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THE SYSTEM OF THE ENCHYTRAEIDAE

by Dr. L. Černosvitov

The question of dividing the Enchytraeidae into subfamilies was raised /263 by Eisen in 1905 and has been the subject of debate for more than thirty years; nevertheless, it cannot be said that we have come any closer to solving the problem during this period. Eisen determined different structural types of penial bulbs in a large number of species of eight genera examined by him. He used them as the basis for his classification of the Enchytraeidae and erected the subfamilies Mesenchytraeinae (with the genus Mesenchytraeus), Enchytraeinae (with the genera Enchytraeus and Michaelsena) and Lumbricillinae (with the genera Lumbricillus, Marionina, Bryodrilus, Henlea and Fridericia). Moreover, he segregated the genus Achaeta as a separate subfamily although at the time the structure of its penial bulb was not yet known.

However, more recent investigations have shown that the structure of the penial bulb in different representatives of one and the same genus does not at all always agree with the scheme erected by Eisen.

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Consequently, Stephenson (1911) questioned the propriety of characterizing a family, or even a genus on the basis of penial bulb structure. Later on Welch (1914) thoroughly tested the problem of the significance of the penial bulb in the systematics of the Enchytraeidae. He was able to confirm Eisen's opinions in many instances; he supplemented and corrected them in some respects, and in a few instances he disagreed. Nevertheless, the major problem remained unanswered. Later on (1920), while examining the genera of the Enchytraeidae, he stated "here seem to be some good grounds for considering the structure of the penial bulb as a basis for the erection of subfamilies, but since its structure is unknown in such genera as Achaeta, Distichopus, Chirodrilus and Stercutus, it does not seem profitable just now to attempt to discuss this problem" (p. 28).

A further attempt at dividing the Enchytraeidae into subfamilies was made in 1910 by Čejka. However, the author did not state the characteristics he used as basis for his division; furthermore, he does not appear to have taken into consideration the facts that have become known as a result of Eisen's studies. He contended himself with the statement: "At this time the family (Enchytraeidae) has received so much attention that it has become advisable to divide it into several well-founded subfamilies for the sake of better clarity. In this context it is easy, for instance, to erect even now the subfamilies Fridericinae, Mesenchytraeinae, Henleinae and others which, as it appears, contain typical forms and are undoubtedly of different phylogenetic origin" (p. 25). Furthermore, the author provides only the diagnosis for the subfamily Henleinae: "with large digestive glands developing by transformation from the wall of the gut and emptying their secretions into its lumen"; he includes in this subfamily the genera *Henlea*, *Buchholzia*, *Hepatogaster* and *Bryodrilus* without taking into account that the intestinal pockets are absent in an entire series of *Henlea* species, currently combined in the genus *Henleanella*. Later on (1913), without stating any reasons, the author segregates the subfamily Enchytraeinae, including the genera *Enchytraeus* and the genus *Litorea* described by himself. Still later (1920) Welch showed that the latter is only a synonym of the former.

Most recently, Stephenson (1930) discussed the problem of the division of the Enchytraeidae in subfamilies in his monograph of the Oligochaeta; he believes it possible to segregate two groups: first, *Henlea* which includes the genera *Buchholzia*, possibly *Bryodrilus*, *Aspidodrilus*, *Fridericia* and *Distichopus*, and *Enchytraeus* as the second group with the genera *Lumbricillus*, *Marioninae* and *Michaelsena*. All other groups (*Propappus*, *Mesenchytraeus*, *Stercutus*, *Chirodrilus*, *Achaeta* and *Litorea*, which he considers independent) remain separate. /264

It is evident from this brief overview that the opinions of the various authors regarding further groupings within the family of the Enchytraeidae are quite divergent.

It is our opinion that due to the great heterogeneity of the individual genera we would never arrive at a positive result if we were to continue on the path started by Eisen, i.e. the search for a taxonomic characteristic for dividing the entire family. Eisen's attempt to see this characteristic exclusively in the structure of the penial bulb may be considered failed at this time, although this is not meant at all to deny the fact that his attempt has contributed much to the elucidation of the problem.

More positive results can only be expected if the groupings are based on the sum total of several mutual characteristics. This task is made easier because in the Enchytraeidae the complex of characterisatics considered generic characteristics has already been laid down. In the present study I shall try to divide the Enchytraeidae into subfamilies; however, I shall use a different basis than heretofore.

Propappus is the most primitive genus of the Enchytraeidae; this is shown by the bifurcate setae, the structure of the seminal funnels which are formed only by one layer of ciliate cells, analogous to the "collar" of the other Enchytraeidae, whereas the glandular thickening of the distal portion of the sperm duct is behind the septum. It is possible that the glandular portion of the sperm duct which is anteseptal in all other Enchytraeidae may be homologized with the glandular ampulla of *Epirodrilus michaelseni* Hrabě, which belongs to the Tubificidae. The histological structure of this organ (Hrabě 1930, 1931) is reminiscent of the "seminal funnel" of the Enchytraeidae. The structure of the nephridia of *Propappus* is also close to other, lower

Oligochaeta. The small, anteseptal portion is constituted only by a narrow funnel; the postseptal part is not compact but narrowly lobed, formed like an irregular ribbon that is tacked together. The structure of the salivary glands is reminiscent of the Naididae and the Tubificidae. In *Propappus* they are not connected to the septa and do not constitute more or less compact organs as in the other Enchytraeidae. In this respect, only a few representatives of the genus *Mesenchytraeus* are similar to *Propappus*; i.e. *M. setorus* Mich., *M. flavus* Lev., *M. celticus* South. and many others, in addition to two or three pairs of true septal glands, have several pairs of salivary /265 glands which are located on the extensions of the ducts and which are in no way connected with the septa. Analogous proliferations of glandular cells are occasionally observed in representatives of other genera; however, always to a substantially lower extent than in *Mesenchytraeus*. Close affinities between the genera *Mesenchytraeus* and *Propappus* are also indicated by a number of other characteristics. In *Propappus* a small pit occurs on the dorsal side of the prostomium; at the same location the cephalic pore occurs in *Mesenchytraeus*. The nephridia of *Mesenchytraeus* have a weakly developed, cellular intermediate substance and are dividied into a series of lobes; in this respect they deviate pronouncedly from the structure of the nephridia of all other genera of the Enchytraeidae and are reminiscent of those in *Propappus*. In both genera the longitudinal muscles are formed by only a single layer of ribbon-like fibres. Peptonephridia are absent. The structure of the male ducts in both genera also shows similar characteristics. The seminal funnels of many representatives of the genus *Mesenchytraeus* have only a very weakly developed, glandular sperm duct portion which opens into the atrium, ending in the more primitive species (*M. bungei* Mich., *M. multispinus* Grube, *M. affinis* Mich. et al.) directly in the genital operculum.

The genus *Mesenchytraeus* is not fully homogeneous and can be divided into two large groups. One includes the species with relatively short sperm ducts, small seminal funnels and seminal vesicles which communicate with the gut, and the other is characterized by long sperm ducts, large seminal funnels and usually long seminal vesicles which extend over several segments and do not communicate with the gut. The first of these two groups is closest to the genus *Propappus*, although the second - as far as the seminal vesicles are concerned - also has similarities to this genus.

These characteristics are indicative of affinities between the genera *Propappus* and *Mesenchytraeus*; because both genera hold relatively isolated positions within the Enchytraeidae I propose to combine them in the subfamily Mesenchytraeinae.

The other group, which is genetically directly adjacent to the first, includes the following genera: *Achaeta*, *Guaranidrilus*, *Hemienchytraeus* and, as we shall see later on, also *Aspidodrilus* and *Stercutus*.

Many researchers attribute great phylogenetic significance to the absence of setae in the genus *Achaeta*. I have already stated in earlier publications that no overly great systematic importance should be given to the form of the setae or their partial or complete absence /266

(Černosvitov 1933, p. 76; 1934, p. 244) because it is a secondary phenomenon. Partial loss of the setae is evident in representatives of the genera *Enchytraeus* and *Pachydrilus*, combined earlier in the genus *Michaelsenia*; complete disappearance of the lateral setal bundles can be observed in *Fridericia* (*Distichopus*) *silvestris* Leidy, notwithstanding that the remaining characteristics clearly indicate that all these species belong to the genus.

The genera *Achaeta*, *Guaranidrilus* and *Hemienchytraeus* are closely related by a number of mutual characteristics, they are also closely related to the Mesenchytraeinae. They are close to the genus *Mesenchytraeus* in the position of the cephalic pore at the tip of the prostomium. The genus *Achaeta* is related to *Propappus* by the presence of pyriform glands that extend into the body cavity; Vejdovsky (1879) considers them homologues of the setal follicles. However, Michaelsen (1926) refers to the great similarity of these structures with the setal glands of *Propappus* and the possibility that they are homologous to them. In this instance we would look at a complete loss of setae and their follicles in *Achaeta* in the same manner as the lateral bundles of *Fridericia silvestris* Leidy and others were lost. This is also indicated by the fact that the pyriform glands occur in 4's in each segment only in *Achaeta eiseni* Vejd., whereas in *A. bohemica* Vejd. only the dorsal glands have been retained and in *A. comeranoi* Cogn. and *A. maorica* Benh. they are absent. Furthermore, all three genera are related to each other and to *Propappus glandulosus* Mich. by the fact that the esophagus changes into the midgut anteclitellially and occasionally develops a noticeable widening or differs in its histological structure. In contrast, the position of the dorsal vessel may be anteclitellial as in P. glandulosus Mich. (Achaeta, Guaranidrilus) or intraclitellial and postclitellial as in Propappus volki Mich. and all Mesenchytraeus species (Hemienchytraeus). Another mutual characteristic of Propappus and the second group of Mesenchytraeus and the aforementioned three genera is the presence of large spermatheca which extend over several segments and do not /267 communicate with the gut.

Mutual characteristics connecting the genera Achaeta, Guaranidrilus and Hemienchytraeus and, at the same time, differentiating them from Mesenchytraeus are the following: 1. presence of peptonephridia, 2. large anteseptal part of the nephridia in which the cilial canal forms numerous loops, 3. well-developed cellular intermediate substance and 4. the presence of two types of muscle fibres as a result of which the muscles - similar to Fridericia - consist of round fibres and ribbon-like fibres. Furthermore, we should mention a number of characteristics which are common to only two or three of the aforementioned genera, or only to a number of species. Primarily, reference must be made to the similar structure of the penial bulb in Achaeta and Guaranidrilus where the seminal tubule is surrounded by a complex of glandular cells which are covered by a mutual layer of muscles; it ends directly at the ventral body surface. However, in Hemienchytraeus just as in the majority of the remaining Enchytraeidae there is a slight, epidermeal curvature, and the structure of the penial bulb is more reminiscent of that of Fridericia and Pachydrilus. Another characteristic, common to the genera Achaeta (except A. maorica Benh.), Guaranidrilus and Hemienchytraeus (H. brasiliensis Cogn.?) is the spiral looping of the seminal tubules, which has not been observed in any other representative of the remaining genera of the Enchytraeidae. All these statements are indicative of genetic affinities of the genera Achaeta, Guaranidrilus and Hemienchytraeus; consequently, I have combined them in the subfamily Achaetinae.

At first sight it may be doubtful whether Aspidodrilus, as the fourth genus, should be placed in the subfamily. After detailed examination the genus may even be considered the intermediate form to the Mesenchytraeinae; in any case, it does not belong in the Henlea group where Michaelsen has placed it (1925, 1926). The problem of homologization of the chylar pockets in Aspidodrilus is of primary importance. They are located within segment 7 and are laterally connected with the esophagus which ends in the centre of segment 8 in the expanded midgut. The walls of the chylar pockets are lined with ciliar epithelium which constitutes the direct continuation of the esophageal epithelium; the change occurs without a defined limit (Michaelsen 1926, Plate IV, Fig. 6, Chy.). All this indicates that these structures are of an entirely different type than the esophageal /268 peptonephridia of the genera Guaranidrilus, Henlea and Bryodrilus. As indicated by the cilio-epithelial lining, they are evaginations of the gut; consequently, they must be homologized with the chylar pockets of Henlea, Michaelseniella and Guaranidrilus. Consequently, I cannot agree with Michaelsen's opinion (1926, p. 148-149) who considers them homologues of the peptonephridia of Buchholzia; he writes: "It is remarkable that quite similar, sparsely branched pockets occur in the anterior part of the esophagus in segment 4 in *Buchholzia appendiculata* Buchh. Vejdovský also illustrates these esophageal appendages of segment 4 but he considers them salivary glands (peptonephridia) (1879, p. 54; Plate II, Fig. 6, spd.). However, their similarity to the chylar pockets of *Aspidodrilus* is so great that their homology with these and their dissimilarity from the peptonephridia of other genera - despite their far-advanced position - can hardly be doubted." (p. 148). He rejects possible homologization of these organs with the intestinal pockets of *Henlea* and the intestinal organ of *Buchholzia* and adds: "Perhaps the short, caecal esophageal appendages of *Henlea ventriculosa* Udek., which previously were interpreted as peptonephridia, may be interpreted as such esophageal chylar pockets corresponding to the similarly shaped organs of *Buchholzia fallax* Mich." (p. 149). However, these organs in *Henlea* and *Buchholzia* are no intestinal structures as in *Aspidodrilus* (or like the intestinal pockets in *Henlea*, *Michaelseniella*, *Guaranidrilus* and *Bryohenlea* where this is indicated by the presence of ciliar epithelium) but they are organs that are probably only secondarily connected with the gut and are of nephridial nature in *Henlea*, according to Stephenson (1922, pp. 1114, 1116). Consequently, I believe the chylar pockets of *Aspidodrilus* to be homologous to these organs in *Henlea*, *Michaelseniella* and *Guaranidrilus*; however, they are not developed in the anterior section of the midgut but arise, as in *Bryohenlea*, from the end of the esophagus. We have no absolutely clear information concerning genuine peptonephridia because Michaelsen only makes the statement that in *A. kelsalli* there do not appear to be any peptonephridia (p. 143). This may be indicative of close affinities between *Aspidodrilus* and the

Mesenchytraeinae because peptonephridia are present in all Achaetinae. As we shall see further on, this assumption is also confirmed to a certain degree by the structure of some other organs.

With regard to the longitudinal muscle we can only say that it is /269 single-layered in the posterior, changed body section of Aspidodrilus; this, in turn, places the genus closer to the Mesenchytraeinae. The muscles in the anterior section of the body where the primitive structure has been better retained have not been studied so far.

The position of the transitory zone of the esophagus to the midgut, which is located in the centre of a segment, is reminiscent of Guaranidrilus and Hemienchytraeus, whereas the dorsal vessel starts at the widening of the gut, as in Propappus, and not in the subsequent segments, as in Achaeta and Guaranidrilus. As in the Achaetinae, there is no heart. The structure of the nephridia in Aspidodrilus is also indicative of its affinities to this subfamily. The anteseptal part is large with the ciliar canal forming several loops in it; the cellular intermediate substance is well-developed.

The structure of the sexual organs also indicates the affinity of Aspidodrilus to the Achaetinae. At first, the strongly developed, thickened distal part of the seminal duct is evident as in all Achaetinae (a similar structure in the Mesenchytraeinae occurs only in a North American group with free seminal vesicles). The seminal ducts are thin as in most Achaetinae, long, and are located in segment 12, rolled up in large loops. On the basis of a very brief description of the penial bulb by Michaelsen (1926, p. 147) it may concluded that it is structured similar to the types of Achaeta and Guaranidrilus. The epidermal curvature is absent and the seminal ducts lead directly to the outside after traversing the nearly round bulbus which consists of many glandular cells. Accessory prostatal glands - well-developed in Mesenchytraeus - are absent. The seminal vesicles are of the type common in many Mesenchytraeinae (the majority of the palearctic Mesenchytraeus species excepted) and in all Achaetinae. According to statements by Michaelsen they consist of muscular tubes extending transversely to the median line, then bending to the posterior and outward, ending with blind, expanded ampullae directly anterior to the chylar pockets.

Definitive determination of the systematic position of Aspidodrilus is difficult due to incomplete knowledge of the only species; in the available description, the important characteristics in particular have not been considered.

Michaelson was unable to determine the position of the cephalic pore definitely; he states (1926, p. 140): "It should be noted that the /270 body cavity at the anterior pole of the cephalic lobe produces a small, circular, relatively deep pit in the body wall. It is possible that pit in our specimen is connected to a closed and, consequently, invisible cephalic pore." If this is truly a cephalic pore, then its position equals to that in the Achaetinae and Mesenchytraeinae.

The setae of Aspidodrilus display rather interesting conditions. They occur only in the ventral bundles, an aspect which brings the genus close to Achaeta where the setae are completely absent; however, based on the number of setae in the bundles of the first 12 unchanged segments, i.e. 2, they approach Hemienchytraeus and Guaranidrilus, in which all bundles always consist of 2 setae. Their form according to Baylis (1914, p. 139) is "simple, short, pointed"; according to Michaelsen (1926, p. 139) it is sharply pointed. I must also make mention here of the rather inexact statement by Michaelsen that one seta of segment 12 (it was not possible to examine the other setae) of his specimen "apparently had a bifurcate ectal end" (p. 139). If this observation is correct, this type of seta on segment 12, which may be considered genital setae, is indicative of close relations between Aspidodrilus and Propappus.

It is evident that the genus Aspidodrilus may assume - on the basis of some characteristics - an intermediate position between the subfamilies Mesenchytraeinae and Achaetinae. The presence of organs homologous to the intestinal pockets of Henlea and Michaelseniella does not confirm the affinity of Aspidodrilus to the Henlea group because similar organs also occur in Guaranidrilus. Most of the characteristics indicate that it is more correct to attach Aspidodrilus to the subfamily Achaetinae. In this regard I am primarily guided by the structure of the nephridia, the penial bulbs, the setae of the anterior body section, and by the structure of esophagus and intestinal pockets.

The correctness of this opinion is also confirmed by the geographical range of the Achaetinae. While all remaining genera of the Enchytraeidae (except a small number of species) belong to the holarctic region, the subfamily Achaetinae occurs almost exclusively in the tropics. The genus *Guaranidrilus* occurs in South America, /271 *Aspidodrilus* in Africa, and *Hemienchytraeus* in South America, Africa and India. Only *Achaeta* is more widely distributed and its representatives have become known from Europe, South America, South Georgia (*Achaeta* sp.? Stephenson, 1932) and New Zealand.

One more genus remains to be attached to the subfamily Achaetinae, i.e. *Stercutus* with the single representative *S. niveus* Mich. Most recently (1937) I had the opportunity to discuss its affinities to other genera of the Enchytraeidae; consequently, at this point I shall deal only with the most important aspects which determine its systematic position.

The structure of the penial bulbs, the shape of the clitellum, the anteclitellial dorsal vessel, and the seminal vesicles which do not communicate with the gut, are indicative of the close relation of *Stercutus* to *Achaeta*. On the other hand, the heart described by Freudweiler (1905) and the ovisacs, the single-layered muscles, absence of peptonephridia, shape of setae and seminal funnels, the structure of seminal vesicles and the gradual transition of the esophagus into the midgut are evidence of its affinities with the genus *Mesenchytraeus*. The anteclitellial dorsal vessel, structure of the penial bulbs and particularly of the nephridia with strongly developed cellular intermediate substance and large anteseptal portion do not allow attachment to the Mesenchytraeinae; similar to Aspidodrilus, it will have to take an intermediate position between the last-mentioned subfamily and the Achaetinae.

In contrast to all other Achaetinae, Stercutus comes close to Aspidodrilus due to the presence of single-layered longitudinal muscles, absence of a cephalic pore and of the peptonephridia (provided they are genuinely absent in Aspidodrilus), the presence of more than two setae per bundle (in Aspidodrilus only on the posterior section of the body), and many other characteristics common to all Achaetinae. Consequently, the two genera assume a separate position in the Achaetinae and constitute a transition to the Mesenchytraeinae. The characteristics common to both genera, however, are not sufficiently important to permit combining them in a separate subfamily.

According to the structure of the longitudinal muscles which consist of round fibres and ribbon-like fibres, furthermore, according to the presence of peptonephridia and the structure of the nephridia with large anteseptal portions in which the cilial canal loops repeatedly, and moreover, in accordance with the well-developed cellular intermediate substance, the genus Fridericia is closest to the /272 Achaetinae. Nevertheless, an entire series of characteristics, e.g. presence of dorsal pores, chylar cells, two types of lymphocytes and the peculiar arrangement of the setae in the bundles convey to this genus a rather isolated position among the Enchytraeidae; consequently, I segregate it in a special subfamily, the Fridericinae. This subfamily includes only the genus *Fridericia*; it must be considered closest to the genus *Hemienchytraeus* and not, as usual, *Henlea*. In addition to the aforementioned characteristics it is related to *Hemienchytraeus* by the intraclitellial or postclitellial position of the dorsal vessel and the structure of the penial bulbs. The peptonephridia in both genera are also of the same type although in *Fridericia* they are paired, whereas in *Hemienchytraeus* they are unpaired. In both instances they are located directly behind the pharynx and consist of a sac-like major part that changes into a tube-like section which, in turn, ends in a bundle of fine branches.

Before Michaelsen described *Propappus* as the most primitive of the genera in the Enchytraeidae, the genus *Henlea* (later divided into four subgenera) was considered the most primitive genus; the closely related genera *Buchholzia*, *Bryodrilus* and *Bryohenlea* were grouped around it.

Nevertheless, despite the obviously close relationship of the genera listed (only Stephenson [1930, pp. 763 & 765] expresses some reservations concerning the membership of *Bryodrilus* in the *Henlea* group) and their undoubted membership in one subfamily, it is rather difficult to characterize the latter clearly. The most important mutual characteristics are: 1. the anteclitellial transition of the esophagus into the midgut, normally accompanied by a sudden distension (probable exceptions are *Henlea scharfi* South. and *Bryodrilus borealis* Čejka); 2. the position of the cephalic pore between prostomium and peristomium; 3. the strongly developed, cellular intermediate substance of the nephridia; 4. the single-layered longitudinal muscles; 5. connection of the seminal vesicles with the gut, which has been lost secondarily only in a few species (e.g. *Michaelseniella brucei* Steph. and some others). In most instances the seminal vesicles are connected with each other and open into a mutual canal from the dorsal side into the gut; exceptions are very rare; 6. the presence of esophageal peptonephridia. Statements by some authors (Bretscher, Friend) /273 concerning the absence of these organs in some species are not overly important because the observations were always made on living specimens or complete mounts. The possibility of homologizing the so-called "intestinal pockets" of *Bryodrilus* with the peptonephridia of other Enchytraeidae has been discussed earlier by me (1928, 1934); the possibility of the presence of these organs in *Bryohenlea* has also been discussed (1934, p. 296); in the following text I consider them true peptonephridia.

Phylogenetically the Henleinae must have developed from the Achaetinae; it is related to the latter by a series of common characteristics, such as the anteclitellial transition of the esophagus into the midgut, the presence of peptonephridia, the position of the dorsal vessel and the structure of the nephridia. Consequently, it seems to me that Delphys' attempt (1919) to derive *Henlea* from *Fridericia* and to use it as an intermediate form seems to have failed. The genus *Edmondiella*, erected by Delphy, was intended to be this connecting link; however, it was erected on the basis of erroneous statements by the author, i.e. that the dorsal vessel in *Fridericia perrieri* Vejd. is of anteclitellial origin. This was caused by Vejdovsky's opinion that cardiac distensions were present in this species in segments 5, 6 and 7, although all other characteristics were typical for *Fridericia*. This opinion by Delphy was later on accepted by Michaelsen (1925, 1926) and he added to the genus *Edmondiella* three *Henlea* species described by Eisen in 1905 (*H. ehrhorni*, *H. californica* and *H. guatemale*) which possess several characteristics similar to *Fridericia* (shape of setae and nephridia), although they are characterized as typical *Henlea* (*Michaelseniella*) by the presence of chylar pockets and the position of the dorsal vessel. However, most recently, Ude (1929, pp. 66-67) (and earlier Friend [1912]) stated that according to his observations the dorsal vessel in *F. perrieri* Vejd. originates postclitellially in segment 18; for this reason *F. perrieri* cannot be included in the genus *Edmondiella*. Based on material from the High Tatra mountains and from Central Africa examined by me in 1937 I can fully confirm Ude's statements and consider the genus *Edmondiella* as entirely artificial; I have stated this opinion already earlier (1931).

Stephenson (1930, pp. 763, 774) also finds the genus *Henlea* connected with *Fridericia* by transitional forms and so close that "the separation /274 of the two genera is not quite easy"; however, he states that "the difficulties are not removed by the proposed institution of the genus *Edmondiella* for the reception of the transitional forms", because the genus is not homogeneous.

Following our familiarization with the genera *Guaranidrilus* and *Hemienchytraeus*, previously accepted concepts concerning mutual relations of *Henlea* and *Fridericia* must be revised. I have already referred above to the close relations of the genera *Hemienchytraeus* and *Fridericia* which are connected with each other through an entire series of mutual characteristics. A group of genera closely related to *Henlea* is directly and closely connected with another member of the Achaetinae, i.e. *Guaranidrilus*. These close relations are evident from the presence - determined in *Guaranidrilus* - of chylar pockets, esophageal peptonephridia located in segment 6 as in most *Henlea* and *Bryodrilus* species, the anteclitellial transition of the esophagus into the midgut, and the anteclitellial position of the dorsal vessel. The structure of the penial bulbs in most *Henlea* species is similar to *Hemienchytraeus*; however, in *Bryohenlea*, due to the absence of the epithelial curvature, it is reminiscent of the *Achaeta* and *Guaranidrilus* type. The position of the dorsal vessel in *Bryodrilus* and *Bryohenlea* corresponds to that in *Hemienchytraeus*, whereas the remaining Henleinae species in this regard resemble the genera *Guaranidrilus*, *Achaeta*, *Aspidodrilus* and *Stercutus*. The structure of the nephridia of the three aforementioned *Henlea* (*Michaelseniella*) species which are placed by Michaelsen in the genus *Edmondiella*, corresponds fully to that in the remaining representatives of the Achaetinae.

In view of these statements we are compelled to assume that the Henleinae and *Fridericia* have evolved from a common ancestor which belonged to the subfamily Achaetinae; however, they developed in different directions. In *Fridericia* the two-layered longitudinal muscles have been retained and chylar cells have developed; they may be considered a functional replacement or a transformation of the chylar pockets (a counterpart is the structure of the intestinal organs of *Hepatogaster* and *Buchholzia*).

Examination of the four subgenera into which *Henlea* is divided, reveals that they cannot be derived from a mutual ancestral form but from different genera. The species with one pair of chylar pockets, combined /275
in the genus *Michaelseniella*, may be derived from *Guaranidrilus* which, as stated above, is also close to *Bryohenlea* and to the latter genus, i.e. *Henlea* (= *Udekemiana*) which has two pairs of chylar pockets just like *Bryohenlea*. *Hepatogaster* must be assumed - as I have demonstrated earlier (1931) - to have originated from *Henlea* (= *Udekemiana*) insofar as the structure of the chylar pockets became more complex, analogous to the development of *Buchholzia* and *Michaelseniella* from a common ancestor. With regard to *Henleanella* the absence of the chylar pockets indicates close relations to *Achaeta* and *Hemienchytraeus*. These considerations bring me to the conclusion that the four subgenera into which *Henlea* has been divided (*Henlea*, *Hepatogaster*, *Michaelseniella* and *Henleanella*) must be considered independent genera; I have discussed this elsewhere at an earlier time (1934). I have investigated their interrelations in another study (1931); consequently, I am not going to deal with these problems in detail at this point.

The last great subfamily, the Enchytraeinae, includes the two large genera *Enchytraeus* and *Pachydrilus* (s.l.) which are connected by the genus *Stephensoniella*. Their interrelations have been discussed in detail in one of my studies (1934) and I shall not repeat my earlier statements at this point. Regardless of the apparent close relationship between these two genera, it is very difficult to list mutual characteristics. The most important characteristics are the following: 1. position of the cephalic pore between prostomium and peristomium; 2. intraclitellial or postclitellial transition of the esophagus into the midgut, without sudden distension; 3. strong development of the nephridial cellular intermediate substance; 4. absence of intestinal pockets and chylar cells; 5. absence of a cardiac body and 6. postclitellial or, more rarely, intraclitellial dorsal vessel. No definite statements can be made at this time with regard to the structure of the longitudinal muscles. In some species it is two-layered, similar to that of Achaetinae and Fridericinae (Enchytraeus buchholzi, Stephensoniella); however, the two-layered condition is not always clearly evident (Enchytraeus albidus). In other forms the longitudinal muscles are single-layered (Pachydrilus arenarius, P. mangeri; Černosvitov, 1937). Peptonephridia are present in Enchytraeus and are absent in Pachydrilus and Stephensoniella. This characteristic and the structure of the penial bulbs connect the two last-mentioned genera; in contrast, the structure of the testes which include large peritonial sacs formed by the septum, is completely /276 identical in Stephensoniella and Enchytraeus albidus (and in a few other species). The structure of the penial bulbs and the seminal vesicles unites the subgenera Pachydrilus and Stephensoniella with some Enchytraeus species. The remaining species show evidence of relations to some, primarily Antarctic, Marionina species by the penial bulb, which breaks up into individual cell complexes.

These statements are evidence of the exceedingly great complexity of the interrelations of the species mentioned; nevertheless, it does not provide sufficient grounds to doubt the connective, direct affinities.

The presence of postpharyngeal peptonephridia in Enchytraeus and the structure of its longitudinal muscles are indicative of some relations to Fridericia and Hemienchytraeus. Affinities to the former genus are also indicated by the connection of the seminal vesicles with the gut, where these organs do not open through a common canal into the gut, as in the largest number of the Henleinae, but separately.

In 1925, E. Reisinger described a very peculiar worm under the name Parergodrilus heideri which he placed with the Archiannelida. Later on, Meyer (1927) stated the opinion that this worm was an oligochaete belonging to the Enchytraeidae and closely related to the genera Achaeta and Henlea. Reisinger objected to this (1929); he held on to this original opinion. With regard to the systematic position of the species, Michaelsen (1928), Ude (1929) and Stephenson (1930) later on supported Meyer's opinion. Without discussing any of the details of the polemics which was kindled by this problem, I wish to state that in view of its peculiar structure Parergodrilus cannot be placed without restrictions in the Enchytraeidae, although I admit the possibility of classifying this species under the oligochaetes. Characteristics such as the absence of septa and of a vascular system, the hermaphroditic gonads whose ovarial portion is located anterior to the testicular portion, the peculiar structure of the sexual ducts and a series of other characteristics demand a special position for this species among the oligochaetes. I tentatively place this species into a special subfamily, the Parergodrilinae, without excluding the possibility that it may turn out to be the representative of a new oligochaete family which then, without doubt, would assume a position close to the Enchytraeidae, similar to the Phreodrilidae in relation to /277 the Tubificidae. In contrast, some characteristics such as the form and number of setae, the presence of setal glands, the position of the seminal vesicles, the sudden transition of the esophagus into the midgut, indicate that Parergodrilus is close to the Achaetinae.

We still have to deal with three inadequately described enchytraeid genera whose systematic position is quite uncertain.

Our knowledge concerning the genus Chirodrilus Verrill with its two species is so inadequate that it is doubtful whether it can be placed in the Enchytraeidae as already stated by Stephenson (1930, p. 78); consequently, I shall not discuss it further at this point.

With regard to the genus Hydrenchytraeus Bretscher, Bretscher himself states the opinion (1901, p. 209; 1913, p. 106) that it may have to be considered a subgenus of Marionina or Lumbricillus (Pachydrilus). The presence of peptonephridia, the gradual transition of the esophagus into the midgut, and the postclitellial position of the dorsal vessel, however, indicate that this genus is either closely related to, or synonymous with, Enchytraeus.

The exceedingly inadequately characterized genus Euenchytraeus Bretscher is undoubtedly a synonym of the subgenus Marionina. In Bretscher's opinion, major characteristics are the presence of nephridia from septum 2/3 on and developed nephridia in the sexual segments even during sexual maturity. However, as evident from the above discussions, this characteristic may not be used as a criterion for the genus. Furthermore, doubts in the accuracy of Bretscher's observations may arise insofar as the septa in the most anterior section of the body of all Enchytraeidae are absent and start only with intersegmental furrow 3/4 or 4/5. It is not improbable that the author erred while counting the segments, and the first pair of nephridia of the genus Euenchytraeus probably belongs to septum 3/4 or 4/5 as we known occurs in some other species. However, even without making this correction we may consider this genus a synonym of the subgenus Marionina from which it does not fundamentally differ in any way.

Consequently, the family of the Enchytraeidae may be divided into the following six subfamilies: 1. Mesenchytraeinae (genus Propappus, Mesenchytraeus), 2. Achaetinae (Achaeta, Guaranidrilus, Hemienchytraeus, Aspidodrilus and Stercutus), 3. Parergodrilinae (Parergodrilus), /278 4. Fridericinae (Fridericia), 5. Henleinae (Henlea, Michaelseniella, Henleanella, Hepatogaster, Buchholzia, Bryodrilus and Bryohenlea) and 6. Enchytraeinae (Enchytraeus, Stephensoniella and Pachydrilus).

I shall now present the diagnoses of the subfamilies erected by me and the revised diagnosis of all genera included in them. Lack of space compelled me to omit the detailed synonymy in the list of the presently known species of the Enchytraeidae and I contend myself with the most necessary remarks.

Fam. Enchytraeidae

Subfam. Mesenchytraeinae

Cephalic pore on the tip of the cephalic lobe or absent (or closed and replaced by a pit). Dorsal pores absent. Longitudinal muscles single-layered. Cellular intermediate substance of nephridia reduced. Anteseptal portion consisting only of the funnel. Peptonephridia, chylar cells and intestinal pockets absent. Sperm sacs and ovisacs present. Sperm ducts proximally distended in an atrium-like manner. Penial bulb without epidermal curvature. Accessory penial glands usually present.

Range: Europe, Siberia, North America.

Gen. Mesenchytraeus Eisen

Four bundles of setae on each segment, starting with the second, sigmoid, simple-pointed, equal length. Cephalic pore on or close to the tip of the cephalic lobe. Dorsal pores absent. Transition of esophagus to midgut gradual. Origin of dorsal vessel postclitellial, rarely intraclitellial; blood hyaline or yellow; cardiac body present. Peptonephridia, chylar cells and intestinal pockets absent.

Longitudinal muscles single-layered, anteseptal parts of the neprhridia consisting only of the funnel, postseptal part lobed with reduced cellular intermediate substance. Copulatory glands absent. Sperm sacs and ovisacs present, long. Seminal funnels cylindric or funnel-shaped with weakly developed, glandular thickening of the sperm duct. Sperm duct proximal with atrial distension, often with atrial glands and accessory penial glands. Epidermal curvature of the penial bulb absent. Communication of seminal vesicles present or absent. Verticulum of seminal vesicles present or absent.

In soil, fresh and brackish water, under the bark of trees, on glaciers.

Range: All of Europe, Spitsbergen, Greenland, Siberia, Baikal Lake, Islands in New Siberia, Bering Island, North America (Arctic Canada, Alaska, U.S.A.).

M. ***affinis*** **Michaelsen 1901**
M. ***armatus*** **(Levinsen) 1884**
M. ***altus*** **Welch 1917**
M. ***asiaticus*** **Eisen 1905**
M. ***beringensis*** **Eisen 1905**
M. ***beumeri*** **(Michaelsen) 1886**

M. ***bisetosus*** **Bretscher 1901**
M. ***bungei*** **Michaelsen 1901**
M. ***celticus*** **Southern 1909**
M. ***čejkai*** **Černosvitov (nom. nov. pro** ***M. eiseni*** **Čejka 1914, non Bretscher 1900)**
M. ***eastwoodi*** **Eisen 1905**

M. *eiseni* Bretscher 1900
M. *eltoni* Stephenson 1925
M. *fuscus* Eisen 1905 f. typica
M. *fuscus* Eisen var. *inermis* Eisen 1905
M. *franciscanus* Eisen 1905
M. *fontinalis* Eisen 1905 (syn. *E. f.* var. *glacialis* Eisen 1905)
M. *flavus* (Levinsen) 1884 (syn. *M. moravicus* Vejdovský 1905)
M. *flavidus* Michaelsen 1887
M. *falciformis* Eisen 1878
M. *gaudens* Cognetti 1903 (syn. *M. mencli* Vejdovský 1905)
M. *gaudens* Cognetti var. *pelicensis* Issel 1905
M. *gaudens* Cognetti var. *glandulosus* Issel 1905
M. *grandis* Eisen 1905
M. *grebnizkyi* Michaelsen 1901
M. *gelidus* Welch 1916
M. *hydrius* Welch 1919
M. *harperi* Stephenson 1926
M. *harrimani* Eisen 1905
M. *johanseni* Welch 1919
M. *konyamensis* Michaelsen 1916
M. *kinkaidi* Eisen 1905
M. *multispinus* (Grube) 1851
M. *monochaetus* Bretscher 1900

M. *mirabilis* Eisen 1878
M. *maculatus* Eisen 1905
M. *nodulosus* Lastočkin nom. nud.
M. *nanus* Eisen 1905
M. *obscurus* Eisen 1905 /279
M. *orcae* Eisen 1905
M. *primaevus* Eisen 1878
M. *penicillus* Eisen 1905
M. *pedatus* Eisen 1905
M. *rhabdogenus* Issel 1905
M. *solifugus* (Emery) 1898
M. *solifugus* (Emery) var. *rainierensis* Welch 1916
M. *setosus* Michaelsen 1888
M. *setschelli* Eisen 1905
M. *unalaskae* Eisen 1905
M. *vegae* Eisen 1905
M. *variabilis* Čejka 1914

Species dubiae:

M. *alpinus* Bretscher 1901
M. *amoeboideus* Bretscher 1901
M. *fenestratus* (Eisen) 1878
M. *glandulosus* (Levinsen) 1884
M. *montanus* Bretscher 1899
M. *oligosetosus* Friend 1913
M. *tigrinus* Bretscher 1902
M. *trisetosus* Bretscher 1903

Gen. Propappus Michaelsen

Four bundles of setae on each segment, starting with the second segment, S-shaped, bifurcate, one setal gland behind each bundle of setae. Cephalic pore and dorsal pores absent. Salivary glands not developed as septal glands. Transition of esophagus to midgut anteclitellial or postclitellial after sudden distension. Dorsal vessel originates at the beginning of the midgut. Cardiac body (always?) present. Peptonephridia, chylar cells and intestinal pockets absent. Longitudinal muscles single-layered. Anteseptal portion of the nephridia consisting only of the funnel, postseptal portion with reduced intermediate substance. Copulation glands absent. Male gonopore anterior to the setal zone of segment 12, pores of seminal vesicles anterior to the setal zone of segment 4. Glandular portion of the sperm duct (seminal funnel) partly or entirely behind septum 11/12, much thinner than the proximal mouth part. Sperm ducts distally extended in an atrium-like manner and opening through the genital operculum. Epidermal curvature and prostatal glands (accessory penial glands) absent. Seminal vesicles free, not communicating with the gut, without diverticulum, extending towards the posterior through several segments.

In freshwater.

Range: Germany (Elbe River), Russia (Volga and its tributaries, Baikal Lake).

P. <u>glandulosus</u> Michaelsen 1905 P. <u>Volki</u> (Michaelsen) 1915

Subfam. Achaetinae

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Cephalic pore on the tip of the cephalic lobe or absent, dorsal pores absent. Longitudinal muscles two-layered, consisting of round fibres and ribbon-like fibres, rarely single-layered. Cellular intermediate substance of nephridia strongly developed, anteseptal portion large. Esophageal or postpharyngeal peptonephridia present or rarely absent. Transition of esophagus to the midgut usually anteclitellial after sudden distension; the boundary between esophagus and midgut rarely (<u>Stercutus</u>) not well marked. Chylar cells absent. Intestinal pockets present or absent. Sperm sacs usually present. Atrium-like distension of the sperm duct absent. Accessory penial glands absent. Penial bulb compact with mutual layer of muscles, with or without epidermal curvature. Seminal vesicles without communication to the gut; diverticulum absent.

<u>Range</u>: Europe, India, North America, South America, South Georgia, Central Africa, New Zealand.

Gen. <u>Achaeta</u> Vejdovský

Setae absent, setal glands usually present. Cephalic pore on the tip of the cephalic lobe. Dorsal pores absent. Transition of esophagus to midgut anteclitellial after sudden distension (always?). Origin of dorsal vessel anteclitellial. Blood hyaline. Esophageal peptonephridia present. Chylar cells and intestinal pockets absent. Longitudinal muscles two-layered, consisting of round fibres and ribbon-like fibres. Cellular intermediate substance of nephridia strongly developed. Anteseptal portion large. Copulatory glands absent. Sperm sacs and ovisacs absent (always?). Sperm duct spiral, long, penetrated by a compact penial bulb with mutual muscle layer; epidermal curvature and accessory penial glands absent. Seminal vesicles without communication to the gut and without diverticula.

In soil, underneath the bark of trees (rare in freshwater ?).

Range: Europe (Switzerland, Germany, Belgium, Czechoslovakia, Italy, Great Britain, Ireland), South America (northern Argentina, new collection site!), South Georgia, New Zealand (South Island).

A. bohemica (Vejdovský) 1879
A. cameranoi (Cognetti) 1899
A. eiseni Vejdovský 1877
A. maorica Benham 1903

Species dubiae:

A. incisa Friend 1912
A. vejdovskýi Bretscher 1902

Gen. Hemienchytraeus Černosvitov

Four bundles of setae on each segment, starting with the second segment, straight, only proximally bent, simple-pointed, of equal length, two in each bundle. Cephalic pore near the tip of the cephalic lobe. Dorsal pores absent. Transition of esophagus to midgut anteclitellial (in /281
segment 9), sometimes with sudden distension. Unpaired postpharyngeal peptonephridia present. Chylar cells and intestinal pockets absent. Longitudinal muscles two-layered, consisting of round fibres and

ribbon-like fibres. Origin of dorsal vessel intraclitellial or postclitellial. Blood hyaline. Cardiac body absent. Nephridia with large anteseptal portion in which the cilial canal loops a few times, cellular intermediate substance strongly developed. Copulatory glands absent. Seminal funnel gradually tapering distally, trumpet-shaped. Sperm duct long and thin, confined to segment 12. Sperm sacs and ovisacs absent. Penial bulbs compact, with mutual muscle layer, opening at the epidermal curvature; accessory penial glands absent. Seminal vesicles without communication to the gut, extending through several segments. No diverticula.

In soil or freshwater.

Range: South America (northern Argentina, Paraguay, Brazil), Central Africa (Kenya), India (Rangoon, Assam).

H. africanus Černosvitov 1935
H. brasiliensis (Cognetti) 1900
H. stephensoni (Cognetti) 1927

Gen. Stercutus Michaelsen

Four bundles of setae on each segment, starting with the second segment, S-shaped, simple-pointed. Cephalic pore absent (or small?, or closed?). Dorsal pores absent. Transition of esophagus to midgut gradual. Peptonephridia absent. Chylar cells and intestinal pockets absent. Origin of dorsal vessel anteclitellial. Blood hyaline. Cardiac body present. Longitudinal muscles single-layered. Cellular intermediate substance of nephridia strongly developed. Copulatory glands absent. Seminal funnels small, funnel-shaped. Ovisacs present. Penial bulbs small, compact, with mutual muscle layer, without epidermal curvature. Sperm duct long, opening directly on the surface of the body. Seminal vesicles without communication to the gut and without diverticula.

On the seashore, in fish dung.

Range: Germany.

S. niveus Michaelsen 1888

Gen. Guaranidrilus Černosvitov nov. gen.

Four bundles of setae on each segment, starting with the second segment, straight, of equal length, two in each bundle. Cephalic pore close to the tip of the cephalic lobe. Dorsal pores absent. Longitudinal muscles two-layered, consisting of round fibres and ribbon-like fibres, Transition of esophagus to midgut anteclitellial after sudden distension, where one pair of large intestinal pockets open. Chylar /282 cells absent. Paired esophageal peptonephridia present (in segment 6). Origin of dorsal vessel preclitellial or intraclitellial. Blood hyaline. Cardiac body absent. Nephridia with large anteseptal portion in which the cilial canal loops several times; cellular intermediate substance strongly developed. Copulatory glands absent. Sperm sacs present, ovisacs absent. Seminal funnel cylindric. Spiral sperm duct, long and thin, confined to segment 12. Penial bulbs compact with mutual muscle layer, without epidermal curvature. Sperm duct opening directly on the surface of the body. Seminal vesicles without communication to the gut. Diverticula absent.

Terrestrial or in freshwater.

Range: Northern Argentina (Misiones), ?Columbia.

G. glandulosus Cernosvitov in lit.	G. rarus Cernosvitov in lit.
G. fridericoides Cernosvitov in lit.	?G. columbianus (Michaelsen) 1913

Gen. Aspidodrilus Baylis

Setae anteclitellial, two ventral bundles on each segment starting with the second, simple-pointed, of equal length, straight, two in each bundle. Anterior part of body vermiform, posterior part dorsoventrally flattened and much broadened, setae arranged in several (up to 20) transverse rows on the ventral surface of the body. Cephalic pore and dorsal pores absent. Longitudinal muscles of the posterior part of the body single-layered. Transition of the esophagus to the distended midgut in the centre of segment 8, the dorsal vessel originates at the same point. Cardiac body absent. One pair intestinal pockets in segment 7. Peptonephridia absent (?). Chylar cells absent. Cellular intermediate substance of nephridia strongly developed, anteseptal portion large. Copulatory glands absent. Seminal funnels cylindric. Sperm ducts thin, confined to segment 12. Penial bulbs compact, with mutual muscle layer, without epidermal curvature; sperm duct opening directly on the surface of the body. Seminal vesicles without communication to the gut and without diverticula.

Epizoic on dew worms.

Range: Africa (Sierra Leone).

A. *kellalli* Baylis 1914

Subfam. Parergodrilidae

Body shortened, number of segments reduced. Cephalic pore and dorsal pores absent. Longitudinal muscles single-layered. Cellular intermediate substance of nephridia strongly (?) developed. Peptonephridia and chylar cells absent. Rudimentary intestinal pockets (?) at the posterior end of the esophagus. Transition of esophagus to the stomach after sudden extension. Small intestine with extended /283 final portion. Septa and vascular system absent. Hermaphroditic gonads surrounded by a tunic which continues in two tubular gonoducts, each with a very large adanal gland. Seminal vesicles rudimentary, without communication to the gut and without diverticula.

Range: Austria, France.

Gen. *Parergodrilus* Reisinger

Body abbreviated, consisting of 11 segments of which the first is homologous to the three or four most anterior segments of the other Enchytraeidae. Cephalic pore and dorsal pores absent. One pair of ventral setal bundles on anterior segments 2-9 and one pair dorsal setal glands. Setae straight, simple-pointed, of equal length, two per bundle. Longitudinal muscles single-layered. Pharynx with a ventral, protrusible pharyngeal pouch. Transition of esophagus to the wide, sac-like stomach/gut after sudden extension; a tubular small intestine originates from the stomach/gut, looping, somewhat distended at the end and may be considered here as the terminal portion of the gut. On each side of the posterior end of the esophagus one or two glands (reduced intestinal pockets?). Septa and vascular system absent. Peritoneal epithelium incomplete and only developed in the gonadal segments. Two pairs nephridia in segments 3 and 4; cellular intermediate substance strongly (?) developed. Peptonephridia and chylar cells absent. Genital organs at the posterior part of the body. One pair of hermaphroditic gonads. Eggs probably develop parthenogenetically. Sperm not fertile. Each gonad surrounded by a tunic which continues in two tubular gonoducts which open into segment 10 shortly before the anus. Shortly before the opening each of the gonoducts bears a very large adanal gland. Subneural glands (copulatory glands) within the region of the genital segment. A pair of rudimentary seminal vesicles without communication to the gut and without diverticula open ventrally directly anterior to the first bundles of setae.

Between decaying leaves and humus layers in deciduous forests.

Range: Austria (Graz), France (Vosges, Alsace).

P. heideri Reisinger 1925

Subfam. Fridericinae

Cephalic pore between prostomium and peristomium. Dorsal pores present. Longitudinal muscles two-layered, consisting of round fibres and ribbon-like fibres. Two forms of lymphocytes. Postpharyngeal peptonephridia present. Transition of esophagus to the midgut /284 postclitellial without sudden distension. Chylar cells present. Intestinal pockets absent. Cellular intermediate substance of nephridia strongly developed. Sperm ducts without atrium-like distension, opening in the epidermal curvature. Penial bulb compact, with mutual muscle layer. Accessory penial glands and atrial glands absent. Seminal vesicles primarily communicating with the gut.

Habits and range see below.

Gen. *Fridericia* Michaelsen

Four bundles of setae on each segment, starting with the second (in exceptional cases only ventral bundles are present), straight or proximally curved, rarely weakly curved, simple-pointed, of unequal length, the interior seta in the bundle is shorter than the exterior. Cephalic pore between prostomium and peristomium. Dorsal pores present. Longitudinal muscles two-layered, consisting of round fibres and ribbon-like fibres. Paired postpharyngeal peptonephridia present. Transition of esophagus to the midgut postclitellial without sudden distension. Chylar cells present. Intestinal pockets absent. Origin of dorsal vessel postclitellial, rarely intraclitellial; blood hyaline, rarely greenish or red. Cardiac body absent. Nephridia with large anteseptal portion in which the cilial canal loops repeatedly; cellular intermediate substance strongly developed. Copulatory glands sometimes present. Seminal funnels cylindric. Sperm sacs and ovisacs usually absent, rarely only weakly developed. Sperm ducts thin and long, confined to segment 12. Penial bulbs compact, with mutual muscle layer, at the epidermal curvature where the sperm ducts open. Seminal vesicles primarily communicating with the gut (this communication is secondarily interrupted only in rare instances). Diverticula absent or present.

In soil, under moss and moist leaves and the bark of trees, rarely amphibian or in freshwater, rarely epizoic on dew worms.

<u>Range</u>: All of Europe, Siberia, Nowaja Semlja, Spitsbergen, all of North America, part of Central America.

Some species are very widely distributed as a result of introduction in South America, Africa, New Zealand, Australia, the Kermadek Islands, India, the Malay Archipelago.

Some species also endemic (?) in South and North East Africa and New Zealand (?).

F. *agilis* Smith 1895
F. *agricola* Moore 1895
F. *alba* Moore 1895
F. *alpinula* Bretscher 1900
F. *aurita* Issel 1905
F. *bedoti* Bretscher 1904
F. *belgica* Černosvitov 1936
F. *biglobulata* Bretscher 1903
F. *bisetosa* (Levinsen) 1884
F. *bollonsi* Benham 1915
F. *bollonsi* var. *oliveri* Benham 1915
F. *bretscheri* Southern 1907
F. *bulbosa* (Rosa) 1887
F. *beddardi* Bretscher 1900
F. *clitellaris* Bretscher 1900
F. *callosa* (Eisen) 1878 (syn. **F.** *striata* Levinsen 1884)
F. *cognettii* Bretscher 1904

F. connata Bretscher [illegible]
F. connata var. *baskini* Černosvitov 1937
F. californica Eisen 1905
F. digitata Cognetti 1901
F. douglasensis Welch 1914
F. exserta Bretscher 1902
F. firma Smith & Welch 1913
F. florentina Dequal
F. fuchsi Eisen 1905
F. fruttensis Bretscher 1900
F. galba (Hoffmeister) 1843
F. galba var. *michaelseni* Bretscher 1899
F. gamotheca Issel 1905
F. gigantea Dequal 1912
F. glandifera Friend 1911
F. glandulosa Southern 1907
F. harrimani Eisen 1905
F. hegemon (Vejdovský) 1877
F. helvetica Bretscher 1896
F. hillmani Friend 1913
F. humicola Bretscher 1900
F. humilis Friend 1912
F. ilvana Issel 1905
F. irregularis Bretscher 1903
F. johnsoni Eisen 1905
F. lacustris Bretscher 1899
F. leydigi (Vejdovský) 1877
F. lobifera (Vejdovský) 1879
F. longa Moore 1895
F. macgregori Eisen 1905
F. magna Friend 1899
F. microcara Friend 1912
F. monopera Cognetti 1903
F. nigrina Friend 1913
F. oconeensis Welch 1914
F. obtusa Friend 1912
F. omeri Stephenson 1932
F. paroniana Issel 1904
F. parasitica Černosvitov 1928
F. perrieri (Vejdovský) 1877
F. ptychaeta Bretscher 1900
F. popofiana Eisen 1905
F. pretoriana Stephenson 1930
F. pseudoargentea Knöllner 1935
F. quadriglobulata Bretscher 1903
F. ratzeli (Eisen) 1872
F. santabarbarae Eisen 1905
F. santarosae Eisen 1905
F. sardorum Cognetti 1901
F. silvestris (Leidy) 1882
F. sima Welch 1914
F. stephensoni Moszynski 1932
F. sonorae Eisen 1905
F. tenera Smith & Welch 1913
F. terrestris Bretscher 1900
F. tusca Dequal 1914
F. uniglandula Stephenson 1931
F. udei Bretscher 1899
F. viridula Issel 1904
F. variata Bretscher 1902
F. valdensis Issel 1905
F. valdarnensis Dequal 1914
F. zykoffi Vejdovský 1903

Species dubiae et incerti generis:

F. anglica Friend 1912
F. inornata Friend 1912
F. peruviana Friend 1911
F. ulmicola Friend 1899

Subfam. Henleinae

Cephalic pore between prostomium and peristomium. Dorsal pores absent. Longitudinal muscles single-layered, consisting of ribbon-like fibres. Esophageal peptonephridia present. Transition of esophagus to the broad midgut anteclitellial, usual after a sudden distension. Chylar cells absent. Intestinal pockets present or absent. Cellular intermediate substance of nephridia strongly developed. Origin of dorsal vessel anteclitellial or intraclitellial. Seminal funnel cylindric. Sperm duct without atrium-like distension, opening in the epidermal curvature which is only rarely absent; then the sperm duct opens on the surface of the body. Penial bulb compact, with mutual muscle layer. Seminal vesicles primarily communicating with the gut, usually dorsally through a mutual canal.

Terrestrial, rarely in freshwater.

Range: All of Europe, Siberia, Arctic, North and Central America.

As a result of introduction some species are widely distributed: Africa, South America, Australia.

Gen. Henleanella Friend /286

Four bundles of setae on each segment starting with the second, straight or only entally slightly curved, thin, of equal length or the interior seta in the bundle somewhat shorter than the exterior. Cephalic pore between prostomium and peristomium. Dorsal pores absent. Longitudinal muscles single-layered. Transition of esophagus to the midgut anteclitellial after sudden distension. Chylar cells and intestinal pockets absent. Origin of dorsal vessel anteclitellial, one segment behind the intestinal distension; blood hyaline; cardiac body absent. Cellular intermediate substance of nephridia strongly developed. Esophageal peptonephridia present. Copulatory glands only rarely present. Sperm sacs and ovisacs absent. Seminal funnel cylindric. Sperm duct thin and long and confined to segment 12. Penial bulbs compact, with mutual muscle layer on the epidermal curvatures where the sperm ducts open. Seminal vesicles communicating with the gut through a mutual canal (or separately ?) (this communication is only rarely secondarily interrupted). Diverticula absent.

In soil, rarely amphibian.

Range: All of Europe, Nowaja Semlja, the New Siberian Islands, Spitsbergen, Greenland, North America (Whaite Mountains).

H. dicksoni (Eisen) 1870
H. glandulosa (Friend) 1913
H. heleotropha (Stephenson) 1922
H. inuritata (Friend) 1913
H. nivea (Černosvitov) 1929
H. puteana (Vejdovský) 1877
H. perpusilla (Friend) 1911
H. rosai (Bretscher) 1899
H. scharfi (Southern) 1910
H. stolli (Bretscher) 1900
H. subterranea Černosvitov 1937

Species dubiae:

H. arenicola Friend 1912
H. marina Friend 1912
H. minima Friend 1913

Gen. Henlea Michaelsen

Four bundles of setae on each segment starting with the second, straight, rarely weakly curved, of equal length or the interior seta in the bundle shorter. Cephalic pore between prostomium and peristomium. Dorsal pores absent. Longitudinal muscles single-layered. Transition of esophagus to midgut anteclitellial after sudden distension. Two pairs of large intestinal pockets open into the midgut at the point of transition. Origin of dorsal vessel anteclitellial, one segment behind the intestinal distension; blood hyaline; cardiac body absent. Chylar cells absent. Esophageal peptonephridia present. Cellular intermediate substance of nephridia strongly developed. Copulatory glands only rarely present. Sperm sacs and ovisacs absent. Seminal funnel cylindric. Sperm duct thin and long, confined to segment 12.

Penial bulbs compact, with a mutual muscle layer at the epidermal /287 curvature where the sperm ducts open. Seminal vesicles communicating with the gut through a mutual canal. Diverticula rarely present.

In soil or amphibian.

Range: All of Europe, Turkestan, northern Siberia, The New Siberian Islands, Greenland, northwestern Canada.

One species (H. ventriculosa) widely distributed as a result of introduction: New Zealand, Chile, South Patagonia, Pennsylvania.

H. arctica Welch 1919
H. diverticulata Čejka 1912
H. groenlandica Černosvitov 1929
H. sibirica (Čejka) 1910
H. tolli Michaelsen 1901

H. ventriculosa (Udekem) 1854

Species dubiae:
H. simplex Michaelsen 1926
?*H. dorsalis* Bretscher 1902

Gen. Michaelseniella Černosvitov

Four bundles of setae on each segment starting with the second, simple-pointed, weakly curved or straight, of equal length or the interior seta in a bundle shorter. Cephalic pore between prostomium and peristomium. Dorsal pores absent. Longitudinal muscles single-layered. Transition of esophagus to midgut anteclitellial after sudden distension. One pair large intestinal pockets open into the midgut at the point of transition. Origin of dorsal vessel between the intestinal pockets; blood hyaline; cardiac body absent. Esophageal peptonephridia present. Chylar cells absent. Cellular intermediate substance of nephridia strongly developed. Copulatory glands absent. Seminal funnels cylindric. Sperm sacs and ovisacs absent. Sperm duct thin and long, confined to segment 12. Penial bulbs compact, with mutual muscle layer at the epidermal curvatures where the sperm ducts open. Seminal vesicles communicating separately or through a mutual canal with the gut. Diverticula absent.

In soil or amphibian.

Range: All of Europe, New Siberian Islands, Spitsbergen, Greenland, Tibet, North America (northwest Canada, U.S.A.), California, Central America (Guatemala).

M. brucei (Stephenson) 1922
M. californica (Eisen) 1905 f. typica
M. californica (Eisen) var. *monticola* (Eisen) 1905
M. ehrhorni (Eisen) 1905
M. guatemalae (Eisen) 1905
M. helenae Černosvitov nom. nov. (pro *H. californica* var. *Helenae* Eisen 1905)
M. nasuta (Eisen) 1878 (syn. *Henlea quadrupla* Friend 1913)
M. stewarti (Stephenson) 1909
M. urbanensis (Welch) 1914

Species dubiae:

Henlea heterotropha Friend 1912
Henlea pusilla Friend 1913
Henlea triloba Friend 1912
Henlea gulleri Bretscher 1903

Gen. Hepatogaster Čejka

Four bundles of setae on each segment starting with the second, straight, of equal length or the interior seta in each bundle shorter and sometimes thinner. Cephalic pore between prostomium and /288 peristomium. Dorsal pores absent. Longitudinal muscles single-layered. Transition of esophagus into the distended midgut anteclitellial. The intestinal organ consists of branched canals opening with several (approximately 10-12) openings into the gut at the point of transition into the midgut. Origin of dorsal vessel one segment (rarely two?) behind the intestinal distension; blood hyaline; cardiac body absent. Esophageal peptonephridia present. Chylar cells absent. Cellular intermediate substance of nephridia strongly developed. Copulatory glands absent. Sperm sacs and ovisacs absent. Seminal funnels cylindric. Sperm ducts thin and long, confined to segment 12. Penial bulbs compact with mutual muscle layer at the epidermal curvatures where the sperm ducts open. Seminal vesicles communicating with the gut. Diverticula absent.

In soil or amphibian.

Range: North Norway, Solowetsky Islands, Nowaja Semlja, Waygatsch Island, Siberia (Jenisej, Tajmyr, Irkutsk), New Siberian Islands, North America, (Alaska, northwestern Canada?, Illinois, Michigan).

H. birulae Čejka 1910
H. tenellus (Eisen) 1879
H. ochraceus (Eisen) 1879
H. moderatus (Welch) 1914
H. tubuliferus (Welch) 1914
H. irkutensis (Burow) 1929

Gen. *Buchholzia* Michaelsen

Four bundles of setae on each segment starting with the second, simple-pointed, S-shaped, of different length, the shorter setae closer to the centre lines. Cephalic pore between prostomium and peristomium. Dorsal pores absent. Longitudinal muscles single-layered. Transition of esophagus to midgut anteclitellial after sudden distension. Intestinal organ (originally paired) consisting of thin canals opening at the point of transition of the esophagus into the midgut. Origin of dorsal vessel anteclitellial, from the tip of the intestinal organ; blood hyaline, cardiac body absent. Esophageal, sac-like peptonephridia present. Chylar cells absent. Cellular intermediate substance of nephridia strongly developed. Copulatory glands absent. Sperm sacs and ovisacs absent. Seminal funnels cylindric. Sperm ducts thin and long, confined to segment 12. Penial bulbs compact with mutual muscle layer on the epidermal curvatures where the sperm ducts open. Seminal vesicles (always?) communicating through a mutual canal with the gut. Diverticula secreted from the ampulli are absent. Sexual organs, except seminal vesicles, sometimes advanced 3-4 segments.

In soil, under leaves and bark of trees. /289

Range: Europe, North Africa (Algeria).

B. africana Černosvitov 1933
B. appendiculata (Buchholz) 1863
B. fallax Michelsen 1877
B. protarum (Bretscher) 1900

Species incerti generis:
B. focale Friend 1914 (*?Bryodrilus*)
B. parva Bretscher 1900 (*?Marionina*)

Gen. Bryohenlea Černosvitov

Four bundles of setae on each segment starting with the second, weakly curved, pointed. Cephalic pore between prostomium and peristomium. Dorsal pores absent. Longitudinal muscles single-layered. Transition of esophagus to the midgut without sudden distension. Two pairs of intestinal pockets with ciliate walls open into the gut in segment 8. (Esophageal peptonephridia present?) Origin of dorsal vessel in segment 12; cardiac body present. Cellular intermediate substance of nephridia strongly developed; anteseptal portion consisting only of the funnel. Copulatory glands absent. Sperm sacs and ovisacs absent. Seminal funnel cylindric. Sperm ducts 3-4 times as long as the seminal funnel. Penial bulbs compact, with mutual muscle layer without epidermal curvature. Sperm duct opening directly on the body surface. Seminal vesicles communicating with the esophagus through a mutual long canal. Diverticula absent.

Range: Alaska.

B. udei (Eisen) 1905

Gen. *Bryodrilus* Ude

Four bundles of setae on each segment starting with the second, weakly curved or S-shaped, simple-pointed, of unequal length, the shorter setae closer to the centre lines. Cephalic pore between prostomium and peristomium. Dorsal pores absent. Longitudinal muscles single-layered. Transition of esophagus to the midgut anteclitellial, often after weak distension. Two pairs of esophageal peptonephridia present (resembling intestinal pockets). Chylar cells and intestinal pockets absent. Origin of dorsal vessel intraclitellial; blood hyaline; cardiac body absent. Cellular intermediate substance of nephridia strongly developed. Copulatory glands absent. Sperm sacs and ovisacs absent (always?). Seminal funnel cylindric. Sperm duct thin and long, confined to segment 12. Penial bulbs compact, with mutual muscle layer on the epidermal curvatures where the sperm ducts open. Seminal vesicles communicating with the gut through a mutual canal. Diverticula absent.

In soil, under moss and bark of trees.

Range: Europe (Germany, Switzerland, Czechoslovakia, Ireland), New Siberian Islands (Kotelny), Greenland.

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B. borealis Čejka 1912
B. diverticulatus Černosvitov 1929
B. ehlersi Ude 1892

Species incerti generis Henleinarum:

Archyenchytraeus lampas Eisen 1878
Archyenchytraeus gemmatus Eisen 1878
Bryodrilus sulphureus Bretscher 1904
Henlea alba Friend 1913
Henlea curiosa Friend 1912
Henlea insulae Friend 1913 < Fridericia ..
Henlea lefroi Beddard 1905
Henlea variata var. *polychaeta* Friend 1912
Neoenchytraeus fenestratus Eisen 1878

Subfam. Enchytraeinae

Cephalic pore between prostomium and peristomium. Dorsal pores absent. Longitudinal muscles single-layered or indistinctly two-layered with irregularly distributed round fibres of different size. Postpharyngeal peptonephridia absent or present. Transition of esophagus to midgut postclitellial without sudden distension. Chylar cells and intestinal pockets absent. Cellular intermediate substance of nephridia strongly developed. Origin of dorsal vessel postclitellial, rarely intraclitellial. Seminal funnel cylindric. Sperm duct without atrium-like distension. Penial bulbs compact or consisting of several glandular complexes. Epidermal curvatures present or absent. Seminal vesicles communicating or not communicating with gut.

Marine, in brackish, salt and freshwater, also terrestrial.

Range: Cosmopolitan.

Gen. Enchytraeus Henle

Four bundles of setae on each segment starting with the second, or occasionally absent from the anterior part of the body. Setae equally long, straight, rarely weakly curved. Cephalic pore between prostomium and peristomium. Dorsal pores absent. Longitudinal muscles indistinctly two-layered with scattered round fibres of various size (or single-layered?). Transition of esophagus to midgut gradual. Postpharyngeal peptonephridia present. Chylar cells and intestinal pockets absent. Origin of dorsal vessel intraclitellial or postclitellial; cardiac body absent; blood hyaline. Cellular intermediate substance of nephridia strongly developed. Copulatory glands present only in exceptional instances. Testes free or included in peritoneal sperm sacs. Seminal funnel cylindric. Sperm duct long, extending to the posterior through several segments or confined to segment 12. Penial bulbs consisting of several separate glandular complexes without mutual muscle layer and with weakly developed epidermal curvature, or compact and with mutual muscle layer and well developed curvature. Seminal vesicles communicating with the gut. /291 Sexual organs, except the seminal vesicles, sometimes advanced 3-4 segments.

Littoral in salt water and brackish water, terrestrial or in freshwater.

Range: All of Europe, Siberia, Nowaja Semlja, Spitsbergen, Iceland, Greenland, North America, South America, South Georgia, Antarctic Islands, Bermudas, northern and eastern Africa.

E. albidus Henle 1837
E. australis Stephenson 1932
E. affinis Levinsen 1884
E. alaskae Eisen 1905
E. buchholzi Vejdovský 1879
E. carcinophilus Baylis 1915
E. fonteinensis Michaelsen 1933
E. gilletensis Welch 1914
E. hyalinus (Eisen) 1878
E. harurami Stephenson 1914
E. issyk-kulensis Hrabě 1934
E. indicus Stephenson 1912
E. kinkaidi Eisen 1905
E. krumbachi (Čejka) 1913
E. lifdeensis Stephenson 1924
E. macrochaetus Pierantoni 1901
E. mediterraneus Michaelsen 1925
E. parasiticus Baylis 1915
E. przewalskyi Hrabě 1934
E. sabulosus Southern 1906
E. silvestris Bretscher 1900
E. spiculus Leuckart 1847

Species dubiae:

E. alpestris Bretscher 1902

Gen. Stephensoniella Černosvitov

Four bundles of setae on each segment starting with the second, simple-pointed, of equal length, straight. Cephalic pore between prostomium and peristomium. Dorsal pores absent. Longitudinal muscles distinctly two-layered, consisting of round fibres and ribbon-like fibres. Transition of esophagus to the midgut intraclitellial or postclitellial without sudden distension. Peptonephridia absent. Chylar cells and intestinal pockets absent. Origin of dorsal vessel intraclitellial or postclitellial; cardiac body absent; blood hyaline. Anteseptal portion of nephridia consisting only of the funnel, cellular intermediate substance strongly developed. Copulatory glands absent. Testes included in large peritoneal sperm sacs. Ovisacs absent. Seminal funnels cylindric. Sperm ducts long, confined to segment 12. Penial bulbs compact, with mutual muscle layer, sperm ducts opening in the epidermal curvatures. Seminal vesicles communicating with the gut. Diverticula present or absent.

On seashores.

Range: Bermudas, French Guayana, India (Barkuda Islands).

S. barcudensis (Stephenson) 1915 S. marina (Moore) 1902

Gen. Pachydrilus Claparède

Four bundles of setae on each segment starting with the second, rarely absent from some of the anterior segments, S-shaped or straight, simple-pointed. Cephalic pore between prostomium and peristomium. Dorsal pores absent. Longitudinal muscles single-layered (or indistinctly two-layered?). Transition of esophagus to midgut postclitellial, rarely intraclitellial, without sudden distension. /292 Peptonephridia absent. Chylar cells and intestinal pockets absent. Origin of dorsal vessel postclitellial, rarely intraclitellial; cardiac body absent; blood red, yellow or hyaline. Nephridia with strongly developed cellular intermediate substance. Copulatory glands often present. Seminal funnel cylindric. Sperm duct short or long, confined to segment 12. Testes free or covered by a peritoneal membrane. Ovisacs only exceptionally present. Seminal vesicles confined to segment 5, or long, extending through several segments. Ampullae of seminal vesicles rarely with diverticula. Communication with gut absent or present. Penial bulbs compact with mutual muscle layer and epidermal curvature where the sperm ducts open, rarely consisting of separate glandular complexes and without epidermal curvature.

Usually in tidal zones, in saline and ammonium-containing locations, in freshwater, in boggy ground and in the soil.

Range: All of Europe, Spitsbergen, Nowaja Semlja, Iceland, Jan Mayen, the Hebrides, the Faeroes, Greenland, Siberia, Turkestan, Kamschatka, North America, South America, South Georgia, Australia, New Zealand, the Australian/Antarctic Islands.

Subgen. Pachydrilus Claparède

Body of testes divided into a number of elongate-pyriform parts, rarely only lobed or split longitudinally, even more rarely simply pyriform. Testes covered by a delicate, peritoneal membrane which forms small sperm sacs at the free ends of the parts or lobes. Blood (perhaps with a few exceptions?) red or red-yellow. Sexual organs in normal position.

P. antarcticus (Stephenson) 1932
P. aegialites (Stephenson) 1932
P. annulatus (Eisen) 1905
P. aestuum (Stephenson) 1932
P. americanus Ude 1896
P. benhami (Stephenson) 1932
P. colpites (Stephenson) 1932
P. catanensis (Drago) 1887
P. crymodes (Stephenson) 1922
P. dubius (Stephenson) 1911
P. eltoni (Stephenson) 1924
P. enchytraeoides St. Loup 1885
P. eiseni Černosvitov (nom. nov. pro *Marionina americana* Eisen 1905 non Ude 1896)
P. fossarum Tauber 1879
P. franciscanus (Eisen) 1905 f. typica
P. franciscanus var. *borealis* (Eisen) 1905
P. franciscanus var. *unalaskae* (Eisen) 1905
P. griseus (Stephenson) 1932
P. helgolandicus Michaelsen 1927
P. insularis Ude 1896
P. kamtschatkanus Michaelsen 1929
P. lineatus (O. F. Müller) 1774
P. lineatus forma *verrucosus* (Claparède) 1861
P. muscicola (Stephenson) 1924
P. maximus Michaelsen 1888
P. maximus var. *Robinson* Michaelsen 1905
P. maritimus Ude 1896
P. mangeri (Michaelsen) 1914
P. macquariensis (Benham) 1905
P. merriami (Eisen) 1905
P. merriami var. *elongatus* (Eisen) 1905
P. minimus Černosvitov 1929
P. minutus (Müller) 1776, Fabricius 1780
P. nervosus (Eisen) 1878
P. niger (Southern) 1909
P. orthochaetus Delphy 1921
P. parvus Ude 1896
P. profugus (Eisen) 1879
P. pagenstecheri (Ratzel) 1869
P. pumillio (Stephenson) 1932
P. pygmaeus Michaelsen 1935
P. ritteri (Eisen) 1905
P. russoi (Drago) 1908

P. scoticus (Elmhirst & Stephenson) 1926
P. santaeclarae (Eisen) 1905
P. tuba (Stephenson) 1911
P. tenuis Ude 1896
P. werthi (Michaelsen) 1905

Subgen. Marionina Michaelsen

Testes without peritoneal membrane. Body of testes compact, rarely only weakly lobed. Blood yellow or hyaline. Sexual organs, except seminal vesicles, sometimes advanced 2-4 segments.

P. (*M.*) *argenteus* (Michaelsen) 1889
P. (*M.*) *atratus* (Bretscher) 1903
P. (*M.*) *arenarius* (Michaelsen) 1889
P. (*M.*) *aliger* (Michaelsen) 1927
P. (*M.*) *anomalus* (Černosvitov) 1928
P. (*M.*) *alaskae* (Eisen) 1905
P. (*M.*) *antipodum* (Benham) 1905
P. (*M.*) *cognettii* (Issel) 1905
P. (*M.*) *crassus* Claparède 1861
P. (*M.*) *ebudensis* Claparède 1861
P. (*M.*) *exiguus* (Ude) 1896
P. (*M.*) *elgonensis* Černosvitov 1937
P. (*M.*) *fontinalis* (Bretscher) 1901
P. (*M.*) *forbesae* (Smith & Welch) 1913
P. (*M.*) *falclandicus* (Michaelsen) 1905
P. (*M.*) *georgianus* Michaelsen 1888
P. (*M.*) *glandulosus* Michaelsen 1888
P. (*M.*) *guttulatus* (Bretscher) 1901
P. (*M.*) *insignis* (Ude) 1896
P. (*M.*) *incisus* (Bretscher) 1905
P. (*M.*) *kinangopensis* Černosvitov 1937
P. (*M.*) *lobatus* (Bretscher) 1899
P. (*M.*) *litteratus* (Hesse) 1893
P. (*M.*) *maculatus* Bretscher 1896
P. (*M.*) *monochaetus* (Michaelsen) 1888
P. (*M.*) *nigrinus* (Bretscher) 1900
P. (*M.*) *nodosus* (Stephenson) 1911
P. (*M.*) *riparius* (Bretscher) 1899
P. (*M.*) *rivularis* (Bretscher) 1900
P. (*M.*) *southerni* Černosvitov (nom. nov. pro *Enchytraeus lobatus* Southern 1909)
P. (*M.*) *sphagnetorum* Vejdovský 1877
P. (*M.*) *semifuscus* Claparède 1861
P. (*M.*) *subtilis* (Ude) 1896
P. (*M.*) *singula* (Ude) 1896
P. (*M.*) *tatrensis* (Kowalewski) 1916
P. (*M.*) *volkarti* (Bretscher) 1904

Species dubiae:

P. (*M.*) *montanus* (Bretscher) 1905
P. (*M.*) *bisetosus* (Bretscher) 1906

Species incerti subgeneris.

Pachydrilus aporus Stephenson 1922
Enchytraeus cavicola Joseph 1880
Enchytraeus citrinus Eisen 1905
Enchytraeus cliarensis Southern 1913
Enchytraeus pugetensis Altman 1931
Enchytraeus saxicola Eisen 1905

Species incerti generis Enchytraeinarum.

Enchytraeus metlakatlensis Eisen 1905
Enchytraeus modestus Eisen 1905
Enchytraeus parvulus Bretscher 1902 (non *E. parvulus* Friend 1897)
Enchytraeoides unisetosus Ferronier 1900
Henlea minuta Friend 1913
Henlea marina Friend 1912
Michaelsena paucispina Eisen 1905
Michaelsena principissae Michaelsen 1907
Pachydrilus charkoviensis Czerniavsky 1820
Pachydrilus gracilis Czerniavsky 1880
Saenuris vagus Johnston 1865

The systematic position of the following genus remains unclear because Bretscher's description is inadequate and it is presently not possible to ascertain the subfamily of the Enchytraeidae into which it should be placed.

Gen. Hydrenchytraeus Bretscher

Four bundles of setae on each segment, simple-pointed, S-shaped, curved. Dorsal pores absent. Transition of esophagus to the midgut gradual. Peptonephridia present. Origin of dorsal vessel /294 postclitellial, blood yellow or red. Nephridia with large or small anteseptal portions. Seminal funnel cylindric. Ampullae of seminal vesicles without diverticula.

In freshwater.

Range: Switzerland.

H. stebleri Bretscher 1901

H. nematoides Bretscher 1901

Species incerti generis Enchytraeidarum:

Archyenchytraeus levinseni Eisen 1878
Enchytraeus parvulus Friend 1897
Enchytraeus maniliformus Udekem 1859
Enchytraeus lataslei Giard 1894
Enchytraeus jaltensis Czerniavsky 1868
Enchytraeus juliformis Kessler 1868
Enchytraeus globulatus Bretscher 1900
Lumbricus vermicularis Müller 1774
Lumbricus jordani Williams 1858
Lumbricus putredinis Hardy 1849
Lumbricus gracilis Leidy 1885
Lumbricus noctilucus Eversman 1838
Michaelsena Normani Michaelsen 1907
Mesenchytraeus alpinus Bretscher
Nais albida Carter 1858
Naidium breviceps Schmidt 1847
Pachydrilus affinis Czerniavsky 1880
Pachydrilus fossor Vejdovský 1877
Pachydrilus lacustris Czerniavsky 1880
Pachydrilus opacus Czerniavsky 1880
Pachydrilus proximus Czerniavsky 1880
Pachydrilus similis Czerniavsky 1880
Saenuris limicola Verril 1871
Saenuris abyssicola Verril 1871
Tubifex pallidus A. Duges 1837

The description of the following species was unfortunately not available; consequently, I was not able to elucidate their true systematic position.

Enchytraeoides immotus Knöllner 1935
Michaelsena postclitellochaeta Knöllner 1935
Marionina sialona Friend 1912
Michaelsena subterranea Knöllner 1935

[illegible] über die Oligochaeten [illegible] suisse Zool., vol. 9, p. 189—223, pl. 14.

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3 ČEJKA, B. (1913): Litorea krumbachi nsp. ngen. — Ein Beitrag zur Systematik der Enchytraeiden. Zool. Anz. Bd. 42, p. 145—151.

4 ČERNOSVITOV, L. (1931): Sur quelques Oligochètes de la région arctique et des îles Faeroer. Ann. Sci. Nat, Zool. vol. 14, p. 65—110.

5 ČERNOSVITOV, L. (1933): Revision der Enchytraeiden-Gattung Distichopus Leidy. Zool. Anz. Bd. 104. p. 73—76.

6 ČERNOSVITOV, L. (1934): Zur Kenntnis der Enchytraeiden I. Zool. Anz. Bd. 105 p. 233—247.

7 ČERNOSVITOV, L. (1934): Zur Kenntnis der Enchytraeiden II. Zool. Anz. Bd. 105 p. 295—305.

8 ČERNOSVITOV, L. (1937): Zur Kenntnis der Enchytraeiden IV. Revision der Michaelsenschen Typen. Zool. Anz. Bd. 118.

9 ČERNOSVITOV, L. (1937): Oligochaeta. Exped. Sci de l'Omo. (im Druck).

✓10 DELPHY, J. (1919): Recherches sur les Oligochètes limicoles. III. Sur quelques genres d'Enchytréidomorphes et la position systematique de l'Enchytraeoides Roule. Bull. Mus. Hist. Nat. no 7, 1919.

11 EISEN, G. (1905): Enchytraeidae of the West Coast of North America. Harriman Alaska Exped. New York 1905.

12 FREUDWEILER, H. (1905): Studien über das Gefässsystem niederer Oligochaeten. Jena Zeitschr. Naturw. Bd. 39.

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