

Diagnosis

Cephalon and pereonite 1 fused medially for short portion of length; pleotelson usually about three-fourths as long as wide; uropods either slightly shorter or slightly longer than pleotelson; swellings (ridges) present on lateral margins of dorsum of pereonites 3-7; pereopod 2 (male) with six-eight setae on process on inner proximal margin of propodus (slightly modified from Schultz 1973). Additionally, pleotelsonal apex truncate and vault shelf wide.

Material Examined

Padre Island, Cameron County, Texas, 5 December 1954, two specimens, collector L. Hubricht, accession no. USNM 209567. Horn Island, Mississippi, 27 March 1958, four specimens, collector J. Y. Christmas, GCRL (Gulf Coast Research Laboratory) no. 160: 50; Horn Island, 5 February 1959, one specimen, collector J. Y. Christmas, GCRL 160: 51; Horn Island, 23 March 1959, 11 specimens, collector J. Y. Christmas, GCRL 160: 52; Horn Island, 9 December 1958, four specimens, collector J. Y. Christmas, GCRL 160: 53; Horn Island, 26 February 1973, four specimens, collector R. Heard and N. Whatley, GCRL 1067.

Discussion with Supplementary Descriptive Notes

Contrary to Schultz's (1973) assertion that the differences between *Ancinus depressus* and

A. granulatus are very slight, we found the two species readily distinguishable. A more difficult distinction, requiring detailed study with quantitative measurements, was that between *A. depressus* and *A. brasiliensis*. Comparison of the width to length ratios demonstrates that *A. depressus* (mean percent and range, 48.1, 45.4-50.8, and median percent 48.4 for $N = 14$) has a wider body than *A. brasiliensis* (mean percent and range 46.4, 44.4-48.2, median percent 46.6 for $N = 20$). This is largely due to the broad pereonites 1-2 in *A. depressus*. The difference is significant at $P < 0.01$ (Mann-Whitney U test). Other statistical differences in the pleotelson (width to length) and the pleotelsonal vault shelf (width) are given in Tables 1 and 2. The pleotelson in *A. depressus* is also strongly arched, has a broad apex, and is notably truncate (Fig. 11D). The only differences observed in dissected appendages were in the antennae. Ant¹ in *A. depressus* has long fine setae on the third peduncular article and flagellar articles 2-7; penicillate setae are relatively sparse (about 16 present along anterior margin versus 18-20 in *A. brasiliensis*); aesthetae are present on the terminal flagellar articles only. Ant² has long simple setae extending to flagellar article 6; in *A. brasiliensis* these setae extend to flagellar articles 3-4 only.

KEY TO SPECIES OF *Ancinus*

1. Body broad, breadth 0.48-0.54 ($\bar{X} = 0.50$) of length; pleotelson truncate or broadly rounded 2
1. Body elongate, breadth 0.44-0.48 ($\bar{X} = 0.46$) of length; pleotelson nearly acute, not broadly truncate 4
2. Pleotelsonal apex broadly rounded; ridges absent from lateral margins of pereonites and epimera; p² (male) dactylus short, closing on propodus; propodus process with three setae. (small species, up to 4.3 mm in length.) *A. panamensis*, new species
2. Pleotelsonal apex truncate; ridges present on lateral margins of pereonites and epimera; p² (male) dactylus long, closing on carpus; propodus process with four-eight setae. (Large species, maximum length exceeding 9 mm.) 3
3. Body surface granulose, eyes elevated on swellings; upper pleotelsonal apex surface cylindrical; Plp⁵ exopod with three squamiferous protuberances; up to 9.5 mm in length. *A. granulatus* Holmes & Gay 1909

3. Body surface smooth, eyes not elevated; upper pleotelsonal apex not cylindrical; pereopod 2 (male) propodus with five squamiferous protuberances; up to 13.5 mm in length *A. depressus* (Say) 19
4. Pleotelsonal apex narrowly truncate; pereopod 2 (male) propodus process with four setae; Ant¹ peduncular article 3 and flagellar article 1 with stemless esthetascs, proximal flagellar articles without numerous fine setae; Plp⁵ exopod with four squamiferous protuberances *A. brasiliensis* Castro 19
4. Pleotelsonal apex acutely rounded; pereopod 2 (male) propodus process with five–seven setae; Ant¹ with normal esthetascs on distal flagellar articles only, proximal flagellar articles with numerous fine setae; Plp⁵ exopod with five squamiferous protuberances *A. ?seticomus* Trask 19

COLOR POLYMORPHISM

This separate treatment of the color forms in Panamanian *Ancinus* is presented to illustrate specific differences of a nonmeasurable kind and to serve as a reference for studies on the balanced polymorphism in these populations. Color identification (after Kornerup and Wanscher 1967) was carried out with reflected light under low magnification ($\times 25$). In this discussion, pattern refers to the distribution of pigment on the dorsum; descriptive color terms denote the coloration of the patterns; ground color is the dominant color of individuals. Laboratory-reared animals showed that the pigmented patterns developed gradually in 1–2 weeks and remained unchanged to maturity and against different colored sand substrata.

Ancinus panamensis n. sp.

All populations of *A. panamensis* examined in Panama (alive or freshly preserved in formalin) exhibited a similar set of pigment patterns (Fig. 6 A–H). In addition, the colors were similar within populations. Colors between populations differed, however; each tended to match the dominant sand color, creating a cryptic effect. The morphs described here are from live adult specimens collected at the type locality near Naos Island, 1 September 1973. Eight types are described, each showing a variety of hues. These are arranged below in approximate order of diminishing pigmentation. Synoptic morph frequencies are noted for samples collected over the period 1970–1973.

UNIFORM (A): Pigmentation on dorsum nearly uniformly distributed. Some individuals with dense pigmentation on anterior margin of cephalon, pereonite 4, and lateral margins of pleotelson. Dominant ground colors are orange (ranging from light and grayish to brownish) and gray (greenish to yellowish gray). Yellow, red, and brown pigmentation is less common. This morph comprised from 10 to 20 percent of the population.

STRIPE (B): Pigmentation nearly uniformly distributed except along midline where it is less dense, extending from the cephalon to the apex of the pleotelson. Width of stripe varies somewhat among different individuals. The dominant ground color is red, ranging from grayish and pastel to dull red. Commonly from 3 to 10 percent of the population.

PATTERN (C): Characteristically with pigment-free areas centrally on cephalon and pereonites 2–4, along posterolateral margins, and often centrally on the pleotelson. Minor variations are common, including (a) complete pigmentation of pereonites 2–4, (b) complete pigmentation of pleotelson, (c) marginal pigmentation of pleotelson reduced or absent, (d) entire body sparsely pigmented over the basic morph pattern. The coloration tends to be intense with orange (grayish and brownish) and red (orange and brownish) hues predominant. Brownish, red and orange areas are commonly present centrally on pereonites 2–4. This morph comprised about 60 percent of the population.

HALF PATTERN (D): Pigmented areas generally less common than in the "pattern" morph.

Variations include: (a) sparse pigmentation on pereonites 6-7, (b) dense pigmentation on pereonites 3 and 7, (c) entire anterior half of body pigmented (from pereonite 4 to cephalon), (d) all of pleotelson pigmented. The ground color is highly variable, ranging from grayish green to reddish brown, violet-white, and dark brown. Reddish orange areas are commonly present centrally on pereonites 3 and 7. This morph comprised about 10 percent of the population.

BICOLOR (E): Anterior half of body from pereonite 4 forward uniformly pigmented. Some pigmentation occasionally present on pereonites 5 and 7 and pleotelson. Lateral margins of pleotelson also often pigmented. Ground color highly variable with shades of brown (grayish and mustard brown), orange (brownish and reddish orange) and red (orange and pastel red) predominating. Uncommon, from 1 to 4 percent of the population.

(F): Similar to "bicolor" except for pigment-free area located centrally on cephalon and pereonite 1. All of pereonite 1 may be pigment-free and often the lateral margins of the pleotelson are pigmented. Red and orange areas are sometimes present centrally on pereonites 2-4. The dominant coloration is brownish gray, gray, or brownish orange. From 3 to 8 percent of the population.

1/2 o (G): Central pigment-free area not entirely enclosed and usually extending posteriorly to pereonite 4. The ground color in one specimen was brownish gray. Uncommon, less than 2 percent of the population.

HALF BELT (H): Pigmentation sparse, usually present along margin of cephalon, on pereonite 4, and laterally on margins of pleotelson. Some pigmentation is often present laterally on pereonites 1-3. Brownish gray is most common ground color. From 3 to 10 percent of the population.

Ancinus brasiliensis

The 10 morphs of *A. brasiliensis* illustrated and described below (Fig. 12A-K) represent the most common forms observed in populations

collected 6 September 1973 from Shimmey and María Chiquita beaches. Although only the first peduncular article of Ant¹ is shown, usually all of the peduncular articles of both Ant¹ and Ant² are pigmented.

UNIFORM-S (A): "S" refers to the conspicuous spots or pigment-free areas astride midline on pereonites 5-7 and pleonite 1; these areas contain faint traces of grayish green or reddish orange pigment. Remainder of body segments with dark gray pigmentation. Reddish orange patch at center of cephalon. Uncommon, about 17 percent of populations sampled.

SPECKLED (B AND C): B—Rounded pigment patches light to dark gray in color present on all body segments. Small nonpigmented to slightly pigmented areas astride midline on pereonites 5-7 and pleonite 1; if pigmented, these areas often contain traces of pastel green or orange-red pigment. Orange-red patch present at center of cephalon. Uropods with dark gray pigment. This dark speckled morph was the most common present at María Chiquita Beach, comprising 72 percent of 136 individuals sampled. C—Similar to the "speckled" morph described in (B) except with fewer pigmented areas. Peduncular articles of antennae pigmented, but mostly light in color with an iridescent sheen. Light orange patch often present on cephalon and orange pigment interspersed on midbody pereonites. This light speckled morph was the most common present at Shimmey Beach; it comprised 66 percent of 196 individuals sampled.

HALFSPECKLED (D): Similar to "speckled" except that gray pigment sparse on pereonites 1-3 and pleotelson. Ground color usually white, but a few individuals golden yellow in color. Pale orange patch sometimes present centrally on cephalon. Uncommon, about 2 percent of the populations sampled.

GIRDLE (E): Dark gray pigment present on cephalon and sometimes pereonite 1, on pereonites 4-7, and posteriorly on pleotelson. Orange patch usually present centrally on cephalon. Traces of pale green pigment often present on pereonites 5-7. Nonpigmented areas usually

white, but light yellow in some individuals. Present only at María Chiquita Beach, about 6 percent of populations sampled.

GIRDLE-B (F): "Girdle-B" refers to the broken pattern of dark gray pigmentation on pereonites 4-7, otherwise similar to the "girdle" morph. Most common ground color is orange; however, some individuals with white on either side of girdle. Present only at María Chiquita Beach, about 8 percent of populations sampled.

BELT (G): Light to dark gray pigment concentrated on pereonites 1 and 4 with an intervening white area. Pigmentation sometimes reduced or absent from pereonites 1-3, but always present on pereonite 4. Superficially similar to "Bi-O" in *Ancinus panamensis* n. sp. except for location of clear area. Present only at Shimmey Beach, about 2 percent of population.

HALF QUADRATE (H): Body dark gray except for nonpigmented (white) areas on pereonites 2 (central patch), 5-7, and pleotelson. Light orange patch present centrally on cephalon. Relatively rare, less than 1 percent of populations sampled.

QUADRATE (I): Violet brown marginally (covering all of epimera), nearly completely enclosing a white or pale orange interior. Cephalon with a central orange patch. Relatively rare, less than 1 percent of populations sampled.

FLECK (J): Small and varying amounts of grayish brown or dark gray (in one case pastel red) pigment spotting pereonites 4-7 near midline. Ground color usually white, but sometimes orange. Nearly 5 percent of population at Shimmey Beach.

UNIFORM (K): Essentially identical with "uniform" morph of *A. panamensis*. Illustrated specimen nearly completely white, but dark gray and orange ground color also common. Orange to pale orange patch on cephalon occasionally present. Of 42 "uniform" morphs sampled from the light-colored sand at Shimmey Beach (about 21 percent of population), 60 percent were white and all of the "uniform" morphs from the dark sand at María Chiquita

Beach (11 percent of the population) were in color (13 grayish brown to gray, two gray orange).

The differences in color polymorphism sufficiently pronounced that specific determinations could be made on this basis alone. For example, the pigment patterns of the dominant morphs "pattern," "half-pattern" (*A. panamensis*) and "speckled," "half-speckled" (*A. brasiliensis*) are markedly distinct. Unique subdominant morphs include, for example, "stripe," "quadrate," and "half-quadrate." Moreover, in *A. brasiliensis* an orange patch was common, present centrally on the cephalon, and peduncular articles of the antennae were unpigmented. Finally, it is our impression that the color polymorphism is more variable in *A. brasiliensis* than in *A. panamensis*. The morphs illustrated for *A. brasiliensis*, plus several additional rare morphs, give a total of 15 morphs found in a sample of 539 individuals. Over 2,000 individuals of *A. panamensis* were classified and these contained only eight defined morphs and three additional morphs.

COUPLING BEHAVIOR

From preliminary observations on coupling frequency between males and females of conspecifics, we felt that this precopulatory step in the mating behavior of the two Panamanian species might differ. In coupling the male grasps a female with the second pereopod and places her below, oriented in the opposite direction. In this position the female, always smaller than the male partner, is carried underneath. The coupling frequency was tested with 30 pairs of each species under comparable conditions on both sides of the Isthmus. The median number of interactions (and confidence limits) observed were 4/pair/hour (2-19/pair/hour) in *A. brasiliensis* and 2/pair/hour (2-9/pair/hour) in *A. panamensis*. These results are not significantly different ($P > 0.05$, Mann-Whitney *U* test). The initial impression of a difference in the coupling frequency could not be demonstrated; indeed, the interactions were highly variable and apparently greatly influenced by the conditions of transport across the Isthmus (approximate time of trip $1\frac{1}{2}$ hours).

Heterospecific pairs (involving both combinations) were also observed and found to undergo coupling rather commonly. Females of *A. brasiliensis* were always matched with larger males of *A. panamensis*. The results were variable, ranging from median coupling frequencies ($N = 10$) of 0 to 2 and 4.5/pair/hour. The short dactylus on pereopod 2 in males of *A. panamensis* did not appear to handicap their coupling with females of *A. brasiliensis*. However, the frequency of precopulatory encounters among heterospecifics would be expected to be less than that between conspecifics because of the specific size differences in the sexes. It was not determined whether or not copulation had taken place.

CONCLUSIONS

On the basis of morphological criteria, reinforced by differences in color polymorphism, we conclude that the tropical ampho-American members of *Ancinus* are separate species. Minor differences, believed intraspecific in kind, were found to exist between populations of *A. brasiliensis* from Brazil and those present in Panama and Costa Rica in the Caribbean. *Ancinus depressus* from the Gulf of Mexico and east coast of the United States is closely related to *A. brasiliensis*, but does demonstrate significant differences that we interpret to be specific in nature. Morphologically, the closest relative of the Atlantic species group is the problematic species *A. seticomvus*. The latter species overlaps in distribution with *A. granulatus* in southern California and the Gulf of California, but continues at least as far south as Mazatlán, Mexico.

With the scant information at hand it is not possible at present to establish any coherent zoogeographic relationships within the genus. Considering the geographic proximity of the new Panamic species to *A. brasiliensis* and the former continuity of this region in Pliocene time (Whitmore and Stewart 1965), it is interesting that the transisthmian species appear to be less closely allied than the more distantly disjunct pair *A. seticomvus*—*A. brasiliensis*. One of several possible factors that may have a bearing on this is the great contrast in the marine environments of the eastern Pacific and

Caribbean (Rubinoff 1968, Glynn 1972) and the extent that this has affected the evolution of the littoral ancinids.

LITERATURE CITED

- CASTRO, A. L. 1959. Descrição de uma nova espécie do género "Ancinus" Milne Edwards (Isopoda, Sphaeromidae). *Revta. bras. Biol.* 19(2): 215–218, 8 figs.
- DEXTER, D. M. 1972. Comparison of the community structures in a Pacific and an Atlantic Panamanian sandy beach. *Bull. Mar. Sci.* 22(2): 449–462, 4 figs., 2 tables.
- GLYNN, P. W. 1972. Observations on the ecology of the Caribbean and Pacific coasts of Panamá. *Bull. biol. Soc. Wash.* (2): 13–30, 3 figs.
- HANSEN, H. J. 1905. On the propagation, structure, and classification of the family Sphaeromidae. *Quart. J. micr. Sci., new ser.*, 49(1): 69–135, 1 pl.
- HOLMES, S. J., and M. E. GAY. 1909. Four new species of isopods from the coast of California. *Proc. U.S. nat. Mus.* 36(1670): 375–379, 6 figs.
- KORNERUP, A., and J. H. WANSCHER. 1967. *Methuen handbook of colour*. 2nd ed. rev. Methuen & Co., London. 243 pp.
- LOYOLA E SILVA, J. 1963. Redescricao de *Ancinus brasiliensis* Castro, 1959 (Isopoda-Crustacea). *Bol. Univ. Paraná, Zool.* 2(1): 1–19, 5 figs.
- . 1971. Sobre os géneros *Ancinus* Milne Edwards, 1840 e *Bathycopea* Tattersall, 1909, da coleção U.S. Nat. Mus. (Isopoda-Crustacea). *Archos. Mus. nac., Rio de J.* 54: 209–223, 7 figs.
- MENZIES, R. J., and J. L. BARNARD. 1959. Marine Isopoda on coastal shelf bottoms of southern California: systematics and ecology. *Pacif. Nat.* 1(11): 1–35, 28 figs., 2 tables.
- MENZIES, R. J., and D. FRANKENBERG. 1966. *Handbook on the common marine isopod Crustacea of Georgia*. University of Georgia Press, Athens. viii + 93 pp.
- MILNE EDWARDS, H. 1840. Pages 115–284 in *Histoire naturelle des Crustacés comprenant l'anatomie, la physiologie et la classification de ces animaux*. Vol. 3, pp. 115–284, 3 pls. Roret, Paris.

- RICHARDSON, H. 1905. A monograph on the isopods of North America. Bull. U.S. nat. Mus. 54. liv + 727 pp., 740 figs.
- . 1909. The isopod crustacean, *Ancinus depressus* (Say). Proc. U.S. nat. Mus. 36(1663): 173-177, 9 figs.
- RUBINOFF, I. 1968. Central American sea-level canal: possible biological effects. Science 161: 857-861, 3 figs.
- SAY, T. 1818. Description of three new species of the genus *Naesa*. (An account of the Crustacea of the United States.) J. Acad. nat. Sci. Philad. 1(2): 482-485.
- SCHULTZ, G. A. 1973. *Ancinus* H. Milne Edwards in the New World (Isopoda, Flabellifera). Crustaceana 25(3): 267-275, 1 fig., 2 tables.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York. xviii + 312 pp.
- TATTERSALL, W. M. 1905. The marine fauna of the coast of Ireland. Part V, Isopoda. Scientific Investigations, 1904, no. 2, pp. 53-100, 11 plates. Department of Agriculture and Technical Instruction for Ireland, Fisheries Branch, Dublin.
- TRASK, T. 1970. *Ancinus seticomvus*, n. sp. (Isopoda), from Santa Barbara, California. Bull. S. Calif. Acad. Sci. 69(3-4): 145-149, 2 figs.
- WHITMORE, F. C., JR., and R. H. STEWART. 1966. Miocene mammals and Central American seaways. Science 148: 180-185, 2 figs.