Insular species of Neotropical freshwater crabs (Crustacea: Brachyura)

G. RODRÍGUEZ and B. LÓPEZ

*Instituto Venezolano de Investigaciones Científicas, Centro de Ecología,
Apartado 21827, Caracas 1020 A, Venezuela;
e-mail: grodrigu@oikos.ivic.ve*

One species of Trichodactylidae and four species of Pseudothelphusidae are present on continental islands in three areas of Central and South America. (1) Trinidad and Margarita Island have, in common with the Venezuelan mainland, the pseudothelphusid *Eudaniela garmani* (Rathbun, 1898); additionally, Trinidad shares with the mainland the trichodactylid *Dilocarcinus dentatus* (Randall, 1839). These disjunct distributions can be attributed to changes in sea level during the Quaternary, but the presence of the endemic pseudothelphusid *Microthelphusa odaelkae* (Bott, 1970) in Trinidad probably reflects an older connection with the continent. (2) A new species, *Potamocarcinus roatensis*, was found on Roatan Island, off the coast of Honduras. A cladistic analysis of the genus *Potamocarcinus* (H. Milne Edwards, 1853) revealed a close association of *P. roatensis* with *P. magnus* (Rathbun, 1896), a widely distributed Central American pseudothelphusid. Possibly both species originated in a pre-Quaternary vicariant event. (3) Another pseudothelphusid, *Hypolobocera gorgonensis* von Prahl, 1983, inhabits disjunct areas on Gorgona Island, off the Pacific coast of Colombia, and on the mainland of Ecuador, reflecting either a wider distribution before the last Holocene transgression or accidental dispersal through natural rafts.

KEYWORDS: Pseudothelphusidae, Trichodactylidae, freshwater crabs, island biogeography, phylogenetics.

Introduction

Insular studies have provided important insights on the interplay of process and pattern in biogeography (Lomolino, 2000). However, the distribution of many organisms, particularly birds, insects and vascular plants, is not very informative about palaeogeographic history because their dispersal methods allow them indiscriminately to penetrate physical barriers isolating oceanic and continental islands. Freshwater crabs, on the other hand, are useful geographical tools for testing dispersalist or vicariant hypotheses because the absence of free-swimming larvae rigorously restricts them to their natural habitats (Ng and Rodríguez, 1995). Exceptionally, the adaptations that Pseudothelphusidae possess for air breathing could enable them to be transported by natural rafts (Rodríguez, 1986).

Of the two Neotropical freshwater crab families, the Pseudothelphusidae, with more than 229 known species, have eight species on oceanic islands in the Caribbean, namely, seven species of *Epilobocera* Stimpson, 1860, in Cuba, Hispaniola and Puerto Rico (Rodríguez and Williams, 1995), and *Guinotia dentata* (Latreille, 1825) in the Lesser Antilles islands of Guadeloupe, Dominica, Martinique, St Lucia and St Vincent. The problems posed by these oceanic distributions have been dealt with by Rodríguez (1986).

The species of Pseudothelphusidae recorded from continental islands are *Eudaniela garmani* (Rathbun, 1898) from Trinidad and Margarita Island, off the coast of Venezuela, *Microthelphusa odaelkae* (Bott, 1970) from Trinidad, and *Hypolobocera gorgonensis* von Prahl, 1983, from Gorgona Island, off the Pacific coast of Colombia. The Trichodactylidae, comprising 44 species (Rodríguez, 1992), have only one representative on continental islands, *Dilocarcinus dentatus* (Randall, 1839) recorded from Trinidad.

The present contribution deals with the geographical distributions of the aforementioned species from land bridge islands, together with a new species of Pseudothelphusidae from Roatan Island, off the coast of Honduras. The materials recorded are deposited in the Museum of Natural History of Tulane University, New Orleans (TU), the Field Museum of Natural History, Chicago (FMNH) and the reference collection of the Instituto Venezolano de Investigaciones Científicas, Caracas (IVIC). Other abbreviations used are cl = carapace length, cb = carapace breadth and ch = carapace height as measured from the sternum to the top of upper surface.

Systematics

Family TRICHODACTYLIDAE H. Milne Edwards, 1853
Genus *Dilocarcinus* H. Milne Edwards, 1853
Dilocarcinus dentatus (Randall, 1839)

Material examined

Mitan, near Nariva Swamp, Trinidad, 27 March 1980, coll. A. E. Esteves, five males, cl 29.1, 30.8, 31.5, 31.8 and 32.3 mm, cb 36.4, 37.5, 39.6, 39.9 and 41.3 mm (IVIC 734). Hato Terecay, 16 km N of El Manteco, Bolivar State, Venezuela, 7 June 1977, coll. S. Gorzula, one male, cl 30.8 mm, cb 37.3 (IVIC 720). Caño Onoto, near El Callao, Bolivar State, Venezuela, one male, cl 33.7 mm, cb 41.7 (IVIC 722). Laguna Campoma, Sucre State, Venezuela, one male, cl 41.6 mm, cb 51.8 (IVIC 732). Hato Piritu, Calabozo, Aragua State, Venezuela, coll. F. Tamayo, January 1963, one male, cl 31.2 mm, cb 39.3 mm (IVIC 724). Naguanagua, Carabobo State, Venezuela, coll. F. Rumbos, 7 November 1965, one male, cl 30.3 mm, cb 39.6 mm (IVIC 729).

Remarks

Pretzmann (1968b) described the subspecies *Dilocarcinus dentatus trinidadensis* based on a male (cl. 35 mm) from Trinidad, for which he gives the following characters: carapace narrower, flatter; 10 blunt lateral teeth; fingers of larger chela slightly gaping; dactylus shorter; gonopod wider, more recurved; colour dark brown. We compared five male specimens from Mitan, near Nariva Swamp, Trinidad, with five male specimens from several different localities on the nearby mainland of

Venezuela, recorded under Material examined, taking the degree of narrowness of the carapace as the ratio cb/cl, its degree of flatness as the ratio cb/ch, and the relative length of the dactylus as the proportion of the dactylus to the length of the ventral border of the chela (table 1). A larger variability of these characters was observed in Venezuelan specimens; the range of variation of Trinidad specimens was included within the range of variation of Venezuelan specimens. The number of lateral teeth is 10 in both groups, except for one mainland specimen which has nine on the left side, and a Trinidadian specimen which has 11 teeth on the right side. No differences could be noted in the morphology of gonopods in both groups. The colour of specimens (preserved in alcohol) is very variable, from grey to brown, as already observed by Rodríguez (1992).

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Family Pseudothelphusidae Rathbun, 1893

Tribe Hypolobocerini Pretzmann, 1971

Genus Hypolobocera Ortmann, 1897

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Hypolobocera gorgonensis von Prahl, 1983.

Hypolobocera gorgonensis von Prahl, 1983: 105, figure 1; 1988: 181, figure 13.

Hypolobocera muisnensis Rodríguez and von Sternberg, 1998: 123, figure 8.

Material examined

Gorgona Island, Colombia, 22 August 1989, received from von Prahl, one male, cl 50.6 mm, cb 83.0 mm (TU 6303). Gorgona Island, Pacific, Cauca Department, Colombia, 1 February 1962, one male, cl 43.2 mm, cb 69.9 mm, one male with broken carapace, cb 81.2 mm, one female, cl 47.2 mm, cb 76.4 mm (FMNH 3687). Estero Lojca More, Muisne Salima, Esmeraldas Province, Ecuador, 21 October 1988, coll. J. C. Vieira, one male holotype of *Hypolobocera muisnensis*, cl 31.1 mm, cb 51.6 mm (IVIC 952). Estero El Cañero, La Concordia, Esmeraldas Province, Ecuador, 1 October 1988, coll. J. C. Vieira, one male, cl 20.7 mm, cb 31.9 mm (IVIC 953). Same data, 8 October 1988, one male cl 24.2 mm, cb 39.5 mm (IVIC 954). Estero Moncauve, Recinto Moncauve, Esmeraldas Province, Ecuador, 5 January 1988, coll. J. C. Vieira, one male cl 24.2 mm, cb 39.5 mm (IVIC 955).

Remarks

Hypolobocera gorgonensis belongs to a group of 10 species of *Hypolobocera* from Ecuador, in which the lateral lobe is very elongated, extending to approximately

Table 1. Comparison of male specimens of *Dilocarcinus dentatus* from mainland Venezuela and Trinidad. Venezuelan specimens are ordered following the list of localities under Material examined.

	Trinidad cb/cl	Venezuela cb/cl	Trinidad cb/ch	Venezuela cb/ch	Trinidad dactylus/chela	Venezuela dactylus/chela
	1.22	1.21	2.00	1.92	0.59	0.55
	1.25	1.23	2.01	1.96	0.59	0.57
	1.25	1.24	2.04	1.99	0.59	0.62
	1.26	1.26	2.04	2.00	0.60	0.63
	1.28	1.31	2.05	2.08	0.61	0.65
Mean	1.25	1.25	2.03	1.99	0.60	0.60
SD	0.019	0.034	0.019	0.053	0.008	0.038

one-third the total length of the gonopod, subtriangular or gently curved; the apex in distal view is elongated, with its lateral half either rounded and horseshoe-shaped, or triangular and ending in an acute spine directed upwards (Rodríguez and von Sternberg, 1998). One of these species, *Hypolobocera muisnensis* from Esmeraldas Province, Ecuador, cannot be distinguished from *H. gorgonensis*, although there are slight differences in the material available for both species, such as the cb/cl ratio which is 1.63 in *H. gorgonensis* ($N=3$) and 1.62 in *H. muisnensis* ($N=4$); and the proportion exognath length/ischium length of endognath which is 0.32 ($N=2$) in *H. gorgonensis* and slightly more, 0.38 ($N=4$), in *H. muisnensis*. The gonopod morphology is similar, except that the distal margin of the lateral lobe of *Hypolobocera gorgonensis* is rounded, whereas in *H. muisnensis* it is angled, and that *H. muisnensis* presents in caudal view a distal slope toward the mesial margin not observed in *H. gorgonensis*. These differences can be regarded as intraspecific variations and consequently *Hypolobocera muisnensis* should be considered a junior synonym of *H. gorgonensis*, notwithstanding the noteworthy disjunction and isolation of the respective areas.

Habitat

Regarding the specimens collected on Gorgona Island (FMNH 3687), the collector F. Medem stated on the label that the species is 'abundant in all the brooks, also in their upper courses and in the small Laguna Cabrera. Eaten by the Spectacled Caiman, *Caiman sclerops* spp.'

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Tribe Potamocarcinini Ortmann, 1897
Genus *Potamocarcinus* H. Milne Edwards, 1853
***Potamocarcinus roatensis* sp. nov.**
(figure 1A–H)

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Material examined

Port Royal, Roatan Island, Honduras, 10 March 1979, coll. D. E. Keith, found dead in streambed, one male HOLOTYPE, cl 59.6 mm, cb 98.4 mm (TU 6267); one immature male PARATYPE, cl 16.2 mm, cb 25.1 mm, 17 March 1979, coll. D. E. Keith (TU6268).

Diagnosis

First male gonopods expanded laterally at middle; apical part bearing two rounded lobes of equal extension, caudal one partially overlapping mesial one, mesial one folded over mesial side and continued toward mesial process; mesial process digitiform, directed mesially; apical cephalic surface with well-developed bifid tooth and shorter lower process, both pointing mesially; field of spines slit-like.

Male holotype description. Carapace 1.65 times as wide as long, with deep and wide cervical groove, curving posteriorly and reaching lateral margin. Anterolateral margin with small postorbital notch, another wider notch at level of cervical groove, seven papillae on margin between these two notches, rest of anterolateral margin covered by 29 small and unequal teeth. Postfrontal lobes well defined, delimited anteriorly by two small scars, median groove obsolete except for slight incision on upper margin of front. Surface of carapace in front of postfrontal lobe flat and inclined anteriorly. Upper margin of front straight in dorsal view, with ill-defined papillae; lower margin visible in dorsal view, with row of papillae, almost straight
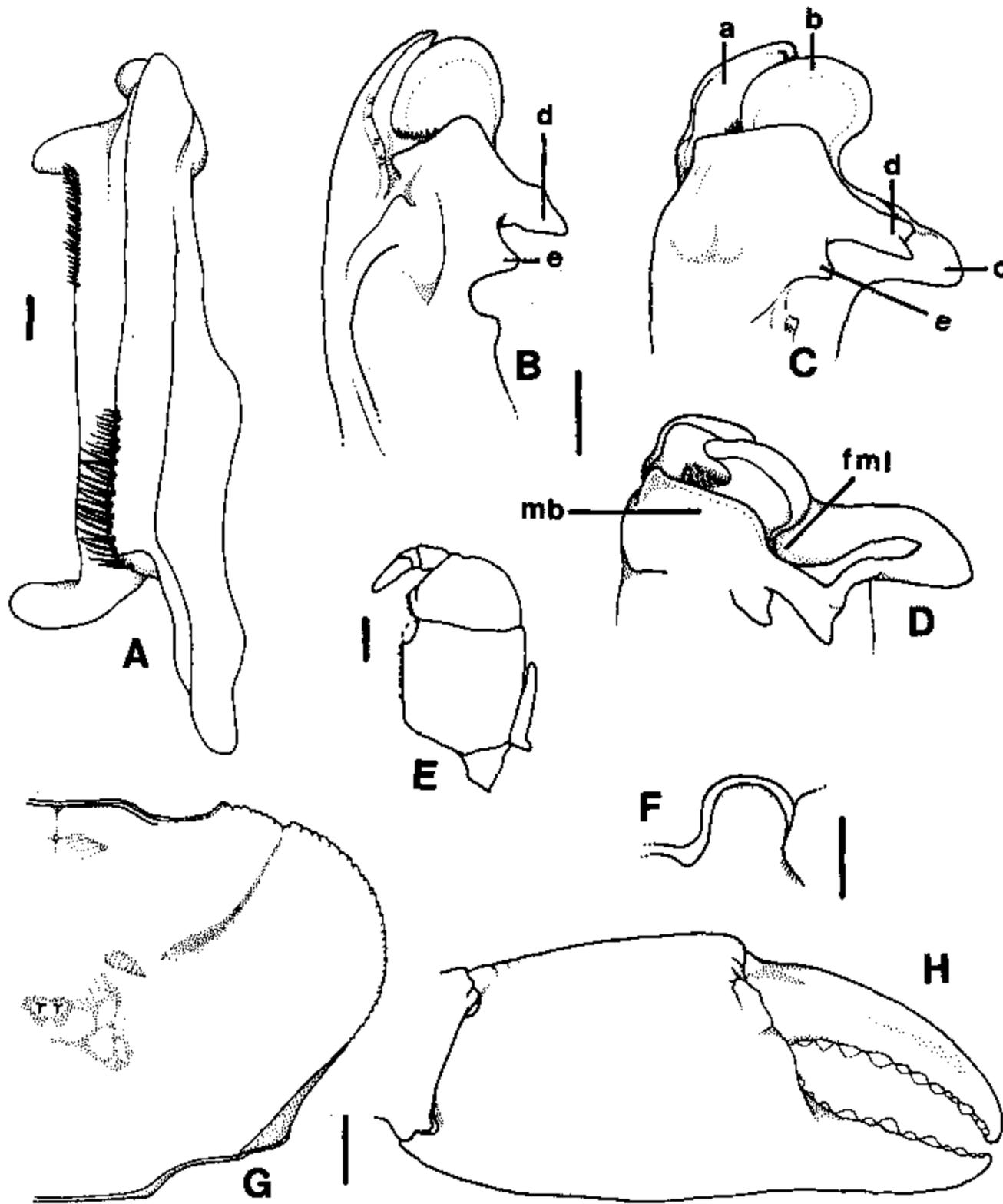
FIG. 1. *Potamocarcinus roatensis*, new species, holotype male from Port Royal, Roatan Island (TU 6267). (A) Left gonopod, caudal view; (B) apex, lateral view; (C) apex, cephalic view; (D) apex, distal view; (E) third maxilliped; (F) opening of left efferent channel; (G) dorsal view of right side of carapace; (H) chela of largest cheliped, external view. a, Caudal lobe; b, mesial lobe; c, mesial process; d, cephalic tooth; e, cephalic process; fml, fold of mesial lobe; mb, mesocephalic border. Scales: (A–F) = 1 mm, (G, H) = 1 cm.

in frontal view, space between upper and lower margin high. Surface of carapace covered by very small papillae, not visible to naked eye.

First pereiopods heterochelous, right cheliped larger than left. Merus with three crests, external crest with round and scattered papillae, internal upper crest with row of tubercles decreasing in size proximally, internal lower crest with row of small teeth. Carpus with row of teeth on internal crest and prominent acute spine at

middle. Inner and outer side of palms of both chelipeds smooth, lower margin with row of scattered small papillae. Palm of larger chela swollen, fingers gaping when closed, tips crossing; palm of smaller chela not swollen, fingers not gaping when closed. *Third maxillipeds absent in holotype, in paratype (juvenile) third maxilliped with exognath 0.73 times length of ischium, merus of endognath curved with slight depression on distal part of external margin, orifice of efferent branchial channel open.*

First male gonopods robust, expanded laterally at middle in caudal view (figure 1A). Apical part bearing two rounded lobes of equal extension (figure 1C: a, b), caudal one partially overlapping mesial one; mesial lobe folded over mesial side and continued toward mesial process (figure 1D: fml). Mesial process digitiform, directed mesially. Cephalic surface with well-developed bifid tooth and lower shorter process, both pointing mesially. Field of spines slit-like, with mesocephalic border advanced (figure 1D: mb).

Remarks

The gonopod of this species resembles that of *Potamocarcinus magnus* (Rathbun, 1896), but its mesial lobe is rounded, not subtriangular as in *P. magnus*, and has a lower apical tooth which is lacking in *P. magnus*.

Other insular species examined

Eudaniela garmani (Rathbun, 1898) is a well-defined species. No differential characters can be found between the populations within their general area of distribution in the Coastal Range of eastern Venezuela, Margarita Island and Trinidad Island (Rodríguez, 1982). *The known altitudinal range of the species in the respective subareas are*: mainland, 20–1500 m; Margarita Island, 20–800 m; Trinidad Island, 50–800 m.

Microthelphusa odaelkae (Bott, 1970) is an endemic species, recorded only from its type locality in Cerro del Aripo, North Range, Trinidad, between 600 and 800 m. The gonopod morphology of *Microthelphusa odaelkae* is very close to that of *M. turumikiri* Rodríguez, 1980 (see figures 115 and 116 in Rodríguez, 1982).

Phylogenetic study of *Potamocarcinus*

Methodology for the analysis of Potamocarcinus

The present cladistic analysis of *Potamocarcinus* includes all the species of this genus (table 2), with the exception of *Potamocarcinus leptomelus* Rodríguez and Hobbs, 1989, a taxon whose somatic and gonopodal characters considerably depart from others in the genus, due to its cave-dwelling adaptations, and *P. armatus aequispinosus* Pretzmann, 1971, which is a controversial species. Although this last is considered the type of the genus, its status is uncertain (Rodríguez, 1982), since the holotype is a female.

The strategy used in the cladistic analysis is similar to that employed in Rodríguez and Campos (1998). From 17 characters selected for the analysis of *Potamocarcinus* (table 3), five were somatic characters which concern the shape of the front, post-frontal lobes, cervical groove, anterolateral margin of carapace, and proportion of the exognath of the third maxilliped. The other characters pertain to the morphology

Table 2. List of species of *Potamocarcinus* used in the cladistic analysis with indication of the extension of the endognath of third maxilliped and the state of this character in parentheses. State (0) corresponds to the outgroup that presents an endognath extension >1.

Species	Extension of endognath
P. aspoekorum	0.79 (1)
P. zilchi	0.91 (1)
P. roatensis	0.72 (1)
P. richmondi	0.52 (2)
P. colombiensis	0.52 (2)
P. magnus	0.59 (2)
P. nicaraguensis	0.53 (2)
P. chajulensis	0.40 (2)
P. hartmanni	0.50 (2)

Table 3. Characters of *Potamocarcinus* compared.

1. Postfrontal lobes: (0) more or less defined; (1) absent and replaced by two small scars.
2. Cervical groove: (0) reaching margin of carapace; (1) not reaching margin
3. Antero-lateral margin between the orbit and cervical groove: (0) with small acute or papilliform teeth; (1) with spines; (2) smooth or with ill-defined papillae; (3) with prominent tuberculated teeth.
4. Anterolateral margin posterior to cervical groove: (0) with small teeth; (1) armed with strong spines; (2) with ill-defined papillae.
5. Border of front: (0) with more or less defined tubercle; (1) with small spines.
6. Third maxilliped, ratio exognath to ischium of endognath: (0) > 1; (1) approximately 1; (2) <1.
7. Caudal lobe of gonopod: (0) not exceeding the apex widely; (1) overreaching the apex widely.
8. Cephalic surface: (0) with a complex process; (1) with two elements (a hump+one sharp tooth); (2) with three elements, being all simple teeth; (3) with three elements including a bifid tooth; (4) with rudimentary processes or teeth.
9. Cephalic surface: (0) with a patch of strong spines; (1) with a patch of weak spines; (2) without a patch of spines.
10. Cephalic surface with a hump or tooth below the bifid tooth: (0) absent; (1) present.
11. Hump below mesial process: (0) absent; (1) present and small; (2) present and prominent.
12. Margin of mesial lobe: (0) with strong spines; (1) with a crenulation; (2) smooth.
13. Mesial process: (0) incipient or not present; (1) like subtriangular plate; (2) like a narrow conic tooth; (3) like sub-rounded tooth; (4) digitiform and bent; (5) like a broad conic tooth.
14. Mesial lobe: (0) not swollen at mesial side; (1) swollen at mesial side.
15. Mesial lobe: (0) not overreaching the apex; (1) exceeding slightly the apex; (2) exceeding widely the apex.
16. Mesial process: (0) rudimentary or not present; (1) acute; (2) blunt; (3) blunt and bent proximally.
17. Apex formed by: (0) three or more distinct lobes; (1) two distinct lobes; (3) two similar lobes.

of the first gonopods. The phylogenetic program used was PAUP version 4.0 beta 8 (Swofford, 1998) and option ALLTREES that guarantees the finding of all the most parsimonious trees.

Table 4. Data matrix of 17 characters of *Epilobocera sinuatifrons*, *Strengeriana risaraldensis* and the species of *Potamocarcinus*.

Species	State of characters																
E. sinuatifrons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S. risaraldensis	0	1	0	0	0	0	0	0	1	0	0	2	0	0	2	0	0
P. aspoekorum	0	1	2	2	0	1	0	1	1	0	0	1	5	0	1	1	1
P. zilchi	1	1	2	0	0	1	0	1	1	0	0	1	5	0	2	1	1
P. richmondi	0	0	0	0	0	2	0	2	2	0	0	2	1	1	1	1	1
P. colombiensis	0	0	3	0	0	2	0	2	2	0	0	2	1	0	1	1	1
P. magnus	0	0	0	0	0	2	1	3	2	1	0	2	2	1	2	1	2
P. roatensis	0	0	0	0	0	1	1	3	2	1	0	2	3	0	2	2	2
P. nicaraguensis	0	0	3	1	0	2	1	3	2	0	2	2	4	0	2	3	2
P. chajulensis	1	1	1	1	1	2	1	4	2	0	1	2	2	0	2	1	2
P. hartmanni	1	1	1	1	0	2	1	4	2	0	1	2	2	0	2	1	2

Homologies in the gonopodal processes of Potamocarcinus

One of the most significant homologies of these species regards the presence and shape of one or two apical lobes (figure 2F: a, b). In *Potamocarcinus aspoekorum* (Pretzmann, 1968a) and *P. zilchi* (Bott, 1956) only the mesial lobe is present; in *P. aspoekorum* it is placed transversally, but leaving exposed the field of spines, and in *P. zilchi* it is bent over the field of spines, forming a lid-like structure. In *Potamocarcinus richmondi* (Rathbun, 1893) and *P. colombiensis* von Prahl, 1987, the mesial lobe is poorly developed and the caudal lobe appears rudimentary. In the rest of the species both lobes are well developed; in *Potamocarcinus magnus* (Rathbun, 1896) the mesial lobe is inclined cephalically, a trend that continues in *P. nicaraguensis* (Rathbun, 1893) where the mesial lobe is applied over the field of spines (figure 2H: b).

A mesial process is present in all species of *Potamocarcinus* (figure 2), with specific differences in its shape and degree of development. In *Potamocarcinus richmondi* and *P. colombiensis* it forms a subtriangular plate directed meso-cephalically; it displays a progressive increase in *P. aspoekorum* and in *P. zilchi*, resembling in both species a broad conical tooth. In *Potamocarcinus magnus*, *P. roatensis*, *P. chajulensis* Alvarez and Villalobos, 1998 and *P. hartmanni* Pretzmann, 1975, this process appears like a narrow conical tooth, although in *P. roatensis* its apex is conspicuously blunt. In *P. nicaraguensis* it appears strongly modified as a finger-like projection, bent in the proximal direction and fused to the mesial lobe.

The cephalic surface of the first gonopods shows two elements in *Potamocarcinus aspoekorum* and *P. zilchi*, a sharp tooth and a spiny hump (figure 2A, E). In the rest of the species the spiny hump is progressively obsolescent while the sharp tooth is divided into two separate elements. In *Potamocarcinus richmondi* and *P. colombiensis* (figure 2B, D: d, d_1) both elements are separated by a wide gap, but are close together in *P. magnus*, *P. roatensis* and *P. nicaraguensis*, forming a bifid tooth (figure 2F, H: d, d_1). In *Potamocarcinus hartmanni* and *P. chajulensis* only rudimentary processes are observed on the cephalic surface.

Outgroup selection

The synapomorphies used to separate the genus *Potamocarcinus* are the following: (1) a mesial lobe that extends beyond the apex; (2) a well-developed mesial process;
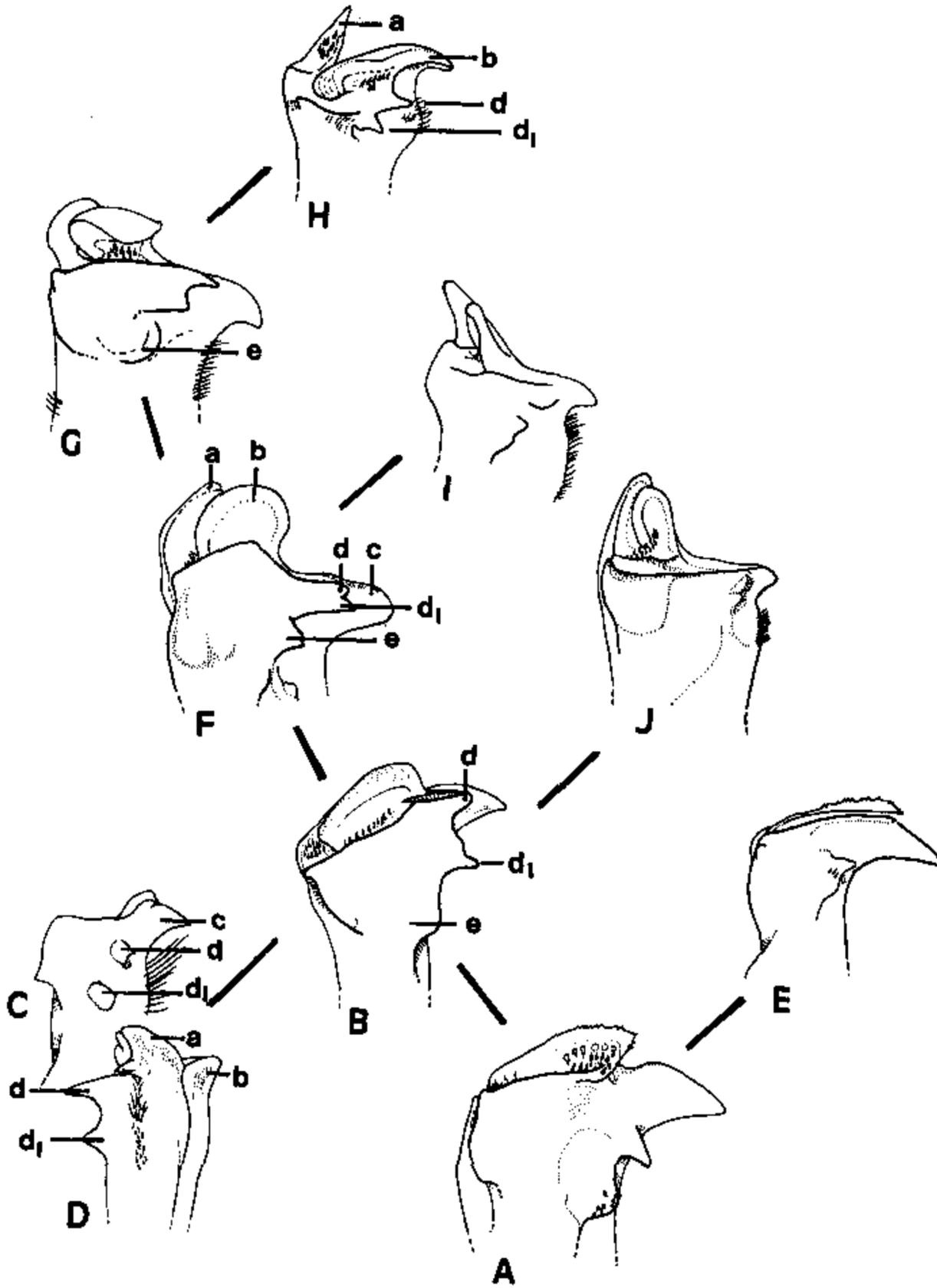
Fig. 2. Homologies in the gonopods of *Potamocarcinus*. (A) *P. aspoekorum*; (B) *P. richmondi*; (C) (D) *P. colombiensis*; (E) *P. zilchi*; (F) *P. roatensis*; (G) *P. magnus*; (H) *P. nicaraguensis*; (I) *P. hartmanni*; (J) *P. chajulensis*. a, Caudal lobe; b, mesial lobe; c, mesial process; d, d_1, cephalic teeth; e, cephalic process. All illustrations are in cephalic view, except (D) which is in mesial view.

(3) a cephalic process composed of a tooth and/or a hump; (4) a caudal lobe, that in some species can reach beyond the apex. The greatest similarity to the cup-shaped mesial lobe of *Potamocarcinus* is found in the more rudimentary mesial lobe of the species of the genus *Strengeriana* Pretzmann, 1971. Furthermore, in the case of

Strengeriana risaraldensis Rodríguez and Campos, 1989, there is an incipient finger-like projection on the mesial side, similar to the well-developed mesial process present in the genus *Potamocarcinus*. For these reasons *S. risaraldensis* can be considered as an outgroup for the polarization of characters.

A distinguishing feature of the Pseudothelphusidae is the reduction of the exognath in the third maxilliped (Rodríguez, 1986). This reduction, however, is not uniform in all species. The genera *Epilobocera* and *Strengeriana* have the exognath slightly larger than the ischium of the endognath, and one species of *Epilobocera* even has a rudimentary flagellum. The irreversible loss of the flagellum represents one of the basic synapomorphies of the Pseudothelphusidae, whereas its presence in *Epilobocera* represents the plesiomorphic condition of this character. Therefore the genus *Epilobocera* can be considered as approaching the ancestral condition of the family and, together with *Strengeriana*, will be used as a second out-group for the polarization of characters (table 4). Variations of this character within *Potamocarcinus* are presented in table 2.

Results of the cladistic analysis

The most parsimonious tree found has 42 steps and CI = 0.82 excluding uninformative characters (figure 3). According to this tree characters 1, 2, 3, 6, 14 and 15 show homoplasic conditions. Character 5 is parsimony uninformative but defines
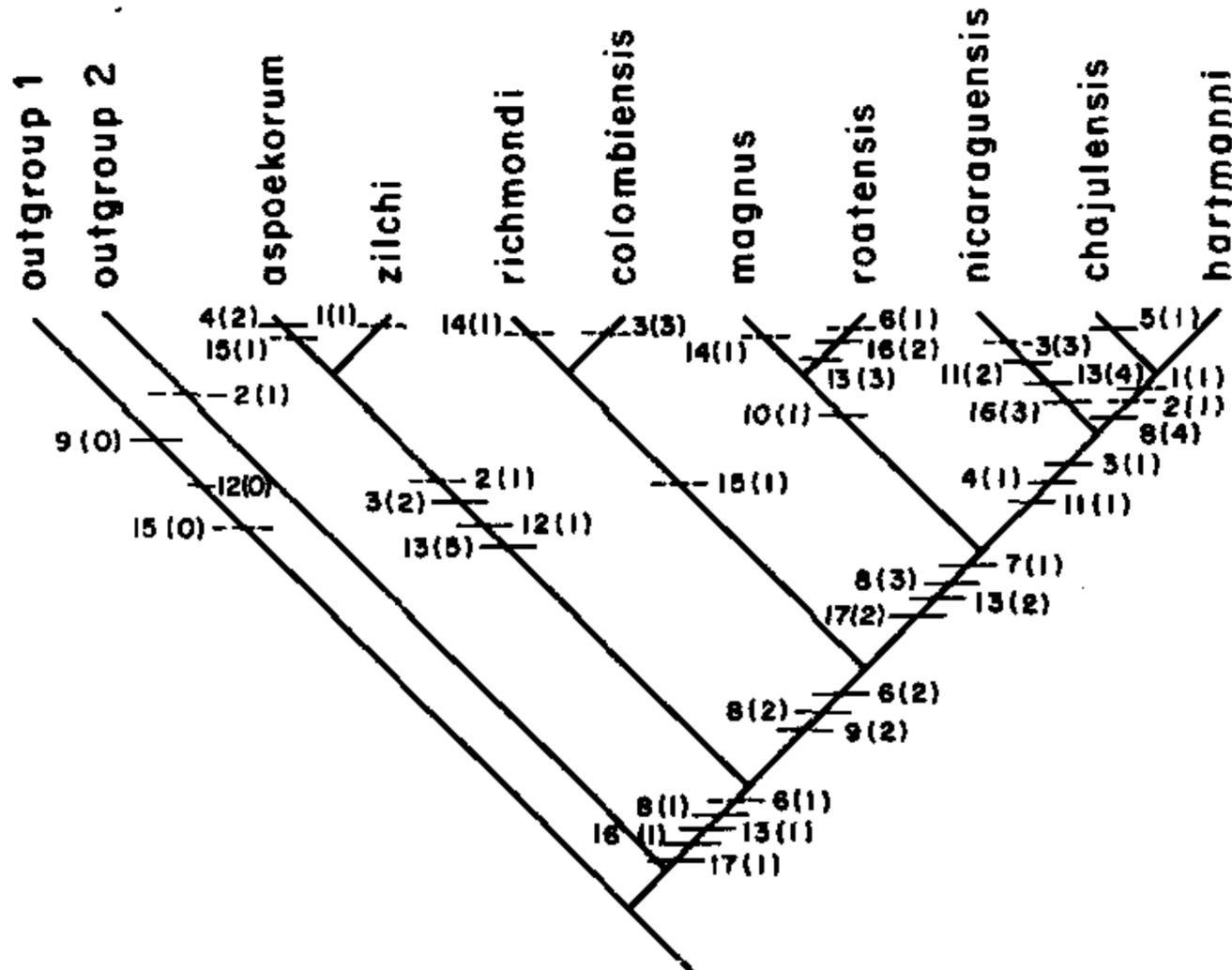

FIG. 3. Most parsimonious cladogram obtained for the species of *Potamocarcinus*, with indication of changes in character states. Outgroup 1, *Epilobocera sinuatifrons*; outgroup 2, *Strengeriana risaraldensis*.

P. chajulensis as valid species. The tree starts with the sister pair *Potamocarcinus aspoekorum–P. zilchi* defined by characters 2(1), 3(2), 12(1) and 13(5). Then follows the cluster *Potamocarcinus richmondi–P. colombiensis* defined by character 15(1) and the rest of the species supported by characters 7(1), 8(3), 13(2) and 17(2). The cluster *Potamocarcinus magnus–P. roatensis* is defined by character 10(1). A final cluster, defined by characters 3(1), 4(1) and 11(1), splits into a branch leading to *Potamocarcinus nicaraguensis*, defined by characters 3(3), 11(2), 13(4) and 16(3), and another branch leading to the pair *P. chajulensis–P. hartmanni*, supported by characters 1(1), 2(1) and 8(4). The branch leading to *Potamocarcinus hartmanni* is not defined by any autapomorphy, and therefore is zero length.

Continental insularity in Neotropical freshwater crabs

Freshwater crabs appear in continental islands on three areas of Central and South America, and involve five species.

Margarita and Trinidad Islands offshore of Venezuelan mainland

Trinidad, Margarita Island and the mainland of Venezuela form an interrelated structural complex. The east–west trending Coastal Cordillera that extends parallel to the northern coast of Venezuela and eastward along the peninsula of Paria (as the Venezuela Eastern Range), crosses the strait which separates Venezuela from Trinidad, and forms the North Range in this island (figure 4A). Margarita Island, although situated geographically to the north of the backbone of the Coastal Cordillera, is usually related with this mountainous chain. It is generally accepted (Bellizia and Dengo, 1990) that there has been, since Tertiary times, a series of periodic submergences which brought about the break-up of the Coastal Cordillera, leaving as a remnant Margarita Island, and isolating Trinidad. At present a shallow platform, less than 60 m deep, connects Margarita Island to the northern coast of Paria, and Trinidad to the southern coast of the peninsula.

Dilocarcinus dentatus, a species widely distributed throughout South America, including many tributaries of the Orinoco River, has also a disjunct sub-area in Trinidad. The nearest mainland locality to Trinidad recorded for this species is in the Orinoco Delta, approximately 30 km from the Trinidad coast, at altitudes less than 2 m above sea level (López and Pereira, 1996).

Eudaniela garmani has disjunct sub-areas of distribution on the Venezuelan mainland, Trinidad and Margarita Island. The nearest recorded locality to Trinidad Island, on the Venezuela Mainland, for this species is at the eastern end of the Paria Penisula, approximately 30 km from the Trinidad North Range, whereas the distance of Margarita Island to the nearest locality of this species on the mainland (Cerro Turumiquiri) is 80 km. Radiocarbon evidence has shown that this species has been present on the mainland for at least 5000 years b.p. (Rodríguez and Díaz, 1977).

Microthelphusa odaelkae is present at high altitude (>800 m) in the Trinidad North Range. The species of the genus closest to *Microthelphusa odaelkae*, both morphologically and geographically, is *M. turumikiri* Rodríguez, 1980, whose area of distribution is at the occidental end of the Venezuela Eastern Range, at 1500 m above sea level. The present distance between the areas of both species is 130 km. The other species of the genus are found at considerable distances from Trinidad, in the Andes, Coastal Cordillera, Venezuelan Guiana and Surinam, all of them above 800 m altitude.

The submarine connections mentioned above emerged during the Pleistocene sea
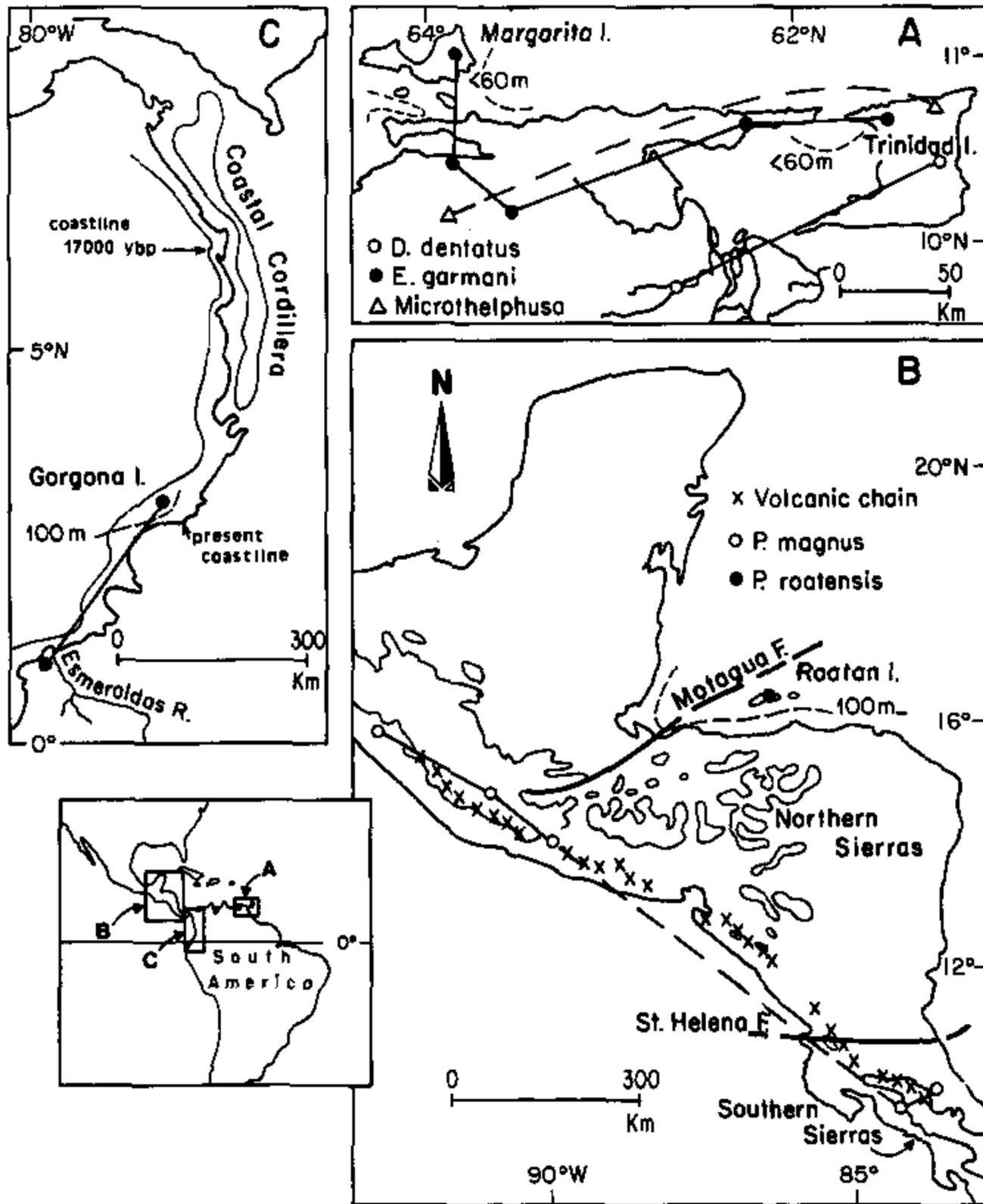
FIG. 4. Geographical setting of the Neotropical freshwater crabs from continental islands. (A) *Dilocarcinus dentatus, Eudaniela garmani* and *Microthelphusa* spp. in Trinidad, Margarita Island and the mainland of Venezuela; *(B) Potamocarcinus roatensis* and its sister species *P. magnus* in Roatan Island and the mainland of Central America; (C) *Hypolobocera gorgonensis* in Gorgona Island and the Pacific coast of South America.

lowering, and attained at least 61 m in this area, before the Holocene transgression that began approximately 11 500 years b.p. A land connection during this period between the Orinoco Delta and the southeastern tip of Trinidad (Galeota Point) has been documented by Carr-Brown (1972). The presence of the Trinidadian sub-area of distribution of *Dilocarcinus dentatus* can be understood in terms of this Pleistocene land bridge. Since *Eudaniela garmani* occurs at present down to low

altitudes, its presence in the three sub-areas can be explained also by a Pleistocene expansion of the mainland sub-area across the Margarita–Venezuela and Trinidad–Venezuela platforms.

The fragmented distributional pattern of the genus *Microthelphusa* and the altitudes at which the various species are found preclude the possibility of a Quaternary vicariant event for the origin of *M. odaelkae*, and rather points to an older Tertiary allopatric event.

Northern coast of Honduras

Two large areas of different tectonic and geologic structure have been recognized in Central America: namely, nuclear Central America, and the Isthmian Link from southern Nicaragua to northwestern Colombia. Nuclear Central America is almost all comprised within the Chortis Block defined to the north by the Motagua Fault in central Guatemala, and to the south by the Santa Helena Fault between Nicaragua and Costa Rica (figure 4B). The morphotectonic units within both areas are the Sierras of northern Central America, the Sierras of southern Central America and the Pacific volcanic Chain (Donnelly *et al.*, 1990).

Roatan Island is part of the Bay Islands that sits on the Bonaca Ridge, north of the Honduras coast. The Bay Islands are probably a continuation of the mountain system of nuclear Central America (Donnelly *et al.*, 1990), but this cannot be absolutely ascertained since Roatan Island has Cretaceous lithologies that are analogous to those of the Motagua Valley and the Cayman Ridge to the north-east.

As shown by our cladogram (figure 3), *Potamocarcinus roatensis* is a sister species of *P. magnus*. This latter species occupies two disjunct areas in both sections of Central America, the first in Chiapas State (Mexico), southern Guatemala and El Salvador, and a second one in Costa Rica (Rodríguez, 1982). In nuclear Central America *Potamocarcinus magnus* occurs along the Pacific volcanic chain, but it does not extend into the northern Sierras. In the Isthmian link *Potamocarcinus magnus* is restricted to Costa Rica in both the Pacific volcanic Chain and the southern Sierras.

Since Roatan Island is separated from the mainland by continuous depths between 200 and 1000 m, a connection of both areas during minimal Quaternary sea level is precluded. The observed modern distributions of *Potamocarcinus roatensis* and the sister species *P. magnus* rather suggest a vicariant event of a widely distributed ancestor in pre-Quaternary times.

Pacific coast of Colombia

A tectonic trait of the northern Andes is a Coastal Cordillera, paralleling the coast, which originated during Eocene times. This cordillera can be followed as a separate unit from Panama to the Colombian Pacific coast, where it disappears at Cabo Corrientes. A small remnant, just touching the west coast of Ecuador at Esmeraldas, may form a missing link to this coastal belt. According to one theory Gorgona and Gorgonilla Islands represent an outcrop of this cordillera, 280 km to the south of Cabo Corrientes. Another theory holds that the islands are Cretaceous blocks from the Western Cordillera, which rotated north-east in relation to its original axis (Llinas *et al.*, 1990).

Hypolobocera gorgonensis occupies two disjunct sub-areas of distribution on Gorgona Island and near the basin of the Esmeraldas River in Ecuador (figure 4C), separated by a sea distance of 300 km. At present the island is separated from the coast of Colombia by depths between 80 and 100 m, but a continuous connection

with the Colombian and Ecuadorian coasts emerged during the last glaciation, 17 000 years b.p., when the sea level dropped by approximately 120 m (figure 4C). Alberico (1986) has shown that many vertebrate species from Gorgona Island are more closely related to species from Ecuador than to those of the nearby Colombian mainland. Thus a plausible hypothesis is that the geographical area of *Hypolobocera gorgonensis* before the Holocene transgression, which began approximately 10 000 years b.p., comprised the two present disjunct areas and the then-emerged intervening lands. The morphological similarity between the insular and continental populations suggests a relatively recent date for the severance of the gene flow. Further study of this species using allozymes or other genetic markers would indicate whether the genetic similarity is as close as the morphological similarity suggests.

An alternative hypothesis is that *Hypolobocera gorgonensis* reached the island dispersed by rafts originating in the Esmeraldas River and transported northwards along the coast. The presence of numerous tree trunks on the west coast of the island, transported by currents, has been documented (Alberico, 1986). The main surface currents in this area have a northwesterly direction during January to March, with current speeds between 20 and 30 cm/s (Forsbergh, 1969). Given these current characteristics, a raft could cover the distance between Esmeraldas, Ecuador, and Gorgona Island in 12–17 days, a passage not impossible for a group of crabs which possess pseudolungs for gas exchange with the fresh water contained in their branchial chambers (Rodríguez, 1986).

Acknowledgements

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