

CLADISTIC RELATIONSHIPS OF FRESH-WATER
CRABS OF THE TRIBE STRENGERIANINI
(DECAPODA: PSEUDOTHELPHUSIDAE)
FROM THE NORTHERN ANDES, WITH
COMMENTS ON THEIR BIOGEOGRAPHY AND
DESCRIPTIONS OF NEW SPECIES

Gilberto Rodríguez and Martha R. Campos

ABSTRACT

The species of Strengerianini are restricted to altitudinal levels between 900 and 3,000 m in the Eastern, Western, and Central Cordilleras, and the Sierra Nevada de Santa Marta in Colombia, and the Sierra de Perija in Venezuela. A cladistic analysis of the genera *Chaceus* and *Strengeriana*, including the new species *Strengeriana risaraldensis*, *Strengeriana bolivarensis*, *Strengeriana huilensis*, and *Strengeriana taironae*, using somatic and gonopodal characters, confirms the separation of both genera and suggests the geographic disjunction of 3 sister groups. Bridging of these disjunctions requires, within a dispersalist hypothesis, the establishment of migratory paths either across extensive areas of lowlands or through a very long stretch of continuous highlands, if the present geography is assumed. It is suggested that the group was widespread in the area by 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. This model requires dating the first radiation of the Strengerianini before the end of the Miocene, after a previous splitting of the family into sister groups, in the Antilles and in the northern Andes, in Eocene times.

During surveys of the fauna of high altitudes in the Colombian Andes, carried out since 1984, several species of pseudoscorpionid crabs were collected. The discovery of four undescribed species of the genus *Strengeriana* in this material revealed further problems in the relationships of some of the genera of Pseudoscorpionidae, such as the distribution of one of the new species in the Sierra de Santa Marta, in complete isolation from the area of the genus in the Cordilleras of Central Colombia. In the present contribution we have explored these problems, basing our work on a cladistic analysis of the genera *Strengeriana* and *Chaceus*.

METHODS AND MATERIALS

Species Examined.—The tribe Strengerianini includes at present the genera *Strengeriana*, *Chaceus*, *Martiana*, and *Phallangothelphusa*. The autapomorphy that defines the group including *Strengeriana*, *Chaceus*, and *Martiana*, is the advancement of the jugal angle to form a closed or partially closed orifice for the efferent branchial channels (Fig. 1f, 2g, 3g, 4e) instead of the U-shaped one found in all other groups of fresh-water crabs (Potamoidea). The cladistic analysis presented below covers all the species of *Strengeriana* and *Chaceus*, including the new species described in this paper (Table 1).

The types of the new species are deposited at the Museum of Natural History, Instituto de Ciencias Naturales, Universidad Nacional, Bogota (ICN-MHN).

The monotypic genus *Phallangothelphusa* was not covered in the analysis because the closure of the efferent branchial channel is achieved by an elongation of the epistome, not homologous to the advancement of the jugal angle found in the Strengerianini. For this reason this genus lies outside the monophyletic group that includes *Strengeriana* and *Chaceus*.

In *Martiana*, another monotypic genus, the gonopod (Fig. 5O) shows a rudimentary digitiform process (n) and a coiled, button-shaped apex resembling the respective parts of *Chaceus pearsei* (Rathbun, 1915) and *C. davidi* Campos and Rodríguez, 1984, but all other gonopodal characters are similar to those of the tribe Hiplobocerini. This intermediate position casts a large uncertainty about *Martiana* forming a monophyletic group with *Strengeriana* and *Chaceus*, and for this reason this genus was also excluded from the analysis.

Characters Examined.—The modern systematics of this family is based on the morphology of the male gonopod (Smalley, 1964a), and for this reason the hypotheses proposed to explain the evolution of these crabs have taken into account only the structure of this organ (Delamare-Deboutteville, 1976; Rodríguez, 1982). In the present contribution we have made an attempt to use both somatic and gonopodal characters. To this end, six characters on the dorsal surface of the carapace related to the shape of the front, postfrontal lobes, cervical and median grooves, and anterolateral margin, were selected for analysis (Table 2). These characters show slight but constant intrageneric differences and are commonly used in the diagnosis of species (cf. Rathbun, 1905; Rodríguez, 1982).

Table 1. List of the known species of the tribe Strengerianini with indication of the extension of the endognath of the third maxilliped, condition of the efferent channel, and binary state of each of these characters in parentheses.

Species	Extension of endognath	Efferent aperture
<i>Strengeriana fuhrmanni</i> (Zimmer, 1912)	1.09 (0)	0.0 (1)
<i>S. foresti</i> Rodriguez, 1980	1.11 (0)	0.4 (1)
<i>S. restrepoi</i> Rodriguez, 1980	1.17 (0)	0.2 (1)
<i>S. tolimensis</i> Rodriguez and Diaz, 1981	1.06 (0)	0.0 (1)
<i>S. chaparralensis</i> Campos and Rodriguez 1984	1.07 (0)	0.0 (1)
<i>S. risaraldensis</i> , new species	1.16 (0)	0.4 (1)
<i>S. bolivarensis</i> , new species	1.07 (0)	0.1 (1)
<i>S. huilensis</i> , new species	1.05 (0)	0.2 (1)
<i>S. taironae</i> , new species	0.96 (0)	0.0 (1)
<i>Chaceus pearsei</i> (Rathbun, 1915)	0.70 (1)	0.1 (1)
<i>C. motiloni</i> Rodriguez, 1980	0.58 (1)	0.1 (0)
<i>C. nasutus</i> Rodriguez, 1980	0.74 (1)	0.6 (0)
<i>C. davidi</i> Campos and Rodriguez, 1984	0.70 (1)	0.0 (1)
<i>Martiana clausa</i> (Rathbun, 1915)	0.81 (1)	0.2 (1)
<i>Phallangothelphusa dispar</i> (Zimmer, 1912)	0.77 (1)	0.9 (0)

The structure and proportions of the exognath of the third maxilliped (character 12, Tables 2, 3) and the degree of aperture of the orifice of the efferent branchial channel (character 4) also display considerable specific fidelity. In the various species of Strengerianini the basal portion of the exognath may be fully developed or somewhat reduced (see below under "Out-group selection"). This character was evaluated as the proportion of the length of the exognath to the length of the external margin of the ischium of the endognath (Table 1). The orifice of the efferent branchial channels were scored as "closed" when the quotient of the ratio (the largest diameter of the orifice/the distance from the jugal angle to the outer end of the epistome) was <0.5 (Table 1).

Homologies in the Gonopodal Processes.—The gonopod of the Pseudothelphusidae is a complex structure, which can be understood according to the criteria established by Smalley (1964a). The possible homologies of the gonopodal processes in the species of the tribe Strengerianini (Fig. 5), postulated on the basis of similarity of morphology, either directly or through an intermediate form, and topographical position within the gonopod apex, are the following. *Strengeriana fuhrmanni* (Zimmer, 1912) (Fig. 5A) shows the simplest arrangement of the gonopod, consisting of three plates, mesial, marginal (caudal), and lateral. *Strengeriana risaraldensis* (Fig. 5B) has a similar gonopod, although slightly distorted. The mesial plate (m) exists as a separate unit in all other species of *Strengeriana* (Fig. 5C, E–J), but the mesial and marginal plates are indistinct. In *Strengeriana restrepoi* Rodriguez, 1980 (Fig. 5C) two new elements appear in the form of a caudal process (u) and a lateral spine (s). The caudal process reappears only in *Strengeriana tolimensis* Rodriguez and Diaz, 1981 (Fig. 5I), with spinulation identical to *S. restrepoi*. The lateral spine (s) is present in *Strengeriana chaparralensis* Campos and Rodriguez, 1984 (Fig. 5G), *Strengeriana huilensis* (Fig. 5H) and *S. tolimensis* (Fig. 5I), together with a second lateral spine (t); in *Strengeriana foresti* Rodriguez, 1980 (Fig. 5E) the second lateral spine (t) is represented only by an inconspicuous swelling. The lateral crenulated prominence (s) in

Strengeriana taironae (Fig. 5J) possibly represents a fusion and simplification of these teeth (s + t).

The cephalic process (r) is rudimentary in *S. restrepoi*, very conspicuous in *Strengeriana bolivarensis* (Fig. 5F), slightly bifid in *S. foresti*, and strongly bifid and prominent in *S. chaparralensis*, *S. huilensis*, and *S. tolimensis*. The strong fingerlike cephalic projection (r) of *S. taironae* possibly represents a simplification of this process; the toothed caudal crest of this species cannot be homologized with any other structure within the Strengerianini.

The homology of the fingerlike (n) and marginal (p) processes of *Chaceus* (Fig. 5K) with the mesial and marginal plates of *S. fuhrmanni* has been discussed by Rodriguez (1982). These processes are present in all species of *Chaceus* (Fig. 5K–N), enormously developed in *Chaceus nasutus* Rodriguez, 1980 (Fig. 5M), reduced in *C. pearsei* (Fig. 5L) and *C. davidi* (Fig. 5N). In the last two species a new morphological element appears in the form of a coiled ridge (q).

Out-group Selection.—The autapomorphy that defines the family Pseudothelphusidae is the possession of a pseudolung in the branchial chamber (Diaz and Rodriguez, 1977). All the taxonomic systems that have been recently devised for the family (Smalley, 1964b; Pretzmann, 1972; Rodriguez, 1982), divide it into two subfamilies, Epilobocerinae with the single genus *Epilobocera* from the Antilles, and Pseudothelphusinae comprising the rest of the South and Central American genera. The distinction between both subfamilies is based on the morphology of the exognath of the third maxilliped, the presence of a "field of spines" in the gonopod of the Pseudothelphusinae, and the presence of a tooth inside the efferent channel of the Epilobocerinae. The last two characters represent synapomorphies of the respective subfamilies.

The structure and proportions of the third maxilliped display considerable variations in the several families of fresh-water crabs (Potamoidea), attributable to different respiratory adaptations (Rodriguez, 1986). The majority show the general brachyuran condition, with the exognath and its palp fully developed and functional. The Epilobocerinae display a trend towards re-

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

1	Cervical groove (0) reaching margin, (1) not reaching margin.
2	Afferent aperture (0) open or almost open, (1) closed or almost closed.
3	Postorbital notch (0) absent or slight, (1) conspicuous.
4	Anterolateral margin (0) with small, acute or papilliform teeth at least on terminal half, (1) completely devoid of teeth.
5	Postfrontal lobes (0) more or less defined, (1) absent and replaced by two small scars.
6	Median groove (0) indicated by frontal notch or shallow postfrontal depression, (1) absent.
7	Upper border of front (0) well defined, with or without row of tubercles, (1) undefined.
8	Third maxilliped, ratio exognath to ischium of endognath (0) approximately 1, (1) exognath < 1.
9	Gonopod, lateral crest (0) present, (1) absent.
10	Gonopod, digitiform processes over field of spines (0) absent, (1) present.
11	Gonopod, process of marginal plate (0) absent, (1) present.
12	Gonopod, tubercle of lateral surface (0) absent, (1) present.
13	Gonopod, bifid or bicuspid cephalic process (0) absent, (1) present.
14	Gonopod, coiled process (0) absent, (1) present.
15	Gonopod, marginal tubercle (0) absent, (1) present.
16	Gonopod, mesial plate (0) undeveloped, (1) developed into crest.
17	Gonopod, toothed crest (0) absent, (1) present.

duction of the exognathal palp. *Epilobocera sinuatifrons* (A. Milne Edwards) from Puerto Rico and *Epilobocera haytensis* (Rathbun) from Hispaniola possess a rudimentary palp; in the other four species of the genus the rudimentary palp may be present or absent. In the Pseudothelphusinae the palp is always absent. Additionally, there is a trend for reduction of the exognath itself, except in several species of *Strengeriana* in which the exognath is completely developed. This suggests that the most primitive species of Pseudothelphusinae are within this genus.

The irreversible loss of the exognathal palp represents one of the basic synapomorphies of the subfamily Pseudothelphusinae, whereas the presence of a rudimentary palp found in *Epilobocera* represents the plesiomorphic condition of this character. Based on the trend towards the reduction of the exognath the genus *Epilobocera* can be considered as the most likely sister group of the Pseudothelphusinae and will be used as an out-group for the polarization of characters.

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

Table 3. Data matrix of 17 characters of the Strengerianini.

Species	State of characters
<i>Strengeriana fuhrmanni</i>	11100100000000010
<i>S. risaraldensis</i>	11100100000000010
<i>S. foresti</i>	11100100100110010
<i>S. restrepoi</i>	11100100100100110
<i>S. tolimensis</i>	11011110100110110
<i>S. chaparralensis</i>	11000100100110010
<i>S. huilensis</i>	11111100100110010
<i>S. bolivarensis</i>	11111100100110010
<i>S. taironae</i>	11111110100110011
<i>Chaceus pearsei</i>	01100001011001000
<i>C. motiloni</i>	01001001011000000
<i>C. nasutus</i>	00011001011000000
<i>C. davidi</i>	01001001011001000

SYSTEMATICS

Family Pseudothelphusidae

Tribe Strengerianini Rodriguez, 1982

Genus *Strengeriana* Pretzmann, 1971

Strengeriana risaraldensis, new species

Fig. 1a–f

Material.—Municipio Pueblo Rico, road between Pueblo Rico and Palo Blanco, 1,350 m above sea level, Risaralda Department, Colombia; 21 August 1987; R. Sanchez collector; 1 ♂ holotype, carapace width (cw) 20.1 mm, carapace length (cl) 12.8 mm (ICN-MHN No. CR 0782).

Description.—Cervical groove straight and deep, ending far from lateral margin. Anterolateral margin with depression behind orbit followed by series of approximately 10 regularly spaced teeth on anterior half and similar series of 8 teeth on posterior half. Postfrontal lobes small, oval and low, marked on anterior margin by row of tubercles. Median groove absent. Surface of carapace in front of postfrontal lobes conspicuously depressed and inclined anteriorly. Upper border of front well defined, almost straight in dorsal view, arched in frontal view, marked with row of conspicuous, well-defined tubercles. Lower margin strongly sinuous in frontal view. Surface of front between upper and lower borders high. Surface of carapace smooth, covered by small papillae not visible to naked eye; regions strongly demarcated.

Palm of larger chela strongly inflated; fingers gaping slightly. Walking legs slender, but not unusually elongated, largest being those of third pair (total length approximately equal to width of carapace); merus

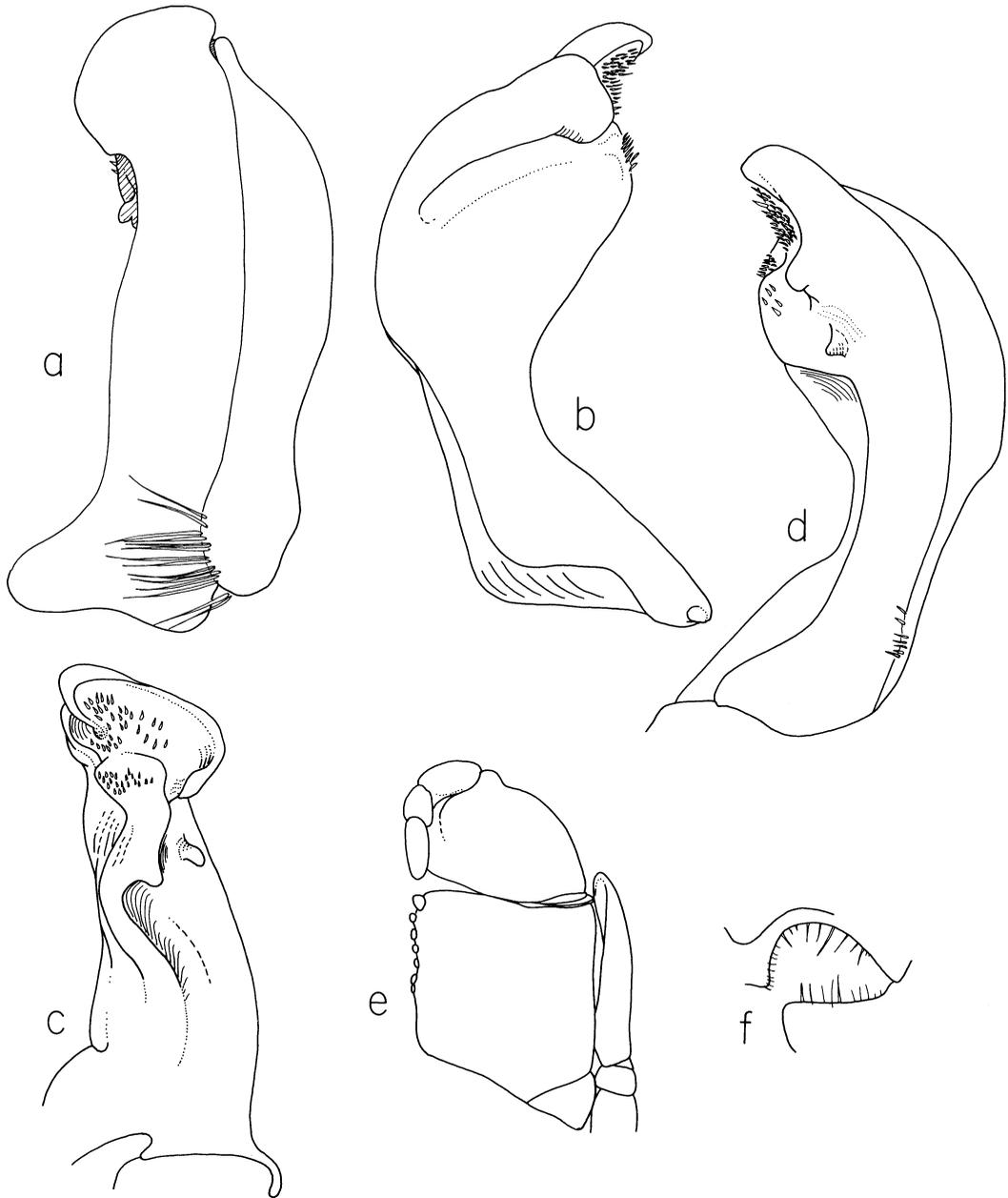


Fig. 1. *Strengeriana risaraldensis*, new species, holotype male, ICN-MHN No. CR 0782: a, left gonopod, caudal view; b, lateral view; c, cephalic view; d, mesial view; e, third maxilliped, left; f, opening of branchial channel, left.

in this pair 2.7 times longer than wide. Exopod of third maxilliped overreaching lateral margin of ischium of exognath. Orifice of efferent branchial channel almost closed by spine at jugal angle and by production of lateral lobe of epistome.

Male gonopod strongly arched in caudo-cephalic plane. Apex formed by 3 distinct

lobes; mesial and marginal lobes rounded, cup-shaped, with their borders strongly demarcated; border of mesial lobe strongly bent at cephalic and caudal ends; cephalic lobe very wide in lateral view, strongly sinuous in cephalic view, with its distal margin partially fused to field of spines. Small fingerlike projection located subapically on

mesial surface. Internal cavity of mesial lobe densely covered by long spines; patch of shorter spines on external surface of cephalic lobe.

Size. — This is a small species (cw 20.1 mm) for the family, but near the mean size of the genus.

Etymology. — The specific name refers to Risaralda Department, where the type locality is situated.

Remarks. — The species is closely allied to *Strengeriana fuhrmanni* (Zimmer, 1912), but the gonopod is conspicuously expanded in the caudocephalic plane, and the caudal lobe thus formed is strongly prominent and sinuous.

***Strengeriana bolivarensis*, new species**

Fig. 2a–g

Material. — Finca El Silencio, Corregimiento Faralones, Municipio Bolívar, 1,500 m above sea level, Antioquia Department, Colombia; 31 August 1987; R. Sanchez collector; 1 ♂ holotype, cw 21.5 mm, cl 13.2 mm, 3 ♂ paratypes, cw 24.9 (broken carapace), 17.9, and 14.0 mm, cl 14.6, 11.2, and 9.0 mm (ICN-MHN No. CR 0785).

Description. — Cervical groove straight and deep, ending far from lateral margin. Anterolateral margin with shallow depression behind orbit, followed by series of approximately 10 regularly spaced papillae on anterior half, and another series of 10 similar papillae on posterior half. Postfrontal lobes wide, but ill defined. Median groove absent. Surface of carapace behind front moderately inclined anteriorly and towards midline. Front almost straight in dorsal view, with slight depression in middle; upper border well defined, marked with row of conspicuous, well-defined tubercles. Lower margin sinuous in frontal view. Surface of front between upper and lower margins high. Surface of carapace smooth, covered by small papillae not visible to naked eye; regions strongly demarcated.

Palm of larger chela moderately inflated. Fingers gaping slightly. Exopod of third maxilliped slightly overreaching end of ischium of endognath. Orifice of efferent branchial channel almost closed by spine of jugal angle and by production of lateral lobe of epistome.

Male gonopod short and stocky, with mesial, marginal, and lateral lobes well developed; marginal lobe cupped and overreach-

ing field of spines; mesial lobe produced laterad to form rounded hood overhanging field of spines; cephalic lobe bearing small acute spines and long, flat process directed proximally; in addition to strong caudal setae and small spines of genital pore, gonopod bearing large patch of small dark spines on lateral side, small spinules over distal border of cephalic lobe and few tiny setae on mesial side.

Size. — This is a small species (cw 24.9 mm) for the family, but near the mean size of the genus.

Etymology. — The species is named after the type locality, Municipio Bolívar.

Remarks. — The shape of the male gonopod strongly departs from the general pattern of organization of the gonopod of *Strengeriana*. The three lobes that constitute the basic structure of the gonopod apex are separated and distinct, as in *S. fuhrmanni*, but in this case they are strongly developed and bent over the field of spines. There is only one spine on the cephalic lobe, and the cephalic process is entire, not bifid as in *S. chaparralensis*, *S. tolimensis*, and *S. huilensis*, although the strong, dark spines over the lateral surface is a character shared with these three species.

***Strengeriana huilensis*, new species**

Fig. 3a–g

Material. — Quebrada Honda, Caserio Tres Esquinas, Municipio Gigante, 1,350 m above sea level, Huila Department, Colombia; 30 August 1986; M.R. Campos collector; 1 ♂ holotype, cw 28.2 mm, cl 17.5 mm, 13 ♂ and 8 ♀ paratypes (ICN-MHN No. CR 0664).

Description. — Cervical groove straight and shallow, deeper in posterior half, not reaching margin of carapace. Anterolateral margin with shallow depression behind orbit followed by few obsolescent papillae. Postfrontal lobes ill defined, their presence being indicated only by 2 small scars. Median groove absent. Surface of carapace behind front moderately inclined anteriorly and towards midline. Upper border of front well defined, almost straight in frontal view, but arched in dorsal view. Lower margin strongly sinuous in frontal view. Surface of front between upper and lower borders high. Surface of carapace smooth to naked eye, with regions strongly demarcated.

Palm of larger chela moderately inflated; fingers gaping slightly. Walking legs not no-

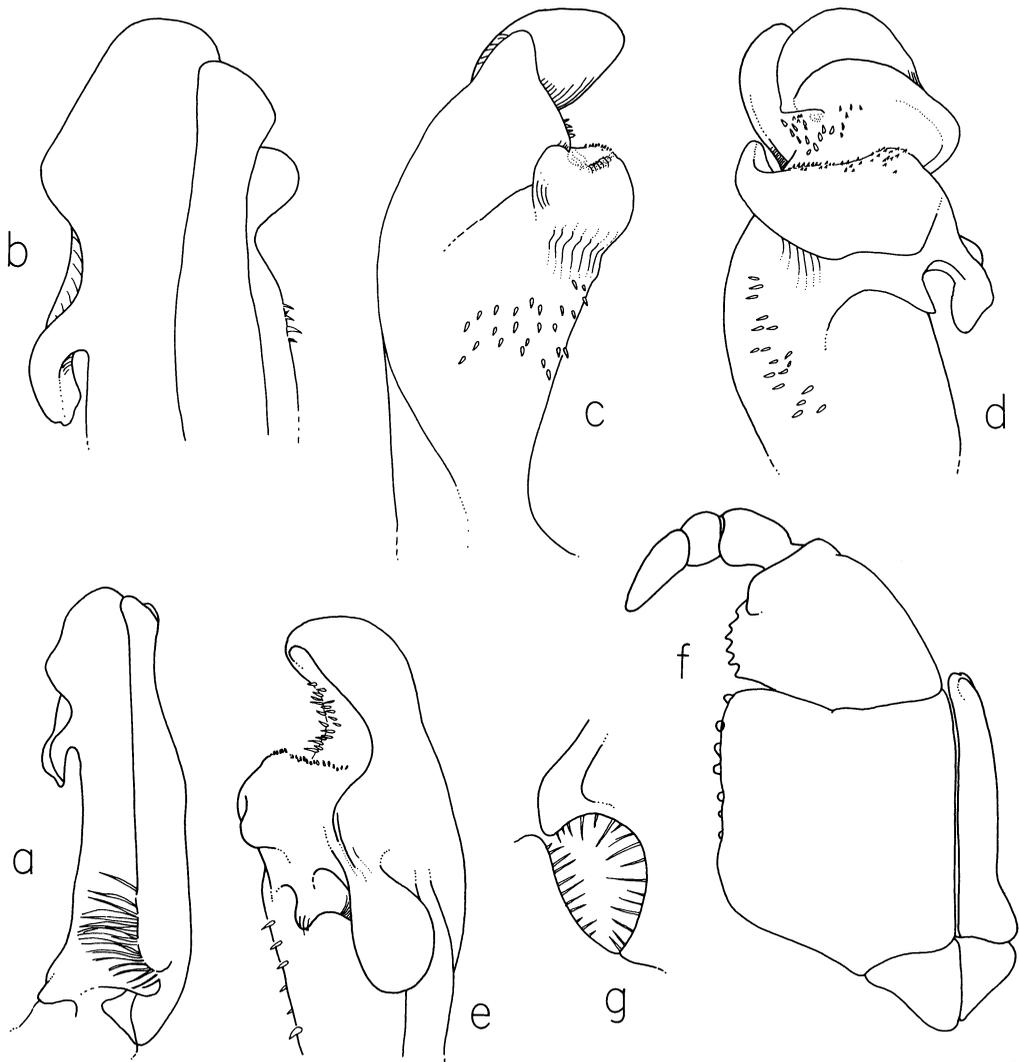


Fig. 2. *Strengeriana bolivarensis*, new species, holotype male, ICN-MHN No. CR 0785: a, left gonopod, caudal view; b, lateral-caudal view; c, lateral view; d, cephalic view; e, mesial view; f, third maxilliped, left; g, opening of branchial channel, left.

ticeably elongate, largest being those of third pair, in this pair merus being 2.9 times longer than wide. Exopod of third maxilliped overreaching lateral margin of ischium. Orifice of efferent branchial channel almost closed by spine at jugal angle and by production of lateral lobe of epistome.

Male gonopod short and stocky, with long apical processes extending proximally to middle of appendage; marginal lobe simple, with short ridge on lateral surface. Mesial lobe forming with cephalic lobe long slit at location of genital pore; mesial border bearing conspicuous rounded tooth on cephalic

side; cephalic lobe bearing 2 strong closely set spines and long bifid process directed proximally; small acute subterminal spine on cephalic surface of bifid process. In addition to strong caudal setae and small spines of genital pore, gonopod bearing large patch of small dark spines on lateral side, small spinules over distal border of cephalic lobe and few tiny setae on mesial side.

Size. — This is a small species (cw 28.2 mm) for the family, but near the mean size of the genus.

Etymology. — The specific name refers to

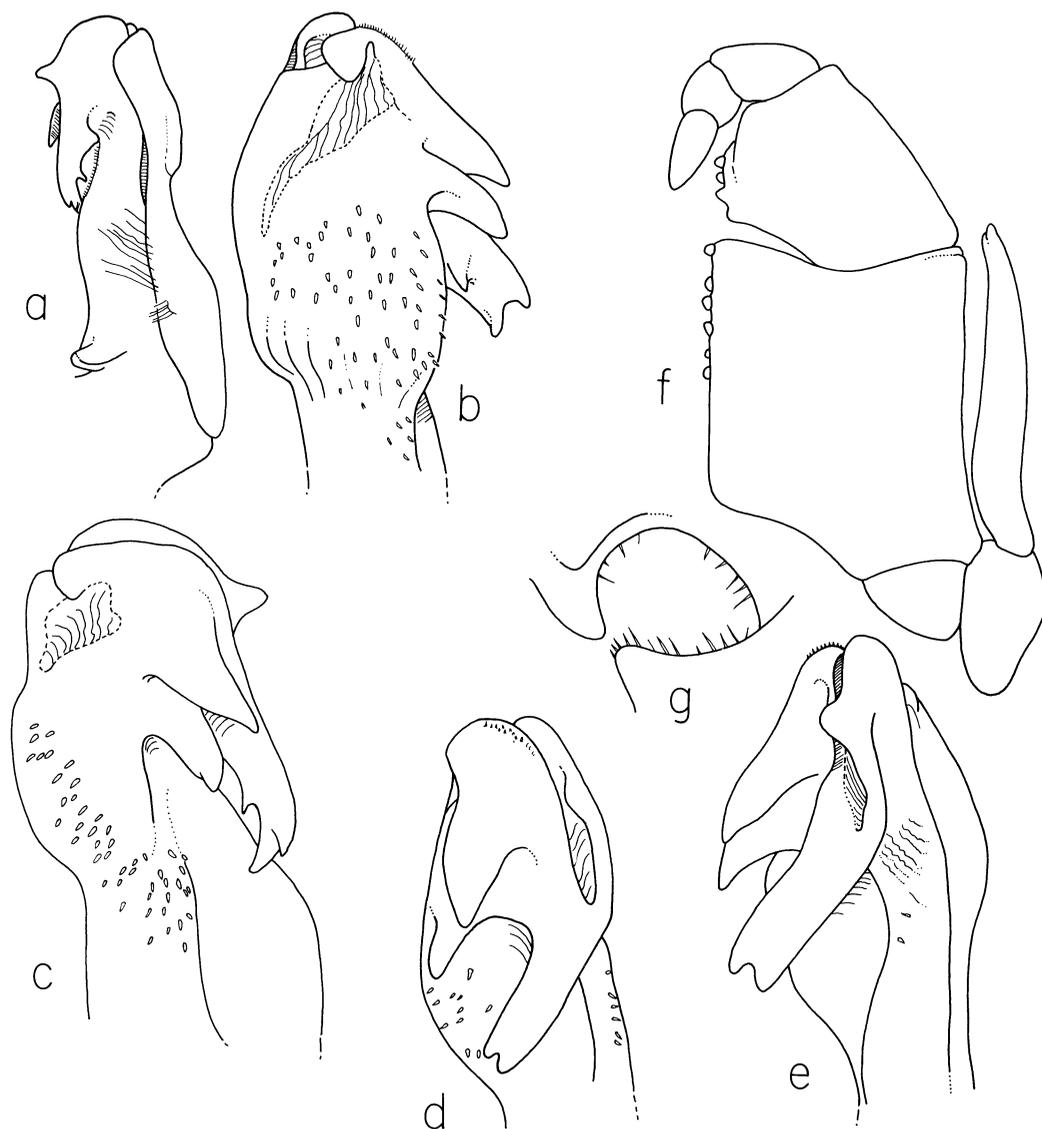


Fig. 3. *Strengeriana huilensis*, new species, holotype male, ICN-MHN No. CR 0664: a, left gonopod, caudal view; b, lateral view; c, cephalic view; d, mesial view; e, mesocephalic view; f, third maxilliped, left; g, opening of branchial channel, left.

Huila Department, where the type locality is situated.

Remarks.—The species is closely allied to *Strengeriana chaparralensis* Campos and Rodríguez, 1984. The main differences are found in the apical processes of the gonopod. The two cephalic spines are closely set in the present species, not widely separated as in *S. chaparralensis*; the bifid process is very long and directed proximally, giving a characteristic appearance to the appendage

in caudal view (Fig. 3a); in *S. chaparralensis* the cephalic end of the caudal margin is bent over toward the slit lodging the gonopore, whereas in *S. huilensis* there is a conspicuous rounded tooth.

***Strengeriana taironae*, new species**

Fig. 4a–c

Material.—Santa Marta, Municipio San Lorenzo, 1,200 m above sea level, Magdalena Department, Colombia; 5 November 1984; A. Rocha collector: 1 ♂ holotype, cw 41.5 mm, cl 21.7 mm, 1 ♀ paratype, cw 37.4 mm,

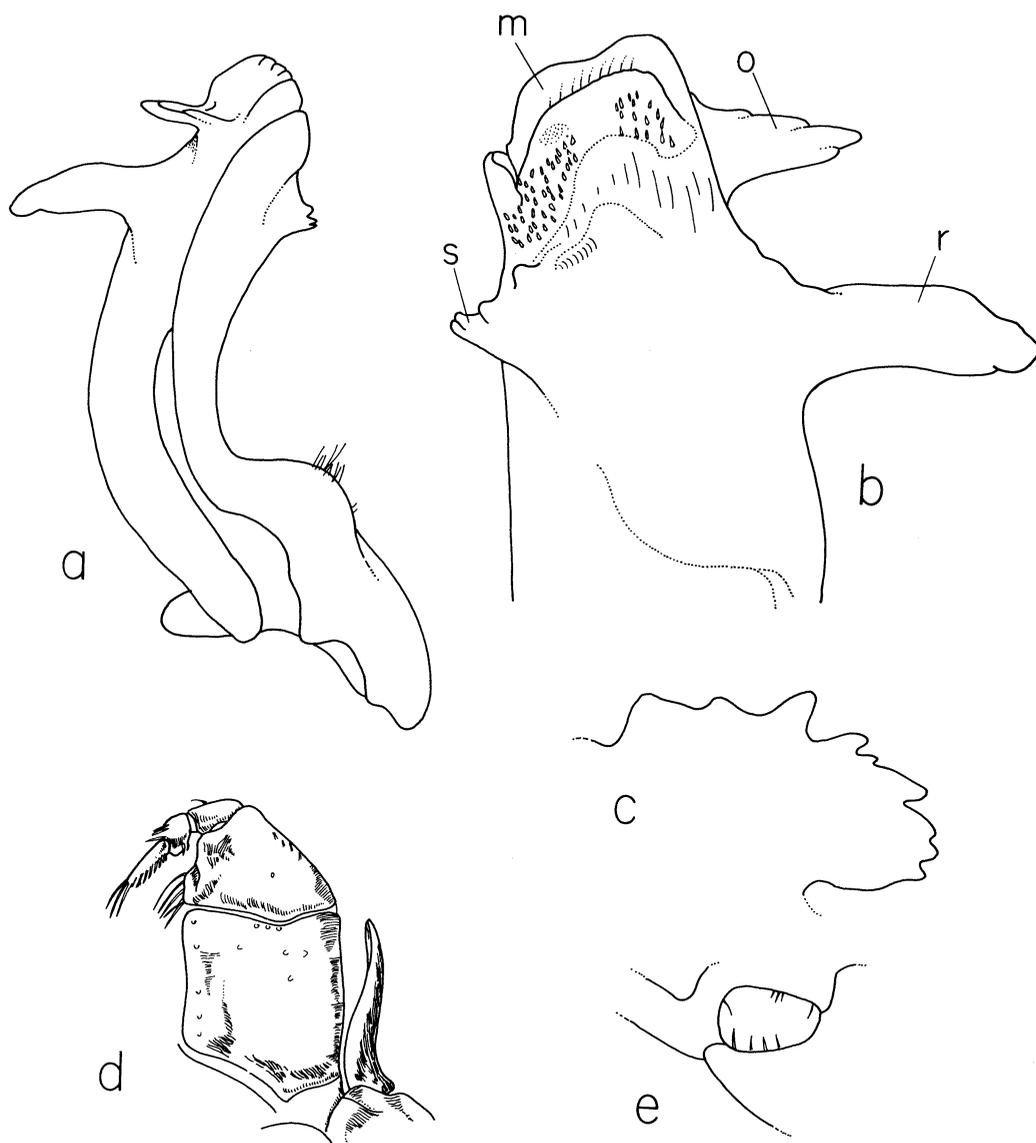


Fig. 4. *Strengeriana taironae*, new species, holotype male, ICN-MHN No. CR 0525: a, left gonopod, caudal view; b, cephalic view; c, apex in distal view; d, third maxilliped, left; e, opening of branchial channel, left.

cl 20.0 mm, 1 juvenile δ , cw 19.8 mm, cl 12.9 mm (ICN-MHN No. CR 0605).

Description.—Carapace exceptionally wide (cw/cl = 1.9 in holotype). Cervical groove slightly arched and shallow, deeper and wider in posterior half. Anterolateral margin with conspicuous notch behind orbit; lateral margin smooth, except for faint crenulation near middle of length. Postfrontal lobes absent and instead small, rounded depression on each side. Median groove forming shal-

low wide depression. Surface of carapace behind front moderately inclined towards midline. Front bilobed in dorsal view. Upper border absent and carapace in this area regularly curving downwards. Lower margin almost straight in frontal view. Surface of carapace polished, with regions strongly demarcated. Over margin of metabranchial region 2 transverse ridges parallel to lateroposterior margin defining shallow groove; merus of last pair of pereopods loosely fit-

ting in these grooves when retracted over carapace.

Palm of larger chela inflated. Fingers strongly gaping; mobile finger strongly arched. Walking legs slender but not unusually elongate, largest being those of third pair (total length approximately equal to width of carapace); in this pair, merus being 3.9 times longer than wide. Exopod of third maxilliped reaching almost to end of ischium of endognath. Orifice of efferent branchial channel almost closed by spine of jugal angle and by production of lateral lobe of epistome.

Male gonopod strongly bent in middle portion giving appendage sickle-shaped appearance. Terminal portion bearing toothed subapical crest, transversely placed on caudal surface, and long fingerlike projection over lateral surface. Apical field of spines directed mesially and bounded distally by well-defined concave middle plate, and proximally by crenulated crest.

Size. — This is a small species, cw 41.5 mm, but, even so, it is the largest of the genus.

Etymology. — The species is named after the Tairona Indians, in whose ancient territory the species was found.

Remarks. — The species is very characteristic and sharply distinct from others in the genus. The carapace is wider than in any other pseudothelphusid and the parallel ridges of the branchial region are found only on this species. The length of the exognath of the outer maxilliped is atypical of the genus, being shorter than in other species. The strongly bent gonopod is very characteristic, and the mesial serrated crest of this appendage is not found in any species of Pseudothelphusidae previously known.

CLADISTIC ANALYSIS

A large number of most parsimonious trees with 25 steps in length and Consistency Index of 0.86 were found. An individual tree with character changes is shown in Fig. 6a. The strict consensus tree in Fig. 6b summarizes the point of agreement in all the trees. The species of *Chaceus* and *Strengeriana* form well-defined monophyletic groups. There is no resolution for the species in the genus *Chaceus*. In the genus *Strengeriana*, *S. fuhrmanni* and *S. risaraldensis* cluster as the most basal. There is a trichot-

omy with *S. foresti*, *S. restrepoi*, and *S. chaparralensis* and an unresolved dichotomy with *S. huilensis* and *S. bolivarensis*. Finally, *S. tolimensis* and *S. taironae* consistently cluster together.

The tree shown in Fig. 6a agrees with our tentative biogeographical model for evolution of the group, as will be discussed further under the biogeographical section. All trees agree on reversal to the plesiomorphic conditions in characters 2 and 3 (see Table 2) as the most parsimonious explanation, and independent development of the derived states in characters 4 and 5, affecting the species of *Chaceus*. The only homoplasy found in the gonopod was the marginal tubercle (character 15) which appears independently in *S. restrepoi* and *S. tolimensis*.

Due to the unresolved trichotomies and tetratomies in the strict consensus tree, the following biogeographical discussion is limited to the three main clades shown in Fig. 6 and to the pair formed by *Strengeriana tolimensis*–*S. taironae*.

BIOGEOGRAPHY

The areas of distribution of the species of Strengerianini are located above 900 m (Table 4) in the Eastern, Western, and Central Cordilleras and the Sierra Nevada de Santa Marta in Colombia, and the Sierra de Perija in Venezuela (Fig. 7). The altitudinal distribution suggests that at present the lowlands operate as a barrier for the dispersion of these organisms.

The geographical distribution, together with the cladogram of relationships, shows three drastic disjunctions: (a) the monophyletic groups formed by the genera *Strengeriana* and *Chaceus*, (b) the species *Chaceus motiloni* Rodriguez, 1980, with respect to the rest of the species of the genus, and (c) *Strengeriana tolimensis* with respect to its sister species, *S. taironae*.

A dispersalist hypothesis requires the establishment of three paths or migratory routes to connect (1) the areas of *Strengeriana* and *Chaceus*, (2) the areas of *C. motiloni* and those of other species of *Chaceus*, and (3) the areas of *Strengeriana tolimensis* and *S. taironae* (Fig. 7). The dispersalist hypothesis presented in Fig. 7 agrees with the cladogram in Fig. 6. It implies a progressive expansion southward of the genus *Strengeriana* across the Central Cordillera, cross-

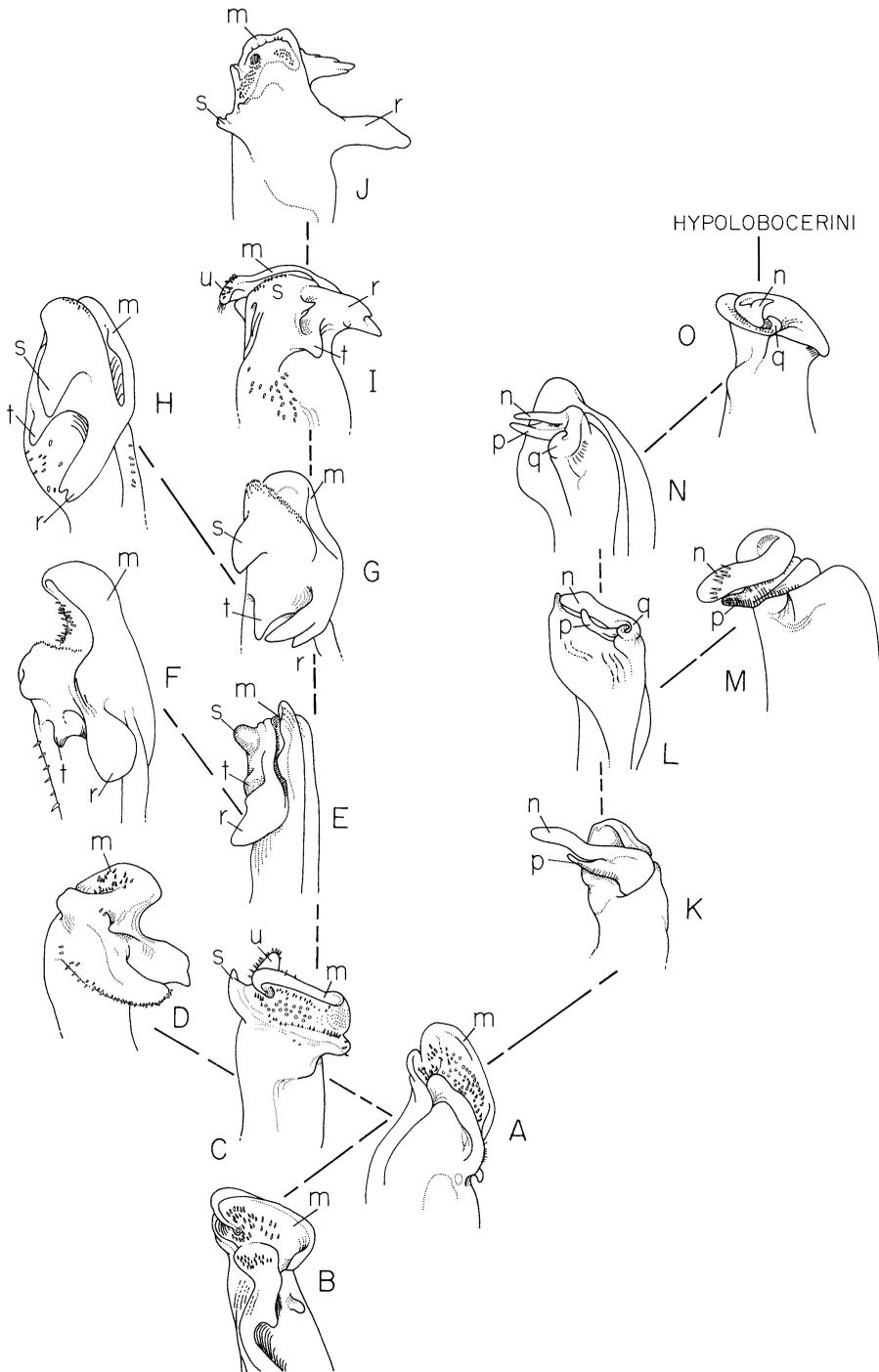


Fig. 5. Homologies in the gonopods of the Strengerianini. A, *Strengeriana fuhrmanni*; B, *S. risaraldensis*; C, *S. restrepoi*; D, *Phallangothelphusa dispar*; E, *Strengeriana foresti*; F, *S. bolivarensis*; G, *S. chaparralensis*; H, *S. huilensis*; I, *S. tolimensis*; J, *S. taironae*; K, *Chaceus motiloni*; L, *C. pearsei*; M, *C. nasutus*; N, *C. davidi*; O, *Martiana clausa*. m, marginal plate; n, digitiform process; p, basal process; q, coiled ridge; r, cephalic process; s, t, lateral spines; u, caudal process. Appendages drawn in cephalic, cephalomesial or cephalolateral view.

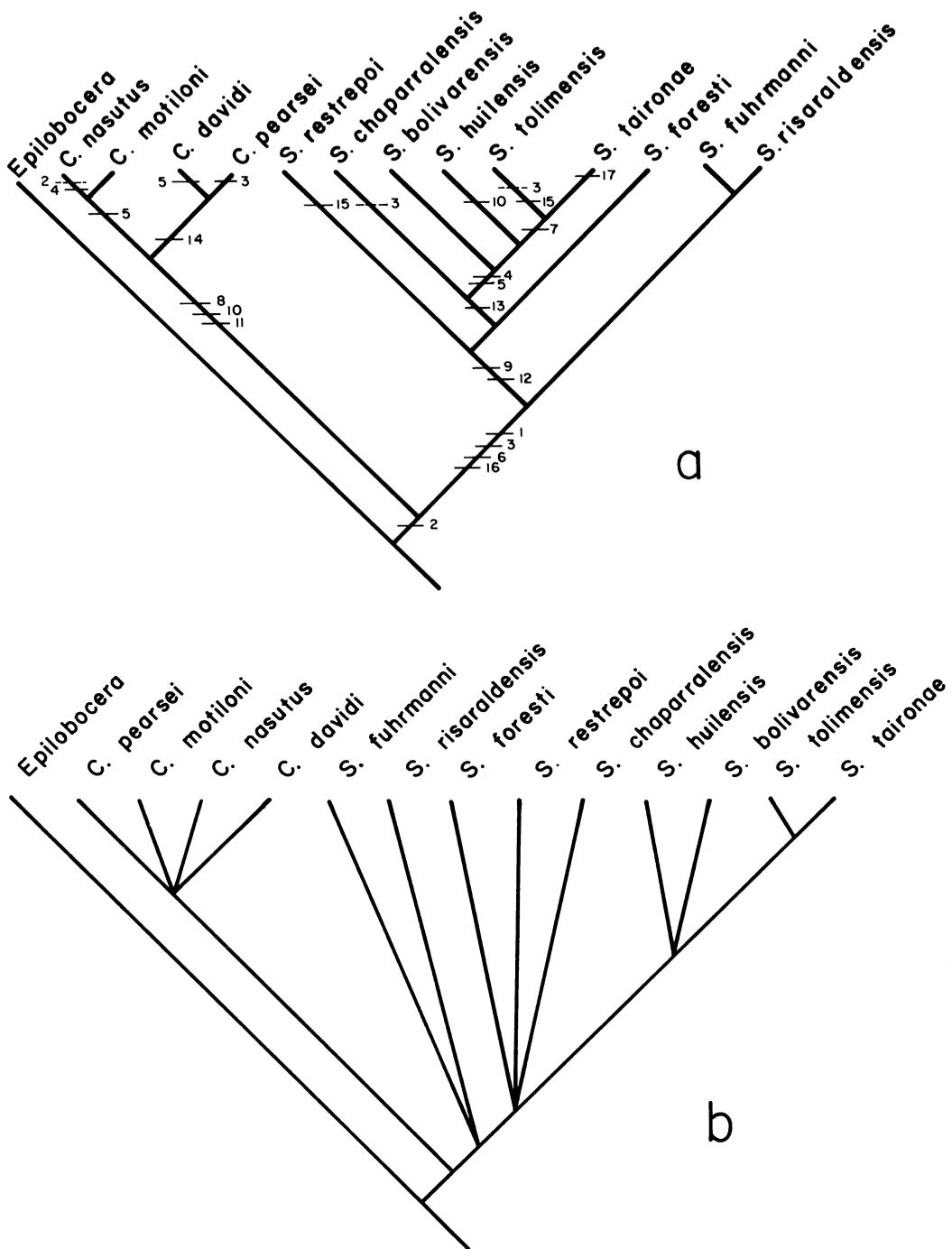


Fig. 6. a, One of the most parsimonious cladograms obtained, with indication of the changes in character states (solid horizontal lines) and reversals (broken lines). b, Strict consensus tree.

ing to the Western Cordillera with *S. risaraldensis* and *S. bolivarensis*, and to the Eastern Cordillera with *S. huilensis*. However, it casts a large uncertainty about the origin of *S. taironae*.

Within the present geographical framework, the three main paths could be either across extensive areas of lowlands or along a continuous course of highlands through the Central Cordillera, the Eastern Cordille-

Table 4. Vertical distribution of the species of Strengerianini.

Species	Meters above sea level
<i>Strengeriana fuhrmanni</i>	1,820
<i>S. foresti</i>	1,870
<i>S. restrepoi</i>	1,770
<i>S. tolimensis</i>	> 1,820
<i>S. chaparralensis</i>	900
<i>S. risaraldensis</i>	1,350
<i>S. bolivarensis</i>	1,500
<i>S. huilensis</i>	1,350
<i>S. taironae</i>	1,200
<i>Chaceus pearsei</i>	1,200–1,600
<i>C. motiloni</i>	1,100
<i>C. nasutus</i>	3,000
<i>C. davidi</i>	1,150
<i>Martiana clausa</i>	1,500
<i>Phallangothelphusa dispar</i>	1,000

ra, Sierra de Perija, and finally across the divide of the Cesar River, to the Sierra Nevada de Santa Marta. A review of the Tertiary geography permits us to suggest an alternative hypothesis.

The three mountainous systems of the Colombian Andes are distinctive geologically and originated at different times. The present Central Cordillera, the central part of the Sierra Nevada de Santa Marta and the Goajira Peninsula already existed at the close of the Paleozoic; the Western Cordillera originated in late Cretaceous. All the area of the northern Andes was submerged by Cretaceous epicontinental seas (Irving, 1975). The "Andean Orogeny," the principal orogenic phase of the Colombian An-

des, took place during Late Miocene–Early Pliocene times. From this time on, its three-pronged configuration was established and suitable lands, as required by the fresh-water crabs, were available uninterrupted through the Quaternary, although not at the same altitude as at present. The present uplift and final modeling probably took place during the late Pliocene or the beginning of the Pleistocene (van der Hammen and Gonzalez, 1964).

In addition to the vertical movement of this belt, considerable horizontal movements have taken place. The Phanerozoic tectonic history of northwestern South America can be understood in terms of the plate tectonic hypothesis of McCourt *et al.* (1984) as a multiple accretionary model resulting from the progressive westward migration of a subduction zone.

Large wrench faults, in part related to the main shear systems in the Caribbean, are major structural features of northern Colombia and Venezuela (Feininger, 1970). The triangular Sierra de Santa Marta Massif (Fig. 8) is bounded by the Oca fault, the Santa Marta fault, and the Cesar lineament (Tschanz *et al.*, 1974). It seems well established now (Campbell, 1968, 1974; Feininger, 1970; Cediell, 1972; Tschanz *et al.*, 1974; McCourt *et al.*, 1984) that, during the Tertiary, dextral and sinistral movement of 65 and 110 km, respectively, occurred along the Oca and Santa Marta faults, displacing the pre-Triassic rocks more than 100 km

Table 5. Geological evolution of the Northern Andes from the Upper Cretaceous and hypothetical biogeographical events as postulated in the text. Numbers indicate either approximate date of geological events (*) or approximate beginning of epochs according to Irving (1975).

Epoch	Ma	Geological events	Biogeography
Cretaceous	86*	Santa Marta Massif in ancient position (Irving, 1975)	
Paleocene	65	Withdrawal of epicontinental seas from northern South America (Irving, 1975)	
Eocene	48*	Separation of proto-Antilles from South America (Durham, 1985)	Splitting of ancestral Epilobocerini and Pseudothelphusini (Rodriguez, 1986)
Miocene	26	Beginning of Andean orogenesis (Irving, 1975)	Ancestral Strengerianini widespread in proto-Andes Splitting of <i>Strengeriana</i> and <i>Chaceus</i> Speciation
Pliocene	12	Santa Marta Massif in present location (Campbell, 1968)	Disjunction of sister groups
Pleistocene	3	Final uplift of Andes (van der Hammen and Gonzalez, 1964)	Vertical isolation of species

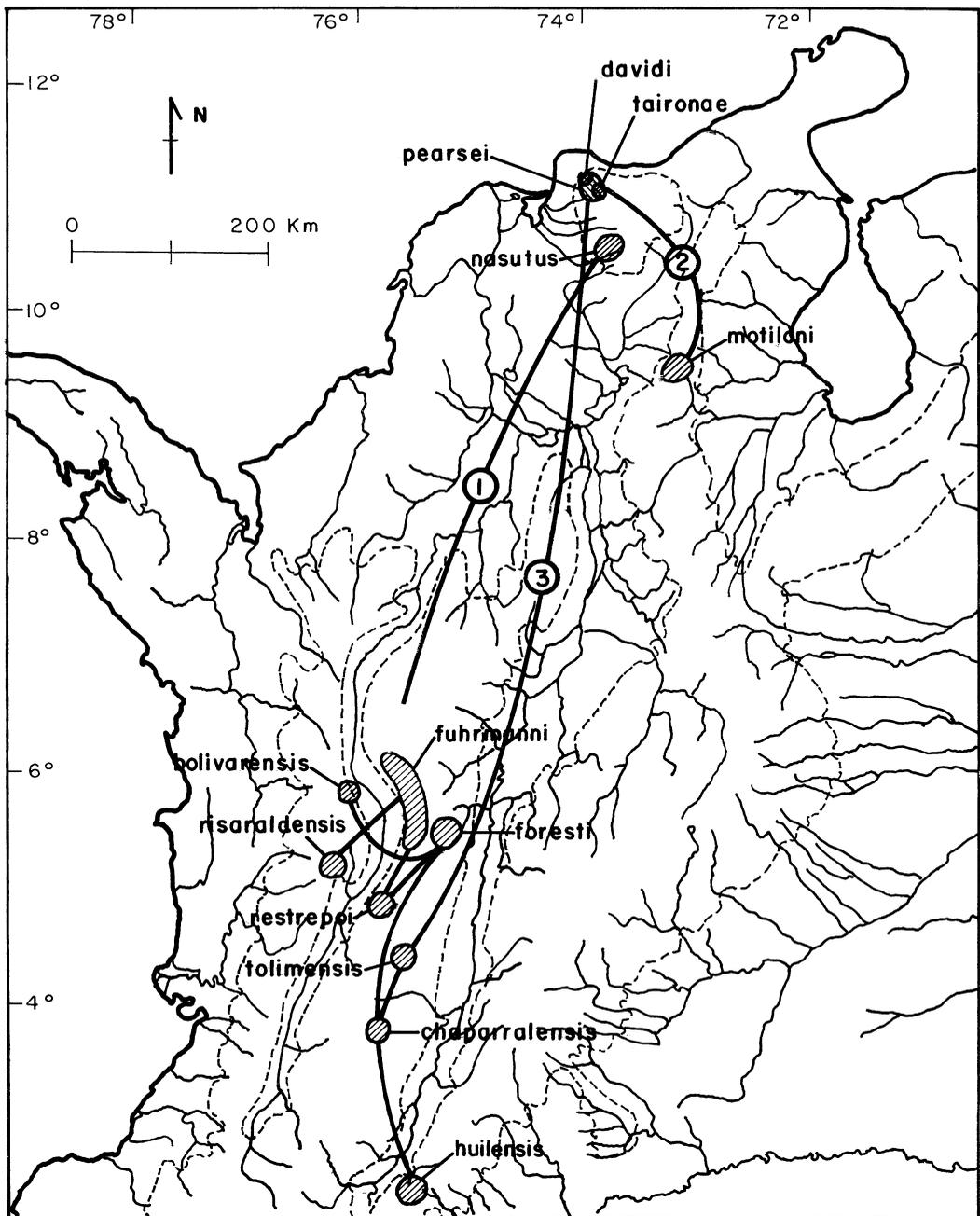


Fig. 7. Geographical ranges of the species of *Strengeriana* and *Chaceus* in Colombia and Venezuela. The paths marked 1 to 3 are hypothetical dispersion routes required to establish the congruence of the observed distributions with the cladogram in Fig. 6. SM, Sierra Nevada de Santa Marta; P, Sierra de Perija; W, Western Cordillera; C, Central Cordillera; E, Eastern Cordillera. Broken lines indicate altitudes above 1,000 m.

north of their place of origin. Subsequently, several thousand meters of uplift produced the present geomorphic setting. Consequently, during the Upper Cretaceous, the Santa Marta Massif was approximately 110

km south of its actual position as a part of the uplifted Central Cordillera. Irving (1975) found confirmation of this hypothesis in the lithology of an oil well perforated in Algarrobo (Fig. 8C). These rocks, with an age of

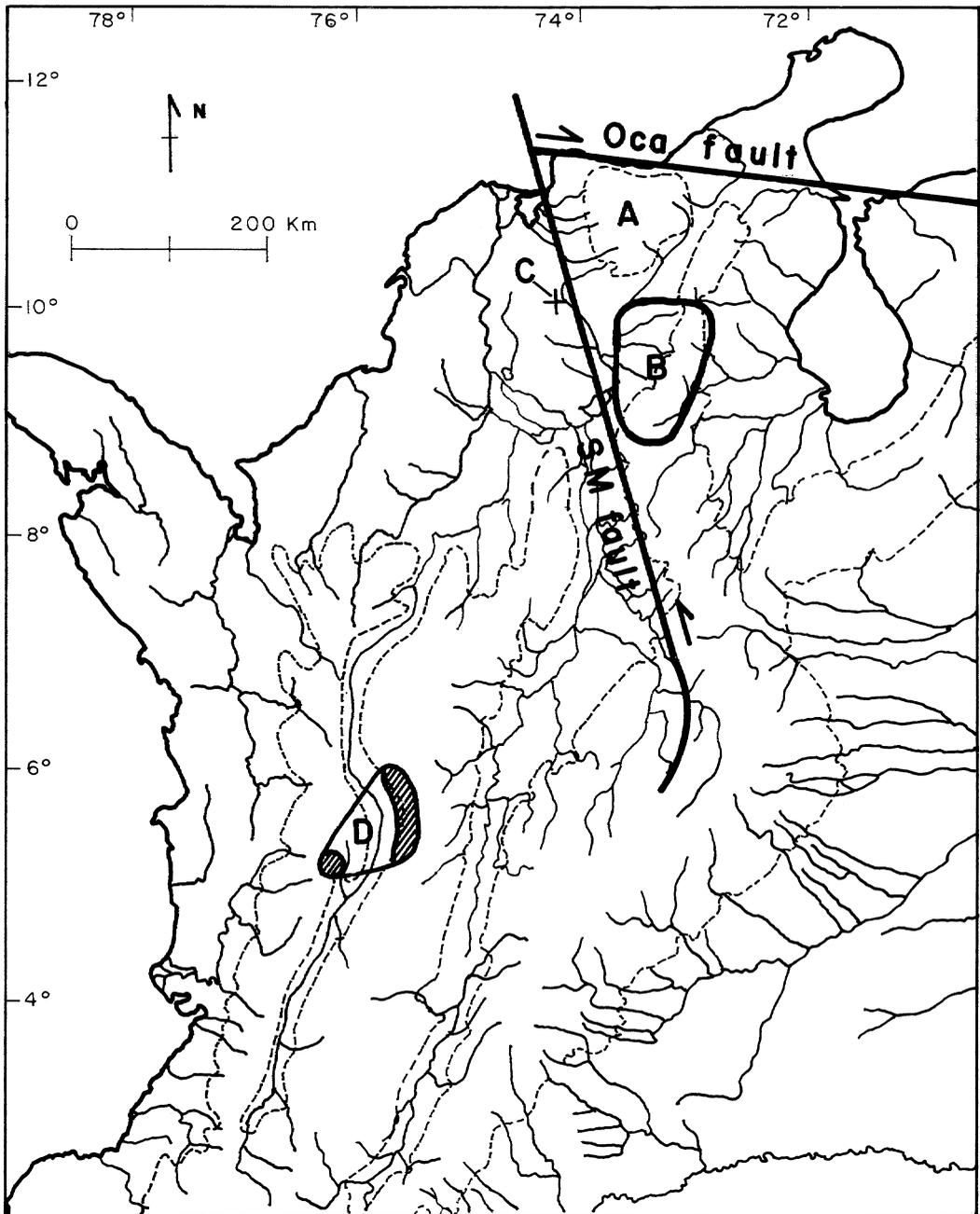


Fig. 8. Location of wrench faults in northeastern Colombia and western Venezuela. The block of the Sierra Nevada de Santa Marta (A) has been moved along the Santa Marta Fault (SM) to its hypothetical position in Upper Cretaceous (B). C indicates the Algarrobo Oil Well referred to in the text and D the areas of distribution of *Strengeriana fuhrmanni* and *S. risaraldensis*. Broken lines indicate altitudes above 1,000 m.

86 Ma, have no similitude to the rocks to the west, at the same latitude, but rather with the schist on the northwest corner of the Sierra Nevada de Santa Marta. This massif was emplaced in its present position

in post-Miocene to Recent times (Campbell, 1968).

If this displacement is taken into account, the general area of distribution of *Strengeriana* on the Central Cordillera is brought

into contiguity with the areas of distribution of *S. taironae* and of the species of *Chaceus* in the Sierra Nevada de Santa Marta, and there is no need to explain the present distribution by migration along paths 1 and 3 (Fig. 7). Thus, the splitting of the ancestral biota into two genera occurred at Miocene times, after early diversification of the family into different lineages (subfamilies), in the Antilles and in the Northern Andes in Eocene times (Rodríguez, 1986), very probably in close association with the geological evolution of the Caribbean (Malfait and Dinkelman, 1972; Sykes *et al.*, 1982; Durham, 1985).

Since the vertical distribution of the species (Table 4) suggests that the lowlands act as a physical barrier to the dispersion, it is probable that the ancestral Strengerianini had a broad distribution before the Andes achieved their present altitude in the Pliocene-Pleistocene (van der Hammen and Gonzalez, 1964). It is possible that the first radiation of the tribe took place at lower altitudes. With further elevation by the raising of the cordilleras, the different groups became isolated in the subtropical zone of the Andes. The sequence of events suggested by the present vicariant hypothesis is summarized in Table 5.

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Caracas 1020A, Venezuela; (MC) Universidad Nacional, Instituto de Ciencias Naturales, Apdo. Aereo 53416, Bogotá, Colombia.

Addresses: (GR) Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Apdo. 21827,

ANNOUNCEMENT

“The revision of the family Lithodidae Samouelle, 1819 (Crustacea, Decapoda, Anomura) in the Atlantic Ocean,” by E. Macpherson, has been published (1988) in “Monografías de zoología marina,” as volume 2, pages 1–153, with 53 figures and 28 plates.

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