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**The freshwater crabs of the Barbilla National Park, Costa Rica (Crustacea: Brachyura: Pseudothelphusidae), with notes on the evolution of structures for spermatophore retention**

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*Abstract.*—The Barbilla National Park, a natural area of high biodiversity on the Caribbean slope of Costa Rica, possesses two species of freshwater crabs that share the same biotope in different localities of the Park. The first species, *Potamocarcinus magnus* (Rathbun, 1896), one of the largest species of the family Pseudothelphusidae, is widely distributed in Middle America, from Costa Rica to Southern Mexico. The other species is a new species, *Ptychophallus barbillaensis*. This is a species of small crabs, possibly restricted to the National Park and neighboring areas. It can be distinguished from all other species in the genus by the form of the receptacle formed in the apex of the male gonopod, possibly for the retention of spermatophora during copulation. The species of *Ptychophallus* Smalley, can be arranged in a morphocline according to the relative development of this receptacle, with the present new species midway between the ancestral condition and the closed channel found in *P. goldmanni* Pretzmann, 1965.

The Barbilla National Park covers 12,830 hectares of humid tropical forest on the Caribbean watershed of the Sierra de Talamanca, Costa Rica. This stretch of mostly primary vegetation is located between the valleys of the Pacuare and Chirripó rivers, between 200 and 1600 m above sea level. The area is noted for its high biodiversity.

During recent surveys carried out by the Mid Sweden University several samples of freshwater organisms have been collected in the ravines that surround the Nairi Field Station, close to the northwestern border of the Park. Two species of freshwater crabs were discovered among the materials in these collections. One of them, a new species belonging to the genus *Ptychophallus* Smalley, 1964a, is described in the present contribution. The materials recorded are deposited in the Reference Collection of the

Instituto Venezolano de Investigaciones Científicas, Caracas (IVIC); the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and the Museum of Natural History of Tulane University, New Orleans (TU). Other abbreviations used are cl, carapace length, and cb, carapace breadth.

Systematics

Family Pseudothelphusidae Rathbun, 1893  
Genus *Potamocarcinus* H. Milne Edwards, 1853

*Potamocarcinus magnus* (Rathbun, 1896)

*Material.*—Costa Rica: Río Caño Seco (10°00'N, 83°26'W), affluent of Río Dantas, Barbilla National Park, 7 Jan 1999, leg. I. Hedström, 300 m above sea level, 1 immature female, cl 17.3 mm, cb 25.0 mm

(IVIC 1070); Casas Negras, Río Dantas, Barbilla National Park, 8 Jan 1999, leg. I. Hedström, 200 m above sea level, 1 immature male, cl 19.8 mm, cb 28.3 mm (IVIC 1071); Río Barbilla, Barbilla National Park, 28 Jan 1999, leg. I. Hedström, 100 m above sea level, 2 immature males, cl 17.0 and 12.4 mm, cb 23.7 and 18.5 mm, 1 immature female, cl 10.0 mm, cb 15.7 mm (IVIC 1072).

*Remarks.*—Although our specimens are immature, they can be referred with certainty to this species. *Potamocarcinus magnus* is widely distributed in Central America, but Rodríguez (1982) distinguish three different morphological groups from (a) Costa Rica, (b) El Salvador, Guatemala and southern Mexico, and (c) Guatemala. The characters of the carapace in our specimens agree with those given for the Costarican form. However, the typical flat tubercles present over the surface of the carapace cover a greater area, a characteristic possibly due to the juvenile condition of the specimens. The right cheliped has the typical long and narrow tubercle over the palm, at the base of the fingers, although it is relatively little developed. In the first male gonopods there is not an abnormal intrusion of the marginal process into the distal lobe, as was the case in the specimen from Costa Rica illustrated by Rodríguez (1982, fig. 72b). *Potamocarcinus magnus* is the largest of all species of Pseudothelphusidae, with a cb of 135 mm reported by Rathbun (1896).

Genus *Ptychophallus* Smalley, 1964a  
*Ptychophallus barbillaensis*, new species  
 Fig. 1, 2C, H

*Material.*—Costa Rica: Río Caño Seco (10°00'N; 83°26'W), affluent of Río Dantas, Barbilla National Park, 7 Jan 1999, leg. I. Hedström, 300 m above sea level, 1 male holotype, cl 16.9 mm, cb 27.7 mm (IVIC 1073), 1 male paratype, cl 13.4 mm, cb 20.7 mm (IVIC 1074); Nairi Field Station (09°59'N; 83°27'W), 3 km north of the bor-

der of Barbilla National Park, 7 Jan 1999, leg. I. Hedström, 2 ovigerous females, cl 15.6 and 13.9 mm, cb 25.0 and 21.1 mm (IVIC 1075); Casas Negras, Río Dantas, Barbilla National Park, 8 Jan 1999, leg. I. Hedström, 200 m above sea level, 2 males, cl 12.2 and 11.9 mm, cb 18.9 and 18.7 mm (IVIC 1076); Las Cuevas, Río Dantas, Barbilla National Park, 11 Jan 1999, leg. I. Hedström, 150 m above sea level, 2 males, cl 14.2 and 11.7 mm, cb 22.5 and 18.6 mm, 1 mature female, cl 14.1 mm, cb 21.5 mm (IVIC 1077); El Recodo, Río Dantas, Barbilla National Park, 6 Jan 1999, leg. I. Hedström, 300 m above sea level, 1 male, cl 15.2 mm, cb 23.3 mm, 1 immature male, cl 9.9 mm, cb 15.0 mm, 1 male juvenile, cl 5.8 mm, cb 13.5 mm (IVIC 1078).

*Diagnosis.*—First gonopods with large lateral lobe divided in 2 subequal rounded segments by median notch; proximal segment smaller, subcircular; distal segment projected anteriorly and bent caudally to form cup-shaped receptacle; apex strongly bent laterally forming, with distal segment of lateral lobe, characteristic sinus; field of spines directed toward latero-cephalic side, oblong, with deep notch on mesial side; cephalic end of apex with 2 expansions, distal subtriangular in lateral and caudal views, with notch on lateral side, proximal rounded in cephalic view, beak-like in mesial view.

*Description of holotype.*—Carapace 1.6 times as wide as long, surface smooth and polished, except for few granules on posterior branchial regions, near margins; cervical grooves recurved backwards, narrow and deep, not reaching margins of carapace; anterolateral margins with shallow and wide postorbital notch bordered by 5 papillae, rest of borders with small papillae that becomes dentiform behind level of cervical grooves. Postfrontal lobes low, delimited anteriorly by transverse depressions; median groove narrow, deep, making incision on upper margin of front. Surface of carapace between postfrontal lobes and front flat, slightly inclined forward and towards mid-

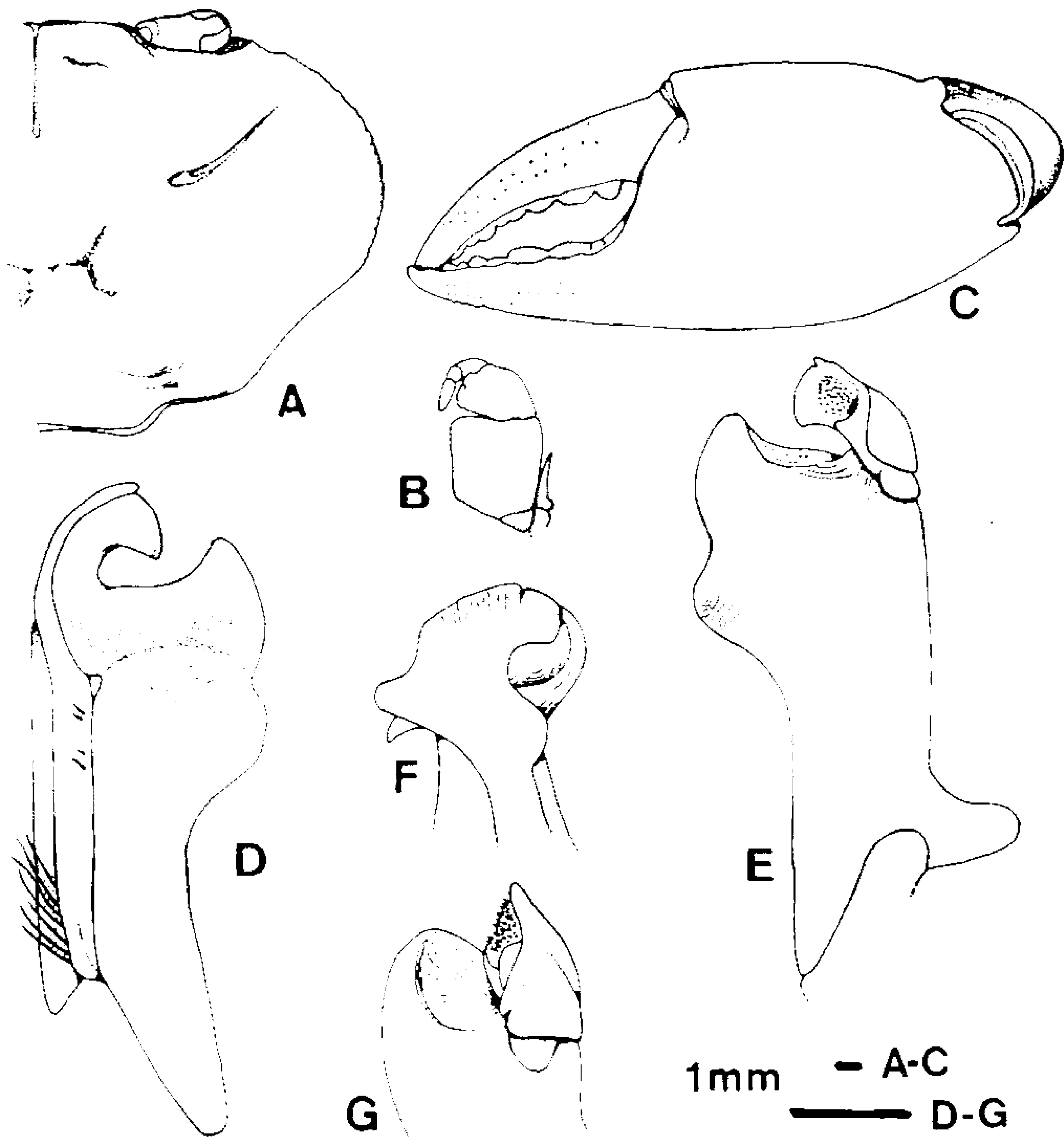


Fig. 1. *Ptychophallus barbillaensis*, new species, holotype from Río Caño Seco, Costa Rica (IVIC 1073): A, dorsal view of right side of carapace; B, third maxilliped, left; C, chela of largest cheliped (left), external view; D, first left gonopod, caudal view; E, same, cephalic view; F, same, apex, mesial view; G, same, apex, cephalic view.

dle line. Upper margin of front in dorsal view slightly convex and divided into two halves by median notch, thin, well marked, with small tubercles; lower margin thin, moderately sinuous, advanced in front of upper margin; both margins subparallel.

Exognath of third maxilliped 0.65 length of ischium of endognath. Palm of largest cheliped moderately swollen, with lower and upper margins convex; fingers gaping,

with rows of small black-brown points on external surface.

First gonopods wide in latero-mesial direction, narrow in caudo-cephalic direction; large lateral lobe divided in 2 subequal rounded segments by median notch; proximal segment smaller, subcircular; distal segment projected anteriorly and bent caudally to form cup-shaped receptacle semi-enclosed by apex of gonopod; apex strongly

bent laterally, forming with distal segment of lateral lobe characteristic sinus; field of spines directed toward latero-cephalic side, oblong, with deep notch on mesial side; cephalic end of apex forming two expansions; distal expansion continuous with margin of gonopod, subtriangular, in lateral and caudal views, with notch on lateral side; proximal expansion rounded in cephalic view, beak-like in mesial view.

*Remarks.*—This species can be distinguished from all others in the genus by the cupshaped expansion of the distal segment of the lateral lobe of the first gonopods and by the strong recurvation of the apical peduncle of gonopod over this expansion.

*Etymology.*—The species is named after the Barbilla National Park, Costa Rica, where the species was collected.

#### Evolution of Structures for Spermatophore Retention in *Ptychophallus*

Although the morphology of the first male gonopods are essential for the discrimination of the species of Pseudothelphusidae, very little is known of the function of the different processes of these appendages during copulation. In all species, the apex is provided with a field of minute spines (Smalley 1964b) which surround the opening of the spermatophore channel and serve to hold the spermatophore once it is extruded by the piston-like pumping action of the second gonopod.

In the species of *Ptychophallus* a trend can be observed towards a reaccommodation of the lateral lobe and the various components of the apex of the gonopod, to form a structure that possibly serves to receive and keep the spermatophore once it is extruded. This is fully developed in *Ptychophallus goldmanni* Pretzmann, 1965, but the other species can be arranged in a morphocline comprising several stages of development of this structure, as follows.

*Stage I* (Fig. 2A, F).—In the primitive condition there is a wide lateral lobe, which is foliose, with a shallow depression or

deeply notched, with the distal portion advanced and transverse. The field of spines is located distant from the lateral lobe, facing caudo-laterally, its long axis forming an angle of approximately  $60^\circ$  with the longitudinal axis of the appendage. Species at this stage are *P. colombianus* (Rathbun, 1893), *P. exillipes* (Rathbun, 1898), *P. kuna* Campos & Lemaitre, 1999, and *P. tristani* (Rathbun, 1896).

*Stage II* (Fig. 2B, G).—Lateral lobe deeply notched as in some species of stage I, but the distal portion is more advanced and joins the caudal side of the apical peduncle. The field of spines approaches the lateral lobe and is directed laterally, with its long axis forming an angle of approximately  $180^\circ$  with the longitudinal axis of the appendage. Species at this stage are *P. micracanthus* Rodríguez, 1994, *P. montanus* (Rathbun, 1898), and *P. tumimanus* (Rathbun, 1898).

*Stage III* (Fig. 2C, H).—Lateral lobe as in stage II, but the distal portion is cupped, and its border is continuous with the caudal margin of the apical peduncle. The field of spines faces the lateral side, and its long axis forms an angle of approximately  $230^\circ$  with the longitudinal axis of the appendage. The only species at this stage is *P. barbillaensis*.

*Stage IV* (Fig. 2D, I).—The lateral lobe has the proximal segment strongly reduced, the distal one very advanced and forms, together with the border of the field of spines, a channel-like receptacle which is wide open. The field of spines is directed laterally, its long axis forming an angle of approximately  $180^\circ$  with the longitudinal axis of the appendage. The only species at this stage is *P. cocleensis* Pretzmann, 1965.

*Stage V* (Fig. 2E, J).—The lateral lobe is reduced to a distal segment, very advanced and forms, together with the border of the field of spines, an almost closed channel-like receptacle. The field of spines is directed laterally, its long axis forming an angle of approximately  $180^\circ$  with the longitudinal axis of appendage. The only species

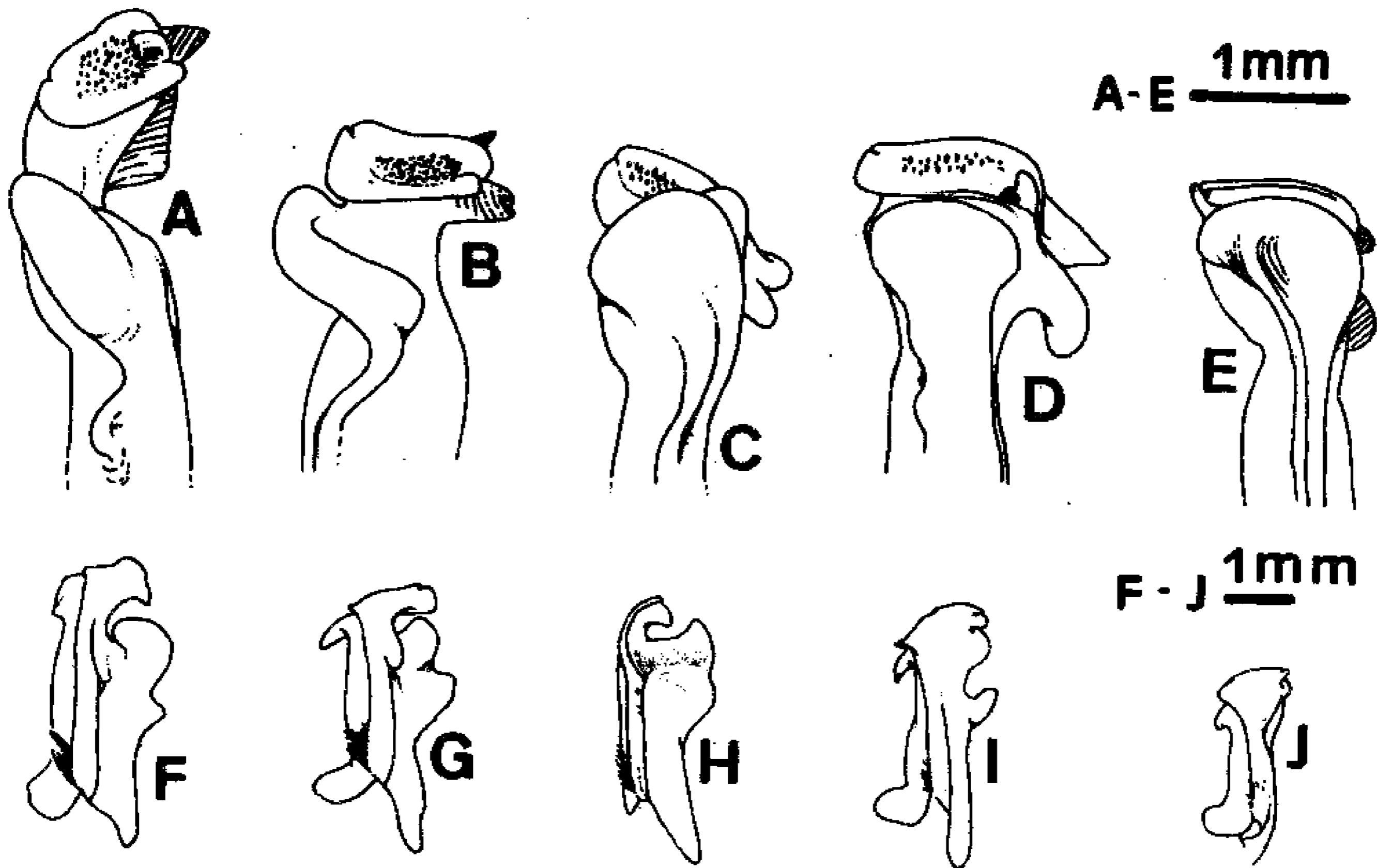


Fig. 2. First left gonopod of *Ptychophallus* species: A, F, *P. tristani* (Rathbun, 1896), male from ~1.8 km E Atenas, San José Province, Costa Rica (TU 4436); B, G, *P. montanus* (Rathbun, 1898), male from ~3 km N San Jerónimo de Moravia, San José Province, Costa Rica (TU 4442); C, H, *P. barbillaensis*, new species, holotype from Río Caño Seco, Costa Rica (IVIC 1073); D, I, *P. cocleensis* Pretzmann, 1965, holotype from Rio Coclé del Norte, Panama (USNM 119869); E, J, *P. goldmanni* Pretzmann, 1965, holotype from Cana, Panama (USNM 54044); A-E, detail of apex, lateral view; F-J, total view, caudal.

at this stage is *P. goldmanni* Pretzmann, 1965.

A similar morphocline, although not leading to the formation of a structure for the retention of the spermatophore, has been observed in the lateral lobe of species of the genera *Pseudothelphusa* Saussure, 1857, and *Tehuana* Rodríguez & Smalley, 1969, in southern Mexico (Rodríguez 1986). In this case the morphocline follows a general westward direction, suggesting an allopatric speciation of primitive demes, encompassing a migration along the same geographical axis. In the case of *Ptychophallus* the pattern is more complex. Species of stages I and II overlap their areas of distribution in Costa Rica, and the areas of *P. kuna* (stage I) and *P. micracanthus* (stage II) are relatively close in Central Panama (see map in Campos & Lemaitre 1999). The area of *P. barbillaensis* (stage III) is nested among the species of stages I and II. *P. cocleensis* (Stage IV) is found

in Central Panama, and *P. goldmanni* (Stage IV) further East, near the Colombian border. Notwithstanding this complex pattern, the general trend of the morphocline is eastward. This direction contrasts with the supposed radiation of the family, that proceeded westward from an ancestral area in northern Colombia (Rodríguez 1986).

Two species of *Ptychophallus* cannot be placed in this morphocline. *P. lavallensis* Pretzmann, 1978, has a field of spines strongly upturned cephalically and a very wide undivided lateral lobe that does not approach the field of spines. *P. paraxanthusi* Bott, 1968, has a field of spines bent mesially and a wide, shallow-notched, lateral lobe that displays distally several ridges but does not form a receptacle. These species possibly represent phyletic lines that differ both among themselves, as with those species in the morphocline described above.



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