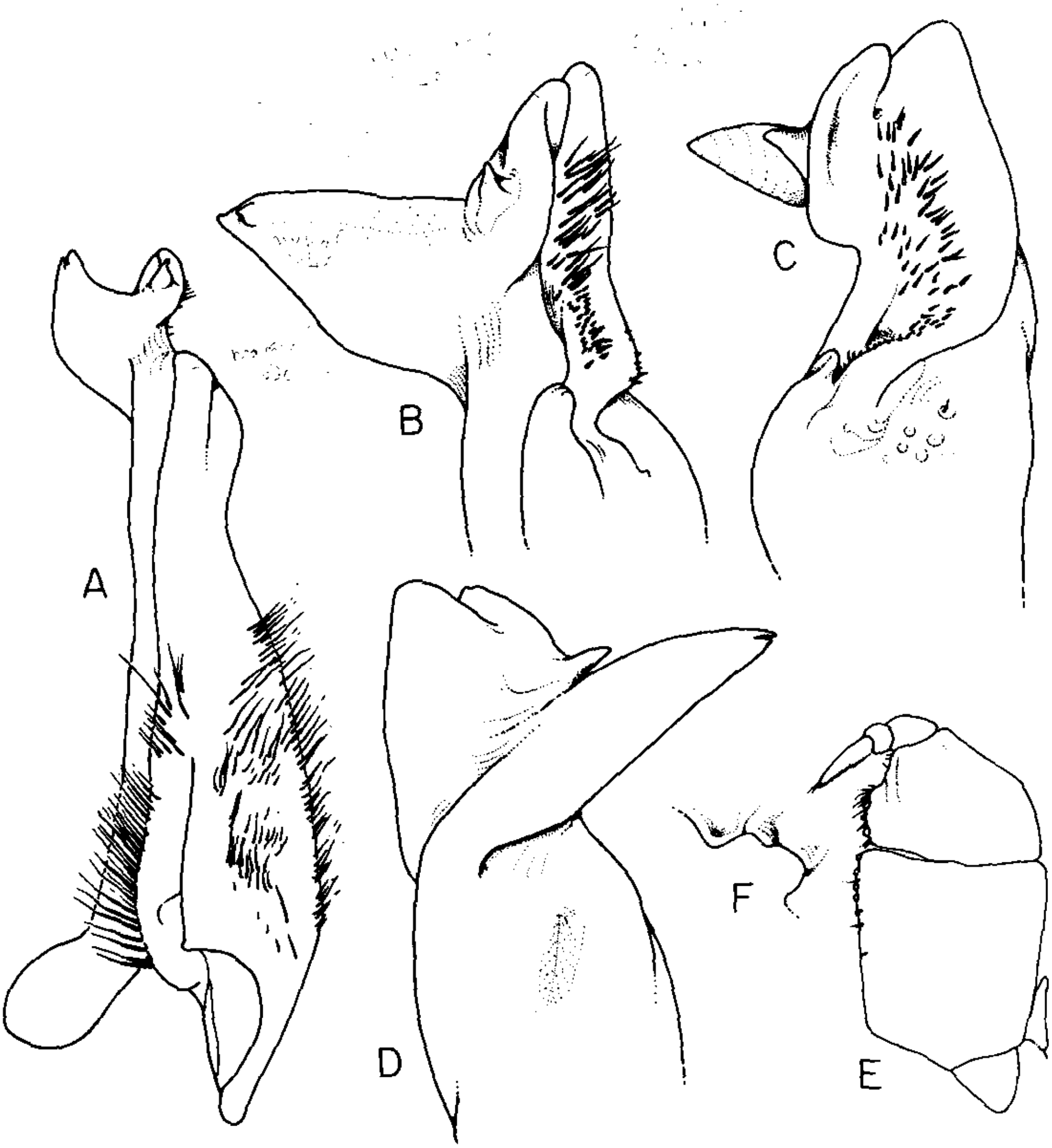

Fig. 3. *Fredius platyacanthus*, new species, holotype male from Rio Icabaru: A, left gonopod, caudal view; B, apex, laterocaudal view; C, apex, cephalic view; D, apex, mesial view; E, third maxilliped; F, opening of left efferent channel.

the branch leading to *F. estevisi* is zero length, and therefore the taxon (valid species) is not defined by any autapomorphy; in tree A it is defined by character 8. We chose tree A as our working hypothesis, because it is better supported by the data at hand in the sense that there are no zero length branches.

Characters 8, 9, 14, 16, and 17 show homoplasic conditions. Tree A (Fig. 5) starts with a cluster of the species *F. platyacanthus–F. estevisi* as the most basal group, then follows the pair *F. beccarii–F. denticulatus,* and, sequentially, *F. chanfajoni, F. adpressus,* and *F. reflexifrons* as the most derived taxa.

The autapomorphies that define each cluster are as follows: 6, 16, and 17 for the *F. platyacanthus–F. estevisi* cluster; 8 and 15 for the rest; 14 and 15 for the *F. beccarii–F. denticulatus* cluster; 6, 7, and 17 for the

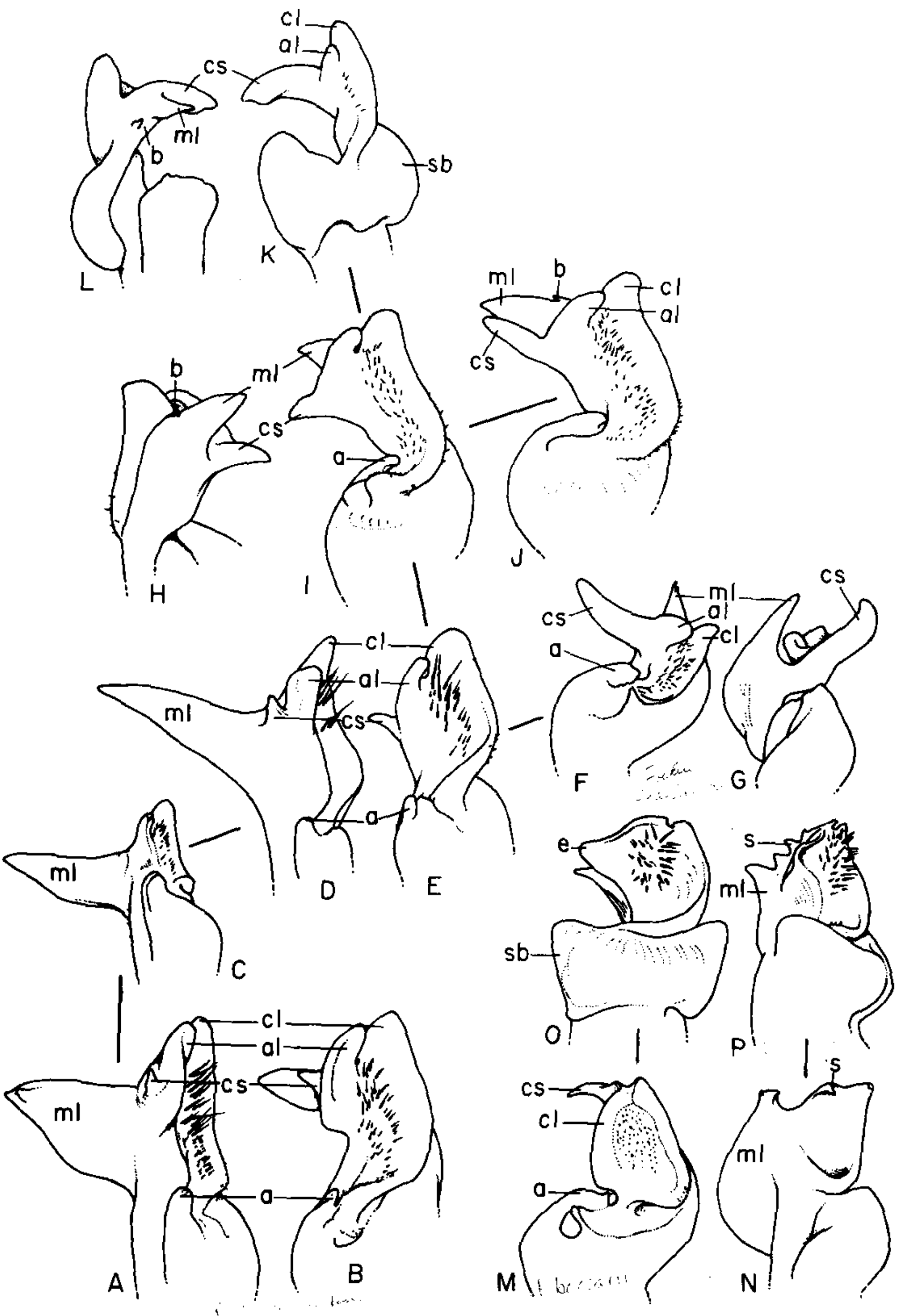

Fig. 4. Homologies in the gonopods of *Fredius*: A, B, *F. platyacanthus*; C, *F. estevisi siapensis*; D, E, *F. estevisi estevisi*; F, G, *F. chaffanjoni*; H, I, *F. adpressus adpressus*; J, *F. adpressus piaroensis*; K, L, *F. reflexifrons*; M, N, *F. beccarii*; O, P, *F. denticulatus*. a, marginal lobe; al, auxiliary lobe; b, basal spine; cl, cephalic lobe; cs, cephalic spine; e, lateral elongation of field of spines; ml, mesial lobe; s, distal denticles; sb, subapical bulge. A, C, D, G, L, N, P, caudal view; B, E, F, I, J, K, M, O, cephalic view; H, mesial view.

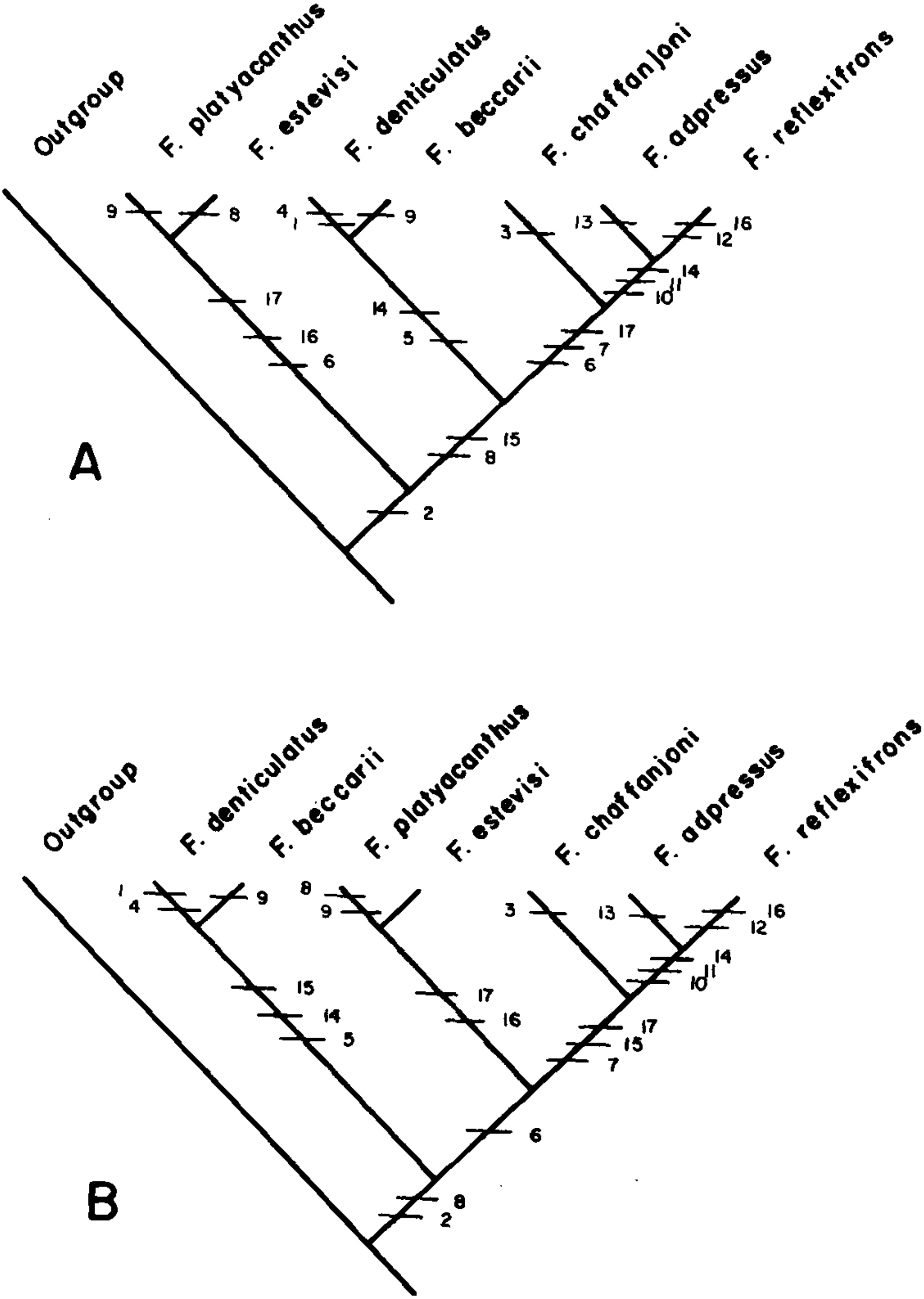

Fig. 5. Two most parsimonious cladograms obtained, with indication of changes in character states.

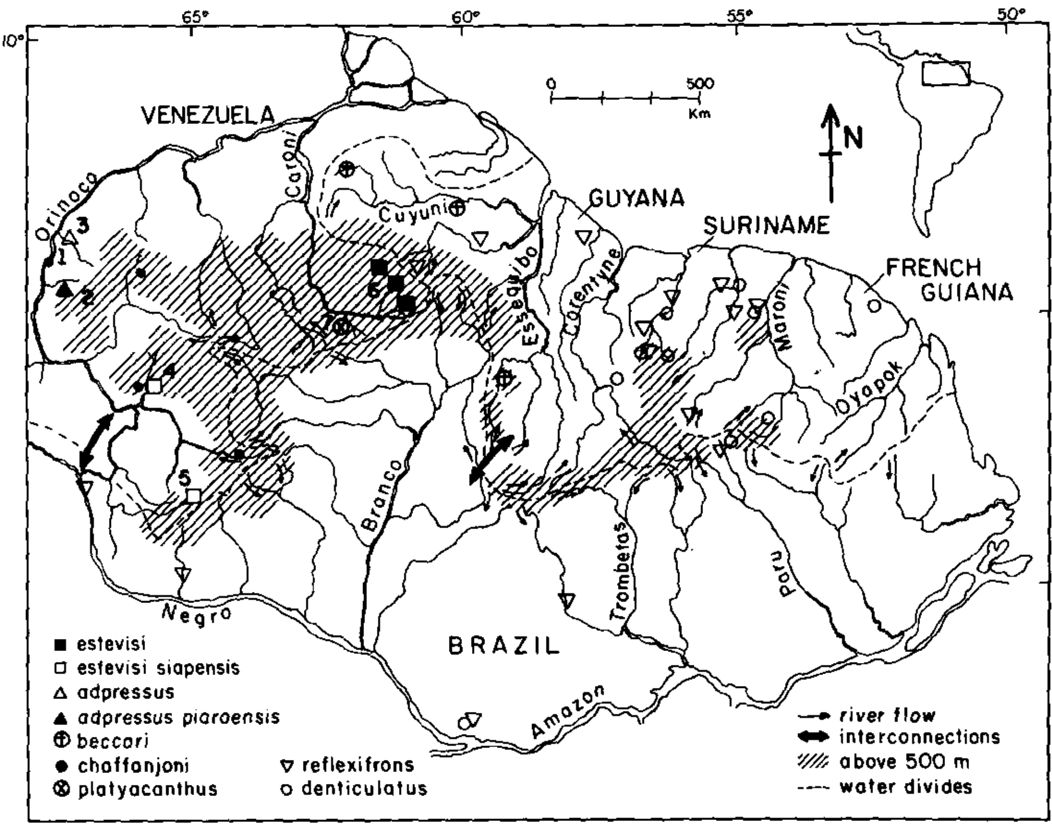

Fig. 6. Map of the Guianas and northern Amazon basin, showing distribution of species of *Fredius*. Records south of Amazon and Negro rivers not included. Numbers referring to localities listed under Material and Methods.

rest; and 10, 11, and 14 for the *F. adpressus–F. reflexifrons* cluster.

BIOGEOGRAPHY

As the available data indicate (Fig. 6), the species of *Fredius* are widely distributed in four major basins: (1) The Orinoco basin comprises the tributaries of the right margin of the Orinoco River which drain the Venezuelan Guiana; (2) the Essequibo-Cuyuni basin, an area of the Venezuelan Guiana separated by low elevations from the Orinoco basin; (3) the lower Amazon basin; and (4) the Atlantic basin formed by the rivers that run through the territories of Guyana, Suriname, and French Guiana, and discharge into the Atlantic. The Orinoco and Amazon basins are connected through the Brazo Casiquiare, a natural waterway between the Negro and Orinoco rivers, while the inundated areas of the Rupununi connect the Essequibo and Cuyuni with the Amazon basin (Rodriguez, 1982b). The continuous mountain chain between the Orinoco and the Amazon affords a barrier to the dispersion of the species, since all the species of *Fredius*, with the exception of *F. estevisi estevisi* from the Gran Sabana plateau, are restricted to altitudes below 500 m (Table 1).

The Venezuelan Guiana possesses the largest number of species and subspecies. The areas of distribution of these forms are very variable in extent. *Fredius adpressus* and *F. platyacanthus* are restricted to minor river basins, while *Fredius chaffanjoni* occupies a relatively large area in the headwaters and the middle course of the Orinoco. The two subspecies of *Fredius estevisi* occupy disjunct areas in the Gran Sabana plateau and the Siapa river, respectively. Only two species are present in the Atlantic and lower Amazon basins: *Fredius denticulatus*, with a wide distribution in the three

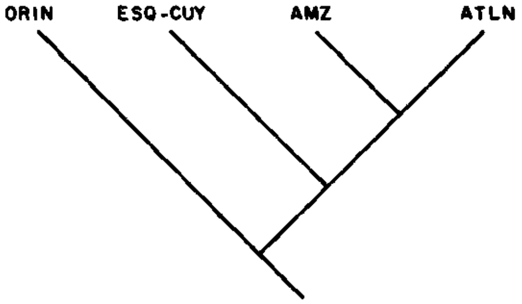

Fig. 7. Tree showing hypothetical relationships of the basins involved in the area of distribution of *Fredius*. ORIN, Orinoco basin; ESQ-CUY, Essequibo-Cuyuni basin; AMZ, lower Amazon basin; ATLN, Atlantic basin.

Atlantic Guianas, and recorded also from the Amazon at Manaos (Magalhaes, 1986); and *F. reflexifrons*, with the largest area of distribution for a pseudothelphusid crab, partially overlapping the area of *F. denticulatus*, but also covering the southern basin of the Amazon (not shown in Fig. 6; see Magalhaes, 1986). *Fredius beccarii* is restricted to the Essequibo-Cuyuni basin.

The area of distribution of *Fredius* comprises one of the oldest on earth with some parts that date to Precambrian times. On the other hand, the present configuration of the water systems is a more recent event (Garner, 1966, 1975). A likely hypothesis for the relationships among the four basins is shown in Fig. 7. This hypothesis suggests that the Orinoco basin (ORIN) is the oldest, following the Essequibo-Cuyuni basin (ESQ-CUY) formed by an early splitting from a once larger Orinoco basin. On the other hand, the part of the lower Amazon basin (AMZ) involved in the area of distribution of *Fredius* (lower Amazon valley) was formed by alluvionic deposition ranging from Tertiary to Holocene (Grabert, 1983). We can safely say that this area is younger than the Orinoco and Cuyuni-Essequibo basin. Finally, the Atlantic area (ATLN), formed mainly by smaller rivers that discharge directly into the Atlantic Ocean, was formed mainly by marine regressions and should be the youngest (Krook, 1979).

Using Brooks parsimony analysis (Wiley, 1988; Brooks, 1990) it was possible to compare our hypothesis of relationships within *Fredius* with the relationships of the areas. The phylogenetic data fully agree (CI = 1.0) with the area cladogram (Fig. 8A, B; see Tables 3, 4 for data). There is some ambiguity about the possible origin of the widespread species *Fredius reflexifrons* and *F. denticulatus* (taxa 3 and 7 in Fig. 8A). The most parsimonious explanation for *Fredius denticulatus* (taxon 3) is that it originated in the Atlantic drainage and then dispersed into the lower Amazon basin. Based on the position of the ancestors within the area cladogram, it can be said that most of them were present in a hypothetical major basin

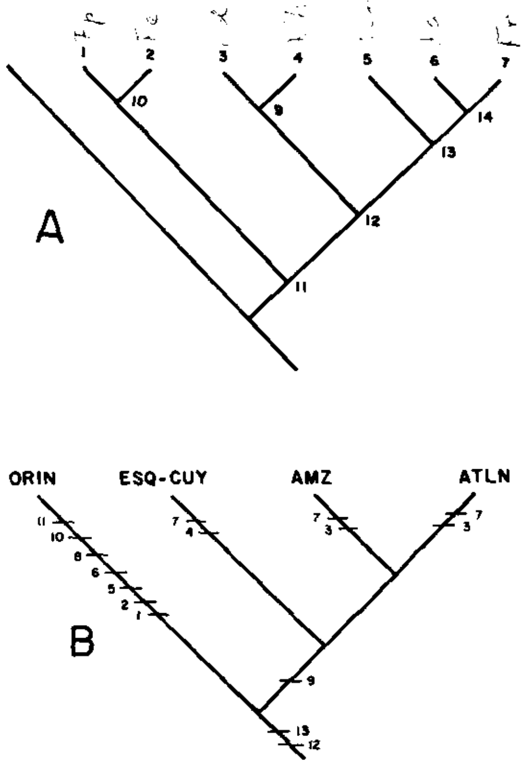

Fig. 8. A: Most parsimonious cladogram (Fig. 5A) with terminal taxa and internodes numbered. B: Area cladogram based on phylogenetic relationships among 7 species of *Fredius* (based on data coded for Brooks parsimony analysis; Brooks, 1990) (CI = 1.0).

Table 3. Data matrix of 17 characters of the species of *Fredius*.

Species	State of characters
Fredius adpressus	01000111011011112
F. beccarii	01001001100001111
F. denticulatus	11011001000001111
F. chaffanjoni	01100111000000112
F. estevisi	01000101000000000
F. platyacanthus	01000100100000000
F. reflexifrons	01000111011101102

Table 4. Data matrix listing binary codes for species of *Fredius* inhabiting four geographic areas. One through 13 refers to species and nodes as listed in tree (see Fig. 7).

	1	2	3	4	5	6	7	8	9	10	11	12	13
Orinoco basin	1	1	0	0	1	1	0	1	0	1	1	1	1
Essequibo-Cuyuni basin	0	0	0	1	0	0	1	0	1	0	0	1	1
Lower Amazon basin	0	0	1	0	0	0	1	0	1	0	0	1	1
Atlantic basin	0	0	1	0	0	0	1	0	1	0	0	1	1

comprising the present Orinoco, Essequibo, and Cuyuni rivers, and much of the evolution of the group occurred there. Ancestors 10, 11, and 13 originated in this area and went into extinction after the splitting of the Essequibo-Cuyuni basin.

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LITERATURE CITED

Bott, R. 1970. Betrachtungen über die Entwicklungsgeschichte und Verbreitung der Süsswasser-Krabben nach der Sammlung des Naturhistorischen Museums in Genf/Schweiz.—Revue Suisse de Zoologie 77(2): 327–344.

Brooks, D. R. 1990. Parsimony analysis in historical biogeography and coevolution: methodological and theoretical update.—Systematic Zoology 39: 14–30.

Coifmann, I. 1939. Potamonidi della Guiana Inglese raccolti dal Prof. Nello Beccari.—Archivio Zoologico Italiano 27: 93–117.

Felsenstein, J. 1984. The statistical approach to inferring evolutionary trees and what it tells us about parsimony and compatibility.—*In:* T. Duncan and T. F. Atussy, eds., Cladistics: perspectives in the reconstruction of evolutionary history. Pp. 169–191. Columbia University Press, New York, New York.

Finkers, J. 1986. Los Yanomami y su sistema alimenticio.—Monografia no. 2, Vicariato Apostolico de Puerto Ayacucho. Editorial Texto, Caracas. Pp. 1–262.

Garner, H. F. 1966. Derangements of the Rio Caroni, Venezuela.—Revue de Géomorphologie Dynamique 2: 50–83.

———. 1975. Rain forests, deserts and evolution.—Annais do Academia Brasileira de Ciencias 47: 127–133.

Grabert, H. 1983. Das Amazonas-Entwässerungssystem in Zeit und Raum.—Geologischen Rundschau 72: 671–683.

Krook, L. 1979. Sedimentary petrographic studies in northern Suriname.—Thesis, Vrije Universiteit Amsterdam. Drukkerij Elinkwijk Bv., Utrech, The Netherlands. Pp. 1–154.

Magalhaes, C. 1986. Revisao taxonomica dos caranguejos de agua doce brasileiros da familia Pseudothelphusidae (Crustacea, Decapoda).—Amazoniana 9: 609–636.

———, and M. Türkay. 1986. *Brasiliothelphusa,* a new Brazilian freshwater-crab genus (Crustacea: Decapoda: Pseudothelphusidae).—Senckenbergiana Biologica 66: 371–376.

Milne Edwards, H. 1853. Mémoire sur la famille des Ocypodien.—Annales des Sciences Naturelles, Zoologie, 3e série, 20: 163–228.

Ortmann, A. 1897. Carcinologische Studien.—Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere 10: 258–372.

Pretzmann, G. 1965. Vorläufiger Bericht über die Familie Pseudothelphusidae.—Anzeiger der mathematisch—naturwissenschaftlichen Klasse der österreichischen Akademie der Wissenschaften (1) 1: 1–10.

———. 1967. Über einige südamerikanische Süßwasserkrabben (Pseudothelphusidae). Vorläufige Mitteilung.—Entomologische Nachrichtenblatt, Wien 14: 23–26.

Rathbun, M. J. 1893. Descriptions of new species of American freshwater crabs.—Proceedings of the United States National Museum 16: 649–661.

———. 1905. Les Crabes d'eau douce (Potamonidae).—Nouvelles Archives du Muséum d'Histoire Naturelle, Paris 7: 159–321.

Rodriguez, G. 1966. Three new species of *Pseudothelphusa* from Venezuela.—Zoologische Mededelingen 41: 259–267.

———. 1980. Description préliminaire de quelques espèces et genres nouveaux de crabes d'eau douce de l'Amérique tropicale (Crustacea, Decapoda, Pseudothelphusidae).—Bulletin du Muséum National d'Histoire Naturelle, Paris (4) 2, section A (3): 889–894.

———. 1982a. Les crabes d'eau douce d'Amérique. Famille des Pseudothelphusidae.—Faune Tropicale 22: 1–223.

———. 1982b. Fresh-water shrimps (Crustacea, Decapoda, Natantia) of the Orinoco basin and the Venezuela Guayana.—Journal of Crustacean Biology 2: 378–391.

———. 1986. Centers of distribution of neotropical fresh-water crabs.—*In:* R. H. Gore and K. L. Heck, eds., Biogeography of the Crustacea. Crustacean Issues 4, pp. 51–67. A. A. Balkema, Rotterdam, The Netherlands.

———, and M. R. Campos. 1989. Cladistic relationships of the fresh-water crabs of the tribe Strengerianini (Decapoda: Pseudothelphusidae) from the northern Andes, with comments on their biogeography and descriptions of new species.—Journal of Crustacean Biology 9: 141–156.

———, and H. H. Hobbs, Jr. 1989. A new cavernicolous crab, *Zilchia falcata,* from Guatemala, with notes on the genera of Potamocarcinini (Crustacea, Decapoda, Pseudothelphusidae).—Bulletin du Muséum National d'Histoire Naturelle, Paris (4) 11, section A: 183–192.

Swofford, D. 1985. PAUP. Phylogenetic analysis using parsimony.—Illinois Natural History Survey, 607 E. Peabody Drive, Champaign, Illinois 61820.

Wiley, O. 1988. Parsimony analysis and vicariance biogeography.—Systematic Zoology 37: 271–290.

Zimmer, C. 1912. Beitrag zur Kentniss der süsswasser Dekapoden Kolumbiens.—*In:* O. Fuhrmann and E. Mayor, eds., Voyage d'exploration scientifique en Colombie.—Mémoires de la Société Neuchâteloise des Sciences Naturelles 5: 1–8.

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