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REVISION OF THE MILLIPED GENUS HARPAPHE COOK FROM WESTERN NORTH AMERICA (POLYDESMIDA:XYSTODESMIDAE)

JOHN S. BUCKETT

AND

MICHAEL R. GARDNER

BUREAU OF ENTOMOLOGY

DEPARTMENT OF AGRICULTURE

SACRAMENTO, CALIFORNIA

BUREAU OF ENTOMOLOGY

CALIFORNIA DEPARTMENT OF AGRICULTURE

1220 N STREET

SACRAMENTO, CALIFORNIA 95814

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REVISION OF THE MILLIPED GENUS HARPAPHE COOK FROM WESTERN NORTH AMERICA (POLYDESMIDA:XYSTODESMIDAE)*

by

John S. Buckett
Systematic Entomologist
Bureau of Entomology
Department of Agriculture
Sacramento, California

and

Michael R. Gardner
Department of Entomology
University of California
Davis, California

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Harpaphe haydeniana scotia (Chamberlin)

INTRODUCTION

The genus *Harpaphe* is composed of moderate-sized dark millipeds with yellow tipped paranota and telson. Though rarely seen, these millipeds occur on the west coast of North America, from Alaska to central California, and are thus far not known to occur further inland than the Sierra Nevada Mountains of California.

Careless taxonomic methods well familiar to students of the Diplopoda have characterized the treatment of the group. Names currently associated with *Harpaphe* have been placed in five other genera. Ten species have been proposed within the group at one time or another; nine species were recognized in the checklist of Chamberlin and Hoffman (1958), but only three species are presently regarded as valid.

The physical and biological conditions which prevail in western North America have at times been misinterpreted by previous workers, resulting in taxonomic confusion. California possesses unusual climatic conditions and a unique geologic history, and these factors have contributed to an unusually diverse milliped fauna. Loomis (1938) stated, "The Pacific Coast States, particularly California, have a larger and more varied milliped fauna than is to be found in any like area of the Eastern United States." Undoubtedly, the factors which have created this diversity are still operating and continuing this very active speciation. For this reason extreme care must be exercised in the analysis of geographic variation in order to assure the erection of valid classifications.

MATERIALS AND METHODS

During the course of the present study 180 specimens were examined, representing all of the names recognized as valid. We have personally collected material of half of the entities, and therefore we were able to gather some ecological data.

Abbreviations of institutions and individuals from which material was borrowed are as follows:

B&G - Collection of J. S. Buckett & M. R. Gardner, Davis, California.
CAS - California Academy of Sciences, San Francisco, California.
CDA - California Department of Agriculture, Sacramento, California.
CMNH - Chicago Natural History Museum, Chicago, Illinois.
NBC - Collection of Dr. Nell B. Causey, Baton Rouge, Louisiana.
RLH - Collection of Dr. Richard L. Hoffman, Radford, Virginia.
USNM - United States National Museum, Washington, D. C.

All drawings were made with an ocular grid mounted in an AO Spencer binocular microscope with the specimens submerged in alcohol. Gonopods and cyphopods were removed before being stu-

died, the surrounding muscle tissue being pulled away. It was found that desiccation of the gonopods caused bending of the slender endites and telopodites, and that clearing in hot KOH (potassium hydroxide) may dissolve the structures of interest or cause them to lose their characteristic form.

Knowledge of typical material is essential if proper placement of all named entities is to be achieved. In the course of our work, we have seen the holotype of *"Paimokia" telodonta* Chamberlin and topotypes of *Harpaphe clara* Chamberlin. In addition, Dr. R. L. Hoffman kindly made gonopod drawings available of the holotypes of *"Fontaria" simoni* Brolemann, *"Polydesmus" intaminatus* Karsch, and *"Pachydesmus" cummingsiensis* Verhoeff. Of the remaining names, *"Polydesmus" haydenianus* Wood, *"Paimokia" scotia* Chamberlin, *"Paimokia" maculifer* Chamb., *Paimokia modestior* Chamb., *Harpaphe penulta* Chamb., *Harpaphe pottera* Chamb., and *Harpaphe inlignea* Chamb., specimens have been examined which agree with the original descriptions.

ACKNOWLEDGEMENTS

At this time we wish to take the opportunity to express our appreciation to Dr. P. H. Arnaud, Jr., for the loan of specimens contained in the California Academy of Sciences, San Francisco; to Mr. George T. Okumura for loan of the specimens in the Bureau of Entomology, California Department of Agriculture, Sacramento; to Mr. Darwin L. Tiemann for color photographs of *Harpaphe* and information on their fluorescence; Dr. Nell B. Causey for material from her private collection and for information on the identity of *"Paimokia" maculifer* and *P. modestior*. We are especially indebted to Dr. R. L. Hoffman for providing us with drawings of certain holotypes and loaning us specimens contained in his collection. We also wish to thank Dr. R. M. Bohart for his valuable suggestions throughout the preparation of this paper. Finally, we wish to express our appreciation to Mr. Ronald C. Gardner, Mr. Stanley E. Harrison, Mr. Jacques R. Helfer, Mr. Peter Richerson, Mrs. Iris Savage, and Mr. Harold Wilson, who collected specimens for us which greatly enhanced the value of this work, and to Mrs. Cindy Sullivan for typing the final manuscript.

LITERATURE REVIEW

Polydesmus haydenianus Wood, 1864, described from Oregon, was the first known species to be included in the genus *Harpaphe* Cook. Wood's description of the gonopods is fully adequate for the generic identification, and at the time of that publication he placed the type in the United States National Museum. However, it is no longer known to be extant. In 1865 Wood published a drawing of the gonopod. The species was next treated by Charles Harvey Bollman (1893) in his checklist of North American Millipeds, and it was placed in the genus *Leptodesmus* Saussure.

Ferdinand Karsch (1881) added an additional species, *Polydesmus (Oxyurus) intaminatus*, included a description useful only at the generic level, and cited "California" as the only locality data. Henry W. Brölemann (1896) described and illustrated the gonopods of a third entity, *Fontaria simoni*, from Washington State. Carl Attems (1899) included *intaminatus* in his monumental work, "System der Polydesmiden," placing it also in the genus *Leptodesmus*.

O. F. Cook (1904) described the genus *Harpaphe* and included both *haydenianus* Wood and *intaminatus* Karsch, the former being the type species. Interestingly, Cook recognized the similarity of the two forms and mentioned that *intaminatus* "may easily prove to be a synonym of *H. haydeniana*."

Harpaphe was not dealt with until 1938 when Attems, in his last great treatise on the Polydesmida, listed *Harpaphe haydeniana* and included *intaminata* in *Pachydesmus*. Hoffman (1958) explained the obvious error in this placement, the two genera bearing only some superficial resemblance.

R. V. Chamberlin (1941) described the genus *Paimokia*, including the new species *modestior*, *maculifer*, and *scotia*, the last of which should have been placed in the genus *Harpaphe*. Chamberlin (1943) described *Paimokia telodonta*, and K. W. Verhoeff (1944) described *Pachydesmus cummingsiensis*, both of the species being other incorrectly placed members of *Harpaphe*. In 1947 Chamberlin treated *Paimokia scotia* as a synonym of *H. intaminata*. Shortly thereafter, Chamberlin (1949) transferred *Paimokia telodonta* into *Harpaphe* and described the new species *H. clara*, *H. inlignea*, *H. penulta* and *H. pottera*. At this point, nine proposed names in three genera representing entities of *Harpaphe* were present in the literature.

In the checklist by Chamberlin and Hoffman (1958) the primary steps toward clarification of the confusion were taken by associating all of the names connected with *Harpaphe*. Nine species were recognized, including *clara* Chamberlin, *inlignea* Chamb., *pottera* Chamb., *penulta* Chamb., *maculifer* (Chamb.), *modestior* (Chamb.), *telodonta* (Chamb.), *haydeniana* (Wood), and *intaminata* (Karsch). *Paimokia scotia* Chamberlin and *Pachydesmus cummingsiensis* Verhoeff were placed as synonyms of *H. intaminata*. *Fontaria simoni* Brölemann was placed in *Harpaphe* as a synonym of *haydeniana*. Also placed in the genus for the first time were *cummingsiensis* Verhoeff, *maculifer* Chamberlin, and *modestior* Chamberlin.

All of the aforementioned names except *Paimokia modestior* and *P. maculifer* are treated here as belonging to *Harpaphe*. *P. modestior* is the only known species presently believed to belong to *Paimokia*, and *P. maculifer* is believed by Dr. Nell B. Causey (personal communication) to actually belong to the genus *Sigmocheir* Chamberlin.

After careful study we have concluded that there are apparently three species in *Harpaphe: haydeniana* (Wood), *pottera*

Chamberlin, and *telodonta* (Chamberlin). The remaining names represent subspecies of *haydeniana* or synonyms.

BIOLOGICAL NOTES

General Ecology: Species of the genus *Harpaphe* possess a distinct and somewhat unique niche among western Xystodesmids. Most Xystodesmids collected by the authors were found in oak woodland with varying degrees of leaf litter on the ground. *Xystocheir*, *Cheirauxus*, *Paimokia*, *Hybaphe*, *Sigmocheir*, *Motyxia*, and *Wamokia* are usually scattered widely over the area where they occur. *Harpaphe*, on the other hand, is not known to occur in oak litter. Of four collections we have made, two have been in alder litter (*Alnus rhombifolia* Nutt.), one in mixed alder and redwood litter [*Sequoia sempervirens* (D. Don) Endl.], and one in redwood. Furthermore, collections we made of *scotia*, *cummingsiensis*, and *maurogona* have indicated a strong tendency toward clustering in the population. Many individuals were collected in a location less than ten feet across in its greatest dimension. In the last two subspecies mentioned, some specimens were encapsulated in individual earthen chambers under a log. This observed capsulation and clustering may be interpreted as a response to drought conditions; yet collections of two species, *scotia* and *cummingsiensis* were made in late December during the wettest part of the season. The true meaning of habits such as these will be elucidated only when further data are available.

Period of Activity: In California, collections of adult *Harpaphe* are generally made from December through June. The latest annual record is from Mendocino, Mendocino County on 1 July. Presumably, the increasing dryness of summer requires the millipeds to burrow into the ground and aestivate, whence they emerge with the winter rains. In northern areas (Oregon, Washington, Canada, and Alaska) where the winters are more severe, this situation is altered, the collections being made from April through September.

Sex Ratio: During the months of December through February, collections usually show an abundance of females over the males. Of three large collections we have seen, one of *cummingsiensis* in December yielded 16 males, 28 females, one of *lanceolata* in February 2 males, 11 females, and one of *scotia* in December 10 males, 8 females. In the spring and summer this ratio seems to be reversed, at least in California where aestivation is necessary for most populations. The collection of *maurogona* made in June yielded 14 males and 2 females. All collections of *Harpaphe* made in California after 15 April totaled 40 males and 15 females.

The more accurate figures for the sex ratio of *Harpaphe* species are probably those of the winter months when the moisture conditions permit full activity. In the spring months when the moisture content is low in the duff in most of Calif-

ornia, at least, specimens of the populations of *Harpaphe* burrow into the soil where aestivation occurs. The greater number of males collected in spring and summer may be due to the females burrowing into the ground before the males, perhaps for oviposition.

Fluorescence: In response to his request we sent a few living specimens of *scotia* to Mr. Darwin L. Tiemann, who reported to us that the specimens fluoresced when exposed to U V light radiation. We repeated Mr. Tiemann's test and found that specimens of *scotia* did glow an off-white color over their entire bodies when subjected to fluorescent black light. Specimens of *H. telodonta*, the only other living species available to us at that time, glowed only very faintly when exposed to the U V light.

Laboratory Rearing: We kept specimens of *scotia* in the laboratory for a period of nearly seven months. With an ample quantity of their native litter, they survived in a variety of containers, including gallon jars, coffee cans, and plastic bags. Juveniles from as young as fourth instar reached adulthood. Pairs of adults kept in jars and observed were not seen to copulate, nor were eggs or larvae found.

TAXONOMIC CHARACTERS

Members of the genus *Harpaphe* can be distinguished from most related western genera by superficial characters, although characterization is greatly facilitated by use of the male gonopods. *Harpaphe* is distinct from other related genera by the possession of both an elongate femoral process and a short truncate prefemoral process of the gonopods. Major superficial features which are useful in distinguishing the group are the dark coloration and yellow-tipped paranota and telson. This exact color pattern is apparently shared only with *Chonaphe*, *Paimokia*, *Hybaphe*, and *Montaphe* among western Xystodesmid and with *Boraria* of the east. Also, the possession of sharply pointed posterior corners of the paranota helps to distinguish *Harpaphe* from *Isaphe*, *Hybaphe*, *Tubaphe*, and *Chonaphe*.

The major characters used to distinguish entities within the genus are dealt with individually.

Size of Body: From the material studied there appears to be a definite relationship between body length and collection locality of the specimens. This character cannot be used in a key, however, since the various forms all overlap in size. *Harpaphe telodonta* is generally smaller than *haydeniana* and *pottera*, but this character cannot be relied upon to separate the species because most Alaskan and some Canadian specimens of *haydeniana* are smaller than the mean length of *telodonta*.

Color Pattern: The color of all species in the genus *Harpaphe* conforms to the same general pattern but differs in shades of color. A freshly collected specimen of *haydeniana* appears

to be jet black dorsally, brown ventrally, and with bright yellow on the lateral extensions of the paranota and telson. In the California populations of *Harpaphe* that we have seen alive, the color appeared to be much less pronounced, the black and yellow appearing lighter. In a population of *scotia* (topotypes of synonym *clara*), the living specimens definitely appeared to be an olive green with yellow paranota. This green color turned to black, however, when the specimens were placed in plastic bags and brought into the lab; the cause of this phenomenon is unknown.

Gonopods: The configuration of the male gonopods offers extremely useful and generally easily discernible taxonomic characters. They have been so useful that some workers have tended toward describing only the gonopods in their characterization of new species, and to recognize every such variant as a distinct species. As is shown in the following pages, lack of consideration for morphological variability in the gonopods can lead to taxonomic confusion.

The large coxa is similar in all known forms. The coxal apodeme, however, varies in length and width, being largest in populations from the Coast Ranges just north of San Francisco Bay.

The prefemur bears a truncate process which is of some taxonomic usefulness. Chamberlin (1949) used the configuration of the apex of the prefemoral process in diagnoses of species, stating whether it was convex, concave, or "highest at anterior end." These features, however, are variable and not always correlated with distribution. Nonetheless, the relative size of the prefemoral process is somewhat constant within populations and is herein used as a supplementary character.

The curved process of the femoral division of the telopodite presents variations which are of prime importance in certain instances. The main genitalic distinction between *telodonta* and the other species within the genus lies in the presence of a broad, bi- or tri-dentate apex of the femoral process. In *pottera* and all subspecies of *haydeniana*, the femoral process is simple, but varies in form. In *scotia* it is unusually broad; in *lanceolata* it is long and strongly curved mesad; in *maurogona* it is broad and strongly twisted counterclockwise when viewed apically. Besides these special modifications all populations exhibit two types of variation: in one, the apex is slightly twisted counterclockwise near the apex; in the other the apex is directed slightly mesad.

The tibiotarsus (solenomerite of some authors and posterior blade of Chamberlin) is the curved distal section of the gonopod. It exhibits geographic variation and has been used as the primary diagnostic character in the erection of *pottera* and two of the forms of *haydeniana*. In *pottera* the tibiotarsus is less curved, the apex being directed distad rather than proximad. In several subspecies of *haydeniana*, namely *haydeniana*, *lanceolata*,

scotia, and *maurogona*, the tibiotarsus is of rather constant width and is evenly curved with the apex acuminate, directed proximad; in *cummingsiensis* the tibiotarsus is unusually long and narrow and is strongly curved basally; in *inlignea* the apex is blunt instead of acuminate. Although the configuration of the tibiotarsus is relatively stable within populations, in at least one case it loses its modified aspects in the extremities of the range; i.e., the tibiotarsus of *cummingsiensis* becomes more like that of *haydeniana* in the northern and southern reaches of its known distribution.

Shape of Paranota: Constant superficial differences lend confidence to the conclusion that two species are distinct when separable by genitalia. In one of the species recognized herein, there is a definite difference in shape of the paranota of the anterior and medial body segments. In *haydeniana* and in *pottera* the anterolateral margins of these segments are rather abruptly curved and the posterior corners are usually obtusely pointed but not projecting caudally. In *telodonta*, however, the corners are broadly rounded anteriorly, acutely pointed posteriorly, and projecting caudally beyond the posterior border of the segment.

Cyphopods: Cyphopods of five subspecies of *haydeniana* were examined and found to provide no suitable subspecific characters, as variation was found to be too slight to be of significant value. The degree of extrusion of the valves from the receptacle varies greatly, and this appears to be a function of the muscles governing the cyphopods. Constant differences were found, however, between two of the species in the shape of the large valvular lobe. In *haydeniana* it is broadly rounded, and in *telodonta* it is rather small and sharply rounded. The single female specimen of *pottera* showed no apparent differences from *haydeniana*.

HARPAPHE Cook

Harpaphe Cook, 1904, in Harriman Alaska Exped., 8:59
Type Species: *Polydesmus haydenianus* Wood, by original designation.

Diagnosis: Body of typical Xystodesmid shape and moderate in length (28-48 mm); color dorsally black or olive cast, with tips of the paranota and telson yellow, ventrally light brown.

Dorsum of mid-body segments rounded, the paranota small, projecting outward laterally from just above mid-body; paranota directed downward about 15° from horizontal and tilted about 20° with posterior margin higher than anterior margin.

Tergites appearing smooth except for 1-4 transverse rows of small tubercles plus lightly scattered random tubercles; prozonites and metazonites separated by prominent furrow crossed by longitudinal striations, the furrow extending ventrally around anterior margin of sternum, thus ringing entire segment; pleural

area of metatergite roughened, forming sub-parallel longitudinal wrinkles; sterna smooth, not produced on legs; legs widely separated, the anterior and posterior pairs equally separated and raised out from the level of the body; legs long, extending beyond both lateral margins of body; leg segments not modified except for large distal spines on the prefemur.

Gonopods of male small, apices crossing in situ, but not projecting between seventh pair of legs; coxae joined by unsclerotized connective tissue and contained almost entirely within gonopod socket, a long basal coxal apophysis present; prefemur with short, truncate process; femur with long process curved distad though not reaching tibiotarsus; tibiotarsus long, curved cephalomesad; seminal canal emerging mesally on coxa, proceeding up prefemur, around anterior face of femur to lateral margin, then along posterior face of tibiotarsus to apex.

Cyphopods of female of usual Xystodesmid shape and size (see figs. 7-9).

GENERIC RELATIONSHIPS

Only two postulations as to the generic relationships of *Harpaphe* have been found in the literature. Cook (1904) began his description of the genus by noting that *Harpaphe* is closely related to *Isaphe* Cook and *Hybaphe* Cook, both by gonopods and superficial characters. Indeed, Cook even questioned the validity of recognizing different genera for the species involved. Hoffman (1958), in discussing the relationships of *Pachydesmus*, placed *Harpaphe* in the *"Rhysodesmus-Boraria* complex", noting the structural similarity between *Harpaphe* and *Boraria*.

Both *Boraria* and *Hybaphe* do seem to be related to *Harpaphe*. Too little is known about *Isaphe* to determine its relationship to *Harpaphe*, although there is some apparent similarity in the gonopods. Like *Harpaphe*, both *Boraria* and *Hybaphe* possess spines only on the prefemur, possess smooth sterna, gonopods which are small in relation to body size, with an indistinct sternal remnant connecting the coxae.

An unusual feature of the gonopods of *Harpaphe* was pointed out by Dr. Hoffman (personal communication). The seminal canal makes a 360° circuit around the gonopod, indicating that the gonopod itself has been twisted one full revolution during the evolution of the genus. The seminal canal of *Hybaphe* follows an almost identical course, indicating a high liklihood that the two genera are closely related. The seminal canal of *Boraria*, on the other hand, follows a more direct course to the apex, revealing the absence of gonopod twisting.

Ecological similarities are present in these genera as well. *Boraria* was observed by Hoffman (1965) to be semi-aquatic, occurring in wet habitats very near streams. The three collections of *Hybaphe* which we have made were also taken a few yards

from streams, although in more conventional terrestrial habitats. *Harpaphe* populations observed by us certainly were not semi-aquatic, but their associations with riparian plants makes the possibility of relationship to a semi-aquatic genus very feasible. Thus, both *Hybaphe* and *Boraria* exhibit morphological and ecological similarities to *Harpaphe* which are probably of phylogenetic significance, but *Hybaphe* seems to be the genus most closely related to *Harpaphe*.

SPECIFIC RELATIONSHIPS

Nominate *H. haydeniana* appears to be the least specialized entity, being morphologically intermediate between the more modified types and ecologically inhabiting the primitive Pleistocene-like habitat. The tibiotarsus is evenly curved and of equal width; the femoral process is relatively narrow and evenly curved distad. Furthermore, the tibiotarsus of nominate *H. haydeniana* is quite similar to that of *H. telodonta*, suggesting ancestral relationship.

A tentative history of the group can be correlated with the recent geologic past. According to Daniel I. Axelrod (1965, p. 7): "Members of the Coast Forest (*Sequoia, Chamaecyparis, Thuja, Abies*, etc.) which occupied the coastward slopes of the northern Sierra Nevada by the close of the Miocene, gradually shifted to a more coastal position during the Pliocene as aridity increased." Through its apparently obligatory association with moisture-requiring plants such as *Sequoia* and *Alnus*, specimens of *Harpaphe* probably also inhabited this coastal forest.

During the Pleistocene the climate became cooler and much more moist, permitting the extension of the Coast Forest southward, *Sequoia sempervirens* reaching as far south as the coast opposite the Channel Islands. The southern Sierras and transverse ranges had been elevated by mid-Pleistocene sufficiently to accommodate the Sierran Flora, of which *Alnus* was a constituent. It is probable that during this moist period, *Harpaphe haydeniana* expanded its range southward along the coast, eastward above the Great Central Valley to the Sierras and southward along the Sierras. Indeed, if the Sierran record of *scotia* is valid, it appears as though that form might have migrated from the Coast Ranges across the Tehachapi Range to the Sierras.

Following this glacial period, *H. haydeniana* migrated northward along with its associated plants from California to its present northern limit in Alaska. During this same period there has been a steady decrease in precipitation in California which has eliminated many populations of plants, especially in the southern Sierras. *Alnus* has become limited to streambed situations for the most part, and populations of *Harpaphe* also have become scattered and isolated. These isolated groups of populations have adapted to the relative dryness and evolved to the subspecies state. It is notable that only *H. pottera* and sub-

species of *haydeniana* have adapted to the dryer habitat. *H. telodonta* is limited to the north coast of California, which is the area most closely resembling the moist Pleistocene conditions (see Stebbins and Major, 1964). Presumably, *telodonta* was unable to adapt to the more recent dryer conditions and was spared from extinction by the climate of the north Pacific coast. On the basis of these more strict ecological requirements as well as morphological differences, *telodonta* is therefore considered a relic species.

A dendrogram based on structural similarities is presented in figure 3.

KEY TO SPECIES AND SUBSPECIES OF *HARPAPHE*

1. Body segments 10-15 with posterior corners of paranota projected caudad, acutely pointed; gonopods with femoral process broad at apex and distinctly bi- or tri-dentate (as in figs. 10 & 11)..... *telodonta* (Chamberlin).
   Body segments 10-15 with posterior corners of paranota not projected caudad, obtuse; gonopods with femoral process simple.....2

2. Tibiotarsus of gonopod directed distad and not much curved; i.e., apex is most distally projecting part of gonopod; femoral process curving distad and slightly laterad (as in fig. 12)..... *pottera* Chamberlin.
   Tibiotarsus proceeding distad, then curving so that apex directed proximad; femoral process curving more directly distad or mesad.....3

3. Terminal portion of tibiotarsus blunt, rounded (see fig. 21); prefemoral process long and wide, with linear apex (as in fig. 21)..... *haydeniana inlignea* Chamberlin.
   Tibiotarsus narrowing gradually to acute apex.....4

4. Tibiotarsus long, quite narrow, strongly bent at base and nearly straight for much of its length (as in fig. 23)... ..... *haydeniana cummingsiensis* Verhoeff
   Tibiotarsus not as above, either more evenly curved or wider.....5

5. Femoral process either strongly curved mesally or twisted 90°.....6
   Femoral process curving evenly distad, only slightly twisted or mesally bent.....7

6. Femoral process strongly bent mesad and twisted counterclockwise so as to appear very narrow from anterior aspect (as in fig. 19)..... ..... *haydeniana lanceolata* Buckett & Gardner

Femoral process not bent mesad, strongly twisted counterclockwise so that apical part appears abruptly narrowed from anterior view (see fig. 20)..... ..... *haydeniana maurogona* Buckett & Gardner

7. Femoral process narrower than tibiotarsus; body length usually 28-36 mm..... *haydeniana haydeniana* (Wood)
Femoral process broad, wider than some parts of tibiotarsus; body length 37-43 mm..... *haydeniana scotia* (Chamberlin)

Harpaphe telodonta (Chamberlin)

Paimokia telodonta Chamberlin, 1943. Bull. Univ. Utah Biol. Ser. 8(2):17, fig. 33.
Harpaphe telodonta, Chamberlin, 1949. Proc. Biol. Soc. Washington, 62:129, fig. 11; Chamberlin and Hoffman, 1958, Bull. United States Natl. Mus. 212:35-36; Buckett, 1964, Annotated List Diplopoda California, p. 8; Buckett and Gardner Proc. New York Entomol Soc. 76(1):60-63, figs. 1-3.

TYPES: Male holotype, now in U. S. National Museum, from Arcata, Humboldt County, California, collected by Earl Mills on December 19, 1942. This type was found in the collection of the Bureau of Entomology, California Department of Agriculture (see Buckett & Gardner, 1968).
DIAGNOSIS: In the male, distinguished by the broad bi- or tridentate apex of the femoral process of the gonopod and by the acute posterior corners of the paranota of middle body segments; in the female by the sharply curved valve of the cyphopods.
DESCRIPTION: Holotype male: (modified from Buckett and Gardner, 1968). Length 33 mm (specimen slightly distended); width 4.5 mm. Body slender, nearly uniform in width; first five segments becoming broader from 3.5 mm to 4.5 mm, this greater width being prevalent through segment 17.

Head both dark and light brown, reticulate, glabrous; coronal suture well developed, with margins smooth and even; a prominent pair of setae present on both sides of coronal suture at its midpoint; three setae present on each side of frons in straight line between median juncture of frontal sutures and lateral margins of labrum; genae (laterad of clypeus and ventrad of antennae) each with two closely situated setae; antennae separated by distance equal to length of third antennal segment, total antennal length 5 mm; first antennal segment as broad as long, with prominent dorsal seta; antennal segments two through five subequal in size and shape, two and three sparsely setose, with a single erect large subterminal dorsal seta; sixth antennal segment slightly shorter and more evenly conical, seventh antennal segment about one quarter the length of sixth, cylindrical, with four terminal sense cones; antennal segments four through seven densely setose, without prominent setae.

Collum narrower than second body segment, its anterior margin evenly convex, posterior margin slightly medially concave, laterally convex, ventrolateral corners rounded.

Dorsum of tergites strongly convex; paranota relatively small, produced laterad and slightly ventrad, making a distinct obtuse angle with the curvature of the tergite; anterior and lateral margins of paranota thickly rounded, posterior margins sharp; repugnatorial pores opening on posterolateral margin of paranota; surface of tergites finely and shallowly reticulate; series of tubercles present in the following pattern: collum and segment 2 with one transverse row of seven or eight tubercles near posterior margin; except for segment 8, segments 3-12 with two transverse rows of tubercles ranging from three to eight on the anterior row and from five to eleven on posterior row; segments 13-18 with three rows of tubercles, anterior with six to eight, middle with six to thirteen, and posterior row with thirteen to seventeen tubercles.

Second segment with anterior and posterolateral corners rounded, not produced; following four segments with posterior corners increasingly developed and lateral margins increasingly convexly curved (as in fig. 6), this condition prevailing to penultimate segment; anal tergite broader than long, subtriangular, with concave lateral margins, truncate apex, two dorsal, four lateral, and six terminal setae; anal scale projecting beyond anal lip; anal lips smooth, moderately produced; preanal scale broad, subtriangular with convex sides and base, possessing one pair of lateral setae.

Pleural region coriaceous, glabrous, posterior margin well defined.

Sterna of metazonites essentially flat, raised beyond level of prozonites and separated by a shallow depression; sternites glabrous, not much produced on legs; coxae of second legs produced into two slender thimble-shaped processes; sternal aperture of seventh segment wider than distance between coxae of eighth legs, anterior margin straight, lateral margins strongly convex and posterior margin weakly convex.

Legs with each coxa possessing one prominent slender ventral seta; prefemur with a long slender ventral seta and many shorter ones; femur with numerous short setae, slightly shorter than prefemur; tibia longer than postfemur, with several spines; tarsus more heavily setose, equal in length to previous two segments combined; tarsal claws strongly developed.

Gonopods attached to one another by a weak band of connective tissue, the tibiotarsi crossing in situ; coxal apodeme fairly long, tapering gradually; coxae enlarged, slightly elongate; prefemur much narrower than coxa, setose, and with horizontally directed sub-rectangular prefemoral process; femur whitish, densely short-setose, and rather blade-like, with an elongate upcurved femoral process emerging at right angle to the telopodite; femoral process with apex wide, blade-like,

bidentate; tibiotarsus, the remainder of telopodite, blade-like, evenly curving in horizontal direction, narrowing gradually to pointed apex; seminal canal emerging on caudal face of coxa, progressing distad of prefemoral process to cephalic face of femur, up the telopodite between femur and tibiotarsus over to caudal face of tibiotarsus and along it to apex; seminal canal thus making a full 360° circuit.

Color (in alcohol) pale brown, but described by Chamberlin (1943) as being "brown...with the keels yellow."

Female: As in male, but averaging a millimeter or two longer. Cyphopods with receptacle possessing two setae along margin adjoining valves; valves densely setose, abruptly rounded distally (see fig. 8).

SPECIMENS EXAMINED: CALIFORNIA: Del Norte County, 7 males, 6 females, Crescent City, 15 June 1956, (N. W. Hope), (NBC); Humboldt County, 1 male (Holotype), Arcata, 19 December 1942, (Earl Mills), (USNM); 1 male, Humboldt County Redwoods, Spring, 1965, (R. Jones), (B & G).

VARIATION: Length ranges from about 30-34 mm, most males being near 32 mm and females 33 or 34 mm. Gonopods of the holotype and males from Crescent City, Del Norte County, possess the rather small, bidentate femoral process; however, one male from Humboldt County Redwoods possessed a broad, tridentate femoral process (see fig. 11). We believe this falls within the normal range of variation to be expected within this species.

ECOLOGY: The area of California in which *telodonta* occurs is densely covered with *Sequoia sempervirens*, so it is most likely that *telodonta* occurs in redwood litter.

DISTRIBUTION: *H. telodonta* occurs from southern Humboldt County to northern Del Norte County, and may occur in Oregon as well, although there are no records of its occurrence there at the present time. The northermost record of *cummingsiensis* lies just 15 miles south of the southern record of *telodonta*, indicating a relatively high possibility of sympatric occurrence.

Harpaphe pottera Chamberlin

Harpaphe pottera Chamberlin, 1949. Proc. Biol. Soc. Washington, 62:129, pl. 8, fig. 10; Chamberlin and Hoffman, 1958, Bull. United States Natl. Mus. 212:35; Buckett, 1964, Annotated List Diplopoda California, p. 8.

TYPES: Holotype (RVC) and other specimens taken from Potter Creek, Mendocino County, California, 15 July 1937, by R. V. Chamberlin.

We have not seen the type of this species. The pertinent part of the original description is therefore presented: "Most readily distinguished by the peculiarities of the gonopods, in particular those of the principal blade which is shorter and less curved than usual and has the distal margin evenly convex."

We have seen two male specimens which are in agreement with this description and are deemed to be *pottera*. A fuller description of one of these males is presented below.

DESCRIPTION: Male: Head smooth above, with 4 setal sockets; coronal suture deep, dividing between antennae; frontal sutures with three evenly distributed setae each; frons densely microspinose; gular areas lightly microspinose, each with two macrosetae and strong convex curvature dorsally; antennae typical, with four large setae on short basal segment; segments 2-5 nearly equal in size, with increasingly dense setae distally; sixth segment slightly shorter, densely setose; seventh segment short, truncate, with four terminal sense cones.

Collum much wider than head, narrower, but about twice as long as second segment; segments 2, 3, 4 and 5 increasing in width and length, anterior corners rounding broadly and posterior corners becoming produced; segments 17 to 20 decreasing in size; tergite 19 mostly concealed under tergite 18, ventrally almost completely covered; epiproct subtriangular in shape, broader than long, with 12 setae visible from above; preanal scale semicircular, with a pair of caudal setae; anal cheeks medially with a pair of setae; anal lips moderately produced, a pair of setae near dorsal margin.

Tergites all with transverse rows of tubercles visible under 20X magnification; segments 1 to 5 with one row of five to nine tubercles along posterior margin of metazonite; segments 6 to 8 with two rows, anterior row positioned just behind mid-transect of segment and containing about seven tubercles, posterior row along caudal margin of segment with about 10 tubercles; following segments with three rows averaging eight, ten, and thirteen tubercles each, respectively, these numbers varying 20% to 50%.

Legs one and two with sternites not produced, coxae projecting ventrad and closely adjacent; beginning with leg three, sternum produced ventrad from level of body cylinder and separated from prozonites by abrupt, prominent groove; coxae attached to lateral margins of sternum and directed laterad; coxae of legpair 3 separated by one-half length of coxa, of legpairs 4 to 7 by about one coxal length, and coxae of following legs by almost two coxal lengths. Coxa and prefemur short, microspinose, with one large distal seta; prefemora of legs near caudal part of body possessing subtriangular apical spine, with long seta attached at base of spine; anteriorly, femur slightly longer than prefemur but much the longest segment near caudal end of body; post-femur short, ventrally spinose; tibia slightly longer, more densely spinose and setose; tarsus long, subconical, densely short-spinose; coxae of second legs produced in short, truncate, cylindrical ventral processes.

Gonopods with long femur and short tibiotarsus which is directed up at about 45° and curved slightly, the apex acuminate, projecting just below horizontal; femoral process rather

blunt, wide, not twisted but slightly bent laterad; prefemoral process small, truncate.
SPECIMENS EXAMINED: CALIFORNIA: Humboldt County, 2 males, 1 female, Fort Seward, 27 May 1935 (E. O. Essig) (RLH).
VARIATION: The specimens we have seen differ from Chamberlin's description in having acute rather than rounded apices of the gonopods, but this character may be of rather trivial importance. In placing the specimens included here under *pottera* we laid heavy emphasis on the erect posture of the tibiotarsus.
ECOLOGY: We made a trip to the type locality, but were unsuccessful in our effort to obtain specimens. There were no redwoods in the area, but alders occurred along Potter Creek.
DISTRIBUTION: This species has been collected inland in both Mendocino and Humboldt Counties; *H. haydeniana cummingsiensis* has been collected coastally in both areas. Thus far, no intergrades have been found between the two and we have, therefore, left the status of this form unchanged pending more complete information.

Harpaphe haydeniana (Wood)

We place most populations of *Harpaphe* in this species, deleting only *telodonta* because of its striking differences and *pottera* because its identity is still not certain. The rationale for this treatment is based on the high variability and lack of distinct differences between populations of *Harpaphe* as is indicated by specimens available to us.

Within this wide ranging species we have found different forms of the male gonopods in different geographic areas, and have recognized the usefulness of utilizing the subspecies concept in this situation. The primary employer and defender of subspecies in millipeds has been R. L. Hoffman (1956, 1958), and we agree with his viewpoint that stable geographic units should be formally recognized. Only one of the subspecies recognized is known from just a single locality, and for most subspecies the ranges are well delimited by the material we have seen.

Since these subspecies differ mainly in the gonopods, a thorough description of general superficial features will be given only for the nominate subspecies.

Harpaphe haydeniana haydeniana (Wood)

Polydesmus (Leptodesmus) haydenianus Wood, 1864. Proc. Acad. Nat. Sci. Philadelphia 16:10; 1865, Trans. American Philos. Soc. 13:226-227, fig. 57.
Leptodesmus haydenianus, Bollman, 1893. Bull. United States Natl. Mus. 46:122.
Harpaphe haydeniana, Cook, 1904. Harriman Alaska Exped. 8:59, pl. 4, figs. 4a-c; Attems, 1938, Das Tierreich 69:198;

Chamberlin, 1949, Proc. Biol. Soc. Washington 62(63!) 125-128; Causey, 1954, Pan-Pacific Entomol. 30(3):221; Chamberlin and Hoffman, 1958, Bull. United States Natl. Mus. 212:34; Buckett, 1964, Annotated List Diplopoda California, p. 8.

Polydesmus intaminatus Karsch, 1881, Arch. Naturg. 47:41 (Type locality: "California"; Type: Berlin Museum). NEW SYNONYMY.

Leptodesmus intaminatus, Attems, 1899. Denkschr. Kais. Acad. Wien 67-387, pl. 6, fig. 135; Bollman, 1893, Bull. United States Natl. Mus. 46:122.

Pachydesmus intaminatus, Attems, 1938, *in* Das Tierreich, 69: 153-154, fig. 175.

Harpaphe intaminata, Chamberlin and Hoffman, 1958. Bull. United States Natl. Mus. 212:35; Buckett, 1964, Annotated List Diplopoda California, p. 8.

Fontaria simoni Brolemann, 1896. Ann. Soc. Entomol. France 65: 65, pl. 5, figs. 19, 20 (Type locality: Washington State; Mus. Hist. Nat., Paris).

Harpaphe penulta Chamberlin, 1949. Proc. Biol. Soc. Washington 62(63!):128, fig. 9; Chamberlin and Hoffman, 1958, Bull. United States Natl. Mus. 212:35 (Type locality: 9 miles south of Belknap Springs, Lane County, Oregon; Type: Collection of R. V. Chamberlin). NEW SYNONYMY.

TYPE SPECIMENS: Collected in Oregon by Hayden and placed in the United States National Museum, but were apparently later lost. A search of the United States National Museum Collection made by the second author in 1967 did not reveal the presence of any type material. Therefore, a male neotype is hereby selected by the authors to stabilize this name. The specimen is labeled as follows: *Polydesmus haydenianus* Wood, 9 miles north of Agness, *in* Coos County, Oregon, 11 March 1968 (J. S. Buckett & M. R. Gardner), J. S. B.-M. R. G. Collection Number 68-28. The type specimen is placed in the arthropod type collection of the Department of Entomology, University of California, Davis, California.

DIAGNOSIS: This subspecies is characterized in the male genitalia by the following: tibiotarsus curved evenly, usually of similar width throughout; prefemoral process small; femoral process narrow and evenly curved distad, the broad face of blade directed cephalolaterad. Closely related to *scotia*, but distinguished by the thinner femoral process, with face of blade not directed cephalad as in *scotia*. Body length 26-38 mm.

DESCRIPTION: Head with coronal suture prominent, dividing between antennae to two obscure frontal sutures; epicranial halves shining, but finely pitted; frontal area densely and very finely spinose, the lateral areas smooth and not spinose; two pairs of supra-antennal setae, three setae along each frontal suture, and two pair of gular setae all present. Antennal sockets well sunk, deep dorsolateral supra-antennal groove present. Antennae sep-

arated by length of third antennal segment; antennae typical, extending caudad to middle of segment three; antennal segments two to five subcylindrical, subequal in length; segment six slightly longer, seven hemispherical, with four terminal peg-like sense cones.

Collum with anterior margin evenly convex, posterior margin slightly concave medially, lateral corners on medial transect of segment; collum laterally narrower but longitudinally twice the length of tergite two; tergites two, three, and four with both anterior and posterior lateral corners of paranota pronounced; succeeding tergites with anterior corners progressively more rounded and posterior corners projected increasingly caudad beyond posterior margin of tergite. Repugnatorial pores opening laterally on paranotal margins.

Last tergite much broader than long, subtriangular, projecting well beyond anal lips, with four terminal, six lateral and four dorsal setae. Anal lips smooth, moderately produced; preanal scale subelliptical, possessing a pair of caudal setae.

Tergites with tubercles visible under 12X magnification and arranged as follows: Tergite one with a single posterior transverse row of 7 tubercles; tergites two - twelve with 2 transverse rows, the anterior averaging 5, the posterior row 7; tergites thirteen - nineteen with 3 transverse rows, the posterior row most numerous, averaging 13 tubercles.

Sterna of metazonites slightly concave, produced well beyond level of prozonites and separated from them by a deep groove; sternites glabrous, produced only slightly up around legs. Coxa with one large ventral seta and many short spines; prefemur beyond segment ten produced apically in a prominent spine-like ventral projection, slightly more pronounced in females than in males; femur nearly as long as coxa and prefemur combined with many short, stout spines; postfemur and tibia together shorter than femur, sparsely spinose; tarsus nearly as long as postfemur and tibia combined, densely setose with large, curved tarsal claw; coxae of second legs in male produced in a pair of cylindrical ventral processes; sternal aperture of seventh segment wider than distance between coxae of eighth legs. Aperture with anterior margin short, straight, curving abruptly caudolaterad, the lateral margins evenly rounded, posterior margin evenly concave.

Gonopods joined with connective tissue, tibiotarsi crossing in situ; coxal apodeme long, nearly straight; coxa large, rounded, with subcircular basal muscular aperture; prefemur much narrower than coxa, with short, flattened truncate prefemoral process; femur elongate, setose, with a long, simple distally curved process; tibiotarsus flattened, subequal in length to femur, generally more slender, curved mesad, apically acuminate. Seminal canal originating on posterior side of coxa, progressing antero-laterally distad of prefemoral process, along anterior face of femur, caudally between femur and tibiotarsus and along

posterior face of tibiotarsus to apex.
SPECIMENS EXAMINED: CANADA: British Columbia: 1 male, 1 female, Copper Island, 30 July 1960, (P. Joslin), (RLH); 1 male, George Island, 30 July 1960, (J. B. Foster), (RLH); 1 male, Harrison Island, 16 June 1960, (J. B. Foster), (RLH); 1 female, Hotspring Island, 27 July 1960, (J. B. Foster), (RLH): 1 female, Huxley Island, 28 July 1960, (J. B. Foster), (RLH); 1 male, Langara Island, 6 June 1960, (J. B. Foster), (RLH); 1 male, Lucy Island, 6 June 1960, (J. B. Foster), (RLH); 1 male, 1 female, Moude Island, 22 June 1960, (P. Joslin), (RLH); 1 fragment, Queen Charlotte Island, Rose Harbor, 16 August 1960, (P. Joslin), (RLH); 1 female, Shooting-Star Island, 20 July 1960, (J. B. Foster), (RLH); 1 male, 2 females, Shawnigan Lake, Vancouver Island, 3 August 1960, (NBC) UNITED STATES: ALASKA: 3 males, 1 female, 1 immature, Dall Island, Rose Inlet, 1 July 1947 (G. Hanna)(CAS); 1 male, 3 females, Forester Island, May 1913, (H. & R. W. Heathe), (RLH) CALIFORNIA: 4 males, Inverness, Marin County, 26 March 1938, (Tilletson), (CAS); 1 male, near Mill Valley, Marin County, 6 June 1965, (Iris Savage), (B&G); 1 male, 1 female, Muir Woods, Marin County, 20 May 1952, (H. S. D Dybas), (CAS) OREGON: 1 male, 1 female and immatures, Reedsport, Douglas County, 24 August 1967, (J. R. Helfer), (B&G); 1 male, Lambs Creek, 1 mile E Cascadia, Linn County, 23 July 1949, (V. D. Roth), (RLH); 1 male, 1 female, Nelscott Beach, Lincoln County, 10 April 1949, (V. O. Roth), (RLH) WASHINGTON: 3 males, 4 females, Seattle, King County, 27 September 1944, (H. S. Dybas), (CMNH); 5 males, 7 females, Bellingham, Whatcom County, 25 July 1950, (J. F. G. Clarke), (USNM).
VARIATION There is a trend in Washington and British Columbia for an increase in the width of the subapical portion of the tibiotarsus with a corresponding decrease in the width of its base. This trend is less evident in specimens from Alaska and Oregon (see figs. 14 and 15).
SYNONYMY: *Fontaria simoni* Brölemann was correctly placed as a synonym of *haydeniana* by Chamberlin and Hoffman (1958). The holotype was sent to the United States from the Paris Museum through the courtesy of Dr. J. P. Mauries, and a drawing made of it by Dr. Hoffman was used in determining its position. *F. simoni* appears to be typical *H. h. haydeniana*. Furthermore, the type locality for *simoni* is Washington State, the center of distribution of *H. h. haydeniana*.

The placement of *H. intaminata* as a junior synonym of *H. h. haydeniana* is a tentative placement, since "California" was the only known locality for *intaminata*. Dr. Hoffman kindly loaned us a drawing of a gonopod of the holotype, but the subspecies of *haydeniana* to which it belongs could not be clearly discerned from the angle from which the drawing was made. As can be seen from the drawing of the type (fig. 13), it appears to resemble *H. h. haydeniana*, even though this subspecies is known to be represented in California only in Marin County.

Harpaphe penulta Chamberlin is included under *H. h. haydeniana* because there is nothing in either the original description or drawings which justifies separate status, the character of a concave apex of the prefemoral process being insufficient for species distinction.

DISTRIBUTION: *H. h. haydeniana* is easily the most wide-ranging subspecies, occurring continuously from southern Oregon to southern Alaska. Its inland distribution is greatly restricted, our specimens indicating its occurrence no more than 75 miles from the Pacific Ocean.

This is one of two known polytopic subspecies of *Harpaphe*, occurring on many islands as well as Marin County, California. Assuming *h. haydeniana* is probably most closely related to the prototype of all entities except *telodonta*, this small Marin population probably became isolated early after the Pleistocene and evolved slower than the neighboring populations to the north.

Harpaphe haydeniana scotia (Chamberlin), New Combination

Paimokia scotia Chamberlin, 1941, Bull. Univ. Utah, Biol. Ser. 8(2):13, fig. 26.

Harpaphe intaminata (Karsch), of Chamberlin (in part), 1947. Proc. Acad. Nat. Sci. Philadelphia 99:24-25; of Chamberlin and Hoffman (in part), 1958, Bull. United States Natl. Mus. 212:35.

Harpaphe clara Chamberlin, 1949. Proc. Biol. Soc. Washington 62(63!):128, figs. 6,7 (Type locality: Santa Clara County, California. Type: Collection of R. V. Chamberlin); Chamberlin and Hoffman, 1958, Bull. United States Nat. Mus. 212:34; Buckett, 1964, Annotated List Diplopoda California, p. 8, NEW SYNONYMY.

TYPES: Holotype (RVC) from 12 miles south of Los Gatos, 20 March 1941, (S. and D. Mulaik).

DIAGNOSIS: Living color sometimes a light olive green; genitalia with tibiotarsus evenly curving ventromesad, of nearly equal width throughout; femoral process as wide as tibiotarsus, facing directly cephalad, and very slightly curved mesad or not curved at all. Distinguished from closely related *h. haydeniana* by green color in life, shape and greater width of femoral process of gonopod, and by generally larger body size, length being 37-43 mm.

SPECIMENS EXAMINED: CALIFORNIA: 1 male, Alder Creek, Monterey County, 28 June 1965, (Peter Richerson), (B&G); 1 male, Palo Colorado Canyon, Monterey County, 24 February 1964, (Ray Johnson), (NBC); 10 males, 8 females, 5.2 miles southwest of Stevens Creek Dam, Santa Clara County, 25 December 1966, (M. R. & R. C. Gardner, S. E. Harrison), (B&G); many immatures, 3 miles south of Holy City, Santa Cruz County, 20 February 1960, (D. Gonzales), (NBC).

VARIATION: Some specimens from Santa Clara County have a longer tibiotarsus with a thinner basal region and wider apical region.

Of two male specimens collected from Yosemite National Park, one fits the typical form given in the diagnosis and the other matches this variant type.
SYNONYMY: In 1947 Chamberlin synonymized *H. scotia* under *H. intaminata* (Karsch), where it remained until the present time. The two are conspecific, as Chamberlin realized, and they may be consubspecific, but this fact will be ascertained only when a more precise type locality is determined for *intaminata*.

There is little doubt that *clara* is a synonym of *scotia*. Although Chamberlin did not describe the gonopods of *scotia*, a drawing he presented appears to be identical with gonopods of topotypes of *clara* collected from Stevens Creek, Santa Clara County. Further evidence is found in the fact that the type localities are situated only a few miles apart along the same ridgeline, in an area with no apparent distribution barriers. Apparently, Chamberlin was unaware of *"P." scotia* when he described *clara*, since he compared *clara* with *intaminata* but not with *scotia*.
ECOLOGY: After unsuccessfully examining many likely areas along Stevens Creek in search of topotypes of *H. clara*, we finally found many specimens in a shallow depression filled with alder leaves and alder and redwood logs. This area was situated about 5 meters from Stevens Creek. The entire population of hundreds of individuals inhabited an area about 3 meters in diameter, the boundaries of the population being rather sharply defined.
DISTRIBUTION: The northern range seems to extend to San Francisco Bay. The southern range limit remains undefined, but if, as suspected, the record from Yosemite National Park represents the natural distribution, it seems plausible that *scotia* at one time ranged across the Tehachapi Range into the Sierras.

HARPAPHE HAYDENIANA LANCEOLATA Buckett and Gardner, subsp. nov.

TYPE: Holotype male, Mt. St. Helena, Napa County, California, (R. O. Schuster); placed in the Entomology Type Collection, University of California, Davis (UCD).
DIAGNOSIS: Characterized by the long femoral process gradually narrowing and curving strongly mesad; prefemoral process moderate in size, tibiotarsus with moderate bend near base, upper part evenly curving, apex directed down at about 30° with vertical; tibiotarsus narrow at basal bend, not much enlarged subapically, acuminate at apex; body length 37-42 mm. females generally larger.
SPECIMENS EXAMINED: CALIFORNIA: Holotype male, Mt. St. Helena, Napa County, 3 February 1959, (R. O. Schuster), (UCD). Paratypes, 1 male, same data as holotype, (RLH); 3 males, 1 female, Calistoga, Napa County, 12 June 1934, (O. Bryant), (CAS); 2 males, 11 females, Anderson Springs, 4 miles northwest of Middletown, Lake County, 21 February 1965, (J. S. Buckett & M. R.

Gardner), (B&G).
VARIATION: Gonopods of males from the type locality and Anderson Springs are very similar, the only significant difference being a slightly smaller and less bent femoral process in the Anderson Springs specimens.
ECOLOGY: The only collection we have personally made of this subspecies was in an area of alder litter and logs at Anderson Springs, Lake County. This area experiences a wet winter, but a hot, dry summer. Individuals were scattered on a hillside about 10' above the high water mark of a perennial stream.
DISTRIBUTION: This entity is probably fairly localized, occurring in the inner coast ranges in Lake and Napa Counties. It seems to intergrade with *cummingsiensis* at Cazadero, Sonoma County, and Calistoga, Napa County. The specimens from Cazadero, near the coast, more closely resemble *cummingsiensis*, and those from Calistoga resemble *lanceolata*.

HARPAPHE HAYDENIANA MAUROGONA Buckett and Gardner, subsp. nov.

TYPE SPECIMENS: Holotype male and paratypes from two miles east of Baxter, Nevada County, California, 18 June 1964, (Buckett and Gardner).
DIAGNOSIS: Gonopod with tibiotarsus strongly curved, moderate in length, relatively broad and with sinuate margins; femur quite broad; femoral process becoming suddenly narrow, being abruptly twisted 90° counterclockwise near apex; prefemoral process well developed; gonopods more darkly sclerotized than in any other form in the genus. Related to *inlignea* Chamberlin, but distinguished in the gonopod by dark color, a strongly twisted femoral process and shape of the tibiotarsus.
SPECIMENS EXAMINED: Holotype Male: CALIFORNIA: 2 miles east of Baxter, Nevada County, elevation 4100', 18 June 1964, (J. S. Buckett & M. R. Gardner), (UCD); Paratypes: 1 female (designated allotype), same data as holotype; 13 males, 2 females, same data as holotype.

The holotype will be placed in the Type Collection of the Entomology Department, University of California, Davis. Paratypes will be placed in the following institutions and collections: Buckett-Gardner Collection, California Academy of Sciences, N. B. Causey Collection, R. L. Hoffman Collection, H. F. Loomis Collection, Miami, Florida, and the United States National Museum.
VARIATION: In the one collection known, variation was minor, being expressed only slightly in amount of anterior bending of the tibiotarsus and the curvature of its margins.
ECOLOGY: Individuals were found concentrated in soil as far as six inches beneath an alder log lying above a small stream. Most were encapsulated in small earthen chambers. The date of collection is almost the latest in the spring that any specimens of

Harpaphe have been found in California. It probably reflects the delay in the arrival of spring in the higher elevations.
DISTRIBUTION: *H. h. maurogona* is known only from the type locality. More records will have to be accumulated before its range and taxonomic status can be properly assessed.

Harpaphe haydeniana inlignea Chamberlin

Harpaphe inlignea Chamberlin, 1949. Proc. Biol. Soc. Washington 62(63!):128, fig. 8; Buckett, 1964, Annotated List Diplopoda California, p. 8.
Harpaphe pottera, Causey (!), 1954. Pan-Pacific Entomol. 30(3): 222; 1955, Proc. Biol. Soc. Wash. 68:90; Buckett, 1964, Annotated List Diplopoda California, p. 4.
TYPES: Holotype (RVC) from Inwood, Shasta County, California.
DIAGNOSIS: Characterized by a marked bluntness in the tip of the tibiotarsus, which is evenly curved and nearly constant in width throughout; prefemoral process long and broad, the apex linear and the mesal margin longer than the lateral margin; femoral process subequal in width to tibiotarsus, curving somewhat laterad, and with tip twisted counterclockwise about 70°, giving the appearance of abrupt narrowing from anterior view; body length 42mm to 48mm.
SPECIMENS EXAMINED: California: 2 males, Bass Creek, Shasta County, 15 April 1953, (J. Gorman), (NBC); 1 male, 1 female, Brock Mountain, Shasta County, 16 April 1952, (J. Gorman), (NBC).
VARIATION: Specimens from Bass Creek have a blunter apex of the tibiotarsus, and a somewhat smaller prefemoral process than the single male from Brock Mountain, yet there appears to be no doubt about the placement of these specimens.
SYNONYMY: The specimens cited here were recorded by Causey (1954, 1955) as representing *Harpaphe pottera.* They resemble the description of *pottera* in having a short tibiotarsus with a rounded apex, but their strongly curved tibiotarsus precludes that placement. The blunt tibiotarsus is the major diagnostic feature described by Chamberlin for *inlignea* too. Also, the proximity of the collection locality to the type locality of *inlignea* further supports the placement of these specimens as *inlignea.*
DISTRIBUTION: Apparently localized; known only from three localities in Shasta County, California. Collecting should be done on both sides of the northern end of the Sacramento Valley to define the bounderies of *inlignea.*

Harpaphe haydeniana cummingsiensis (Verhoeff), new combination

Pachydesmus cummingsiensis Verhoeff, 1944. Bull. Southern California Acad. Sci. 43(2):64, fig. 14.
Harpaphe intaminata (Karsch), of Chamberlin and Hoffman (in part), 1958. Bull. United States Natl. Mus. 212:35; Buckett (in part), 1964, Annotated List Diplopoda California, p. 8.

TYPES: Holotype from Cummings, Mendocino County, California, collected by Michelbacher; now in the Zoologische Sammlung des Bayerischen Staats, Munich.
DIAGNOSIS: Gonopods with tibiotarsus long and narrower than femoral process, a strong bend near base of tibiotarsus and another near its apex; femoral process twisted counterclockwise about 80° near apex, and sometimes bent slightly mesad; in situ, gonopods strongly crossed, tips of femoral processes curving mesad and touching or nearly touching tibiotarsus of opposite gonopod. *H. h. cummingsiensis* is primarily characterized by the tibiotarsus being long, narrow, and strongly bent near base. Body length, 36-40 mm.
SPECIMENS EXAMINED: CALIFORNIA: 1 male, Richardson Grove State Park, Humboldt County, 15 May 1966, (Harold Wilson), (B&G); 16 males, 28 females, County Road 409, 5 miles northeast of Mendocino, Mendocino County, 22 December 1964, (J. S. Buckett, M. R. Gardner, and J. R. Helfer), (B&G); 1 female, Mendocino, Mendocino County, 1 July 1967, (J. R. H.), (B&G); 3 males, 1 female, Cazadero, Sonoma County, 18 April 1918, (H. Vanduzee), (CAS).
VARIATION: The type specimen (fig. 24) possesses a distorted femoral process. An identical effect was produced by drying the gonopod of another specimen, so it is presumed that this condition is probably an artifact of the preservation technique used.

Specimens from Mendocino County are all somewhat similar but vary in mesial curvature of the femoral process and in the length of the tibiotarsis and angle to which it is bent. The male specimen from Richardson Grove, Humboldt County, is clearly assignable to this subspecies, but possesses a shorter tibiotarsus with a widened subapical region, thus showing some resemblance to *H. h. haydeniana*. Specimens from Cazadero, Sonoma County, are also placed here, although they show intermediate characteristics between *cummingsiensis* and *lanceolata*. In the male sex these specimens possess a tibiotarsus shorter than is usual in *cummingsiensis* but with two distinct bends in it. The femoral process is curved more mesad than in typical *cummingsiensis*, but much less than in typical *lanceolata*.
SYNONYMY: In Chamberlin and Hoffman (1958), *"Pachydesmus" cummingsiensis* was placed as a junior synonym of *Harpaphe intaminata*, which is correct at the specific level, though *intaminata* is itself a synonym of *haydeniana*. However, *cummingsiensis* represents a subspecies not previously recognized as such, and is therefore retained at the subspecific level. This designation is based on a drawing of the gonopod of the holotype provided us by Dr. Hoffman which clearly shows the diagnostic characters mentioned above.
ECOLOGY: Collections from Richardson Grove State Park, Humboldt County, and 5 miles northeast of Mendocino, Mendocino County, were made in a redwood situation. At the latter locality we found nearly sixty individuals in and under a single small redwood log, and many of them were encapsulated. Surface litter was

inches thick and moist. A collection made there by Helfer on 1 July provides the record for the latest seasonal collection of *Harpaphe* in California. The individuals are apparently able to remain active longer than elsewhere because of the cool, moist summers of the northern coast ranges.

DISTRIBUTION: The most typical specimens of *cummingsiensis* that we have seen occur near Mendocino, California. The subspecies occurs coastally north as far as Humboldt County, where at Richardson Grove State Park it shares traits with *H. h. haydeniana*. It occurs southward to Sonoma County, where at Cazadero it apparently intergrades with *lanceolata*.

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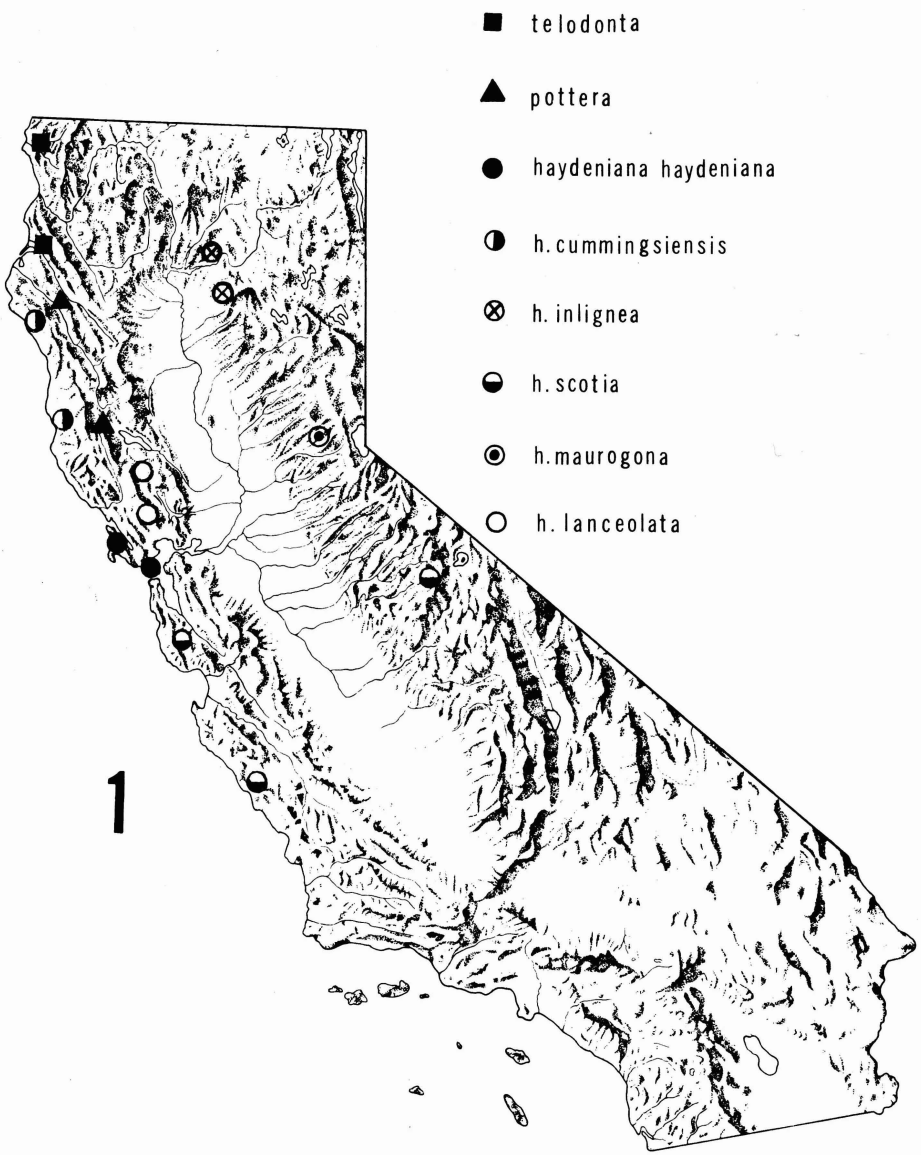


PLATE 1

fig. 1. Map showing distribution of *Harpaphe* in California.

PLATE 2

fig. 2. Map showing distribution of *H. haydeniana haydeniana* on the Pacific Coast north of California

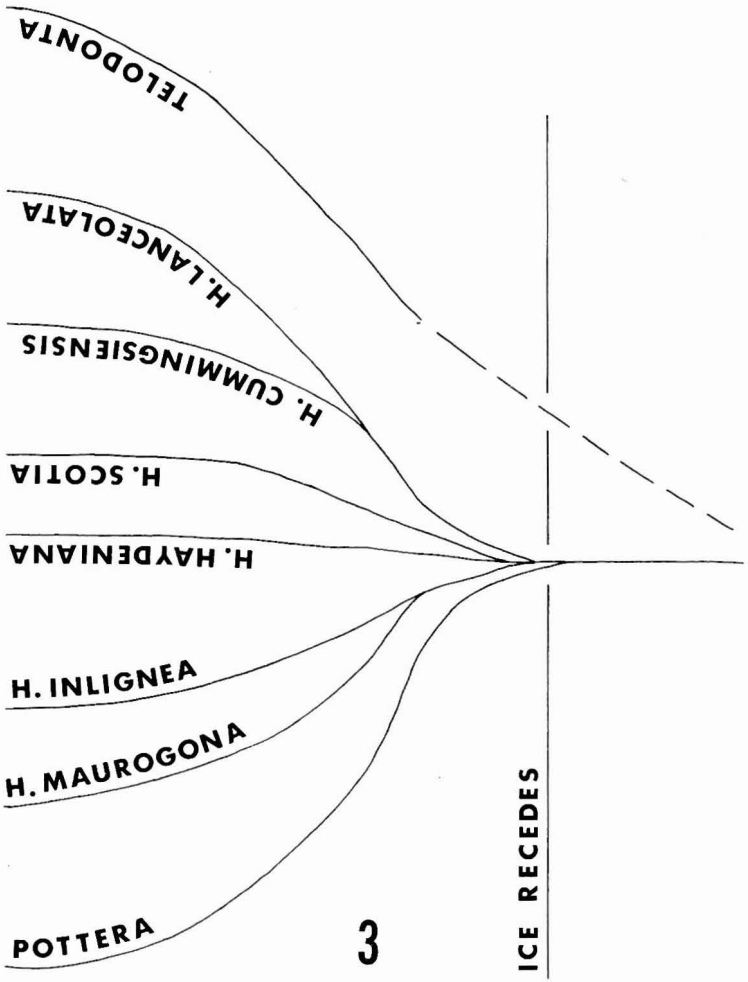
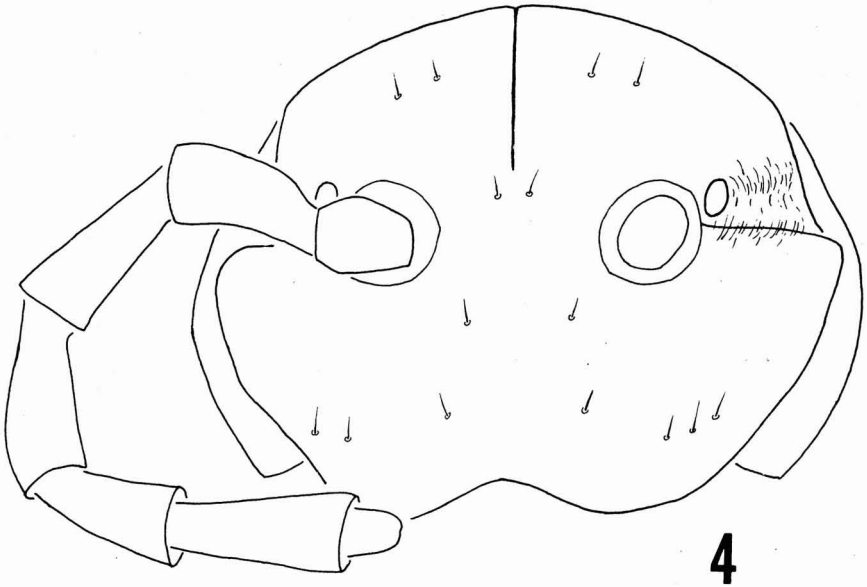


PLATE 3

fig. 3. Proposed dendrogram of relationships within *Harpaphe*.



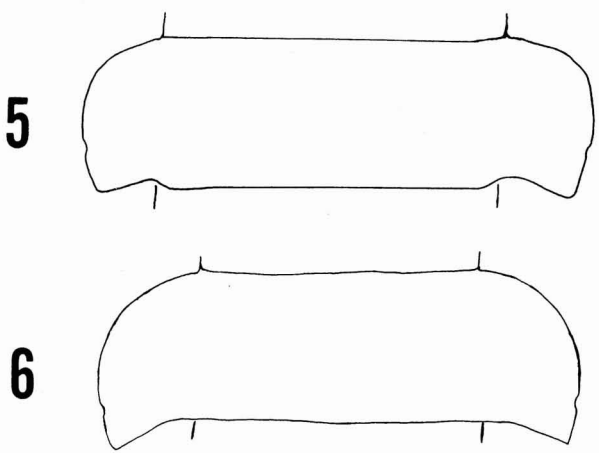


PLATE 4

fig. 4. *H. haydeniana haydeniana* head, anterior aspect.

fig. 5. *H. h. haydeniana* eleventh tergum, dorsal view. Reedsport, Oregon.

fig. 6. *H. telodonta* eleventh tergum, dorsal view. Crescent City, California.

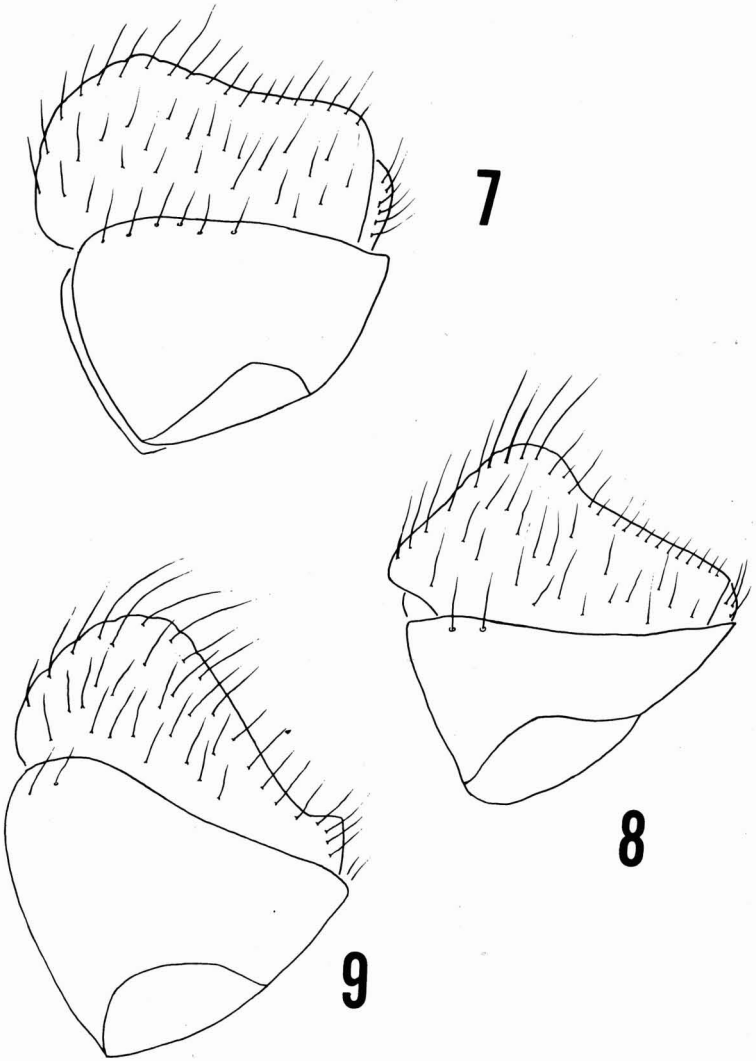
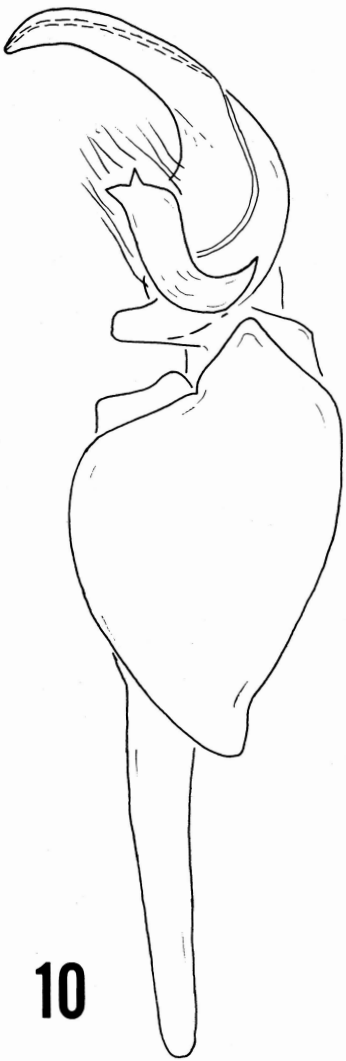


PLATE 5

fig. 7. *H. h. scotia*, Stevens Creek, Santa Clara County, California.

fig. 8. *H. telodonta*, Crescent City, California.

fig. 9. *H. h. cummingsiensis*, Mendocino, California.



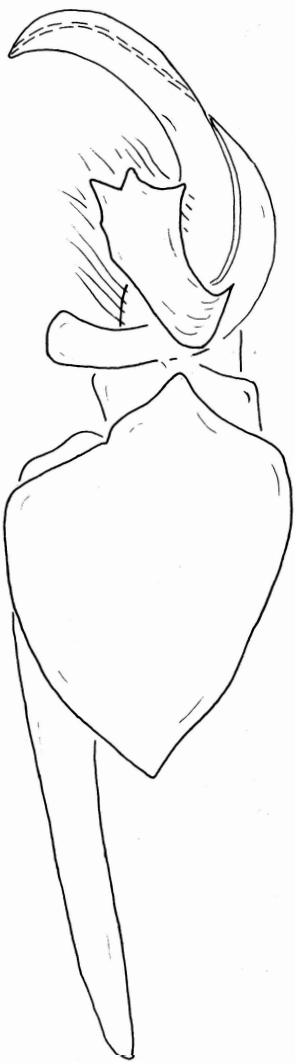


PLATE 6

fig. 10. *H. telodonta*, holotype male.

fig. 11. *H. telodonta*, Humboldt County Redwoods, California.

PLATE 7

fig. 12. *H. pottera,* Fort Seward, Humboldt County, California.

fig. 13. *Polydesmus intaminatus* Karsch, holotype, left male gonopod, lateral aspect (drawn by R. L. Hoffman).

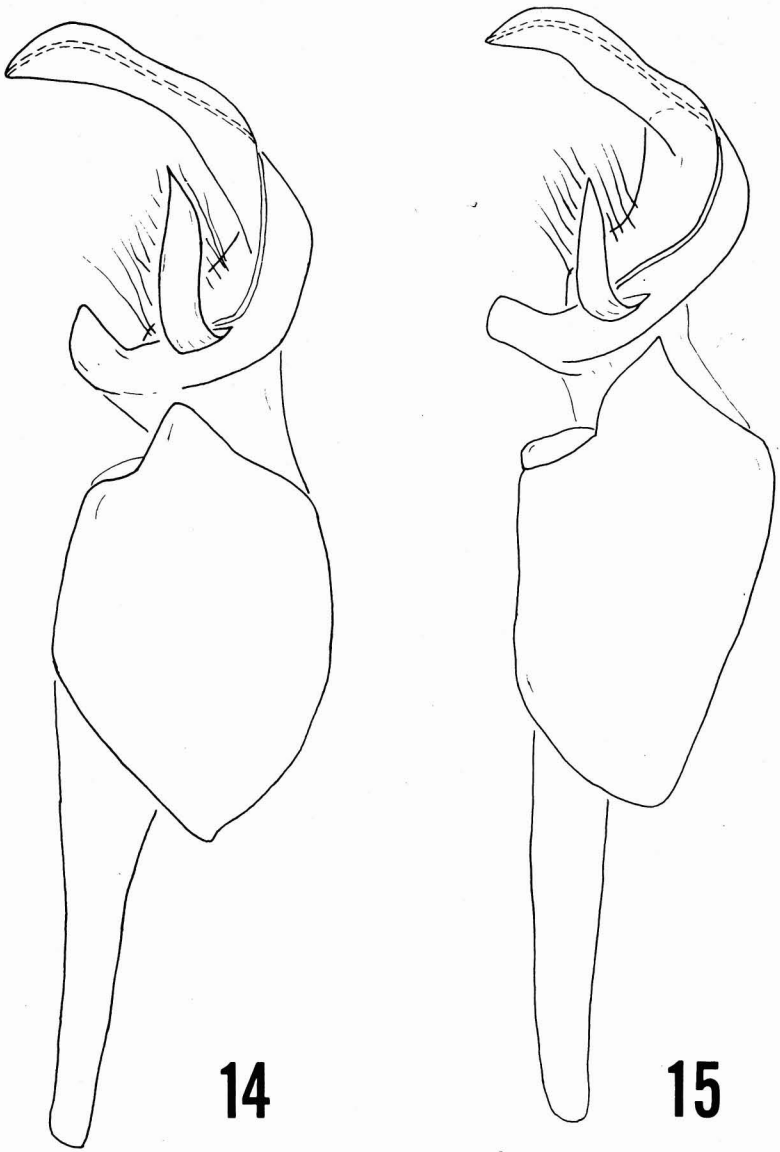


PLATE 8

fig. 14. *H. h. haydeniana*, Seattle, Washington.

fig. 15. *H. h. haydeniana*, Dall Island, Alaska.

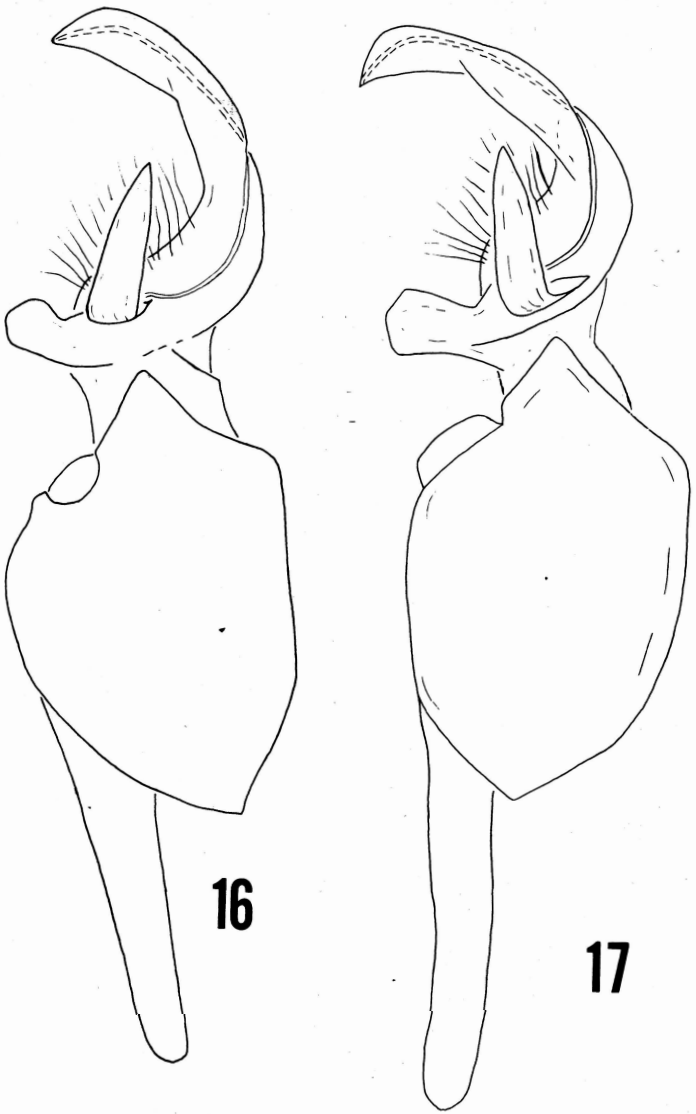


PLATE 9

fig. 16. *H. h. scotia*, Big Basin, Yosemite National Park, California.

fig. 17. *H. h. scotia*, Stevens Creek, Santa Clara County, California.

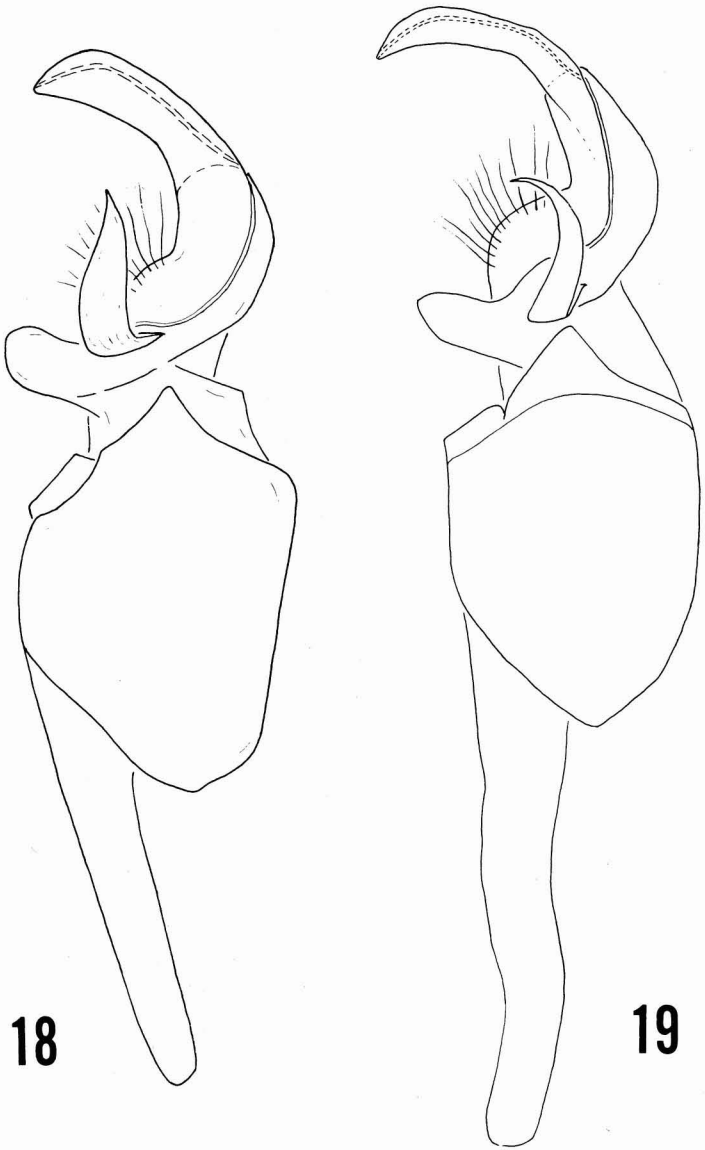


PLATE 10

fig. 18. *H. h. scotia*, Stevens Creek, Santa Clara County, California.

fig. 19. *H. h. lanceolata*, holotype.

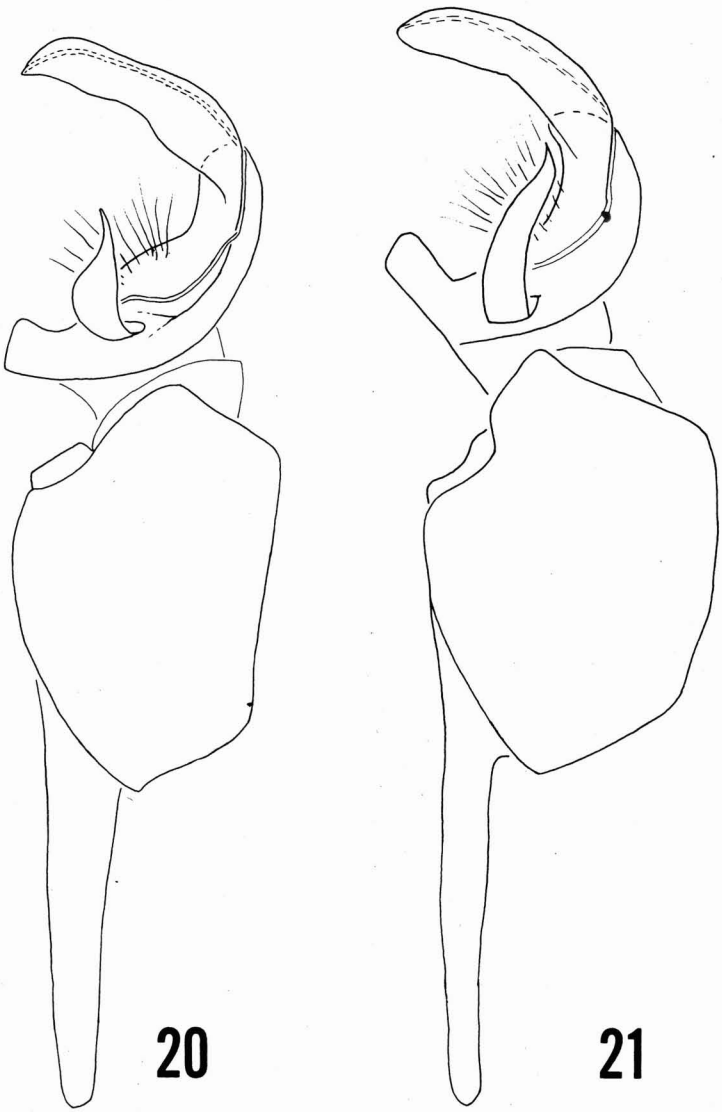


PLATE 11

fig. 20. *H. h. maurogona*, paratype.

fig. 21. *H. h. inlignea*, Bass Creek, Shasta County, California.

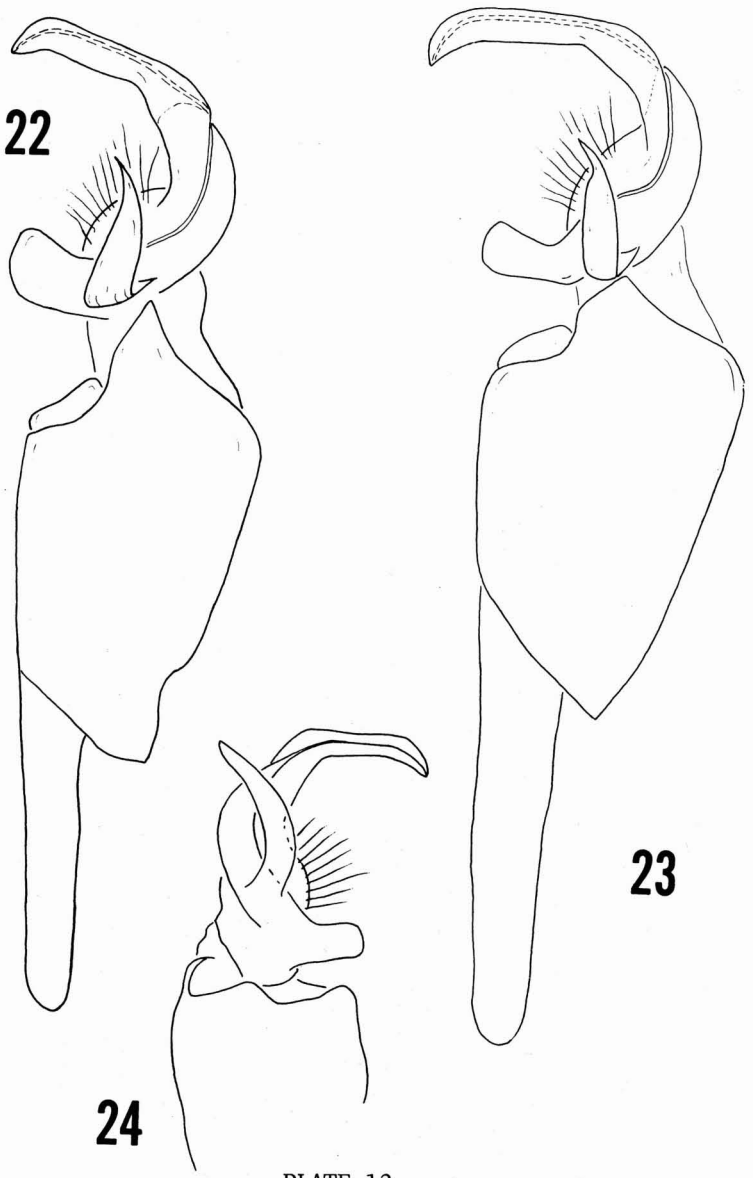


PLATE 12

fig. 22. *H. h. cummingsiensis*, Mendocino, California.

fig. 23. *H. h. cummingsiensis*, Mendocino, California.

fig. 24. *H. h. cummingsiensis*, holotype, left male gonopod, sublateral aspect (drawn by R. L. Hoffman).