

REVISION OF THE MILLIPED GENUS *CHEIROPUS* (POLYDESMIDA: XYSTODESMIDAE)

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Abstract.—The xystodesmid milliped genus *Cheiropus* is the southernmost genus in the tribe Apheloriini and is located primarily in the Coastal Plain physiographic province. The nominal genera *Stelgipus* and *Lyrranea* are subjective synonyms of *Cheiropus*, which consists of four allopatric species: *plancus* Loomis, *agrestis* (Loomis), *persicus* (Hoffman), and *serratus*, new species. A separate solenomerite in various positions on the lateral side of the acropodite stem diagnoses the genus, and the position of the solenomerite and the distal configuration of the acropodite are important specific characters. *Cheiropus* appears closely related to the Appalachian genus *Prionogonus* and represents ancestral stock that penetrated the lowland provinces of South Carolina, Georgia, and Florida. Cladal variation in the degree of serration, the breadth of the acropodal expansion, and the curvature of the acropodite reflects ancestral variation that has been retained independent of phylogeny.

The center of diversity and abundance of the xystodesmid milliped tribe Apheloriini is the southern Blue Ridge Province, occupied by seven genera and over 35 species. At both taxonomic levels, numbers decline to the east and south, so that only five genera and six species occur in the Coastal Plain of the Carolinas, and only three genera and four species inhabit coastal Georgia. Two of these nominal Georgian genera, *Cheiropus* and *Stelgipus*, are monotypic; so is *Lyrranea*, which occurs in the central Fall Zone region near Macon. I have long been intrigued by the prospect of three monotypic lowland genera in such close proximity, and I was prompted to review their concepts by discovering a new species in southeastern Georgia. This new species appeared to belong to *Stelgipus*, but since none of the taxa had been adequately diagnosed, I had to consider all of them in describing the new form. Eventually I concluded that only one genus was justified, and *Cheiropus* has priority, since it was published three pages before *Stelgipus* by Loomis (1944). The chief diagnostic character of *Cheiropus* is a lateral solenomerite that is distinct from the acropodite proper; specific differences obtain in the shape of the solenomerite, its position on the acropodite, and the distal configuration of the latter. *Cheiropus* is endemic to the southeastern Atlantic lowlands, and it is the genus farthest removed from the center of tribal abundance. However, it seems related to the Appalachian taxa through affinity to *Prionogonus*.

The history of *Cheiropus* begins with Loomis (1944), and with *Cheiropus*, *Stelgipus*, and their single species. Chamberlin and Hoffman (1958) recognized the former genus and *C. plancus* Loomis, but they synonymized *Stelgipus* with *Fontaria* thus publishing *F. agrestis* (Loomis), as recommended by Hoffman (1952). Hoffman (1963) proposed *Lyrranea* for a species from Peach County, Georgia, which he named *L. persica*. In 1979 Hoffman revived *Stelgipus*, which he included with *Cheiropus* and *Lyrranea* as components of the Apheloriini, and I (1979)

revived Loomis' original combination, *S. agrestis*, for a form from Jacksonville, Florida. This record, however, was a misidentification of the new species, which is here named *serratus*.

In the present contribution I present a modern diagnosis of *Cheiropus*, a description and redescription of the four species, and discussions on ecology, distribution, and relationships. A key and detailed gonopodal illustrations are presented to facilitate identifications. I have been fortunate in having access to the small amount of preserved study material, whose repositories are indicated in the species accounts by the following acronyms:

AMNH—American Museum of Natural History, New York, New York.

FSCA—Florida State Collection of Arthropods, Gainesville, Florida.

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

NCSM—North Carolina State Museum of Natural History, Raleigh, North Carolina. The invertebrate catalog numbers of specimens in this collection are indicated in parentheses after appropriate locality citations.

RLH—Private collection of Richard L. Hoffman, Radford, Virginia.

WAS—Private collection of William A. Shear, Hampden-Sydney, Virginia.

ZMC—Zoologisk Museum, Copenhagen, Denmark.

Taxonomic Characters

The taxonomic characters of *Cheiropus* are found exclusively on the gonopods. Color pattern is of no value in making determinations because sympatric or nearly sympatric species of other apheloriine genera demonstrate the striped pattern with colors similar to those displayed by *Cheiropus*. Likewise, differences in the lengths and configurations of the processes of the fourth sterna in species of *Cheiropus* and sympatric taxa are insufficient to allow for valid determinations.

The chief diagnostic character of *Cheiropus*, the segregation of the solenomerite from the stem of the acropodite on the gonopods, is clearly visible in *persicus* and *plancus*, but it is masked by the expanded distal extremity of the acropodite in *agrestis* and *serratus*. Thus to distinguish *Cheiropus*, one has only to look for a separate solenomerite or an apically expanded acropodite.

At the species level the taxonomically useful characters involve the position of the solenomerite, the configuration of the acropodite, and the condition of its distal margin. *Cheiropus persicus* is distinguished by the relatively narrow acropodite that tapers to an acuminate tip and by the nearly basal origin of the solenomerite. The other three species have distally expanded acropodites, and the solenomerite is located on the under (concave) surface of the expansion in *F. agrestis* and *serratus* and laterally at its base in *plancus*. The expansion in western populations of *plancus* lacks marginal teeth, being smoothly rounded with one or two blunt terminations, but in eastern forms there are from one to five sharp dentations. The expansion in *agrestis* and *serratus* is truncate and variably jagged. These two species differ in the configuration of the solenomerite (slender and falcate in *serratus*; a thick, heavy boss in *agrestis*) and the marginal condition of the acropodite (with a single row of up to 12 distinct teeth in *agrestis*; with two or more rows of numerous small teeth and serrations in *serratus*).

Cheiropus Loomis

Cheiropus Loomis, 1944:170–171.—Chamberlin and Hoffman, 1958:25.—Hoffman, 1979:159.

Stelgipus Loomis, 1944:173.—Hoffman, 1979:159.

Fontaria: Chamberlin and Hoffman, 1958:33.

Lyrranea Hoffman, 1963:114–115; 1979:159.

Type species.—Of *Cheiropus*, *C. plancus* Loomis, 1944, by original designation; of *Stelgipus*, *S. agrestis* Loomis, 1944, by original designation; of *Lyrranea*, *L. persica* Hoffman, 1963, by original designation.

Description.—A genus of moderate to large xystodesmids with the following characteristics:

Body composed of head and 20 segments in both sexes; size varying from 8.0–10.5 mm wide and 32–40 mm long; W/L ratio similarly varying from around 23–27%. Body essentially parallel-sided in midbody region, tapering at both ends.

Color in life: paranota red, pink, or orange; metaterga black with red, pink, or orange stripes along caudal margins connecting paranotal spots; collum with concolorous stripe along anterior margin.

Head of normal appearance, smooth, polished. Epicranial suture shallow, distinct, terminating in interantennal region; interantennal isthmus moderately wide; genae not margined laterally, with shallow central impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Antennae moderately slender, varying in length, becoming progressively more hirsute distally, with 4 conical sensory cones on ultimate article; no other sensory structures apparent. Facial setae reduced; epicranial and interantennal absent; frontal, genal, clypeal, and labral present.

Terga generally smooth, polished, becoming slightly coriaceous anteriorly. Collum variably broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, generally continuing slope of dorsum, caudolateral corners rounded on anteriormost segments, becoming blunt in midbody region and progressively more acute posteriorly. Peritremata distinct, strongly elevated above paranotal surface; ozopores located just caudal to midlength, opening dorsolaterad. Prozonites smaller than metazonites; strictures distinct, smooth.

Caudal segments normal for family.

Sides of metazonites smooth or irregular, with varying shallow, curved impressions. Strictures sharp, distinct. Pregonopodal sterna of males modified as follows: that of segment 4 with low, apically divided process between 3rd legs, much shorter than widths of adjacent coxae; that of segment 5 with two small projections between 4th legs, much shorter than widths of adjacent coxae, and unmodified or with low, flattened areas between 5th legs; that of segment 6 convexly recessed between 7th legs to accommodate apices of acropodites when body segments compressed. Postgonopodal sterna generally with broad, subtriangular lobes on segments 8–9, becoming flattened with shallow transverse and longitudinal grooves or depressions caudally. Gonapophyses on 2nd leg pair of males distinctly elevated above coxal surfaces, with round, apical knobs. Pregonopodal legs densely hirsute; postgonopodal legs becoming progressively less hirsute caudally. Coxae with variable, low tubercles beginning on pregonopodal or postgonopodal legs; prefemoral

spines moderately long and sharply pointed; tarsal claws bisinuate. Hypoproct broadly rounded; paraprocts with margins strongly thickened.

Gonopodal aperture ovoid to elliptical, with slight or strong anteriolateral indentations, front flush with metazonal surface, sides and caudal edge elevated. Gonopods in situ with acropodites projecting ventrad from aperture, extending either anteriorly in subparallel arrangement to beyond anterior margin of aperture, or anteriorly, crossing in midline, and located wholly within aperture. Coxae moderate to large, without apophyses, connected by membrane only, no sternal remnant. Prefemora moderate to large, without prefemoral process, though occasionally with vestige. Acropodites moderately thick and heavy, well sclerotized, extending sublinearly from prefemur in most species, curving broadly anteriorly through a single vertical plane in *agrestis*; either tapering smoothly to acuminate tip or with a cupulate, apically truncate, distal expansion at $\frac{2}{3}$ length, apical margin of expansion variable, smooth or with a few or many sharply acute teeth and serrations on one or more rows, undersurface of expansion also variable, smooth, striated, or with numerous minute teeth, becoming larger and denser near apical margin. Solenomerite variable, a long to moderate process arising from stem of acropodite near base or at origin of distal expansion, or a short falcate projection or thickened boss located on undersurface of expansion. Prostatic groove arising in pit on medial side of prefemur, crossing to lateral side at variable distances along acropodite stem, opening apically on solenomerite.

Cyphopodal aperture broad, encircling 2nd legs, sides slightly elevated above metazonal surface. Cyphopods in situ located lateral to 2nd legs, usually with valves and corner of receptacle visible in aperture. Receptacle small to moderate in size, variously positioned with respect to valves, surface rugulose to granulate, without lobes. Valves moderate and subequal in size, surfaces finely granulate. Operculum minute, hidden under free end of valves.

Distribution.—Outer Coastal Plain of South Carolina to mid-peninsular Florida, ranging inland to the Fall Zone and central Piedmont Plateau of Georgia. The Cooper-Santee River may be the northern range limit in South Carolina, but there is no tangible southern boundary, as *plancus* extends beyond the Withlacoochee River. Likewise, there is no definite western limit; *agrestis* occurs well into piedmont Georgia and might be found along the base of the Blue Ridge escarpment. *Cheiropus* is chiefly a Coastal Plain genus, one of the few occurring on the coastal islands of Georgia and southeastern South Carolina.

Species.—Four.

Remarks.—To Loomis, the position of the solenomerite with respect to the distal acropodal expansion in *plancus* suggested a cupped hand with its palm outward opposed by the thumb, and hence he based the generic name on the Greek word for hand.

Because of the gonopodal variability of *Cheiropus*, I decided against using the terminology devised for *Sigmoria* and adopted for *Prionogonus* (Shelley 1981, 1982), although *Cheiropus* appears to share a common ancestor with the latter (see relationships section). The gonopods of *persicus*, for example, are highly modified and the zones of “sigmoid” acropodites are not apparent, so this terminology would be meaningless. The acropodites of the other three species terminate at the distal extremity of the “peak,” but the solenomerite, which represents the repositioned “distal zone,” is neither distal nor stationary in *Cheiropus* and thus cannot be characterized by this terminology. Consequently, new language

is required for the species of *Cheiropus*, and their accounts cannot be compared directly with those of the “sigmoid” species.

Key to Species of *Cheiropus* (Based on Adult Males)

1. Acropodite broadened distally into cupulate expansion or cap; solenomerite either beneath and partly or completely obscured by cap, or located laterally at its base 2
- Acropodite relatively narrow, widest basally, tapering smoothly to acuminate tip; solenomerite about half the length of acropodite, arising near base of, and running subparallel to, acropodite; Fall Zone of central Georgia *persicus* (Hoffman)
2. Solenomerite distinctly visible on lateral side of acropodite at base of expansion; except for eastern populations, margin of expansion not strongly serrated; Thomas Co., Georgia, to Hernando Co., Florida *plancus* Loomis
- Solenomerite located beneath cap and partly or completely obscured; margin of expansion strongly serrated 3
3. Acropodite in form of continuous, broadly curved arc, extending in medial view beyond level of prefemur; margin of expansion with a single row of up to 12 teeth; solenomerite a thickened, sclerotized boss; Charleston Co., South Carolina, to Clarke and Burke cos., Georgia *agrestis* (Loomis)
- Acropodite in form of inverted L, stem relatively straight, bent sharply anteriad at level of cap, overhanging prefemur in medial view; margin of expansion highly serrate, with two or more rows of variable teeth; solenomerite a thin, falcate projection tucked under teeth, distal to boss; Liberty Co., Georgia, to Duval Co., Florida *serratus*, new species

Cheiropus plancus Loomis
Figs. 1–7

Cheiropus plancus Loomis, 1944:171–172, Fig. 3.—Chamberlin and Hoffman, 1958:26.

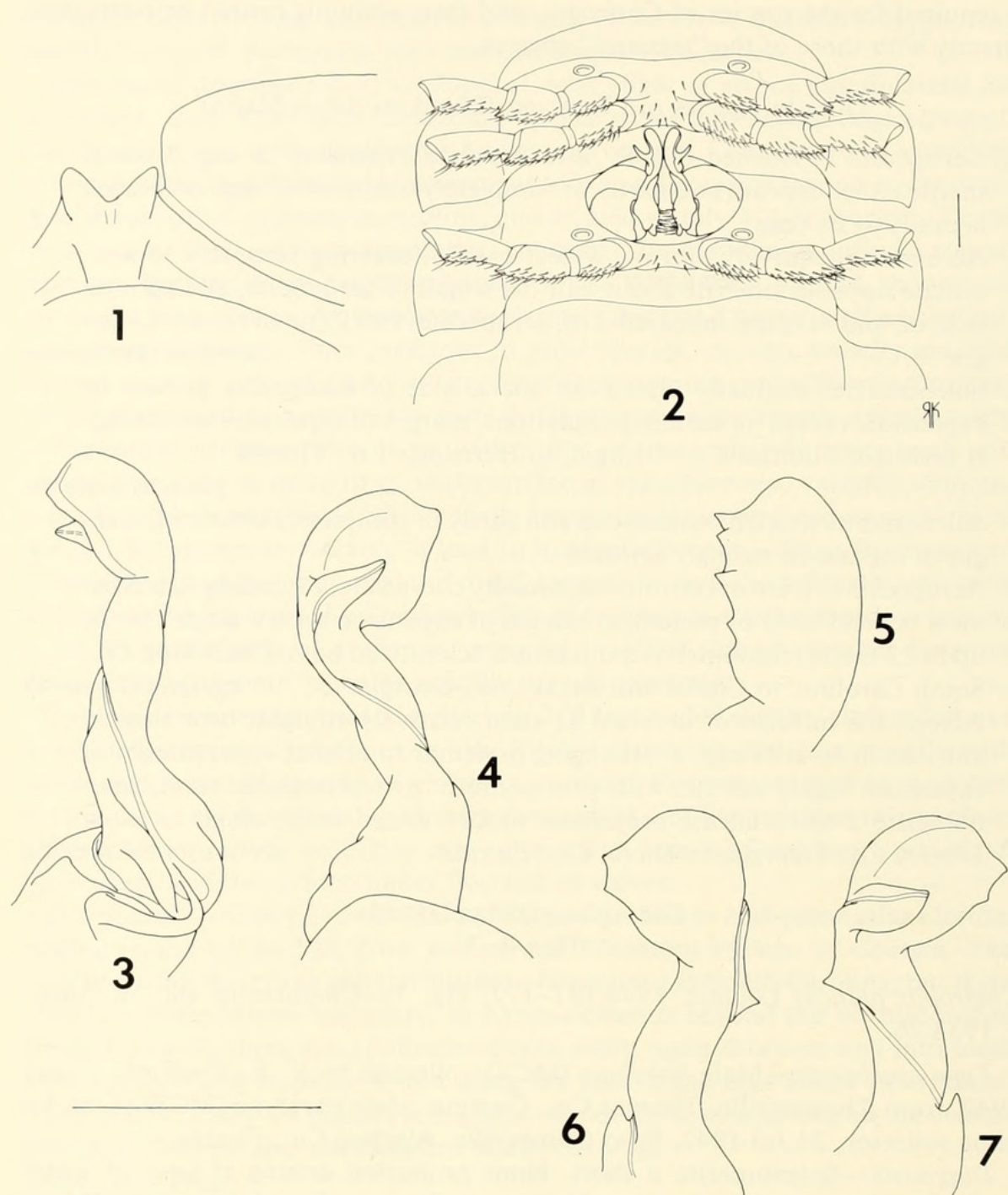
Type specimens.—Male holotype (MCZ) collected by V. E. Shelford, 27 Jul 1942, from Thomasville, Thomas Co., Georgia. Male paratype (MCZ) taken by same collector, 24 Jul 1942, from Gainesville, Alachua Co., Florida.

Diagnosis.—Solenomerite a short, blunt projection arising at base of distal expansion of acropodite; margin of latter usually smooth with one or two blunt terminations, occasionally sharply pointed teeth; stem of acropodite twisted at midlength.

Holotype.—Length 39.2 mm, maximum width 9.8 mm, W/L ratio 25.0%; depth/width ratio 56.1%. Segmental widths as follows:

collum 5.8 mm	8th–14th 9.8
2nd 7.4	15th 9.5
3rd 8.3	16th 9.1
4th–5th 9.1	17th 8.3
6th–7th 9.5	18th 5.7

Color in life unknown; the pigments reported by Loomis (1944) are obviously the faded colors of preservation.



Figs. 1-7. *Cheiropus plancus*. 1, Process of 4th sternum of holotype, caudal view; 2, Gonopods in situ, ventral view of near toptotypical male from Thomas Co., Georgia; 3, Left gonopod of holotype, medial view; 4, The same, lateral view; 5, Acropodite expansion of paratype, submedial view; 6, Telopodite of left gonopod of male from Alachua Co., Florida, medial view; 7, The same, lateral view. Scale line for Fig. 2 = 1.00 mm; line for other Figs. = 1.00 mm for 1, 6-7; 1.33 mm for 3-4; and 0.80 mm for 5. Setation is omitted from all sternal and dissected gonopod drawings in this paper.

Head capsule smooth, polished, width across genal apices 4.1 mm, interantennal isthmus 1.5 mm. Epicranial suture thin but distinct, terminating in interantennal region, bifid. Antennae reaching back nearly to caudal margin of 4th tergite, becoming progressively more hirsute distally; relative lengths of antennomeres

2>3>6>4=5>1>7. Genae not margined laterally, with distinct medial impression, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Facial setae as follows: epicranial and interantennal absent; frontal 1-1, genal 4-4, clypeal about 11-11, labral about 28-28.

Terga smooth, polished, becoming slightly coriaceous on paranota. Collum broad, ends slightly beyond those of following tergite. Paranota moderately depressed, angled slightly ventrad and continuing slope of dorsum; anterior corners rounded, caudolateral corners rounded through segments 4, becoming blunt and progressively more pointed posteriorly. Peritremata thick and conspicuous, sharply set off from paranotal surface. Ozopores located in slight swellings near middle of peritremata, opening dorsad.

Sides of metazonites relatively smooth. Strictures sharp, distinct. Sternum of segment 4 with two small, blunt, widely spaced and diverging lobes, much shorter than adjacent coxal widths (Fig. 1); of segment 5, with two minute, widely separated tubercles between 4th legs, unmodified between 5th legs; of segment 6, convexly recessed between 7th legs to accommodate apices of telopodites. Postgonopodal sterna with two broad, subtriangular lobes along caudal edges on segments 7-8 and two blunt tubercles subtending posterior coxae on remaining segments; with shallow, central impressions and shallow, transverse grooves between leg pairs. Pregonopodal legs densely hirsute, postgonopodal legs becoming progressively less hirsute caudally. Small coxal tubercle present on legs of segments 9-17; prefemoral spines beginning on segment 6, becoming progressively longer and sharper caudally; tarsal claws bisinuate curved. Hypoproct broadly rounded; paraprocts with margins strongly thickened.

Gonopodal aperture elliptical, 2.4 mm wide and 1.3 mm long at midpoint, without indentations, caudolateral edges raised above metazonal surface. Gonopods in situ (Fig. 2, not this specimen) with telopodites projecting anteriad from aperture, either lying beside each other in parallel fashion or crossing distally, extending forward just beyond anterior margin of aperture. Gonopod structure as follows (Figs. 3-4): Acropodite extending ventrad from prefemur, widening at about $\frac{2}{3}$ length into broad, rounded, cupulate distal swelling or expansion, shielding and obscuring base of solenomerite in medial view; acropodite stem proximal to bend strongly twisted, with low, rounded shoulder laterally at base of solenomerite; expansion with wide, central impression on lateral side, margin smoothly curved proximad, indented slightly at midlength and extending into single, blunt termination. Solenomerite short and blunt, subtriangular, about half as long as expansion, arising from lateral side of acropodite stem at base of expansion, base obscured by latter in medial view, tip directed toward distalmost point of swelling. Prostatic groove arising in pit in base of prefemur, crossing to lateral side at torsion in midlength of acropodite stem, running behind lateral shoulder onto solenomerite, opening apically.

Male paratype.—The male paratype from Gainesville, Alachua County, Florida, designated by Loomis (1944) was taken some 125 miles SE of the type locality. It differs most notably from the holotype in the irregular margin of the expansion, which is lined with five sharply pointed teeth (Fig. 5). Other characteristics of the Alachua County population are discussed under variation.

Female topotype.—Length 38.8 mm, maximum width 10.2 mm, W/L ratio

26.2%, depth/width ratio 65.7%. Somatic features agreeing essentially with holotype, except paranota more strongly depressed, giving appearance of more highly arched body.

Cyphopods in situ with opening of valves and corner of receptacle visible in aperture. Receptacle relatively small, cupped around caudolateral surface of valves, surface finely granulate.

Variation.—Western populations in Jefferson County, Florida, and the vicinity of Tallahassee agree closely with the holotype. Eastern males from Bradford to Hernando counties differ, however, in that the margin of the expansion possesses from one to five sharp teeth. Some have a vestigial prefemoral process (Figs. 6–7), and a basal spine on the shoulder of the acropodite. The shoulder is larger in these males and is slightly visible in medial view, along with the prostatic groove, which passes behind it before entering the solenomerite.

Ecology.—*Cheiropus plancus* is available during the hot summer months. Most specimens were collected from June–August, and I have not encountered it in October or November at Devil's Millhopper State Park, where it is common in the summer. According to Loomis (1944), the holotype came from climax magnolia-beech woods, and numerous specimens have been collected from damp slopes along Hogtown Creek in Gainesville. The sinkhole at Devil's Millhopper is surrounded by hardwoods, and *plancus* occurs under leaves in moist spots. At Ichetucknee Springs it was found on damp moss in cracks on a concrete retaining wall a few feet above the river. The material from Brooksville was discovered under thin leaf layers on hard, moist substrate in an area dominated by sweet gum trees and overgrown with kudzu. I have never found *plancus* under live oaks and believe it occurs solely in litter of broad-leaved species. Tracts of these are rare in Florida, but *plancus* may be expected in the few that do exist west of the St. John's River.

Distribution.—Southern Georgia to west-central, peninsular Florida, from Thomasville to Brooksville. The area lies east of the Ochlockonee River and extends across the Suwannee and Withlacoochee rivers. The easternmost known locality is some 35 miles west of the St. John's River. Specimens were examined as follows:

GEORGIA: *Thomas Co.*, Thomasville, M, 27 Jul 1942, V. E. Shelford (MCZ), and Millpond Plantation, Thomasville, M, 16 Jul 1973, F. A. Coyle (WAS), and 3M, 3F, 25 Jun 1978, H. W. Levi (MCZ) TYPE LOCALITY; S of Boston, Bar-M-Ranch, M, 2F, Apr 1968, and 2M, 15 Jul 1973, W. Sedgwick (WAS), and M, 25 Jun 1978, H. W. Levi (MCZ).

FLORIDA: *Leon Co.*, Tallahassee, 2M, 30 Jun 1952, H. H. Humm (FSCA); and Tall Timbers Research Station, M, 25 Oct 1972, D. L. Harris (FSCA); M, 8 Apr 1968, A. M. Chickering (MCZ); M, F, 17 Jul 1972, W. W. Whitcomb (FSCA); and 2M, 2F, 30 Jul 1973 (FSCA). *Jefferson Co.*, Monticello, Big Bend Horticultural Lab, M, date and collector unknown (FSCA). *Hamilton Co.*, Stephen Foster St. Pk., 10M, 4F, 15 Jun 1959, A. Williams (FSCA). *Columbia Co.*, Ichetucknee Springs, 4F, 22 Jun 1977, J. E. Cooper (NCSM A1599). *Bradford Co.*, 3 mi. NNE Brooker, M, F, 9 Aug 1959, L. Hubricht (RLH). *Alachua Co.*, Gainesville, M, 24 Jul 1942, V. E. Shelford (MCZ), along Hogtown Cr. in Gainesville, 11M, 7F, 23 Jun 1959, H. V. Weems and W. J. Platt (FSCA), and many other males and females collected in May, June, July, and August (FSCA); Devil's Mill Hopper

St. Pk., 2M, F, 5 Jun 1959, N. B. Causey (FSCA), other males and females in summers of various years (FSCA), and 2M, F, 9 Jun 1983, R. M. Shelley and J. L. Staton (NCSM A4149). *Hernando Co.*, Brooksville, corner of Bailey and Lamar Sts., 7M, 4F, 13 Jun 1983, R. M. Shelley (NCSM A4159).

Remarks.—In life the proterga of *plancus* are black, and the metaterga are black with orange stripes along the caudal edges. The stripes become wider on the caudal halves of the paranota, and the peritremata are also orange; however, the anterior halves of the paranota are black. There is also an orange stripe along the anterior margin of the collum, which connects laterally with the caudal stripe.

Cheiropus plancus is the southernmost representative of the tribe Apheloriini. The only xystodesmids known from farther south in Florida are *Dicellarius okefenokensis* (Chamberlin) and *Pleurolooma cala* (Chamberlin), of the tribes Pachydesmini and Rhysodesmini, respectively. Until 1983, Gainesville was the southernmost known locality, but the discovery of a population in Brooksville, Hernando County, represents a range extension of around 85 miles and establishes its presence in the western side of the northern half of the peninsula.

Cheiropus persicus (Hoffman), new combination

Figs. 8–11

Lyrranea persica Hoffman, 1963:115–119, Figs. 1–4.

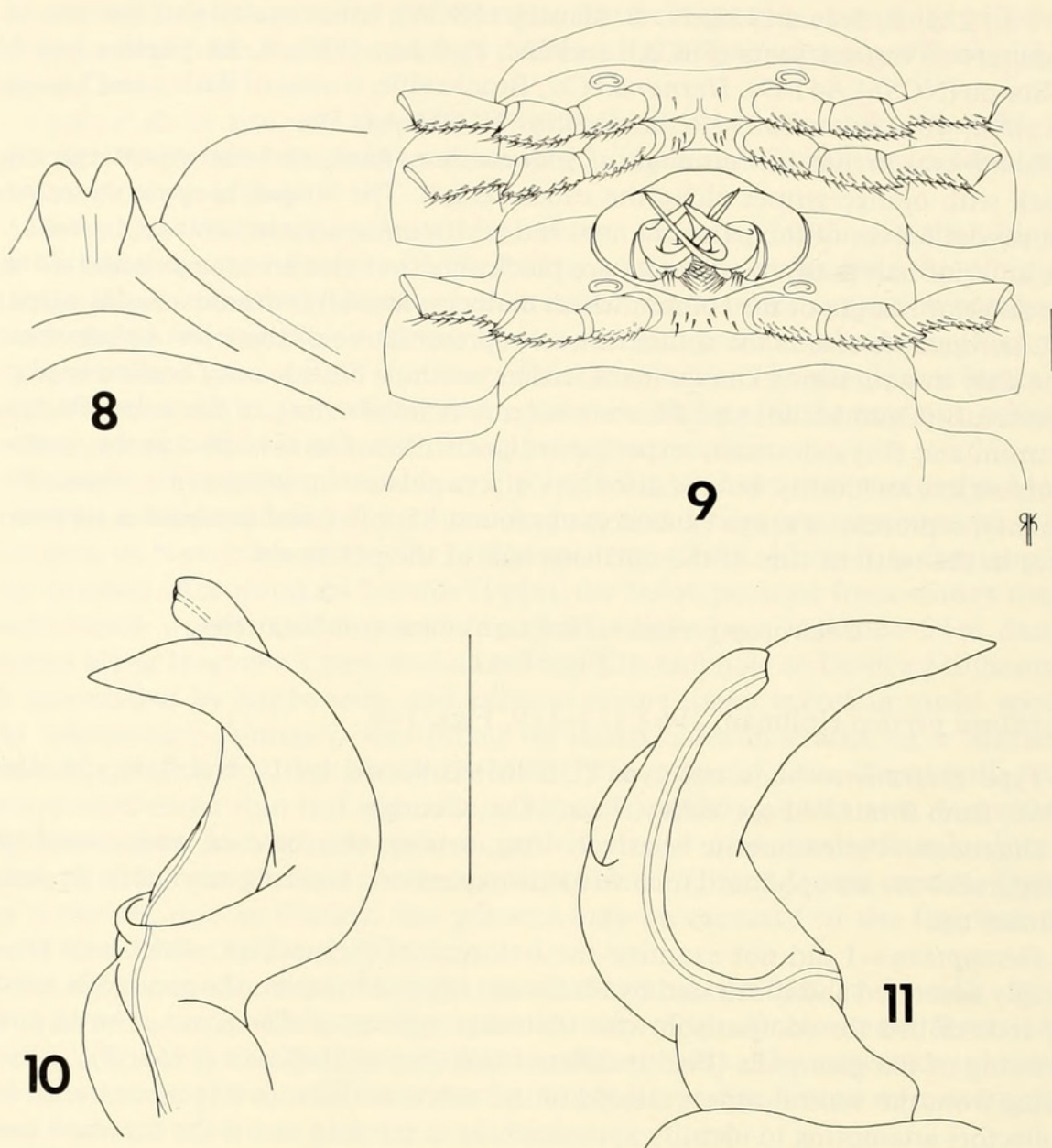
Type specimen.—Male holotype (USNM) collected by L. Hubricht, 24 Apr 1960, from 3 mi. W Fort Valley, Peach Co., Georgia.

Diagnosis.—Solenomerite relatively long, arising near base of, and extending subparallel to, acropodite; latter without expansion, tapering smoothly to acuminate tip.

Description.—I did not examine the holotype of this species, which was thoroughly described and illustrated by Hoffman (1963). However, the gonopods must be redescribed for comparison with the other species of *Cheiropus*. The in situ drawing of the gonopods (Fig. 9) differs from that of Hoffman (1963, Fig. 1) in being from the ventral aspect instead of the anterior. This view is more useful to collectors attempting to identify xystodesmids in the field and is the standard one I present in papers. I also show in Fig. 8 the process of the 4th sternum, which Hoffman verbally characterized. The following is a composite description of the gonopods of all males available to me, encompassing all aspects of variation.

Gonopodal aperture subovoid, about 3.5 mm wide and 1.8 mm long at midpoint, indented anteriolaterad, sides elevated above metazonal surface. Gonopods in situ (Fig. 9) with telopodites projecting ventrad from aperture, extending over opposite side of aperture and crossing in midline, either lying entirely over aperture or tips extending just beyond anterior margin. Gonopod structure as follows (Figs. 10–11): Solenomerite diverging laterally from acropodite at about $\frac{1}{3}$ length, extending subparallel to acropodite for about $\frac{3}{4}$ of length of latter, directed ventrad, slightly curved and wider distad, apically blunt. Acropodite with concavity subtending solenomerite, curved broadly anteriad and extending beyond level of prefemur, margin smooth, sides narrowing smoothly to acuminate tip. Prostatic groove arising in pit in prefemur, running along anterior edge of concavity onto solenomerite, opening apically in center of latter.

Description of female.—Length 36.3 mm, maximum width 8.9 mm, W/L ratio



Figs. 8–11. *Cheiropus persicus*. 8, Process of 4th sternum of male from Houston Co., Georgia, caudal view; 9, Gonopods in situ, ventral view of male from Houston Co.; 10, Telopodite of left gonopod of male from Houston Co., medial view; 11, The same, lateral view. Scale line for Fig. 9 = 1.00 mm; line for other Figs. = 1.00 mm for each.

24.5%, depth/width ratio 71.9%. Agreeing closely with males in somatic features, except paranota more strongly depressed, creating appearance of more highly arched body.

Cyphopods in situ with opening of valves and corner of receptacle visible in aperture. Receptacle relatively small, subtriangular, located medial to valves, surface finely granulate.

Ecology.—*Cheiropus persicus* occurs in typical piedmont apheloriine habitat, under thin layers of leaves (usually dogwood or maples) on relatively hard substrates near water sources.

Distribution.—Known only from four counties in the Fall Zone region of west-

central Georgia, but doubtlessly occupies a larger area in the Fall Zone and adjacent parts of the Piedmont Plateau and Coastal Plain. Specimens were examined as follows: all were collected by the author or an assistant:

GEORGIA: *Peach Co.*, 2 mi. W Fort Valley, along Georgia hwy. 96, 2F near topotypes, 12 Apr 1978 (NCSM A1839). *Houston Co.*, 4 mi. NW Perry, along US hwy. 341 at Bay Cr., 5M, 16 Sep 1979 (NCSM A2880); and 4 mi. SW Perry, along US hwy. 341 at Flat Cr., M, 16 Sep 1979 (NCSM A2878). *Crawford Co.*, 4 mi. E Roberts, along Georgia hwy. 42, 2.6 mi. E US hwy. 80, M, 16 Sep 1979 (NCSM A2883). *Taylor Co.*, along Georgia hwy. 96 just E of Reynolds, F, 12 Apr 1978 (NCSM A1839).

Remarks.—In life *persicus* displays the red striped color pattern of many apheloriine xystodesmids. The metaterga are black with wide red stripes along the caudal edges connecting red paranota. There is a concolorous red stripe along the anterior margin of the collum.

The highly modified acropodites of *persicus* lack cupulate distal expansions and are thus distinct from those of its congeners. Some may therefore question the congeneric status of *persicus*, but as discussed elsewhere in this paper, the basal origin of the solenomerite from the acropodite culminates the trend in these lowland forms to more proximal derivation. Thus, absence of the expansion, like the basal origin of the solenomerite, are best regarded as autapomorphic traits of *persicus* rather than as criteria for a distinct generic taxon. Were *Lyrranea* to be retained for *persicus*, *Stelgipus* would have to stand for *agrestis* and *serratus*, since their solenomerites are in different positions from that of *plancus*. Since the species are linked by common, inferred, ancestral species, only one genus is justified, which is defined as having a variably positioned solenomerite. It is also worth noting that the acropodal curvature of *persicus* is similar to that of the geographically proximal population of *agrestis* (compare Figs. 10 and 13).

Cheiropus agrestis (Loomis), new combination

Figs. 12–16

Stelgipus agrestis Loomis, 1944:173–174, Fig. 5.

Fontaria agrestis:—Chamberlin and Hoffman, 1958:33–34.

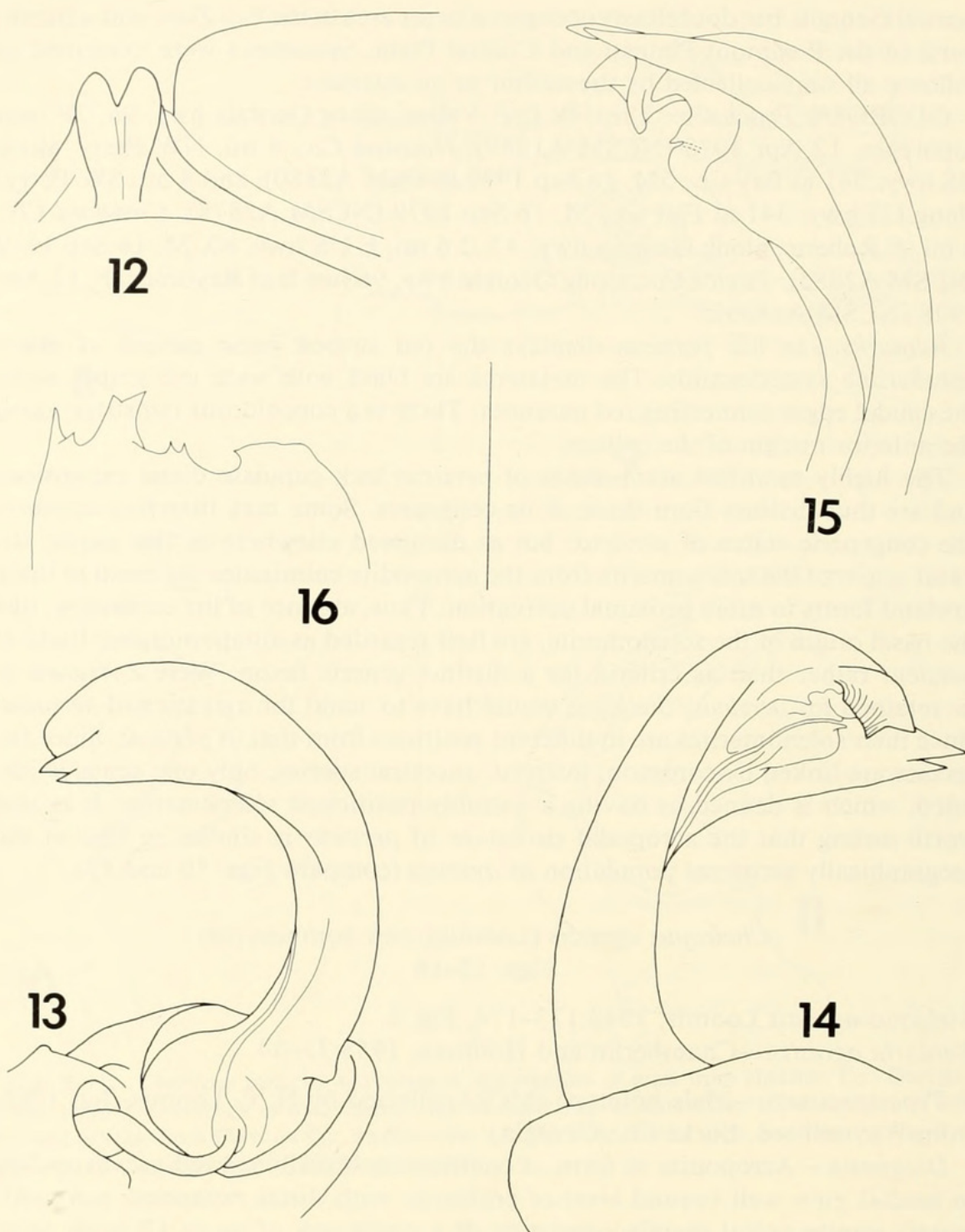
Type-specimen.—Male holotype (MCZ) collected by H. F. Loomis, Jun 1943, from Waynesboro, Burke Co., Georgia.

Diagnosis.—Acropodite in form of continuous, broadly curved arc, extending in medial view well beyond level of prefemur, with distal expansion and moderately serrate apical margin consisting of a single row of up to 12 teeth; solenomerite a thick, heavy boss located on undersurface of expansion.

Holotype.—Length 37.4 mm, maximum width 9.4 mm, W/L ratio 24.9%; depth/width ratio 63.4%. Segmental widths as follows; segments 2–7 are damaged and cannot be measured.

collum 7.6 mm	13th–15th 9.4
8th 8.8	16th 9.1
9th–10th 9.0	17th 8.0
11th–12th 9.2	18th 6.1

Color in life unknown; Loomis (1944) reported that it was bleached when found.



Figs. 12-16. *Cheiropus agrestis*. 12, Process of 4th sternum of holotype, caudal view; 13, Left gonopod of holotype, medial view; 14, The same, lateral view; 15, Distal half of acropodite of same, submedial view; 16, Distal extremity of expansion of same, subventral view. Scale line = 1.00 mm for Figs. 12-15, 1.33 mm for 16.

Somatic features similar to those of *plancus*, with following exceptions:

Width across genal apices 4.7 mm, interantennal isthmus 1.8 mm. Antennae reaching back only to caudal margin of 2nd tergite, relative lengths of antennomeres $2 > 3 = 5 > 6 > 4 > 1 > 7$. Facial setae as in *plancus* except genal 3-3, clypeal

about 16-16, labral about 22-22, merging with clypeal series and continuing for short distance along genal margins.

Sides of metazonites with several shallow, grooved impressions. Sternum of segment 4 with small, apically divided process between 3rd legs, much shorter than widths of adjacent coxae (Fig. 12); of segment 5, produced into two paramedial knobs between 4th legs, shorter than adjacent coxal widths, and two broad elevated areas between 5th legs; of segment 6, convexly recessed between 7th legs to accommodate apices of telopodites. Postgonopodal sterna with caudal margins produced into broad, subtriangular lobes on segments 7-9 and short, blunt teeth subtending adjacent coxae on remaining segments; center of sterna slightly depressed, with transverse groove between leg pairs. Coxae without projections; prefemoral spines beginning on segment 5.

Gonopodal aperture subelliptical, about 3.8 mm wide and 2.4 mm long at midpoint, strongly indented anteriolaterally, sides flush with metazonal surface. Gonopods in situ not observed but probably similar to condition in *serratus* or with apices overlapping. Gonopod structure as follows (Figs. 13-16): coxa massive, surrounding base of prefemur. Acropodite short but massive, heavily sclerotized, curving strongly but smoothly at midlength and extending in arc well beyond level of prefemur; portion distal to bend greatly widened into umbrellar-shaped expansion shielding and protecting solenomerite, inner surface deeply concave and highly irregular with numerous scattered striae and minute teeth, striae and teeth clustered distally near solenomerite; apical margin of expansion with two lobes, two sharply pointed, irregularly subdivided spines on medial lobe, lateral lobe with two small inner teeth, becoming smooth and straight laterally and overhanging short, vertical, striated lamina; latter extending nearly to level of solenomerite and continuing as thin, irregularly toothed lamella to base of solenomerite. Solenomerite a short, thickened, heavily sclerotized boss or callus located distally on lateral part of acropodite beneath lateral marginal lobe, visible only in lateral view, masked by medial marginal lobe in medial view; solenomerite apically broad, with numerous minute teeth and one longer, curved tooth at opening of groove. Prostatic groove arising in pit in base of prefemur, crossing to lateral side of acropodite stem basally, continuing onto solenomerite to apical opening.

Variation.—The acropodite expansion is broader in the Clarke County male and curves dorsad medially so that its overall configuration resembles an umbrella. In the South Carolina male the expansion is reduced and flattened, and does not curve dorsad medially thus resembling the condition in *serratus*. The acropodite is also more serrated in the latter individual.

Distribution.—Piedmont Plateau and Coastal Plain of northern Georgia and southern South Carolina. *Cheiropus agrestis* is one of the few apheloriine millipeds occurring in both physiographic provinces and one of only two traversing the Savannah River, the other being an undescribed species of *Hubroria*. Specimens were examined as follows:

SOUTH CAROLINA: *Charleston Co.*, Wadmalaw Island, Rockland Plantation, M, 28 Jun, year unknown, O. F. Cook (RLH).

GEORGIA: *Clarke Co.*, Bogart, M, 2 Jul 1973, R. M. Duffield (RLH). *Burke Co.*, Waynesboro, M, Jun 1943, H. F. Loomis (MCZ) TYPE LOCALITY; and 5 mi. SE Waynesboro, M, 22 May 1960, L. Hubricht (RLH).

Remarks.—Males of *agrestis* are the largest in the genus and are equivalent in size to those of *Cleptoria rileyi* (Bollman) and *C. abbotti* Hoffman. No females have been discovered, so the cyphopodal condition is unknown.

Cheiopus agrestis has been encountered only four times, with a single male being taken each time. I have searched for it repeatedly but unsuccessfully, even on Wadmalaw Island and at Waynesboro. Never having collected a specimen myself, I cannot report the living color or preferred habitat. No useful notes were in the sample vials, but the preserved specimens exhibit a striped pattern that suggests the red paranota and metatergal stripe coloration of other apheloriine species. The South Carolina male resembles *serratus* in the acropodite expansion and its occurrence in the outer Coastal Plain. However, it has the solenomerite boss of *agrestis*, and I include it with this species because of the importance of the solenomerite in the taxonomy of this genus. Additional material between Burke County, Georgia, and Charleston County, South Carolina, would help clarify this matter.

Cheiopus serratus, new species

Figs. 17–22

Type-specimens.—Male holotype (NCSM A3589) and three male and four female paratypes collected by R. M. Shelley and R. W. Jones, 2 Oct 1980, from Crooked River State Park, Camden Co., Georgia. Male paratype collected by R. M. Shelley at same locality, 3 Jul 1977. Male and female paratypes deposited in FSCA.

Diagnosis.—Acropodite in form of inverted L, stem relatively straight, bent sharply anteriad at $\frac{2}{3}$ length and overhanging prefemur in medial view, with distal expansion and highly serrate, jagged apical margin consisting of two or more rows of variable teeth; solenomerite thin and falcate, located on undersurface of expansion beneath overhanging rows of teeth.

Holotype.—Length 35.8 mm, maximum width 8.3 mm, W/L ratio 23.2%, depth/width ratio 62.7%. Segmental widths as follows:

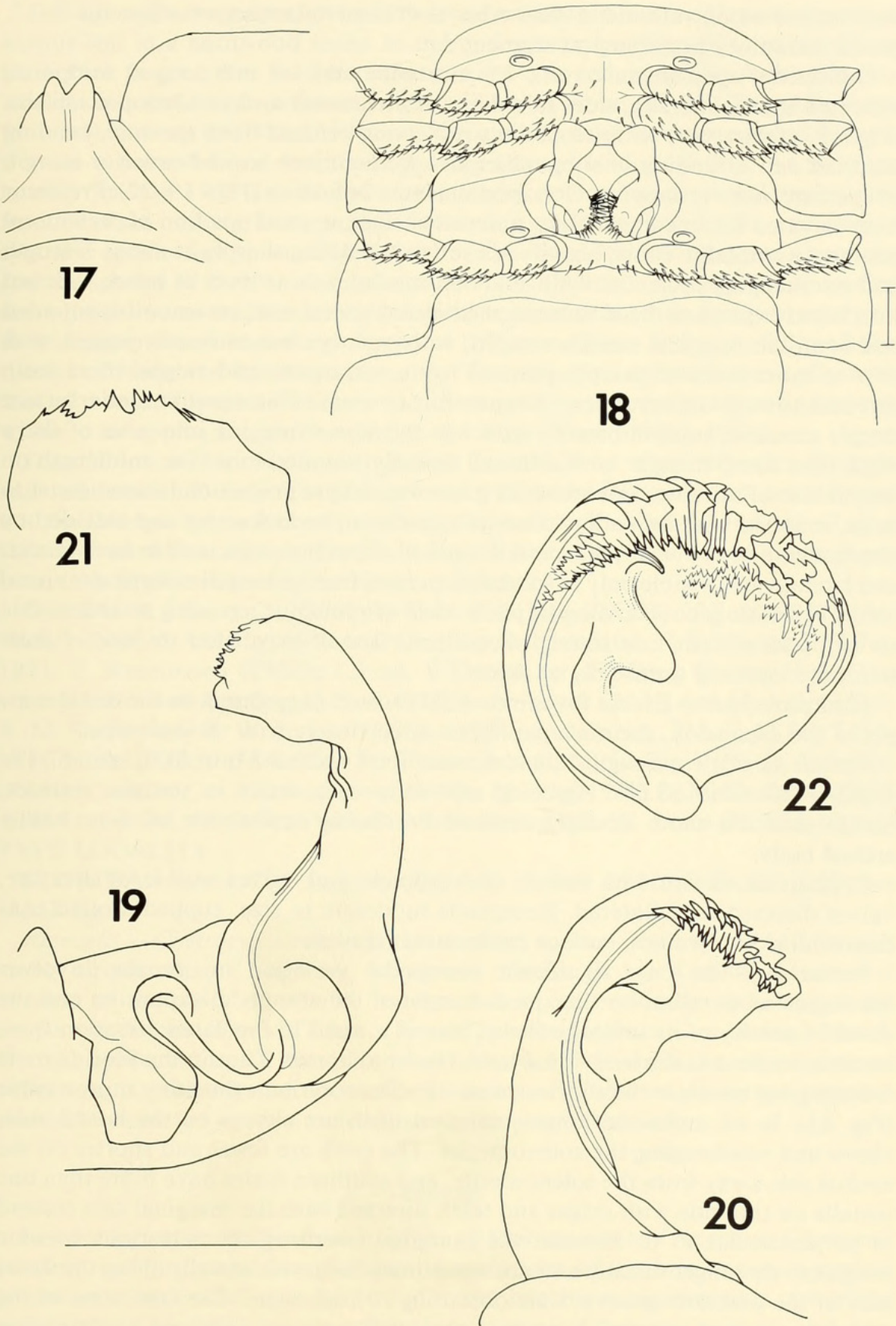
collum 5.2 mm	6th–14th 8.3
2nd 6.8	15th 8.0
3rd 7.3	16th 7.6
4th 7.8	17th 6.4
5th 8.1	18th 4.6

Color in life: paranota pink-orange, metaterga black with narrow, pink-orange stripes along caudal margins connecting paranotal spots; collum with stripes along both anterior and caudal edges.

Somatic features similar to those of *plancus*, with following exceptions:

Width across genal apices 3.6 mm, interantennal isthmus 1.3 mm. Facial setae as in *plancus* except genal 2-2, clypeal about 10-10, and labral about 15-15.

Sides of metazonites with several curved, shallow impressions. Sternum of segment 4 with two minute lobes between 3rd legs, much shorter than widths of adjacent coxae (Fig. 17); that of segment 5 with two low paramedial knobs between 4th legs, shorter than width of adjacent coxae, and two low elevated areas between 5th legs; that of segment 6 with deep, convex recession between 7th legs to accommodate apices of acropodites. Postgonopodal sterna flat and unmodified, with narrow transverse grooves between leg pairs and wide, shallow, longitudinal



Figs. 17–22. *Cheiropus serratus*. 17, Process of 4th sternum of holotype, caudal view; 18, Gonopods in situ, ventral view of paratype; 19, Left gonopod of holotype, medial view; 20, The same, lateral view; 21, Distal extremity of expansion of same, subventral view; 22, Undersurface of expansion of male from Duval Co., Florida, subdorsal view. Scale line for Fig. 18 = 1.00 mm; line for other Figs. = 1.00 mm for 17 and 20–22, and 1.33 mm for 19.

depressions along midline. Coxae with low blunt tubercles on segments 9–17; preformal spines beginning on segment 5.

Gonopodal aperture subovoid, 2.8 mm wide and 1.4 mm long at midpoint, indented anteriolaterally, sides raised above metazonal surface. Gonopods in situ (Fig. 18, of paratype) with telopodites projecting ventrad from aperture, bending antiad and extending in subparallel arrangement just beyond anterior margin of aperture, not overlapping. Gonopod structure as follows (Figs. 19–22): Prefemur with elevated flattened area along anterior surface at usual position of prefemoral process. Acropodite short, heavily sclerotized, bending sharply at about $\frac{2}{3}$ length and overhanging prefemur, with folds on medial side at level of bend; widened into broad expansion distal to bend, medial and lateral margins smoothly rounded and continuous, apical margin straight, without lobes but extremely jagged, with two or more rows of sharply pointed teeth, serrations, and ridges, most teeth directed toward undersurface of expansion or stem of acropodite; undersurface deeply concave, smooth basally, with fine serrations merging into rows of sharp teeth near distal margin, with a broad, apically rounded lobe near midlength on lateral side of midline. Solenomerite a narrow, falcate projection located distal to large, rounded boss on undersurface of expansion, tucked under and shielded by overhanging rows of teeth on apical margin of expansion, obscured in both medial and lateral view, visible only in subdorsal perspective looking directly under apical teeth. Prostatic groove arising in pit in base of prefemur, crossing to lateral side on acropodite stem, continuing on undersurface of expansion to base of solenomerite, opening terminally on latter.

Male paratypes.—Except for minor differences in jaggedness on the distal margin of the expansion, the male paratypes agree closely with the holotype.

Female paratype.—Length 32.1 mm, maximum width 8.8 mm, W/L ratio 27.4%, depth/width ratio 63.6%. Agreeing especially with males in somatic features, except paranota more strongly depressed, creating appearance of more highly arched body.

Cyphopods in situ with corner of receptacle and valves visible in aperture, valves directed caudolaterad. Receptacle moderate in size, cupped around caudomedial side of valves, surface moderately rugulose.

Variation.—The only significant gonopodal variation in *serratus* involves the degree of serration on the apical margin of the acropodal expansion and the distal extremity of its undersurface. There is a trend to increased serration from north to south, but the individual teeth become shorter. Thus in the Florida male the marginal teeth are the shortest, and the solenomerite is therefore more visible (Fig. 22). In all males the longer marginal teeth are always on the lateral side, above and overhanging the solenomerite. The teeth are fewer and shorter on the medial side away from the solenomerite, and southern males have more than one lamella on this side with ridges and teeth directed with the marginal axis instead of perpendicular to it. Beneath the marginal overhang the serrations become progressively longer distally and are sometimes clustered laterally along the distal part of the prostatic groove, thus obscuring it from view. The best view of the solenomerite and prostatic groove is the subdorsal one, obtained by “standing the gonopod on its head” with the coxa and apodeme directed up. This view also shows the serrations on the undersurface of the expansion, which lie in rows of increasing size distally, in an arrangement similar to shark’s teeth.

Ecology.—The type specimens were found under thin layers of leaves on sandy-humus soil in a hardwood forest in the undeveloped section of Crooked River State Park beyond the vacation cabins. Live oak and magnolia dominate this locality, but *serratus* was absent from the litter of these species. The male from McIntosh County (NCSM A3591) was discovered under leaves in a small depression on a mowed lawn outside Fort King George Historical Site. At the type locality in July 1977 I collected one male of *serratus* and several males and females of an undescribed species of *Hubroria*, the first time I have ever found syntopic apheloriine species. However, in October 1980 *serratus* was abundant and the species of *Hubroria* was absent. Perhaps the life histories of these species are adjusted so as to minimize ecological competition, with *serratus* emerging in midsummer and becoming dominant by late summer and early fall, and the species of *Hubroria* dominant in spring. This situation contrasts markedly with that of montane species of *Sigmoria*, where only one occurs at a given site even within overlapping ranges, thus avoiding competition (Shelley 1981).

Distribution.—The coastal islands and Coastal Zone of southeastern Georgia and northeastern Florida. The precise locality of the Jacksonville male is unknown, but the Georgia specimens were collected east of highways I-95 and US 17, less than five air miles inland. The St. John's River is a plausible southern range boundary. Specimens were examined as follows:

GEORGIA: *Liberty Co.*, Sunbury State Hist. Site, 2M, 2F, 20 Jun 1983, R. M. Shelley (NCSM A4161). *McIntosh Co.*, Sapelo Island, M, F, 8 May and 27 Jun 1971, E. Rasmussen (ZMC); 1.3 mi. E Darien, nr. Ft. King George Hist. Site, several males and females, 15 Nov 1959, L. Hubricht (RLH) and M, 1 Oct 1980, R. M. Shelley and R. W. Jones (NCSM A3591); and Darien, 2M, F, 11 Sep 1959, L. Hubricht (RLH). *Glynn Co.*, St. Simons Island, M, 12 Sep 1959, L. Hubricht (RLH). *Camden Co.*, Crooked River St. Pk., M, 3 Jul 1977, R. M. Shelley (NCSM A1604) and 4M, 4F, 2 Oct 1980, R. M. Shelley and R. W. Jones (NCSM A3589) TYPE LOCALITY.

FLORIDA: *Duval Co.*, Jacksonville, M, 13 Feb 1921, collector unknown (AMNH).

Remarks.—*Cheiropus serratus* is the smallest species in the genus and considerably smaller than *C. agrestis*, its closest relative. It has a spotty occurrence because of the rarity of suitable habitat, but it can be locally abundant under proper conditions. The MCZ has a female apheloriine from Cumberland Island, Georgia, collected by O. Bangs in March–April 1896, which, based on time of collection, is probably the undescribed species of *Hubroria*. However, *serratus* should be expected on this national seashore later in the year.

Ecology

Few ecological generalizations hold for all four species of *Cheiropus*. *Cheiropus persicus*, and probably also piedmont populations of *agrestis*, occur in typical piedmont climax-subclimax hardwood tracts, but this environment is rare in the coastal areas occupied by the other three species. *Cheiropus plancus* and *serratus* therefore occur in a variety of predominantly hardwood sites, which are the best spots available in the generally unfavorable coastal environments. The same is probably also true for coastal populations of *agrestis*.

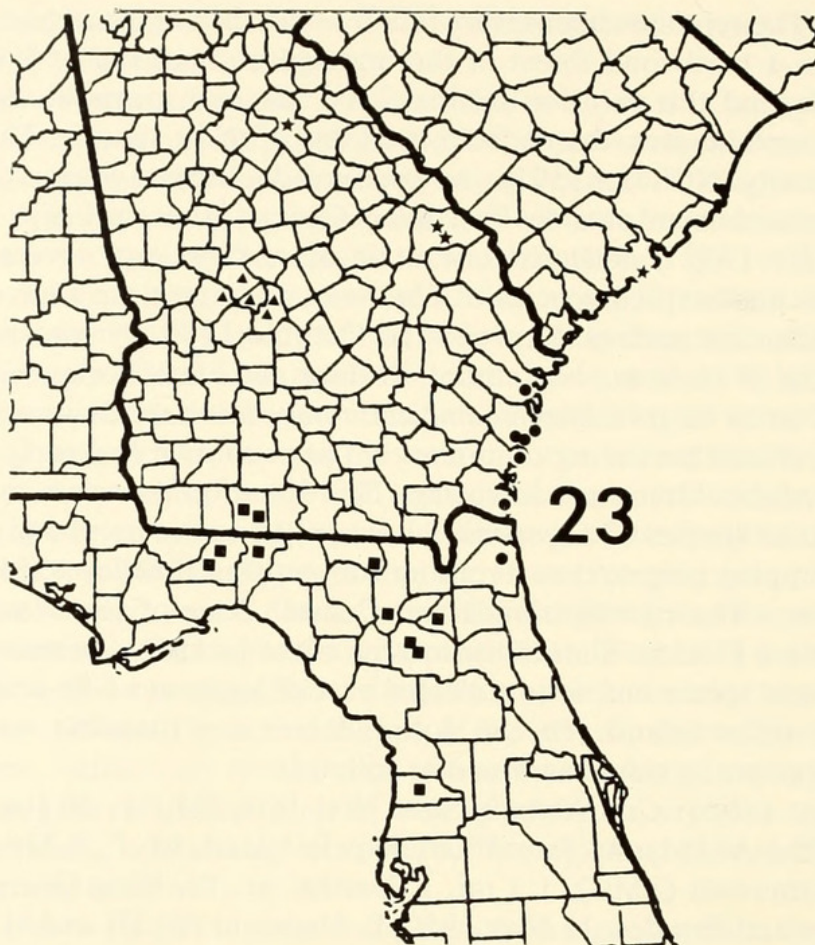


Fig. 23. Distribution of *Cheiropus*. dots, *serratus*; squares, *plancus*; triangles, *persicus*; stars, *agrestis*.

The species also occur at different times of the year. *Cheiropus plancus* is prevalent in midsummer but absent in autumn when *serratus* is available. On the other hand, *persicus* has been encountered in both spring and fall, but as its area has not been sampled in summer I do not know if it is available throughout the warm seasons of the year.

Distribution

The distribution of *Cheiropus* extends in the north-south direction from the Coastal Plain of southeastern South Carolina to west-central peninsular Florida, and east-west from the Atlantic Ocean to the central Piedmont Plateau of northern Georgia (Fig. 23). It is the most southern and most coastal apheloriine genus, and its type species is the southernmost in the tribe. Only *Dicellarius* and *Pleuroloma* occur farther south, each represented by one species in peninsular Florida, but the centers of abundance for these taxa lie outside the Atlantic Coastal Plain.

The four species of *Cheiropus* are entirely allopatric. Except for *persicus*, all span large rivers, and except for *agrestis*, all are limited to a single physiographic province. The known range of *serratus* is unusual for an apheloriine millipedin being linear and extremely narrow, resembling in this regard that of *Furcellaria aequalis* Shelley (Shelley 1981b). The two southernmost taxa, *plancus* and *serratus*,

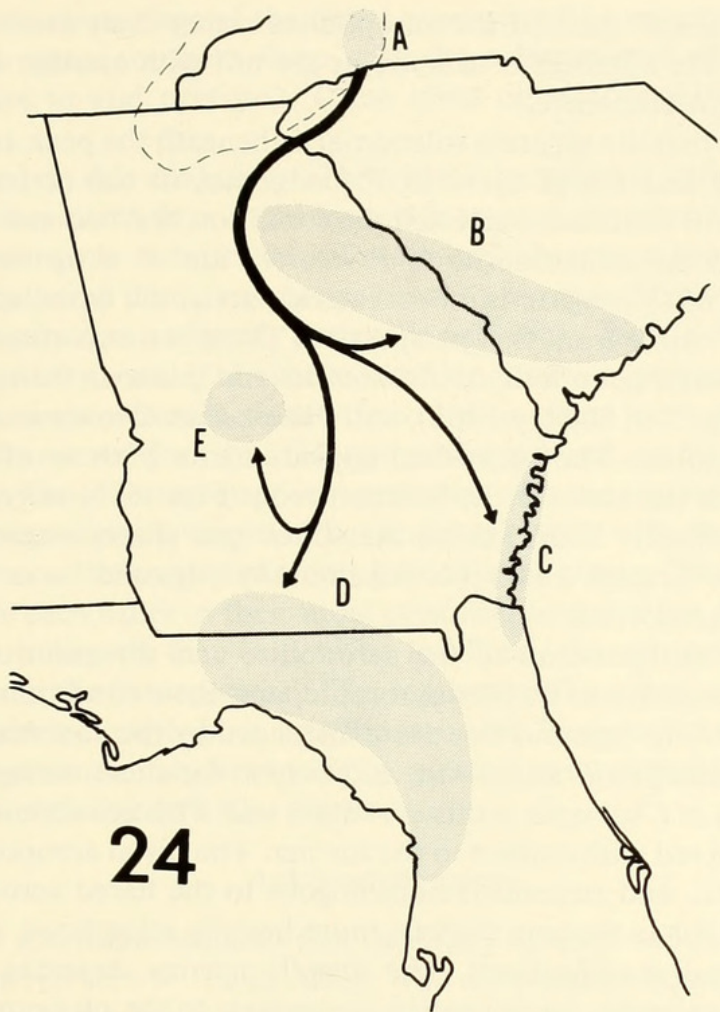


Fig. 24. Relationships in *Cheiropus* and *Prionogonus*. A, *Prionogonus*; B, *agrestis*; C, *serratus*; D, *plancus*; E, *persicus*. The dashed line is the approximately boundary of the southern Appalachian (Blue Ridge) Mountains.

are partly sympatric with the undescribed species of *Hubroria*, and in central Georgia, the range of *persicus* is near those of *Dynoria medialis* Chamberlin and *Cleptoria rileyi* (Bollman) (Shelley in press; Hoffman 1967). *Cheiropus agrestis* spans the ranges of several species of *Crotania*, *Brevigonus*, and *Cleptoria* in both South Carolina and Georgia (Shelley 1977, 1981c; Hoffman 1967).

The distributions within the ranges differ. *Cheiropus persicus* occurs continuously in its known area, but the other three species have patchy distributions reflecting the spotty occurrence of suitable lowland and coastal habitat. Thus, sizeable hiatuses, spanning a number of counties, exist between sample sites of *agrestis*, and smaller ones occur within the ranges of *plancus* and *serratus*.

Relationships

The generic affinities of *Cheiropus* are not easily inferred, because there are no obvious similarities with other genera. Of the geographically proximal taxa, *Hubroria* is closely related to *Sigmoria* (Shelley 1981a), and the gonopods of *Cleptoria*, *Crotania*, and *Brevigonus* conform to different patterns from that of *Cheiropus*. *Dynoria* and *Furcellaria* have separate but non-homologous solenomerites because

they are on the medial sides of the acropodites rather than on the lateral as in *Cheiropus*. Thus, the affinities of *Cheiropus* are not with another lowland genus and must be sought elsewhere.

In 1982 I stated that the separate solenomerite beneath the peak and the absence of the distal zone and apical curve in *Prionogonus*, in the eastern Blue Ridge Mountains of North Carolina, suggested the condition in *Cheiropus*, and it should also be noted that the solenomerite in *P. haerens* and *P. divaricatus* Shelley, as in all four species of *Cheiropus*, is on the lateral part of the flared acropodite peak and most clearly visible from this perspective. There is a superficial similarity in medial view between gonopods of *P. haerens* and *plancus* (compare Fig. 3 of this paper with Fig. 3 of Shelley 1982), and I think that *Cheiropus* is most closely related to *Prionogonus*. The occasional appearance in *plancus* of a spur on the lateral shoulder at the base of the solenomerite (Figs. 6–7) may be additional evidence of this affinity. Thus, I think that *Cheiropus* shares a common ancestor with *Prionogonus*, through which it is linked to the “sigmoid” taxa that constitute the bulk of the Apheloriini.

I consider the configuration of the acropodite and the position of the solenomerite in *Prionogonus* to be plesiomorphic, and their conditions in *Cheiropus* to be apomorphic. The sigmoid curvature displayed by the vast majority of apheloriine taxa is retained in *Prionogonus*, and only in the short, straight acropodites of the four species of *Cheiropus* is this curvature lost. This condition may therefore be considered derived with respect to the former. The distal acropodite expansion in *plancus*, *agrestis*, and *serratus* is homologous to the flared acropodite peak in *Prionogonus*, but it has become thicker, more heavily sclerotized, and developed secondary marginal modifications. The distally narrow, tapering acropodite of *persicus* is an apomorphic specialization in contrast to the plesiomorphic state in the other species and *Prionogonus*.

Most apheloriine species lack a solenomerite, and the prostatic groove opens terminally at the tip of the acropodite. Comparatively few species possess a divided acropodite or a separate projection from the stem of the latter that carries the groove and hence is termed a solenomerite. The presence of a solenomerite is thus considered apomorphic with respect to its absence. The most plesiomorphic position possible for a solenomerite in this tribe is terminally on the acropodite as in *Prionogonus*, since the groove opens terminally in the majority of species. More proximal locations are thus apomorphic with respect to more distal ones. Hence, *persicus* exhibits the most apomorphic solenomerite, since it arises basally just distal to the prefemur. The position in *plancus* is apomorphic with respect to that in *agrestis* and *serratus*, which in turn is apomorphic with respect to that in *Prionogonus*. Consequently, there is a southward cline from distal to more proximal solenomerites that is interrupted by *persicus* in central Georgia. *Cheiropus*, then, represents apheloriine stock that dispersed in a southeastward direction from a probable source area in the eastern Blue Ridge Mountains and escarpment where *Prionogonus* occurs today. *Prionogonus* probably originated there since it appears to share a common ancestor with the sympatric species, *Sigmoria stibarophalla* Shelley (Shelley 1982). Its limited range suggests that *Prionogonus* represents a relict population that remained in the area when the proto-*Cheiropus* stock dispersed. The sequence of events in the evolution of *Cheiropus* probably involved an early dichotomy in northern Georgia into one form with the solen-

omerite on the undersurface of the distal expansion (the ancestor of *agrestis* and *serratus*) and a more southern form with the solenomerite shifted basally (the ancestor of *plancus* and *persicus*). These ideas on relationships are depicted in Fig. 24.

Superimposed on this analysis of *Cheiropus* is geographic variation that crosses cladistic lines. For example, a trend toward increased serration in the eastern part of the generic range is manifested by more and sharper acropodal teeth in the populations of *plancus* that are most proximal to *serratus*. Likewise, the acropodal expansion in *agrestis* is reduced, flattened, and more serrate in the Charleston County male, which occurs at about the same longitude as *serratus*. The acropodite in this individual also resembles that of *serratus* in being more upright and linear than the broadly curved forms in Georgia whose general configurations resemble that of *persicus*. These features appear to conflict with the phylogeny of *Cheiropus*, but they are geographically logical if an ancestral stock with clines in such characters undergoes vicariance partitioning in several places. The resultant clades would resemble each other in their most proximal populations, and in non-vagile organisms like millipeds that tend to be localized, the similarity would persist indefinitely. Thus, the four species of *Cheiropus* exhibit residual ancestral variation that is independent of phylogeny, and the same can be expected in other diplopod taxa. This phenomenon may be especially valuable in interpreting mosaic patterns of species in complex genera like *Sigmoria*.

Acknowledgments

The types of *Cheiropus plancus* and *Stelgipus agrestis* were examined through the courtesy of Herbert W. Levi, MCZ, who also loaned non-type material and donated two Kodachrome slides of *C. plancus* from which the living color was determined. Material in the FSCA and AMNH was loaned by Howard V. Weems, Jr., and Norman I. Platnick, respectively. My colleagues Richard L. Hoffman and William A. Shear kindly donated specimens from their private collections. The samples from Crooked River State Park, Georgia, were taken with permission of the Parks, Recreation, and Historic Sites Division, of the Georgia Department of Natural Resources. I thank Donald R. Whitehead, for his astute, invaluable review, and Renaldo G. Kuhler, NCSM scientific illustrator, for preparing Figs. 2, 9, 14–16, and 19–22. This project was supported in part by NSF Grants DEB 7702596 and 8200556.

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