

THE OPILIONID FAMILY CADDIDAE IN NORTH AMERICA, WITH NOTES ON SPECIES FROM OTHER REGIONS (OPILIONES, PALPATOIRES, CADDOIDEA)

William A. Shear

Biology Department
Hampden-Sydney, College
Hampden-Sydney, Virginia 23943

ABSTRACT

Species belonging to the opilionid genera *Caddo*, *Acropsopilio*, *Austropsopilio* and *Cadella* are herein considered to constitute the family Caddidae. The subfamily Caddinae contains the genus *Caddo*; the other genera are placed in the subfamily Acropsopilioninae. It is suggested that the palpatorid Opiliones be grouped in three superfamilies: Caddoidea (including the family Caddidae), Phalangoidea (including the families Phalangiidae, Liobunidae, Neopilionidae and Sclerosomatidae) and Troguloidea (including the families Trogulidae, Nemostomatidae, Ischyropsalidae and Sabaconidae). North American members of the Caddidae are discussed in detail, and a new species, *Caddo pepperella*, is described. The North American caddids appear to be mostly parthenogenetic, and *C. pepperella* is very likely a neotenic isolate of *C. agilis*. Illustrations and taxonomic notes are provided for the majority of the exotic species of the family.

INTRODUCTION

Considerable confusion has surrounded the taxonomy of the order Opiliones in North America, since the early work of the prolific Nathan Banks, who described many of our species in the last decade of the 1800's and the first few years of this century. For many species, no additional descriptive material has been published following the original descriptions, most of which were brief and concentrated on such characters as color and body proportions. Only recently have a few generic revisions begun to appear. This paper is the first in a projected series of generic and familial revisions of North American opilionids, beginning with those of the superfamily Troguloidea (roughly, but not completely, equivalent to the old "Group" Dyspnoi). The family Caddidae was at first thought to belong to this group, and therefore seemed like a good starting point, but later study has shown that it is best considered a separate superfamily as will be explained below.

Species of the family Caddidae are small, inconspicuous, superficially mite-like opilionids usually found in leaf litter, moss, and vegetable debris, or running about on tree trunks and fallen logs. They may be immediately distinguished from any other opilionids by the enormous eyes, which occupy most of the carapace.

The first species of the family, *Caddo agilis*, was described from Long Island, New York, by Banks in 1892. Crosby (1904) described two more American species, *C. glaucopsis* and *C. boopis*, in a rather confusing paper in which a figure of *C. boopis*' pedipalp was labelled as pertaining to *C. glaucopsis*. This error was perpetuated by Roewer

(1923) in his enormous compendium *Die Weberknechte der Erde*. Crosby (1924) realized his error and published a correction, also stating that *C. glaucopsis* was a synonym for *C. agilis*. Crosby had been misled by Banks' published description of *agilis*, which neglected to mention that the type was not a mature specimen—this information appeared in a short paragraph by Banks (1924; printed on the same page as the last paragraph of Crosby's description of *C. glaucopsis*!) in which Banks reported *C. agilis* from the area of Washington, D.C. As a further complication, the type series of *C. agilis* contained a second, until now undescribed species, from which Banks' description was at least partly drawn.

Meanwhile, Silvestri (1904) described a peculiar, *Caddo*-like opilionid from Chile under the name *Acropsopilio chilensis*. Roewer (1923) established the new family Acropsopilionidae for this species, but because of his limited view of family level characters placed it incorrectly in the "Group" Dyspnoi. Roewer did not see specimens, but Silvestri's Latin description contains all the information necessary for a proper placement. Hirst (1925) and Lawrence (1931, 1934) described a total of three species in this nominal family from South Africa. Forster (1948, 1955) and Hickman (1957) described five species from New Zealand and Australia.

Further developments in *Caddo* proper are the description of *Caddo chomulae* from Mexico by Goodnight and Goodnight (1948), and the report by Suzuki (1958) of *C. agilis* from Japan. Although males of *Caddo agilis* Banks have been "described" several times in the literature, authentic members of this sex were only recently discovered. Males of the other New World species remain unknown, and indeed may not exist; there is evidence that they are parthenogenetic.

Unless indicated otherwise, all specimens mentioned in the distribution sections are in the American Museum of Natural History. Other museums and private collections as designated as follows: Chicago Natural History Museum (CNHM), Museum of Comparative Zoology (MCZ). Private Collections of W. A. Shear (WAS), Arlan L. Edgar (ALE), Joseph A. Beatty (JAB), Andrew A. Weaver (AAW), George Klee (GK), Charles R. McGhee (CRM), and R. L. Hoffman (RLH).

PROBLEMS IN HIGHER CLASSIFICATION OF THE CADDIDAE

The problem of generic groupings in the Caddidae has not been closely examined up to this time, and several redundant generic names have been proposed. *Oonopsopilio* Lawrence was later recognized by its describer to be a synonym of *Caddella* Hirst (Lawrence, 1934). *Zeopsopilio* Forster is here placed in the synonymy of *Acropsopilio* Silvestri, and *Tasmanopilio* Hickman is placed in the synonymy of *Austropsopilio* Forster. These synonymies will be found in the appropriate sections. Furthermore, two species described in *Caddo*, *C. boopis* Crosby, and *C. chomulae* Goodnight and Goodnight, are clearly members of *Acropsopilio*.

On the family level, there has been great confusion. Banks (1892) considered *Caddo agilis* to represent a distinct tribe which he called Caddini, but subsequently treated as a subfamily of Phalangiidae. Roewer, while placing *Acropsopilio* in a family of its own, put *Caddo* first in the subfamily Oligolophinae of the family Phalangiidae (Roewer, 1923). Later, Roewer (1957) placed the name Acropsopilionidae in the synonymy of the subfamily Caddoinae under the Phalangiidae, attributing the name to Banks but ignoring Banks' original orthography.

In a short paper on higher classification of the order Opiliones in general, Silahvy (1962) essentially retained Roewer's placement.

After the relationship of *Caddo* to the acropsopilionines was recognized, several authors speculated on the position of the group. Kauri (1950-1951) discussed species of *Caddella* in detail but came to no certain conclusions regarding *Caddo*. He retained the name Acropsopilionidae in the "Dyspnoi," Ringuelet (1962), in a restudy of *Acropsopilio*, using the sets of characters that classically have divided "Eupnoi" and "Dyspnoi," decided that *Caddo* should remain in the Oligolophinae and that the acropsopilionines should also be left as they were. However, some of Ringuelet's observations on *Caddo* were not correct, and he did not emphasize the mixture of features exhibited by species of *Caddella* and *Austropsopilio*. Suzuki (1967) felt that *C. agilis* bridged the classical groups, and depending on the key characters used, could go in either category. A perusal of the descriptive material below will demonstrate clearly the validity of Suzuki's position. Furthermore, the relictual distribution of the family indicates that we have to deal with an ancient group whose subunits have long been isolated from one another.

All of the authors cited above have indicated that some caddids may fit in either of the classical Hansen-Sorensen "groups," Dyspnoi or Eupnoi (Some Opilionid taxonomists have called these *tribes*, but treated them as superfamilies. The tribe is usually considered a division of the subfamily.). However, I think the time has come for bold measures with regard to this outmoded dichotomy. Too much effort has been spent surveying the literature and erecting higher categories without reference to species or actual specimens. Higher categories in taxonomy derive their standing from groupings of lower categories and do not exist as *a priori* pigeonholes in which the lower categories must be stuffed. I have earlier pointed out, in studies on diplopod taxonomy, that it is not inconsistent to have large actively speciating genera or families, or even superfamilies, in the same orders with small, perhaps even monobasic genera or families which qualified investigators feel represent the ends of old, expiring phyletic lines. Thus it follows that to consider certain single characters of "family value," or some such procedure, is logically inconsistent. Categories above the genus should be based on a holistic, not reductionistic, view.

Within the suborder Palpatores, two groups are well-defined and probably monophyletic: one includes the Troglulidae, Nemastomatidae, Ischyropsalidae and Saboconidae and the other families Neopilionidae, Phalangiidae, Liobunidae and Sclerosomatidae. Silhavy (1961) rejects the division of the Opiliones into the suborders Laniatores, Palpatores and Cyphophthalmi—instead he breaks the Laniatores up into two suborders, Gonyleptomorphi and Oncopodomorphi and raises the old names "Eupnoi" and "Dyspnoi" to subordinal status, leaving Cyphophthalmi as it stands. The evidence for this arrangement is not very clear, and it essentially involves the same reductionistic views as the arrangement of Roewer. I think that a greater level of stability would be maintained by continuing with the three classical, well-established suborders and by using superfamily names for divisions within them. The use of superfamily names to replace the "group" names Eupnoi and Dyspnoi has some clear advantages: 1) superfamily names are protected by the ICZN and thus finding and using the oldest identifiable name will lend stability to the nomenclature; 2) such names will reflect at least partially the content of the group by being based on the name of a type-genus; 3) a hierarchy of categories, rather than a series of coordinate categories, is established.

Thus, I propose to group the suborder Palpatores into three superfamilies. The superfamily Troguloidea Sundevall, 1833 contains the families Troglulidae, Nemastomatidae, Ischyropsalidae and Saboconidae. The type-genus is *Trogulus* Latrielle, 1802. The super-

family Phalangioidea Sundevall, 1833 contains the families Phalangiidae, Neopilionidae, Liobunidae and Sclerosomatidae. The type-genus is *Phalangium* Linnaeus, 1758. The superfamily Caddoidea Banks, 1892 contains only the family Caddidae; the type genus is *Caddo* Banks, 1892. All three of these are formed and characterized by the included families, rather than by more or less arbitrarily chosen diagnostic characters.

The superfamily status of the Caddoidea is justified by the combination of characters elaborated on at length in the section below. This action removes from the Troguloidea the nonconforming element of the family Acropsopilionidae and from the Phalangioidea the nonconforming element of the subfamily Caddinae. A greater uniformity within superfamilies is thus achieved. When an overview of the order Opiliones in general has been completed, it will be possible to discuss these categories more fully.

DESCRIPTIONS OF THE CADDIDS OF NORTH AMERICA

Superfamily CADDOIDEA Banks, 1892, NEW STATUS

A superfamily of the suborder Palpatores, containing only the family Caddidae Banks, 1892, as defined below.

Type-genus—*Caddo*, Banks, 1893.

Diagnosis—Differs from the superfamily Phalangioidea in lacking accessory spiracles on the tibiae of the legs, and in having the abdominal spiracles comparatively large and partially bridged over with granules; and from the superfamily Troguloidea in having pedipalps with usually large, sometimes movable claws and armed with spine-bearing processes.

Description—The characters of the superfamily are the same as those of the Family Caddidae.

Family Caddidae Banks, 1892

Caddini Banks, 1892, Canadian Entomol. 25:205; Roewer, 1957 (Caddoinae), Senck. Biol. 38:331; Silhavy, 1961, 11th Int. Cong. Entomol. 1:267. Acropsopilionidae Roewer, 1923, *Die Weberknechte der Erde*, p. 678; Lawrence, 1931, Ann. South African Mus. 29(2):469; Kauri, 1950-51, S. Afr. Animal Life 8:135; Ringuelet, 1959, Rev. Mus. Arg. Cien. Nat. 5(2):206; 1962, Physis 23:77-80; NEW SUBJECTIVE SYNONYMY.

Type-genus—*Caddo* Banks, 1892.

Diagnosis—See superfamily diagnosis above.

Description—Carapace nearly as broad as long, thoracic tergites well-marked, cuticle leathery, unarmed. Eye tubercle occupying nearly all of carapace, deeply depressed in middle, in some species extending forward over chelicerae (*Austropsopilio*, see Fig. 17). Eyes large, nearly at lateral margins of carapace. Scent gland pores at anteriolateral margins of carapace, small, not conspicuous. Abdominal tergites not heavily sclerotized, usually unarmed, not well separated from one another. Labrum subtriangular, small. Labium rounded, as wide as long. Sternum well-sclerotized, armed with setae, usually wider than long, sometimes with long processes (*Caddella africana*, Fig. 29). Chelicerae with toothed fingers, with or without a ventral spine on the basal article. Palpus with spined processes, lacking a claw in females of some species. Coxal endites of pedipalp large, mostly membranous, sclerotic portion crescentic, sometimes with a large spine; of coxae I with membranous part longer than wide, sclerotic part longer than wide, armed with setae; of coxae II longer than wide, about one-third the size of those of coxae I; of coxae III and IV vestigial, not movable. Genital operculum large, blunt, covering

sternum or articulating with it (*Caddella africana*, Fig. 29). Spiracles large, partially operculate, partially bridged over with enlarged cuticular granules. Male genitalia poorly known, variable, see subfamilies. Ovipositor usually ringed, with large furcae each bearing single sensory organ.

Distribution—Appalachian Mountains of North America, including area surrounding the Great Lakes; Chiapas, Mexico; southern South America, including parts of Chile, Argentina and Brazil; Union of South Africa; Queensland and Tasmania, Australia; New Zealand; Japan.

KEY TO SUBFAMILIES AND GENERA

- 1a. Basal articles of chelicerae each with a ventral spur; North America, Japan . . .
 Subfamily Caddinae Banks, *Caddo* Banks
- 1b. Basal articles of chelicerae without ventral spurs; all southern hemisphere localities, Great Lakes region of North America, and Chiapas, Mexico
 Acropsopilioninae Roewer 2
- 2a(1b). Palpal tibia unarmed (Figs. 23, 28, 31); South Africa *Caddella* Hirst
- 2b. Palpal tibia armed with spine-bearing tubercles (Figs. 8, 18) 3
- 3a(2b). Basal spined tubercles of palpal femora blunt, rounded (Fig. 18), Australia . . .
 *Austropsopilio* Forster
- 3b. Basal spined tubercles of palpal femora acute, tipped with a large terminal spine (Fig. 8); New Zealand, Chile, Chiapas, Great Lakes region of U.S.
 *Acropsopilio* Silvestri

Subfamily Caddinae Banks, 1893

Caddini Banks, 1892, Canadian Ent. 25:205.

Type-genus—*Caddo* Banks, 1892.

Diagnosis—Distinct from the Acropsopilioninae in being generally more phalangoid in appearance; in having the palpal tarsus longer than the tibia, armed with a movable claw; ovipositor with more than three annuli; male genitalia simple, symmetrical.

Description—With the characters of the family, and in addition: palpus of females with femur armed with three evenly spaced acute spined tubercles and a mesal apical lobe; tibia not armed, shorter than tarsus; tarsus with movable claw. Chelicerae with basal article armed ventrally with short, sharp spur. Ovipositor with 10-12 annuli distinctly sclerotized; sensillae of furcae small articulated lobes with socketed setae. Penis (when males are known) simple, shaftlike, symmetrical, not twisted, apically bifurcate.

Distribution—North America and Japan, with a single fossil species from the Baltic Amber [*Caddo dentipalpis* (Koch and Berendt); see Bishop and Crosby, 1923].

Included genera—*Caddo* Banks, 1892.

Genus *Caddo* Banks, 1892

Caddo Banks, 1892, Proc. Entomol. Soc. Washington 2:249; Crosby, 1904, J. New York Entomol. Soc. 12:253; Roewer, 1912, Abh. Geb. Naturwiss. 20:33; 1923, *Die Weberknechte der Erde*, p. 712; 1957, Senck. Biol. 38:331; Bishop and Crosby, 1924,

New York State Mus. Dir. Rep. 1923:83; Bishop, 1949, Proc. Rochester Acad. Sci. 9:174-175 (complete references to 1948).

Type-species—*Caddo agilis* Banks.

Description—With the characters of the subfamily, and in addition: palpus of female with three large spine-bearing tubercles on ventral surface of femur, large spine-bearing knob on inner distal surface of femur; of male (when known) with large subquadrate lobe in place of spine-bearing tubercles. Ovipositor with 6-12 chitinous rings, deeply bifurcated distally, each furca with 10 setae arranged as in Fig. 4; seminal receptacles of most specimens obsolete; penis (when males are present) simple, shaftlike, with dorsal spinous branch and ventral glans.

Distribution—(Maps 1, 2) North America, from North Carolina to the Great Lakes region, New England, and southern Canada; Japan, region of Mt. Hoki-Daisen, Tottori Pref.

Key to Species of *Caddo*

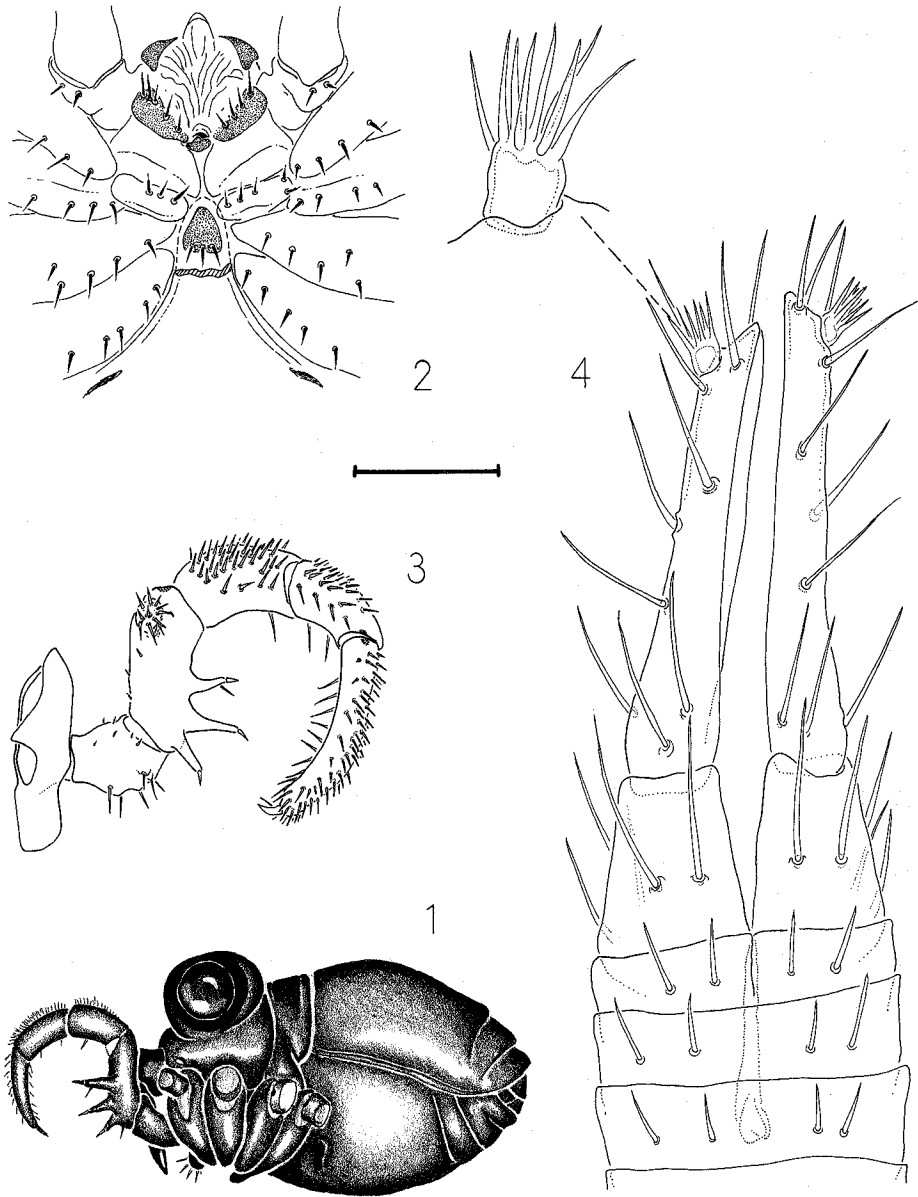
- 1a. Width of eye tubercle of *adults* 1.3-1.5 mm; body strongly marked purplish brown and silver; north-eastern United States and southern Canada, south to North Carolina and Tennessee in mountains, Japan *C. agilis* Banks
- 1b. Width of eye tubercle of *adults* 0.6-0.8 mm; body more or less evenly colored medium brown; eastern New York, Long Island, southern New England
 *C. pepperella* n. sp.

Caddo agilis Banks

Figs. 1-4, Map 1

Caddo agilis Banks, 1892, Proc. Entomol. Soc. Washington 2:249-251, Figs. 1-6, ♀; Roewer, 1912, Abh. Geb. Naturwiss. 20:33, no figures, 1923, *Die Weberknechte der Erde* p. 712-713, Figs. 889a-889b; ♀; 1957 Senck. Biol. 38:331, no figures; Bishop and Crosby, 1924, New York State Mus. Bull. 1923:83-84, Fig. 3, ♀; Bishop, 1949, Proc. Rochester Acad. Sci. 9:175-176, Pl. 1, Figs. 9-14, ♀ (complete references to 1948); Suzuki, 1958, Ann. Zool. Japan, 31:226-228, Figs. 1-6, ♀. *Caddo glaucopis* Crosby, 1904, J. New York Entomol. Soc. 12:253-254 [Fig. 4, labelled as pertaining to *C. glaucopis*, depicts palpus of *Caddo* (= *Acropsopilio*) *boopis*]; Roewer, 1928, *Die Weberknechte der Erde*, p. 713-714.

Types—Female cotypes from Long Island, New York deposited in Museum of Comparative Zoology, Harvard University, Cambridge, Mass. The type series consists of several females of both *Caddo agilis* and the heretofore unrecognized species *C. pepperella*. It is obvious from Banks' original description, particularly of the color pattern, that his concept of *C. agilis* was drawn mostly from specimens of *C. pepperella*. In 1904, Banks published a brief note mentioning that the type of *C. agilis* was immature; *C. pepperella* closely resembles immature *C. agilis*. It is possible that Banks added the "mature" specimens (real *C. agilis*) at a later date; this was a common practice of taxonomists of the day. Despite the evidence that the name *Caddo agilis* ought to be applied to the newly recognized species referred to here as *C. pepperella*, and that the more widespread familiar species now known as *C. agilis* ought to be called *C. glaucopis* (a name proposed by Crosby for mature specimens of the present *C. agilis* before publication of Banks' note on the maturity of the types of *agilis*) I think that stability and



Figs. 1-4.—Anatomy of *Caddo agilis*: 1, body, lateral view; 2, ventral side of cephalothorax, ventral view; 3, left palpus of female, mesal view; 4, ovipositor, ventral view; enlargement: right sensillum. Scale line = 1.00 mm for Fig. 1, 0.35 mm for Figs. 2, 3. Fig. 4 not to scale, 400X enlargement 900X.

continuity of nomenclature would best be preserved by continuing to refer to the larger, widespread species as *Caddo agilis*, and providing a new name for the smaller, more restricted species. In accordance with this, I have designated as a neoelectotype a mature specimen of *Caddo agilis* from the original type series.

The female holotype of *C. glaucopis* is from Ithaca, N.Y., collected on a tree trunk in August, 1903. It is in the AMNH (specimen examined). Because of the great difference, particularly in color and size, between his specimen and the original description of *C. agilis*, Crosby described *C. glaucopis*. In the same journal, and actually on the very page carrying the last few paragraphs of Crosby's article, Banks published a note on a collection of opiliones from Washington, D.C., which mentioned in passing that the types of *C. agilis* were immature. Actually, as shown above, they belonged to a different species. Bishop and Crosby (1923) synonymized the two names, but Roewer's *Die Weberknechte der Erde* (1923) had already been published, including *C. glaucopis* as a valid species, largely because a drawing of the palpus of *Caddo boopis* had been labelled as pertaining to *C. glaucopis*.

All of this remarkable confusion has been further compounded by the fact that although "males" have been repeatedly described and recorded (Roewer, 1923; Bishop, 1949, etc.), true males of this species were not found until very recently. The state of development of American opilionid taxonomy is indicated by the fact that no one has described the genitalia of some of the commonest species.

Description—Female from Coudersport, Pennsylvania: Length of body (Fig. 1), 3.0 mm; width of eye tubercle, 1.4 mm. Eye tubercle occupying nearly entire width of cephalothorax, deeply divided along median line by broad furrow; eyes circular in outline, somewhat protruding when seen from above. Free thoracic tergites separated from carapace by lightly impressed suture, from dorsum of abdomen by deeper suture running laterally and ventrally behind coxae IV. Dorsum of abdomen indistinctly segmented, cuticle soft, leathery. Dorsal surface without tubercles, spines, or prominent setae. Ventral surface as in Fig. 2. Labium small, moderately sclerotized, dark, vaguely divided into three anterior lobes. Endites of pedipalps with unsclerotized part posterior, three times size of sclerotized parts; sclerotized parts three times as long as wide, armed with row of stout black setae. Endites of first coxae not strongly sclerotized, slightly more than twice as long as wide, armed with row of setae. Coxae with rows of stout black setae, somewhat irregular on posterior coxae. Sternum subtriangular, apex anterior, posteriorly with row of three stout setae, covered by genital operculum. Segments of venter with scattered small setae. Palpus as in Fig. 3. Trochanter with a few setae on small prominences. Femur with three large, pointed tubercles bearing apical and sometimes subapical setae, distally with a large mesal setose lobe. Patella, tibia and tarsus heavily armed with stout setae, mostly on mesal surfaces. Claw large, movable, heavily sclerotized. Tarsus about twice length of tibia. Legs long, slender. Femora I-IV 1.3, 1.8, 1.3, 1.7 mm long respectively. Tibiae I-IV 1.8, 2.6, 1.6, 2.6 mm long respectively. Metatarsi with 1-6 false articulations; tarsi multiarticulate, claw single, not toothed. Ovipositor as in Fig. 4, seminal receptacles vestigial, sensilla setose lobes. Coloration: cephalothorax bright metallic silver, eye tubercle tinged dusky brown, eyes heavily ringed in black. Dorsum dark brown to purplish brown with median and lateral silver stripes; impression is one of silver background with parallel rows of brown spots. Venter off-white to silver, variable in specimens from the same population. Legs yellowish white proximally, darkening to medium brown on tibiae and metatarsi.

Notes—No genuine males of *Caddo agilis* have been described, and indeed, probably do not exist in most populations. A single real male was collected with numerous females, in 1956, by the late Wilton Ivie, near Jamison, Pennsylvania. Previous descriptions of males allude to slender females probably not as yet carrying eggs, or to juveniles. In all of the populations examined by me, the seminal receptacles of the females were virtually

vestigial, indicating that even if males sporadically appeared, the females probably could not be fertilized by them.

The male collected by Ivie was given to Herr Jürgen Gruber of the Vienna Natural History Museum. In 1970, Herr Gruber very kindly sent me a copy of his manuscript on the animal and Xerox copies of his illustrations. At this writing (June, 1973) his paper has not to my knowledge appeared. A full description of the male will be presented by Gruber, but for the time being, Gruber's drawings show that the pedipalp of the male differs from that of the female in having a single, quadrate femoral lobe in place of the three acute tubercles of the female and in having the tarsus set with very stout, black setae. The penis consists of a long shaft with a short, tubular glans and a dorsal (?) spinous process. Taking into account the complexity of the male genitalia of related forms, it seems likely that this organ is either not functional or represents a rather drastic simplification.

The rarity of males (one having been collected for literally hundred of females) forces the conclusion that *Caddo agilis* is usually parthenogenetic. This might also help to account for the lack of variability, even when Japanese specimens are compared to ones from eastern North America, if parthenogenesis became established before the animal reached its present wide distribution. *Caddo dentipalpis* (Koch and Berendt), a fossil from the Baltic Amber of Oligocene Age, does not differ in any important respects, according to the account of Crosby and Bishop (1923), from *C. agilis*. There is a strong possibility that they are really the same species, and this indicates a much wider previous distribution for *Caddo*.

Most mature specimens are taken in late summer and fall, and the species probably winters over in the egg stage or as very small young. Detailed collection notes are sparse, but specimens are usually found in very humid, densely shaded areas, such as ravines, and there is usually a coniferous element in the forest, most frequently hemlock. Specimens have also been taken from moss, from beneath logs and stones, from tree trunks and the outside walls of buildings. The southwesternmost record (Pickett Co., Tenn.) is from a cave. In North Carolina, I collected *C. agilis* on the slopes of Mt. Mitchell. *Caddo agilis* is a rapid runner; the body is held high, and the excellent vision makes individuals even harder to catch. The diet is unknown, but they are undoubtedly predators.

Distribution—New England and southern Canada; south, mostly in the mountains, to Virginia, North Carolina, and Tennessee; northwest through Kentucky (?) to Ohio (Map 1). CANADA: QUEBEC: St. Joseph d'Alma (Alma), 29 July 1934, C. Crosby and H. Zorsch, ♀; Bagotville, 26 July 1934, H. Zorsch, juvs. ONTARIO: Sandford, June 1906, no. coll., juv. UNITED STATES: VERMONT: *Washington Co.*, Marshfield, 4 July 1969, A. M. Chickering, ♀♀ (MCZ). MASSACHUSETTS: *Barnstable Co.*, Cape Cod, South Chatham, from oak-pine woods, 16-18 June 1971, H. and L. Levi, juvs. (MCZ). CONNECTICUT: *New Haven Co.*, Bethany Bog, 29 May 1963, W. Ivie, ♀ (ALE). NEW JERSEY: *Warren Co.*, Jenny Jump State Forest, 27 June 1966, F. Coyle, juv. (WAS). NEW YORK: *Suffolk Co.*, Montauk Point, 24 May 1924, N. Banks, juv.; Cold Spring Harbor, July 1932, no coll., juv.; *Leviw Co.*, Michigan Mills, 1 Sept. 1926, no coll., ♀♀; *Catteraugus Co.*, Rock City Park, Olean, 22 July 1962, W. Shear, ♀♀ (WAS); Alleghany State Park, 21 May 1957, R. L. Hoffman, juv. (RLH); *Albany Co.*, E. N. Huyck Preserve, Rensselaerville, 8 July 1948, S. Bishop, juv.; *Oneida Co.*, Boonville, 23 July 1931, no coll., ♀; *Herkimer Co.*, Big Moose Lake, 14 June 1931, S. Bishop, juv.; *Tompkins Co.*, Woodwardia Swamp, Freeville, 10 Aug. 1924, no coll., ♀; Ithaca, 2 May 1926, Seeley and Fletcher, juv.; *Franklin Co.*, Wawbeek, 19 July 1931, C. Crosby, juv.

Bishop (1948) reports the following New York localities: *Delaware Co.*, Delhi, May; *Niagara Co.*, Olcott, Sept.; *Seneca Co.*, Covert, July. PENNSYLVANIA: *Potter Co.*, 4 mi east of Coudersport, on buildings and tree trunks in dense woods, 10 June 1963, 2 Aug. 1970, W. Shear, ♀♀ (WAS); *Bucks Co.*, Neshaminy Cr. near Jamison, 23 May 1965, W. Ivie, ♀♀ (this collection also contained the male Ivie sent to Gruber). MICHIGAN: *Cheboygan Co.*, Gorge, 2 Aug. 1967, A. Edgar, ♀♀ (ALE). OHIO: *Ashland Co.*, Mohican State Forest, 31 May 1962, ♀♀ juvs., J. Beatty (JAB), R. MacArtor (WAS), A. Weaver (AAW); *Hocking Co.*, Cantwell Cliffs State Park, 30 May 1927, M. Walker, ♀♀; *Wayne Co.*, Ohio State Agricultural Experiment Station, Wooster, 4 Sept. 1963, J. Beatty, juv. (JAB); Funks Hollow, R14W, T15N, Sec. 23, A. Weaver, ♀ (AAW). WEST VIRGINIA: *Mercer Co.*, immediate vicinity of Athens, 1966-1969, W. Shear, numerous collections, ♀♀ (WAS); Cove Branch Hollow, 3 mi northwest of Athens, 14 May 1967, W. Shear, juv. (WAS); Brush Creek Falls, *Rhododendron* and hemlock litter, 9 May 1967, juv. (WAS); *Pocahontas Co.*, Hills Creek Falls Scenic Area, Monongahelia National Forest, 8 July 1967, W. Shear, ♀♀ (WAS); VIRGINIA: *Augusta Co.*, Ramsey's Draft, 18 mi north of Staunton, virgin cove forest dominated by hemlock, 19 June 1969, W. Shear, ♀♀ (WAS); *Carroll Co.*, Fancy Gap, pine forest, 27 Apr. 1969, H. Levi, juv. (MCZ); *Grayson Co.*, south slope of Mt. Rogers, ca. 4500' 20 Oct. 1963, R. Hoffman, ♀ (RLH); *Craig Co.*, Clover Hollow Mtn., 6 June 1957, R. Hoffman, juv. (RLH); NORTH CAROLINA: *Yancey Co.*, slopes of Mt. Mitchell above Black Mountain Campground near Busick, 14 July 1969, W. Shear, ♀♀ (WAS); TENNESSEE: *Pickett Co.*, Pickett State Park, Hazard Cave, 25 June 1967, C. R. McGhee, ♀♀ (CRM). Bishop (1948) reports: Princeton, N.J., Washington, D.C., Mt. Katahdin, Maine, Swannanoa Valley, North Carolina.

***Caddo pepperella*, new species**

Fig. 5, Map 2

Types—Female holotype from Pepperell, Middlesex Co., Massachusetts, collected July 1964 by H. W. Levi, deposited in MCZ. The specific epithet is derived from the type locality.

Diagnosis—Differs from *C. agilis* in color, size, and form of the ovipositor. *Caddo agilis* is marked with metallic silver, while *C. pepperella* is an even, dark brown dorsally. *Caddo pepperella* is about 1.6-1.9 mm long, and *C. agilis* is from 2.8 to 3.2 mm long. The apical sensory lobes of the ovipositor of *C. pepperella* are much smaller than those of *C. agilis*.

Description of female holotype—Length of body, 1.7 mm; width of eye tubercle, 0.72 mm. Structure essentially as in *Caddo agilis*. Legs short, somewhat stouter than in *C. agilis*; femora I-IV 0.52, 0.91, 0.65, 0.78 mm long respectively, tibia I-IV 0.78, 1.17, 0.78, 1.04 mm long respectively. Ovipositor with 7-9 sclerotized rings, seminal receptacles completely lacking, apical sensory organ (Fig. 5) reduced in size. Coloration: eye tubercle and cephalothorax white, dorsum of abdomen medium to dark brown, with two narrow, parallel white stripes on posterior part. Venter and legs yellowish white.

Males unknown, probably do not exist.

Notes—This species has gone unrecognized for many years, even making up a part of the collection from which Banks described *C. agilis*, and, as mentioned above, his concept of that species was apparently based primarily on *C. pepperella*.

The problem of the relationship of this species to *Caddo agilis* is most interesting. I might postulate, in the absence of any real evidence, that *C. pepperella* originated from *C. agilis* by neoteny in one parthenogenetic population sometime during the Pleistocene,

probably on the glacial margins. Neoteny would shorten the life cycle of the population in the severe periglacial climate, and thus be a definite selective advantage. During the final retreat of the glaciers, such a form would be in an excellent position to invade newly exposed glaciated territory, but might be extinguished in the south by competition from surviving populations of the ancestral form moving north into the new forest. This view is supported by the present limited distribution of *C. pepperella*, in a corner of the glaciated territory of southern New England, southeastern New York and Long Island. Throughout most of this range, both species of Caddo are sympatric, and at least on Long Island, they are syntopic.

I am aware that naming this form "opens a can of worms" in that the status of parthenogenetic or neotenic isolates is controversial. But since *C. pepperella* is a recognizable, distinct genetic entity, I feel it is nameworthy.

Distribution—(Map 2) CONNECTICUT: *Litchfield Co.*, Mohawk Mtn. 21 Aug. 1956, R. L. Hoffman, ♀ (RLH). MASSACHUSETTS: *Middlesex Co.*, Pepperell July 1964, H. and L. Levi, ♀ (MCZ). NEW YORK: *Albany Co.*, E. N. Huyck Preserve, 21 July 1956, ♀♀ 25 Aug. 1954, ♀♀ R. L. Hoffman, (RLH); *Suffolk Co.* Brookhaven National Laboratory, from *Sphagnum* spp., 11-17 July 1960, G. Klee, ♀ (GK), "Long Island (type locality of *C. agilis*)" no collector or date, ♀♀ (MCZ).

Subfamily Acropsopilioninae Roewer

Acropsopilionidae Roewer, 1923, *Die Weberknechte der Erde*, p. 678; Lawrence, 1931, Ann. South Africa Mus. 29(2):469-470; Ringuelet, 1959, Rev. Mus. Arg. Cien. Nat. "Bernardo Rivadavia" 5(2)206-207.

Type genus—*Acropsopilio* Silvestri 1904, by original designation.

Diagnosis—Generally more troguloid in appearance; the palpal tibia is longer than the tarsus, and in some species a claw is absent in females, ovipositor with at most three annuli; male genitalia, when known, complex (Figs. 19, 25-27), sometimes twisted.

Description—With the characters of the family, and in addition: palpus with patella and tibia armed with spine-bearing tubercles, armature of femur various, tarsus shorter than tibia, with small, fused claw, or without a claw. Basal article of chelicera not armed ventrally. Ovipositor short, with at most three annuli, sensilla complex branched setae. Penis (when males are known) complex, composed of several plates and articulated spines, bearing a membranous glans and sometimes subject to 180 degrees of torsion.

Distribution—Great Lakes region and northern Appalachian Mts. in the United States and Canada; Chiapas, Mexico; southern South America, Australia; Tasmania and New Zealand; South Africa.

Included genera—*Acropsopilio* Silvestri 1904; *Cadella* Hirst 1925; *Austropsopilio* Forster 1955. See the key given under the discussion of the family.

Genus *Acropsopilio* Silvestri

Acropsopilio Silvestri, 1904, Redia 2:254-255. Canals 1932, Physis 11:150; Mello-Leitao, 1938, Ann. Acad. Bras. Sci. 10:317; Roewer, 1923, *Die Weberknechte der Erde*, p. 678; Ringuelet, 1959, Rev. Mus. Arg. Cien. Nat. "Bernardo Rivadavia" 5(2)207; 1962, Physis 23:77-80. *Zeopsopilio* Forster, 1948, Trans. Royal Soc. New Zealand 77(1):140; NEW SUBJECTIVE SYNONYMY.

Type species—*A. chilensis* Silvestri by monotypy and original designation. Type species of *Zeopsopilio*, *Z. neozealandiae* Forster, by monotypy.

Diagnosis—*Acropsopilio* is nowhere sympatric with other members of the subfamily. A comparison of the figures given here will suffice to separate members of the genus *Cadella* and *Austropsopilio* species.

Description—With the characters of the subfamily, and in addition: palpus with patella armed with two or three spine-bearing tubercles femur with two basal one ventromedial and one distal spined tubercle, also with a lobe bearing macrosetae near the dorsomedial distal end of femur, or group of stout macrosetae in that position, patella with one or two ventral spined tubercles, tibia and tarsus with ventral rows of macrosetae on low tubercles, claw stout, not movable. Ovipositor (when known) with three chitinized rings, or such rings reduced and indicated by rows of setae, seminal receptacles (in *A. boopis*) absent or vestigial, apical sensilla branched setae. Males unknown.

Distribution—Great Lakes region of U.S. and Canada, and northernmost Appalachian Mountains; mountains of Chiapas, Mexico; southern South America (parts of Argentina, Chile, and Brazil); New Zealand.

KEY TO SPECIES OF *ACROPSOPILIO*

- 1a. Femur of palpus with distal medial lobe bearing setae (Fig. 7); United States and Canada *A. boopis*
 1b. Femur of palpus without such a lobe; with or without a group of setae in its place 2
 2a.(1b). Femur of palpus without a group of distal setae (fig. 11); Chiapas Mexico *A. chomulae*
 2b. Femur with distal group of setae 3
 3a(2b). Trochanter of palpus with two spined tubercles (Fig. 15); New Zealand *A. neozealandiae*
 3b. Trochanter of palpus with three spined tubercles (Fig. 13); Chile, Argentina, Brazil *A. chilensis*

Of the four species considered as valid, the two most closely related are *A. chomulae* and *A. chilensis*, while *A. neozealandiae* is more distantly related to the first two, and *A. boopis* distinct from the other species.

Acropsopilio boopis (Crosby), new combination

Figs. 6-9, Map 1

Caddo boopis Crosby, 1904, J. New York Entomol. Soc. 12(4):255, Fig. 4, ♀; Roewer, 1912, Abh. Geb. Naturwiss. 20(1):35-36; 1923, *Die Weberknechte der Erde* p. 714, Fig. 890, ♀; Bishop, 1949, Proc. Rochester Acad. Sci. 9(3):176-177, Figs. 15-18, ♀.

Types—A female specimen in the American Museum of Natural History (examined) is labelled as a lectotype, but the designator is not known. Locality data: 'Ithaca, N.Y. VIII-1904.' In the original description, the palpus of *A. boopis* was illustrated but labelled as being that of *Caddo glaucopis*, a synonym of *C. agilis*. Roewer (1923) perpetuated the error in *Die Weberknechte der Erde*. Bishop (1949) claims to figure a male, but the specimen was probably not dissected, and no genuine males are known from the 25-30 specimens of *A. boopis* in collections.



Fig. 5.—Anatomy of *Caddo pepperella*, right furca of ovipositor, ventral view.

Figs. 6-9.—Anatomy of *Acropsopilio boopis*: 6, body of female, lateral view; 7, anterior ventral part of female, ventral view; 8, left palpus of female, mesal view; enlargement: claw and glandular setae; 9, ovipositor, ventral view; enlargement: seft sensillum. Scale line = 0.65 mm for Fig. 6, 0.25 mm for Figs. 7, 8. Figs. 5, 9, not to scale, Fig. 9 400X, Fig. 5 900X.

Description—Drawn from female specimen from bog 4 mi east of Columbiaville, Michigan, in Field Museum of Natural History, Chicago. Length of body (Fig. 6), 0.91 mm; width of eye tubercle, 0.44 mm. Eye tubercle occupying entire width and length of cephalothorax when seen from above, deeply impressed along median line; eyes circular

in outline, protruding when seen from above. Free thoracic tergites not distinct from cephalothorax, set off from abdomen by suture. Body soft, leathery, not strongly sclerotized. Dorsal surface without spines or tubercles. Labrum prominent, pointed. Labium rounded, small, 2-lobed. Only endites of pedipalp coxae show sclerotized part; coxae and endites (Fig. 7) about as in *Caddo agilis*. Spiracles very small and indistinct, covered in some specimens by fourth coxae. Palpus as in Fig. 8; trochanter with two basally fused ventral spined tubercles; femur with two tubercles at base, one near middle of segment, one distal; tubercle bearing macrosetae present near distal end; patella with three vague rows of median macrosetae, two ventral spined tubercles. Tibia with area of macrosetae more dorsal, with three ventral spined tubercles; tarsus about 80% length of tibia, heavily set with macrosetae; claw (Fig. 8) stout, not movable. Legs relatively short, fourth leg much the longest (all specimens studied lacked legs II). Femora I, III, IV 0.30, 0.40, 0.73 mm long respectively, tibiae I, III, IV 0.34, 0.38, 0.43 mm long respectively. Ovipositor as in Fig. 9, with three chitinous rings, distal two with single rows of setae, apex bifurcate, with three vague rows of setae; sensilla flattened, complexly branched setae (Fig. 9). Coloration; eye tubercle and cephalothorax off-white, remainder of body medium brown, dorsum unmarked. Venter slightly lighter, speckled black. Pedipalps and legs dark brown.

Notes—No males are known; the species is probably parthenogenetic. *Acroposopilio boopis* may be rare, or it may be that the small size of the species makes it difficult to collect. Ecological data on labels is sparse, but the species is usually taken by sifting or in Berlese samples from *Sphagnum* moss or from pine needles. In Quebec and Indiana, it has been sifted from leaf litter. Most of the labels (see below) refer to lakes, ponds and streams, so *A. boopis* may have an affinity for littoral situations. Curiously, all records are from glaciated territory.

Distribution—In addition to Map 1, detailed records are given here to establish for the first time the range of the species: CANADA: QUEBEC: Latériere, Laurentide Park, from leaf litter, 29 Aug. 1956, H. Dybas, ♀, juv. (CNHM). ONTARIO: Island 1024, Lake Temagami, 15-25 Aug. 1946, C. Goodnight and T. Kuarata, ♀♀. UNITED STATES: CONNECTICUT: *Litchfield Co.*, Salisbury, Wachocastinook Creek, 29 June 1930, no coll., 3 ♀♀. INDIANA: *Porter Co.*, Dune Acres leaf litter, 16 Oct. 1948, H. Dybas, ♀ (CNHM). MAINE: *Aroostook Co.*, Presque Isle, 26 Aug. 1925, no. coll. ♀. MICHIGAN: *Lapeer Co.*, bog 4 mi east of Columbiaville, from nonsphagnum mosses 25 Aug. 1963, Suter and Graves, 3 ♀♀, 3 juvs. (CNHM); *Montmorency Co.*, T31N, R6E, Sec. 3, Berlese of moss from jack pine plantation, 10-20 Aug. 1967, G. V. Manley, ♀ (GK). NEW YORK: *Saratoga Co.*, Ballston Lake, 5 Aug. 1923, A. Wolf, ♀; *Franklin Co.*, Wawbeek 9 Aug. 1931, N. W. Davis, ♀; *Fulton Co.*, East Caroga Lake, 14 July 1934, no. coll. ♀; *Oswego Co.*, North Pond, 27 July 1935, C. Crosby, ♀; *Albany Co.*, Uly Creek near Voorheesville, 30 Aug. 1923, D. Leonard, ♀; *Tompkins Co.*, Six Mile Creek, Ithaca, 24 Apr. 1926, Seeley and Fletcher, ♀; *Queens Co.*, Flushing, Spring 1938, K. Cooper, ♀.

NOTES ON CADDID SPECIES FROM OTHER REGIONS

Special collecting will be required for a worldwide revisionary treatment of the family, but in the course of this study, I have compiled the following notes on some of the other species.

Acropsopilio chomulae (Goodnight and Goodnight)

Figs. 10, 11

Caddo chomulae Goodnight and Goodnight, 1948, J. New York Entomol. Soc. 55:201, Figs. 1, 2 juvenile. *Acropsopilio "chommulae"* [sic], Ringuélet 1962, Physis 23(64):79.

Type—Juvenile from San Cristobal de las Casas Chiapas, Mexico, collected 22 July 1947 by M. Goodnight, in AMNH, examined.

The detailed description of the juvenile holotype by Goodnight and Goodnight (1948) needs no amplification, but I here present a lateral view of the holotype (Fig. 10) and a mesal view of the trochanter and femur of the right palpus (Fig. 11). In 1950, Goodnight and Goodnight, reporting on a collecting trip to Chiapas, stated, "The interesting species *Caddo chomulae* Goodnight (sic) was found in large numbers." (Goodnight and Goodnight, 1950, p. 143). However, no specimens other than the holotype were in the American Museum, nor could any be located in the Goodnights' collection (C. Goodnight, in litt.). Mature specimens are needed to complete the description, and in particular, males, if they exist, should be searched for.

Ringuélet (1962) first placed *A. chomulae* in the proper genus, but did not mention *A. boopis*.

Acropsopilio chilensis Silvestri

Figs. 12, 13

Acropsopilio chilensis Silvestri, 1904, Redia 2:256, Figs. 35-48, ♀; Roewer, 1923, *Die Weberknechte der Erde*, p. 678, Figs. 846-848, ♀ (copies of Silvestri's figures); Canals, 1932, Physis 11:151, 2 figures unnumbered, ♀ (copies of Silvestri's figures); Ringuélet, 1959, Rev. Mus. Arg. Cien. Nat. "Bernardo Rivadavia" 5(2):207, Fig. 14, (supposed to be a male, but this cannot be verified; no figures of the genitalia given). *Acropsopilio chilensis* var. *ogloblini* Canals, 1932, Physis 11:152, 5 figures, sex not indicated. *Acropsopilio ogloblini*, Ringuélet, 1959, Rev. Mus. Arg. Cien. Nat. "Bernardo Rivadavia" 5(2):209, no figures; NEW SYNONYMY.

Type—Female holotype from Pitrufquén, Chile, whereabouts unknown.

Acropsopilio chilensis was described from the southern Andes, near Pitrufquén, Chile, and has also been collected at Laguna Frías, Rio Negro, Argentina (Ringuélet, 1959). Canals (1932) described *A. ogloblini* as a "variety" from Loreto, Misiones, Argentina, and Ringuélet (1959) raised the name to species status but at the same time indicating that there were no significant differences between the two, and that *ogloblini* might be at most a subspecies. In a subsequent paper, Ringuélet (1962) used the name *A. ogloblini* to indicate a separate species from *A. chilensis*, without further comment, except to report a population he regarded as *A. ogloblini* from the subtropical jungle of Punta Lara, on the Río de la Plata, Argentina, where it was collected in a Berlese sample of mosses. No figures were presented. Since no one has ever demonstrated any significant degree of difference between the three widely separated populations, and as several other caddid species have wide, disjunct distributions, I think *A. ogloblini* should be relegated to the synonymy of *A. chilensis*.

According to Ringuélet (1962), the ovipositor of his specimens is short and not ringed, and he considers this as a troguloid ("Dyspnoi-like") character. Undoubtedly, this is really of little importance and is an adaptation to small size, the ovipositor is definitely ringed in *A. boopis*, and rings of setae indicating such structures occur in *A. neozealandiae* and in two species of *Caddella*.

I illustrate here an immature specimen (Figs. 12, 13) from Pinares, Province Concepción, Chile, collected Oct. 23, 1971, and forwarded to me through the kindness of Dr. T. Cekalovic of the Universidad de Concepción, Chile. Dr. Cekalovic is preparing a detailed treatment of South American *Acropsopilio* populations from new material. When properly searched for, *A. chilensis* may actually prove to be a rather common species in southern South America.

Acropsopilio neozealandiae (Forster)

Figs. 14, 15

Zeopsopilio neozealandiae Forster, 1948, Trans. Royal Soc. New Zealand 77(1):140, Figs. 1-4, sex not indicated. NEW COMBINATION.

Types—Female cotypes from Johnson's Park, Fielding, collected 25 March 1943, by R. Forster, in Dominion Museum, Wellington, examined.

Forster (in litt.) states that he has collected males of this species, but none could be located. The cotypes are both females; Forster (1948) makes no reference to the sex of his specimens in the original description, which is very complete as regards nonsexual characters. The ovipositor *apparently* lacks seminal receptacles; the specimen I dissected was in poor condition and almost transparent. The outer form of the ovipositor is much as it is in *A. boopis*, but definite chitinous rings are lacking. However, the setae of the ovipositor are arranged in rows that indicated a derivation from a three-ringed condition, and the apical sensilla are large, bifurcate setae.

According to Forster (1948), the species occurs under logs, in moss and leaf litter, and in other similar habitats over most of New Zealand, without significant variation.

The figures provided here of the body (Fig. 14) and palpus (Fig. 15) will demonstrate the above synonymy.

Genus *Austropsopilio* Forster

Austropsopilio Forster, 1955, Aust. J. Zool. 3(3):357. Type species, *A. novahollandiae* Forster 1955, by original designation and monotypy. *Tasmanopilio* Hickman, 1957, Papers Proc. Royal Soc. Tasmania 91:65. Type species, *T. fuscus* Hickman 1957, by original designation; NEW SUBJECTIVE SYNONYMY.

The genus *Tasmanopilio* was distinguished from *Austropsopilio* solely on the basis of the elongate eye tubercle (Fig. 16) in the latter genus. Since the foundation of the generic category is the grouping of related species, and since no differences of the level of significance separating other acropsopilionine genera are to be found between species of the two Australian nominate genera, no purpose is served by having two generic names. Unfortunately, I was unable to obtain material of either of the Tasmanian species for detailed study.

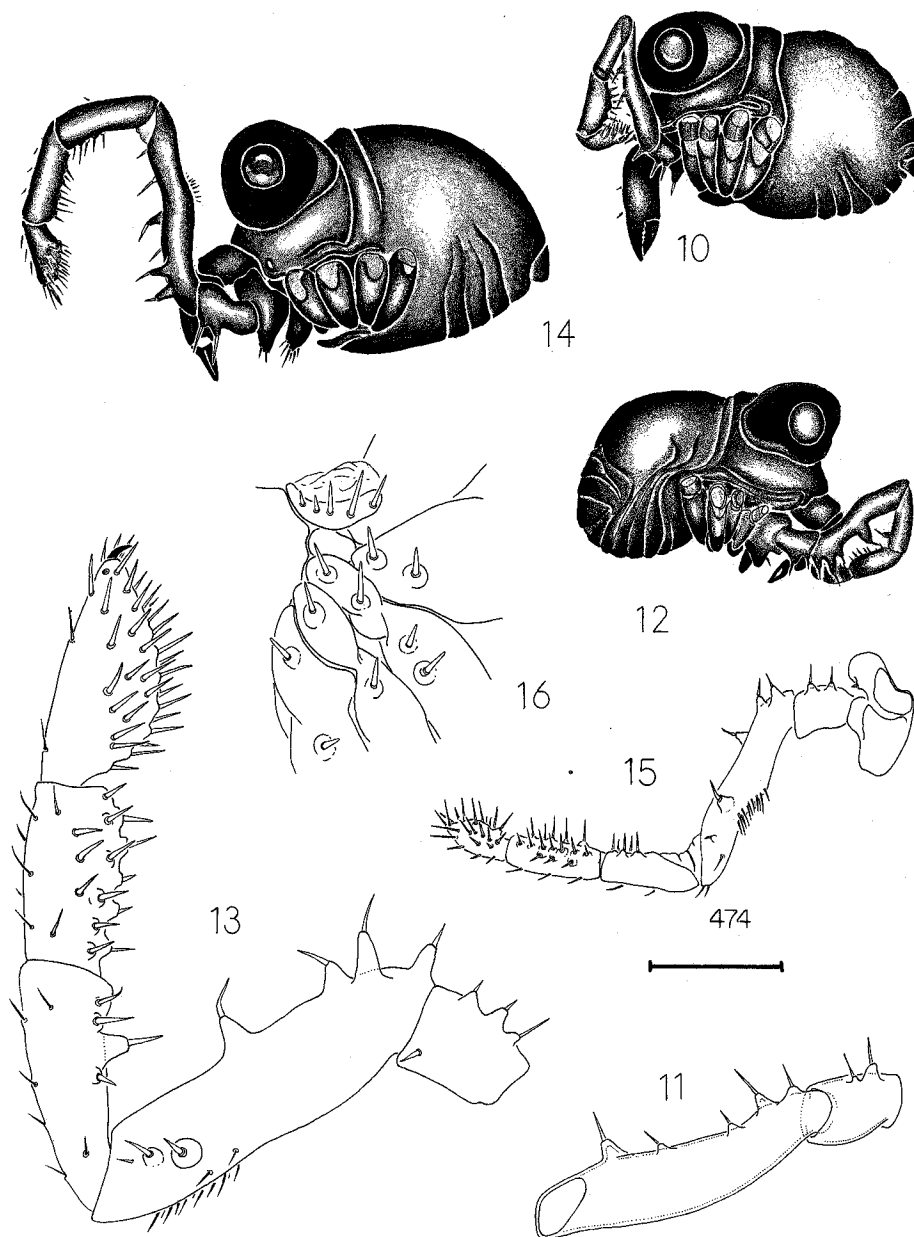
Austropsopilio novahollandiae Forster

Figs. 16-18

Austropsopilio novahollandiae Forster, 1955, Aust. J. Zool. 3(3):358-359, Figs. 8-11, juvenile.

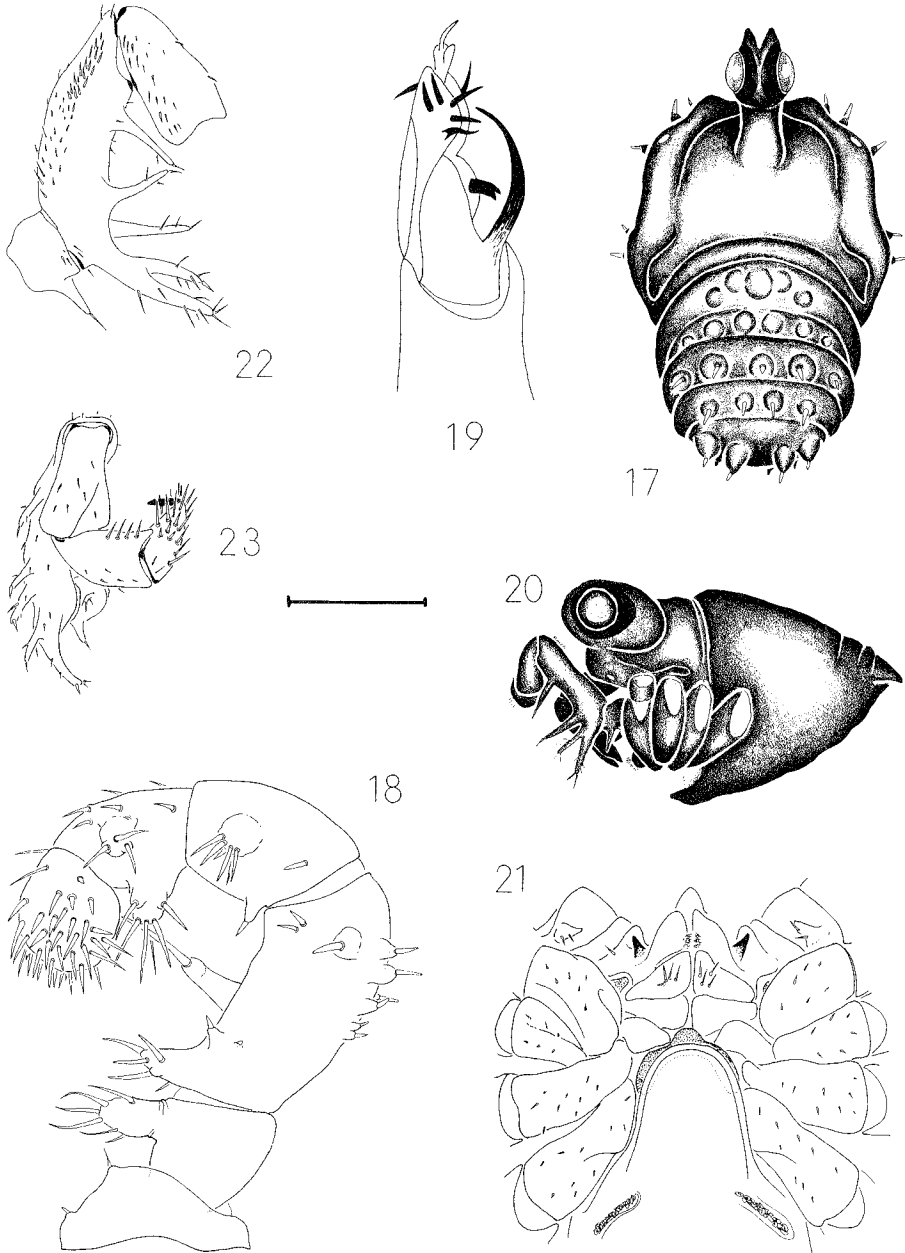
Types—Juvenile holotype from Mt. Hobwee, Lamington Plateau, south Queensland, collected from leafmold, 27 August 1953, by T. W. Woodward, in Queensland Museum, examined.

This species is unique in the elongate eye tubercle (Fig. 16), which projects forward from the anterior edge of the cephalothorax; the eyes are much smaller than in other



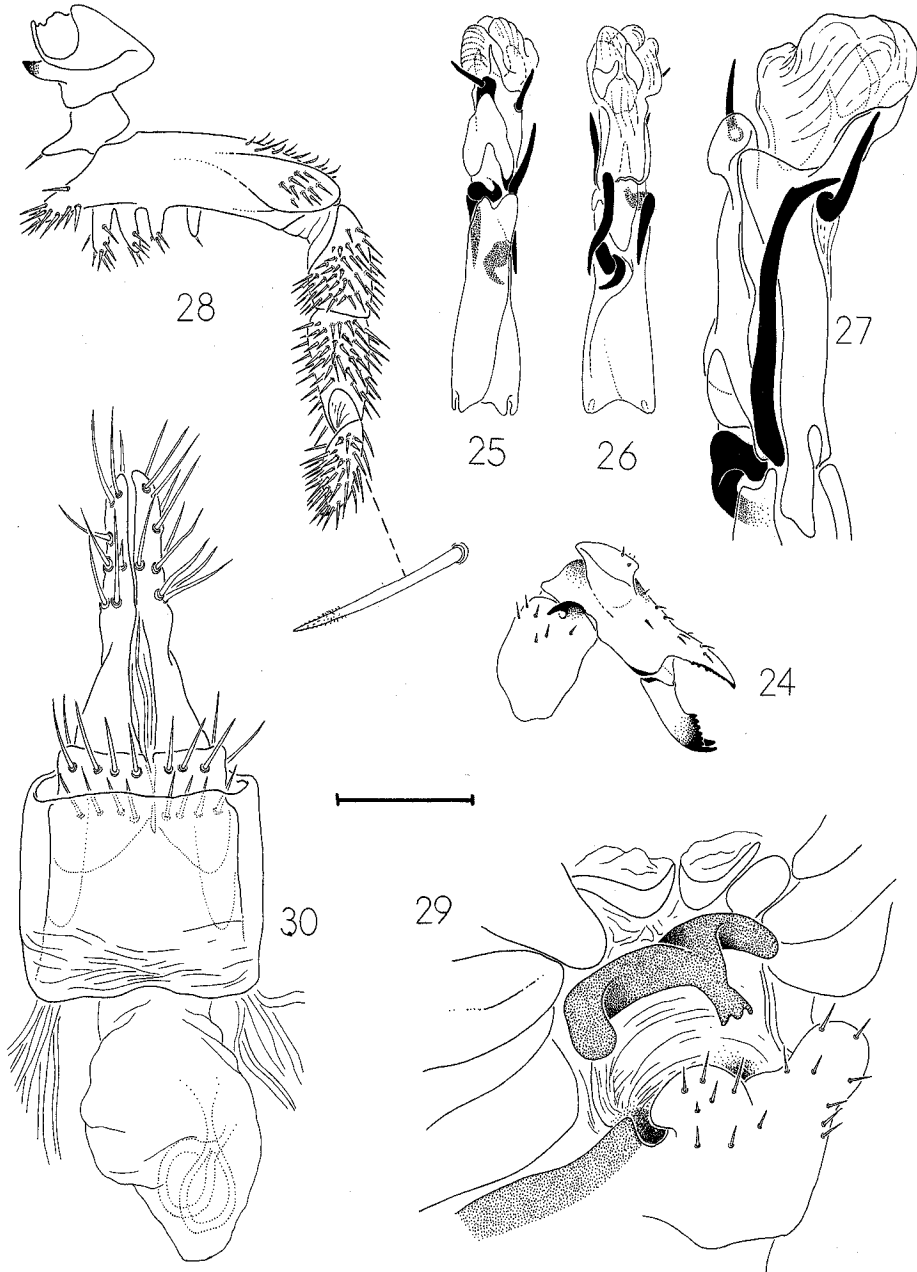
Figs. 10-16.—Anatomy of *Acropsopilio* and *Austropsopilio* species: 10, *A. chomulae*, body of juvenile, lateral view; 11, *A. chomulae*, trochanter and femur of left palpus of juvenile, mesal view; 12, *A. chilensis*, body of juvenile, lateral view; 13, *A. chilensis*, left palpus of juvenile, mesal view; 14, *A. neozealandiae*, body of female, lateral view; 15, *A. neozealandiae*, left palpus of female, mesal view; 16, *Austropsopilio novahollandiae*, left coxal endites of juvenile, ventral view. Scale line = 0.5 mm for Figs. 10, 12, 14, 0.35 mm for Fig. 15, 0.20 mm for Figs. 11, 16, 0.15 mm for Fig. 13.

caddis. The dorsal surface of the body (Fig. 16) is ornamented with rows of stout setae on tubercles. Ventrally, the coxal endites (Fig. 17), which are more prominent than in other members of the family, are likewise studded with stout setae. The species *A.*



Figs. 17-23.—Anatomy of *Austropsopilio* and *Caddella* spp: 17, *A. novahollandiae*, body of juvenile, dorsal view; 18, *A. novahollandiae*, right palpus of juvenile, mesal view; 19, *A. fuscus*, penis (after Hickman); 20, *C. capensis*, body of male, lateral view; 21, *C. capensis*, venter of cephalothorax of male, ventral view; 22, *C. capensis*, left palpus of male, lateral view; 23, *C. capensis*, left palpus of male, anterior view. Scale line = 1.00 mm for Fig. 20, 0.5 mm for Figs. 17, 21-23, 0.25 mm for Fig. 18.

cygneus Hickman, (Hickman, 1957) probably represents mature material of *A novahollandiae*, but the species synonymy should be confirmed by an examination of the type of *A. cygneus*, which I was unable to obtain.



Figs. 24-27.—Anatomy of *Caddella capensis*: 24, left chelicera of male, mesal view; 25, penis, dorsal view; 26, penis, ventral view; 27, penis, lateral view.

Figs. 28-30.—Anatomy of *Caddella africana*: 28, left palpus of female, mesal view; enlargement: glandular seta from tarsus; 29, sternum and genital operculum of female, oblique view; 30, ovipositor, dorsal view. Scale line = 0.5 mm for Figs. 24, 28, 0.20 mm for Fig. 29, 0.10 mm for Fig. 30, Figs. 25-27 not to scale, 400X.

Austropsopilio fuscus (Hickman), originally described as the type of *Tasmanopilio*, would appear from Hickman's (1957) illustrations to be somewhat intermediate in form. The eye tubercle projects slightly forward, the eyes are somewhat smaller than usual, and the palpi are of the *Austropsopilio* type. The dorsal surface lacks armed tubercles. Males and females of *A. fuscus* have been described, and there is some sexual dimorphism, as the palpus of the female lacks a claw, while that of the male is somewhat less robust and has a stout black claw. The penis (Fig. 19, redrawn from Hickman, 1957) is enigmatic, but could be construed as being intermediate between the complex organ of species of *Caddella* and the simple one of *Caddo agilis*. A third species, *A. megalops* (Hickman), is known only from females (Hickman, 1957).

Genus *Caddella* Hirst

Caddella Hirst, 1925, Proc. Zool. Soc. London 1925:1276. Type species, *C. capensis*, by monotypy. Kauri, 1950-1952, S. Afr. Anim. Life 8:137. *Oonopsopilio* Lawrence, 1931, Ann. S. Afr. Mus. 29(2):470. Type species, *A. africanus*, by monotypy. *Caddella*, Lawrence, 1934, Ann. S. Afr. Mus. 30.

Lawrence (1934) recognized the synonymy of his generic name *Oonopsopilio* with *Caddella*. The genus itself forms a fairly compact group most closely related to species of *Austropsopilio*, and showing about the same range of species types. Three species have been described from South Africa and are discussed individually below. *Caddella* species are large, about the size of *Caddo agilis*.

Caddella capensis Hirst

Figs. 20-27

Caddella capensis Hirst, 1925, Proc. Zool. Soc. London 1925:1276-1277, Figs. 5A-C, ♂; Kauri, 1961, S. Afr. Anim. Life 8:137-138, Figs. 77-78, ♀.

Types—Male holotype collected by J. Hewitt, at Port Alfred, South Africa, in the British Museum (Natural History). I examined it through the characteristic generosity of the late Mr. D. Clark.

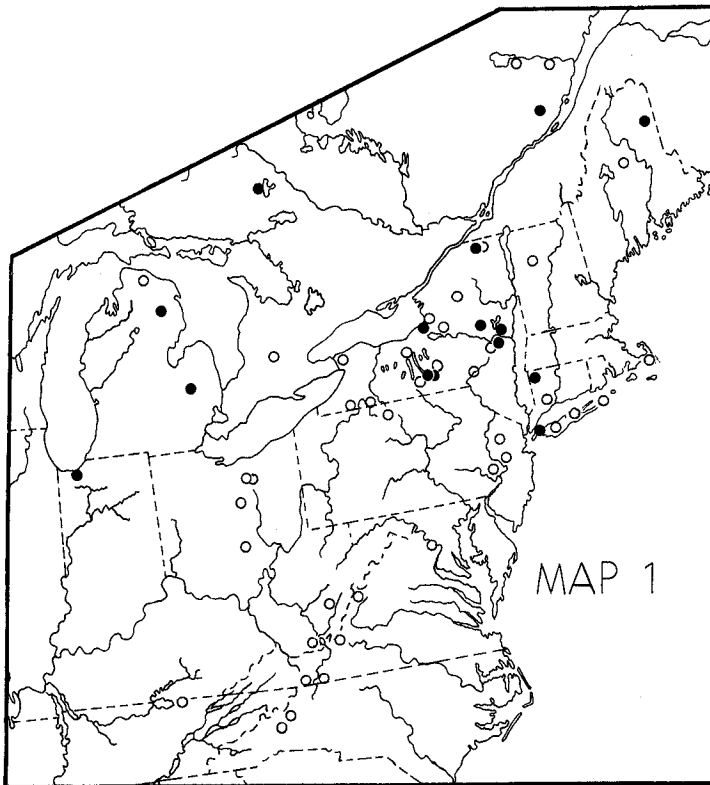
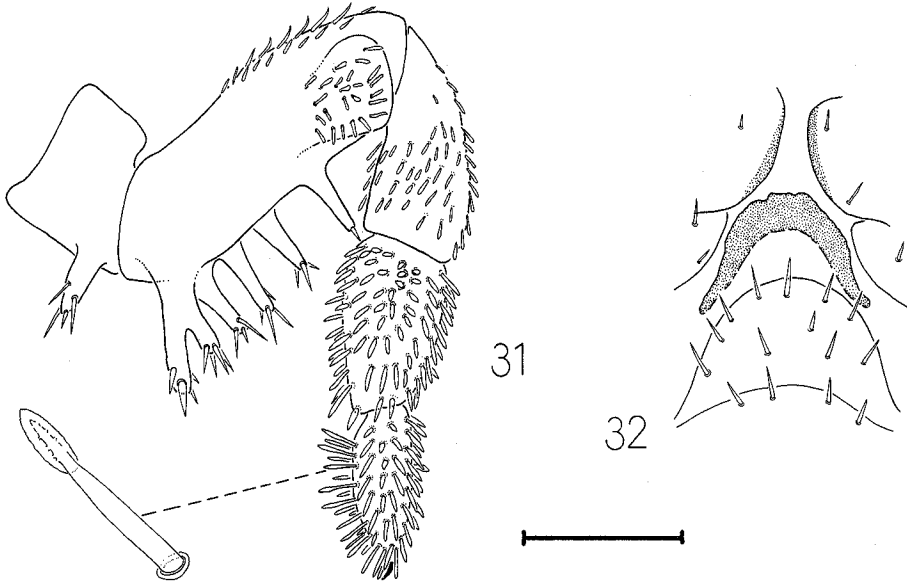
Kauri (1961) reported a female specimen from the Tzitzikama Forest, Stormsrivierpiek. I was unable to obtain this specimen. I illustrate here the body (Fig. 20), pedipalp (Figs. 22, 23) and chelicera (Fig. 24) of the male holotype. Of particular interest is the mesal sclerotized hook on the basal article of the chelicera. The relationship of this structure to the ventral spine of the same article in *Caddo agilis* is not known. The anvil-like process of the distal article is not glandular.

The penis of the male (Figs. 25-27) is unique in the Opiliones, but shows some relationship with that of *Austropsopilio fuscus* (Fig. 19), as illustrated by Hickman (1957), which also could conceivably be simplified to the form found in *Caddo agilis*. There appear to be four basic plates, two proximal and two distal, fitted with heavy, curved spines. The glans is membranous, and the seminal duct could not be traced with certainty. The relative positions of the plates and spines indicate that the penis has, at some time in its ontogeny or phylogeny, undergone 180 degrees of torsion.

Caddella africana (Lawrence)

Figs. 28-30

Oonopsopilio africanus Lawrence, 1931, Ann. S. Afr. Mus. 29(2):470-472, Figs. 66A-E, sex not indicated. *Caddella africana*, Lawrence, 1934, Ann. S. Afr. Mus. 30:584; Kauri 1961, S. Afr. Anim. Life 8:139-140, Figs. 76-78, ♂.



Figs. 31-32.—Anatomy of *Caddella spatulipalpis*: 31, left palp of female, mesal view; enlargement: glandular seta from tarsus; 32, sternum and genital operculum of female, ventral view. Scale line = 0.5 mm for Fig. 31. Fig. 32 not to scale, 250X.

Map 1.—Northeastern United States and southeastern Canada, showing distribution of *Caddo agilis* (circles) and *Acropsopilio boopis* (dots).

Type—Female holotype from Ladismith, Cape Province, South Africa, in South African Museum (examined).

The palpus differs from that of *C. capensis*, and resembles that of *C. spatulipalpus*, in having rounded setose lobes rather than spined tubercles. The coxa, as in *capensis*, has a sharp basal thorn. The body form is typical of *Caddella*. The penis is illustrated by Kauri (1950-1951), and is much like that of *C. capensis*. The ovipositor (Fig. 30) is likewise typical, with obvious seminal receptacles. Most peculiar is the interlocking apparatus involving the sternum and the genital operculum of the female (Fig. 29). Kauri (1961), in describing the female of *C. capensis*, mentions no such structure, and it is not present in females of *C. spatulipalpus*.

The species is known from a number of localities in South Africa, generally to the west of the range of *C. capensis*.

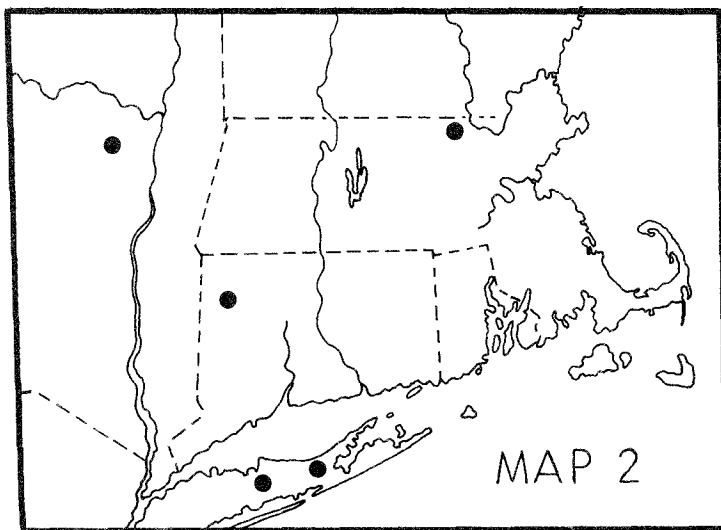
Caddella spatulipalpis Lawrence

Figs. 31-32

Caddella spatulipalpis Lawrence, 1934, Ann. S. Afr. Mus. 30:582-584, Fig. 18, ♀; Kauri, 1961, S. Afr. Anim. Life 8:140-141, no. figs.

This species is known only from the type collection from Jonkershoek, Cape Province, South Africa, and is closely related to *C. africana*, differing mostly in the details of the palpus (Fig. 31). Also, the sternum and genital operculum of the female of *C. spatulipalpis* (Fig. 32) are not modified as in *C. africana*. Males have not been collected. The type is in the South African Museum, Cape Town (examined).

Map 2.—Southern New England, showing distribution of *Caddo pepperella* (dots).



ACKNOWLEDGEMENTS

I thank the following museums and their respective curators for the loan of types and other materials: American Museum of Natural History, New York (Dr. J. A. L. Cooke); Chicago Natural History Museum, Chicago (Mr. H. Dybas and Dr. J. Kethley); Museum of Comparative Zoology, Cambridge (Dr. H. W. Levi); British Museum (Natural History), London (Mr. D. Clark); Entomology Museum of Michigan State University, East Lansing

(Dr. R. Fisher); New Zealand Dominion Museum, Wellington (Dr. R. Ordish); South African Museum of Natural History, Cape Town (Dr. A. J. Hesse); Queensland Museum, Brisbane (Dr. R. Monroe); Senckenburg Museum, Hamburg (Dr. O. Kraus); Natal Museum, Pietermaritzburg (Dr. B. Lamoral).

The following individuals loaned material from their private collections, or provided information and advice: Dr. Arlan Edgar, Alma Michigan; Dr. Richard Hoffman, Radford, Virginia; Mr. George Klee, East Lansing, Michigan; Mr. Charles McGhee, Murfreesboro, Tennessee; Dr. Joseph A. Beatty, Carbondale, Illinois; Dr. Andrew A. Weaver, Wooster, Ohio; Dr. R. Lawrence, Grahamstown, South Africa; Dr. R. Forster, Dunedin, New Zealand; Dr. T. Cekalovic, Concepción, Chile; Dr. R. Ringuet, Buenos Aires, Argentina; Dr. R. Capocasale, Concepción, Uruguay; Dr. V. V. Hickman, Hobart, Tasmania.

Staff members of the Yen Ching Library at Harvard University provided translations of Japanese articles, and Professor Margot Ormes, Hollins College, Roanoke, Virginia, translated several articles from Spanish.

I especially thank Jürgen Gruber, Natural History Museum, Vienna, Austria, for sending me a copy of his unpublished manuscript and illustrations on *Caddo* and the acropsopilionines.

LITERATURE CITED

- Banks, N. 1892. A new genus of Phalangiidae. Entomol. Soc. Washington 2(2):249-251.
- Banks, N. 1904. Phalangids from Washington, D.C. J. New York Entomol. Soc. 12(4):256.
- Bishop, S. C. 1949. The Phalangida (Opiliones) of New York. Proc. Rochester Acad. Sci. 9(3):159-235.
- Bishop, S. C., and C. R. Crosby. 1924. A fossil species of *Caddo* (Opiliones) from the Baltic Amber, and its living relatives.. Bull. New York State Mus. 253:83-84.
- Canals, J. 1932. Hallago de una variedad del *Acropsopilio chilensis* Silv. en nuestro pais (Nota previa). Physis 11:150-154.
- Crosby, C. R. 1904. Notes on some phalangids collected near Ithaca, N.Y. J. New York Entomol. Soc. 12(4):253-256.
- Forster, R. R. 1948. A new genus and species of the family Acropsopilionidae (Opiliones) from New Zealand. Trans. Roy. Soc. N. Z. 77(1):139-141, Pl. 1.
- Forster, R. R. 1955. Further Australian harvestmen. Aust. J. Zool. 3:354-411.
- Goodnight, C. J., and M. L. Goodnight. 1948. A new member of the genus *Caddo* (Phalangida). J. New York Entomol. Soc. 56:201-203.
- Goodnight, C. J., and M. L. Goodnight. 1950. Grant No. 1219 (1950), Distribution and taxonomic relationships of the phalangid fauna of Chiapas, Mexico. Year Book Amer. Phil. Soc. 1950:142-145.
- Hickman, V. V. 1957. Some Tasmanian harvestmen of the sub-order Palpatores. Papers Proc. Royal Soc. Tasmania 91:65-79.
- Hirst, S. 1925. On some new genera and species of Arachnida. Proc. Zool. Soc. London 1925:1271-1280.
- Kauri, H. 1950-1951. Opiliones. S. Afr. Anim. Life Vol. 8.
- Lawrence, R. F. 1931. The harvest spiders of South Africa. Ann. S. Afr. Mus. 29(2):341-508.
- Lawrence, R. F. 1934. New South African Opiliones. Ann. S. Afr. Mus. 30:549-586.
- Ringuet, R. A. 1959. Los arachidos Argentinos del Ordre Opiliones. Rev. Mus. Arg. Cien. Nat. "Bernardo Rivadavia" 5(2):126-439.
- Ringuet, R. A. 1962. Notas sobre Opiliones. I. *Acropsopilio ogloblini* Canals en la selva marginal de Punta Lara y la ubicacion taxonomica del género *Acropsopilio* Silvestri. Physis 23(64):77-81.
- Roewer, C. F. 1912. Revision der Opiliones Palpatores. II Teil. Familie der Phalangiidae (Subfamilien: Sclerosomini, Oligolophini, Phlangiini). Abh. Geb. Naturwiss. 20:1-295.
- Roewer, C. F. 1923. Die Weberknechte der Erde. Gustav Fischer, Jena. 1116 pp.
- Roewer, C. F. 1957. Über Oligolophinae, Caddoinae, Sclerosomatinae, Liobuninae, Neopilioninae und Leptobuninae (Weitere Weberknechte XX). Senck. Biol. 38:323-358.

- Silhavy, V. 1961. Die Grundsätze der modernen Weberknechtetaxonomie und Revision des bisherigen Systems der Opilioniden. 11th. Int. Cong. Entomol. (Wien) 1960, Verh. 1:262-267.
- Silvestri, F. 1904. Descrizione di un nuovo genere di Opilionidi del Chile. Redia 2:254-256, Tav. 23.
- Suzuki, S. 1958. Occurrence in Japan of *Caddo agilis* Banks (Opiliones). Ann. Zool. Japan 31:225-228.
- Suzuki, S. 1967. Zoogeographical relationships of the Japanese Opiliones (in Japanese). Jap. Soc. Syst. Zool. Circ. 36:1-7.