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ON A NEW SPECIES OF CALIFORNIA EARTHWORM,
HAPLOTAXIS ICHTHYOPHAGOUS
(OLIGOCHAETA, ANNELIDA)¹

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Earthworms, on hooks, have been used, at least for one millenium by man as bait to catch fish. In California, the worm has turned, according to Briggs (1953), and even gets its fish as food without human assistance. Such worms may prove to be of considerable economic importance and should be of general interest because of the unusual diet and adaptation thereto.

Several examples received directly or indirectly from Briggs in 1951 were juvenile. Further material was requested in hope of securing adults to enable description of the genitalia. Again only juveniles were provided. Various subsequent efforts to obtain additional specimens all were futile.

Fortunately, researches of the last quarter century have shown that somatic megadrile anatomy, previously derogated or ignored by oligochaetologists of the classical school, is, rather generally, much more conservative phylogenetically than the genitalia. Accordingly a very short esophagus comprising parts functioning as a pharynx and as a gizzard, the long but simple intestine, presence of only two longitudinal vascular trunks, absence of hearts but presence of a pair of long and much looped, lateral (in sensu stricto) commissures in each segment, enabled assigning the Californian juveniles to the presently monogeneric family Haplotaxidae. Furthermore, pedestals of Timm under the nerve cord indicate to

¹ The worms were studied during research financed by the National Science Foundation.

which one of the few, little-known species of that family the new form seems most likely to be related.

Haplotaxis ichthyophagous new species

Material examined: California, Humboldt County. Prairie Creek near Orick, from 8 inches below gravel surface and under 6 inches of water near stream center, 15 March 1951, 8-0-0. J. C. Briggs (in part per Dr. C. Berkeley). Subsequently, 165-0-0. J. C. Briggs. Types and permanent transverse and longitudinal sections, at the Tall Timbers Research Station, Tallahassee, Florida.

External characteristics: Length at first could only be estimated as each worm was in a tightly coiled mass of loops 30-40 mm long, straightening then (1951) impossible without breaking the body wall. Length in **mm/segment** number (in 1961 by which time formalin as well as spirit specimens could be straightened without rupture), 205/339, 210/412, 250/433, 270/462. Diameter (maximum), of most specimens 2-2½ mm. Near the hind end thickness decreases to less than a millimeter. Color (formalin material), greyish in regions where gut contains black granules but elsewhere, i.e., in much of the body and most worms, only cuticular iridescence and muscular sheen is recognizable. A yellowish to brownish color, lacking in 1951, now (1961) characterizes specimens kept in spirit since receipt. Head, neck and dorsal pores, lacking. Mouth, ventral, 1 + mm from anterior end of body, transversely elliptical, always open, closure probably impossible but the anterior part of the body can be bent ventrally so as to conceal it from view. Anus, very small, perfectly circular, terminal. Annulation, intersegmental furrows obvious, one secondary presetal furrow in each metamere from v back for some distance but gradually becoming less obvious and finally **unrecognizable** in the posterior portion of the body. The presetal annulus is slightly less than half the length of the next portion of the segment.

Three furrows are recognizable in front of the first setae. The foremost is completely circumferential and marks off a large lobe distinguished by a pebbled appearance of its surface. A second furrow ends **ventrally** at the lateroanterior margins of the mouth. The third, though unrecognizable in the ventrum behind the mouth, elsewhere seemingly forms the anterior boundary of the first setigerous segment and so should be intersegmental furrow 1/2 unless deviation from normal is involved. Confirmation for that interpretation seemingly is provided by gonad locations in the usual haplotaxid segments x—xiii, if the first setigerous segment really is **ii**. But then, segment i is very short in the ventrum. However, three haplotaxid species supposedly do have a bipartite prostomium, perhaps somewhat as in the Californian worms. Here the anterior section is about twice the length of the other portion, and the two-part prostomium is about three times the length of the peristomium even dorsally. On the largest worms, length of the region from the anterior end to the

postoral furrow (1/2) about equals combined lengths of ii-iii and presetal annulus of iv or even all of ii-iv.

Setae, four to two per segment, located about at the equators of the longer secondary annuli. Even in the last few segments where secondary annulation is lacking, the setae are nearer the posterior than the anterior intersegmental **furrows**. For convenience only, the dorsal setae are assumed to be the d shafts (which of course implies that the b and c setae had disappeared) thus enabling characterization of setal intervals as, AA ca. = DD < AD. The ventral setae are larger, protuberant to the exterior, with simply pointed tip posteriorly directed. A major ental portion of the shaft, from the nodulus just within the parietes, is nearly straight. The shorter external portion beyond the nodulus is slightly curved so as to be faintly suggestive of a shape characterizing a and b setae posteriorly (cf. Omodeo, 1958, fig. 4, p. 20) in *Pelodrilus falcifer*. A considerable portion of the shaft between the nodulus and the ectal tip is ornamented with frequently and irregularly interrupted circles of fine serrations. Dorsal setae are within the parietes and are lacking behind the 250th segment if not also from some more anterior level. Tips are simply pointed. No ornamentation was recognized.

Nephropores and genital apertures are unrecognizable. No indications of possible sites could be distinguished, even in microscope mounts of the cuticle. Nor is any trace of a **clitellum** distinguishable. Accordingly, all specimens were rated as juvenile.

Longitudinal greyish lines mL and mV, like similar lines sometimes visible at A and D, presumably are due to gaps in the longitudinal musculature.

The cuticle, in 1951, was firmly adherent and could not be removed without damage to the epidermis. Ten years later the cuticle of formalin material is wholly free of the epidermis but from alcoholic specimens still comes away with occasional bits of tissue attached. The cuticle is tough (cuts with difficulty), strong (does not tear easily) and seems to be thicker than in most megadriles. It is continued into the buccal cavity and to the hind end of the esophagus as well as into the parietes to form a lining of the setal follicles. Within the gut the cuticle seems to be thinner than externally. Inner ends of cuticular tubes lining the follicles are smooth and appear to have been in the region of the nodulus. Walls of the a tubules are thicker than those of the d tubules. Posteriorly very small dorsal tubules were without **setae** which presumably had been dehisced as the follicles atrophied. Thus, in cuticle of the 200th to 203d segments of one specimen only a single tube was found and no seta.

In the mounted cuticle, small markings like a plus sign each comprising four short and straight, dark lines from a dark dot, appeared to be scattered about in a random manner. They certainly are less numerous than the epidermal fenestrae. Pinkish patches, that appeared under the 16 mm objective of the inverting microscope to be circular spots of thinness, do have a more regular arrangement, being in equatorial circles in both segmental annuli, more numerous in the setal annuli, in several

cephalic segments in bands rather than circles. The patches, under 4 mm objective, are resolved into closely crowded dark or pinkish dots in regular parallel rows so that each area now has a squarish or rectangular outline. Those patches probably are present throughout the body as they still are recognizable, though fewer in number, in cuticle from segments in front of the anus.

The epidermis is perforated, except in immediate vicinity of follicle apertures and at primary and secondary furrows, by small, closely crowded fenestrae so that the epidermis has a rather honeycomb appearance. Through those **fenestrae** circular muscle fibers are distinguishable. Each fenestra presumably indicates site of a unicellular mucus gland contents of which had disappeared completely. No trace of nephrophores or of genital apertures was recognized, either in cuticle or epidermis and even in vicinity of the follicle apertures. Because of location of the supposed nephridial ducts, possibility of their opening into setal follicles was considered but no evidence for it was recognized in cuticular tubes lining the follicles.

Internal anatomy: Septa, present at least from 5/6 which is somewhat funnel-shaped and bulged posteriorly, none especially thickened. The circular muscle layer is thin, seemingly only 3-5 fibers thick. The longitudinal muscle layer, in transverse section, certainly cannot be called pinnate and so presumably should be termed fasciculate. The size of the discrete muscle blocks varies from small to large and also from one section to another. The number of blocks may be as many as 20 or even more. Setal follicles protrude into coelomic cavities, the d follicles much less conspicuously. Two bandlike retractor muscles pass, close to the parietes, from each a follicle to the d follicle of its own side and segment. A single functional shaft is associated with each follicle aperture but a follicles often have one or two reserve setae, the smallest seen being no longer than the thickness of the functional shaft. A single reserve rarely is associated with a d follicle.

The digestive system comprises three macroscopically distinguishable regions, the buccal cavity, the next portion which is called esophagus and the intestine. Calciferous glands, caeca, typhlosoles and suprainestinal glands are lacking. The buccal cavity is large and its thin wall is firmly adherent to the parietes. The esophagus is white, thick-walled, with a slight flange at the posterior end on which is the insertion of septum 5/6, with but little external indication of demarcation into a pharynx and gizzard. The anterior portion (presumably to be regarded as pharyngeal) is circular in cross section. The posterior portion (presumably gizzard) is squarish in cross section and thereby distinguished from the circular cross section of most megadrile gizzards. Numerous muscle bands pass posterolaterally from the esophagus to the parietes. The gut behind 5/6, being of uniform calibre and without regional differentiation presumably is to be considered as all intestine. **Chlorogogen** may first be recognizable in vii in which case the intestine of vi is white like the esophagus. On each side of the intestine, slightly lateral to mD,

a longitudinal ridge, seemingly uninterrupted for considerable distances, protrudes conspicuously into the gut lumen. The ridge is rounded, never lamelliform. In other regions of some specimens longitudinal ridges, also rounded, are protuberant from the dorsal surface of the gut, instead of into the intestinal lumen. These protuberances, in either case, always are filled with blood. These longitudinal sinuses, often elliptical to nearly circular in cross section, are so constant and regular as to seem to require special structure of the channel walls. They must contain most of the blood of the gut and perhaps a large portion of the total amount of the animal.

The vascular system has only two longitudinal trunks each of which runs from one end of the body to the other. The dorsal is slender, circular or nearly so in cross section, with a thick opaque wall seemingly covered with chlorogogen. The ventral trunk, usually much larger, thin-walled, and transparent, elliptical in cross section, deeply constricted in region of each septal insertion, bifurcates behind the mouth. Black bodies, seemingly aggregations of small granules, are just behind each of the constrictions. A small blood vessel was seen at anterior end of the prostomium but was not traceable to one of the major trunks. A pair of slender commissures just in front of each septum connects the dorsal and ventral trunks. Each commissure is much longer than height of the coelom and is looped, one long loop with closed end ventrally almost reaches the ventral parietes on lateral face of the a follicle. A vessel on the median face of each nephridium passes off ventrally and to the posterior septum where it becomes unrecognizable. Only the nephridial vessels and the dorsal spaces in the intestine were red, other vessels were colorless or perhaps slightly yellowish. Hearts are lacking.

Nephridia are lacking in the first 15 or 16 segments and are small (vestigial?) in xvii—xviii or xix. Posteriorly these holoic organs nearly fill coelomic cavities. Tubular structure is unrecognizable and if present is concealed by massive distention (by metabolites?) of the investing **peritoneal** cells. A slender cord (duct?) from the lower side of a nephridial mass passes ventrally, almost on the anteroventral face of an a follicle, and into the parietes. **Nephric** funnels were not seen.

The bibbed brain is pre-oral, nearly filling the coelomic cavity of its annulus which is assumed to be the hinder portion of the prostomium. Circum-oral commissures are long, slender, and unite at mV behind the mouth. Shortly behind the **commissural** junction the nerve cord is widened into two obvious ganglia that are fairly close to each other. Posteriorly the cord is ribbon like and with little indication of ganglionic widenings. Three pairs of nerves probably do pass out from the cord in each segment. Only a single giant fibre was recognized dorsally in cross sections of the cord. Nerve cord pedestals (organs of Timm) are present.

Gonads, fairly large, are present in at the usual megadrile sites. Distal ends of those in xfi and xiii are continued into three discrete and gradually narrowing processes. Such continuations were not seen in

x-xi but could have been broken off and unrecognized. Rudiments of male and female funnels, gonoducts, seminal vesicles and ovisacs, or of any sort of genital glands were not seen.

Growth: Four small juveniles were available. Length, 76-113 mm. Maximum diameter, 1 mm. Setigerous segments, 184, 197, 210, 237. A **metamerically** undifferentiated region behind the last setigerous segment is little more than one tenth of a millimeter thick though 1-1+ mm long. Several slight furrows (possibly rudimentary intersegmentals?) may be indicated. The anus is of the usual pin-prick sort.

Post embryonic growth, in *H. ichthyophagous*, presumably involves production of new segments.

Regeneration: Tail regenerates: 1) Small, conical bud, much narrower than the substrate, metamerically undifferentiated, anus terminal, at 260/261. 2) Tail had been lost at 265/266 along with ventral halves of 263'd to 265th segments. Missing ventral tissues had been replaced but were marked off into 7 setigerous segments. Remainder of the regenerate comprised 13 setigerous segments and a terminal region with several rudimentary intersegmental furrows but no setae. 3) At 277/278, regenerate with 15 setigerous segments followed by two asetal segments and the periproct. 4) Tail had been lost at 284/285 along with left half of the 284th segment. Regeneration bud, distal and bluntly rounded, without indications of metameric differentiation, had been growing posterolaterally from ^{21/2} left side of the 284th segment. 5) At 327/328, a regenerate about ^{21/2} times length of last substrate segment, without metameric differentiation. 6) At 330/331, regenerate with six setigerous segments, and a terminal region in which rudimentary intersegmental furrows are recognizable but no setae. 7) At 347/348 a 24 segment regenerate, the proximal segment and the periproct without setae. 8) At 356/357, a regenerate about 1 mm long apparently marked off by rudimentary furrows into several segments none of which is setigerous.

The anus is terminal, in each case, and of the usual pin-prick sort. At distal end of regenerate No. 5, there is a slight transverse cleft at bottom of which is the anal aperture.

Some specimens, perhaps nearly a dozen, may be unregenerate posterior amputees. (Posterior ends of 23 worms had been broken off at time of collection or subsequently.)

Abnormality: Metameric abnormality should be easily recognizable as intersegmental furrows are distinct. Only two abnormal segments were noted, in the middle of the body of two specimens. No. 1. Segment with setae but length about equal only to the posterior secondary annulus of neighboring metameres. No. 2. Segment without setae, about half as long as adjacent **metameres**, somewhat asymmetrical as the left side is shorter. No. 3. A caudal growth of 12 setigerous segments and periproct from right-side of 264th and 265th segments of a worm with 285 segments and a short area with rudimentary intersegmental furrows but no setae recognizable. A branch from the gut of the main axis passes through the outgrowth to a terminal anus of the usual sort. The nerve

cord of the appendage emerges from the parietes well lateral to the main cord and apparently as a thickening of a lateral nerve. No. 4. Anus of one worm longitudinally slitlike, dorsal, lateral margins in apposition, without a terminal lobe.

Ingesta: The gut usually was empty except for black granules in a short pre-anal region.

Biology: *H. ichthyophagous* lives at unknown depths in the gravel of northern California streams. It is believed (Briggs, 1953) to be able to detect presence of salmon eggs from considerable distances. During February—May, the worms aggregate to a depth of a foot in the redds where salmon and trout had deposited their eggs, 400 + worms having been found in a single redd. The worms give off mucus copiously and that was thought to kill the fish embryos more by oxygen deprivation than by toxicity. No mechanical damage to fish eggs was evident and worms were believed to feed on the yolk only after decomposition had ruptured the tough outer chorion.

A very strong odor proved that these worms really had been associated with fish.

The species presumably should be called limocolous rather than aquatic. Haplotaxids have been thought to be inhabitants of wells or other subterranean waters primarily because most specimens known were secured from just such or similar situations. However, Thienemann (1912) and Hesse (1923) maintained that *H. gordioides* really is terrestrial and breeds only in earth.

Remarks: The formalin specimens provided a control for color which appeared only in alcoholic material. References to golden, yellow, and yellowish-brown color of earthworm specimens in classical descriptions then are likely to have no taxonomic significance. Long enough stay in alcohol sometimes does produce a browning of tissues in which little optical differentiation is recognizable. A yellow color at posterior end of the body of certain megadriles may be due to accumulation in coelomic cavities of detached chloragog cells.

When first received the completely circumferential furrow marking off the prostomium into two segments was invariably obvious. That furrow, as one result of the softening and relaxation that has taken place during the last 19 years, now seems less distinct or even in part lacking. Reports as to intraspecific variation of the furrow may then have little significance. Apparent absence in any species with an elongated prostomium may also be an artefact.

The mouth of most megadrile oligochaetes is terminal. If the oral segment of the California worms is the same as the **buccal** segment of other megadriles, then the prostomium has been enlarged, extended anteriorly and demarcated into two portions. The mouth also has been enlarged at the expense of the peristomium which is very short ventrally.

Histological structure of the short esophagus may be quite different from that of most megadriles in which case adequate histological **characterization** may provide additional differences of systematic importance.

Mention now is made of only one of the interesting questions posed by the species: Is **presence** of the brain in the prostomium, instead of somewhere in the pharyngeal region of ii—iv as in most megadriles, primitive or secondary?

Systematics: The California worms are distinguished from those of all other megadrile families by several unusual characters. Unfortunately none of them was allowed any importance in the past when oligochaete systematics was mainly concerned with setae and genitalia. In the latest key to species of the Haplotaxidae (Brinkhurst, 1966, p. 44), the present form runs down to *H. gordioides* (Hartmann, 18Z1). That species now has been recorded from Denmark, Germany, Poland, Russia, Belgium, France, Switzerland, CSR, Yugoslavia, Hungary, Italy, Corsica, Central Asia, Siberia (including Kamchatka), Japan, and Washington, Illinois, Indiana, Ohio, Virginia and New York states. All other earthworm ranges presently equalling or approximating that of *H. gordioides* were attained as a result of transportation by man. No records have been found of interception of haplotaxids. However, the European *Criodrilus laccum* Hoffmeister, 1845, also never intercepted, was introduced to North America at least once though probably without attainment of domicile. Furthermore, mud along with aquatic plants is known to have been carried around the world.

If, however, the present range of *H. gordioides* was self-attained the time involved, especially in view of the restricted habitat, would seem to have been much greater than that which would have allowed considerable speciation in so wide a domain. Such evolution of course should be expected first of all in the reproductive system.

From *H. gordioides* as now defined, the Californian taxon is distinguished, in absence of so much data about somatic systems, only by the setal ratio $AA = DD < AD$ instead of $aa = al, al >$ or $= ld, aa = \frac{1}{2}dd$.

Information also is lacking about segment number in *H. gordioides*. Neither Michaelsen (1900) nor Brinkhurst (1966) mention that character in their definitions nor in those of one other pre-1900 species. The California taxon is defined tentatively by its somatic anatomy alone as follows.

Digestive system, with a transversely elliptical, permanently open mouth, large buccal cavity in ii with its wall firmly adherent to the parietes, a short, thick-walled esophagus in **iii—v** without obvious external demarcation into **pharynx** and gizzard, an intestinal origin in vi, a terminal pin-hole anus, but without intestinal caeca and typhlosoles or calciferous and supra-intestinal glands. Vascular system, with complete dorsal and ventral but no other longitudinal trunks, with a large vascular space in intestinal roof on either side of mD, with long, looped, segmental vessels connecting longitudinal trunks but without hearts. Excretory system, of holoic nephridia (avesiculate?), lacking in interior segments, with investing peritoneal cells distended by metabolites, ducts passing into parietes in region of A. Nephropores, inconspicuous, (in vicinity of A?). Nervous system, with brain in prostomium, two ganglia in anterior end of nerve

cord but little evidence of ganglionic widenings elsewhere, with but one small dorsal giant fibre. Pedestals of Timm, present. Septa, present from 5/6, none especially thickened. Circular muscle layer, thin. Longitudinal muscle layer, fasciculate, muscle blocks numerous and with marked **variation** in size and number. Setae, four per segment, two dorsal, small and disappearing posteriorly, two ventral, much larger, with posteriorly directed, simply pointed tip, anteriorly $AA \text{ ca.} = DD < AD$. Head, neck and dorsal pores, lacking. Prostomium, long, marked off by an annular furrow into two segments. Segments, to 462, with posthatching production of new **metameres**. Size to 270 by $2\frac{1}{2}$ mm.

Some of those characters will be definitive at genus if not at family level. Little is to be gained by guessing as to which characters and at what level. Good generic characters are those which are invariant in all species of the genus, just as good species characters are those that are invariant in all normal individuals of the taxon. What is invariant in one megadrile genus may vary interspecifically or even intraspecifically elsewhere. However, the author is inclined to think that some vascular characters may prove to be definitive at the family level.

According to Stephenson (1930, p. 803) "The interest of the family lies in its probably having given origin to all the families of the Megadrili—the earthworms'. The scattered distribution represents the remains of a formerly general occurrence of the family, and the surviving members are relicts." The Haplotaxidae, according to Brinkhurst (1966), "may be regarded as primitive or, more reasonably, as descendants of a primitive group of oligochaetes." The esotery on which the classical system was based is now known to have been erroneous. *Eobippus* could not give rise to *Equus* while remaining *Eobippus* (cf. Stephenson, 1930, p. 711). The sole reason previously for believing haplotaxids to be ancestral or even primitive is the possession of only four pairs of gonads located in segments x—xiii. Evidence accumulating slowly since 1907 indicates that such an octogonadal battery is by no means primitive and that early megadriles are likely to have had a much longer series of gonads perhaps extending through v—xx or even further back.

Megadrile, as indicated above in the quotation from Stephenson, means earthworms. They are in the following families: Acanthodrilidae, Alluroididae, Criodrilidae, Eudrilidae, Glossoscolecidae, Haplotaxidae, **Hormogastridae**, Lumbricidae, Megascolecidae, Microchaetidae, Moniligastridae, Ocnodrilidae, Octochaetidae, Sparganophilidae. Those **megadrile** families in formal classifications are called by Michaelsen (1930) Oligochaeta opisthopora or by Yamaguchi (1953) Opisthopora diplotesticulata. Non-earthworm **oligochaetes** are microdriles. The size indications are in general valid even though a few megadriles are smaller than an occasional large microdrile. Ectoparasitic worms formerly regarded as **oligochaete** now are in distinct groups, the Acanthobdellida and Branchiobdellida.

The Haplotaxidae, along with the Alluroididae, and to a lesser extent the Moniligastridae, are of interest because of certain characters shared

with microdriles, such as: 1) Seminal vesicles and ovisacs, when present, are simple, unpartitioned, posteriorly directed outpocketings of the septa. 2) Ova, large and **yolky**. 3) A supposedly unilayered condition of the clitellum though that has been denied for at least one of the families. 4) Location of male pores in front of the female pores. However, it should be noted that in one rather common morph of a widely distributed European **lumbricid**, the parthenogenesis has enabled a return to the microdrile condition.

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