THE TAXONOMY, ECOLOGY AND HOST-SPECIFICITY OF SOME PHYLLOBOTHRIIDAE (CESTODA: TETRAPHYLLIDEA), A CRITICAL REVISION OF *PHYLLOBOTHRIUM* BENEDEN, 1849 AND COMMENTS ON SOME ALLIED GENERA

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Two new and twelve little known species of *Phyllobothrium* or of allied genera, mainly from elasmobranchs and teleosts caught off the British Isles, have been investigated. As some of these could not be identified to species and the others presented difficulties, material from various other sources was obtained and examined for comparison. In addition, the literature on about 100 species allocated to *Phyllobothrium* was consulted and brought together. A critical appraisal of this literature is given and the genus is revised for the first time. Information on most of the species was found to be inadequate to provide a key and, therefore, a host-parasite list was compiled. As only about fifty species of *Phyllobothrium sensu lato* have been found in about 100 of the 3000 species of elasmobranchs known to exist, it is estimated that a very large number of *Phyllobothrium* spp. remains to be discovered and described. The possible significance of this fact is discussed. Brief descriptions of the most well-known species of *Phyllobothrium* are given and reasons against listing synonyms for these are emphasized. Of the 100 species already allocated to the genus only twenty-two are accepted at present; further studies may show that only three of these, viz. *P. lactuca*,

* On the appearance of a valuable paper by Dollfus (1964) it was decided to give only a brief account of larvae of *Phyllobothrium* in marine mammals.

P. dagnallium and *P. serratum*, show the typical features of the genus, as originally described. Fourteen of the twenty-two may, eventually, be placed in *Anthocephalum* Linton, 1890, if this genus is revived; the erection of a new genus or genera may be necessary for the remainder. *P. britannicum* sp.nov., from *Raja montagui*, is provisionally placed near *P. lactuca* but the bothridia are only slightly bifid, their margins are not so folded and the species is euapolytic. *P. minutum* sp.nov. from *R. fullonica* closely resembles *P. auricularia*, *P. foliatum* and *P. loculatum* and may, eventually, fall as a synonym of one of these; at present they are all little-known forms. Reasons are given for provisionally retaining *Crossobothrium* and *Monorygma*, with about ten species in each. It is suggested that three species originally placed in *Phyllobothrium* may be allied to *Sphaerobothrium lubeti* Euzet, 1959. An examination of the type material of *P. ketae* Canavan, 1928, previously regarded as unique or as a neotenic form, has shown that the original description was partly based on a pseudophyllidean and possibly on the larvae of *P. caudatum*. A number of larvae of *Phyllobothrium* in invertebrates, teleosts and marine mammals, fourteen little-known species of the genus and invalid members are discussed. A detailed discussion is given of the ecology, host specificity and attachment of *Phyllobothrium* and allied genera to the gut mucosa of elasmobranchs. In a general discussion brief comments are made on life-history, the identification and classification of *Phyllobothrium*, self-fertilization and on 'segmentation'. Almost 200 references are cited.

I. Introduction

Wardle & McLeod (1952, p. 247) correctly referred to *Phyllobothrium* Beneden, 1849, as 'a lumber room of forms which cannot be fitted into other phyllobothriid genera'. A revision of the genus has, therefore, been attempted as a result of finding about forty tetraphyllidean species, including several phyllobothriids, in elasmobranchs caught off the British Isles. The fishes were obtained using methods similar to those described by Williams (1958, 1959*a*, 1961, 1966). It was possible to identify many of the species mentioned in this paper only after extended observations on the biology of the hosts and of the cestodes found; living material collected at the Plymouth Marine Laboratory and the Marine Laboratory, Sète was invaluable in this respect. Additional preserved specimens were examined at the British Museum (Natural History), and at the Institute of Zoology, University of Neuchâtel. The main results of the investigation show that: (i) of about 100 species previously referred to *Phyllobothrium* only about twenty-two are now recognized; of these twenty-two only three show the typical features of the genus as deduced from the original description of *Phyllobothrium lactuca*, the type species; (ii) *Phyllobothrium ketae* Canavan, 1928, is invalid; hitherto it was regarded as unique in its host distribution or, possibly, as a neotonic form; (iii) the taxonomy of *Crossobothrium* and of *Monorygma* is extremely complex; (iv) five species, previously referred to *Phyllobothrium*, show affinities with *Sphaerobothrium lubeti* Euzet, 1959; (v) the rigid host-specificity of adult Tetraphyllidea may be due partly to ecological factors and to the characteristic morphology of the gut mucosa of the host in different species of elasmobranchs; and (vi) two new species of *Phyllobothrium* are described. For convenience of presentation and discussion of these results and other aspects of the biology of *Phyllobothrium* and allied genera the paper is arranged as indicated in the table of contents above.

II. Summary of the taxonomic history of the genus *Phyllobothrium* Beneden, 1849

The genus *Phyllobothrium* was first defined by van Beneden (1849) as having four sessile bothridia which show great mobility, each being curled like the leaves of a lettuce. From 1849 to 1912 a large number of references to *Phyllobothrium* was published, but as the information was summarized by Stiles & Hassall (1912, pp. 285–287) it will not be repeated here; they gave about thirty references and mentioned thirty-two species including nine unnamed forms.

Meggitt (1924) referred to '*Phyllobothrium* Beneden, 1850' and included *Crossobothrium* Linton, 1889, as a synonym of the genus which he very briefly described, with '*P. lactuca* Beneden, 1850' as type species. He also gave a diagnosis of the family *Phyllobothriidae* Braun, 1900, with '*Phyllobothrium* Beneden, 1850' as type genus. Meggitt referred to the adults of the Phyllobothriidae, including *Phyllobothrium*, as parasites of fish and mammals but in this revision it will be shown that adults of *Phyllobothrium* are restricted to elasmobranchs.

Southwell (1925) defined *Phyllobothrium* and gave the following synonyms: *Anthrobothrium* (*musteli*) Ben., 1850 *pro parte*; *Tetrabothrium*, of Molin, 1858 *pro parte*; *Monorygma* Diesing, 1863; *Orygmatobothrium* Diesing, 1863 *pro parte*; *Trilocularia* Olsson, 1867; *Dinobothrium* Ben, 1889; *Crossobothrium* Linton, 1889; *Pelichnibothrium* Monticelli, 1889; *Anthocephalum* Linton, 1890; *Calyptrobothrium* Monticelli, 1893; *Rhinebothrium* (*ceylonicum*) Shipley & Hornell, 1906, and *Bilocularia* Obertseiner, 1914. As with the taxonomy of the genus *Echeneibothrium*, however, discussed by Williams (1966), it is now known that a number of previous workers has erroneously suggested long lists of synonyms for various Tetraphyllidea without adequate knowledge of certain aspects of their biology. As with *Echeneibothrium* this revision of *Phyllobothrium* will show that it is premature to suggest synonyms for most of the genera included in the Tetraphyllidea; at specific level the taxonomic difficulties are so great that some 'species' are unidentifiable. Poche (1926) referred to the order 'Taeniidea nom.nov.', to the superfamily 'Phyllobothrioidea Carus, 1863', the family Phyllobothriidae Braun, 1900, and listed synonyms for the Taeniidea and the Phyllobothrioidea. Few authors have followed Poche in including *Phyllobothrium* in the Taeniidea, but Prudhoe & Baylis (1957, p. 89) are an exception. Further comments on the classifications of elasmobranch cestodes will be given when revisions of other genera are completed. Southwell (1929) discussed classifications of the Cestoda by Poche in 1926, Woodland in 1927 and by Pintner in 1928 and referred to the position of *Phyllobothrium* in the schemes proposed. Southwell (1930, p. 179) briefly discussed previous work on *Phyllobothrium* and gave a key to eleven species with notes on each of these.

Joyeux & Baer (1936, p. 50) referred to *Phyllobothrium* with *Monorygma* Diesing, 1863; *Trilocularia* Olsson, 1867; *Crossobothrium* Linton, 1889; *Pelichnibothrium* Monticelli, 1889; *Anthocephalum* Linton, 1890; *Calyptrobothrium* Monticelli, 1893, and *Bilocularia* Obersteiner, 1914, as synonyms. This reduction in the number of synonyms, compared with Southwell (1925), is an indication of the progress made in solving taxonomic problems connected with *Phyllobothrium*. Joyeux & Baer gave a key to six of the eight species known from France; they referred to seventeen valid species and to two inadequately known forms, *P. gracile* and *P. rotundum*. Three of the species included in the key by Joyeux & Baer are no longer accepted as valid members of the genus; *P. unilaterale* is thought to be a synonym of *P. thridax*, while *P. acanthae-vulgaris* and *P. rigii* are included in other genera.

Hyman (1951) included some general comments on *Phyllobothrium* and a figure of a species 'from a skate'. Wardle & McLeod (1952) quoted Beneden's original definition of the genus and correctly emphasized that later definitions by Braun (1900), Linton

(1924*a*) and Southwell (1925, 1930) are not an improvement on that by Beneden. They also stated that 'it seems almost impossible to find characteristics which are peculiar to this genus alone, and which occur in every species of it'. They gave a provisional key to and notes on twenty-six species of the genus which is defined as follows: 'With the bothridia stalked or sessile, their adherent surfaces simple, completely curled, or folded, their margins entire or completely frilled or bearing minute, suckerlike organs. An accessory sucker commonly but not invariably present in each bothridium. A neck present or absent.' Polyanski (1955) referred to *Phyllobothrium* as a world-wide polymorphic genus with over twenty species parasitic in the spiral valve of sharks and skates.

Riser (1955) proposed a new super order Trixenidea, in which he included the order Tetraphyllidea with four superfamilies including the Phyllobothrioidea Southwell, 1930. He re-defined *Phyllobothrium* as follows: 'Craspedote apolytic cestodes with large, circular, leaflike phyllidea each bearing an anterior acetabulum. Genital atria muscular, irregularly alternating. Excretory vessels internal to or at medial ends of vitellaria and lateral to testes; one dorsal and one ventral vessel on each side, lying one above the other. Testes in two or more layers. Ova spherical or subspherical.'

A classification differing from that of Riser was proposed by Euzet (1956), who suggested three new superfamilies, namely, the Phyllobothriidea, Lecanicephaliidea and the Prosobothriidea, the former comprising the Phyllobothriidea and the Onchobothriidae. Euzet (1959, p. 49), however, referred to the order Tetraphyllidea Carus, 1863; superfamily Phyllobothrioidea Southwell, 1930; family Phyllobothriidae Braun, 1900, and the subfamily Phyllobothriinae Beauchamp, 1905. The definition of *Phyllobothrium* given by Euzet (1959) emphasized, among other features, that the testes are numerous, the vagina opens in front of the cirrus sac, the uterus is sac-like and that each bothridium has an apical accessory sucker. Joyeux & Baer (1961) quoted some of the information given by Euzet (1959) on *Phyllobothrium* and on its systematic status. The invaluable study by Euzet is of particular interest in that it differs from those of Southwell (1925), Joyeux & Baer (1936) and Yamaguti (1959). Euzet, in our present state of knowledge, correctly avoided listing synonyms for *Phyllobothrium*. Yamaguti (1959), however, gave a key to genera of the Phyllobothriidae and included *Crossobothrium* Linton, 1889; *Anthocephalum* Linton, 1890; *Calyptrobothrium* Monticelli, 1893, and *Bilocularia* Obersteiner, 1914, as synonyms. He gave a detailed definition of *Phyllobothrium* and listed thirty-three species with their hosts and geographical distribution.

A definition of *Phyllobothrium* and a discussion of its place in a classification of the cestodes of elasmobranchs will not be given in this revision; apart from a scant knowledge of the morphology of a few adults, little is known of the biology of these tapeworms. One of the aims of this revision, therefore, is to provide a basis for further studies by arranging the species already described into a series which may indicate relationships. The species referred to in the revision must still be regarded as little-known forms. To aid further work, therefore, it was decided to list the hosts and localities from which each species had been previously recorded. With the exception of the type species, *P. lactuca*, no attempt has been made to criticize these records; criticisms of the kind offered in connexion with previous records of *P. lactuca* are probably applicable to other species.

III. Taxonomic histories and brief accounts for twenty-two species of the genus

1. **Phyllobothrium lactuca** Beneden, 1849
(Figures 1 to 9, 61, 67; figure 74, plate 13; figure 92, plate 15)

Previous records: *Mustelus lenticulatus*, New Zealand, Alexander (1963); *Hexanchus griseus*, Britain, Baylis (1939); *M. vulgaris*, Beneden (1849); *M. vulgaris*, Belgium, Beneden (1850 *b*); *M. vulgaris*, Belgium, Beneden (1858); *M. vulgaris*, European waters, Beneden (1870); *Spinax acanthias*, Beneden (1870); *Raja batis*, European waters, Beneden (1870); *R. clavata*, European waters, Beneden (1870); *Trygon pastinaca*, Black Sea, Borcea (1934); *M. vulgaris*, Mediterranean, Carus (1884); *M. vulgaris*, Diesing (1863); *T. pastinaca* Diesing (1863); *Sepia officinalis*, Dollfus (1958); *M. canis*, Concarneau, Sète, Euzet (1959); *M. mustelus*, Concarneau, Sète, Euzet (1959); *Raja*, Fuhrmann (1931); *Squalus mitsukuri*, Tsingtao, Hsü (1935); *R. batis*, Carnarvon Bay, Wales, Johnstone (1906); *R. circularis*, Beaumaris Bay, Wales, Johnstone (1906); *R. clavata*, Carnarvon Bay, Wales, Johnstone (1906); *Acanthias vulgaris*, Manche, France, Joyeux & Baer (1936); *M. hinnulus*, Manche, France, Joyeux & Baer (1936); *M. laevis*, Manche, France, Joyeux & Baer (1936); *Oxyrhina spallanzanii*, Manche, France, Joyeux & Baer (1936); *R. batis*, Manche, France, Joyeux & Baer (1936); *R. clavata*, Manche, France, Joyeux & Baer (1936); *Squatina angelus*, Manche, France, Joyeux & Baer (1936); *Trygon pastinaca*, Manche, France, Joyeux & Baer (1936); *M. vulgaris*, Linstow (1878); *R. batis*, Linstow (1878); *R. clavata*, Linstow (1878); *Scymnus glacialis*, Linstow (1878); *Lamna* sp., Meggitt (1928); *M. vulgaris*, Wimereux (Pas-de-Calais), Monticelli (1889); *M. laevis*, Oerley (1885 *a*, *b*); *T. pastinaca*, Oerley (1885 *a*, *b*); *R. clavata*, Olsson (1867); *R. radiata*, Olsson (1867); *Micropogon undulatus*, Montevideo, Parona (1900); *Mustelus laevis*, Mediterranean, Parona (1900); *Hexanchus griseus*, Plymouth, Prudhoe & Baylis (1957); *H. griseus*, Britain, Rees & Llewellyn (1941); *Triakis semifasciata*, Monterey Bay and Obispo Bay, California, Riser (1955); *Carcharodon carcharias*, New Zealand, Robinson (1959); *M. lenticulatus*, New Zealand, Robinson (1959); *Squatina angelus*, Britain, Scott (1909); *Trygon walga*, Ceylon, Shipley & Hornell (1906); '*H. brevirostris*', Dry Tortugas, Shuler (1938); *Galeocerdo tigrinus*, Ceylon, Southwell (1912); *T. kuhli*, Ceylon, Southwell (1912); *T. kuhli*, Ceylon, Southwell (1925); *T. walga*, Ceylon, Southwell (1925); *Dasybatus kuhli*, Ceylon, Southwell (1930); *D. walga*, Ceylon, Southwell (1930); *G. arcticus*, Ceylon, Southwell (1930); *G. tigrinus*, Ceylon, Southwell & Prashad (1920); *Squalus mitsukuri*, Tsingtao, China, Tseng (1933); *M. mustelus*, Britain, Williams (see p. 293); *M. vulgaris*, Plymouth, Woodland (1927); *M. manazo*, Sea of Japan, Yamaguti (1952); *Cynias manazo*, Hiroshima, Yoshida (1917).

Phyllobothrium lactuca Beneden, 1849, has been known since 1819 but Euzet (1959) was the first to give an adequate account of its main features. His observations are confirmed and slightly enlarged in this revision after discussing some aspects of the history of the name *P. lactuca*. This historical account is intended as a basis for further studies on species previously misidentified as *P. lactuca*. For a number of reasons some of the references to *P. lactuca* in the above list of its previous records are omitted from the following discussion.

The specimens described and illustrated by Leuckart (1820) as *Bothriocephalus echeneis* and as *B. flos* probably included a species now known as *Phyllobothrium lactuca*. His figures 6 and 7, Plate I, show a scolex almost identical with that described by Euzet (1959) and in the present instance; but his figures 8 to 11, Plate I, and the hosts given by Leuckart, namely '*Rajae Pastinacae, R. Torpedinis intestinis, Squali Galei, S. glauci* and *S. squatinae*' suggest that he was dealing with a complex of cestode species which probably included *P. thridax*. Rudolphi (1819) and Bremser (1824), in a discussion of *Bothriocephalus auriculatus*, were probably dealing with a species of *Phyllobothrium*, possibly *P. lactuca* or *P. thridax*; '*Torpedinis marmoratae, Squali Galei* (?) and *Squali glauci*' were given as hosts.

Dujardin (1845) referred to *Bothriocephalus auriculatus* Rudolphi and included '*Bothriocephalus Flos* Leuckart' and '*Bothr. auriculatus* Bremser' as synonyms of the species. He gave a diagnosis for the species based on specimens from *Raja clavata*; he also referred to specimens from '*Squalus galeus*', '*glaucus*', '*squatina*' and the '*torpille*'.

The name *Phyllobothrium* was first used by Beneden (1849), who referred to *Phyllobothrium lactuca* in *Mustelus vulgaris* and *P. thridax* in *Squatina angelus*; Beneden stated that the former resembled specimens described by Leuckart as '*Bot. echeneis* ou *Tumidulus* de Rud.'

Beneden (1850*a*, *b*) referred to the four notched, sessile bothridia of *Phyllobothrium* as each with great mobility, very much folded and divided like the leaves of a lettuce. It is remarkable, therefore, that in later studies of *Phyllobothrium* little attention has been given to these features. *P. lactuca* was first described by Beneden (1850*b*), who stated that the strobila was 250 mm long and 3·0 and 4·0 mm wide; the proglottid measurements were given as 12 to 15 mm long by 4 to 5 mm wide. These measurements and a figure of a free proglottid of '*P. lactuca*' suggest that Beneden was dealing with more than one species under the same name; but only one host is named, i.e. *Mustelus vulgaris*. Beneden (1858) referred to *M. vulgaris* as host, emphasizing that species of *Phyllobothrium* were difficult to identify and again figured a free proglottid of *P. lactuca*. Diesing (1863) gave a concise definition of *P. lactuca*, but referred to both *Trygon pastinaca* and *Mustelus vulgaris* as hosts and to *Bothriocephalus echeneis* of Leuckhart, *Tetrabothrium tumidulum* of Rudolphi, *Phyllobothrium lactuca* of Beneden and to *Tetrabothrium* (*Phyllobothrium*) *lactuca* of Diesing 1854 as synonyms.

Much of the information which accumulated on *P. lactuca* between 1867 and 1912 is of particular interest only in so far as the hosts are concerned and will not be discussed further here. Many of the authors who have previously recorded *P. lactuca* were probably dealing with another species.

The material described by Yoshida (1917) as '*Phyllobothrium lactuca*' from *Cynias manazo* (Bleeker) caught near Hiroshima, Japan, is worthy of further study especially if additional material could be obtained from the same host and locality. He referred to specimens measuring 60 to 80 mm long with a subglobular head, 2·0 to 3·0 × 2·50 mm, and to the most remarkable feature being a dehiscence of the posterior proglottids to liberate eggs, i.e. he suggested that the specimens, as in *P. lactuca*, are anapolytic but he did not describe the eggs. Yoshida briefly described the genital organs, vas deferens, vagina, ovary, uterus, yolk gland and musculature but did not refer to the number of testes. In his brief discussion of the affinities of the species he implied that it may not be *P. lactuca*.

The species briefly described by Southwell & Prashad (1920) as *Phyllobothrium lactuca* from *Galeocerdo tigrinus* caught in the Pearl Bank, Ceylon, should be referred to as *Phyllobothrium* sp. pending further investigations. The specimens they described were apolytic; a clear figure of the proglottid was given.

Southwell (1925) described '*Phyllobothrium lactuca*' van Ben., 1850, from several specimens found in *Trygon kuhli* and *T. walga* in the Pearl Bank, Ceylon, but he reproduced Beneden's figure of the scolex of the species. Southwell's list of synonyms for the species are unacceptable at present; he included *Phyllobothrium crispatissimum* Monticelli, 1889, but an examination of Monticelli's material, now at the British Museum (Natural History) has confirmed that he was dealing with a species of *Thysanocephalum*. Southwell also included *P. inchoatum* Leidy, 1891, as a synonym of *P. lactuca* but as Dollfus (1964*a*) has indicated *P. inchoatum* may be a synonym of *P. delphini* or of *Monorygma delphini*, a species discussed elsewhere in this revision. *Rhinebothrium ceylonicum* Shipley & Hornell, 1906, was included by Southwell (1925) as a synonym of *P. lactuca* but the species is worthy of further investigation in relation to *Sphaerobothrium lubeti* Euzet, 1959, and similar forms, e.g. *P. compacta* Southwell & Prashad, 1920, which Southwell (1925) also included as a synonym of *P. lactuca*.

The references to *P. lactuca*, between 1927 and 1961, may conveniently be divided into two groups: (i) those which probably deal with the species or similar forms and are now of interest only in so far as the host and locality are concerned, and (ii) those which give incomplete descriptions of species as *P. lactuca*, from unusual hosts and localities. Woodland (1927) gave an interesting discussion of *P. lactuca* as an apolytic species, but he incorrectly referred to Yoshida (1917) as having given an excellent description of the species; Fuhrmann (1931) figured a scolex of a species which appears identical to that of *P. lactuca* but *Raja* is given as the host; Joyeux & Baer (1936) gave a useful diagnosis for the species but referred to *Mustelus hinnulus*, *M. laevis*, *Squatina angelus*, *Acanthias vulgaris*, *Oxyrhina spallanzanii*, *Trygon pastinaca*, *Raja batis* and *R. clavata* as hosts; Baylis (1939) referred to *P. lactuca* in *Hexanchus griseus* caught off south Devon; Rees & Llewellyn (1941) referred to the species in the same host caught in the Porcupine Bank, west of Ireland. Wardle & McLeod (1952) gave a very brief diagnosis for the species, pointing out the controversy as to whether the species is apolytic or anapolytic and referred to the views of Southwell (1925) on its synonymy. Reichenbach-Klinke (1956) gave a figure of the scolex of *P. lactuca* but no other details. Yamaguti (1959) repeated the list of synonyms given by Southwell (1925) for *P. lactuca*, with the exception of *Rhinebothrium ceylonicum*, and referred to a number of unlikely hosts for the species. Tseng (1933) briefly described '*P. lactuca*' from *Squalus mitsukuri* (Jordan & Snyder) at Tsingtao, China and referred to a number of fragments from this host. He stated that they were macerated and that the form of the scolex was impossible to detect; he did, however, describe the scolex as massive and globular measuring $1{\cdot}332 \times 0{\cdot}888$ mm with suckers $166 \times 222\,\mu$m. Owing to poor preservation, details of the internal anatomy could not be worked out but he refers to 250 testes.

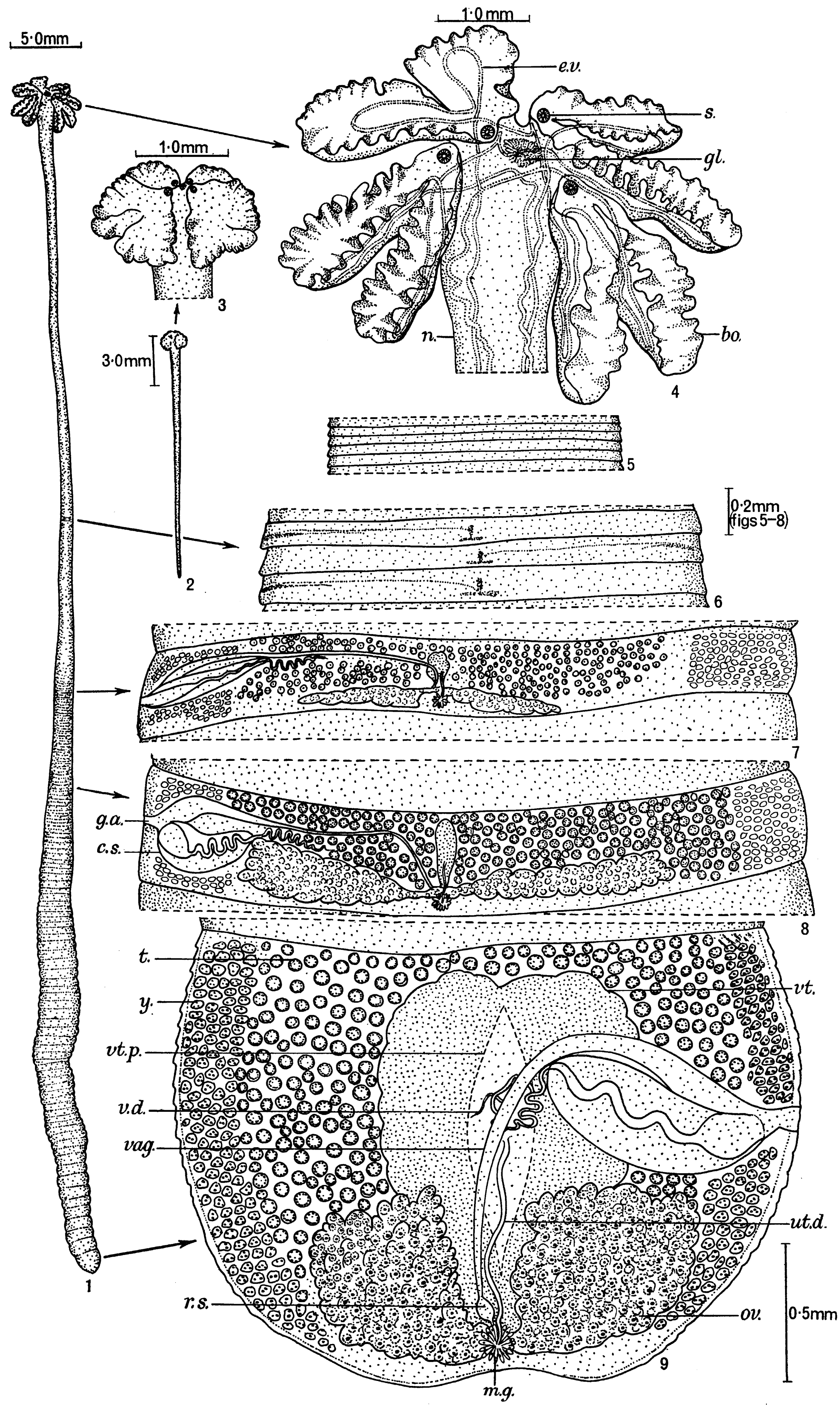
Shuler (1938) referred to '*P. lactuca*' from '*H. brevirostris*' at the Biological Laboratory, Carnegie Institute of Washington, Dry Tortugas, Florida, and stated that although his specimens were much smaller than those previously described there seemed to be no other differences which might be specific. Yamaguti (1952, p. 23) gave a brief illustrated description of *P. lactuca* from *Mustelus manazo* in the Sea of Japan. Riser (1955) described briefly and figured '*Phyllobothrium lactuca* van Ben., 1850 nec *P. lactuca* Southwell, 1925, 1930' but the specimens should be re-examined and, if possible, compared with additional material from *Triakis semifasciata* Girard in Monterey Bay, California, and from the same host in San Luis, Obispo Bay, California. Riser compared his material with that described by Yoshida (1917) and Woodland (1927). He appears to agree with Woodland, who pointed out that the material described by Southwell (1912), from *Galeocerdo tigrinus* Mueller & Henle, and by Southwell (1925) from *Trygon kuhle* Mueller & Henle and from *T. walga* Mueller & Henle, was not *P. lactuca*. He disagreed with Woodland's view that the free proglottids described by Beneden as *P. lactuca* were probably those of *Calliobothrium verticillatum*, a species which has proglottids with a laciniated posterior margin and already described by Beneden. Riser also stated that the specimens described by Young (1954) as *P. radioductum* Kay were those of *P. lactuca*. This requires confirmation because the specimens described by Riser as *P. lactuca* may not belong to the species.

Robinson (1959) stated that nine of the twelve specimens of *Mustelus lenticulatus* Phillips which he examined in New Zealand harboured *P. lactuca*, which was also present in two *Carcharadon carcharias*. He referred to the great variation in size amongst worms from the same host specimen; frequently the scoleces of the larger worms were a pale orange colour and contrasted sharply with the cream-coloured strobilae. Robinson emphasized that the size of the scolex was considerably smaller than that recorded by many authors; being 2·4 mm long with a maximum width of 3·6 mm towards the posterior margin. The only other information given by Robinson is a suggestion that his specimens were anapolytic. Alexander (1963) also referred to *P. lactuca* from *Mustelus lenticulatus* Phillips at Cook Strait, Oamura Harbour, New Zealand, seven of the host specimens examined being infected. He described living unembryonated eggs in sea water as spherical and measuring 0·22 to 0·024 mm in diameter. Euzet (1959), however, referred to eggs being 0·030 to 0·040 mm in diameter, the hexacanth embryo developing in about 6 days and measuring 0·018 to 0·020 mm in diameter.

The strobila of *P. lactuca* is scaly and up to about 150 mm long with a maximum breadth of about 3·0 mm (figure 1). Except for the posterior-most, the proglottids are broader than they are long and craspedote; the species is anapolytic. The scolex is almost spherical in shape, up to 5·0 mm in diameter, and clearly divided into four distinctly bilobed and very much folded bothridia, each with a small apical sucker about 0·1 mm in diameter. The bothridia are covered with minute spines. A myzorhynchus is absent but a distinct glandular organ, the exact function of which is unknown, occurs at the apex of the scolex. The genital atrium is lateral, irregularly alternate and midway between the anterior and posterior borders of the proglottid. There are about 200 testes. The cirrus sac is about 0·50 mm long by 2·50 mm broad. The uterus is sac-like and that of the posterior proglottid is filled with eggs measuring about 0·035 mm in diameter. There is no evidence of protandry and as in *P. sinuosiceps*, to be discussed later, self-fertilization occurs. The adults are restricted to the anterior region of the spiral valve intestine of species of *Mustelus* in European waters.

2. **Phyllobothrium dagnallium** Southwell, 1927

Previous records: *Raja scabrata*, Canada, Heller (1949); *R. stabuliformis*, Canada, Heller (1949); *Lamna nasus*, St Lawrence, Canada, Myers (1959); *R. laevis*, Canada, Myers (1959); *Chiloscyllium indicum*, Pearl Bank, Ceylon, Southwell (1927); *Galeocerdo tigrinus*, Ceylon, Southwell (1927); *Rhynchobatus ancylostomus*, Ceylon, Southwell (1927); *C. indicum*, Ceylon,



FIGURES 1 to 9. For legends see facing page.

Southwell (1930); *G. arcticus*, Ceylon, Southwell (1930); *Rhina ancylostoma*, Ceylon, Southwell (1930).

Phyllobothrium dagnallium was originally found by Southwell (1927) in *Rhynchobatus ancylostomus* caught in the Pearl Bank, Ceylon. He recovered a large number of specimens from the spiral valve intestine of this host but he also referred to several specimens in *Chiloscyllium indicum* and *Galeocerdo tigrinus* from the same locality. Specimens of *P. dagnallium* preserved in formaldehyde are up to 18 cm long with a maximum breadth of 2·10 mm. An 'enormous ventral uterine pore' occurs in the mature and partly gravid proglottids; the largest proglottids measure 2·20 mm long × 1·0 mm broad. It is significant that the folds of the four bothridia are disposed into eight principal parts, each bothridium is roughly divided into two and is very much folded. The margins of the bothridia are armed with minute spines. Four minute accessory suckers can be seen in whole mounts of *P. dagnallium*, each measuring 150 μm in diameter. Southwell stated that the head of *P. dagnallium* is not massive and fleshy, as in *P. lactuca* but is delicate and membranous in appearance, being 1·70 mm long × 2·20 mm broad. The number of testes is not given but in one proglottid about 180 are shown while in the other more than 300 can be seen. This variation may be significant in relation to its alleged occurrence in three different host species. The distribution of the testes may also be of importance in further studies of the species as none was present behind the pouch on the poral side. This kind of distribution is known to occur in other species of the genus, e.g. *P. gracilis* as described by Euzet (1959).

Southwell (1927) was of the opinion that his *P. dagnallium* closely resembled *P. pulvinatum* (Linton, 1890), *P. tumidum* Linton, 1922, and *P. laciniatum* (Linton, 1890) and tabulated the differences between the four species. *P. dagnallium* was considered to be particularly close to *P. tumidum* from which it differed in size, position of genital pore, which was in the middle of the proglottid in *P. dagnallium*, and in that the testes were absent behind the cirrus pouch on the poral side.

P. dagnallium Southwell, 1927, is here considered to be close to *P. lactuca* mainly from the form of each bothridium and the number of testes. Further investigation into this species is necessary with some reference to the following records of the species. Southwell (1930) again referred to the species with '*Anthobothrium pulvinatum* Southwell, 1925' as its synonym. Wardle & McLeod (1952) gave a very brief diagnosis of the species, based mainly on the information of Southwell (1927) and suggest that the species may be synonymous with *Anthobothrium pulvinatum* of Southwell (1925). This interesting suggestion requires further investigation. The records by Myers (1959) of *P. dagnallium* in *Raja laevis* and *Lamna nasus* in the Gulf of St Lawrence, Canada, are also of considerable interest; that from *Raja* is accepted by Yamaguti (1959).

FIGURES 1 to 9. *Phyllobothrium lactuca* from *Mustelus mustelus*

FIGURE 1. Complete strobila of mature adult, about 80 mm long.
FIGURE 2. Complete strobila of immature specimen approximately 15 mm long.
FIGURES 3 and 4. Scoleces of specimens shown in figures 1 and 2 drawn to same scale for comparison.
FIGURES 5 to 9. Proglottids from different regions of the same strobila, dorsal view.

3. **Phyllobothrium serratum** Yamaguti, 1952

Phyllobothrium serratum was first described by Yamaguti (1952) from specimens found in *Triacis scyllium* at Hamazima, Japan. The species is up to 22 cm long and 3·0 mm broad, with a maximum depth of about 1·0 mm. The scolex is almost spherical, 2·0 to 3·0 mm in diameter, the bothridia being sessile and almost identical with those of *P. lactuca*. The accessory suckers measure 0·125 to 0·175 mm in diameter. The cirrus pouch is 0·90 mm × 0·50 mm and the genital pores are at the middle of the lateral margins of the proglottids being irregularly alternate. The outer egg shell is 21 to 24 × 19 to 22 μm while the embryo is 17 to 21 × 15 to 18 μm. Yamaguti emphasized that the species resembles *P. lactuca* so closely that a very careful comparison is necessary to identify the species; he pointed out that in *P. serratum* the strobila is longer and thinner and the eggs are smaller. A more detailed description of *P. serratum* should prove interesting and valuable.

4. **Phyllobothrium radioductum** Kay, 1942

Previous records: *Triakis semifasciata*, California, Young (1954).

This species was originally found, frequently in great numbers, in *Raja binoculata* (Girard) at Friday Harbour, Washington. It is about 26 to 58 mm long (average length being 39 mm), about 1·20 mm broad and consists of 144 to 290 proglottids. The scolex is 1·80 to 2·0 mm long, about 1·80 to 2·0 mm broad and the outer surface of each bothridium, which has an accessory sucker, is armed with closely set minute spines. The neck is about ¼ the length of the strobila. The lateral genital pores are irregularly alternate and equidistant from the anterior and posterior margins of the proglottid. The species was described as having 100 or more testes but over 200 are shown in a figure of the proglottid. An approximately oval cirrus pouch extends towards the middle of the proglottid from the genital atrium. The egg is thin-shelled, non-operculate and nearly spherical with a diameter of about 35 μm. A hexacanth embryo, a pair of refractile globules, and some granular material is present in the mature eggs.

Kay stated that *P. radioductum* is distinguished from other species of *Phyllobothrium* in having a spiny cuticle on the outer surface of the bothridia, in the complex highly branched excretory system of the scolex and in the form of the egg. The species was thought to be more closely related to *P. lactuca* Beneden, 1850, and *P. vagans* Haswell, 1902, than to other species of the genus and to differ from these two in absolute size and proportion. Kay also gives the following diagnostic information on *P. radioductum* to distinguish it from the two species. 'From *P. lactuca* it is further set off by the dorsal union of the primary and secondary uteri and by the internal arming of the ejaculatory duct. The egg of *P. vagans* is very distinct from that of *P. radioductam* and in the latter the shell gland is diffuse and distinctly smaller than the seminal receptacle. The very large number of testes and the muscular termination of the vagina appear to be other characters which distinguish this species from all others.'

Wardle & McLeod (1952) accepted and gave a brief diagnosis for *P. radioductum*, while Riser (1955) gave a brief redescription of the species from material found in *Raja rhina* Jordan & Gilbert, *R. montereyensis* Gilbert and *R. binoculata*, from Monterey Bay, California, and briefly compared it with *P. lactuca*. Riser also refers to an examination of the material identified by Heller (1949) as *P. dagnalli* Southwell, 1927, and concludes that the specimens are morphologically identical with *R. radioductum.* In the light of our present knowledge of species of *Phyllobothrium* a re-examination of the material studied by Riser may show that he was dealing with a species other than *P. radioductum.* Yamaguti (1959) refers to *P. radioductum* including a record of the species from *Triakis semifasciata.* The exact relationships of *P. radioductum* and *P. britannicum* sp.nov., to be described briefly below cannot be decided at present.

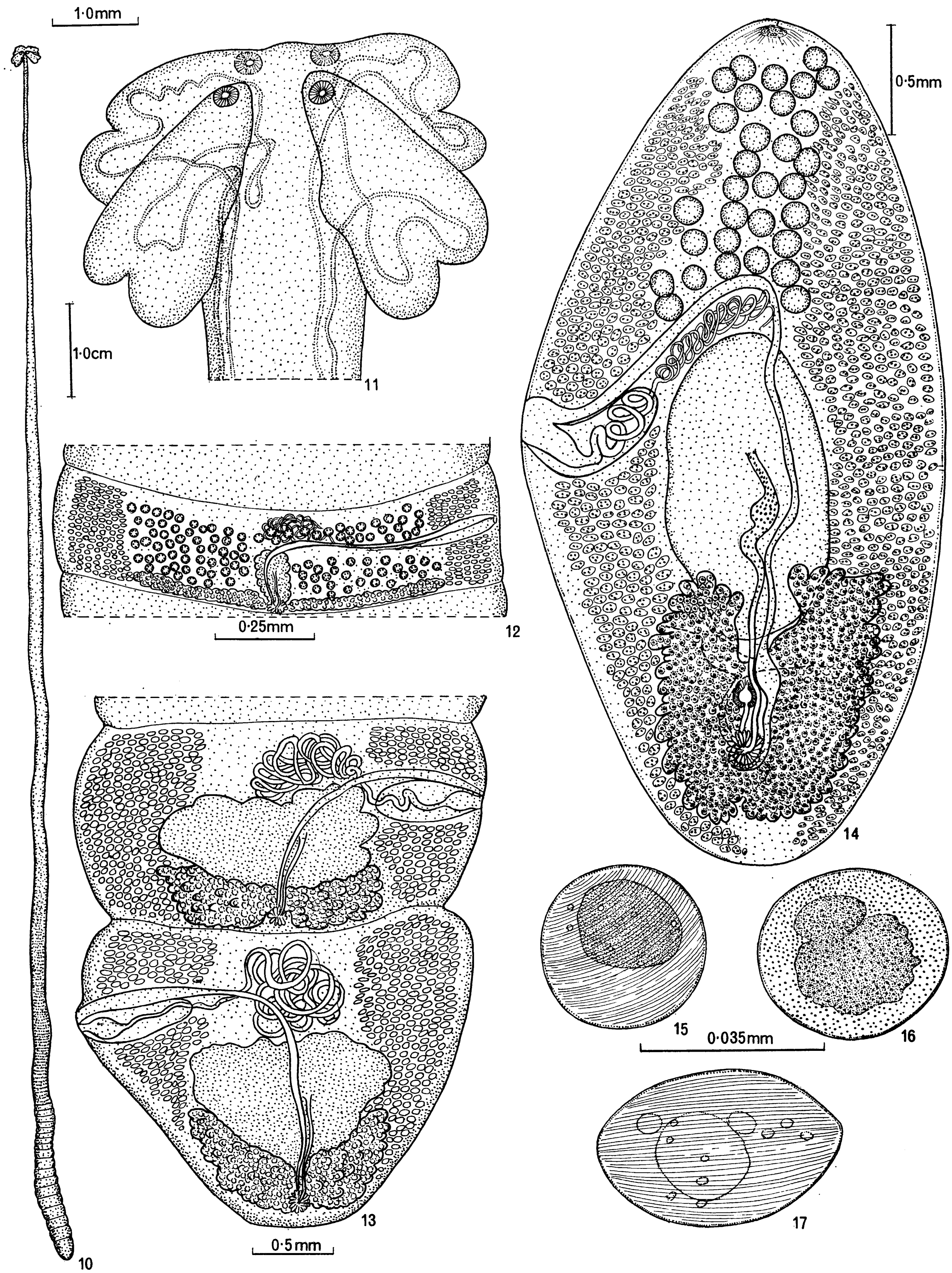
5. **Phyllobothrium britannicum** sp.nov.

(Figures 10 to 15, 18 and 19, 70; figure 73, plate 13 and figure 81, plate 14)

The following description of *Phyllobothrium britannicum* sp.nov. is based on a study of five entire adult strobilae, six immature specimens (figure 73, plate 14) and about twelve free proglottids found in the spiral valve of four specimens of *Raja montagui* trawled off Plymouth in the months of August and September during 1958 and 1959. Sixty-six specimens of *R. montagui* were thoroughly examined so it is reasonable to assume that in late summer the species is comparatively rare at Plymouth.

The scolex, in living specimens when attached to the mucosa, covers a roughly circular area up to 8·0 mm in diameter (figure 18). In this figure it may be seen that one bothridium has released its grip and lost its distinctly bifid shape. In all the stained permanent whole mounts examined, however, this characteristic feature was retained (figure 19). Four small accessory suckers are present, one at the apex of each bothridium and measuring about 0·16 mm in diameter. The strobila may attain a length of about 250 mm but on being fixed in formaldehyde it may contract to about 170 mm. The strobila is about 1·0 mm broad immediately behind the scolex and about 2·50 mm at the posterior end (figures 10, 11, 13). The neck appears to occupy about half the length of the body. Distinct proglottids showing some details of the arrangement of the genitalia are visible only in the posterior half of the strobila. The posterior-most proglottid may be 2·0 mm long in fixed specimens. *P. britannicum* sp.nov. is euapolytic, that is, growth and egg production continue after the proglottids have become detached. Detached living proglottids are very mobile and are capable of attaching themselves to the mucosa by means of a distinctive anterior 'sucker' (figure 14). Fixed specimens of the detached proglottids vary in shape, but their length, 3·50 to 4·0 mm, is always considerably greater than the maximum breadth of about 2·0 mm. The genital pore is lateral, irregularly alternate and at about the middle of the proglottid. The nervous and excretory systems have not been studied, but traces of the latter in the scolex could be made out in living specimens (figure 11). The general arrangement of the excretory vessels in the scolex is like that for *P. dohrnii* as described by Rees (1946) and for *P. sinuosiceps* Williams (1959*a*).

The male and female genitalia appear to ripen together in the same region of the strobila, as in *P. sinuosiceps*, there being no evidence of protandry. There are about 100 testes in each proglottid in the mid-strobila region (figure 12), but the number of testes could not be easily counted in the posteriormost proglottids (figure 13) possibly due to the thickness of the cuticle and to the expansion of the vas deferens and uterus as they become filled with spermatozoa and eggs respectively. About forty to eighty testes were counted in these proglottids in living specimens, but this count requires confirmation when further



FIGURES 10 to 17. For legends see facing page.

material becomes available. In the free proglottids, however, the testes are clearly visible even in stained permanent whole mounts and it is very significant that only about thirty could be seen. At present, therefore, the number of testes in *P. britannicum* sp.nov. must for taxonomic purposes be assumed to be about 100, being the maximum number clearly visible in young proglottids about the mid-region of the strobila. Vasa efferentia could not be seen but the ciliated vas deferens is conspicuous in most proglottids, especially those at the posterior end where it occupies most of the mid anterior region of the proglottid. The cirrus sac lies postero-dorsal to the vagina and is 0·60 mm long, i.e. about a third of the breadth of the proglottid. The detailed arrangement of the cirrus within its sac appears to be the same as that in *P. sinuosiceps*; but this, especially the exact form of the cirrus hooks, will require confirmation when further specimens become available. The general arrangement of the ovary and female ducts is also similar to that in *P. sinuosiceps* and a description will not, therefore, be given here. The eggs are spherical measuring 0·031 mm in diameter (figure 15), the capsule having a characteristic pattern of striations arranged equatorially.

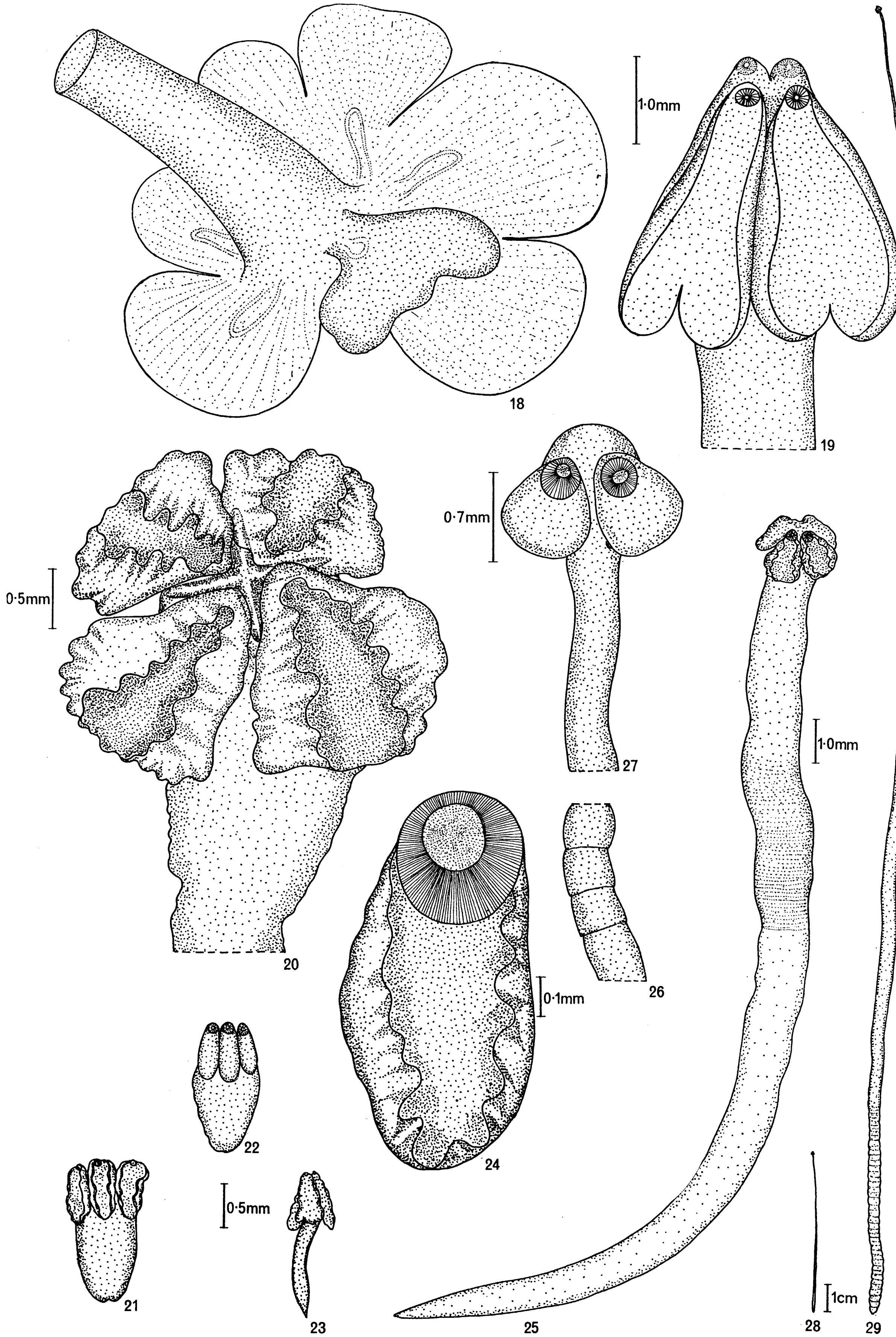
P. britannicum sp.nov. is of considerable interest in that the bothridia are slightly bifid as in *P. lactuca*, but their margins are not so folded, and in sharp contrast to *P. lactuca* the species is euapolytic. The species may eventually be considered far removed from *P. lactuca* but at present there appears to be no alternative but to place it somewhere near this form. In deciding on its position in the present revision some weight has been given to the fact that it is euapolytic. In this respect, therefore, it may have affinities with *P. tumidum* and *P. sinuosiceps*, but these occur in different hosts. Further knowledge of *Phyollbothrium* in *Raja* is desirable, especially that of *P. radioductum* Kay, 1942, and of the new species described briefly here.

6. **Phyllobothrium tumidum** Linton, 1922
(Figure 20)

Previous records: *Todaropsis eblanae*, Finistere, Dollfus (1958); *Isurus* (*Oxyrhina*) *spellanzanii*, Mediterranean, Euzet (1952*c*); *I. oxyrhynchus*, Sète, Concarneau, Euzet (1959); *Cynias manazo*, Tsingtao, China, Hsü (1935); *Dasyatis akajei*, Tsingtao, Hsu (1935); *Triakis scyllium*, Tsingtao, Hsü (1935); *Carcharadon carcharias*, Woods Hole, Massachusetts, Linton (1922); *I. dekayi*, Woods Hole, Linton (1922); *C. carcharias*, California, Riser (1955); *Lamna ditropis*, Monterey, California, Riser (1955); *Scoliodon terrae-novae*, Dry Tortugas,

Figures 10 to 15. *Phyllobothrium britannicum* sp.nov. from *Raja montagui*.

Figure 10. Complete strobila of mature adult, about 130 mm long.
Figure 11. Scolex.
Figure 12. Mature proglottid from mid-strobila region.
Figure 13. Gravid proglottids at posterior region of strobila.
Figure 14. Free proglottid showing male and female genitalia, dorsal view.
Figure 15. Egg.
Figure 16. *Phyllobothrium thridax* from *Squatina squatina*, egg.
Figure 17. *Monorygma* (*Phyllobothrium*?) sp. from *Scyliorhinus caniculus*, egg.
Figures 15 to 17 drawn to same scale.



Figures 18 to 29. For legends see facing page.

Shuler (1938); *Hemigaleus balfouri*, Southwell (1927); *H. balfouri*, Ceylon, Southwell (1930); *Cynias manazo*, Tsingtao, China, Tseng (1933); *Dasyatis akajei*, Tsingtao, Tseng (1933); *Triakis scyllium*, Tsingtao, Tseng (1933); *L. cornubica*, Britain, Williams *loc. cit.*

The original description of *P. tumidum* Linton, 1922, is based on material from the mackerel shark, *Isurus dekayi*, and the man-eater, *Carcharadon carcharias*. The bothridia have frilled or crumpled (lacinio-crispate) margins and a conspicuous apical sucker. The anterior end of the scolex is prolonged beyond the bothridia to form an eminence which is dome-shaped in outline, in dorso-ventral, and conical, in marginal view. Linton refers to a few specimens killed whilst still attached to the host; in these the bothridia were very thin and leaf-like. A loop of the excretory system enters each bothridium where it follows a course in the main parallel with the margin. The species is apolytic, the free proglottids being much longer than broad, the anterior end usually more or less rounded or knob-like. A free proglottid mounted in balsam is 7·0 mm long and 2·10 mm broad in the region of the genital pore. The genital pores are on the lateral margins, irregularly alternate and in the anterior third of the proglottids. Linton does not refer to the number of testes but about 200 are figured.

In September 1903 Linton found fifty specimens, most of them immature, in a small man-eater shark at Woods Hole. The specimens were associated with the jaws and pens of squid and thought to have been 'introduced by the squid'. Linton (1922) referred to examinations of other man-eater and mackerel sharks and to having found the remains of squids in their intestines; he concentrates on evidence for believing that the larval cestodes often found in *Ommastrephes illecebrosa* and in *Loligo peali* are the young of *P. tumidum*. Further details from Linton (1922) will, therefore, be given later (p. 272) in a discussion of *P. loliginis*. Other hosts thought by Linton to be involved in the life-cycle of *P. loliginis* are *Mustelus canis*, *Squalus acanthias*, *Raja ocellata*, *R. laevis*, *Thunnus thynnis*, *Xiphias gladius*, *Spheroides maculatus*, *Hemitripterus americanus*, *Lopholatilus chamaeleonticeps*, *Merluccius bilinearis*, *Pollachius virens*, *Phycis tenuis*, *Lophius piscatorius* and *Leptocephalus conger*; but this list requires critical analysis preferably with reference to the specimens they harboured.

FIGURES 18 and 19. *Phyllobothrium britannicum* sp.nov. from *Raja montagui*.

FIGURE 18. Scolex showing form assumed by three bothridia when attached to a glass slide in sea water; the 4th bothridium retracted from the slide.

FIGURE 19. Same specimen as that shown in figure 18, drawn to same scale a few minutes later.

FIGURE 20. *Phyllobothrium tumidum*? from *Lamna cornubica*, scolex.

FIGURE 21. Immature specimen (post-plerocercoid?) of *P. minutum* sp.nov., from *Raja fullonica*.

FIGURE 22. 'Young' plerocercoid of *Phyllobothrium caudatum* from *Oncorhynchus nerka*.

FIGURE 23. Immature specimen (post-plerocercoid?) of *Phyllobothrium thridax* in *Squatina squatina*.

FIGURES 24 and 25. *Phyllobothrium caudatum* from *Oncorhynchus nerka*, bothridium and 'old' plerocercoid respectively.

FIGURES 26 and 27. *Monorygma* (*Phyllobothrium*?) *chlamydoselachi* from *Chlamydoselachus anguineus*; posterior proglottids and scolex respectively of an incomplete immature specimen, measuring 15 mm long.

FIGURES 28 and 29. *Phyllobothrium minutum* sp.nov. from *Raja fullonica* and *P. thridax* from *Squatina squatina* showing size relationships of complete strobila.

Southwell (1925) gave a very brief diagnosis of *P. tumidum* from information given by Linton (1922), while Southwell (1927, 1930) referred to the species in *Hemigaleus balfouri* in Ceylon and, in 1927, briefly described the specimens as follows: 'The worms measure up to 90 mm in length and 1·4 mm in breadth. The largest eggs in the uterus measured 35 μ[μm] by 25 μ, and bore about 12 short filaments, each measuring from 6 μ to 10 μ.' Southwell (1930) supplemented this account but reproduced figures of the scolex and proglottid from the original description by Linton. The specimens collected and examined by Southwell require further investigation.

P. tumidum was found in *Triakis scyllium*, *Cynias manazo* and *Dasyatis akejei* at Tsingtao, China by Tseng (1933); these records are repeated by Hsu (1935). Shuler (1938) recorded the species from *Scoliodon terrae-novae* in Dry Tortugas, Florida, U.S.A. Euzet (1952*c*) briefly referred to *P. tumidum* from *Isurus* (*Oxyrhina*) *spallanzanii* in the Mediterranean and remarked on the occurrence of its plerocercoid stage in cephalopods and on its wide range of geographical distribution; this latter feature of its biology, however, is questionable at present.

Riser (1955) gave a brief redescription of *P. tumidum* based on material found in *Lamna ditropis* at Monterey, California and in *Carcharadon carcharias* at La Jolla, California. He included several measurements of the species but did not refer to the number of testes. He stated that the musculature of *P. tumidum* is strikingly different from that of other members of the genus in that 'the longitudinal muscles are restricted to a narrow zone just inside the circular layer except at mid-line where they fill the subcuticula. The strong development of the dorso-ventral fibres and the unbalanced arrangement of the longitudinal muscles allow a rather unusual type of contraction to occur. The margins of the strobila curl inwards and the worms coil upon themselves so that a specimen 73 mm long when relaxed was observed to contract into a tight spiral 12 mm long.' Riser stated that the ovary is not X-shaped in transverse section and consists only of a dorsal wing; and that the species differs from all other members of the genus in that the bothridia 'arise posteriorly from the lateral walls of the scolex leaving an anterior cone-like projection visible, the vitellaria extend almost to mid-line and the ventral wing of the ovary is absent'. In a reference to transverse commissures in the proglottids of *P. tumidum*, Riser points out that Subramaniam (1939) described a phyllobothriid as a monozootic cestode, *Biporophyllaeus madrassensis*, for which Wardle & McLeod (1952) established a new order.

Except for the original account, the only description which is of value in identifying *P. tumidum* is that by Euzet (1959), who figured and discussed specimens found in *Isurus oxyrhynchus*, caught in the Mediterranean. A specimen of *P. tumidum* found in *Lamna cornubica* caught off Britain was provisionally identified as this species in consultation with Dr Euzet; the scolex is shown (figure 20), but the strobila was unsuitable for further examination. Euzet (1959) has shown that in specimens from *I. oxyrhynchus* there are 270 to 330 testes.

P. tumidum must still be regarded as a little-known form in spite of having the distinction of being the only member of *Phyllobothrium* for which suggestions as to the probable course of part of its life history have been made. Further evidence of its occurrence in cephalopods was given by Dollfus (1958), who recorded plerocercoids in *Todaropsis eblanae* caught off Finistere, France; but Yamaguti (1959) recorded the species and also gave the following information: 'Southwell (1936), Johnston & Mawson (1939) regard this species as a synonym of *Phyllobothrium delphini* Bosc (1802) which was found in the larval form in *Otania, Hydranga, Arctocephalus* of Falkland Isl.,—Southw.; *Kogia breviceps* of South Australia —Johnston & Maws.'

7. **Phyllobothrium sinuosiceps** Williams, 1959

(Figure 83, plate 14 and figure 87, 88, plate 15)

Previous records: *Hexanchus griseus*, Williams (1959*a*); *H. griseus*, Williams (1960); *H. griseus*, Britain, Williams (see p. 291).

In the original description of *P. sinuosiceps* it was pointed out that the species differs from *P. lactuca* in the host species, in the absence of well-defined bothridia, in the nature of the cuticle, in the larger number of testes, in the size of the cirrus sac relative to the proglottid in which it is contained, in the nature of the vagina and in the absence of uterine pores. It was also very briefly compared with *P. radioductum* Kay, 1942. *P. britannicum* sp.nov. and *P. tumidum* may also be compared with *P. sinuosiceps* which can be identified from the following features: strobila up to 350 mm long, cuticle scaly; attached segments craspedote, broader than long; euapolytic, free segments longer than broad; scolex almost spherical in shape, 3·20 to 6 mm in diameter, possessing four apical suckers not clearly divided into four distinct bothridia but bearing two to four complicated folds encircling the scolex, the folds are subdivided and their edges frilly; myzorhynchus absent; arrangement of the deep longitudinal muscles not correlated with the overlapping of the segments; excretory and nervous systems of the scolex simple; genital atrium covered permanently by a cuticular membrane; testes between 700 and 800; cirrus pouch 1·95 to 2·40 mm long, 0·15 to 0·30 mm broad; evaginated cirrus 5·25 mm long, swollen basally, armed with small hooks, 0·014 mm in length, with sharp points and swollen cylindrical bases; vagina thin walled, dilated proximally to form a 'vulva'; uterine pore absent. Host: *Hexanchus griseus* Gmelin. Location: spiral valve.

8. **Phyllobothrium dohrnii** (Oerley, 1885) Zschokke, 1888

Previous records: *Notorhynchus pectorosus*, Cape Campbell, New Zealand, Alexander (1963); *Ommastrephes todarus*, Dollfus (1923*b*); *Hexanchus griseus*, Mediterranean, Euzet (1952*c*); *H. griseus*, Concarneau, Sete, Euzet (1959); *Heptanchus cinereus*, Mediterranean, Joyeux & Baer (1936); *Hexanchus griseus*, Mediterranean, Joyeux & Baer (1936); *Mustelus hinnulus*, Mediterranean, Joyeux & Baer (1936); *Scymnus lichia*, Mediterranean, Joyeux & Baer (1936); *Todarodes sagittatus*, Mediterranean, Joyeux & Baer (1936); *Odontaspis littoralis*, Joyeux & Baer (1961); *H. griseus*, Britain, Rees (1946); *Notorhynchus pectorosus*, Cape Palliser, New Zealand, Robinson (1959); *H. griseus*, Britain, Williams (1958); *H. griseus* Williams (1960); *H. griseus*, Britain, Williams (see p. 291).

Rees (1946) has already described and figured *Phyllobothrium dohrnii* and discussed its complicated synonymy. She points out that since the appearance of the original description by Oerley several cestodes described by various writers are probably synonymous with the species, e.g. *Crossobothrium laciniatum* Linton (1889) from *Odontaspis littoralis* at Woods Hole, *C. campanulatum* Klaptocz (1906) from *Hexanchus griseus* in the Gulf of Trieste and

Orygmatobothrium velamentum Yoshida (1917) from *Cynias manazo* at Hiroshima, Japan. With increased knowledge of *P. dohrnii* it may be advisable to exclude *O. velamentum* as one of its synonyms; a more detailed description is necessary of the original specimens and of additional material of *O. velamentum.* In a discussion of the validity of *Crossobothrium* Rees points out that Klaptocz (1906), in a key to the genera of the Phyllobothriidae, indicated that the key was unsatisfactory in those instances where the distinction depends on the bothridia being either pedunculated or sessile and having either smooth or crinkly margins; the genus *Crossobothrium* is tentatively accepted in this revision. Various descriptions of *P. dohrnii* are not entirely in accord and are incomplete and it is obvious that more than one species have been given the same name.

Hyman (1951) refers to a description by Curtis (1906) of an unusual method of proglottid formation in *Phyllobothrium dohrnii* (= *Crossobothrium laciniatum*) in which the strobila after proliferating in the usual manner at the rear end of the neck begins to form proglottids immediately behind the scolex. This feature is discussed further in the general discussion of this paper. Brief references to *P. dohrnii* were made by Wardle & McLeod (1952), Euzet (1952*c*), Williams (1958, 1960), Yamaguti (1959) and Joyeux & Baer (1961). Yamaguti referred to Riser (1955) having retained 'Oerley's original combination of *Orygmatobothrium dohrnii*'.

Euzet (1959) described and figured specimens of *P. dohrnii* from *Hexanchus griseus* in the Mediterranean and listed *O. dohrnii* Oerley 1885, *Crossobothrium lacinatum* Linton, 1889, and *C. campanulatum* Klaptocz, 1906 as synonymous. His reference to marginal loculi in the bothridia will be of particular interest in deciding the relationships of this species with other members of the genus. In view of the valuable accounts by Rees (1946) and by Euzet (1959) no further description of *P. dohrnii* will be given here. The specimens mentioned by Alexander (1963) as *P. dohrnii* from *Notorhynchus pectorosus* in Cape Campbell, New Zealand, are inadequately described. He stated that the eggs have an outer capsule 0·025 to 0·028 mm in diameter and an inner denser mass of 0·017 to 0·020 mm in diameter; but Euzet (1959) gave the egg measurement as 0·035 to 0·040 mm in diameter. It is probably inadvisable to consider *P. dohrnii* as occurring in Japanese, American, British and Australian waters.

9. **Phyllobothrium vagans** Haswell, 1902

Haswell (1902) stated that *Phyllobothrium vagans* occurs usually in abundance in *Heterodontus portusjacksoni*, the Port Jackson shark in New Zealand; the proglottids being set free from the posterior end of the strobila long before they are mature. The strobila in preserved specimens is 9 to 10 cm long with a breadth of about 0·50 mm in the neck region; the last proglottid is 5·0 mm long × 2·0 mm broad and the free proglottids are 11·0 × 1·75 mm. The bothridia are 'not divided or reticulated' and 'appear to use the suckers more in connexion with progression than as organs of permanent attachment'. Haswell pointed out that 'the only recorded observations on the development of any member of the genus appear to be a few notes on *P. thridax* by Moniez. No hooked embryos were found in the uterus of any of the numerous specimens examined. When the eggs were kept in sea water for 5 days, a large proportion developed fully formed hexacanth embryos.'

10. **Phyllobothrium thridax** Beneden, 1849

(Figures 16, 23, 29, 39; and figure 72, plate 13.)

Previous records: *Raja brachyura*, Britain, Baylis (1939); *R. clavata*, Britain, Baylis (1939); *R. blanda*, Britain, Baylis & Jones (1933); *R. clavata*, Britain, Baylis & Jones (1933); *Squatina angelus*, Belgium, Beneden (1849, 1850*b*); *S. angelus*, Beneden (1858); *S. angelus*, Beneden (1870); *S. angelus*, Diesing (1863); *Heterodontus philippi*, Australasia, Drummond (1937); *S. squatina*, Concarneau, Arcachon, Banyuls, Sète, Euzet (1959); *R. clavata*, Wales, Johnstone (1906); *R. batis*, Manche, France, Joyeux & Baer (1936); *R. clavata*, Manche, France, Joyeux & Baer (1936); *S. angelus*, Manche, France, Joyeux & Baer (1936); *Trygon pastinaca*, Manche, France, Joyeux & Baer (1936); *R. batis*, Linstow (1878); *R. radiata*, Linstow (1878); *S. angelus*, Linstow (1878); *R. radiata*, Murman, Linstow (1903); *S. angelus* Oerley (1885*b*); *R. radiata*, Olsson (1867); *R. batis*, Scandinavia, Olsson (1893); *R. clavata*, Mediterranean, Parona (1900); *S. angelus*, Mediterranean, Parona (1900); *Squatina* sp., Mediterranean, Parona (1900); *R. radiata*, Poliansky (1955); *R. brachyura*, Plymouth, Prudhoe & Baylis (1957); *R. clavata*, Plymouth, Prudhoe & Baylis (1957); *S. squatina*, Plymouth, Prudhoe & Baylis (1957); *S. angelus*, Britain, Scott (1909); *S. squatina*, Britain, Williams (1960); *S. squatina*, Britain, Williams (see p. 294).

From the figures, brief description and hosts listed by Leuckart (1820) for '*Bothriocephalus Flos*' it is obvious that he was dealing with more than one species, probably those now recognized as *Phyllobothrium lactuca* and *P. thridax*. Rudolphi (1819), Bremser (1824) and Dujardin (1845) may also have described specimens of *P. thridax* as *B. auriculatus*; the last named author stating that he had found specimens in *Raja clavata* and that it occurred also in '*Squalus galeus*', '*glaucas*' and '*squatina*' and in the '*torpille*'. The name *Phyllobothrium thridax* was first proposed by Beneden (1849) and later, Beneden (1850*b*) described specimens from '*Squatina angelus*' as having a scolex without folds and never spherical. Beneden (1858) again emphasized that the species occurs in *S. angelus* and attains an extraordinary length.

As I have recently obtained *Phyllobothrium thridax* in abundance in *S. squatina* from the English channel and the species is inadequately known it is hoped to publish a full description of this cestode at a later date. The following comments are offered on the taxononic status and distribution of some species described as *P. thridax*. Drummond (1937) may have been dealing with *P. vagans*. Wardle & McLeod (1952) accepted both *P. thridax* and *P. unilaterale* Southwell, 1925, as valid species, but Euzet (1959) in a description of *P. thridax* included *P. unilaterale* as its synonym. Polyanski (1955) stated that in the Barents Sea *P. thridax* is most frequently found in the spiral valve of *Raja radiata*, 73·3 % being infected and as many as 100 specimens sometimes being found in one individual fish. He thinks that the species is apparently adapted to northern latitudes and refers to previous records of the species from *R. radiata* in the Barents Sea, by Lyaiman & Borovkova in 1926 and by Basikalova in 1932. Yamaguti (1959) agreed with Wardle & McLeod (1952) in accepting both *P. thridax* and *P. unilaterale* as valid species.

11. **Phyllobothrium marginatum** Yamaguti, 1934

Phyllobothrium marginatum from *Squatina japonica* in Toyama Bay, Japan, is placed as a synonym of *P. thridax* by Euzet (1959), but is accepted by Wardle & McLeod (1952) and Yamaguti (1959). It is about 6·0 cm long by 0·8 mm broad, the mature proglottids being

0·70 to 1·60 × 0·53 to 0·80 mm and the detached gravid proglottids about 2·50 to 3·20 × 0·87 to 1·10 mm. The accessory suckers of the bothridia are about 0·08 mm in diameter. The genital pore is a third of the length of the proglottid from its anterior end. There are 220 to 240 testes and the cirrus sac is 0·30 to 0·40 mm long. The eggs measure 0·035 to 0·045 × 0·035 to 0·042 mm.

This species differs from *P. thridax* in its host distribution, in being apolytic and in the size of its accessory suckers and eggs. A detailed study of *P. marginatum* should prove valuable.

12. **Phyllobothrium dasybati** Yamaguti, 1934

Phyllobothrium dasybati is a little-known form originally described from a specimen found in *Dasybatus akajei* in Japan. The specimen, consisting of about sixty proglottids, is 57·0 mm long and about 0·90 mm in maximum breadth. The accessory suckers of the bothridia measure 0·08 mm in diameter. Yamaguti (1934) described 'a cupola-like myzorhynchus not projecting beyond the anterior ends of the bothridia' and 250 to 350 testes; but only about 130 are figured. The genital pores are unilateral and about a third of the length of the proglottid from its anterior end. The species was compared with *P. thridax* and *P. unilaterale*, but Yamaguti referred to these two as 'too inadequately described to permit comparison'. It is surprising, therefore, that *P. dasybati* was not compared with *P. marginatum* Yamaguti 1934. Further work should also include a detailed comparison of *P. dasybati* with *P. triacis* Yamaguti, 1952, a species placed by Euzet (1959) as a synonym of *Crossobothrium triacis* (Yamaguti 1952).

Shuler (1938) referred to '*Phyllobothrium dasybati*' from *Hypoprion brevirostris* in Dry Tortugas, Florida, but emphasized that his specimens 'especially the strobila, are smaller than that of the original description and the cirrus sac is globose, rather than oval'. Shuler conceded that if more reliable criteria were known to differentiate species of *Phyllobothrium*, his specimens might be recognized as a different species.

13. **Phyllobothrium auricula** Beneden, 1858

Previous records: *Trygon pastinaca*, Belgium, Beneden (1858); *T. pastinaca*, Belgium, Beneden (1870); *T. pastinaca*, Diesing (1863); *T. pastinaca*, Mediterranean, Euzet (1952*c*); *Dasyatis pastinaca*, Concarneau, Arcachon, Sète, Euzet (1959); *Laemargus borealis*, Linstow (1878); *Scymnus glacialis*, Linstow (1878); *Trygon pastinaca*, Linstow (1878); *T. pastinaca*, Oerley (1885*b*).

The original description of *Phyllobothrium auricula* is very brief but its occurrence in '*Trigon pastinaca*' and the presence of marginal loculi in the bothridia is emphasized by Beneden (1858). It is surprising that Wardle & McLeod (1952) and Yamaguti (1959) omit *P. auricula* from their lists of species of *Phyllobothrium*. Euzet (1952*c*) stated that an examination of Linton's original material showed that *P. foliatum* Linton, 1890 from *Trygon centrura* at Woods Hole, was a synonym of *P. auricula*; but that *P. foliatum* of Southwell 1927 did not resemble the form described by Linton. In a valuable redescription of *P. auricula* Euzet (1959) again referred to *P. foliatum* Linton, 1890 as its synonym, but this view is not accepted here; the life histories of *P. auricula* and *T. pastinaca* in European waters and of *P. foliatum* from '*T. centrura*' in American waters are unknown; stages in the life-histories in the two localities may reveal constant differences which may be of importance in recognizing the two species.

14. **Phyllobothrium minutum** sp.nov.

(Figures 21, 28, 30–38, 59, 71; figure 75, plate 13.)

The following description of *Phyllobothrium minutum* sp.nov. is based on a study of five entire adult strobilae, four immature specimens and eight free proglottids found in the spiral valve intestines of two *Raja fullonica* trawled off the west coast of Scotland, in September 1957 at 57° 50′ N. and 9° 15′ W. and a depth of 160 fathoms; eight other specimens of the same host species from the same locality were not infected with the cestode. Measurements given in this description are from specimens fixed and preserved in 4% formaldehyde and then studied as whole mounts stained in acetocarmine.

The strobila is about 90·0 mm long, 0·30 mm broad immediately behind the scolex and has a last proglottid measuring 1·20 mm long × 1·0 mm broad (figures 30, 32 to 34). *P. minutum* sp.nov. is euapolytic, considerable growth and egg(?) production taking place after the last proglottid becomes detached (figures 36 to 38). Detached proglottids may attain a length of 8·0 mm and a breadth of almost 3·0 mm. The scolex is about 0·90 mm in diameter, each bothridium measuring approximately 0·45 × 0·45 mm and having indistinct marginal loculi. The apical accessory suckers are also inconspicuous, being 0·085 mm in diameter.

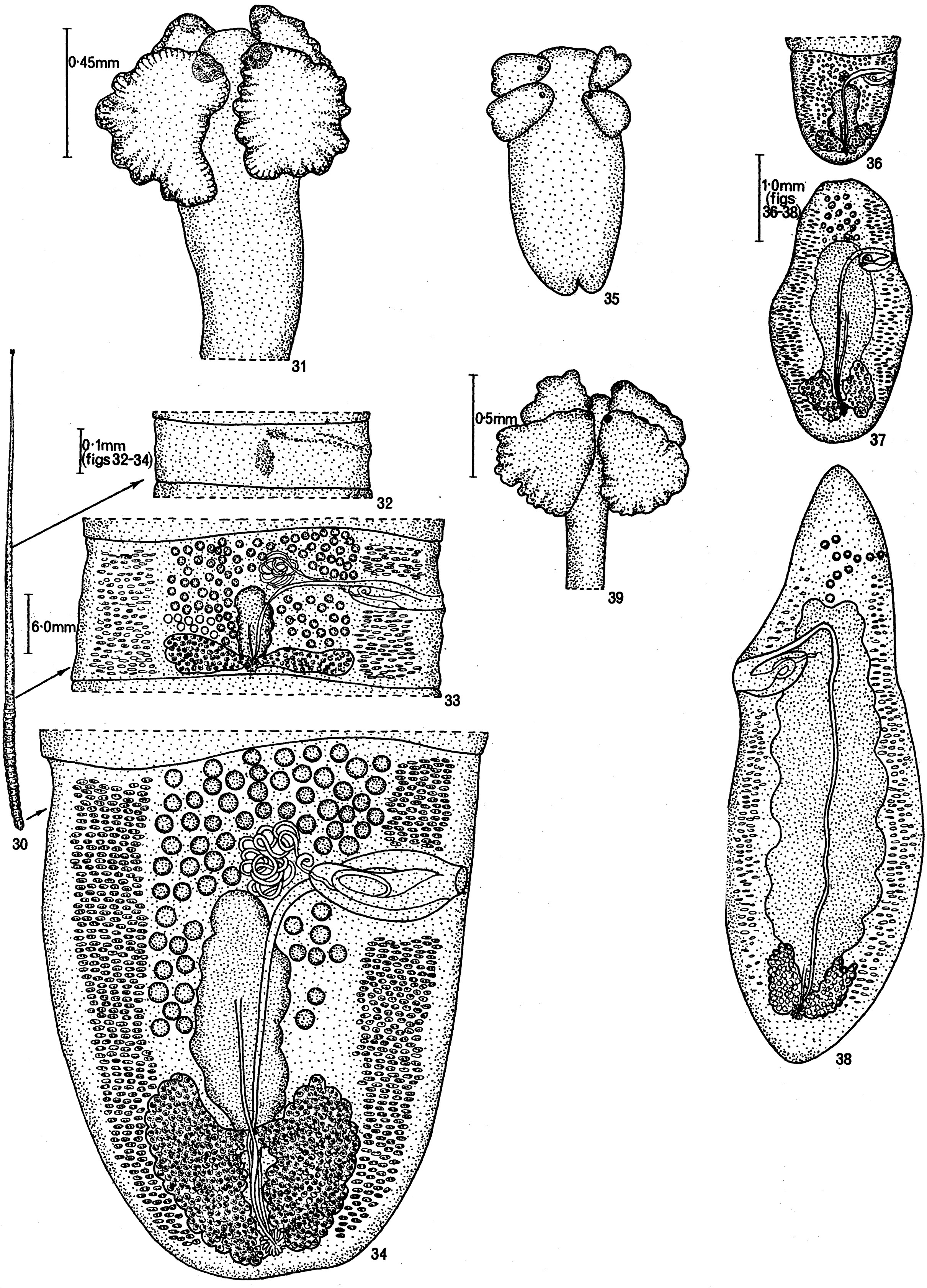
The genital pore is lateral at about a third of the length of the proglottid from the anterior end. There is no evidence of protandry. About 80 to 100 testes can be seen in the proglottids of the posterior region of the strobila. The cirrus sac is about 0·35 mm long × 0·15 mm broad.

P. minutum sp.nov. is of considerable interest in that it occurs in a species of *Raja*, but is a little-known form requiring further investigation especially if living specimens become available for study. It closely resembles *P. auricula*, *P. foliatum* and *P. loculatum*, and may eventually fall as a synonym of one of these species; but they are all little-known forms; information on their life-histories, especially on the form of the eggs and larvae, would be of particular value in solving this taxonomic problem. Immature specimens of *P. minutum* sp.nov. were also found (figures 21, 35, 59; and figure 75, plate 13).

15. **Phyllobothrium foliatum** Linton, 1890

Previous records: *Trygon centrura*, Woods Hole, Massachusetts, Linton (1890); *Dasyatis centrura*, Woods Hole, Linton (1897*b*); *Dasyatis centrura*, Woods Hole, Linton (1901); *Carcharinus obscurus*, Beaufort, North Carolina, Linton (1905*a*); *Dasyatis say*, Beaufort, North Carolina, Linton (1905*a*); *Dasybatis centrura*, Woods Hole, Massachusetts, Linton (1924*b*); *Raja stabuliformis*, Woods Hole, Linton (1924*b*); *Rhynchobatus djeddensis*, Ceylon, Southwell (1912); *R. djeddensis*, Ceylon, Southwell (1927); *R. djeddensis*, Ceylon, Southwell (1930); *R. djeddensis*, Ceylon, Southwell & Prashad (1920).

The original description of *Phyllobothrium foliatum* was based on a large number of specimens from the intestine of *Trygon centrura* at Woods Hole, Massachusetts. In this and subsequent references by Linton (1897*b*, 1901, 1905*a*, 1924*b*) there is little of value for identifying *P. foliatum*. As already indicated by Euzet (1952*c*) *P. foliatum* of Southwell &



FIGURES 30 to 39. For legends see facing page.

Prashad (1920) and of Southwell (1927) is not identical with the specimens described by Linton. Southwell (1925) gave a brief diagnosis of *P. foliatum* based on information by Linton (1890). A detailed study of specimens, in all stages of development, from the original host and locality is essential for a detailed comparison of *P. foliatum* with *P. auricula* and *P. centrurum*. *Taenia rosaeformis* Macallum, 1921, from *Dasybatis pastinacus* at Woods Hole, may be a synonym of *P. foliatum* or, as indicated by Euzet (1959), of *P. centrurum* Southwell, 1925.

16. **Phyllobothrium centrurum** Southwell, 1925

Previous records: *Dasyatis pastinaca*, Sète, Euzet (1959); *Hexanchus griseus*, Britain, Rees & Llewellyn (1941).

Southwell (1925) stated that the specimens described by Linton (1890) as *Anthocephalum gracile* are really members of *Phyllobothrium*; as *P. gracile* is a valid species described by Wedl (1855*b*) the name *P. centrurum* was proposed by Southwell for Linton's *A. gracile* from *Trygon centrura*. Euzet (1959) briefly redescribed and figured *P. centrurum* from *Dasyatis pastinaca* in the Mediterranean, with the following synonymy: '*Anthocephalum gracile* E. Linton, 1890. *Taenia rosaeformis* G.-A. MacCallum 1921. *Phyllobothrium gracile* K. Weld, T. Southwell 1930'. According to Euzet *P. centrurum* is 20·0 to 25·0 mm long, 0·35 mm broad and euapolytic, the free proglottids measuring 2·40 × 0·60 mm. The bothridia have loculate margins and accessory suckers 0·60 to 0·080 mm in diameter. The genital pore is in the posterior region of the proglottid and the forty to sixty testes are confined to a region in front of the vagina. The cirrus sac is 0·150 × 0·075 mm. It is of particular interest that gravid proglottids have not yet been found.

17. **Phyllobothrium gracile** Wedl, 1855

Previous records: *Torpedo marmorata*, France, Beauchamp (1905); *Trygon pastinaca*, Black Sea, Borcea (1934); *Torpedo marmorata*, Trieste, Carus (1884); *T. marmorata*, Diesing (1863); *T. marmorata*, Euzet (1952*b*); *T. marmorata*, Mediterranean, coasts of European Atlantic and Morocco, Euzet (1952*c*); *T. marmorata*, Concarneau, Archachon, Sète, Euzet (1959); *Squatina angelus*, Banyuls (Pyrenees-Orientales); Joyeux & Baer (1936); *T. marmorata*, Banyuls, Joyeux & Baer (1936); *T. marmorata*, Linstow (1878); *T. marmorata*, Oerley (1885); *Heptanchus cinereus*, Mediterranean, Parona (1900); *Hexanchus griseus*, Mediterranean, Parona (1900); *T. marmorata*, Mediterranean, Parona (1900); *T. marmorata*, Pintner (1896); *T. nobiliana*, Williams (1958); *T. nobiliana*, Britain, Williams (see p. 297).

Previous records of *P. gracile* show that its taxonomic history is complicated. The species was described in detail by Beauchamp (1905) and redescribed and figured by Euzet (1959),

FIGURES 30 to 38. *Phyllobothrium minutum* sp.nov. from *Raja fullonica*.
FIGURE 30. Complete strobila of mature adult, about 50 mm long.
FIGURE 31. Scolex of largest specimen found, drawn from temporary whole mount in formaldehyde.
FIGURES 32–34. Proglottids from different regions of the same strobila, dorsal view.
FIGURE 35. Immature specimen (post-plerocercoid?) to same scale as figure 31.
FIGURE 36–38. Posterior proglottid of strobila and two free proglottids, all to same scale to show growth change, as uterus becomes filled with eggs.
FIGURE 39. Scolex of *Phyllobothrium thridax* for comparison with that of *P. minutum* n.sp.

who gave *Anthobothrium auriculatum* Rudolphi, 1819 and *A. auriculatum* Zschokke, 1888 as its synonyms. Euzet pointed out that the species does not correspond with that described by Southwell (1930) as *P. gracile*. The adults are 40 to 50 mm long and 2·0 mm broad; Zschokke (1888) gave the length as 140 to 200 mm. The accessory suckers of the bothridia are 0·080 to 0·100 mm in diameter. The species is apolytic, the free proglottids measuring 2·50 × 1·0 mm. The genital pore is almost at the posterior margin of the proglottid and the 100 to 130 testes are confined to a region in front of the vagina. The cirrus sac is 0·200 mm × 0·150 mm. The eggs, which measure 0·150 mm × 0·060 mm, are characteristic in having 2 polar filaments each of about 0·500 mm long.

18. **Phyllobothrium loculatum** Yamaguti, 1952

Phyllobothrium loculatum from the intestine of *Heterodontus zebra* in the East China Sea is 20·0 to 40·0 mm long, 1·0 to 2·40 mm broad and has a scolex 1·0 to 1·50 mm broad with an 'apex projecting forwards more or less prominently between dorsal and ventral bothridia'. The surface of the bothridium is divided into irregularly arranged loculi and fifty prominent marginal loculi. The genital pores are irregularly alternate and slightly post-equatorial. The testes were described as numerous, about 190 being figured. The vagina is postero-dorsal to the cirrus sac and opening into the genital atrium immediately dorsal to the cirrus. Yamaguti (1952) compared the species with *P. foliatum* from which it differs in lacking pedicels supporting the bothridia. In *P. foliatum* the vagina opens in front of the cirrus.

19. **Phyllobothrium typicum** Subhapradha, 1955

Phyllobothrium typicum occurred in the intestines of *Carcharias acutus*, *C. walbeehmi* and *Mustelus manazo* in the coastal waters of Madras; but this lack of host specificity requires confirmation. The largest specimen was only 3·68 mm long with a maximum breadth of 0·167 mm. The margins of the bothridia are thickened and the apical suckers measure 0·028 to 0·038 mm in diameter. The strobila consists of about 6 to 10 proglottids. The genital pore is in the anterior third of the proglottid and the 50 to 60 testes extend from the ovary to the anterior region of the proglottid. The vitellaria consist of a number of follicles arranged in a double row, one above the other on each side, in lateral fields. The species was compared with *P. prionacis* Yamaguti, 1934, from which it differs in being much smaller, in the absence of spines on the cirrus and in the position of the genital pore. *P. typicum* is inadequately described for comparison with other species; it may be related to *P. prionacis*, but further work on the type specimens and on additional material from the type hosts and locality should also consider *Crossobothrium* (*Phyllobothrium*?) *filiforme* (Yamaguti 1952), a species which Euzet (1959) included with 6 others as synonyms of *C. angustum* (Linton 1889).

20. **Phyllobothrium chiloscylli** Subhapradha, 1955

Phyllobothrium chiloscylli was found in the intestines of *Chiloscyllium griseum*, *Rhynchobatus djeddensis*, *Rhinobatus granulatus* and *R. schlegeli* in the coastal waters of Madras. The largest of the specimens was 12 mm long. Each bothridium has distinct marginal loculi and an anterior accessory sucker 0·075 mm in diameter. The strobila is composed of 6 to 18 proglottids. The unilateral genital pores are in the anterior third of the proglottid, there are 55 to 80 testes and the cirrus has no spines. The vitellaria consist of a double row of small follicles on each side of the proglottid. The species was compared with *P. foliatum* Linton, 1890, and '*P. centrurum* (Linton, 1890)' in having marginal loculi in the bothridia. It was said to differ from *P. foliatum* in size, position of genital pore and absence of cirrus spines; and from *P. centrurum* in the position of the genital pore and distribution of the testes.

21. **Phyllobothrium minimum** Subhapradha, 1955

Phyllobothrium minimum was originally described and figured from specimens found in *Rhynchobatus djeddensis* in the coastal waters of Madras. The largest specimen was only 2·0 mm long with a maximum breadth of 0·117 mm. Each bothridium has distinct marginal loculi and an accessory sucker 0·048 mm in diameter. The strobila consists of about four to five proglottids. Thirty-nine to fifty-seven testes are arranged in two rows, close together, along the mid-line. There is a double row of vitelline follicles on each side of the proglottid. The species was compared with *P. chiloscylli*, from which it differs in the arrangement of testes and genital ducts and in that the vitellaria do not extend behind the ovary; the testes of *P. chiloscylli* are described as being arranged in a double row on either side of the median longitudinal axis while in front of the cirrus sac they extend to the median field. Subhapradha also compared *P. minimum* with *Anthobothrium septatum* Subhapradha 1955 from *Rhynchobatus djeddensis* and *Trygon imbricatus*.

22. **Phyllobothrium biacetabulum** Yamaguti, 1960

Yamaguti (1960) refers to twelve mature specimens of *P. biacetabulum* from *Rhinobatus schlegeli*, originally from the Inland Sea, Japan, and which had subsequently died in the aquarium of Tamano Oceanographical Museum at Shibukawa, Okayama Prefecture. The specimens measured 3·50 to 8·50 mm, the nearly circular bothridia measure about 0·30 mm in diameter and each bears two fused acetabula, one behind the other; the anterior acetabulum being 0·060 to 0·075 mm and the posterior 0·100 to 0·115 mm in diameter. Each bothridium also possesses about forty marginal loculi. There are eighteen to thirty testes. Yamaguti did not compare the species with another member of the genus; further work on *P. biacetabulum* may show that it resembles *P. chiloscylli* Subhapradha, 1955.

IV. The complex of species in *Crossobothrium* Linton, 1889

The genus *Crossobothrium* was first proposed and defined by Linton (1889, p. 469) to accommodate *C. laciniatum*, a new species which he had found in *Odontaspis littoralis* at Woods Hole, Massachusetts. *C. laciniatum* Linton, 1889 is now generally accepted as a synonym of *Phyllobothrium dohrnii*, but this synonymy is not accepted in the present revision, mainly to avoid further confusion in a discussion of names of species on which few detailed biological investigations have been carried out. Linton (1889, p. 470) emphasized that *Crossobothrium* is closely allied to *Phyllobothrium*, but differs from it in having the 'bothria pediceled instead of sessile, and in the absence of a distinct neck'. The following ten species require further investigation, preferably with living specimens from the type hosts and locality.

1. **Crossobothrium (Phyllobothrium?) angustum** (Linton, 1889)

Linton (1889, p. 468) described and figured a new species from '*Carcharias obscurus*' as *Orygmatobothrium angustum* but Linton (1901, p. 426) referred to this species as *Crossobothrium angustum*, with '*Carcharinus milberti*, Blue Shark' and '*Carcharinus obscurus* (*Carcharias obscurus*), Dusky Shark' as hosts. Euzet (1959) redescribed and figured *Crossobothrium angustum* from *Galeus glaucus* and *Alopias vulpinus* in European waters and listed the following seven synonyms: *Orygmatobothrium angustum* Linton, 1889; *O. paulum* Linton 1897; *C. angustum* Linton, 1901; *Phyllobothrium prionacis* Yamaguti, 1934; *P. musteli* (Beneden *pro parte*) Guiart, 1936; *P. angustum* of Euzet (1952*c*) and *P. filiforme* Yamaguti, 1952. In other words, the species is thought to occur in different host species from widely separated geographical areas; in addition to the four hosts mentioned above for *C. angustum* the following are also involved: *Galeocerdo tigrinus* at Woods Hole and '*Alopias vulpinus*' and '*Prionace glauca*' in the Pacific.

This interesting suggestion concerning the wide host and geographical distribution of *C. angustum* requires confirmation. At present it is considered inadvisable to accept long lists of synonyms for inadequately described species; reasons for this view were given by Williams (1966).

2. **Crossobothrium (Phyllobothrium?) filiforme** Yamaguti, 1952

Phyllobothrium filiforme was found in the intestine of *Alopias vulpinus* in the Pacific. It is 13·0 to 24·0 mm long, 0·30 to 0·45 mm broad, has bothridia 0·25 to 0·30 mm in diameter and submarginal accessory suckers 0·055 to 0·075 mm in diameter. Yamaguti (1952) referred to 100 to 120 testes but only about ninety are figured. The cirrus sac is 0·16 to 0·19 × 0·08 to 0·12 mm. The species was compared with *P. rotundum*, a little-known form.

Further work on *P. filiforme* should consider the similarity between *Anthobothrium parvum* of Yamaguti (1934, fig. 89), from *Alopias vulpinus*; and the information given by Yamaguti (1952, Plate IV, figs. 17 and 18); but Yamaguti (1952, p. 27) gave a description of '*Anthobothrium parvum* Stossich, 1909 nec *A. parvum* Yamaguti, 1934 (renamed *A. exigum* Yamaguti, 1935)', from *Mustelus manazo* in Obama, Hukui Prefecture, Japan. According to Euzet (1959) *P. filiforme* Yamaguti, 1952, is a synonym of *Crossobothrium angustum* (Linton, 1889).

3. **Crossobothrium (Phyllobothrium?) laciniatum** Linton, 1889

Crossobothrium laciniatum Linton, 1889, from *Odontaspis littoralis* at Woods Hole, Massachusetts, is generally regarded as a synonym of *Phyllobothrium dohrnii* (Oerley 1885*b*), a species originally found in '*Heptanchus cinereus*' in the Mediterranean; but it is here considered advisable to recognize *C.* (*Phyllobothrium*?) *laciniatum* mainly because the alleged occurrence of *P. dohrnii* in American, European and Japanese waters is not confirmed. Johnstone (1906) referred to *C. laciniatum* from *Raja batis* in British waters, while Yamaguti (1952) gave a redescription of *P. laciniatum* from *Squalus sucklii* in the East China Sea.

4. **Crossobothrium (Phyllobothrium?) longicolle** (Molin 1858)

Crossobothrium longicolle, from *Scyliorhinus stellaris* at Sète was redescribed by Euzet (1959). He gave the following synonyms: *Tetrabothrium longicolle* Molin, 1858; *Monorygma perfectum* of Zschokke, 1888, and *M. elegans* Monticelli, 1890. It is 150 to 300 mm long, with a maximum breadth of 2·50 mm. The scolex is 0·600 to 0·800 mm long × 0·300 to 0·400 mm broad. The accessory sucker is 0·150 mm in diameter. The posterior proglottids which are gravid are 2·0 mm long × 1·0 mm broad. The species is anapolytic. The genital pore is in the anterior third of the proglottid. There are 170 to 230 testes and the cirrus sac is 0·350 mm long × 0·200 mm broad. The spherical eggs which are ornamented by a fine punctation are 0·030 mm in diameter.

5. **Crossobothrium (Phyllobothrium?) prionacis** (Yamaguti 1934)

The specimens found by Yamaguti (1934) in *Prionace glauca* in the Pacific were not gravid, the largest being 12·0 mm long and of about 15 proglottids, the last being 1·125 mm long and 0·36 mm in maximum breadth. The accessory suckers of the bothridia are about 0·11 mm in diameter. The genital pore is mid-lateral and there are 35 to 40 testes. Yamaguti (1934) compared *C. prionacis* with a new species which he described as *Anthobothrium parvum* from *Alopias vulpinus*. He stated that *C. prionacis* differed from *A. parvum* 'chiefly by the possession of accessory suckers and the position of the genital pore'. *Anthobothrium parvum* of Yamaguti (1934) was briefly discussed above under *P. filiforme* Yamaguti, 1952, also a cestode of *Alopias vulpinus*.

6. **Crossobothrium (Phyllobothrium?) squali** (Yamaguti 1952)

Yamaguti (1952) described *Phyllobothrium squali* from *Squalus sucklii* in Onahama, Hukusima Perfecture, Japan. *P. squali* is 140·0 mm long × 2·15 mm broad with a scolex 2·85 mm in diameter. The accessory sucker is 0·30 to 0·35 mm in diameter. The last four proglottids are fully gravid, the terminal measuring 3·0 × 2·30 mm. The lateral genital pore is in the anterior half and the 80 to 100 testes are confined to the middle of the proglottid in front of the ovary. The cirrus sac is 0·50 mm long × 0·15 to 0·20 mm broad. The eggs are described as subglobular and measuring 0·040 × 0·030 mm. Yamaguti stated that 'this species resembles *P. thridax* van Beneden, 1850, but the latter, being inadequately described, satisfactory comparison is not possible'.

Euzet (1959) redescribed *C. squali* (Yamaguti 1952) from *Squalus acanthias* at Concarneau and from *Etmopterus spinax* at Naples and stated that he had never found the species in *S. acanthias* or *S. fernandinus* at Sète. The specimens described by Euzet differ from those of Yamaguti in size of the strobila (50 to 60 mm long × 2·0 mm broad), size of scolex (1·0 mm long × 1·2 mm broad), diameter of accessory sucker (0·200 to 0·220 mm), in being apolytic, the free proglottid being 7·0 mm long × 2·50 mm broad, in having 130 to 170 testes and in the size of the cirrus sac (0·300 mm long × 0·100 mm broad).

The specimens referred to by name only as *P. squali*, by Williams (1960) are here further considered as *C.* (*Phyllobothrium?*) sp. 1 and *C.* (*Phyllobothrium?*) sp. 3.

7. **Crossobothrium (Phyllobothrium?) triacis** (Yamaguti 1952)

Crossobothrium triacis was first described by Yamaguti (1952), from *Triacis scyllium* in the Pacific and very briefly redescribed and figured by Euzet (1952*c*), from *Mustelus canis* at Sète and Concarneau and *M. mustelus* at Sète.

According to Yamaguti the species is 35·0 to 46·0 mm long and 0·80 to 0·90 mm broad, with a strobila of 40 to 50 proglottids. The scolex is 0·68 mm in diameter with bothridia 0·40 to 0·50 mm in diameter and accessory suckers measuring 0·060 × 0·065 to 0·075 mm. 180 to 230 testes are present, but only 107 can be seen in a photomicrograph of the proglottid and about 160 are shown in a figure. The genital pores are unilateral, about a third of the length of each proglottid from its anterior end. The cirrus sac is 0·27 to 0·35 × 0·11 to 0·175 mm. According to Yamaguti (1952, p. 16): 'This species resembles *Phyllobothrium dasybati* Yamaguti, 1934, very closely, but differs from it distinctly in the cirrus being conspicuously spinose. In *P. dasybati* the cirrus is entirely devoid of spines. In this species the serration of the cuticle is also present throughout the strobila though not mentioned in my previous description.'

8. **Crossobothrium (Phyllobothrium?)** sp. 1 from **Spinax spinax**

(Figures 40 to 45)

Specimens, referred to by Williams (1960, p. 709) as *Phyllobothrium squali* from *Spinax spinax*, are now left unnamed in view of increasing evidence that *Squalus* and *Spinax* harbour different species of *Crossobothrium* (*Phyllobothrium*?). There is also some evidence showing that more than one species of *C.* (*Phyllobothrium*?) occur in each of these two host genera, if records from different geographical areas are considered. Specimens from *Spinax spinax* differ from those in *Squalus* particularly in the general appearance of the strobila (figures 40, 46) and in the size and shape of the scolex (figures 41, 47).

9. **Crossobothrium (Phyllobothrium?)** sp. 2 from **Spinax spinax**

(Figures 79, 80, plate 13.)

After recording differences between *Crossobothrium* from *Spinax* and *Squalus*, photomicrographs of a cestode from *S. spinax* caught in the outer Oslo fjord, Norway, were received from Professor Rolf Vik; these, (figures 79 and 80, plate 13) being unlike the specimens already referred to as *Crossobothrium* (*Phyllobothrium*?) sp. 1 (figures 40 to 45) are provisionally mentioned as *Crossobothrium* (*Phyllobothrium*?) sp. 2.

10. **Crossobothrium (Phyllobothrium?)** sp. 3 from **Squalus acanthias**

(Figures 46 to 51, 60; and figure 84, plate 14.)

The specimens here described as *Crossobothrium* (*Phyllobothrium*?) sp. 3, from *Squalus acanthias*, were referred to as *Phyllobothrium squali* by Williams (1960, p. 709) but they are now left unnamed with a view to erecting a new species when further material becomes

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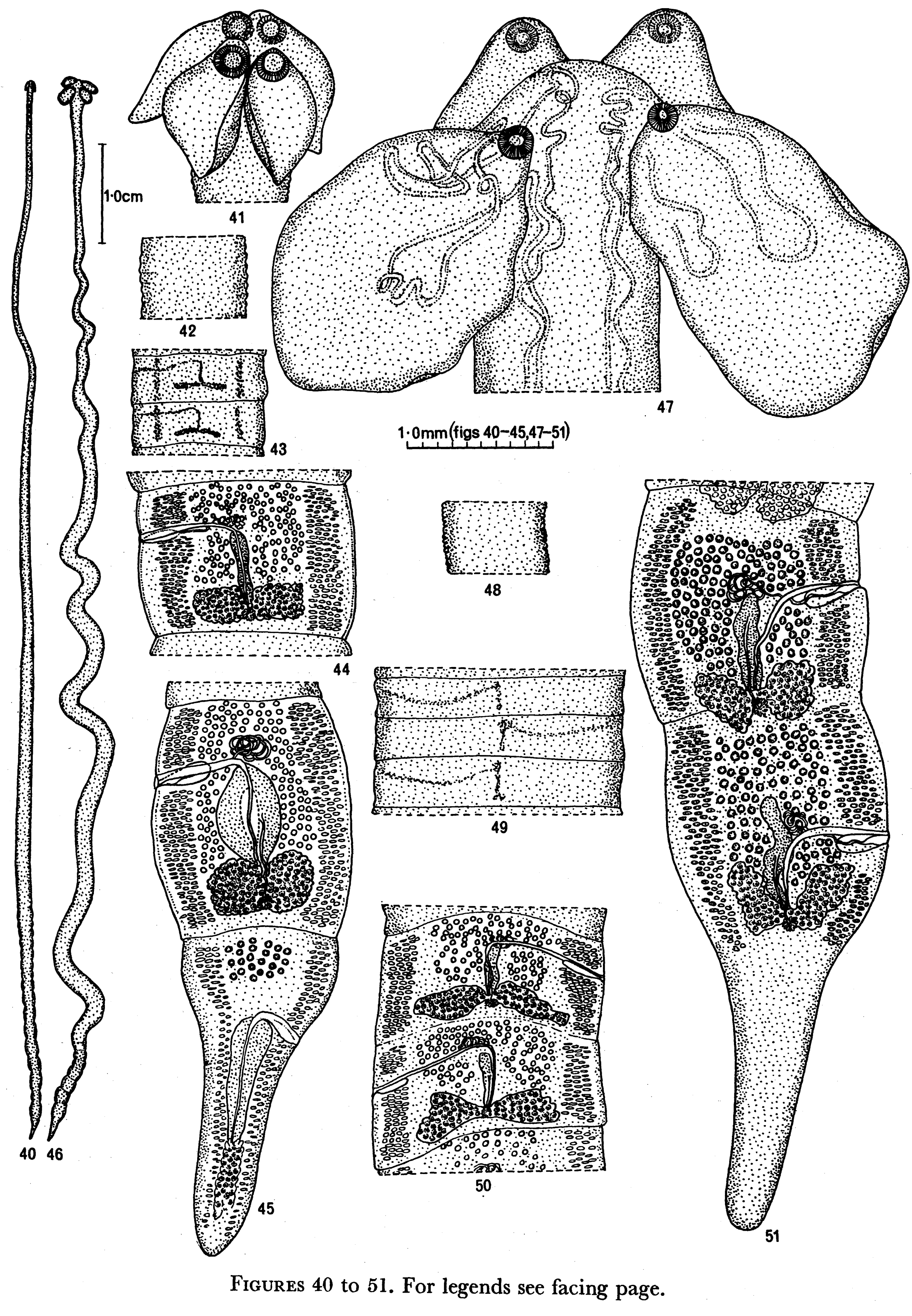
FIGURES 40 to 45. *Crossobothrium* (*Phyllobothrium*?) sp. 1 from *Spinax spinax*
FIGURE 40. Complete strobila of mature adult, about 140 mm long.
FIGURE 41. Scolex.
FIGURES 42 to 45. Proglottids from different regions of the same strobila, dorsal view.
FIGURES 46–51. *Crossobothrium* (*Phyllobothrium*?) sp. 3 from *Squalus acanthias*.
FIGURE 46. Complete strobila of mature adult, about 160 mm long.
FIGURE 47. Scolex.
FIGURES 48 to 51. Proglottids from different regions of the same strobila.



FIGURES 40 to 51. For legends see facing page.

available for confirmation of certain morphological features and aspects of their biology. The following comments on the specimens are based on a study of six entire strobilae found in the intestines of four of twenty *S. acanthias* caught off the British Isles. Measurements are based on material fixed in 4% formaldehyde and subsequently stained in acetocarmine. The strobila is up to 350 mm long and 3·0 mm in maximum breadth (figure 46). The species is anapolytic with a characteristically shaped last proglottid which is distinctly elongated and pointed posteriorly (figure 51); it is about 3·50 mm long × 1·50 mm broad in the region of the genital pore.

The scolex is about 2·0 mm in diameter, each bothridium measuring approximately 2·50 mm long × 1·50 mm broad and having an apical sucker 0·12 mm in diameter (figure 47; and figure 84, plate 14). The genital pore is lateral and midway along the length of the proglottid. About 80 to 100 testes are clearly visible in some of the proglottids examined but this feature requires confirmation. The cirrus sac is 0·50 mm long × 0·15 mm broad.

These specimens from *S. acanthias* in British waters closely resemble *P. squali* Yamaguti, 1952, but differ from those described by Euzet (1959) as *C. squali*, in size of the strobila, size of the scolex, diameter of accessory suckers, in being anapolytic, in the number of testes and in the size of the cirrus sac.

Specimens of *C.* (*Phyllobothrium*?) from *Squalus* in Japanese and European waters require further more detailed examination and comparison.

V. The complex of species in *Monorygma* Diesing, 1863

The genus *Monorygma* was proposed by Diesing (1863) to accommodate *Anthobothrium perfectum* Beneden, 1853, and was originally defined as follows: 'body segmented, and taenia-like; head separated from the body by a neck. There are four sessile bothridia, opposite with margins entire, each bearing a single accessory sucker at its apex. Myzorhynchus present and terminal.' *Monorygma* is tentatively accepted in this revision because further detailed observations on the biology of the following nine 'species', preferably of material from the type host and locality, is essential before establishing or rejecting the genus.

1. **Monorygma (Phyllobothrium?) elegans** Monticelli, 1890

Stiles & Hassall (1912) gave an indication of the early history of *Monorygma elegans*. The name was proposed by Monticelli (1890) for a cestode of *Scyliorhinus catulus* and *S. stellaris* described by Zschokke (1888) as *M. perfectum* Beneden, 1853. Euzet (1952*c*) briefly referred to *M. elegans* from '*Scyllium stellare* L = *Scyllium catulus*' at Wimereux, coast of Manche, and in the Mediterranean, stating that Zschokke (1888) and Beauchamp (1905) described the species adequately for its identification. Euzet (1959, p. 81), however, placed *M. perfectum* of Zschokke, 1888, and *M. elegans* Monticelli, 1890, as a synonym of *Crossobothrium longicolle* (Molin 1858), also a cestode of *Scyliorhynus stellaris* at Sète. It appears, therefore, that only one host, *S. stellaris*, is implicated in this taxonomic problem, but in view of the two localities involved, the Mediterranean and the North Sea, further work on *M. elegans* is considered advisable in order to confirm or reject its synonymy with

C. longicolle Molin, 1858, and/or its relationships to a cestode of *S. canicula*, briefly discussed below as *M.* (*Phyllobothrium?*) sp.

2. Monorogma (Phyllobothrium?) chlamydoselachi Loennberg, 1898

(Figures 26, 27)

Baer (1956) and Euzet (1959) place *Monorygma chlamydoselachi* Loennberg (1898) as a synonym of *M. perfectum* Beneden, 1853, thus suggesting that the latter occurs in several hosts and localities; this feature will be further discussed below. *M. chlamydoselachi* is provisionally accepted in this revision after examining about twelve specimens of a cestode at the British Museum (Natural History), identified as '*Monorygma? chlamydoselachi* (Loennberg 1898)', and originally found in *Chlamysdoselachus anguineus* caught off the west coast of Ireland at 53° N 13° W and 300 to 350 fathoms. The scolex of these specimens (figure 27) differs greatly from that of *M. perfectum* as described by Euzet (1959).

3. Monorygma (Phyllobothrium?) galeocerdonis MacCallum, 1921

Monorygma galeocerdonis MacCallum, 1921, is a little-known species of uncertain systematic status briefly described and figured from material found in *Galeocerdo tigrinus* at Woods Hole, Massachusetts.

4. Monorygma (Phyllobothrium?) hyperapolytica (Obersteiner 1914)

This species was briefly discussed by Williams (1958) and Alexander (1963). The latter identified specimens found in *Dalatius licha* (Bonnaterre) at Palliser Bay, New Zealand, as *Monorygma hyperapolytica* and listed four synonyms including *Phyllobothrium hyperapolytica* of Williams (1958). For reasons already given by Williams (1966), in a revision of *Echeneibothrium*, I am unable to accept this procedure in regard to erecting several synonyms for little-known Tetraphyllidea. Alexander's synonymy is also questionable because he did not examine the specimens I described and figured, from *Scymnus licha* caught off Britain. This confusion may also be linked with that on host identity. According to Alexander (1963) *D. licha* and *S. licha* are synonymous, but Golvan (1962) placed *Scymnus* as a synonym of *Scymnorhinus*, in the family Scymnorhinidae, and *Centrophorus* as a synonym of *Dalatias*, in the Squalidae. Other problems of this nature require investigation in connexion with the validity of '*Bilocularia hyperapolytica* Obersteiner, 1914', preferably with reference to material from *Centrophorus* (= *Dalatias?*) *granulosus* caught in the vicinity of Naples, the type host and locality. At present, the species referred to as *Phyllobothrium hyperapolytica* by Williams (1958) will not be renamed; this would confuse further an already complicated taxonomic problem.

5. Monorygma (Phyllobothrium?) macquariae Johnston, 1937

Monorygma macquariae Johnston, 1937, was placed as a synonym of *Monorygma magnum* by Johnston (1937) and of *M. perfectum* by Baer (1956) and by Euzet (1959), but the species is tentatively accepted in this revision, mainly in view of its host(?) and geographical occurrence, size of accessory suckers and eggs and number of testes.

M. macquariae was found in a large shark cast up on the beach at Macquariae Island and determined as '*Somniosus* sp., one of the Scymnorhinidae'. This cestode is over 500 mm long with a greatest breadth of about 7·0 mm, the end proglottids being 3·50 to 4·0 mm long × 2·50 mm broad. The scolex has a maximum breadth of 4·50 mm and a length of 3·10 mm; each bothridium being up to 2·50 mm broad and 1·9 to 2·30 mm long from the hind border of the accessory sucker. The accessory sucker is about 0·90 mm in diameter.

The lateral genital pores alternate irregularly and are situated at about the middle of the proglottid or just in front of it. The cirrus sac is from 1·80 to 2·0 mm long with a maximum diameter of 0·40 to 0·50 mm. About 200 testes are figured. Uterine eggs are elliptical, measuring 0·07 to 0·08 mm long by 0·033 to 0·037 mm broad with bluntly rounded extremities. Euzet (1959), however, gave the following data on *M. perfectum*: up to 850 mm long and 4·50 mm broad; a scolex 1·80 to 2·0 mm long and 1·30 to 1·70 mm broad with bothridia 1·5 to 2·0 mm long, 0·60 to 0·80 mm broad; the accessory suckers were shown to be less than 0·200 mm in diameter; about 300 to 350 testes; and fusiform eggs measuring 0·145 to 0·155 mm long × 0·030 to 0·040 mm broad.

Johnston described *M. macquariae* in detail, stating that the species is obviously closely related to *Monorygma perfectum* and that 'it is quite possible that this species of *Monorygma* collected from an insufficiently known large Subantarctic shark, allied to the Arctic shark, may be synonymous with *M. perfectum* described from the latter'. He agreed with Beauchamp (1905), Linton (1924*b*), Meggitt (1924) and Baylis (1932) in accepting the genus *Monorygma*; the well-developed thick bothridia devoid of a crenulate border, the large projecting accessory suckers and the fact that the proglottids reach maturity while remaining attached, serving to distinguish the genus from *Phyllobothrium*. He, therefore, disagreed with Southwell (1925) and Fuhrmann (1931) in placing *Monorygma* as a synonym of *Phyllobothrium*.

The confusion concerning the identity of species of *Monorygma* described by various authors from various localities and hosts is well illustrated in the following remarks in Johnston's discussion: Linton (1924*b*) recorded *M. perfectum* from *Somniosus brevipinna* from Alaska, while Beneden's type material came from the same host species from the Belgian coast; Beneden's *Scymnus glacialis* and *Laemargus borealis* are synonyms of *Somniosus brevipinna*, according to Linton. *M. macquariae* was thought to resemble much more closely the species described by Linton as *M. perfectum* than that by Zschokke from *Scyllium* spp., apparently from Naples. Southwell (1925) regarded *M. dentatum* Linstow as a synonym of *Phyllobothrium perfectum* but *M. dentatum* was an immature specimen from an undetermined shark in the north equatorial Atlantic. According to Johnston, Linstow's figure indicates a form (perhaps a *Phyllobothrium*) quite distinct from *M. perfectum*. No definite myzorhynchus was seen by Linton or Johnston in their specimens, but Beneden (1853) and Euzet (1959) figured a myzorhynchus and Diesing regarded its presence as a generic character. Johnston also emphasized that the scolex in his material is larger than in those described by Linton & Beneden. Linton stated that the genital pores, as well as the cirrus sac, are nearer the anterior border and Beneden's figure indicates a similar position, but in *M. macquariae* they are just in front of the mid-margin. In an addendum Johnston stated that his *M. macquariae* is a synonym of *P. magnum* Hart, 1936, a species to be discussed below; but he also referred to the relatively few testes in the latter which was recorded from *Somniosus microcephalus* in the north-eastern Pacific.

6. **Monorygma (Phyllobothrium?) magnum** Hart, 1936

Monorygma (Phyllobothrium?) magnum was placed as a synonym of *M. perfectum* by Baer (1956) and Euzet (1959), but in view of the differences between *M. macquariae* and *M. perfectum*, discussed above, and Hart's discussion of the relationships of *M. magnum*, it is here considered valid pending further examination of specimens from the type host and locality; *Somniosus microcephalus* in Puget Sound, Washington. The following information in the specific diagnosis given by Hart is of value: 'Size up to 48 cm in length and 5 mm in width. Scolex 4·2 mm in diameter and 2·5 mm in length. Bothridia up to 2·50 mm in length and 2·0 mm in width. Each bothridium has an accessory sucker measuring up to 1·0 mm in diameter located in its anterior position. No neck present. Genital pores marginal and irregularly alternate and located in middle, or slightly anterior to middle, of proglottids. Eggs spindle-shaped measuring 0·08 mm × 0·04 mm.'

Hart stated that '*P. magnum*' differs from '*P. perfectum*' in size of scolex; size relationship of proglottids; manner in which the vagina opens; location of the opening of the uterine duct into the uterus; location of the vas deferens; type, shape and size of the ovary; and size and shape of eggs. He considered *M. perfectum* of Linton (1924*b*) nearer to '*P. magnum*' than to '*P. perfectum*' and agreed with Linton, who considered his material as probably being a different species from the types described by other workers as *P. perfectum*.

7. **Monorygma (Phyllobothrium?) megacotyla** Yamaguti, 1952

Monorygma megacotyla occurs in the intestine of *Cephaloscyllium umbratile* in Nagasaki, Japan. Yamaguti (1952) gave the following information and measurements: 'Length 80 mm or more; breadth up to 2·0 mm. Number of segments over 600 in a specimen 72 mm long. Scolex pyramidal, 0·5 to 1·1 mm broad at base dorsal and ventral pair of bothridia, with disc-shaped myzorhynchus 0·1 to 0·105 mm in diameter at its apex. Bothridia pyriform 0·35 to 0·6 mm broad, pressed one against the other in median line, hollowed out near posteromedial corner, each pair 0·7 to 1·4 mm in combined breadth; accessory sucker muscular, well marked out, 0·25 to 0·26 × 0·2 to 0·21 mm. Neck 1·5 to 2·0 mm long × 0·4 to 0·95 mm broad.'

The species was briefly compared with *M. perfectum* and '*M. longicolle* (Molin 1858)'.

8. **Monorygma (Phyllobotherium?) perfectum** (Beneden 1853)

Monorygma perfectum has often been recorded and discussed and occasionally confused with other species. It may, however, be a cosmopolitan member of the genus showing considerable morphological variation in different hosts and localities. Olsson (1867) referred to *Monorygma* sp. from *Gadus melanostomus* as being possibly the larva of '*Anthobothrium (Monorygma) perfectum*, from *Scymnus glacialis*', of van Beneden, but his figure of the larva does not support this view. Olsson (1893) briefly discussed an adult of the species, from *Scymnus borealis* in the Skagerrack and a larval form in *Sebastes norvegicus*. Other early records of *M. perfectum* were listed by Stiles & Hassall (1912), while Southwell (1925) discussed six synonyms of the species including some of the species of *Monorygma* already discussed above and *Orygmatobothrium forte* of Linton (1924*b*). Polyanski (1955) gave a brief illustrated description of '*P. perfectum*' with *M. perfectum* and *Anthobothrium perfectum* as its synonyms. His account was based on three specimens found in two of ten *Somniosus microcephalus*. The largest strobila was 15 cm long with a scolex 3·0 mm long, neck 1·50 mm wide and a last proglottid measuring 3·50 mm long and 3·0 mm wide. These measurements differ from those given by Baer (1956) and Euzet (1959), who also recorded the cestode from *S. microcephalus*; in addition Euzet referred to *Dalatias licha* as a host at Nice. Baer referred to two specimens of *Lycichthys minor*, a large portion of *Eumicotremus spinosus* and beaks of cephalopods in the stomach of one of the sharks he examined. His account is also of interest in that he stated that if *M. perfectum* occurred in *Somniosus* sp. in the Antarctic, as indicated by Johnston (1937), one must suppose that a specimen of this deep-sea shark might have migrated through the cold, deep waters beneath the equator into the Antarctic. The measurements and data given by Euzet (1959) for *M. perfectum* were given above for comparison with *M. macquariae*.

9. **Monorygma (Phyllobothrium?)** sp. from **Scyliorhinus caniculus**

(Figures 17, 52 to 57, 66; and figure 82, plate 14.)

The possible identity of this species was discussed in detail by Williams (1958), who concluded that, since much confusion exists over the use of the name *Phyllobothrium musteli*, the cestode from *Scyliorhinus caniculus* should be considered as belonging to an indeterminate species of *Phyllobothrium*. Additional specimens have now been recovered from *S. caniculus* at Plymouth and are here briefly described and figured; they are, however, left as an indeterminate species until further material becomes available for comparison with *Crossobothrium* (*Phyllobothrium*?) *longicolle* and *Monorygma* (*Phyllobothrium*?) *elegans*.

Four entire strobilae and twelve free proglottids were examined. The strobila is about 100 mm long, 0·80 mm broad immediately behind the scolex and 2·0 mm in maximum breadth in the mid-region. The last proglottid is about 2·0 mm long × 1·85 mm broad, the free proglottid 5·0 mm long × 3·0 mm broad. Each bothridium is about 1·0 mm long × 1·0 mm broad and has an accessory sucker 0·20 mm in diameter. The genital pore is lateral and midway along the length of the proglottid. In the mid-region of the strobila 140 to 150 testes are visible in each proglottid but only about seventy are visible in the free proglottids. The cirrus sac is 0·75 mm long × 0·20 mm broad. The egg is elliptical with pointed ends and measures 0·038 mm long × 0·030 mm broad. In many features the species resembles *C. longicolle* as described by Euzet (1959) but differs in being apolytic and in the shape of the bothridium and eggs.

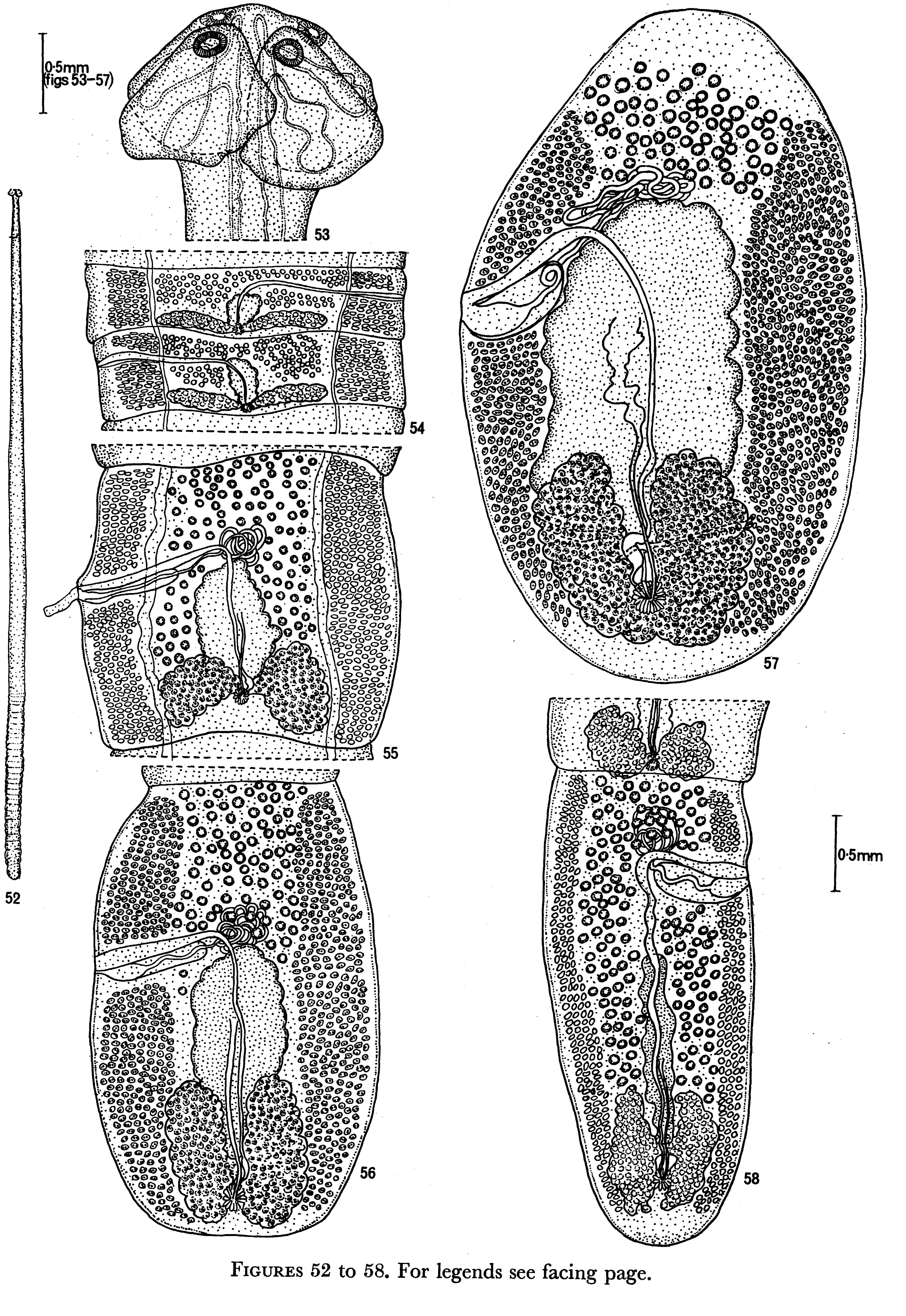
FIGURES 52 to 57. *Monorygma* (*Phyllobothrium*?) sp. from *Scyliorhynus caniculus*

FIGURE 52. Complete strobila of mature adult, about 65 mm long.

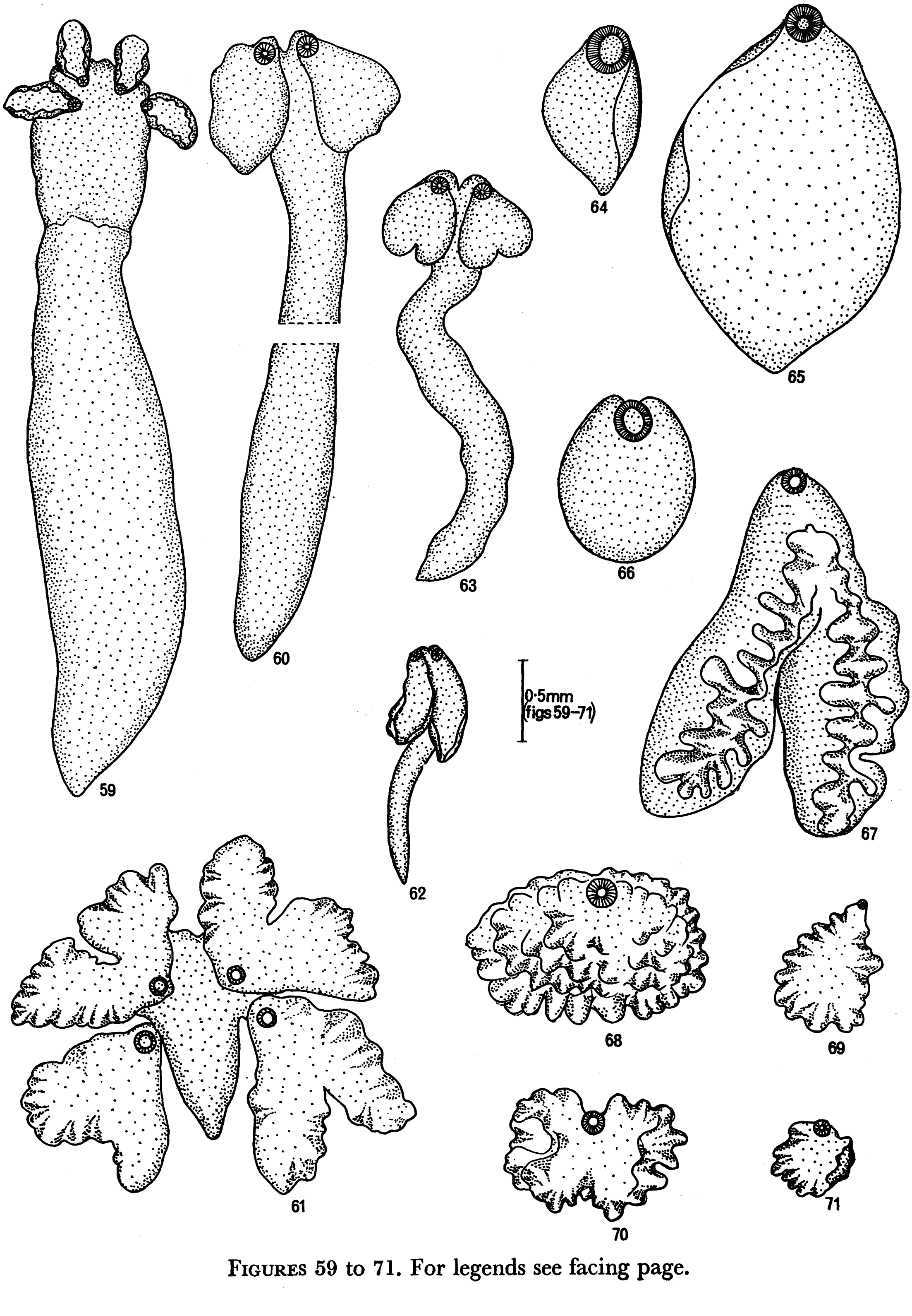
FIGURES 53 to 56. Proglottids from different regions of the same strobila, dorsal view.

FIGURE 57. Free proglottid showing male and female genitalia, dorsal view.

FIGURE 58. *Phyllobothrium thridax* from *Squatina squatina*; posterior proglottid from a strobila about 200 mm long.



FIGURES 52 to 58. For legends see facing page.



Figures 59 to 71. For legends see facing page.

VI. SPHAEROBOTHRIUM LUBETI EUZET, 1959 AND SOME ALLIED SPECIES

Euzet (1959) described and figured an interesting new genus and species, *Sphaerobothrium lubeti*, from *Myliobatis aquila* in Arcachon. Very large numbers of this have now been found in *M. aquila* caught off Britain. A comparison of the morphology with that of other cestodes, previously described as species of *Phyllobothrium*, has revealed several interesting features which may be of value in establishing a classification showing the relationships of *Phyllobothrium* to other genera.

The cestodes briefly referred to and illustrated by Guiart (1935) as *P. crispatissimum* Monticelli, 1889, were probably those now known as *S. lubeti*. He found a massive infection in '*Leiobatis aquila*' and compared the specimens with *P. lactuca*. The specimens described by Monticelli as *Phyllobothrium crispatissimum* and deposited at the British Museum (Natural History) are known to be *Thysanocephalum crispum* Linton, 1890.

1. **Sphaerobothrium lubeti** Euzet, 1959

Synonym: *Phyllobothrium crispatissimum* of Guiart (1935)
(Figure 76, plate 13.)

Sphaerobothrium differs from *Phyllobothrium* in the absence of accessory suckers on the bothridia and from *Anthobothrium* in that the margins of the bothridia are very much folded. According to Euzet (1959) *S. lubeti* is 80·0 to 250·0 mm long and 2·0 to 4·0 mm broad. The scolex bears four very much folded bilobed bothridia as in *P. lactuca*. It is apolytic, the free proglottids being 4·0 mm long × 2·0 mm broad. The genital pore is marginal and about midway along the length of the proglottid. 120 to 160 testes are present, about 20 of which are post-vaginal. The eggs measure 0·150 mm in diameter.

A thorough comparison should be made of *S. lubeti*, the specimens described by Guiart (1935) as *P. crispatissimum* and the following five species.

FIGURES 59 to 63. Immature specimens (post-plerocercoids?) of various *Phyllobothrium* species and *Crossobothrium* (*Phyllobothrium*?) sp. from elasmobranchs; drawn to same scale

FIGURE 59. *P. minutum* sp.nov. from *Raja fullonica*.
FIGURE 60. *Crossobothrium* (*Phyllobothrium*) sp. from *Squalus acanthias*.
FIGURE 61. *P. lactuca* from *Mustelus mustelus*.
FIGURE 62. *P. thridax* from *Squatina squatina*.
FIGURE 63. *P. britannicum* sp.nov. from *R. montagui*.

FIGURES 64 to 71. Bothridia from mature adults of various *Phyllobothrium*, *Crossobothrium* and *Monorygma* spp., all drawn to same scale.

FIGURE 64. *Crossobothrium* (*Phyllobothrium*?) sp. from *Spinax spinax*.
FIGURE 65. *C.* (*Phyllobothrium*?) sp. from *Squalus acanthias*.
FIGURE 66. *Monorygma* (*Phyllobothrium*?) sp. from *Scyliorhynus caniculus*.
FIGURE 67. *Phyllobothrium lactuca* from *Mustelus mustelus*.
FIGURE 68. *Phyllobothrium* sp. from *Raja batis*.
FIGURE 69. *Phyllobothrium thridax* from *Squatina squatina*.
FIGURE 70. *P. britannicum* n.sp. from *R. montagui*.
FIGURE 71. *P. minutum* n.sp. from *R. fullonica*.

2. **Phyllobothrium blakei** Shipley & Hornell, 1906

Phyllobothrium blakei, originally found in *Trygon kuhli* in Ceylon, may be a member of *Sphaerobothrium*. Shipley & Hornell (1906) described the bothridia as having 'thickened edges, which are so twisted they show numerous little bays and rounded recesses which at first sight might easily be taken for small circular suckers. These bothridia spring with practically no stalk from the edge of a hollow which show some circular markings as if there were here two rings of circular muscles.' Southwell & Prashad (1920) referred to *P. blakei* from *T. khuli* in Ceylon, while Southwell (1925) placed *P. blakei* as a synonym of *Anthobothrium pulvinatum*; but Southwell (1930) referred to *P. blakei* as a *species inquirenda*.

3. **Phyllobothrium compacta** Southwell & Prashad, 1920

Southwell & Prashad (1920) gave a very brief illustrated description of *Phyllobothrium compacta*, from *Trygon kuhli* at Anaivilundum Paar, Ceylon. They stated that accessory suckers are absent from the bothridia. Their specimens should, therefore, be compared with *P. blakei*. Southwell (1930) referred to '*P. compactum* Southwell & Prashad, 1920' and to the scolex having 'a very compact appearance owing to the sessile nature of the large fleshy and well-developed bothridia'. He stated that 'although an accessory sucker could not be seen, this species is identical with *P. lactuca*.'

4. **Phyllobothrium pammicrum** Southwell, 1915

Previous records of *Phyllobothrium pammicrum* Shipley & Hornell, 1906, are as follows: *Carcharias melanopterus*, Ceylon, Shipley & Hornell (1906); *Urogymnus asperrimus*, Ceylon, Southwell (1912); *Hypolophus sephen*, Southwell (1915); *C. melanopterus*, Pearl Bank, Ceylon, Southwell (1930); *C. melanopterus*, Dutch Bay, Ceylon, Southwell & Prashad (1920); *H. sephen*, Chilka Lake, Southwell & Prashad (1920); *Urogymnus asperrimus*, Ceylon, Southwell & Prashad (1920).

Of these records the cestodes from *H. sephen* and *U. asperrimus* discussed by Southwell (1915), and Southwell & Prashad (1920) should be re-examined and compared with species of *Sphaerobothrium*. Southwell (1925) is of the opinion that *P. pammicrum* (Shipley & Hornell 1906) is a synonym of *Anthobothrium giganteum* Beneden, 1858.

5. **Anthobothrium panjadi** Shipley, 1909

Shipley (1909) published the following note: 'In Part v of the *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar*, published by the Royal Society 1906, and on page 57, I described under the name of *Anthobothrium crispum* a new species of Tape worm collected by Mr J. Hornell from the intestine of an Eagle Ray *Myliobatis maculata*. Within the last few days Mr A. Hassall of Washington has kindly pointed out to me that this specific name is preoccupied having been used by Molin for a Cestode from *Mustelus plebejius*, (*SB. Ak. Wien*. xxx, 1858, p. 135). I therefore propose to re-christen the species from Ceylon *Anthobothrium panjadi*, the specific name being the Tamil equivalent of the host.'

The host, *Myliobatis maculata*, and description given by Shipley for '*Anthobothrium crispum*' suggest a similarity with *Sphaerobothrium lubeti*. A transfer of *A. panjadi* to this genus should therefore be considered when our knowledge of the species is increased. Southwell (1930) referred to '*Phyllobothrium panjadi* (Shipley & Hornell 1909)', see Shipley (1909) with *A. crispum* Shipley & Hornell 1906, as a synonym and with *Aetomyloeus maculatus* and *Stoasodon narinari* in Ceylon as hosts; an examination of these for cestodes should be rewarding.

6. **Anthobothrium pulvinatum** Linton, 1890

Linton (1890, p. 759) referred to having previously described this species as a member of a new genus, *Rhodobothrium*, 'in a communication to the *American Journal of Science and Arts*, March, 1889'. His figures and description of *Anthobothrium pulvinatum*, especially of the margins of the bothridia entire at the base, with their upper edges frilled or ruffled and their faces thrown into corrugated folds, show similarities with Euzet's description of the bothridia of *Sphaerobothrium lubeti*. Other features in Linton's description appear to support the view that *A. pulvinatum* may belong to *Sphaerobothrium*, e.g. mature adults of the species are about 550 mm long and occur in *Trygon centrura* at Woods Hole. It is apolytic, the uterus containing oval eggs measuring 0·036 × 0·028 mm.

VII. Larvae of *Phyllobothrium* in invertebrates and teleosts

The following references will be of particular significance in future work on larval phyllobothriids in invertebrates and teleosts: Dollfus (1923*a*, *b*, 1929, 1931, 1953, 1958, 1964*a*, *b*), Cleave (1927), Joyeux & Baer (1936), Jepps (1937) and Euzet (1959).

Ctenophores as hosts of phyllobothriids were discussed by Dollfus (1923*a*) who also referred to a record by Panceri in 1868 of a 'Scolex of *Phyllobothrium* in *Cydippe densa* [*C. densa* Panceri = *Hormiphora plumosa* (Sars)] at Naples'. Several records of larval tetraphyllids and tetrarhynchs in cephalopods are also discussed by Dollfus (1923*b*), including the following references to *Phyllobothrium*: (i) 'Scolex phyllobothrii' believed to be *P. dohrnii* by Monticelli in 1888, (ii) *Taenia loliginis* of Leidy (1887), a form compared with *P. tumidum* by Linton (1922), and (iii) the frequent occurrence of *Phyllobothrium* larvae in *Ommastrephes illecebrosus* and in *Loligo peali*. Dollfus (1929) discussed and figured the plerocercoids of a *Phyllobothrium* sp. in the stomach of *L. loligo* at Arcachon. They were 10·0 mm long with four bothridia having frilly margins and apical accessory suckers measuring 0·200 mm in diameter; the apical sucker of the scolex is 0·150 mm in diameter. The bothridia measured 0·170 mm long × 0·210 to 0·270 mm broad. Joyeux & Dollfus (1931) briefly described and figured the plerocercoids of *Phyllobothrium* sp., from *L. loligo*, of unknown origin, stating that they resembled those described by Dollfus (1929), but the accessory suckers are 0·260 to 0·280 mm, and the apical sucker 0·100 to 0·110 mm in diameter. Larval phyllobothriids were listed under several cephalopod hosts by Dollfus (1958), namely *Scolex phyllobothrii* and *P. loliginis* in *O. sagittatus*; plerocercoids of *P. tumidum* in *Illex illecebrosus conidetti* and in *Todaropsis eblane*; plerocercoids of *Phyllobothrium* in *Sepia elegans*, *L. loligo* and *L. vulgaris*; the plercocercoids of *Phyllobothrium*, possibly *P. latuca*, in *S. officinalis*; and *Phyllobothrium* sp. in *S. elegans*. Dollfus (1964*b*) summarized information on larval phyllobothriids in marine invertebrates.

Cleave (1927) briefly described and figured *Scolex* sp. from the ctenophores *Pleurobrachia pileus*. Joyeux & Baer (1936) referred to larval cestodes in ctenophores and cephalopods, including *Scolex acalepharum* Sars, 1845; *Tetrastoma playfairi* Forbes, 1840: *Scolex pleuronectis* Muller, 1788; *Scolex* sp. Dollfus, 1923, and three records of *Phyllobothrium*. *Phyllobothrium* sp. Joyeux & Baer, 1936, which is briefly described and figured, occurs in great abundance in the stomach of *Todaropsis eblanae* at Concarneau. In addition over sixty host species, mainly teleosts, were listed by Joyeux & Baer (1936) for '*Scolex pleuronectis*' which is now generally accepted as representing a complex of genera and species. Dollfus (1953) stated that the forms grouped under the name '*S. polymorphus*' are the young plercercoid larvae of diverse Onchobothriidae and Phyllobothriidae. Jepps (1937) briefly described some very early stages in the development of larval cestodes in *Calanus*, stating that infected copepods are fairly common in the Clyde area of Britain. Euzet (1959, pp. 221–237) made valuable speculations on the probable course of the life-history in tetraphyllideans; his comments are soundly based on detailed observations of adult Tetraphyllidea in selachians and larval forms, recovered experimentally and/or naturally, in crustaceans, cephalopods and teleosts.

The following larvae of *Phyllobothrium* are known from teleosts:

1. **Phyllobothrium caudatum** (Zschokke & Heitz 1914)

(Figures 22, 24, 25; and figure 107, plate 17.)

Previous records: *Oncorhynchus*, White Sea, Barents Sea and Baltic, Dogiel, Petrushewski & Polyanski (1961); *O. nerka*, North Pacific, Margolis (1963); *Coregonus ussuriensis*, Russia, Zenejev (1936); *Mesocottus haitjei*, Russia, Zenejev (1936); *O. keta*, Russia, Zenejev (1936); *O. gorbuscha* Russia, Zenejev (1936); *Parasilurus asotus*, Russia, Zenejev (1936).

The species described by Zschokke & Heitz (1914) as *Pelichnibothrium caudatum* from salmon in Kamchatka, U.S.S.R., is the subject of much controversy in relation to *P. speciosum* Monticelli, 1889. The latter was accepted by Southwell (1925), with *P. caudatum* as its synonym. As Southwell reproduces details from the original account by Zschokke & Heitz (1914) and includes a figure of *Phyllobothrium caudatum* no further account will be given here.

I agree with Margolis (1963) in identifying larval phyllobothriids from *Oncorhynchus nerka* in the North Pacific and adjacent seas as *P. caudatum*, especially as a representative sample of the salmon he examined was obtained from two U.S.S.R. (Kamchatka) rivers and from close to the east coast of Kamchatka, the type locality. From a preliminary examination of a sample of the cestodes collected by Margolis no obvious differences from *P. caudatum* were observed.

2. **Phyllobothrium loliginis** (Leidy 1887)

[? larva of *P. tumidum* Linton, 1922]

Previous records: *Ommastrephes illecebrosus*, Dollfus (1923*b*); *O. sagittatus*, Leidy (1887); *O. illecebrosus*, Woods Hole, Massachusetts, Linton (1897*a*); *Hemitripterus americanus*, *Leptocephalus conger*, *Loligo pealii*, *Lophius piscatorius*, *Lopholatilus chamaeleonticeps*, *Merluccius bilinearis*, *Mustelus canis*, *Ommastrephes illecebrosus*, *Paralichthys dentatus*, *P. oblongus*, *Phycis chuss*, *P. tenuis*, *Pollachias virens*, *Raja laevis*, *R. ocellata*, *Spheroides maculatus*, *Squalus acanthias*, *Thunnus thynnis* and *Xyphias gladius*, Linton (1922); *Paralichthys dentatus* and *P. oblongus*, Ronald (1959).

The history of *P. loliginis* is complicated as is suggested by the above list of previous references to the species. This list will not be further discussed at present, except for comments on some of the information given by Linton (1922). He recorded immature *P. loliginis* from nineteen host-species including four selachians, but Linton concluded that its development to the adult stage in *Mustelus canis*, *Squalus acanthias*, *Raja laevis* and *R. ocellata* is highly improbable. Adults of *P. loliginis*, which are described as *P. tumidum*, were found in *Carcharodon carcharias* and *Isurus dekayi*. Evidence which suggests that *P. tumidum* is the probable adult stage of *P. loliginis* is based on similarities in structure of the scolex. In making this comparison Linton interprets the terminal sucker of *P. loliginis* as 'an evanescent, larval structure, as in *Scolex polymorphous*'. He states also that 'The feature which presents the greatest difficulty is that part of the scolex which is posterior to the bothridia. In *P. loliginis* there is a rather conspicuous neck portion which is sharply marked off from the strobila proper. In *P. tumidum* the strobila appears to begin close to the bothridia, although segments do not make their appearance at once. In the structure of the bothridia and auxillary suckers, and in the axial portion of the scolex, there is close agreement.'

Further comments on *P. loliginis* and *P. tumidum* are given by Dollfus (1964*b*).

3. **Phyllobothrium rudicornis** Drummond, 1838

Ronald (1959, p. 70) refers to *Phyllobothrium rudicornis* as a larval cestode in *Hippoglossus hippoglossus* as having been first described by Drummond (1838). No evidence exists at present for rejecting this name.

4. **Phyllobothrium salmonis** Fujita, 1922

The status of *Phyllobothrium salmonis* Fujita, 1922, relative to *P. speciosum* and *P. caudatum*, is controversial. Further examination of material from the type hosts and localities is essential to solve this problem. Fujita (1922) recorded the species from *Onchorhynchus keta* and *O. masou* in Japanese waters. Yamaguti (1959) listed *P. salmonis* as a phyllobothriid larva in *Onchorhynchus* sp., Japan, but suggested that it may be a synonym of *Pelichnibothrium speciosum*. The adult of *P. speciosum* from *Prionace glauca* in the Pacific was described and figured by Yamaguti (1934) and in the same paper he briefly described *Pelichnibothrium* larvae, from *Loligo* sp. and *Salmo keta* in Japanese waters; in a brief discussion of the larvae they were provisionally assigned to *P. speciosum*, with *P. caudatum* Zschokke & Heitz, 1914, and *Phyllobothrium salmonis* Fujita, 1922, as synonyms. Riser (1956), however, described the plerocercoid larvae of *Pelichnibothrium speciosum*, from *Alepisaurus ferox*, off Carmel, California, and made the following comments. The larvae described by Zschokke & Heitz (1914) as *P. caudatum* and the '*Pelichnibothrium larvae*' of Yamaguti (1934) were not strobilate, and possibly, when phyllobothriid life-histories become known, may prove to be plerocercoids of *Phyllobothrium*. Riser's description is of particular interest in that he refers to specimens of *Pelichnibothrium speciosum* as measuring up to 1450 mm, with a tail constituting 640 mm of the length; the worms being strobilate and the proglottids containing complete sets of genitalia. About 300 to 400 testes were present. This possibility of the occurrence of a mature tetraphyllidean in a teleost is of considerable interest; but Riser stated that although the scolex of *Pelichnibothrium* is that of a phyllobothriid, the relationship of the vitellaria and uterus to the longitudinal muscles, and the nerve ring lying internal to the vitellaria, makes it impossible to place the species at present. He referred to the remarkable similarity in arrangement of organs to some of the aberrant proteocephalids described by Woodland in 1933. Riser also pointed out that Yamaguti (1934), in his description of *P. speciosum* from *Prionace glauca*, referred to only 200 testes, and stated that 'if this animal normally parasitizes *P. glauca* as indicated by Yamaguti's work, it has a peculiar life-history pattern. *P. glauca* was the most frequently autopsied shark from Monterey Bay, California, during four years of work on cestodes of elasmobranch fishes and *Pelichnibothrium* was never encountered in any species of shark.'

In view of this controversy regarding *P. speciosum* it was decided to accept *Phyllobothrium salmonis* in the present revision; it may fall as a synonym of *P. caudatum* as our knowledge of phyllobothriid larvae from salmon in Canadian, Russian and Japanese water increases. There is increasing evidence, however, that *Pelichnibothrium speciosum* may be widely separated from *Phyllobothrium caudatum* and *P. salmonis*.

Wardle (1932) briefly referred to *Phyllobothrium* sp. from 'all species of *Oncorhynchus*, straits of Georgia, British Columbia', stating that it is identical to *P. salmonis* and that it resembles '*Phyllobothrium dohrnii* Oerley described as *O. velamentum* by Yoshida (1917)'. Wardle (1933) referred to *P. salmonis* Fujita, 1922, as a *larva inquirenda* which is particularly common in *Oncorhynchus* spp., especially *O. gorbuscha* in British Columbia; he stated that the adult had been recorded as *Phyllobothrium keta* by Canavan (1928), from a specimen of *O. keta* in Alaskan waters. Wardle & McLeod (1952, p. 252) accept *P. ketae* as a valid species despite its peculiar distribution as a mature adult in a teleost. In this revision, however, evidence will be given for rejecting *P. ketae*.

5. **Phyllobothrium (Pelichnibothrium?) speciosum** Monticelli, 1889

Pelichnibothrium speciosum was discussed above relative to *P. caudatum* and *P. salmonis* and mainly in view of its controversial systematic status was considered distinct from those two species. Joyeux & Baer (1961, p. 363), however, briefly referred to a figure of *Pelichnibothrium* sp. (larva of *Phyllobothrium*) of *Oncorhynchus kisutch*. Bikhovskaya-Pavlovskaya *et al.* (1962) described *P. speciosum* with *Phyllobothrium caudatum* as its synonym. They gave the following information. The larvae reach a length of 5 to 24 mm and a width of 0·6 to 1·50 mm in the anterior region of the strobila. The head is 0·70 to 1·0 mm in

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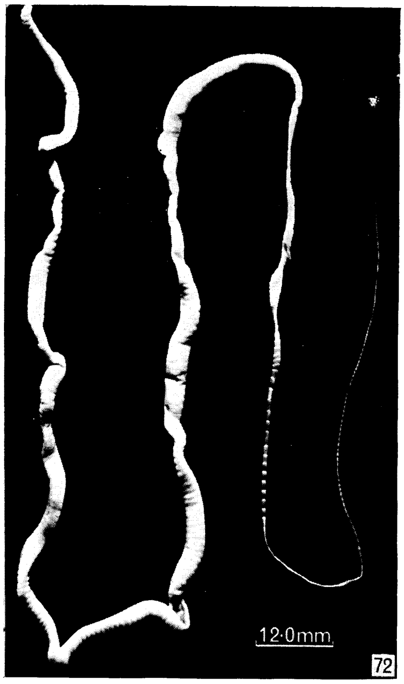
DESCRIPTION OF PLATE 13

FIGURE 72. *Phyllobothrium thridax* from *Squatina squatina*.
FIGURE 73. *P. britannicum* sp.nov. from *Raja montagui*; immature specimen (post-plerocercoid?).
FIGURE 74. *Phyllobothrium lactuca*, adult.
FIGURE 75. *Phyllobothrium minutum* sp.nov. from *Raja fullonica*, immature specimen (post-plerocercoid?).
FIGURE 76. *Sphaerobothrium lubeti*, adults showing form of scolex and strobila.
FIGURES 77 *a* to *e*. *Phyllobothrium* sp. plerocercoids from *Trachypterus arcticus*.
FIGURES 78 *a*, *b*. *Phyllobothrium* sp. plerocercoids from *Paralepis coregonoides*.
FIGURES 79 and 80. *Crossobothrium* (*Phyllobothrium*?) sp. 3. from *Spinax spinax*.
FIGURE 79. Whole strobila.
FIGURE 80. Scolex.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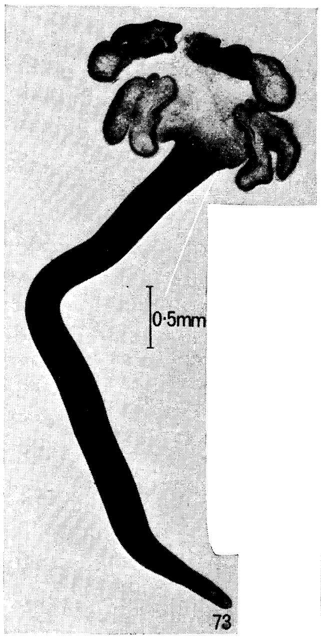
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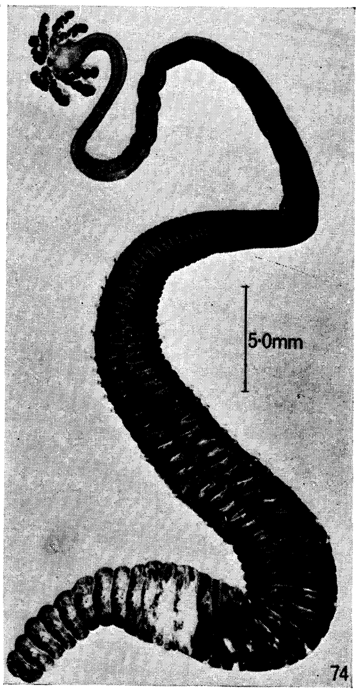
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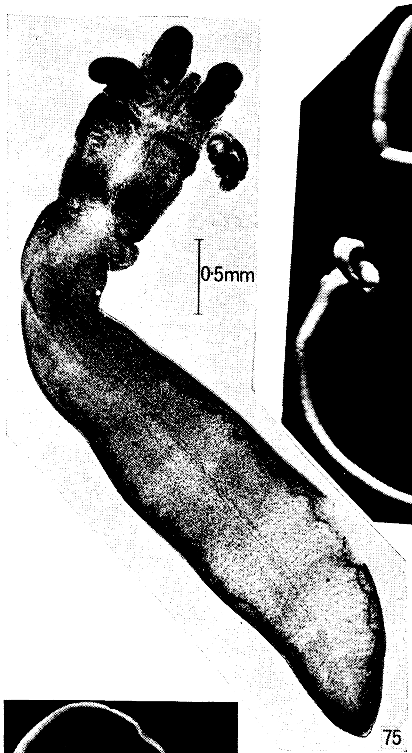
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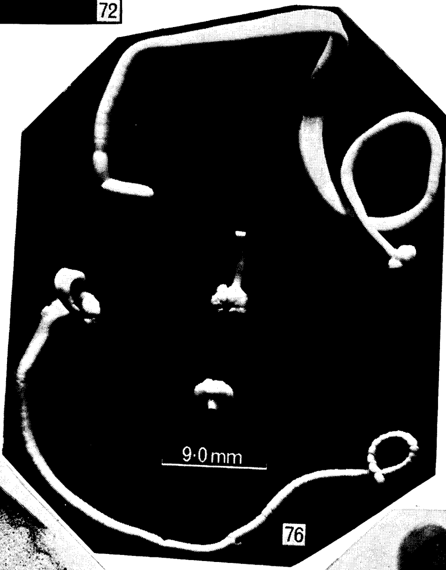
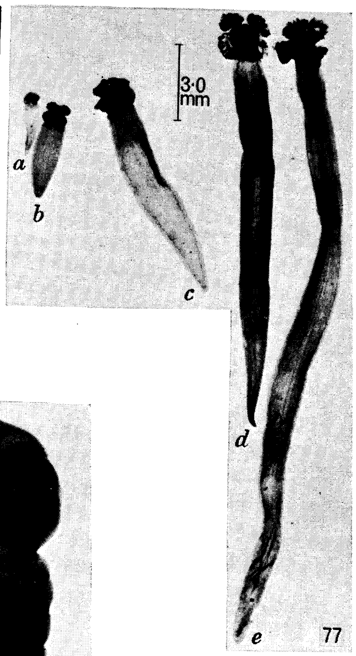

9·0mm
76


3·0 mm
a
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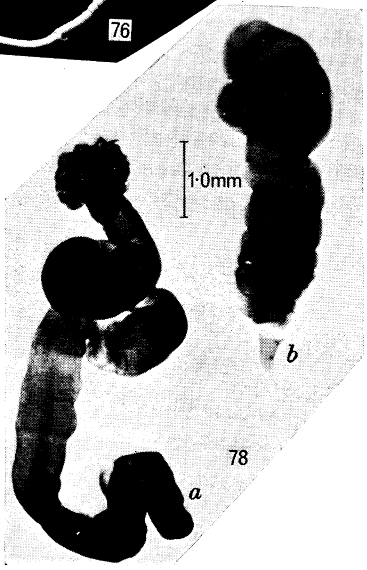
77


1·0mm
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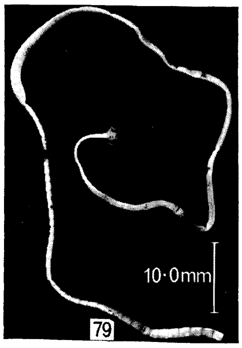
a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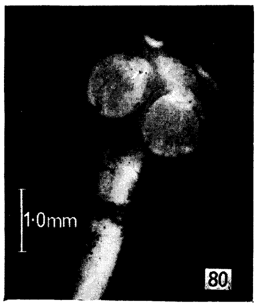
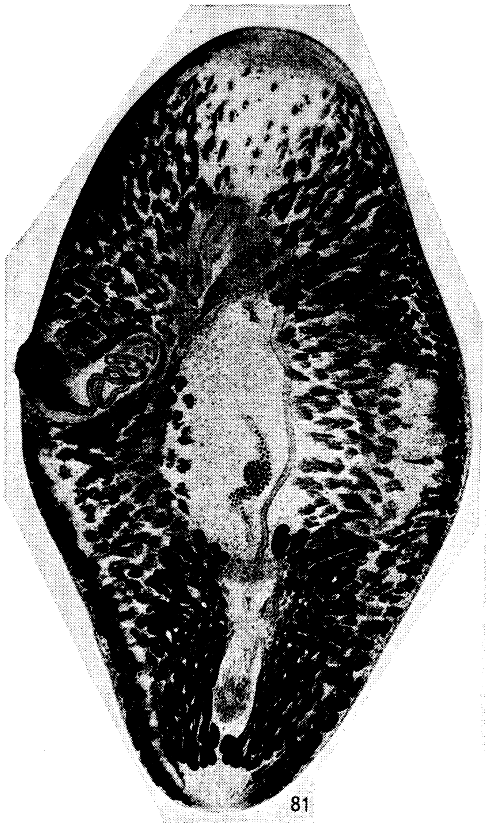
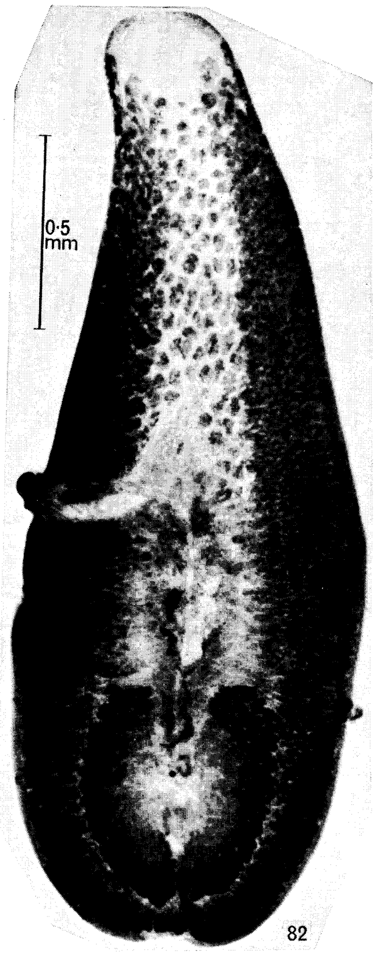

1·0mm
80

(*Facing p.* 274)





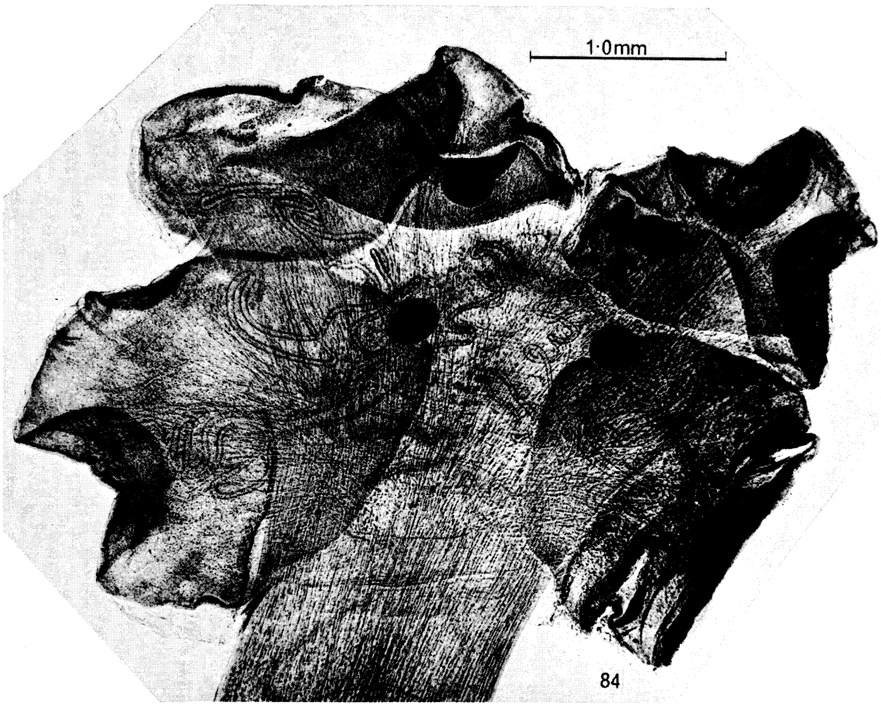
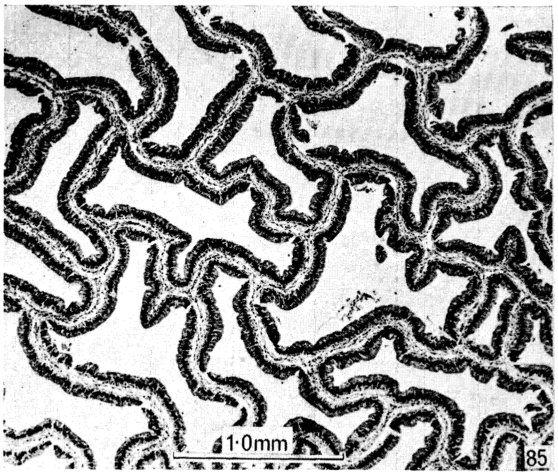
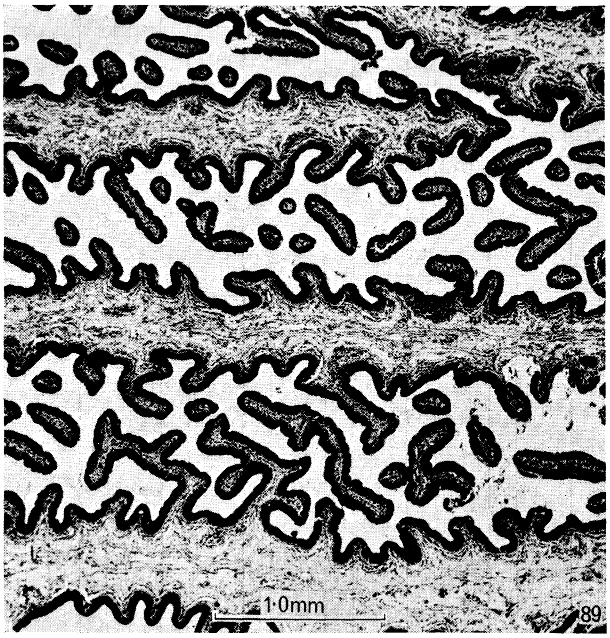
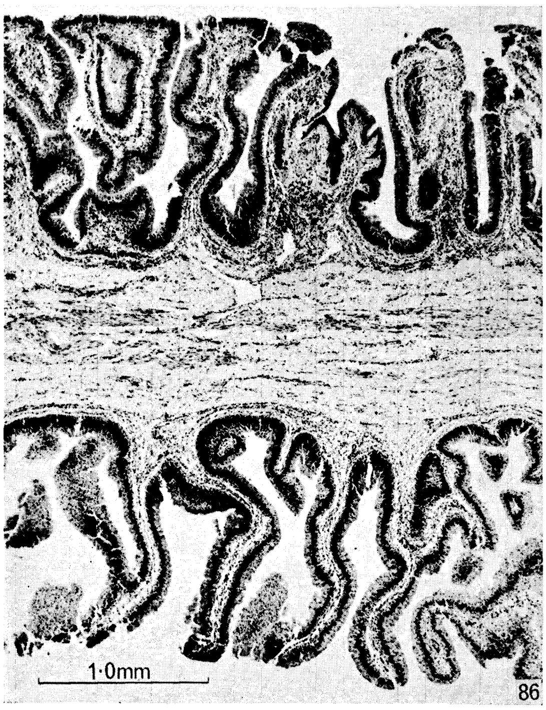


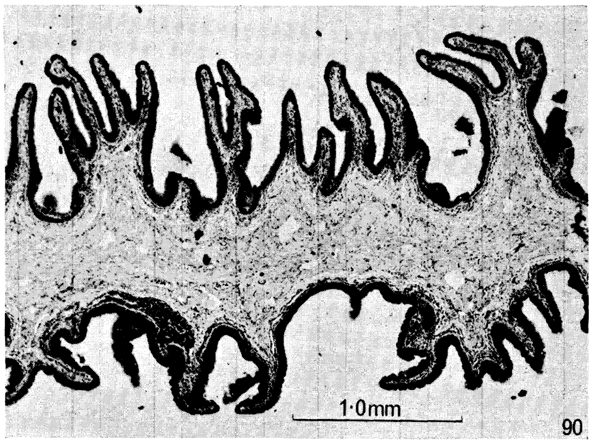
FIGURE 81. *Phyllobothrium britannicum* sp.nov., proglottid.
FIGURE 82. *Monorygma* (*Phyllobothrium*?) sp. from *Scyliorhinus caniculus*, proglottid.
FIGURE 83. *Phyllobothrium sinuosiceps*, proglottid.
FIGURE 84. *Crossobothrium* (*Phyllobothrium*?) sp. 3 from *Squalus acanthias*, scolex.

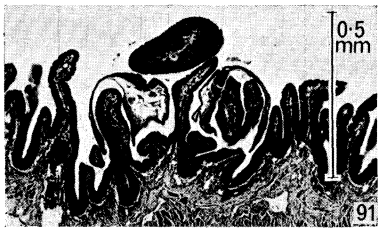
FIGURE 91. Vertical section of the gut mucosa of *Mustelus mustelus*; from posterior region of intestine, i.e. area of attachment of *Orygmatobothrium musteli*.
FIGURE 92. *P. lactuca*, scolex.

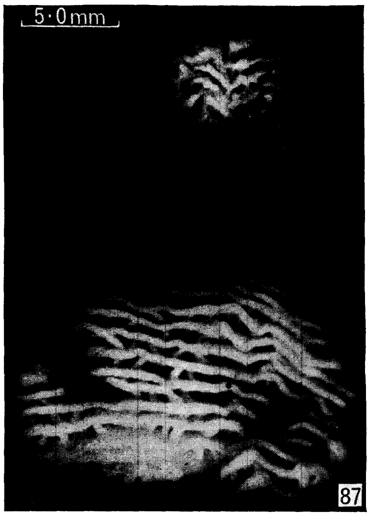


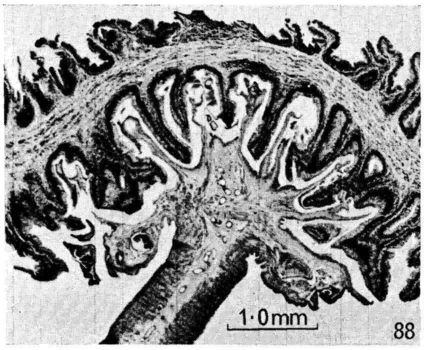


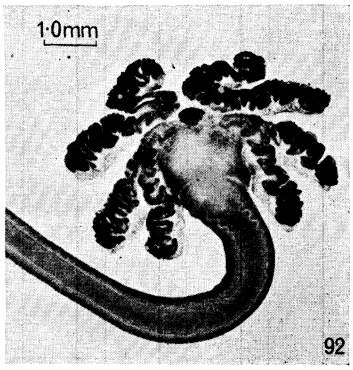










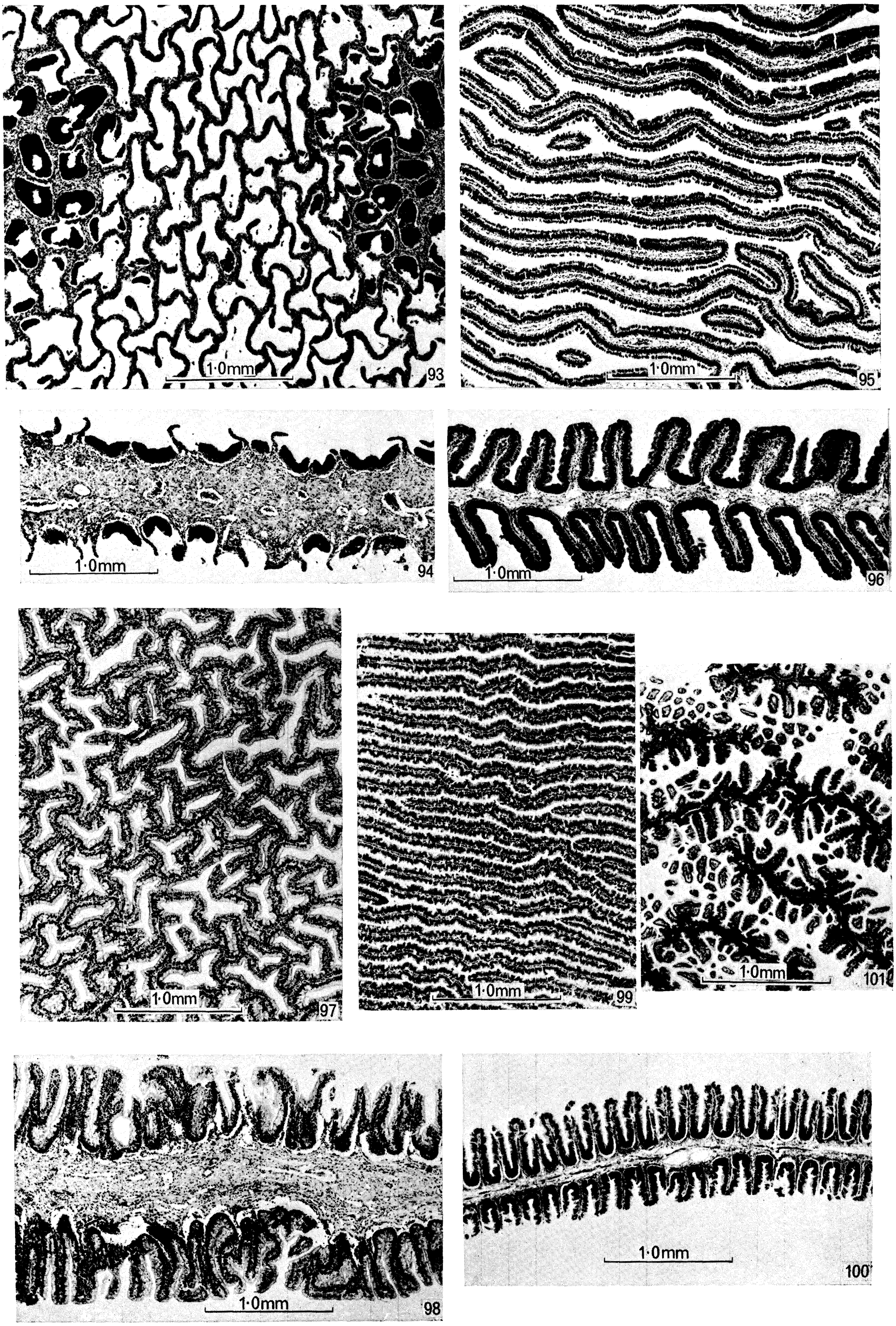


Figures 85 and 86. Facial and vertical sections of the gut mucosa of *Hexanchus griseus*; from anterior spiral of intestine, i.e. area of attachment of *Phyllobothrium sinuosiceps*.

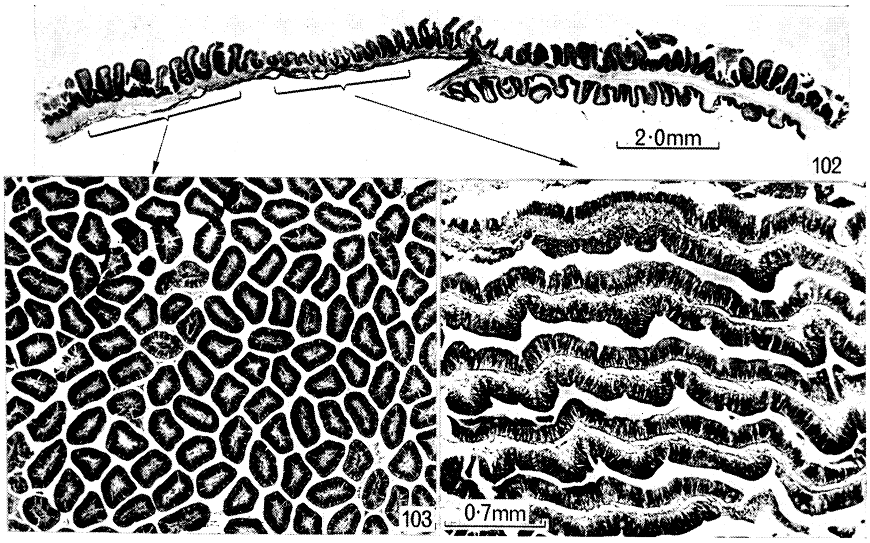
Figure 87. *P. sinuosiceps*, scolex photographed alongside piece of mucosa from anterior spiral of intestine of *H. griseus*.

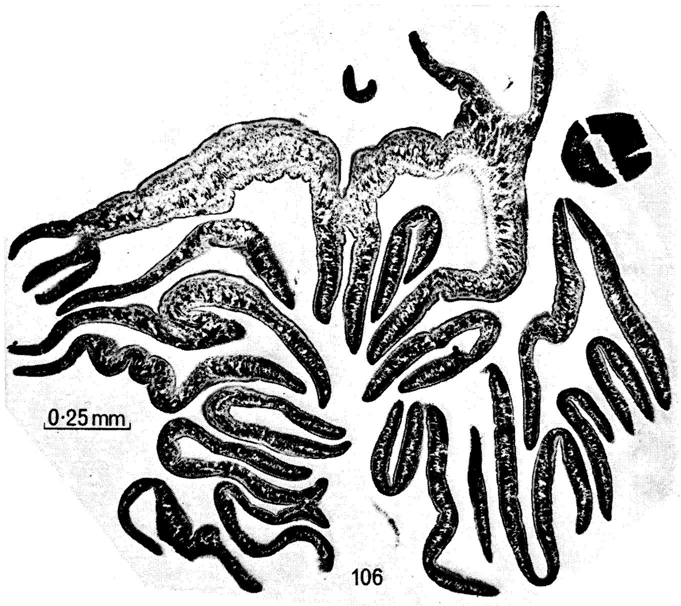
Figure 88. Vertical section of *P. sinuosiceps* attached to mucosa of *H. griseus*.

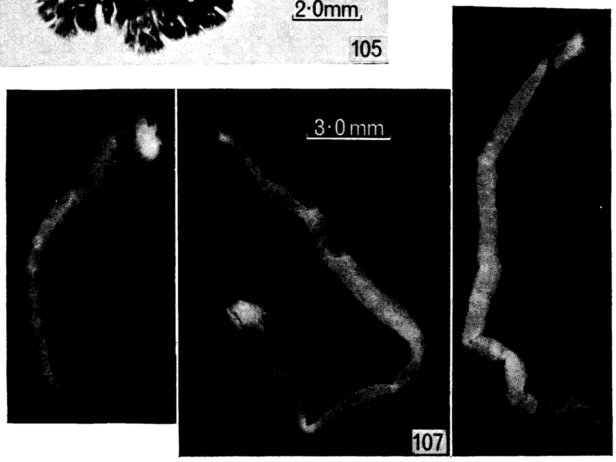
Figures 89 and 90. Facial and vertical sections of the gut mucosa of *Mustelus mustelus*; from anterior spiral of intestine, i.e. area of attachment of *P. lactuca*. (*Continue at foot of plate* 14.)

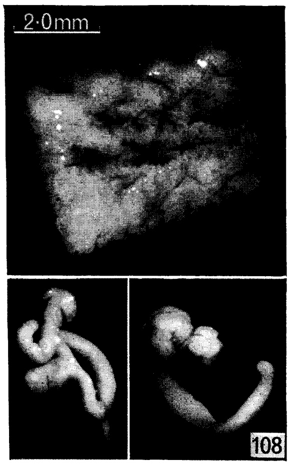


FIGURES 93, 94. Facial and vertical sections of the gut mucosa of *Squalus acanthias*.
FIGURES 95, 96. Facial and vertical sections of the gut mucosa of *Scyliorhinus stellaris*.
FIGURES 97, 98. Facial and vertical sections of the gut mucosa of *S. squatina*.
FIGURES 99, 100. Facial and vertical sections of the gut mucosa of *Eugaleus galeus*.
FIGURE 101. Facial section of the gut mucosa of *Raja batis*.









Figures 102–104. Variation in a small area of the gut mucosa of *Chimaera montrosa*.

Figure 105. *Gyrocotyle* showing posterior adhesive organ.

Figure 106. Section through posterior adhesive organ of *Gyrocotyle*.

Figure 107. *Phyllobothrium caudatum* from *Oncorhynchus nerka*, plerocercoids.

Figure 108. *Phyllobothrium* sp. in *Paralepis coregonoides*, plerocercoids and piece of intestinal mucosa of the host to which they are attached.

diameter; in small specimens the bothridia have smooth edges while in large individuals the edges become ruffled. The diameter of the apical sucker is 0·19 to 0·25 mm and that of the apical suckers of the acetabula are 0·19 to 0·41 mm. The anterior part of the body is condensed with marked strobilization, in the larger specimens, and the posterior part is uniformly delicate. *P. speciosum* occurs in the intestine and pyloric caeca of marine and anadromous salmonid fishes: *Coregonus ussuriensis*, *Oncorhynchus gorbuscha*, *O. keta*, *O. kisutch*, *O. nerka*, *O. tschwytcha*, *O. masu*, *Salvelinus malma* and *S. leucomaenis*, all in the Amur river basin.

6. **Phyllobothrium** sp. Linton, 1901

A plerocercoid of *Phyllobothrium* from *Merluccius merluccius* at Woods Hole was briefly described and figured by Linton (1901). The three specimens resembled larvae found in the common squid in the area; they had a scolex of four bothridia with crumpled margins, accessory suckers and an apical sucker. The largest specimens were 44 mm long, of which the scolex occupied 3 mm and the 'neck' 23 mm.

7. **Phyllobothrium** sp. Subhapradha, 1948

Phyllobothrium sp. of Subhapradha (1948) from *Uroconger lepturus* is briefly referred to by Anantaraman (1963).

8. **Phyllobothrium** sp. Hutton, 1961

Hutton (1961), in a brief illustrated description of *Phyllobothrium* sp. plerocercoids, from *Regalecus glesne* in Florida waters, gave the following measurements which may be of diagnostic value: pars. antica scoleces, 1·95 mm; pars postica scoleces, 9·75 mm; pars bothridialis 0·78 mm; pars proliferens, 1·17 mm; length of myzorhynchus, 0·20 × 0·25 mm; accessory sucker 0·190 mm in diameter.

9. **Phyllobothrium** sp. in **Trachipterus arcticus**

(Figures 77*a* to *e*, plate 13.)

The species here referred to as *Phyllobothrium* sp. from *Trachipterus arcticus* show some features in common with *Phyllobothrium* sp. Hutton, 1961. The host, a 112 cm female, was obtained in February 1959, about 15 miles south-east of Fuglo Corner, Faroes.

10. **Phyllobothrium** sp. in **Paralepis coregonoides borealis**

(Figure 78, plate 13, and figure 108, plate 17.)

It is hoped that the specimens here referred to as *Phyllobothrium* sp. in *Paralepis coregonoides borealis* will be discussed in greater detail elsewhere. The host was obtained in August 1964 at 62° N 33° W at a depth of 200 m.

11. **Phyllobothrium** sp. Linstow, 1878

Stiles & Hassall (1912) listed *Phyllobothrium* sp. Linstow, 1878, in *Clupea harengus*, *Gobius niger* and *Labrus maculatus*.

12. **Phyllobothrium** sp. Monticelli, 1887

Parona (1900) referred to *Phyllobothrium* sp. Monticelli, 1887, from *Alosa sardinia* in the Mediterranean.

13. **Phyllobothrium** sp. Margolis, 1952

Ronald (1959) referred to *Phyllobothrium* sp. Margolis, 1952, from *Hippoglossus elassodon.*

VIII. Larvae of *Phyllobothrium* in mammals

The literature on larval cestodes in Cetacea is extensively reviewed by Dollfus (1964*a*) and arranged in chronological order, from 1864 to 1955; in an appendix to the paper he includes information on larval cestodes in Pinnipedia. Sixty-seven references are cited by Dollfus, and the present account, therefore, is restricted to some of the facts given in the more relevant papers on the three generally accepted species and on some unnamed forms; for completeness it is considered essential to include details of this nature in a revision of *Phyllobothrium.*

1. **Phyllobothrium chamissonii** (Linton 1905)

Linton (1905*b*) referred to two kinds of cysts from the mesentery of a skunk porpoise, *Lagenorhynchus acutus,* caught at 'Menemsha Bight, Vineyard Sound'. He stated that the cysts from *Delphinus delphis,* described by Beneden (1870), undoubtedly belong to *Phyllobothrium* and are identical with *Cysticercus delphini* of Rudolphi (1810, vol. 2, p. 36); but that *C. delphini* of Rudolphi (1810, p. 551) are identical with the form described by Linton (1905*b*) as *Taenia chamissonii.* Linton emphasized that he agreed with Cobbold, who believed that the final host of *Cysticercus delphini* is a shark, and with Rudolphi (1810, p. 551) that the final host of *T. chamissonii* is more likely to be a predaceous mammal, e.g. the killer whale, *Orcinus orca.* Baylis (1932) stated that *Monorygma chamissonii* (Linton 1905), Meggitt, 1924 is possibly identical with *M. grimaldi* (Moniez 1889) and that *M. delphini* (Gervais 1870), Meggitt, 1924 occurs in the diaphragm of *Delphinus delphis* and is synonymous with *Stenotaenia delphini* Gervais, 1870. The confusion concerning the identity of plerocercoids from marine mammals is summarized by Dollfus (1964*a*). He concluded that they fall into the two groups recognized by Baer in 1932, namely, '*grimaldii*' and '*delphini*'; members of the former having scoleces at the end of long (12 cm to 1 m) filament-like invaginations and the latter at the end of shorter invaginations (12 to 15 mm). Dollfus stated that Linton (1905*b*), Baylis in 1919 and Guiart (1935) described plerocercoids of the '*grimaldi*' type; and described and figured as *Monorygma delphini,* a cyst of this group, found in the peritoneum of the cetacean *Tursiops truncatus* at Banyuls, France.

As Linton (1905*b*) appears to be the first to have emphasized the existence of two kinds of cestode cysts in marine mammals and described one species as '*Taenia chamissonii*', this specific name is provisionally accepted in the present revision. As already pointed out by Dollfus (1964*a*) '*T. chamissonii*' may be a member of *Monorygma* but in the present revision the views of Southwell & Walker (1936) are accepted who mentioned five definite species of larval cestodes, including *P. chamissonii,* from Cetacea and Phocidae.

2. **Phyllobothrium delphini** (Bosc 1802)

Previous records: *Mesoplodon bidens,* Belgium, Adam (1938); *Delphinus delphis,* Falkland Islands, Baylis (1932); *Grampus griseus,* Falkland Islands, Baylis (1932); *Tursiops truncatus,* Falkland Islands, Baylis (1932); *Globicephala melaena,* Cornwall, Baylis (1939); *D. delphis,* Beneden (1870); *Physeter catadon*, Falkland Islands, Hamilton (1934); *Kogia breviceps*, Australia, Johnston & Mawson (1939); *P. catadon*, Margolis & Pike (1955); *D. delphis*, Meggitt (1924); *Grampus griseus*, Meggitt (1924); *P. tursio* Meggitt (1924); *P. catadon*, Sokolov (1955); *Arctocephalus australis*, Falkland Islands, Southwell & Walker (1936).

The history of *Phyllobothrium delphini* is confused and extremely complicated, possibly because of the difficulties in distinguishing *Monorygma* from *Phyllobothrium* and of the different hosts, localities and authorities involved. The following is a summary of the difficulties.

Meggitt (1924) referred to *Phyllobothrium delphini* (Rudolphi 1810) and listed four synonyms, three hosts and ten authors who had published information on the species, from 1810 to 1920.

Southwell (1925), however, listed '*Phyllobothrium delphini* Gerv., in Carus, 1885 (= *Taenia chamissonii*, Linton, 1905)' as a doubtful species.

Baylis (1932) accepted *Monorygma delphini* (Gervais 1870), Meggitt, 1924; *Scolex delphini* Stossich, 1898, from the rectum of *Grampus griseus*; and *Phyllobothrium delphini* (Bosc 1802), Gervais, 1885. For this last-named species he gave seven synonyms and cited thirteen references to twelve authors who had discussed the species.

Guiart (1935) described *Phyllobothrium delphini* (Bosc 1802), with a list of nine synonyms, from *Delphinus delphis* in the Atlantic (Azores and Finisterre); he also referred to specimens from *Globicephala melaena* in the Mediterranean and from *Physeter macrocephala*, north-west of the Azores.

The information given by Southwell & Walker (1936) is worthy of further consideration. These authors discuss *P. delphini* (Bosc 1802), Gervais, 1885 in detail, compare it with closely related species and remark on its probable life-history and adult stage. Five specimens found in the musculature of the abdominal wall of a Falkland Islands fur seal, *Arctocephalus australis*, are described and figured. Four membranaceous bothridia with thickened margins, each wrinkled and folded exactly as in *P. lactuca*, are present. The specimens measure up to 32 mm long, comprising a bladder 18 mm long, a distinct neck 12 mm long and a head 2 mm long × 3 mm broad. The diameter of the accessory sucker is 0·20 to 0·35 mm and that of the apical sucker, which is placed on a prominence termed a myzorhynchus, is 0·12 to 0·15 mm.

Southwell & Walker discussed the species given by Baylis (1932), Guiart (1935), Baer (1932) and other records of larval cestodes from Cetacea, including *Phyllobothrium* sp. Rennie & Reid, 1912, from the blubber of *Ogmorhinus weddelli* in which suckers are said to be absent. At present I agree with Southwell & Walker, who emphasized that it should be obvious from the lists given by Baylis, Guiart and by Baer that the synonymy of what is generally known as *P. delphini* is most involved, and that it is impossible to decide with any degree of certainty which larvae the various authors were dealing with; in many instances the description given is inadequate and the specific characters are not given.

In a discussion of the life-cycle of *P. delphini* Southwell & Walker referred to specimens from *Hydrurga leptonyx* and *Otaria bryonia* as having a terminal sucker, this being the first record of a fifth sucker in the species. They concluded that a terminal sucker is present in young 'cysticerci' but that when it has grown to its full size it disappears. Their further conclusion, however, is unacceptable at present, i.e. they 'agree with

Linton that the larval form known as *Phyllobothrium delphini* (Bosc, 1802) = *Phyllobothrium loliginis* (Leidy 1887), found in seals, dolphins, whales and squids, becomes adult in the man-eating and mackerel sharks and that the adult worm is *P. tumidum* Linton, 1922. No other adult *Phyllobothrium* is known having a scolex like that of *Cysticercus delphini*. If our conclusion is correct then *P. tumidum* is a synonym of *P. delphini*.' The scolex illustrated in the present revision, however (figure 20), shows some features in common with Southwell & Walker's figure 2, the main difference being the apparent absence of suckers in that shown here.

Sokolov (1955) provided information which may be of value in elucidating the life-cycle of *Phyllobothrium delphini* and/or related species. In sperm whales the larvae of *P. delphini* congregate 2 to 5 cm deep in the dermal fat layer of the skin but are absent in the fibrous layers. The larvae are particularly concentrated at the dorsal fin in males and, in females, around the genital pore. Generally females are more heavily infected. No larvae were found around the pectoral and tail fins and only occasionally on the head. The exact status of *Monorygma grimaldi* relative to *P. delphini* is still little known. *M. grimaldi* was discussed by Baylis (1932), Guiart (1935), Joyeux & Baer (1961) and Dollfus (1964*a*).

3. **Phyllobothrium inchoatum** Leidy, 1891

According to Southwell (1925, p. 152) *Phyllobothrium inchoatum* was originally described as having a depressed fusiform body from 14 to 18 mm long and 3 to 4 mm broad, the scolex being globose, quadrate and provided with four longer globose and plicated bothridia. Although Southwell stated that accessory suckers are not mentioned in the original account he placed the species as a synonym of *P. lactuca*. Baylis (1932) accepted *P. inchoatum* stating that it may be identical with *P. lactuca*: it was recorded in the blubber of *Mesoplodon bidens* in the Falkland Islands.

4. **Phyllobothrium physeteris** (Diesing 1863), Meggitt, 1924

Meggitt (1924) and Baylis (1932) accepted *Phyllobothrium physeteris* as a valid species, quoting previous records, and stated that it may be identical with *P. delphini* (Bosc.). It occurs in *Balaena mysticetus* and *Physeter catodon*; this latter was recorded as a host for cestode larvae by Markowski (1955).

5. **Phyllobothrium** sp. Johnston 1937

Johnston (1937) referred to three specimens from the blubber of a sea elephant, *Mirounga proboscidea*, Macquarie Island; they were named '*Phyllobothrium* sp. (larva) near *P. unilaterale*, (Southwell). Synonyms—*Phyllobothrium* sp. Rennie & Reid (1912), 450–1, pl. 2. figs. 13, 14; Fuhrmann (1931), 184, fig. 216'. He stated that an infection of those seals which are restricted to the Antarctic and Sub-Antarctic, e.g. *Leptonychotes weddelli* and *Mirounga proboscidea* presupposes the presence of some elasmobranch in these waters. In a discussion of the possible course of the life-history, Johnston referred to *Monorygma perfectum* a cestode of the Greenland shark, *Laemargus borealis*, which has the habit of biting pieces of the flesh of living cetaceans, and that a large shark, ?*Somniosus* sp. allied to the Greenland shark was found in 1912 by the Australian Antarctic Expedition, washed ashore on Macquariae Island. Johnston concluded that it seems likely that the cestode larvae found in the southern seal belongs to *Phyllobothrium unilaterale* or to a closely related species such as *P. tumidum*, or perhaps *P. thridax*.

6. **Phyllobothrium** spp.

Little information is contained in the literature on the following five species: *Phyllobothrium* sp. '(Carnot, 1822)', Meggitt, 1924 of *Tursiops truncatus* in the Falkland Islands, a species also referred to by Baylis (1932); *Phyllobothrium* sp. Linton, 1905, in *Lagenorhynchus acutus*, Woods Hole and in *L. acutus* in the Falkland Islands, according to Baylis (1932); *Phyllobothrium* sp. Markowski 1955 in *Lagenorhynchus obscurus* and *Physeter catodon*, a species which, according to Dollfus (1964*a*), cannot be placed in either the '*delphini*' or '*grimaldii*' group of larval cestodes from marine mammals; *Phyllobothrium* sp. Megrin, 1822, in the 'Common dolphin', according to Stiles & Hassall (1912); and *Phyllobothrium* sp. Rennie & Reid, 1912, in *Ogmorhinus weddelli*, according to Meggitt (1924).

IX. Annotated list of the little known and/or doubtful species of *Phyllobothrium*

An examination of the original descriptions and specimens, in addition to new material from the type hosts and localities, should, if possible, be carried out before the following are rejected, transferred to other genera or made synonyms of other species.

1. *Phyllobothrium crispum* (Molin 1858), with *Tetrabothrium* (*Anthobothrium*) *crispum* as synonym occurs in *Mustelus plebejus*, according to Southwell (1925, p. 178). This species is not synonymous with *Anthobothrium crispum* Shipley & Hornell, 1906, described above as *P. panjadi*.
2. *Phyllobothrium dentatum* (Linstow 1907), with *Monorygma dentatum* Linstow, 1907, as synonym, according to Southwell (1925, p. 180); from an unidentified shark in the Atlantic in the vicinity of the equator according to Johnston (1937).
3. *Phyllobothrium dipsadomorphi* Shipley, 1900, was placed in *Anthobothrium* by Southwell (1925, p. 191). It occurs in the Malagea snake, *Dipsadomorphus irregularis*, in the Western Pacific and was recorded by Hughes, Baker & Dawson (1941) from *Boiga irregularis*.
4. *Phyllobothrium floriforme* (Southwell 1912), according to Southwell (1930, p. 199), occurs in *Carcharias bleekeri* and *Carcharias* sp. in the Pearl Bank, Ceylon; but he stated that accessory suckers were absent from the bothridia.
5. *Phyllobothrium giganteum* (Ben. 1858) of Southwell (1930, p. 186) occurs in *Dasybatus walga* in the Pearl Bank, Ceylon.
6. *Phyllobothrium lintoni* (Southwell 1912) occurs in *Rhynchobatus djeddensis* and *Urogymnus asperrimus* in Pearl Bank, Ceylon, and is redescribed by Southwell (1925, p. 197).
7. *Phyllobothrium microsomum* Southwell & Hilmy, 1929, occurs in *Ginglymostoma concolor* in the Pearl Bank, Ceylon.
8. *Phyllobothrium pammicrum* Shipley & Hornell, 1906, from *Carcharias melanopterus* in the Pearl Bank, Ceylon is regarded as a *species inquirenda* by Southwell (1930, p. 207), but as already indicated above (p. 270) other records of *P. pammicrum* suggest a complex of species. In the original description it is stated that accessory suckers are absent.

9. *Phyllobothrium minutum* Shipley & Hornell, 1906, from *Carcharias melanopterus* is briefly discussed by Southwell (1925, 1930). Linton (1924*a*) described a cestode from the same host as *Crossobothrium angustum*.

10. *Phyllobothrium musteli* (Beneden 1850) was briefly referred to above in a discussion of *Phyllobothrium* sp. from *Scyliorhinus caniculus*. Drummond (1937) discussed *P. musteli* from *Mustelus antarcticus*, with *Anthobothrium musteli* Beneden, 1850, and *P. musteli* Southwell, 1925, as synonyms. He stated that the species had been fully described by Yoshida (1917). Furhmann (1931) referred to specimens of *P. musteli* from *Mustelus laevis*, while Guiart (1935) gave *Carcharias taurus* as a host.

11. *Phyllobothrium paulum* (Linton 1897) was discussed by Southwell (1925, p. 165) with *Orygmatobothrium paulum* Linton, 1897, and *O. crenulatum* Linton, 1897, as synonyms; the hosts are *Galeocerdo tigrinus* and *Dasyatis centrura*, respectively, at Woods Hole, Massachusetts.

12. *Phyllobothrium rotundum* (Klaptocz 1906) was listed by Wardle & McLeod (1952) and Yamaguti (1959), it was originally recorded as *Monorygma rotundum* from *Hexanchus griseus* in the Mediterranean. The species was discussed by Southwell (1925) and Joyeux & Baer (1936).

13. *Phyllobothrium variabile* (Linton 1889) with *Spongibothrium variabile* Linton, 1889, and *Echeneibothrium simplex* Shipley & Hornell, 1906, as synonyms and *Dasybatis kuhli* and *D. walga* as hosts in Ceylon, was discussed by Southwell (1930, p. 187). Stiles & Hassall (1912) also listed the species, but Southwell (1925) placed it as a synonym of *E. variabile*.

14. *Phyllobothrium* spp. The following are host-records of cestodes from elasmobranchs, recorded as *Phyllobothrium* sp.: *Lamna cornubica*, Belgium, Beneden (1870); *Raja laevis*, *R. ocellata*, *R. radiata* and *Squalus acanthias*, St Lawrence, Canada, Myers (1959); *Isurus glaucus*, Japan, Yamaguti (1934); and *Scymnus microcephalus*, Stiles & Hassall (1912).

X. Species previously allocated to *Phyllobothrium* but now in other genera

The following species previously allocated by various authors to the genus *Phyllobothrium*, are now generally accepted as members of other genera. The species are listed here, followed by their present systematic status, and some recent references to more detailed discussion of their taxonomy and/or biology.

1. *Phyllobothrium acanthae-vulgaris*, now *Trilocularia acanthae-vulgaris* (Olsson, 1867), see Rees (1953) & Euzet (1952*a*, 1959).

2. *Phyllobothrium rigii*, now *Calyptrobothrium rigii* Monticelli, 1893, see Polyansky (1955), Euzet (1959) and Alexander (1963).

3. *Phyllobothrium septaria*, now *Dinobothrium septaria*, see Baylis (1950), Euzet (1955, 1959) and Kulemina (1964).

XI. Invalid members of *Phyllobothrium*

Southwell (1925) discussed *Phyllobothrium brassica* and pointed out that it is a *nomen nudum*. It was originally recorded by Beneden (1870), from '*Spinax acanthias*' and by Linstow (1878), from *Scymnus glacialis*. *P. fallax* Beneden, 1870, was also discussed by Southwell (1925) as a *nomen nudum*; it was originally recorded from *Raja rubus* and *Spinax*, and later by Linstow (1878) from *R. rubus*. I agree with Euzet (1959) in placing *P. unilaterale* Southwell, 1925, as a synonym of *P. thridax* Beneden, 1849. The species was accepted by Baylis (1939), Joyeux & Baer (1936), Wardle & McLeod (1952), Woodland (1927), and Yamaguti (1959). An examination of the specimen identified by Woodland (1927) as *P. unilaterale* and alleged to have unilateral pores has shown that the pores are alternate.

P. ketae is not accepted as a valid species in this revision. From an examination of specimens obtained on loan from the Beltsville Parasitological Laboratory, Beltsville, Maryland, U.S.A., and labelled 'U.S.N.M. Helm. Coll. 49817, *P. ketae* type', the following comments are made. Canavan's description of *Phyllobothrium ketae* was based on the plerocercoid of a tetraphyllidean and on the strobila of a pseudophyllidean (possibly *Eubothrium oncorhynchi* Wardle, 1932). The plerocercoid appeared identical with those described in this revision as *P. caudatum* (Zschokke & Heitz 1914). *P. ketae* is, therefore, rejected. Wardle & McLeod (1952) stated that it is a perfectly valid species despite its peculiar distribution, and Yamaguti (1959) suggested that it is a neotenic form. Canavan omitted to discuss his *P. ketae*, from *Oncorhynchus*, Excursion Inlet, Alaska, in relation to *P. caudatum*. Ronald (1959) referred to *P. ketae* from *Eopsetta jordani*.

XII. Ecology, host specificity and attachment of *Phyllobothrium* in relation to the form of the gut mucosa in elasmobranchs

Williams (1960) briefly described the mucosa of the intestine in members of the genus *Raja* and host-specificity in the Tetraphyllidea, with particular reference to *Echeneibothrium*. Variations in the structure of the mucosa in different species were discussed and it was suggested that they might explain, in part, the high degree of host specificity in some of the Tetraphyllidea. The present studies on *Phyllobothrium* have shown that fourteen species occurred, one in each of fourteen species of elasmobranchs, i.e. the high degree of host-specificity alleged to occur in the Tetraphyllidea and previously recorded for *Echeneibothrium* by Williams (1966) is confirmed for a number of *Phyllobothrium* spp. As with *Echeneibothrium*, a considerable variation in the scolex was observed in the species of *Phyllobothrium* studied, the scolex and its bothridia being fairly characteristic of a given species. Unlike *Echeneibothrium*, however, very few members of *Phyllobothrium* can be fixed and preserved for further studies whilst still attached to the host mucosa. Nevertheless, it was considered advisable to note the area of attachment and preserve suitable portions of the mucosa for further investigation, together with portions of the mucosa far removed from the point of attachment of the scolex. The results have shown that the mucosa in the various hosts of *Phyllobothrium* show striking morphological variations similar to those previously recorded for species of *Raja*, the hosts of *Echeneibothrium*. The form of the mucosa in the hosts of *Phyllobothrium* may be an important factor influencing host-specificity in these cestodes. In emphasizing this it should also be stressed that other factors are probably equally important, e.g. physiological and ecological factors which could not be investigated with the material available. Some physiological aspects of specificity were recently discussed by Smyth & Haslewood (1963).

The results of studies of the mucosa of various species of elasmobranchs will be summarized below. First, however, reference will be made to the invaluable but neglected work of Hilton (1902), who emphasized that confused ideas have been prevalent concerning the form and occurrence of mucosal folds and villi in different groups of vertebrates and that it was not clear just where folds cease and villi begin. He pointed out that comparatively few investigators have made extensive studies of the folds and villi in the different classes, although quite a number had made careful investigations of a single vertebrate class and much work had been done upon the folds and villi of different species when the general form of the digestive system of a 'typical' species was known. Hilton, however, gave little detailed information on the spiral valve of elasmobranchs and stated that his own observations seemed to confirm the description by Pilliet (1885) of villi in the spiral valves of selachians. Hilton also discussed many varieties of mucosal elevations in different ganoids and teleosts including a net-like arrangement of folds in *Amia*, these being broken down in many places into free projections which are true villi; no true villi were found in the teleosts examined and in *Esox lucius*, for which villi had been described, a simple network of true folds was found. In the following account Hilton's classification of the general types of folds and villi will be used. Four types of folds were described, namely, long, straight and parallel; wavy and parallel; zigzag and parallel and a net arrangement of the folds. The four types of villi were, thin and leaf-like; thread-like or long and cylindrical, cylindrical or finger shaped and low columnar or wart-like. The present preliminary account of the gut mucosa is, in most instances, restricted to a very small area around the point of attachment of the scolex, but as in Hilton's study it is hoped, in the near future, to select suitable elasmobranch hosts for detailed studies of the whole gut especially as it is thought at present that there might be a simple explanation for the occurrence of cestodes with almost identical scoleces, e.g. *Acanthobothrium* in widely different host species which show striking variations in the form of the mucosa.

Mustelus mustelus

Only two specimens of this host species became available for examination and both harboured *Phyllobothrium lactuca* attached at the anterior end of the spiral valve. At the point of attachment the gut mucosa is in the form of a series of long, straight and parallel primary folds (figure 89, plate 19). These primary folds are very much branched into secondary and tertiary folds and it is not clear at which point the smaller folds might be termed villi; Hilton (1902) described ways in which villi are formed from folds. The subdivisions of the primary muscular folds of *Mustelus mustelus* into a number of smaller folds can be clearly seen in transverse section of the gut (figure 90, plate 19); here it can be seen that some of the primary folds are either subdivided from the apex or from the base in which latter case the point of origin of the main fold becomes masked. So far, attempts to fix *P. lactuca* while still attached to the gut of *Mustelus mustelus* have been unsuccessful, but another cestode, *Orygmatobothrium musteli*, which is attached in the posterior region of the intestine, is easily available for study in this manner. *O. musteli* has a considerably smaller bothridium, about 0·6 to 0·8 mm long, than that of *P. lactuca*, and it can be seen (figure 91, plate 19) that about half of the bothridium occupies the depth of the main folds of the mucosa. It is, therefore, reasonable to speculate that adult

P. lactuca with a bothridium measuring up to 3 mm long could not attach itself in this region. It is of interest that not only are the bothridia in *P. lactuca* clearly visible and very much folded but each is bifid (figure 92, plate 15). Further studies should, therefore, investigate the precise orientation of each bothridium in relation to the primary folds of the mucosa in search for a possible explanation of such a division of the bothridium. The study of Euzet (1959, p. 212) showing the various regions of the intestine of *Mustelus canis* occupied by seven tetraphyllidean species is an essential basis for further work on this aspect of the biology of cestodes.

Raja montagui and R. batis

The intestinal mucosa of *R. montagui* was briefly described and illustrated by Williams (1960, 1961) in relation to the ecology of *Echeneibothridium maculatum*. To some extent the mucosa might be compared with that of *Mustelus mustelus* in that it is divided into folds but in *R. montagui* the folded ridges are variously arranged and sometimes join to form a complicated network. As in *P. lactuca* the species of *Phyllobothrium* in *R. montagui* could not be fixed while still attached to its host or even examined in the attached position after the spiral valve had been opened. Observations on living *P. brittanicum* sp.nov., however, showed that the bothridia were extremely mobile and flexible in their movements and, on becoming attached to a glass plate in sea-water, could spread out to occupy a circular area, the bothridium becoming a flat, plate-like structure (figure 18). From this behaviour and their various movements it must be assumed that the bothridia can become attached to the ridged mucosa of the host and in so doing they must form a pattern corresponding with that of the mucosa. The mucosa of *R. batis* (figure 101, plate 16) is also interesting in that it resembles, to some extent, that of *Mustelus mustelus*, but there is greater division of the primary and secondary folds which resemble low columnar villi. On one occasion a cestode, with a scolex showing a striking resemblance to that of *P. sinuosiceps*, was found in *R. batis*, but the species was anapolytic; as only one specimen was found no description is included in this revision.

Hexanchus griseus

Each of the seven *H. griseus* examined harboured *P. sinuosiceps* in the anterior spiral valve and unlike *P. lactuca* the species can easily be preserved while still attached. In sharp contrast the very much folded scolex of *P. sinuosiceps* is not clearly divisible into bothridia; the form of the gut mucosa of its host, *Hexanchus griseus*, might be an explanation. From an examination of the surface of the mucosa and from horizontal sections its net-like arrangement of folds can be clearly seen (figures 85, 86, plate 15). The scolex of *P. sinuosiceps* occasionally shows a strikingly similar arrangement of its folds, being almost a mirror-image of the mucosa (figures 87, 88, plate 15). The depths of the folds of the scolex correspond with those of the mucosa. In view of this the exact area of attachment of *P. dohrnii*, another species found in this host and which has a considerably smaller scolex than that of *P. sinuosiceps*, is worthy of further study.

Squalus acanthias

The gut mucosa of this host shows a fine even network (figure 93, plate 16) of folds, as seen in horizontal sections; but in vertical section the folds (figure 94, plate 16) appear as thread-like, short and collapsible villi. Darkly staining ?glandular areas occur between the folds. The comparatively flat but uneven surface of the mucosa, therefore, may explain the large flat and leaf like bothridia of *Crossobothrium* (?*Phyllobothrium*) sp. (figure 84, plate 14) found in this host-species. A suitably preserved area of the gut mucosa of *Spinax spinax* was unavailable for comparison with *Squalus acanthias*.

Scyliorhinus stellaris and *S. canicula*

The mucosa of the spiral valve of *Scyliorhinus stellaris* and *S. canicula* is folded. The folds, according to the scheme proposed by Hilton, may be described as wavy and parallel (figures 95 and 96, plate 15). The mode of attachment of *Monorygma* (?*Phyllobothrium*) sp. to this type of gut is not yet clear, as no specimens have been preserved whilst still attached, but it may be significant that the folds are separated by narrow clefts and that the depth of the scolex, being considerably less than its breadth, may correspond with the width of the clefts. The length of the scolex in relation to the depth of the fold at the point of attachment should also be investigated.

Squatina squatina

The gut mucosa of this host is comparable with that of *Hexanchus griseus* but the net-like and narrower folds are much closer, resulting in a very fine mesh (figures 97 and 98, plate 15). The very small scolex of *P. thridax* (figure 72, plate 13), therefore, may be capable of extending into the space between the folds. In surface view, however, the mucosa appears uniformly flat and smooth and the intervening spaces are difficult to detect with the naked eye. This arrangement may necessitate the attachment of the bothridia of *P. thridax* to the outersurface of the ridges. Preliminary observations indicate that the strobila of *P. thridax*, one of the largest members of the genus, is delicately attached along its length to the surface of the mucosa; it also appears that one surface only (?ventral) is involved in this attachment.

Eugaleus galeus

Anthobothrium cornucopia, but no member of *Phyllobothrium*, has been found attached to the mucosa of this host. The arrangement of the mucosal folds (figures 99 and 100, plate 16) resembles that of *Scyliorhinus*.

Chimaera monstrosa

An area of the mucosa of this host is included here to show differences which occur in the surface pattern in adjacent regions of the gut in one host-species (figures 102 to 104, plate 17), i.e. wavy and parallel folds and villi are present. Preliminary observations indicate that *Gyrocotyle* (Platyhelminthes: Cestodaria), a common parasite of this host, is attached to the villous area of the gut mucosa. It has a posterior adhesive organ folded to give the same general appearance as the scolex of some members of *Phyllobothrium*. Other species of elasmobranchs should, therefore, be examined for similar mucosal variations and the consequent effect, if any, on the distribution of cestodes in the gut.

The above very brief account of the mucosa in various elasmobranchs is further evidence in support of morphological factors operating in the host-specificity of cestodes. Williams (1957, p. 173) speculated that 'our knowledge of host specificity can be greatly increased if the ecology of the parasite is investigated in greater detail and its morphology correlated with that of the organ in which it occurs'. This statement was based on an examination of the helminths of a number of marine fish, particularly the cestodes of elasmobranchs, studies on which appeared to confirm the observations made by Euzet (1954). A comment with similar implications was independently made by Professor Baer in 1957, in the discussion of a paper by Euzet (1957, p. 269); he stated that work on the comparative histology of the spiral valve in elasmobranchs might eventually lead to a clue on the structure and specificity of their cestodes. In a further discussion of the paper by Euzet it was suggested that the mucosa of the intestine in elasmobranchs had not been studied in detail. Williams (1957, p. 93), however, had independently drawn attention to the description by Bridge (1904) of the highly characteristic and complicated mucosal folds in elasmobranchs, and to the gut mucosa of *Hexanchus griseus* in relation to its cestode, *Phyllobothrium sinuosiceps*. He also stated that a thorough study of many members of the genus *Phyllobothrium* in relation to the mucosa of the host may show that well-developed as opposed to weakly developed suckers are present only when a folding of the mucosa of the host's intestine is not complicated; it was suggested that an accessory sucker would certainly be at its maximum efficiency on a relatively flat smooth surface. The present revision of the genus appears to confirm this suggestion. Williams (1958, 1960, 1961, 1966), Rees (1958, 1959, 1961) and Rees & Williams (1966) have confirmed that several interesting correlations may occur between the structure of the cestode scolex and that of the intestine in fish; but further work is necessary in order to confirm the exact significance of this correlation in relation to classification, host specificity and phylogeny and to other more important factors which probably influence specificity. Further knowledge of the host intestine in particular would be of value in this connexion. Some information of this kind was discussed by Parker (1879), Al-Hussaini (1949) and Bullock (1963), but little information is yet available on elasmobranchs. The importance of the host alimentary canal as an environment for other helminths was described by Mykytowycz (1964). He referred to some factors affecting the distribution of nematodes in kangaroos. While the occurrence of *Filarinema* spp. in the pyloric region seems to be controlled by pH levels, the concentration of *Rugopharynx* and other small species on the mucous membrane of the stomach may be the result of the higher oxygen requirements of these worms. Superficial observation of the stomach suggested a distinct histological structure of the separate parts and an understanding of the role of these different areas in the distribution of worms is considered important; different species were found to occupy separate niches within the stomach of the kangaroo.

It is now abundantly clear that a correlation of the results from physiological, ecological, morphological and other studies on cestodes is necessary before any definite conclusions can be made on their biology in relation to that of the host.

XIII. Discussion

This revision, based on original work on living material and/or on specimens collected by the writer from freshly killed hosts, presents additional information supporting the views expressed by Williams (1957, 1958, 1960, 1961, 1966), on some aspects of the attachment, ecology and host-specificity of the Tetraphyllidea. It is hoped that the revision, together with that of *Echeneibothrium* (1966) and *Acanthobothrium* (in preparation), will establish a provisional basis for future studies on other aspects of the biology including further taxonomic work and classification of the Tetraphyllidea. Further work on the embryology, functional morphology, physiology, biochemistry, life-history and detailed morphology of the known forms referred to in these revisions is essential for taxonomic and other purposes including phylogenetic speculations on the Cestoda. The present discussion will be restricted to some general comments on (i) the taxonomy of *Phyllobothrium*, (ii) life-history of phyllobothriids, (iii) self-fertilization in the Tetraphyllidea, and (iv) segmentation in *Phyllobothrium*.

(i) *The taxonomy of* Phyllobothrium

This appears to be the first revision of the genus *Phyllobothrium*, although Joyeux & Dollfus (1931) emphasized that such an investigation was necessary and Wardle & McLeod (1952) indicated that *Phyllobothrium* was a collective name and had become a 'lumber room' of phyllobothriid genera. The revision became necessary because of the difficulties encountered in identifying fourteen species of *Phyllobothrium* or of related genera found in 'British' elasmobranchs. Although all the literature on *Phyllobothrium* was consulted, i.e. about 150 references to almost 100 members previously allocated to the genus, some of the species found could not be named, partly due to the lack of adequate descriptions of the morphology of adults and to the absence of information on other aspects of the biology of these cestodes. Difficulties on host taxonomy are also apparent in the literature. For this reason, it is emphasized that the present arrangement of the species must be modified as our knowledge increases and as new species are discovered. So far about twelve of the twenty-four species of 'British' elasmobranchs examined for cestodes have revealed a species of *Phyllobothrium* or of a related genus, each species being strictly host-specific. About 100 species of elasmobranchs, known to have been examined for cestodes in different areas of the world, have revealed about fifty species which have been allocated to *Phyllobothrium*. Since it is generally recognized that there are about 3000 species of elasmobranchs it follows that a large number of *Phyllobothrium* species remains to be discovered and described. For this reason redescriptions are essential of the forms already discovered, especially of the little-known species; and a greater concentration is required on the study of other aspects of the biology of those species for which the descriptions of adults appear adequate. Without a basis of this nature, for classifying new species, *Phyllobothrium* will remain a 'lumber room' and grounds for phylogenetic speculations will be inadequate.

Views on the tendency of other authors to list synonyms for little-known cestodes were discussed in detail by Williams (1966) in an account of *Echeneibothrium*; these views apply in particular to *Phyllobothrium*, e.g. it is difficult to accept the fact that *P. lactuca* occurs in a number of host species caught in European, Australasian, Japanese, Indian and American waters especially as it occurs only in *Mustelus* in 'British' waters. The various records of *Phyllobothrium lactuca* and the synonyms which have been listed for it probably indicate a complex of species. It is becoming increasingly evident that before it can be decided with any degree of certainty that two helminthologists working in different geographical areas are in fact dealing with the same tetraphyllidean species, observations must be made on living specimens from both localities, preferably with close collaboration by the two authors concerned. The different species of *Crossobothrium* (*Phyllobothrium*) from *Spinax spinax* and *Squalus acanthias* discussed in this revision illustrate the difficulties involved.

Important taxonomic characters of adult *Phyllobothrium* are difficult to investigate after fixation in 4% formaldehyde or other chemicals. The principle generally agreed upon among zoologists should, therefore, be applied, i.e. an apparent similarity in superficial morphological characters of the adults from two populations found in different hosts and localities is not a basis for placing the two in one species. There is considerable evidence that the strobila and free proglottids of *Phyllobothrium* show convergent evolution (figure 81 to 83, plate 14), but there is no indication that this has been considered in identifying species. Tetraphyllidea have been identified and classified mainly on the form of the scolex, although some helminthologists have opposed such classifications. It has now been shown that the form of the scolex corresponds, to some degree, with the form of the mucosa of the intestine, e.g. *P. lactuca* (figure 87, plate 15), but it is not known if these scoleces are really preadapted and how many, if any, become adapted to a particular kind of mucosa. Until information of this nature is available the value of using the size and form of the scolex alone as a taxonomic character should be questioned. In comparison with Tetraphyllidea other groups of cestodes appear to show considerably less variation in the size and structure of the scolex in different genera and species, but it is not known if this is really a reflexion of the fairly uniform pattern of the mucosa in their vertebrate hosts. This also applies to some tetraphyllidean genera which contain a large number of species and show a basic pattern in the form of the scolex, e.g. *Acanthobothrium*, and which inhabit species of elasmobranchs showing a wide variation in the form of the mucosa. This feature is being investigated.

With due regard to the caution expressed above and in a previous paper (Williams 1966) the species of *Phyllobothrium* and of related genera recorded so far have been provisionally arranged as shown in the table of contents. The main new features of this scheme can be summarized as follows: of the twenty-two named species of *Phyllobothrium*, numbered 1 to 22 in the table of contents, only the first ten show certain features in common, and these concern the scolex, namely a folding of the margins of the bothridia and a lack of distinct marginal loculi. Eventually *Phyllobothrium* may be restricted to include these species with distinctly bilobed bothridia and at least some indication of the presence of a myzorhynchus as in *Phyllobothrium lactuca*. Further work may show that at present these two features are restricted to the first three species discussed, viz. *P. lactuca*, *P. dagnallium* and *P. serratum*. The species of *Phyllobothrium* numbered 11 to 22 should, when knowledge increases, be further considered in relation to *Anthocephalum*, a new genus proposed by Linton (1890, p. 76) and characterized by having marginal loculi in the bothridia and no myzorhynchus.

In view of the confusion relative to synonymy, host and geographical distribution and the lack of detailed descriptions there is no alternative, at present, to accepting *Crossobothrium* and *Monorygma*, with about ten species in each. The differences between these two genera and *Phyllobothrium* cannot be clearly defined with the information already available.

There is strong evidence, mainly from the morphology of the scolex and partly from host distribution for the transference of five species to *Sphaerobothrium* Euzet, 1959; but these are not given as new combinations for reasons similar to those used against listing synonyms without adequate supporting information.

Larval phyllobothriids are unsatisfactorily arranged in the present scheme according to the three main groups of hosts in which they occur; but it is felt that the arrangement given, when used with the host-parasite list, may be of value in life-history speculations and future work on elucidating this aspect of the biology of *Phyllobothrium*.

(ii) *Life history of phyllobothriids*

Among the authors who have given clues to certain stages in the life history of some phyllobothriids are Linton (1897*a*, 1922), Dollfus (1923*a*, *b*, 1929, 1931, 1958, 1964*a*, *b*), Cleave (1927), Joyeux & Baer (1936), Jepps (1937) and Euzet (1959). They considered copepods, crustacea, cephalopoda, teleosts and marine mammals as probable intermediate hosts. The host-species mentioned by these authors were discussed in the systematic section of this revision and are given in the host-list. Little further progress will be made until more detailed observations are carried out and correlated with available information, e.g. it is not known if the eggs of those species of *Phyllobothrium* and of related genera occurring in open ocean sharks are able to float in surface waters. Experiments have shown that the eggs of certain species of *Echeneibothrium*, cestodes of rays, sink in a column of sea water. If the eggs of some other phyllobothriids, e.g. those of *Gastrolecithus planus* and *Reesium paciferum* behave similarly the mode of infection of *Cetorhinus maximus* should be investigated. Infection of this shark may occur in shallow waters and/or the diurnal migrations of planktonic organisms may facilitate contact with infective eggs, if they do sink. Structures resembling oil globules were seen in the eggs of *Phyllobothrium brittanicum* and of *Monorygma* (?*Phyllobothrium*) sp. (figures 15, 17), suggesting the presence of an aid to flotation; but these two species occurred in hosts which spend much of their time on the sea bottom. Further speculations of this nature are considered inadvisable, as nothing is known of the rate of proglottid formation or of egg production in the Tetraphyllidea and little information is available on the rate of development of the egg. Euzet (1959) showed that the hexacanth embryo of *P. lactuca* develops in about 6 days after release of the egg into sea water. He demonstrated that the eggs were infective to copepods, but *Gobius* was not a suitable second intermediate host. As indicated in the present host-list, cephalopods, teleosts and mammals have often been recorded as hosts of the plerocercoids of *Phyllobothrium*, but their mode of infection and subsequent behaviour of the late procercoid and developing plerocercoid is not known. Linton (1897*a*, p. 789) referred to 'enormous numbers of larvae' in the 'cystic duct' of most of the *Cynoscion regalis* examined at Woods Hole, while Kulemina (1964) recorded about 100 plerocercoids of a new species of *Dinobothrium*, at different stages of development in *Gadus morrhua* in the Barents Sea. The remarkable cestode described by Southwell & Prashad (1918*a*, *b*) as *Ilisha parthenogenetica* may, according to the same authors (1923), be a plerocercoid larva; heavy infections were found in the mesentery and liver of *Hilsa ilisha* in Bengal. The authors described and illustrated parthenogenetic reproduction in the species which was first referred to as an adult tapeworm of doubtful affinities but subsequently as a plerocercoid. Further examination of this unique cestode larva in relation to other plerocercoid larvae in teleosts may prove interesting.

Linton (1922) discussed evidence for linking *Phyllobothrium loliginis* of various cephalopods and teleosts, with *P. tumidum* in sharks. Southwell & Walker (1936) agreed with Linton, but concluded that *P. tumidum* is a synonym of *P. delphini* originally described as a larval form from marine mammals. Johnston (1937) further confirmed this view and referred larval *Phyllobothrium* from the sea elephant, *Mirounga proboscidea* to *P. tumidum* or *P. thridax*. Of particular interest are Johnston's remarks on the behaviour of sharks which might act as hosts of *Phyllobothrium*, e.g. he stated that the Greenland shark, *Laemargus glacialis* (*borealis*), attacks whales and presumably smaller aquatic mammals, biting out pieces of flesh of living cetaceans. If this is true the description by Sokolov (1955), of the larvae of *P. delphini* migrating to certain areas of the body of sperm whales, e.g. to the dorsal fin or the genital pore region, may be relevant.

(iii) *Self-fertilization in Tetraphyllidea*

This aspect of the biology of Tetraphyllidea was discussed in relation to *Phyllobothrium sinuosiceps* by Williams (1959*a*) and to *Echeneibothrium* by Williams (1966), the latter reference including views on its possible significance in the taxonomy of these cestodes. This revision of *Phyllobothrium* has revealed that Johnston (1937) referred to the swollen rounded base of the cirrus in *Monorygma macquariae* as an 'organ which serves as a holdfast during self-impregnation'. Most of the sexually mature proglottids he examined showed various stages in the process of 'self-copulation'. The cirrus extended into the vagina to a length greater than that of the cirrus sac. He is of the opinion that 'an ejaculation of semen apparently takes place at this stage, because in the proglottids in which the cirrus was fully everted into the vagina, the latter was greatly distended by a compact mass of spermatozoa just beyond the termination of the male duct, the end of the mass remote from the cirrus being large and rounded, while the part towards and adjacent to it was rather tubular and of only slightly larger diameter than the duct of the male organ, suggesting that the whole mass was ejected at one ejaculation'.

(iv) *Segmentation in* Phyllobothrium

The method of proglottid formation in *Phyllobothrium* was not examined for this study, but the following brief remarks may have a bearing on future observations of this kind. Hyman (1951, p. 351) referred to an unusual method of proglottid formation as reported by Curtis in 1906 for *Phyllobothrium dohrnii* (= *Crossobothrium laciniatum*) in which the strobila after proliferating in the usual manner at the rear end of the neck begins to form proglottids immediately behind the scolex from before backwards, i.e. contrary to the usual method. If this is true for other tetraphyllideans it may have considerable significance as pointed out by Rausch (1964) for some diphyllobothriids. He described the process of sexual reproduction by means of transverse subdivision of primary proglottids in *Diplogonoporus balaenopterae*, stating that this method of growth is unique in cestodes of this genus. He summarized previous records of its occurrence in *Diplogonoporus* and pointed out that in his material secondary and even tertiary subdivision had taken place in the proglottids immediately following the scolex; continuation of the process had resulted in the formation in the posterior part of the strobila of as many as 8 to 10 reproductively functional proglottids from each primary proglottid derived from the neck region. A similar process was observed in *D. tetrapterus*. This asexual method of reproduction and the diplogonadic structure of these cestodes are considered to be adaptations to increase the production of eggs and thereby enhance the chances of success in a marine habitat. These remarks have also a bearing on some of those made on the life history.

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XIV. Host-parasite list

A classified list of hosts from which cestodes, identified as *Phyllobothrium*, have been recorded. The host names used are those given in the original papers and they are arranged according to Joyeux & Baer (1936) for the Ctenophora and Cephalopoda; Golvan (1962) for the teleosts and elasmobranchs; and Dollfus (1964*a*) and Joyeux & Baer (1936) for the marine mammals. Whenever possible locality and references are given.

A. CTENOPHORA

Cydippidae

1. *Cydippe densa: Phyllobothrium* sp., Mediterranean, Parona (1900); *Phyllobothrium* sp., Mediterranean, Dollfus (1923*a*).

B. MOLLUSCA

Cephalopoda

Ommatostrephidae

2. *Ommastrephes illecebrosus: Phyllobothrium loliginis*, Woods Hole, Massachusetts, Linton (1897*a*); *P. loliginis*, Woods Hole, Linton (1922); *P. thysanocephalum*, Woods Hole, Dollfus (1923*b*); *P. loliginis*, Woods Hole, Dollfus (1923*b*).
3. *Ommastrephes sagittatus: Phyllobothrium loliginis*, Leidy (1887).

4. *Ommastrephes todarus: Phyllobothrium dohrni*, Dollfus (1923*b*).
5. *Todaropsis eblanae: Phyllobothrium* sp., Concarneau, Joyeux & Baer (1936); *P. tumidum* plerocercoid, Finistere, Dollfus (1958).
6. *Todarodes sagittatus: Phyllobothrium dohrni*, Naples, Joyeux & Baer (1936).

SEPIIDAE

7. *Sepia elegans: Phyllobothrium* sp., Dollfus (1958).
8. *Sepia officinalis: Phyllobothrium lactuca* of Dollfus (1958).

LOLIGINIDAE

9. *Loligo: Phyllobothrium* sp., Joyeux & Dollfus (1931); *Phyllobothrium* sp., Dollfus (1931).
10. *Loligo loligo: Phyllobothrium* sp., Arcachon, Joyeux & Baer (1936); *Phyllobothrium* sp., Arcachon, Dollfus (1929).
11. *Loligo pealii: Phyllobothrium loliginis*, Linton (1922); *Phyllobothrium* sp., Dollfus (1923*b*).
12. *Loligo vulgaris: Phyllobothrium* sp., Dollfus (1958).

C. SELACHII

HEXANCHIFORMES

HEXANCHIDAE

13. *Heptanchus cinereus: Phyllobothrium dohrnii*, Mediterranean, Joyeux & Baer (1936); *P. gracile*, Mediterranean, Parona (1900).
14. *Hexanchus griseus: Phyllobothrium lactuca*, Britain, Baylis (1939); *P. dohrnii*, Mediterranean, Euzet (1952*c*); *P. triacis*, Mediterranean, Euzet (1952*c*); *P. dohrnii*, Concarneau, Sète, Euzet (1959); *P. rotundum*, Joyeux & Baer (1936); *P. dohrnii*, Mediterranean, Joyeux & Baer (1936); *P. gracile*, Mediterranean, Parona (1900); *P. lactuca*, Britain, Prudhoe & Baylis (1957); *P. dohrnii*, Britain, Rees (1946); *P. lactuca*, Britain, Rees & Llewellyn (1941); *P. centrurum*, Britain, Rees & Llewellyn (1941); *P. dohrnii*, Britain, Williams (1958); *P. sinuosiceps*, Britain, Williams (1959*a*); *P. sinuosiceps*, Britain, Williams (1960); *P. dohrnii*, Britain, Williams (1960); *P. dohrnii*, Britain, Williams (see p. 249); *P. sinuosiceps*, Britain, Williams (see p. 249).
15. *Notorhynchus pectorosus: Phyllobothrium dohrnii*, New Zealand, Alexander (1963); *P. dohrnii* New Zealand, Robinson (1959).

CHLAMYDOSELACHIDAE

16. *Chlamydoselachus anguineus: Phyllobothrium chlamydoselachi*, Scandinavia, Southwell (1925); *P. chlamydoselachi*, Britain, Williams (see p. 263).

HETERODONTIFORMES

HETERODONTIDAE

17. *Cestracion: Phyllobothrium vagans*, Port Jackson, New Zealand, Haswell (1902).
18. *Heterodontus philippi: Phyllobothrium thridax*, Australasia, Drummond (1937).
19. *Heterodontus zebra: Phyllobothrium loculatum*, Japan, Yamaguti (1952).

GALEIFORMES

ISUROIDEI

ALOPIIDAE

20. *Alopias vulpinus: Phyllobothrium filiforme*, Japan, Yamaguti (1952).

GINGLYMOSTOMIDAE

21. *Ginglymostoma concolor: Phyllobothrium microsomum*, Ceylon, Southwell (1930); *P. microsomum*, Ceylon, Southwell & Hilmy (1929).

ISURIDAE

22. *Carcharadon carcharias: Phyllobothrium tumidum*, Woods Hole, Massachusetts, Linton (1922); *P. tumidum*, California, Riser (1955); *P. lactuca*, New Zealand, Robinson (1959).
23. *Isurus dekayi: Phyllobothrium tumidum*, Woods Hole, Massachusetts, Linton (1922).
24. *Isurus glaucus: Phyllobothrium* sp., Japan, Yamaguti (1934).
25. *Isurus oxyrhynchus: Phyllobothrium tumidum*, Sète, Concarneau, Euzet (1959).
26. *Oxyrhina spallanzanii: Phyllobothrium lactuca*, France, Joyeux & Baer (1936).
27. *Isurus (Oxyrhina) spallanzanii: Phyllobothrium tumidum*, Mediterranean, Euzet, (1952*c*).
28. *Lamna cornubica: Phyllobothrium* sp., Europe, Beneden (1870); *P. tumidum*, Britain, Williams (see p. 245).
29. *Lamna ditropis: Phyllobothrium tumidum*, Monterey, California, Riser (1955).
30. *Lamna nasus: Phyllobothrium dagnalli*, St Lawrence, Canada, Myers (1959).
31. *Lamna* sp.: *Phyllobothrium rigii*, Meggitt (1928); *P. lactuca*, Meggitt (1928).

ODONTASPIDAE

32. *Odontaspis littoralis: Phyllobothrium dohrnii*, Joyeux & Baer (1961).

CARCHARHINOIDEI

CARCHARHINIDAE

33. *Carcharhias bleekeri: Phyllobothrium floriforme*, Ceylon, Southwell (1930).
34. *Carcharhias melanopterus: Phyllobothrium pammicrum*, Ceylon, Southwell & Prashad (1920); *P. pammicrum*, Ceylon, Shipley & Hornell (1906); *P. pammicrum*, Ceylon, Southwell (1930); *P. minutum*, Ceylon, Shipley & Hornell (1906); *P. minutum*, Ceylon, Southwell (1930).
35. *Carcharhias taurus: Phyllobothrium musteli*, Guiart (1935).
36. *Carcharhias walbeehmi: Phyllobothrium typicum*, Madras, India, Subhapradha (1955).
37. *Carcharhias* sp.: *Phyllobothrium floriforme*, Ceylon, Southwell (1930).
38. *Carcharhinus glaucus: Phyllobothrium angustum*, Mediterranean, coasts of European Atlantic and Morocco, Euzet (1952*b*, *c*).
39. *Carcharhinus obscurus: Phyllobothrium foliatum*, Beaufort, North Carolina, Linton (1905*a*).
40. *Cynias manazo: Phyllobothrium tumidum*, Tsingtao, China, Tseng (1933); *P. tumidum* Tsingtao, Hsü (1935); *P. lactuca*, Hiroshima, Yoshida (1917).
41. *Galeocerdo arcticus: Phyllobothrium dagnalli*, Pearl Bank, Ceylon, Southwell (1930); *P. lactuca*, Ceylon, Southwell (1930).

42. *Galeocerdo tigrinus: Phyllobothrium thysanocephalum*, Woods Hole, Massachusetts, Linton (1889); *P. galeocerdonis*, Woods Hole, Massachusetts, MacCallum (1921); *P. lactuca*, Ceylon, Southwell (1912); *P. dagnallium*, Ceylon, Southwell (1927); *P. lactuca*, Southwell & Prashad (1920).
43. *Galeus canis: Phyllobothrium giganteum*, Ceylon, Southwell (1930).
44. *Hemigaleus balfouri: Phyllobothrium tumidum*, Ceylon, Southwell (1927); *P. tumidum*, Ceylon, Southwell (1930).
45. *Mustelus antarcticus: Phyllobothrium musteli*, Australasia, Drummond (1937).
46. *Mustelus canis: Phyllobothrium lactuca*, Concarneau, Sète, Euzet (1959); *P. loliginis*, Linton (1922).
47. *Mustelus hinnulus: Phyllobothrium triacis*, Euzet (1952*c*); *P. lactuca*, Manche et l'Ocean, Joyeux & Baer (1936); *P. dohrnii*, Mediterranean, Joyeux & Baer (1936).
48. *Mustelus laevis: Phyllobothrium triacis*, Mediterranean, Euzet (1952*c*); *P. musteli*, Fuhrmann (1931); *P. lactuca*, 'Manche et l'Ocean', Joyeux & Baer (1936); *P. lactuca*, Oerley (1885*a*, *b*); *P. lactuca*, Mediterranean, Parona (1900).
49. *Mustelus lenticulatus: Phyllobothrium lactuca*, New Zealand, Robinson (1959); *P. lactuca*, New Zealand, Alexander (1963).
50. *Mustelus manazo: Phyllobothrium lactuca*, Sea of Japan, Yamaguti (1952); *P. typicum*, Madras, India, Subhapradha (1955).
51. *Mustelus mustelus: Phyllobothrium lactuca*, Concarneau, Sète, Euzet (1959); *P. lactuca*, Britain, Williams (see p. 236).
52. *Mustelus plebejus: Phyllobothrium crispum*, Southwell (1925).
53. *Mustelus vulgaris: Phyllobothrium lactuca*, Belgium, Beneden (1849, 1850*b*); *P. lactuca*, Belgium, Beneden (1858); *P. lactuca*, European waters, Beneden (1870); *P. lactuca*, Mediterranean, Carus (1884); *P. lactuca*, Diesing (1863); *P. lactuca*, Linstow (1878); *P. lactuca*, Wimereux (Pas-de-Calais), Monticelli (1889); *P. lactuca*, Plymouth, Woodland (1927).
54. *Prionace glauca: Phyllobothrium prionacis*, Japan, Yamaguti (1934).
55. *Scoliodon terrae-novae: Phyllobothrium tumidum*, Dry Tortugas, Shuler (1938).
56. *Triakis scyllium: Phyllobothrium tumidum*, Tsingtao, China, Hsü (1935); *P. tumidum*, Tsingtao, Tseng (1933); *P. serratum* Japan, Yamaguti (1952); *P. triacis* Japan, Yamaguti (1952).
57. *Triakis semifasciata: Phyllobothrium lactuca*, Monterey Bay, California and Obispo Bay, California, Riser (1955); *P. radioductum*, California, Young (1954).

Hemiscylliidae

58. *Chiloscyllium griseum: Phyllobothrium chiloscyllii*, Madras, India, Subhapradha (1955).
59. *Chiloscyllium indicum: Phyllobothrium dagnallium*, Pearl Bank, Southwell (1927); *P. dagnalli*, Ceylon, Southwell (1930).

Scylliorhinidae

60. *Scyliorhinus caniculus: Phyllobothrium* sp., Britain, Williams (1958); *Phyllobothrium* sp., Britain, Williams (see p. 236).

SQUALIFORMES

SQUALIOIDEI

SQUALIDAE

61. *Acanthias vulgaris: Phyllobothrium acanthiae-vulgaris*, Scandinavia, Joyeux & Baer (1936); *P. lactuca*, 'Manche et l'Ocean', Joyeux & Baer (1936).
62. *Spinax acanthias: Phyllobothrium brassica*, Europe, Beneden (1870); *P. lactuca*, Europe, Beneden (1870).
63. *Spinax spinax: Phyllobothrium squali*, Britain, Williams (1960); *Phyllobothrium* sp. 1, Norway, Williams (see p. 260); *Phyllobothrium* sp. 2, Britain, Williams (see p. 260).
64. *Squalus acanthias: Phyllobothrium* sp., St Lawrence, Canada, Myers (1959); *Phyllobothrium acanthae-vulgaris*, Iceland, Rees (1953); *Phyllobothrium squali*, Britain, Williams (1960); *Phyllobothrium* sp. 3, Britain, Williams (see p. 260); *P. loliginis*, Linton (1922).
65. *Squalus mitsukuri: Phyllobothrium lactuca*, Tsingtao, China, Hsü (1935); *P. lactuca*, Tsingtao, Tseng (1933).
66. *Squalus sucklii: Phyllobothrium squali*, Japan, Yamaguti (1952); *P. laciniatum*, East China Sea, Yamaguti (1952).

SCYMNORHINIDAE

67. *Scymnus glacialis: Phyllobothrium auricula, P. acanthae-vulgaris, P. brassica* and *P. lactuca*, Linstow (1878).
68. *Scymnus lichia: Phyllobothrium dohrnii*, Mediterranean, Joyeux & Baer (1936); *P. hyperapolytica*, Britain, Williams (1958).
69. *Scymnus microcephalus: Phyllobothrium* sp., Stiles & Hassall (1912).

SOMNIOSIDAE

70. *Laemargus borealis: Phyllobothrium auricula*, Linstow (1878).
71. *Somniosus microcephalus: Phyllobothrium magnum*, Puget Sound, Washington, Hart (1936); *P. perfectum*, Russia, Poliansky (1955).

SQUATINOIDEI

SQUATINIDAE

72. *Squatina angelus: Phyllobothrium thridax*, Belgium, Beneden (1849, 1850*b*, 1858); *P. thridax*, Europe, Beneden (1870); *P. thridax*, Diesing (1863); *P. gracile*, Banyuls (Pyrénées-Orientales), Joyeux & Baer (1936); *P. lactuca*, 'Manche et l'Ocean', Joyeux & Baer (1936); *P. thridax*, Manche, France, Joyeux & Baer (1936); *P. unilaterale*, Mediterranean, Joyeux & Baer (1936); *P. thridax*, Linstow (1878); *P. thridax*, Oerley (1885*a*, *b*); *P. thridax*, Mediterranean, Parona (1900); *P. thridax*, Britain, Scott (1909); *P. lactuca*, Britain, Scott (1909); *P. unilaterale*, Britain, Woodland (1927).
73. *Squatina japonica: Phyllobothrium marginatum*, Japan, Yamaguti (1934).
74. *Squatina squatina: Phyllobothrium unilaterale*, Britain, Baylis (1939); *P. thridax*, Concarneau, Arcachon, Banyuls, Sète, Euzet (1959); *P. thridax*, Plymouth, Prudhoe & Baylis (1957); *P. thridax*, Britain, Williams (1960); *P. thridax*, Britain, Williams (see p. 251).
75. *Squatina* sp.: *Phyllobothrium thridax*, Mediterranean, Parona (1900).

RAJIFORMES

RHINOBATOIDEI

RHINIDAE

76. *Rhina ancylostoma: Phyllobothrium dagnalli*, Ceylon, Southwell (1930).
77. *Rhynchobatus ancylostomus: Phyllobothrium dagnallium*, Ceylon, Southwell (1927).
78. *Rhynchobatus djeddensis: Phyllobothrium foliatum*, Ceylon, Southwell (1912); *P. foliatum*, Ceylon, Southwell (1927, 1930); *P. lintoni*, Ceylon, Southwell (1930); *P. foliatum*, Ceylon, Southwell & Prashad (1920); *P. chiloscyllii*, Madras, India, Subhapradha (1955); *P. minimum*, Madras, India, Subhapradha (1955).

RHINOBATOIDAE

79. *Rhinobatus granulatus: Phyllobothrium chiloscyllii*, Madras, India, Subhapradha (1955).
80. *Rhinobatus schlegeli: Phyllobothrium chiloscyllii*, Madras, India, Subhapradha (1955); *Phyllobothrium biacetabulum*, Japan, Yamaguti (1960).

RAJOIDEI

RAJIDAE

81. *Raja batis: Phyllobothrium lactuca*, Europe, Beneden (1870); *P. thridax*, Europe, Beneden (1870); *P. lactuca*, Carnarvon Bay, Wales, Johnstone (1906); *P. lactuca*, 'Manche et l'Ocean', Joyeux & Baer (1936); *P. thridax*, Manche, France, Joyeux & Baer (1936); *P. lactuca*, Linstow (1878); *P. thridax*, Linstow (1878); *P. thridax*, *Scandinavia*, Olsson (1893).
82. *Raja binoculata: Phyllobothrium radioductum*, Washington, Kay (1942).
83. *Raja blanda: Phyllobothrium thridax*, Britain, Baylis & Jones (1933).
84. *Raja brachyura: Phyllobothrium thridax*, Britain, Baylis (1939); *P. thridax*, Britain, Prudhoe & Baylis (1957).
85. *Raja circularis: Phyllobothrium lactuca*, Beaumaris Bay, Wales, Johnstone (1906).
86. *Raja clavata: Phyllobothrium thridax*, Britain, Baylis (1939); *P. thridax*, Britain, Baylis & Jones (1933); *P. lactuca*, Europe, Beneden (1870); *P. thridax*, Wales, Johnstone (1906); *P. lactuca*, Wales, Johnstone (1906); *P. lactuca*, 'Manche et l'Ocean', Joyeux & Baer (1936); *P. thridax* Manche, France, Joyeux & Baer (1936); *P. lactuca*, Linstow (1878); *P. lactuca*, Olsson (1867); *P. thridax*, Mediterranean, Parona (1900); *P. thridax*, Plymouth, Prudhoe & Baylis (1957).
87. *Raja fullonica: Phyllobothrium minutum* sp.nov., Britain, Williams (see p. 253).
88. *Raja laevis: Phyllobothrium loliginis*, Linton (1922); *P. dagnalli*, St Lawrence, Canada, Myers (1959); *Phyllobothrium* sp., St Lawrence, Myers (1959).
89. *Raja montagui: Phyllobothrium britannicum* sp.nov., Britain, Williams (see p. 243).
90. *Raja ocellata: Phyllobothrium loliginis*, Linton (1922); *Phyllobothrium* sp., St Lawrence, Canada, Myers (1959).
91. *Raja radiata: Phyllobothrium thridax*, Linstow (1878); *P. thridax*, Murman-Kuste, Linstow (1903); *Phyllobothrium* sp., St Lawrence, Canada, Myers (1959); *P. lactuca*, Scandinavia, Olsson (1867); *P. thridax*, Scandinavia, Olsson (1867); *P. rigii*, Russia, Polyanski (1955); *P. thridax*, Russia, Poliansky (1955).
92. *Raja rubus: Phyllobothrium fallax*, Europe, Beneden (1870); *P. fallax*, Linstow (1878).
93. *Raja scabrata: Phyllobothrium dagnalli*, Canada, Heller (1949).

94. *Raja stabuliformis: Phyllobothrium dagnalli*, Canada, Heller (1949); *P. foliatum*, Woods Hole, Massachusetts, Linton (1924*b*).
95. *Raja: Phyllobothrium fallax*, Europe, Beneden (1870); *P. lactuca*, Fuhrmann (1931).

DASYATOIDEI

DASYATIDAE

96. *Dasyatis akajei: Phyllobothrium tumidum*, Tsingtao, China, Hsu (1935); *P. tumidum*, Tsingtao, Tseng (1933).
97. *Dasyatis centrura: Phyllobothrium foliatum*, Woods Hole, Massachusetts, Linton (1897*b*); *P. foliatum*, Woods Hole, Linton (1901); *P. paulum*, Woods Hole, Southwell (1925).
98. *Dasyatis pastinaca: Phyllobothrium auricula*, Concarneau, Arcachon, Sète, Euzet (1959); *P. centrurum*, Sète, Euzet (1959).
99. *Dasyatis say: Phyllobothrium foliatum*, Beaufort, North Carolina, Linton (1905*a*).
100. *Dasybatus akajei: Phyllobothrium dasybati*, Japan, Yamaguti (1934).
101. *Dasybatus centrura: Phyllobothrium foliatum*, Woods Hole, Massachusetts, Linton (1924*b*).
102. *Dasybatus kuhli: Phyllobothrium blakei*, Ceylon, Southwell (1930); *P. lactuca*, Ceylon, Southwell (1930); *P. variabile*, Ceylon, Southwell (1930).
103. *Dasybatus walga: Phyllobothrium giganteum*, Ceylon, Southwell (1930); *P. lactuca*, Ceylon, Southwell (1930); *P. variabile*, Ceylon, Southwell (1930).
104. *Hypolophus sephen: Phyllobothrium pammicrum*, Southwell (1915); *P. pammicrum*, Chilka Lake, Southwell & Prashad (1920).
105. *Leiobatus aquila: Phyllobothrium crispatissimum*, Morocco, Guiart (1935).
106. *Trygon centrura: Phyllobothrium foliatum*, Woods Hole, Massachusetts, Linton (1890).
107. *Trygon kuhli: Phyllobothrium blakei*, Ceylon, Shipley & Hornwell (1906); *P. blakei*, Ceylon, Southwell (1912); *P. lactuca*, Ceylon, Southwell (1912, 1925); *P. blakei*, Ceylon, Southwell & Prashad (1920); *P. compacta*, Ceylon, Southwell & Prashad (1920).
108. *Trygon pastinaca: Phyllobothrium auricula*, Belgium, Beneden (1858); *P. auricula*, Europe, Beneden (1870); *P. gracile*, Black Sea, Borcea (1934); *P. lactuca*, Black Sea, Borcea (1934); *P. auricula*, Diesing (1863); *P. lactuca*, Diesing (1863); *P. auricula*, Mediterranean, Euzet (1952*c*); *P. lactuca*, 'Manche et l'Ocean', Joyeux & Baer (1936); *P. thridax*, Manche, France, Joyeux & Baer (1936); *P. auricula*, Linstow (1878); *P. auricula*, Oerley (1885*a*, *b*); *P. lactuca*, Oerley (1885*a*, *b*).
109. *Trygon walga: Phyllobothrium lactuca*, Ceylon, Shipley & Hornell (1906); *P. lactuca*, Ceylon, Southwell (1925).
110. *Urogymnus asperrimus: Phyllobothrium pammicrum*, Ceylon, Southwell (1912); *P. lintoni*, Ceylon, Southwell (1930); *P. pammicrum*, Ceylon, Southwell & Prashad (1920).

AETOBATIDAE

111. *Aetomylaeus maculatus: Phyllobothrium panjadi*, Ceylon, Southwell (1930).
112. *Stoasodon narinari: Phyllobothrium panjadi*, Ceylon, Southwell (1930).

TORPEDINIFORMES

TORPEDINIDAE

113. *Torpedo marmorata: Phyllobothrium gracile*, France, Beauchamp (1905); *P. gracile*, Trieste, Carus (1884); *P. gracile*, Diesing (1863); *P. gracile*, Mediterranean, Euzet (1952*b*); *P. gracile*, Mediterranean, coast of European Atlantic and Morocco, Euzet (1952*c*); *P. gracile*, Concarneau, Arcachon, Sète, Euzet (1959); *P. gracile*, Banyuls (Pyrenees-Orientales); Joyeux & Baer (1936); *P. rigii*, Mediterranean and Western Atlantic, Joyeux & Baer (1936); *P. gracile*, Linstow (1878); *P. gracile*, Oerley (1885); *P. gracile*, Mediterranean, Parona (1900); *P. gracile*, Pintner (1896).

114. *Torpedo nobiliana: Phyllobothrium rigii*, Mediterranean and Western Atlantic, Joyeux & Baer (1936); *P. gracile*, Britain, Williams (1958); *P. rigii*, Britain, Williams (1958); *P. rigii*, Britain, Williams (1960); *P. gracile*, Britain, Williams (see p. 255).

D. OSTEICHTHYES

CLUPEIFORMES

CLUPEOIDEI

CLUPEIDAE

115. *Alosa sardinia: Phyllobothrium* sp., Mediterranean, Monticelli (1887) and Parona (1900).

116. *Clupea harengus: Phyllobothrium* sp., Stiles & Hassall (1912).

SALMONOIDEI

SALMONIDAE

117. *Oncorhynchus: Phyllobothrium ketae*, Excursion Inlet, Alaska, Canavan (1928); *P. caudatum*, White Sea, Barents Sea, Baltic, Dogiel, Petrushevski & Polyanski (1961); *P. salmonis*, Fujita (1922); *Phyllobothrium* sp., Straits of Georgia, British Columbia, Wardle (1932); *P. salmonis*, British Columbia, Wardle (1933).

118. *Oncorhynchus gorbuscha: Phyllobothrium caudatum*, Russia, Zenejev (1936).

119. *Oncorhynchus keta: Phyllobothrium caudatum*, Russia, Zenejev (1936).

120. *Oncorhynchus nerka: Phyllobothrium caudatum*, North Pacific, Margolis (1963); *Phyllobothrium caudatum*, British Columbia, Williams (see p. 272).

COREGONIDAE

121. *Coregonus ussuriensis: Phyllobothrium caudatum*, Russia, Zenejev (1936).

MYCTOPHOIDEI

SUDIDAE

122. *Paralepis coregonoides borealis: Phyllobothrium* sp., Britain, Williams (see p. 275).

ALEPISAUROIDEI

ALEPISAURIDAE

123. *Alepidosaurus ferox: Phyllobothrium speciosum*, Madeira, Monticelli (1889).

TETRAODONTIFORMES

TETRAODONTOIDEI

TETRAODONTIDAE

124. *Spheroides maculatus: Phyllobothrium loliginis*, Linton (1922).

CYPRINIFORMES

SILUROIDEI

SILURIDAE

125. *Parasilurus asotus: Phyllobothrium caudatum*, Russia, Zenejev (1936).

BAGRIDAE

126. *Liocassis brazhnikowi: Phyllobothrium caudatum*, Russia, Zenejev (1936).

ANGUILLIFORMES

CONGROIDEI

CONGRIDAE

127. *Leptocephalus conger: Phyllobothrium loliginis*, Linton (1922).
128. *Uroconger lepturus: Phyllobothrium* sp., India, Anantaraman (1963); *Phyllobothrium* larva, Subhapradha (1948).

GADIFORMES

MERLUCCIIDAE

129. *Merluccius bilinearis: Phyllobothrium loliginis*, Linton (1922); *Phyllobothrium* sp., Woods Hole, Massachusetts, Linton (1901).

GADIDAE

130. *Phycis chuss: Phyllobothrium loliginis*, Linton (1922).
131. *Phycis tenuis: Phyllobothrium loliginis*, Linton (1922).
132. *Pollachius virens: Phyllobothrium loliginis*, Linton (1922).

LAMPRIDIFORMES

TRACHIPTERIDAE

133. *Trachipterus arcticus: Phyllobothrium* sp. larva, Britain, Williams (see p. 275).

REGALECIDAE

134. *Regalecus glesne: Phyllobothrium* sp., Florida, Hutton (1961).

PERCIFORMES

PERCOIDEI

LATILIDAE

135. *Lopholatilus chamaeleonticeps: Phyllobothrium loliginis*, Linton (1922).

SCIAENIDAE

136. *Micropogon undulatus: Phyllobothrium lactuca*, Montevideo, Parona (1900).

LABROIDEI

LABRIDAE

137. *Labrus maculatus: Phyllobothrium* sp., Stiles & Hassall (1912).

SCOMBROIDEI

THUNNIDAE

138. *Thunnus thynnis: Phyllobothrium loliginis*, Linton (1922).

XIPHIIDAE

139. *Xiphias gladius: Phyllobothrium loliginis*, Linton (1922).

GOBIOIDEI

GOBIIDAE

140. *Gobius niger: Phyllobothrium* sp., Stiles & Hassall (1912).

COTTOIDEI

COTTIDAE

141. *Mesocottus haitjei: Phyllobothrium caudatum*, Russia, Zenejev (1936).

HEMITRIPTERIDAE

142. *Hemitripterus americanus: Phyllobothrium loliginis*, Linton (1922).

PLEURONECTIFORMES

PLEURONECTOIDEI

PARALICHTHYIDAE

143. *Paralichthys dentatus: Phyllobothrium loliginis*, Linton (1922); *P. loliginis*, Ronald (1959).

144. *Paralichthys oblongatus: Phyllobothrium loliginis*, Linton (1922), *P. loliginis*, Ronald (1959).

HIPPOGLOSSIDAE

145. *Eopsetta jordani: Phyllobothrium ketae*, Ronald (1959).

146. *Hippoglossoides elassodon: Phyllobothrium* sp., Ronald (1959).

147. *Hippoglossus hippoglossus: Phyllobothrium rudicornis*, Ronald (1959).

LOPHIIFORMES

LOPHIODEI

LOPHIIDAE

148. *Lophius piscatorius: Phyllobothrium loliginis*, Linton (1922).

E. REPTILIA

SERPENTES

BOIGINAE

149. *Boiga irregularis: Phyllobothrium dipsadomorphi*, Ceylon, Hughes, Baker & Dawson (1941).

150. *Dipsadomorphus irregularis: Phyllobothrium dipsadomorphi*, Western Pacific, Shipley (1900).

F. MAMMALIA

CETACEA

BALAENIDAE

151. *Balaena mysticetus: Phyllobothrium physeteris*, Falkland Islands, Baylis (1932); *P. physeteris*, Meggitt (1924).

152. *Delphinus delphis: Phyllobothrium delphini*, Meggitt (1924); *P. delphini*, Belgium, Beneden (1870); *P. delphini*, Falkland Islands, Baylis (1932).

153. *Globicephala melaena: Phyllobothrium delphini*, Britain, Baylis (1939).

154. *Grampus griseus: Phyllobothrium delphini*, Falkland Islands, Baylis (1932); *P. delphini*, Meggitt (1924).

155. *Kogia breviceps: Phyllobothrium delphini*, Australia, Johnston & Mawson (1939).

156. *Lagenorhynchus acutus: Phyllobothrium chamissonii*, Southwell & Walker (1936); *Phyllobothrium* sp. larva, Woods Hole, Massachusetts, Linton (1905 *a*); *Phyllobothrium* sp., Falkland Islands, Baylis (1932).

157. *Lagenorhynchus obscurus: Phyllobothrium* sp. larva, Markowski (1955).
158. *Mesoplodon bidens: Phyllobothrium delphini*, Belgium, Adam (1938); *P. inchoatum*, Falkland Islands, Baylis (1932); *P. inchoatum*, Leidy (1891). *P. inchoatum*, Meggitt (1924).
159. *Ogmorhinus weddellii: Phyllobothrium* sp., Antarctic, Rennie & Reid (1912); *Phyllobothrium* sp., Meggitt (1924).
160. *Physeter catadon: Phyllobothrium delphini*, Falkland Islands, Hamilton (1934); *P. physeteris*, Falkland Islands, Baylis (1932); *P. delphini*, Sokolov (1955); *P. delphini*, Margolis & Pike (1955); *P. physeteris*, South Georgia, Mathews (1938); *Phyllobothrium* sp. larva, Markowski (1955).
161. *Physeter macrocephalus: Phyllobothrium physeteris*, Meggitt (1924).
162. *Tursiops truncatus: Phyllobothrium delphini*, Falkland Islands, Baylis (1932); *Phyllobothrium* sp., Falkland Islands, Baylis (1932).
163. *Tursiops tursio: Phyllobothrium delphini*, Meggitt (1924); *Phyllobothrium* sp., Meggitt (1924).

PINNIPEDIA

PHOCIDAE

164. *Arctocephalus australis: Phyllobothrium delphini*, Falkland Islands, Southwell & Walker (1936).
165. *Mirounga leonina: Phyllobothrium* sp., Antarctic, Johnston (1937).

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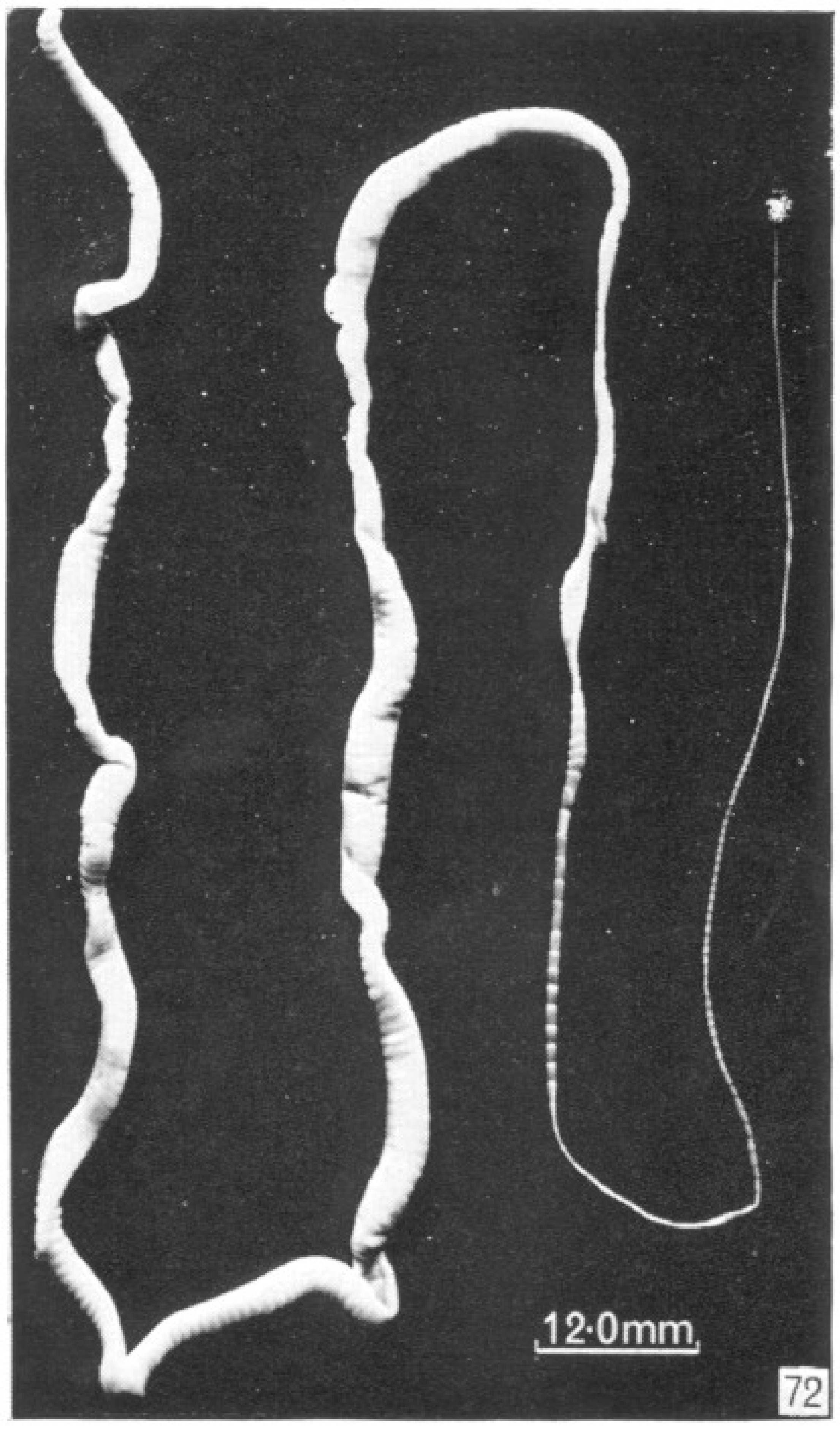
List of abbrevations used in the figures

bo.	bothridium	*s.*	sucker
c.s.	cirrus sac	*t.*	testis
e.v.	excretory vessel	*ut.*	uterus
g.a.	genital atrium	*ut.d.*	uterine duct
gl.	glandular myzorhynchus	*ut.p.*	uterine pore
m.g.	Mehlis's gland	*v.d.*	vas deferens
n.	neck	*vag.*	vagina
ov.	ovary	*y.*	yolk gland
r.s.	receptaculum seminis		



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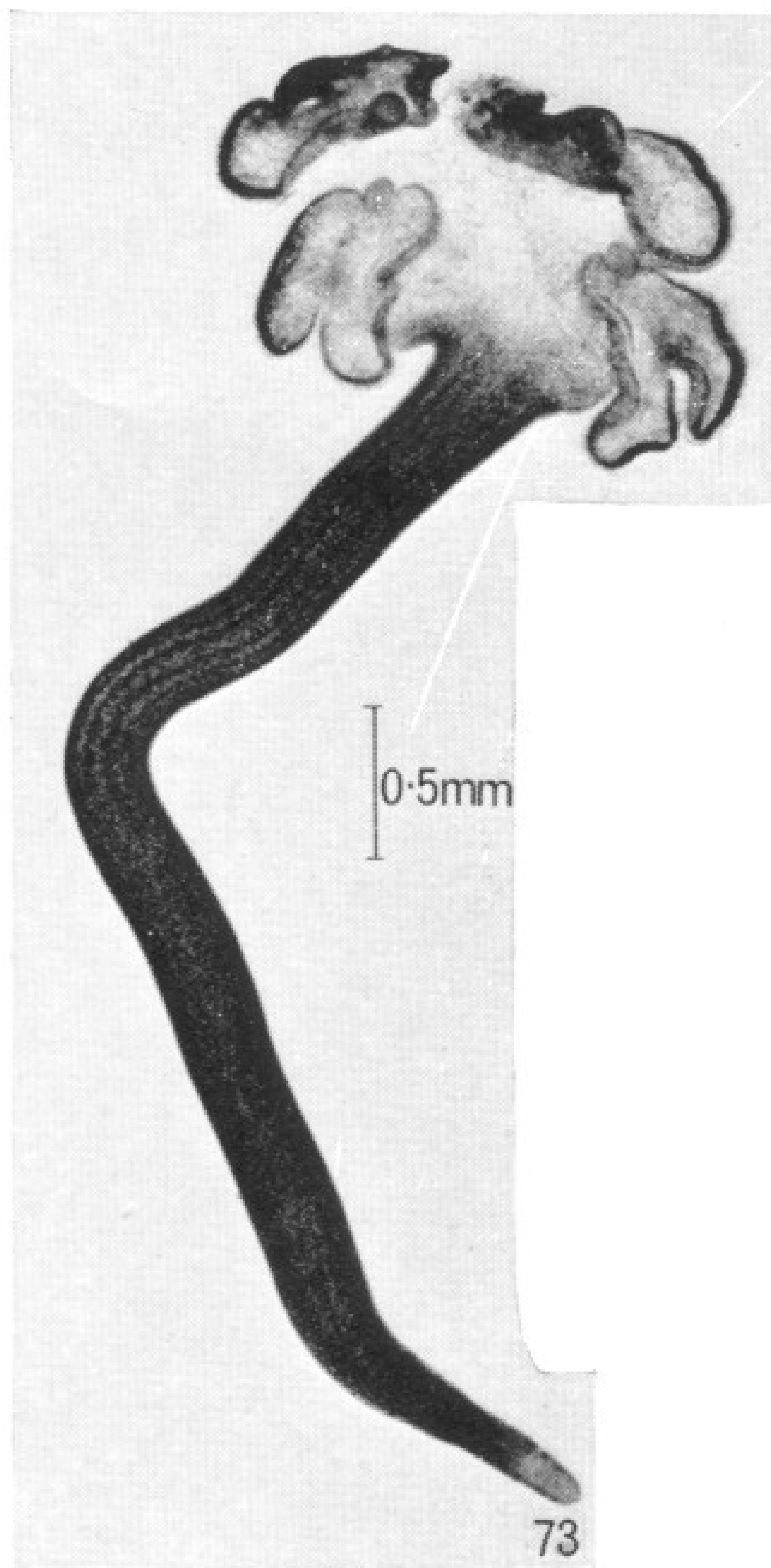

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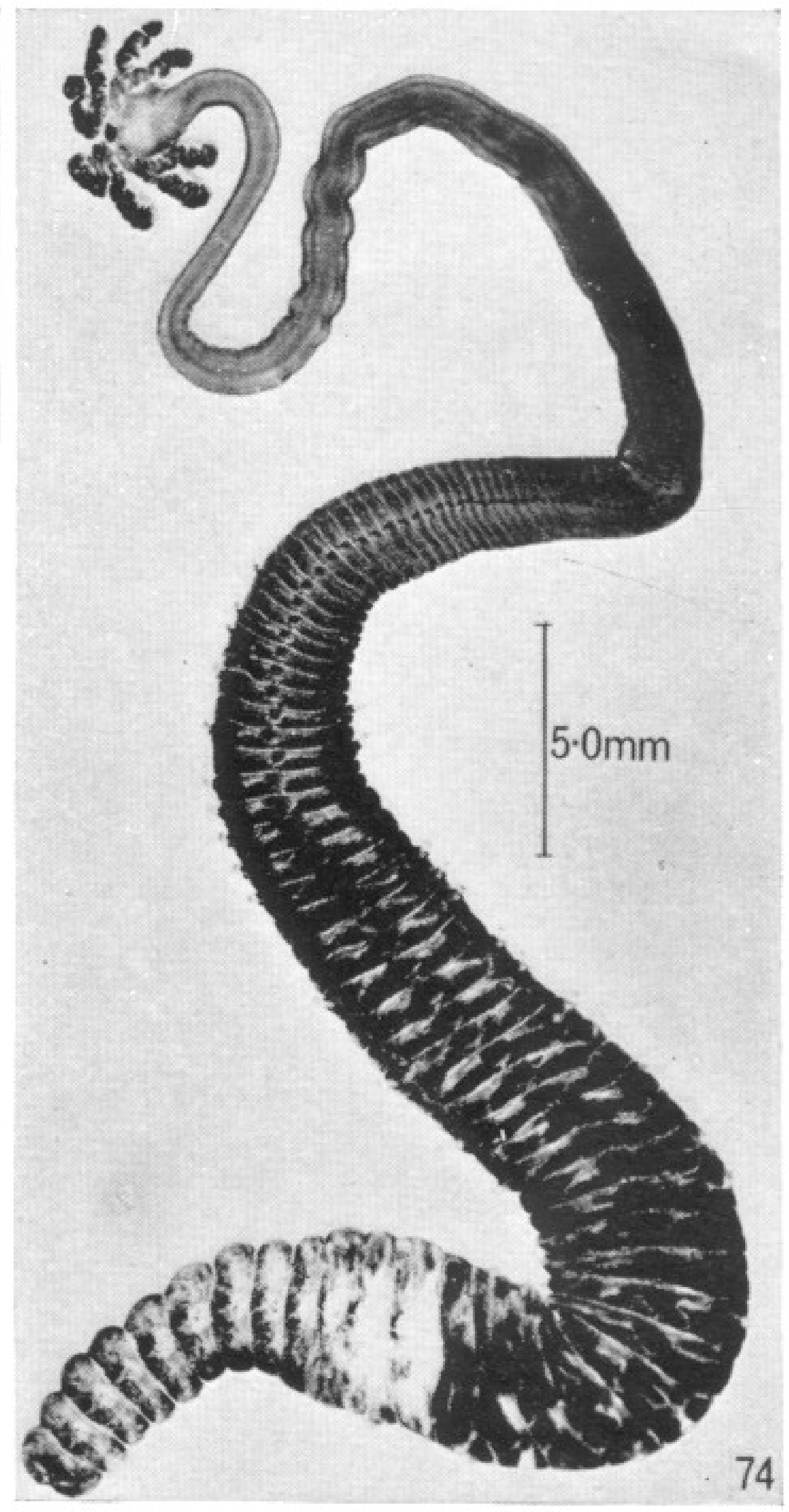

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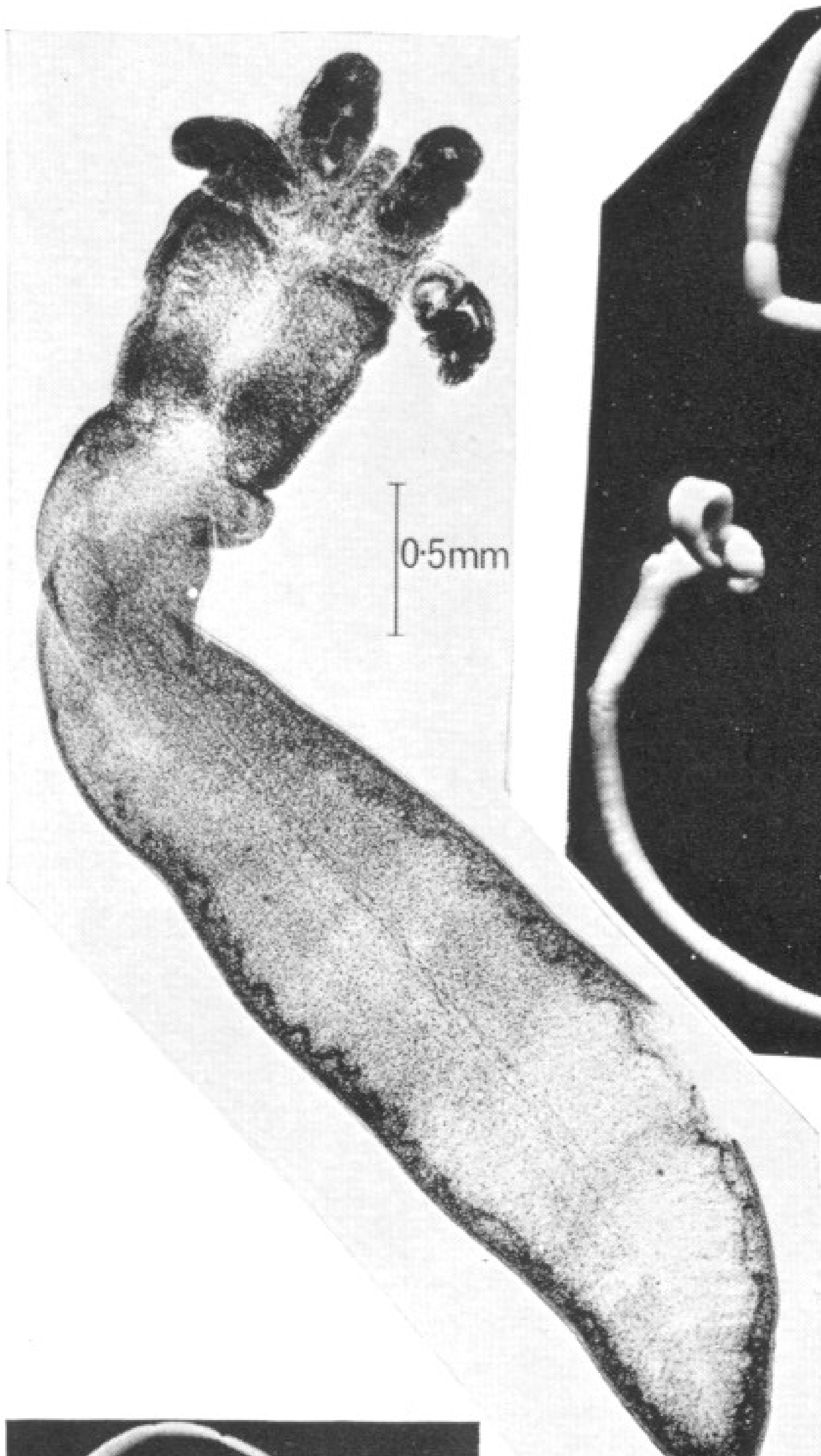

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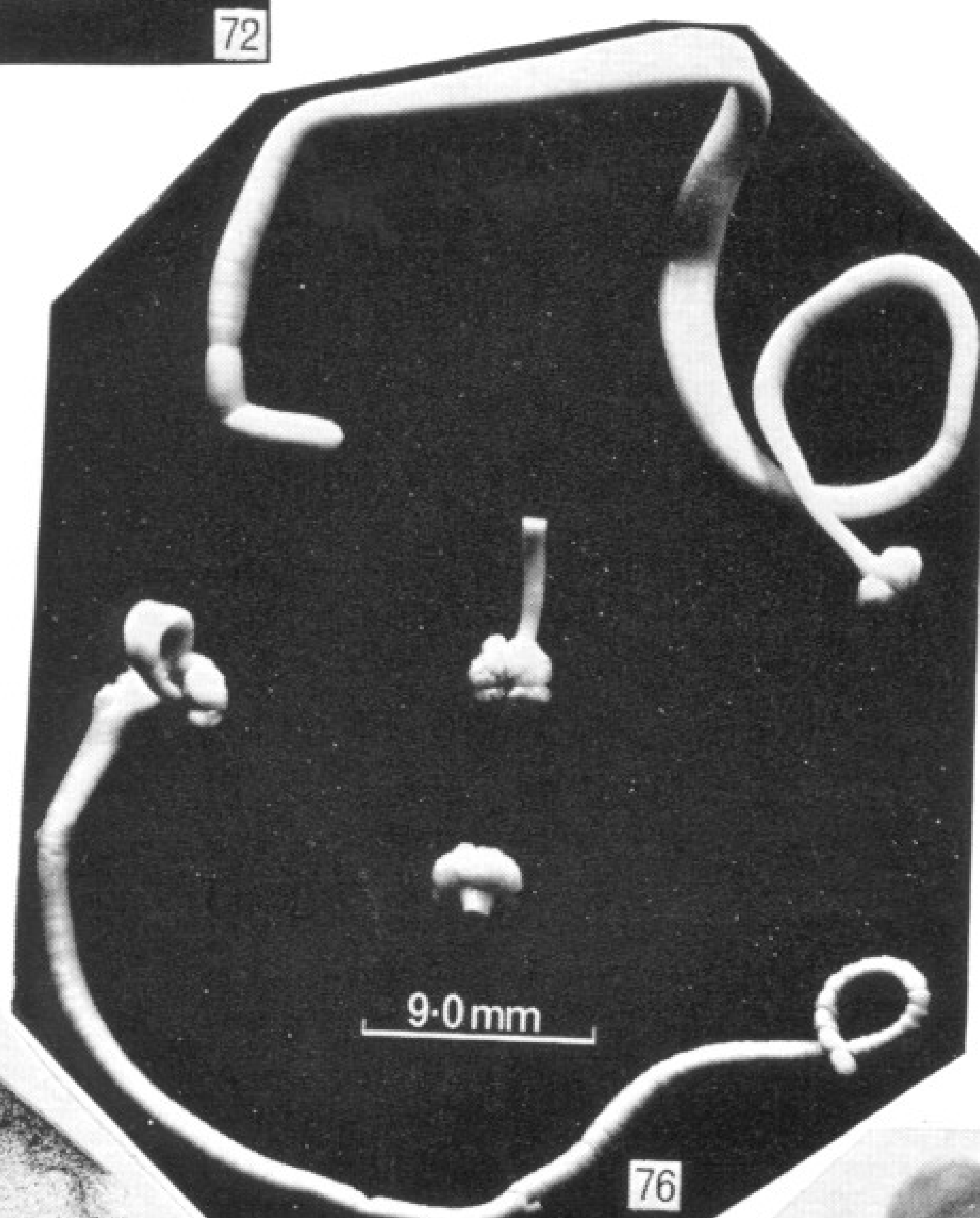

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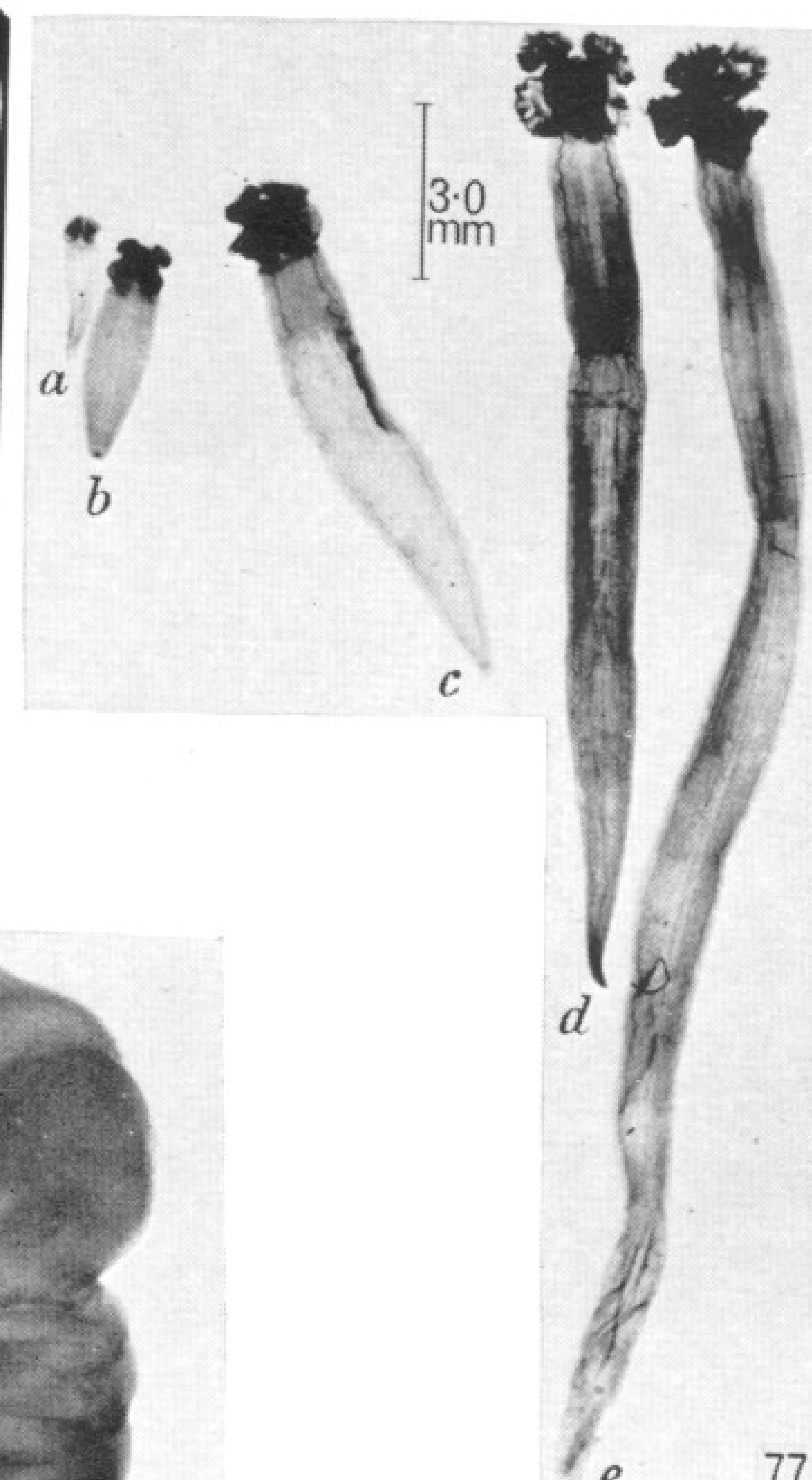

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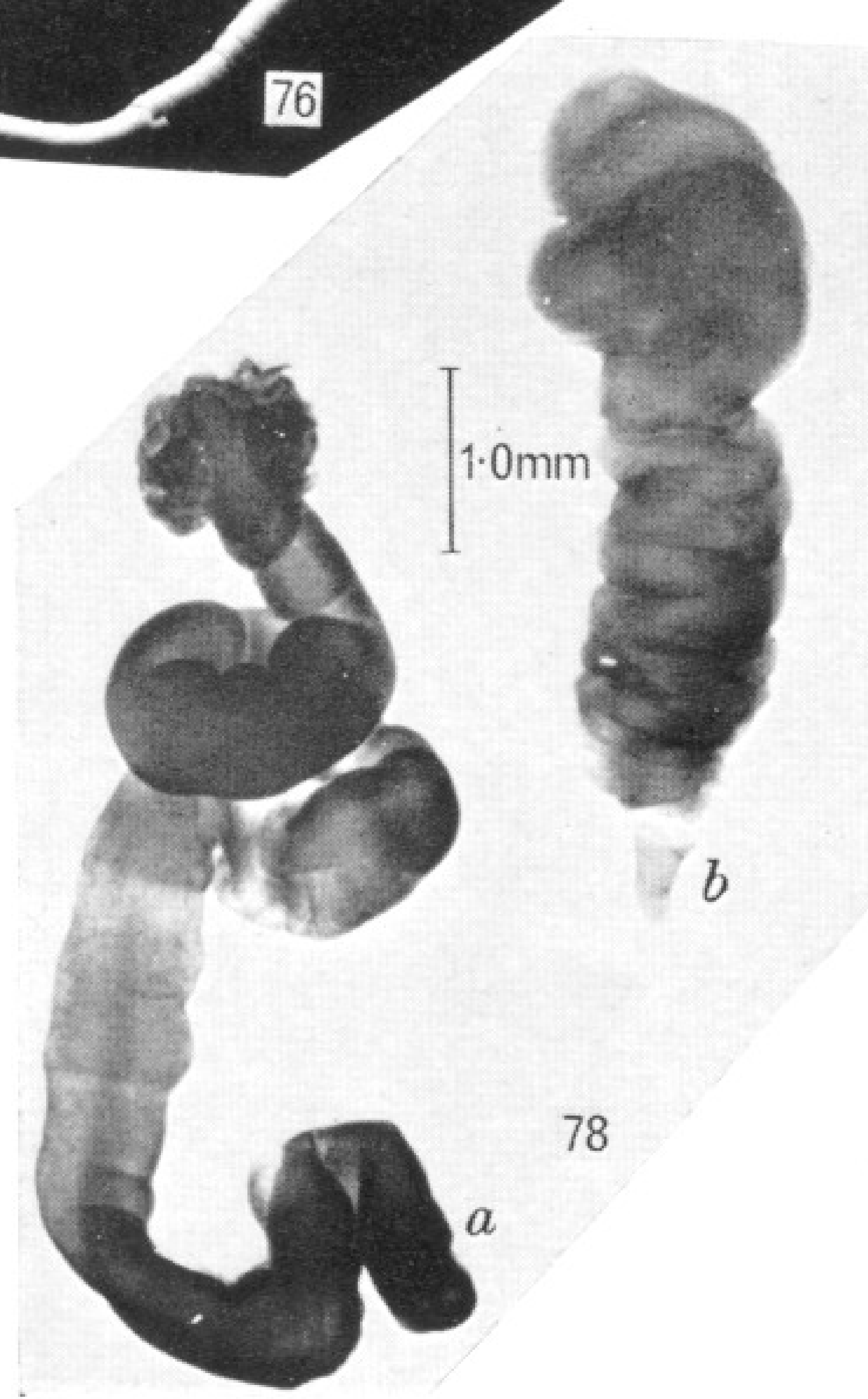

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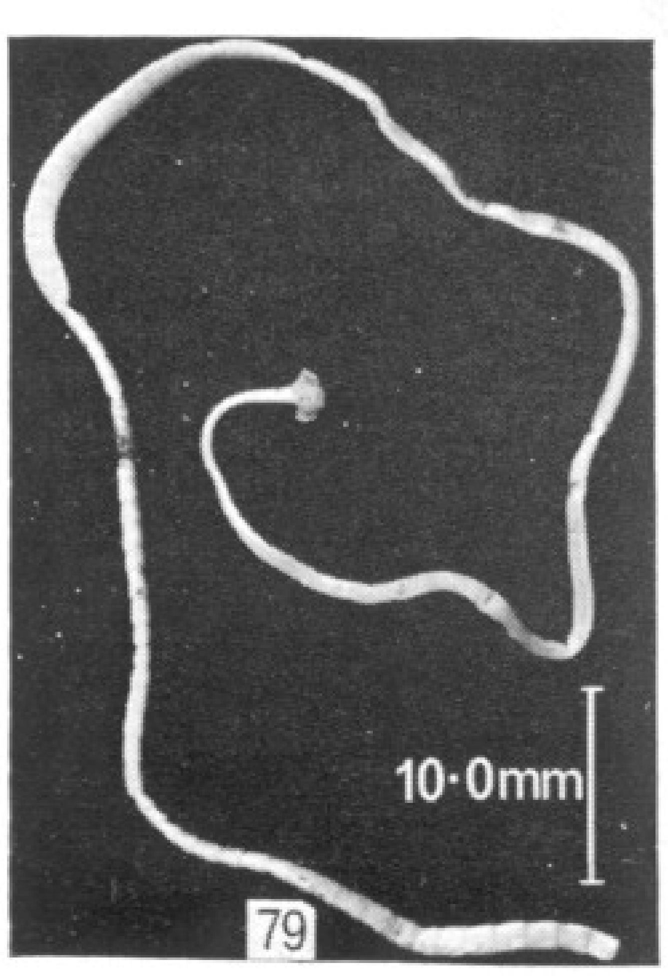

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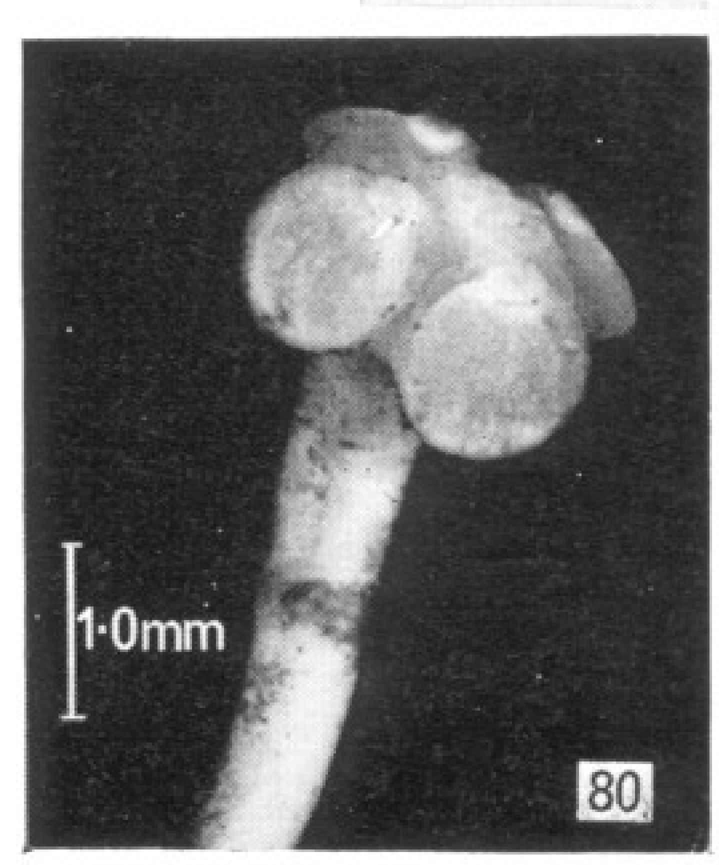

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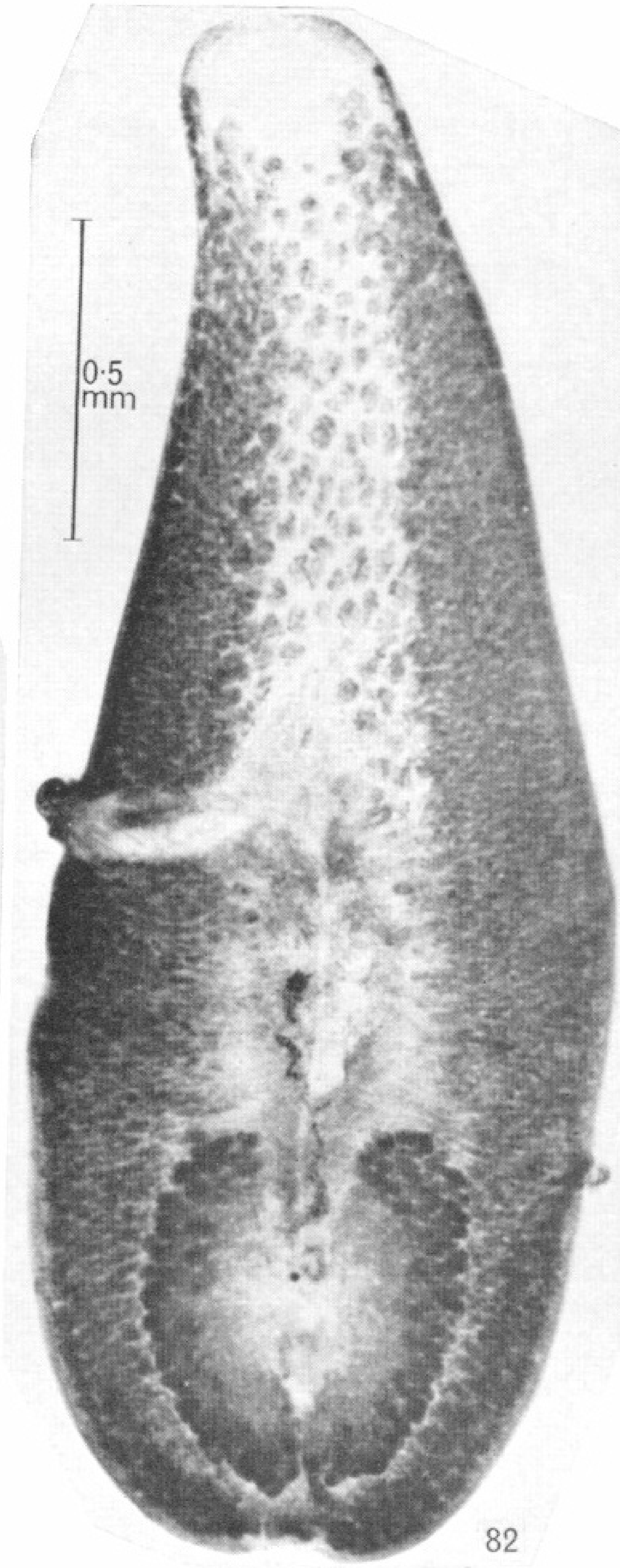
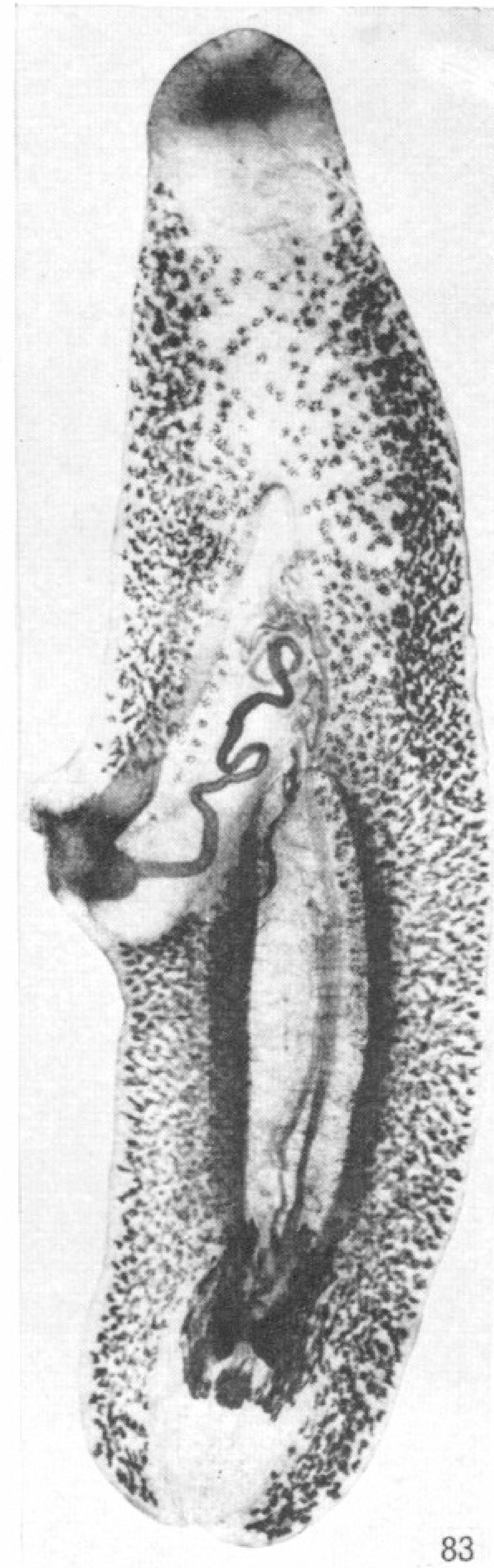




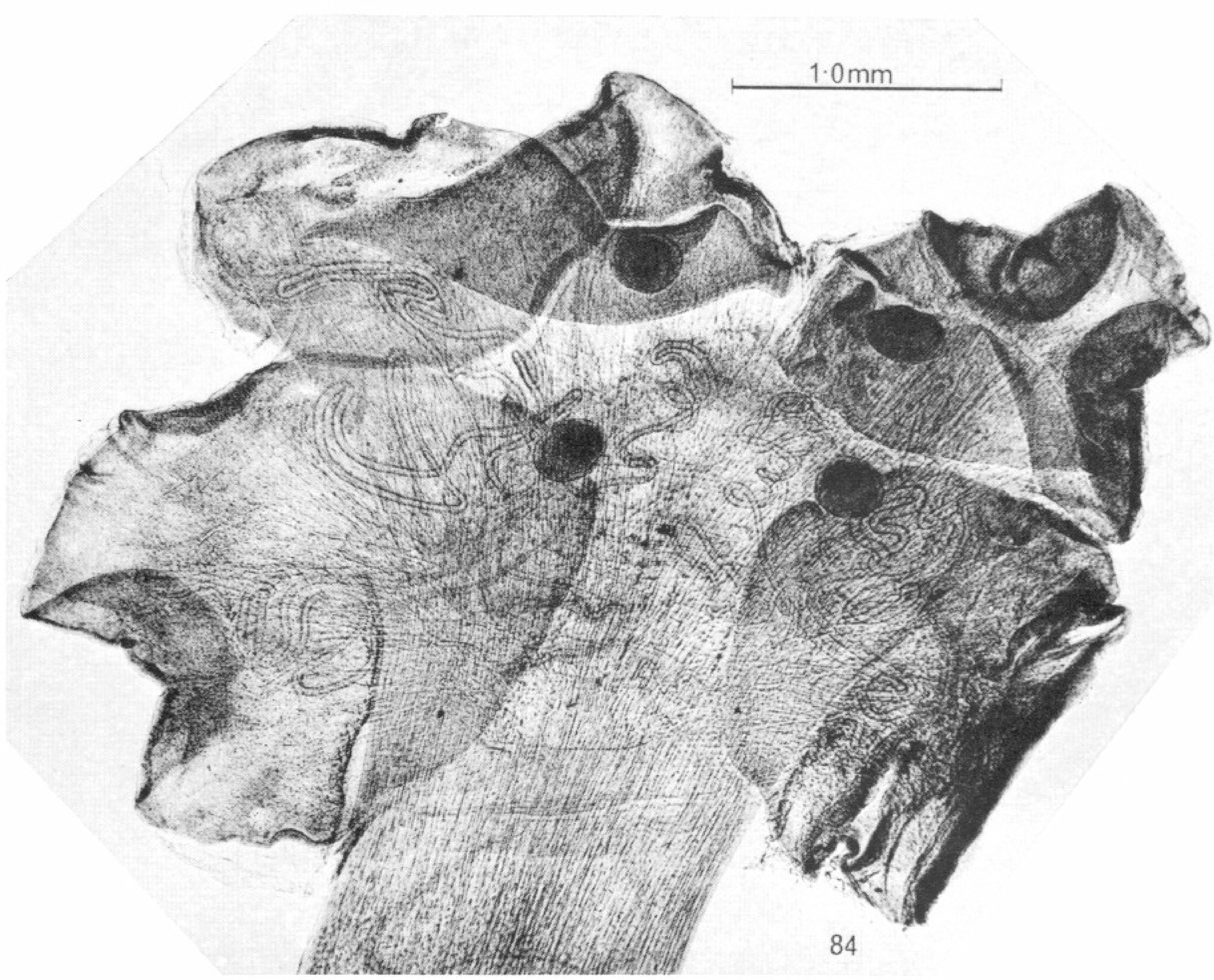
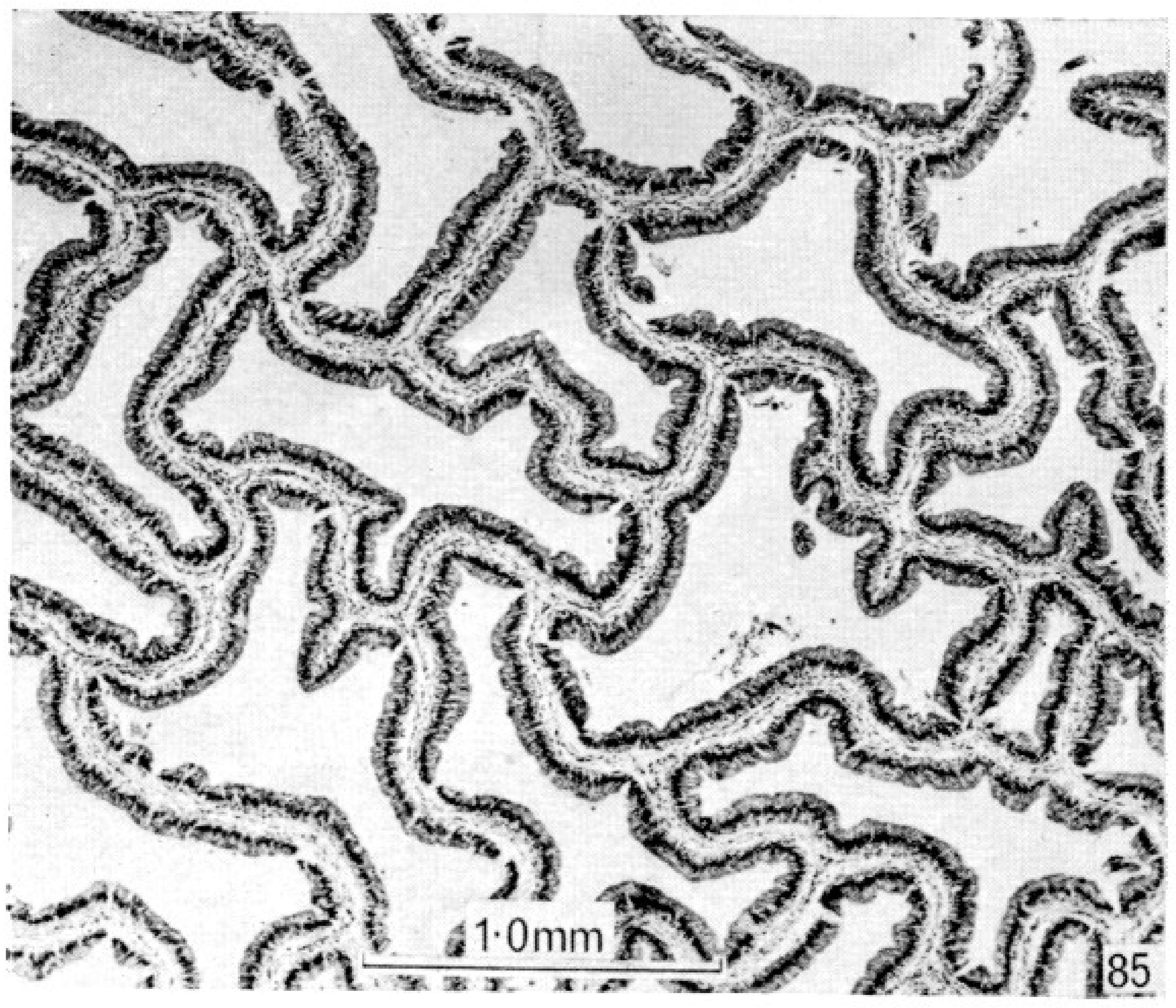
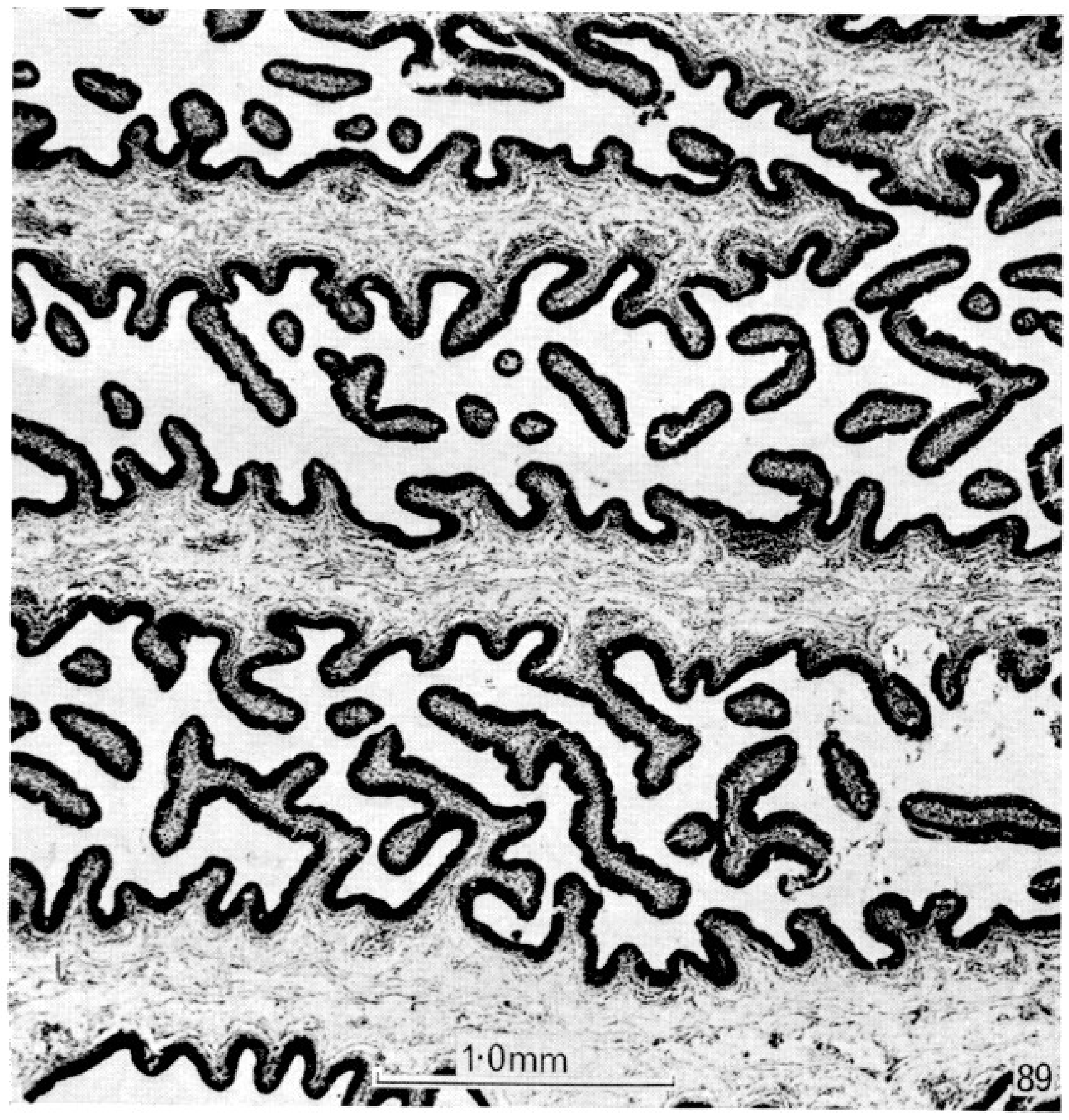
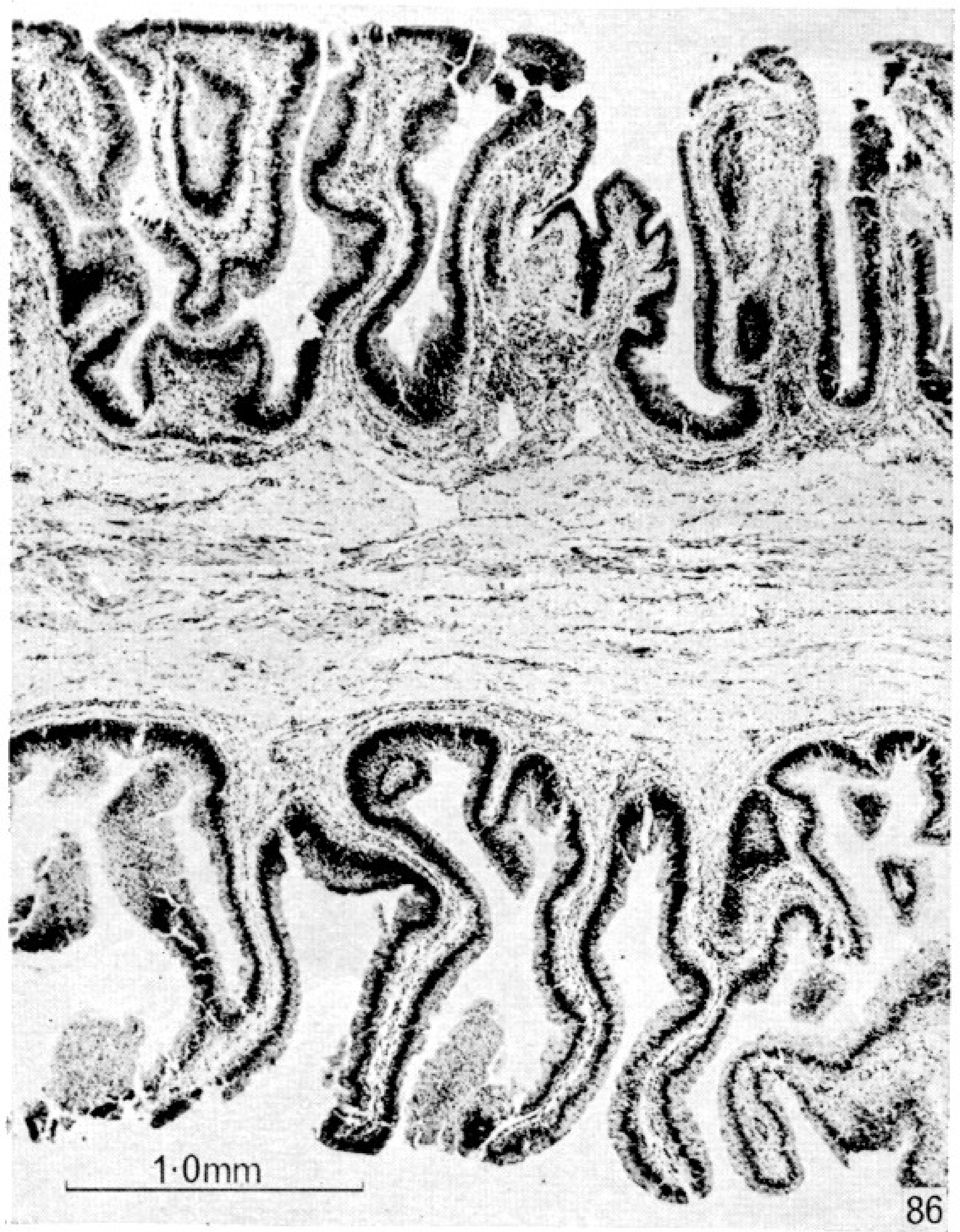
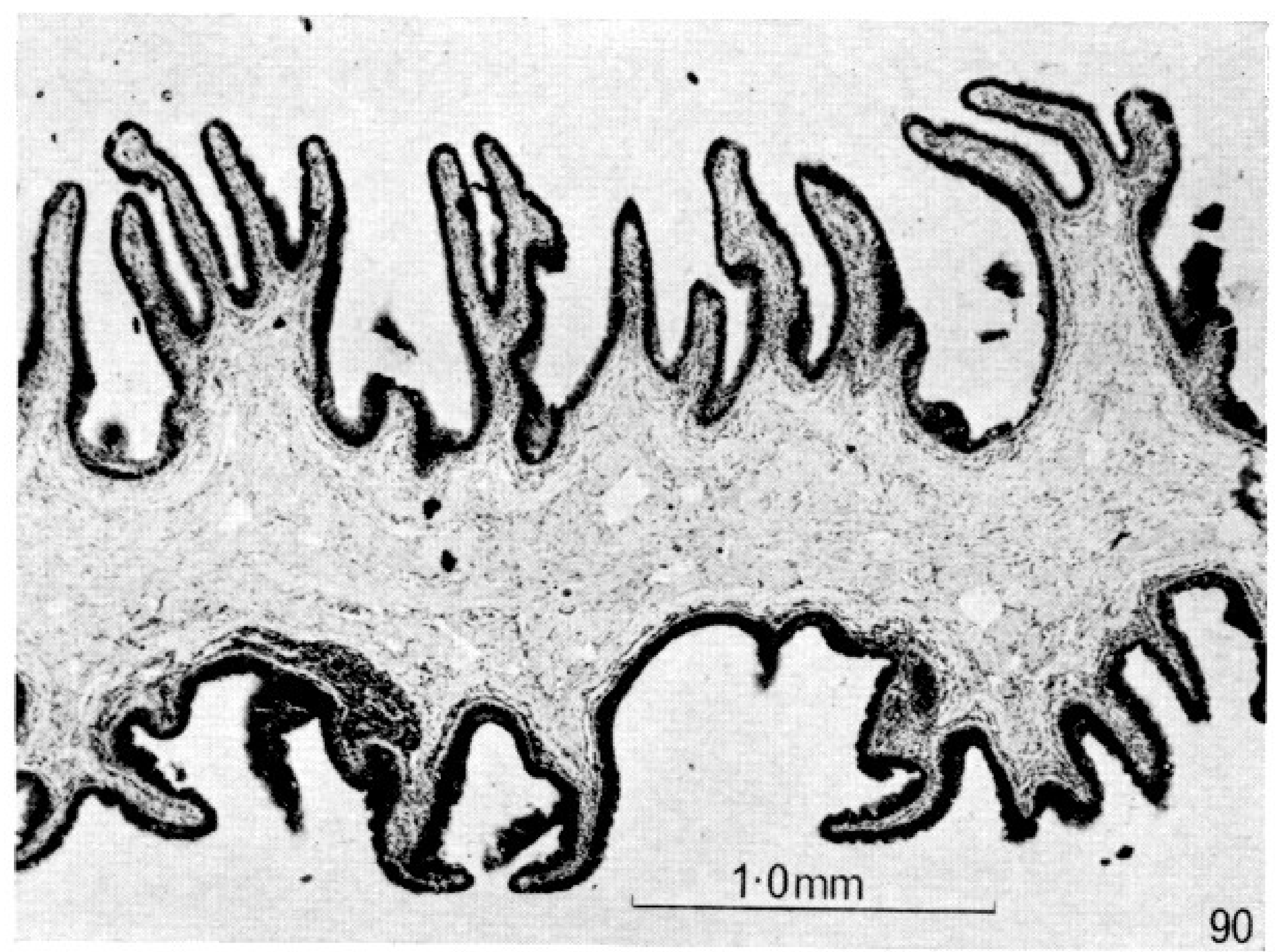


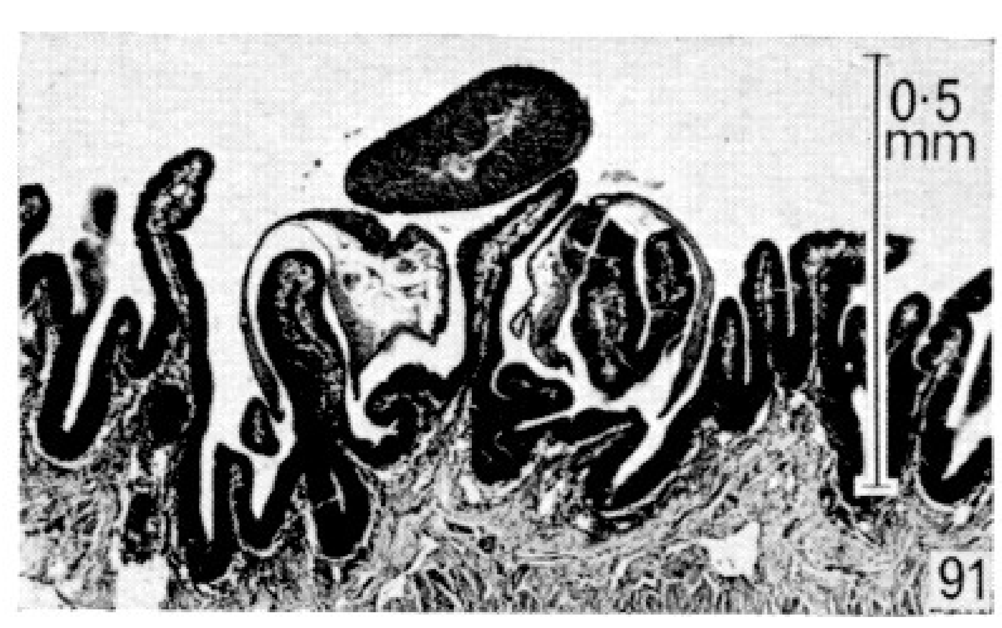
FIGURE 81. *Phyllobothrium britannicum* sp.nov., proglottid.
FIGURE 82. *Monorygma* (*Phyllobothrium*?) sp. from *Scyliorhinus caniculus*, proglottid.
FIGURE 83. *Phyllobothrium sinuosiceps*, proglottid.
FIGURE 84. *Crossobothrium* (*Phyllobothrium*?) sp. 3 from *Squalus acanthias*, scolex.

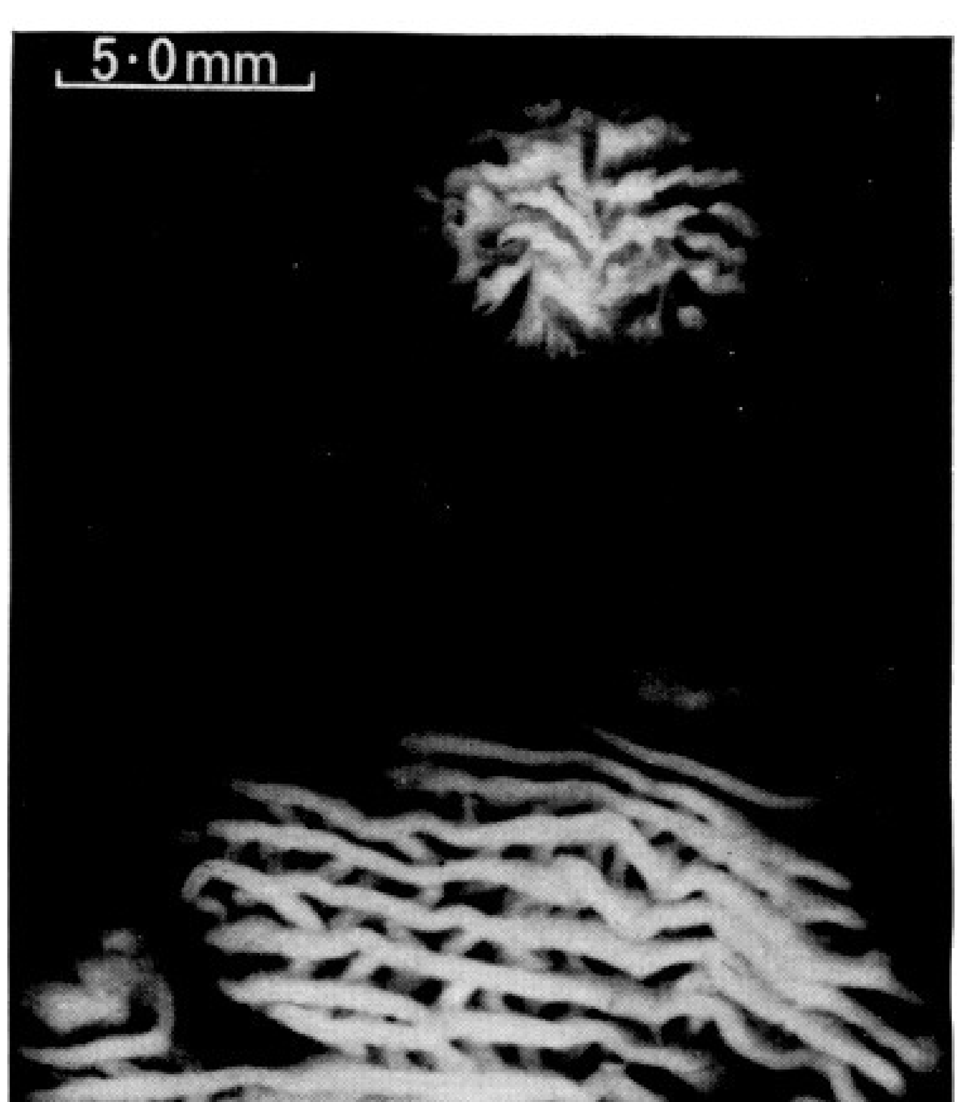


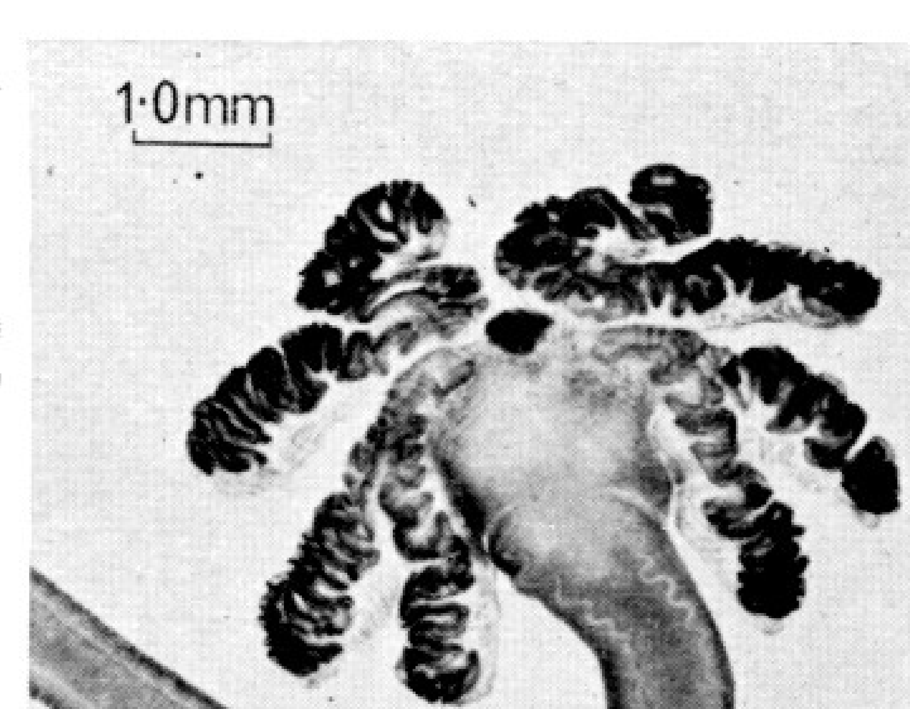










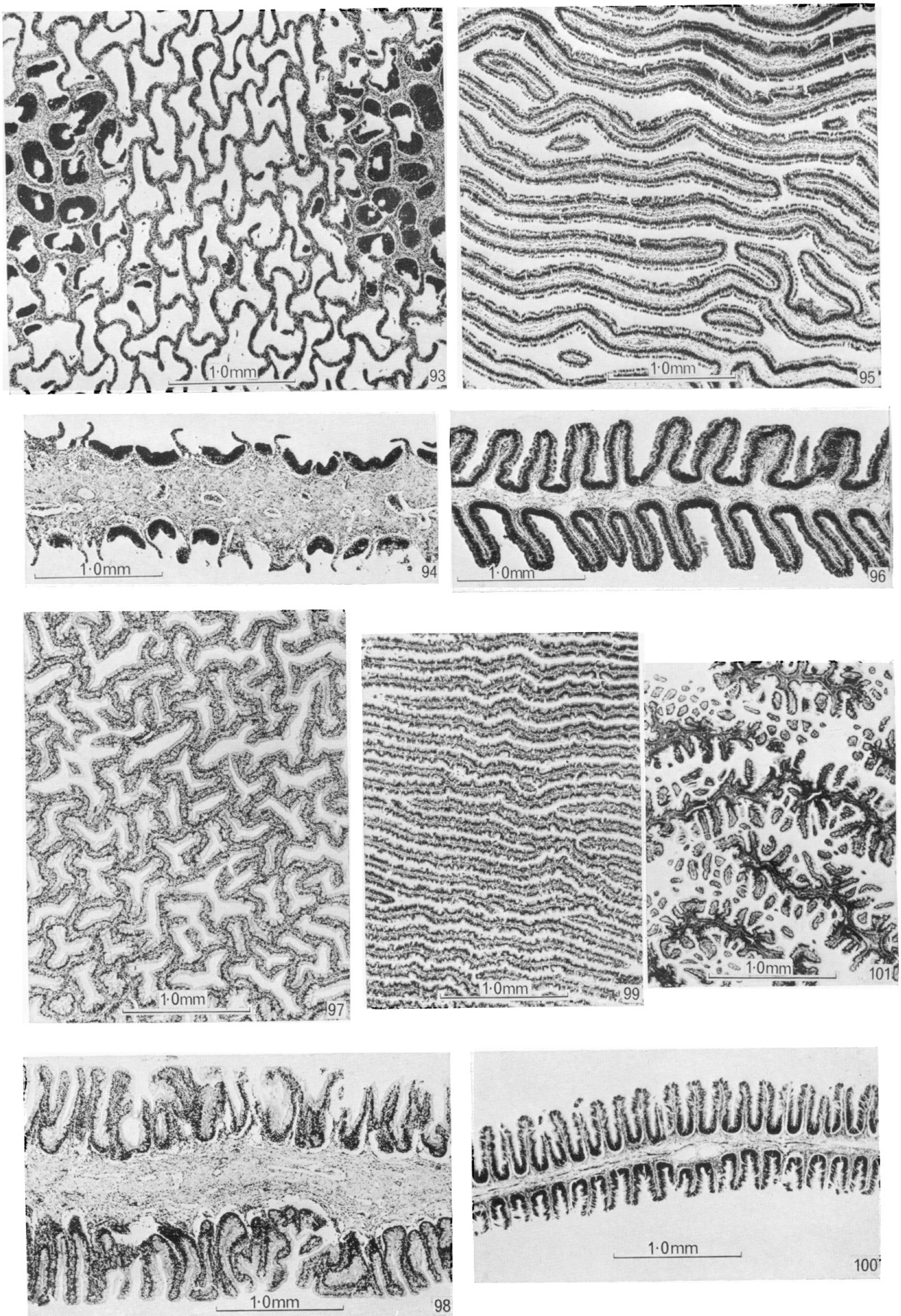


FIGURES 85 and 86. Facial and vertical sections of the gut mucosa of *Hexanchus griseus*; from anterior spiral of intestine, i.e. area of attachment of *Phyllobothrium sinuosiceps*.

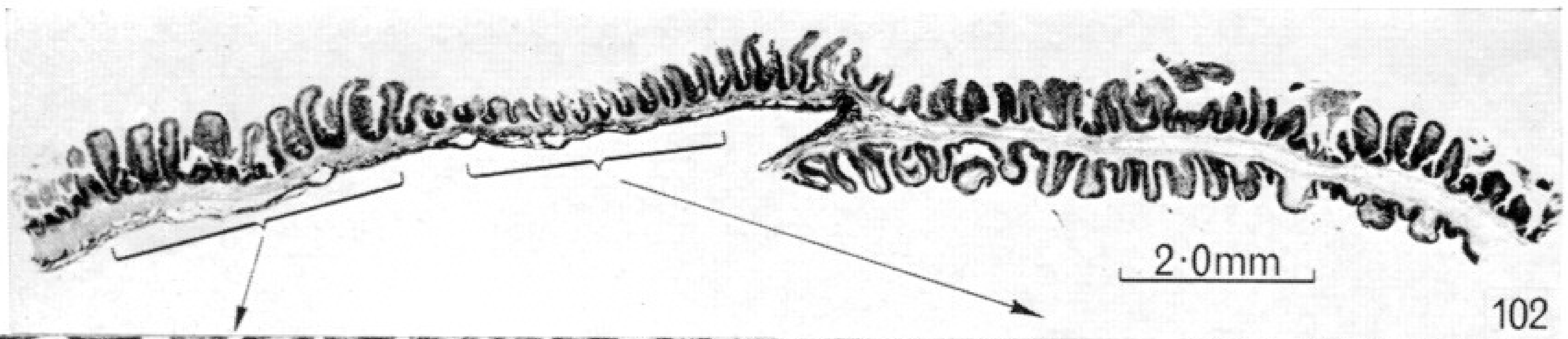
FIGURE 87. *P. sinuosiceps*, scolex photographed alongside piece of mucosa from anterior spiral of intestine of *H. griseus*.

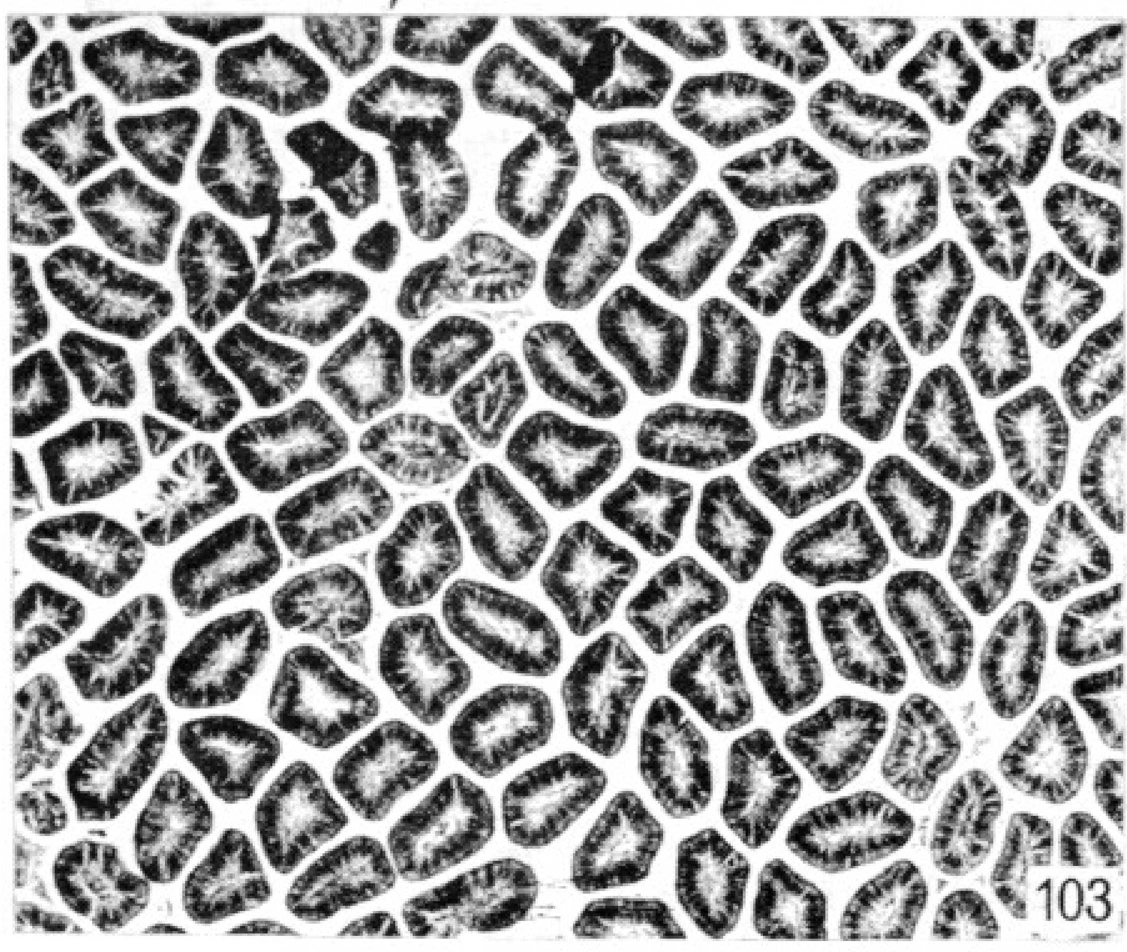
FIGURE 88. Vertical section of *P. sinuosiceps* attached to mucosa of *H. griseus*.

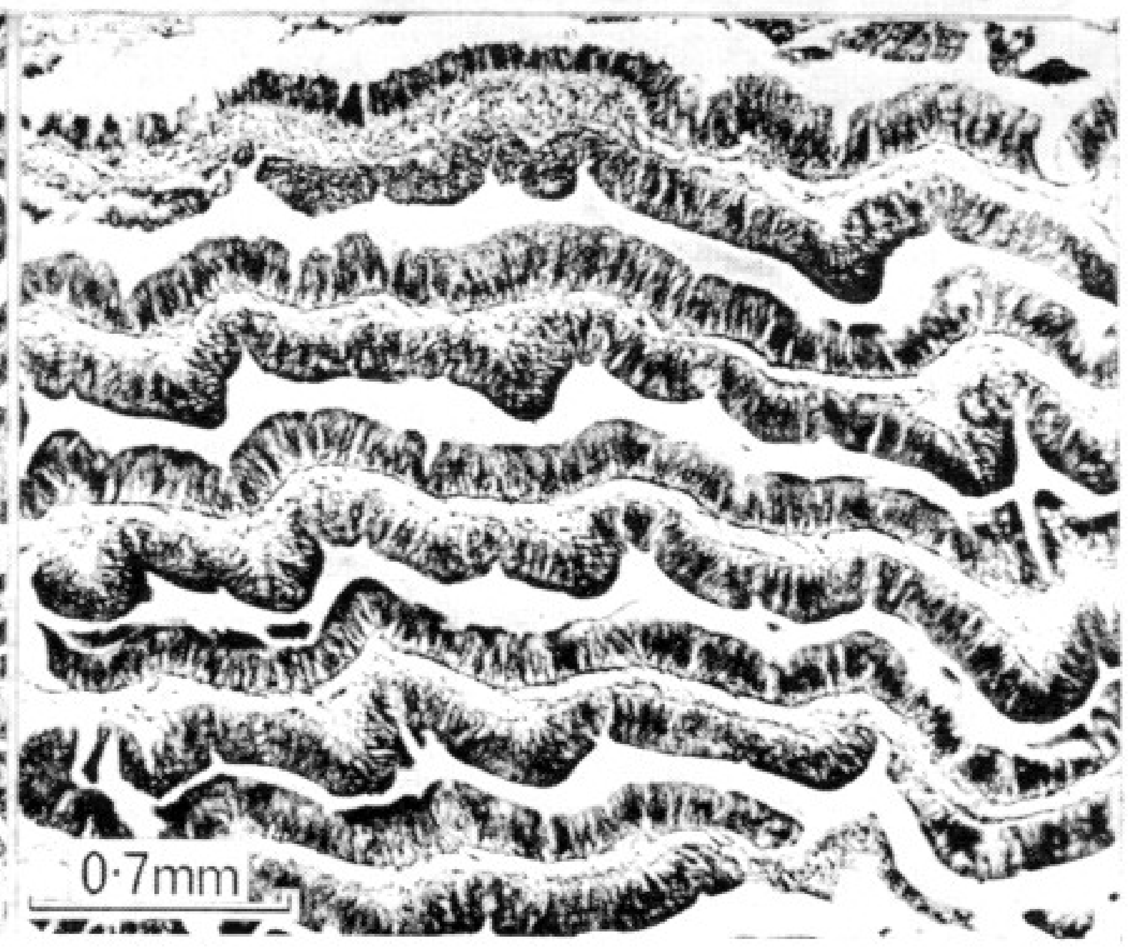
FIGURES 89 and 90. Facial and vertical sections of the gut mucosa of *Mustelus mustelus*; from anterior spiral of intestine, i.e. area of attachment of *P. lactuca*. (*Continue at foot of plate* 14.)

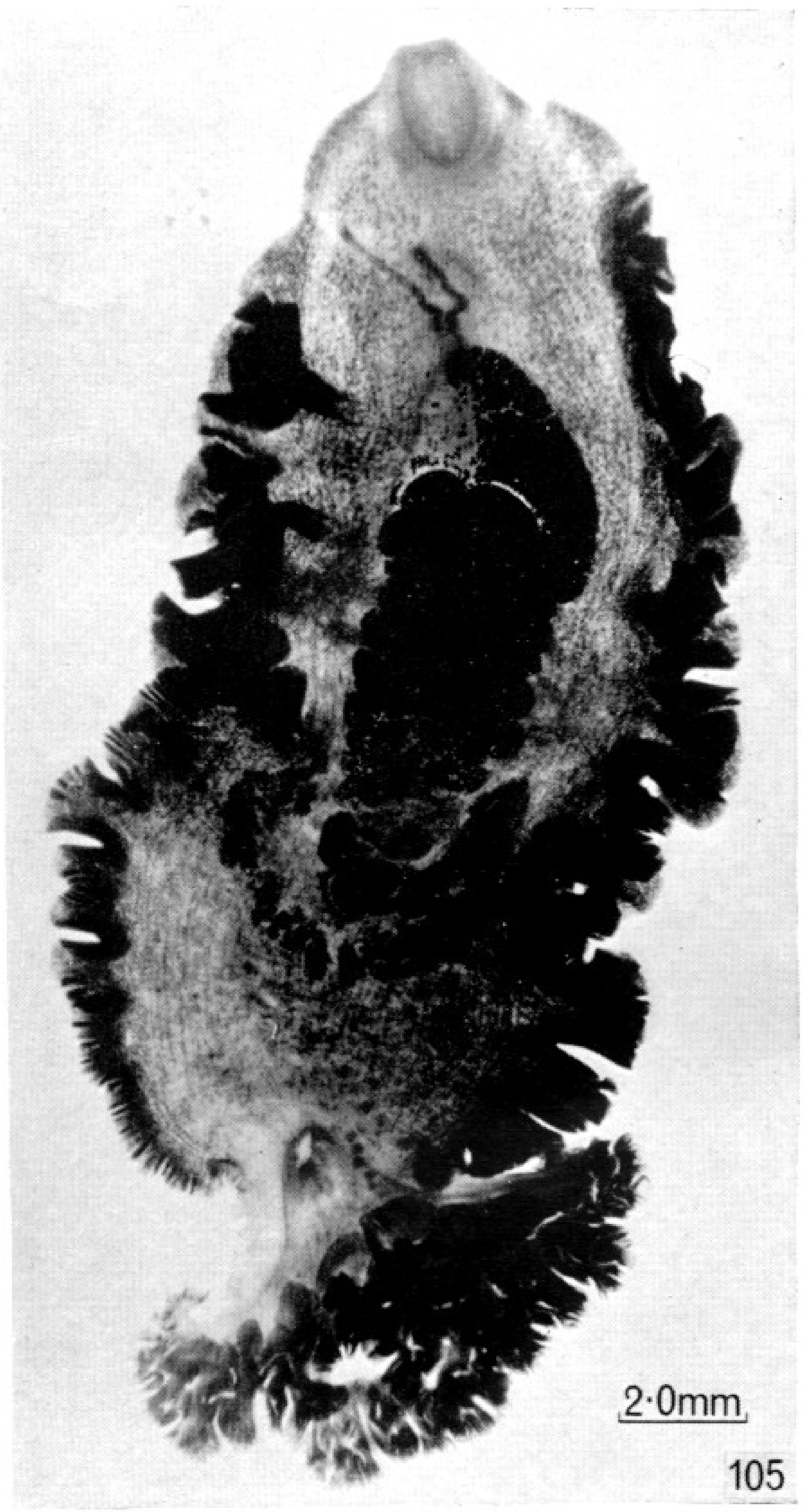


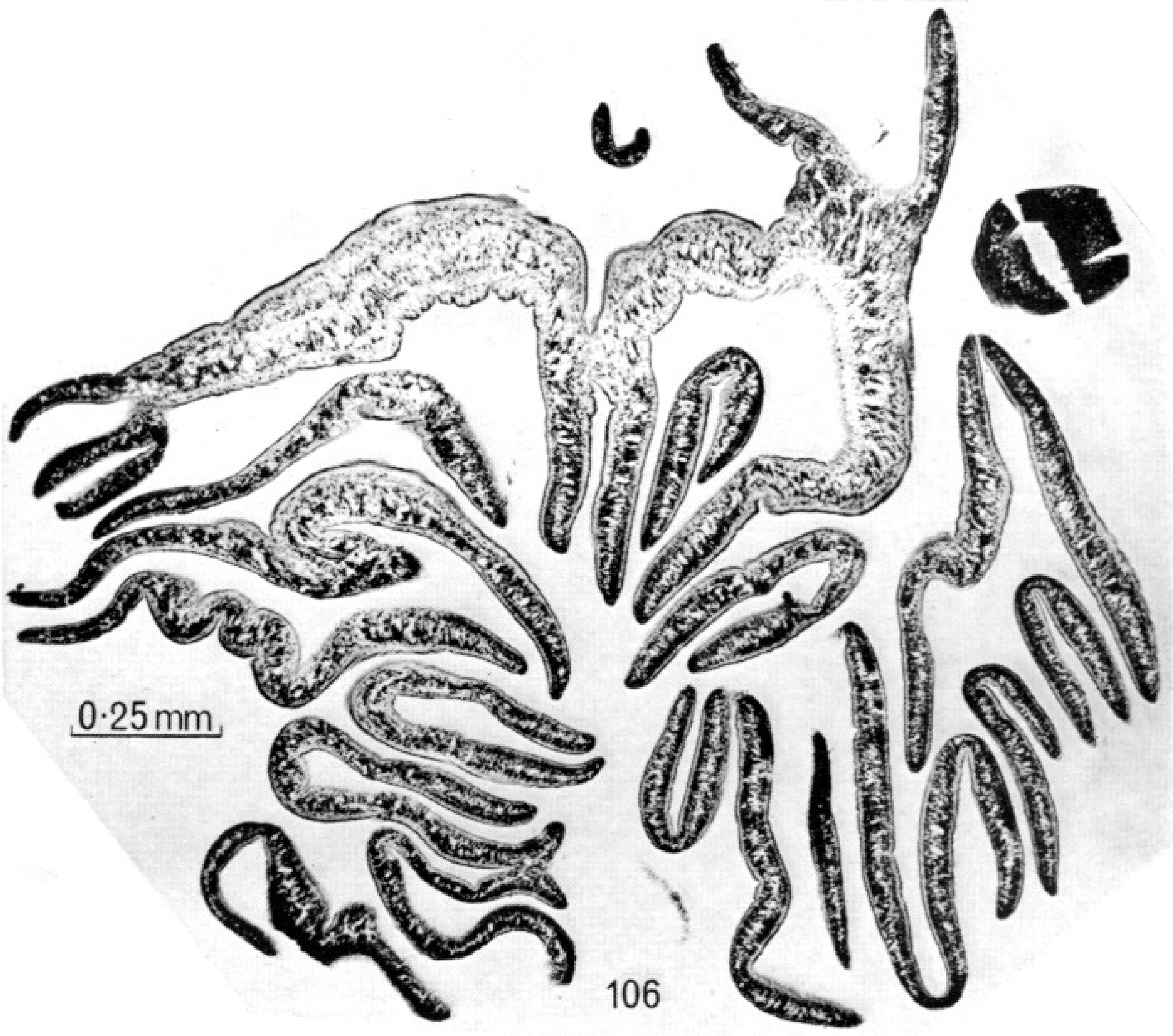
FIGURES 93, 94. Facial and vertical sections of the gut mucosa of *Squalus acanthias*.
FIGURES 95, 96. Facial and vertical sections of the gut mucosa of *Scyliorhinus stellaris*.
FIGURES 97, 98. Facial and vertical sections of the gut mucosa of *S. squatina*.
FIGURES 99, 100. Facial and vertical sections of the gut mucosa of *Eugaleus galeus*.
FIGURE 101. Facial section of the gut mucosa of *Raja batis*.

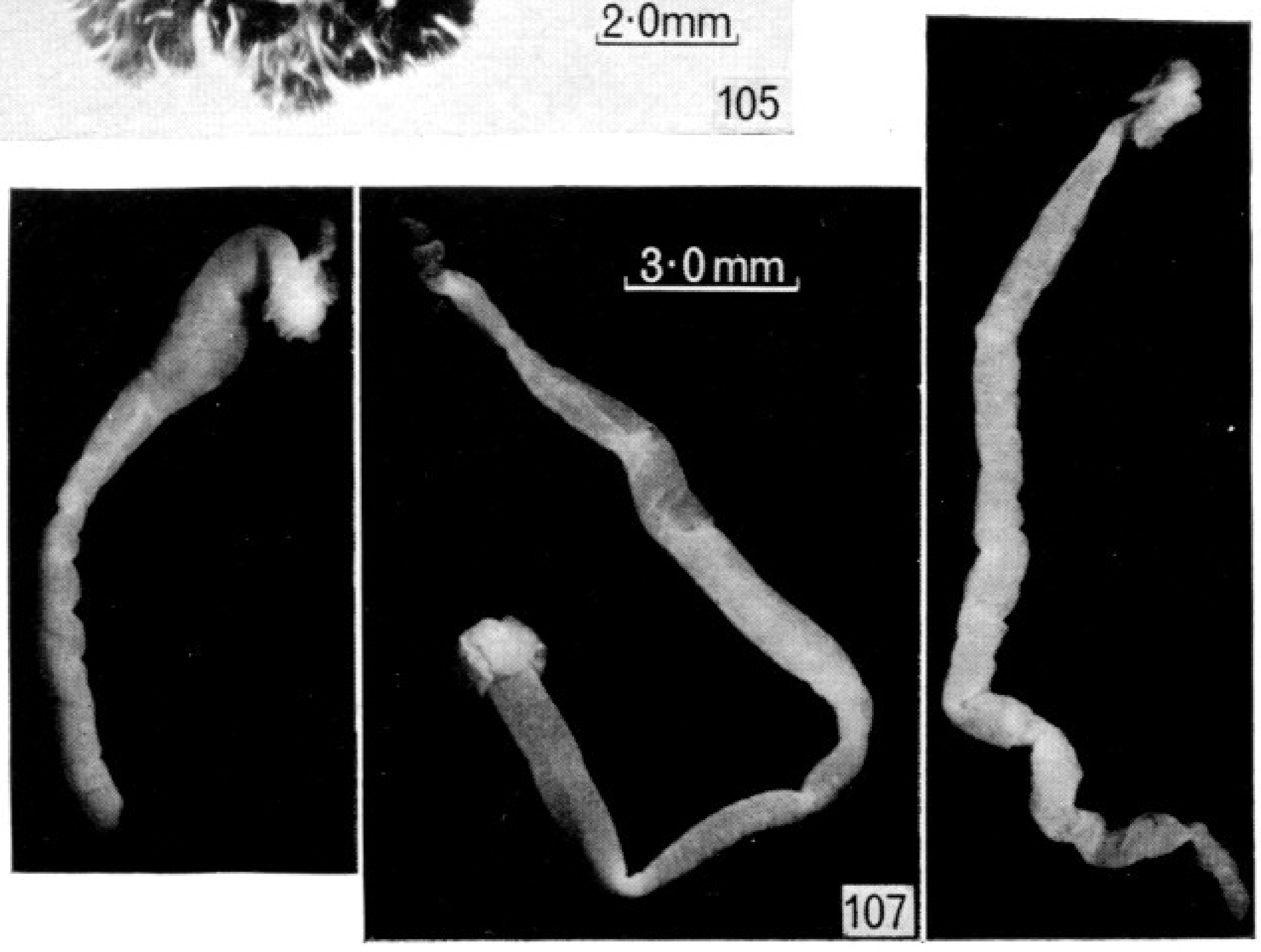


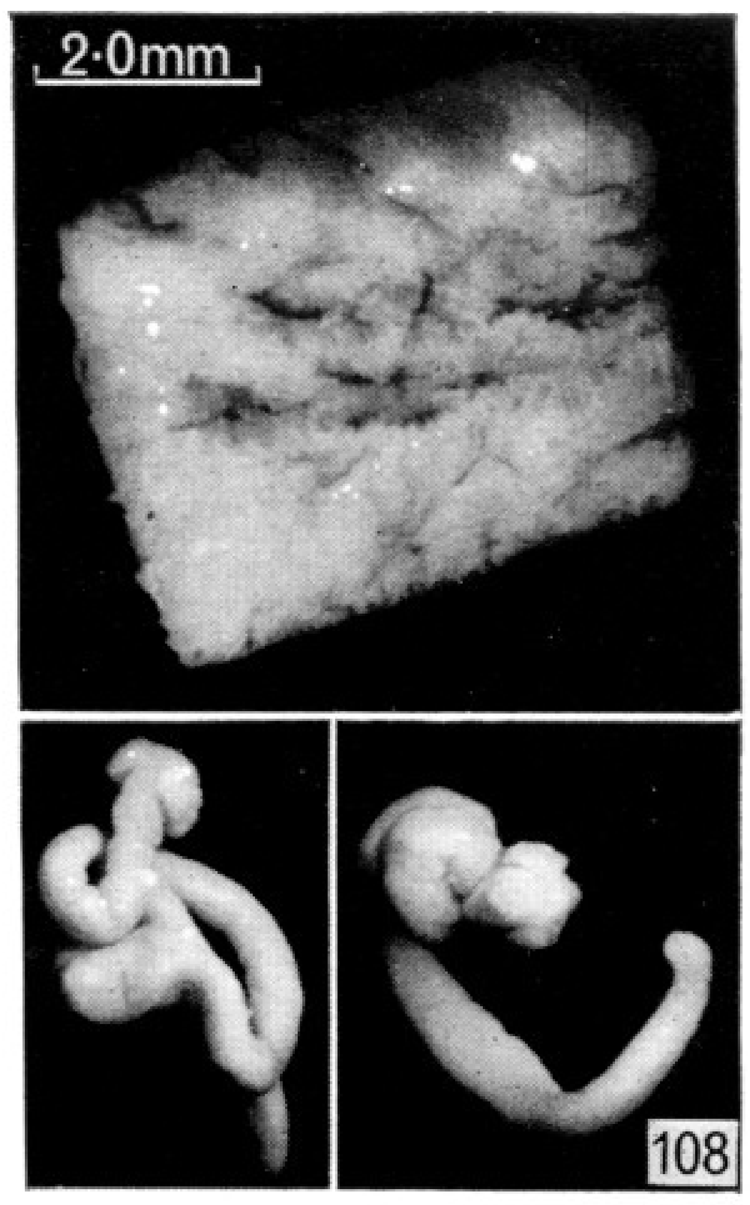












FIGURES 102–104. Variation in a small area of the gut mucosa of *Chimaera montrosa*.
FIGURE 105. *Gyrocotyle* showing posterior adhesive organ.
FIGURE 106. Section through posterior adhesive organ of *Gyrocotyle*.
FIGURE 107. *Phyllobothrium caudatum* from *Oncorhynchus nerka*, plerocercoids.
FIGURE 108. *Phyllobothrium* sp. in *Paralepis coregonoides*, plerocercoids and piece of intestinal mucosa of the host to which they are attached.