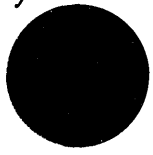


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with a Key to the Middle American Genera
(Crustacea Decapoda, Pseudothelphusidae)

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A New Genus of Freshwater Crabs from Guatemala, with a Key to the Middle American Genera (Crustacea Decapoda, Pseudothelphusidae)

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ABSTRACT: *Phrygiopilus*, a new genus of Pseudothelphusidae, and two new species, *P. chuacusensis* and *P. acanthophallus*, are described from Guatemala. The structure of their gonopods is entirely different from that of any other crabs in the family, and their relationships are unknown. Notes on identification and distribution of freshwater crabs of the West Indies, Mexico, and Central America are given, along with a key to the genera and subgenera, and a table listing generic and subgeneric names appearing in the literature.

INTRODUCTION

A species of freshwater crab with a very unusual gonopod was collected in Guatemala; subsequently, another species with the same basic gonopod type was received from the U. S. National Museum. These two species are described, along with a new genus to accommodate them.

An increase in research on American freshwater crabs has resulted in a confusing number of new genera and species, and several different classifications (see, for example, Bott, 1969; Pretzmann, 1965). The taxonomic publications seem to be directed principally toward other specialists, but nonspecialists also need to learn more about these widespread and interesting animals. Not only are tropical freshwaters increasingly studied by limnologists, but the role of freshwater crabs as intermediate hosts of *Paragonimus*, the human lung fluke, is becoming more significant as parasitologists report an alarming number of cases of human paragonimiasis in the New World.

I am presenting some notes on field identification, the more important facts about the distribution of the genera of Mexico, Central America, and the West Indies, a table of generic and subgeneric names appearing in the literature, and a key to the genera and subgenera.

Phrygiopilus new genus

Diagnosis.—The first male gonopod bears a large process which extends beyond the “apex” a distance about equal to the length of the gonopod from the marginal setae to the apex, and is as wide or wider than the main part of the gonopod. The margin is strongly curved laterad. The spine field and apical spines are in a groove formed by the proximal part of the gonopod and the supra-apical process, and this area projects strongly laterad.

Type species.—*Phrygiopilus chuacusensis*, n. sp.

Etymology.—The name *Phrygiopilus* (masc.) refers to the resemblance of the distinctive supra-apical process of the gonopod of the type species to the “liberty cap” of the ancient Phrygians.

Phrygiopilus chuacusensis new species

Description.—Carapace moderately convex, particularly anteriorly, smooth, with scattered very small punctae. Front narrow, upper margin without tubercles, median sulcus moderately deep, broad, poorly defined. Orbits wide, posterior margin sinuous. Cervical suture moderately deep, broad, terminating before reaching anterolateral margin of carapace, not producing notch in margin. Lower margin of orbit with single row of small tubercles.

Chelae of adult males with two series of teeth, large alternating with one or two small, contrast in size somewhat greater than usual for family. Chelae unequal, palm of larger swollen, fingers gaping, inner margin of carpus with median tooth, three small proximal teeth. Inner dorsal margin of merus with single row of 15 teeth, varying irregularly in size; scattered tubercles mesial to marginal row. Width of third pereopod (second walking leg) about 30% of length.

First gonopod long, reaching beyond thoracic sternum of second pereopod. Margin of gonopod curving laterad, sperm channel opening on cephalic surface. Caudal surface of gonopod produced into very large helmet- or cap-shaped process, about as long and broad as proximal part of gonopod from setae to apical spines. Spine field concealed between supra-apical process and cephalic border of apex. Gonopod approximately flat in transverse plane, but apical area (bearing spine field) folded into strong cephalic projection. Tip of supra-apical process with smaller fold. Low V-shaped elevation proximal to apex at about level of marginal setae. Mesial margin bearing blunt tooth at level of apical spines. Supra-apical process bearing numerous flat spines on lateral and mesial surfaces.

Second gonopod with tip flattened; lateral surface bearing spines or

TABLE 1.—Measurements (in mm) of *Phrygiopilus*. Breadth is greatest carapace breadth; length is median carapace length; exorbital width is distance between the junction of the carapace margins and the orbits; front is the length of the lower margin of the anterior border of the carapace

Sex	Breadth	Length	Fronto-orbital width	Front
<i>P. chuacusensis</i>				
F (soft shell)	28.0	17.0	16.0	7.2
F	24.0	14.2	13.8	6.1
M	20.2	12.2	12.2	5.6
M (holotype)	20.2	12.1	12.1	5.6
M	18.9	11.1	11.8	5.6
M	16.5	10.4	10.7	4.8
M	15.4	9.7	9.8	4.4
M	15.0	9.1	9.5	4.2
F	10.9	7.2	7.1	3.6
F	11.4	7.1	7.5	3.8
F	10.7	6.7	6.9	3.7
F	9.7	6.4	6.3	3.2
<i>P. acanthophallus</i>				
M	21.6	12.5	11.6	5.2

bristles on distal 16% of flagellar segment of gonopod; mesial surface with flat spineless area shorter than spine-covered surface both distally and proximally.

Specimens examined.—6 males, 6 females (Table 1), all from the same locality; small stream, 96 km by highway N Guatemala City, near the summit of Sierra de Chuacus, Departamento Baja Verapaz, Guatemala, lat 15° 00'N, long 90° 26'W; 19 Aug. 1967; coll. A. and I. Smalley.

Disposition of types.—Male holotype (USNM-126113, four male and six female paratypes (USNM-126114) in the U. S. National Museum. One male paratype (TU-6090) in the Tulane University collections.

Size.—Measurements of the specimens are given in Table 1. The smallest male (carapace breadth 15.5 mm) can be easily identified by the gonopods, which have already assumed the adult configuration.

***Phrygiopilus acanthophallus* new species**

Description.—Carapace slightly convex, front almost vertical, without distinct upper border. Carapace with scattered small punctae, anteriorly with close-set flat tubercles. Anterior border of front with strongly produced median convexity. Posterior orbital border arcuate, tuberculate. Anterolateral margin of carapace tuberculate, tubercles not becoming spiniform. Cervical groove shallow, bordered posterolaterally by low ridge.

Chelae of holotype male and only specimen unequal, the larger chelae only slightly swollen, fingers not gaping. Inner border of carpus with large sharp tooth about two-thirds distance from proximal articulation. Three small, low teeth posterior to large tooth, small tubercles anterior to tooth, outer border irregularly tuberculate. Upper anterior border of merus with irregular blunt teeth, lower border with smaller blunt teeth or large tubercles.

Walking legs long, slender, particularly the merus.

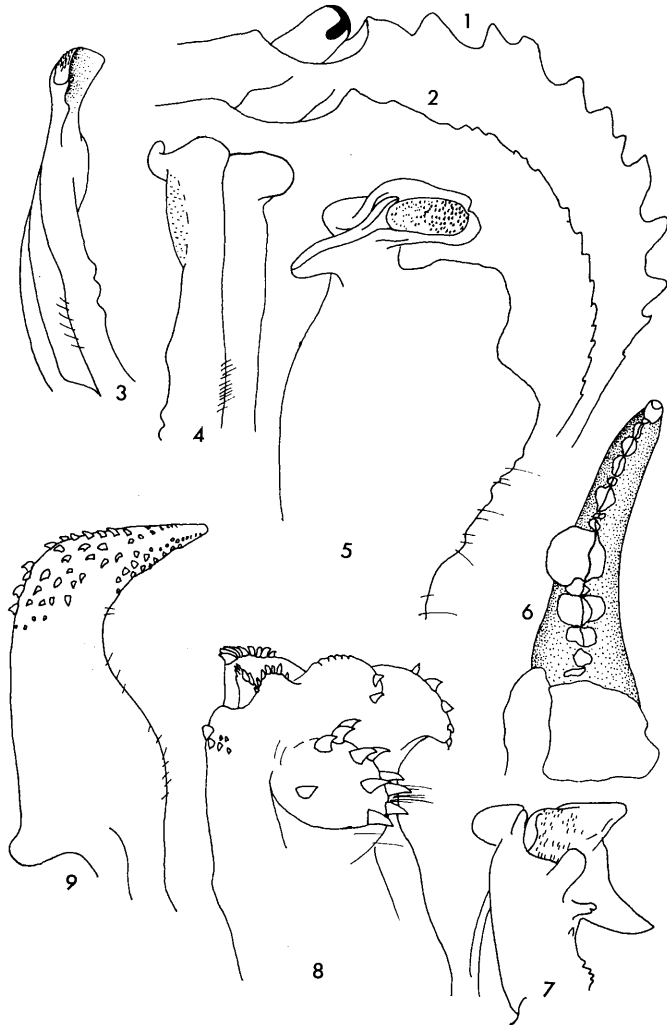
Gonopod with margin curving strongly laterad, sperm channel opening on cephalic surface. Supra-apical process broadly rounded, curving strongly mesiad, bearing numerous flat teeth. Spine field and apical teeth concealed between supra-apical process and cephalic border of apex, this area strongly produced cephalad. V-shaped cephalic prominence on proximal part of gonopod. Sharp mesial tooth at level of spine field.

Specimens examined.—Male holotype and only specimen (USNM-126110; Seamay Cave, 1 km S Senahu, Alta Verapaz, Guatemala; 10 February 1968; collected by Brother G. Nicholas.

Size.—Measurements of the holotypes are given in Table 1. The single specimen is probably close to maximum size for the species, since the gonopods are well developed. The chelae are not greatly swollen, and the fingers do not gape, but the walking legs are very slender, and the form of the chelae may be an adaptation to a cave habitat.

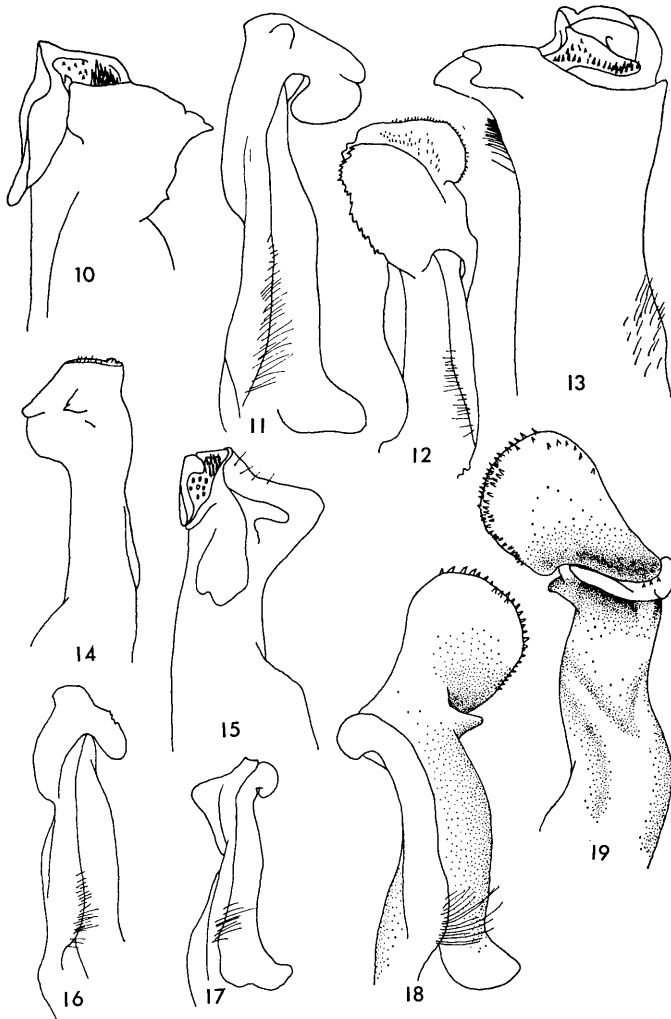
REMARKS

The genera and subgenera of the Pseudothelphusidae are the subject of considerable disagreement among specialists—an unfortunate situation likely to persist for many years. Criteria for the different



Figs. 1-9.—1. *Potamocarcinus* (*P.*) *nicaraguensis*, anterolateral margin of carapace; 2. *Potamocarcinus* (*P.*) *magnus*, same; 3. *Achlidon agrestis*, 1. gonopod, caudal surface; 4. *Allacanthos pittieri*, r. gonopod, caudal surface; 5. *Ptychophallus tumimanus*, r. gonopod, cephalic surface; 6. *Potamocarcinus* (*Raddaus*) sp., fixed finger of larger claw, from above; 7. *Epithelphusa mixtepens*, 1. gonopod, caudal surface; 8. *Epilobocera sinuatifrons*, r. gonopod, cephalic surface; *Trichodactylus constrictus*, r. gonopod, cephalic surface.

taxonomic levels have not been adequately discussed in the literature. Furthermore, the male gonopod has proven to be so useful in making generic distinctions that taxonomists have been remiss in using other characters. The definition of the genus *Phrygiopilus* is based solely on

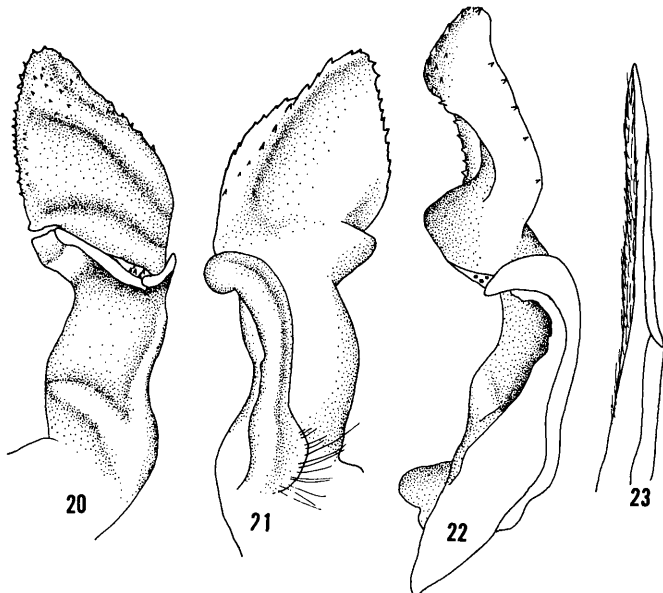


Figs. 10-19.—10, 16. *Pseudothelphusa (P.) juyi*, r. gonopod, cephalic surface; same, caudal surface; 11. *Pseudothelphusa (Tehuana) veracruzana*, r. gonopod, caudal surface; 12. *Spirothelphusa verticalis*, 1. gonopod, caudal surface; 13. *Potamocarcinus (P.) magnus*, r. gonopod, cephalic surface; 14. *Potamocarcinus (Raddaus) probably cobanensis*, same; 15, 17. *Elsalvadoria zurstrasseni*, r. gonopod, lateral surface; same, caudal surface; 18-19. *Phrygiopilus acanthophallus* r. gonopod, caudal and cephalic surfaces.

gonopod characters after due consideration of the inherent limitations of this procedure. The use of other characters would imply that they possess a diagnostic value, which in fact has not been shown to be true.

Phrygiopilus does not appear to be related to any other genus of Pseudothelphusidae. The supra-apical process of *Phrygiopilus* is apparently not a modification of a process found in other genera, but is a structure without any obvious homolog in other crabs. Low projections above the spine field are found in *Potamocarcinus* (Fig. 13), *Ptychophallus* (Fig. 5), and *Spirothelphusa* (Fig. 12). In these genera, some changes in the orientation of the spine field and apical spines take place. In *Phrygiopilus*, which has an apical modification extremely large in proportion to the rest of the gonopod, the apical spines retain their "original" or usual position, just as in a simple gonopod like *Achlidon* (Fig. 3) or *Potamocarcinus* (*Raddaus*) (Fig. 14). Therefore, I conclude that not only do these two species deserve separate generic status, but in addition their relationships to other genera of Pseudothelphusidae cannot be presently recognized.

P. acanthophallus can be readily distinguished from *P. chuacusensis* by the rounded supra-apical process, compared with the roughly triangular process in the latter species. The supra-apical process of *P. acanthophallus* curves markedly mesiad and is more spiny than that of *P. chuacusensis*. The mesial tooth of *P. acanthophallus* is sharp, not blunt and rounded. The anterior border of the front of the carapace



Figs. 20-23.—*Phrygiopilus chuacusensis*. 20-22. r. gonopod, cephalic, caudal and lateral surfaces; 23. r. second male gonopod, cephalic surface.

in *P. acanthophallus* is strongly curved, but in *P. chuacusensis* is nearly straight.

Isabellagordonia longipes (Pretzmann, 1965) has the very long and slender appendages associated with a cave existence, but differs from *P. acanthophallus* in the shape of the carapace and armature of the chelae. The legs in *I. longipes* are much longer than in *P. acanthophallus*. The holotype of *I. longipes* is a female, and the relationships of this species cannot be determined until a male can be examined.

IDENTIFICATION OF MIDDLE AMERICAN FRESHWATER CRABS

The taxonomy of these crabs is based mostly on the gonopods (the modified male pleopods), but crabs can occasionally be identified in the field by other means. Four species have distinct teeth on the antero-lateral margin of the carapace; *Potamocarcinus* (*Potamocarcinus*) *armatus* H. Milne Edwards, 1853, of southern Mexico, *P. (P.) nicaraguaensis* Rathbun, 1893, of Nicaragua and Costa Rica (Figs. 1 and 2; the latter showing the more typical carapace condition of *P. (P.) magnus* (Rathbun, 1896), and two of the three species of *Trichodactylus*, which are keyed out to species. Large individuals of both sexes of the subgenus *Potamocarcinus* (*Raddaus*) can be identified by the way one or more teeth of the fixed finger of the larger claw project conspicuously outward (Fig. 6).

Identification can also be aided by some distributional notes.

(1) The genus *Epilobocera* is restricted to the Greater Antilles (but not Jamaica, which has no Pseudothelphusidae); the freshwater crab of the Lesser Antilles is *Guinotia dentata* (Latreille, 1825), and of Surinam *G. garmani* (Rathbun, 1898), a South American genus not considered here. *Pseudothelphusa* has been reported from Cuba and Haiti, but the records are probably due to errors or misidentification of *Epilobocera*.

(2) Apparently only one species of crab occurs in each of the larger lakes of the region:

Lago de Chapala, Mexico—*Pseudothelphusa joutyi* Rathbun, 1893.

Lago de Atitlán, Guatemala—*Potamocarcinus* (*Raddaus*), species uncertain but probably *cobanensis* (Rathbun, 1905).

Lago de Amatitlán, Guatemala—*Potamocarcinus* (*P.*) *magnus guatemalensis* Rathbun, 1905 (this species also introduced into Atitlán). Lago de Managua, Lago de Nicaragua, and the volcanic lakes of Nicaragua ("lagunas")—*Potamocarcinus* (*P.*) *nicaraguaensis*.

(3) The cave crab of Cueva del Tío Ticho, Chiapas, Mexico, is *Potamocarcinus* (*Typhlopseudothelphusa*) *mocinoi* Rioja, 1952.

The perceptive field worker will often find differences in ecology, as well as differences in color, size and shape of the carapace and claws. However, initial identification must be made from the morphology of the first gonopod of preserved specimens. One of the gonopods of the largest available male should be removed, and thereafter kept in a small, cotton-stopped vial in the same jar with the rest of the crab. Only the terminal segment, or flagellum (an inappropriate term for

TABLE 2.—A list of generic and subgeneric names used for Middle American Pseudothelphusidae, listed alphabetically

This paper	Pretzmann, 1965	Other generic names and combinations applied to species in genus
<i>Achlidon</i> Smalley, 1964	<i>Pseudothelphusa</i> ; <i>P. (Achlidon)</i>
<i>Allacanthos</i> Smalley, 1964	<i>Pseudothelphusa</i> ; <i>P. (Allacanthos)</i>
<i>Elsalvadoria</i> Bott, 1967	<i>Pseudothelphusa</i> ; <i>Potamocarcinus (Elsalvadoria)</i>
<i>Epilobocera</i> Stimpson, 1860	<i>Epilobocera</i>	<i>Pseudothelphusa</i> (by error); <i>Opisthocera</i> S. I. Smith, 1870; <i>Boscia</i> A. Milne Edwards, 1866
.....
<i>Epithelphusa</i> Rodriguez y Smalley, 1969
<i>Isabellagordonia</i> Pretzmann, 1967	<i>Gordonia</i> Pretzmann, 1965
<i>Phrygotilus</i> , new genus
<i>Potamocarcinus (Potamocarcinus)</i>	<i>Potamocarcinus (Potamocarcinus)</i>	<i>Pseudothelphusa</i> ; <i>P. (Megathelphusa)</i> Smalley, 1964
H. Milne Edwards, 1853	<i>Pseudothelphusa</i> ; <i>P. (Anaphyrmos)</i> Smalley, 1965; <i>Boscia</i> ; <i>Potamocarcinus (Anaphyrmos)</i>
<i>Potamocarcinus (Raddaus)</i> Pretzmann, 1965	<i>Potamocarcinus (Raddaus)</i>	<i>Typhlopseudothelphusa</i>
.....
<i>Potamocarcinus (Typhlopseudothelphusa)</i>	<i>Potamocarcinus (Typhlopseudothelphusa)</i>
Rioja, 1952	<i>(Typhlopseudothelphusa)</i>
<i>Pseudothelphusa (Pseudothelphusa)</i>	<i>Pseudothelphusa (Pseudothelphusa)</i>
Saussure, 1857
<i>Pseudothelphusa (Tehuana)</i>	<i>Pseudothelphusa (Pseudothelphusa)</i>
Rodriguez and Smalley, 1969
<i>Psychohallus (Psychohallus)</i>	<i>Psychohallus (Psychohallus)</i>	<i>Pseudothelphusa</i> ; <i>Pseudothelphusa (Psychohallus)</i>
Smalley, 1964	<i>Pseudothelphusa (Camptophallus)</i>
<i>Psychohallus (Camptophallus)</i>
Smalley, 1965
<i>P. (Microptychophallus)</i>	<i>P. (Microptychophallus)</i>
Pretzmann, 1965
<i>P. (Semiptychophallus)</i>	<i>P. (Semiptychophallus)</i>
Pretzmann, 1965
<i>Spirothelphusa</i> Pretzmann, 1965	<i>Strengeria (Spirothelphusa)</i>	<i>Pseudothelphusa</i>

Notes: *Guinotia fuhrmanni* (Zimmer, 1912) was originally placed in *Epilobocera* by error. *Chaceus pearsei* (Rathbun, 1915) is considered by Pretzmann (1965) a subgenus of *Pseudothelphusa*, but I think this decision is questionable. Both species are South American.

the stout gonopod of the Pseudothelphusidae) is used. The orientation of the gonopod varies slightly *in situ*, and the crab can twist the gonopod considerably in mating, so it is best to first orient the gonopod so that the margin and marginal setae are facing the viewer. The margin is the line which marks the external opening of the sperm channel, and can always be located by the tuft of marginal setae on the proximal part of the gonopod, as shown on many of the accompanying drawings. The sperm channel opens near the tip of the gonopod (except in *Phrygiopilus*) in a well-defined area, the *spine field* (German *Borstenfeld*), which bears a variable number of cornified *apical spines*. Sometimes scattered spines are found on the gonopod, but the term apical spines is restricted to the spines found at the distal opening of the sperm channel. The remaining terms are more or less topographical; the surface bearing the marginal setae is the caudal surface, the opposite is the cephalic surface, and the other sides the mesial and lateral surfaces. The additional terms: distal, proximal, tooth, spine and process will suffice in nearly every case.

Table 2 is a guide to the generic and subgeneric names which have been used for Middle American Pseudothelphusidae. The first column is a list of the genera and subgenera separated in the key, with the exception of the subgenera of *Ptychophallus*, which are not keyed out, and the genus *Isabellagordonia*, which is omitted from the key because the male is unknown.

Achlidon, *Allacanthos*, and *Elsalvadoria* are given full generic status for the first time. The proliferation of genera in the Pseudothelphusidae is sometimes distressing to the non-specialist, but treating these taxa as separate genera is actually the more conservative alternative. Classifying species and subgenera together without demonstrating their relationships is an uncritical approach which causes incorrect concepts to persist in the literature, and may lead to entirely false zoogeographical conclusions.

In the key, only genera and subgenera are considered. For species identification, the interested student must resort to the literature cited at the end of this paper. For many species, perhaps a majority, direct comparison with related species is necessary, and specimens should be sent to one of the several specialists currently working on freshwater crabs.

For monotypic genera, the species is named in the key.

- | | |
|--|---|
| 1. Gonopod gradually tapering toward apex, without prominent teeth or lobes, without spine field or apical spines; tip of gonopod typically bearing numerous spines. TRICHODACTYLIDAE (Fig. 9) | 2 |
| 1. Gonopod expanded at tip, usually with teeth and lobes, well-defined spine field bearing apical spines, tuft of marginal setae along proximal part of gonopod. PSEUDOTHELPHUSIDAE | 4 |
| 2. Anterolateral margin of carapace without teeth (Chiapas, Mexico).
..... <i>Trichodactylus villalobosi</i> Rodriguez y Manrique, 1967 | |
| 2. Anterolateral margin of carapace with teeth | 3 |
| 3. Anterolateral margin of carapace with three teeth (Veracruz and Chiapas, Mexico).
..... <i>Trichodactylus constrictus</i> Pearse, 1911 | |

3. Anterolateral margin of carapace with five teeth (Nicaragua and Colombia).*Trichodactylus quinquedentatus* Rathbun, 1893
4. Tip of gonopod with numerous large, flat spines in addition to the apical spines (Greater Antilles, Fig. 8)*Epilobocera* Stimpson, 1860
4. Tip of gonopod with only apical spines, occasionally other scattered spines (see *Phrygiopilus*) 5
5. Margin strongly curved (Figs. 3, 18, 21) 6
5. Margin straight, or curving slightly near tip (Figs. 11, 17) 7
6. Margin curving laterad; large, spine-bordered supra-apical process. (Guatemala, Figs. 18-23)*Phrygiopilus* new genus
6. Margin curving mesiad, entire gonopod twisted, simple, without sharply delimited lobes or teeth (Costa Rica, Fig. 3)
.....*Achlidon agrestis* (Rathbun, 1898)
7. Margin visible to apex, or nearly so (Figs. 4, 17) 8
7. Margin distally hidden by one or more lobes which are folded across the caudal surface of the gonopod (Figs. 11, 12, 16)13
8. Apical spines directed cephalad (Fig. 5) 9
8. Apical spines directed distally; spine field may slope laterad or cephalad (Figs. 10, 13, 14, 15)10
9. Gonopod with a well-defined patch of small sub-apical spines on the cephalic surface (Costa Rica, Fig. 4)*Allacanthos pittieri* (Rathbun, 1898)
9. Apical spines only (Costa Rica, Nicaragua, Fig. 5)
.....*Potamocarcinus* (*Typhlopseudothelphusa*) Rioja, 1952
10. Mesial projection a strong tooth (Fig. 13)11
10. Mesial projection a lobe (Figs. 14, 17)12
11. Epigeal species with normal eyes (S. Mexico to Panama, Fig. 13)
.....*Potamocarcinus* (*Potamocarcinus*) H. Milne Edwards, 1853
11. Cave species with reduced eyes (Chiapas, Mexico)
.....*Potamocarcinus* (*Typhlopseudothelphusa*) Rioja, 1952
12. Spine field curved laterad, with triangular lateral lobe, two strong projections on lateral surface; small species (El Salvador and Guatemala, Figs. 15, 17)*Elsalvadoria zurstrasseni* (Bott, 1956)
12. Spine field normal to long axis of gonopod, large flat mesial lobe with one or two teeth on cephalic surface; usually large species (S. Mexico-Nicaragua, Fig. 14)*Potamocarcinus* (*Raddaus*) Pretzmann, 1965
13. Strong apical process curving caudad so that the spine field faces caudad or at least is exposed caudad instead of apically or cephalad (Mexico, Fig. 12)*Spirothelphusa* Pretzmann, 1965
13. Spine field not exposed caudad14
14. Two distinct lobes folding mesiad over the margin; spine field facing laterad; two distinct lobes in front of spine field (Mexico, Fig. 7)
.....*Epithelphusa mixtepecensis* Rodriguez y Smalley, 1969
14. A single lobe folding mesiad over margin (actually the two lobes of *Epithelphusa* in fused condition); spine field facing laterad, slanting obliquely, but the spines pointing apically. *Pseudothelphusa* (Figs. 10, 11, 16)15
15. Mesial process an elongate lobe, variously shaped but not strongly recurved, sometimes bilobed but dorsal process never as prominent as in *P. (Tehuana)*; upper margin not tuberculate except in *P. guerreroensis* Rathbun, 1933 (Mexico, Figs. 10, 16)
.....*Pseudothelphusa* (*Pseudothelphusa*) Saussure, 1857
15. Mesial process large and strongly recurved; always bilobed with strong dorsal process; cephalic process high, so the apical spines are not as easily

seen as in *P. (Pseudothelphusa)*; upper border of front marked by conspicuous line of tubercles (Tehuantepec peninsula of Mexico; Fig. 11)
*Pseudothelphusa (Tehuana)* Rodriguez y Smalley, 1969

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