THE BIOLOGY OF SOME FRESHWATER OLIGOCHAETES

Being a thesis submitted for the degree of Ph.D.
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by

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CHAPTER 1

INTRODUCTION

Although several families of oligochaetes occur in fresh water it is members of the family Tubificidae that are frequently encountered in general biological surveys. The widespread distribution of the family and the abundance of tubificids under certain environmental conditions, especially in organically polluted waters, have long been recognised, but little is known of the biology and ecological requirements of individual species. The Tubificidae are primarily inhabitants of muddy substrata in inland waters, but despite the obvious importance of the family in limnological studies they have received very little attention compared to other groups of freshwater organisms. In most publications of a general limnological nature no attempt is made to identify species, and they are commonly referred to as Tubificidae indet. Occasionally references are made specially to Tubifex tubifex and Limnodrilus hoffmeisteri, the two most widespread and abundant species, but since these identifications are rarely checked little reliance can be placed on them.

The principal reason for the neglect of biological studies on the Tubificidae has been the difficulties of identification of specimens. The lack of uniformity of approach of earlier workers, the definition of species on morphological characters alone, with no account being taken of their variation, and the scattering of the species descriptions throughout an extensive literature have all combined to increase the difficulties of identification for persons who were not specialists in the group. The last complete taxonomic revision of the family was made by Michaelsen (1900) at a time when very few species were recognised. Although Stephenson (1930) described all the genera then recognised, he made no attempt to describe the species. Furthermore, the insistence of the earlier workers that identifications could only be made on live specimens or preferably even from serial sections greatly hindered the development of studies of a biological or ecological nature. The great majority of published works on the family have been of a taxonomic nature, with occasional biological notes. Apart from the studies on reproduction by Gavrilov (1931 et.seq.), the first papers on the life history of any species did not appear until comparatively recently, when Poddubnaya (1959) published an account of the life cycles of three species of Tubificidae.

A year later Brinkhurst (1960) described a technique for the examination of whole mounts which enabled large numbers of specimens to be examined fairly rapidly. At the same time he was preparing a taxonomic revision of the family, and a key that could be used by ecologists. The preliminary results of his studies on the British Tubificidae were published in 1960. It was evident from this work that further detailed studies were needed on some genera, in particular the genus *Limnodrilus* Claparède, 1862. Brinkhurst (1960) recorded three British species of *Limnodrilus*, but was not certain of their validity or the status of some specimens found by him. In a discussion on *L.hoffmeisteri* he stated that "There is a chitinous penis tube in segment 11, and in this species it is usually 11 - 12 times longer than the width, but immature specimens have tubes as short as *L.udekemianus*, and I have observed several specimens with the tube as long as that of *L.claparedeanus*". He also expressed some doubt as to the correct taxonomic status of *L.parvus*? It was apparent that information on the value of specific characte within the genus and on the biology of each species was required before the true relationships of the various entities could be determined.

The following points in particular required clarification. The relative values of the chaetae, the length and shape of the penis tube as taxonomic characters were known, as also was the range of variation exhibited by each structure. It was also important to determine whether these structures varied with the age of the specimen as well as with its condition or habitat. The validity of some species and the status of some entities also required investigation. In particular it was desired to know whether L. parvus was a valid species or whether it was only a young stage of another species, and what was the status of the forms with a long penis tube described by Brinkhurst (1960) under L. hoffmeisteri. Finally, it was necessary to determine whether there were any biological and ecological differences between the species in addition to morphological ones. It was evident that morphological characteristics alone were not sufficient to separate the entities: a knowledge of the biology of each was essential to an understanding of the systematic relationships within the genus.

The answers to the problems posed above could only come from a detailed study of the morphology and biology of the species of Limnodrilus, and it is this study that forms the basis of the present work. The problem has been approached along the lines indicated above. A study of the taxonomic characters and their temporal and seasonal variations has resulted in seven valid species of Limnodrilus being recognised and described. The geographical distribution of these species has been studied, and also their distribution and abundance in a variety of types of habitat. The reproductive biology and the relative importance of sexual and asexual reproduction was studied in detail for L.hoffmeisteri. Finally, detailed investigations were carried out into the life histories of each of the British species of Limnodrilus under different sets of field and laboratory conditions. The information gained from these studies will provide a basis for future work of a more ecological nature, but in the limited time available for the present study it was not possible to investigate the ecology of the species in any detail.

One further aspect of the biology of Limnodrilus was treated in some detail although it was not directly relevant to the problems ennumerated above. This was the relationship between Limnodrilus and its Cestode parasites, and the biology of the parasites themselves. Infected specimens of Limnodrilus were frequently encountered during the examination of routine samples, and in the almost total absence of any published information on the biology of the parasites or the host - parasite relationship it was decided to investigate these topics in rather more detail than is customary in studies of a more general biological nature.

The sampling methods are discussed in the appropriate chapters, but it is convenient to refer here to the methods of examination of specimens. The majority of specimens were examined as whole mounts, having been killed and prepared for examination by the technique described by Brinkhurst (1960, 1963). For detailed morphological studies additional specimens were dissected and serial sections were examined. Specimens kept in cultures in the laboratory were generally examined alive, after first being narcotised in commercial "soda water". The methods of preparation and examination of the parasites are dealt with in the appropriate chapter.

CHAPTER 2

THE TAXONOMY OF LIMNODRILUS, CLAPARÈDE 1862.

a) THE GENITALIA OF LIMNODRILUS

In accordance with the views of Brinkhurst (1963) the genitalia are accepted as providing the most satisfactory generic characters. Before proceeding to a discussion of the taxonomy of Limnodrilus, therefore, a bried description of the genitalia will be given.

The arrangement of the genitalia in Limnodrilus is shown in semi-diagramatic form in figure 1. With the exception of the sperm sacs and egg sac all organs are paired. The testes lie in segment X, attached to the intersegmental septum 9/10. The spermathecae are also situated in segment X. Each spermatheca is divisible into a thin-walled sac-like portion and a thick walled duct which opens into a spermathecal pore situated close to the mid line on the ventral surface of the segment. After copulation spermatophores are present in them (Fig. 2.)

The sperm funnels lie in segment X, but the vas deferens passes through the intersegmental septum 10/11 close to them and lies in segment XI. The vas deferens is both elongate and convoluted and passes terminally, not laterally as in Tubifex, into a small elongate kidney-shaped atrium. There is a large solid prostate

Figure 1

Semi-diagrammatic view of the genitalia of L. hoffmeisteri.

Legend

Roman numerals indicate segments.

A = atrium

ATS = anterior testis sac

EJ = ejaculatory duct

O = ovary

OD = oviduct

OS = ovisac

P = penis and chitinous penis sheath

PS = prostate

PTS = posterior testis sac

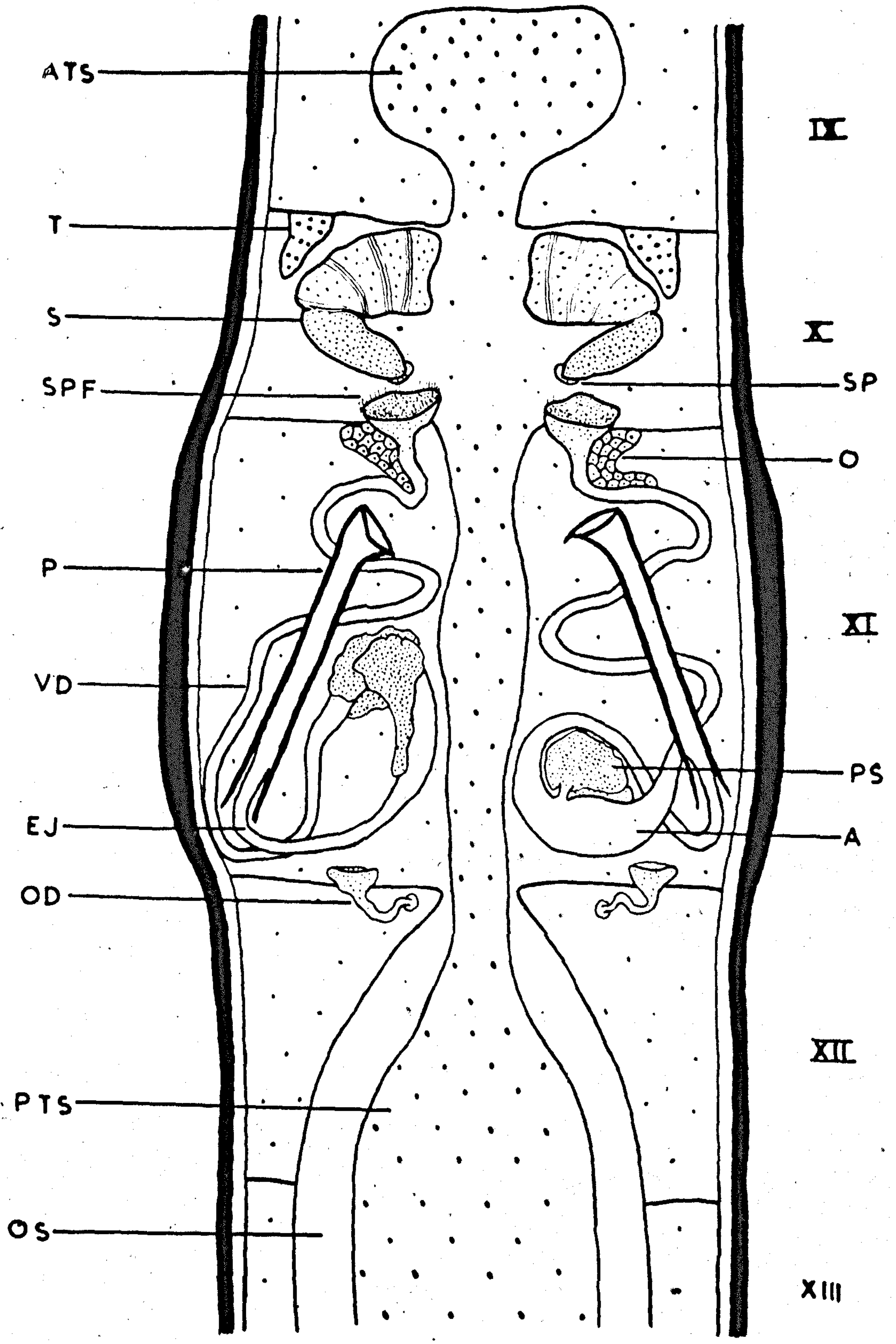
S = spermatheca

SP = spermathecal pore

SPF = sperm funnel

T = testis

VD = vas deferens


ATS
T
S
SPF
P
VD
EJ
OD
PTS
OS
IX
X
SP
O
XI
PS
A
XII
XIII

gland opening centrally by a stalk into the atrium. The gland may be closely applied to the atrium (Fig. 2). A long ejaculatory duct leads from the atrium to the more-or-less elongate penis. The penis is surrounded by a thick chitinous sheath, with a characteristic terminal portion, which is a continuation of the cuticle. The penis and sheath lie within a pocket formed by an invagination of the body wall (figs. 2 and 3). The invaginations open as paired male pores on the ventral surface of segment 11. The penis, its sheath and body-wall sac, which is closely applied to the sheath except near the male pores (fig. 3), are in turn surrounded by layers of muscles arranged in a spiral fashion. These attach to the body wall musculature close to the male pores. Their contraction serves to evert the penis and sheath (figs. 2 and 3). The sperm funnels, vas deferens and ejaculatory ducts are ciliated. In species with a short penis tube the male efferent ducts, with the exception of the sperm funnels, lie completely in segment XI, but in species with a very long penis sheath, as L. cervix and L. claparedeanus, this structure may either push back the intersegmental septum 11/12 and sometimes also 12/13, or break through them (fig. 2). In this case the male ducts come to occupy several segments. It must be emphasised that this is a secondary condition.

Figure 2

Longitudinal section through genital segments of *L. cervix*.

Legend

AS = stalk of prostate entering atrium

bWI = body wall invagination surrounding penis sheath

IT = intestine

PM = spiral muscles surrounding penial apparatus

SM = spermatophore

Other abbreviations as Figure 1.

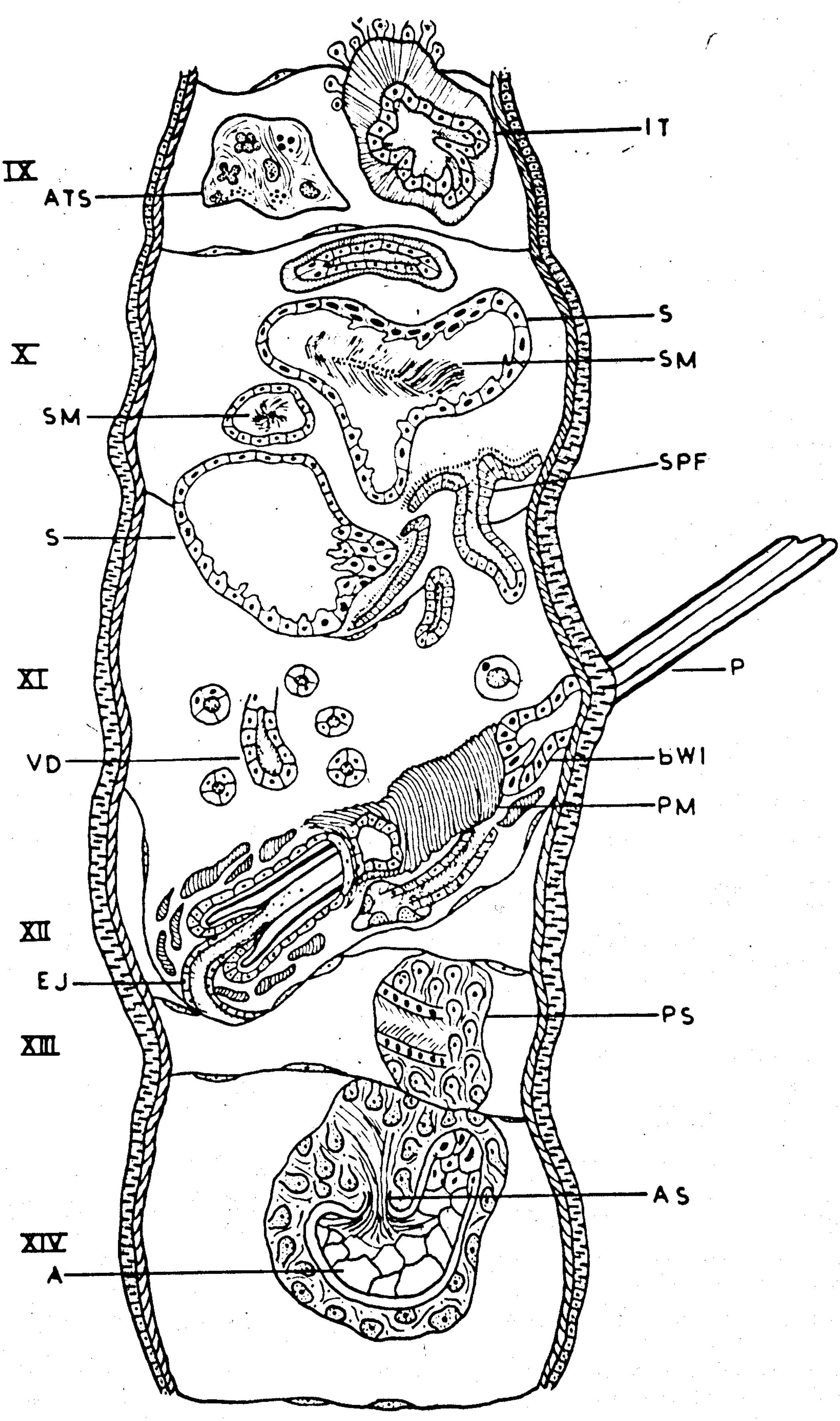

IT
IX
ATS
S
X
SM
SM
SPF
S
P
XI
VD
BWI
PM
XII
EJ
PS
XIII
AS
XIV
A

Figure 3

Longitudinal section through segment 11 of *L. hoffmeisteri*.

Legend

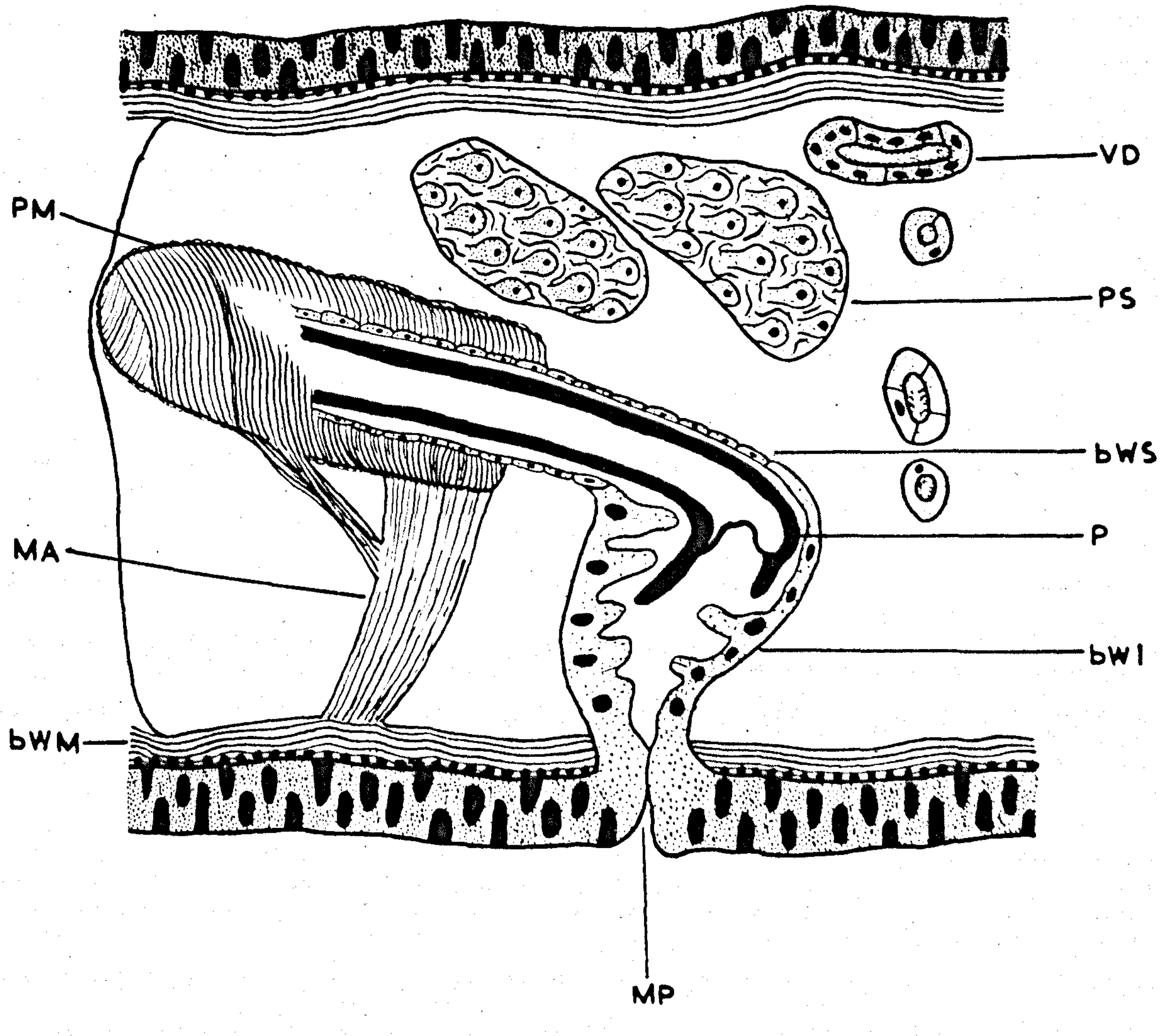
bWM = body wall musculature

bWS = body wall sac closely applied to penis sheath

MA = muscle band joining body wall musculature to penial musculature

MP = male pore

Other abbreviations as Figures 1 and 2.


VD
PM
PS
bWS
P
MA
bWl
bWM
MP

The ovaries, attached to the intersegmental septum 10/11, lie in segment XI and are often closely applied to the vas deferens. The oviducts are very short and pass through septum 11/12 to open ventrally and anteriorly on segment XII.

At maturity the anterior sperm sac is formed from the intersegmental septum 9/10 and does not often extend further forwards than segment IX (figs. 1 and 2). The posterior sperm sacs are formed from the septum 10/11 and enter the egg sacs on septum 11/12. The posterior egg and sperm sacs project back through several segments, usually 3 but occasionally as many as 6. At maturity a clitellum is formed on segments X-XIV. The ovaries may disappear at maturity, maturation of the eggs taking place in the egg sac. No copulatory bursa is formed.

All specimens so far examined have had the male pores on segment XI, but there remains the theoretical possibility that if regeneration has occurred in some of the anterior segments, as is known to occur in Aulodrilus and Bothrioneurum (Hrabě, 1934, 1937), the male pores could apparently come to lie on a more anterior segment. Although typically only one pair of testes and a single pair of male ducts are present, Claparède (1862) records specimens with three testes, while the author has occasionally observed specimens with three atria and corresponding genital ducts. These duplications are probably caused by developmental abnormalities and have no taxonomil significance.

As the genera of Tubificidae are now characterised on the nature of their male ducts no attempt is made to describe the vascular system. A full description of this and of the nervous and excretory systems may be found in Vejdovsky (1884), Nomura (1913) and Marcus (1942). A description and key to all the genera of Tubificidae may be found in Brinkhurst (1963).

b) GENERIC CHARACTERS.

The original description of *Limnodrilus* by Claparède (1862) is incomplete, and lacks many important details of the genitalia. In view of the inaccessibility of this description to many modern authors ahd its obvious importance in this study, the generic diagnosis as it appeared in Claparède's paper (opp.cit.) is here given in its original form in full:- "Diagnose. Oligochaetes presentant tous les caracteres des *Tubifex*, moins les soies capillaires, et possedant en outre des vaisseaux circulant entre les deux couches musculaires de la paroi du corps". The characters that originally served to distinguish *Limnodrilus* were thus the absence of hair chaetae and the presence of a vascular complex in the body wall. In the generic diagnosis there is no mention of the presence of an elongate penis sheath as has been suggested by some later authors, including Brinkhurst (1963). Claparède, in common with most of his contemporaries, failed to appreciate the true nature and relationships of the genital ducts, and considered the penis sheath to be of value as a specific character only. A third species of <u>Limnodrilus</u> was described by Ratzel (1868) and characterised on the shape of the penis sheath, but no alteration was made to the generic diagnosis.

The genus was re-defined by Eisen in 1883. He recognised that the atrium was longer and narrower than in either <u>Tubifex</u> or <u>Ilyodrilus</u> and that a prominent feature of the copulatory organs was their elongation and narrowness. He still held, however, that the principle generic characteristic was the absence of hair chaetae. In the following year the genital organs were correctly described for the first time by Vejdovsky (1884). He considered the male ducts to be important specific characteristics, but continued to define the genus on the nature of the chaetae.

A full appreciation of the importance of the nature of the genital ducts in the diagnosis of the tubificid genera was due to Michaelsen (1900). He separated some of the genera on the nature of the male efferent ducts, in particular on the nature of the atrium and prostate gland. He considered both of these structures to be important generic characteristics. In his diagnosis of <u>Limnodrilus</u> he referred to the length of the sperm ducts; their opening into the proximal part of the atrium; the presence of a single large prostate gland and the presence of a chitinous penis sheath. The genus, however, was still separated from others by the absence of hair chaetae, and the form of the male ducts in Limnodrilus was considered to be of secondary importance.

Pointer (1911) described a new species of tubificid which did not possess hair chaetae and which differed from Limnodrilus in the absence of a chitinous penis sheath. He erected a new genus, Isochaeta, to contain this species, and thereby implied that the possession of a penis sheath was a characteristic of Limnodrilus. Piguet and Bretscher (1913) repeated Michaelsen's (1900) definition of the genus, but suggested that species without a chitinous penis sheath should be transferred to Isochaeta. This view was not generally accepted, and Michaelsen (1926) re-defined the genus and characterised it on the absence of hair chaetae. He included in Limnodrilus several species that did not possess a chitinous penis sheath and that had hitherto been assigned to Isochaeta or Lycodrilus. Michaelsen's views continued to influence other authors, including Ude (1929) and Stephenson (1930). This latter author in his monograph on the oligochaetes defined Limnodrilus by the following characters:- Dorsal and ventral bundles with double-pronged crotchets only; vas deferens long; atrium with bulky solid prostate;

true penis usually with chitinous penis sheath. He specifically stated that the chaetae furnished the best generic characteristic and that the penis tube could not be used as a diagnostic character in the generic definition.

In the following year Hrabě (1931) re-described Tubifex blanchardi. This species did not possess hair chaetae, but, relying on the form of the male genital ducts alone, he placed it in the correct genus. His studies on Ilyodrilus published in the same year (Hrabě, 1931a), also showed the importance of the male ducts and the unreliability of the chaetae as generic characteristics. The implications of this work, however, in relation to Limnodrilus were generally slow to be appreciated. Although Chen (1940) diagnosed the genus on the form of the male ducts, and in particular on the presence of a chitinous penis tube, Marcus (1942) and Cekanovskaya (1962) were still diagnosing the genus on the absence of hair chaetae, although both authors did include a description of the genitalia. It remained for Brinkhurst (1962) to apply the results of Hrabě's (1931) work to Limnodrilus. He removed two species from this genus and transferred them to Tubifex on the basis of the nature of their male genital ducts, despite the fact that both species do not possess hair chaetae.

A year later Brinkhurst (1963) re-defined all the genera of Tubificidae on the nature of their male genital ducts and showed that although chaetae were often valuable specific characters, they could not be used to distinguish genera.

In accordance with these views of Brinkhurst (1962, 1963), with which the author is in complete agreement, the genus Limnodrilus may be re-defined as follows:-

Tubificidae having the characters of the family. The paired male ducts are distinct, each comprising a long convoluted vas deferens opening terminally into an elongate, narrow, kidney-shaped atrium. The atrium receives a large solid prostate gland, opening centrally to it by a stalk. A long ejaculatory duct leads from the atrium to the more-or-less elongated penis. The penis is enclosed in a thick, well developed chitinous sheath, the length and shape of which varies specifically.

c) SPECIFIC CHARACTERS

There has existed in the past considerable confusion over the specific limits within the genus. This has arisen as the result of several factors. The original descriptions of many species have been inadequate, while in some cases the relationships of the genital organs have been imperfectly understood. The cosmopolitan nature of some species has led to their being described as different species in different parts of their range. Perhaps most important of all, however, has been the failure of the great majority of workers to give any account of the variation of the characters that they have used to delimit their species. Species were frequently described on the basis of the study of one or a few specimens, and then rigidly defined in terms of a few characteristics.

The characters that have been used by the earlier workers, including Claparède (1862), Ratzel (1868), Vejdovsky (1884) and Michaelsen (1900), to separate the species within the genus were the length:breadth ratio of the chitinous penis sheath and the shape of the chaetae. The use of the length:breadth ratio without any account being given of its natural variation led to several species being described which differed from each other only with respect to slight differences in this ratio. The principle objections to the use of this ratio were stated by Brinkhurst (1960). He considered the length of the penis tube to be unsatisfactory because it developed slowly, because it was a growing organ and because the length of the tube in mature specimens of different species overlapped considerably. Evidence will be presented later to show that the penis tube in fact develops rapidly, and that the length:breadth ratio of the penis tube at maturity can provide a useful secondary specific character. A study of the variation in this ratio, however, has revealed that an overlap may exist between some species, and that this ratio alone cannot serve to characterise the species. The form of the penis sheath, and in particular the shape of the terminal portion, has proved to be a suitable alternative character.

The use of the shape of the chaetae as a specific character has also led to confusion, as the natural variation in shape has generally been ignored. It is considered here that the chaetae in general exhibit a greater degree of variability within each species than is consistent with their use as specific characters. There are one or two exceptions to this, but in most species the chaetae have been found to be more useful as additional characters. This contrasts with the view of Brinkhurst (1960) who considered that the shape of the chaetae could provide a useful specific character. All species of Limnodrilus so far described have only bifid crotchets in both dorsal and ventral bundles. Hair chaetae, pectinate chaetae and specialised genital chaetae are absent, and such interspecific differences as do exist are differences in the relative proportions and sizes of the two teeth.

d) HISTORY OF THE GENUS

The genus Limnodrilus was originally erected by Claparède (1862) to contain two species that differed from the known species of Tubifex in the absence of hair chaetae. Claparède, however, failed to understand the true nature of the genital ducts and their relationships, and his description lacked many important details. A third species of Limnodrilus was described by Ratzel (1868), but the genus was not re-described or the diagnosis amended as a result. Eisen (1883) redognised the true nature of the male ducts, but not the female ones, and established a new genus, Camptodrilus, which differed from Limnodrilus in that the male genitalia were surrounded by spiral muscles. The major advance in the understanding of the genus came from Vejdovsky (1884), who described the genital ducts and their relationships correctly for the first time. On finding spiral muscles surrounding the penis sheath of L.hoffmeisteri he concluded that Camptodrilus Eisen had no validity and was in fact a synonym of Limnodrilus.

Vejdovsky's conclusions were accepted by Beddard (1895) in his monograph on the tubificids, but in addition he considered Clitellio Savigny, 1820, to be synonymous with Limnodrilus. This conclusion was largely based on the absence of hair chaetae in both genera. In the taxonomic revision of the Tubificidae by Michaelsen (1900), *Clitellio* was re-established as a valid genus, and was separated from *Limnodrilus* on the nature of the male ducts. In 1904, Ditlevsen synonomised *Limnodrilus* with *Tubifex*, but this view was not accepted.

In 1901, Michaelsen described a species of *Limnodrilus* with bifid crotchets but without a penis sheath. In 1905 he transferred this species to *Lycodrilus*, Grube, 1873. *Tubifex (Limnodrilus) newaensis*, a species described by him earlier (Michaelsen, 1903), was considered to be a 'link' between *Limnodrilus* and *Lycodrilus*, as it possessed a minute penis sheath. Pointer (1911) described another species without a penis sheath and without hair chaetae, and he created a new genus, *Isochaeta*, to contain it. The removal of species from *Limnodrilus* on the grounds of the absence of a chitinous penis sheath met with little acceptance, and in 1926 Michaelsen re-defined *Limnodrilus* and removed the criterion of the penis sheath. He accordingly considered that *Lycodrilus* and *Isochaeta* must be regarded as synonyms of *Limnodrilus*. The genus thus returned to its original state - being defined on the nature of the chaetae, and the genital ducts being of secondary importance. Stephenson (1930) followed Michaelsen's views, and included in Limnodrilus all the species previously assigned to Lycodrilus and Isochaeta. He arranged all the species in the genus into a series showing the progressive reduction of the penis sheath.

The work of Hrabě (1931, 1931a) on Tubifex blanchardi and on the genus Ilyodrilus showed the importance of the male ducts as generic characters. The importance of this work, however, was not realised until comparatively recently. Svetlov (in Cekanovskaya, 1962) re-erected Lycodrilus and raised it to family rank. Cekanovskaya herself still retained within the genus Limnodrilus some species that did not possess a chitinous penis tube. Brinkhurst (1962) was able to transfer some of the species of Limnodrilus to Tubifex, on the nature of their genital ducts. Finally, Brinkhurst (1963) re-defined all the tubificid genera on the nature of the male efferent ducts, and re-established Isochaeta as a genus. Thus, the genus Limnodrilus was at last clearly defined on the nature of its genital ducts and could now be separated from the genera that had at various times been synonomised with it.

e) LIST OF SPECIES TRANSFERRED TO OTHER GENERA

In accordance with the re-definition of the genera of tubificids by Brinkhurst (1963), as outlined in the above section, and the diagnosis of Limnodrilus as it appears on page 2.8, several species hitherto assigned to Limnodrilus have been transferred to other genera. These are tabulated below.

Species	New genus
L.heterochaetus (Michaelsen)	Peloscolex
L.chacoensis (Stephenson)	Tubifex
L.newaensis Michaelsen	Tubifex
L.pseudogaster Dahl	Tubifex
L.siolii Marcus	Tubifex
L.kleerekoperi Marcus	Tubifex
L.baikalensis Michaelsen	Isochaeta
L.arenarius Michaelsen	Isochaeta
L.michaelseni Lastockin	Isochaeta
L.lastockini Jaroschenko	Psammoryctes
L.dybowskii Grube	Lycodrilus
L.schizochaetus Michaelsen	Lycodrilus
L.grubei Michaelsen	Lycodrilus
L.parvus Michaelsen	Lycodrilus
L.phreodriloides Michaelsen	Lycodrilus

The remaining species that have been assigned to *Limnodrilus* will be dealt with in a later section.

f) DESCRIPTION AND DISCUSSION OF SPECIES

The taxonomy of the genus *Limnodrilus* has recently been discussed by Brinkhurst (1963) in the course of his revision of the Tubificidae. In a work of this scope, however, much detail had to be omitted and many details in his revision are in need of amplification. Furthermore, as his review was written while the studies outlined below were in progress, publication delays made it possible to include the results of the present work in condensed form. These results, and the evidence from which they were derived, appear in more detailed form in the following account.

Before proceeding to a consideration of the species currently recognised as belonging to Limnodrilus, it is convenient first to mention briefly those species described by Eisen and Friend respectively. Eisen (1879, 1883) described nine species that are clearly referable to Limnodrilus from the structure of their male genital ducts. Eisen failed to realise the true relationships of the parts of the genitalia, and the illustrations and descriptions are consequently difficult of interpretation. Several authors, including Michaelsen (1900), Cernosvitov (1939) and Chen (1940) have attempted to relate these species to other well-established species in the genus, but no agreement has been reached by them. Only L.alpestris has subsequently been recorded. Michaelsen (1914) claimed to have found it in West Africa. From his description it would appear that he found L.udekemianus. Cernosvitov (1936) also claimed to have found L.alpestris, but only one of his specimens was mature. He expressed doubt as to its identity, and with reluctance assigned his specimens to this species. Both records must be regarded as dubious. Further speculation as to their identity is at present pointless. Brinkhurst recently visited the type localities and it is to be hoped that his collections will help to clear up their identity.

There remain the species described by Friend to be considered. A detailed study of these was made by Cernosvitov (1941), and his views are followed here. A summary of them is given below.

Friend's species	Date	Status	Probable Identity
L.wordsworthianus	1898	Synonym	L.udekemianus
L.aurantiacus	1911	Synonym	L.hoddmeisteri
L.galeritus	1912	Synonym	L.hoffmeisteri
L.inaequalis	1912	Incertae generis	
L.nervosus	1912	Species dubium	Immature *Limnodrilus* sp.
L.papillosus	1912	Incertae generis	
L.trisetosus	1912	Incertae generis.	

L.hoffmeisteri v. tenellulus was regarded by him as being either a synonym of *L.udekemianus* or a specimen of *L.hoffmeisteri* that had not yet attained full maturity. A study of the type specimen indicates that the latter is more likely.

It is now convenient to consider the species currently recognised as belonging to *Limnodrilus*. In each case a list of synonomies will be given first, followed by a description of the species and an account of the variation of the specific characteristics. A discussion of the synonomies will be deferred to a later section when an account of the variations will be particularly relevant.

Limnodrilus hoffmeisteri Claparède, 1862.

L.hoffmeisteri Claparède, 1862, p.100, f. 75-85.
L.claparedeanus: Vejdovsky, 1884, p. 166.
L.dugesi Rybka, 1889, p. 382-388. pl. 5, f. 1-7.
L.gotoi Hatai, 1899 (in part) p.5, f.3.
L.lucasi Benham, 1903, p.216-217, pl.25, f.18-22.
L.vejdovskyanum Benham, 1903, p.213-216, pl.25, f.10-17.
L.subsalsus Moore, 1905, p.392-394, pl.33, f.19-22. (in part)
L.aurostriatus Southern, 1909, p.136-137, f. 3.
L.parvus Southern, 1909, p.137-138, f.5.
L.aurantiacus Friend, 1911, p.44.
L.galeritus Friend, 1912, p.104, f.1b.
L.socialis Stephenson, 1912, p.294, f.9-16.
L.gotoi Nomura, 1913, p.3-34, f.1-27.
L.pacificus Chen, 1940, p.118, f.33.
L.hoffmeisteri f. divergens Marcus, 1942, p.169-174, pl. 2-4.

Description:

20 - 35 mm. 55 - 95 or more segments. Anterior dorsal bundles with 3 - 10 crotchets, with a mean of 5.4 for immature and 6.9 for mature specimens. Simple bifid crotchets only present, with the upper tooth typically a little longer and thinner than the lower, but sometimes considerably shorter. In mature specimens penis tube averaging 9.5 times as long as broad, but with a range of from 1 - 14 times. The penis tube may be straight or curved, and the wall is of even thickness along its length. The distal end is expanded to form a hood with a laterally situated outlet and of apparently variable form but referable to a single pattern, (figs. 6 and 11).

Discussion:

Thus stated, with the variation in the specific characteristics taken into account, the definition of this species is unambiguous. In accordance with custom the length and number of segments are included in the definition, but not too much attention should be paid to them. As both characters vary with the age and condition of the specimen they are of little value in the separation of species. Because it is customary, the number of chaetae per bundle is also quoted here. It is frequently quoted as part of the specific diagnosis but it is evident from table 1a that it is of little importance. The mean number of chaetae per bundle in the anterior dorsal bundles, which will subsequently be referred to as the chaetal number, varies with the state of maturity of the specimen, although it is never less than three or more than ten. The addition of chaetae with age is discussed more fully in chapter 4. There is a narrower range of variation of the chaetal number in mature specimens, but a comparison with other species, (table 6), shows that the chaetal number for mature specimens and the standard deviations are very similar.

The shape of the chaetae is also very variable, (fig. 4c,d). Although pectinate chaetae do not occur, occasional specimens with three teeth are encountered (fig. 4c6). The upper tooth is more commonly longer and thinner than the lower one, but may be considerably shorter (fig. 4d4) and all stages of reduction are known (fig. 4d). Furthermore, if the chaetae of *L.hoffmeisteri* (fig. 4c and d) are compared with those of *L.claparedeanus* (fig.4b) or *L.cervix* (fig. 4e) or *L.helveticus* (fig. 4f) it will be seen that they may be indistinguishable. This is particularly true of immature specimens of *Limnodrilus*. With the exception of *L.udekemianus*

TABLE I

The variation in the specific characteristics of L.hoffmeisteri

1a) The variation in the average number of chaetae per bundle in the dorsal bundles of segments 2 - 7.

	Average number of chaetae per bundle								M	S	T
	3	4	5	6	7	8	9	10			
Immature Specimens	10	250	530	375	110	30	10	0	5.37	-	1305
Mature Specimens	0	6	75	160	212	120	28	6	6.9	1.13	597

1b) The variation in the length: breadth ratio of the penis sheath.

	Length: breadth ratio of the penis tube													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
All specimens	1	3	3	6	9	19	52	128	134	124	55	33	14	5
Breeding specimens	0	0	0	0	2	9	27	76	89	82	36	17	9	0

All specimens M = 9.5 S = 1.7 T = 586

Breeding " M = 9.7 S = 1.16 T = 347

Legend

M = mean S = standard deviation T = total number of observations

Figure 4

The variation in the chaetal shapes of the British species of *Limnodrilus*.

A. The chaetae of *L. udekemianus*

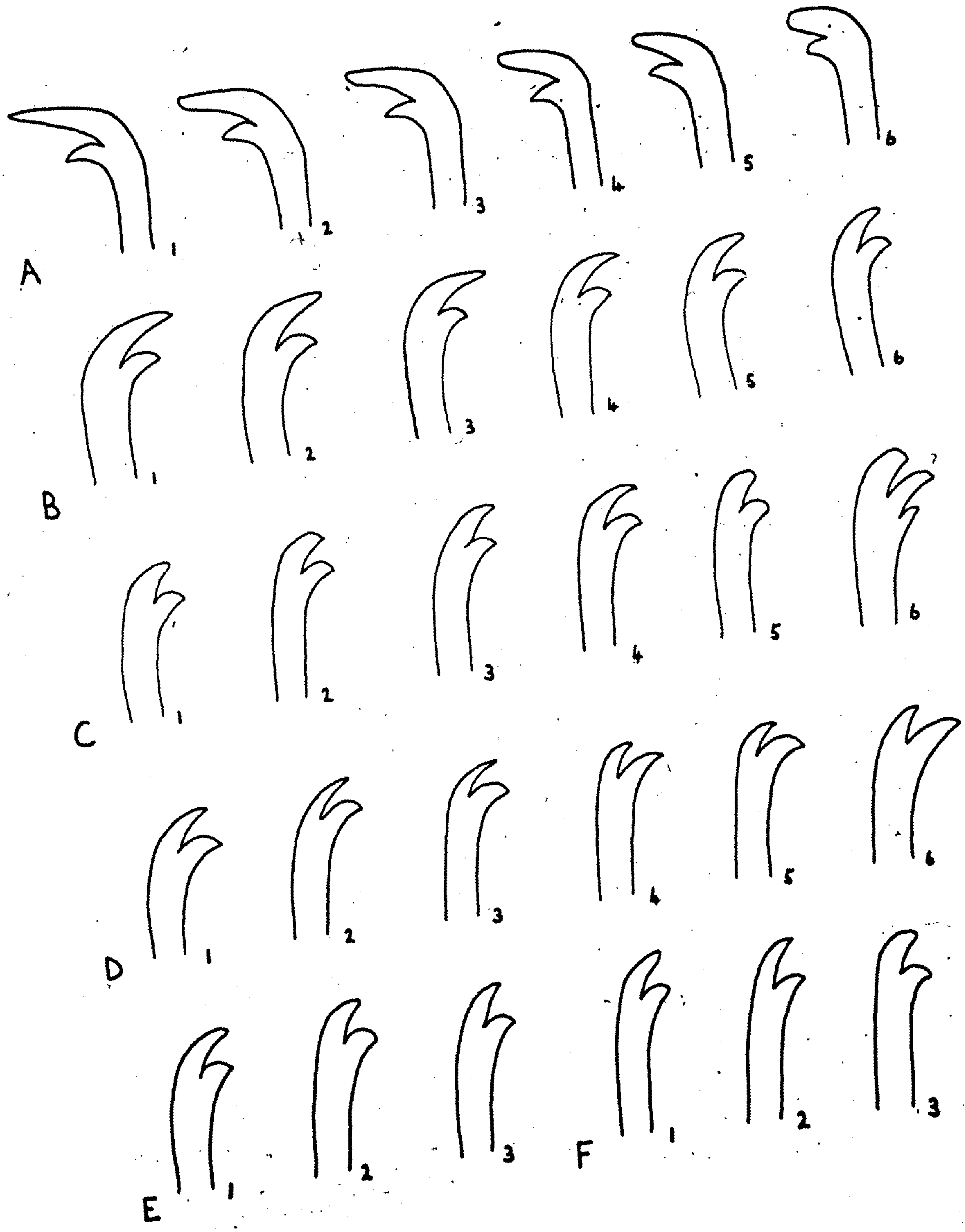
B. The chaetae of *L. claparedeanus*

C. The chaetae of *L. hoffmeisteri*

D. The chaetae of *L. hoffmeisteri* showing stages in reduction of the upper tooth

E. The chaetae of *L. cervix*

F. The chaetae of *L. helveticus*


1
2
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A
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3

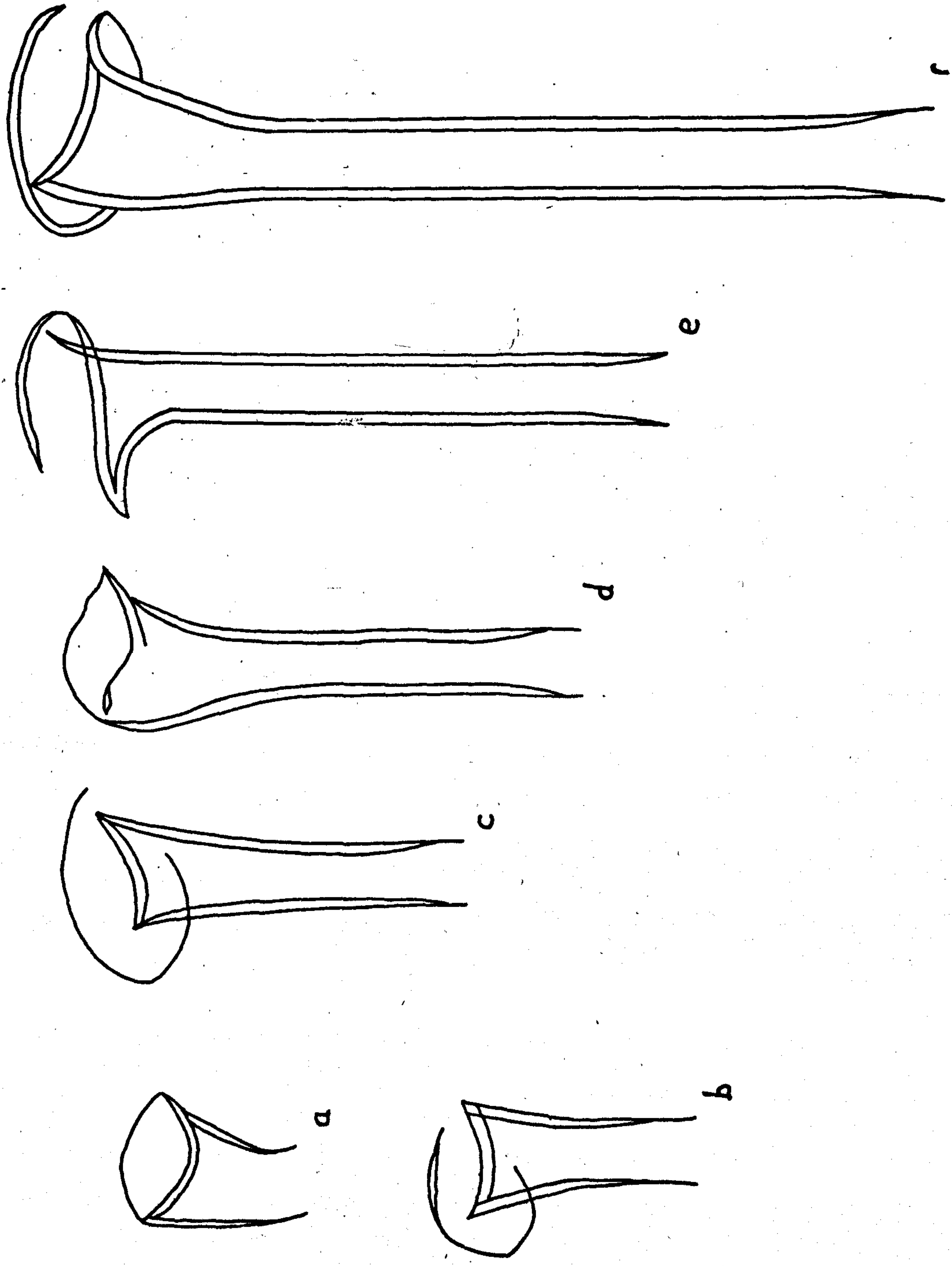
these cannot be identified to species on chaetal characteristics. To date no suitable alternative characters for the identification of immature specimens have been discovered. From the foregoing account it is evident that the chaetal number and shape are very variable, and the chaetae must consequently be regarded as being unsuitable diagnostic characteristics, (c.f. Brinkhurst, 1960).

The length:breadth ratio of the penis tube has long been used as a specific character. The length of the penis sheath is taken from base to tip, but the width is only taken at the base. The variation in this ratio based on the analysis of 500 specimens is shown in table 1b. It will be noticed that the range is fairly wide and the standard deviation fairly high (as opposed to L.udekemianus, table 2b). Further, the range and standard deviation are reduced when only breeding specimens i.e. those with spermatophores, are considered. When the variation in this ratio for L.hoffmeisteri is compared with the variation in other species (tables 1-5, table 6), two important facts emerge. The mean length: breadth ratios are significantly different and serve to characterise each species, but when the full range of variation is considered there exists a considerable overlap between the different species. This overlap is reduced if only breeding specimens are considered.

An objection to the use of the penis tube as a specific character by Brinkhurst (1960) was that the tube developed slowly, immature worms all having short tubes regardless of the species, and this would lead to confusion. From the relative paucity of observations of ratios below 6:1 compared to those above this figure (table 1b) this would not appear to be so. The stages of growth of a penis tube are shown in fig. 5, drawn to scale. It will be noticed that the basal width only increases slightly during growth, and that the change in ratio is due to the increase in length. This negates the possibility that a high length:breadth ratio may be obtained from an immature specimen if both length and breadth were initially small. The observations on which table 1b were based took place over a period of a year, when all specimens were measured, so if the occurrence of small tubes was seasonal they could not have been overlooked. It must be concluded therefore that the penis tube develops rapidly, and Brinkhurst's objection, whilst valid, is of little importance in practice. It is also relevant to note at this stage that in specimens which survive their first breeding period and go on to breed again in subsequent years the penis tube is developed anew, and the length:breadth ratio falls within the normal

Figure 5

Stages in the growth and development of the penis tube of *L. hoffmeisteri*. (Drawn to scale.)


f
e
d
c
a
b

range of the species. The penis tube does not persist throughout the non-reproductive season and then increase in length during the subsequent breeding season as was considered possible at one time (Brinkhurst, pers.comm.) It is apparent therefore that whilst the length:breadth ratio of the penis tube may prove a useful additional aid in the identification of species, the overlap that exists between species renders it unsuitable as a diagnostic specific character.

The most suitable diagnostic character has proved to be the shape of the head of the penis tube, despite the fact that earlier authors, in particular Cornosvitov (1939), Chen (1940) and Brinkhurst (1960) considered this structure to be very variable. A study of this variation has been made and several of the 'variations' are shown in fig. 6. The author is of the opinion that these variations are only apparent and are artifacts resulting principally from the following:- the condition of the specimen; its position and the angle from which it is viewed; the degree to which it has been stained or cleared and the degree of pressure exerted upon it when mounting it. It appears that all the examples figured may be derived by a combination of these factors from the typical example shown in fig. 6a. Many of the earlier workers described these forms as separate

Figure 6

Variations in the head of the penis tube of *L. hoffmeisteri*.

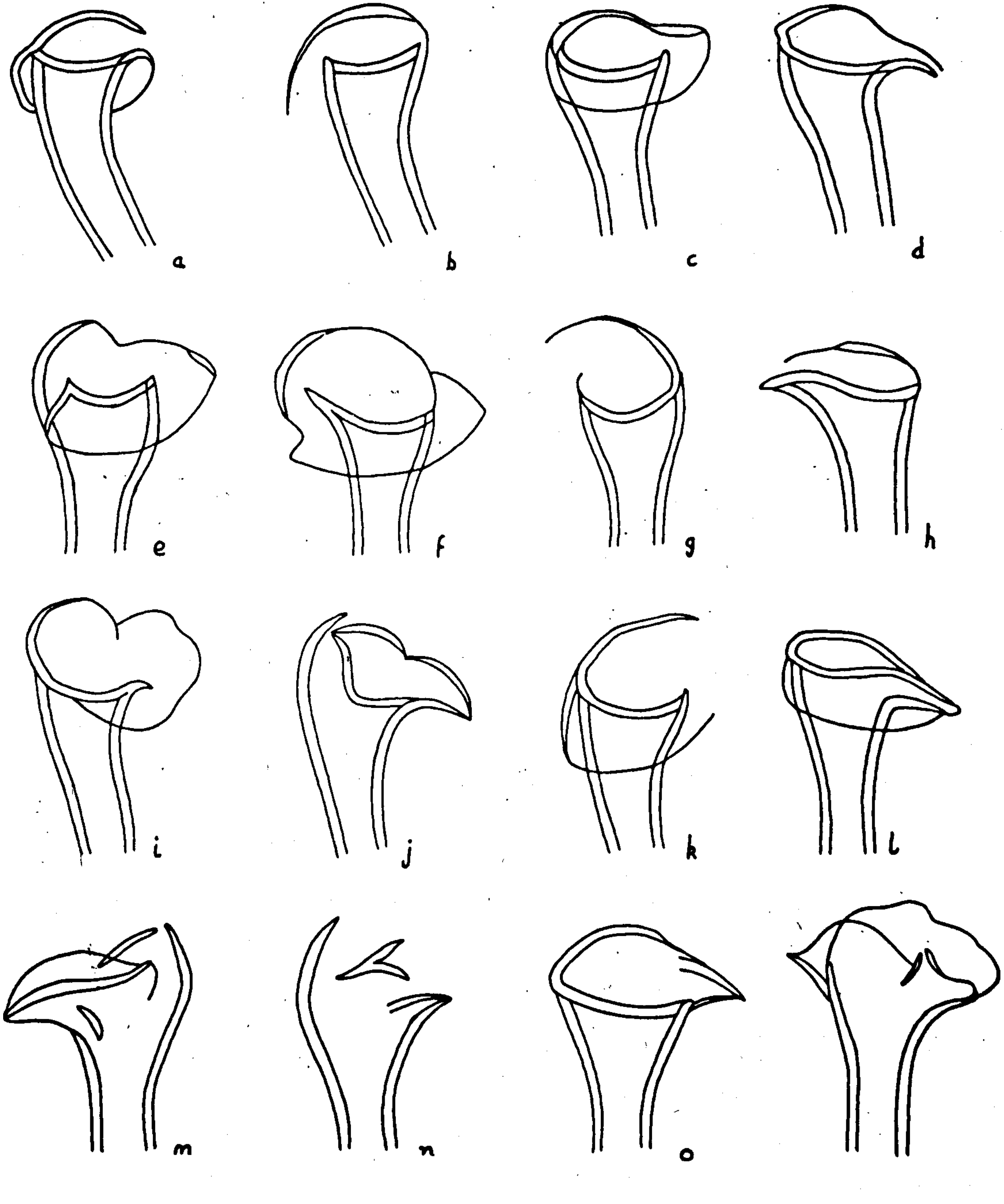
a and b ..... pair from the same specimen

g and h ..... pair from the same specimen

k and l ..... pair from the same specimen

o and p ..... pair from the same specimen

e and f ..... same specimen under different degrees of pressure.


a
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species, but the absurdity of this is obvious when it is considered that figs. 6a and b, 6k and l, 6o and p are pairs from the same specimens. As the chitin at the distal end of the tube is thinner than at the proximal end it is more liable to distortion under pressure. Fig. 6e shows a head under slight pressure, fig. 6f shows the same head after heavier pressure has been applied to it. A comparison of the typical shape, fig. 6a, with the shape of the head of other species is made in fig. 11. It will be seen that it is quite distinct from that of other species and does serve to characterise L. hoffmeisteri. If the penis tube is exposed on dissection or naturally everted (figs. 1 and 3), the head is usually of the type figured in fig. 6a. Individual variation must obviously be taken into account but the author is of the opinion that this is not as important as previous workers considered. Since the head of the penis tube is the first region to be formed, (fig. 5), this character may be used for identification for a longer period than the length:breadth ratio. The use of any portion of the genitalia as a diagnostic character has the serious disadvantage that immature specimens cannot be identified. In the apparent absence of any alternative characters this is at present unavoidable.

Having considered the variation in the specific characteristics it is now possible to discuss the synonyms of L.hoffmeisteri. The species was defined by Claparède (1862) as having the characters of the genus and with a copulatory organ about six times as long as broad. Although he quotes a ratio of 5 - 6 : 1, his figure shows one of 43 by 4 units or 10 : 1, which is closer to the average as recorded above. Vejdovsky (1884) repeated Claparède's description of L.hoffmeisteri but included a description of L.claparedeanus in which he gave the ratio as 8 - 10 : 1 and a figure that showed a head of L.hoffmeisteri shape, not of L.claparedeanus. There can be little doubt that he confused the two species and that his L.hoffmeisteri and L.claparedeanus were both in fact L.hoffmeisteri. Several workers who followed Vejdovsky, as Michaelson (1900) and Galloway (1911) also described specimens of L.claparedeanus that were undoubtedly more correctly attributable to L.hoffmeisteri.

Limnodrilus duresi was considered to be a valid species by Michaelsen (1900), but was considered a synonym of L.hoffmeisteri by Chen (1940). It was later referred to as forma duresi by Gavrilov and Paz (1950), but a study of their specimens by the author showed that the so-called differences come within the range of variation of *L.hoffmeisteri* as figured here. *Limnodrilus gotoi* Hatai was shown by Nomura (1913) to consist of two species, one of which he renamed *L.gotoi* but considered to be closely related to *L.socialis* Stephenson. This latter species was considered to be a synonym of *L.hoffmeisteri* by Michaelsen (1935). After a study of the co-type this synonomy is confirmed here. The discussion of Michaelsen in considering *L.socialis* a synonym of *L.hoffmeisteri* is also valid for *forma socialis* as described by Gavrilov and Paz (1950).

Limnodrilus lucasi and *L.vejdovskyanum* are considered to be synonyms of *L.hoffmeisteri* by Brinkhurst (1963), but no reasons are given. They were considered by Benham (1903) to be distinct species on the lengths of the penis sheaths and the form of their ends. Both of these characters for both species fall within the range of variation for *L.hoffmeisteri* as given here and Brinkhurst's synonomy is therefore accepted. *Limnodrilus subsalsus* was considered to be synonomous with *L.hoffmeisteri* by Cernosvitov (1939). It was considered to be related to *L.pacificus* by Chen (1940), but to differ from this species in the absence of spermatophores. As spermatophores are only present after copulation this distinction cannot be accepted. Marcus (1944) claimed to recognise *L.subsalsus* as a distinct species. It was considered by Moore (1905) to be similar to *L.hoffmeisteri*, but one of the principle differences was held to be its occurrence in brackish water. *Limnodrilus hoffmeisteri is now* known to be able to live in brackish water (Brinkhurst and Kennedy, 1962). Dr. R. O. Brinkhurst was able to examine the type specimens and confirmed Cernosvitov's synonomy, but showed that some specimens also belonged to *L.claparedeanus*. This synonomy is accepted here.

Brinkhurst (1963) without giving any reasons also considered *L.aurostriatus* Southern to be a synonym of *L.hoffmeisteri*. Berg (1939) recorded *L.aurostriatus* from Denmark, and it proved possible to examine both his specimens and the type specimen. For a full discussion of this synonomy see Kennedy (1964). It is sufficient to indicate here that the length of the penis tube and the shape of its distal end falls within the range of *L.hoffmeisteri*. *Limnodrilus parvus*, also described by Southern (1909) has proved a more difficult problem. Lastockin (1927) accepted the validity of this species and described a *v.biannulatus* and a *v.okaensis*. Cernosvitov (1939) considered it to be a synonym of *L.hoffmeisteri*, but later (1945) changed his mind and considered it a valid species. He suggested (after Hrabě) that it might possibly be a stage in the life history of *L.hoffmeisteri*. Hrabě (1954,1958) continued to regard it as a valid species. Marcus (1942) and Cekanovskaya (1962) have reduced it to the rank of form, Brinkhurst (1963) reduced it to complete synonomy with L.hoffmeisteri but Gavrilov and Paz (1950) regarded it as a valid species. It has again proved possible to examine the type specimens, and in addition to examine both Cernosvitov's and Gavrilov's material. A full discussion of these specimens is given in Kennedy (1964). The length and form of the penis tube fall within the range of L.hoffmeisteri, while chaetae of the type figured by Southern (1909) are often found in conjunction with penis tubes of different shapes. Chaetae of this type with a shorter, thinner upper tooth do occur (fig. 4d4-6) and there is a complete series in the reduction of the upper teeth to form this type (fig. 4d) which grades imperceptibly into chaetae of the more common L.hoffmeisteri type, (fig.4c). Life cycle studies have shown that this form does not occur at any particular stage in the life cycle of L.hoffmeisteri, nor is it associated with any particular ecological conditions although similar forms have been produced in specimens in a rough substratum under laboratory conditions (fig. 6d6). In view of the variability of L.hoffmeisteri chaetae, the existence of a continuous series and the inability to characterise the shape or length of the penis tube, L.parvus must be considered a synonym of L.hoffmeisteri.

Limnodrilus pacificus was discussed and reduced to synonomy with *L.hoffmeisteri* by Brinkhurst (1963). *Limnodrilus hoffmeisteri f. divergens* differs from *L.hoffmeisteri* only in the length of the penis sheath and the shape of the chaetae. Both appear to fall within the range of variation exhibited by *L.hoffmeisteri*. It is accordingly considered that *f.divergens* is a synonym of *L.hoffmeisteri*.

Limnodrilus udekemianus Claparède, 1862.

L.udekemianus Claparède, 1862, p.243, f.45.
L.gotoi Hatai, 1899, (in part), p.5, f.3.
L.wordsworthianus Friend, 1898, p.120.
L.willeyi Nomura, 1913, p.33-34, f.25-34.
L.inversus Gavrilov and Paz, 1949, p.541-555, f.1-5.

Description:-

20 - 90 mm. Approximately 160 segments. Anterior dorsal bundles with 3 - 8 crotchets (with a mean of 5.4 for immature specimens) decreasing to 2 posteriorly. Simple bifid crotchets only present with, in the anterior bundles, the upper tooth longer and stouter than the lower. In the posterior bundles the teeth are of equal length. In mature specimens penis tube averaging 3.7 times as long as broad, with a range of from 2 to 4 times. The distal end is slightly expanded to form a hood of relatively simple form (figs. 7 and 11) with

a terminal outlet. The wall of the penis tube thickens towards the distal end.

Discussion:

The chaetal number is given only for immature specimens because insufficient observations were made on mature specimens. As the chaetal number increases with age it was considered that an estimate of the standard deviation would be of little value. It will be seen from table 2a that both the mean and range are smaller than for the corresponding mean and range of immature L.hoffmeisteri. The mean is quoted for comparative purposes in table 6, and from this table it can be seen that the chaetal number does not differ significantly from that of other species, and is therefore unsuitable as a diagnostic specific characteristic.

The shape of the dorsal anterior chaetae however is characteristic of this species. The upper tooth is longer and stouter than the lower one (fig. 4a). Whilst this difference is pronounced in typical specimens, in others the upper tooth may be reduced in length to varying degrees (fig. 4a1-6). In all these cases the upper tooth remains stouter than the lower one: even if the upper tooth has been reduced its stoutness serves to distinguish this species from the other species of Limnodrilus (fig. 4). This difference in the shape and relative sizes of the two teeth is less pronounced

TABLE 2

The variation in the specific characteristics of L. udekemianus

2a) The variation in the average number of chaetae per bundle in the dorsal bundles of segments 2 - 7.

	Average number of chaetae per bundle								M	S	T
	3	4	5	6	7	8	9	10			
Immature specimens	17	52	118	66	37	5	1	0	5.24	-	295

2b) The variation in the length:breadth ratio of the penis sheath

	Length:breadth ratio					M	S	T
	2	3	4	5	6			
All specimens	40	170	81	10	0	3.7	0.64	301
Breeding specimens	0	80	20	0	0	3.7	0.28	100

Legend

M = mean S = standard deviation T = total number of observations

in the ventral bundles, and diminishes in both dorsal and ventral bundles along the length of the specimen.

The length:breadth ratio of the penis sheath is fairly constant (table 2b). It can be seen from this table that the range for breeding specimens is less than that for all mature specimens but the mean is the same in both cases. It can be seen from table 6 that the mean ratio is significantly different from that of other species, and is closest to L.helveticus. L.udekemianus may be separated from this latter species by the shape of the chaetae and the form of the distal end of the penis sheath. The range of variation of the ratio overlaps with most other species.

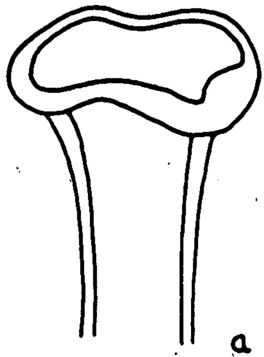
The variations in the shape of the hood of the penis sheath are shown in fig. 7. It will be seen that the head is always fairly simple in form. The differences arise principally from the width of the hood. An idea of the individual hood variation may be gained from the fact that figs. 7e and f, and 7h and i are pairs from the same specimens. The remarks made concerning the variation of this organ in L.hoffmeisteri are also relevant here. The penis tube is always short and narrows in the middle region before expanding to form the hood (figs. 7e and g). The wall also thickens closer to the hood (figs. 7a, b, d and f).

Figure 7

Variations in the head of the penis tube of *L. udekemianus*.

e and f ...... pair from the same specimen

h and i ...... pair from the same specimen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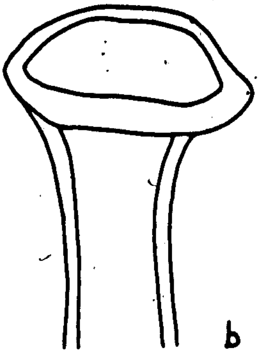
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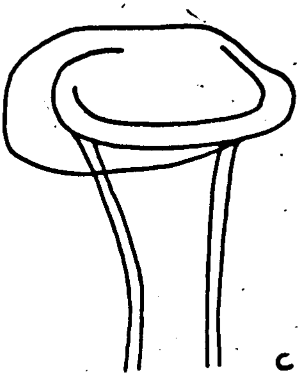
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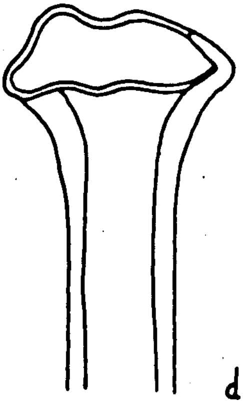
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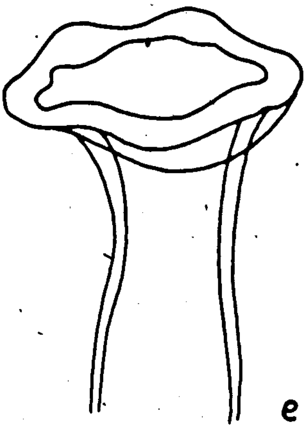
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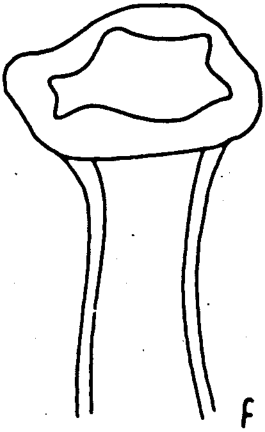
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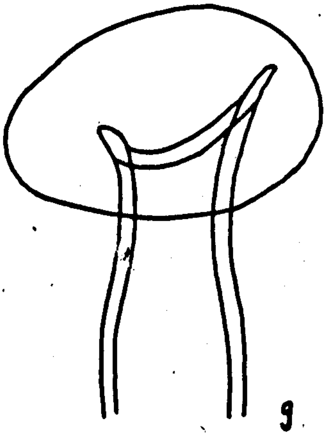
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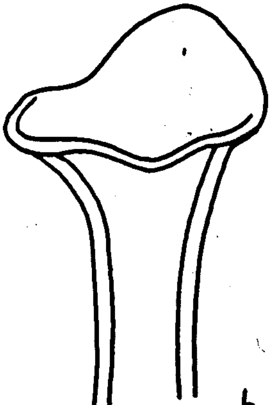
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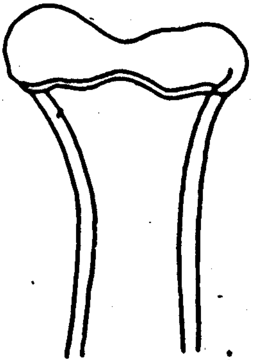

i

This species was defined by Claparède (1862) on its length, its colour and the length:breadth ratio of the copulatory organs. He quoted these as being about three times as long as broad. The distinctive shape of the chaetae was first appreciated by Vejdovsky (1884). Nomura (1913) separated *L.gotoi* Hatai into two species, *L.gotoi* Nomura, considered here under *L.hoffmeisteri*, and *L.willeyi*. The identity of this latter species was discussed by Chen (1940) who reduced it to synonomy with *L.udekemianus*, a view accepted here. *Limnodrilus wordsworthianus* was considered to be a synonym of *L.udekemianus* by Southern (1909), and this was confirmed by Cernosvitov (1941). *Limnodrilus inversus* was considered by Brinkhurst (1963) to be a synonym of *L.udekemianus*, but no reasons were given by him. The principle distinguishing feature of *L.inversus* was held by Gavrilov and Paz (1949) to be the bi-annulate anterior segments. This feature is commonly observed in *L.udekemianus*. It has proved possible to examine the type specimens of *L.inversus* which have been found to be indistinguishable from specimens of *L.udekemianus*. Brinkhurst's synonomy is therefore accepted here.

Limnodrilus claparedeanus Ratzel, 1868

L. claparedeanus Ratzel, 1868, p. 108.

Tubifex rivulorum Budge, 1850, p. 1.

L. longus Brtescher, 1901, p.204-205, pl.14, f.2-3.

L. subsalsus Moore, 1905 (in part), p. 392-394, pl.33, fig.19-22.

L. gracilis Moore, 1909.

Limnodrilus form C Nomura, 1913, p.2.

L. notomurai Nomura, 1929, p.131-137, pl.11.

L. hoffmeisteri Clap.: Brinkhurst, 1960 (in part), p.401.

Description:-

30 - 60 mm. 50 - 120 segments. Anterior dorsal bundles with 4 - 9 crotchets, with a mean of 6.8 in mature specimens. Simple bifid crotchets only present, with the upper tooth a little longer and thinner than the lower, but sometimes considerably longer. In mature specimens penis tube averaging 25.9 times as long as broad, with a range of from 17 - 43 times. The penis sheath is straight and thin walled along its length. The distal end is expanded to form a pear shaped hood, with the opening situated in the centre of the hood (figs. 8 and 11).

Discussion:

The chaetal number is here quoted only for mature specimens, as this species cannot be identified when immature. It can be seen from table 3a that the mean is in the same region as that of L.hoffmeisteri and L.cervix (table 6), but that the standard deviation is lower.

The variation in the shape of the chaetae is shown in fig. 4b. In specimens from England the upper tooth is slightly longer and thinner than the lower one (fig. 4b4,5 and 6), but occasional specimens are encountered in which the upper tooth is distinctly longer (fig. 4b3). In specimens from America and Germany the upper tooth is typically longer and nearly as stout as the lower one (fig. 4b1 and 2). These individuals may easily be confused with L.udekemianus but in this latter species the upper tooth is always very much stouter than the lower one. Since this chaetal character is not constant it cannot be used to distinguish L.claparedeanus unless the genitalia are also present.

The length:breadth ratio of the penis tube in this species is very variable (table 3b). If the range and the mean are compared with the values for other species (table 6), it can be seen that the variation in the ratio is greater in this species than in any species other than L.cervix, and that the mean value serves to distinguish it from all other species

TABLE 3

The variation in the specific characteristics of L. claparedeanus

3a) The variation in the average number of chaetae per bundle in the dorsal bundles of segments 2 - 7.

	Average number of chaetae per bundle									
	4	5	6	7	8	9	10	M	S	T
Mature specimens	1	13	37	46	16	5	0	6.8	1.02	118

3b) The variation in the length:breadth ratio of the penis sheath

Ratio	17	18	19	20	21	22	23	24	25	26	27	28	29
All specimens	14	5	2	8	6	6	9	8	9	12	9	8	6
Breeding specimens	0	0	0	0	2	2	3	4	2	3	3	2	1

Ratio	30	31	32	33	34	35	36	37	38	39	40	41	42
All specimens	6	7	7	9	1	2	7	1	4	0	1	4	2
Breeding specimens	2	3	3	5	1	0	2	0	2	0	0	2	1

All specimens M = 25.9 S = 6.52 T = 158

Breeding specimens M = 29.8 S = - T = 43

Legend

M = mean S = Standard deviation T = total number of observations

except L.cervix. In view of the scarcity of material the value of the standard deviation for breeding specimens only has not been calculated. L.claparedeanus and L.cervix may be distinguished by the form of the penis tube and the shape of its hood.

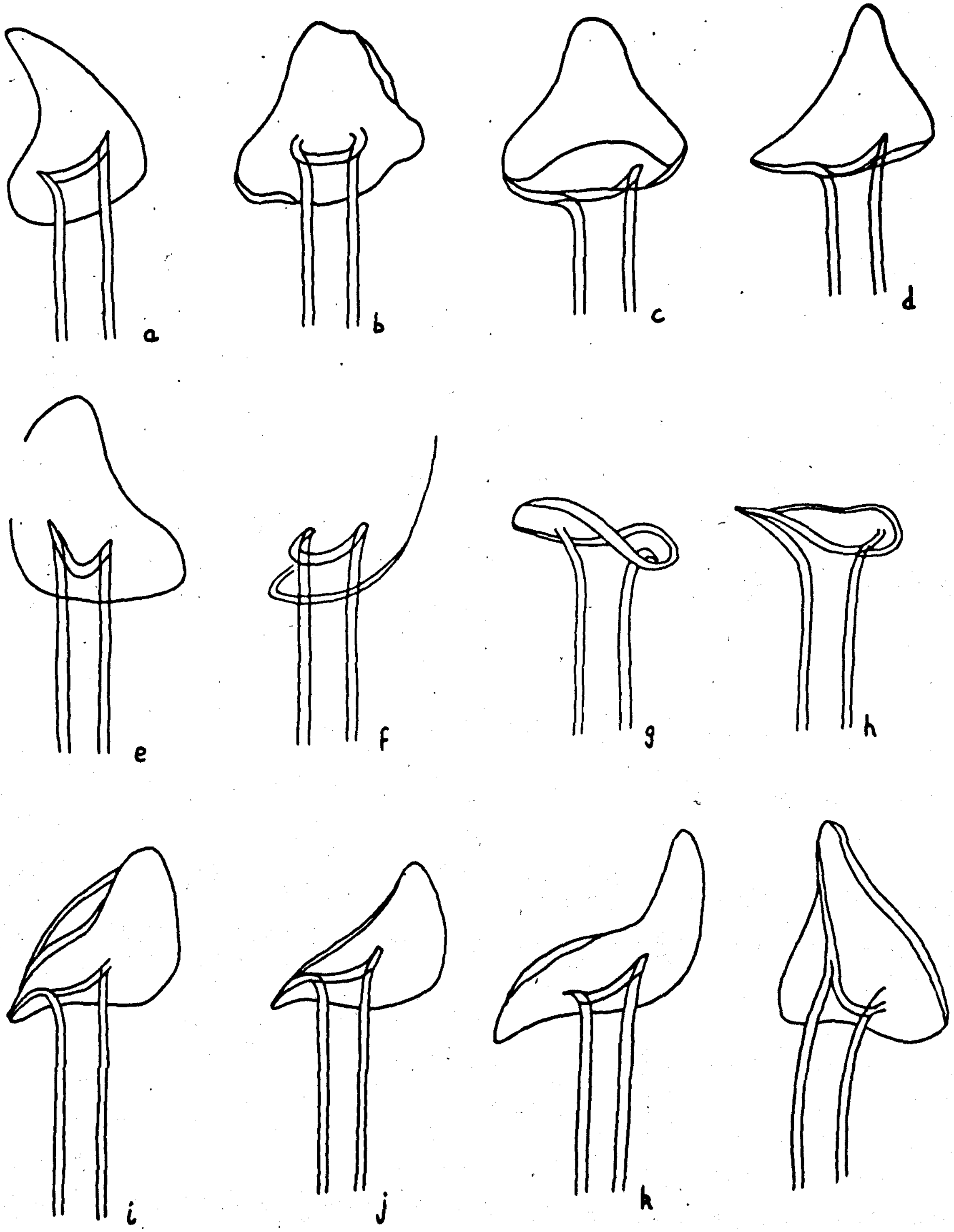
The shape of the head of the penis tube in L.claparedeanus is, by contrast with the length:breadth ratio, not very variable. The variations are shown in fig. 8. The penis sheath is straight and of equal diameter along its entire length, and widens suddenly into a more or less pear shaped hood. In fig. 8 it is apparent that the specimens figured may all be referred to a basic pattern, similar to fig. 8a. The 'variations' are due in the main to the angle at which the specimens were observed, and to the size and angle set of the hood. The specimens figured in 8f and 8g belong to the same individual, and give some idea of the slight individual variation. The opening of the sheath is situated in the centre of the hood (figs. 8a, b, e, and 1).

Since its description by Ratzel (1868) there has been considerable confusion over the identity of this species. The early confusion was due mainly to an incorrect identification of this species by Vejdovsky (1884). He figured two specimens, one of which was probably L.claparedeanus but the other was undoubtedly

Figure 8

Variations in the head of the penis tube of *L. claparedeanus.*

F and G ..... pair from the same specimen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L.hoffmeisteri. In the text he described the specimen of *L.hoffmeisteri.* Despite this mistake he correctly recognised *Tubifex rivulorum* as described by Budge (1850) as a synonym of *L.claparedeanus.* This mis-identification by Vejdovsky caused many later authors to make the same mistake. Dieffenbach (1886), Michaelsen (1900) and Galloway (1911) all confused *L.claparedeanus* and *L.hoffmeisteri.* Other authorities, as Beddard (1895), by reference to Ratzel's original description described it correctly. Finally Bretscher (1901) described a new species (*L.longus*) which was said to differ from *L.claparedeanus* in the length:breadth ratio of the penis sheath. He used almost exactly the same words as Ratzel (1868) to describe the shape of the hood of the penis sheath, referred to Ratzel's original description of *L.claparedeanus*, yet followed Vejdovsky's incorrect description of this species. By re-describing *L.claparedeanus* with reference to the original description Piguet (1913) cleared up the position. He reduced *L.longus* to synonomy with *L.claparedeanus*, and separated this latter species from *L.hoffmeisteri.* The species was then described correctly in later works by Piguet and Bretscher (1913) and Ude (1929).

Reference to the type specimens of L.subsalsus, some of which are undoubtedly L.claparedeanus, make it necessary to regard this species as a synonym of L.claparedeanus (in part). For further discussion of this synonomy see under L.hoffmeisteri. The form referred to by Nomura (1913) as Limnodrilus C was later described by him (Nomura, 1929) as a new species under the name of L.motomurai. The penis sheath ratio and the shape of the head as described by him leave no doubt that L.motomurai must be considered a synonym of L.claparedeanus.

The identity of L.claparedeanus had thus been clarified, but further confusion was to follow. Brinkhurst (1960) described two forms of Limnodrilus with long penis sheaths. One of these he described as a variation of L.hoffmeisteri as 'several specimens with the tube as long as that of L.claparedeanus', and referred to its thin walled penis sheath of uniform diameter and the triangular hood. The other form he distinguished from L.hoffmeisteri by the thick wall of the penis sheath, the abrupt narrowing of the sheath before the hood and by the hood possessing a forward and backward projection. He considered this form to be L.claparedeanus. After an examination of Brinkhurst's specimens the author was able to distinguish the form described under L.hoffmeisteri, to be referred to in this discussion as form a, from L.hoffmeisteri on the basis of the penis tube ratio and the shape of the hood. The author considered that form a should have been correctly attributed to L.claparedeanus, as it conformed to the diagnosis on p.2.33. The form described by Brinkhurst as L.claparedeanus, form b, was tentatively considered to be a new species, as it did not conform to the diagnosis of any existing species. In an effort to clear up the problem the author examined some specimens of L.claparedeanus collected and identified by Piguet, and these proved to be identical to form a. This confirmed the author's opinion that form a was correctly assignable to L.claparedeanus and that form b was a new species.

Brinkhurst, however, was unwilling to accept this view, and in order to keep the two forms distinct but avoid describing a new species assigned form a and Piguet's specimens of L.claparedeanus to L.longus Bretscher, maintaining that Ratzel's (1868) description could have fitted either form a or b. These views were expressed in a joint report on Piguet's collection (Brinkhurst and Kennedy, 1962a), and L.longus was recorded as a valid species in the check list of British oligochaetes compiled by Brinkhurst (1962a).

In the meanwhile this author had been engaged upon a study of the geographical distribution of the species of Limnodrilus, and was able to show that form b was absent from continental Europe and Asia. It occurred only in North America and Britain, and its distribution in Britain strongly suggested that it had been introduced there, (see chapter 3 for full discussion). If Brinkhurst's identification had been correct and form b was in fact the same entity as L.claparedeanus Ratzel (sensu Piguet, 1913), this would have created a situation whereby this species, although described from continental Europe, was absent from its type locality and the continent. Faced with this geographical and morphological evidence Brinkhurst accepted the views of this author. Accordingly Brinkhurst (1963) described form b as a new species under the name of L.cervix, and reduced L.claparedeanus sensu Brinkhurst (1960) to synonomy with it. In the same work L.hoffmeisteri Clap. (in Brinkhurst, 1960) in part, L.longus (in Brinkhurst and Kennedy, 1962a) and L.longus (in Brinkhurst, 1962) were regarded as synonyms of L.claparedeanus Ratzel.

In order to clarify the problem of the identity of L.cervix and L.claparedeanus, the following table is given below.

Species	Author	Date	Correct identity
L. hoffmeisteri (in part)	Brinkhurst	1960	*L. claparedeanus*
L. claparedeanus	Brinkhurst	1960	*L. cervix*
L. longus	Brinkhurst & Kennedy	1962a	*L. claparedeanus*
L. longus	Brinkhurst	1962a	*L. claparedeanus*
L. claparedeanus	Brinkhurst	1962a	*L. cervix*

Limnodrilus cervix Brinkhurst, 1963

L. cervix Brinkhurst, 1963, p. 2, f. 20.

L. claparedeanus: Brinkhurst, 1960, p. 402, f. 4.

L. claparedeanus: Brinkhurst and Kennedy, 1962, p. 188.

Description:

30 - 80 mm. 60 - 120 segments. Anterior dorsal bundles with 4 - 9 crotchets, with a mean of 6.9 for mature specimens. Simple bifid crotchets only present, with the upper tooth a little longer and thinner than the lower. In mature specimens penis tube averaging 28.2 times as long as broad, with a range of from 7 - 14 times. The penis sheath is straight and thick walled along most of its length, but narrows near to the distal end. This end is expanded to form a hood bearing forward and backward projections (figs. 9 and 11), with the opening situated in the centre of the hood.

Discussion.

The mean number of chaetae per bundle is given for mature specimens only (table 4a) as this species cannot be identified in the immature stages. The chaetal number and standard deviation are close to the values for the other species of Limnodrilus (table 6), and do not characterise this species.

The shape of the chaetae is not very variable in this species (fig. 4e). The upper tooth is slightly longer and thinner than the lower, but never appears to be as reduced as in L. hoffmeisteri or as elongated as in L. claparedeanus. The chaetae of L. cervix are usually indistinguishable from those of L. hoffmeisteri and L. helveticus.

The length: breadth ratio of the penis tube is very variable (table 4b), and the standard deviation exceeds that of all other species (table 6). In the case of all mature specimens the length: breadth ratio overlaps that of most other species, but if the ratio in breeding specimens only is considered it overlaps only with L. claparedeanus. The wide range of the ratio in L. cervix is attributed to the fact that observations were made on several specimens in which the penis tube was still developing. Observations on breeding specimens only would consequently be expected to narrow the range.

Limnodrilus cervix may be distinguished from all other species of Limnodrilus by the form of the penis sheath and the shape of the hood. The penis sheath appears to be composed of two layers of chitin for most of its length (figs. 2 and 9). There is a thin inner layer of the same thickness as that of the wall of other species of Limnodrilus and a thicker outer layer about two to three times as wide as the inner one which terminates close to the distal end, producing the very characteristic narrowing of the sheath in this region. The inner layer then expands slightly to form the hood. This consists of a flat plate bearing a forward and backward projection, each projection having an approximately triangular shape. The shape of the hood is not very variable (fig. 9). It is apparent that most of the variation arises from the degree of pressure exerted on the specimen (figs. 9f and g) are the same specimen under different pressures, or the angle from which it is viewed. The opening of the sheath is situated in the centre of the hood.

A discussion on the identity of this species and its synononies has already been given under L. claparedeanus.

TABLE 4

The variation in the specific characteristics of L. cervix

4a) The variation in the average number of chaetae per bundle in the dorsal bundles of segments 2 - 7.

	Average number of chaetae per bundle							M	S	T
	4	5	6	7	8	9	10			
Mature specimens	3	10	55	57	18	9	0	6.9	1.06	146

4b) The variation in the length:breadth ratio of the penis sheath.

Ratio	7	9	11	12	13	14	15	16	17	18	19	20	21	22
All specimens	1	5	5	3	1	4	2	3	3	2	2	6	0	3
Breeding specimens	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Ratio	23	24	25	26	27	28	29	30	31	32	33	34	35
All specimens	12	5	9	14	14	18	18	15	11	8	11	11	10
Breeding specimens	3	4	2	8	9	9	12	9	6	1	6	7	4

Ratio	36	37	38	39	40	41	42	43	44	45	46	47	48
All specimens	6	9	2	4	3	0	0	4	0	0	0	0	1
Breeding specimens	2	3	1	2	1	0	0	1	0	0	0	0	0

	M	S	T
All specimens	M = 28.2	S = 7.57	T = 226
Breeding specimens	M = 30.2	S = -	T = 91

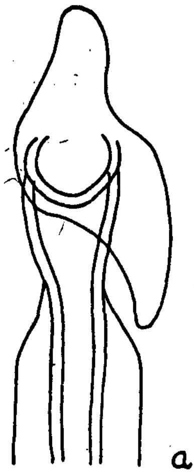
Legend.

M = mean S = standard deviation T = total number of observations.

Figure 9

Variations in the head of the penis tube of L. cervix

c and d ..... pair from the same specimen



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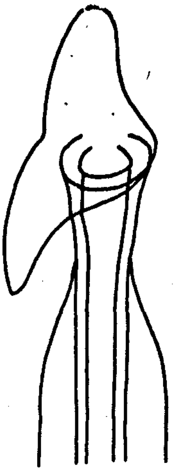

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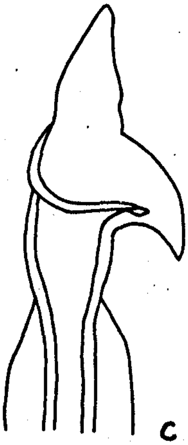

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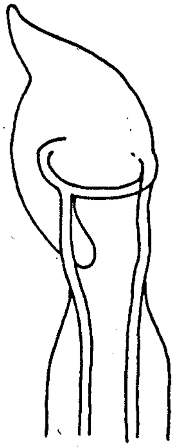

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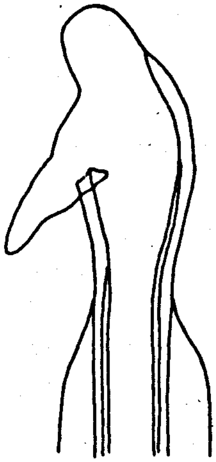

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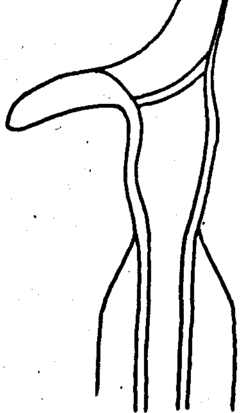

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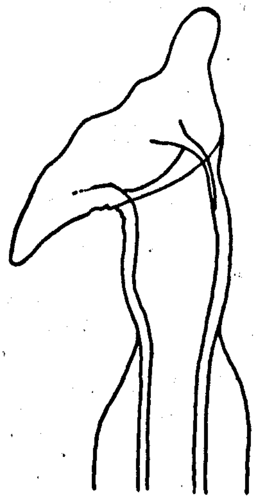

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Limnodrilus helveticus Piguet, 1913

L. helveticus Piguet, 1913, p.136, fig. 8-10.

Description:

20 - 45 mm. 50 - 90 segments. Anterior dorsal bundles with 5 - 9 crotchets, with a mean of 6.4 for mature specimens. Simple bifid crotchets only present, with the upper tooth a little longer and thinner than the lower. In mature specimens penis tube averaging 4.5 times as long as broad, with a range of from 2 - 7 times. The penis sheath is short and straight, expanding distally to form the hood which is reflected back over the tube (figs. 10 and 11).

Discussion:

The mean number of chaetae per bundle is quoted only for mature specimens as this species cannot be identified from immature specimens. If these figures (table 5a) are compared with the values for other species (table 6) it can be seen that they are generally lower, but as this difference is not very pronounced little importance should be attached to it.

The shape of the chaetae is uniform, and the upper tooth always appears to be a little longer and thinner than the lower one, (fig. 4f). Piguet (1913) claimed that the teeth in lacustrine specimens were short and rounded whilst those of riverine specimens were sharply pointed. No trace of such a distinction has been found in specimens examined by the author, but it must be admitted that none have been from true lacustrine habitats. An examination of Piguet's specimens from both types of habitat (Brinkhurst and Kennedy, 1962a) failed to show any such distinction. The chaetae of L.helveticus are indistinguishable from those of L.hoffmeisteri and L.cervix.

The length:breadth ratio of the penis tube is not very variable (table 5b). The mean and the standard deviation are lower than for most other species except L.udekemianus (table 6) and possibly L.neotropicus. Limnodrilus helveticus may be separated from these species by the shape of the penis tube hood. There is no significant difference between the range and the mean for all mature specimens and for breeding specimens only.

The hood of the penis sheath takes the form of a circular plate which is reflected back over the end of the sheath (figs. 10a - d). Under pressure, however, it may assume a trumpet shape (figs. 10i - l). Intermediate stages in this process are shown in figs. 10e - h. It is considered that all these forms are referable to a basic type, fig. 10a. The different forms may occur in a single specimen, as figs. 10f and k. Where the hood has assumed the trumpet-shape it may closely resemble specimens of L.hoffmeisteri which have also been subjected to pressure, (compare fig. 10l with fig. 6p). In these cases the penis tube ratio will usually serve

TABLE 5.

The variation in the specific characteristics of L.helveticus

5a) The variation in the average number of chaetae per bundle in the dorsal bundles of segments 2 - 7.

	Average number of chaetae per bundle							M	S	T
	4	5	6	7	8	9	10			
Mature specimens	0	17	60	29	10	3	0	6.4	0.91	119

5b) The variation in the length:breadth ratio of the penis tube.

	Length:breadth ratio						M	S	T
	2	3	4	5	6	7			
All specimens	3	26	39	19	2	1	4.5	0.86	90
Breeding specimens	3	19	29	10	1	0	4.3	0.74	62

Legend.

M = mean S = standard deviation T = total number of observations

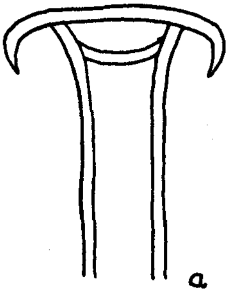
Figure 10

Variations in the head of the penis tube of *L. helveticus*

d and g ...... pair from the same specimen

f and k ...... pair from the same specimen

h and j ...... pair from the same specimen



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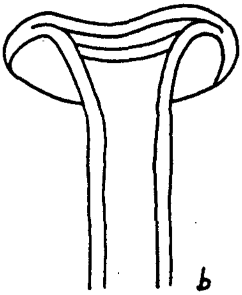

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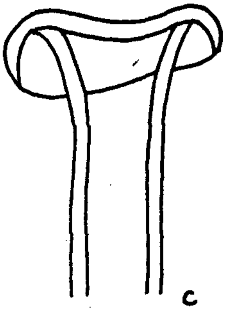

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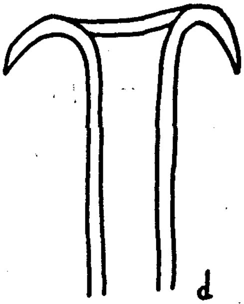

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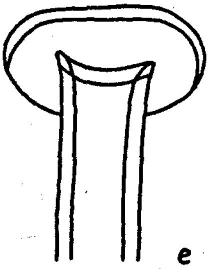

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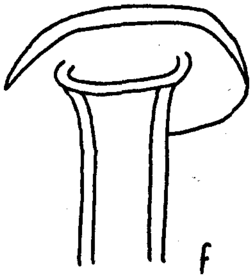

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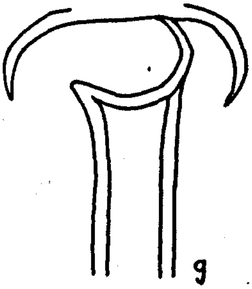

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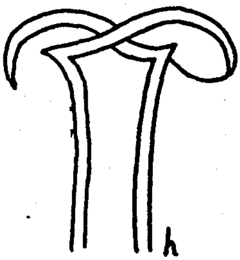

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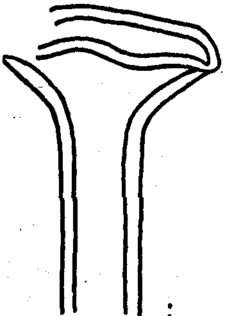

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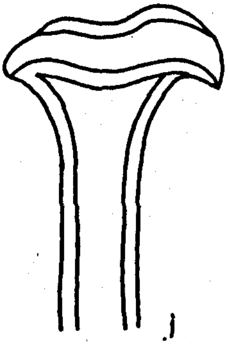

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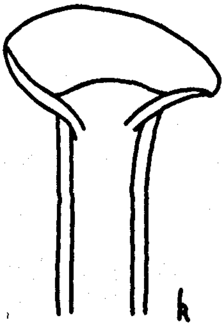

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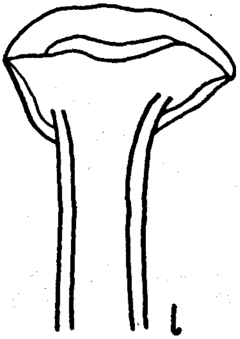

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to identify the specimens. The reflected tip, when present, is quite distinctive and serves to distinguish L. helveticus from other species, (fig. 11).

Limnodrilus grandisetosus Nomura, 1932

L. grandisetosus Nomura, 1932, p. 511, f. 1-5, pl. 13-17.

Description:

80 mm. 85 - 95 segments. Anterior dorsal bundles with 3 - 4 chaetae, decreasing to 2 in the post clitellar region. Ventral chaetae of segments 4 - 10 very broad and long, and disproportionately larger than the corresponding dorsal ones. All other chaetae bifid crotchets with the upper tooth longer and stouter than the lower one. Penis tube short, with a length:breadth ratio of 2:1, forming a shovel-shaped hood (fig. 11g).

Discussion:

The above description is that of Nomura (1932). No account is given of the variation in the shapes of the chaetae or penis sheath, or of the dimensions of the latter organ.

The species appears to be similar to L. udekemianus, but without reference to the original specimens it is not possible to discuss its relationships in detail. Enlarged chaetae are frequently related to regeneration in the Naididae, but the presence of numerous specimens in Nomura's original locality suggests that this may not have been responsible for the enlarged chaetae in L. grandisetosus. Further, no such enlarged chaetae have been observed following regeneration in Limnodrilus by the author (chapter 4).

Limnodrilus neotropicus Cernosvitov, 1939

L. neotropicus Cernosvitov, 1939, p.106-108, f.86-101.

Description:

50 mm. 45 - 170 segments. Anterior dorsal bundles with 3 - 4 crotchets, decreasing to 2 or 1 posteriorly. Simple bifid crotchets only present, with the upper tooth strongly curved and about twice as long as the lower in the anterior bundles, but with the upper one as long as, but thinner than, the lower one in the posterior bundles. The penis sheath is short and narrows towards the distal end. It then expands to form a large round dilation, with a wide laterally displaced opening (fig. 11c). The length: breadth ratio of the penis sheath with a range of from 4 : 1 to 5.5 : 1.

Discussion:

The above description is that of Cernosvitov (1939). Reference to the type specimens confirms his descriptions. The variations in the shape of the chaetae and the hood of the penis sheath are figured by Cernosvitov (op.cit.).

Species dubia

L.corallinus (Eisen) 1883, p.900, f.14.
L.californicus (Eisen), 1883, p.901, f.16.
L.igneus (Eisen) 1883, p.900, f.14.
L.monticola (Eisen) 1883, p.896, f.10.
L.ornatus Eisen, 1883, p.894-895, f.8.
L.silvani Eisen, 1883, p.897-898, f.12.
L.spiralis (Eisen), 1883, p.899-900, f.15.
L.steigerwaldi Eisen, 1883, p.895, f.9.
L.alpestris Eisen, 1883, p.896-897, f.11, 18.

These species dubia have been discussed briefly on pages 2.12 and 2.13.

L.bogdonovi Grimm, 1877.

This was considered a species dubium by Michaelsen (1900). It has never subsequently been recorded. The original descriptions of this entity (Grimm, 1877, 1878) have not been seen by the author.

L.crassus Andrussof, 1914, p.92-97, f.1-3.

This was considered to be a species dubium by Marcus (1942). It has recently been considered to be a synonym of *Tubifex newaensis* by Brinkhurst (1963).

L.aequatorialis Michaelsen, 1935, p.34-36.

This species was recorded from the Belgian Congo. It was poorly described and few details of the genitalia were given. It was transferred with considerable doubt to *Bothrioneurum* by Cernosvitov (1938).

L.benedii d'Udekem

L.elongatus d'Udekem

L.hyalinus d'Udekem

These three species were considered species dubia by Vejdovsky (1884). *Limnodrilus benedii* is now considered to be *Peloscolex benedeni* in all probability. The author has not seen the original descriptions.

L.novaezelandiae Nomen nudum in Beddard (1895).

This species is referred to by Beddard in earlier publications (1889, 1892). No description was given by him, but he considered the species to be a link between *Limnodrilus* and *Clitellio*. He then further remarked that his specimens were immature and possibly not even assignable to *Limnodrilus*. The species was listed under species dubia by Michaelsen (1900). Benham (1903) described the occurrence of *Limnodrilus* sp. in New Zealand and considered his specimens to be the same as those of Beddard. Neither he nor the author has been able to trace a description of this species in the literature.

c) KEY TO THE SPECIES OF LIMNODRILUS

For comparative purposes a summary of the variation in the number of chaetae per bundle and the length: breadth ratio of the penis tubes of the British species of Limnodrilus is given in table 6. The variations in the chaetal shape of each species are shown in fig. 4, and a comparison of the hoods of the penis sheaths of all species of Limnodrilus is shown in fig. 11.

Much of the information in the previous sections of this work has been used in the preparation of a key to the species of Limnodrilus in Brinkhurst (1963), and to the British species of Tubificidae in Brinkhurst (1964). The key that appears below is essentially the same as that appearing in Brinkhurst (1963), but with some slight modifications.

The key is useful for mature specimens only, as immature specimens cannot yet be identified. In using the key the variation in the form of the hoods as figured elsewhere (figs. 6 - 10) should be considered.

TABLE 6.

Comparison of the variation of the specific characteristics of the species of *Limnodrilus*.

Information compiled from tables 1 - 5. Insufficient information is available on the variation of *L. grandisetosus* and *L. neotropicus* for inclusion here.

	Lh.	Lu.	Lhe.	Lcl.	Lce.
Mean number of chaetae/bundle of mature specimens	6.9	5.3*	6.4	6.8	6.9
Standard deviation of chaetae	1.13	---*	0.91	1.02	1.06
Range of penis tube ratio in all specimens	1 - 14	2 - 5	2 - 7	17-42	7-48
Mean ratio in all specimens.	9.5	3.7	4.5	25.9	28.2
Standard deviation in all specimens	1.7	0.64	0.86	6.52	7.57
Range of penis tube ratio in breeding specimens only	5 - 13	3 - 4	2 - 6	21-42	20-43
Mean ratio in breeding specimens only	9.7	3.7	4.3	29.8	30.2
Standard deviation in breeding specimens only	1.16	0.28	0.74	---	---

Legend.

Lh = *L. hoffmeisteri* Lu = *L. udekemianus* Lhe = *L. helveticus*

Lcl = *L. claparedeanus* Lce = *L. cervix*

* the mean for immature specimens was quoted for this species as insufficient information is available for mature specimens.

1a. Ventral chaetae of segments 4 - 10 broader and longer than other chaetae. Penis sheath short with shovel-shaped ending (fig. 11g).......*L.grandisetosus*

b. Ventral chaetae of segments 4 - 10 normal. Penis sheath not of this form..........................2

2a. Anterior dorsal chaetae with upper tooth up to twice as long as lower one. Penis sheath always short 3

b. Anterior dorsal chaetae with teeth more or less equal in length, or upper tooth only slightly longer than lower one.
Penis tube long or short..........................4

3a. Penis sheath short with a simple tip (fig. 7)
L.udekemianus

b. Penis sheath narrowing towards distal end, then expanding to form rounded dilation with lateral opening, (fig. 11c)..................*L.neotropicus.*

4a. Penis sheath short, with reflected tip (fig.10)
...............*L.helveticus.*

b. Penis sheath of medium length, curved, with the distal end expanding to form a trumpet-shaped hood with a lateral opening (fig. 6)....*L.hoffmeisteri.*

c. Penis sheath long, thin walled and straight, with a pear shaped hood (fig. 8).........*L.claparedeanus.*

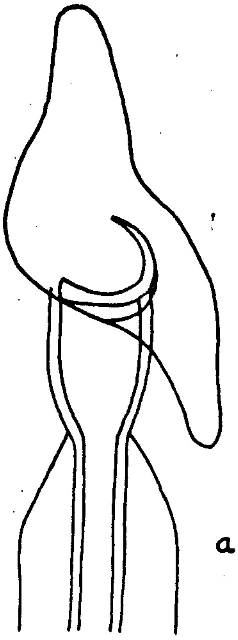
d. Penis sheath long, thick walled and narrowing suddenly at the tip. Slightly expanded hood bearing a backward and a forward projection (fig. 9)......*L.cervix.*

Figure 11

A comparison of the heads of the penis tubes of all species of *Limnodrilus*.

a ..... *L. cervix*
b ..... *L. Claparedeanus*
c ..... *L. neotropicus*
d ..... *L. helveticus*
e ..... *L. hoffmeisteri*
f ..... *L. udekemianus*
g ..... *L. grandisetosus*

a - f original; g after Nomura (1932).



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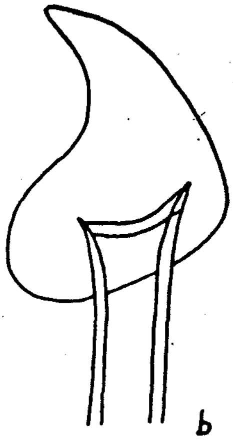

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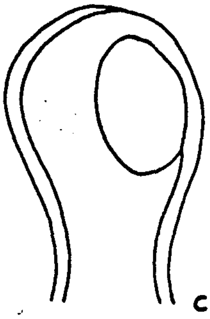

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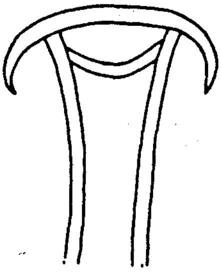

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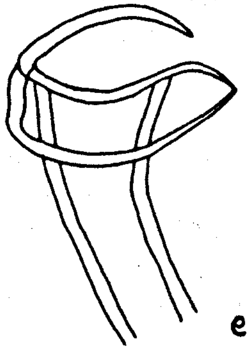

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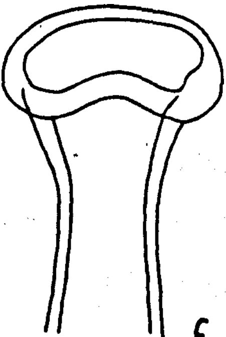

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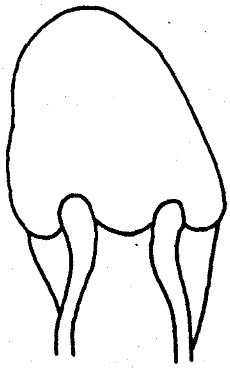

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CHAPTER 3

THE DISTRIBUTION OF LIMNODRILUS

a) THE GEOGRAPHICAL DISTRIBUTION OF LIMNODRILUS

Since the work of Michaelsen (1903) there has been no major attempt to make a comprehensive survey of the distribution of the genus Limnodrilus. Check-lists have been compiled for several countries (Marcus, 1942: Hrabě 1954: Cekanovskaya 1962: Moszynska, 1962: Brinkhurst 1962a, 1963), but most of the information on distribution still lies scattered in the extensive literature. In compiling the following information reference has been made exclusively to these check lists only when the country in question is small. In the case of larger countries, as the U.S.S.R., additional references have been given in order to indicate the distribution of the species within such a vast area. Records in which the identity of the specimens is considered dubious have generally been omitted.

For all species except L. claparedeanus the literary records have been accepted on their merits. In the case of L. claparedeanus, because of the confusion with other species discussed in the previous chapter, the literary records have only been accepted when a description has been included such that the identity of the specimens is clear, or if it has proved possible to examine the specimens in question.

The distribution of Limnodrilus in Britain is discussed in more detail in section 2 of this chapter.

1) The distribution of Limnodrilus outside Britain.

The distribution is given for each species in terms of its occurrence in zoogeographical regions and then in countries. The boundaries of the zoogeographical regions are given by de Beaufort (1951). The boundaries of the countries are those indicated in the Oxford Atlas (1st Edn.1951). Since the boundaries of several European countries have changed since the original records, the countries given here are not necessarily those in which the original record was located.

Limnodrilus hoffmeisteri

Palaearctic.

Europe.... Lithuania (Grigelis; 1959,1962): Estonia (Timm; 1959, 1962, 1962a, 1963): Czechslovakia (Hrabě; 1938, 1941, 1954): Poland (Ryoska; 1935, 1936: Szczepanski, 1953: Moszynska, 1962 - check-list): Rumania (Cernosvitov, 1928): Yugoslavia (Cernosvitov, 1930, 1931, 1938; Sapkarev, 1956; Hrabě, 1958): Albania (Cernosvitov, 1931, 1938; Hrabě, 1955):

Germany (Michaelsen, 1900, 1901; 1903, 1909; Ude, 1929 - summary): Switzerland (Piguet and Bretscher, 1913 - summary):
Italy (Sciacchitano, 1934; Brinkhurst, 1963a-check list): France (Juget, 1957; Brinkhurst, 1963):
Britain (Brinkhurst, 1962a - check list):
Ireland (Southern, 1909; Kennedy, 1964 - check list):
Sweden (Amstedt, 1946; Piguet, 1919):
Denmark (Berg, 1939, 1948): Finland (Brinkhurst, pers.comm.): Austria (Brinkhurst, 1963).
Eurasia and Asia.... Palestine (Cernosvitov, 1938):
U.S.S.R. (Hrabě, 1936; Jaroshenko, 1957; Cekanovskaya, 1959; Sokolskaya, 1961, 1961a; Cekanovskaya, 1962 - check list and summary): Japan (Nomura, 1913): China (Chen, 1940).

Oriental

Java (Michaelsen and Boldt, 1932): Phillipines (Brinkhurst, pers. comm.): India and Ceylon (Stephenson, 1912, 1923).

New Zealand

New Zealand (Benham, 1903)

Ethiopan

Belgian Congo (Cernosvitov, 1939, 1945): South Africa (Brinkhurst, pers.comm.)

Nearctic

U.S.A. (Altman, 1932; Collins, 1937; Brinkhurst, in preparation - check list): Mexico (Rybka, 1898).

Neotropical

Brasil (Marcus, 1942, 1944): Argentine (Cernosvitov, 1939; Gavrilov and Paz, 1950): Peru (Cernosvitov, 1939).

Limnodrilus udekemianus

Palaearctic

Europe.......Lithuania (Grigelis, 1959, 1962): Estonia (Timm, 1959, 1962, 1962a, 1963): Czechoslovakia (Hrabě, 1941, 1958): Poland (Ryoska, 1935, 1936; Szczepanski, 1953; Moszynska, 1962 - check list): Yugoslavia (Cernosvitov, 1938; Sapkarev, 1956): Albania (Cernosvitov, 1938): Germany (Michaelsen, 1900, 1901, 1903, 1909; Ude, 1929 - summary): Austria (Brinkhurst, 1963): Switzerland (Piguet and Bretscher, 1913 - summary) Italy (Brinkhurst, 1963a - check list): France (Brinkhurst, 1963): Britain (Brinkhurst, 1962a - check list): Ireland (Southern, 1909; Kennedy, 1964 - check list): Sweden (Amstedt, 1946): Denmark (Berg, 1939, 1948): Finland (Munsterhejlm, 1905).

Eurasia and Asia... U.S.S.R. (Boltovskoi, 1961; Sokolskaya, 1961, 1961a; Cekanovskaya, 1959, 1962 - summary): Tibet (Cernosvitov, 1941a): China (Chen, 1940): Japan (Nomura, 1913).

Oriental

India (Stephenson, 1923).

Ethiopan

South West Africa (Michaelsen, 1914 as L.alpestris)

Nearctic

U.S.A. (Brinkhurst, in preparation - check list): Mexico (Rybka, 1898).

Neotropical

Brasil (Marcus, 1942): Argentine (Gavrilov and Paz, 1949).

Limnodrilus claparedeanus

In view of the confusion that has existed over the identity of this species an attempt has been made to verify the literary records, where possible. Most European and American records of this species, prior to 1913, have been ignored as the distinction between this species and L.hoffmeisteri was not generally appreciated until this year (see chapter 2).

The following symbols will be used to indicate the status of the records listed below:-

? ....Very dubious. Insufficient indication is given in the publication for the identity of the specimens to be confirmed.

X ....Sufficient evidence is given by the original author to confirm the identity of the specimens.

* ....It has proved possible for the author to examine the original specimens or specimens from the same locality.

Palaearctic

Europe .....Lithuania (X Grigelis, 1959 and pers.comm.): Estonia (X Timm, 1959, 1963 and pers.comm.): Czechoslovakia (X Hrabě, 1941): Poland (? Ryoska, 1935, 1936; * Szczepanski, 1953; X Moszynska, 1962 - check list): Austria (* Brinkhurst, 1963): Germany (* Ude, 1929): Switzerland (* Piguet and Bretscher, 1913; Brinkhurst and Kennedy, 1962a): Italy (* Brinkhurst, 1963 - check list): Britain (* Brinkhurst, 1962a, but see also chapter 2): Ireland (* Southern, 1909; * Kennedy, 1964): Denmark (* Berg, 1948; not as Berg, 1939).

Eurasia and Asia... U.S.S.R. (? Jaroshenko, 1957; * Boltovskoi, 1961; X Sokolskaya, 1961a; X Cekanovskaya, 1962 - summary): Japan (X Nomura, 1929): China (X Chen, 1940).

Nearctic

U.S.A. (? Causey, 1953; X Teter, 1960; * Brinkhurst, 1963 and pers.comm.)

Neotropical

Uruguay (?? Cordero, 1931).

Limnodrilus cervix

Palaearctic

Europe .... Britain (Brinkhurst, 1963).

Nearctic

U.S.A. (Brinkhurst, 1963 and pers.comm.).

For further discussion on the distribution of this species see section 2A of this chapter.

Limnodrilus helveticus

Palaearctic

Europe.... Lithuania (Grigelis, pers.comm.): Czechoslovakia (Hrabě, 1941): Switzerland (Piguet and Bretscher, 1913; Juget, 1958): France (Juget, 1957): Britain (Brinkhurst, 1962 supplement): Sweden (Piguet, 1919; Brinkhurst and Kennedy 1962a).

Eurasia and Asia... U.S.S.R. (Hrabe, 1936; Jaroshenko, 1957; Boltovskoi, 1961; Sokolskaya, 1961; Cekanovskaya, 1962 - check list and summary).

Limnodrilus grandisetosus

Palaearctic

Asia... U.S.S.R. (Sokolskaya, 1958, 1961a; Cekanovskaya, 1962 summary): Japan (Nomura, 1932; Yamaguchi, 1940).

Oriental

Burma (Stephenson, 1939 - described as *Limnodrilus* sp. and believed by Nomura (1932) to be this species.

Limnodrilus neotropicus

Neotropical

Argentine (Cernosvitov, 1939): Paraguay (Cernosvitov, 1939): Peru (Cernosvitov, 1939).

Discussion

It will be obvious from the above lists that the distribution of the species of *Limnodrilus* is to some extent a reflection of the locations of collectors. The tubificid fauna of Europe, except Spain and Norway, Northern Asia and Japan is fairly well known. North America, South America and China have been less thoroughly studied, but sufficient collections have been made to indicate the commoner species of tubificids in these regions. Other regions, however, are still very poorly known, and the absence of a particular species from them can not, as yet, be regarded as significant. These regions include Africa, the Middle East, India, the Pacific Islands, Australasia and the Arctic and Antarctic regions. The knowledge of the tubificid faunas of these regions has been compiled from the results of occasional expeditions. Several expeditions have been made to Africa, and it does appear possible that the scarcity of observations of *Limnodrilus* there may truly reflect a scarcity of the genus in that continent. Occasional expeditions have been made into Antarctica (Michaelsen, 1905), and into the Arctic to the Faroes (Ditlevsen, 1936) and Iceland (Zoology of Iceland series). Few tubificids have been recorded and it again seems possible that many species may be absent in these regions. It seems very probable, however, that some members of the genus *Limnodrilus* will be found to occur in all other geographical regions when they are searched for.

Despite these reservations it is still possible to attempt a summary of the distribution of the genus and species of *Limnodrilus* from the foregoing records. The genus as a whole is cosmopolitan, having been found in all the regions surveyed, but some species appear to be restricted in their distribution to varying degrees. *L.hoffmeisteri* appears to be a cosmopolitan species. It appears likely that *L.udekemianus* will also prove to have a wide distribution species. It never occurs as abundantly as *L.hoffmeisteri*, and this may be the reason for its absence in regions that have not as yet been thoroughly worked. The indications are that it is able to withstand extremes of climate, being known in Tibet (Cernosvitov, 1931) and Brasil (Marcus, 1942). It seems probable that it will be found to occur in other regions and to have a world-wide distribution.

L.claparedeanus, on the other hand, shows some evidence of a more restricted distribution. It is present throughout the holarctic region and the only record outside this region is a very dubious one. Cordero (1931), who claimed to have found it in Uruguay, based his identification on Michaelsen (1900). It has been shown in the previous chapter that Michaelsen's identification with regard to this species was inaccurate. On the present evidence, therefore, it appears that this species is restricted to the holarctic region. The distribution of L.cervix will be discussed in more detail in a later section (p.3.14) when evidence will be presented to show that it has probably been introduced into Britain comparatively recently. Outside of Britain it is only known from U.S.A. It is probable that this is a true nearctic species but is now spreading into the palaearctic region. Limnodrilus helveticus, by comparison, appears to be a palaearctic species, and even within this region its distribution is restricted when compared with that of L.hoffmeisteri. Evidence will again be presented to show that it has only recently been introduced into Britain.

The remaining two species appear to have very restricted distributions. Limnodrilus grandisetosus was described from Japan but was later found by Sokolskaya (1958) in the Soviet province of Amura. The record from Burma must be considered dubious, but even if it is correct it still indicates a restricted distribution. If this species is present in Japan and Burma it would be expected that it would also occur in China. Since there are relatively few records from China, its absence from there cannot be regarded as established. The distribution of L.neotropicus is even more restricted. It is confined to South America and appears only to occur in the centre of the continent. It is probable that it will also be found in Bolivia, since it occurs in Lake Titicaca (Cernosvitov, 1939) which forms part of the boundary between Bolivia and Peru.

The information summarised in the preceding pages on the distribution of the species of Limnodrilus in Europe has been incorporated by Brinkhurst in his chapter on the Oligochaeta in the Limnofauna Europea (in preparation).

2) The distribution of Limnodrilus in Britain

The distribution of the genus in Britain has been little studied. At the beginning of the century numerous records were published by Friend (1898 et seq.), but his identifications have been shown to be unreliable (Cernosvitov, 1941). They are ignored here. A few English and Manx records were included in a work on Irish tubificids by Southern (1909). These have recently been checked and brought up to date (Kennedy, 1964). Some British records are to be found in Brinkhurst (1960), but in view of the taxonomic confusions in that work some of these cannot be accepted in a study of the distribution of the genus. The check list of British Tubificidae compiled by Brinkhurst (1962a) is of no value here because localities are not given. The distribution of tubificids in the Isle of Man has been recorded by Brinkhurst and Kennedy (1962). References to Limnodrilus sp. and to L.hoffmeisteri occur extensively in the general freshwater literature, but in the absence of confirmation it is considered safer to discard them.

The distribution of Limnodrilus recorded in the following pages has been based to a large extent on personal collections. Literary records have only been accepted when it proved possible to examine the specimens. Distribution has been recorded on a vice-county basis, as there is insufficient information for maps on a smaller scale to be meaningful. In addition to showing a region where a species has been found to occur, the regions where it has been searched for and not found are also shown. This clearly distinguishes the regions which have not been surveyed and enables more reliance to be placed on negative records.

Collections were only made at sites where Limnodrilus was considered likely to be present. Particular attention was paid to canals, in view of the apparent restriction of L.cervix to this habitat. Most of the collections were made in spring and early summer, when the chances of finding more easily identifiable breeding individuals was greater. In the relatively short time available it was not possible to cover all of Britain but attention was given to England and Wales. Records from the North of England and Scotland are few.

In the following account the distributions of L.cervix and L.helveticus are considered separately from that of the other British species of Limnodrilus as preliminary observations had shown a very restricted distribution for both species. It was finally concluded that both were not native species but had recently been introduced into Britain (pp.3.14 - 3.21) The remaining species of Limnodrilus are considered together because all three appear to be native to this country and their distribution shows no peculiarities.

A) The distribution of L. cervix and L. helveticus.

Limnodrilus cervix

The distribution of this species is shown on a vice county basis in fig. 12a. It is evident that it is restricted to two areas. The larger area occupies the whole of the midlands and the smaller one is confined to the county of Cheshire. A closer study of the distribution of L. cervix within these areas shows that it is either confined to canals or to rivers in close connection with, or receiving overflows from, a canal system. Its distribution throughout the canal system is shown in more detail in fig. 13. Both the sites where found and where not found are shown. A single negative record is not accepted, but several negative records close to each other or from a particular canal or river system are accepted as evidence of its absence in that region.

It can be seen then from fig. 13 that it is present in the R. Thames as far as Oxford, but is not found beyond it or in any of the tributaries of the Thames, as the Churwell or Thame. It is present in the two main branches of the S.E. canal system i.e. the Oxford canal and the Grand Union Canal. It is present in the R.Ouze close to Bedford and the R.Nene just above Northampton, but both rivers are in direct

Figure 12

The distribution by vice-counties of *L. cervix* and *L. helveticus* in Britain.

A ..... *L. cervix*

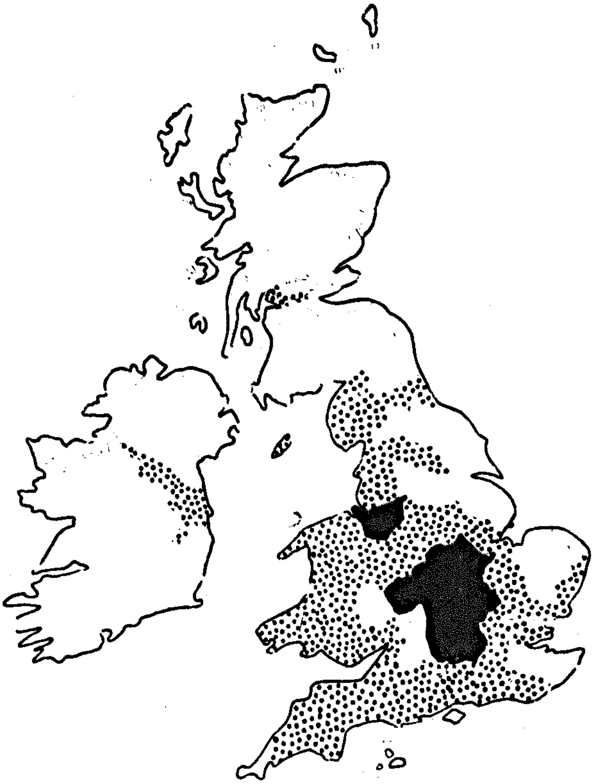
B ..... *L. helveticus*

Legend

Vice counties blocked in indicates the presence of the species in the area.

Vice counties stippled indicates that collections have been made in the area but the species has not been found there.

Vice counties left blank indicates that no published records are available for the area and no collections have been made there.



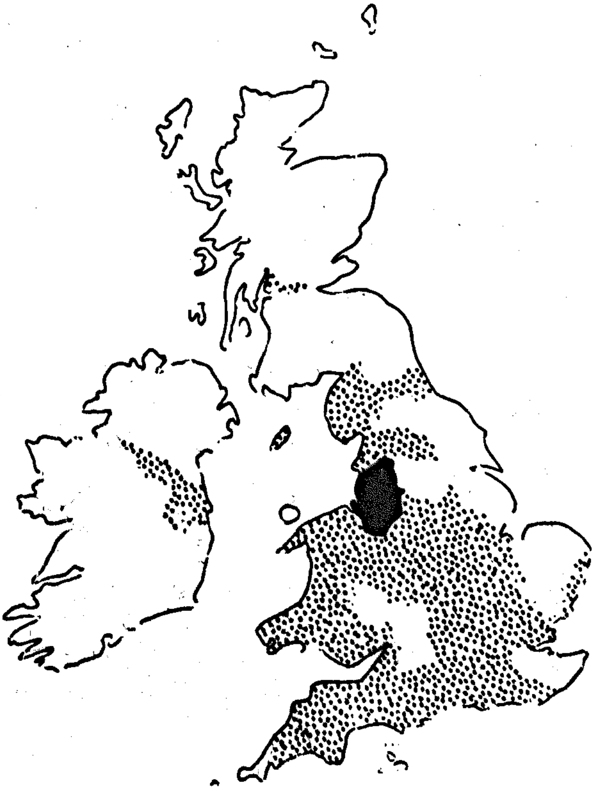


Figure 13

The distribution of L. cervix throughout the canal system of England and Wales. Only those waterways specifically named in the text are labelled.

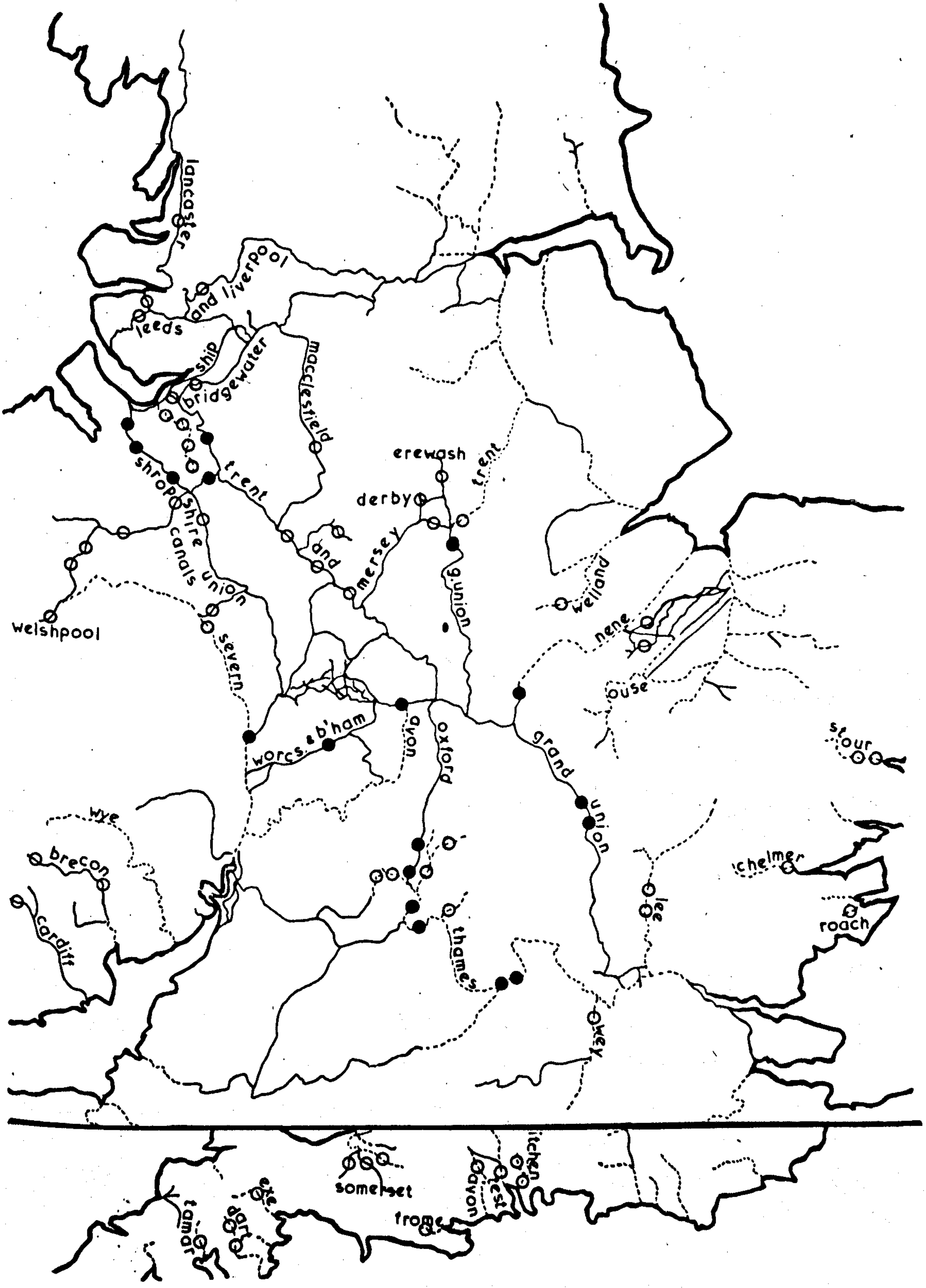
Legend

Unbroken lines = canals

Broken lines = rivers

Solid circles = localities from which L. cervix has been recorded

Hollow circles = localities from which L. cervix has not been recorded.


lancaster
leeds and liverpool
ship
bridgewater
macclesfield
shropshire
canals
union
trent
and
mersey
erewash
derby
trent
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welland
nene
ouse
welshpool
severn
worcs & b'ham
avon
oxford
grand union
stour
wye
brecon
cardiff
chelmer
roach
lee
thames
key
somerset
frome
avon
test
itchen
exe
dart
tamar

connection with the Grand Union. It is present in the Grand Union canal above Leicester and below its junction with the R. Trent. This would appear to be the northernmost limit of its distribution along the system, as it has not been found in the R. Trent, the Erewash Canal, the R. Derwent (where a series of detailed surveys have been made over recent years - Brinkhurst, in press) or in the Trent and Mersey canal. In the Oxford canal system it is present in the R. Avon at Warwick, where it connects with the canal system, the Worcester and Birmingham canal and the R. Severn at Stourport, where it joins the Staffordshire and Worcester canal. It is not known whether it is present in the Rivers Severn and Avon below their junctions with the respective canals. No attempt has been made to look for it in the Birmingham canal system. It is not, however, present in the two N.W. canals leaving the Birmingham system (its absence in the N.E. exit has already been referred to). Several collections have been made in the Trent and Mersey canal between Stoke and Lichfield, where it has not been found. It is also absent in the Shropshire Union canal and from its Shrewsbury and Llangollen branches.

It occurs in several localities in both the Shropshire Union and the Trent and Mersey canals and their junction branch in Cheshire, in several localities. It has not been searched-for extensively north of the line from the R.Mersey to the Wash. These Northern canals are main canal system joined to the Southern by four branches: The R.Trent, the Macclesfield canal, the Bridgewater canal and the Manchester Ship canal. The first three mentioned branches have been sampled and L.cervix has been found to be absent from them. The ship canal has not been sampled, but in view of its high salinity it is considered unlikely that any freshwater species is able to survive there. It may thus tentatively be concluded that L.cervix is absent from the northern canal system. The pattern, as shown in fig. 12, of two restricted and discontinuous areas of distribution is thus confirmed by this more detailed survey.

There appear to be three possible explanations for such a pattern of distribution. The first of these is that at some previous time L.cervix had a much wider distribution in the deeper, slow flowing rivers and due to increased organic pollution it has now become restricted to canals. The main objection to this theory is that canals are frequently more polluted than many rivers. Limnodrilus cervix is present in canals in most stages of pollution (pers.obsvn.) Even if this were true, it might be expected that the species would be found in some rivers not necessarily connected with the canal system. It will be shown that this is not the case. A second possible explanation is that this species exhibits an ecological preference for deep, slow blowing rivers, and that it has spread into canals as these provide a similar type of habitat. If this were the case it would be expected that the species should occur in rivers of this nature, and possibly also in canals outside the main system. Reference to fig. 13 shows that this is not so. Outside of the main canal system collections have been made in the Neath, Swansea, Brecon and Abergavenny, Bridgewater (Somerset), Lancaster and Leeds and Liverpool canals. Collections have also been made in the following large rivers:- Tamar, Dart, Exe, Hampshire Avon, Test, Blackwater, Itchen, Roach, Crouch, Chelmer, Stour, Lee, Ouse, Nene and fen drains, Welland, tributaries of the Thames and the Thames above Oxford. It has not been found in any of these canals or rivers. It is also absent in all the rivers and canals so far examined in Ireland. Accordingly, this theory is rejected.

The third possible explanation is that <u>L. cervix</u> is not a native species but has been introduced into Britain and is now spreading slowly through the canal system. Outside Britain it is known only from U.S.A. (p.3.7). It may be significant that its two areas of distribution in Britain are based on the transatlantic ports of Liverpool and London. On this theory L. cervix is still only in the early stages of introduction and is only beginning to spread from the canals into the connecting rivers. It has not yet had time to spread into rivers or canals not closely connected with the main systems, and its noted absence in these bodies of water is thus readily explicable. The distribution of L. cervix shows a very similar pattern to that of Gammarus tigrinus, and it was concluded by Hynes (1955) that this species had been introduced from North America. To the author this theory appears to be the most plausible of the three, as it satisfactorily explains the known distribution of the species. It is therefore concluded that L. cervix is a North American species that has been introduced into Britain within comparatively recent times.

It is also possible to consider the sites of introduction. Since the two areas of distribution are distinct and discontinuous it is suggested that two introductions have taken place. From the wider spread of the species in the midlands it would appear likely that this was the earlier introduction of the two. It would seem likely that the introduction took place into the R. Thames, probably above London since it is absent from the Lee Navigation canal. From the R. Thames the species could have entered the Grand Union canal at

Richmond, or more possibly from Kew. Another species of tubificid, *Branchiura sowerbyi*, is known to have entered the R.Thames at Kew, and then to have spread upstream (Mann, 1958). *Limnodrilus cervix* may then have spread northwards and westwards up the R.Thames, i.e. along the waterways indicated in the preceding paragraphs. It does not seem to have spread beyond the Birmingham canal system. This may be a result of the time factor, or possibly it is unable to tolerate the heavy pollution in the canals of that region. It has not, however, made contact with the Northwestern introduction. The restricted area of spread of the species in this region suggests that this is a more recent introduction than the southern one. It seems possible that this occurred in the Manchester Ship canal at Ellesmere Port, where the Shropshire Union canal joins it. It is not suggested that *L.cervix* is present in the ship canal, but that it passed into the Shropshire Union canal at this point and spread along it, as far as the branch joining this canal to the Trent and Mersey canal. It then spread into the Trent and Mersey canal, and back along it in the direction of Runcorn. This suggestion is preferred to that of its direct entry from the ship canal to the Trent and Mersey canal via the Bridgewater canal, as it has not been found in several samples from the latter canal. This appears to be the limit of the Northwestern distribution of L. cervix, at present. It has not spread into the Northern canal system, or any farther South along the Shropshire Union or Trent and Mersey canals or any of their branches. It must be emphasised that such conjectures must inevitably remain hypothetical, as it is virtually impossible to prove conclusively that a species has been introduced. Nevertheless, it is the opinion of the author that this is the only explanation of the distribution of L. cervix in Britain that embraces the observed facts and satisfactorily accounts for them.

The implications of this theory in so far as it concerns the taxonomic confusion between L. cervix and L. claparedeanus has been discussed elsewhere (p. 2.37). It is sufficient to state here that the knowledge of the distribution of L. cervix as compared with that of L. claparedeanus was of considerable help in the recognition and separation of the two species.

Limnodrilus helveticus

The distribution of this species on a vice county basis is shown in fig. 12b. Compared with the large areas examined it is obvious that its distribution in Britain is very restricted. It is known, in fact, from only three localities, all on Merseyside. In

Cheshire it occurs in a small pond at Raby (for full description see chapter 5a1). It has not been found in other ponds in this locality despite an intensive search. In Lancashire it is known from a small brook at Ditton (for full description see chapter 5a1) and from the Leeds and Liverpool canal near Burscough. The two Lancashire localities are closely connected to the R.Mersey and the port of Liverpool. The Cheshire pond, however, is an isolated locality about five miles from the R.Mersey and without any water connection to it.

In continental Europe and Asia where this species is more common its typical habitats are deep lakes (Piguet and Bretscher, 1913; Piguet, 1919; Boltovskoi, 1961) or large rivers (Hrabě, 1941; Jaroshenko, 1957). It is occasionally found in small streams (Piguet and Bretscher, 1913; Brinkhurst and Kennedy, 1962a). It has not been found in any of the British lakes so far examined (Brinkhurst in press b) Its occurrence in such a restricted area and in sites so unlike its normal habitat is not readily explicable. On the basis of the peculiarity of these habitats and their proximity to a large port it is tentatively suggested that L.helveticus may be an introduced species in this country, although there is very little evidence to support this suggestion.

b) The distribution of other species.

The remaining three species of *Limnodrilus* to occur in Britain appear to be native to this country and their distributions show no peculiarities. The distribution of *L.hoffmeisteri* is shown in fig.14a, *L.udekemianus* in 14b and *L.claparedeanus* in 14c.

As might be expected from such a cosmopolitan species as *L.hoffmeisteri* its distribution in Britain shows no evidence of a restricted pattern. It has been found in all areas investigated, and in the opinion of the author it will be found in suitable sites in all the remaining areas when they are searched.

The distribution of both *L.udekemianus* and *L.claparedeanus* is patchy and more local. Both species are generally scarce in habitats where they occur, and are consequently more likely to be overlooked. The distribution of both species is widespread, however, and it is considered likely that they will be found to occur in most areas when these have been searched more thoroughly.

b) THE DISTRIBUTION OF LIMNODRILUS IN RELATION TO ITS ECOLOGY

Ecological studies on the Tubificidae have been hampered by difficulties in the identification of specimens. Such ecological information as is available

Figure 14

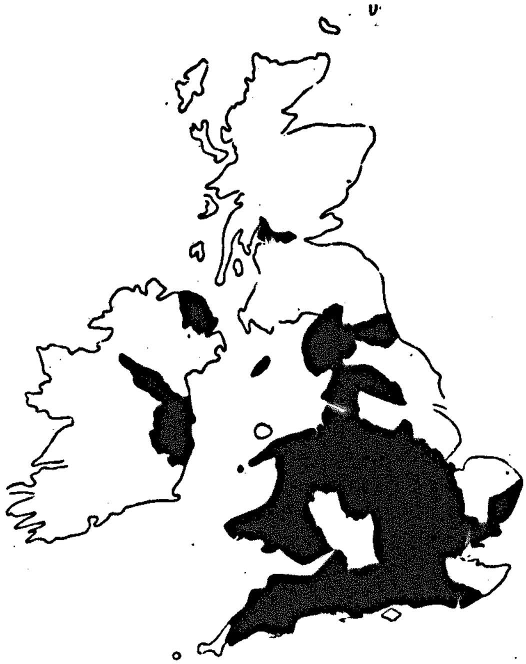
The distribution by vice counties of L. hoffmeisteri, L. udekemianus and L. claparedeanus in Britain.

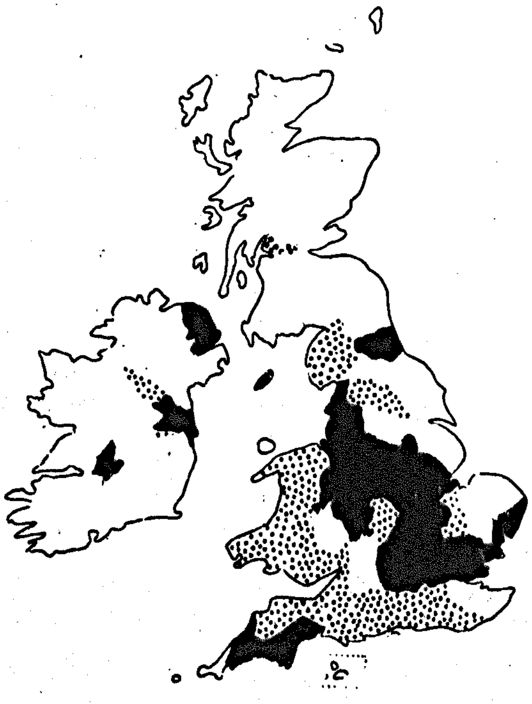
A ..... L. hoffmeisteri

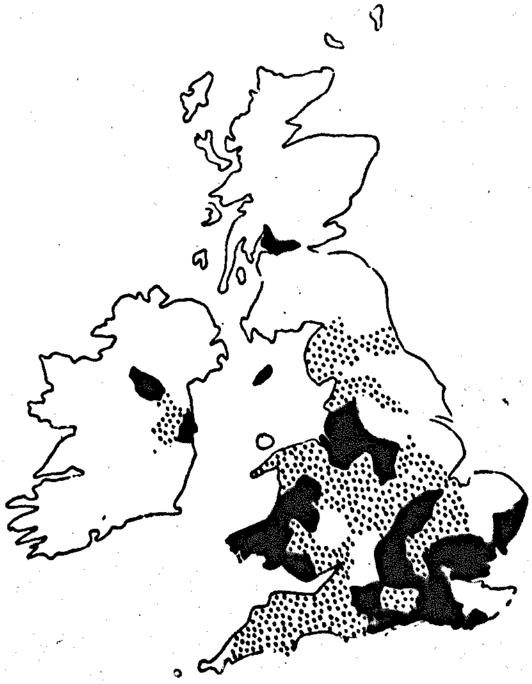
B ..... L. udekemianus

C ..... L. claparedeanus

Legend as in figure 12.







has recently been summarised by Brinkhurst (in press, a and b). He concluded that for most species there is no apparent relationship between the presence or absence of a species and any known factors in the physical or chemical nature of the environment. He suggested, however, that the nature of the substratum might influence the abundance of a species in a particular habitat.

In the present study particular attention is paid to the distribution of Limnodrilus in a number of habitats. Few attempts have been made to determine the abundance of Limnodrilus in relation to the nature of the habitat, although this was originally intended. Detailed studies on the distribution and abundance of species of Limnodrilus within a particular locality (discussed in part 4 of this section) show that a considerable range of variation may exist within an apparently uniform habitat. It was evident from these studies that the relative abundance of the species in any particular locality could not be determined from a single sample and that a large number of samples would be required. Within the time available for the present study it proved impossible to examine large numbers of samples from every locality visited, and so the quantitative aspects of the distribution of Limnodrilus have largely been ignored.

In the following account the distributions of L.cervix and L.helveticus are not considered in any more detail than is given to them in the previous section. As both species still appear to be at the immigration stage, their absence in many of the habitats examined in Britain can not be regarded as significant or as proof of their inability to survive there..

1) The distribution of Limnodrilus in relation to the nature of the habitat.

a) The distribution of Limnodrilus in rivers.

There is relatively little information available in the literature on the distribution of Limnodrilus in rivers. Hrabě (1941) gave details of collections in the R.Danube and summarised the literature on several European rivers. He found L.hoffmeisteri to be amongst the ten commonest species, whereas L.udekemianus and L.claparedeanus occurred only locally and never abundantly. He also recorded occasional specimens of L.helveticus from the R.Danube. Boisen Bennike (in Berg, 1948) found L.hoffmeisteri occurring in all types of substrata in the R.Susaa, but sparser on sandy substrata. L.udekemianus and L.claparedeanus occurred rarely during the Susaa survey.

Szczepanski (1953) tried to relate the distribution and abundance of the tubificids in the R.Vistula to the type of substratum. He concluded that L.hoffmeisteri is a ubiquitous species, whereas L.udekemianus and L.claparedeanus are restricted to a permanently muddy substratum. Although L.hoffmeisteri is the dominant species of the genus in the river, its numbers decline on a sandy substratum. He considered that the composition of the bottom fauna in the river was the result of two principle interdependant factors; the nature of the substratum and the velocity of the current.

The above conclusions are confirmed by the author's own collections (table 7). Limnodrilus hoffmeisteri occurs more frequently than either of the other two species of Limnodrilus in each type of habitat, and occurred in 51 out of the 57 localities sampled. The occurrence of both L.udekemianus and L.claparedeanus was local, and showed no correlation with the nature of the habitat. Limnodrilus hoffmeisteri occurred in all types of substrata, and appears to be the most abundant species of Limnodrilus. The other two species rarely appeared to occur abundantly.

b) The distribution of Limnodrilus in lakes.

Brinkhurst (in press, a and b) in a review of the biology of the Tubificidae in lakes stated that in general there seemed to be no correlation between the presence of species and the physical and chemical factors usually estimated in lakes. A detailed study of the distribution of Limnodrilus in lakes confirms his conclusions.

TABLE 7

The occurrence of *Limnodrilus* in riverine habitats in Britain.

Nature of habitat.	Number examined	Number containing L.hof.	 L.ude.	 L.clap.
Rivers	23	21	8	5
Streams	14	10	1	6
Canals	20	20	3	3
Totals	57	51	12	14

Legend.

L.hof. = *L.hoffmeisteri* *L.ude.* = *L.udekemianus*
L.clap. = *L.claparedeanus*

The distribution of Limnodrilus in the Swiss lakes has been summarised by Piguet and Bretscher (1913). Limnodrilus hoffmeisteri occurs in the majority of the lakes surveyed, L.udekemianus, L.claparedeanus and L.helveticus in only a few. No clear pattern emerges from the presence or absence of a species and the trophic status of the lake. They show, however, that L.helveticus occurs more frequently in lakes than in any other type of habitat, an observation confirmed by Piguet (1919) in his studies on Swedish lakes.

The Danish lakes have been studied by Berg (1938) and Dunn (1954), but in both works the identifications of the tubificids are not always correct. Some of these have been corrected by the author. Limnodrilus hoffmeisteri is shown to be present in eutrophic and oligotrophic lakes, but there is no evidence of it occurring in dystrophic ones. Limnodrilus udekemianus is known only from the very eutrophic lake Esrom. Neither L.claparedeanus nor L.helveticus was found in any of the lakes surveyed.

A summary of the distribution of Limnodrilus in the British lakes has been given by Brinkhurst (in press, a). Limnodrilus hoffmeisteri occurs in the majority of lakes surveyed in the Lake District, but is absent in the more oligotrophic lakes in the series, as were all tubificids. Limnodrilus udekemianus and Limnodrilus claparedeanus are apparently absent from all the lakes in the series. In the more eutrophic Shropshire meres investigated in this survey *L.hoffmeisteri* is absent in only two out of the nine surveyed, *L.udekemianus* is only present in four of them and *L.claparedeanus* is absent in all. In the one dystrophic lake examined no tubificids were found.

There are several studies on individual lakes. Juget (1958) found *L.hoffmeisteri*, *L.claparedeanus* and *L.helveticus* in the Léman, but only the first occurred abundantly. Poddubnaya (1960) found all three species and *L.udekemianus* in the Rybinsky reservoir, but *L.hoffmeisteri* is the commonest species. Brinkhurst (1963a) found only *L.hoffmeisteri* and *L.udekemianus* in samples from L.Maggiore. Lastockin (1927) failed to find any species of *Limnodrilus* in dystrophic lakes surveyed by him.

Two studies in which an attempt has been made to relate the presence of various species of tubificids to the altitude of the lake deserve attention. Bretscher (1903) showed that whilst *L.hoffmeisteri* is a common species in lakes up to 700 m. above sea level; above this height it is of very rare occurrence. Hrabě (1938) studied the tubificid fauna of the high Tatra lakes and found that *Limnodrilus* is absent from the highest ones.

The following conclusions may be tentatively drawn from these observations. All species of Limnodrilus are absent from or rarely occur in a) dystrophic lakes, b) extreme oligotrophic lakes and c) lakes of high altitude. Limnodrilus helveticus appears to be more commonly found in lakes than in any other type of habitat, and may be considered to be primarily a lacustrine species. Limnodrilus hoffmeisteri occurs in eutrophic and some oligotrophic lakes. Its presence cannot therefore be held to be indicative of the trophic status of the lake. Limnodrilus udekemianus occurs more frequently in eutrophic lakes, although it is also present in some oligotrophic ones. Limnodrilus claparedeanus, on the other hand, has not been found in any eutrophic lakes so far surveyed. There does not appear to be any correlation between the size of the lake and the presence of this species. It occurs in both large and small Swiss lakes (Piguet and Bretscher, 1913) and is absent from large eutrophic lakes. It is also absent, however, from many of the oligotrophic lakes here surveyed, especially the British ones. The presence or absence of this species may therefore be related to some factor, such as the nature of the substratum, other than to the trophic status of the lake.

2) The distribution of Limnodrilus in relation to salinity.

No species of Limnodrilus is known to be able to survive under marine conditions. The genus as a whole is strictly fresh water in its distribution, but there is evidence that L.hoffmeisteri is more tolerant of saline or brackish conditions than other species of the genus. Moore (1905) recorded this species (as L.subsalsus) in estuarine waters that became brackish at flood tide. Chen (1940) recorded it as L.pacificus in fresh water bodies along the sea shore where the saline content of the water was undoubtedly high. Brinkhurst and Kennedy (1962) recorded L.hoffmeisteri from saline conditions in an estuary in the Isle of Man. Kennedy (1964) records the presence of this species in ditches in a marine salt marsh. There is no evidence that other species of Limnodrilus are able to tolerate saline conditions.

3) The distribution and abundance of Limnodrilus in relation to pollution.

a) Organic pollution.

The effect of organic pollution on tubificids has been described and summarised by Hynes (1959,1960) and Brinkhurst (in press). The following account has been compiled from these works. Limnodrilus hoffmeisteri is one of the most resistant species of tubificids to organic pollution. It is one of the last two species to disappear when the degree of pollution reaches a toxic level. It is also one of the first species to re-appear in the recovery stages. Whilst it may be absent immediately below a source of pollution it may reach very large numbers in the region where its predators are still absent.

Limnodrilus udekemianus is only slightly less resistant to organic pollution than *L.hoffmeisteri*. Its numbers increase with the degree of pollution, but it disappears before and re-appears after *L.hoffmeisteri*.

Limnodrilus claparedeanus seems to be more sensitive to pollution and to occur mainly in unpolluted habitats. It appears to be able to withstand slight pollution, but probably only if the oxygen level is high. Little is known of the tolerance level of *L.cervix*, but it is common in polluted waters in U.S.A. (Brinkhurst pers.comm.) Nothing is known however of the relationship between *L.helveticus* and organic pollution.

b) *Inorganic pollution.*

The effect of heavy metal ions on *Tubifex* was reviewed by Jones (1938). The identification of his specimens is somewhat suspect and it is probable that at least one species of *Limnodrilus* was present in his collections. He showed that copper was lethal to tubificids, but that the relationship was a complex one and that the presence of other ions could greatly influence the survival rate of the specimens. A more direct effect of copper was shown by Pentelow and Butcher (1938) in the R. Churnet. Here, immediately below an effluent containing copper ions no tubificids were present, whereas they were fairly common above the effluent. A survey on the same river was carried out in 1960 by Mr. J. B. Leeming, and the author was kindly permitted to examine the tubificids collected by him. A similar pattern to that observed by Pentelow and Butcher was found. Above the effluent L. hoffmeisteri was one of the commonest species of tubificid, but L. udekemianus also occurred in small numbers. Immediately below the effluent no tubificids were present. Limnodrilus hoffmeisteri was one of the first species to appear downstream but L. udekemianus did not appear for a considerable distance.

The effect of lead and arsenic upon a tubificid population in Raby pool is shown in table 8, although here it must be emphasised that the evidence for the influence of the metal ions is circumstantial. Between March and July 1962 the mean number of specimens per sample fluctuated, but no pattern was observable in these fluctuations. From late July to October the

TABLE 8

The seasonal changes in abundance of the tubificids in Raby pool.

	1962													1963			
Month	**M**	**M**	**A**	**M**	**M**	**J**	**Jl**	**Jl**	**A**	**S**	**S**	**O**	**N**	**D**	**F**	**M**	**A**	**M**
Mean number of specimens per sample	89	116	77	100	33	135	108	73	64	55	13	25	6	8	12	4	10	3

The following species of tubificid were present in the pond:-

L. hoffmeisteri, *L. helveticus*, *L. claparedeanus*, *T. tubifex*.

population decreased in size. Between October and November a further decrease followed, and from November until the termination of the sampling programme in May 1963 the population remained at a consistently low level. The size of the population in March, April and May 1963 was considerably smaller than in the corresponding months in 1962. It appears that some factor came into operation in October 1962 when the size of the population was already declining and operated in such a manner that the decline continued into November and maintained a low level until the termination of the sampling programme.

This factor is thought to be inorganic pollution due to lead arsenate. The pond receives drainage from an adjoining golf course. In October 1962 parts of the course were dressed with lead arsenate to remove earthworms. In the following month the size of the tubificid population in the pond decreased to a very low level and several decaying specimens were observed in the sample. In February, 1963, it was apparent that the population size was being maintained at this lower level than in the previous year, but not until March was it realised that the golf course had been with toxic chemicals. When this was appreciated a sample of the substratum was analysed, but the results did not show either lead or arsenic to be present.

The tests for lead and arsenic are complex, and this, together with the probable minute concentrations of the ions, may explain why the results were negative. This cannot, however, be taken as conclusive proof that the ions were absent. The golf course was not dressed in 1961 or 1962. The higher density of the population before the application of this toxin; the decline of the population; the presence of decaying specimens in the month following its application and the persistent low level of the population in the subsequent months all suggest that lead arsenate was the factor responsible for the decline in the population in the pool. There is no direct evidence for this, however, so it cannot be proved conclusively that this was the factor responsible for the observed population decrease.

4) The distribution of *Limnodrilus* within a single locality.

In the preceding sections the distribution of *Limnodrilus* in several habitats has been considered, and an attempt has been made to relate the presence or absence of *Limnodrilus* to the nature of the habitat. In this section the distribution of *Limnodrilus* within a single locality is considered in detail, by reference to studies in three different sites.

The first of these is a study of the distribution of the tubificids in Sweat Mere, a small eutrophic lake. A description of the mere and its vegetation is given by Sinker (1962). Seven samples were taken by means of an Ekman grab at different depth stations in a single afternoon and all the oligochaetes from each sample examined. The results are shown in table 9. The vegetation at each station differed, but the substratum was similar at all stations and differed principally in the amount of vegetable detritus present. Nevertheless the relative and absolute abundance of L.hoffmeisteri varied considerably from station to station (table 9b). The relative abundance of L.hoffmeisteri varied from 0.0% - 63.5% and the absolute abundance from 0 - 106 per. grab in the course of seven samples. There is no obvious correlation between these variations and the nature of the substratum, the vegetation present or the depth at each station. Thus, in an apparently uniform habitat in which only two species of tubificid are present the distribution and abundance of each species may vary in a manner unrelated to any observable characteristic of the habitat.

The second locality studied was the R.Thames at Reading. Fourteen species of tubificid are known to occur in the river in this region. A survey by Brinkhurst (1960) showed that in four transects across the river there is no apparent relationship between the

TABLE 9

The tubificid fauna of Sweat Mere on 15 July, 1961

a) Description of the collecting stations

Station	Depth	Description of substratum
1. *Typha* beds	2 ft.	Fine mud and *Typha* debris
2. *Nymphaea* beds	2 ft.	Fine mud but less debris than in 1
3. *Carex* beds	1.5 ft.	Fine mud, large amount of plant debris
4. *Nymphaea* beds	2. ft.	Fine mud, little debris
5. *Typha* beds	3 ft.	Fine mud, large amount of plant debris
6. Typha beds	3.5 ft.	Fine mud, large amount of plant debris.
7. Open water	6.0 ft.	Fine mud, little debris.

b) The percentage composition of the tubificid fauna.

Species	Station 1	2	3	4	5	6	7
Limnodrilus hoffmeisteri	60.0	63.0	0.0	50.0	63.5	0.0	14.0
Euilyodrilus hammoniensis	40.0	37.0	0.0	50.0	36.5	100	86.0
Total number of specimens	7	171	0	8	69	9	43

presence and absence or abundance of a species and any of the physical characteristics recorded at each station. His results are confirmed in the present survey. In table 10 the relative abundance of each species of *Limnodrilus* along a single transect in the R. Thames (results from all stations combined) is shown for two successive years. The relative overall abundance of each species, except *L. udekemianus*, was very similar each year, despite the greater number of specimens examined in 1962. The increase in the relative abundance of *L. udekemianus* in 1962 is due to the inclusion in this transect of a station not sampled in the previous year in which this species occurs abundantly. The relative abundance of each species at each station on the transect, however, differed in the two years (table 11) despite the constancy of the relative overall abundance. No pattern is discernible in these differences. There is no evidence of an increase of any species at all stations, nor of all species at any one station. Thus in a non-uniform habitat the overall proportion of each species present remains fairly constant in successive years, but the proportion of each species at each station may differ in a manner that cannot be correlated with any observable physical characteristics of the micro-habitat.

TABLE 10

The relative abundance of the species of Limnodrilus along a transect across the R.Thames at Reading.

Species	Abundance of each species expressed as a percentage of the total number of specimens examined.	
	December 1961	December 1962
L.cervix	6.6	7.8
L.hoffmeisteri	20.6	14.7
L.claparedeanus	5.8	1.7
L.udekemianus	3.7	21.4
Limnodrilus indet.	9.2	11.6
Total number of specimens examined.	240	997

TABLE 11

The relative abundance of the species of *Limnodrilus* at each station along a transect across the R. Thames at Reading.

December 1961

Species	Yards from North Bank					
	1	5	10	30	69	72
L. cervix	10.0	5.8	0.0	8.3	9.7	6.0
L. hoffmeisteri	20.0	1.7	20.0	8.3	19.5	28.0
L. claparedeanus	12.0	3.8	5.7	16.7	2.4	2.0
L. udekemianus	0.0	9.6	2.9	0.0	0.0	6.0
Limnodrilus indet.	2.0	7.7	17.2	25.2	12.2	6.0
Number of specimens examined	50	52	35	12	41	50

December 1962

Species	Yards from North bank					
	1	5	10	30	69	72
L. cervix	2.6	4.8	18.2	36.1	12.5	0.0
L. hoffmeisteri	5.2	43.4	10.4	12.7	18.7	4.5
L. claparedeanus	0.8	2.4	1.3	0.0	0.0	3.5
L. udekemianus	0.0	0.0	0.0	0.0	0.0	66.5
Limnodrilus indet.	6.9	7.2	11.7	6.4	15.7	6.5
Number of specimens examined	116	42	77	47	64	200

The abundance of each species is expressed as a percentage of the total number of specimens of all species examined.

The third locality studied was a small tributary of Ditton brook. All samples were taken on one day. Three stations (A, B, and C), approximately 25 yards apart were chosen. Observation revealed no differences in the rate of flow or the nature of the substratum between each station. Five samples were taken at each station; one in the centre of the stream (3), one on either side, below water level (2 and 4) and one on either side at water level (1 and 5). A single sample, D1, was taken in the centre of the stream where it entered Ditton brook. The percentage composition of tubificid fauna in each sample, based on the examination of subsamples of 100 specimens, is shown in table 12. With the exception of B5 and C5 L.hoffmeisteri is never the dominant species. Apart from these two samples the relative abundance of L.hoffmeisteri varies from 22.0% - 48.0%. There is no evident correlation between the relative abundance of each species and the position of the sample. Nevertheless, a statistical analysis of these results showed that the probability of the observed distribution and abundance of these two species being due to chance alone was less than 0.001. It is evident, therefore, that some factor or factors, as yet undetected, influence the distribution and abundance of the species within this locality.

In contrast to the situation in the R.Thames, several authors, notably Rzoska (1936), Szczepanski (1953),

TABLE 12

The percentage composition of the tubificid fauna of a small tributary of Ditton Brook on 21 November 1960.

Station	Sample	Tubifex tubifex	Limnodrilus hoffmeisteri
A	1	52.9	46.6
	2	56.0	44.0
	3	70.0	30.0
	4	56.1	43.8
	5	78.0	22.0
B	1	65.2	34.0
	2	64.0	36.0
	3	51.9	48.0
	4	60.0	40.0
	5	38.6	62.4
C	1	55.6	42.4
	2	57.9	42.1
	3	58.0	42.0
	4	61.8	38.2
	5	38.0	60.0
D	1	66.1	33.9

An analysis of the above results gave a chi^{2} value of 64.456 to 15 degrees of freedom. The probability value was less than 0.001.

Della Croce (1955) and Grigelis (1958,1961) have noted correlations between the presence and abundance of species and the nature of the substratum within a single locality. Szczepanski (1953) and Grigelis (1961) considered that the substratum was the most important factor in determining the distribution and abundance of tubificids. Della Croce (1955) studied the relationship in considerable detail and claimed to have discovered a causitive relationship between the substratum and the abundance of the species. Brinkhurst (in press) has claimed, using Della Croce's figures, that no such relationship exists.

It is evident, then, that within a single locality there may be a superficial relationship between the presence of a species and the nature of the substratum. More usually it appears that no such relationship exists. Within a non-uniform or an apparently uniform habitat the proportions of the species present may vary in a manner unrelated to any physical characteristics of the habitat. Over long periods of time the relative proportions of the species may remain constant, although at any one time considerable spatial variation may be found. The existence of such a large degree of variability within a single locality presents many problems in the selection of a suitable sampling technique, a point which will be discussed more fully in chapter 5. It is evident that a single sample may give a totally false picture of the species present and their abundance, and that several samples must be taken in each locality. The labour involved in this procedure has prevented the abundance of Limnodrilus being considered in the current section.

c) DISCUSSION

One of the major aims in the present study was to determine whether any differences existed in the distribution of the species of Limnodrilus. The problem has been approached by studying the distribution of Limnodrilus in areas of progressively decreasing size, and by attempting to discover the factors responsible for the distribution of each species within each area.

A study of the geographical distribution of the genus showed that some species were apparently restricted to certain zoo-geographical regions, while others were cosmopolitan. The distribution of L. grandisetosus and L. neotropicus, the two most restricted species, was not considered any further. The remaining five species of the genus occur in Britain. A study of their distribution in this country suggests that two of them have recently been introduced. Limnodrilus cervix appears to be a nearctic species now spreading throughout the canal system and L.helveticus a palaearctic species, hitherto confined to the continental mainland, but now established in Britain. Since both species still appear to be in the immigration stage of invasion their distribution in Britain was not considered any further. The remaining three species are widespread throughout the country, but L.udekemianus and L.claparedeanus show evidence of being patchy and more local.

The relationship between the distribution of these three species and the abiotic factors of the environment was then considered in detail. Correlations have been noted between the distribution of the species and some chemical factors, such as salinity and metal ions. Despite the existence of such correlations, however, it is still not possible to recognise the habitat preferences of each species. All three species occur in all types of habitat examined, although the occurrence of L.udekemianus and L.claparedeanus was more sporadic than that of L.hoffmeisteri. The attempt to recognise habitat preferences was considerably hampered by the inability to consider the abundance of each species in each habitat. Studies in the literature suggested that the nature of the substratum might be of importance in this respect, as correlations between the nature of the substratum and the relative abundance of each species have been noted by authors on several occasions.

Factors limiting the distribution of the genus as a whole were noted, but it proved impossible to recognise factors that limited the distribution of individual species. That such factors must exist is evident from the restricted distribution of *L.udekemianus* and *L.claparedeanus*. The absence of monospecific populations of either of these two species suggests that their ecological requirements may be the same as those of *L.hoffmeisteri* but that their tolerance limits may be more restricted. It appears, then, that with a few exceptions, abiotic factors are of little importance in determining the distribution of the species of *Limnodrilus*. This is confirmed by studies in apparently uniform habitats in which it was shown that the relative abundance of *L.hoffmeisteri* in particular varied in a manner unrelated to any observed abiotic factors, but that such variations were unlikely to be due to chance alone. Even in an obviously non-uniform habitat it was found that, despite a superficial appearance of stability, the relative abundance of all the species of *Limnodrilus* and their distribution varied in a manner that could not be related to observable abiotic factors.

From the foregoing remarks it is evident that it may well be biotic factors that are important in determining the distribution and abundance of the species of Limnodrilus. Little is known about the relationship between any species of tubificid and the biotic factors of their environment. The effect of parasitism on a population of Limnodrilus will be discussed in Chapter 6. It will be shown that this is negligible. The literature on predation is sparse, and nothing can be said about its possible effects.

The biotic factor that appears most likely to influence the distribution and abundance of the species of Limnodrilus is the availability of a suitable food supply. The exact nature of the tubificid food is unknown. They are known to feed by ingesting the substratum, digesting only the organic detritus or bacteria present. Poddubnaya (1961) has shown that the nature of the substratum is of importance in the feeding behaviour of the tubificids and that although some degree of specific selectivity may occur different species appear to ingest particles of similar size and nature. Nevertheless, the possibility that different species may be utilising different components of the food matter remains. If this is so, correlations observed between the abundance of a species and the nature of the substratum may be explicable in terms of the abundance of the food supply in different types of substratum. Similarly, the differences in the relative abundance of species in an apparently uniform habitat may be related to hitherto undetected differences in the nature of the food supply. If L. udekemianus and L. claparedeanus have a more restricted food preference than L. hoffmeisteri it may explain their restricted distribution and their relative paucity, where they do occur. At present these are only speculations unsupported by any direct evidence but, with the failure to explain the distribution and abundance of Limnodrilus in terms of abiotic factors, they provide a possible explanation for the observed facts and hence require fuller investigation.

CHAPTER 4

THE GROWTH AND REPRODUCTION OF LIMNODRILUS

Since one of the primary aims of the present study was to investigate the life histories of the species of Limnodrilus a knowledge of the growth and reproduction of the species was obviously necessary. These aspects of the biology of Limnodrilus have been little studied. Knowledge of the life histories and of the reproductive behaviour in the genus is based primarily upon inference from the morphology of the genitalia and from observations on other genera. Accordingly, an attempt has been made here to clarify certain aspects of the growth and reproduction of Limnodrilus that were considered to be of importance if an understanding of data derived from field observations is to be arrived at. In particular, it was considered that more information was needed on methods of age determination; on the length of time spermatophores were retained in the spermathecae; on the degeneration of the gonads after breeding and on the extent to which asexual reproduction occurred. Most of the observations were made on L. hoffmeisteri, as sufficient specimens were readily obtainable at all times of the year.

a) THE GROWTH OF LIMNODRILUS HOFFMEISTERI.

In studies on invertebrate life histories both the length and weight of individual specimens have frequently been used as indications of their age and to determine growth rates (Mann, 1961, Reynoldson, 1960). In an analysis of any animal population it is obviously desirable to be able to recognise age classes. Both length and weight provide easily measurable criteria of these since both normally increase in a definite relationship.

In the case of tubificids, however, there are serious objections to the use of both criteria. Both the length and weight of a worm depend not only on its age but also on its condition. Regeneration or autotomy, both of which occur in L.hoffmeisteri, will upset the normal length or weight to age relationship. Furthermore, the preserving agents in use for tubificids generally cause shrinkage and frequently also distorsion, making length measurements very difficult. These latter difficulties could be overcome by examining live specimens, but this involves considerably greater labour. It is considered, therefore, that neither length nor weight are suitable criteria for age determinations of specimens of Limnodrilus.

In a search for alternative characters that increased with age, attention was drawn to the number of segments and the number of chaetae per bundle. Since the number of segments is to a large degree dependant upon the extent to which regeneration has occurred, it was considered to be unsuitable for present purposes. Attention was therefore directed to the number of chaetae per bundle. It was shown in table 1 that average number of chaetae in a dorsal bundle of segments 2 - 7 (referred to henceforth as the chaetal number) increases with the age of the specimens - the mean number for immature specimens being 5.4 and for mature specimens being 6.9. It was decided to investigate this relationship more closely. Two laboratory cultures of *L.hoffmeisteri* were set up, one on muddy sand and one on mud. Both cultures commenced with breeding specimens. All specimens were examined at monthly intervals and the state of maturity and chaetal number recorded for each specimen. The results are shown in figs. 15 and 1

Several interesting results emerge from these observations. No chaetal number of less than 3 was recorded, and it must be concluded that specimens do not hatch with a number less than this. It is apparent that the chaetal number does increase with age, but the relationship is not a linear one and the number cannot be used to determine the age of individual specimens. After hatching with a chaetal number of 3 or more, the number increases rapidly to 5. It may then increase slowly to 6 or remain at 5 for a long period.

Figure 15

The relationship between the average number of chaetae per bundle in the anterior dorsal segments, the state of maturity and the age of specimens from a laboratory population of *L. hoffmeisteri* living in sandy mud. Solid segments indicate breeding specimens, hollow segments mature and immature ones. The number given above the month is the number of specimens examined.

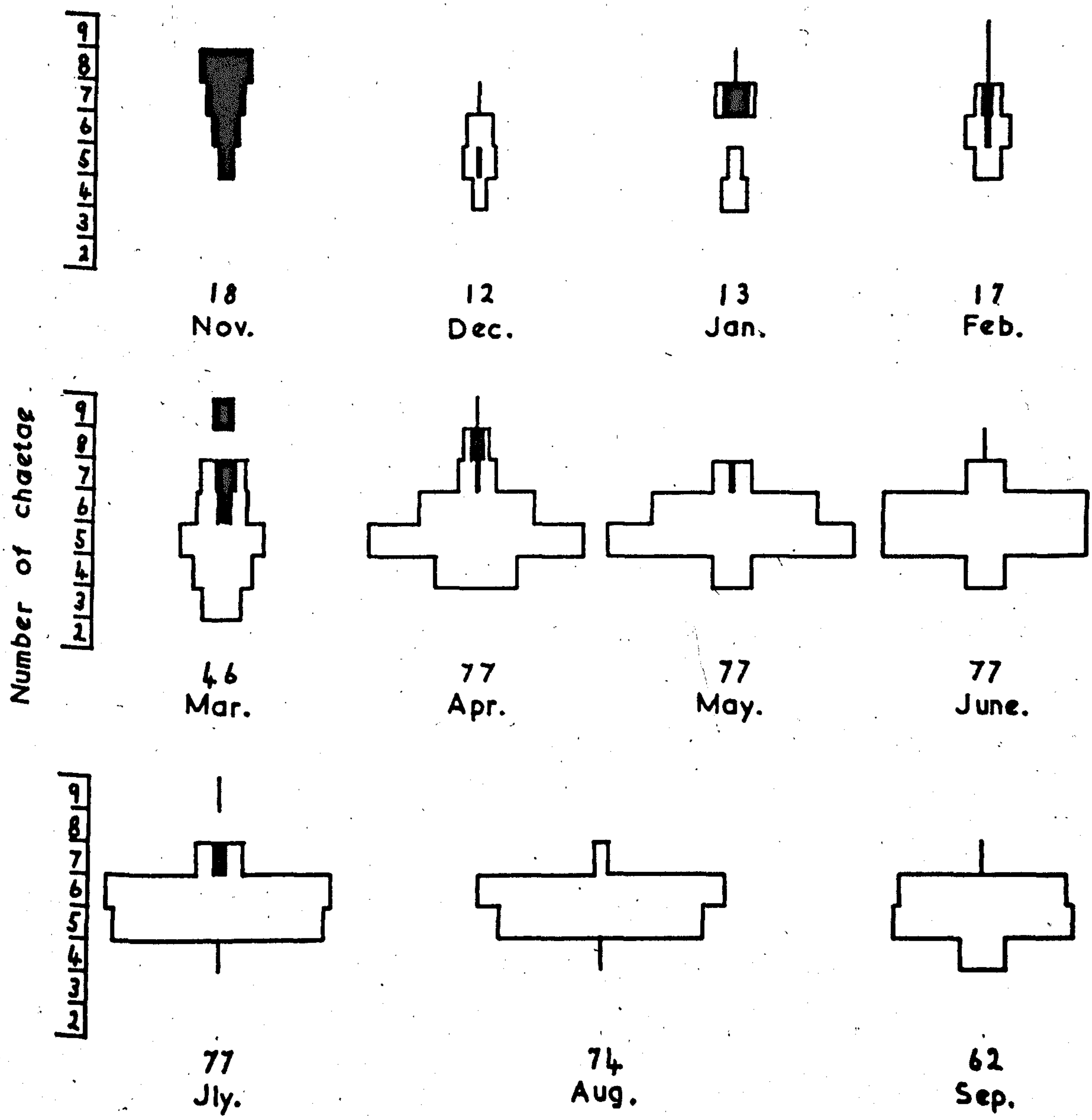
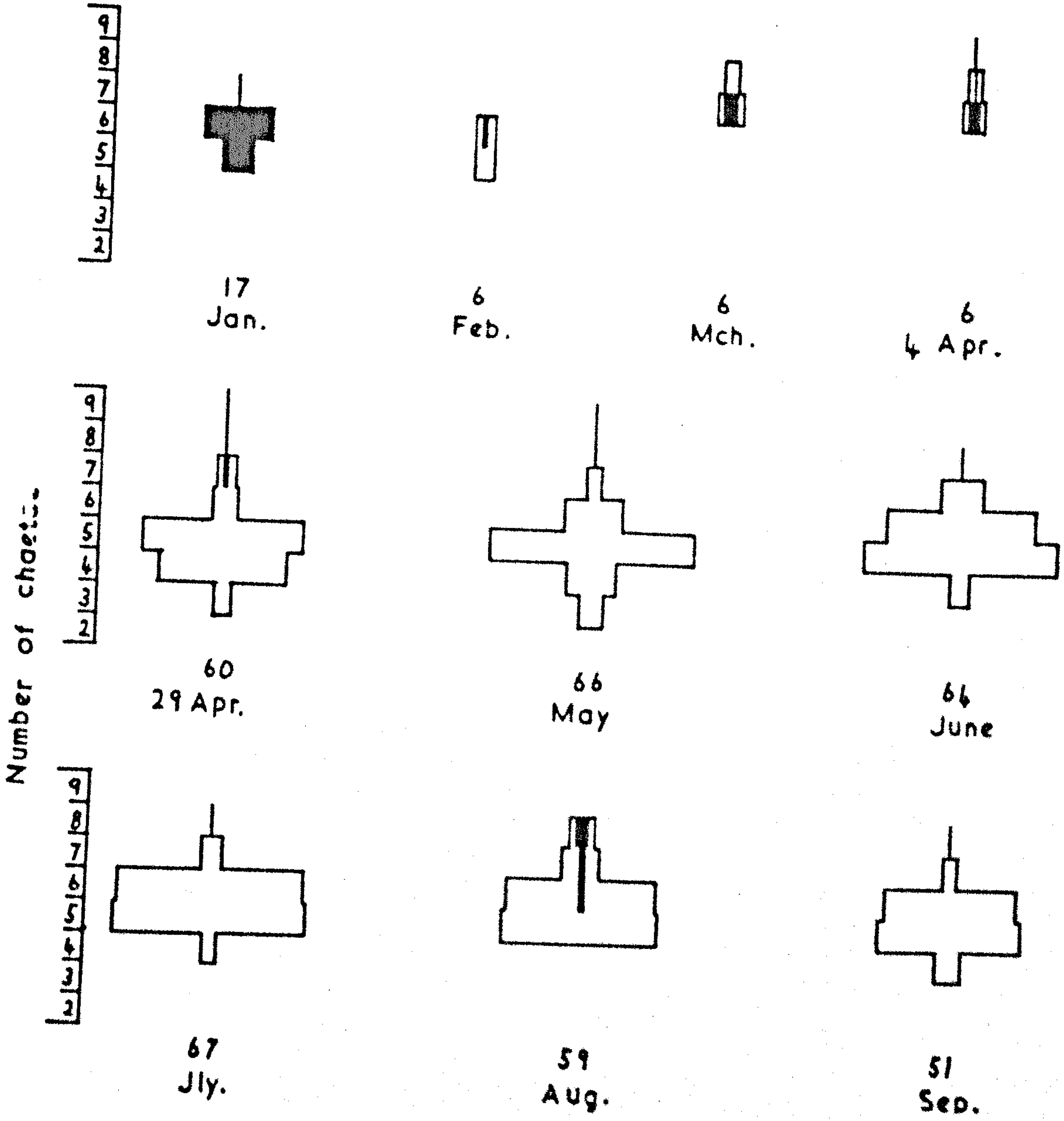

Number of chaetae
2
3
4
5
6
7
8
9
18
Nov.
12
Dec.
13
Jan.
17
Feb.
46
Mar.
77
Apr.
77
May.
77
June.
77
Jly.
74
Aug.
62
Sep.

Figure 16

The relationship between the average number of chaetae per bundle in the anterior dorsal segments, the state of maturity and the age of specimens from a laboratory population of *L. hoffmeisteri* living in mud.

For explanation of symbols see figure 15.


Number of chaet
9
8
7
6
5
4
3
2
17
Jan.
6
Feb.
6
Mch.
6
4 Apr.
60
29 Apr.
66
May
64
June
67
Jly.
59
Aug.
51
Sep.

This is shown clearly in the figures for June to September for both cultures, as by this time no further increase in the number of specimens occurred. The increase in the size of the population was slower and the time taken for the chaetal number of 5/6 to be attained by the majority of specimens took longer for the specimens on the muddy sand (fig. 15). The rate of addition of chaetae is thus also influenced by the nature of the substratum. A specimen with a chaetal number of 5 may therefore be from less than 1 up to 6 months old. These observations (figs. 15 and 16) confirm the earlier one (table 1), that the chaetal number of mature specimens is higher than that of immature ones, but shows clearly that a considerable overlap may exist.

The change in chaetal number after breeding is shown more clearly in fig. 15. During the breeding period the chaetal number increases and after breeding it may continue to increase up to 9 (Dec. to Feb., and March to April). Occasionally specimens with a chaetal number of 10 have been encountered (table 1). This appears to be the maximum attainable. Observations of isolated specimens has shown that at this stage the specimens either die, or the chaetal number starts to decrease, falling to 5 or 6. The worms are then indistinguishable from immature ones. It may be concluded that although the chaetal number does increase with the age of the specimens, it is unsuitable for determining the age of individual specimens. It is also unsuitable for distinguishing immature specimens from specimens that have already bred.

At present, therefore, it is not possible to separate a population of L.hoffmeisteri into age classes. The most that can be done in this respect is to separate the population into classes based on the state of maturity of the specimens, since breeding and mature specimens are older than immature ones. This must be considered far from satisfactory but no alternative is yet possible.

It is convenient at this stage to refer briefly to the work of Poddubnaya (1959, 1963). In considering populations of Tubifex newaensis she was able to use length and weight in order to distinguish age classes. This species is readily identifiable alive, so that many of the objections raised earlier do not apply here. She used the length and diameter of individual chaetae as criteria of age, and found a relationship similar to that of the chaetal number and age. She also used the biomass of L.hoffmeisteri to demonstrate the changes in the structure of a population, but divided the specimens into the same three groups of immature, mature and breeding specimens as is proposed here. She gives no indications as to whether her specimens were examined dead or alive.

b) REPRODUCTION OF LIMNODRILUS HOFFMEISTERI

1) The breeding cycle.

In the development of the gonads and genitalia the testes are the first organs to appear. They persist throughout the whole period of maturity and, even after breeding, seldom degenerate completely. The ovaries, on the other hand, appear slightly later and decrease in size as the ovisac develops until, at maturity, they are frequently absent. Maturation of the ova occurs in the ovisac. The gonads may be present for several months before the genitalia start to develop.

The rudiments of the genital ducts appear first, followed by the rudiments of the spermathecae. The atrium first appears as a swelling in the genital ducts and later develops into its characteristic shape. The prostate gland then develops. The spermathecal rudiments appear as a solid ball of cells which later hollows out to form a thin walled sac and a thicker walled duct. The testes sacs and ovisacs then make their appearance and increase in size as proliferation of cells from the testes and ovaries begins. The male, female and spermathecal pores then appear. After the appearance of the male pores the chitinous penis sheaths develop. The stages in development of a sheath are shown in fig. 5. The head is laid down first. Increase in length and thickening of the wall are brought about by the activity of the cells of the invagination of the body wall, especially those close to the base of the sheath. The invagination necessarily penetrates deeper into the body cavity as the sheath lengthens. There is very little increase in the width of the sheath or in the thickness of its walls as it lengthens. Even in <u>L.cervix</u> the wall develops to its full thickness at an early stage. The development of the penis sheath takes place very rapidly.

The present study most of the specimens were cleared in Amman's lactophenol for examination. Whilst this rendered the chitinous structures readily visible it often proved difficult to see other details of the genitalia. Accordingly, only three stages of maturity are recognised here. The first stage is that of immaturity, before the penis sheath has appeared. The second stage is that of maturity, when the penis sheath has appeared. The presence of the sheath alone is taken to indicate this stage, and no account is taken of its length. The third stage recognised is that of breeding. This is recognised by the presence of spermatophores in the spermathecae, signifying that copulation has taken place. As explained in the previous section it is not possible to sub-divide the immature stage or to recognise a post-breeding stage.

According to the views of earlier authors, biparental reproduction, due to reciprocal fertilisation, is the predominant method of reproduction in Limnodrilus. This view is based upon indirect evidence and on inference from the anatomical arrangement of the genitalia. Spermatophores were always considered to have been formed from sperm from another individual. Gavrilov, in a series of papers (1931 et seq.), has challenged this view and has shown that self fertilisation is not only possible but also common in some species of Limnodrilus.

In L.udekemianus, Gavrilov (1931, 1935, 1949) showed that self fertilisation took place by autocopulation. The penis tube was so short that by bending the worm could fertilise itself. The existence of uniparental reproduction in L.hoffmeisteri and L.claparedeanus was also demonstrated (Gavrilov, 1931) but no suggestion was made at that time as to its mechanism. Later (Gavrilov, 1939, 1948) it was suggested that self fertilisation or parthenogenesis was equally possible. In a review of the subject (Gavrilov, 1959) it was considered that auto copulation was most unlikely owing to the length of the penis tubes in these two species.

He considered that self fertilisation i.e. fertilisation of the eggs in the cocoon while the cocoon was in the process of formation, or fertilisation of the eggs in the ovisac, was more likely than parthenogenesis. It was stated, however, that when spermatophores were present they were probably formed from the sperm of other individuals. It must be presumed that this remark did not apply to L. udekemianus where self copulation is possible.

Gavrilov's conclusions were based entirely upon laboratory experiment and observation, so the extent to which uniparental reproduction occurs in the field is still unknown. Even if it does occur to any great extent, it does not invalidate the category of breeding specimens as understood by the author. The presence of spermatophores is still an indication that copulation has occurred. There remains the possibility that specimens assigned to the mature class because of the absence of spermatophores may in fact have undergone self fertilisation. This can not be detected by the present methods of examination. Since, however, in field populations large numbers of mature specimens were nearly always followed by large numbers of breeding specimens, it was concluded that if uniparental reproduction did occur it did not do so to any extent, and it was accordingly ignored. Specimens were occasionally encountered in which the genitalia, including the penis tube, were not fully developed, but which possessed spermatophores. This appears to be evidence for non-reciprocal copulation, but it occurred only in approximately 0.02% of all specimens examined.

Since the presence of spermatophores was taken to indicate that copulation had occurred, it is obviously of importance to know how long they are retained in the spermathecae. Accordingly, breeding specimens were taken from field populations and observed at regular intervals in the laboratory. The results of these observations are shown in Table 13. It must be emphasised that this only indicates the minimum period for which spermatophores were retained, as there was no way of knowing how long they had been present before the specimens had been collected. It can be seen that on a sandy substratum spermatophores persist in some individuals for up to 1½ months, but that the majority have disappeared after two weeks. On a muddy or sandy-mud substratum the majority have disappeared after two weeks also, but in some individuals they persist up to a month.

TABLE 13

The period of retention of spermatophores in the spermathecae of L. hoffmeisteri living in different types of substrata.

	Nature of substratum					
Date	Sand		Sandy-mud		Mud	
	N	T	N	T	N	T
24 Oct.	55	55				
1 Nov.	17	21				
12 Nov.	5	15				
19 Nov.	5	15	18	18		
28 Nov.	5	15	14	14		
6 Dec.	3	15	8	12		
13 Dec.	2	15	2	12		
20 Dec.	0	15	1	12		
8 Jan.	0	13	1	12		
23 Jan.	0	12	4	13	17	17
7 Feb.	0	10	6	14	3	6
20 Feb.	0	10	6	17	1	6
9 Mar.	1	10	8	19	3	6
22 Mar.	0	9	9	46	4	6
4 Apr.	0	9	7	59	3	6
29 Apr.			0	77	2	60
21 May					0	66

Legend. N = Number of specimens with spermatophores.

T = Total number of specimens in the population.

It is also apparent from Table 13 that some individuals may breed twice within the same season. This is shown more clearly for the specimens cultured on the muddy substratum. The total number of specimens remained constant from 7 February to 4 April, but during this time the number of specimens with spermatophores first fell to 1 then increased again to 4. There was no evidence of recruitment into the population during this period, so the only possible explanation is that specimens had shed their spermatophores and then some individuals have bred again. There is also evidence of breeding occurring for a second time in the specimens cultured on the sandy-mud, but since recruitment was occurring in the population this is not as apparent. It is shown in figs. 15 and 16 that individuals do not attain maturity for at least 4 months, so the observed increase in the number of breeding specimens in February and March must again be due to specimens breeding for a second time. There is no evidence of this occurring in specimens cultured in sand. In order to confirm this, observations were made on isolated specimens cultured in the same three media. The observations confirmed the above suppositions. The specimens in mud and sandy-mud did breed twice, but those in sand did not.

A further interesting feature emerged from these observations. The specimens cultured in sand did not produce any young and the size of the population continued to dwindle. In contrast, young individuals were produced from the specimens cultured in mud and sandy-mud, and the size of both populations increased approximately 4 times. As is apparent from figs. 15 and 16, the increase took place in a shorter time in the population living in mud. The three cultures were kept under similar physical and chemical conditions, and the specimens were all taken originally from the same locality. The only difference between them was in the nature of the substratum. It must be concluded therefore that this can influence the rate of increase of the chaetal number, the number of times a specimen breeds within each season, the number of individuals produced and the rate of increase of the population. The implications of these findings in relation to the interpretation of field data will be considered in chapter 5.

The fate of individuals after breeding is also of importance to a study of the life history. It can be seen from table 13 that, regardless of the nature of the substratum, there is a heavy post-breeding mortality. This is less for specimens cultured on the sandy-mud (33%), but for the other two cultures is fairly high (64% and 73%). Nevertheless, some specimens do survive and may breed again as indicated above. It is not clear whether those specimens that have bred twice then die or whether they can survive until the next season. The evidence suggests the latter. In table 13 it can be seen that second breeding is not followed by any noticeable mortality, but the recruitment into the population at this time would tend to obscure this. Observations on isolated specimens show that some can survive until the next season.

Degeneration of the genitalia following breeding has been shown to occur in Tubifex tubifex by Cernosvitov (1930). It has been observed in L.hoffmeisteri in the present study, and the process is essentially the same as that observed in T.tubifex. After the shedding of the spermatophores degeneration begins simultaneously in all the genital organs. The remains of the disintegrating tissues are devoured by lymphocytes. The genital ducts disappear first, then the spermathecae and penis sheaths. The testes and ovaries remain as rudiments throughout the non-reproductive season.

No mention has so far been made of the clitellum. This structure is present at maturity in all species of Limnodrilus, but its degree of development varies individually and specifically. It may be well developed in *L.udekemianus* and *L.helveticus*, but is poorly developed in *L.hoffmeisteri*, *L.claparedeanus* and *L.cervix*. In these three species it is generally little more than a slight swelling of the epidermis with a few scattered papillar, and is relatively transparent. Although Poddubnaya (1959) uses the presence of a clitellum in *L.hoffmeisteri* as an indication of breeding specimens, it is considered that the presence of spermatophores is a more reliable criterion. No relationship has yet been established between the degree of development of the clitellum and the incidence of breeding.

A discussion on the time taken to attain maturity and on the period of breeding is deferred until Chapter 5. It is sufficient to indicate here that it appears that most specimens breed in their first year, but others may take two years to attain maturity. The period of breeding depends on the site and the nature of the substratum. It may take place all the year round or be confined to a short season. The average life span is not known. Since most specimens take one year to attain maturity and the majority die after breeding it is estimated at one year. Some few specimens will continue longer than this, but they will undoubtedly decrease in number each year. Cernosvitov (1930) records a laboratory specimen of *T.tubifex* over 10 years old.

Development in tubificids, in common with all oligochaetes, is said to take place in cocoons. Cocoons of L.hoffmeisteri have been found and reported by Poddubnaya (1958) and Gavrilov (1935), and of L.udekemianus and L.claparedeanus by Gavrilov (1935 et seq.). Cocoons of other species of tubificids have been found by several authors. The whole subject is treated in detail by Stephenson (1930) and Cekanovskaya (1962). In the course of the present study cocoons of L.udekemianus and L.claparedeanus have been observed in both field and laboratory populations. The author, however, has completely failed to find cocoons of L.hoffmeisteri, L.helveticus and L.cervix. Since the latter two species do not occur abundantly and cocoons are only produced over short period, it is possible that they could have been overlooked. It proved impossible to establish populations of either species in the laboratory where closer examinations could have been made.

The absence of cocoons in L.hoffmeisteri, however, is not so readily understood. All cocoons taken from field localities where this species occurred were brought back to the laboratory and hatched out. No specimens of L.hoffmeisteri were obtained from the cocoons. In some localities where this species occurs no live cocoons were found in the samples at any time. It was considered that the sampling methods in operation might possibly have been unsuitable for collecting cocoons, but no cocoons have been found in the laboratory cultures either. Cultures in mud and sandy-mud (referred to above and in figs. 15 and 16) were sieved through meshes of 0.4 mm. diameter, a size known to retain cocoons of other species, but no cocoons were obtained. Nevertheless, development must have occurred, as young worms appeared in the populations and the populations continued to increase in size. Cultures kept for other purposes in sand were examined and although the population again increased and young specimens were found, no cocoons were observed.

Poddubnaya (1958) records the cocoons as being attached to vegetation, and although this could explain their absence from bottom field collections, it does not explain their absence from laboratory populations. She records the time of development in cocoons as 28 - 35 days at 14 - 15 deg. C. Since the author's laboratory cultures were examined at weekly intervals it is unlikely that they can have been overlooked. It must be concluded, therefore, that L.hoffmeisteri has the ability to complete its development without the production of cocoons. The details of this form of development are unknown, and require further study. It is possible that other species of Limnodrilus may also possess this ability. It appears likely that Poddubnaya may have encountered this problem to some extent, as she refers (1958) to L.hoffmeisteri producing very few cocoons in her laboratory. She herself attributed this to the conditions of the cultures. In her field observations (1959) she does not say how she identified cocoons of this species. Since several other genera were present in her samples there is no indication that the cocoons found by her were in fact produced by L.hoffmeisteri. It is not suggested here that L.hoffmeisteri is incapable of producing cocoons; the works of Poddubnaya (opp.cit.) and Gavrilov (1931 et.seq.) indicate clearly that it can. It is suggested, however, that this may not be the only, or exclusive, method of propagation.

2) Asexual reproduction and regeneration.

Throughout the foregoing discussions on the reproduction of Limnodrilus it has been assumed that sexual reproduction is the dominant method of propagation in the genus. From the little information on this subject in the literature this does appear to be so. Asexual reproduction does not seem to attain the same importance in the Tubificidae as in the Naididae, where it is frequently the dominant method of reproduction.

It is dismissed as being of little importance in the family by Stephenson (1930) and Cekanovskaya (1962). Poddubnaya (1958) states that it is known that tubificids only breed sexually. There is some evidence that it may be of some importance in some genera, principally Aulodrilus (Hrabě, 1934) and Bothrioneurum (Hrabě, 1937). The general concensus of opinion, as summarised by Vorontsova and Liosner (1960), is that asexual reproduction plays little, if any, part in the reproduction of tubificids.

Nevertheless, in the absence of any information relating specifically to Limnodrilus, it was decided to conduct a short series of experiments on the regenerative ability of species of the genus. Autotomy, which has been shown to occur extensively in Tubifex newaensis (Poddubnaya, 1959), has on occasions also been observed in L. hoffmeisteri. It was further observed that specimens frequently fragmented (as distinct from autotomy) during handling, or as a result of mechanical damage. It was desired to know the fate of these fragments, and whether new individuals could develop following fragmentation. The relationship between regenerative powers and asexual reproduction is a close one (Vorontsova and Liosner, 1960). It was considered that these experiments on regeneration would also give an indication of the degree of asexual reproduction that was possible.

Specimens with regenerated posterior portions, recognisable as such by their transparency and by the narrower diameter of their segments, were commonly encountered in field collections. The incidence of specimens with a regenerated head, recognisable in the same manner, was very low, being less than 0.01%. It was also observed that specimens that had fragmented did not die or decay, but normally survived. It was accordingly determined to cut specimens of *L.hoffmeisteri* and *L.udekemianus*, the two most easily obtainable species, between certain specified segments and record the fate of both fragments. Controls were set up simultaneously to obtain an indication of the mortality subsequent to such fragmentation.

The results of these experiments are summarised below:-

L.hoffmeisteri

Position of cut	Fate of fragments	
	Anterior	Posterior
3/4	Decayed and lost.	May heal over and eventually decay, or may grow new head of prostomium, peristomium and mouth.
8/9	Decayed and lost.	Usually just heals over. Only 1% developed a new head.

	Anterior	Posterior
12/13	Heals over. New tail rarely developed.	Heals over. Does not grow a new head.
24/25	Grows a new tail.	Heals over. Does not grow a new head.
44/45	Grows a new tail.	Decayed and lost.

L. udekemianus

Position of cut.	Fate of fragments	
	Anterior	Posterior
3/4	Decayed and lost.	May just heal over, but usually develops a new head.
12/13	Heals over, but often grows new tail.	Heals over. Does not grow a new head.
24/25	Grows a new tail	Heals over. Does not grow a new head.

The average mortality following fragmentation was 50%.

In the case of posterior portions that healed over and did not develop a new head, mortality did not occur for a considerable period after the operation. They survived for up to two months in some cases, but eventually decayed and were lost.

The general picture presented by these experiments is that two new individuals are never produced following fragmentation. If separation has occurred anterior to segment 12, an individual develops only from the posterior portion; if posterior to segment 12, only from the anterior portion. Posterior regeneration appears to be better developed than anterior, as fragmentation has to take place very close to the head to produce a new head. Abnormalities with two tails were of frequent occurrence. These results are in agreement with those of Poddubnaya (1959) on *T. newaensis*, who failed to find regeneration of the head after autotomy, and of Krecker (1910) on *L. claparedeanus*, who found that no new head was formed unless fragmentation occurred in the first seven segments.

There is therefore no evidence from these experiments that *L. hoffmeisteri* and *L. udekemianus*, and by inference other species of *Limnodrilus*, can reproduce by asexual methods to any great extent. Regeneration appears to be fairly well developed, but the major effect of this will be to upset the length: age relationship. Fragmentation, whether due to autotomy or accident, does not result in the formation of new individuals. In future discussions on the reproduction of *Limnodrilus* no further reference will therefore be made to the possibility of asexual reproduction, and the genus will be considered to exhibit only sexual reproduction.

CHAPTER 5

THE LIFE HISTORIES OF THE BRITISH SPECIES OF LIMNODRILUS

a) FIELD INVESTIGATIONS

Several factors were important in selecting localities for regular seasonal sampling. These may conveniently be grouped together under physical and biological factors. The principal biological factors were that at least one species of Limnodrilus should occur in the locality and in sufficient numbers to ensure that results would be reliable. It was also desired to study the life history of each species in at least two sites; one in which it formed a single species population or was the dominant species, and one in which it occurred in a mixed species population. Sites were also selected on the basis of their physico-chemical characteristics, so the nature and suitability of the substratum for quantitative samplin had also to be considered. It was hoped that ultimately it would be possible to compare the life history of each species in different habitats and then to compare the life histories of the different species and their population biology in the same habitat. On the basis of these criteria, regular samples were taken over a period of a year or more at six localities i.e. a canal, a small stream, a large river, a small pond and two lakes.

1) Description of localities.

In the following section only a brief description is given of each locality from which regular samples were taken. Where possible reference is given to a work in which the locality is described in greater detail. Only the tubificid fauna of each locality is listed. No indication is given of the relative abundance of each species. It has been shown in chapter 3 that the relative abundance of species may vary considerably from site to site within a single locality. An estimate of the overall abundance of a species in any locality may therefore obscure the fact that it may be common in one site and rare in another, and consequently such an estimate will have little meaning. The relative abundance of the species of Limnodrilus in each sample from each locality are given in appendix 1.

The Shropshire Union Canal, near Backford, Cheshire.

A detailed account of the history, the physiography, the flora and the fauna of this canal is given by Twigg (1959). The canal in the Backford region is a broad canal; the width of the bed was estimated at 30 feet with a maximum depth of 6 feet in the centre. The canal is seldom used for commercial or pleasure traffic and is rapidly falling into disuse. During the course of this survey the vegetation, although it is still cut at intervals, has spread along the banks and into the shallower regions of the canal. Backford is situated at the base of the Wirral peninsula and on the edge of the fertile Cheshire plain. The canal in this region receives drainage from rich arable pastures. The basic substratum is clay, on top of which is a layer of rich organic mud. The fauna is rich and varied and, together with the physical and chemical characteristics, indicates a very productive habitat. The following tubificid species occur:-

L.hoffmeisteri
L.claparedeanus
L.cervix
L.udekemianus
Euilyodrilus moldaviensis
E.hammoniensis

Ditton Brook, Cronton, Lancs.

This is a small stream about 10 feet wide and 2 feet deep in summer. In winter, the water level may rise considerably and the rate of flow increases causing scouring of the banks and substratum. The main stream receives coal washings from a nearby colliery. Just above the sampling site the stream receives a small tributary, which is enriched by an organic effluent from a farm. The substratum consists of mud and organic debris, and also some small coal particles. The stream, undoubtedly, suffers from organic pollution but little de-oxygenation occurs due to the rapid rate of flow and shallow depth. The fauna is indicative of pollution, being low in the number of species but rich in the number of individuals. The following tubificid species occur:-

L.hoffmeisteri
L.udekemianus
L.helveticus
T.tubifex

Raby Pool, Near Raby, Cheshire.

This is a small pond serving as a water supply for cattle. About half of the total area is covered by emergent vegetation. The open water is about 2 feet deep. The substratum is thick clay overlain by a thin layer of sand and organic debris, the latter derived primarily from animal faeces. The pond receives drainage water from the field and from a nearby golf course. It is thought that this drainage at certain seasons contains lead arsenate (p.3.31). The fauna of the pond is sparse, and the tubificids form the dominant group. The following species occur:-

<u>L.hoffmeisteri</u>
<u>L.helveticus</u>
<u>L.claparedeanus</u>
<u>L.udekemianus</u>
<u>T.tubifex</u>

<u>River Thames, Reading, Berks.</u>

The R.Thames at Reading is about 50 yards wide and about 12 feet deep in the centre. It has a medium flow rate, and is subject to heavy flooding in winter and early spring. The substratum varies, and emergent vegetation is found only on one bank (Brinkhurst, 1960). The river receives both organic and inorganic pollution from the town of Reading. The fauna is nevertheless a rich and varied one, and the following 15 species of tubificids are known to occur:-

<u>L.hoffmeisteri</u>
<u>L.udekemianus</u>
<u>L.cervix</u>
<u>L.claparedeanus</u>
<u>E.moldaviensis</u>
<u>E.hammoniensis</u>
<u>E.bavaricus</u>
<u>T.tubifex</u>
<u>T.ignotus</u>

Psammoryctes barbatus
P.albicola
Rhyacodrilus coccineus
Aulodrilus pluriseta
Peloscolex velutinus
Branchiura sowerbyi
The habitat must be regarded as a rich and productive one.

Windermere

This lake has been the subject of many generalised and many specialised studies, and reference to the following works may be made for details; Moon (1934), Humphries (1936) Boycott (1936). The distribution of the tubificids in the lake has been studied by Brinkhurst (in press, b). The lake is considered by the above authorities to be mesotrophic one. The tubificids known to occur are:-

L.hoffmeisteri
T.tubifex
T.templetoni
A.pluriseta
P.ferox

Llyn Tegid.

This lake has been the subject of several ecological studies. A general account of its physiography and of the bottom fauna is given by Dunn (1961). The lake is considered by her to be an oligotrophic one tending towards mesotrophy. The tubificids known to occur are:-

<u>L.hoffmeisteri</u>

<u>T.ignotus</u>

<u>E.hammoniensis</u>

<u>P.ferox</u>

<u>A.pluriseta</u>

2) Methods.

The variation in abundance of tubificid species within a single locality (discussed in chapter 3) presents a considerable problem in the preparation of a sampling programme. The existence of such a high degree of spatial variation necessitates the taking of duplicate samples on all occasions. In order to obtain an accurate indication of the degree of spatial variation a large number of samples must be taken. The number of samples that can be taken, however, is limited to a large extent by the time available for their sorting and identification. The sampling programme must therefore aim to strike a balance between the two requirements. In the present study a series of preliminary samples was taken at each locality in order to give an indication of the spatial variation in abundance that existed. The number of samples to be taken on regular visits to each locality was then determined on the basis of the degree of spatial variation that had been shown to exist, the amount of material present in each sample and the time available for its examination.

The sampling method varied in different localities. It was determined primarily according to the nature of the substratum and the accessibility of the locality. The size of sampler used was determined by the density of the tubificid population.

In the Shropshire Union Canal, samples were taken with a dredge of 1 mm. mesh. All samples in which the dredge was not full of mud were rejected. Although the dredge is not regarded as an instrument suitable for quantitative estimates, the duplicate samples agreed very well with each other (Appendix 1) both in regard to the total numbers of tubificids and the number and maturity classes of the individual species. The agreement is sufficiently accurate to enable deductions to be made from the changes in overall abundance. After a preliminary sieving in the field the samples were brought back alive to the laboratory and sieved through a 1 mm. mesh. Initially, they were sorted by hand, but as this was time consuming a less laborious method was adopted. The sample was spread out evenly on the mesh of the sieve, which was then suspended over a dish of water so that the mesh was just level with the surface of the water. A strong light was arranged about 1 foot above the sieve and in such a manner that it illuminated all parts evenly. This was left overnight and by morning the tubificids had passed into the dish from which they were easily removed. The method has been estimated as being on the average 99.4% efficient. Very small worms which are often missed by hand sorting are readily obtained by this method. Initially samples were taken at 3 weekly intervals, but after 12 months the interval was increased to 1 month. In the summer months sampling often proved difficult owing to the extensive growth of Rhizoclonium hieroglyphicum which blocked up the dredge. During January and February 1963 the canal was covered by 18 inches of ice, making sampling with the dredge impossible. An attempt was made to sample with an Ekman grab, but no reliable samples were obtained.

At Ditton brook the samples were taken by means of a corer. This consisted of a perspex tube of 15 mm. diameter and 2 ft. 6 inches in length. It was sealed at one end and fitted with a plunger of the same diameter as the tube. In use it was inserted into the substratum to a constant depth (10 cm.) and removed with a core of substratum of known volume. This could then be transferred to a bottle by means of the plunger. The agreement between samples was satisfactory in regard to maturity classes, but rather less so in regard to the total number of specimens (Appendix 2). The cores were brought back to the laboratory and sieved through a mesh of 0.41 mm. The specimens were sorted by hand. Sampling took place at monthly intervals over a period of 12 months. The rapid flow of water prevented the stream from becoming iced in the winter so that continuous sampling was possible.

At Raby pool were taken by means of a corer of similar construction to the one described above, but of 18 inches in length and 5 cm. diameter. The length of the core was determined by the thickness of the sandy layer, as the tubificids were not present in the thick clay. Initially two samples were taken at each visit, but as the size of the population declined (see p.3.32) up to 8 samples were taken. The agreement between samples was not very satisfactory (Appendix 3). The cores were brought back to the laboratory and sieved through a mesh of 0.41 mm. The specimens were sorted by hand. Sampling took place at three weekly intervals from March to October 1962, after which the interval was increased to 1 month. The thickness of the ice in January 1963 prevented sampling, which was, however, resumed the following month.

In the R.Thames the samples were taken by Dr. K. H. Mann in the course of a more general study on the productivity of the river. He kindly allowed me to examine the tubificids for the purpose of life cycle studies. The samples were taken at approximately 2 monthly intervals and at a series of regular stations on a transect across the river. Duplicate samples were taken at each station, with a grab biting an area of 20 by 22 cm. The agreement between samples is not very satisfactory (Appendix 6), but there is reason to believe (p. 5.53) that the sampling technique was not quantitative with regard to tubificids. The samples were sieved through a series of meshes graded down to 0.6 mm and sorted by hand.

The samples from Windermere and Llyn Tegid were made available to me through the kindness of Dr. R.O. Brinkhurst, who investigated the life cycles of other genera of tubificids. In Windermere each sample consisted of the contents of 2 Ekman grabs taken from 34 m. depth. The content of each sample was sieved in the laboratory and preserved, and later sorted by hand. The agreement between samples was fairly satisfactory (Appendix 4). In Llyn Tegid the samples were also taken with an Ekman grab, each sample consisting of the contents of 2 grabs. They were sieved in the field and sorted later. The agreement between samples was not very satisfactory with respect to L.hoffmeisteri (Appendix 5). At both localities samples were taken at monthly intervals over a period of 12 months.

In the Shropshire Union Canal, and occasionally in other localities, the number of specimens obtained in each sample was so large that in the time available it was only possible to examine subsamples. In such cases approximately 100 specimens from each sample were examined. The specimens were selected at random, the technique having first been tested and proved accurate (Appendix 7). For the reasons discussed on page 4.2 no attempt was made to weigh or measure specimens.

3) Interpretation of field data.

The interpretation of data derived from field investigations presents several problems. The principal of these arises from the variation in abundance of species from site to site within a single locality that may be observed in the field (pp. 3.33 - 3.38). The existence of such variation increases the difficulty of interpretation of data derived from monthly samples, as it is possible that the same population is not being sampled each month. The degree of variation that occurs in any one locality is indicated by the agreement of the duplicate samples. It can be seen from appendices 1 - 6 that this is generally satisfactory with regard to the proportions of the maturity classes of each species. The agreement is less satisfactory with regard to the number of specimens in each maturity class, the number of each species and the total number of specimens. The difficulties this presents in determining the density of each species will be dealt with in a later section.

In view of the agreement of results from duplicate samples with regard to the state of maturity of each species and the small number of specimens in many samples, after examination the samples were considered together for the purpose of compiling life history tables. Where possible the results are expressed in terms of the percentage of individuals in each maturity class. Whilst there are cogent objections to expressing data in percentages, this method of expression is adopted here for the following reasons; a) the direct use of numbers may be misleading due to the variation that exists between samples, as discussed above, b) in a discussion on the incidence and duration of breeding in a population the relative proportions of specimens in each maturity class is often more informative than the actual numbers, c) the use of percentages facilitates comparison of the life cycles in different localities.

There are several other difficulties in the interpretation of field data. The inability to identify immature specimens of Limnodrilus, except in the case of L.udekemianus, presents a problem. Where one species of Limnodrilus is dominant in a particular locality it has been assumed that the majority of immature specimens belong to that species. Where two or more species are co-dominant no such assumption may be made. In these localities where immature specimens can not be assigned to any one species, the results are expressed directly in numerals. The failure to find cocoons of Limnodrilus (p. 4.15) means that the presence of spermatophores must be taken as the sole criterion of breeding. The ability of Limnodrilus to breed twice in the same season (p. 4.11) must also be considered. The inability to recognise age classes makes it impossible to distinguish specimens that have bred and whose genitalia have regressed from immature specimens.

The time taken for specimens to attain maturity will also affect the interpretation of results. This will be dealt with in greater detail in a later section, but it is sufficient to indicate here that it takes several months at least. It is therefore impossible to recruit breeding specimens from cocoons between the sampling dates.

A further difficulty that arises is the paucity of some species, particularly L.helveticus and L.claparedeanus, in all the localities sampled. Little confidence could therefore be placed in the results obtained. In these cases it was considered that there was insufficient information to express the results in percentages.

4) Life histories as revealed by field investigations.

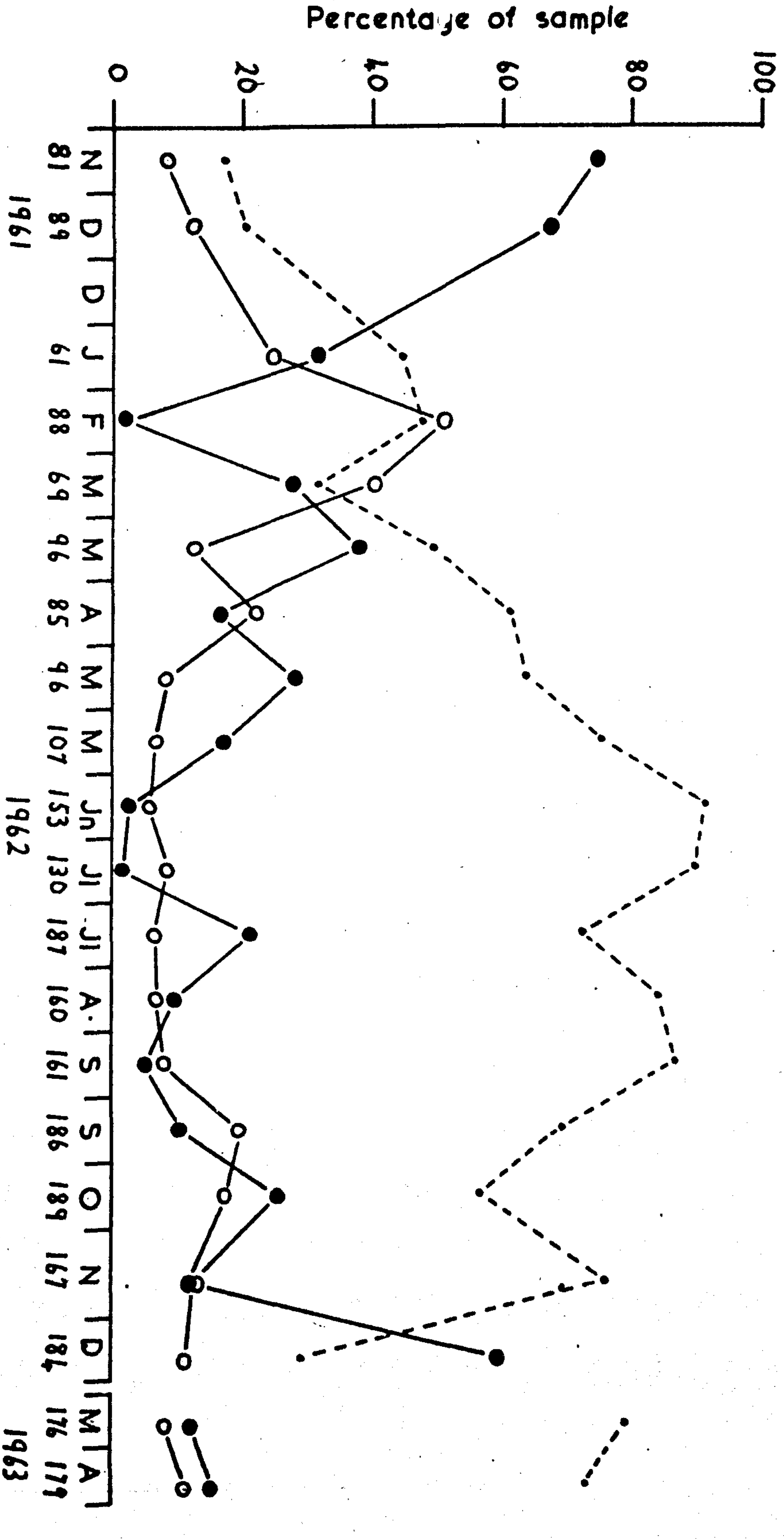
L.hoffmeisteri

The life history of this species in the Shropshire Union Canal is shown in fig. 17. As L.hoffmeisteri is the dominant species of Limnodrilus in this locality

Figure 17

Breeding in *L. hoffmeisteri* in the Shropshire Union Canal. Breeding specimens are indicated by solid circles; mature specimens by open circles. Immature specimens are indicated by a broken line. The figure given under each month refers to the number of specimens examined.

No samples were taken in January and February 1963 owing to unfavourable weather conditions.


Percentage of sample
0
20
40
60
80
100
N
D
D
J
F
M
M
A
M
M
Jn
Jl
Jl
A
S
S
O
N
D
M
A
81
89
61
88
69
96
85
96
107
153
130
187
160
161
186
189
167
184
176
179
1961
1962
1963

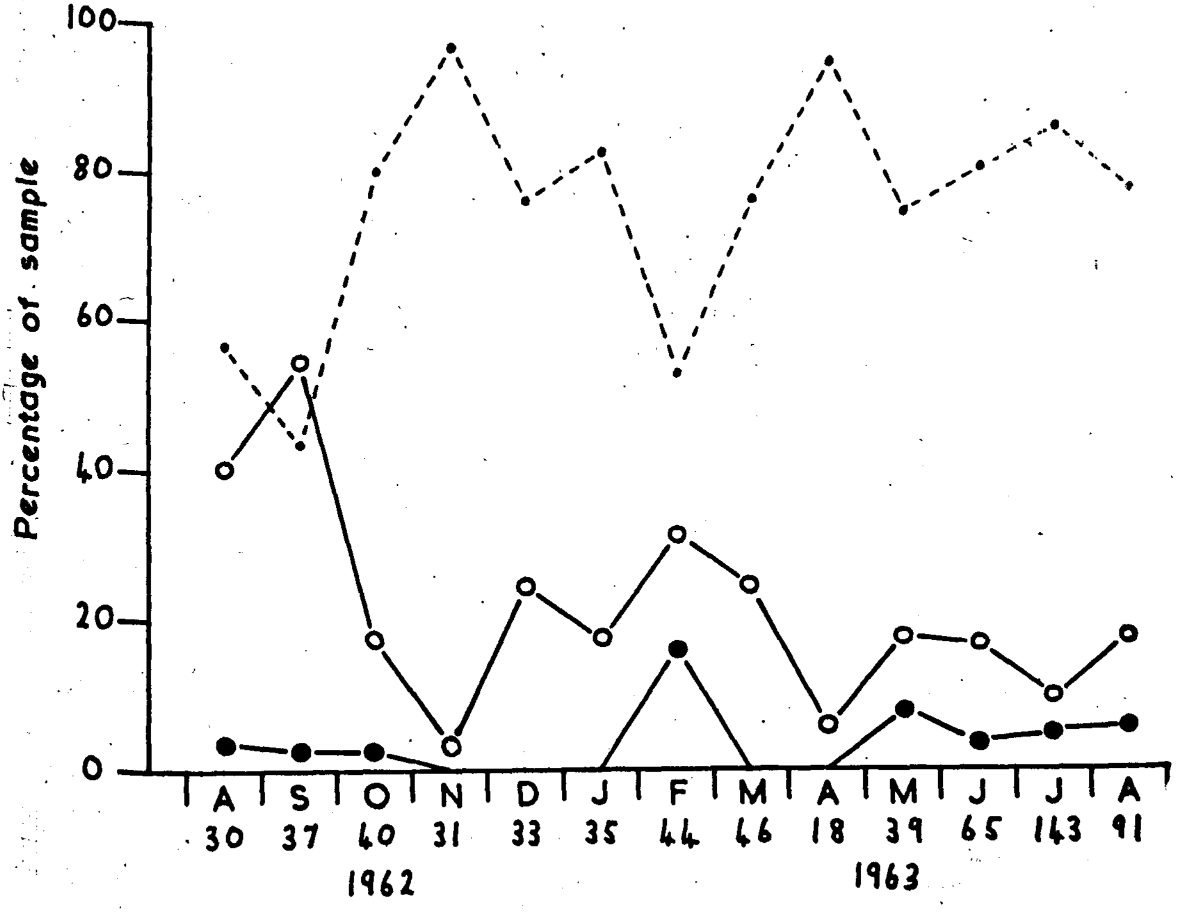
it is assumed that all immature specimens belonged to this species. The first observation was made in November 1961, when there was a high proportion of breeding specimens. The proportion of breeding specimens fell off steadily until July 1962, with the exception of a sudden drop in January - February. The proportion of mature worms showed a steep rise in February - March. This is probably directly attributable to the temporary cessation of breeding in February, and recruitment into this class has occurred from the breeding category. The proportion of immature worms also fell off in March, probably again due to the cessation of breeding activity in February. In late summer the proportions of mature and breeding specimens rise again, and there is a peak of breeding specimens in December, 1962. The population was not sampled when the canal was covered by ice in the winter of 1962/63, but by March 1963 the population structure was similar to that observed in the previous September.

It would seem that worms hatched in the spring and early summer matured in late summer and began to breed in the winter. The breeding period is apparently interrupted in mid-winter when the canal is frozen. This may be directly attributable to cold or to the shortage of oxygen which occurs under the ice. The severe winter of 1962/63 appears to have had a more drastic effect on the population than that of 1961/62. Breeding is then resumed in the late winter and early spring, although at a lesser intensity than in the early winter. The resumption of breeding probably involves the same specimens as before the lag in breeding activity. Breeding then declines further during the summer, although it never entirely ceases. The ensuing autumn breeding is probably due to the maturation of a fresh generation, but whether they were hatched 7 months or 19 months before is difficult to establish. From the high proportion of specimens that breed each year it would appear that only one year class was present in the population and it would therefore seem more likely that the specimens had been hatched 7 months before. If this is so, the cycle of L.hoffmeisteri in the canal is an annual one.

The life history of L.hoffmeisteri in Ditton Brook shows rather a different pattern (fig. 18). From November to February the proportion of mature specimens rose, and was followed by the peak of breeding in February. The proportion of breeding specimens then fell off, and breeding continued at a lower level for most of the year. The proportion of mature specimens also falls off after breeding in February. It remains at a low level throughout the summer, but rises to a peak in August and September. This peak in the proportion of mature

Figure 18

The breeding of L. hoffmeisteri in Ditton Brook. Details as in figure 17.


Percentage of sample
0
20
40
60
80
100
A 30
S 37
O 40
N 31
D 33
J 35
F 44
M 46
A 18
M 39
J 65
J 143
A 91
1962
1963

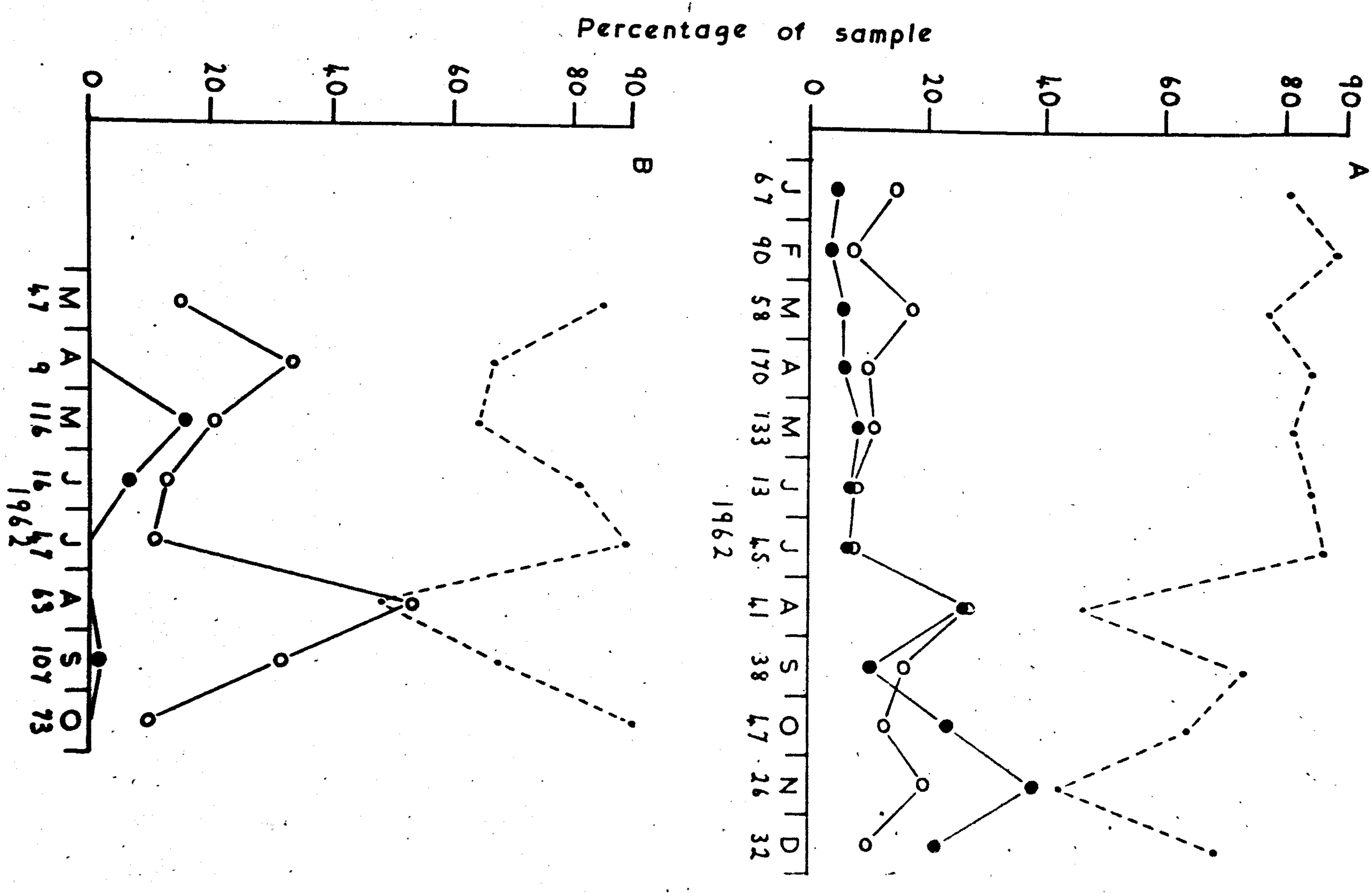
specimens is not followed by a peak of breeding. Instead, there is a fall off in the proportion of mature specimens accompanied by a rise in the proportion of immature worms between September and November.

It would seem that in this locality worms hatch in the spring and mature in late summer and early autumn. They are apparently unable to breed at this time, and by regression of the gonads return to the immature category. The reason for this failure to breed is unknown. The increase in the mature class from November onwards is probably brought about by these specimens re-developing their gonads, and they then go on to breed in February. Breeding activity then declines, but continues throughout the summer at a lower level.

The life history of L.hoffmeisteri in Windermere is shown in fig. 19a. The proportion of mature and breeding specimens remains fairly steady at a low level from January to July. From July onwards there appears to be a rapid recruitment of specimens into the more mature classes, and the proportions of these rise. There is a temporary halt in recruitment in September, but this is then resumed. The proportion of breeding specimens reaches its maximum from August to December. Subsequent to December, breeding declines again to its

Figure 19

Breeding in L. hoffmeisteri in (A) Windermere and (B) Llyn Tegid. Details as in figure 17.


Percentage of sample
A
0
20
40
60
80
90
J
F
M
A
M
J
J
A
S
O
N
D
67
90
58
170
133
13
45
41
38
47
26
32
1962
B
0
20
40
60
80
90
M
A
M
J
J
A
S
O
47
9
116
16
47
63
107
73
1962

normal level. There appears in this locality to be a simple annual cycle, with breeding occuring all year round but rising to a peak in late autumn to early winter. The cycle here is not obscured by irregular fluctuations in the proportions of the maturity classes as in the canal.

In Llyn Tegid, however, which is hydrochemically similar to Windermere, the cycle is very different (fig.19b). The agreement between samples was less satisfactory than in other localities, and L.hoffmeisteri was not found in the samples during the winter months. Nevertheless, there is sufficient information to indicate the general outline of the cycle. The proportion of mature specimens increases from March to April. Breeding commences abruptly in May and is terminated by June. From April to July the proportion of mature specimens decreases, due probably to the recruitment of specimens into the breeding class. From July onwards, however, the proportion of mature specimens rises rapidly by recruitment from the immature class. Some of these specimens may breed in September, but the majority appear to return to the immature class. This appears to be the same phenomenon as occurs at Ditton, and a similar explanation may be presumed.

Rather less can be said about the life cycles of L.hoffmeisteri in the R.Thames (table 14) and Raby pool (table 15), as in both localities several other species of Limnodrilus are present and it is not possible to assign the immature specimens to any one species. In the R.Thames it is apparent that breeding occurs at a high level throughout the whole year. The level is somewhat lower in October and February than in other months. It must be presumed that production of young also occurs for most of the year. It is not possible to detect any cyclic trend due to the limitations in interpretation of the data. Nevertheless, the ability of the species to breed at a high level throughout the year is of considerable interest.

In Raby, however, despite the same limitations in interpretation, there is evidence of a cyclic trend. In 1962 the peak of breeding occurred in May. The high number of mature specimens in June may be due to the presence of specimens that had bred, but not yet died or lost their gonads. Breeding does not take place throughout the summer. The increase in mature specimens from September onwards would seem to be due to maturation of the new generation. This generation then breeds from December through to February. The cycle is thus similar to that determined in the canal and Windermere, but the peak of breeding occurs later in Raby and breeding is restricted to the winter months.

From the foregoing account it is evident that the life history of L.hoffmeisteri is an annual cycle. The peak of breeding occurs during winter or early spring,

TABLE 14

The seasonal changes in maturity in the species of Limnodrilus, excluding L.udekemianus, in the R.Thames at Reading.

		1962			1963	
		Oct.	Dec.	Feb.	May	Jly.
Limnodrilus	immature*	131	113	104	39	51
L.hoffmeisteri	mature	40	72	61	19	23
	breeding	26	73	39	46	70
L.cervix	mature	17	35	29	5	5
	breeding	7	43	33	27	27
L.claparedeanus	mature	6	3	11	2	0
	breeding	0	12	17	4	0
Total number of specimens examined		227	351	294	142	176

* There is some evidence (p.5.53) that suggests that this class is under-represented in the samples.

TABLE 15

The seasonal changes in maturity in the species of Limnodrilus in Raby pool.

		1962														1963			
		M	M	A	M	M	J	JL	Jl	A	S	S	O	N	D	F	M	A	M
Limnodrilus sp.	Immature	18	31	18	26	32	48	53	96	53	56	23	18	26	21	47	19	38	7
L. hoffmeisteri	mature	5	7	2	6	5	15	2	2	1	6	3	5	6	5	1	1	0	1
	breeding	1	1	4	11	8	1	0	0	0	1	0	0	0	2	3	0	0	0
L. helveticus	mature	4	3	0	9	1	8	0	0	0	1	0	0	1	2	10	0	1	2
	breeding	5	4	4	18	12	5	4	3	3	11	4	6	3	4	0	0	1	1
L. claparedeanus	mature	4	6	0	2	11	0	0	0	1	0	0	2	0	0	5	0	1	2
	breeding	2	2	0	4	0	1	0	0	0	0	0	0	0	0	3	4	1	1
Number of specimens examined		39	54	28	76	59	78	59	101	58	85	30	31	36	34	69	24	42	14
Cocoons		p	p	p	p	p	p	p	a	a	a	a	p	a	a	p	p	p	p

Owing to the thickness of the ice in January 1963 no sample was taken.

the new generation appears in spring and goes on to breed the following winter. The timing and duration of the breeding period, however, varies in different localities. In the R.Thames there is no well defined breeding period since breeding continues at a high level throughout the year. In the canal breeding continues at a low level in summer, starts to increase in July and reaches a peak in November or December, then declines gradually to June. In Windermere breeding also occurs throughout the year at a low level, but the peak occurs from August to November. In Ditton brook there is a clearly defined peak in February, but for most of the year breeding also takes place at a lower level. On the other hand, in Llyn Tegid, apart from a small peak in September, breeding appears to be confined to May and June. The situation in Raby is similar, as breeding occurs in April and May and ceases during the summer months before resuming in the following year. The pattern may be obscured by specimens breeding for a second time at some localities and by specimens becoming mature but failing to breed at others.

The factors influencing the time and duration of breeding are not known. That climatic factors have some effect has been shown in the canal. It would seem likely that the nature of the substratum and consequently the availability of nutrient matter is important. Where the substratum is rich organic mud, as in the R. Thames and the canal, breeding occurs for most of the year at a fairly high level, although in the latter site there is a peak in winter and a decline in summer. In Windermere and Ditton the winter peak is more pronounced, and breeding at other seasons takes place at a lower intensity. The substratum in Windermere contained a fair proportion of undecomposed vegetation debris, and at Ditton a considerable amount of inorganic mineral matter. In Llyn Tegid and Raby the breeding period is shorter and more strictly seasonal, and the substrata at both sites contained a high proportion of undecomposed vegetation debris and inorganic particles, particularly sand.

There would thus appear to be a correlation between the duration of the breeding period and the nature of the substratum, but it is not possible at this stage to say whether the relationship is a causal one. The nature of the substratum and the availability of food are related, and it is possible that the abundance of food may influence the breeding cycle. It has been suggested in Chapter 3 that food may determine the abundance of a species, and in Chapter 4 that the nature of the substratum may influence the reproductive cycle. The failure of mature specimens to breed in Llyn Tegid and Ditton in

September may be related to the availability of the food supply. Further discussion on this topic must be left until the life history of *L.hoffmeisteri* has been studied under laboratory conditions.

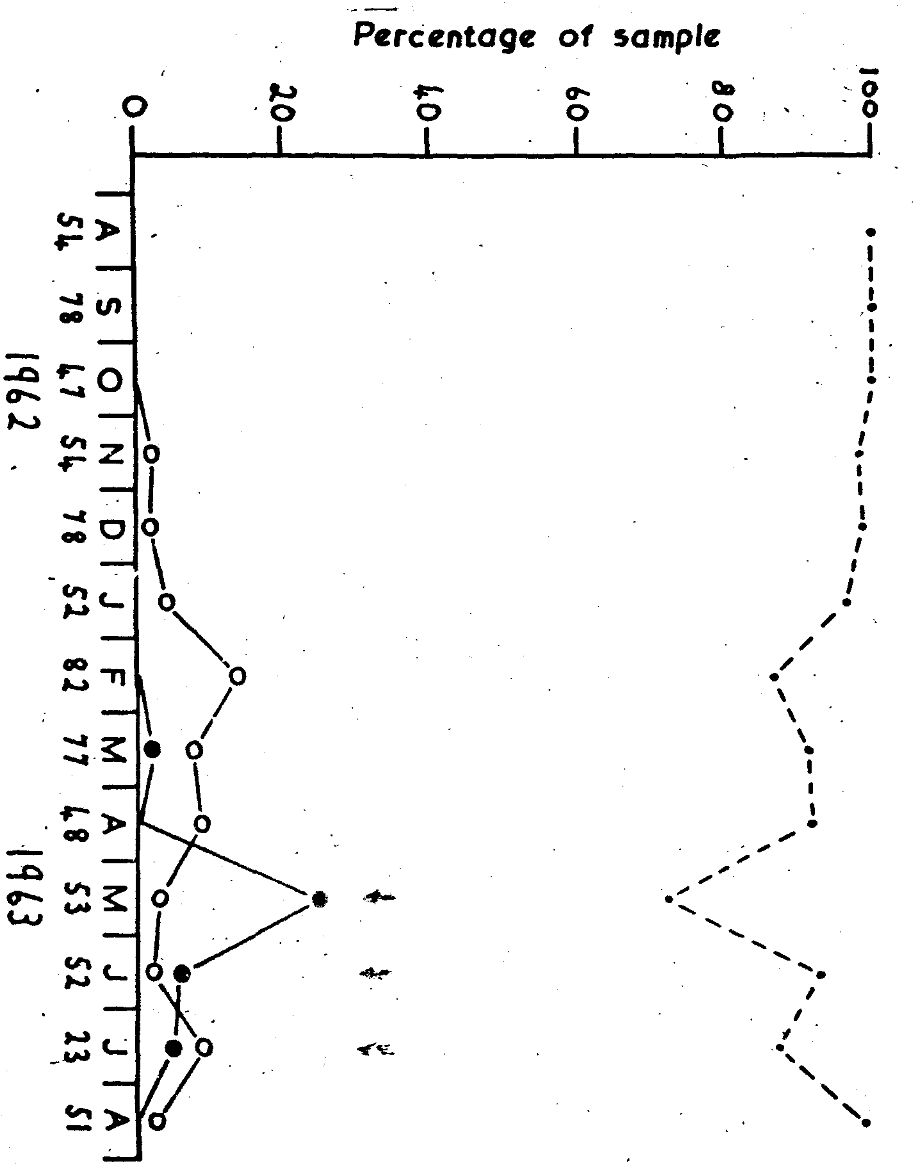
L.udekemianus

The life history of this species presented rather less difficulty in interpretation as it is possible to identify immature specimens. The life history in Ditton brook is shown in fig. 20. Specimens begin to mature in November and December, reaching a peak in February. Thereafter the proportion of mature specimens declines, presumably as specimens are recruited into the breeding class. Breeding begins in March, but rises to a sudden peak in May. The proportion of breeding specimens then falls off rapidly, due almost certainly to post breeding mortality, to about June, continues to decline slowly, and ceases by August. The rise in the proportion of mature specimens in July is possibly due to breeding specimens in the initial stages of degeneration of the gonads. Cocoon production starts in May and declines through June and July, following closely on breeding.

The overall proportion of breeding specimens is not very great and it appears that only part of the total population breeds each year. This suggests the existence of two year classes in the population, one

Figure 20

Breeding in L. udekemianus in Ditton Brook. Details as in figure 17. Arrows indicate the presence of cocoon.

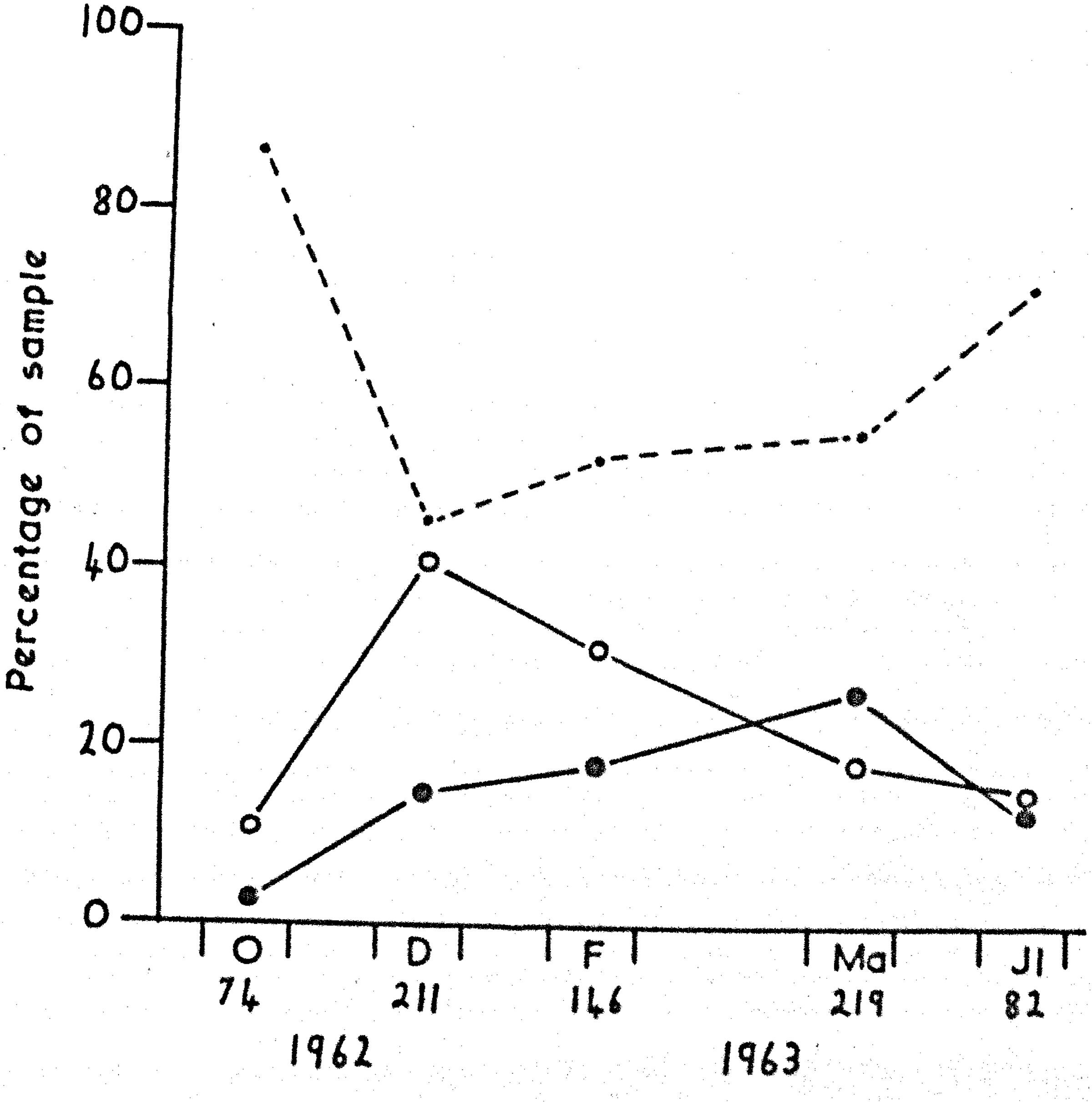

Percentage of sample
0
20
40
60
80
100
A
S
O
N
D
J
F
M
A
M
J
J
A
54
78
47
54
78
52
82
77
48
53
52
23
51
1962
1963

of which breeds each year. It would seem that the life cycle of L.udekemianus in this locality is as follows. In September all specimens are immature, but the population consists of specimens of two year classes. One of these, the 0+, is composed of specimens that hatch out in June or July, whilst the other, the 1+, is composed of individuals that hatched out 15 months before, in the previous July. The 1+ specimens start to become mature in November and breed from March to July, the peak occurring in May. The majority of these specimens die after breeding, although some may undergo gonad regression and survive to breed again the following year as 2+. It is possible that these are the early March breeders. Cocoons appear during this period which hatch to give the new generation. This generation takes about 16 months to attain maturity and breeds at 21 months. The population in September will again be a mixture of 0+ and 1+ specimens. The cycle is a relatively simple biannual one, and breeding takes place over a short period each year.

The cycle in the R.Thames (fig. 21) is probably similar, but the pattern is obscured by the continuation of breeding for most of the year. It seems likely that the cycle is again a 2 year one, and the peak of breeding, though less well defined, occurs in May.

Figure 21

Breeding in L. udekemianus in the River Thames. Details as in figure 17.


100
80
60
40
20
0
Percentage of sample
O
74
D
211
F
146
Ma
219
Jl
82
1962
1963

The fall in the proportion of mature specimens from December onwards is paralleled by a rise in the proportion of breeding ones. Cocoons were not found in the samples. By October the bulk of the population is in the immature class, and from October to December the decline in the proportion of this class is probably due to the recruitment of the 1+ generation into the mature class. Breeding throughout the year, assuming it is accompanied by a continual production of young individuals, obviously obscures any cyclic trends, and will be directly responsible for the existence of continuous breeding in subsequent years.

The life cycle of L.udekemianus appears then to be a two year one in both localities. The peak of breeding occurs in May, but in the R.Thames breeding continues over a longer period. This situation is similar to that found in L.hoffmeisteri, where breeding continued at a higher level and for a longer period in the R.Thames than in any of the other sites examined. It has been suggested that this is due to the greater productivity of this habitat and the availability of food, and the same arguments are equally valid for L.udekemianus. That two species should show a similar trend in otherwise different life cycles in the same habitat suggests that the same factor is responsible. Thus in L.udekemianus there is also a correlation between the duration of breeding and the productivity of the habitat.

L. claparedeanus

The difficulties in interpreting the life histories of this and the two remaining species of Limnodrilus are considerable. The inability to identify them when immature made it impossible to calculate the proportions of individuals in each maturity class. Furthermore, none of these three species occurred abundantly in any locality. Conclusions had of necessity to be based on the examination of too few specimens. Only the time, the duration and some idea of the intensity of breeding could be obtained.

The occurrence of L. claparedeanus in the canal is shown in table 16. It can be seen that mature specimens were present from November to May 1962 and from November to April 1962. No breeding specimens were discovered in 1962. Their absence may be due solely to the low numbers of specimens examined. In 1963 breeding specimens were found in March. Despite the paucity of material, it does appear that breeding may be seasonal and is possibly confined to the winter and early spring. It may not occur in summer.

In Raby (table 15) breeding takes place from March to May 1962 and from February to May 1963. The majority of mature specimens were found during the same periods. Breeding does not appear to take place during the summer and autumn. The mature specimens found in

TABLE 16.

The incidence of breeding in L.claparedeanus in the canal.

	1961		1962												1963	
	N	D	J	F	M	A	M	J	J	A	S	O	N	D	M	A
Mature	1	0	4	5	2	2	1	0	0	0	0	0	5	2	1	1
Breeding	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Number of specimens	1	0	4	5	2	2	1	0	0	0	0	0	5	2	3	1

No samples were taken in January and February 1963 owing to unfavourable weather conditions.

August and October may be specimens breeding for a second time. Despite the small numbers examined, breeding again appears to be strictly seasonal with the peak occurring in spring.

In the R. Thames (table 14) breeding takes place over a longer period, from December to May. The largest numbers of breeding specimens are found in December and February. Mature specimens are also present in October, but no mature or breeding specimens were found in July.

Despite the paucity of material it is possible to draw some preliminary conclusions regarding the breeding cycle of _L. claparedeanus._ Breeding in this species appears to be strictly seasonal, and to be confined to late winter and early spring. A similar pattern to that found in the previous two species of _Limnodrilus_ discussed was found here also. The breeding period was of longer duration in the more productive R. Thames, but even in this locality it was still restricted to the winter months. It is not possible on the information obtained to determine whether year classes are present in a population.

L. cervix

The occurrence of this species in the canal is shown in table 17. Mature and breeding specimens were found throughout the year. From February to July inclusive approximately 50% of the specimens were breeding.

TABLE 17

The incidence of breeding in L.cervix in the canal.

	1961		1962												1963	
	N	D	J	F	M	A	M	J	J	A	S	O	N	D	M	A
Mature	3	0	4	14	3	1	2	5	6	0	0	1	4	4	1	0
Breeding	1	1	0	10	1	2	1	6	5	1	0	1	1	2	1	3
Total number of specimens	4	1	4	24	4	3	3	11	11	1	0	2	5	6	2	3

No samples were taken in January and February 1963 owing to unfavourable climatic conditions.

There is insufficient evidence to indicate whether breeding of this species in this locality is seasonal or not.

In the R.Thames (table 14) mature and breeding specimens were also found throughout the year. There is no clear evidence that a peak of breeding occurs in any month. It is of interest to note that in every month except October the number of breeding specimens was greater than the number of mature ones.

From the little information available it must be concluded that this species is capable of breeding throughout the year. There is no evidence of a seasonal cycle in either locality. Breeding apparently occurs at a greater intensity in the R.Thames, but this may be due merely to the greater abundance of this species in this locality. It is impossible to determine whether the cycle is an annual or a biannual one.

L.helveticus

The seasonal changes in maturity in this species in Raby are shown in table 15. In 1962 breeding specimens were found throughout the year. There is no clear evidence that a peak of breeding occurs at any particular period, although the highest breeding: mature ratios occurred in May and September. From the little information available it appears that this

TABLE 18

The incidence of breeding in L.helveticus in Ditton Brook.

	1962			1963			
	Aug.... Feb.	Mar.	Apr.	May	Jne.	Jly.	Aug.
Mature specimens	0	8	0	1	0	3	2
Breeding specimens	0	0	4	7	4	0	2
Total number of specimens	0	8	4	8	4	3	4

species is able to breed at a fairly steady intensity throughout the year, with possibly an increase in May and September.

Few conclusions concerning the breeding cycle of this species can be drawn from its occurrence in Ditton Brook (table 18). Breeding in this site shows some slight evidence of being seasonal, as breeding specimens were absent from August 1962 to March 1963. Mature specimens first appeared in this latter month and persisted until August. However, since so few specimens were examined, the apparent absence of winter breeding in this locality may be of no significance.

Little can be said concerning the life cycle of this species. It is apparently capable of breeding throughout the year, and there is little evidence of a cyclic pattern.

b) LABORATORY INVESTIGATIONS

In order to clarify and confirm many of the field observations a series of species populations were set up under laboratory conditions. Information was particularly required on the aspects of the biology that would affect the interpretation of the field data. The most important factor in this respect was the time taken by specimens to attain maturity and the length of the life cycle of each species. Under these conditions it was also decided to investigate the relationship between the nature of the substratum and the duration of the breeding period.

Finally, it was hoped that it would be possible to obtain more detailed information on the life histories of those species that could not be identified when immature.

All laboratory populations commenced with breeding specimens. The specimens were taken from field populations and acclimatized before regular observations commenced. The temperature was maintained at around 14 deg. C, and did not fall below 12 deg. C. Species populations were kept in isolated containers, but with a common water supply. A population of each species was reared on a substratum of sand which had previously been kept dry for 6 months, but which was seeded with a small amount of organic debris. In addition, populations of L.hoffmeisteri were reared two other types of substrata. One was rich organic mud, previously sterilised to remove any tubificid eggs or cocoons. The other was sandy-mud, formed by the artificial mixing of equal volumes of the dried sand and organic mud.

All populations were examined at monthly intervals after the period of acclimatization. The entire substratum of each container was sieved through a mesh of 0.4 mm, and the substratum and water then returned to the original container. The specimens were lightly anaesthetised to facilitate examination. After examination they were placed in a dish of water to recover from the anaesthetic. Any mortality due to this could then be estimated. At no time was any evidence of post anaesthetic mortality found. All specimens in each population were examined. Any cocoons present were counted and returned to the container.

The populations on a sandy substratum were examined over a period of a year. Those on a muddy substratum had to be terminated before this period due to the author's transfer to another department.

L. hoffmeisteri

The life history of this species on the three different types of substratum is shown in table 19. Considering first the life history on the sandy substratum (table 19a) it can be seen that a heavy mortality takes place in the first month after breeding. The number of breeding specimens then declines less rapidly until the fifth month, after which it starts to rise again. The re-commencement of breeding in the sixth month is probably due to specimens breeding for a second time. The rapid increase in the number of breeding specimens in the tenth and eleventh months is undoubtedly due to specimens recruited from the mature class, which has been increasing from the seventh month onwards. The increase in the number of immature specimens occurred in the fourth month after the commencement of the culture, but took place more gradually following the peak of breeding in the tenth and eleventh months. No cocoons were observed at any time.

TABLE 19

The breeding cycle of L.hoffmeisteri under laboratory conditions.

a) Sandy substratum

	Months after commencement of observations													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
Immature	0	4	-	16	127	91	70	57	63	83	117	141	225	219
Mature	0	12	-	8	11	16	1	11	20	36	27	20	5	12
Breeding	78	15	-	13	3	0	4	6	8	5	21	26	2	5
Total	78	31	33	37	141	107	75	74	91	124	165	187	232	236

In the second month the population was not divided into maturity classes although the total number of specimens was counted.

b) Sandy-mud substratum

	Months after commencement of observations										
	0	1	2	3	4	5	6	7	8	9	10
Immature	0	1	7	10	34	74	76	75	74	71	61
Mature	0	9	2	1	3	0	0	2	0	3	0
Breeding	18	2	4	6	9	3	1	0	3	0	0
Total	18	12	13	17	46	77	77	77	77	74	62

c) Muddy-substratum

	Months after commencement of observations								
	0	1	2	3	4	5	6	7	8
Immature	0	1	3	56	62	64	67	47	48
Mature	0	4	0	2	4	0	0	8	3
Breeding	17	1	3	2	0	0	0	4	0
Total	17	6	6	60	66	64	67	59	51

It would seem, then, that worms hatching in the fourth month begin to mature when four months old and go on to breed at about seven months. It is difficult to estimate what proportion of this generation breeds in its first year. The minimum population size before breeding is 74 specimens (in the seventh month) and the number of breeding specimens observed at the height of the breeding period (in the tenth and eleventh months) is 46. Since spermatophores are generally retained for less than four weeks (p. 4.10) it is evident that the same individuals were not being observed in the breeding class in both of these months. It would seem likely, then, that the majority of specimens are breeding in their first year. It is also apparent that even a population which commenced with all specimens at the same stage of maturity can result in a population in which specimens of all stages of maturity are present within 1 month, and in which breeding may occur throughout the year. This demonstrates clearly how the existence of a cyclic pattern in the life history may be obscured under field conditions where specimens in all three maturity classes are present at the commencement of the breeding season.

On a substratum of sandy-mud (table 19b) some differences are apparent in the life history. The post breeding mortality was considerably less than in other cultures. Specimens assumed to be breeding for a second time appear in the second month, increase into the fourth month and fall off into the sixth. The three specimens breeding in the eighth month may be specimens breeding for a second time or they may be the first specimens of the new generation. Five to six months after the appearance of most of the specimens of the new generation there is no sign of their reaching maturity. On a sandy substratum the new generation bred after seven months. This suggests that under these conditions specimens either do not breed until they are a year old or over, or that breeding will set in rapidly in the population without the gradual increase in the number of mature specimens that normally preceeds it. It is not possible to determine which is the case.

On a muddy substratum (table 19c) the life history is in many ways intermediate between the two patterns considered above. Breeding is followed by a heavy mortality as in a sandy substratum. Specimens assumed to be breeding for a second time are present in the second and third months. In the seventh month 12 specimens were present in the mature and breeding classes, but only six of these could have been specimens from the parent generation. Some few specimens of the new generation, therefore, must be maturing at 5 - 6 months old. There was no evidence of the majority of the new generation reaching maturity, although they were six months old at the termination of experimental observations.

It is evident from the studies outlined above that the age at which specimens of L.hoffmeisteri attain maturity may vary between populations. Specimens may become mature at four months old, but they do not appear to breed until they are at least six or seven months old. This must be considered to be the minimum age. More often, there was no evidence of specimens even attaining maturity at 5 - 6 months old. In one example, however, it was shown that the majority of specimens became mature in their first year of life. Under field conditions of a lower temperature, it is probable that the time taken to attain maturity will be even longer. However, if four months is taken as a minimum period, it does show that it is impossible to recruit mature specimens from cocoons in between the sampling dates. These results also confirm some of the conclusions arrived at from the field studies. The life history of L.hoffmeisteri appears to be basically an annual cycle, with peaks of breeding occurring at approximately 12 monthly intervals. The breeding period, even under stable environmental conditions, is not sharply defined but is spread over several months. There is no indication in table 19 that this is influenced by the nature of the substratum. This cannot be regarded as conclusive proof that no such relationship exists, as any evidence would have to be based on the length of the breeding period of the new generation. The termination of observations on two of the cultures occurred before the commencement of this second breeding period, and therefore no conclusions could be drawn. The relationship between the general breeding pattern and the nature of the substratum will be discussed in a later section (section cl).

L.udekemianus

The life history of this species under laboratory conditions is shown in table 20. Breeding fell off rapidly at first, then more slowly and had ceased by the fifth month. The post breeding mortality was slight as compared with L.hoffmeisteri. There is no evidence of specimens breeding for a second time, at least in the same season. The specimens maturing from the seventh month onwards and the single specimen breeding in the eleventh month may be specimens of the parent generation breeding for a second time. Although the majority of specimens of the new generation appeared in the fourth and fifth months, there was no evidence of large numbers nearing maturity at the termination of observations, when they were nine to ten months old. It appeared instead that the new generation did not reach maturity or breed in its first year of life. It is interesting to note that the peak of cocoon production did not occur until 3 months after copulation. The interval of time between the two might be expected to be considerably shorter.

TABLE 20

The breeding cycle of L.udekemianus under laboratory conditions.

	Months after commencement of observations													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
Immature	0	2	-	9	63	89	94	80	63	63	60	59	64	65
Mature	0	4	-	6	4	5	0	1	1	1	3	2	0	0
Breeding	14	6	-	4	1	0	0	0	0	0	0	1	0	0
Total number of specimens	14	12	13	19	68	94	94	81	64	64	63	62	64	65
Cocoons	0	3	1	12	0	0	0	0	0	0	0	0	0	0

In the second month the population was not divided into maturity classes although the total number of specimens was counted.

It is evident from the above account that specimens of L.udekemianus do not attain maturity in their first year. The age at breeding must therefore be 1+ years. It would seem then that the life history of this species is a 2 year cycle, although some specimens may survive to breed in their third year. This confirms the results from field investigations, where the existence of a two year cycle and the presence of two year classes in a population was suggested. The life hitory as determined above is in fact very similar to the life history of this species at Ditton brook. Breeding took place over a short period, with a peak in spring, and only a small proportion of the population bred each year.

L.claparedeanus

The life history of this species under laboratory conditions is shown in table 21. Breeding fell off rapidly, and terminated in the fourth month. Mature specimens began to appear in appreciable numbers in the seventh month, increased up to the eleventh and then declined slowly. Breeding re-commenced at a low rate in the seventh month and continued at this low rate through to the eleventh. During this period a total of 17 breeding specimens was observed, but since only 8 specimens had survived of the parent generation it is evident that some of these specimens at least were members of

TABLE 21

The breeding cycle of L.claparedeanus under laboratory conditions.

	Months after commencement of observations													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
Immature	0	3	-	38	40	38	37	24	50	71	54	47	62	42
Mature	0	3	-	0	2	1	0	7	9	11	7	2	1	1
Breeding	16	2	-	1	0	0	0	5	1	3	4	4	0	0
Total number of specimens	16	8	11	39	42	39	37	36	60	85	65	53	63	43
Cocoons	0	0	7	0	0	0	0	0	0	0	0	0	0	0

In the second month the population was not divided into maturity classes although the total number of specimens was counted.

the new generation. It is difficult to estimate the proportion of the new generation that was breeding. Assuming that all these specimens belonged to the new generation and that spermatophores were retained for less than a month, the highest estimate was about 50%. The number of breeding specimens appeared to be less than the number of mature specimens, suggesting that some specimens of the new generation may have attained maturity but not gone on to breed.

From the above considerations it is evident that some specimens of L. claparedeanus may breed in their first year, but a large number do not breed until during the second year. The minimum age at maturity appears to be about 5 months, and at breeding 5 - 6 months. Most specimens breeding in their first year did so at seven to nine months old. It would seem that the life history of this species may be a one or two year cycle, and it must be concluded that a field population may contain a mixture of two year classes. Breeding occurs over a longer period than was generally found in the field, but this may be attributable to the higher temperature under laboratory conditions.

L. cervix and L. helveticus

Breeding specimens of both species were isolated and removed to cultures as described earlier (p. 5.29).

In both species the number of specimens steadily declined, and ultimately all specimens died. No new individuals were produced.

c) POPULATION STUDIES.

In the previous sections the life histories of the British species of Limnodrilus under field and laboratory conditions have been considered, but no account was taken of the overall changes in abundance of each species in each locality. In the present section an attempt is made to evaluate certain population trends of each species, in particular birth and death rates, and to relate them to the changes in density of each population.

1) Population biology under laboratory conditions.

L.hoffmeisteri

The data on which the following calculations are based is given in table 19. In order to compare the three populations attention was concentrated upon three aspects of the population. These were the fecundity of individual specimens; the post breeding mortality and the interval between the peak of breeding and the maximum number of immature specimens.

In the absence of cocoons (p. 4.15) an estimate of fecundity presented many difficulties. It was not possible to determine directly the number of young produced by each individual or the proportion of these surviving to the stage of hatching. Instead, an indirect estimate of the number of young produced was obtained. It will be seen from table 19a that the maximum number of individuals, 141, occurred in the fourth month after the first breeding season. Of these 31 at the most could have been specimens of the parent generation which had survived breeding. Assuming that no mortality had occurred in these specimens, a minimum number of 110 new individuals must have been produced. If mortality had occurred, this estimate will be too low. At the setting up of the culture 78 breeding specimens were present, and it was assumed that these were responsible for the production of the young specimens. On average, therefore, each breeding specimen had produced 1.41 individuals. This was taken to be the minimum fecundity of L.hoffmeisteri under this set of conditions. The estimate is undoubtedly too low, as it assumes that all the specimens that survived breeding did not die later, and that no mortality had occurred amongst the juvenile specimens. Both assumptions are liable to be incorrect, but nevertheless an estimate of fecundity that may be used for comparative purposes can be obtained. In general terms,

$$\text{fecundity} = \frac{\text{maximum size of population} - \text{number of individuals surviving breeding}}{\text{total number of breeding specimens.}}$$

This formula will be used in future calculations of fecundity.

The post breeding mortality was simpler to calculate. It was assumed that specimens that survived the initial post breeding mortality survived at least for several months. Using the data in table 13a, 31 specimens survived breeding out of an initial total of 78 breeding specimens. The mortality was therefore 47, or, expressed as a percentage of the original size of the population, 60%. In general terms

$$\text{post breeding mortality} = \frac{\text{original number of breeding specimen} - \text{number of specimens surviving breeding}}{\text{original number of breeding specimen}}$$

This formula will be used in future calculations of post breeding mortality. The interval between the peak of breeding and the maximum number of immature specimens is determinable directly from table 19a.

A comparison of these statistics for populations of L.hoffmeisteri reared on three different types of substratum under laboratory conditions is given in table 22. It is apparent that the minimum fecundity is directly related to the nature of the substratum, and increases with its nutritive value. The post breeding mortality for the sand and the mud substrata is of the same order, but is considerably less on the sandy-mud substratum. The reason for this is not readily apparent, as it might be expected that the mortality under these conditions would

TABLE 22

The population statistics of three species of Limnodrilus reared under laboratory conditions

	Lhoff.			L.udek.	Lclap
Substratum	S	SM	M	S	S
Minimum fecundity	1.4	3.1	3.5	5.8	2.1
Post-breeding mortality	60%	33%	64%	14%	50%
Interval between peak of breeding and peak of immature specimens in months	4	5	4	5	4

For explanation of terms and methods of calculation see text.

Legend

Lhoff = L.hoffmeisteri   L.udek = L.udekemianus

L.clap = L.claparedeanus

S = sand   SM = sandy-mud   M = mud be of the same order as in the other two cultures. The maximum number of immature specimens appears at about the same time after the peak of breeding in all three cultures. In the sandy-mud and mud cultures the population did not breed again in large numbers during the period of observation, and it was not possible to calculate a second value for any of the statistics. A second breeding period was observed on the sandy substratum, and an estimate of the minimum fecundity gave a minimum value of 2.2. This is higher than the value of 1.41 obtained earlier for specimens on the same substratum, but is still significantly lower than the values for the other two cultures.

<u>L. udekemianus</u>

The population statistics for this species on a sandy substratum are shown in table 22. They were calculated in the manner described for <u>L. hoffmeisteri</u> on the basis of the data shown in table 20. The fecundity value of 5.8 is considerably higher than the value for <u>L. hoffmeisteri</u> both on the same substratum and on more productive substrata. It is also possible with this species to obtain an estimate of the mortality in the cocoon stage. Sixteen cocoons were found up to the third month after breeding, with a total of 81 eggs. The number of young produced is estimated at 82 from table 20, suggesting that there is little or no mortality in the early stages of development.

This appears rather unlikely, and it would seem that some cocoons must have been overlooked, or that some specimens have not produced cocoons. The maximum number of young occurred 5 months after the peak of copulation and two months after the peak of cocoon production. The post breeding mortality is very much lower than in either of the other two species of Limnodrilus studied.

L. claparedeanus

The population statistics for this species on a sandy substratum are shown in table 22. They were calculated in the manner described for L. hoffmeisteri on the basis of the data given in table 21. The fecundity value of 2.1 approximates very closely to the value determined for the second generation of L. hoffmeisteri on the same substratum. The post breeding mortality value of 50% is closer to the figures for L. hoffmeisteri than for L. udekemianus. The maximum number of immature specimens appeared 4 months after the peak of breeding 7 cocoons only were found in the second month after breeding, with a total of 29 eggs. The number of young produced was estimated at 34 from the data in table 21. This suggests that either some cocoons were overlooked, or that some individuals can be produced without cocoons, as is known for L. hoffmeisteri (p. 4.15). The latter alternative seems more probable, as from the seventh to the eleventh month breeding was continuing at a steady rate but no cocoons were observed. Nevertheless, the population size increased during this period indicating that the production of new individuals must have occurred.

If the results in table 22 are compared, several interesting facts emerge. The interval between the peak of copulation and maximum number of immature specimens is of the same order for all three species. It does not appear to be related to the nature of the substratum. Fecundity, however, appears to be a variable factor. It varies from species to species, and in L.hoffmeisteri it also varied in relation to the productivity of the substratum. The post breeding mortality also varies, but the variations show no relation to the nature of the substrata. It is perhaps significant that L.udekemianus, the only species with an obligatory two year life cycle, had a higher fecundity value and a lower post breeding mortality than either of the other two species, both of which appear basically to have an annual life cycle. It must be concluded that specific differences do exist between populations of different species cultured under the same conditions, but that the nature of the substratum can influence the population biology of any one species.

2) Population biology under field conditions

The major problem in the study of field populations arises from the local variations in abundance of a species from site to site in a single locality. The importance of this variation in relation to the interpretation of data has been discussed elsewhere (p. 5.12), but in the present context it is obvious that such variation makes estimates of specific densities very difficult. The agreement between duplicate samples was not very satisfactory with regard to the total numbers of each species present. Nevertheless, an estimate of density is essential if the seasonal changes in population abundance are to be considered. In view of the existence of such spatial variation it was considered that the density expressed in terms of a unit area would have little meaning, and accordingly density is expressed in numbers per sample, by taking the mean of the samples. A further difficulty, also discussed on page 5.12, was that samples taken at the same place may not be sampling the same population in successive months. If this is happening, it is evident that it will seriously affect the interpretation of any observed changes in population size. This possibility must therefore be considered in the interpretation of results, and an attempt made to assess its importance.

In the present section the overall changes in the abundance of Limnodrilus will be considered in each locality. This will be considered in relation to the changes in the size of the breeding and immature classes. This will give an indication of the occurrence of breeding and the production of the new generation. The number of mature specimens has been omitted from the figures, as this class does not contribute to changes in the population size.

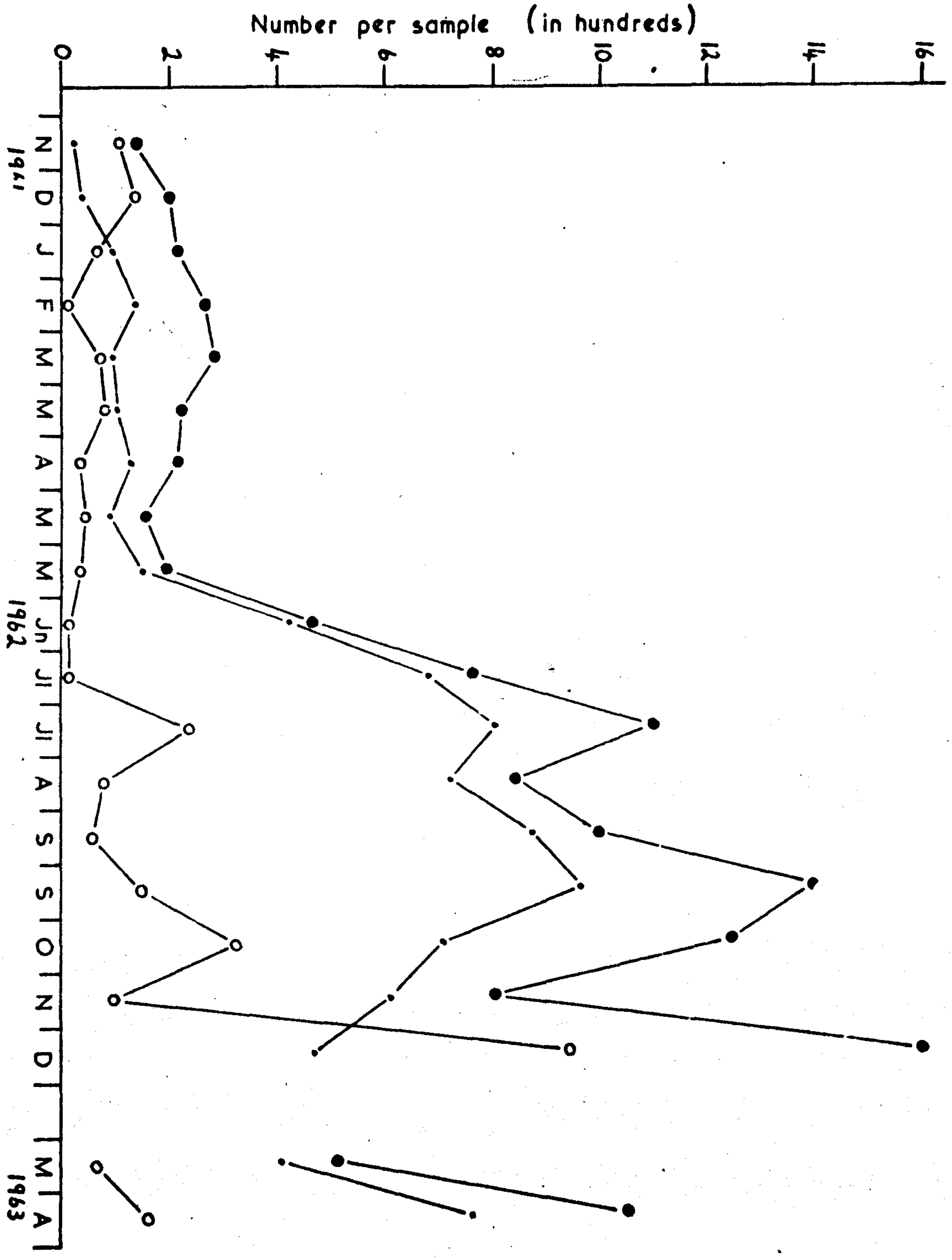
The Shropshire Union Canal

In considering the changes of abundance in this locality it has been assumed that all immature specimens should be assigned to L.hoffmeisteri. As this was the dominant species this assumption does not appear to be unreasonable. The seasonal changes in abundance are shown in fig. 22.

It is evident that the increase in the size of the population from May to July, 1962, is due to the appearance of large numbers of immature specimens. The steep rise in the number of immature specimens in July is not readily explicable. It has been shown from the laboratory studies (p.5.40) that the interval between the peak of breeding and the maximum number of immature specimens is between four and five months. In the canal, however, there is no peak of breeding

Figure 22

The seasonal changes of abundance of L. hoffmeisteri in the Shropshire Union Canal. Solid circles indicate the total number of specimens of Limnodrilus present in each sample. Breeding specimens are indicated by open circles; immature specimens by solid dots.


Number per sample (in hundreds)
0
2
4
6
8
10
12
14
16
N
D
J
F
M
M
A
M
M
Jn
Jl
Jl
A
S
S
O
N
D
M
A
1961
1962
1963

activity equivalent to the rise in July in the previous six months. The peak of breeding occurred in December, eight months before the rise, and breeding activity then gradually diminished. If it is assumed that the specimens breeding in March were responsible for the large production of young, this would agree with the interval between the two events of four months observed in the laboratory. Assuming the maximum fecundity observed in the laboratory was realised in the field, the specimens breeding in March could only be responsible for the production of about 350 specimens. Even if specimens breeding after March are included, the number of young produced is still less than the 800 observed in July. It is therefore difficult to see from where the immature specimens were derived. A higher fecundity value under field conditions appears most unlikely. A further possibility, that the production of immature specimens has been concentrated into one month, also appears unlikely in view of the long interval of seven to eight months between the peak of breeding activity and the maximum number of young. It is particularly unfortunate that no cocoons were found, as their presence would have given a further indication of the time of breeding activity. The possibility that a major change in the environment occurred at this time will be discussed later.

Breeding re-commences in July and October, and the size of the population rises again in September and December. The incidence of breeding is followed by an increase in the number of immature specimens except in December, where the very large breeding population has undoubtedly been produced by recruitment from the immature class that had built up during the summer. The population is maintained at a high level in the spring of 1963, despite the severe winter of 1962/1963. It is probable that the recruits from the high breeding population in December 1962 are entering the population in April 1963.

A part from the inexplicable increase in the size of the immature class in July, a further aspect of the population changes of L.hoffmeisteri in this canal deserves attention. Between November 1961 and May 1962 the size of the population fluctuated between 140 and 280 specimens per sample, but from June 1962 to April 1963 the size of the population never fell below 470 specimens per sample. If the size of the population for the same month in successive years is compared it is seen that the figures from June 1963 onwards are consistently higher than those for the preceeding months. Over the period of observation there was evidently a permanent increase in the size of the population in the canal. It would appear that during 1961, or perhaps even during 1960, some factor was operating on the population of

Limnodrilus that kept the size low, but that during 1960 the influence of this factor was greatly reduced so that the population was able to increase and maintain itself at a high level. The nature of this factor is unknown. It would appear unlikely that it was a climatic one as the climate was more severe during the period when the population was maintained at the higher level. During the period of observation no pronounced physical, chemical or biotic changes in the canal were recorded, although it is possible that such changes may have occurred before observations commenced. There was no evidence that a source of organic pollution entered the canal during 1962, although this could have caused an increase similar to the one observed. It is perhaps significant that the higher population level was initiated by the unexplained increase in the number of immature specimens in July, and it seems unlikely that the two events were independent of each other. Despite the fact that the identity of the factors responsible was not determined, it is, nevertheless, of considerable interest to note that large changes in the mean density of the population may occur from year to year.

Ditton Brook

The seasonal changes in abundance of the species of Limnodrilus in this locality are shown in table 23. Because of the failure to identify immature specimens, L.hoffmeisteri and L.helveticus are considered together.

It is evident from table 23a that immature specimens form the bulk of the population throughout the year. It seems likely that the increase in the number of immature specimens in October 1962 was due to specimens that had bred earlier in the same year. The size of the population then gradually declined until April 1963. From thos month onwards the size of the population increased due to the recruitment of large numbers of specimens into the immature class. This recruitment had ceased by August 1963.

In 1963 the maximum number of immature specimens was found in the same month as the maximum numberof breeding specimens. In laboratory studies the interval between these two maxima was 4 - 5 months, but in February only 7 breeding specimens were found. Prior to July 1963, only 34 breeding specimens had been observed, and even assuming the maximum fecundity recorded under laboratory conditions is realised in the field and that there is a very rapid production of young, it does not seem possible for them to have produced 389 individuals

TABLE 23

The seasonal changes in abundance of Limnodrilus in Ditton Brook

a) L. hoffmeisteri and L. helveticus

	1962					1963							
	A	S	O	N	D	J	F	M	A	M	J	J	A
Number of immature specimens	17	16	94	65	56	29	23	35	17	52	143	389	131
Number of breeding specimens	1	1	3	0	0	0	7	0	4	15	15	19	13
Total number of specimens	30	37	117	67	74	35	44	54	22	70	178	454	170

b) L. udekemianus

	1962					1963							
	A	S	O	N	D	J	F	M	A	M	J	J	A
Number of immature specimens	27	78	138	171	216	50	71	70	44	57	116	62	89
Number of breeding specimens	0	0	0	0	0	0	0	1	0	19	7	3	0
Total number of specimens	27	78	138	174	219	52	82	77	48	79	126	71	91

by July. It is evident, therefore that either breeding specimens are under-represented in the sample, or that the sampler has not sampled the same micropopulation each month. This latter explanation would seem the more likely, as it has been demonstrated in a previous section (p.3.36) that considerable variation in the relative abundance of each species from site to site exists in this locality. It is possible that the proportions of the different maturity classes within each species may also vary from site to site. This was not indicated by the duplicate samples, which agreed fairly well in this respect, but it is possible that it might have been indicated had a larger number of duplicates been taken. As has been explained earlier, (p.5.7), the number of samples taken was limited by the time available. If agregation or clumping of specimens occurs, this will accentuate the variability between samples. A further factor that may be of importance is the scouring of the stream bed (p.5.3) which may cause micro populations to move about. All these factors will tend to increase the variability of the samples.

A similar situation was observed in relation to the abundance of L. udekemianus in the same locality, (table 23b). Between October and December 1962 an increase in the number of immature specimens was observed. This increase was occurring at a time when recruitment from the individuals hatched out in May and June, the breeding time for this species, was no longer possible. The sudden fall in number of immature specimens between December 1962 and January 1963 is inexplicable. Apart from the increase in the number of immature specimens in June 1963 following closely upon the breeding activity in the previous month, the fluctuations in the number of immature specimens during the period of observation appear to bear no relationship to the incidence of breeding in the population. It must be concluded, therefore, that as in the case of L.hoffmeisteri the same population is not being sampled each month.

It would appear then that in this locality agregation and clumping of individuals and mobile local populations resulted in non-representative samples, at least as far as the size of the populations was concerned. The sample appeared to give a good indication of the incidence of breeding, and its duration, but were less reliable with regard to its intensity. Under these circumstances, the changes in the sizes of the populations in this locality will not be considered any further.

Windermere

The changes in abundance of L.hoffmeisteri in this locality are shown in table 24. The sudden rise in the number of specimens, due entirely to a rise in the total number of immature specimens, between January and February is inexplicable. In this locality breeding occurs all the year round, but the monthly fluctuations in the number of immature specimens bear no relationship to the incidence or intensity of breeding activity. The same situation as found in Ditton brook appears to occur here, in that samples taken from the same place do not sample the same population from month to month. In this respect it is of interest to note that the occurrence of Tubifex templetoni in the samples showed no seasonal pattern. The fluctuations in population size occurred in such an irregular manner that the population changes will not be considered any further. It is evident that any seasonal changes are being obscured by spatial variation.

Llyn Tegid.

The changes in abundance of L.hoffmeisteri in this locality are shown in Appendix 5. The species was not found in samples for four months of the year. Even when L.hoffmeisteri was present there was little

TABLE 24

The seasonal changes in abundance of L.hoffmeisteri in Windermere.

	J	F	M	A	M	J	J	A	S	O	N	D
Number of immature specimens	54	405	45	144	108	11	39	19	28	30	11	22
Number of breeding specimens	3	15	3	10	11	1	3	11	4	11	10	7
Total number of specimens	67	455	58	170	133	13	45	41	38	47	26	32

agreement between duplicate samples, both with regard to number of specimens and the size of the maturity classes. No attempt is therefore made to consider the changes in abundance of this species in view of the discrepancies between samples.

Raby Pool

Three species of Limnodrilus were found in this locality. Two of them, L. hoffmeisteri and L. helveticus, were co-dominant. The agreement between samples was not very satisfactory, both with regard to the number of specimens and the sizes of the maturity classes, (Appendix 3). Furthermore, it has been suggested earlier (p.3.32) that during the period of observation the pool was being poisoned by inorganic chemicals. This would obviously invalidate any attempts to relate the observed changes in population size to the breeding biology of Limnodrilus, and consequently the population changes in this locality will not be considered any further.

The River Thames

The changes in abundance of the species of Limnodrilus, except L. udekemianus, in this locality are shown in table 25. In view of the inability to identify immature specimens all species are considered together.

TABLE 25

The seasonal changes in abundance of Limnodrilus in the R. Thames.

	Oct.	Dec.	Feb.	May	July
Number of immature specimens	131	113	104	39	51
Number of breeding specimens	33	128	89	77	97
Number of mature and breeding specimens	96	238	190	103	125

In compiling the above table all species except L. udekemianus, were considered together.

From a consideration of this table two factors emerge. The first is that the number of breeding specimens forms a high proportion of the total population throughout the year. The second is that the number of nature and breeding specimens when considered together is greater than the number of immature specimens in four out of the five samples. This is in marked contrast to the other populations considered, where the number of immature specimens is always greater than the number of mature and/or breeding ones, except at the breeding season. This strongly suggests that the immature specimens are under-represented in the samples. On the data given in table 25 there are insufficient immature specimens to maintain the population at the same level of abundance. In an account of the life histories of the species occurring in this locality the incidence and abundance of immature specimens were ignored for this reason. As immature specimens are under-represented in the samples no further attempt is made to analyse the seasonal changes of abundance of Limnodrilus in this locality.

General considerations.

It was suggested in the introduction to this section (p. 5.12) that because of the spatial variation that exists it is possible that samples taken in the same place do not necessarily sample the same population each month. In the foregoing account it has been shown that this has been responsible for the observed variation in the abundance of species in most of the localities examined. It has accordingly proved impossible to analyse the observed population changes in terms of the breeding biology of each species.

At the commencement of the sampling programme it was impossible to determine the extent to which populations might change from month to month. The preliminary surveys of each locality gave an indication of the spatial variation in abundance at that time, but could not reveal the existence of temporal variation also. The extent to which different micro populations had been sampled in different months could only be revealed at the conclusion of the sampling programme. It was not revealed by the duplicate samples, as they were sampling the same micro population at any one time. It is possible that had a larger number of duplicate samples been taken at each visit and the intervals between visits been shorter, the movements of the micro populations might have been suspected sooner. However, the choice lay between very detailed studies in one locality or rather less detailed studies in a number of localities. In the time available it was not possible to do both. It was considered at the beginning of this study that it would be more useful to determine the life history of each species under a number of different sets of conditions, and consequently detailed studies on one locality were not possible.

It is evident from the above remarks that future studies of the population biology of Limnodrilus must take the form of detailed investigations in a single locality. This will involve a large number of duplicate samples being taken at each visit, and the interval of time between visits should be shorter than a month. Future studies should also aim at determining whether the micro populations remain discreet or are only temporary associations. In the former case they must aim at trying to follow and sample the same micro population, rather than to sample at the same place as was done in the present study. Only by such a programme will it prove possible to analyse the population biology of Limnodrilus.

d) DISCUSSION

There is little published information on the life histories of any species of Limnodrilus with which the results of this work can be compared. Poddubnaya (1959) gives a brief account of the life history of L.hoffmeisteri. She divided her specimens into the same three classes of maturity as are recognised here. She found mature specimens present from April to

September, but breeding specimens only in June and July. The maximum production of young occurred in August and September. She considered that *L.hoffmeisteri* bred only once a year and that breeding was strictly seasonal. It is difficult to compare her results here as she was unable to take samples during the winter months. In view of the totally different climatic factors operating in the localities in which she worked little significance may be attached to the differences in duration and timing of the breeding period as revealed by her and by the author. Nevertheless, it is of interest to note that she came to the same conclusion that the life cycle of *L.hoffmeisteri* is an annual one. There are several observations in the literature of the occurrence of breeding specimens of the species of *Limnodrilus* and the month in which they were found. No importance can be attached to these, as it has been shown that most species of *Limnodrilus* in suitable localities are capable of breeding throughout the year. In the absence of any other studies, therefore, the subsequent discussion will be based entirely on the results presented in this work.

Considering first *L.hoffmeisteri*, there is evidently no set cycle of events in the life history of this species. The time and duration of the breeding period and the age at maturity appears to depend on local conditions. Under favourable conditions breeding may take place all the year round, as in the R.Thames. Under less favourable conditions, as at Raby, it may be more strictly seasonal. Laboratory investigations indicate that specimens may attain maturity at any time from four months up to over a year old. The time taken to attain maturity and the duration of the breeding period may be influenced by the nature of the substratum. As the productivity of the habitat increases, maturity is attained at an earlier age and breeding continues over a longer period. L.hoffmeisteri must therefore be considered to be a very adaptable species. This adaptability is completely consistent with its cosmopolitan distribution and tolerance to a wide range of environmental conditions.

In the other species of Limnodrilus a set cycle of events in the life histories is more evident. L.udekemianus appears to be a more strictly seasonal breeder, although under favourable conditions the duration of the breeding period may increase. Specimens do not attain maturity until they are at least a year old, and the cycle is a bi-annual one. This pattern agrees more closely with the life histories of species of other genera; in particular Tubifex costatus, Aulodrilus pluriseta and Peloscolex ferox, all of which also seem to have two year cycles (Brinkhurst, pers.comm.) L.claparedeanus is also a seasonal breeder. Some specimens may attain maturity in less than a year, but the majority appear to take a year or over. It would seem that the cycle of this species is primarily a two year one. Both of these species are less adaptable than L.hoffmeisteri, and both are more local in their distribution although generally widespread.

Little can be said concerning the cycles of L.helveticus and L.cervix. Both species appeared to be able to breed all the year round, but their age at maturity was not determined.

Perhaps the most important conclusion to be drawn from these life history studies is the difficulty of making any generalisation concerning the life cycles of the species of Limnodrilus. When several species in different localities are considered, certain trends are evident. There is some evidence that the time taken to attain maturity may be a characteristic of a species, but in general the variation in pattern within each species is so great as to obscure any specific differences that may exist. Many of the variations appear to be related to the productivity of the habitat or to the nature of the substratum. Even if a cyclic pattern of events is characteristic of a species, several factors may combine to obscure it. The most important of these factors are the ability of specimens to breed twice in the same season and to attain maturity at different ages. Furthermore, the existence of a more or less prolonged breeding period followed by a prolonged production of young specimens will give rise to a similar situation in the following season. The life history of most species of *Limnodrilus* appears to be fairly adaptable, and there can be little doubt that this adaptability is largely responsible for their widespread distribution.

CHAPTER 6

THE CESTODE PARASITES OF LIMNODRILUS

a) INTRODUCTION

In the course of the routine examination of specimens of *Limnodrilus* it was found that a small proportion of them was infected with cestode parasites. These were identified as belonging to the genus *Archigetes*, Leuckart, 1878, whose members are capable of producing eggs and becoming whilst still in the invertebrate host. A study of the relevant literature showed that the taxonomy of *Archigetes* was in a state of confusion. It was considered by several authors that this genus was probably a generic complex and that species assigned to it were progenetically developed larvae of species from other genera. Such conclusions had generally been arrived at by comparative morphological studies. Studies on the life histories of the species concerned, which would appear to be of fundamental importance in determining the true relationships of the entities, were almost entirely wanting. There was also very little information available on the relationship between the parasite and the invertebrate host. Such information would undoubtedly be relevant to the current investigation, and it was accordingly decided to investigate in some detail the biology of the parasites.

The scope of the investigation was limited to two major fields; to determine more about the relationship between the parasite and its invertebrate host, and to investigate the growth, development and life cycles of the parasites themselves. It was important to ascertain whether _Archigetes_ was specific to _Limnodrilus_, as preliminary observations had indicated, and whether the presence of parasites had any deleterious effects on the host. It was considered that a knowledge of the biology of the parasites would be a help towards their correct identification. There were two further reasons for pursuing this course of investigation. The parasites were found during routine collections of _Limnodrilus_ and their biology could hence be studied without much additional increase in labour. Furthermore, the information gained would be of considerable importance in the elucidation of the _Archigetes_ problems. It was considered that a comparison of the biology of the genus in this country with current studies in Russia and America would be particularly interesting.

As a consequence of these studies, five species of Caryophyllaeidae were found to occur in Britain. Three of them are new British records. The species recorded are:-

Family Caryophyllaeidae, Leuckart 1878.

Subfamily Caryophyllaeinae, Nybelin 1922.

Genus Caryophyllaeus, Gmelin 1790

Caryophyllaeus laticeps (Pallas, 1781)

Genus Archigetes, Leuckart 1878.

Archigetes sieboldi Leuckart, 1878 New British record.

A. brachyurus Mrazek, 1908 New British record.

A. gobii (Szidat), 1938 n. comb. New British record.

Subfamily Lytocestinae Hunter, 1927

Genus Caryophyllaeides Nybelin, 1922

Caryophyllaeides fennica (Schneider, 1902) em. Nybelin, 1922

The genus Caryophyllaeides was found in the vertebrate host only. This list is probably not complete, and further investigations will no doubt add to it. Archigetes, as can be seen, is retained as a valid genus and is redescribed, together with the species recorded in the survey. Preliminary studies were carried out on the biology of A. gobii. Information on host specificity and the effect of the parasite on the host was gained for all species of parasite and host. The studies of the life histories of Archigetes also involved an examination of possible vertebrate hosts. Finally, an attempt has been made to relate the life cycles and the degree of progenetic development exhibited by Archigetes to the life cycles of the Caryophyllaeidae in general.

b) METHODS.

Initially parasites were collected during routine examination of hosts. It was later found necessary to obtain more specimens than was possible in this way, and additional methods were tried. Instead of examining individual specimens, large numbers of tubificids were immersed alive in a solution of pepsin. It was hoped that the hosts would be digested and the parasites left. It was later found that young parasites were also digested and the method was consequently abandoned. It subsequently proved possible to recognise infected tubificids with the naked eye, and large collections of worms could be examined rapidly in this way. This was the only method used in the examination of laboratory cultures. It had the advantage that information could be obtained on most aspects of the host-parasite relationship, but had the disadvantage that the degree of infection could not be determined.

After recording the necessary information on the hosts, the parasites were dissected out of them. If the parasites were alive at this stage they were transferred to water and allowed to swell until stimulation produced no response. They were then transferred to a solution of alcohol-formol-acetic. If the hosts had been cleared in Amman's lactophenol for routine examination, the parasites were removed in the same way but were preserved in lactophenol.

Initially, several stains were tried, including cotton blue and aceto-orcein, but these proved unsatisfactory. Latterly Mayer's paracarmine was used for all whole mounts. The procedure was the same whichever fixative had been used. Specimens were transferred to 45% acetic acid and left for 20 minutes. They were then stained in Mayer's paracarmine, made up by diluting a 5 ml. aliquot of concentrated stock stain to 100 ml. with 45% acetic acid. Staining was for approximately 6 hours. After staining, the specimens were transferred to 45% acetic acid and rinsed for 5 mins. They were then dehydrated in glacial acetic acid for 5 to 20 mins. Clearing took place in three stages. The specimens were left in 3:1, 1:1 and 1:3 glacial acetic acidmethyl salicylate mixtures until they sank. They were then transferred to pure methyl salicylate. Specimens were mounted in Canada balsam or Hymount (E. Gurr Ltd.). No counter stain was used.

For examination of possible vertebrate hosts adult fish were collected by use of a gill net of 29 mm. mesh, knot to knot. The intestines were examined as soon after capture as possible. The parasites were fixed in A.F.A. and stained as above.

c) THE HOST

1) Host specificity

Wisniewski (1930) concluded that the genus *Archigetes* was specific to *Limnodrilus* and especially to *L.hoffmeisteri.* These conclusions are confirmed in the present study. Table 26 shows the occurrence of some of the British species of Caryophyllaeidae in relation to the possible tubificid hosts. It is evident that *Archigetes* is, in fact, specific to *Limnodrilus*, whereas *Caryophyllaeus* is apparently unable to infect specimens of this genus. The larval stage of *Caryophyllaeides fennica* and its intermediate host have not been seen in Britain.

Experimental studies confirmed that *Archigetes* is specific to *Limnodrilus*. Populations of several species of several genera of tubificids, including specimens of *L.hoffmeisteri* parasitised by *Archigetes*, were set up in the laboratory. The development of the parasites was followed through two generations. It was found that only species of *Limnodrilus* were ever infected. Similar situations were found under field conditions. In the R.Thames all three British species of *Archigetes* and fourteen species of tubificids occur, but *Archigetes* was found only to infect *Limnodrilus*.

TABLE 26

The host specificity of the British species of Caryophyllaeidae (Invertebrate hosts only).

Host species	Parasite species 1	2	3	4	5
Limnodrilus indet.	21	25	1	1	0
L.hoffmeisteri	5	26	17	5	0
L.cervix	0	17	0	0	0
L.claparedeanus	0	6	0	0	0
L.udekemianus	0	0	0	0	0
Euilyodrilus	0	0	0	0	7
Psammoryctes	0	0	0	0	7
Tubifex	0	0	0	0	1
Other genera	0	0	0	0	0

The numbers indicate the frequency of occurrence of the particular combination of host and parasite.

Legend

1 = Archigetes indet. 2 = A.gobii 3 = A.sieboldi

4 = A.brachyurus 5 = C.laticeps

Table 26 also shows that there is no clear relationship between the species of Archigetes and the species of Limnodrilus. The commonest host appears to be L.hoffmeisteri, but this is almost certainly because it is the commonest species of Limnodrilus in Britain. Only A.gobii was recorded from both L.cervix and L.claparedeanus, but this is not necessarily evidence for a greater range of specificity. Both species of tubificid are restricted in their distribution, whereas A.gobii was the commonest species of Archigetes encountered. As L.helveticus is very restricted in its distribution the failure to find infected specimens cannot be considered significant.

The failure to find infected specimens of L.udekemianus deserves further consideration. This species occurred abundantly in regions of the R.Thames in which Archigetes was also found, but no infected specimens were ever recorded. In laboratory cultures all attempts to infect L.udekemianus proved unsuccessful. It would appear, then, that this species is immune to infection by Archigetes, or that it is liable to infection but by reason of its feeding behaviour avoids it. Either of these explanations may also account for the absence of Archigetes in other genera and the absence of Caryophyllaeus in Limnodrilus. It is not possible at this stage of investigation to determine which explanation is correct.

In an attempt to determine whether Archigetes also infected a vertebrate host, fish were examined at regular intervals throughout the summer from the Shropshire Union Canal. No Archigetes were found. Outside of Britain all species of Archigetes have been recorded from fish, generally species of the family Cyprinidae (Kulakowskaya, 1962; Calentine, 1962), but A. gobii is also known from the Cobitidae (Yamaguti, 1934).

The above conclusions concerning the specificity of Archigetes agree well with the observations of many authors. Wisniewski (1930) found the genus to be specific to Limnodrilus under field and laboratory conditions. Archigetes brachyurus has been recorded from L. hoffmeisteri and L. claparedeanus (Kulakowskaya, 1961, 1962). Archigetes gobii (as Glaridacris limnodrili) has only been recorded from Limnodrilus indet. (Yamaguti, 1934). Archigetes sieboldi, however, appears to be less specific outside Britain. It has been recorded from L. hoffmeisteri, L. claparedeanus and Tubifex tubifex (Kulakowskaya, 1962). In view of the taxonomic confusion that has long existed in the tubificids and the failure of Kulakowskaya to record whether her oligochaete identifications were confirmed, it would be interesting to have these identifications checked. Archigetes sieboldi has also been reported in L. udekemianus (Marcus '42) and this record is of particular interest as it is the only record of L.udekemianus being infected with Archigetes. There is little doubt that the identification of the host was correct but the identity of the parasite is less certain. Archigetes iowensis, a North American species, was also found to be specific to Limnodrilus (Calentine, 1962). Experimental investigations showed that it was unable to infect L.udekemianus or any species of Tubifex, (Calentine, pers.comm.) It has also been shown (Calentine, pers.comm.) that Biacetabulum, a genus often confused with Archigetes, is specific to Tubifex. It would seem possible that Kulakowskaya's (1962) record of A.sieboldi from T.tubifex may have been a record of Biacetabulum, as these two genera were often confused by her (p.6.26).

Outside Britain other species of Caryophyllaeides are known to infect Limnodrilus. Glaridacris catostomi and G.oligorchis have been found to infect L.udekemianus under experimental conditions by MacCrae (1961). Under field conditions Khavia sinensis has been found in L.hoffmeisteri and L.udekemianus and Caryophyllaeus brachycolis in L.hoffmeisteri by Kulakowskaya (1962).

2) The host - parasite relationship

In the following account all species of parasite and all species of host respectively are considered together, as observation failed to indicate any specific differences in the host - parasite relationship.

The site of the parasite in the host varies with the state of maturity of both the host and the parasite. Very young parasites are usually found in coelom of the posterior segments of the tubificid (Kulakowskaya, 1962a; and personal observation). They then move forward and come to lie in the region of segments 9 to 15. If more than one parasite is present they may extend more posteriorly. In immature hosts the parasites lie in the general body cavity, but they move into the testes-sacs as soon as these develop. The parasites are generally reported to occur in the body cavity of tubificids (Joyeux and Baer, 1961), but it is suspected that this is due largely to the failure to record the exact position in the host. The scolex of the cestode may be directed either toward the anterior or posterior end of the host.

The number of parasites per host appears to be related to the state of maturity of the parasite (Table 27). A maximum number of 20 parasites per host was found by the author, but Kulakowskaya (1962a) has recorded an infection of 29 parasites per host. Such high

TABLE 27

The number of parasites per host and its relationship to the state of maturity of the parasite.

Maturity of parasite	Number of parasites per host											
	1	2	3	4	5	6	7	8	9	10...	14...	20
I and II	6	4	2	5	3	2	1	0	0	3	1	1
III	28	10	2	1	0	1	0	0	0	0	0	0
IV	17	2	0	0	0	0	0	0	0	0	0	0
V	23	3	1	0	0	0	0	0	0	0	0	0

Only parasites of the genus Archigetes and hosts of the genus Limnodrilus are considered.

Legend.

I and II = Parasites without genitalia.
III = Parasites with genitalia but without eggs.
IV = Parasites starting to produce eggs.
V = Parasites gravid.

numbers are recorded only under experimental conditions; under natural conditions the maximum recorded by this author was 4, and by Kulakowskaya (1962a) 8. As the maturity of the parasites increases, the number per host declines so that there is generally only a single gravid specimens per host. This decline in the number of parasites per host has also been observed in isolated specimens of Limnodrilus. It would seem to indicate that either intra-specific competition occurs among the parasites, or that there is a host mechanism for preventing excessive parasitisation. Under natural conditions, specimens in multiple infections are generally at the same state of maturity. Under experimental conditions, the parasites may be at all stages of maturity. Mixed-species infections have not been found.

The relationship between the state of maturity of the parasite and that of the host is shown in table 28. When all observations are considered (Table 28a) no relationship is apparent. Mature parasites are found in hosts of all stages of maturity. When observations from naturally occurring infections only are considered (Table 28b), a more definite relationship is apparent. It is evident that mature parasites tend to occur in mature hosts. A more detailed consideration of this relationship is not possible at present as the determination of the state of maturity of both host and parasite is

TABLE 28

The relationship between the state of maturity of Archigetes and the state of maturity of Limnodrilus.

a) Laboratory and field observations

Maturity of host	Maturity of parasite 1	2	3	4	5
1	4	10	22	3	9
2	3	5	19	8	2
3	1	0	6	6	19

b) Field observations only

Maturity of host	Maturity of parasites 1	2	3	4	5
1	2	2	12	1	3
2	0	3	15	7	3
3	0	0	5	3	19

For explanation of stages of maturity see text.

somewhat arbitrary, and the states of maturity recognised for each are not necessarily homologous.

This tendency of the host and parasite to mature together represents an interesting adaptation of the parasite. As indicated in Chapter 4 the majority of Limnodrilus die after breeding, and hence an immature parasite in a mature worm would have a remote chance of completing its life cycle. This factor would be of less importance if the parasite normally completed its development in a fish host, provided that it reached an infective stage early in its development and that the feeding behaviour of the fish was not selective with regard to the state of maturity of the tubificid. Where the parasite customarily undergoes neotenous development, as appears to be the case here, such an adaptation appears to be of obvious survival value to the parasite. On the other hand if the parasite matures in an immature host, it may reduce the chance of the host completing its life cycle (see section 3) which could ultimately also be disadvantageous to the parasite. That such a relationship is not evident under experimental conditions should not be regarded as significant. At the commencement of the experiments selection was exercised in favour of gravid parasites and breeding and very young tubificids. Such arbitrary selection may have upset the natural timing of the life cycles and the relationship between them. Possibly correlated with this adaptation is the observation by Calentine (pers.comm.) that immature tubificids are more easily infected than mature ones.

The degree of infection by the parasite and its seasonal variation is shown in table 29. The infection is expressed as a percentage, in terms of the number of Limnodrilus containing parasites in relation to the number of Limnodrilus examined. No account is taken of the number of parasites per host or the number of tubificids of other genera examined. In the R.Thames the number of L.udekemianus examined is also ignored, as this species does not appear to become infected in Britain. It is apparent from table 29 that there is no pattern of seasonal infection, and the percentage infection for the same month in successive years may be very different. It is further apparent that there is no similarity between the seasonal patterns of infection in different localities. It is considered unwise to attempt to draw any further conclusions from these results at this stage as it is evident that the presence or absence of a single specimen could cause a large variation in the percentage infection.

The overall rate of infection is very low. The maximum degree of infection is higher in the Canal than in the River (10.1% as opposed to 5.6%), but the

TABLE 29

The seasonal variation in the degree of infection of Limnodrilus by Archigetes.

a) The Shropshire Union Canal, Backford.

	1961	1962											1963	
	D	J	F	M	A	M	J	J	A	S	O	N	D	M	A
Number of Limnodrilus examined	159	69	193	101	91	207	164	335	160	347	189	167	184	176	179
Number infected	8	7	10	4	2	4	5	3	1	4	1	0	2	3	3
Percentage infection	5.0	10.1	5.2	3.9	2.2	1.9	3.1	0.9	0.6	1.2	0.5	0	1.1	1.7	1.7

b) The R.Thames, Reading

	1962		1963		
	Oct.	Dec.	Feb.	May	Jly.
Number of Limnodrilus examined	227	351	292	142	179
Number infected	3	9	1	2	10
Percentage infection	1.3	2.6	0.3	1.4	5.6

degree of infection in both localities rarely exceeds 4.0%. This agrees quite well with the degree of infection recorded by other workers. Calentine (pers.comm.) found an overall infection of 3.7% with a maximum of 5.4%, and Kulakowskaya (1962) 1 - 2%, under natural conditions. Both authors were investigating riverine localities. The degree of infection in ponds and small streams is usually higher. Kulakowskaya (1962) records 8-10%, Berg (1948) 30% and the author has recorded 14% for a pond. Under experimental conditions Calentine (pers.comm.) and the author have found low degrees of infection, in the region of 1-2%, but Kulakowskaya (1962a) has recorded experimental infections of up to 50%.

3) The effect of the parasite on the host.

Kulakowskaya (1962a) made an intensive study of the effects of the parasite on the host. She concluded that the cestodes were capable of causing considerable damage to the tubificids. According to her account an infection of 10 or more Archigetes per host ultimately caused its death. The development of the parasite in the oligochaete prevented its genitalia from developing, or, if their development had commenced, caused them to disappear. She further reported that infection resulted in the tubificids becoming thin; in the body wall becoming weak in the segments occupied by the parasites; and that liberation of the parasite caused the death of the host.

None of her findings has been substantiated here. As indicated on p.6.11, a heavy infection of parasites results in the death of most of the parasites, not of the host. It has been shown (p. 6.11 and table 28) that mature parasites are usually found in mature hosts i.e. tubificids possessing genitalia, and that the host and parasite tend to mature together. Observation on the development of parasites in isolated specimens of Limnodrilus has shown that the development of the host's genitalia is unaffected by the presence of the parasite. The author has been unable to find any evidence that infected worms become weak and thin; on the contrary infected specimens are often large and robust.

In the present study it has been found that the presence of parasites has no apparent deleterious effect on the host until egg liberation occurs. The mechanism of this varies. If the eggs are shed into the body cavity of Limnodrilus, as occasionally happens in A.gobii and commonly in A.iowensis (Calentine, 1962), little damage occurs. If, however, the parasite is liberated intact by rupture of the host, as in A.gobii (p.6.40), then death of the tubificid may follow. Even this is by no means inevitable. It has been shown in Chapter 4 that Limnodrilus is capable of regenerating posterio segments provided sufficient anterior segments are still present, and such regeneration following liberation of the parasite has occasionally been observed. Nevertheless, the possibility of mortality occurring must be considered to be higher as a direct result of rupture of the host. This appears to be the only deleterious effect of Archigetes upon Limnodrilus.

From the foregoing account it is evident that the relationship between Archigetes and Limnodrilus is a balanced one in which little mutual interference occurs. Both host and parasite show certain adaptations which help to maintain this balance. It cannot be accepted, as Kulakowskaya (1962a) suggested, that the parasite causes considerable damage to the hosts, and that this is the sign of an unstable relationship. The degree of infection of the host is so low and the effect of the parasite so slight, except on a few individuals, that the overall influence of the parasite population on that of the host must be considered to be negligible.

d) THE PARASITE

In the following account of the taxonomy and biology of Archigetes it has been found convenient to treat the aspects studied under appropriate headings. It must be emphasised, however, that these divisions are artificial and for convenience only, and that the knowledge of one aspect of the biology often contributed greatly to an understanding of the knowledge of other aspects. In particular it is considered that the taxonomy of the genus can no longer be studied on the basis of morphological characters only. A knowledge of the biology of the species proved essential to an understanding of the systematic relationships of the genus.

Before proceeding to an account of the biology of <u>Archigetes</u> the terminology employed requires consideration. Many of the terms in general use for describing stages in cestode life cycles were found to be inappropriate when applied to <u>Archigetes</u>, due mainly to the ability of specimens to undergo neotenous development. Thus, the procercoid is described by Wardle and McLeod (1952) as a solid-bodied larva in which the onchospheric hooks are retained and in which the future holdfast has not yet differentiated, and the plerocercoid as a solid larva in which the future holdfast is present but from which the embryonic hooks have disappeared. The plerocercoid stage is said to begin with the shedding of the cercomer or loss of the hooks and to differ from the adult only in the absence of segmentation and genitalia. In the case of <u>Archigetes</u>, however, the onchospheric hooks and the cercomer persist throughout most, if not all, of its life, and occur simultaneously with the bothria and genitalia. It is evident, therefore, that the terms procercoid and plerocercoid have little meaning in relation to the life cycle of Archigetes, and they have consequently been abandoned. Reference is made instead to the larval and adult stages. The adult is characterised by the presence of eggs. The terms intermediate and definitive also have little meaning in relation to the hosts of Archigetes. If specimens mature in fish, then the tubificid is the intermediate host; if they mature in tubificids the invertebrate is the definitive host. To avoid confusion these terms are not used, and reference is only made to invertebrate and vertebrate hosts.

1) The taxonomy of Archigetes.

The systematic position of Archigetes and the relationship of this genus to others in the family Caryophyllaeidae has long been a problem. It was regarded by Wisniewski (1930) and subsequent authors as an aberrant genus, the members of which were to be regarded as neotenic procercoids maturing in the invertebrate host. In accordance with this view species morphologically resembling Archigetes but occurring in fish were automatically assigned to other genera (Szidat, 1937, 1938; Janiszewska, 1950). As more information on life cycles became available and more species were recorded from fish the genus became depleted, and according to Kulakowskaya (1962) contained only *A. sieboldi*. Co-incidental with these changes the view of *Archigetes* as a distinct genus came to be questioned (Janiszewska, 1950, 1954) and it was considered that 'species' of *Archigetes* were in fact progenetic larvae of species of other genera known from fish. This led to the inclusion of species, hitherto assigned to *Archigetes*, in other genera with which they frequently showed little affinity. As a necessary corollary, progenetic development was recognised as occurring in several genera. The fundamental reasons behind these transfers would appear to be the assertion by Wisniewski (1930) that species of *Archigetes* could not infect fish, and the failure to realise that the designation of a genus described from progenetic larvae was not invalid.

The alternative view, that Wisniewski (1930) may have been incorrect and that species of *Archigetes* might be capable of infecting fish, appears not to have been considered. The designation of the genus is perfectly valid according to the International Code of Zoological Nomenclature. Accordingly, when forms that resembled *Archigetes* were later described from fish it would have seemed more logical to have recognised them as belonging to this genus rather than assigning them to other genera. The mere fact that Wisniewski (opp. cit.) did not find any specimens from fish did not mean that they did not occur in a vertebrate host; the possibility that they might later be found should have been recognised. Conclusive proof, however, could only come from life cycle studies in which it could be shown that specimens recognisable morphologically as belonging to *Archigetes* were also capable of infecting fish. Such studies were carried out by Calentine (1962) and Nybelin (1962), who showed that species of *Archigetes* could and did infect fish.

Once this is appreciated, a re-appraisal of the systematic position of *Archigetes* can be made. The genus may now be re-defined to take account of the morphology and life cycles of the species. All species originally described as belonging to *Archigetes* are known to be capable of undergoing progenetic development, and these may now be united again into a single genus. Wisniewski's (1930) definition of the genus is accepted here, but with reservations relating to the life cycle. In particular the genus is now characterised on, in addition to morphological structures, the ability of specimens to become gravid in the invertebrate, but this is no longer considered to be obligatory. The genus is re-defined as follows:-

Genus *Archigetes* Leuckart, 1878.

Diagnosis

Small (2 mm. - 6 mm.) caryophyllaeids with the characters of the family. The larval stage parasitic in the body cavity of tubificids, almost exclusively those of the genus Limnodrilus. The adult stage may be parasitic in either the body cavity of tubificids or in the intestine of freshwater teleosts, particularly those of the family Cyprinidae. All species are capable of attaining maturity in the invertebrate host. Two or more bothria present on the scolex. A cercomer, bearing 6 embryonic hooks at the posterior end, is present in the larval stage and may persist into the adult. Frontal glands not extending posteriorly to the scolex. Uterine glands present or absent. Genital opening covered by a tegument. Vagina possessing a distinct seminal receptacle. Cirrus opening into a genital atrium. Cirrus pouch round. Well developed excretory system in the form of an irregular net, appearing at the posterior end in 6 to 7 ampullae. Eggs operculate, not hatching in free state. Invertebrate host infected by ingestion of embryonated eggs. Ciliated oncosphere lacking.

As pointed out by Calentine (1962) the presence or absence of a cuticular covering of the genital pore and the possession or lack of an excretory bladder may be considered as differences between the larva and the adult.

The morphological characteristics of Archigetes as described above are very similar to those of Biacetabulum as described by Hunter (1927), and there has been considerable confusion between the two genera. This has been compounded by the fact that Hunter described his specimens from fish hosts at a time when it was not realised that *Archigetes* could also parasitise a vertebrate host. When *Archigetes* was first discovered from a fish host it was consequently assigned to *Biacetabulum*. The major differences between the two genera appear to be in the arrangement of the excretory system, the specificity of the invertebrate hosts and the inability of *Biacetabulum* to undergo progenetic development (Calentine, pers. comm.) It may also be noted that with the exception of *B. appendiculatum*, to be discussed later, all described species of *Biacetabulum* can be distinguished from all described species of *Archigetes*. Species of *Archigetes* have also been attributed to *Glaridacris*, principally by Yamaguti (1959). These transfers will be discussed later. Most of them appear to have been occasioned solely by the fact that the specimens were found in a fish host, and in the absence of any evidence can not be accepted here, for the reasons discussed above.

Many of the characters originally used to designate the species of *Archigetes* have since been found to be unsatisfactory owing to the range of variation exhibited by them. This applies particularly to the shape of the scolex and the number of bothria. Other characters appear to depend upon the state of maturity of the specimen, in particular the continuity of the vitelline glands in the region of the ovary, the extension of the uterine loops to the level of or beyond the cirrus sac and possibly also the presence or absence of uterine glands. In the present study particular emphasis has been placed upon the number and arrangement of the testes and whether they extend beyond the vitellaria in the anterior region of the body. These appear to provide the most diagnostic characters.

Archigetes sieboldi Leuckart, 1878

Synonyms:

A. appendiculatus Mrazek, 1897.
Biacetabulum sieboldi: Szidat, 1937
B. appendiculatum: Janiszewska, 1950.

Description:-

With the characters of the genus. At the commencement of egg production average length 1.5 mm (1.1 to 2.5), average breadth 0.4 mm. (0.3 to 1.0). Scolex bearing single distinct bothrium on dorsal and ventral surfaces. Testes numbering 90 (75 to 99), and extending from neck region to cirrus pouch. Anteriorly, they begin behind the vitellaria and are scattered through the medulla. Preovarian vitellaria principally located in two lateral bands, but scattered follicles occur in the median region. The follicles begin in front of the testes, usually curving in towards the mid line (figs. 23 - 26), and may or may not extend laterally along the ovarian wings (figs. 23 - 26). Postovarian vitellaria present. Uterus loops frequently extending as far as cirrus pouch. Uterine glands may be present or absent. Eggs measuring 54u (50 to 58) by 33u (28 to 40).

Parasites of the body cavity of *Limnodrilus* and the intestine of Cyprinidae.

Discussion.

The early descriptions of this species as *A. sieboldi* and *A. appendiculatus* and the authorship of the latter name have been discussed in some detail by Calentine (1962). Mrazek's (1897) original figure of *A. appendiculatus* showed that the vitellaria did not extend laterally along the ovarian wings but were clearly divisible into pre- and post-ovarian groups. In all other respects his specimens closely resembled *A. sieboldi*. Wisniewski (1930) believed that *A. appendiculatus* was a synonym of *A. sieboldi*, and concluded that the attainment of sexual maturity in the invertebrate host was obligatory for this species. This synonomy was accepted by Joyeux and Baer (1936, 1961) and Wardle and McLeod (1952). These authors all figured *A. sieboldi* under that name, but illustrated it with a reproduction of Mrazek's figure. Janiszewska (1950), on the other hand, separated the two entities on the continuity of the vitellaria and recognised them as valid species. Her views were followed by Kulakowskaya (1961) and Calentine (1962), although the latter author did state that the true identity of these two entities required further study.

The identity of the two entities was confused even further. Hunter (1927) had created the genus *Biacetabulum* to contain specimens taken from fish, and his definition was very similar to the definition of *Archigetes*. Szidat (1937) found specimens of the *sieboldi* type in fish and accordingly called them *Biacetabulum sieboldi*. He considered that *Archigetes* was a generic complex containing the progenetic larval forms of species of other genera, and that the adult forms of the other species would also be found in fish. Janiszewska (1950) found specimens of the *Appendiculatus* type in both oligochaetes and fish, and therefore transferred *appendiculatus* to *Biacetabulum*. She considered Szidat's specimens to be in fact of the *appendiculatus* type, and so retained the name *Archigetes* for *sieboldi*. She considered, however, that the adults of *sieboldi* would eventually be found in fish, and in fact later (1954) decided that *Archigetes* was probably located in *Biacetabulum* and *Glaridacris*. Kulakowskaya (1961, 1962) accepted Janiszewskaya's views on the basis of her own experimental evidence, but she made an exception for sieboldi which she retained in Archigetes as the adult form had not been found from fish.

In accordance with the views expressed elsewhere in this work and the generic diagnosis on p.6.20 the transfer of species from Archigetes to Biacetabulum cannot be accepted merely because the specimens were found in fish. There is nothing in Janiszewskaya's (1950,1954) descriptions to suggest that her specimens are more correctly assignable to Biacetabulum either on morphological or biological characters, and they must accordingly be assigned to Archigetes. The specimens figured by Kulakowskaya (1962) from oligochaetes show the presence of eggs in the uterus, and accordingly they should be referred to Archigetes. B.sieboldi as recognised by Szidat (1937) and B.appendiculatum as recognised by Janiszewska (1950, 1954) and Kulakowskaya (1961,1962) are consequently recognised as being correctly assignable to Archigetes.

The problem of the synonomy of A.sieboldi and A.appendiculatus still remains. Specimens of both types were present in the author's collections and a comparison of them is given below:-

	sieboldi	*appendiculatus*
Length	0.7-1.6 mm.(1.1 mean)	1.1-2.6 mm.(1.5 mean)
Width	0.2-0.7 mm.(0.4 mean)	0.3-1.0 mm.(0.4 mean)
Testes number	85-96 (91 mean)	75-99 (88 mean)
Testes arrangement	Scattered in medulla	Scattered in medulla
Vitellaria - start	Anterior to testes	Anterior to testes
continuity	Continuous lateral to ovary, at least on one side.	Discontinuous lateral to ovary
Uterine glands	Generally absent	Generally absent
Number of specimens examined	15	13

It can be seen that the two entities are very similar indeed apart from the continuity of the vitellaria in the region of the ovaries. If the above descriptions are compared with the descriptions of other species of the genus, it will be seen that they constitute a single unit with regard to the testes number and arrangement and the anterior position of the vitellaria. The difference in length is not held to be significant, as specimens of the *appendiculatus* group were at a more advanced stage of maturity than those of the *sieboldi*. The general similarity between them is shown in figs. 23-26. The difference in the mean testes number is very slight. The most important factor of all, however, is that the continuity of the vitellaria is not a stable characteristic. It can be seen in fig. 24 that the

Figure 23

Archigetes sieboldi

Note apparent break in vitellaria on either side of ovary.

Legend

B = Bothrium

C = Cirrus pouch

CR = Cercomer

O = Ovary

S = Seminal vesicle

T = Testes

U = Uterus

VD = Vas deferens

VG = Vitelline glands

Note

The same convention in the representation of organs has been adopted in figures 24 -31. These are not, therefore, labelled and reference may be made to this figure for identification of structures. All specimens were collected from *Limnodrilus*.

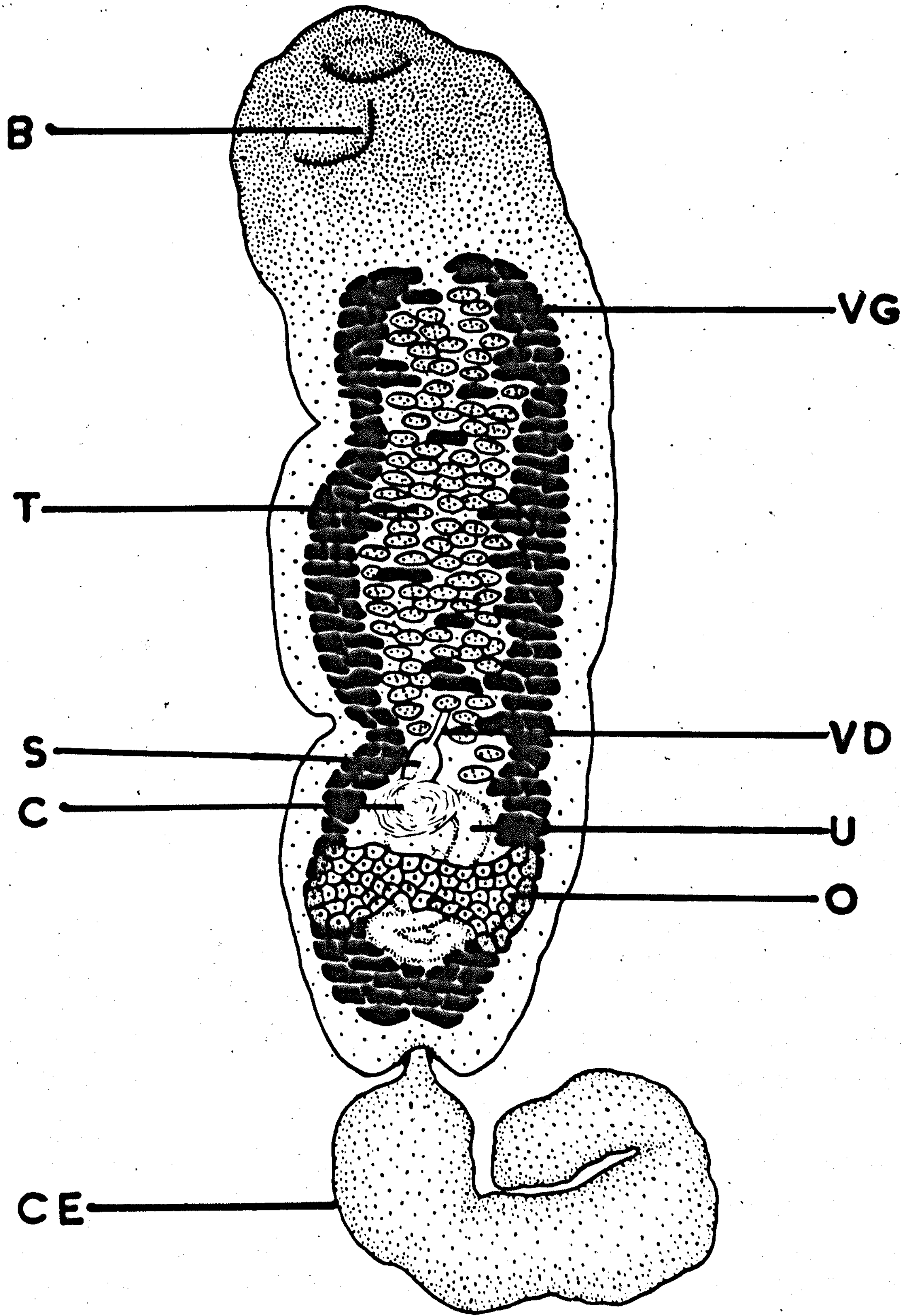

B
VG
T
VD
S
C
U
O
CE

Figure 24

Archigetes sieboldi

Note the thinning of the vitellaria on one side of the ovary and the resulting separation into pre and post ovarian vitellaria.

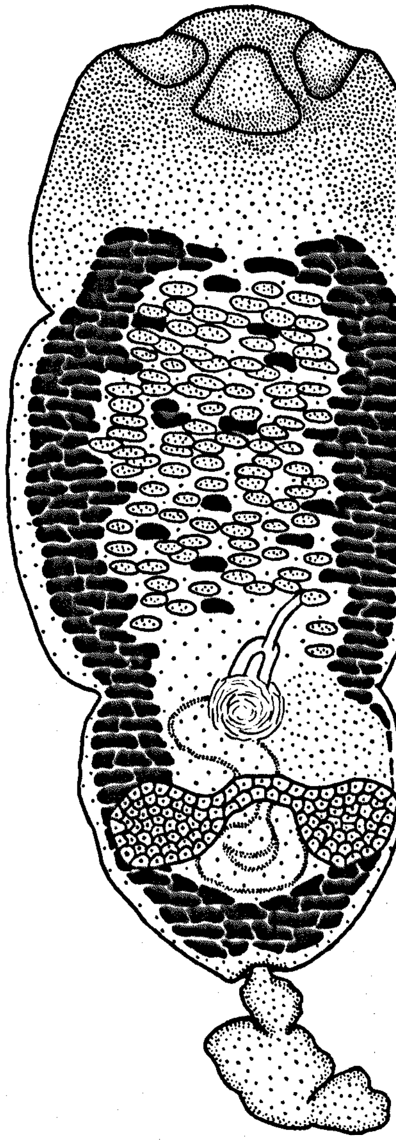


Figure 25

Archigetes sieboldi

Note the complete division into pre and post ovarian vitellaria on either side and the presence of small deformed eggs in the uterus.

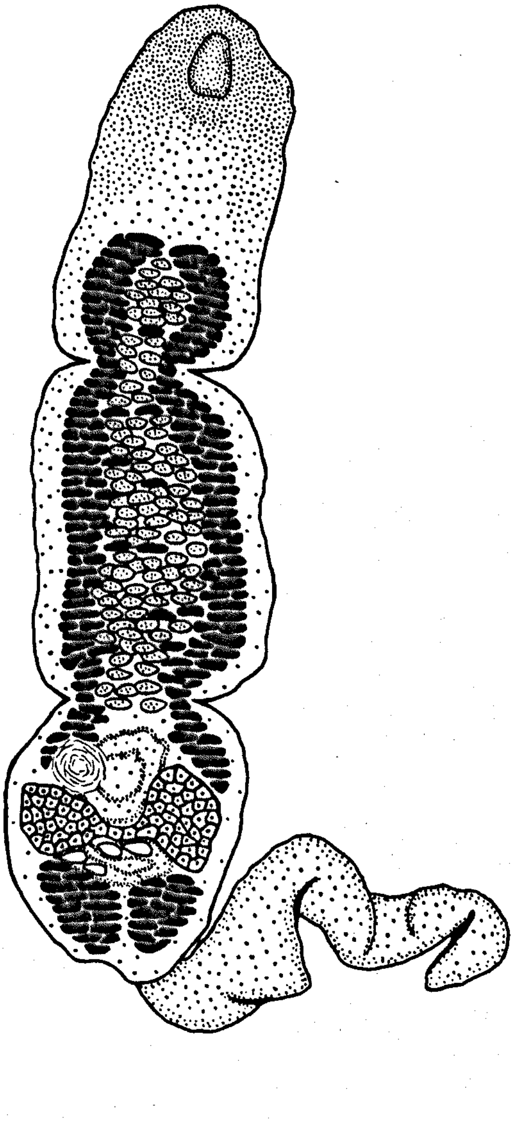
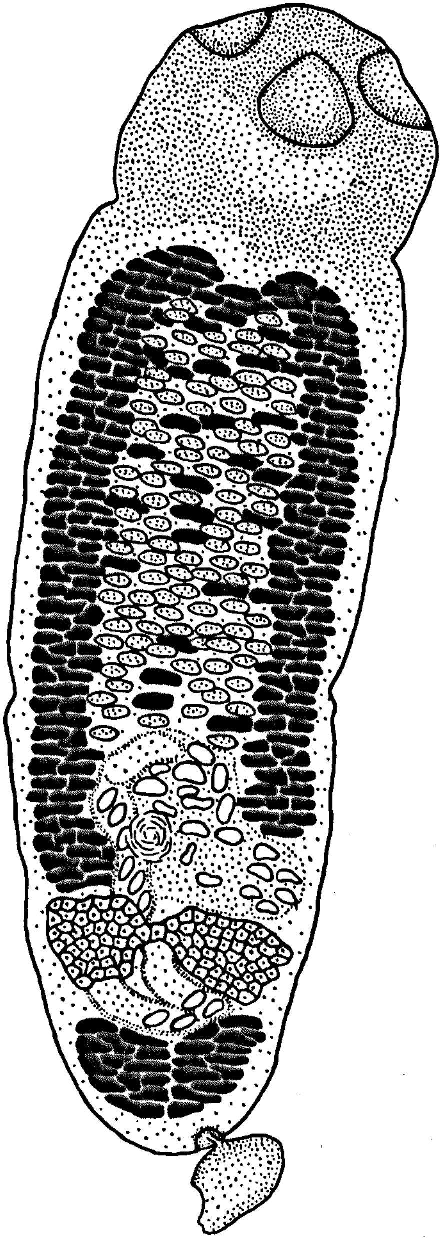


Figure 25

Archigetes sieboldi

Note.

The complete division into pre and post ovarian vitellaria. The presence of deformed and normal eggs in the uterus. The broken cercomer.



vitellaria may be continuous on one side of the ovary, but thin and broken on the other. The thinning and interruption of the vitellaria in this region is known to occur in other species of Archigetes (Yamaguti, 1934; Szidat, 1938) as the specimens approach maturity and the ovaries and uterus increase in size.

It is suggested that this may be true here also, and that the appendiculatus type is only a more mature stage of A.sieboldi. Further confirmation of this suggestion comes from the fact that specimens of the sieboldi type have never been found with eggs, whereas only one specimen of the appendiculatus type has been found without eggs. A survey of the literature reveals the same situation. Specimens of the sieboldi type have never been recorded from fish or with eggs. Those specimens recorded from fish or as gravid in the oligochaete have always been of the appendiculatus type, (Szidat, 1937; Janiszewska, 1950, 1954; Kulakowskaya, 1961, 1962). Since Wisniewski (1930) believed the two types were synononous his life cycle studies of A.sieboldi give no indication of which types were present, or if they occurred at different stages in the life cycle. An attempt was made by the author to study the development of A.sieboldi in the laboratory in an effort to clear up this problem. It only proved possible to take one specimen through the complete life cycle, but in this specimen a thinning of the vitellaria in the region of the ovaries was observed at the commencement of egg production. Such a result cannot be regarded as conclusive. Despite the absence of experimental studies, it is considered that at present the balance of all the circumstantial evidence presented above confirms the suggestion that *A.appendiculatus* is only a more mature stage of *A.sieboldi*, and must hence be regarded as a synonym of this species.

Archigetes brachyurus Mrazek, 1908

Synonyms:

Brachyurus brachyurus Szidat, 1938.

Paraglaridacris silesiacus Janiszewska, 1950.

Glaridacris brachyurus Yamaguti, 1959.

Description:-

With the characters of the genus. At the commencement of egg production average length 3.0 mm. (2.4 to 3.5), average breadth 0.45 mm. (0.4 to 0.5). Scolex bearing three distinct bothria on dorsal and ventral surfaces. Testes numbering 137 (120 to 159), and extending from the neck region to the cirrus pouch. Anteriorly, they begin in front of the vitellaria and are arranged in longitudinal rows of 30 to 40 per row. Preovarian vitellaria located in two lateral bands, extending laterally along the ovarian wings (figs. 27, 28). Postovarian vitellaria present. Uterine loops extend as far as the cirrus pouch. Uterine glands present. Eggs measuring 62u by 32u.

Parasites of the body cavity of Limnodrilus and the intestine of Cyprinidae.

Discussion

This appears to be the least common species of Archigetes. It is described by Kulakowskaya (1961,1962) as being rare in tubificids and very rare in fish. This current record is the first from Western Europe since the original description of this species from Czechoslovakia by Mrazek (1908). The author's specimens approximated very closely to the descriptions of Mrazek (1908) and Wisniewski (1930). They differed from Kulakowskaya's (1961,1962) and Dubinina's (in Bykhovski, 1962) descriptions in that the vitellaria are continuous lateral to the ovarian wings (figs. 27, 28). No mention is made of this character in the type description and its importance has already been discussed with reference to A.sieboldi (p.6.27).

This species was originally described from gravid specimens found in L.hoffmeisteri. It was accepted as a species of Archigetes by Joyeux and Baer (1936) and Wisniewski (1930). Szidat (1938) described specimens of Archigetes from fish and created a new genus to contain

Figure 27

Archigetes brachyurus

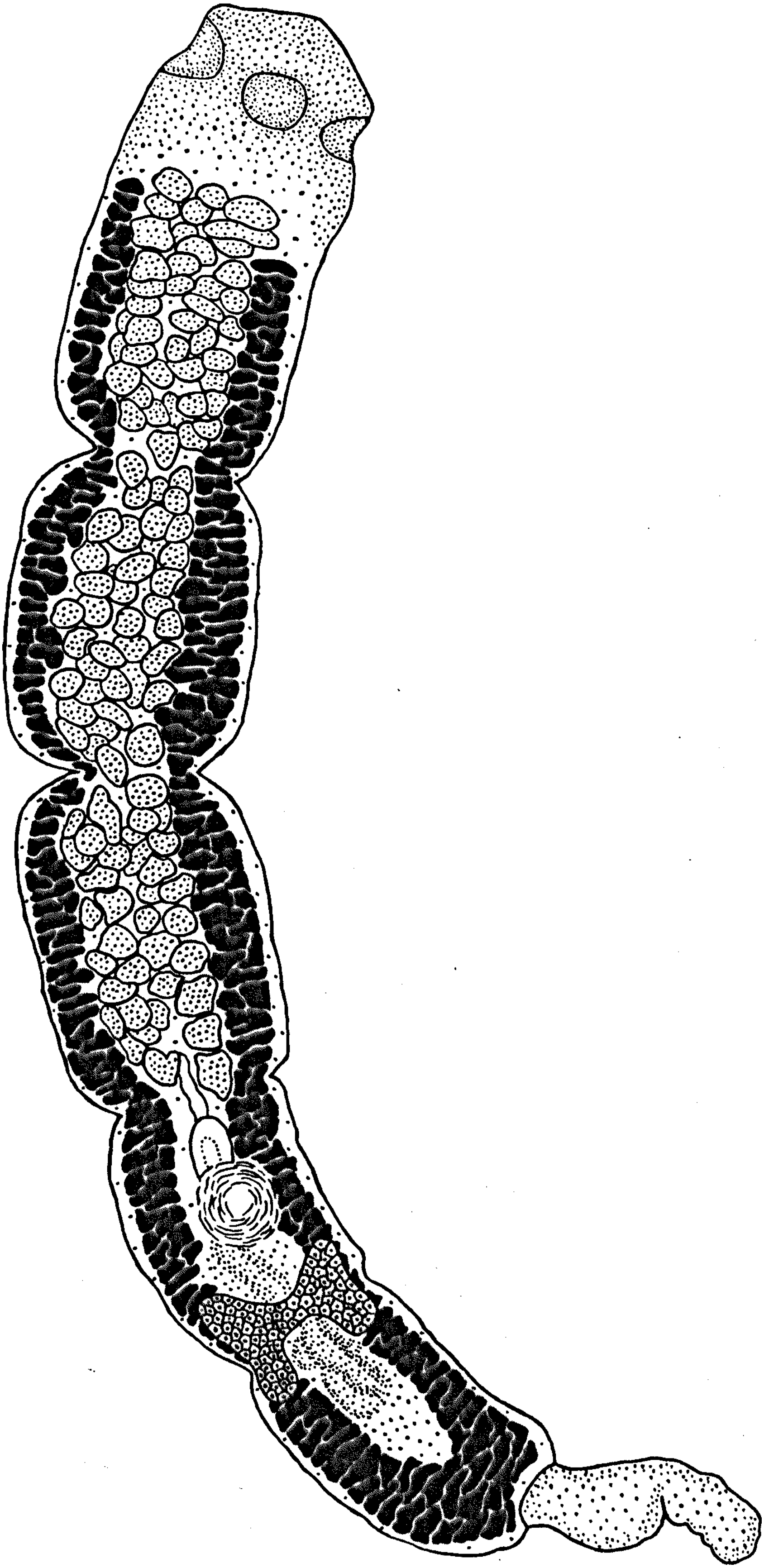
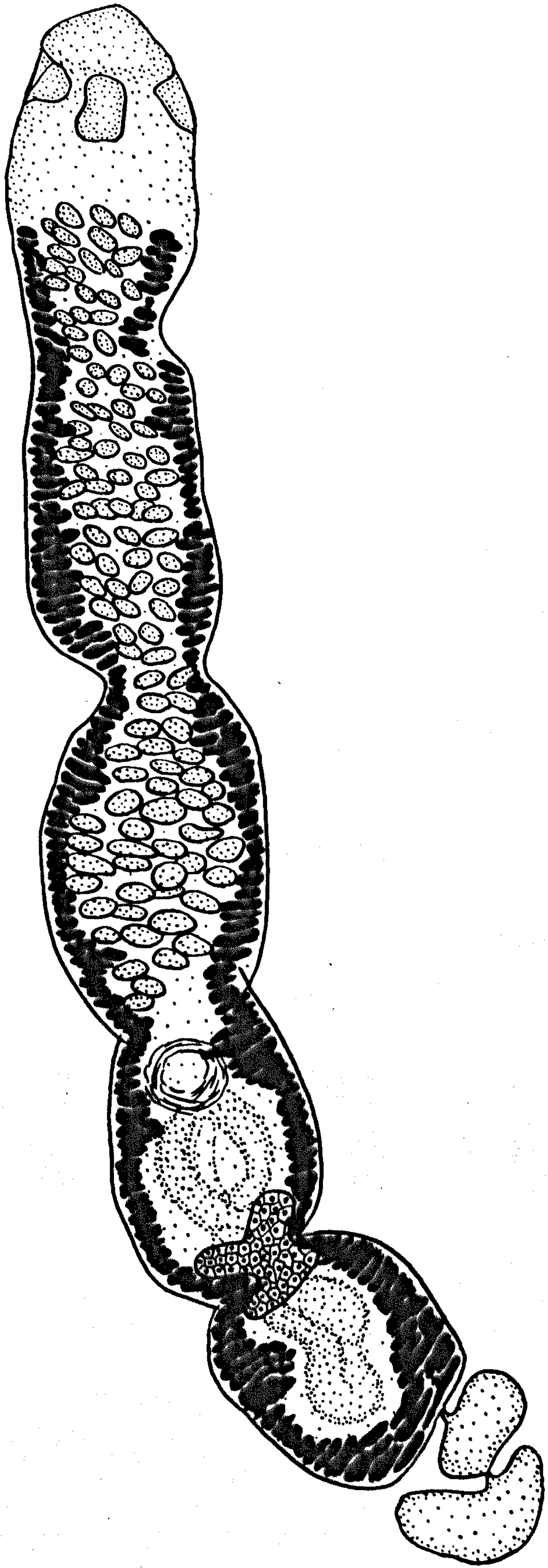


Figure 28

Archigetes brachyurus



them. He described his specimens as *Brachyurus gobii*, n.sp.,n.gen. He considered that *A.brachyurus* was the progenetic larva of a second species of this genus, the adult stage of which had not yet been found in fish, and designated it as *Brabhyurus brachyurus*. Fischthal (1951) pointed out that Brachyurus as a generic name was already in use. This was taken up by Yamaguti (1959) who transferred both species of *Brachyurus* to *Glaridacris*. His justification for doing so was that both species occurred in fish and were similar to *G.limnodrili*, a species previously described by him (Yamaguti, 1934). The possibility that all three species might be more correctly assigned to *Archigetes* was ignored. Kulakowskaya (1961) retained *brachyurus* in *Archigetes*, but later (1962) accepted the views of Yamaguti and transferred both species of *Brachyurus* to *Glaridacris*. At the same time she recognised that *Paraglaridacris silesiacus*, Janiszewska, 1950, was a synonym of *G.brachyurus*.

The transfer of *A.brachyurus* to a new genus cannot be accepted here. The genus *Brachyurus* was created only because specimens morphologically resembling *Archigetes* had been found from fish. Both *brachyurus* and *gobii* were transferred to *Glaridacris*, with which genus they showed little affinity, instead of being returned to *Archigetes* for the same reason. Both species conform morphologically and biologically to the definition of Archigetes on p.6.20, and should be located in this genus. The question of the similarity of both species to G.limnodrili will be dealt with under A.gobii.

Archigetes gobii (Szidat, 1938) n.comb.

Synonyms:

Brachyurus gobii Szidat, 1938.

Glaridacris limnodrili Yamaguti, 1934

G.gobii: Yamaguti, 1959

Description

With the characters of the genus. At the commencement of egg production average length 1.5 mm. (1.1 to 2.1), average breadth 0.45 mm. (0.3 - 0.5). Scolex bearing three bothria on dorsal and ventral surfaces, although some may disappear during fixation. Testes numbering 50 (39 to 63) and extending from the neck region to the cirrus pouch. Anteriorly, they begin in front of the vitellaria and are arranged in two dorsal and two ventral longitudinal rows with twelve to each row. Preovarian vitellaria located in two lateral bands, extending laterally along the ovarian wings, although they may be thinner in this region (fig.29). Postovarian vitellaria present. Uterine loops may extend as far as the cirrus pouch. Uterine glands generally present. Eggs measuring 53u (45 to 63) by 32u (27 to 36).

Parasites of the body cavity of Limnodrilus and the intestine of Cyprinidae and Cobitidae.

Discussion

This was the commonest species of Archigetes occurring in Britain. This is the first record of the larva of this species from Western Europe. The author's specimens approximated very closely to the descriptions of the adult given by Szidat (1938) and Kulakowskaya (1961,1962).

The original description of this species as Brachyurus gobii by Szidat (1938), its similarity to A.brachyurus, and the transfer of both species to Glaridacris has been discussed under A.brachyurus (p.6.31). The species is morphologically similar to the described species of Archigetes, it conforms to the definition on p.6.20, and it is able to mature in the invertebrate host. It is accordingly considered that B.(G.) gobii should be located in Archigetes and it is here designated as A.gobii.

When Szidat (1938) created the genus Brachyurus he recognised the similarity of A.gobii to G.limnodrili, and accordingly transferred this latter species to his new genus. This similarity between the two species was largely responsible for their transfer to Glaridacris by Yamaguti (1959). G.limnodrili was described from

Figure 29

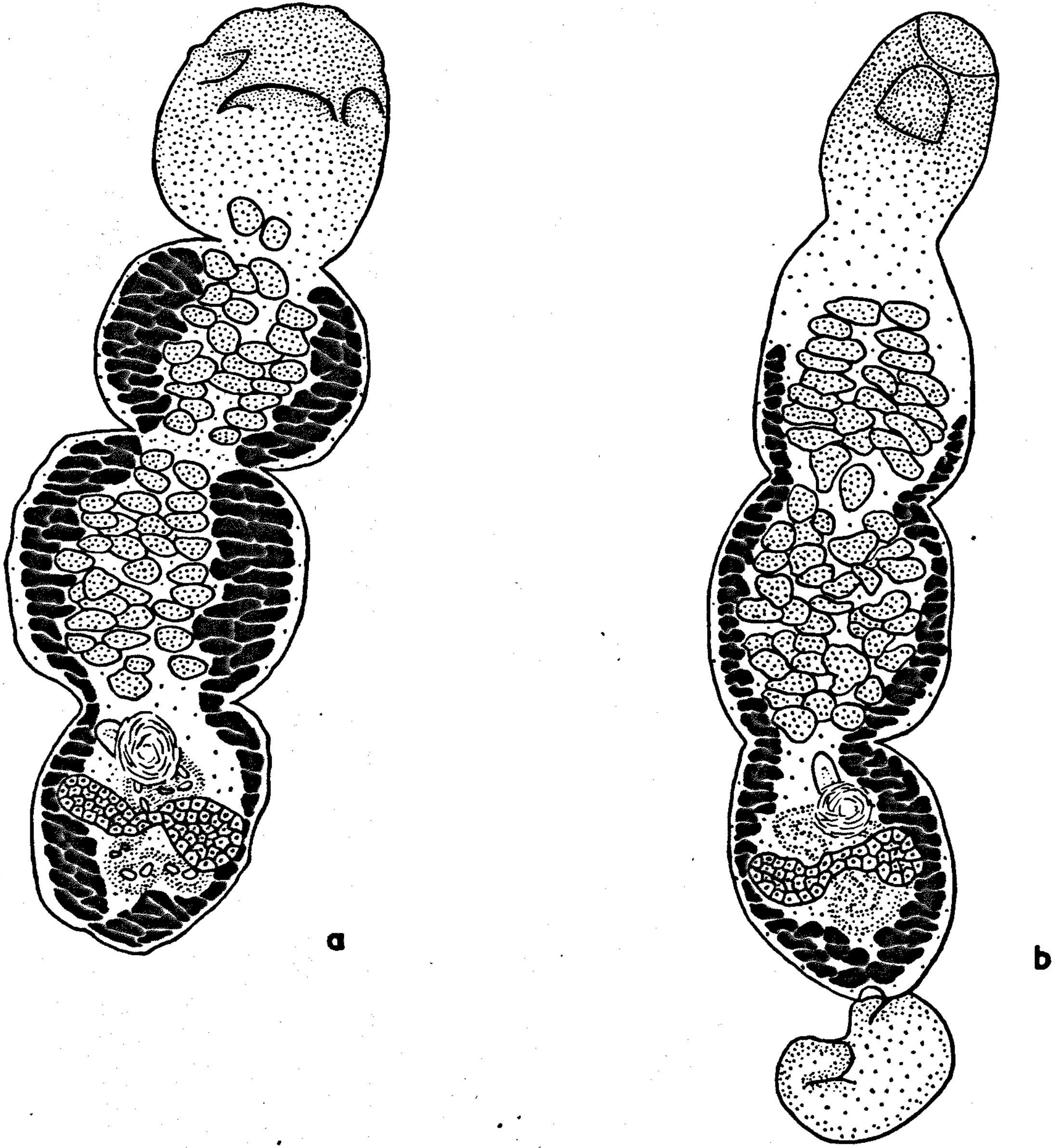
Archigetes gobii

Note.

The variation in shape of the scolex and arrangement of the bothria.

The presence of deformed eggs and the absence of a cercomer (broken off during the removal of the specimen from the host) in specimen a.

The arrangement of the testes in two rows in the anterior region of specimen b.


a
b

L.hoffmeisteri and from fishes by Yamaguti (1934). In the same work he demonstrated that the species was able to attain maturity in either host. No reasons for its inclusion in Glaridacris were given, other than that it possessed the characters of the genus and had been recorded from fish. The description and figures show that it is unlike any of the other species of Glaridacris. Furthermore, no other species of this genus is able to mature in the invertebrate host. A comparison of the description of A.gobii given above and figs. 29-31 with the description and figures of G.limnodrili given by Yamaguti (1934) reveals no significant differences. The similarity between these two species was also noted by Kulakovskaya (1962) and Calentine (pers.comm.) Both morphologically and in its life cycle G.limnodrili is indistinguishable from A.gobii and must therefore be regarded as a synonym of this latter species.

Two other species of Archigetes have been described but have not yet been recorded from Britain. A.cryptobothrius was described by Wisniewski (1928) and later (1930) compared by him with other species of the genus. It has not subsequently been found. A.iowensis was described from North America by Calentine (1962). A full description of its morphology is given and enough evidence to show that it may mature in invertebrate and vertebrate hosts.

A key to the genus *Archigetes* is given by Calentine (1962). In view of the systematic changes proposed above it is considered advisable to include a new key. This is based on examination of specimens of *A.sieboldi*, *A.brachyurus* and *A.gobii* from the author's collections; of specimens of *A.iowensis* kindly loaned by Dr. Calentine; and of published descriptions of *A.cryptobothrius*. The key may be used for specimens obtained from either invertebrate or vertebrate hosts.

1a Testes arrangement not clear; testes beginning after the vitellaria in the anterior part of the body; Testes number 75-95 (mean 90).

A.sieboldi Leuckart

1b Testes arranged in longitudinal rows, easily observable in the anterior part of the body. Testes beginning level with or in front of the vitellaria..............2

2a Testes number 120 - 159 (mean 137), beginning in front of vitellaria and arranged in rows of 30 to 40 each.

A.brachyurus Mrazek

2b Testes number averaging 154, beginning level with vitellaria, and arranged in several longitudinal rows of 18 to 26 each.

A.cryptobothrius Wisniewski

2c Testes number 57 - 76 (mean 66); scolex clearly demarcated from body.

A. iowensis Calentine

2d Testes number 39 - 63 (mean 50); scolex not clearly demarcated from body.

A. gobii (Szidat)

2) Geographical distribution of Archigetes

Although few records of the genus are available, it appears to be of fairly widespread occurrence but to have been frequently overlooked. It would seem likely that its distribution will ultimately be found to parallel that of *Limnodrilus*, which is cosmopolitan.

The distribution will be given by species and by the country of occurrence. New records are indicated as such.

A. sieboldi Germany (Szidat, 1937). Italy (new record). Sweden (Nybelin, 1962). Denmark (Kennedy and Chubb, 1962). Poland (Wisniewski, 1930). U.S.S.R. (Kulakowskaya, 1962). France (Joyeux and Baer, 1936). Czechoslovakia (Mrazek, 1908). Britain (Brinkhurst, Chubb and Kennedy 1962) Brasil (Marcus, 1942).

A. brachyurus Czechoslovakia (Mrazek, 1908) U.S.S.R. (Kulakowskaya, 1962). Britain (new record).

A.gobii Germany (Szidat, 1938). U.S.S.R. (Kulakowskaya, 1961). Japan (Yamaguti, 1934). Britain (new record).

A.iowensis U.S.A. (Calentine, 1962)

A.cryptobothrius Poland (Wisniewski, 1930). Denmark (Berg, 1948).

The genus has also been recorded from Finland (Brinkhurst, pers.comm.), Lithuania (Grigelis, pers.comm.) and Ireland (new record), but it was not possible to identify the specimens owing to their condition.

3) The growth and development of *A.gobii* in *Limnodrilus*.

Development of the embryo within the egg commences while the egg is still retained within the body of the cestodes. After liberation, the eggs lie in the substratum and development of the embryo is completed during this period. The eggs are presumably ingested during the course of the tubificid's normal feeding. Hatching of the oncosphere does not take place until ingestion has occurred, and there is no free living coracidium in this or any other species of *Archigetes* (Wisniewski, 1930). After ingestion the eggs pass to the posterior region of the intestine where the oncosphere hatches. They penetrate the intestinal wall and come to lie in the body cavity of the posterior segments where future development takes place. Hatching of the eggs and penetration of the intestine wall was not observed, but it is presumed that this takes place in the same manner as described by Wisniewski (1930). Eggs were recorded from the posterior regions of the intestinal tract and the presence of developing oncospheres in the body cavity in this region has also been observed. The shape and structure of the cestode at this stage is shown in fig. 30a. The scolex and cercomer have not yet differentiated, the six embryonic hooks are present at the posterior end of the body and there is no trace of the genitalia. The length of the larvae at this stage is shown in fig. 32. If several eggs have been ingested, up to 20 larvae may be present in the body cavity.

Within a short time the larvae pass rapidly to the anterior region of the body cavity, not slowly as reported by Kulakowskaya (1962a), to lie in the coelom of the genital segments. If the initial infection has been heavy, considerable larval mortality may occur during this migration, as there are rarely more than 2 or 3 larvae in the genital segments. All further growth and development of the larvae takes place in this region.

The cercomer now begins to differentiate by the cutting-off of the protrubrance bearing the hooks of the oncosphere. The cercomer increases in length but the hooks do not increase in size. The bothria and scolex also make their appearance at this stage. The larvae increase in length up to 1.2 mm. (fig. 32). The appearance of the larva at this time is shown in fig. 30b, where the female and male genitalia have made their appearance. The cercomer reaches its full development, and the bothria and scolex differentiate further. The greatest degree of growth takes place at this stage (fig. 32), and individual differences appear in development, usually related to the number of testes (fig. 29), or the shape of the scolex (figs. 29 - 31). If the genital organs of the host start to develop, the larvae come to lie in the testes sacs.

Egg formation now begins. Those formed first are usually mis-shapen and sterile, but the later ones assume normal dimensions (53u by 32u) and are fertile. As egg development proceeds the uterine loops increase in size, may extend as far as the cirrus sac (fig. 31a), and cause thinning of the vitellaria in the region of the ovaries. Growth of the larva continues, but the rate slows down (fig. 32). Production of eggs continues, and they come to occupy most of the body of the adult (fig. 31b).

For convenience in considering growth and life cycles of <u>Archigetes</u> five stages in development are recognised. Stage 1 (fig. 30a) is recognised by the

Figure 30

Stages in the development of A. gobii

(a) Stage 1. Note absence of cercomer and internal organs.

(b) Stage 2/3. Note poorly developed scolex.

(c) Stage 3.

For explanation of stages see text.

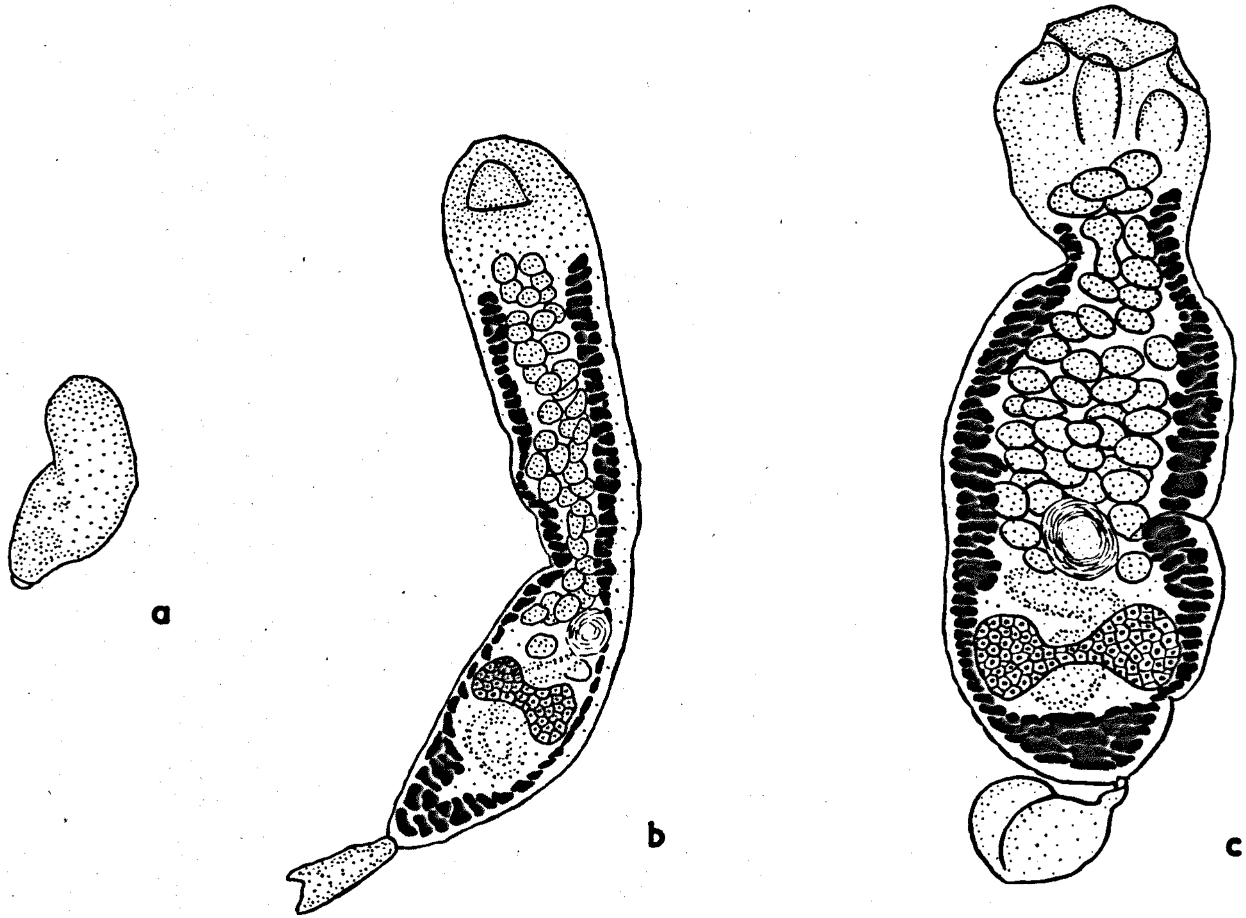
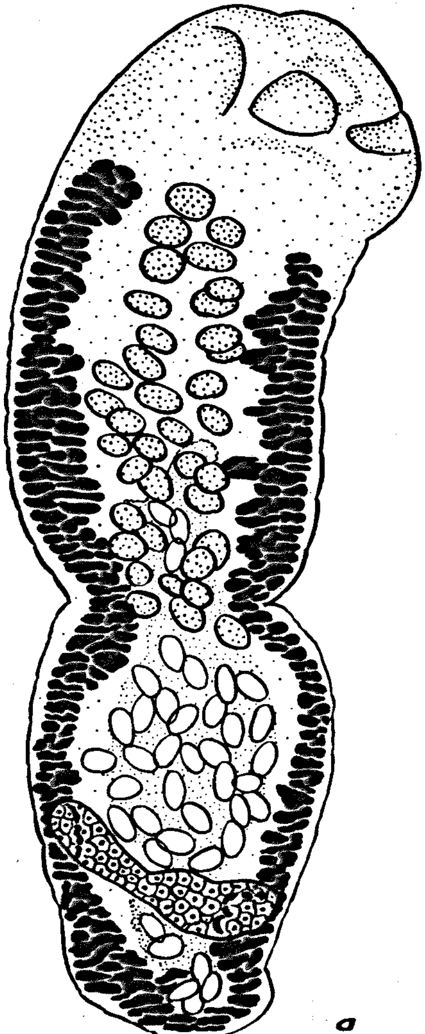

a
b
c

Figure 31

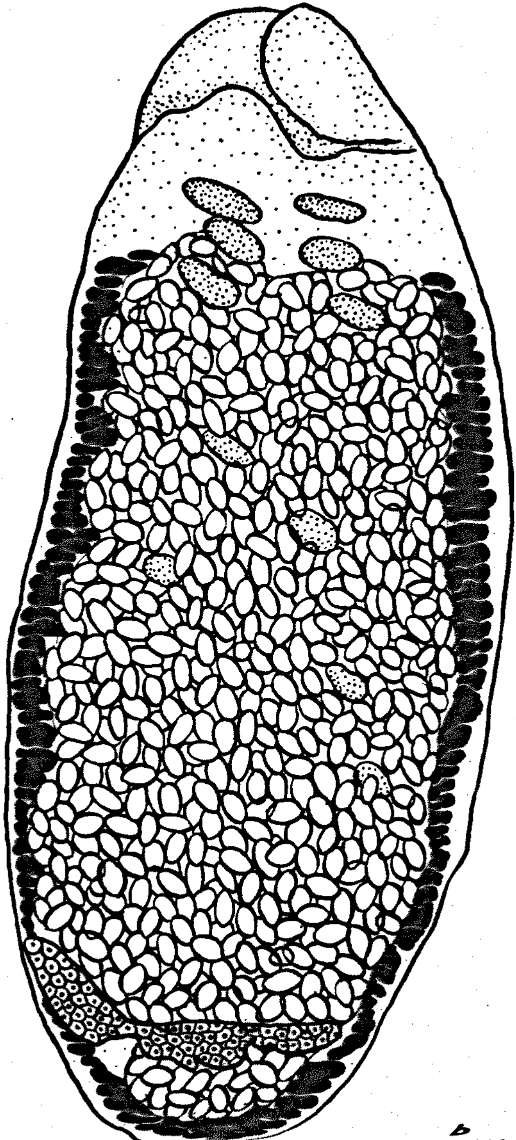
Stages in the development of A. gobii

(a) Stage 4. Commencement of egg production. Note the absence of the cirrus pouch and enlargement of the uterus.

(b) Stage 5. A gravid specimen. Note the reduction in the number of testes.



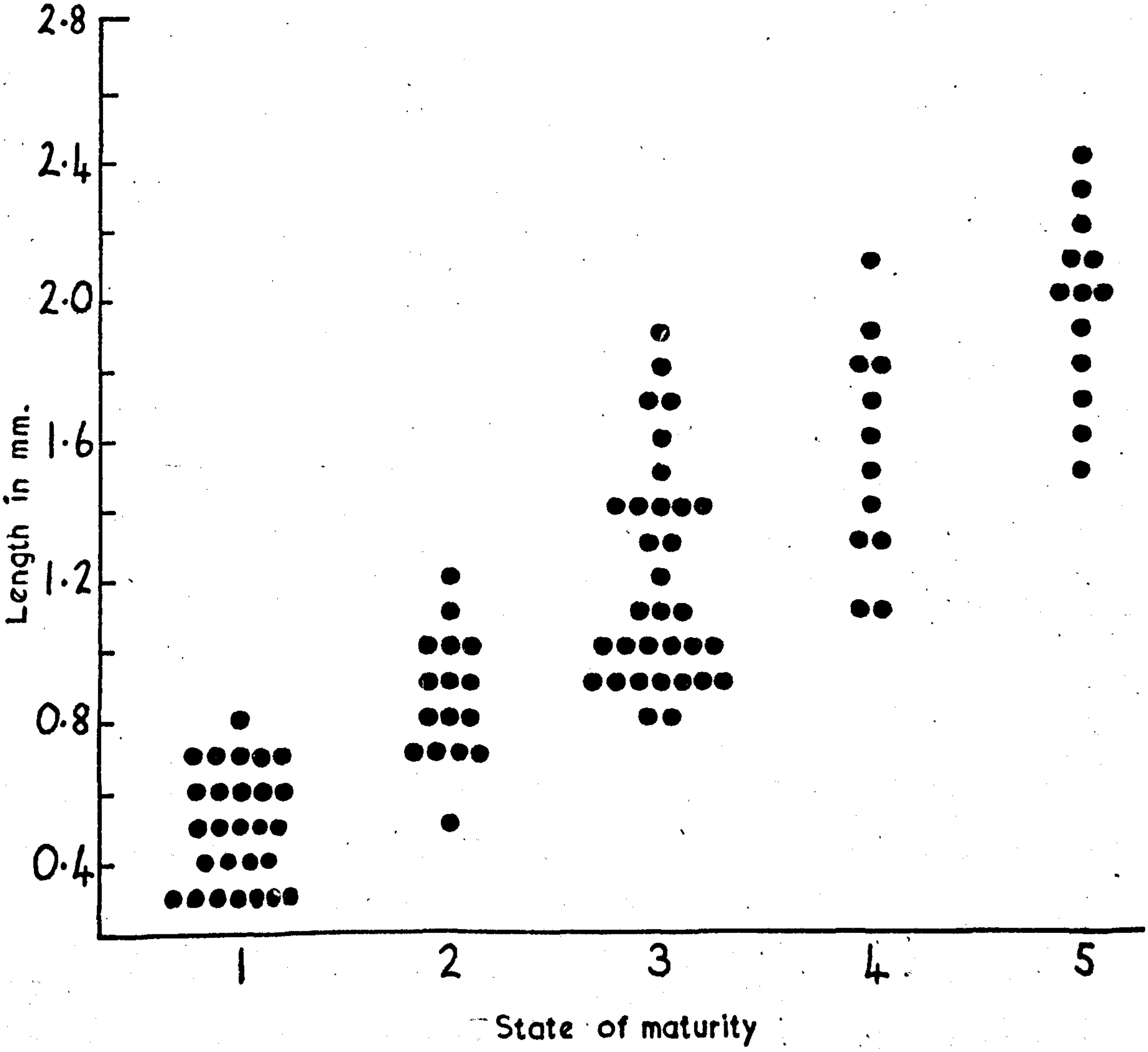
a



b

Figure 32

The length of Archigetes gobii at differeht stages of maturity. The data is based on the analysis of 100 specimens.


2·8
2·4
2·0
1·6
1·2
0·8
0·4
Length in mm.
1
2
3
4
5
State of maturity

absence of any genital structures in the larva. Stage 2 is recognised by the presence of testes and a cercomer. In stage 3 the female genitalia have appeared (figs. 30b and c). Stage 4 is characterised by the commencement of egg production (fig. 31a), and stage 5 by the attainment of complete maturity, when the adult is full of eggs (fig. 31b). The size of specimens at each stage is shown in fig. 32.

Up to this stage the development of A.gobii is similar to that of A.sieboldi (Wisniewski, 1930) and B.appendiculatum (= A.sieboldi ?) (Kulakowskaya, 1962a). The method of release of the eggs, however, appears to vary from species to species. In A.gobii eggs are retained in the adult in utero. The uterus then increases in size, and would seem eventually to rupture, as the eggs come to lie in the body and are not apparently surrounded by any pouch. Liberation almost invariably occurs by release of the parasite from the host. The parasite ruptures the body wall by active movements and passes out into the substratum. Occasionally the parasite itself becomes ruptured during this process, and eggs are shed into the testes sacs of the host or direct into the surrounding medium. More usually the parasite lies on the surface of the substratum, and release of the eggs is accomplished by decay of its body. In A.sieboldi eggs are also retained in utero (Wisniewski, 1930), but eggs of A. cryptobothrius collect into a cuticular pouch (Wisniewski (1928). In A. iowensis eggs are generally shed into the testes sacs of the host. The shedding of eggs into the testes sacs is also reported to occur in A. brachyurus (Mrazek, 1908). Whatever the method of release, the eggs come to lie free in the substratum, whence they can be ingested by the tubificid.

The length of the life cycle in A. gobii under experimental conditions was determined by regular observations on isolated infected hosts. Few specimens were examined for this purpose, as at that time the parasites were required for morphological and developmental observations which required their being killed. The results are expressed below:

	Stage of maturity				
	Eggs	1	2/3	3	4/5
Days after eggs deposited	0	50	116	143	213

According to Wisniewski (1930) A. sieboldi was able to complete two generations each year. The duration of the cycle depended on temperature, being approximately 110 days in warm weather and 210 days in cold weather. The duration of the cycle for 213 days agrees well with Wisniewski's observations, as the observations also took place during the colder months. Calentine (pers. comm.) on the other hand found a cycle of 100 days for

A.iowensis. This agrees well with Wisniewski's figure for warmer months, but Calentine did not specify the temperature of his experiments.

Nothing can be said from personal observation on the duration of life or the development of A.gobii in fish as no fish infected by this cestode were found. In Britain, progenesis is apparently the dominant form of development. The only person to have studied the development of Archigetes in fish was Calentine (1962 and pers.comm.) who worked on A.iowensis. He concluded that their occurrence in fish was strictly seasonal, of a short duration only, and that the eggs were generally shed into the intestine of fish. Of the specimens found by him in fish, 80% were gravid, which would suggest that the procercoids do not become infective until about stage 3. He recorded one point of particular interest: whereas the tubificid cycle took 100 days, specimens of A.iowensis hatched from eggs taken from specimens in fish successfully infected and developed in specimens of Limnodrilus, but had not produced eggs 600 days after infection. He suggested that this might be evidence for the existence of two races (pers.comm.) A.gobii has been recorded from fish hosts (Szidat,1938; Kulakowskaya, 1961, 1962; Dubinina, in Bykhovski, 1962), but no details of its development are given in these accounts.

4) The life history of A.gobii from field investigations.

The life history of this species was investigated in two localities; the Shropshire Union Canal, at Backford Cheshire and the R.Thames, at Reading. Both localities are described in chapter 5,a,1. It must be emphasised that it is difficult to draw many conclusions from these studies as the number of specimens examined was small. This was inevitable in view of the low degree of infection at these sites (table 29) and the method of examination whereby a limited number of hosts was examined in detail. Nevertheless, in the absence of any other studies on the life history of this species it was considered that these results, despite their preliminary nature, were of some value.

The results of these studies are shown in table 30. The life cycles are expressed solely in terms of the seasonal changes in maturity, as the length at different stages was considered to be too variable (fig. 32) to divide the population into size classes. In compiling the table the maturity of all parasites found was considered, regardless of whether they occurred as single or multiple infections.

In both localities breeding specimens were only found between May and September. The majority of specimens found throughout the year were at stage 3 but it is difficult to know whether this has a valid

TABLE 30

Seasonal changes in the states of maturity of field populations of A.gobii.

a) The Shropshire Union Canal.

	1961						1962							1963		
Maturity	D	J	F	M	A	M	J	J	A	S	O	N	D	M	A	
1 & 2	5	5	5	3	0	3	3	2	0	5	1	0	3	4	4	
3	7	4	5	3	1	0	3	0	1	3	0	0	2	0	0	
4	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	
5	0	0	0	0	0	1	2	1	0	1	0	0	0	0	0	
Total	12	9	10	6	1	4	9	3	1	10	1	0	5	4	4	= 79

b) The R.Thames, Reading.

	1962			1963		
Maturity	Oct.	Dec.	Feb.	May	Jly.	
1 and 2	0	8	0	4	0	
3	2	5	1	1	1	
4	0	2	0	0	1	
5	0	0	0	0	9	
Total	2	15	1	5	11	= 34

For explanation of states of maturity see text.

meaning or not. Stages 1 and 2 are more difficult to detect in the hosts because of their small size. It has also been suggested that development may proceed rapidly up to stage 3 (p.6.39), after which it proceeds at a slower rate. The majority of specimens might therefore be expected to occur at this stage. It is evident in both localities that the number of specimens fluctuates considerably from month to month, and there is no indication of a seasonal production of young larvae. The presence of stage 2 specimens in February and March in the Canal, and of stage 4 specimens in February in the River suggests that breeding may also be taking place during the winter. It must be concluded, therefore, that although breeding may take place throughout the year in both localities, there is no indication of periodicity in the occurrence or development of _A.gobii_.

In order to try and determine the importance of fish hosts in the life cycle, specimens of fish were examined throughout the summer of 1963 in the canal. It was not possible to carry out similar examinations of fish from the R.Thames. The numbers examined were as follows:-

	Mch.	_Apr._	_May_	_June_	_Jly._	_Aug._
Rutilus rutilus (L.)	8	32	22	12	8	7
Abramis brama (L.)	0	2	0	0	0	0
Perca fluviatilis (L.)	11	8	0	0	9	0
Esox lucius (L.)	4	3	3	3	1	2

No species of Archigetes was found in the fish, and it may be concluded that A.gobii in the canal is maintained by progenesis. This differs from the life cycle of A.iowensis as determined by Calentine (pers.comm.), where adults were found in the intestine of a fish, Cyprinus carpio, in April. He calculated the overall percentage of gravid Archigetes present in oligochaetes in one year in his locality as 3.2% and in fish as 80%, and concluded that the production of eggs in tubificids is apparently not sufficient to maintain the species. There is no evidence for such a conclusion, as the minimum degree of progenesis that will support the continued existence of the parasite population is unknown. Similar calculations of the degree of progenesis give a value of 6.3% for the canal and 26.5% for the R.Thames. In the former locality this must be sufficient to maintain the species as it is the only type of development to occur. Calentine (pers.comm.) also found evidence of seasonal production of gravid specimens of A.iowensis, as these only occurred in tubificids in March and April. This contrasts with the situation as found in the Canal, where gravid specimens were found for several months of the year.

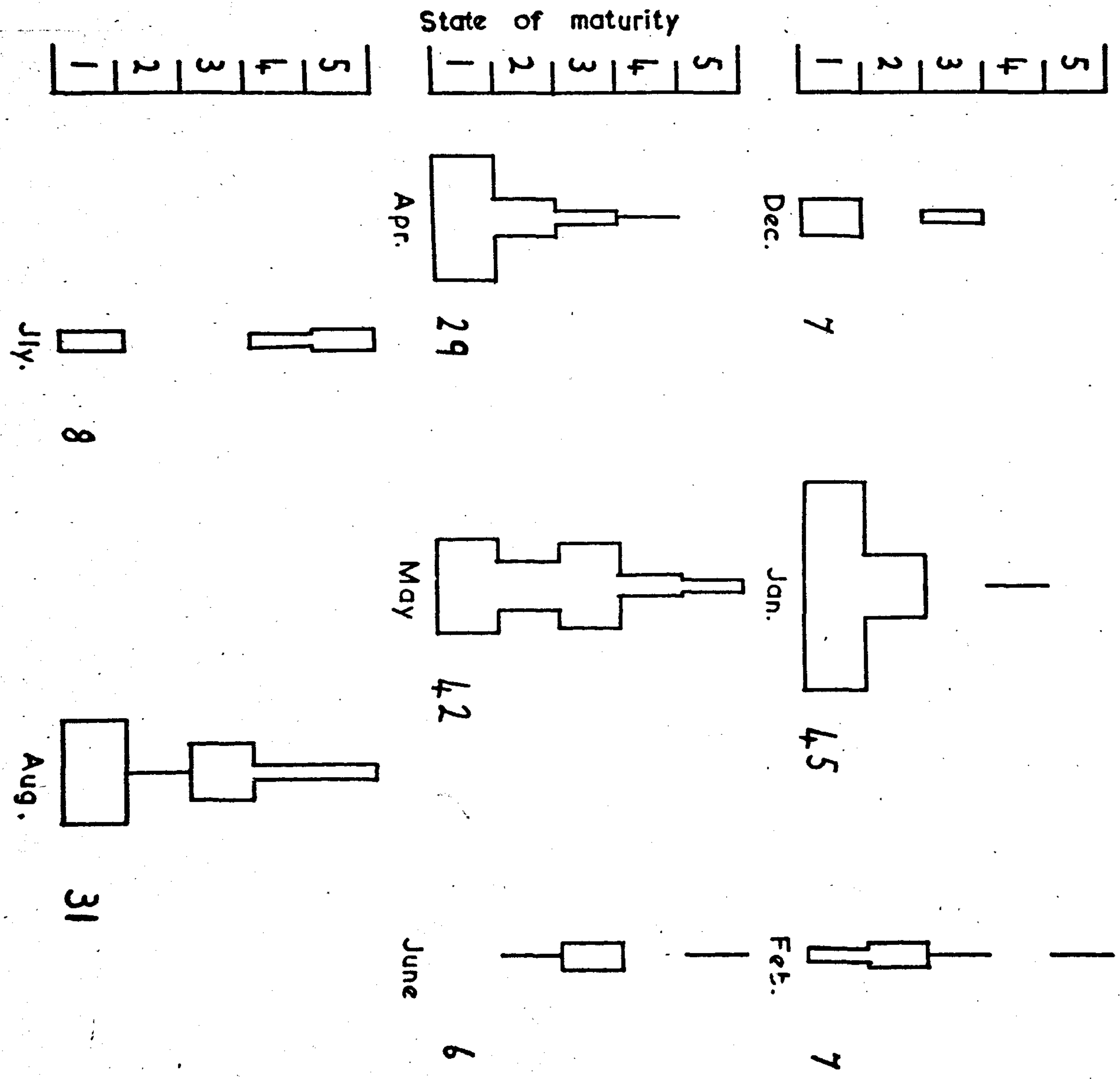
5) The life history of *A.gobii* from laboratory investigations.

It proved possible to maintain a culture of infected specimens of *Limnodrilus*, to infect uninfected specimens under laboratory conditions, and consequently to study the life cycle of *A.gobii* in rather more detail than was possible under field conditions. The study was aided both by the higher degree of infection and the greater number of cestodes present in the laboratory cultures. As a result greater reliance may be placed on the conclusions. Certain other factors, however, indicate that some care is necessary in the interpretation of the results. In the first place, life cycles determined under laboratory conditions do not necessarily have any relevance to happenings under natural conditions. Secondly, in the earlier stages of investigation specimens were frequently removed and killed for the purposes of taxonomic and growth studies. No examination of specimens was made during March, following the removal of specimens, as it was considered advisable to allow natural development to proceed without interference for a period.

The results of these studies are shown in fig. 33. The first factor that is evident, both by the presence of gravid specimens and immature specimens following them, is that progenesis does occur. The presence of gravid specimens from February to August, and of

Figure 33

The seasonal changes in the state of maturity of specimens of *A. gobii* in an infected population of *Limnodrilus* under laboratory conditions. The figures represent the number of specimens examined in each sample.


State of maturity
1
2
3
4
5
Dec.
7
Jan.
45
Feb.
7
Apr.
29
May
42
June
6
Jly.
8
Aug.
31

stage 1 specimens in January suggests that breeding can take place all the year round. The majority of breeding specimens were found from May to August, suggesting the incidence of breeding may vary seasonally. As in the field populations, however, there is no clear evidence of periodicity in the occurrence or development of specimens. There is also no clear evidence for the existence of two generations per year, as was suggested for *A. sieboldi* under similar conditions by Wisniewski (1930). The degree of progenesis was calculated at 5.05%, which approximates closely to the value for the Canal.

In conclusion, the life cycle of *A. gobii* under field and laboratory conditions may be briefly summarised. In Britain, reproduction in this species appears to be exclusively progenetic, but in continental Europe and Asia gravid specimens have been recorded from fish. Breeding apparently occurs all the year round, but the majority of gravid specimens are found between May and September. There is no other evidence of periodicity of occurrence or development of specimens. In view of the small numbers of specimens examined, these must be regarded as preliminary conclusions only, and they require confirmation from more detailed studies.

6) <u>The life histories of other British species of Caryophyllaeidae.</u>

During the course of this study other species of caryophyllaeids were encountered, but never in such abundance as <u>A.gobii</u>. It was, therefore, impossible to determine their life cycles in any detail, under natural conditions. It also proved impossible to obtain sufficient specimens to maintain laboratory populations. Nevertheless, in the total absence of any other information on the biology of these species in Britain it is considered that these preliminary observations may be of value as forming the basis for future studies.

<u>A.sieboldi</u>

Next to <u>A.gobii</u> this was the commonest species encountered. Its systematic relationships have been discussed elsewhere (p.6.24). Specimens of stages 3 - 5 were only encountered between March and August. The failure to record any specimens outside of this period may be due to the inability to determine the specific identity of immature specimens. Gravid or ovigerous specimens were found in every month during its period of occurrence in the samples. Although it was found in <u>L.hoffmeisteri</u> in the Shropshire Union Canal it was not found in fish.

An attempt was made to establish a population of Limnodrilus infected with this species in the laboratory, but it proved largely unsuccessful. A single specimen, however, underwent its complete developmental cycle in 201 days, thus confirming the existence of progenesis in this species. As further confirmation specimens at stage 3 brought in from field collections became gravid in the laboratory. This species has frequently been found in fish (Szidat, 1937; Kulakowskaya, 1961, 1962).

A. brachyurus

This is the rarest British species of Archigetes, and occurred in very small numbers in only two of the sites examined. No immature or stage 5 specimens were found, but stage 4 specimens occurred in April and October. This confirms the existence of progenesis in this species, first reported by Mrazek (1908). It has not been found in fish in Britain, but adults have been recorded from the intestine of Cyprinidae by Kulakowskaya (1961, 1962) and Dubinina (in Dykhovski, 1962). Because of its scarcity it was not possible to establish laboratory populations of infected Limnodrilus.

Caryophyllaeus laticeps

It was shown in table 26 that this species never infected *Limnodrilus*, and accordingly little information about its biology was recorded. The life cycle has been studied by Sekutowicz (1934) and Kulakowskaya (1962a).

The invertebrate hosts (table 26) appear to be species of *Psammoryctes*, *Euilyodrilus* and *Tubifex*. The genus infected varied from site to site. It was more commonly found in *P. barbatus*, but where this species was absent it was found in *Euilyodrilus*. Where species of both genera were found in the same locality it was only recorded from *P. barbatus*. Commonly there was only a single specimen per host; occasionally two were found. The parasite was invariably situated in the coelom of the genital segments or in the testes sacs. Parasites of stage 3 were always found in hosts of stages 2 or 3. Specimens of stages 4 or 5 were never found in the invertebrate host.

In the canal, specimens of stages 3 and 4 were found in roach and bream throughout the period of examination of fish. Progenesis does not occur in this species (Sekutowicz, 1934; Kulakowskaya, 1962a). The latter author has also shown that the larvae can remain in the tubificid from 4 months to two years, a considerably longer period than for *Archigetes* even if it ultimately passes through a fish host (Calentine, pers. comm.)

Caryophyllaeides fennica

This species was only found in fish in the present survey. Its life cycle has not yet been worked out in detail, and the identity of the intermediate host is uncertain. It is generally considered to be a species of Naididae, possibly of the genus Stylaria (Joyeux and Baer, 1936, 1961).

From the little information available it appears that only a short period of time is spent in the intermediate host, and that the larvae are capable of infecting fish at a very early stage in their development. In the present survey it was found to occur in both roach and bream throughout the period of examination of fish. Specimens of stages 2 to 4 were recorded, thus confirming the above observations.

7) DISCUSSION

The relationship of Archigetes to other genera of the Caryophyllaeidae has long been a problem. It was regarded by Wisniewski (1930) and subsequent authors as an aberrent genus, in which progenesis was the exclusive method of development. The members were therefore regarded as neotenic procercoids, and were considered to be unable to infect vertebrate hosts.

Species morphologically resembling *Archigetes* but occurring in fish were hence automatically assigned to other genera. The concept of Archigetes as a distinct genus was later questioned, and it was considered that 'species' of *Archigetes* were in fact only progenetic larvae of species of other genera of the family known from fish. *Archigetes* was finally regarded as a genus of historic interest only (Janiszewska, 1954).

The recognition that species of *Archigetes* may mature in both the invertebrate and the vertebrate hosts has resulted in a redefinition of the genus (p.6. 20). All species capable of undergoing progenetic development may now be united into a single genus, and *Archigetes* is thus recognised as a distinct and valid genus and characterised on the basis of its morphology and life cycles. The restriction of all species exhibiting progenesis to a single genus also enables the relationships between the genera of *Caryophyllaeidae* to be clarified.

The genera may now be arranged in a series showing the stages in the attainment of progenesis. *Caryophyllaeides* and *Khavia* spend a relatively short time in the invertebrate host, and development of the genitalia does not commence until they have successfully infected the vertebrate host (Kulakowskaya, 1962; and p.6.51). *Caryophyllaeus* is also capable of infecting the vertebrate host very early in its development, but on the other hand it may be retained in the tubificid up to 2 years (Kulakowskaya, 1962a). During this time development of the genitalia may take place, but eggs production does not commence until it has infected a fish (Sekutowicz, 1934; Kulakowskaya, 1962a). Biacetabulum has a shorter life cycle than Caryophyllaeus, but like this genus development of the genitalia takes place in the invertebrate host and egg production only in the fish (Kulakowskaya, 1962a; Calentine, pers. comm.) The final stage in the series is represented by Archigetes. In this genus development of the genitalia and egg production may take place in the invertebrate host. The vertebrate host may be eliminated from the life cycle altogether, but this is not obligatory and egg production may occur in either host. Archigetes is consequently seen not to be an aberrant genus but only to represent the final stage in the progressive diminution of the importance of the vertebrate host. There is evidently a tendency in the family for the reproductive organs to appear earlier in development, with a corresponding lengthening of the duration of the procercoid larval stage and the time spent in the invertebrate host. The logical conclusion of such a trend is the attainment of complete sexual maturity in the larval stage, and this occurs in Archigetes.

The position of other genera in the family, not mentioned above, in this series is as yet unknown. Very little information on their life histories is available, although none of the species studied to date show any traces of progenetic development. In several genera, including Monobothrium and Glaridacris, it appears that development of the genitalia may take place in the invertebrate host. It is considered, however, that when sufficient information on their life cycles becomes available it will prove possible to fit them into the general pattern outlined above.

CHAPTER 7

DISCUSSION

The aims of this investigation are set out in the introduction to this work, and at its conclusion it is as well to consider to what extent they have been achieved. A study of the variation of possible specific characters has resulted in the acceptance of some as being suitable for taxonomic purposes and the rejection of others. On the basis of these characters seven species of Limnodrilus are now recognised. Of the other species that have at some time been assigned to Limnodrilus some are recognised as being correctly located in other genera while others have been reduced to synonomy with the species of Limnodrilus. These have been described in detail, taking into account the variation in their specific characteristics, and a key for their identification constructed. In the genus the genitalia provide the most satisfactory specific characters, but this has meant that, with one or two exceptions, it is not possible to identify immature specimens. This is a considerable disadvantage, as it hinders the interpretation of results derived from field investigations.

The genus as a whole proves to be cosmopolitan in its distribution, but individual species are restricted to a greater or lesser degree. *Limnodrilus hoffmeisteri* and *L. udekemianus* are truly cosmopolitan species; *L. claparedeanus* appears to be confined to the holarctic region, *L. helveticus* to the palaearctic and *L. neotropicus* to the nearctic. *Limnodrilus grandisetosus* is restricted to Eastern Asia. *Limnodrilus cervix* appears to be of nearctic origin, but evidence is presented that suggests that it has comparatively recently been introduced into Britain and is spreading slowly throughout the country. Distributional studies in relation to the ecological requirements of individual species failed to show any specific habitat preferences or the existence of any abiotic limiting factors. *Limnodrilus hoffmeisteri* occur in almost every available type of habitat, but *L. udekemianus* and *L. claparedeanus* are local in their distribution. Correlations between the distribution and abundance of some species and physical or chemical characteristics of the environment are noted, but no evidence of any causal relationships was found. The very considerable overlap that exists in the distribution of all species and the presence of mixed species populations suggests the unimportance of abiotic factors and the corresponding importance of biotic factors in determining the distribution and abundance of each species.

A detailed study of the reproductive biology was confined to one species, L.hoffmeisteri. It is presumed that the observed changes take place in a similar manner in other species. The ability of specimens to regenerate lost segments and of the genitalia to regress following breeding and later to regenerate is demonstrated. It is suggested, however, that asexual reproduction does not occur to any significant degree. The existence of these phenomena and the inability to age specimens, combined with other factors, increase the difficulties of interpretation of data derived from field investigations. One problem that emerged from these studies and will require further attention is the observed paucity or absence of cocoons in some species, and the possibility that these are able to breed without their formation.

The life histories studies show that no breeding pattern is characteristic of the genus. Nevertheless, there is some evidence to show that the time and duration of breeding, and the age at which specimens attain maturity, are characteristic of each species. Some species, as L.claparedeanus, are strictly seasonal breeders, others, as L.udekemianus, are less so. Within each species, however, there is considerable variation with regard to the breeding pattern, and in particular to the duration of the breeding period. In all species the same pattern of a longer breeding period in more productive habitats is demonstrated. Limnodrilus hoffmeisteri, unlike most other species of tubificids studied, attains maturity in its first year of life. The other species of Limnodrilus generally breed in their second year. These results are confirmed by laboratory studies, and these also demonstrated that the pattern of breeding is directly related to the nature of the substratum. The existence of micro populations and their mobility within a single locality, the problems of identification and age determination hampered population studies in the field. It was evident that studies of this nature will have to be carried out in considerable detail within a single locality, and a large number of samples taken at frequent intervals.

It has, therefore, proved possible to characterise the species of Limnodrilus on the basis of their morphology, distribution and biology. In the course of this study, however, several new problems have been posed that are important to the study of all tubificids. The inability to identify immature specimens and to age specimens must be overcome. The problems of sampling and the validity of the sampling techniques in current use must also be investigated. The uneven distribution of tubificids within a small area presents difficulties with respect to the selection of a sampling technique, but the reliability of the technique determines the accuracy of the results.

The information gained in the present study, as well as solving some of the original problems, contributes to information on the basic biology of the genus which will provide a background for future ecological studies. In the present work, due to lack of time, such studies have largely been neglected. Before they are undertaken, the problems referred to in the previous paragraph must first be overcome. Nevertheless, some of the lines along which such studies may be expected to proceed are indicated in the present work.

The fundamental approach to a study of the ecology of a species must be the determination of the factors that limit its distribution and abundance. It is evident that it is going to be more difficult to determine these factors for some species of Limnodrilus than for others. Limnodrilus hoffmeisteri, for example, has been shown to be the commonest species of the genus, both in terms of occurrence and abundance. It is cosmopolitan, and occurs in almost every type of habitat, under certain conditions in considerable abundance. Its life history shows it to be a very adaptable species. On the other hand, a species like L.claparedeanus shows evidence of a restricted distribution, rarely occurs abundantly and has a well defined breeding cycle. A study of the ecology of this species would appear to present rather fewer difficulties than a study of L. hoffmeisteri.

Some indications of the factors that are of importance in the ecology of Limnodrilus have emerged from the present study. The preliminary investigation of the distribution of the species of Limnodrilus demonstrated the relative unimportance of abiotic factors and emphasised the importance of biotic ones. The inherent adaptability of each species also assumes considerable importance in this context. The biotic factors may be subdivided into parasites, predators, food and inter or intra specific competition. The relationship between Limnodrilus and its cestode parasites has been investigated, and the stability of the relationship demonstrated. It was shown that the effect of the parasites on a population of Limnodrilus is negligible. Little information is available on the importance of predation. Several species are known to feed on tubificids, either by direct observation or by indirect assumption, but more information about their relative importance is required. In particular, the nature of the predators; the extent to which Limnodrilus forms an essential part of their diet, and the effect of predation on tubificid populations must be determined.

The most important factor in the ecology of Limnodrilus, however, would appear to be the nature and abundance of its food supply. The significance of this is discussed briefly in Chapter 3. In the life cycle studies it was shown that the breeding pattern was dependent upon the productivity of the habitat and the nature of the substratum. The importance of the latter and the availability of food has been commented on several times in the course of this work. The lack of information on the nature of tubificid food and feeding habitats has also been referred to. In view of the possible importance of food in determining the distribution and abundance of Limnodrilus future work must be directed towards this end.

Little can be said at this stage about the importance of competition as a factor in the ecology of Limnodrilus. However, the absence of monospecific populations requires more detailed investigation. The existence of multi-specific and multi-generic populations in an apparently homogenous substratum, as in Ditton Brook and the R. Thames, appears to contradict 'Gause's hypothesis'. It is possible that under these circumstances competition is prevented by different species utilising different constituents of the substratum, thus the feeding habits of each species will assume considerable importance in this context. Should competition occur, the adaptability of the species may well determine the outcome. In the face of current controversy over the importance of interspecific competition as a biological factor, the existence of multi specific populations must present a problem to all interested in this field. The explanation of this phenomenon will not only be a major advance in the understanding of tubificid ecology but may also have considerable influence on the development of modern ecological thought.

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APPENDIX 1

Details of the samples from the Shropshire Union Canal

	1961								1962			
	N	D	J	F	F	M	A	M	M	J	Jl	Jl
L. hoffmeisteri												
Sample 1												
Immature	14	18	27	22	13	20	18	40	37	62	57	61
Mature	7	11	15	19	14	5	11	3	4	5	6	7
Breeding	60	60	19	1	5	19	8	7	12	3	1	20
Sample 2												
Immature	-	-	-	20	9	27	34	21	44	78	60	74
Mature	-	-	-	26	14	7	8	5	3	4	5	5
Breeding	-	-	-	0	12	18	6	20	7	1	1	19
L. claparedeanus												
Sample 1	1	0	4	4	0	2	0	0	0	0	0	0
Sample 2	-	-	-	0	1	0	2	1	0	0	0	0
L. cervix												
Sample 1	4	1	4	2	12	0	2	1	0	8	3	2
Sample 2	-	-	-	3	7	4	1	2	0	3	5	1
Total number of specimens												
Sample 1	138	200	213	136	149	116	41	71	116	243	455	580
Sample 2	-	-	-	128	131	103	171	80	78	224	307	530

From November 1961 until February 1962 no duplicate samples were taken.

APPENDIX 1 ctd.

	1962						1963	
	A	S	S	O	N	D......	M	A
L.hoffmeisteri								
Sample 1								
Immature	59	68	62	50	74	29	87	68
Mature	4	5	18	12	11	12	3	9
Breeding	12	5	15	32	2	50	2	10
Sample 2								
Immature	75	72	67	57	53	25	52	63
Mature	7	7	19	21	9	9	12	12
Breeding	3	4	5	17	18	59	20	17
L.claparedeanus								
Sample 1	0	0	0	0	2	1	2	1
Sample 2	0	0	0	0	3	1	1	0
L.cervix								
Sample 1	1	0	0	0	0	4	1	1
Sample 2	0	0	0	2	5	2	1	2
Total number of specimens								
Sample 1	535	600	607	712	282	809	169	450
Sample 2	310	426	793	552	526	802	341	612

No samples were collected in January and February 1963 owing to unfavourable weather conditions.
In each month a subsample of approximately 100 specimens from each sample were examined.

APPENDIX 2

Details of the samples at Ditton Brook

	1962					1963							
	A	S	O	N	D	J	F	M	A	M	J	J	A
L. hoffmeisteri													
Sample 1													
Immature	8	5	15	14	11	22	20	18	6	7	27	57	31
Mature	7	11	6	0	4	6	11	3	1	4	6	8	8
Breeding	0	0	0	0	0	0	7	0	0	2	2	3	3
Sample 2													
Immature	9	11	17	16	14	7	3	17	11	22	25	66	39
Mature	5	9	1	1	4	0	3	8	0	3	5	6	8
Breeding	1	1	1	0	0	0	0	0	0	1	0	3	2
L. udekemianus													
Sample 1													
Immature	14	26	21	20	40	40	63	38	19	26	27	16	30
Mature	0	0	0	0	0	1	9	1	1	1	1	2	0
Breeding	0	0	0	0	0	0	0	1	0	2	2	1	0
Sample 2													
Immature	13	52	26	33	37	10	8	32	25	12	21	4	20
Mature	0	0	0	1	1	1	2	5	3	1	0	0	1
Breeding	0	0	0	0	0	0	0	0	0	11	1	0	0

APPENDIX 2 ctd.

	1962					1963							
	A	S	O	N	D	J	F	M	A	M	J	J	A
L.helveticus													
Sample 1													
Mature	0	0	0	0	0	0	0	8	0	1	0	2	0
Breeding	0	0	0	0	0	0	0	0	4	0	2	0	2
Sample 2													
Mature	0	0	0	0	0	0	0	0	0	0	0	1	2
Breeding	0	0	0	0	0	0	0	0	0	7	2	0	0
Total number of specimens													
Sample 1	35	64	198	105	242	113	130	96	54	95	247	321	19
Sample 2	31	88	350	251	131	19	45	72	72	132	254	298	18

Owing to the large number of specimens present subsamples were examined in October, November, December, June, July and August.

Tubifex tubifex was present in all the samples but is not included in this table.

All immature *Limnodrilus*, excepting specimens of *L.udekemianus*, have been assigned to *L.hoffmeisteri* as this species is more abundant than *L.helveticus*.

APPENDIX 3

Details of the samples from Raby Pool

The duplicate samples from March to early September are compared in detail. Subsequent to September 1962, the number of specimens in each sample was so small that a comparison of samples with regard to the number of specimens of each species and the number in each maturity class can have little meaning. Accordingly, from September 1962, until the termination of the sampling programme samples are only compared with respect to the total number of specimens and the number of Limnodrilus.

		1962									
		M	M	A	M	M	J	Jl	Jl	A	S
Limnodrilus indet.											
Sample 1		6	20	7	12	17	12	26	37	2	15
Sample 2		13	11	11	14	15	36	27	59	51	41
L. hoffmeisteri											
Sample 1	Mature	4	4	0	5	1	4	1	2	0	1
	Breeding	1	0	3	9	3	1	0	0	0	0
Sample 2	Mature	1	3	2	1	3	11	1	0	1	5
	Breeding	0	1	1	2	6	0	0	0	0	0
L. helveticus											
Sample 1	Mature	4	1	0	6	0	3	0	0	0	1
	Breeding	2	3	2	6	3	2	2	2	0	5
Sample 2	Mature	0	2	0	3	1	4	0	0	0	0
	Breeding	3	1	2	12	9	4	2	1	3	6
L. claparedeanus											
	Sample 1	6	5	0	2	0	0	0	0	1	0
	Sample 2	0	3	0	4	1	1	0	0	0	0
Total number of specimens											
	Sample 1	56	72	44	102	46	159	53	111	4	40
	Sample 2	48	83	55	99	43	111	223	96	74	70

APPENDIX 3 ctd.

Total number of specimens

	1962				1963			
	S	O	N	D	F	M	A	M
Sample 1	12	22	8	8	12	8	7	10
Sample 2	6	28	3	2	1	1	13	0
Sample 3	23	25	10	18	11	3	1	8
Sample 4		6	16	0	5	0	11	2
Sample 5			19	22	0	6	16	0
Sample 6			0	9	23	0	14	2
Sample 7				4	48	14	2	6
Sample 8				0	3	1	22	0

Total number of Limnodrilus

	1962				1963			
	S	O	N	D	F	M	A	M
Sample 1	12	10	6	4	8	6	3	4
Sample 2	2	7	2	2	1	0	3	0
Sample 3	12	11	6	9	7	2	1	3
Sample 4		2	11	0	3	0	10	1
Sample 5			12	13	0	4	6	0
Sample 6			0	2	22	0	5	0
Sample 7				2	25	12	1	3
Sample 8				0	2	0	11	0

APPENDIX 4

Details of the samples at Windermere

The occurrence of L.hoffmeisteri in the samples

	1962											
	J	F	M	A	M	J	J	A	S	O	N	D
Sample 1												
Immature	41	39	31	81	51	5	9	9	17	25	5	17
Mature	8	6	5	4	7	1	1	4	4	5	2	1
Breeding	0	3	3	1	3	1	2	4	2	9	3	2
Total number of specimens	49	520	43	139	76	7	14	18	26	55	10	20
Sample 2												
Immature	13	41	14	63	57	6	30	10	11	5	6	5
Mature	2	1	5	12	7	0	2	7	2	1	3	2
Breeding	3	0	0	9	8	0	1	7	2	2	7	5
Total number of specimens	18	435	21	70	114	7	42	24	17	11	19	13

Owing to the large number of specimens present in February subsamples were examined. Tubifex templetoni was present in many of the samples but is not included in this table.

APPENDIX 5

Details of the samples at Llyn Tegid

The occurrence of L.hoffmeisteri in the samples

	1962											
	J	F	M	A	M	J	J	A	S	O	N	D
Sample 1a												
Immature	0	0	8	4	2	0	0	0	48	12	0	0
Mature	0	0	3	1	0	1	0	0	25	1	0	0
Breeding	0	0	0	0	0	0	0	0	1	0	0	0
Sample 1b												
Immature	0	0	8	0	0	0	2	18	24	0	0	0
Mature	0	0	1	0	0	0	2	17	9	0	0	0
Breeding	0	0	0	0	0	0	0	0	0	0	0	0
Sample 2a												
Immature	0	0	13	2	54	7	11	12	0	33	0	0
Mature	0	0	2	2	17	0	2	16	0	4	0	0
Breeding	0	0	0	0	16	0	0	0	0	0	0	0
Sample 2b												
Immature	0	0	11	0	18	6	29	-	0	21	0	0
Mature	0	0	1	0	7	1	1	-	0	2	0	0
Breeding	0	0	0	0	2	1	0	-	0	0	0	0

Samples a and b are duplicate samples taken at the same site.
Samples 1 and 2 are samples taken at different sites.
No sample 2b was taken in August owing to unfavourable weathe conditions.

APPENDIX 6

Details of the samples from the R. Thames.

In this locality *L. udekemianus* was apparently restricted to two stations. At both of these it occurred relatively abundantly, and the duplicate samples could consequently be compared in detail (a). At the remaining stations the number of *Limnodrilus* in each sample was so small that a comparison of duplicates with regard to the number of specimens of each species and the number in each maturity class can have little meaning. The samples from these stations are therefore compared only with respect to the total number of *Limnodrilus* present (b).

(a) The occurrence of *L. udekemianus* in the samples

			1962		1963		
			O	D	F	M	Jl
Station 71	A)	Immature	0	18	18	31	19
		Mature	0	14	3	10	5
		Breeding	0	4	3	10	4
	B)	Immature	1	29	14	28	3
		Mature	0	9	5	9	0
		Breeding	0	4	3	18	0
Station 72	A)	Immature	29	22	24	23	11
		Mature	5	26	19	10	0
		Breeding	1	14	11	13	1
	B)	Immature	31	26	20	28	24
		Mature	3	36	17	10	3
		Breeding	1	9	9	16	2

APPENDIX 6 ctd.

b) The occurrence of other species of Limnodrilus in the samples.

Station		1962		1963		
		Oct.	Dec.	Feb.	May	Jly.
0	A	7	12	21	13	23
	B	7	6	10	18	11
5	A	7	1	11	9	16
	B	21	23	5	9	7
10	A	4	13	16	3	1
	B	5	19	8	3	1
15	A	25	4	0	0	5
	B	2	4	5	2	3
30	A	4	12	6	0	2
	B	0	14	2	1	2
45	A	13	3	4	1	7
	B	5	22	1	1	1
60	A	14	11	18	0	6
	B	5	13	6	0	0
67	A	3	55	26	9	6
	B	1	40	21	14	4
69	A	21	28	8	17	12
	B	11	3	24	10	9
71	A	2	20	18	6	49
	B	16	23	41	25	12
72	A	26	17	12	8	3
	B	30	12	21	7	4

The station numbers refer to the distance of the site from the North bank of the river.

APPENDIX 7

The validity of the subsampling technique

When it proved necessary to examine subsamples, it was essential to know if the technique was selective for a particular species or maturity class. The subsampling technique consisted of transferring all specimens in the sample into a petri dish. The dish was then shaken to ensure mixing of the specimens. A segment of the dish containing approximately 50 specimens was then selected at random, and all specimens in the segment were removed for examination. The procedure was repeated to bring the size of the subsample up to approximately 100 specimens. In order to test if the technique was selective, the entire contents of two samples were subsampled and the subsamples compared. The results are shown below:-

a) Sample from the Canal on December 12, 1961.

	Subsample					
L. hoffmeisteri	1	2	3	4	5	6
Immature	18	14	17	19	21	22
Mature	11	13	10	13	9	10
Breeding	60	58	66	63	59	57
L. cervix	2	2	0	1	2	1
L. claparedeanus	0	1	0	0	1	2
E. hammoniensis	3	1	6	4	3	7
Total number of specimens	94	89	99	100	95	99

Since all species, except *L.hoffmeisteri*, were present in such small numbers, they were not divided into maturity classes. The fourteen specimens remaining in the sample were not included in the table.

b) Sample from Bromborough Stream on 14 October 1961.

	Subsample						
	1	2	3	4	5	6	7
L.hoffmeisteri							
Immature	6	6	8	6	10	7	8
Mature	4	2	3	1	7	3	2
Breeding	0	0	1	0	1	2	0
L.udekemianus							
Immature	22	18	24	23	16	20	19
Mature	0	0	0	0	0	0	0
Breeding	0	0	0	0	0	0	0
T.tubifex							
Immature	70	70	80	72	75	73	78
Mature	16	13	15	13	17	16	18
Breeding	2	0	3	2	0	1	4
Total number of specimens	120	109	134	117	126	122	129

It can be seen by inspection of these tables that there
no evidence that the technique is selective for a
cular species or maturity class. The data was not,
fore, analysed numerically. The subsampling technique
nsidered to be valid and non-selective, and was
the whenever it was necessary to examine subsamples.
was
employed

A REPORT ON A COLLECTION OF AQUATIC OLIGOCHAETA DEPOSITED AT THE UNIVERSITY OF NEUCHATEL BY D^{r} E. PIGUET

by

R. O. BRINKHURST and **C. R. KENNEDY**
Department of Zoology, University of Liverpool

With plate VII

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This report was made possible by the loan of the Piguet collection of slides of aquatic Oligochaeta deposited in the Department of Zoology, Neuchâtel. We are indebted to Dr. Dottrens and Professor Baer for their assistance and the loan of the collection.

1. The Collection

The slides consist of whole mounts and sections of *Tubificidae*, *Lumbriculidae*, *Haplotaxidae* and *Enchytraeidae*. Most of the slides bear a number, and most have either a locality label or a date, and, less often, the name of the species concerned. The slide trays are also labelled, but many slides have apparently been moved from one tray to another and so this does not always give a clue to the identity of the worms. We now give a list of the number, locality, date and name of the species where these facts are available and, finally, the current name of the species concerned. A revision of the taxonomy of the *Tubificidae* is in the press (Brinkhurst 1962) and further details of the changes in nomenclature will be found therein.

2. Comments on the collection

a) Specimens numbered 53, 64. Bretscher (1901) described *Limnodrilus longus*. Later this species was regarded by that author as a synonym of *L. claparedeanus* Ratzel, 1868. Up to the present time the identity of these species has been established solely on the length of the chitinous penis sheath, but in our studies we have found that the

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Number	Date	Name	Current name and notes
13	15th Dec. 1896	*Psammoryctes barbatus*	*P. barbata:* few rather poor sections.
13c-d	—	*Psammoryctes barbatus*	
13e-f	16th Dec. 1896	*Psammoryctes barbatus*	
13g	16th Dec. 1896	*Psammoryctes barbatus*	
14-14i	21st Jan. 1897	*Embolocephalus velutinus*	*Peloscolex velutinus:* transverse sections (5 slides).
15-15g	21st Jan. 1897	*Embolocephalus velutinus*	*P. velutinus* t. s. (4 slides).
19-19j	3rd Feb. 1897	*Embolocephalus*	*P. velutinus* t. s. (4 slides).
22-22n	5th Feb. 1897	*Embolocephalus*	*P. velutinus* t. s. (5 slides).
23-23k	5th Feb. 1897	*Embolocephalus*	*P. velutinus* t. s. (4 slides).
24-24e	5th Feb. 1897	*Embolocephalus*	*P. velutinus* l. s. (3 slides).

The slide trays containing *Peloscolex* slides are labelled *Tubifex velutinus* and bear the signature of E. Piguet. The handwriting is that observed on all the labels on the slides and serves to identify the material as that belonging to D^{r} Piguet.

29-29b	22nd Feb. 1897	*Tubifex rivulorum*	Two specimens under each of three cover-slips. Note on the rear of the slide reads « Tous des *Tubifex* sauf le dernier qui est un *Embolocephalus plicatus* et l'avant-dernier *(Limnodrilus)*.» The specimens are 1. *Tubifex tubifex* 2-4. *Tubifex* sp. 5. *Euilyodrilus heuscheri* 6. *Peloscolex ferox* (specimen lacks papillae).
32	23rd Feb. 1897	*Lumbriculus variegatus*	Two whole mounts of *L. variegatus.*
35	25th Feb. 1897	*Lumbriculus variegatus*	
37-37b	9th Mar. 1897	*Limnodrilus*	Mature specimens are of *Limnodrilus hoffmeisteri*, but several immature specimens can only be labelled ? *Limnodrilus.*

Number	Locality	Name	Current name and notes
47	Léman	*(Embolocephalus plicatus)*	*Peloscolex ferox*: 2 specimens.
47a	Lac de Neuchâtel	*Peloscolex ferox*	Name corrected on slide at later date.
53-53c	Seime	*Limnodrilus claparedeanus* in P. and B. 1913	*L. longus*: 7 specimens on two slides (see below).
54-54c	Seime	*Limnodrilus udekemianus* in P. and B. 1913	*L. udekemianus*: 10 specimens on 2 slides.
56	Lac de Neuchâtel	*Tubifex velutinus*	5 specimens of *Peloscolex velutinus*
56a	Léman	(on slide tray only)	on 1 slide.
57	Lac de Neuchâtel	*Trichodrilus*? (in pencil)	4 specimens of *Dorydrilus michaelseni* (see Hrabe 1936).
58b, c	Lac de Neuchâtel	*Stylodrilus heringianus* (on slide tray only)	Transverse and longitudinal sections.
64, 64a	Lac de Neuchâtel	*Limnodrilus claparedeanus* in P. and B. 1913	*L. longus*: several specimens and dissected genital regions (see below).
64d, 64e	Lac de Neuchâtel		
68	Lac de Neuchâtel	*Limnodrilus helveticus*	5 specimens and 3 anterior ends dissected,
68a	Lac Vättern (Suède)	(on slide tray only)	*L. helveticus*.
68b	Petit ruisseau près d'Oerlikon	*Limnodrilus helveticus* (on slide tray only)	see note below.
76, 76a	Riveau de la Ferme (Royan)	—	*Tubifex* sp. 1 specimen has dried up, the other has the same fine chaetae, a *Tubifex* type of atrium and a penis sheath like *T. tubifex*.
79	Riveau de la Ferme (Royan)	—	A dried specimen, as 76.
79a	Riveau de la Ferme (Royan)	—	*Euilyodrilus? heuscheri*.
91, 91a	Rhôni	—	Two specimens of *Haplotaxis gordioides*.
93, 93a	Lac Vättern (Suède)	*Stylodrilus heringianus*	Whole mounts of *S. heringianus*. Material from S. Ekman.
93b	Lac Torne Träsk (Laponie)	*Stylodrilus heringianus*	
93c	Lünersee	*Stylodrilus heringianus*	
93d	Lac Torne Träsk (Torne Lappmark)	*Stylodrilus heringianus*	

Number	Locality	Name	Current name and notes
93e-f	Lac Torne Träsk (Torne Lappmark)	*Stylodrilus heringianus*	9 slides of transverse and longitudinal sections.
93g-o	Lac Torne Träsk (Torne Lappmark)	*Stylodrilus heringianus*	
95	Environs de Bâle		
95a-c	Lac Vättern (Suède)	*Rhynchelmis limosella*	8 specimens together with cocoons.
95d	Dans un puits (Sodbrunnen) Bâle	(on tray or (95d) on slide	*R. limosella.*
96b-c	Lac de Bret	*Tubifex (I) bedoti*	*Euilyodrilus bedoti*, several specimens, only 1 mature.
115	Tronchet	—	This slide has dried up and the worm is unidentifiable.
121 I. S. a			
121 II. S. a			
121*b	Lac Vättern (Suède)	*Rhyacodrilus palustris* (deleted)	
121**b	Dr. S. Ekman	*coccineus* (deleted)	Serial sections. For identity see note below.
121 Ic	Dr. Piguet	*ekmani* Piguet 1928	
121 IIc			
121 IIIc			
123a	Lac de Morat	*Tubifex (Peloscolex) ferox* (Eisen)	*P. ferox*—dried up slides.
123b	Lac Vättern (Suède)	*Tubifex ferox*	*P. ferox*—dried up slides.
123c	Lac Saggat (Sarekgebirge, Suède)	*Tubifex ferox*	*P. ferox.* Canada balsm mounts. Several slides signed by Dr Piguet.
123d	Lünersee	*Tubifex (Peloscolex) ferox* (Eisen)	
123e	Lac de Sils	*Tubifex (Peloscolex) ferox* (Eisen)	
124	Lac de Bienne	*Tubifex barbata*	*Psammoryctes barbata.* Dried up slides but
124a	Lac de Lugano	(on slide tray)	chaetae still recognisable.
138gI, gII	Petit ruisseau près d'Oerlikon (Zurich)	*Trichodrilus sanguineus* original de Bretscher Dr Piguet	*Bichaeta sanguinea.* HRABE (1936) saw a specimen from Piguet labelled 138 b.

Number	Locality	Name	Current name and notes
139b	Seyon	—	8 immature specimens of *Aulodrilus pluriseta.*
140	Fürstenalp	*Hydrenchytraeus stibleri*	10 individuals – Neither species listed by Nielsen and Christensen (1959).
141	Fürstenalp	*Hydrenchytraeus nematoides*	8 individuals
145	Lünersee	—	*Mesenchytraeus setosus* (1 specimen).
146	3 Tumpel beim Altjaure Sarekgebirge	*Lumbriculus variegatus* (on slide tray)	2 specimens of L. *variegatus.*
149	Léman	*Haplotaxis gordioides*	2 specimens of this sp. on 1 slide.
149a	Lac de Sils		
149b	Un ruisseau de Banyuls-sur-Mer (Pyrénées orientales) A. Vandel leg.	*Haplotaxis gordioides*	1 specimen of *H. gordioides.*
157b, c	La Limmat près de Baden	*Tubifex (Ilyodrilus) moldaviensis* Dr Piguet	8 specimens of *Euilyodrilus moldaviensis.*
157d	La Limmat près de Baden	*Tubifex (Ilyodrilus) moldaviensis* Dr Piguet	3 specimens of *Euilyodrilus moldaviensis.*
157eI, II	La Limmat près de Baden	par P. Steinmann	longitudinal sections – *E. moldaviensis.*
157fI, IV	La Limmat près de Baden	par P. Steinmann	transverse sections
166-167	Récolte Robert Müller dans lacs périodiques d'Eichen près de Schopfheim (Forêt-Noire)	Enchytréidés (in pencil) Dr Piguet	Enchytraeidae sp. indet.

form of the distal expansion of the sheath and the thickness of its wall provide reliable characters. These points are dealt with in detail elsewhere (Brinkhurst 1962) but perhaps we should indicate that *L. longus* Bretscher has a thinwalled sheath with a pear-shaped distal expansion with a single, forward, projection. The second species, *L. claparedeanus*, has a very thick-walled penis sheath with a triangular tip with a long forward projection and also a long backward projection as figured in Brinkhurst (1960).

b) Specimen 68*b*. These specimens of *Limnodrilus helveticus* are from a riverine habitat. Piguet and Bretscher (1913) mentioned that specimens from such habitats had different chaetae from those found in lakes, but no riverine locality was named. These specimens include one which is clearly that employed for figure 20*b* and thus we believe that the riverine locality concerned is that detailed above (specimen 68*b*). However, we are unable to find any difference in the form of the chaetae between these and other lacustrine specimens of the same species.

c) Specimens 121—serial sections only. *Rhyacodrilus ekmani* Piguet, 1928 differs only very slightly from *R. palustris* and *R. coccineus* (see Brinkhurst 1962). It is of interest to note that the original author was also in some doubt about the identity of this material. On some of the slides it is noticable that the spermathecal walls appear to join together (pl. VII *a*) and to the dorsal side of the gut wall (pl. VII *b*), but we can find no evidence of any actual communication between any of the three cavities concerned. The other character upon which these three species are separated concerns the abundance oft he hair chaetae and the presence or absence of pectinate chaetae in the dorsal bundles. These variations may lead to the recognition of species *(Tubifex tubifexbergi-blanchardi)* or of varieties (*Psammoryctes ochridanus* f. *typica*—f. *variabilis*). There is as yet insufficient evidence on which to bases decision in these cases.

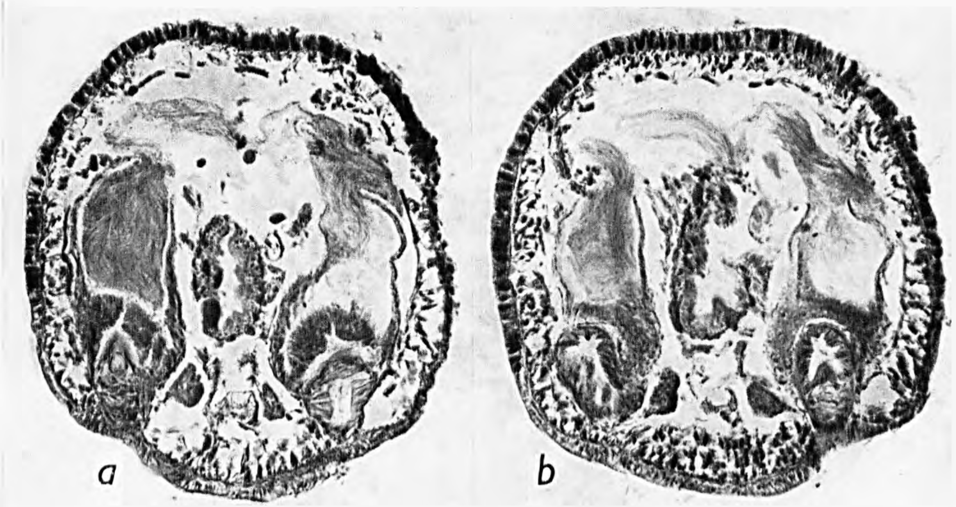

Plate VII

Transverse sections of *Rhyacodrilus ekmani* by Dr. Piguet showing the spermathecae on each side of the gut. Fig. *a* shows strands of tissue joining the two spermathecae dorsally. In fig. *b* the junction with the dorsal wall of the gut can be seen.

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Occurrence of the Genus *Archigetes* in Britain

DURING the course of investigations into the taxonomy and ecology of aquatic Oligochaeta we have observed two species of *Archigetes*, a genus not to our knowledge previously recorded from Britain. *Archigetes appendiculatus* Mrazek, 1897 (non Ratzel, 1868) was first observed in a specimen of *Limnodrilus hoffmeisteri* Claparède, 1862 obtained from a Liverpool pet shop along with a large number of uninfected 'Tubifex' worms. The same species of parasite was later found in a pond near Fornalls Green Lane, Meols, Cheshire, on May 28, 1959. A second species *A. sieboldi* Leuckart, 1869, also from *L. hoffmeisteri*, was found from the Shropshire Union Canal near Chester on March 20, 1962. The cestodes were readily identified from recent descriptions of the genus[1,2]. In each instance the parasites were located in the genital segments of the tubificids. Both

Fig. 1. *Archigetes appendiculatus* in the genital segments of *Limnodrilus hoffmeisteri*. Both host and parasite are sexually mature, eggs being clearly visible in the uterus of the parasite. Note the separation of the vitellaria into four distinct lobes. (× *c*. 17)

specimens of *A. appendiculatus* had eggs in the uterus (Fig. 1), while two specimens of *A. sieboldi*, from one oligochaete, contained no eggs.

At present we are collecting further data on the incidence and occurrence of *Archigetes* and other cestode parasites of Oligochaeta. We should appreciate correspondence with other workers who may find such material during the course of their studies on related fields of freshwater biology.

We thank Mr. T. B. Greenan for translation of Russian literature.

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C. R. KENNEDY

STUDIES ON THE IRISH TUBIFICIDAE

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13.

STUDIES ON THE IRISH TUBIFICIDAE

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ABSTRACT

The study of the Irish Tubificidae has been largely neglected since the publication of a check list by Southern in 1909. The only other person to have concerned himself with them was Friend, whose taxonomic studies and identifications are unreliable (Cernosvitov 1941). Accordingly, it appeared that a complete revision of the Irish tubificids was long overdue. In this paper an attempt is made to bring knowledge of the Irish tubificids up to date and into line with the European species.

The literature pertaining to the Irish tubificids is here reviewed. In addition, the results of an examination of Southern's specimens are presented, together with information gained from visiting sites and making further collections. It has proved possible to confirm or correct the identity of most of the earlier records by a study of their descriptions, by examination of specimens or by both and to bring the nomenclature up to date. As a result of this survey, seventeen species are now recognised as occurring in Ireland, six of which are new Irish records. All of these are encountered, more or less commonly, in Britain.

Introduction

The study of the Irish tubificids has been neglected since the publication of a check list by Southern (1909). In this paper he lists the tubificids occurring in Ireland, with a brief description of some of them, and describes four new species. Since that time there has been a greater appreciation of the important characters used in delimiting the various taxa. Many of the species recorded by him have now been assigned to different genera. Of the new species which he described, *Tubifex thompsoni* has never subsequently been recorded; *T. templetoni* has been recorded from a few places in Britain, the U.S.A. and the Continent; *Limnodrilus aurostriatus* has only been recorded from two other sites and *L. parvus* has been the subject of considerable discussion. In a later paper, Southern (1911) records the presence of two species of Tubificidae in the course of the Clare Island Survey.

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The earliest records of Irish tubificids, however, are those of the Rev. H. Friend. Towards the end of the last century he visited Ireland to collect oligochaetes. The results of his collections are published in the Irish Naturalist (1896 et seq.) and the Zoologist (1898). It appears that he may report a single collection more than once. Some of his records have been incorporated in Southern's paper (1909) and Southern's records have in turn been incorporated in Friend's review (1912). Friend's identifications of aquatic oligochaetes are always suspect (Cernosvitov 1941) and his nomenclature was frequently out of date, even at the time of publication. Accordingly, very little reliance can be placed on his records. As Friend published in rather obscure journals, many of which are now rather difficult to obtain, the list of records in the following pages may not be complete.

It seemed that a critical re-examination of Southern's specimens would be of considerable value as a contribution towards the taxonic revision of the Tubificidae. Accordingly, a visit was made to Dublin and his material located in the Natural History Department of the National Museum. This material comprises the types and co-types of species described by him, together with a miscellaneous collection of specimens. Whilst in Dublin several of the localities named by Southern were visited and collections made there. This often proved difficult as the localities are described very vaguely, while in two cases urban development has occurred in the regions named and several pools have disappeared as a consequence.

In this paper an attempt is made to bring the knowledge of the Irish tubificids up to date, by reviewing the pertinent literature, by giving an account of Southern's specimens and by listing contemporary field records. It is hoped that this paper will form the basis for future work of an ecological nature.

SYSTEMATIC PART

The list of synomyms and references given under each species refers to Irish records only. For a fuller synonomy than this reference must be made to Brinkhurst (1963). This work, however, does not treat the Irish records in any detail. The nomenclature used in this paper follows the check list of Brinkhurst (1962). None of the specimens here recorded is figured, as the important ones have already been figured by Southern and the diagnostic characters of the remaining species and the species recorded as new to Ireland are figured by Brinkhurst (1963). In this same work may be found full descriptions of all the valid species. No attempt has been made to construct a key to the Irish tubificids as one to the British Tubificidae is currently in preparation by Brinkhurst and includes all the known Irish species and species likely to occur in Ireland.

A list of the species recorded from Ireland to date is given below, together with their known distribution in Ireland. The symbols refer to counties and vice-counties. The symbol * indicates a new Irish record.

Species	*Distribution*
Tubifex tubifex (Müller, 1774.)	DU. WI.
Tubifex costatus Claparède, 1863.	DU. AN.
Tubifex templetoni Southern, 1909.	DU.
**Tubifex ignotus* (Stolc), 1886.	DU. AN.
Limnodrilus hoffmeisteri Claparède, 1862.	DU. AN. ME. CV. KD.
Limnodrilus claparedeanus Ratzel, 1868.	DU. CV.
Limnodrilus udekemianus Claparède, 1862.	DU. AN. NT. ME.
Peloscolex benedeni (Udekem), 1855.	DU. WM.
Peloscolex ferox (Eisen), 1879.	DU. ME. WI. EM. WM.
Psammoryctes barbatus (Grube), 1861.	DU. AN. KD.
Clitellio arenarius (Müller), 1776.	DU. WM. WC.
Branchiura sowerbyi Beddard, 1892.	DU.
**Euilyodrilus bavaricus* (Oschmann), 1913.	DU.
**Euilyodrilus hammoniensis* (Michaelson), 1901.	ME. AN.
**Aulodrilus pluriseta* Piguet, 1906.	DU. ME. CV.
**Rhyacodrilus coccineus* (Vejdovsky), 1875.	DU. ME. CV.
**Monopylephorus rubroniveus* Levinsen, 1883.	DU.

Key to counties and vice-counties:

AN. . . . Antrim;
DU. . . . Dublin;
ME. . . . Meath;
KD. . . . Kildare
CV. . . . Cavan;
EM. . . . East Mayo;
NT. . . . Nth. Tipperary;
WC. . . . West Cork;
WM. . . . West Mayo;
WI. . . . Wicklow.

Tubifex tubifex

T. rivulorum: Friend, 1897b, p.296.
T. tubifex: Southern, 1909, p.138.

Material.

2 slides, *T. rivulorum* coll. Southern. Murphystown[1]. DU.
1 slide *Tubifex* sp. coll. et det. Southern. Calary Bog. WI.
1 slide *Tubifex* sp. coll. et det. Southern. Glasnevin. DU.
Numerous specimens *T. tubifex* coll. et det. Kennedy. Howth, Carrickmines and Montpelier. D.U.

Both Friend's and Southern's records of this species must be doubted as they neither figure nor describe it in any detail. All the surviving specimens collected by Southern are immature and hence cannot be identified with certainty. His identifications are probably correct, however, as he correctly identified some non-Irish material, which is also present in his collection. The majority of specimens taken during recent collecting in localities indicated by Southern were mature and readily identifiable.

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[1] The location of Murphystown could not be ascertained from Southern's papers but it is assumed that it is in a townland (Glencullen) in County Dublin.

T. costatus

Heterochaeta costata: Friend, 1897a, p.63.
H. costata: Friend, 1897b, p.297.
Tubifex costatus: Southern, 1909, p.139.
Tubifex thompsoni: Southern, 1909, p.140, fig.7.
Heterochaeta costata: Friend, 1912, p.284.
H. thompsoni: Friend, 1912, p.284.

Material.

1 slide *T. costatus* coll. et det. Southern. Malahide. DU.
1 specimen *T. costatus* coll. et det. Southern, Malahide. DU.
1 slide *T. thompsoni,* type no.106, 1909. Coll. et det. Southern. Howth. DU.
Several specimens *T. costatus* coll. Healy, det. Kennedy. Bull Marsh. DU.

All the records by Friend seem to refer to a single collection. In none of his papers is the species described in detail, but it is almost certain that his records of *H. costata* refer to *T. costatus*. Southern's records of *T. costatus* are also valid.

The listed records of *T. thompsoni* are the only two known and of these Friend's is an incorporation of Southern's previous record. It was hoped, therefore, that an examination of *T. thompsoni* specimens would be interesting but, unfortunately, it was not possible on examination to make out any details of the internal anatomy, in particular of the genitalia, which, according to Southern, served to distinguish it from other species of the same genus.

Palmate chaetae occurred in the dorsal bundles of segments 2–15, not 5–18 as stated by Southern. The remaining dorsal bundles contained only bifid chaetae, with two equal teeth and no trace could be found of any penial chaetae. As noted, the genitalia were not distinct and no trace of a chitinous penis sheath could be found. When a chitinous penis sheath is present it is usually visible in specimens mounted in balsam. It is, however, possible that this specimen was not mature. Southern claimed that the structure of the genitalia of this species served to characterise it and to distinguish it in particular from *T. costatus,* which he considered it otherwise closely resembled. The genital ducts, as figured by him (fig.7), make little sense in relation to the form and function of the penis and his interpretation of these structures is open to doubt. This specimen of *T. thompsoni* was the only one in the collection and as the genitalia could not be seen, it was indistinguishable from *T. costatus*. In view of its close similarity to *T. costatus* and the probable misinterpretation of the genital ducts, it may be presumed that *T. thompsoni* Southern is a synonym of *T. costatus* Claparède.

T. templetoni

T. templetoni Southern, 1909, pp.140–141, fig.6.
T. templetoni: Friend, 1912, p.292.

Material.

1 slide *T. templetoni.* Type no.110. 1909. Coll. et det. Southern. Phoenix Park. DU. (0132348)

3 slides T. templetoni. Co-types. Coll et det. Southern. Phoenix Park. DU. Friend's record is again an incorporation of Southern's. This species has since been recorded from Britain, U.S.A. and the Continent.

T. ignotus

Material.

Worms labelled *T. barbatus* coll. et det. Southern. Lough Neagh. AN. (in part). 3 specimens *T. ignotus* coll. et det. Kennedy. Carrickmines and Killakee. DU.

This species occured in two of the localities visited. One of these was also a locality visited by Southern (Carrickmines) but he did not record its presence there. A sub-sample of Southern's collection from Lough Neagh (the specimens identified by him as *T. barbatus,* see page 234) contained one specimen of *T. ignotus.*

This is a new Irish record.

Limnodrilus hoffmeisteri

L. aurostriatus Southern, 1909, pp.136–137, fig.3.
L. parvus Southern, 1909, pp.137–138, fig.5.
L. aurostriatus: Friend, 1912, p.274.
L. parvus: Friend, 1912, p.274.
L. hoffmeisteri: Friend, 1913, p.171.

Material.

1 slide *L. Aurostriatus.* Type no. 103. 1909. Coll. et det. Southern. Carrickmines. DU.

2 slides *L. aurostriatus.* Co-types. Coll. et det. Southern. Carrickmines. DU.

1 slide *L. parvus.* Type no.111. 1909. Coll. et det. Southern. Montpelier. DU.

1 slide *L. parvus.* Coll. et det. Southern. R. Annalee. CV.

1 specimen labelled *P. barbatus.* Det. Friend. Lough Neagh. AN.

Several specimens *L. hoffmeisteri.* Coll. et det. Kennedy. Carrickmines, Montpelier and Grand Canal. DU. R. Blackwater. ME. Grand Canal. KD.

3 specimens *L. hoffmeisteri.* Coll. Healy, det. Kennedy. Bull Marsh. DU.

L. aurostriatus was considered by Southern to be most nearly related to *L. Hoffmeisteri.* He considered the chief distinguishing characters to be :—

1. Pharynx reaches back to fifth segment.
2. Unbranched integumental vessels.
3. Shape of chaetae.
4. Shape of penis sheath.
5. Shape of spermathecae.
6. Shape of spermatophores.

In the preserved specimens it was not possible to observe the length of the pharynx or the condition of the spermatophores. Brinkhurst (1963), in his review of the Tubificidae, does not consider characters 1 and 5 to be of importance in the differentiation of species. In two of the specimens examined there are no parallel arranged teeth on the anterior chaetae (3), as described by Southern for this species. All teeth diverge markedly throughout the length of the worm. In the remaining specimen the teeth do approximate to this description. The dimensions of the penis sheath (4) of all material examined are of the same order as those given by Southern and the shapes are similar to those figured by him, although he did over-emphasise the twist in the heads of the sheaths. Sheath heads of this shape have been observed in typical specimens of *L. hoffmeisteri,* taken in regular collections in England (Kennedy unpublished). The spermathecae (5) in these specimens are of a shape, as figured by Southern, which conform to those of *L. hoffmeisteri.* Spermatophores (6) are present in one specimen but no difference between them and the spermatophores of *L. hoffmeisteri* could be detected.

L. aurostriatus sensu Southern (1909) has been recorded from only two other localities. One record by Friend, to be considered later, and the other from Lake Esrom in Denmark (Berg 1939), the identification was made by Moszynski. Thanks to the kindness of Professor Berg I have been able to examine these specimens. The chaetae are of the normal *L. hoffmeisteri* type. The dimensions of the penis tube are similar to those given by Southern, but shapes of their distal ends, however, are intermediate between *L. hoffmeisteri* and *L. aurostriatus,* as shown by Southern. The former species appears to possess a penis head of variable shape but, nevertheless, a basic type appears to underline these variations. (The results of this study on *L. hoffmeisteri* will appear at a later date.) The specimens from Esrom can undoubtedly he assigned to *L. hoffmeisteri* but, because the characters used by Southern to distinguish *L. aurostriatus* are variable and unreliable, it would appear that his specimens also belong to this species.

Many of the chaetae, which are considered to be so important in distinguishing the doubtful species, *L. parvus,* are badly damaged in both specimens of this species. Those undamaged are of the type figured by Southern with the upper tooth shorter and thinner than the lower one. The average number per bundle in the anterior segments is five. The shape of the head of the penis sheath is also similar to those in his figures. The length : breadth ratio, however, varies from 8·6 : 1 to 11·1 : 1.

The validity of this species has often been questioned. Cernosvitov (1939) regarded it as synonomous with *L. hoffmeisteri* Clap., but later (1945) regarded it as a valid species. Brinkhurst (1960) initially refers to it as *L. parvus* but considers it to be synonomous with *L. hoffmeisteri.* Cekanovskaya (1962) referred to it as *L. hoffmeisteri f. parvus.* Brinkhurst (1963) in his world review of the Tubificidae now considers it to be synonomous with *L. hoffmeisteri.* From a study of the type specimens and from personal observations on specimens of *L. hoffmeisteri* this synonomy is accepted here. Chaetae of the type figured by Southern for *L. parvus* are often found in conjunction with penis sheaths which do not conform to the type described by him for this species. The remarks made earlier concerning the apparent variability of the specific characteristics of *L. hoffmeisteri,* in particular that of variability of the penis sheath is also relevant here. At present, it appears, from personal experimental evidence, that the reduction of the upper tooth of the chaetae is a direct result of wear. *L. parvus Southern* must, therefore, be regarded as a synonym of *L. hoffmeisteri.*

Friend's records of *L. aurostriatus* and *L. parvus* (1912) from Ireland are only incorporations of Southern's. In recording *L. hoffmeisteri* (1913) he does not give a description of his specimens so his record must be regarded as dubious. *L. hoffmeisteri* occurred commonly in recent collections and abundantly in both localities named by Southern for *L. aurostriatus* and *L. parvus* (Carrickmines and Montpelier).

L. claparedeanus

L. longus: Southern, 1909, p.136.
L. longus: Friend, 1912, p.274.

Material.

1 slide *L. longus.* Coll. et det. Southern. R. Annalee. CV.

This mount consisted of a single penis sheath. It was dried up and in very poor condition but it was possible to see that it was, in fact, a sheath of *L. claparedeanus* Ratzel. *L. longus* Bretscher is regarded as a synonym of this species by Piquet and Bretscher (1913). Recently, the two species were again separated (Brinkhurst and Kennedy 1962), but the separation is now recognised as incorrect. The confusion arose as a result of the presence of a third and now recognised new species to be described in a later publication by Brinkhurst (1963). In this same work a full discussion of the relationships of the species concerned will be found.

Friend's record is again an incorporation of Southern's.

L. udekemianus

L. udekemianus: Friend, 1896, p.127.
L. udekemianus: Friend, 1897a, p.297.
L. udekemianus: Friend, 1897b, p.207.
L. udekemianus: Friend, 1898, p.120.
L. udekemianus: Southern, 1909, pp.135–136.
L. udekemianus: Friend, 1912, p.292.
L. udekemianus: Friend, 1913, p.171.
L. udekemianus v. wordsworthianus: Friend, 1912, p.292.

Material.

None.

Friend (1896) gives a brief description of his specimens and from this it appears that his identification is correct. His first few records all refer to these same specimens. His later records incorporate Southern's. Southern (1909) had synonomised *L. wordsworthianus* Friend with *L. udekemianus* Clap., but Friend (1912) refused to accept this synonomy. He reduced it to subspecific rank and referred to it as *L. udekemianus v. wordsworthianus.* From this work (1912) it appears that he considered Southern's specimens of *L. udekemianus* to be more correctly assignable to *L. udekemianus v. wordsworthianus,* whereas his earlier records (1896 et seq.) were of *L. udekemianus typica.* As Friend nowhere describes any clear or valid distinction between *L. udekemianus* and *L. wordsworthianus,* Southern's synonomy must be accepted.

Southern's records of *L. udekemianus* for Ireland are, however, dubious. There is no Irish material in his collection but there is one slide and two specimens from Lancashire. The slide is of an immature specimen possessing hair chaetae and is consequently not *L. udekemianus,* although labelled as such. The other two specimens are undoubtedly *L. udekemianus.* In view of this, Southern's record can only be accepted with reservation. Although Friend is, in many cases, not to be relied upon completely, his records must be accepted here.

The species did not occur during the survey. In collections made since this survey it has been found in the Navan and Drogheda Canal, ME.

Limnodrilus sp.

Material.

1 slide *Tubifex* sp. Coll. et det. Southern. R. Annalee. CV.
1 slide, unlabelled. Coll. Southern. Calary Bog. WI.
1 slide, unlabelled. Coll. Southern Mornington. ME.

All three slides contained immature specimens and hence could not be identified.

Peloscolex benedeni

Tubifex benedeni: Southern, 1909, p.139.
T. benedeni: Southern, 1911, p.5.

Material.

Several specimens of *P. benedeni.* Coll. et det. Healy. Bull Marsh. DU.

As a result of misidentification by Friend, considerable confusion has arisen in the Irish literature between this species and *P. ferox.* The only reliable records of its occurrence in Ireland are those of Southern. These records will be dealt with under *P. ferox.*

P. ferox

Hemitubifex benedii: Friend, 1896, p.128.
H. benedii: Friend, 1897b, p.297.
H. benedeni v. pustulatus Friend, 1898b, p.120.
Tubifex ferox: Southern, 1909, p.139.
Tubificid indet.: Friend, 1911, p. 14.
H. benedeni: Friend, 1912, p.290.
H. pustulatus: Friend, 1912, p.290.
Spiroserma ferox: Friend, 1912, p.291.
H. pustulatus: Friend, 1912a, p.74.

Material.

2 slides *Tubifex* sp. . Coll. et det. Southern. Calary Bog. WI.

1 slide *Tubifex* sp. . Coll. Friend, det. Southern. Lough Mask. EM. WM.

6 specimens *P. ferox*. Coll. et det. Kennedy. Unnamed lough. CV. Blackwater. ME. Grand Canal. DU.

This species, more than any other, has been incorrectly identified by workers in Ireland. This, no doubt, is due to the changing ideas as to the limits of the genus *Peloscolex*. Species now recognised as belonging to this genus have, at various times, been assigned to the genera *Hemitubifex, Tubifex* and *Spiroserma*. Generic confusion has arisen from time to time in the above mentioned genera because of misinterpretation of specific characters. The earliest Irish record is that of *H. benedeni* (Friend, 1896 et seq.). He describes specimens taken from freshwater as covered with papillae and with hair chaetae. Because of the presence of papillae they are undoubtedly attributable to the genus *Peloscolex*, as currently defined. They could not be *P. benedeni* as this species is characterised by the absence of hair chaetae. It is, also, a marine littoral species (Brinkhurst & Kennedy, 1962a). From the brief description given by Friend, it seems probable that the specimens are more correctly assignable to *P. ferox*. In the cases of *H. benedeni v. pustulatus* and *H. pustulatus* the views of Cernosvitov (1941), who made a detailed study of the species described by Friend, are accepted. Friend (1898) described a variety of *H. benedeni* as *H. benedeni v. pustulatus* and later (1912) raised it to specific rank, i.e. *H. pustulatus*. His description, however, is vague and Cernosvitov (1941) considers the species to be synonomous with *P. ferox*. *Spiroserma ferox*, despite a lack of description, is also believed to be *P. ferox*. The tubificid indet. referred to by Friend (1911) is a single specimen taken from Lough Mask, Co. Mayo, and sent to the National Museum, Dublin. In the collection in the Museum a slide, with a single specimen of *P. ferox* and labelled *Tubifex* sp. by Southern but collected by Friend, was found. It is possible that this is the specimen to which Friend referred.

Southern (1909) refers to *T. ferox* but does not describe it. Specimens of *P. ferox* are present in his collections but they are always labelled as *Tubifex* sp. . At this time *Peloscolex* was regarded as being synonomous with *Tubifex* but the species now recognised as belonging to *Peloscolex* are identifiable, even when the specimens are immature. From his remarks on *P. benedeni* (as *T. benedeni*) in the same paper, it is obvious that Southern could correctly identify one species as *Peloscolex*, yet he failed to identify the other species when it occurred. It seems likely, therefore, that *P. ferox* as recorded by Southern was, in fact, a misidentification and his record must be considered dubious. The true identity of these specimens unfortunately cannot be ascertained.

Psammoryctes barbatus

Psammoryctes sp.: Friend, 1897, p.102.
Psammoryctes sp.: Friend, 1897a, p.297.
Tubifex barbatus: Southern, 1909, p.139.
P. barbata: Friend, 1912, p.291.

Material.

5 specimens *P. barbatus*. Det. Friend. Lough Neagh. AN.
Numerous specimens *T. barbatus*. Coll. et det. Southern. Lough Neagh. AN.
2 specimens *P. barbatus*. Coll. et det. Kennedy. Grand Canal. DU. KD.

No description of the specimen is made by Friend but the locality is given as Lough Neagh. It would, therefore, seem likely that the specimens mentioned above and determined by him as *Psammoryctes* species are those referred to. Tentatively, one may consider *Psammoryctes* sp. to be *P. barbatus*. This collection also contained single specimens of *L. hoffmeisteri* and *T. ignotus*. Southern's collection contained, besides *P. barbatus*, several *Lumbriculidae* indet.

Clitellio arenarius

C. arenarius: Southern, 1909, p.134.
C. arenarius: Southern, 1911, p.4.

Material.

1 slide *C. arenarius*. Coll. et det. Southern. Malahide. DU.
1 slide *C. arenarius*. Coll. et det. Southern. Sandymount. DU.
1 slide unlabelled. Coll. Southern. Bantry Bay. WC.
1 specimen *C. arenarius*. Coll. Healy, det. Kennedy. Bull Marsh. DU.

None of Southern's specimens is in good condition and all have some of their chaetae broken. Nevertheless, all belong to this species.

Branchiura sowerbyi

B. sowerbyi: Southern, 1909, pp.134–135.
B. sowerbyi: Friend, 1912, p.290.

Material.

5 slides *B. sowerbyi*. Coll. et det. Southern. Glasnevin. DU. (0153374).
1 specimen *B. sowerbyi*. Coll. et det. Southern. Glasnevin. DU.

All specimens immature but in good condition.

Euilyodrilus bavaricus

Material.

3 specimens *E. bavaricus*. Coll. et det. Kennedy. Carrickmines and Grand Canal. DU. (0228238 and 0160325).

This is a new Irish record for this rare species.

E. hammoniensis

Material.

Numerous specimens. Coll. et det. Kennedy. R. Blackwater. ME.
Numerous specimens *E. hammoniensis*. Coll. Hynes, det. Brinkhurst. Lough Neagh. AN.

This is a new Irish record.

Aulodrilus pluriseta

Material.

Several specimens *A. pluriseta*. Coll. et det. Kennedy. Killakee and Grand Canal. DU. R. Blackwater. ME. Unnamed lough. CV.

This is a new Irish record.

Rhyacodrilus coccineus

Material.

Numerous specimens *R. coccineus*. Coll. et det. Kennedy. Howth and Carrickmines. DU. R. Blackwater. ME. R. Annalee. CV.

This species occurred very abundantly at all sites visited. Two of these were sites visited by Southern. Reference will be made to its absence from his collections in the discussion later.

This is a new Irish record.

Monopylephorus rubroniveus

Material.

1 specimen M. rubroniveus. Coll. Healy, det. Kennedy. Bull Marsh. DU. (0230366).

This is a new Irish record.

Aegliana sigma Friend

Saenuris lineata: Friend, 1912a, p.221.
A. sigma: Friend, 1916, p.25.

This is considered by Cernosvitov (1941) to be a species of uncertain genus.

DISCUSSION

As mentioned in the introduction, some of the sites named by Southern in his paper were visited. It will be noted that identifications of material from these field collections confirm those of the preserved specimens. This is more apparent when Southern's nomenclature has been brought up to date. In addition, several species not found by Southern at these sites have now been recorded. A few remarks on this point may not be out of place here. *R. coccineus* and *T. ignotus* are not easily distinguishable from *T. tubifex*, especially when immature, and it is possible that these two species were present in Southern's collections but that he failed to distinguish them. Nowhere in his collections are there any undoubted specimens of *T. tubifex*, labelled as such, and it would appear that he was not certain of his identification of these species. Although this is one of the commonest British species, positive identifications cannot be made unless mature specimens are obtained, so it is possible that he never found any mature specimens to confirm his identification. Whichever is the case, it points to the possibility that he may have failed to recognise both *R. coccineus* and *T. ignotus*. The above remarks concerning maturity in *R. coccineus* apply also *E. hammoniensis*. There is also in this case the further possibility that he may never have taken it in his collections, as this species has occurred only rarely and in small numbers in recent surveys.

Nowhere in Southern's collections or in recent collections did *L. udekemianus* occur.† This omission is rather surprising as this species is cosmopolitan, though in few sites does it occur in abundance.

Southern's record of this species must be regarded as dubious for reasons already considered, but Friend's appears valid. It is likely that further collections will reveal that this species is widely distributed in Ireland.

Of the remaining species recorded as new to Ireland *E. bavaricus* and *M. rubroniveus* occurred in very small numbers and are not easily identifiable unless fully mature. *A. pluriseta,* whilst readily identifiable at all stages of maturity, not infrequently occurs only as single specimens and is consequently easily overlooked.

ACKNOWLEDGEMENTS

My visit to Ireland was financed by a special grant from the Nature Conservancy, to whom I wish to express my gratitude. I should also like to thank Miss G. Roche, National Museum of Ireland, for help in locating Southern's specimens; the Director of the Museum for permitting me to examine them and Professor C. F. Humphries, University College, Dublin, for placing her knowledge of the localities at my disposal and taking me to many sites. I should like to thank Mrs. B. Healy, University College, Dublin,

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†It has now (5.12.63) been recorded from one locality in County Kildare.

for allowing me to include some of her unpublished records. Finally, I should like to thank Dr. R. O. Brinkhurst for revision of this manuscript and for his constant advice and encouragement.

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Some Aquatic Oligochaeta from the Isle of Man with special reference to the Silver Burn Estuary

By **R. O. BRINKHURST** and **C. R. KENNEDY,**
Zoology Department, Liverpool University

With 3 figures and 2 tables in the text and on 1 Eddes

The only previous published records of Oligochaeta from the Isle of Man appeared in the Monograph of British and Irish Oligochaeta (SOUTHERN, 1909) and these were restricted to the families Enchytraeidae and Lumbricidae. In this paper we record 14 species of aquatic Oligochaeta from localities south of a line Peel—Douglas. The distribution of nine of these species is followed in some detail in the estuary of the Silver Burn at Castletown.

Most of the streams in the area studied are unsuitable for the development of rich tubificid faunas as they are fast-flowing and stony. Ponds are scarce and so the most rewarding habitats are the estuaries of the larger rivers, especially those at Peel and Castletown. At Douglas the estuary is not readily accessible owing to the development of the harbour and of the town, and so the nearest point to the estuary at which collections could be made was Purt-ny-shee on the River Dhoo where the silty bed of the river contained five species. Most of the smaller streams (at Fleshwick, Colby River, Port Soderick, Poyllvaaish, Arbory) do not have a zone of brackish¹) water as these tiny estuaries have been blocked by the accumulation of large, rounded stones through which the freshwater drains to re-appear on the surface below the high-water line.

The localities examined are shown on Fig. 1 and will now be dealt with individually. It should be noted that collections were made primarily to record Tubificidae and so many Naididae may have been overlooked.

A. Stations at which no Tubificidae were obtained.

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¹) The word "brackish" is prefered to the term "poikilohaline". As salinites are so variable in estuaries, the classification proposed by the International Limnological Society based on relatively narrow salinity ranges cannot be applied. (Symposium on the classification of brackish waters. Arch. Ocean. Limnol. 1959, 11 Suppl.)

These are included as, in the absence of more than fragmentary notes on the habitats of Tubificidae, negative records are as valuable as positive ones. They mostly comprise small stony streams such as those at Fleshwick (2), Colby foreshore (3), Arbory stream (shore) (4), Poyllvaaish foreshore (5), Santon Burn (7), Port Soderick stream and shore (8), River Glas at Tromode (9) and Abbeylands (10). In addition some shallow, muddy pools near Rushen (1) and the stony shore of a flooded quarry near Castletown (6) were also searched unsuccessfully.

B. Stations at which Oligochaeta were obtained

Station 11. In a very small, muddy stream at Rushen *T. tubifex* was obtained together with the lumbriculid *Stylodrilus heringianus.*

Station 12. Stream at Glen Maye. This stony torrent receives a small sewage effluent just below the road bridge and this had created a bed of silt which supports a population of *Tubifex tubifex.* This species is common in all types of habitat, but usually exists alone where the available oxygen is low, especially where organic pollution is severe as it probably is here immediately below the effluent outfall.

Stations 13 and 15. *T. tubifex* and *Limnodrilus hoffmeisteri* were found together in the River Nebb (Glenfaba Mills) and the Arbory stream (Ballanorris). Both are stony streams with silty patches. *Nais pseudobtusa* became very abundant here after sheepdip had been spilt into the stream (HYNES p. c.).

Stations 14 and 16. *Limnodrilus hoffmeisteri* was found alone in the streams at Cronkmoor and the Colby River close to the shore. In the former stream the worms all had extremely long penis-sheaths, and many authors have referred specimens like this to *L. claparedeanus,* but BRINKHURST (1960) has shown that the form of the sheath is characteristic in the latter species. The length of the sheath alone cannot be used as a taxonomic character as it clearly grows throughout the life of the animal. Other specimens with elongate penis-sheaths have been observed, in every other instance together with more normal *L. hoffmeisteri* and for the moment we regard these as one species. Now to be referred to *Limnodrilus longus* BRETSCHER.

Station 17. Stream at Poyllvaaish. Just above the foreshore a bed of silt contained a large number of *L. hoffmeisteri* and two *Peloscolex ferox.*

Station 18. Silverburn at Ballasalla. A shallow stony stream with some silt contained *T. tubifex, L. hoffmeisteri* and *Tubifex ignota.*

Station 19. River Dhoo, Purt-ny-shee. This was the only really muddy stretch of lowland river available and it contained many *L. hoffmeisteri* together with *T. tubifex, T. ignota, Aulodrilus pluriseta* and the lumbriculid *Stylodrilus heringianus.*

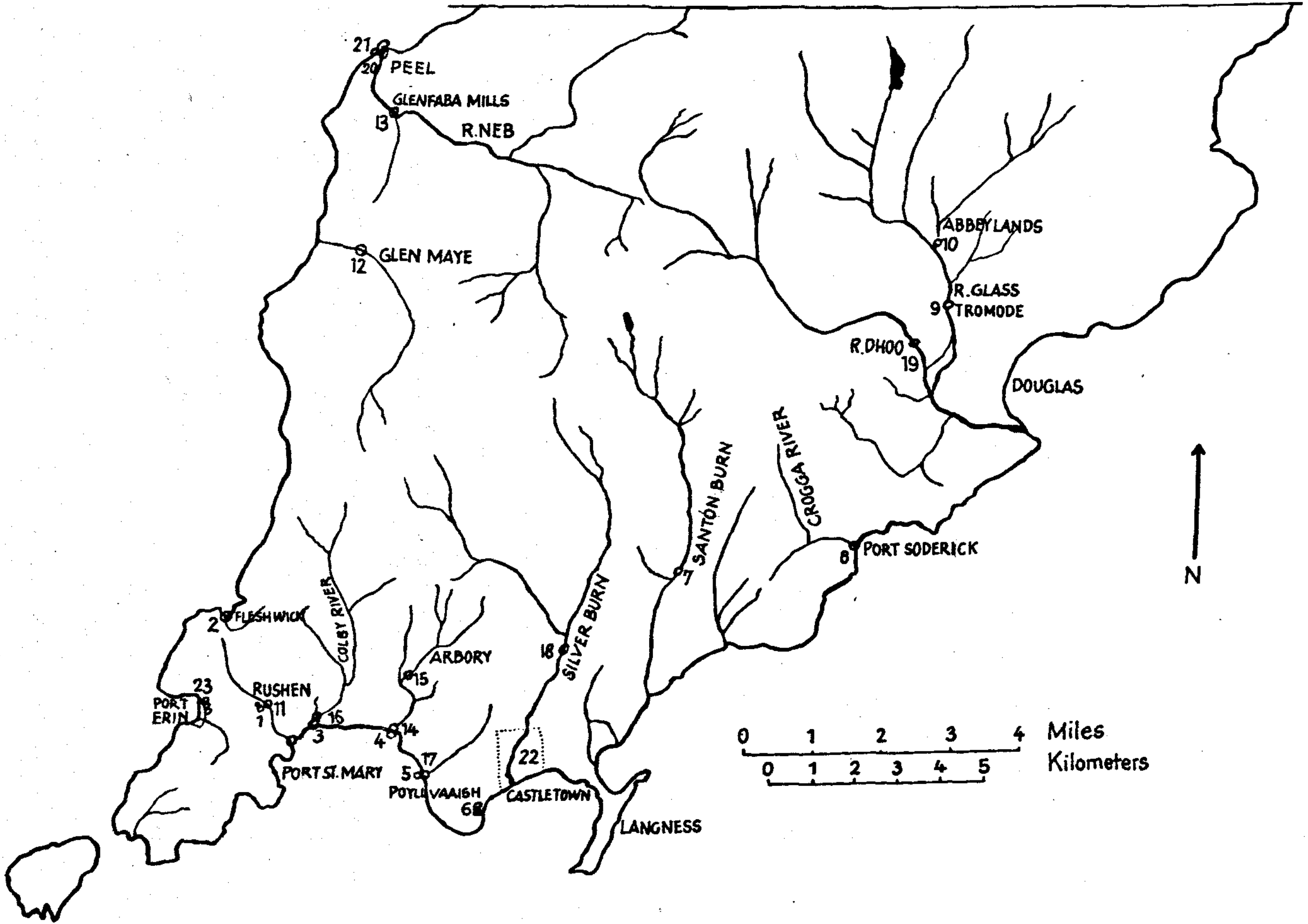

Fig. 1. Map of the southern half of the Isle of Man showing major streams and collecting stations.

ad p. 369.

Station 20. A single specimen of *Tubifex costatus* was found in a pocket of mud between rocks above the tide-line at Peel. A trickle of freshwater ran over the mud.

Station 21. In the estuary at Peel four species were found in gravel just below the lowest road bridge. These were *Peloscolex benedeni* (2), *Tubifex pseudogaster* (12), *T. costatus* (8) and *Clitellio arenarius* (1), the figures in brackets being the numbers observed. The distribution of these species was followed in more detail in the estuary at Castletown (St. 22).

Station 22. Castletown estuary has been examined by the staff and students of this Department on many of their Marine Biology field courses. Like most estuaries of any size in Britain it has been developed as a harbour and weirs have been constructed to limit the extent of the tidal flow. Fig. 2 shows a plan of the estuary. From its source, the Silverburn is a typical trout-stream with a rich fauna, but below a small weir the gradient is reduced and more silt accumulates (Station N—M). Between the bridges and the first weir (which is in effect a dam) the water gradually deepens and the bottom becomes more silty until 2—3 feet of mud was observed just above the weir (Stations L—K). Sea water occasionally gets above this weir and may therefore accumulate below the freshwater but none was observed during the salinity survey (Fig. 3) which was carried out at neap tides. Just below this is a simple waterfall referred to as the lower weir, and between the weirs the bottom is stony with much gravel (Station J). Considerable mud banks are exposed throughout most of the tide cycle on the south-west shore above and below the swing-bridge (Stations G and D), but the main channel remains gravelly, with more silt in the stretch from the lowest bridge to the mouth of the estuary (Stations A—B) than from the upper weir to the bridge (Stations C, E, F, H, J). This last stretch is apparently uniform in substratum and is now almost level owing to recent dredging and rock-blasting. A sewer enters the river just above the swing-bridge and the mud banks on that side of the river are black and deoxygenated. A small effluent enters the estuary from a brewery on the north-east shore opposite the sewer. This is derived from washing water and, once a week, is very hot and contains caustic soda from the cleansing process applied to the vats and piping of the brewery.

Salinity records

At the very highest spring tides a slight increase in salinity can be observed as far as a hundred yards above the railway bridge (Fig. 2). The highest point to which mean tides flow is given as the upper weir. Fig. 3 shows the results obtained during a study of the salinity changes carried out on April 4—5th, 1960. The samples were taken from the surface and from the bottom of the river simultaneously at hourly intervals at each of five stations and more frequently before and after high tide, and when there was no evident stability. In addition a tide curve was prepared from a tide-gauge close to the lowest bridge. A sample was placed in a perspex chamber and a hydrometer was used to obtain a reading of the percentage of sea water in the sample. The readings obtained were sufficiently accurate to indicate the changes occuring under the particular conditions of wind

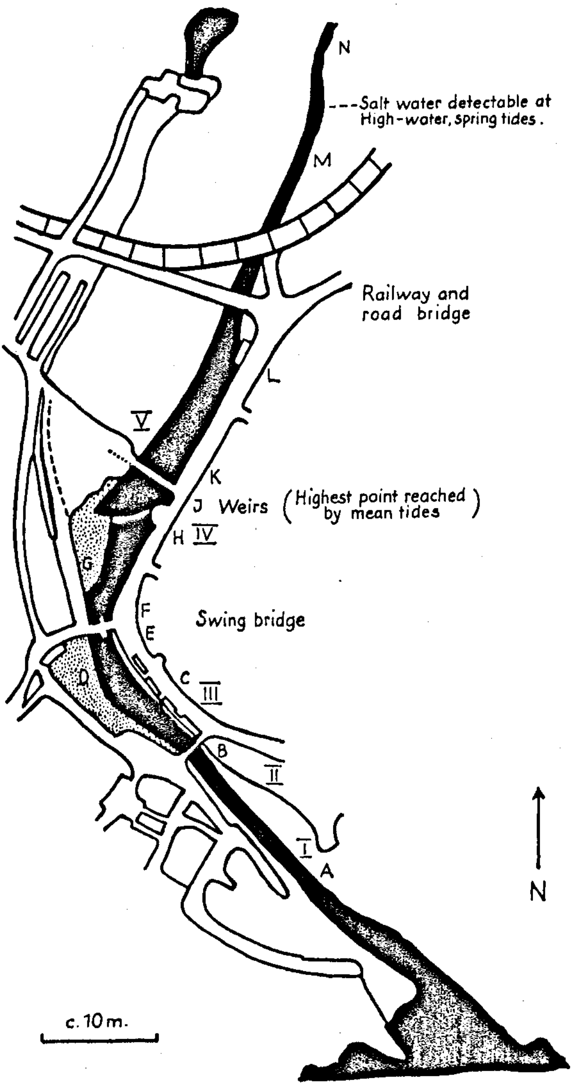

Fig. 2. Map of the Silverburn estuary, Castletown. The two weirs are shown as white lines on either side of J. A—N sites of collections detailed in Table 1—2. Stippled areas — mud banks. I—V Stations used in salinity survey.

and (neap) tides. Observations in the field showed that considerable impoundment of freshwater occured as the tide rose until the freshwater flowed out over the top of the advancing sea water. Thus differences in salinity between top and bottom samples became apparent very rapidly and little mixing occured at first. The surface water became steadily more saline, especially at stations 1 and 2.

Whilst the freshwater flowed over the sea water at high tide a transitional layer one foot deep and two to three feet from the surface was observed at Station III. These results compare well with the more detailed survey of the Blyth estuary by Capstick (1957). Under the combination

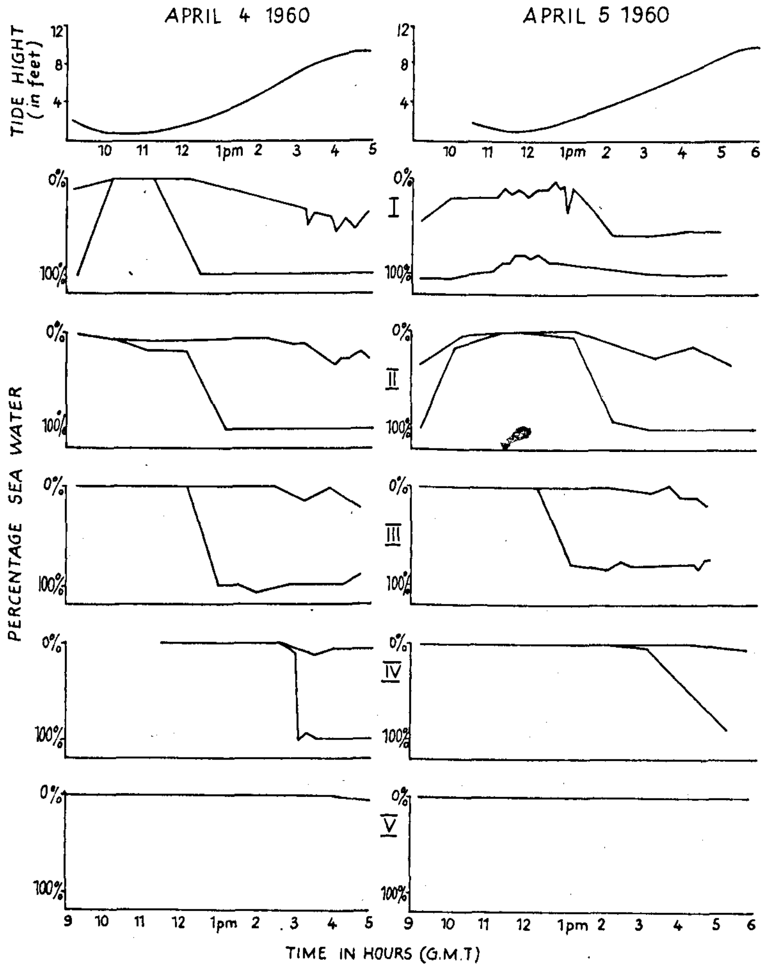

Fig. 3. Tide curves and salinity records for 5 stations on the Silverburn estuary, the stations being indicated on the sketch map (Fig. 2). Top line = surface water, lower line = bottom water.

of neap tides and a strong onshore wind almost no salt water was observed at Station V. All the salt-water receeded from the estuary at low tide on April 4th but on the 5th sea-water remained at Station 1 throughout the cycle possibly owing to the increased strength of the onshore wind. From this it can be seen that the influence of salinity above the upper weir is much less than below it, where the bottom sediments are covered first with freshwater and then with salt, with hardly any transitional phase. The length of time that the sediments are covered with sea-water depends on the distance from the mouth of the estuary, the state of the tide, and the strength and direction of the wind. The latter may be responsible for the fact that the tide apparently turned earlier at Station III than at II on April 5th (Fig. 3) the sampling points being on opposite banks. This apparently circular tidal wave has been observed in the larger Port Erin Bay but it would appear that such effects can operate even in such a narrow channel as this estuary.

The fauna

Many freshwater species do not extend further down the stream than a waterfall just above the stretch of stream shown in Fig. 2 but several penetrate as far as the railway bridge. Some species disappear at about the highest point at which salt water has been detected but *Hydrobia jenkinsi* becomes abundant from here to the bridges. Brackish water species such as *Nereis diversicolor, Corophium volutator, Sphaeroma rugicauda* and *Jaera* spp. extend from the weirs to various extents down the estuary and the more usual marine littoral forms appear in the lower pool (now only sparcely owing to rock-clearance and dredging). Despite the abrupt change in salinity regime produced by the weirs there is no really sudden change in the fauna at this point, but rather a gradual transition as one proceeds downstream. Much of this may be due to the impoundment of water above the upper weir which causes a reduction in current speed from the waterfall mentioned above and, below the weir, to the different substrata found as well as the salinity changes.

In contrast to this there is a marked change in the oligochaete fauna at the upper weir. Above it the species found at Station 18 are present (*T. tubifex, L. hoffmeisteri*) together with *Limnodrilus udekemianus, Stylodrilus heringianus,* and *Eiseniella tetraedra.* However, *Tubifex nerthus* replaces *T. ignota,* and a few *Peloscolex benedeni* were obtained, both probably owing to the slight increase in salinity occasionally observed at this point. Very few worms were found in the deep pool immediately above the weir where sea-water possibly becomes trapped after spring tides, but below the weir tubificids are again abundant (Table 1) but different species are concerned. *Tubifex costatus, T. pseudogaster* and *Clitellio arenarius* occur at all stations below the weir together with *Peloscolex benedeni* at four of the nine stations examined in this section of the estuary. A single specimen of *T. tubifex* was found below the weir (Station J) but otherwise none of the freshwater species was present.

Table 1: Total number of worms obtained in five-minute samples from Station 22 A—N

A	B	C	D	E	F	G	H	J	K	L	M	N
275	450	750	510	160	1350	1100	625	500	9	20	47	138

Table 1 shows the number of oligochaetes obtained in roughly quantitative samples obtained by kicking up the bottom deposits upstream of a pond-net (as supplied by the F. B. A.) for a period of five minutes at each station. Table 2 shows the percentage composition of a subsample of about fifty worms (all specimens from stations K, L and M) in which each individual was identified. From these data the following points emerge.

Table 2: Percentage composition of worms obtained in subsamples of about fifty specimens from Station 22 A—N

	A	B	C	D	E	F	G	H	J	K	L	M	N
Tubifex tubifex									1.7	0	41.8	40.5	28.3
T. nerthus											8.3	4.2	3.8
Limnodrilus hoffmeisteri										87.5	16.6	16.6	22.7
L. udekemianus										12.6	8.3	7.1	11.3
Stylodrilus heringianus												6.4	5.6
Enchytraeidae indet.											16.5	24.8	28.3
Tubifex costatus	19.2	33.4	21.6	29.3	59.1	29.2	45.1	41.0	32.0				
T. pseudogaster	42.3	8.8	40.2	44.9	30.7	43.5	48.5	35.7	30.4				
Clitellio arenarius	36.6	57.9	38.5	12.1	2.0	27.3	1.5	23.2	35.7				
Peloscolex benedeni	1.9	0	0	13.8	8.4	0	4.5	0	0	0	8.3		

a) *Peloscolex benedeni* seems to be most abundant in the deposits of mud below the swing bridge (Station D). This was also observed in preliminary surveys. It occured both above and below the upper weir.

b) *Tubifex pseudogaster* is abundant throughout the brackish zone with the single exception of Station B, for which no explanation can be given. This decrease in abundance was not observed in preliminary surveys made at the same time but on the opposite shore of the estuary.

c) *Tubifex costatus* is as common as the above at most stations in the brackish zone, but decreases in number in the channel at the seaward end of the estuary.

d) *Clitellio arenarius* is found abundantly among small stones but is uncommon in mud.

Thus, whilst the primary factor controlling the distribution of species in this estuary is undoubtedly the great variation in salinity below the weirs as compared with above, substratum differences account in part for the distribution of *Clitellio arenarius* and possibly for the small differences in relative abundance of *T. psudogaster* and *T. costatus*. The decrease in total numbers observed from Stations M—K probably reflects the increase in depth of water and slackening of the rate of flow of the water approaching the upper (dam-like) weir. Worms were most abundant at F and G, close to the sewer and the brewery effluent.

Station 23

A series of collections were made in small streams and seepages on the shore at Port Erin, but Tubificidae were chiefly observed in those where the freshwater ran over fine gravel between stones. Only 1 specimen of *C. arenarius* was found in the large stream running across the sand at Port Erin bay itself, and none was observed on stony beaches. Amongst the gravel in Spaldrick and Boats for Hire Bays (Port Erin) *C. arenarius* was abundant and at the latter *Peloscolex benedeni* also occured in considerable numbers.

These observations support the view that both substratum and salinity are factors affecting the distribution of tubificid oligochaetes.

Discussion

Tubificidae in general inhabit mud or silty gravel in rivers, lakes and ponds and some small streams, but are absent from stony trout-streams such as the Afon Hirnant (Hynes 1961). Some of the factors affecting their distribution are substratum, salinity and organic pollution. Certain species (*Peloscolex benedeni, Tubifex costatus, T. pseudogaster* and *Clitellio arenarius*) appear to be limited to brackish water and may occur on the sea-shore but, in my experience, only where freshwater seeps across the shore. There are a few marine species (Brinkhurst 1962 a) but they were not obtained in this survey. Organic pollution gradually reduces the number of species present as it increases in severity (Brinkhurst unpublished) much as with other groups of freshwater invertebrates (Hynes 1960) until, when the pollution is severe enough to exclude *Erpobdella octoculata*, very large populations of *T. tubifex* are observed, with *L. hoffmeisteri* in addition in all but the most severe. These two species are apparently the least demanding in their ecological requirements, occurring in a wide range of habitats and withstanding the effects of pollution and, in many instances, salinity (as at J and other, unpublished observations) better than other predominantly freshwater species. Substratum is also important in many instances. Ravera (1951) showed that Tubificadae (? *Psammoryctes barbata)* became increasingly abundant with increasing deposition of silt, and *Aulodrilus pluriseta* seems also to prefer fine mud although it is among the least common of the British species (Brinkhurst 1962 b).

Two other species are notable, *Tubifex ignota* being one of the least well-known tubificids (described in error as *T. nerthus* in Brinkhurst 1960, redescribed Brinkhurst 1962 a, b) and *T. nerthus*, a species new to Britain. The latter was described as inhabiting springs and streams (Michaelsen 1908) but has subsequently been recorded from brackish water (Knöllner 1935, Bulow 1957).

Finally it is again apparent that several species of these small worms can inhabit the same locality despite their apparent similarity in habit (Brinkhurst 1960) and frequently two species of the same genus are found in close association. Further studies will be aimed at the ellucidation of this situation.

Species recorded

1. Tubificidae
   - *Tubifex*
     - *Tubifex tubifex*
     - *Tubifex ignota*
     - *Tubifex costatus*
     - *Tubifex pseudogaster*
     - *Tubifex nerthus*
   - *Limnodrilus*
     - *Limnodrilus hoffmeisteri*
     - *Limnodrilus udekemianus*
     - *Limnodrilus claparedeanus*
   - *Peloscolex*
     - *Peloscolex ferox*
     - *Peloscolex benedeni*
   - *Clitellio*
     - *Clitellio arenarius*
   - *Aulodrilus*
     - *Aulodrilus pluriseta*
2. Lumbriculidae
   - *Stylodrilus*
     - *Stylodrilus heringianus*
3. Lumbricidae
   - *Eiseniella*
     - *Eiseniella tetraedra*
4. Naididae
   - *Nais*
     - *Nais pseudobtusa*

Summary

1. Fourteen species of aquatic oligochaete were recorded from the Southern half of the Isle of Man.
2. The distribution of nine of these was followed in some detail in the estuary of the Silverburn, Castletown.
3. The nature of the substratum (and hence the rate of flow of the water), the degree of organic pollution and salinity have all been shown to effect distribution and abundance of Tubificidae.
4. It would appear to be characteristic for several species of tubificid, often more than one in the same genus, to coexist in the same habitat.

Zusammenfassung

1. 14 Arten wasserlebender Oligochaeten wurden in der Südhälfte der Isle of Man gefunden.
2. Die Verbreitung von 9 Arten wurde etwas eingehender im Silverburn-Aestuar, Castletown, untersucht.
3. Die Beschaffenheit des Untergrundes (und im Zusammenhang damit die Fließgeschwindigkeit des Wassers), der Grad der organischen Verunreinigung und der Salzgehalt wurden als wirksame Faktoren für die Verbreitung und Häufigkeit der Tubificiden herausgestellt.
4. Für mehrere Tubificiden-Arten scheint es charakteristisch zu sein, daß oft mehr als eine Art derselben Gattung im gleichen Habitat zusammenleben.

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Occurrence of the Genus *Archigetes* in Britain

DURING the course of investigations into the taxonomy and ecology of aquatic Oligochaeta we have observed two species of *Archigetes*, a genus not to our knowledge previously recorded from Britain. *Archigetes appendiculatus* Mrazek, 1897 (non Ratzel, 1868) was first observed in a specimen of *Limnodrilus hoffmeisteri* Claparède, 1862 obtained from a Liverpool pet shop along with a large number of uninfected 'Tubifex' worms. The same species of parasite was later found in a pond near Fornalls Green Lane, Meols, Cheshire, on May 28, 1959. A second species *A. sieboldi* Leuckart, 1869, also from *L. hoffmeisteri*, was found from the Shropshire Union Canal near Chester on March 20, 1962. The cestodes were readily identified from recent descriptions of the genus[1,2]. In each instance the parasites were located in the genital segments of the tubificids. Both

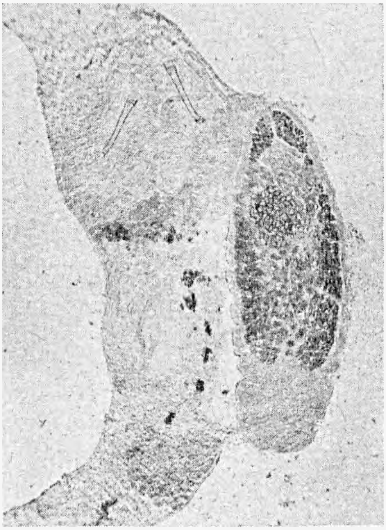

Fig. 1. *Archigetes appendiculatus* in the genital segments of *Limnodrilus hoffmeisteri*. Both host and parasite are sexually mature, eggs being clearly visible in the uterus of the parasite. Note the separation of the vitellaria into four distinct lobes. (× c. 17)

Særtryk af „Flora og Fauna", 69. årg., 1. hæfte, 1963

Forekomsten af bændelorme-slægten *Archigetes* Leuckart 1869 (Cestoda: *Caryophyllidea*) i Danmark

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Ved en undersøgelse, som fornylig er foretaget af nogle oligochaeter fra Esrom Sø – venligst udlånt til os af professor Kaj Berg – bemærkede vi nogle individer af *Archigetes*, en slægt som kun én gang tidligere er blevet fundet i Danmark (Berg et alia, 1948). Den af os fundne *Archigetes* blev observeret i et dyr af *Limnodrilus aurostriatus* Southern, 1909 (= *L. hoffmeisteri* Claparède, 1862), som blev taget i Esrom Sø af Berg ved hans undersøgelse af denne (Berg 1938). På grund af dyrets alder og fordi det var ufarvet, er vi ikke fuldstændig sikre på artsbestemmelsen, men vi mener, at det drejer sig om *Archigetes sieboldi* Leuckart, 1869. Bestemmelsen blev foretaget efter nogle nyere beskrivelser af slægten (Janiszewska, 1954; Kulakowskaja, 1961). Parasitten blev lokaliseret i tubificidens genitalsegmenter og indeholdt æg i uterus (se fig. 1). I et andet dyr af *L. aurostriatus* fandt vi en juvenil cestode, men denne kunne end ikke bestemmes til slægt.

Archigetes er tidligere blevet fundet i Danmark i Susaa og i en dam nær Lyngby (Jylland) af Boisen-Bennike (Berg et al., 1948).

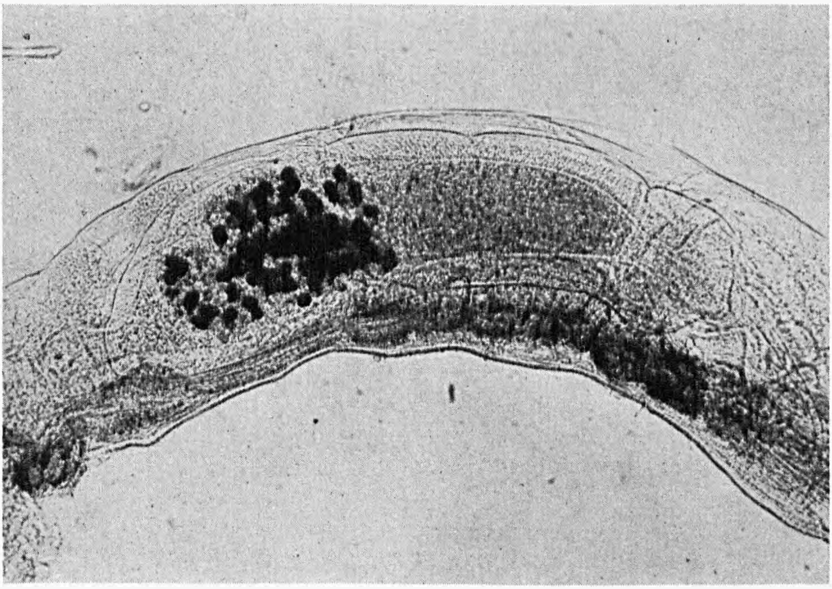

Fig. 1. *Archigetes* sp. i genitalsegmenterne hos *Limnodrilus aurostriatus*, ca. 50 × forstørrelse. Både vært og parasit er kønsmodne; man ser klart æggene i uterus hos parasitten. Dyrene er ufarvede og konserverede i kanadabalsam.

Dyrene fra Susaa bestemte han som *A. cryptobothrius*, og dyrene fra Lyngby som *A. sieboldi*. Ovennævnte fund er det første fra en dansk sø. Udbredelsen af slægten *Archigetes* er i det hele taget kun undersøgt i ringe grad, dog tror vi, den har en hyppig forekomst, men at den ofte bliver overset. Vi er nu i gang med at indsamle yderligere oplysninger om forekomsten af *Archigetes* og andre af oligochaeternes parasitiske cestoder. Vi ville sætte stor pris på korrespondance med andre, som finder et sådant materiale under deres ferskvandsbiologiske studier af beslægtede områder.

Vi vil gerne takke professor Kaj Berg for tilladelsen til at fotografere dyret samt for oversættelsen af denne meddelelse fra engelsk til dansk.

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THE BIOLOGY OF SOME FRESHWATER OLIGOCHAETES

The majority of publications on the genus Limnodrilus Clap. (Tubificidae) have been of a systematic nature. A large number of species had been described on the basis of morphological characters, but in the absence of any account of the variations of the characters used and the biology of the species the systematic position of many of them was dubious. The aim of the present investigation was therefore to determine the true relationships of these species by a study of their morphology, distribution and life histories, and then to give an account of the taxonomy and biology of the species of Limnodrilus.

As a result of morphological and life history studies the genus is re-defined and seven species recognised. These are described and are distinguishable primarily on the nature of the male efferent ducts. An account of the variation of the specific characters is given. Of the remaining species of Limnodrilus that had been described, some were recognised as being correctly located in other genera, some were reduced to synonomy and a few were retained as species dubia.

The genus as a whole proves to be cosmopolitan in its distribution, but differences in the geographical distribution of the species were found. Two species are cosmopolitan, one holarctic, one nearctic, one palaearctic and one neotropical. The remaining species is restricted to eastern Asia. Of the five species that occur in Britain, two appear to have been recently introduced. The distribution of the remaining three species overlaps considerably, and they frequently formed mixed species populations. No specific habitat preferences or limiting factors were recognised.

In a study of the life histories of the British species under laboratory and field conditions it was apparent that no breeding pattern is characteristic of the genus. There is some indication that the time of breeding and the age at which specimens attained maturity are specific characteristics, but within each species the breeding pattern varies considerably. The duration and, to a lesser extent, the time of breeding appears to be related to the productivity of the habitat and the nature of the substratum. The life histories of some species are more variable than that of others, and the more adaptable species prove to be those that have a widespread distribution.

It appeared that abiotic factors of the environment are of little importance in determining the distribution and abundance of the species of Limnodrilus, and that of the biotic factors food is likely to be the most important. The relationship between Limnodrilus and its cestode parasites was considered in detail, but it was shown that these parasites have a negligible effect on the population density of Limnodrilus.

It has, therefore, proved possible to characterise the species of Limnodrilus on the basis of their morphology, distribution and biology. It was not possible to recognise the ecological requirements of each species, or the factors that determine the distribution and abundance within any habitat, but from the available evidence it is apparent that the nature and abundance of the food supply requires further investigation.

English version of "Forekomsten af baendelorme-slaegten _Archigetes_ Leuckart 1869 (Cestoda: Caryophyllidea) i Danmark" Flora og Fauna 69. arg. 1. haefte 1963.

During the course of a recent examination of some Oligochaeta from Lake Esrom, kindly loaned to us by Professor Kaj Berg, we observed a species of _Archigetes_, a genus of which there is only one previous record from Denmark, (Berg et alia, 1948). The _Archigetes_ we observed occurred in a specimen of _Limnodrilus aurostriatus_ Southern, 1909 (L. hoffmeisteri Claparede, 1862), taken from Lake Esrom by Berg during the course of his survey of the lake (Berg, 1938). Owing to the age of the specimen and its unstained condition we cannot be completely certain of its specific identity, but we are of the opinion that it is _Archigetes sieboldi_ Leuckart, 1869. The identification was made from recent descriptions of the genus (Janiszewska, 1954; Kulakowskaja, 1961). The parasite was located in the genital segments of the tubificid, and contained eggs in the uterus (see fig. 1). Another specimen of _L. aurostriatus_ contained a juvenile cestode, but this was not identifiable even to genus.

Archigetes has previously been recorded from Denmark from the River Susaa and from a pool near Lyngby (Jutland), by Boisen-Bennike (Berg et al., 1948). The specimens from the River Susaa he identified as _A. cryptobothrius_, and those from Lyngby as _A. sieboldi_. The above record is the first from a Danish lake. The distribution of the genus _Archigetes_ has on the whole been little studied, but we suspect that it is of wide occurrence, but has been frequently overlooked. Currently we are collecting further data on the incidence and occurrence of _Archigetes_ and other cestode parasites of Oligochaeta. We would appreciate correspondance with other workers who may find such material during the course of their studies on related fields of freshwater biology.

We wish to record our thanks to Professor Kaj Berg for permitting us to photograph the specimen, and for translating this paper into Danish.

Figure 1 _Archigetes_ sp. in the genital segments of _Limnodrilus aurostriatus_, ca. 50 X magnification. Both host and parasite are sexually mature, eggs being clearly visible in the uterus of the parasite. Specimens unstained and mounted in Canada balsam.