

FIGURE 44.—*Asellus obtusus*, A-D, holotype; E, allotype: A, first pleopod; B, second pleopod; C, D, respectively dorsal and ventral surfaces of tip of endopodite of second pleopod; E, terminal segments of first peraeopod.

coll. W. G. Moore, 29.iv.1967; Red River Valley, Rapides Parish, 2♂♂, coll. W. G. Moore, 29.iv.1967; near Grand Bayou, Red River Parish, 2♂♂, coll. W. G. Moore, 29.iv.1967.

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY.—As may be seen from the map (Figure 39) in which the above localities are plotted, *A. obtusus* is known only from a relatively small region in the southeastern corner of the United States. Within this region it seems to inhabit a variety of waters and has been recorded from swamps, roadside ditches, temporary ponds, and in one case each a river and a small stream.

FURTHER DESCRIPTION (♂).—Body: The largest ♂ examined was 12.5 mm long, and the smallest 6.0 mm.

First antenna: Flagellum 12- to 23-merous; flagellum tip reaching one-third along or to distal margin

of the last segment of the peduncle of the second antenna.

Second antenna: Length 0.81 to 1.5 times that of body, but usual length subequal to body length. Flagellum 50- to 85-merous, depending on size.

Mouthparts: See Table 1.

First peraeopod: 2 to 4 spines may occur on the proximal margin of the low proximal projection of the palm; shape of palm shows little variation from that illustrated for the holotype.

First pleopod: Total length of appendage 0.85 to 1.19 times as long as second pleopod. Inner margin of sympod with 2 to 5 coupling hooks. Maximum width of distal segment 0.52 to 0.66 times maximum length. Distal spines few to numerous, but always simple and

of moderate length. The typical shape of the distal segment is subovate.

Second pleopod: Maximum length of sympod from 1.07 to 1.50 (usually 1.1 to 1.3) times maximum width. Proximal segment of exopod without marginal spines; distal segment with 11 to 16 plumose marginal spines. The shape of the distal segment is always ovate, the maximum length, however, ranging from 1.42 to 2.19 (usually 1.6 to 1.9) times the maximum width. Endopod shape is relatively constant (cf. *A. forbesi*), the maximum length ranging from only 1.39 to 1.84 (usually 1.4 to 1.7) times the maximum width; the length in proportion to the length of the distal segment of the exopod varies from 0.64 to 1.06.

Although constant in fundamental construction, the morphology of the tip of the endopod seems to provide a variety of appearances depending upon the state of preservation of the specimen, the position of the endopod when examined, real differences between individuals, and perhaps other factors also. Figure 45 illustrates in part the extent of this variation; it is based mainly on paratype material. As shown, the outer lip of the cannula is developed to different degrees, the ventral groove may be relatively narrow or broad and open, and the caudal outline (including the caudal process) while always rounded exhibits some variation in shape. The mesial process shows the most variation of all; it may be relatively narrow and long, wide and short, rounded or pointed. Like *A. forbesi*, *A. obtusus* appears to be one of the more variable of North American epigeic species with regard to the conformation of the tip of the endopod.

Uropoda: See Table 2. Peduncle and rami always with many long fine lateral spines.

DISCUSSION.—The morphology of the tip of the endopod of the second male pleopod in typical specimens of *A. obtusus* is sufficiently unlike that of any other *Asellus* species to suggest that the taxon warrants specific status on this criterion alone. Because this morphology is basically similar in general plan to that shown by *A. forbesi* for the same structure, however, it is occasionally possible to be uncertain of the specific identity using the morphology of the endopod tip by itself. The two species can, nevertheless, always be separated on a number of other characters: (1) *A. obtusus* is a smaller species than *A. forbesi*; (2) the second antennae are longer relative to body length in *A. obtusus*; (3) the proximal projection on the palm of the first ♂ peraeopod of *A. obtusus* bears apically a long stout spine and never a toothlike spine as is usual in *A. forbesi*; (4) the proximal segment of the exopod of the second ♂ pleopod never has marginal spines in *A. obtusus*, whereas it frequently does in *A. forbesi*; (5) the endopod of the second ♂ pleopod in *A. obtusus* is more squat, wider relative to length, always without a developed outer basal apophysis, and with the inner proximal angle almost a right angle; (6) the telson and uropoda are much more spinose in *A. obtusus* than *A. forbesi* (cf. Figures 43c, 37f, g); and (7) the uropoda of *A. obtusus* relative to telson length are generally longer than those of *A. forbesi*. Many of these differences are quantified in Table 5. Considered together with the differences in the morphology of the

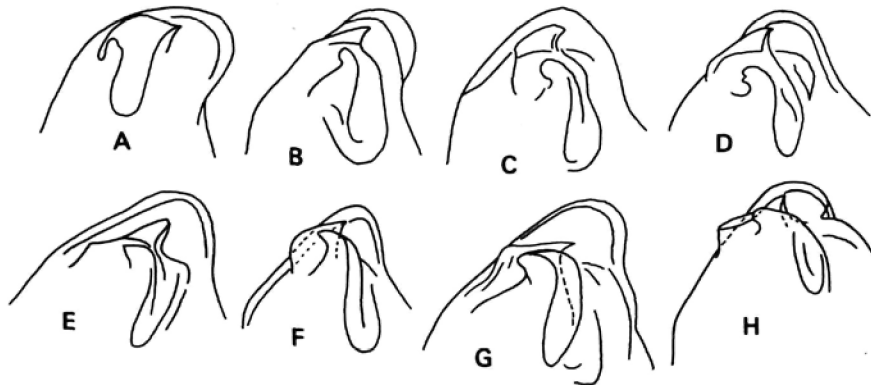


FIGURE 45.—*Asellus obtusus*, extent of variation in morphology of endopodite tip of male second pleopod: A, Jefferson County, Florida; B-E, G, H, paratypes; F, Red River Valley Parish, Louisiana.

endopod tip of the second ♂ pleopod, they provide firm grounds for the specific separation of the two taxa.

Asellus laticaudatus, new species

FIGURES 46-48

ETYMOLOGY.—From the Latin *latus*, broad, and *caudatus*, having a tail.

TYPE MATERIAL AND TYPE LOCALITY.— Holotype: adult ♂, USNM 122055. Allotype: adult nonovigerous ♀, USNM 122056. Paratypes: 8 ♂♂, 1 nonovigerous and 1 ovigerous ♀, USNM 122057. Type locality: roadside ditch near Haynes Boulevard, New Orleans, Orleans Parish, Louisiana. The type collection was made 29 April 1961 by Dr. W. G. Moore.

DESCRIPTION OF HOLOTYPE.—Body: Length, 8.0 mm.

Head: Eyes large and distinct.

First antenna: Flagellum 10-merous and tip reaching to point about two-thirds along last segment of peduncle of second antenna; last 3 segments bear aesthetascs. Second segment of peduncle longest; first, three-quarters length of second; third, two-thirds length of second. First peduncle segment about 1.5 times as long as wide.

Second antenna: Length (5.0 mm) about two-thirds (0.63) body length. Flagellum broken near tip; flagellum at least 61-merous and at least twice length of peduncle.

First peraeopod (Figure 46A): Propodus 1.2 times as long as wide, subtriangular; palm with a broad and large triangular projection near midpoint, a smaller blunt projection between larger projection and point of attachment of dactylus, 3 teethlike spines at proximal end, and a submarginal row of spines on inner and outer surfaces.

First pleopod (Figure 46B): Total length 1.34 times that of second pleopod. Sympod subrectangular, about 1.5 times as long as broad; inner margin with 5 (left) or 6 (right) hooklike protuberances for coupling. Distal segment also subrectangular, but distal margin somewhat rounded; maximum width half maximum length; distal margin and distal half of outer lateral margin with numerous short to moderately long simple spines rather irregularly arranged; inner distal angle with a single simple spine.

Second pleopod (Figures 46C-E): Sympod subquadrate, maximum length only slightly greater (1.20) than maximum width; medial and lateral margins slightly convex. Proximal segment of exopod subtrapezoidal, with 5 short and simple spines on outer margin. Distal segment of exopod ovate, 1.45 times as long as wide, with 19 short to long plumose spines arranged marginally, and a row of fine short spines on inner margin. Endopod four-fifths total length of exopod, and the same length as the distal segment of the exopod; endopod slightly greater (2.62) than two and a half times as long as maximum width (regarded in all specimens of *A. laticaudatus* as the distance between the inner and outer margins of the endopod immediately distal to the basal apophyses). Both inner and outer basal apophyses prominent and well developed. Cannula long and wide and protruding prominently at distal end of endopod. Ventral groove short, narrow, and not prominent. Mesial, lateral, and caudal processes not developed, but distal part of mesial side of ventral groove sclerotized and forming a flaplike structure. At the distal end of the endopod on the dorsal surface numerous groups of about 3-6 minute setae occur in the form of small combs.

Uropod (Figure 46F): Slightly longer (1.11) than telson. Peduncle twice as long as maximum width. Exopod about two-thirds (0.62) length of peduncle, endopod as long as peduncle; both rami are flat, lanceolate, and broad, the exopod being 3 times as long as the maximum width, and the endopod 2.23 times. Rami and peduncle bear numerous short to moderately long spines on their lateral margins.

Telson (Figure 46G): Subsquare; lateral and distal margins with numerous short and moderately long fine and simple spines.

PARTIAL DESCRIPTION OF ALLOTYPE (♀).—First peraeopod (Figures 47A, B): Relatively stout in general proportions, and dactylus and propodus arranged in a subchelate manner. Dactylus about same length as palm of propodus and with 5 teethlike spines on inner margin and a long terminal claw. Propodus broadly subovate, 1.7 times as long as wide; palm with a single long toothlike spine near midpoint, a very small triangular projection between long spine and point of attachment of dactylus, and several long simple submarginal spines. Otherwise as described for a female paralectotype of *A. attenuatus*.

"First" pleopod (Figure 47C): Shape similar to that described for the allotype of *A. forbesi*, but setation

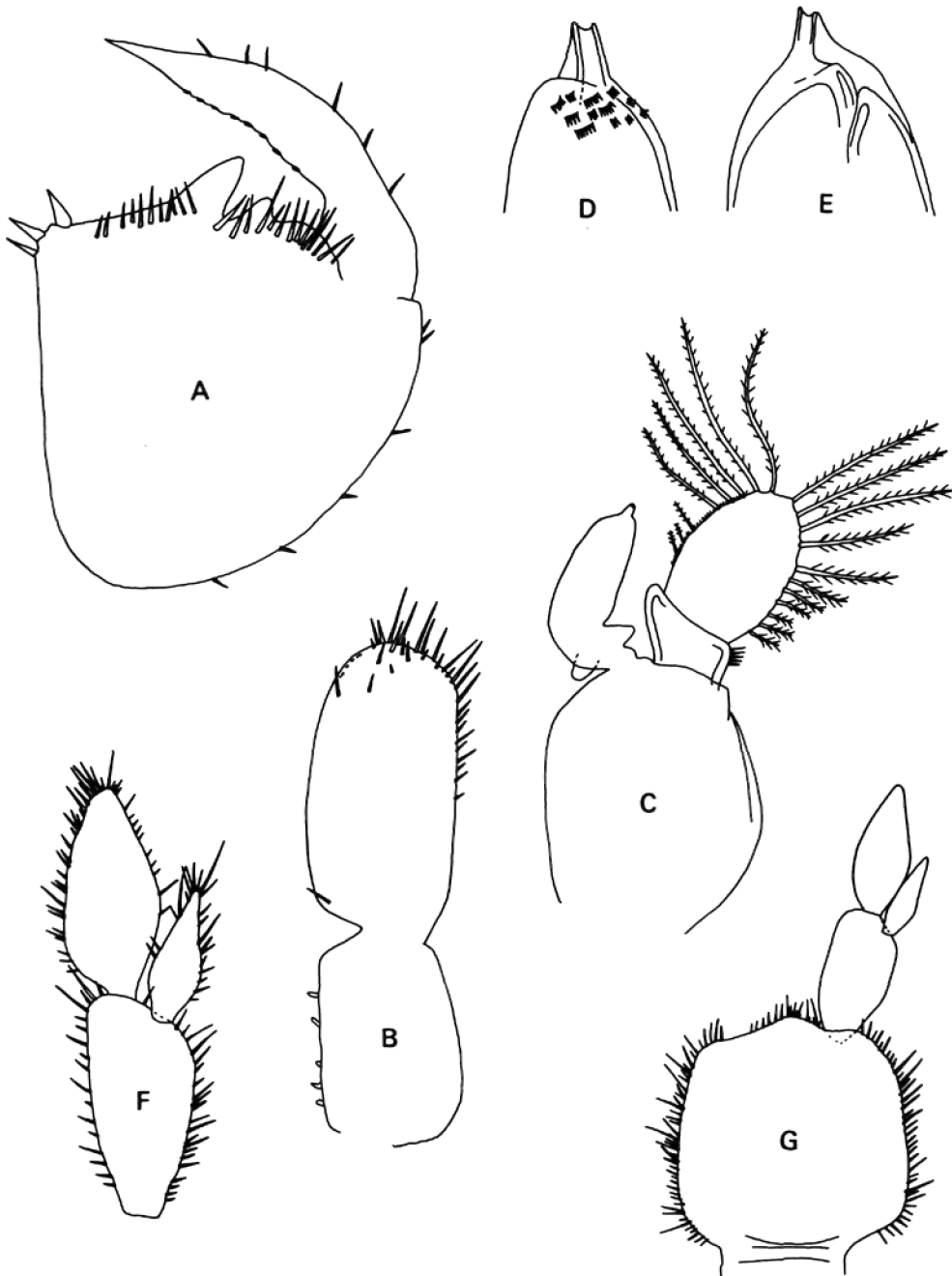


FIGURE 46.—*Asellus laticaudatus*, holotype: A, dactylus and propodus of first pereopod; B, first pleopod; C, second pleopod; D, E, respectively dorsal and ventral surfaces of tip of endopodite of second pleopod; F, uropod; G, uropod and telson.

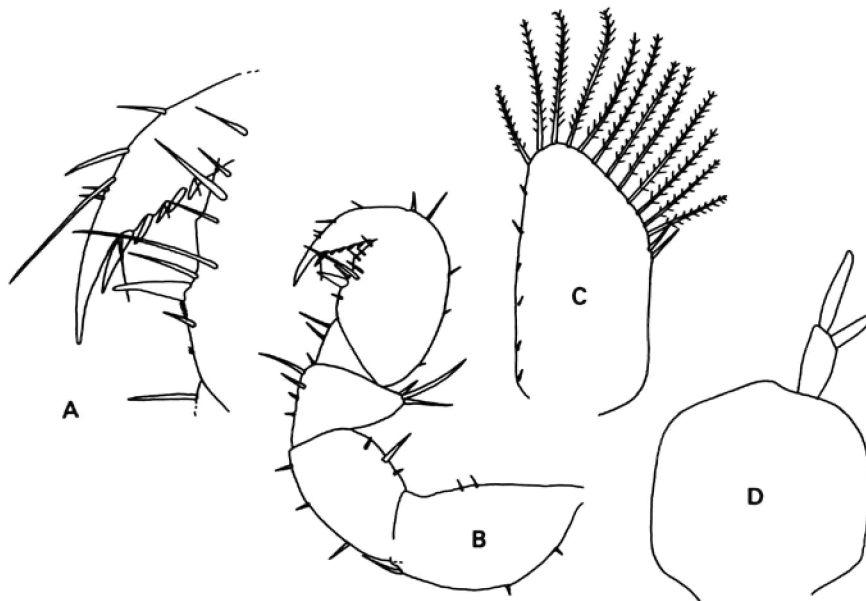


FIGURE 47.—*Asellus laticaudatus*, allotype: A, dactylus and palm of first pereopod; B, first pereopod; C, "first" pleopod; D, uropod and telson.

slightly different; inner margin with 6 short simple spines, outer distal margin with 12 long plumose spines and 2 short simple ones.

Uropod (Figure 47d): Distinctly shorter (0.71) than telson. Peduncle twice as long as maximum width. Exopod about three-quarters (0.71) length of peduncle, endopod slightly longer (1.14) than peduncle; both rami narrow and not markedly lanceolate.

MATERIAL EXAMINED.—KENTUCKY: Beargrass Creek, Louisville, 14 ♂♂, coll. G. A. Cole, 15.ix.1955; Louisville, 1 ♂, coll. G. A. Cole, December 1956.

LOUISIANA: Haynes Boulevard, New Orleans, 10 ♂♂, coll. W. G. Moore, 29.iv.1961.

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY.—The above records together with the type locality are plotted in Figure 13. The great distance between the two regions from where the species is presently known suggests that the species has a wide distribution in southeast United States. Unfortunately no collections of *Asellus* from the intermediate states of Alabama, Mississippi, or Tennessee were available for study during the present investigation. A study of such collections is present for confirmation or otherwise of this distribution.

FURTHER DESCRIPTION (♂).—Body: The largest ♂ examined was 11.5 mm long, and the smallest 6.0 mm.

First antenna: Flagellum 10- to 12-merous; last 3 segments bear aesthetascs.

Second antenna: Length 0.6 to 1.0 times that of body. Flagellum about 65-merous.

Mouthparts: See Table 1.

First pereopod: 2 or 3 spines at proximal end of palm.

First pleopod: Total length of appendage 1.16 to 1.34 times as long as second pleopod. Inner margin of sympod with 4 to 6 coupling hooks. Maximum width of distal segment 0.49 to 0.58 times maximum length.

Second pleopod: Maximum length of sympod from 1.03 to 1.26 times maximum width. Proximal segment of exopod with 2 to 5 short and simple spines on outer margin; distal segment with 13 to 23 plumose, marginal spines. The shape of the distal segment of the exopod is always ovate, the maximum length, however, ranging from 1.23 to 1.63 times the maximum width. Endopod shape is relatively constant, the maximum length ranging from only 2.47 to 2.93 times the maximum width; the length in proportion to the length of the distal segment of the exopod varies from 0.84 to

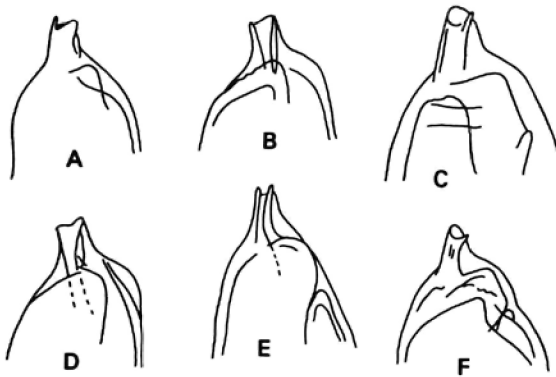


FIGURE 48.—*Asellus laticaudatus*, extent of variation in morphology of endopodite tip of male second pleopod: A, Beargrass Creek, Kentucky; B, D, Haynes Boulevard, Louisiana; C, Louisville, Kentucky; E, F, paratypes.

1.14. The morphology of the tip of the endopod is relatively constant, only minor differences being apparent between individuals (Figure 48).

Uropoda: See Table 2. Both rami are always flat, lanceolate, and broad; the endopod is from 2.23 to 2.5 times as long as maximum width.

Asellus scrupulosus, new species

FIGURES 49, 50

ETYMOLOGY.—From the Latin *scrupulosus*, rough or jagged.

TYPE MATERIAL AND TYPE LOCALITY.—Holotype: adult ♂, USNM 122069. Allotype: adult nonovigerous ♀, USNM 122070. Paratypes: 25 ♂♂, 21 nonovigerous and 4 ovigerous ♀♀, USNM 122071. Type locality: Lick Creek Road, Summers, 5 miles NE of Athens, West Virginia. The type collection was made 19 March 1966 by Dr. W. A. Shear.

DESCRIPTION OF HOLOTYPE.—Body: length, 8.5 mm.

Head: Eyes distinct.

First antenna: Flagellum 10-merous and tip reaching to point about two-thirds along last segment of peduncle of second antenna; penultimate 3 segments bearing aesthetascs. Second segment of peduncle longest; first, three-quarters length of second; third, about two-thirds length of second. First peduncle segment about 1.5 times as long as wide; second and third respectively 3.5 and 3 times as long as wide.

Second antenna: Length (6.0 mm) about three-quarters (0.71) body length. Number of segments in

flagellum unknown (impossible to count accurately) but flagellum about 2.5 times length of peduncle.

First pereopod (Figure 49A): Dactylus slightly longer than palm of propodus, with numerous very small denticles on inner margin. Propodus 1.24 times as long as wide, subtriangular; palm drawn out centrally into a very large triangular projection, and with a much smaller projection between large projection and point of attachment of dactylus, 1 large and 2 smaller teethlike spines at proximal end, and with a submarginal row of spines on inner and outer surfaces.

First pleopod (Figure 49B): Total length 1.18 times that of second pleopod. Sympod subrectangular, about 1.5 times as long as wide; inner margin with 4 hooklike protuberances for coupling. Distal segment subovate, but slightly curved outward so that the distal part of the outer lateral margin is shallowly concave and the inner lateral margin convex; maximum width occurring about one-third toward distal margin and half maximum length; distal margin with 5 very long plumose spines and 5 very short simple submarginal spines; inner distal angle with a single simple spine.

Second pleopod (Figures 49C-E): Sympod subrectangular, maximum length 1.54 times maximum width; medial and lateral margins more or less straight. Proximal segment of exopod cupulate, with 3 short and simple spines on outer margin and a distinctly sclerotized inner margin. Distal segment of exopod subcircular, maximum length only 1.3 times maximum width, with 8 very long plumose spines on outer and outer-distal margins, 4 shorter plumose and 3 shorter simple spines on inner-distal margin, numerous minute setae on inner and inner-distal margins, and with both proximal angles distinctly sclerotized. Endopod slightly longer (1.05) than total length of exopod, and 1.4 times as long as the distal segment of the exopod; endopod about (2.44) two and a half times as long as maximum width (exclusive of apophyses). Both inner and outer basal apophyses prominent and well developed. Cannula small and narrow. Ventral groove distinct, but short and narrow. Mesial process prominent, wide, long, and 4-toothed marginally. Lateral process also prominent, but narrower and hooklike. Caudal process not developed.

Uropod (Figure 49F): As long as telson. Peduncle slightly longer (2.28) than twice maximum width. Exopod three-quarters length of peduncle, endopod slightly shorter (0.91) than peduncle.

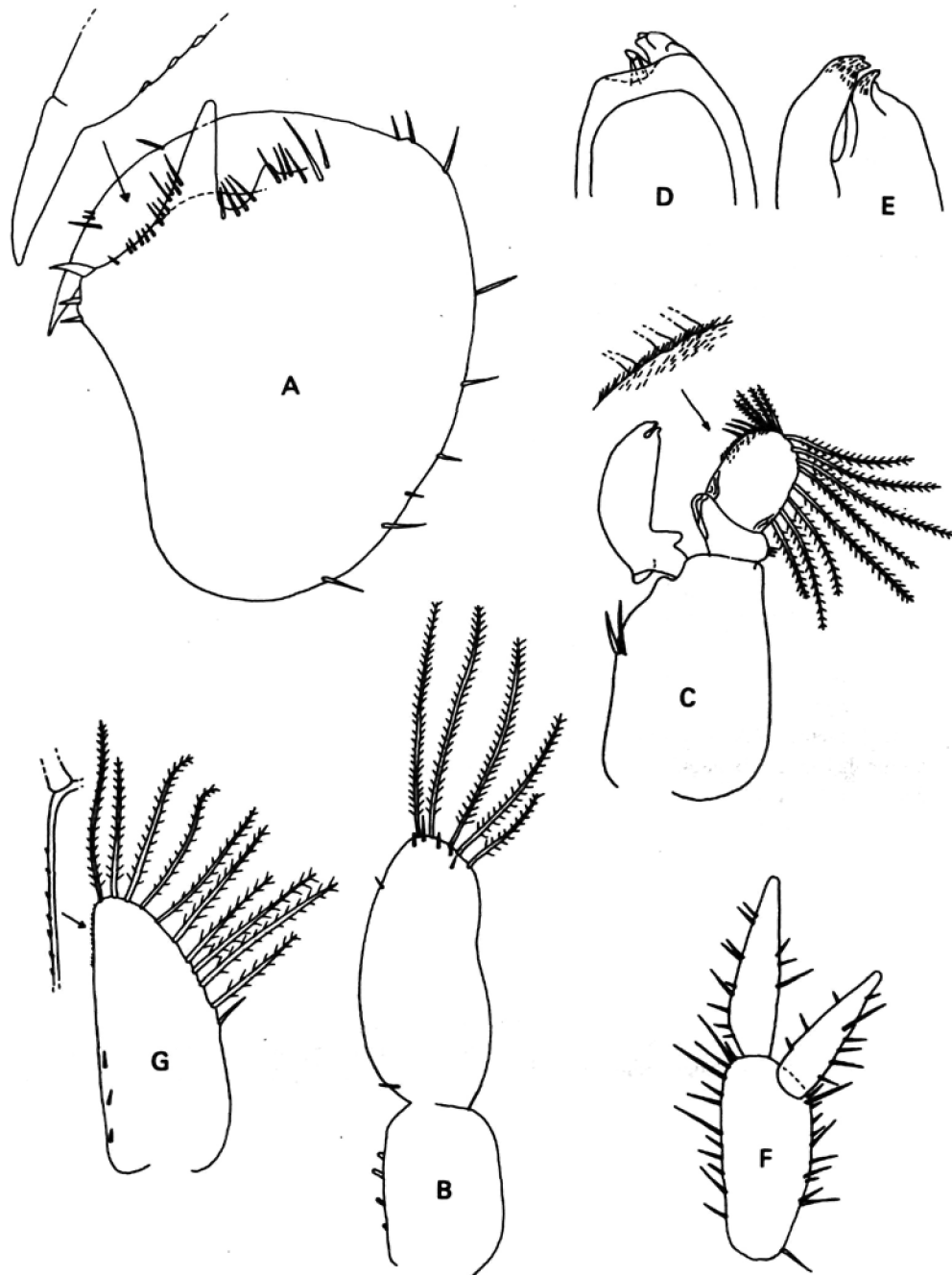


FIGURE 49.—*Asellus scrupulosus*, A–F, holotype; G, allotype: A, dactylus and propodus of first pereopod; B, first pleopod; C, second pleopod; D, E, respectively dorsal and ventral surfaces of tip of endopodite of second pleopod; F, uropod; G, "first" pleopod.

PARTIAL DESCRIPTION OF ALLOTYPE (♀).—First peraeopod: Relatively slender, but dactylus and propodus almost subchelate, as in the allotype of *A. obtusus* (cf. Figure 44E). Dactylus slightly longer than palm of propodus and with 5 teethlike spines on inner margin and a long terminal claw. Otherwise similar to the description given for this appendage in a female paralectotype of *A. attenuatus*.

“First” pleopod (Figure 49G): Shape subtriangular, but outer margin gently convex with 1 short and simple and 10 long and plumose spines on distal half. Inner margin with a row of minute spinules near distal end and 3 short simple spines on proximal half.

MATERIAL EXAMINED.—WEST VIRGINIA: Summers County, 3 ♂♂, coll. A. Weaver, 1.xii.1966; Camp Creek State Forest, Mercer County, 3 ♂♂, coll. W. A. Shear, 22.iii.1967; Hacker Valley, Webster County, 2 ♂♂, coll. A. Weaver, 25.iii.1967.

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY.—The species is known only from West Virginia (Figure 27), where it has been collected from vernal and woodland pools.

FURTHER DESCRIPTION (♂).—Body: The largest ♂ examined was 11.5 mm long.

First antenna: Flagellum 10- to 15-merous; last 3 penultimate segments bear aesthetascs.

Second antenna: Length 0.58 to 0.71 times that of body. Flagellum 59- to 71-merous.

Mouthparts: See Table 1.

First peraeopod: 2 or 3 teethlike spines at proximal end of palm. The shape of the palm seems to display little variation.

First pleopod: Total length of appendage 1.17 to 1.34 times as long as second pleopod. Inner margin of sympod with 3 to 4 coupling hooks. Maximum width of distal segment 0.4 to 0.5 times length; distal margin with 3 to 6 very long plumose spines.

Second pleopod: Maximum length of sympod from 1.2 to 1.5 times maximum width. Proximal segment of exopod with 3 or 4 short and simple spines on outer margin; distal segment with 12 to 15 long and shorter marginal spines, and maximum length 1.2 to 1.55 times maximum width. Endopod shape is relatively constant, but the maximum length varies from 2.4 to 3.3 times the maximum width; the length in proportion to the length of the distal segment of the exopod varies from 1.2 to 1.4. The morphology of the tip of the endopod

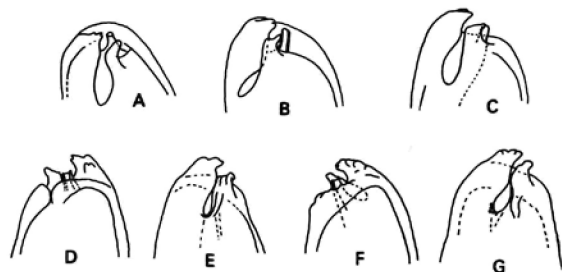


FIGURE 50.—*Asellus scrupulosus*, extent of variation in morphology of endopodite tip of male second pleopod: A, B, Summers County, West Virginia; C, Webster County, West Virginia; D/E, F/G, two paratypes. A-C, E, G, ventral views; D, F, dorsal views.

is quite constant, only minor differences being apparent between individuals (Figure 50).

Uropoda: See Table 2.

Asellus nodulus, new species

Figures 51, 52

ETYMOLOGY.—From the Latin *nodulus*, nobbly.

TYPE MATERIAL AND TYPE LOCALITY.—Holotype: adult ♂, USNM 122058. Allotype: adult ovigerous ♀, USNM 122059. Type locality: boggy ground in Gray's Cypress Swamp, below Prince Frederick, Calvert County, Maryland. The type collection was made 17 April 1938 by C.R. Shoemaker, and was formerly labeled USNM "147/533."

DESCRIPTION OF HOLOTYPE.—Body: Length, 7.0 mm.

Head: Eyes small but distinct.

First antenna: Flagellum 13-merous and tip reaching to about midpoint of last segment of peduncle of second antenna; penultimate 3 segments bearing aesthetascs. Second segment of peduncle longest; first, three-quarters length of second; third, two-thirds length of second. First peduncle segment twice as long as wide; second and third respectively 2.5 and 3 times as long as wide.

Second antenna: Length (6.0 mm) slightly less (0.86) than that of body. Flagellum 67-merous and about 2.5 times as long as peduncle. Fifth segment of peduncle about 5 times as long as wide.

First peraeopod (Figures 51A,B): Dactylus with 4 teethlike spines on inner margin and a very long terminal claw. Propodus 1.78 times as long as wide, ovate;

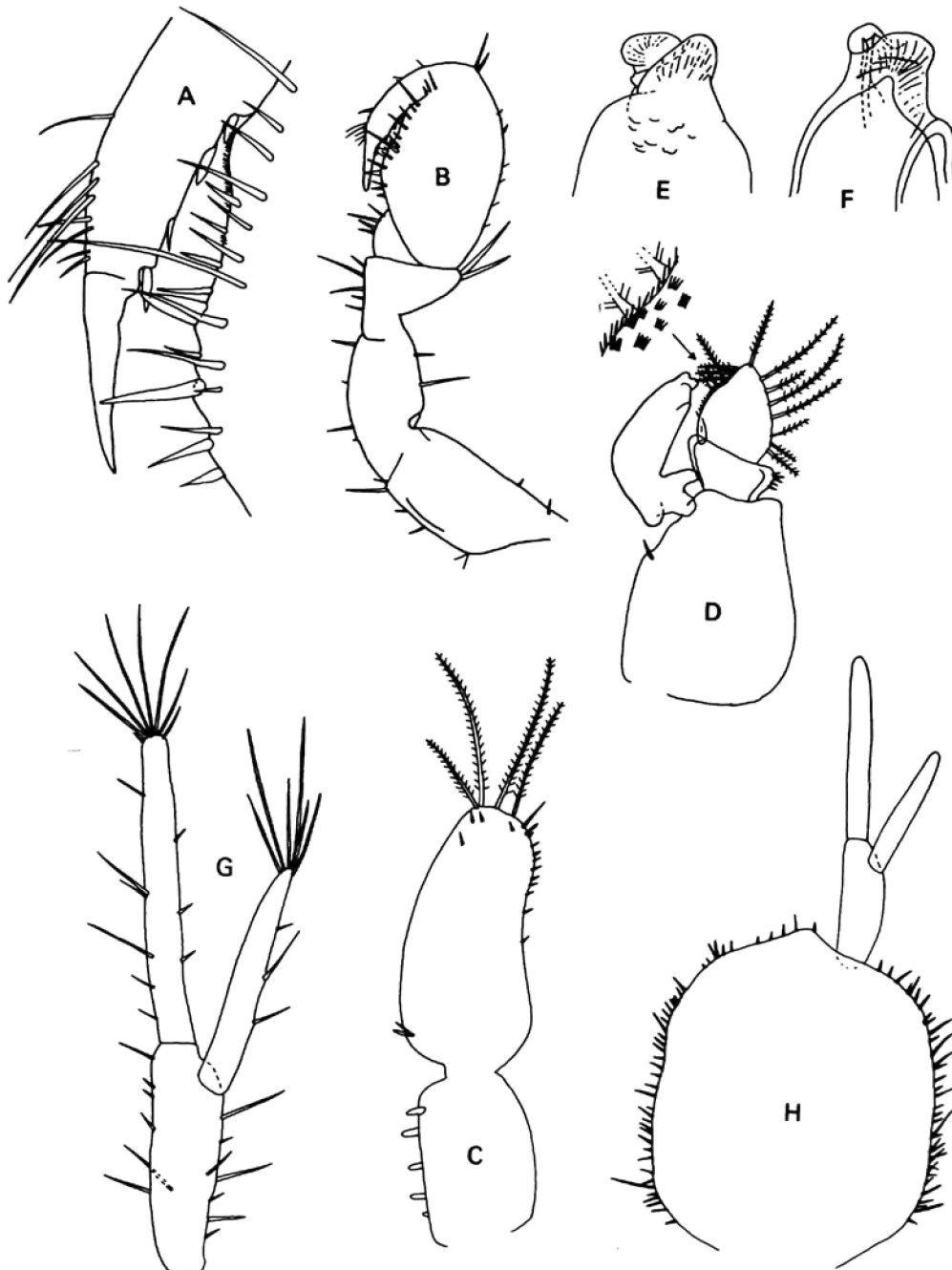


FIGURE 51.—*Asellus nodulus*, holotype: A, dactylus and palm of first peraeopod; B, first peraeopod; C, first pleopod; D, second pleopod; E, F, respectively dorsal and ventral surfaces of tip of endopodite of second pleopod; G, uropod; H, uropod and telson.

palm without triangular projections, but with 4 strong teethlike spines on proximal half, and several short to long spines in a submarginal row on inner and outer surfaces.

First pleopod (Figure 51c): Total length 1.34 times that of second pleopod. Sympod subrectangular, about 1.33 times as long as wide; inner margin with 4 large and 1 small hooklike protuberances for coupling. Distal segment subovate, but curved outward so that the outer lateral margin is shallowly concave and the inner lateral margin convex; maximum width about one-third toward distal margin, and half maximum length; distal margin with 4 very long plumose spines; distal half of outer distal margin with several short and simple spines, and some similar spines also occur submarginally near distal margin; inner distal angle with 2 simple spines.

Second pleopod (Figures 51d-f): Sympod subsquare, maximum length 1.28 times maximum width; medial and lateral margins more or less straight. Proximal segment of exopod irregularly triangular, with 5 short and simple spines on outer margin. Distal segment of exopod broadly subtriangular, maximum length only 1.19 times maximum width, with 7 long plumose spines on outer margin, 1 long plumose spine at apex, 6 moderately long plumose spines on distal half of inner margin, a fringe of very short setae on inner margin some setae of which extend submarginally in the form of small combs of 3-5 minute setae, and a distinctly sclerotized inner proximal angle. Endopod same length as total length of exopod, and 1.5 times as long as the distal segment of the exopod; endopod about (2.64) two and a half times as long as maximum width (exclusive of apophyses). Both inner and outer basal apophyses prominent and well developed, particularly the outer which is subtriangular in side view. Cannula short, relatively narrow, and completely enclosed between prominent and heavily sclerotized ventral and dorsal processes. The total morphology is unique and difficult to homologize with other North American species of *Asellus*; apparently the tip of the endopod has been subject to some torsion, so that the ventral groove has come to lie near the outer lateral margin; the prominent, broadly rounded ventral process perhaps represents an enlarged and slightly twisted (as indicated by striata) mesial process, whereas the prominent, triangular, dorsal process perhaps represents the caudal process.

Uropod (Figure 51g): Almost (0.93) as long as telson. Peduncle slightly longer (3.3) than three times maximum width. Exopod as long as peduncle, endopod 1.33 times as long as peduncle; both rami with almost parallel sides, several long fine setae on rounded distal tips, and only sparsely spinose laterally.

Telson (Figure 51h): Subcircular, but maximum length 1.2 times maximum width.

PARTIAL DESCRIPTION OF ALLOTYPE (♀).—First peraeopod: Relatively slender, but dactylus and propodus almost subchelate, as in the allotype of *A. obtusus* (cf. Figure 44e). Dactylus about as long as palm of propodus and with 5 teethlike spines on inner margin and a long terminal claw. Otherwise similar to the description given for this appendage in a female paralectotype of *A. attenuatus*.

"First" pleopod: Shape similar to that described for the allotype of *A. scrupulosus* (cf. Figure 49g), but setation rather different; 1 long and simple and 13 long plumose spines present on distal lateral margin, 4 short and simple spines irregularly arranged near inner proximal corner, and 1 short and simple spine at outer proximal angle.

MATERIAL EXAMINED.—MARYLAND: Ridge, St. Mary's County, 2♂♂, coll. W. H. Ball, 26.iv.1930 (USNM); Mechanicsville, St. Mary's County, 1♂, coll. W. H. Ball, 11.v.1937 (USNM); Bristol, 1♂, coll. A. Pizzini, 31.x.1937 (USNM).

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY.—The species is known only from Maryland (Figure 27), where it has been collected from a variety of habitats: boggy ground in a swamp, rainwater in roadside ditch, a woodland stream, and the outlet of a spring. All known localities lie on the small peninsula southeast of Washington, D.C., bounded by the Potomac River and Chesapeake Bay.

FURTHER DESCRIPTION (♂).—Body: The longest ♂ examined was 10.5 mm long.

First antenna: Flagellum 13- or 14-merous; last 3 penultimate segments bear aesthetascs.

Second antenna: Length 0.67 to 0.89 times that of body. Flagellum 61- to 85-merous.

Mouthparts: See Table 1.

First peraeopod: Considerable variation was apparent in the setation and palmar shape of the propodus in the material examined. Thus referring to Figure 51a (holotype) and Figure 52 (all other known male material), it can be seen that the extent of develop-

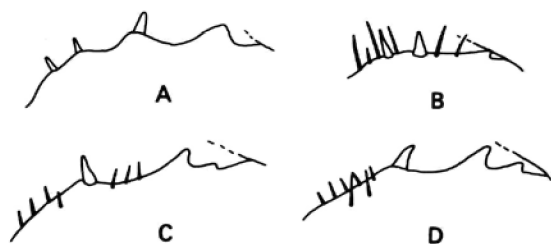


FIGURE 52.—*Asellus nodulus*, extent of variation in palm shape of male first peraeopod: A, C, Ridge, St. Mary's County, Maryland; B, Mechanicsville, St. Mary's County, Maryland; D, Bristol, Maryland.

ment of triangular processes on the palm is variable, as also is the number of proximal toothlike spines.

First pleopod: Total length of appendage 1.27 to 1.36 times as long as second pleopod. Inner margin of sympod with 5 to 6 coupling hooks. Maximum width of distal segment 0.48 to 0.52 times length; distal margin with 3 to 5 very long plumose spines.

Second pleopod: Maximum length of sympod from 1.2 to 1.3 times maximum width. Proximal segment of exopod with 5 or 6 short and simple spines on outer margin; distal segment with 4 to 9 shorter and 8 to 10 longer plumose marginal spines (total: 12 to 17), and maximum length 1.2 to 1.3 times maximum width. Endopod shape is relatively constant, but the maximum length varies from 2.5 to 3.0 times the maximum width; the length in proportion to the length of the distal segment of the exopod varies from 1.3 to 1.5. The morphology of the tip of the endopod is quite constant.

Uropod: See Table 2.

Telson: Maximum length 1.0 to 1.2 times maximum length.

Asellus occidentalis, new species

FIGURES 53, 55, 56

ETYMOLOGY.—From the Latin *occidentalis*, western.

TYPE MATERIAL AND TYPE LOCALITY.—Holotype: adult ♂, USNM 122063. Allotype: adult nonovigerous ♀, USNM 122064. Paratypes: 9 ♂♂, 6 nonovigerous and 1 ovigerous ♀♀, USNM 122065. Type locality: Klamath River, near Falls between Lake Ewuana and Upper Klamath Lake, Oregon. The type collection was made 16 November 1965 by Mr. W.C. Johnson and forwarded for study by Dr. J. B. Ander-

son, Federal Water Pollution Control Administration, United States Department of Interior.

DESCRIPTION OF HOLOTYPE.—Body: Length, 7.0 mm.

Head: Eyes distinct.

First antenna: Flagellum 11-merous and tip reaching to midpoint of last segment of peduncle of second antenna; penultimate 3 segments bearing aesthetascs. Second segment of peduncle longest; first, three-quarters length of second; third, about two-third length of second. First peduncle segment about 1.5 times as long as wide; second and third about 3.5 times as long as wide.

Second antenna: Length (6.5 mm) almost (0.93) equal to that of body. Flagellum 55-merous and about 3 times as long as peduncle.

First peraeopod (Figure 53 A): Dactylus with about 7 toothlike spines on inner margin. Propodus 1.76 times as long as wide, subovate; palm without triangular processes, with 4 prominent toothlike spines on proximal half, and with numerous simple spines submarginally.

First pleopod (Figure 53 B): Total length 1.34 times that of second pleopod. Sympod subrectangular, about 1.5 times as long as wide; inner margin with 3 hooklike protuberances for coupling. Distal segment subovate, but inner margin more or less straight; maximum width occurring about two-thirds toward distal margin, distinctly greater than width of sympod, and about two-thirds maximum length; distal and outer-distal margins with several long plumose spines and numerous shorter and simple spines somewhat irregularly arranged.

Second pleopod (Figures 53 C-E): Sympod subrectangular, maximum length 1.23 times maximum width; medial and lateral margins gently convex; several moderately long simple spines occur near the inner distal angle. Proximal segment of exopod irregularly triangular, without marginal spines. Distal segment of exopod broadly subtriangular, maximum length 1.5 times maximum width, with 17 long to moderately long plumose spines on outer margin and distal half of inner margin, a fringe of marginal setae on distal two-thirds of inner margin, and a distinctly sclerotized inner proximal margin. Endopod slightly shorter (0.92) than total length of exopod, and 1.28 times as long as distal segment of exopod; endopod about (2.57) two and a half times as long as maximum width. Endopod bent at approximately right

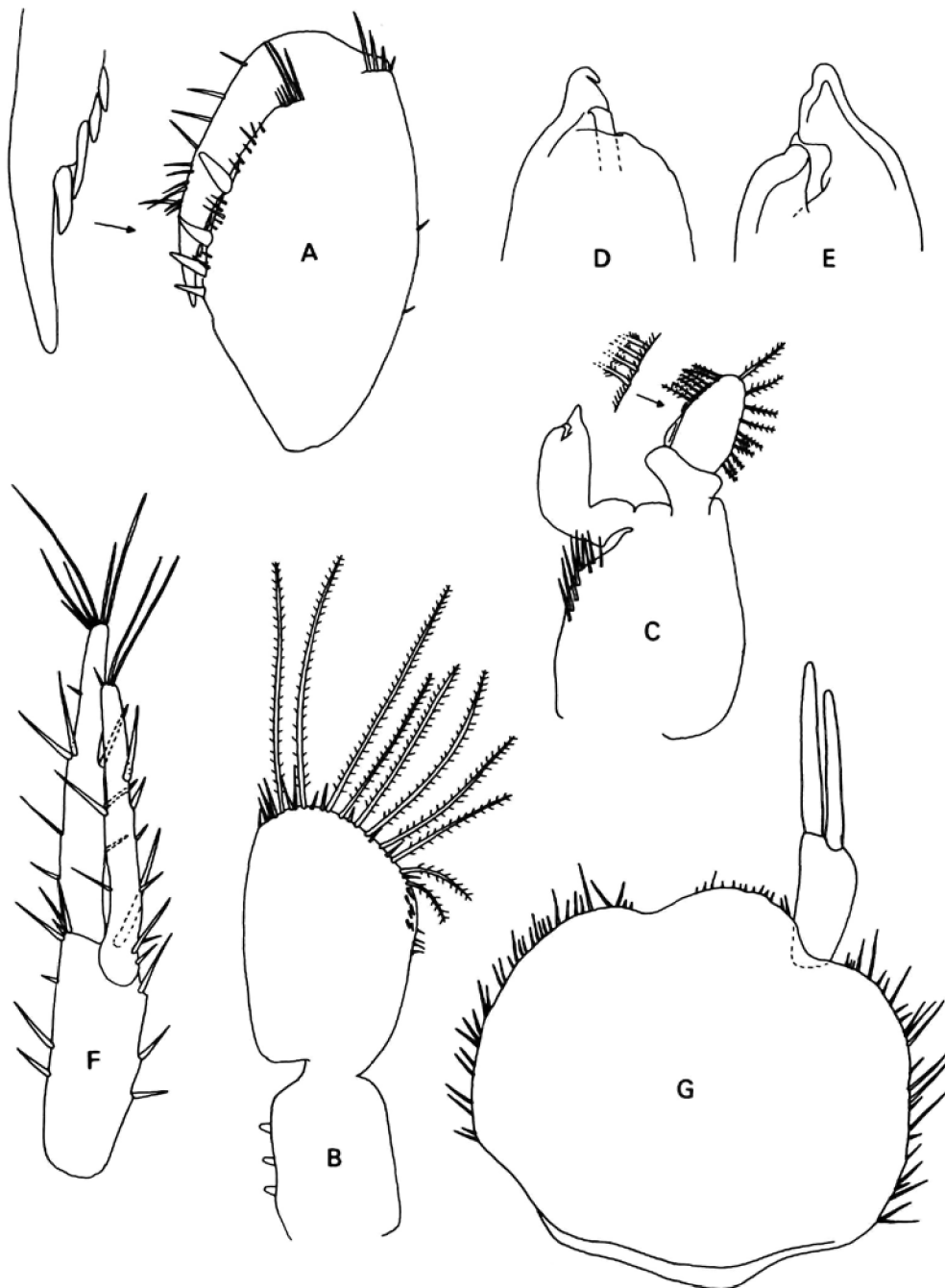


FIGURE 53.—*Asellus occidentalis*, holotype: A, dactylus and propodus of first peraeopod; B, first pleopod; C, second pleopod; D, E, respectively dorsal and ventral surfaces of tip of endopodite of second pleopod; F, uropod; G, uropod and telson.

angles near basal apophyses; outer basal apophysis rounded, not well developed; inner basal apophysis distinct, well developed, flaplike. Cannula short, moderately narrow, and completely hidden in ventral view behind lateral process. Ventral groove prominent, short, and wide. Mesial and caudal processes scarcely developed. Lateral process well developed, large, subtriangular, bent dorsally at tip, and without associated setae or spines.

Uropod (Figure 53F): Not quite (0.83) as long as telson. Peduncle about 2.5 times as long as wide. Exopod distinctly longer (1.27) than peduncle, and ended slightly longer (1.03) than exopod; both rami with several long fine spines on distal tips and several stout long spines laterally.

Telson (Figure 53G): Subcircular, but maximum width greater (1.17) than maximum length; uropodal sinuses distinct.

PARTIAL DESCRIPTION OF ALLOTYPE (♀).—First peraeopod: General shape and setation similar to that described for a female paralectotype of *A. attenuatus*, but propodus with 2 long and stout toothlike spines near middle of palm. Palmar margin of dactylus with 7 toothlike spines.

“First” pleopod: Shape similar to that described for a female paralectotype of *A. intermedius* (cf. Figure 18c). Distal margin and distal half of outer margin with 10 finely plumose spines.

MATERIAL EXAMINED.—**BRITISH COLUMBIA:** Nanaimo, Vancouver Island, 3♂♂, coll. E. L. Bousfield, 24.vii.1955 (NMC); Clayoquot Island, 10♂♂, coll. E. L. Bousfield, 6.viii.1955 (NMC); Double Bay, Vancouver Island, 6♂♂, coll. E. L. Bousfield, 5.viii.1959 (NMC).

OREGON: Philomath, Benton County, 2♂♂, coll. G. B. Wiggins, 24.iv.1964 (ROM); Klamath River, 10♂♂, coll. U.S. Dept. Interior, 1.xii.1965; Klamath River, 1♂, coll. U.S. Dept. Interior, no date marked.

WASHINGTON: Fort Simcoe, near Yakima, 3♂♂, coll. Margaret Anderson, 26.vi.1967.

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY.—The species is recorded only from the far northwestern part of the United States and the extreme southwestern corner of British Columbia (Figure 54). Within this area of distribution it has been collected from spring-brooks, streams, rivers, and on one occasion from the marshy edge of a lake.

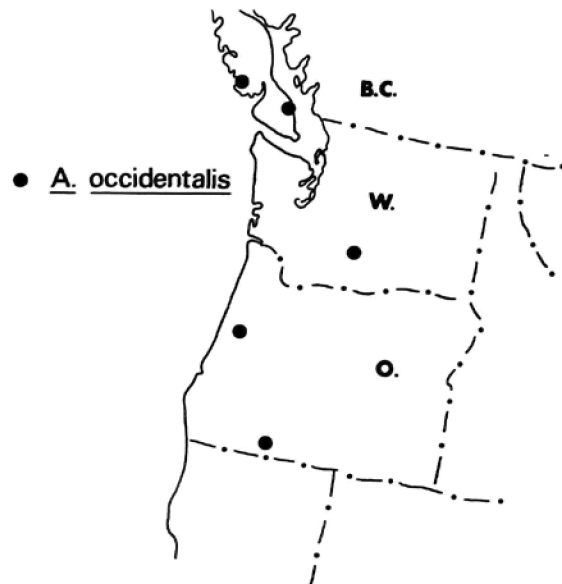


FIGURE 54.—Geographical distribution.

FURTHER DESCRIPTION (♂).—Body: The longest ♂ examined was 11.0 mm long.

First antenna: Flagellum 9- to 12-merous; last 2 or 3 penultimate segments bear aesthetascs.

Second antenna: Length 0.68 to 0.93 times that of body. Flagellum 42- to 60-merous.

Mouthparts: See Table 1.

First peraeopod: Palm of propodus always without triangular process, with 3 to 5 prominent toothlike spines variously arranged (Figure 55), and with numerous simple spines submarginally.

First pleopod: Total length of appendage 1.15 to 1.45 times as long as second pleopod. Inner margin of sympod with 2 to 4 coupling hooks. Maximum width of distal segment 0.56 to 0.73 times length; distal margin with 7 to 13 long plumose spines.

Second pleopod: Maximum length of sympod from 1.08 to 1.27 times maximum width. Proximal segment of exopod with 0 to 1 short and simple spine on outer margin; distal segment with 8 to 18 marginal spines (apart from fringe of setae on inner margin), and maximum length 1.06 to 1.57 times maximum width. Endopod shape more or less constant in character, length 2.06 to 2.72 times maximum width, and 1.15 to 2.24 times length of distal segment of exopod.

A little variation is displayed by the terminal arrangement of the endopod (Figure 56).

Uropod: See Table 2.

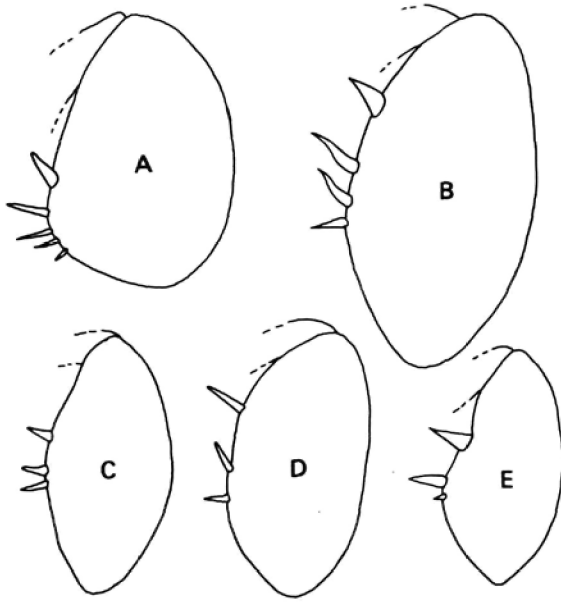


FIGURE 55.—*Asellus occidentalis*, extent of variation in shape and spinulation of propodus of male first pereopod: A, Victoria Island, British Columbia; B, Clayoquot Island, British Columbia; C, Klamath River, Oregon; D, Fort Simcoe, Washington; E, Nanaimo, British Columbia.

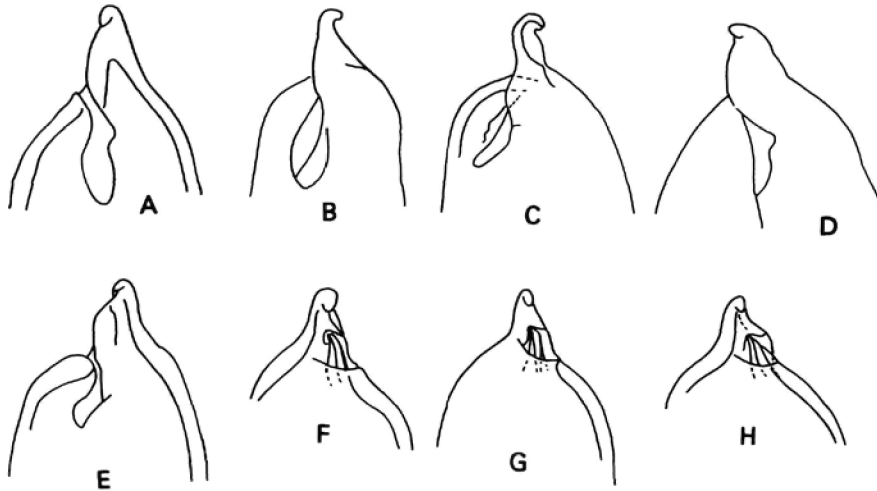


FIGURE 56.—*Asellus occidentalis*, extent of variation in morphology of endopodite tip of male second pleopod: A, B, Victoria Island, British Columbia; C, Clayoquot Island, British Columbia; D, Benton County, Oregon; E-H, paratypes. A-E, ventral views; F-H, dorsal views.

Uncertain Name

The name *Asellus tomalensis* was first proposed by Harford in 1877 (pp. 54-55) for a single specimen of *Asellus* obtained from "Tomales Bay and vicinity." The description was very short, unaccompanied by drawings, and was impossible to use for the certain identification of the taxon involved. Richardson (1900, p. 297) was aware of this, and consequently only tentatively referred to *A. tomalensis* some material that had been collected from Lake Washington, Seattle (1904a, b). This material was actually compared (by Dr. W. E. Ritter) with the single specimen of *A. tomalensis* identified by Harford, but the comparison was clearly superficial as indicated by Richardson's report of it (1904a, pp. 224-225). Richardson did provide a description of her material, but this description likewise is insufficient for diagnostic purposes, and gives, for example, no details for any pleopod (cf. Van Name, 1936, p. 406). Harford's type was redescribed in 1904 by Holmes, but the redescription, though more complete, provided no further clarification of the species identity; moreover, it indicated that the specimen was a female: "first pair of pleopods very small and oblong; second pair not fused in the middle, and forming an operculum over the succeeding ones" (1904, p. 322). This specimen, which had been deposited in the California Academy of Sciences, Registration No. 2609, was subsequently destroyed by fire and earthquake in

1906 according to D. Chivers and G. E. Lindsay, respectively staff member and director of the California Academy of Sciences, San Francisco (personal communication, 27 July 1967).

In view of the certain destruction of the type, the absence of an adequate description, the failure of colleagues (Drs. N. H. Anderson and G. E. Clothier) to collect *Asellus* from the Tomales Bay area of California, and the occurrence of at least three distinct epigeal taxa of *Asellus* (*A. racovitzai racovitzai*, *A. communis*, and *A. occidentalis*) in the western part of North America, *Asellus tomalensis* is here regarded as a name not certainly applicable to any known taxon. The application of the name by several authors (e.g. Carl, 1937; Hatch, 1947) to material examined by them is without firm foundation. It is possible that the new species described in this paper as *A. occidentalis* is conspecific with Harford's taxon but this cannot be verified, and the situation seems best resolved by the course of action here adopted.

Species Originally Referred to *Asellus*

In addition to the names mentioned in this paper, reference should also be made to species originally described as species of *Asellus* but subsequently transferred to the genus *Lirceus*. The original names are *Asellus lineatus* Say, *Asellus tenax* Smith, *Asellus hoppinae* Faxon, *Asellus hoppiae* Packard, and *Asellus incisus* Van Name.

Lirceus lineatus was described by Say in 1818. The description although exceedingly brief and without figures did indicate that there was on the head "a sinus each side in the middle" (p. 438); it may be presumed that this refers to a lateral incision of the head margin, a feature of frequent occurrence in the genus *Lirceus* but never present in *Asellus*. Its occurrence provides firm support for the inclusion of the species in the genus *Lirceus* (Hubricht and Mackin, 1949). The name *Asellus tenax* was put forward by Smith (in Smith and Verrill, 1871). Smith noted (see also Smith, 1874) that his taxon lacked mandibular palpi, and after transference to the genus *Asellopsis* by Harger (1874) and then *Mancasellus* (Harger, 1876), it was synonymized by Hubricht and Mackin (1949) with *L. lineatus*. The lack of a mandibular palp certainly excludes it from the genus *Asellus*.

Lirceus hoppinae was described by Faxon (in Garman, 1889) and was treated as a species of *Asellus* until

fairly recently (e.g., Van Name, 1936; Mackin and Hubricht, 1938). It was transferred to the genus *Lirceus* and redescribed by Hubricht and Mackin in 1949, although these authors did not state what specimens they used as a basis for their description and do not mention type material. Through the courtesy of Miss A. B. Bliss, Museum of Comparative Zoology, original type material (three slightly damaged adult males in alcohol) was located in that Museum, and from the labels inside the container and the state of the material itself it seems not to have been examined by Hubricht and Mackin. There is no record that these authors examined this material (Miss A. B. Bliss, personal communication, 11 December 1967). The labels read: "Mus. Comp. Zoöl. Cambridge Mass. No. 4203 Coll. Miss Ruth Hoppin *Asellus hoppinae* Fax. Typus Day's Cave, Mo.," "25: J-4," "Dave's Cave in mud under stones," and "4203." Examination of this material confirmed the correctness of the generic transference effected by Hubricht and Mackin and also of critical details in their specific redescription. Thus, the specimens have the typical body outline facies of *Lirceus*, and have 3-jointed mandibular palps, third pleopoda with the exopodite divided by a diagonal suture into a large proximal portion and a smaller moon-shaped distal portion, and in appearance of the telson, uropoda and gnathopoda agree with the drawing given by Hubricht and Mackin (1938; plate 3 A-C) for *L. hoppinae hoppinae*. Packard's (1894) name, *Asellus hoppiae*, was synonymized by Van Name (1936) with *Asellus hoppinae* and accordingly becomes a synonym of *L. hoppinae hoppinae*.

A further synonym of *L. hoppinae*, according to Hubricht and Mackin (1949), is *Asellus incisus* described by Van Name (1936). The generic transference, at least, is undoubtedly warranted for Van Name's original description includes a clear diagram of the head (fig. 202), showing incised lateral margins and the frontal shape typical for the anterior head margin of *Lirceus*.

Coexistence of Species

The vast majority of collections examined during the present investigation were unispecific, at least as far as males were concerned. A few, however, were not, emphasizing the need for care in determining material. The number of collections containing two species, and the species involved, are indicated below:

<i>A. communis</i> + <i>A. racovitzai racovitzai</i>	2 collections
<i>A. intermedius</i> + <i>A. racovitzai racovitzai</i>	1 collection
<i>A. intermedius</i> + <i>A. brevicauda brevicauda</i>	1 collection
<i>A. obtusus</i> + <i>A. racovitzai australis</i>	3 collections

Phylogenetic Relationships

It is clear that any attempt to determine phylogenetic relationships within the North American epigeal species of *Asellus* must be based almost entirely upon the structure of the male genital pleopods, and particularly upon the morphology of the endopod tip of the male second pleopod; apart from the shape of the palm of the male first peraeopod, other parts of the body while providing some characters of diagnostic use may be more or less discounted in this respect. Steeves (1966), who dealt with the evolution of North American troglitic *Asellus*, clearly recognized this and indeed based his conclusions upon only the endopodial tip of the male second pleopod. On other grounds, however, certain general criticisms can be raised against Steeves' method of evolutionary analysis. Thus, his evolutionary scheme was the result principally of a series of hypothetical derivations of increasing complexity from ancestors that to him appeared to have the simplest (= most primitive) structure of endopod tip. Further, it took no account of sister groups and involved multiple derivation of species from a single taxon ("*alabamensis*"), a concept which is, as emphasized generally by Brundin (1966), unrealistic. Steeves' method of evolutionary analysis, like all such methods, is therefore open to the same type of criticism that Brundin (1966) has leveled, justifiably for the most part in the opinion of the present author, at the numerous "phylogenies" purporting to indicate phylogenetic relationships but which take no cognizance of the sort of strict phylogenetic principles first enunciated clearly by Hennig (1950).

Hennig's ideas, which emphasize the relative importance of plesiomorphic (primitive) and especially apomorphic (derived) characters, and the importance of sister group delimitation, provide a much more precise basis for determining phylogenetic relationships, and in the following discussion dealing with the relationships of North American epigeal species of *Asellus* an attempt is made to apply them. Although there are many difficulties in such an application, resulting mainly from the paucity of useful characters, and, in part consequence of this, from varying degrees of uncertainty as to whether a given character is plesio-

morphic or apomorphic, it is felt that it is only by the application of Hennig's ideas that true relationships within *Asellus* can be ascertained.

It should perhaps first be stated that it seems valid to deal with the evolution of the North American epigeal asellids as a single entity without involving intercontinental relationships (*A. aquaticus* is not considered in this section), for only two phylogenetic groups seem to be involved. One group, the largest and containing all but one species, seems to be of monophyletic origin in that with two exceptions all included taxa possess the undoubtedly synapomorphic character of a large triangular projection on the palm of the propodus of the male first peraeopod. The exceptions, *A. brevicauda bivittatus* and *A. nodulus*, may reasonably be regarded as having secondarily lost the triangular process; there can be no doubt of the close relationship of *A. brevicauda bivittatus* to *A. brevicauda brevicauda* which has the triangular process, and the triangular process is in fact sometimes present in *A. nodulus*. Secondary loss of the triangular process cannot reasonably be advanced to explain its absence in the western species, *A. occidentalis*, and we must therefore regard this taxon as constituting a second phylogenetic group of uncertain affinities with the first. No synapomorphic characters seem to be possessed by these two groups which set them apart as a single unit from Palearctic species of *Asellus*. The great extension of the lateral process and the absence of either well-developed caudal or mesial processes on the endopod of the male second pleopod of *A. occidentalis* is also a structural pattern not displayed by any other North American epigeal species of *Asellus* and gives further support for regarding *A. occidentalis* as part of a separate phylogenetic group.

In dealing with the relationships of the major phylogenetic group, we may take as an arbitrary starting point the decidedly apomorphic species *A. montanus*. It is difficult to equate the morphology of the endopod tip of the male second pleopod of this species with any other species, but there can be no doubt that the torsion of the endopod is an apomorphic character. The only other species which displays torsion of the endopod is *A. nodulus*, and it is this species, therefore, which must be regarded as the sister species of *A. montanus*. Parallel evolution may have been involved in producing the torsion effect, but as pointed out by Brundin (1966) unless there is proof to the contrary synapomorphies must in the first instance be regarded

as indicating phylogenetic relationship and not used to anticipate parallelism.

Both *A. montanus* and *A. nodulus* possess a first pleopod that is distinctly longer than the second, and which has an elongate distal segment with long plumose spines on its distal margin. The only other eastern species to possess a similar first pleopod are *A. brevicauda*, *A. scrupulosus*, *A. kenki*, and *A. dentadactylus*; the remaining species have a first pleopod that is shorter or more or less subequal in length to the second and lacks plumose distal spines. It is not possible to be certain as to which of these two structural patterns is apomorphic and which plesiomorphic, but the distinction between them is so clear and must surely involve so many genic differences that it seems reasonable to regard the distinction as of considerable phylogenetic significance. Accordingly, the four species *A. brevicauda*, *A. scrupulosus*, *A. kenki*, and *A. dentadactylus*, are here regarded as comprising the sister group to *A. montanus* and *A. nodulus*. For present purposes, we may regard all six species as related principally by their synapomorphic first pleopods.

Apart from *A. montanus* and *A. nodulus*, the structure of the endopod tip of the male second pleopod in all other North American species of *Asellus* may be conceived as a series of developments of three main structures associated with the ventral groove and terminal cannula: the mesial, lateral, and caudal processes. It seems reasonable to presume that any of these structures that is highly or peculiarly developed constitutes an apomorphic character, and, conversely, that absence or slight development indicates plesiomorphy.

The lateral process is variously developed in *A. brevicauda*, *A. scrupulosus*, and *A. kenki*, but not in *A. dentadactylus*, in which species, however, the caudal process is well developed and dentate. The first three species, therefore, may be regarded as the sister group to *A. dentadactylus*. In *A. kenki* the mesial process, according to Bowman (1967), is a simple rounded structure, but in *A. brevicauda* and *A. scrupulosus* it is sclerotized and either rugose or dentate. The latter condition is probably the apomorphic one, and it unites these two species as the sister group to *A. kenki*. The basic structure of the endopod tip of the male second pleopod in *A. scrupulosus* and *A. brevicauda* is very similar, but in the former species the mesial process is dentate and the lateral process heavily sclerotized, suggesting that of these two species *A. scrupulosus* is the more apomorphic. It may be noted, however, that

the very short uropoda of *A. brevicauda* are certainly apomorphic.

Turning now to those species that have a first pleopod of an apparently plesiomorphic nature, that is, short and lacking plumose setae, two distinct sister groups are clearly involved: one in which the mesial process is well developed, and one, presumably more plesiomorphic, in which it is not. Of the former group, *A. racovitzai* appears to be the most apomorphic species, showing relative prolongation of the cannula and mesial process, and with a well developed and pointed caudal process having a series of setal combs on its dorsal surface. The sister species to *A. racovitzai* is unquestionably *A. attenuatus*. Both *A. forbesi* and *A. obtusus* have caudal processes of a simple and apparently plesiomorphic nature, and in both the cannula is short and wide; they probably represent, therefore, the more plesiomorphic sister group to the *A. racovitzai/A. attenuatus* group. The relatively greater development of the mesial process of *A. forbesi* suggests that it is more apomorphic with regard to its endopodial armature than *A. obtusus*.

Of the three species without a well developed mesial process, namely, *A. communis*, *A. intermedius*, and *A. laticaudatus*, the former two appear to be related by their possession of a more or less well-developed caudal process, and they form, consequently, the sister group to the more plesiomorphic species *A. laticaudatus* which lacks a caudal process.

The tentative phylogenetic relationships suggested above are expressed in diagrammatic form in Figure 57.

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Without the cooperation of a very large number of North American colleagues the extent of this work

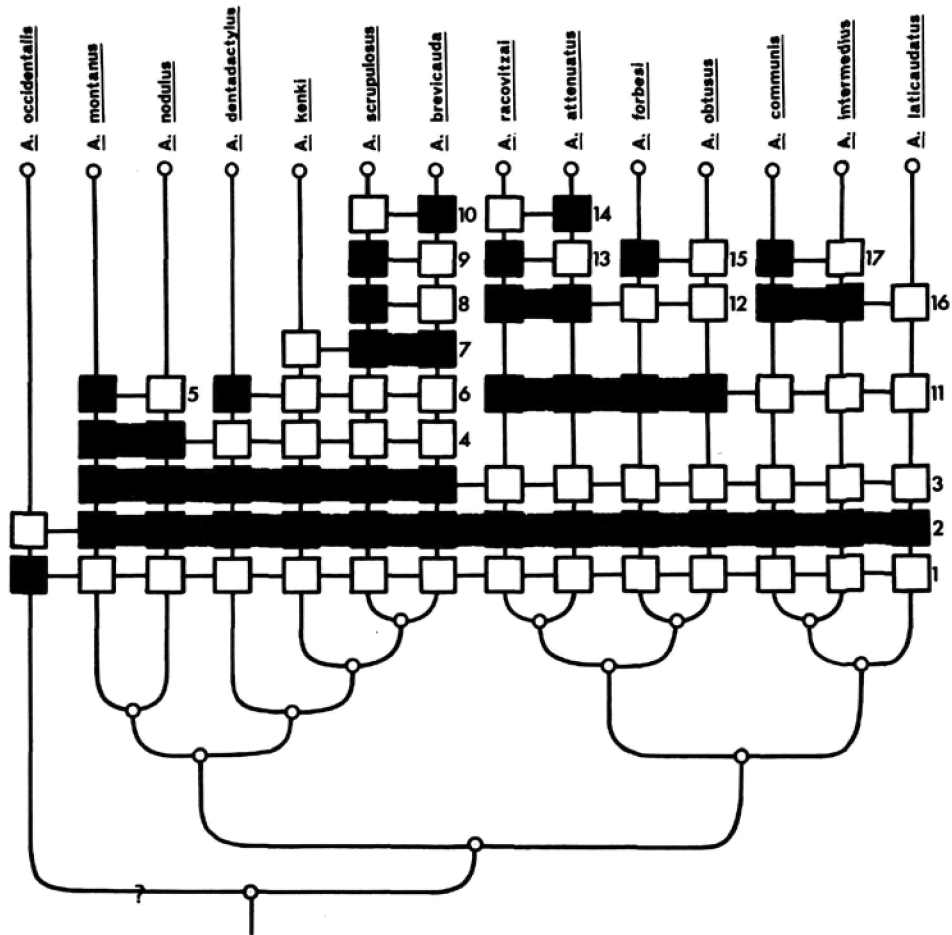


FIGURE 57.—Tentative phylogenetic relationships of North American epigeal species of *Asellus*, arranged according to the ideas of Hennig (1950). Black squares indicate apomorphic grades, empty squares plesiomorphic grades. Synapomorphies are indicated by darker stippling. The following characters are referred to and are indicated by the number to the right of the linked apomorphic and plesiomorphic grades (a, apomorphic grade; p, plesiomorphic grade. Cannula, and lateral, caudal, and mesial processes refer to the endopodial armature of the male second pleopod; endopod also refers to this appendage): 1, lateral process greatly extended (a) or not (p); 2, propodus of male first peraeopod with large triangular process on palm or having secondarily lost this (a) or primitively without such a process (p); 3, male first pleopod distinctly longer than second, with an elongate distal segment having long plumose spines on distal margin (a) or male first pleopod shorter or more or less subequal in length to second and lacking plumose distal spines (p); 4, endopod displaying torsion (a) or not (p); 5, tip of endopod coiled spirally (a) or not (p); 6, caudal process dentate (a) or not (p); 7, mesial process sclerotized and either rugose or dentate (a) or simple and rounded (p); 8, mesial process dentate (a) or not (p); 9, lateral process heavily sclerotized (a) or not (p); 10, uropoda very short (a) or of moderate length (p); 11, mesial process well developed (a) or not (p); 12, cannula long and narrow (a) or short and wide (p); 13, caudal process well developed with associated setae on dorsal surface (a) or not well developed and lacking such setae (p); 14, male first pleopod reduced (a) or not (p); 15, mesial process prominent (a) or less well developed (p); 16, caudal process present (a) or absent (p); 17, cannula long and narrow (a) or short and wide (p).

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* Not seen.