NEW TROPICAL MILLIPEDS OF THE ORDER MEROCHETA, WITH AN EXAMPLE OF KINETIC EVOLUTION.

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EVOLUTION OF USELESS CHARACTERS IN MILLIPEDS.

The adaptive characters of the higher animals and plants, corresponding to differences of habits and external conditions of existence, have furnished the principal arguments for the theory that evolutionary changes of organisms are brought about by the selective action of the environment. A special evolutionary interest attaches to the structural diversities of lower groups like the millipeds because they enable the theory of selection to be tested by application to large series of biological facts.

In comparison with the specialized differences of habits, habitats, and food requirements found among the members of the higher classes of plant and animal life, the millipeds may be said to have an almost complete ecological unity. Nearly all the members of the group have essentially the same habits and live in closely similar environments. They pass their lives buried in the humus layer of the soil or among the dead leaves or other decaying vegetable matter that furnishes their food. With such uniformity of external conditions the influences of natural selection should be expected to work in the same direction, so that the structural unity of the group would be preserved.

The facts do not correspond with this inference from the theory of selection. Elaborate structural specializations have taken place among the millipeds, quite as elaborate as in groups exposed to the selective requirements of specialized external conditions. Darwin and many other writers have argued that evolution would not continue in a group of organisms that remained in a uniform environment. Evolutionary progress in the development of new characters is supposed to be called forth by adaptive response to the stress of external conditions. The theory that selection is the cause of evolution implies that new characters must be useful, but a very large part of the evolution of the millipeds represents the production of characters that seem to be quite useless in any environmental relation.

In a recent number of these Proceedings Gerrit S. Miller, jr., has described examples of divergent evolution under uniform environments in the color characters of the Malayan species of mouse-deer. These are small, nocturnal, forest creatures whose inconspicuous habits might be compared with those of the millipeds.¹

It is the regular rule for related species of millipeds to show such differences of color, not only in neighboring regions, but often in the same localities. With the millipeds the general uniformity of habits makes it also apparent that such nonadaptive differences are not limited to small details of color or proportion, but include elaborate structural specializations, characters of families and orders, as well as of species and genera.

While there can be no absolute certainty that any particular specialization of a milliped or of any other creature is entirely useless, and always has been, the range of speculation regarding the adaptive value of characters is greatly narrowed because of the general uniformity in the habits of the group, a uniformity that must be supposed to have existed in the past as well as in the present. The general relation of natural selection to the evolution of the millipeds is not determined by the usefulness or uselessness of some particular character, but is to be judged from the larger and more general fact that the structural differentiation of the members of the group is out of all proportion to their environmental differences.

Even if it were to be admitted that natural selection had accomplished all that has been claimed for it in the evolution of special characters in specialized environments, as in some of the higher groups, such theories would still be inadequate to account for elaborate diversification among the members of lower groups that have continued in essentially the same environments. General facts of the ecology of whole orders or classes of animals and plants can be appreciated, of course, only by those who have detailed familiarity with such groups. The public can consider only the special cases that may be adduced as illustrations. The example of kinetic evolution afforded by the new Porto Rican milliped does not differ essentially from many other examples of useless structural differences already specified, but this case affords an unusually definite evidence of the uselessness of a very elaborate structural specialization.²

The animal described below belongs to a cosmopolitan tropical group (Stylodesmoidæ) characterized by a peculiar roughening of the dorsal surfaces of the segments by a dense felt of short hairs. Small particles of earth are caught and matted into the hairs, so that

¹ G. S. Miller, jr., The Mouse-Deer of the Rhio-Linga Archipelago: A Study of Specific Differentiation under Uniform Environment, Proceedings of the U. S. National Museum, vol. 37, 1910, pp. 1-9.

³ O. F. Cook, Evolutionary Inferences from the Diplopoda, Proc. Ent. Soc. Washington, vol. 5, No. 1, 1901, p. 14.

the animal gains not merely a protective coloration, like the surrounding soil, but a firmly attached coating of the actual soil material.

From the evolutionary standpoint the hairy covering that holds the soil particles may be considered as an adaptive character of the same general class as protective colorations and mimetic resemblances. It certainly renders the earth-covered animals much more difficult to collect for scientific purposes than members of other families with clean surfaces. An experiment with one of these earth-covered types (Stylodesmus) in Liberia showed that the unpracticed eye could detect the creatures only with great difficulty against their natural background of earth, even after the location of the specimens had been quite definitely pointed out. After my friends had been told how many specimens were under a particular leaf they often took several minutes to find them.

Yet there is nothing to indicate that other families of millipeds have suffered any evolutionary advantage or disadvantage from the lack of the protective covering. There is a very wide range of colors and combinations. Some are black, some white, some with inconspicuous grays and browns. Bright yellows, reds, purples, and even blue shades, are also found that might be considered as sexual attractions or warnings to enemies, were it not for the fact that the animals are all completely eyeless and nocturnal in their habits.

The new Porto Rican milliped is of interest quite apart from the question of the protective value of the earthy covering, which it shares with many related genera. If natural selection by external agencies were needed to bring about changes of characters, no further evolution of the dorsal surfaces of these hairy earth-covered millipeds would be expected after the object of protective coloration had been so perfectly attained. Different environments could make no new demands for more adequate protection, for in this respect the creatures are equally well adapted for every environment in which their other limitations would enable them to exist. They can assume completely the color and texture of any kind of soil in which they may happen to live. And yet evolution has continued to go on underneath this covering of earth.

It seems impossible to imagine that any use can attach to the elaborate and highly specialized lobing of the margins of the segments, the peculiarity that distinguishes the new Porto Rican milliped from the two closely related West Indian genera, Tridesmus and Docodesmus. For animals with naked surfaces such lobing would involve a practical change in the outlines of the segments and the general appearance of the body, that might be of significance in relation to the external environment, but in the actual case extensive changes

¹ See p. 455.

in the forms of the segments underneath the earthy covering have produced no apparent external result. The hairs that clothe the surfaces of the segments project into the narrow incisions and bridge them over, so that the adherent layer of earth is not interrupted. The gaps in the margins of the segments are narrower than the deeper parts of the incisions, as if to keep the outlines of the segments and the general form of the body unmodified. The practical result is quite the same as though the margins of the segments had remained entire, as in the related genera. It would be difficult to imagine a more gratuitous evolutionary change, by which the structure of the segments could be so elaborately modified with so little effect upon the external form or environmental relations of the body as a whole.

It would be rash to insist upon a generalization from any one example of a useless evolutionary change, or even from any one group of animals in which such examples are so abundant as among the millipeds. But if detailed study of many other groups convinces one that the great majority of the differences that distinguish the species and genera are of the same generally useless, nonadaptive character, it becomes impossible to avoid the inference that evolutionary change is not at all limited to the characters subject to the selective action of the natural environment.

That selection may interfere to retard or forbid the spread of a harmful variation among the members of a species is easy to understand, but no concrete explanation has been offered to show how selection can call forth a new character or even bring about any increased development of a character already in existence. Selection is able, undoubtedly, to raise the average of expression of any preferred character in a species or other group of organisms, either wild or domesticated, by restricting reproduction to lines of descent in which the preferred character is expressed with the greatest regularity. Yet such an increase in the regularity of expression of a character is not the same as the production of a new character or an increase in the development of a character beyond a previous maximum. further selection be applied to the progeny of individuals selected for the expression of a certain character, still higher degrees of expression may sometimes be found, but this does not prove that the increased expression represents a new character, or that it is due to selection. The same degree of expression might have been found by wider selection among the members of the parent group.

The idea that natural selection is the actuating cause of evolutionary progress lacks evidence of fact and force of logic. The wide range of diversity found everywhere among the freely interbreeding members of wild species forbids the assumption that the intraspecific differences are all of adaptive value or that the natural tendency is toward a stable, uniform expression of characters. The general

facts of diversity and interbreeding support the opposite view that evolutionary change of characters in species is a spontaneous, kinetic process, independent of the selective action of the environment.¹

Recognizing evolution as an antecedent fact, the influence of natural selection can be understood, for it represents the power of the environment to determine the directions that evolutionary progress may take. It is plain that natural selection must favor the expression of characters that prove useful, and forbid or restrict the expression of those that prove harmful. That such a regulation of the characters of a species by the standards of the environment may profoundly affect the subsequent course of evolution is also easy to understand, without supposing that selection actuates the progressive development of the new characters.

The causes of evolution are to be sought, not in the environment, but in the organization of species as groups of individually diverse, freely interbreeding organisms. The results of the evolutionary process, as shown in such groups as the millipeds, indicate that variations not only occur but become established in expression as new characters without having any direct adaptive value for selection to work upon. Thousands of differences between species, genera, families, and orders have come into existence while the environment of the group as a whole has remained practically unchanged. Instead of evolution being limited to the adaptive characters that are fostered by selection there seems to be full liberty of change in all directions that are not too harmful to the environmental interests of the species.

A NEW GENUS FROM PORTO RICO.

The following is a formal description of the animal discussed in the preceding section:

IOMUS, new genus.

Type.—Iomus incisus, new species, from Porto Rico.

Diagnosis.—Related to Tridesmus Cook, also from Porto Rico, and to Docodesmus Cook from St. Vincent, but with the margins of the carinæ deeply incised, the last segment reduced and concealed, the broad trilobed apex exceeded by large subclavate dorsal processes of the penultimate segment.

Description.—Body small, oblong, abruptly rounded at the ends, about four times as long as broad; dorsum rather strongly convex, the carinæ depressed nearly in the direction of the dorsal arch. Dorsum with four longitudinal rows of dorsal tubercles, enlarged into subclavate processes on posterior segments.

Head concealed and compressed under the expanded first segment, facing ventrad; vertex covered to the level of the antennæ with a

^{10.} F. Cook, Methods and Causes of Evolution, Bull. 136 Bureau of Plant Industry, U. S. Department of Agriculture, 1908.

rounded shield of rough black integument; posterior corner somewhat excavate to accommodate the antenna; clypeus of thin, transparent, white, finely rugulose integument, with four equidistant punctuations below; labrum indistinctly tridentate with a transverse row of eight small, setiferous punctuations.

Antennæ rather long and slender, but distinctly clavate and strongly geniculate at joint 4; joint 3 slightly longer than 1 and 2 taken together; joint 5 the longest, about twice as long as joint 4

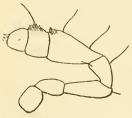


Fig. 1.—Iomus incisus. Antenna.

and about three times as long as 2, 6, or 7. Surface of all the joints densely hirsute with short hairs; joints 4-6 with a single long bristle near the end on the outer face. (See fig. 1.)

First segment distinctly narrower than the second, triangular flabellate, the anterior margin rounded, the posterior very oblique on each side, transverse for a short distance in the middle. Anterior half of dorsal surface occupied by 10 radiating areas separated by

slightly impressed grooves above and below; not incised like the other segments. Posterior part of segment above with 10 tubercles arranged in two transverse rows of four and six; anterior tubercles equidistant, posterior with the inner tubercles very close together and the outer remote from the others.

Second segment with carinæ broadened outward to embrace the first segment, anterior margin entire, lateral margin with two deep incisions, posterior margin with two more shallow incisions. Third

segment with carinæ somewhat broader than the fourth, but with anterior and lateral margins similarly incised.

Segments with four longitudinal rows of dorsal tubercles, three tubercles to each row; tubercles of two median rows larger and more regularly placed than those of outer rows, the anterior tubercle somewhat enlarged and projecting forward on anterior segments, the posterior tubercle enlarged and projecting backward on posterior segments. The outer

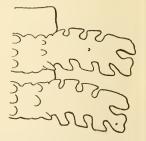


Fig. 2.--Iomus incisus. Ca-RINÆ OF SEGMENTS 8 AND 9.

rows well separated from the inner, somewhat curved or oblique, the middle tubercle of the row always largest and somewhat higher up than the posterior tubercle.

Carinæ nearly as broad as the body cylinder, over twice as broad as long; lateral margin with a deep oval incision near the middle; anterior and posterior margins with three or four similar smaller incisions, nearly closed by the connivent angles of the lobes, but with a broad sinus. (Fig. 2.)

Repugnatorial pores indicated by a small elevation at the base of the posterior lobe of the carina of segments 5, 7, 9, 10, 12, 13, 15–18; these segments also lack a distinct conic tubercle near the middle of the carina, present on other segments. (Fig. 2.)

Supplementary margins divided into minute oblong plates, over

twice as long as broad, the distal end entire and rounded.

Anterior subsegments separated by a very deep and abrupt transverse constriction; surface very minutely reticulate-punctate, the markings arranged in transverse rows on the posterior part of the subsegment, the last row very regular and elongate.

Segments 17-19 with last tubercle of dorsal row enlarged into a papilliform or cylindric process projecting obliquely backward:

process of segment 18 largest.

Last segment reduced and almost completely covered from above, exceeded by the produced carinæ and dorsal processes of segment 19; setiferous apex of segment covered with a broadly rounded median lobe, with a smaller and more pointed lobe on each side, also two distinct setiferous tubercles farther down along the posterior margin. Anal valves nearly flat. Last sternum broadly rounded with two

minute setiferous tubercles, the apex not

produced.

Sterna very narrow, scarcely as wide as the articulations of the legs; surface smooth, with a rather slight longitudinal and a more distinct transverse impression.



FIG. 3.—IOMUS INCISUS. GONO-PODS, ANTERIOR SIDE.

Legs rather slender, joint 2 over twice as

long as joint 1, about two-thirds as long as joint 3; joints 4 and 5 short, subequal, rather robust, about as broad as long; joint 6 very

slender, longer than joint 3.

Gonopods with a large hollow, clypeate basal joint closing over the small apical joint. Basal joint, viewed from in front, with a rounded-triangular outline, tuberculate near the outer angle and with a small notch near the lower inner angle; broadly and deeply emarginate on the posterior face. Second joint with three simple plates, two narrow on the anterior side and one on the posterior, shorter, broader, and more strongly incurved at apex. The longer anterior plates cross the median line. (Figs. 3 and 4.)

Pocock says that the sterna of *Docodesmus* are "as large as in *Polydesmus*" and that the sternum of the eighth segment is "furnished in front with a pair of tubercles tipped with a brush of hairs, a somewhat similar tubercle being noticeable upon the coxa of the anterior legs of this somite." The sterna of *Iomus* are much narrower than in *Polydesmus* and show no indications of such tubercles

either on segment 8 or elsewhere. The sternum of the third segment of the female has a slight transverse ridge and a very broadly trian-

gular process in the middle fitting closely against the strongly compressed, square-cornered, thin-edged, basal joints of the legs.

The last segment of *Docodesmus* is larger than in *Iomus* and with two large tubercles on its upper surface, as well as having the posterior border trilobate, but in *Iomus* the tubercles end with segment 19, the last segment having no exposed surface for the accommodation of such tubercles, only the lobed margin being exserted beyond the rim of segment 19. In *Tridesmus* also the last segment is distinctly exposed behind the posterior edge of the penultimate segment.

IOMUS INCISUS, new species.

Type-specimen.—Cat. No. 806 U.S.N.M., collected near Mayaguez, Porto Rico, November 30, 1899, by O. F. Cook.

Length of male 10.5 mm., width 2.8 mm.; female 12.5 mm. by 3.4 mm.

Color of dorsal surfaces black, also the vertex of the head, the under surfaces of the first segment and carinæ and the sides of the segments below the carinæ. Sterna, legs, antennæ, lower half of

head, anal valves and preanal scale, whitish or hyaline.



Fig. 4.—Iomus incisus. Gonopods, posterior side.

Head strongly depressed, much exceeded by the projecting margins of the first segment. Vertex rather strongly convex, sulcus rather deep, surface strongly granular-hispid like the surfaces of the segments. Clypeus smooth and

nearly flat, with three rather sharp teeth in a shallow emargination subtended by ten or twelve widely separated setæ arranged in two rows.

First segment distinctly narrower than the second, but over three times as long in the middle line; anterior margin entire, nearly transverse in the middle, with a shallow notch on each side near the lateral corner.

Segments with dorsal surface densely hispid with minute subcapitate hairs, matted with adherent particles of earth; removal of these shows a granular-uneven surface without distinct markings other than the dorsal tubercles and the marginal lobes. Median rows of tubercles as far from each other as from the lateral rows.

Posterior segments abruptly narrowed from about the seventeenth; the posterior dorsal tubercles distinctly enlarged, those of segments 17–19 forming oblique cylindric-conic processes, largest on segment 18, those of segment 19 set close together, projecting horizontally.

Last segment with a short decurved apex distinctly exceeded by the enlarged posterior tubercles of segment 19; dorsal black, roughened surface of segment slightly produced into a broad median lobe and two smaller lateral lobes; apex proper narrow, smooth and white, slightly decurved, scarcely exceeded by the broad median lobe.

Anal valves horizontal, smooth, slightly convex, with distinctly raised margins, though not very prominent. Preanal scale very broadly triangular rounded, not produced in the middle, with a small setiferous tubercle on each side.

Seven adult animals were obtained, three males and four females, all in one locality a few miles to the northeast of Mayaguez, along the road toward Las Marias.

The type of *Tridesmus sectilis* (Berlin Museum, No. 900) was probably collected near Mayaguez where Krug resided. *Iomus* is apparently more common than *Tridesmus*, for no additional specimens of the latter genus have been obtained during two visits to Porto Rico. A second specimen has been reported, however, from Utuado, by Professor Silvestri, who describes it as a second species of *Tridesmus*, *T. portoricensis*.¹

Other specimens of *Iomus* from Barrio Plata and from Bayamon were supposed at first to represent the same species, but more detailed examination shows definite differences that appear to require taxonomic recognition. As the specimens from the other localities are all females, only preliminary diagnoses can be offered.

IOMUS PLATANUS, new species.

Type-specimen.—Cat. No. 807, U.S.N.M., collected in Barrio Plata, Porto Rico, November, 1899, by O. F. Cook.

Closely similar to *I. incisus*, but somewhat more robust, the females attaining 13.5 mm. by 3.7 mm.

First segment with anterior margin more convex than in *I. incisus*, and slightly but distinctly scalloped.

Middle rows of dorsal tubercles distinctly closer to each other than to the outer rows, instead of at equal distances, as in *I. incisus*.

These differences may appear rather small, but they are quite definitely shown in all the members of the two series of specimens.

Eleven adult female specimens and one immature male were collected under a rotting log. The male specimen has 18 segments and 26 pairs of legs, and measures 5.5 mm. by 1.8 mm. Sternum of segment 7 unmodified; carinæ notched as in adult, but the dorsal tubercles somewhat less pronounced; repugnatorial pores more distinct. This specimen is of interest as showing that *Tridesmus* does not represent a younger stage of *Iomus*, a question naturally suggested by the close external resemblance of the two genera.

¹ F. Silvestri, Myriapoda from Porto Rico and Culebra, Bull. Amer. Mus. Nat. Hist., vol. 24, p. 577 August, 1908.

IOMUS OBLIQUUS, new species.

Type-specimen.—Cat. No. 808, U.S.N.M., collected near Bayamon, Porto Rico, November, 1899, by O. F. Cook.

Closely similar to *I. incisus* and *I. platanus*, but slightly more slender, the female measuring about 13.5 mm. by 3.4 mm.

First segment with anterior margin more transverse in the middle than in *I. incisus*, but also more distinctly scalloped than in *I. platanus*.

Dorsal tubercles of middle rows distinctly closer to each other than to the outer rows, but the posterior tubercles of the middle rows much farther apart than the anterior, so that the rows appear distinctly oblique, or converging forward, especially on segments near the middle of the body. On the anterior segments the anterior tubercles of the middle rows are distinctly enlarged. The same tendency is shown to a slight extent in I. incisus, while in I. platanus the middle tubercle of the inner rows are often somewhat larger than the others as in the outer rows. In the present species the enlarged anterior tubercles are united with two broad median lobes of the margins of the subsegments. There are two somewhat smaller lobes on each side separated by notches like those of the margins of the carinæ. The raised margins project somewhat forward and are more prominent in this species. The surface of the segments shows a suggestion of division into areas by very slight impressed lines. The carinæ appear shorter and somewhat more widely separated than in I. platanus, and the marginal incisions are somewhat deeper and more open.

The wider separation of the posterior tubercles of the inner rows in this species may be considered as an approximation to the arrangement of the outer rows, in the same way that the tendency to the enlargement of the middle tubercles of the inner rows in *I. platanus* approximates the specialization of the middle tubercle of the outer rows.

A single female specimen was found on limestone rocks near Bayamon. The color is a deep brown, not completely black, as in the other species, and especially in *I. platanus*.

SYNOPSIS OF WEST INDIAN GENERA OF CHYTODESMIDÆ,

The Chytodesmidæ are more nearly related to the African families Stylodesmidæ and Hercodesmidæ than to the true Cryptodesmidæ of South America. The gonopods agree with those of the African families in having the basal joint large and clypeate to contain the small folded terminal joint, but the segments lack the huge dorsal processes that characterize the African families. The slight development of the dorsal tubercles gives these West Indian genera a superficial resemblance to a third African family, the Pterodesmidæ, but the gonopods are of entirely different patterns in the two groups.

- Carinæ divided by deep incisions into numerous lobes; lateral margin with two lobes. Genus *Iomus*, type *I. incisus* Cook, from Porto Rico.
- Carinæ with dorsal areas separated only by shallow grooves and notches.
- Dorsum strongly and evenly convex, with three transverse rows of convex smooth rounded or polygonal areas; lateral carinæ narrow, depressed, the pores large and distinct. Genus *Chytodesmus*, type *C. laqueatus* (Karsch), from Cuba.
- Dorsum slightly convex, with indistinct transverse or radiating, roughened or hispid areas; lateral carinæ broad, nearly horizontal; pores very small.
- Poriferous carinæ with four marginal areas or lobes, the others with three; posterior area not strongly enlarged; last segment rather long, truncate at apex, with a distinct rounded lobe on each side. Genus *Docodesmus*, type *D. vincentii* (Pocock), from St. Vincent.
- All the carinæ with three marginal areas except at posterior end of body; posterior area much enlarged and somewhat produced on poriferous segments; last segment very small, triangular rounded at apex, entire. Genus Tridesmus, type T. sectilis Cook, from Porto Rico.

NOTE ON SOUTH AMERICAN CHYTODESMIDÆ.

Another member of the Chytodesmidæ was recognized several

years ago in the Berlin Museum among the specimens from Bogota, Colombia, included by Peters in his composite species Cryptodesmus alatus. The repugnatorial pores open on a special tubercle near the posterior corner of the carinæ, as in the West Indian genera Docodesmus and Tridesmus. It differs from these West Indian relatives in the very small size of the body and the very slight and poorly defined dorsal sculpture, consisting of a few large rectangular or polygonal areas. The following characters are described from notes and figures drawn at Berlin:

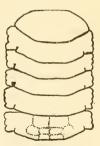


Fig. 5.—Stictodesmus creper. Segments 1-6. Dorsal view

STICTODESMUS CREPER Cook.

Stictodesmus creper Cook, Brandtia, p. 20, June, 1896.

Body composed of 19 segments, length 4.2 mm., width about 0.8 mm., being the smallest of the specimens originally assigned by Peters to his *Cryptodesmus alatus*.

First segment much narrower than the second, not completely concealing the head and the distinctly clavate antennæ; shape of segment subelliptic, or broadly fusiform, much more nearly symmetrical than usual; a line connecting the lateral angles would nearly bisect the segment. (See fig. 5.)

Segments with two rows of somewhat distinct dorsal areas on each side of the impressed median line; other areas not distinct.

Lateral carinæ less than half as wide as the body-cylinder, deeply grooved and notched in the middle of the otherwise entire posterior

margin; lateral margin slightly impressed and notched to form four rounded lobes on poriferous segments, three lobes on other segments; posterior corners of carinæ narrower than the anterior, not produced backward except on posterior segments. (See figs. 5 and 6.)

Repugnatorial pores rather large, opening toward the side, near the margin of the carina, just in front of the sinus between the third and

fourth lobes.

Last segment rather broadly triangular, projecting far beyond the small and slightly produced carinæ of the penultimate segment. (See fig. 6.)

A NEW GENUS FROM ST. PAUL DE LOANDA.

A report was published in 1893 on a small collection of myriapoda obtained from the U.S. National Museum by Mr. Heli Chatelaine at St. Paul de Loanda, West Africa.¹ The specimen to be described

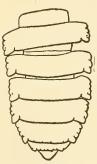


Fig. 6.—Stictodesmus creper. Segments 13-19. Dorsal view.

below was not included when the others were sent to me for identification, perhaps because it was broken into so many pieces. It did not come to my attention until five or six years afterwards, when descriptions and figures were prepared, to await another long delay in publication.

Though the antennæ and most of the legs have been lost, the structural characters of the segments and of the copulatory apparatus show that the animal represents, not only a new generic type, but one that is not closely related to any other hitherto described. The habit is quite similar to that of the other West African and American genera belonging

to the family Pterodesmidæ, but the resemblance proves to be a merely superficial analogy, another of the numerous approximations in external characters between millipeds that belong to unrelated families.

Notwithstanding the flattened dorsum and the broad wing-like carinæ, the affinities of the new genus lie with the Stylodesmidæ, Hercodesmidæ, Chytodesmidæ, and other related families that have the basal joint of the gonopods very large and hollowed out to contain and conceal the much smaller and more complicated distal joint. This feature seems to be diagnostic of a cosmopolitan natural group often confused with the South American family Cryptodesmidæ.

In addition to the large clypeate basal joint of the gonopods, the Stylodesmidæ and their allies are characterized by the prominent positions of the repugnatorial pores, which are borne on special lobes, processes, or tubercles, whereas the pores of the Pterodesmidæ, though seldom or never really absent, as at first supposed, are ex-

tremely small and are often quite remote from the margins of the carinæ.

The bodies of the Stylodesmidæ and most of their allies are characterized by the strongly convex dorsum and strongly decurved carinæ, which contrast with the flat, depressed bodies and horizontal carinæ of the Pterodesmidæ and related types, but this new form shows that no general distinction in the shape of the body can be maintained. It is one of those forms that are usually called aberrant, because they do not readily find places in previous classifications. The study of this type has led to a comparison of members of several other groups and a review of the pertinent literature. It has also been necessary to consider the characters of some undescribed forms that were accessible for comparison.

The new genus is named in honor of Mr. Chatelaine, not only because he collected the specimen on which it is based, but in recognition of his services to science in the study of the language and customs of the natives of Angola, as shown in his writings on these subjects.¹

CHATELAINEA, new genus.

Plate 60, figs. 1a-1n.

Type.—Chatelainea pterodesmoides, new species.

Body rather small, oblong, depressed, the segments with broad, nearly horizontal carinæ.

First segment large, projecting in front of the head; subflabelliform, about twice as broad as long, widest near the middle, twice as wide as the head; anterior margin evenly curved, divided by fine notches and radiating impressed lines into 10 subequal lobes; lateral angles rounded.

Segments plane or somewhat concave above, the carinæ slightly elevated; dorsal surface covered with minute hairs and irregular granules or tubercles, becoming definitely raised areas along the margins of the carinæ and in the middle of the dorsum.

Lateral carinæ with three or four deep notches in the posterior border and one or two in the lateral border, deeper on poriferous segments. The lobes between the notches form convex areas distinct from the more irregularly roughened remainder of the surface. The anterior margin is bordered by a narrow raised ridge. (Pl. 60, fig. 1a.)

Repugnatorial pores located on the dorsal surface at the base of the posterior lateral lobe of the carina, which is more deeply notched and more prominent above on poriferous segments. Poriferous lobe shorter than the others on anterior segments, but longer on posterior, and finally extended into a long tooth with an oblique or backward direction. (See pl. 60, fig. 1n.) Pore formula probably normal, but, with so many of the segments separated, all that can be definitely ascertained is that segment 7 has pores, and also the last nine segments of the body, with the exception of segments 14 and 20.

Supplementary margin well developed, consisting of a row of oblong or broadly spatulate appendages, those of the ventral side broader and with truncate entire margins, those of the dorsal side distinctly angled in the middle and with the margins very minutely toothed. (See pl. 60, figs. 1f and 1g.)

Posterior segments gradually narrowed, the last three more abruptly, and with the margins more deeply lobed; the posterior margins more deeply notched or toothed, and the poriferous lobes of the carinæ produced into long recurved spines.

Last segment small, conic, not concealed under the penultimate; the decurved apex ending in a small truncate tubercle, not definitely indicated in the drawing. (Pl. 60, fig. 1n.) Anal valves rather flat, the surface minutely granular but without distinct tubercles.

Preanal scale very broadly triangular, the lateral edges distinctly concave; apex rounded in the middle, but produced on each side into a distinct papilliform tubercle, bearing a long bristle. (Pl. 60, fig. 1i.)

Sterna narrow, with a distinct, but rather narrow and shallow median groove, and a broader and deeper transverse groove; no spines at the bases of the legs. (Pl. 60, fig. 1c.)

Legs rather slender; joint 2 nearly as long as joint 3, slightly exceeded by joint 6; joint 5 nearly twice as long as joint 4 and half as long as joint 6. (Pl. 60, fig. 1h.)

Copulatory legs with a large clypeate basal joint inclosing and concealing the complicated terminal joint. (Pl. 60, figs. 1j, k, l, and m.) The basal joint has a strong tooth near the middle of the posterior border. The upper part of the basal joint, as seen on the mesial face (pl. 60, fig. 1m) has a large depression to accommodate the strongly recurved terminal spine of the apical joint which bends backward toward the depression. Anterior margin of rim of aperture with a triangular median process. (Pl. 60, fig. 1j.)

CHATELAINEA PTERODESMOIDES, new species.

Type-specimen.—Cat. No. 802, U.S.N.M., collected by Heli Chatelaine at St. Paula de Loanda. Accession 23,400.

Length of male probably about 18 mm.; width 3.5 mm.

Color of alcoholic specimen a dull slightly reddish brown, paler below. As in *Stylodesmus* and other related forms, the finely hispid or pilose surface doubtless holds small particles of earth that lend the living animal the exact color of the soil in which it happens to live.

Head small and depressed, facing nearly ventral, concealed far under the projecting margin of the first segment. Vertex rather obscurely and irregularly granular, with a rather distinct rounded prominence at each of the posterior corners, behind the antennæ; surface pilose like that of the segments. Clypeus rather long and narrow, distinctly emarginate on the sides, with a rather broadly sloping transverse ridge; surface nearly smooth, scarcely pilose, labrum narrow, smooth, with a shallow emargination and three rather sharp teeth.

Antennæ rather slender, moderately pilose; second joint over twice as long as the first and somewhat exceeding the third; other joints lost.

First segment distinctly narrower than the second, over half as long as broad, widest in front of the middle. Dorsal surface strongly convex in the posterior part, concave in front, the anterior margin distinctly upturned; irregularly granular, more even on the marginal areas; densely and very minutely pilose.

Second and following segments with three lateral lobes or areas and three or four posterior, the latter separated by larger notches. Surfaces of lobes rather evenly convex, the remainder of the surface roughened with low irregular granules.

Posterior segments somewhat gradually narrowed from about the sixteenth. Carine rather more strongly upturned than on the middle segments and with the poriferous posterior lobe produced into a long oblique spine bearing the pore near the base. Posterior margin more distinctly scalloped in the middle than on anterior and middle segments. Segments 18 and 19 have the two middle tubercles of the posterior margin specially enlarged.

Last segment distinctly projecting beyond segment 19 in the middle, though evidently exceeded by the long poriferous tubercles of segment 19, incomplete in this specimen, as the figure indicates. Surface less uneven than on preceding segments, but still distinctly granular and pilose. Two minute setiferous tubercles along the lateral margins on each side below the apex.

RELATIONSHIPS OF THE FAMILY CRYPTODESMIDÆ.

The difficulty of assigning Chatelainea to a satisfactory place in the classification is due, in large measure, to the confusion that has been allowed to gather around Cryptodesmus, the genus to which some writers might refer Chatelainea. This name belongs, in reality, to a little-known South American milliped, but has been used for many and very diverse species from all parts of the tropical world. It is generally considered that the tropical forms referred to the genus Cryptodesmus or to the family Cryptodesmide constitute a distinct group, but most writers have hesitated to recognize the true extent

of the structural diversities inside this group, perhaps because of the uncertainty that still attaches to the original genus *Cryptodesmus* and the family Cryptodesmidæ.

Comparison of African material with the original specimens of Cryptodesmus in the Berlin Museum showed that the reference of African species to this genus was without warrant, and the presence of many constant structural differences among the members of a rich African fauna led to the recognition of a considerable series of new genera, and finally to the grouping of these genera into families. It was also found that some of the tropical American millipeds were much more related to the African genera than the first species that Peters assigned to Cryptodesmus, so that some new American genera were established and assigned, provisionally at least, to African families.

As the American fauna becomes better known it appears more and more probable that the original genus *Cryptodesmus* stands well apart from the other members of the series of forms usually associated with it. Indeed, in Pocock's recent treatment of the Central American millipeds in the Biologia Centrali-Americana a new family Peridontodesmidæ is established for the genus that seems to be more nearly related to *Cryptodesmus* than any other member of the Central American fauna. The first segment of *Peridontodesmus* is not expanded as in *Cryptodesmus* and the carinæ are broader and more deeply notched, but such differences would not be considered very serious if other features were alike.

It may be that the rough outlines of the first and last segments of the type of Cryptodesmus shown on pl. 60, figs. 2a and 2c, will help to explain the tendency to look upon any 20-segmented tropical milliped with a large first segment as a relative of Cryptodesmus, and to show at the same time that such conclusions are generally unwarranted. Apart from the broadly expanded first segment, the original type of Cryptodesmus does not show any tendency toward either of the two forms of specialization that characterize most of its supposed relatives. The segments do not have radiating marginal areas as in the Pterodesmidæ, nor enlarged dorsal tubercles, crests, or processes as the Stylodesmidæ, Hercodesmidæ, and Chytodesmidæ. repugnatorial pores are equally unspecialized. They are not located on the anterior part of the segment as in the Pterodesmidæ, nor on a special lobe or tubercle as in the Stylodesmidæ and their allies, but are located near the margin on a slight elevation, somewhat as in Scytonotus. The segments have simple piliferous tubercles as in Peridontodesmus and Scytonotus, and in the pore characters also there is more agreement with these genera than with the Pterodesmidæ or the Stylodesmidæ. There would seem to be better justification for the recognition of the family Scytonotide than for the

family Peridontodesmidæ. Scytonotus is a specialized type that certainly stands well apart from the now rather numerous genera of true Polydesmidæ in the structure and sculpture of the segments, as well as in the numerous and highly specialized secondary sexual characters. This has been recognized by Attems in his System der Polydesmiden, where our North American Scytonotus is associated with members of the South American family Trachelodesmidæ, though the lack of any true relationship is admitted. The structure of the gonopods of Scytonotus is also peculiar in that the basal joint is unusually large and somewhat hollowed out to accommodate the second joint. Though the specialization is not carried to any such extent as in the Stylodesmoid series, the analogy is suggestive. In Peridontodesmus, according to Pocock, the basal joints of the gonopods are fused together, a unique condition, as far as known, in the entire order.

A NEW SOUTH AMERICAN GENUS RELATED TO CRYPTODESMUS AND PERIDONTODESMUS.

The relations between *Peridontodesmus* and *Cryptodesmus* appear to be very close, both in the characters of the segments and in the more significant features of the structure of the gonopods. A Brazilian species described by Attems as *Cryptodesmus pusillus*, though not as similar to *C. olfersii* as its author supposed, is at least to be considered as a member of a related genus. A comparison of Attems's description and figures of *Cryptodesmus pusillus* with notes and drawings made from the type-specimen of *C. olfersii* shows several important discrepancies, though not such as to destroy the probability of family relationship with *Cryptodesmus*.

The body of *C. pusillus* is much smaller and more slender, seven times as long as wide (7 mm. by 1 mm.), instead of about four times (11 mm. by 2.5 mm.), in *C. olfersii*. The segments appear to be relatively longer and narrower than those of *C. olfersii* and the body is said to be broader in front, while that of *C. olfersii* is somewhat narrowed, with the first segment not as wide as the second.

The antennæ of *C. olfersii* are distinctly clavate. Those of *C. pusillus* are large and robust, but the terminal joints are not strongly thickened.

First segment of *C. pusillus* is much more expanded than in *C. olfersii*, semicircular in shape, two-thirds as long as broad; that of *C. olfersii* transversely elliptic, less than half as long as broad. Anterior margin even in both species, bordered in *C. olfersii* by a simple row of flattish granules; smooth in *C. pusillus*, with twenty yellow lobes of the inner tissues showing through the transparent chitin.

Carinæ of *C. pusillus* very angular and with the posterior corners produced; those of *C. olfersii* narrowed and rounded. The delicate,

transparent lateral margins of the anterior carinæ of *C. pusillus* are produced into distinct teeth, each with a large projecting bristle, instead of rather obscurely and unevenly sinuate-dentate as in *C. olfersii*. Posterior margins with fewer and less distinct teeth than in *C. olfersii*.

The segments of *C. pusillus* are distinctly convex in the middle, and the adjacent tubercles of the anterior row run together to form a transverse ridge. Neither of these features was noted in *C. olfersii*, the segments of which have three regular transverse rows of simple granules, each provided with a short hair.

Repugnatorial pores in *C. pusillus* located in distinct furrows that separate the bases of the marginal teeth, in front of the first tooth before the posterior corner. In *C. olfersii* there is no such distinct development of the marginal teeth, and the pores are located on a slight broad elevation, rather close to the margins of the segments.

APOMUS, new genus.

Such differences would seem to require the recognition of a distinct genus, for which the name *Apomus* is proposed, with *Apomus pusillus* (Attems) as the type. Though the specialization of the first segment in *Apomus* is carried even farther than in *Cryptodesmus*, the gonopods are distinctly of the same peculiar pattern as those of Pocock's *Peridontodesmus flagellatus* from Guatemala.

NOTES ON THE SOUTH AMERICAN GENUS CHONODESMUS.

The genus Chonodesmus, based on Cryptodesmus alatus Peters, from Bogota, Colombia, has been referred to the African family Pterodesmidæ on account of a very close approximation in the form and ornamentation of the segments, and the location of the repugnatorial pores in the anterior part of the carina. Nevertheless, it is possible that Chonodesmus belongs to the true Cryptodesmidæ or to the Peridontodesmidæ, if these groups are distinct. The situation of the repugnatorial pores at the side of a small elevation is much as in Peridontodesmus and the gonopods are quite complicated, much more so than those of any of the African genera of Peterodesmidæ. The first segment is much shorter than in Cryptodesmus and Apomus, being less than one-third as long as broad, and the posterior margin is nearly transverse, instead of being turned forward at the sides. The following notes and figures were drawn from the type-specimen in the Berlin Museum.

CHONODESMUS ALATUS (Peters).

Cryptodesmus alatus Peters, Monatsber. königl. Akad. Wiss. Berlin, 1864, p. 621. Chonodesmus alatus Cook, Brandtia, p. 23, June, 1896.

Antennæ rather short and robust, distinctly clavate; joints 5 and 6 subequal, much larger than the others; joint 2 only slightly longer

than joints 1, 3, 4, and 7, which are subequal in length. Surfaces of all the joints rather densely hirsute with rather short hairs. Outer side of joints 5 and 6 with a large rounded prominence

bearing numerous sense-cones. (Fig. 7.)

First segment subcrescentic, very short and broad, only slightly exceeded by the second segment. Anterior margin evenly rounded, lateral corners rather sharp, but scarcely produced; posterior edge with a



FIG. 8.—CHONODESMUS ALATUS. SEGMENTS 1 AND 2. DORSAL VIEW.

distinct median emargination and a much slighter and broader emargination on each side of the middle. Surface covered with nu-



Fig. 7.—Chonodes-Mus alatus. An-Tenna.

merous small convex areas, about twenty along the anterior margin, those of the posterior margin somewhat larger and less numerous. (Fig. 8.)

Dorsal surface of the segments occupied by three transverse rows of convex, piliferous areas, smaller and more regular than those of the carinæ. Margins of carinæ divided by radiating impressed lines into broad, slightly angled or rounded lobes, four on the lateral edge and four or five on the posterior. (Fig. 9.)

Repugnatorial pores not opening on the margins of the carinæ, but at the side of a small elevation near the base of the second lateral area, somewhat in front of the transverse middle of the carina.

Last segment with apex rather broadly rounded, only slightly exceeding the broad, triangular projections of the carinæ of the penultimate segment. (Fig. 10.)

It was on this specimen that Peters evidently relied in drawing his description of *Cryptodesmus alatus*, and he stated in particular that his measurements,



FIG. 10.—CHONODES-MUS ALATUS. SEG-MENTS 18-20. DOR-SAL VIEW.

11 mm. by 2.7 mm., applied to the largest of the specimens. All the other characters that Peters gives in the original description apply to this individual.



Fig. 9.—Chonodesmus alatus. Segments 4 and 5. Dorsal view.

In the second species of *Chonodesmus*, *C. regularis*, the dorsum is more convex and the carinæ less horizontal, the piliferous dorsal areas are more

equal in size, more regularly placed on the dorsal surface, and provided with longer hairs. The body measured 8 mm. by 2.2 mm., but may not have been mature, as only 19 segments were counted.

A NEW SPECIES OF PERIDONTODESMUS FROM GUATEMALA.

The small size of the first segment is the most striking external feature that differentiates *Peridontodesmus* from *Cryptodesmus*. Pocock considers this as a primitive character in justifying the erection of a family, but it seems more reasonable to look upon the peculiarities of this segment as specializations in both cases.

PERIDONTODESMUS PURULICUS, new species.

Another species of *Peridontodesmus*, not studied by Pocock, has the first segment less reduced, scarcely narrower than the rounded anterior corners of the second segment, and with the lateral corners less pointed than in the species studied by Pocock, though more specialized in other ways. The teeth that border the anterior margin of the first segment are of different sizes, five or six near the lateral corners being much larger than those farther toward the middle.

The antennæ are distinctly clavate, but not geniculate; joints 1-5 short and robust, increasing in length and diameter; joint 6 about twice as long as joint 5, more than twice as long as joint 7; joint 3 scarcely longer than joints 2 and 4 instead of much longer, as in *P. flagellifer*. These proportions are also widely different from those found in *Scytonotus* where joint 3 is the longest, and joints 4 and 5 are nearly as long as joint 6.

The dorsal tubercles are reduced so that the segments are nearly smooth, though beset with three transverse rows of long hairs. Poriferous segments have the carine dark brown like the middle of the

body, while segments without pores have yellowish carinæ.

The gonopods end in three prongs, somewhat as in *P. flagellifer*, with the short inner prong sharply decurved, as in that species, but not so much exceeded by the relatively short and straight outer prong. Middle prong expanded into a short, incurved plate, truncate-emarginate at apex, and with the corners produced into small teeth. The long retrorse basal prong of *P. flagellifer* is replaced by a large rounded ventral prominence with a pencil of compact bristles on its distal slope. Female genitalia broadly clavate globose, the apical surface with a deep transverse groove.

This species may be called *Peridontodesmus purulicus*. The type is deposited in the U. S. National Museum (Cat. No. 809), a male specimen collected at Purula, Baja Verapaz, Guatemala, by O. F.

Cook in June, 1904, measuring 8 mm. by nearly 2 mm.

The bearing of these new forms upon the classification of *Chatelainea* lies in the fact that their characters connect *Cryptodesmus* with the American series represented by *Peridontodesmus* and *Scytonotus*, and perhaps even with the true Polydesmidæ, rather than with the African and other tropical types which it has been customary to refer to the genus *Cryptodesmus* or to the family Cryptodesmidæ.

In other words, the true Cryptodesmide of South America have no close relationship with the African families Pterodesmide and Stylodesmide.

THE SYSTEMATIC POSITION OF CHATELAINEA.

Though the structure of the gonopods shows that the affinities of *Chatelainea* undoubtedly lie with Stylodesmidæ and Hercodesmidæ, rather than with the Pterodesmidæ, the radical difference in the form of the body forbids the reference of the genus to either of the related African families, both of which are characterized by strongly convex segments, strongly depressed carinæ, and longitudinal ridges of large dorsal tubercles or processes.

Chatelainea was compared also with the West Indian genera referred to the family Chytodesmidæ, for in some of these the form of the body approaches that of Chatelainea, at least to the extent that the segments are nearly flat, the carinæ nearly horizontal, and the dorsum without any specially developed tubercles or ridges. Two such genera have been known for some years from the West Indies, Docodesmus from St. Vincent and Tridesmus from Porto Rico. Another genus from Porto Rico, hitherto undescribed, offers a still closer approximation to Chatelainea, in that the carinæ are deeply incised instead of having the margins entire or slightly scalloped, a feature that distinguishes it at once from the other West Indian genera of the group.

The carinæ of *Iomus*, as the new Porto Rican genus is now called, are fully as wide or wider than those of *Chatelainea*, and more deeply lobed. The lateral edge, in particular, is cut near the middle by a very deep notch, often completely closed at the margin by the projecting connivent corners of the lobes. The other notches are also partly closed along the edge, somewhat as in *Chatelainea*, but more so. The anterior margin, entire in *Chatelainea*, is notched in *Iomus* like the posterior margin, though not quite so deeply.

The carinæ of *Iomus* are strongly depressed, leaving the middle of the body very convex instead of nearly flat as in *Chatelainea*. Four longitudinal rows of distinctly enlarged tubercles ornament the segments of *Iomus*, but are not developed in *Chatelainea*. Each row is represented by three tubercles on each segment, the two inner rows having somewhat larger tubercles than the outer, and arranged with more regularity. The posterior tubercles of the middle row, on segments 17, 18, and 19 are distinctly enlarged into

¹ The family name Pyrgodesmidæ Silvestri (1896) is used by Pocock in the Blologia instead of Stylodesmidæ Cook (1895), on the ground of a conjecture by Attems that the generic name Stylodesmus is a synonym of Urodesmus Porath, and therefore not available as the basis of a family designation. In reality, Urodesmus is quite distinct from Stylodesmus and more likely to belong to the Hercodesmidæ than to the Stylodesmidæ. At most it may serve to connect the two groups. This would not interfere with the utility of Stylodesmidæ as a family name, but would only extend its application.

prominent papilliform processes, a tendency only faintly suggested on the posterior segments of *Chatelainea*.

The repugnatorial pores are extremely minute, much more so than in *Chatelainea*, but they occur on the same segments, near the base of the posterior lobe of the carina, near the base of the lateral notch. A further peculiarity of *Iomus* is that the segments without pores, 4, 6, 8, 11, and 14, have a distinct tubercle near the middle of the carina, while such tubercles are usually quite absent on poriferous segments. (Fig. 2.)

The basal joints of the antennæ are rather more slender in *Iomus* than in *Chatelainea*, and the second joint is much shorter than the third, whereas in *Chatelainea* it is distinctly longer than the third.

The first segment of *Iomus* has the anterior margin only slightly upturned and the marginal areas are indicated below by very faint impressed lines. The last segment does not project as in *Chatelainea*, but is covered and concealed under segment 19, somewhat as in *Stylodesmus*.

In the absence of any definite indication of affinity with members of other families of Stylodesmoidæ, it seems to be necessary to consider *Chatelainea* as representing a distinct group.

CHATELAINEIDÆ, new family.

African millipeds of the superfamily Stylodesmoidæ, but with external similarity to the Pterodesmoidæ.

Body small, oblong, depressed, with horizontal or slightly ascending carinæ, deeply lobed on the lateral and posterior margins.

First segment moderately large, rounded in front, covering the rather small, depressed head.

Dorsal surface of segments nearly flat, covered with slightly convex rounded or radiating areas and hispid with short hairs, but without prominent spines, crests or tubercles. Poriferous carinæ deeply lobed on the lateral margins; posterior corners produced into long recurved teeth on posterior segments.

Repugnatorial pores opening on the dorsal surface, near the base of the posterior lobe of the carinæ, not borne on a prominent cylindrical or conical tubercle.

Supplementary margin dissected into minute oblong lobes.

Last segment with a projecting conical apex, not covered by the penultimate segment, but exceeded by the greatly produced posterior corners of the penultimate.

Legs slender, joint 2 nearly as long as joints 3 and 6.

Gonopods with basal joint expanded and hollowed out to contain the small retracted second joint.

EXPLANATION OF PLATE 60.

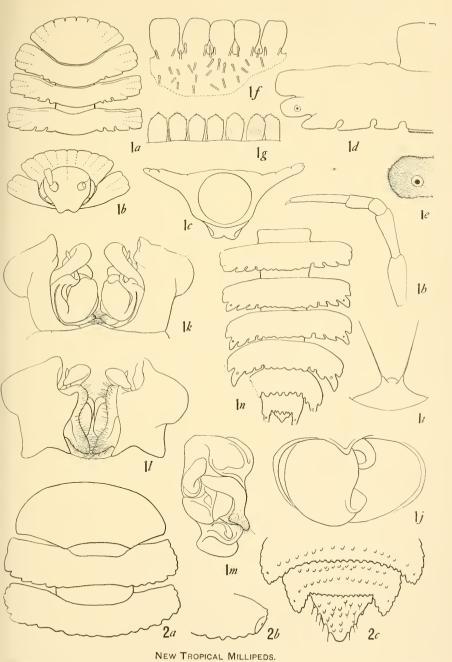
Chatelainea pterodesmoides, new species.

- Fig. 1a. First four segments from above.
 - 1b. Head and first two segments from below.
 - 1c. A segment, posterior view, showing the position of the carinæ.
 - 1d. Lateral carina, showing position of repugnatorial pore.
 - le. Poriferous lobe of carina more magnified.
 - 1f. Supplementary margin from ventral part of segment, seen from the outside.
 - 1g. Supplementary margin from dorsal part of segment, seen from the inside.
 - 1h. Five distal joints of leg.
 - 1i. Preanal scale with long setæ.
 - 1j. Copulatory leg in situ, ventral view, showing rim of aperture.
 - 1k. Copulatory legs, anterior view.
 - 11. Same, posterior view.
 - 1m. Same, mesial view.
 - 1n. Last seven segments, dorsal view.

Cryptodesmus olfersii (Brandt).

- Fig. 2a. First three segments, dorsal view, drawn from type-specimen in the Berlin Museum.
 - 2b. Carina of segment 5, with repugnatorial pore.
 - 2c. Last three segments, dorsal view.





FOR EXPLANATION OF PLATE SEE PAGE 473.

