

THE SYSTEMATIC AND BIOGEOGRAPHICAL STATUS OF *Fredius reflexifrons* (ORTMANN, 1897) AND *Fredius fittkai* (BOTT, 1967) (CRUSTACEA: BRACHYURA: PSEUDOTHELPHUSIDAE) FROM THE AMAZON AND ATLANTIC GUIANAS RIVER BASINS.

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ABSTRACT - There is considerable confusion in the literature regarding the systematic position and distribution of two pseudothelphusid crabs originally described as *Potamocarcinus reflexifrons* Ortmann, 1897 and *Potamocarcinus reflexifrons fittkai* Bott, 1967, and now included in the genus *Fredius* Pretzman, 1965, as *F. reflexifrons* and *F. fittkai*. Study of numerous specimens from recent collections, together with a critical analysis of the data published in the literature, shows that both taxa could be easily separated by gonopodal characters. The two species occupy discrete areas of distribution along the main axis of the Amazon River and in the upper Rio Negro Basin, respectively, with an overlap in the Atlantic Guianas. It is postulated that they originated from a common ancestor, through a process of vicariance, in the two areas observed at present. Permeability of barriers allowed their further occupancy of the Atlantic Guianas after the marine regressions in this area.

Key-words: Pseudothelphusidae, *Fredius*, freshwater crabs, Amazon region, biogeography

Situação Sistemática e Biogeográfica de *Fredius reflexifrons* (Ortmann, 1897) e *Fredius fittkai* (Bott, 1967) (Crustacea: Brachyura: Pseudothelphusidae) das Bacias do Rio Amazonas e dos Rios Costeiros das Guianas.

RESUMO - Há uma considerável confusão na literatura a respeito da posição sistemática e distribuição de duas espécies de caranguejos pseudotelfusídeos originalmente descritos como *Potamocarcinus reflexifrons* Ortmann, 1897 e *Potamocarcinus reflexifrons fittkai* Bott, 1967, atualmente incluídos no gênero *Fredius* Pretzmann, 1965 como *F. reflexifrons* e *F. fittkai*. O estudo de numerosos espécimes obtidos em coletas recentes, complementado por uma análise crítica dos dados publicados na literatura, mostra que ambos os taxa podem ser facilmente separados por caracteres do gonópodo. As duas espécies ocupam áreas de distribuição distintas ao longo do eixo principal do rio Amazonas e no alto rio Negro, respectivamente, com uma sobreposição na região das Guianas. Postula-se que essas espécies se originaram de um ancestral comum, por meio de um processo de vicariância, nas duas áreas observadas atualmente. A permeabilidade das barreiras permitiu uma posterior distribuição na região das Guianas após as regressões marinhas ocorridas naquela área.

Palavras-chaves: Pseudothelphusidae, *Fredius*, caranguejos dulcícolas, Amazônia, biogeografia

Introduction

There is considerable confusion in the literature regarding two conspicuous species of pseudothelphusid crabs, originally described as *Potamocarcinus reflexifrons* Ortmann, 1897, and

Potamocarcinus reflexifrons fittkai Bott, 1967. The large size, abundance and ubiquitous distribution of specimens attributed to one or the other species make them important components of the Amazonian and Guianese freshwater biotas. Due to their edibility for indig-

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enous communities, they are also potential vectors of the liver fluke *Paragonimus westermanni* (Kerbert, 1878). Notwithstanding this importance, there are wide discrepancies on the taxonomic treatment, and consequently geographical distribution, of both taxa in all recent revisions of the family for this area of South America (Pretzmann, 1972; Rodríguez, 1982a; Magalhães, 1986).

In the present contribution we re-describe both species using the abundant material available in several museums and collections, and discuss the respective ranges and the possible explanations for the observed distributions.

All the materials recorded are deposited in the Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA), the Museu de Zoologia da Universidade de São Paulo (MZUSP), the Museu Paraense Emílio Goeldi, Belém (MPEG), the Reference Collection of the Instituto Venezolano de Investigaciones Científicas, Caracas (IVIC), the Collection of the Universidade Santa Úrsula, Rio de Janeiro (USU), the Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main (SMF), the Natural History Museum, London (BM), and the Muséum National d'Histoire Naturelle, Paris (MNHN). The terminology used in the present contribution for the description of the first gonopod is according to the criteria established by Smalley (1964) and Rodríguez (1982a). Measurements of carapace breadth and carapace length are given after the number of specimens examined.

Systematic Account

Family Pseudothelphusidae Rathbun,
1893

Tribu Kingsleyini Bott, 1970

Genus *Fredius* Pretzmann, 1965

***Fredius reflexifrons* (Ortmann, 1897)
Figs. 1A-D; 3A**

Potamocarcinus reflexifrons Ortmann, 1897, p. 321, pl 17, fig. 6.

Pseudothelphusa reflexifrons, Rathbun, 1898, p. 535; Young, 1900, p. 207; Rathbun, 1905, p. 305, fig. 95; Coifmann, 1939, p. 109; Holthuis, 1959, p.231.

Pseudothelphusa colosii Coifman, 1939, p. 112, fig. 3, 4b, pl. 3. figs. 3-4.

Potamocarcinus (Kingsleya) reflexifrons reflexifrons, Bott, 1967, p. 309, figs. 11a, b; 1969, p. 53, pl. 14, figs. 26a,b, pl. 22. figs. 58a,b.

Guinotia (Guinotia) reflexi-frons, Pretzmann, 1965, p. 3.

Guinotia (Fredius) dunoonen-sis colosii, Pretzmann, 1967, p. 24.

Guinotia (Fredius) reflexifrons reflexifrons, Pretzmann, 1967, p. 24.

Eudaniela (Fredius) duno-onensis colosii, Pretzmann, 1971, p. 16; Pretzmann, 1972, p. 14, figs. 38-40.

Eudaniela (Fredius) reflexi-frons reflexifrons, Pretzmann, 1971, p.16; Pretzmann, 1972, p. 13, figs. 29-31, 41-44.

Eudaniela (Fredius) duno-onensis duno-onensis, Pretzmann, 1972, p. 14, figs. 49-52 (part).

Fredius reflexifrons, Rodríguez, 1982a, p. 183 (part).

Not *Fredius reflexifrons*, Rodríguez, 1982a, p. 183 (part), and fig. 128.

Fredius reflexifrons, Magalhães, 1986, p. 620, figs. 16-19, 34, 35.

Material Examined. — French Guiana: Station de Recherche de Saint Eugène,

17-19.iv.1996, J.C. de Massry, 1 male, 55.6:36.9, 1 female, carapace broken (MNHN 413-414). — Brazil, Amapá: Serra do Navio, Serra do Veado, 7.v.1994, leg. Projeto Diversitas Neotrópica, 1 male (USU 523);

idem, 1 male, 47.8:31.3 (INPA 583); Itauba do Piririm, Fazenda Parabrillo, 00° 52'N 50°53'W, 25.vi.1997, J.M. Cardoso, 1 male (MPEG 512). Pará: Belém, 1.ii.1966, W.D. Edmonds, 1 male, 48.6:30.6 (MZUSP 6385);

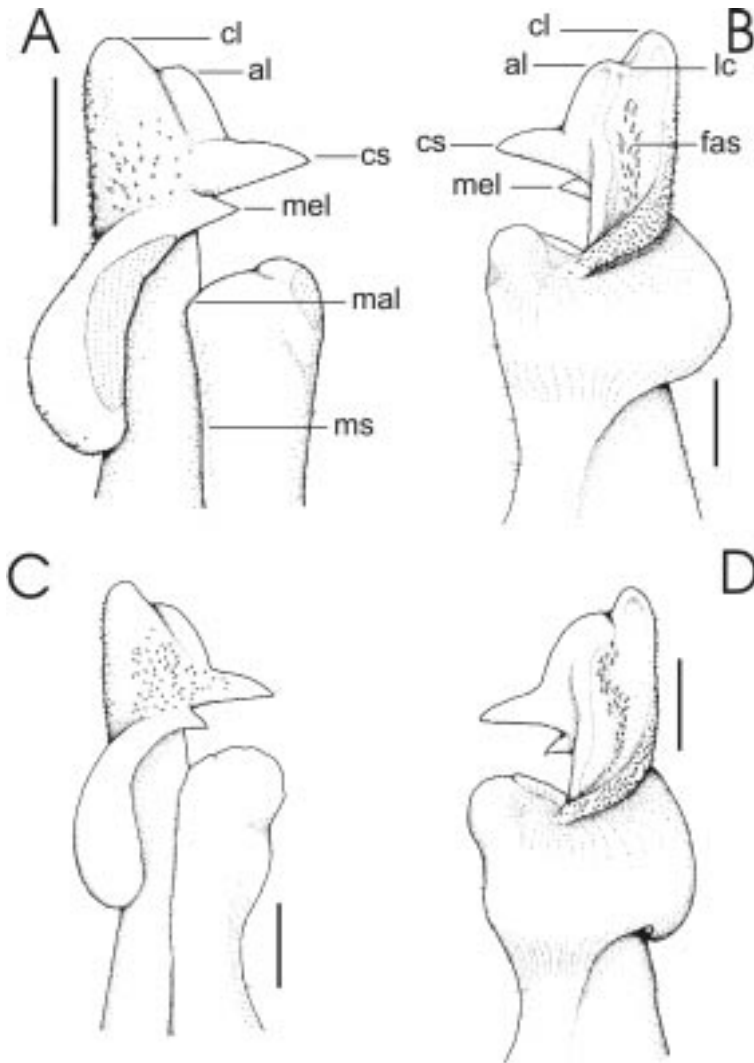


Figure 1. *Fredius reflexifrons* (Ortmann, 1897). A, B, male specimen from Rio Ampiyacu, Loreto, Peru (MZUSP 6389), first left gonopod: A, mesial view; B, lateral view; C, D, male specimen from Rio do Peixe Boi, Pará, Brasil (INPA 851), first left gonopod: C, mesial view; D, lateral view; al, auxiliary lobe; cl, cephalic lobe; cs, cephalic spine; fas, field of apical spines; lc, lateral channel; mal, marginal lobe; mel, mesial lobe; ms, marginal suture. Scale bars = 1mm.

rio do Peixe Boi, 01°11'30"S 47°18'54"W, 3-4.xi.1995, E. Matos & A. Henriques Jr., 1 male, 48.5:32.3 (INPA 851); Melgaço, Floresta Nacional de Caxiuanã, Estação Científica Ferreira Pena, rio Aruá, 2.ii.1998, J.A.R. Bernardi, 1 male (MPEG 575); idem, L.A. Quarema, 1 male (MPEG 535); Tomé-Açu, rio Acará-Mirim, 1 male (SMF 2882). Amazonas: Manaus, Reserva Ducke, igarapé Acará, 15.vii.1985, W. Magnusson, 1 male, 42.7:27.5 (INPA 159); Manaus, igarapé na Reserva Ducke, ii.1942, leg. unknown, 1 male, 39.7:25.4 (INPA 160); Manaus, Reserva Ducke, ii.1994, L. Schiesari, 1 male, 30.3:21.0 (INPA 850); Manaus, ZF 3, reserva do Km 41 (INPA/PDBFF), 02°26'56"S 59°46'13"W, 1 male, 35.5:23.1 (INPA 889); Município de Iranduba, Sítio Anaíra, rodovia AM-070, Manaus-Manacapuru, 03°10'39"S 60°07'39"W, 12.ix.1999, G.M. Santos, 1 male, 38.2:25.0 (INPA 852). — Peru, Loreto: Río Ampiyacu, Estirón, 15-25.iv.1966, B. Malkin, 1 male, 42.8:28.6 (MZUSP 6389).

Description of gonopod — First male gonopods robust, stronger at base, narrower at middle; subapical bulge well developed around lateral and cephalic sides. Marginal suture straight, situated on mesial side. Marginal lobe not differentiated, continuous with caudal surface. Mesial lobe distinct, acuminate, pointing in caudal direction. Cephalic spine longer than mesial lobe, distinctly acuminate, pointing in caudo-lateral direction. Cephalic lobe projected apically, rounded distally, with patch of very small spines along mesial and cephalic sides. Auxiliary lobe on caudal side, slightly shorter than cephalic lobe and continuous with cephalic spine, placed slightly obliquously in relation

to cephalic lobe in lateral view, their junction forming lateral channel running apically in almost straight direction and ending subterminally. Field of apical spines developed, forming elongated curved patch along lateral side, delimited by cephalic and caudal borders of apex.

Type — The type locality of *Potamocarcinus reflexifrons* is given only as "Upper Amazon" (*oberer Amazon*, Ortman, 1898). The syntypes were probably collected by Louis Agassiz during the Thayer Expedition in 1866 (Agassiz and Agassiz, 1868) and are deposited in the Academy of Natural Sciences of Philadelphia. Rathbun (1905) examined and illustrated the gonopod of the holotype. Magalhães and Türkay in 1985 designated as lectotype the specimen CA 3896 from this series (Spamer & Bogan, 1992). These syntypes are "partially disarticulated and very fragile" (Spamer & Bogan, 1992) and "dry" (Magalhães, 1986).

Distribution — Coastal river basins of the Guianas, and Amazon basin in Brazil and Peru, mainly near the Amazon River itself.

Remarks — Since its description, the species has been listed or mentioned, without examination of either the holotype or additional material, by Young (1900), Coifmann (1939), Holthuis (1959), and Pretzmann (1965, 1967, 1971).

The following authors have published additional data for the species: (1) Pretzmann (1972) illustrated the gonopod of a male from Brasil, without other data, collected by Natterer.

His two illustrations coincide with those of the gonopod of *Pseudothelphusa colosii* given by Holthuis (1959: 226, fig. 57e,f) (see below) in position and shape, but the cephalic spine in the former is somewhat more reduced. Pretzmann (1972) also illustrated the gonopod of a specimen, that he placed under *Guinotia (Fredius) dunoensis dunoensis*, which correspond to the gonopodal morphology of *Fredius reflexifrons*, but unfortunately he does not state whether this specimen came from British Guiana (Guyana) or Brazil. (2) Bott (1967, 1969) gives as “locus typicus” Pará, Belém, for *Potamocarcinus (Kingsleya) reflexifrons reflexifrons*. His illustrations coincide with the gonopod morphology of the male SMF 2882, although the locus typicus is erroneous since Pará is not in the “upper Amazon”. (3) Coifmann (1939) described her *Pseudothelphusa colosii* from Fawacuri on the Berbice River, British Guiana. The holotype and only specimen is an immature male, with a carapace breadth of 36.5mm in which the subapical bulge is not fully developed, but the lateral channel, cephalic spine and cephalic lobe of the gonopod, as given in the illustration, is characteristic of *Fredius reflexifrons*. (4) Holthuis (1959) ascribed to his *Pseudothelphusa colosii* specimens from several localities in Suriname. The gonopod, at least for the specimen illustrated from the Nassau Range, also corresponds both in the lateral channel, cephalic spine and cephalic lobe with *Fredius reflexifrons*, and most probably all the Surinamese specimens listed by this author also belong in this species.

Other names associated with this species, and that must be excluded from it, are the following: (1) *Pseudothelphusa agassizii* Rathbun, 1898, described from a female from Pará, collected by the Thayer Expedition. Rodríguez (1982) placed this name in the synonymy of *Fredius reflexifrons*. Pretzmann (1976) considered it a distinct species and later (Pretzmann, 1971, 1972) gave it subgeneric rank as *Eudaniela (Fredius) reflexifrons agassizii*, without adding any new materials. Actually, *Pseudothelphusa agassizii* cannot be either separated as a distinct taxa or synonymized under *Fredius reflexifrons* due to the female holotype and the presence in Pará of other pseudothelphusids with likely somatic characters. Accordingly, it must be considered as a *nomen dubium*. (2) *Potamocarcinus dunoensis* Rathbun, 1919, was also described from a female holotype, in this case from British Guiana (Guyana). Pretzmann (1972) referred specimens from British Guiana to his subspecies *Eudaniela (Fredius) dunoensis dunoensis*; however, at least the one illustrated by him, and possibly all the rest of his material (except those from the lot “BM 1935.6.4.1-3), belongs in *Fredius reflexifrons*.

Several records given in the literature for *Fredius reflexifrons* are based in females specimens and should be regarded as uncertain: (1) From Rodríguez (1982a), Guyana, without other data (BM); Guyana, Mazaruni River (BM 1935.5.20.59); Suriname, Suriname River, near Kaaimanston (BM 1959.3.20.2.). French Guiana, upper Oyapok river (MP B 5342); French Guiana, Village Zidok (MP B 5343). (2)

From Magalhães (1986), Rio Mapuera, Pará (INPA CR 380); Rio Gurupi, Pará (MZUSP 6386); Santa Cruz da Serra, Rondônia (MZUSP 7047); Nova Esperança, Rondônia (MZUSP 6382); Rio Tapirapé, Mato Grosso (MZUSP 6379).

We have left out of our analysis the two male specimens from Guyana, mont Roraima, (BM) and Suriname, Donderberg (BM 1959.3.20.4), that we have not reexamined.

Finally, Rodríguez (1982a) recorded and illustrated under *Fredius reflexifrons* 1 male from Guyana, collected by G.S. Ashby, Oxford University Expedition (BM 1935.6.14.1-3) and recorded another male from Venezuela, San Carlos de Rio Negro (MBC). Both specimens are presently transferred to *Fredius fittkai*.

Fredius fittkai (Bott, 1967)

Fig. 2A-D; 3B

Potamocarcinus (Kingsleya) reflexifrons fittkai Bott, 1967, p. 310, fig. 12a,b; 1969, p. 54, pl. 15, figs. 27a,b, pl. 22, figs. 59a,b.

Eudaniela (Fredius) duno-onensis dunoensis, Pretzmann, 1972, p. 14, (part, "Museum London 1935.6.4.1/3").

Fredius fittkai, Rodríguez & Campos 1998, p. 768.

Material Examined — Guyana:

British Guiana, 14.vi.1935, 1 male (BM 1935.6.14.1-3).— Venezuela, Amazonas: San Carlos de Rio Negro, vi.1976, R. Herrera, 1 male, 79.6:53.1 (IVIC 890); 10.5 km ENE de San Carlos de Rio Negro, 27.v.1978, J. Hall, 2 males, 59.2:41.2, 85.9:57.1, 1 female, 63.9:41.8 (IVIC 583); rio Negro, shoreline, San Carlos de Rio Negro, 13.iii.1977, J. Hall, 97.7:61.9 (IVIC 584). Brazil, Amazonas: Chamata, upper rio Negro (Gebirgsbach Chamata, am oberer Rio Negro, Chamata-Gou), 17.i.1963, E.-J. Fittkau, 1 male holotype, 69.4:44.7 (SMF 2879a); Município de

Barcelos, Balawa-ú, igarapé Loahik, trib. of Rio Demini, 01°47'91"N 63°46'88"W, ca. 180m alt., 18.v.1995, L.S. Aquino & U.C. Barbosa, 3 males, 55.3:37.5-64.0:42.5, 3 females, 58.9:38.8-64.4:41.3 (INPA 856); Município de Barcelos, Toototobi, igarapé unnamed, 01°45'57"N 63°37'02"W, ca. 340m alt., 13.viii.1994, L.S. Aquino & U.C. Barbosa, 1 male juvenile, 22.5:15.6, 1 male, 63.7:40.4, 4 females, 30.2:20.2-61.3:41.2 (INPA 860); idem, 1 male juvenile, 23.9:17.0 (IVIC 1093); Município de Santa Izabel do Rio Negro, Maturacá, igarapé Powo-Powo, tributary left bank rio Maturacá, 00°37'33"N 66°07'20"W, 1.iv.1995, V. Py-Daniel & U.C. Barbosa, 1 male, 65.0:43.2, 3 females, 64.5:40.9-77.5:50.0 (INPA 854); idem, 1 male, 48.2:32.3, 1 female, 79.2:51.9 (IVIC 1094); Município de Barcelos, Novo Demini, rio Demini, igarapé unnamed, 01°36'55"N 63°39'13"W, ca. 270m alt., 6.viii.1994, L.S. de Aquino & U.C. Barbosa, 1 juvenile male, 22.5: 15.6, 1 male, 63.7:40.4, 2 females, 62.1:41.0; 64.0:42.6 (INPA 859); idem, 1 male, 61.0:40.6, 1 female, 51.3:34.5 (IVIC 1092); Município de Santa Izabel do Rio Negro, Marará, rio Marará, igarapé unnamed, 01°11'45"N 64°48'33"W ca. 460m alt., 8.viii.1994, L.S. Aquino & U.C. Barbosa, 2 males, 67.8:45.1; 84.4:53.0, 2 females, 70.9:46.8; 82.4:52.4 (INPA 863); Município de Barcelos, igarapé da Missão Aracá, trib. rio Aracá, 01°10'17"N 65°35'33"W, 120m alt., 30.viii.1996, L.S. Aquino & U.C. Barbosa, 3 males, 59.8:39.4-56.5:37.9, 5 females, 46.9:31.5-79.9:51.6 (INPA 855); idem, 1 male, 52.3:35.1, 1 female, 51.3:34.1 (MZUSP 13902); Município de Santa Izabel do Rio Negro, Pukima, rio Marauíá, igarapé unnamed, 00°41'34"N 65°03'45"W, 30.xi.1994, L.S. Aquino & U.C. Barbosa, 2 males, 60.3:39.0, 74.4:47.6, 1 female, 76.0:50.7 (INPA 861); Município de Santa Izabel do Rio Negro, Pohoro, igarapé Irapirapi, trib. rio Marauíá, 00°34'16"N 65°14'57"W, 29.ii.1994, L.S. Aquino & U.C. Barbosa, 2 males, 54.1:36.5; 72.2:47.6, 4 females, 71.5:48.8-96.8:62.4 (INPA 857); Município de Santa Izabel do Rio Negro, Maiá, rio Maiá, igarapé Poko Poko, 00°30'00"N 65°49'32"W, 5.iv.1995, V. Py-Daniel & U.C. Barbosa, 1 male, 47.7:31.4, 1

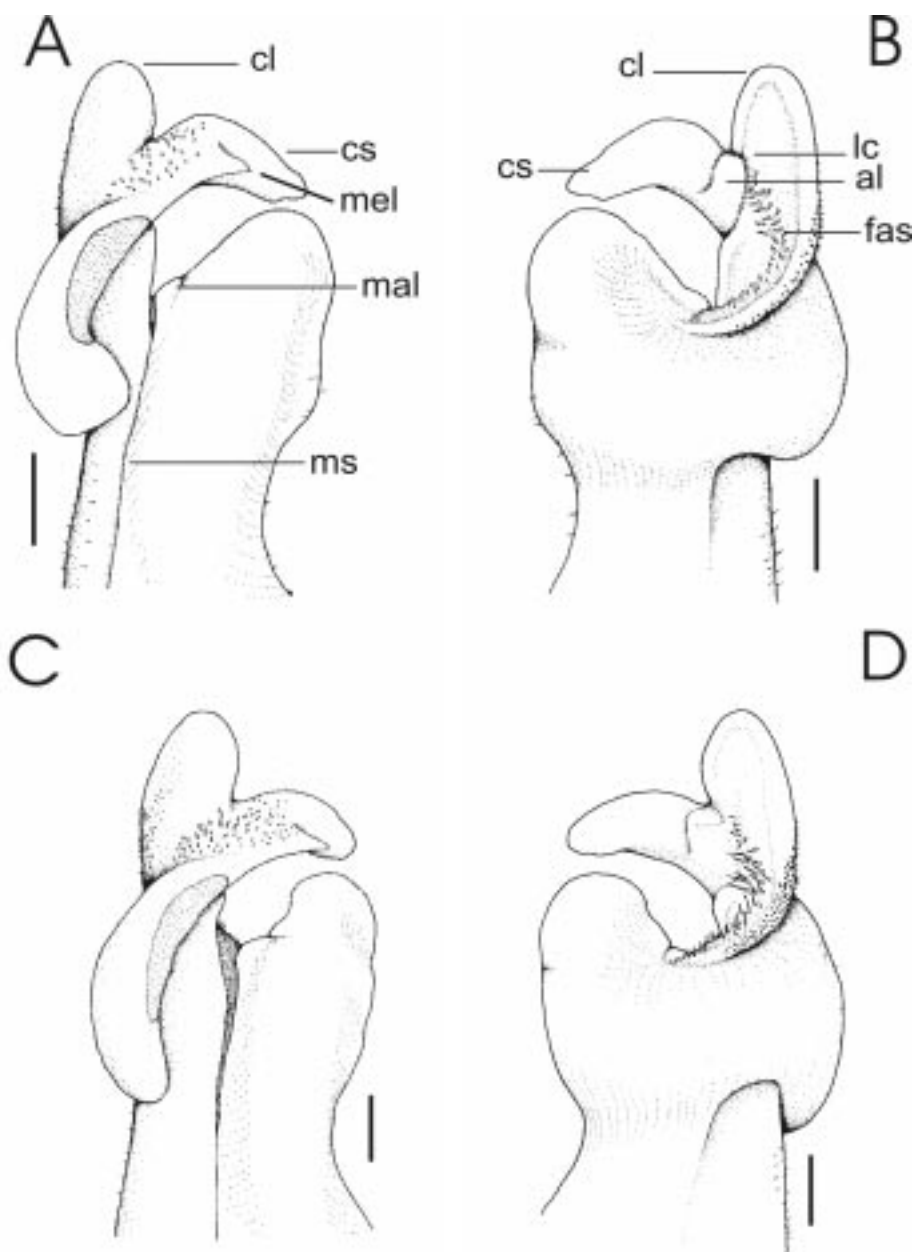


Figure 2. *Fredius fittkaui* (Bott, 1967). A, B, holotype specimen from Chamata (= Xamata, Rio Marauíá basin), upper Rio Negro region, Amazonas, Brasil (SMF 2879a), first left gonopod: A, mesial view; B, lateral view; C, D, male specimen from San Carlos de Rio Negro, Estado Amazonas, Venezuela (IVIC 584), first left gonopod: C, mesial view; D, lateral view; al, auxiliary lobe; cl, cephalic lobe; cs, cephalic spine; fas, field of apical spines; lc, lateral channel; mal, marginal lobe; mel, mesial lobe; ms, marginal suture. Scale bars = 1mm.

female, 72.6:47.8 (INPA 862); idem, 1 male, 58.6:38.3 (IVIC 1095); São Gabriel da Cachoeira, 00°07'S 67°04'W, morro Fortaleza, 2.iv.1990, J. Zuanon & P. Petry, 2 males, 32.1:22.6-77.0:50.5, 4 females, 28.0:18.4-93.0:61.9 (INPA 853); São Gabriel da Cachoeira, 00°07'S 67°04'W, Igarapé da Serra, 17.ii.1994,

1 immature male, 32.5:22.1 (INPA 858).

Description of gonopod — First gonopod robust, stronger at base, narrower at middle, subapical bulge well developed around lateral and cephalic sides. Marginal suture straight, situated on mesial side. Marginal lobe not



Figure 3. *Fredius reflexifrons* (Ortmann, 1897). A, male specimen from Rio Acará, Tomé-Açu, Pará, Brasil, (SMF 2882), dorsal view. *Fredius fittkaui* (Bott, 1967). B, holotype specimen from Chamata (= Xamata, Rio Marauíá basin), upper Rio Negro region, Amazonas, Brasil (SMF 2879a), dorsal view. Scale bar = 10mm.

differentiated or sometimes forming small projection which produces slight discontinuity from the caudal surface. Mesial lobe distinct, acuminate, pointing in caudal direction. Cephalic spine well developed, finger-like, strongly projected laterally, much longer than mesial lobe. Cephalic lobe projected apically, rounded distally, with patch of very small spines along mesial and cephalic sides. Auxiliary lobe situated on lateral side, much shorter than cephalic lobe, not visible in mesial view, placed obliquely in relation to cephalic lobe in lateral view, its terminal portion situated mesially in relation to cephalic lobe; lateral channel formed by junction of both lobes, slightly curved towards lateral side, ending mesially. Field of apical spines developed, forming elongated, curved patch along lateral side, delimited by cephalic and caudal borders of apex.

Type — The type locality of *Fredius fittkaui* is Chamata-Gou (= Xamata). According to Bott (1967, 1969), this is in the upper Rio Negro area, between Tapuruquara (currently Santa Izabel do Rio Negro) and Rio Marauiá. However, Xamata (00°27'100"N 65°04'335"W) is a Yanomami village in the Rio Marauiá basin, which flows into the upper Rio Negro just upstream from Santa Izabel.

Distribution — Brazil and Venezuela, in the upper Rio Negro region, and Guyana.

Remarks — *F. reflexifrons* and *F. fittkaui* can be separated by the following characters of the male first gonopod: (a) Cephalic spine: in *F.*

reflexifrons, this spine is straight and acuminate, being distinctly shorter than in *F. fittkaui*, in which it is well developed and clearly curved, with a rounded tip. (b) Auxiliary lobe: in *F. reflexifrons* it lays on the caudal side and is slightly shorter than cephalic lobe, its proximal portion being continuous with the cephalic spine, the distal portion ending just subterminally in relation to the cephalic lobe; in *F. fittkaui* it is situated on the lateral side and is distinctly shorter than cephalic lobe, its terminal portion situated mesially in relation to cephalic lobe. (c) Lateral channel: in *F. reflexifrons* this channel runs apically in an almost straight direction and ends subterminally, while in *F. fittkaui* it is slightly curved towards the lateral side, ending mesially.

Except for the original locality and the statement in Rodríguez & Campos (1998) to the effect that material from Rio Negro, Venezuela, listed under *Fredius reflexifrons* in Rodríguez (1982a) actually belong in *F. fittkaui*, the species has not being recorded in the literature under this name. Pretzmann (1971; 1972) included it under *Pseudothelphusa dunoensis* Rathbun, first as a synonym of *Pseudothelphusa colosii* Coifman (as *Eudaniela (Fredius) dunoensis colosii*), and later (Pretzmann, 1972) as a synonym of the typical form (as *Eudaniela (Fredius) dunoensis dunoensis*), but did not add any new material. Among the material examined by Pretzmann (1972), at least one lot (BM 1935.6.14.1/3) belongs in *F. fittkaui*.

As stated above, Rodríguez (1982a) recorded it erroneously as *Fredius reflexifrons*, from Guyana (BM 1935.6.14.1-3) and recorded another male from San Carlos de Rio Negro, Venezuela (MBC).

Biogeography

Taking into account only reliable records, as stated above, the geographical areas of distribution can be discriminated as follows (Fig. 4). *Fredius reflexifrons* has a wide distribution along the Amazon River, at elevations below 100m above sea level, where it occurs in association with terra firme forest streams. The most westerly record is in the Rio Ampyiacu, a tributary on the left bank of the Rio Amazonas, near Pebas, in Peru. Another area is at the junction of the Rio Solimões and Rio Negro, near Manaus. A third area covers some of the secondary Atlantic rivers around the mouth of the Rio Amazonas (Rio Araguari, Rio Anapú and Rio Capim), and continues in the rivers of the Atlantic Guianas (Guyana, Suriname and French Guiana). The area of *Fredius fittkai* is restricted to the upper reaches of the Rio Negro in Venezuela and Brazil, and the smaller left tributaries of this river, usually in localities higher than those of *F. reflexifrons*. So far the species has not been recorded in the Rio Branco basin; collections along the Rio Uraricoera by Victor Py-Daniél and associates (personal communication) has revealed the presence of three other species of *Fredius*, but not of *F. fittkai*.

There is an isolated record of *F. fittkai* in Guyana, without indication of a precise locality, pointing to an

overlap of both species in the Atlantic basin formed by the rivers that run through the territories of Guyana, Suriname and French Guiana, and discharge into the Atlantic. The continuous mountainous chain between the Orinoco, the Amazon and Atlantic Guianas affords a barrier to the dispersion of these species of *Fredius*, since all these seem to be restricted to altitudes below 500m (see also Rodríguez & Campos, 1998: 768, 772). However, the Amazon Basin is accessible along the lowlands between Amapá and the French Guiana and through the inundated areas of the Rupununi, which connect the Essequibo and Cuyuni with the Amazon Basin (Rodríguez, 1982b). These connections and weakened interspecific competition due to the paucity of Pseudothelphusid species in the Atlantic Guianas, could explain this overlap.

On the other hand *F. fittkai* do not penetrate the Orinoco basin, notwithstanding its connection of the Brazo Casiquiare, a natural waterway between the Rio Negro and Rio Orinoco (Rodríguez, 1982b). Five species of *Fredius* are found in the Orinoco Basin neighboring the area of distribution of *F. fittkai* (see Rodríguez & Campos, 1998), and this could be one reason for its exclusion from the Orinoco Basin.

Some parts the Guianas are one of the oldest on earth, dating to precambrian times, while the present configuration of the water system is a more recent event (Garner, 1975). A likely hypothesis, according to the evidence summarized by Rodríguez &

Pereira (1992), suggests that the Orinoco Basin is the oldest, following the Essequibo-Cuyuni Basin formed by an early splitting from a once larger Orinoco Basin. The middle and lower Amazon valley is younger than the Orinoco and Cuyuni-Essequibo Basin and was formed by alluvionic deposition ranging from Tertiary to Holocene (Grabert, 1983). Finally, the Atlantic area, 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 Rodríguez & Campos (1998) have theorized that, although most species of *Fredius* were present in an hypothetical major basin comprising the present Rio Orinoco, Rio Essequibo and Rio Cuyuni and much of the evolution of the group occurred there. *Fredius reflexifrons* possibly originated from an ancestor in the Amazon region and then dispersed into the present territory of French Guiana after the marine regression in this area. Taken into account the cladistic analysis of Rodríguez & Campos (1998)

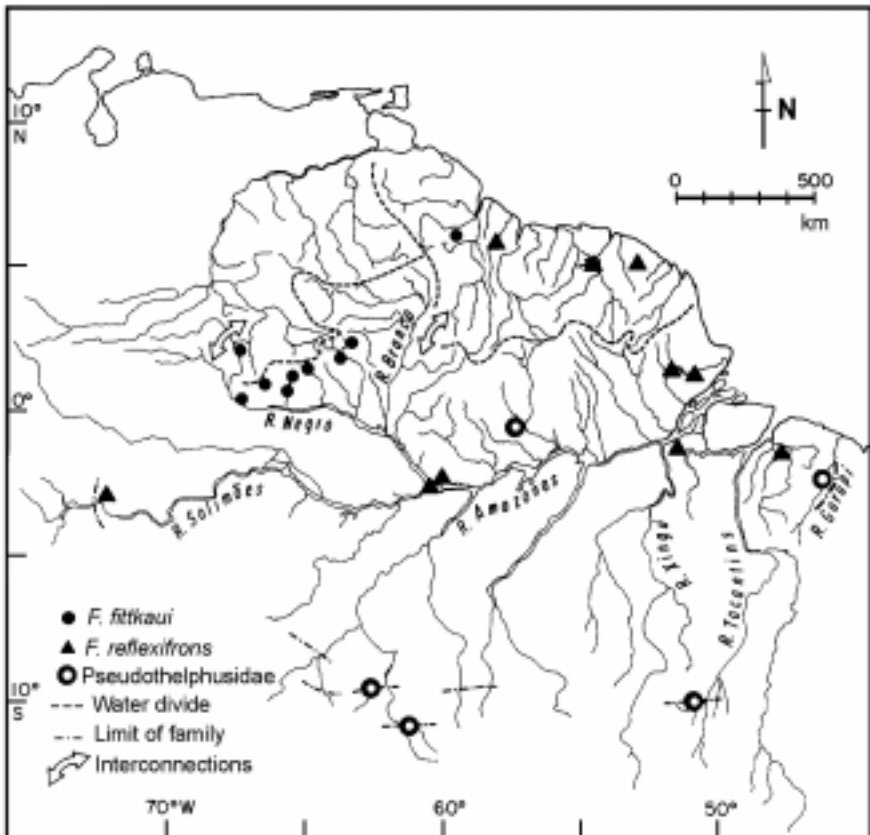


Figure 4. Geographical distribution of *Fredius reflexifrons* (Ortmann, 1897) and *Fredius fittkauri* (Bott, 1967) in the Amazon Basin and the Atlantic Guianas.

which shows a sister taxon for the pair *F. reflexifrons* and *F. fittkaui*, and the distribution patterns presented in the present analysis, it can be postulated that the common ancestor of the species covered both the Amazon River axis and the surrounding northern piedmonts of the basin. The separation of the areas induced a process of allopatry that originated the two vicariant species observed at present. The permeability of barriers allowed their overlap in the Atlantic Guianas.

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