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SOME CONTROVERSIAL PROBLEMS IN CLASSIFICATION OF MONOGENEANS

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Abstract. The paper contains the main objections of foreign specialists (Llewellyn and others) to Bykhovsky's system of monogeneans. Llewellyn's interpretation of anchors and marginal hooks which is the basis of his phylogenetic scheme is proved to be erroneous by a number of data on morphology of chitinoid formations and on their mutual position. Thus the phylogenetic scheme loses its integrity and cannot be accepted. The system of Bykhovsky remains now the most natural. Some additions or changes do not break its principles.

The most recent classification of Monogenea, proposed in full and well founded in detail, was that of Bykhovsky (1957). A later classification proposed by Yamaguti (1963), which represented a revision of Sproston's (1946) monumental monograph, will be mentioned below. Amendments of, and additions to, Bykhovsky's classification (Gussev 1969, 1977, Lebedev 1972, Mamaev and Lebedev 1977, etc.) have not altered its salient features. It has, however, been vigorously rejected by some investigators, Llewellyn (1963, 1970) being outstanding among them. There is no need to review its essence and principles here; they are well known. On the other hand, it is worthwhile to subject the views of its leading opponent to a critical analysis, especially because they are shared, entirely or in part, by a number of other specialists. The root cause of these differences is the paucity of material available on many groups, prompting different answers to the key questions on classification. This paper is devoted to the discussion of some reasons underlying these differences.

Llewellyn (1970) does not propose a classification of his own; he only reviews "inter-relationships of only those 28 families recognized by Bykhovsky" (incorrect, there are 29 of them), "that perhaps a foundation may be laid for the future erection of a classification of monogeneans" (p. 494). He does not think it necessary to use full scientific names of taxa, using only their anglicized versions. This usage creates some difficulties in understanding how, according to his views, they are coordinated.

Both Bykhovsky and Llewellyn saw the origin of Monogenea in broadly similar terms: the adaptation of rhabdocoel turbellarians to parasitism on early vertebrates, followed by the appearance of an attachment disc or haptor of udonellid type. Hooks developed subsequently in that disc, improving attachment to the increasingly more active fishes. The two authorities differ in detail. According to Bykhovsky, the first organs of attachment were spicules, or hooks (marginal only); they were numerous (according to his drawing), while the haptor was bilaterally symmetrical. Llewellyn, on the other hand, sees the first organ of attachment as a sucker, a disc without hooks. The latter appeared later, 16 in number, and were distributed octodiametrally; the anchors arose between the second and the third posterior hooks. These are not differences in principle. What is more, both investigators believe that the subsequent evolution of monogeneans was based on changes in their haptors, that the number of hooks especially in larvae is an important systematic characteristic, that the ontogenetic evidence is the main criterion for setting up classification of the group. This view is now shared by almost all specialists. The greatest differences between Bykhovsky and Llewellyn are in the way they treat the number of larval hooks; this has been used by Bykhovsky as the basis for the division of the class into subclasses. Contradictions in Bykhovsky's work in regard to these structures made him open to the accusations of inconsistency and served to strengthen the position of his opponent. Indeed, Bykhovsky (1957, p. 99) stated that the larvae of the first type, characteristic of the subclass Polyonchoinea, have 14—16 marginal hooks. At another place (p. 343) he attributed to them 12—16 hooks. For larvae of the second type (subclass Oligonchoinea) he assigned on one occasion 10—12 hooks (p. 99), on another — 10 (p. 402). These contradictions are due to insufficiency or erroneous nature of earlier data. They made him unsure, whether in some groups certain hooks, which he considered non-homologous structures, should be treated as anchors or as marginal hooks (pp. 28, 101, 175 and 383 of the Russian edition). This difficulty was of principal importance, since such inaccuracy in some measure discredited the reason for dividing the class into two stems.

All the hooks, the number and relative positions of which have been used by Llewellyn as the basis for his evolutionary scheme, are divided by him, as they are by ourselves, into marginal hooks and anchors. In place of the English name anchor, now in use for the latter, he preferred to use that favoured by our French colleagues, a Latin name hamulus. His reason for doing so was the fact that the term anchor has been used to denote various types of median hooks, some of which are ontogenetically prior marginal hooks, i.e., the true larval hooks, while others (hamuli) develop later. It is true that such confusion existed. Far from clearing it up, however, Llewellyn's proposal rather made it worse, since, as he himself observed, hamuli exist also in larvae of many groups. Bykhovsky did stress that, as the level of organisation rises, they appear in ontogeny earlier and earlier, to be found eventually in larvae within eggs (p. 100). Moreover, knowing that marginal hooks characteristically possess a heel or guard, and loop or domus, Llewellyn and some other colleagues, French included, placed among them also the posteriormost pair (first according to Llewellyn's postero-anterior sequence, or sixth according to his earlier sequence in the opposite direction, proposed for diclidophorids). The hooks of that pair are devoid of heels and loops, are larger than the remaining ones, almost always have a different shape and, logically and on morphological grounds, should be considered as hamuli (Fig. 1).*). He gave no explanation of the differences between this pair of "hooks" and others, referring only to their special function (?). The loop he considered simply as having been lost in all except polystomatids. He has also undoubtedly been aware of the fact that the marginal hooks of adult higher monogeneans retain their embryonic character (in some they are present during the postlarval period). This has also been noted by Bykhovsky (p. 100). However, Llewellyn did not find it at all surprising that these posteriormost "hooks" in some higher monogeneans grow strongly and change their shape in the course of ontogeny (Fig. 1B). Again, he only noted the fact, offering no explanations. Finally, he followed Kearn (1963) in taking the third pair of anchors of capsalids for the first pair of marginal hooks which become modified into auxiliary supporting structures. However these centrally placed "hooks" possess neither heel nor loop (it is usual for anchors and for these considered by Llewellyn to be the first, "crochet en fleau" included, to have instead of a loop a structure of wing type (Fig. 10), as exemplified by Dactylogyrinea, Discocotylidae, Microcotylidae, and Diclidophoridae). Besides in dionchids and in certain capsalids there is only one pair of anchors and in some even this pair is missing. It means that these genera have only 14 marginal

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*) We are not sure what is the difference between the similarly shaped (judging from earlier drawings) anchors and marginal hooks of Mazocraeidae, and *Nitzschia* Anchorophoridae. This calls for careful re-examination, which we plan for the near future.

hooks, not 16 as stipulated by Llewellyn. Moreover, as the latter points out, his "first pair of marginal hooks" in capsalids grows and changes shape during ontogeny, whereas the remaining ones do not. Does this fact not suggest that this "first pair of hooks" is not of the same character as others which are undoubtedly marginal? Finally, we know of no instances of marginal hooks changing into supporting structures, while changes of this kind do occur in anchors on occasions, e.g., in *Anchoradiscus* among dactylogyrids, and perhaps in *Bothitrema* among Tetraonchidea.

Thus, Llewellyn artificially increased by one the number of the marginal hooks in larvae of the higher and of some lower monogeneans (capsalids). Unfortunately, this error received currency among some other specialists. Its author himself went further: he made it the basis for his original phylogenetic scheme (Fig. 2A). The essence of his scheme is as follows. In all monogeneans which have anchors, these anchors are located between the second and third pairs of marginal hooks. In promonogeneans all hooks were

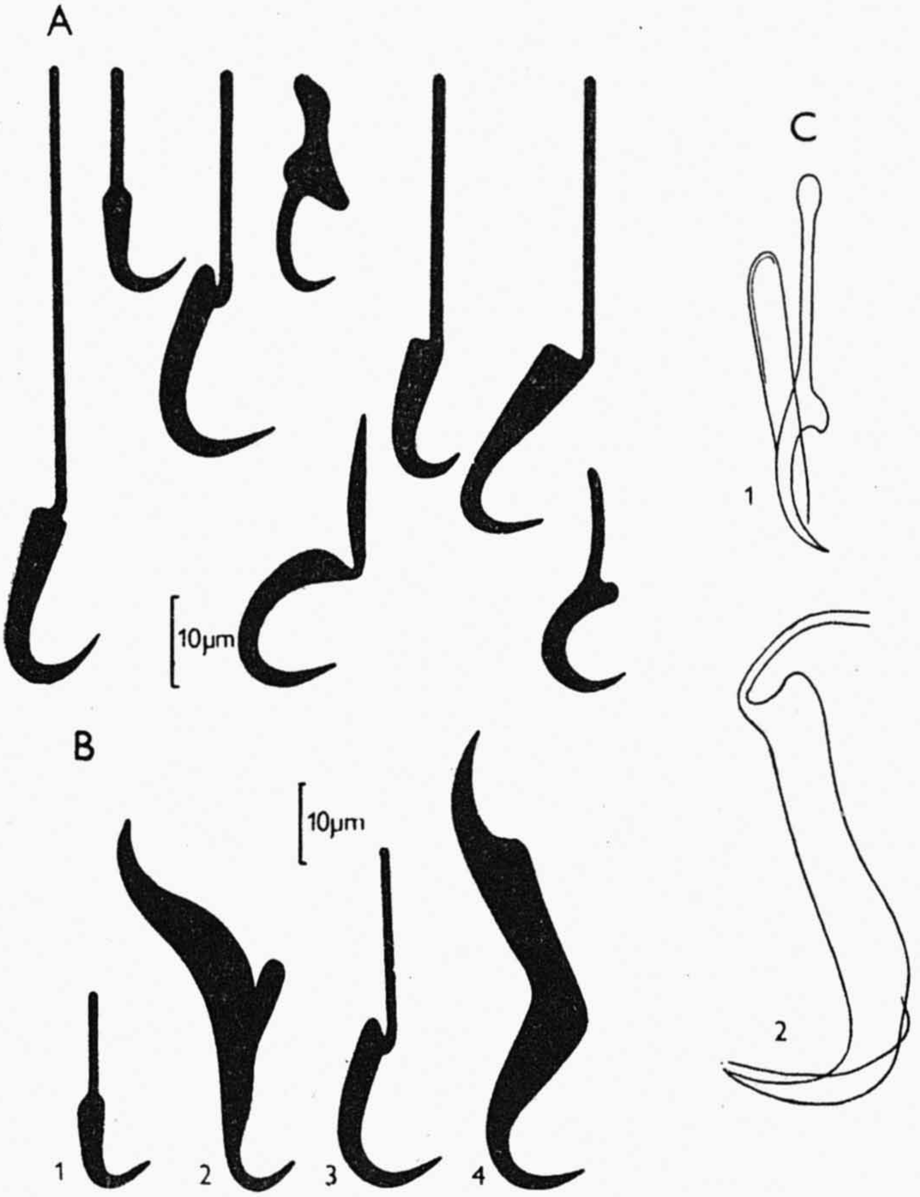
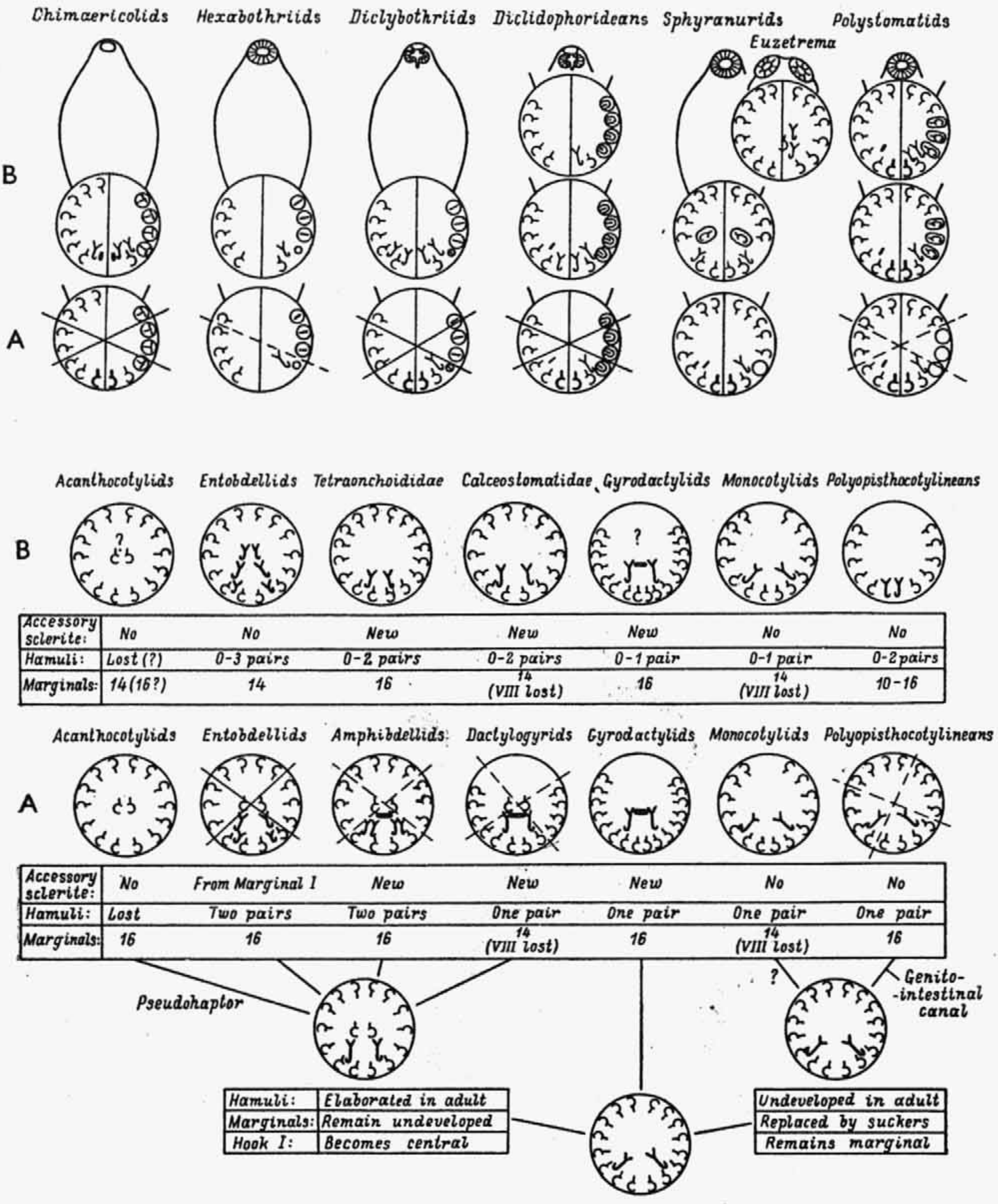


Fig. 1. Anchors and hooks: A — treated by us as anchors and by Llewellyn (1963) as posteriormost marginal hooks (in different groups: of higher monogeneans); B — the growth of anchors (1-st pair of marginal hooks according to Llewellyn 1963) during ontogenesis (1, 2 — *Plectanocotyle*, 3, 4 — *Anthocotyle*, 1, 3 — in larvae, 2—4 — in adult specimens). Both drawings from Llewellyn 1963. C: 1 — Marginal hook of *Dactylogyrus* and its loop or domus, 2 — anchor (1-st marginal hook according to Llewellyn) and its wing which are characteristic for many groups of Oligonchoinea.

arranged allong the periphery of the haptor. Two stems developed from them; in one the posterior pair of marginal hooks (the first according to Llewellyn, the seventh or eighth in our numeration) became displaced towards the centre of the haptor (the dactylogyrid stem); in the second stem (more correctly a group of stems) these hooks retained their peripheral position. From this second stem branched off two lines: the gyrodactylid



	Acanthocotylids	Entobdellids	Tetraonchoididae	Calceostomatidae	Gyrodactylids	Monocotylids	Polyopisthocotylineans
Accessory sclerite:	No	No	New	New	New	No	No
Hamuli:	Lost (?)	0-3 pairs	0-2 pairs	0-2 pairs	0-1 pair	0-1 pair	0-2 pairs
Marginals:	14 (16?)	14	16	14 (VIII lost)	16	14 (VIII lost)	10-16

	Acanthocotylids	Entobdellids	Amphibdellids	Dactylogyrids	Gyrodactylids	Monocotylids	Polyopisthocotylineans
Accessory sclerite:	No	From Marginal I	New	New	New	No	No
Hamuli:	Lost	Two pairs	Two pairs	One pair	One pair	One pair	One pair
Marginals:	16	16	16	14 (VIII lost)	16	14 (VIII lost)	16

Hamuli:	Elaborated in adult
Marginals:	Remain undeveloped
Hook I:	Becomes central

Undeveloped in adult
Replaced by suckers
Remains marginal

Fig. 2. A — Patterns of development of the haptor in monogeneans after Llewellyn 1963; B — the same schemes taking into consideration facts and our interpretation of anchors and marginal hooks. Groups which keep their place in Llewellyn's scheme only partly are crossed out by dotted lines; groups which fall out from his scheme completely are crossed out by continuous lines.

line of viviparous monogeneans and the second one of oviparous forms. The latter, in its turn, produced two branches: monocotylids and polyopisthocotylineans, including polystomatids and all higher monogeneans. In other words, there are four stems (orders, subclasses?). In those instances when, in a group, the number of marginal hooks is less than 16, he quite rightly believes that one or two pairs of anterior hooks have been lost. However, when only one pair, not two, of marginal hooks is present between the anchors, he also believes that one pair of hooks has been lost here (in hexabothriids and, apparently, in some capsalids and dionchids). This assumption is probable and logical only if one tries to preserve the integrity of the entire concept.

In consequence, Llewellyn produced an elegant and orderly, but artificial scheme. However, if the posterior "the first marginal hook" of higher monogeneans and "the central hooks" of capsalids are restored to their apparently true status of anchors and if one takes into account all subsequently obtained data, then the following picture is produced. At the posterior extremity of the haptor in almost all larval Oligonchoinea there is a pair of anchors (hamuli or crochet en fleau, according to Euzet 1957). The second pair of anchors is located between the first and second true marginal hooks. The anchors are between the first and second marginal hooks also in hexabothriids, capsalids, entobdellids, dionchids, calceostomatids, iagotrematids (*Euzetrema*) and tetraonchoidids. In polystomatids one pair of anchors is between the first and second marginal hooks, and the second between the second and third marginal hooks (see diagram in Ktari 1971). According to Bykhovsky and Nagibina (1975), among larvae of chimaericolids, *Callorhynchicola* has 16 (or 14?) marginal hooks, the two posteriormost being rudimentary (it is not clear whether they are hooks, and if so, which hooks), and two pairs of anchors. One of the latter appears already in the egg, before the hatching of the larva, between the rudimentary and next hooks but not between second and third hooks, as it should according to Llewellyn's scheme. Apparently he took this pair of anchors as being the first marginal and overlooked the rudimentary hooks. Even dactylogyrids (sensu Bykhovsky 1957) do not all comply to Llewellyn's scheme. Thus in *Anchoradiscus* all marginal hooks are placed on margin of haptor.

Beside these data which disturb the order set out in Llewellyn's scheme, his proposals contain some obvious lapses. Thus he includes all tetraonchideans in the dactylogyridean branch and he thinks that dactylogyrids and diplectanids arose from tetraonchids (Llewellyn 1970, p. 496). However, a group with 16 marginal hooks cannot be placed in the same phylogenetic stem with one that possesses 14, especially when they differ from each other in their entire organisation. The erroneous nature of such a combination needs no special proof. Calceostomatids have 14 marginal hooks, not 12 as stated by Llewellyn. It is also puzzling why he places *Anonchohaptor* in that family.

One can only be surprised at the one-sided and selective use of some tetraonchoidids by Llewellyn in support of his hypothesis. He observed that in *Pavlovskioides pearsoni* Bychowsky, Gussev et Nagibina, 1965, one pair of marginal hooks is situated at some distance from the others and from the anterior margin of the haptor towards its centre. A similar pair of hooks exists on the anterior "accessory disc" of *Allotetraonchoides rhigophilae* Dillon et Hargis, 1968. Llewellyn postulated that the first (posterior) pair of hooks is displaced forwards by the connecting bar. However another pair of marginal hooks, the second, remains behind it, between the anchors. It would be probable and would fit his cheme, if he kept in mind that a single pair of marginal hooks between the anchors is also present in the remaining species of tetraonchoidids, in which there are no grounds to suspect similar displacement. Hence the conclusion that this pair of anterior hooks in *Pavlovskioides pearsoni* (and in *Allotetraonchoides*) is not a displaced posterior pair but an originally anterior one which moved backwards. Llewellyn's example can be used, therefore, as an argument against him.

Finally, it is by no means always that two pairs of marginal hooks are also present between the anchors of gyrodactylideans (?). And so, if one disregards the problem of "marginal" of "hamular" nature of the posterior, "first pair of hooks", still in need of detailed review, and if one excludes 14-hooked calceostomatids, dionchids and some capsalids, in which disappearance of the first pair of hooks has been assumed (as has been "decided" about hexabothriids), then also in the remaining 16-hooked forms form various groups (Tetraonchoididae, *Euzetrema*, Polystomatidae, or Chimaericolidae with a full set of hooks from which there is nothing to disappear) the comparative distribution of anchors and marginal hooks does not conform to Llewellyn's scheme. If one also takes into account all the facts and views quoted above and if one introduces appropriate corrections to these views, then the scheme becomes fairly chaotic (Fig. 2B). Complete groups of only monocotylids, and perhaps acanthocotylids (and gyrodactylids?) will keep their place in Llewellyn's scheme, as shown in his drawing.

The position of acanthocotylids in the system will remain uncertain until their larvae and morphogenesis are more thoroughly studied. If it is proved that the hooks in the centre of their haptor are marginal, nor anchors, then their inclusion into Monopisthocotylidea would be unjustified. In that case their affinity with Tetraonchidea would appear more probable. This is also suggested by some other structural features similar to those of Amphibdellatidae: both have a copulatory organ of dactylogyrid type, both are eyeless, both are parasitic on skates, etc. Microbothriidae also require detailed reinvestigation to make their place in the system more precise. Their known larva with three pairs of "spicules" is as yet of uncertain shape and, unfortunately, is virtually useless for this purpose.

There was a lot that was controversial and confusing in the views on the phylogenetic interrelationships of the families in the abundant order Dactylogyrinea, which constitutes the bulk of the freshwater and a large part of the marine monogenean fauna. However, the situation was rendered even more complicated by arbitrary and unwarranted treatment of pairs of auxiliary a needle-like structures ("4A" of American authors) and later of two pairs of analogous (or homologous?) similar sclerites in South-American *Anacanthorus*. Ligaments, rudiments of marginal hooks, or of anchors such are the three interpretations of these structures, based almost entirely on theoretical conclusions. None the less, the supporters of each (or rather of the last two) hasten to "correct" accordingly their diagnoses of taxa and to make premature phylogenetic conclusions. The situation was further aggravated by the description of *Curvianchoratus*, a dactylogyrid allegedly possessing three (?) pairs of anchors (a new suborder?), as well as by descriptions of about 15 other genera from India, South America and Africa, based on very scanty, sometimes false, characters (*Archidiplectanum*, *Indocotylus*, *Onchiodiscus*, *Urocleidoides*, etc.). To "bring order" to dactylogyrineans we need accurate data on the fine morphology of representatives of various groups and faunas. Also required is a correct, non-formalistic approach to interpretation of material (Gussev 1977).

The key problem in the classification of monogeneans is correct understanding of the place occupied by polystomatids and sphyranurids, the majority of which continue to be referred to Odhner's Polyopisthocotylea, i.e., to the higher Monogenea. Llewellyn sharply disagrees with Bykhovsky, who places them in one order with gyrodactylids. In Llewellyn's view that order is "unnatural" (1963, p. 317), and "incongruous grouping" (1970, p. 500). Bykhovsky also pointed out extensive differences between its suborders, but stressed that they result from far-reaching specialization of both suborders, and from the viviparity of gyrodactylids. In Bykhovsky's view, their relative closeness to each other is indicated not so much by gyrodactylids' ability to parasitize tadpoles, as by the discovery in Africa of *Gyrdicotyle*, an interesting and specialized gyrocotylid bearing a pair of suckers. It was found in the intestine of a frog, one of the common hosts of polystomatids. On the other hand, *Eurolystoma* was described from Australian *Neoceratodus*. These facts are hardly a coincidence; rather are they evidence of some ancient relationships. Parasitization by *Isancistrum* of cephalopod molluscs (sometimes of fishes?) is also a fact in favour of the ancient age of gyrodactylids. Llewellyn is probably right in treating gyrodactylids as a separate branch. More likely than not, their separation from the stem of Polyonchoinea occurred not in Jurassic but considerably earlier, not later than Carboniferous. This is equally true of polystomatids.

Bykhovsky established satisfactorily that polystomatids and sphyranurids belong to Polyonchoinea. Here are some corroborative facts. In adult Polyopisthocotylidea all marginal hooks are retained and remain in the haptor (Llewellyn made a mistake, when he spoke of their replacement by suckers, 1963, p. 312), which (with few exceptions) occurs in the subclass Polyonchoinea. On the other hand, in Oligonchoinea all marginal hooks except one pair are lost during ontogeny and are replaced by newly-formed clamps or suckers (Nagibina 1969, Wiskin 1970). As Llewellyn (1963) points out, the number of ciliated cells, which is 45 or more in larvae of lower Monogenea and polystomatids, "never exceeds 30" in higher ("diclydophorideans"). This calls for confirmation, since in *Diplozoon* alone there are 36—41. In most lower monogeneans and polystomatids the excretory ducts are fused anteriorly, while in the higher ones they are separate. Llewellyn's reference to the similarity of intestinal epithelium of the higher monogeneans and polystomatids must be rejected. Electron microscope data show only an external similarity. The gastrodermis cells of these two groups show many differences in details of morphology and function (Gussev 1977). In the pharynx of polystomatids and lower monogeneans.

The key to the differences in views on the position of polystomatids lies in the fact that they, like lower monogeneans, have a genito-intestinal duct. However, they also possess bucco-oesophageal ducts which are absent from lower monogeneans. The description of two monogeneans, both from the urinary bladder, *Iagotrema* from a South American turtle and *Euzetrema* from the Corsican salamander has a direct bearing on this problem. The former is without a vaginal duct, while the latter has a paired vaginal one. Neither has a genito-intestinal and buccal ducts but both have typically polystomatid 16 marginal hooks (in the former, a pair of central hooks was overlooked), and two pairs of anchors, as well as two cephalic suckers. They have simple circular intestines and a single testis. Llewellyn (1970) tentatively placed them in capsalids, which is not surprising, since in his view they also have 16 marginal hooks, rather than the 14 determined by Bykhovsky. His decision was, indeed, supported by other features, such as the two cephalic suckers and the absence of the genito-intestinal duct. And yet, Bykhovsky's and our first reaction to the description of *Euzetrema* was: this is a member of Polyopisthocotylinea! (sensu Bykhovsky 1957). Information recently received on the development and life cycle of *Euzetrema* (Combes et al. 1974) has reinforced this view even more. After all, the hosts, biology and type of life cycle are also taxonomic characteristics in the view of modern (non-formalistic) systematics at a higher level. The life cycle, just like any morphological or biological feature, develops as a result of a long process of adaptation of the organism to its environment. For a parasite, particularly for one narrowly specific, this means in the first place the host, a representative of a group characterized by a life rhythm which has also been historically determined. T. A. Timofeeva's investigation carried now on *Euzetrema* (sp.n. from urinary bladder of *Mertensiella caucasica*, Urodela) confirmed our view that this genus belongs to Polyopisthocotylidea, which will be discussed by us in a special paper. Thus Bykhovsky's view on convergent origin of genito-intestinal duct (and bucco-oesophageal canal) in different groups is proved.

Underestimation of the very widespread process of convergent development of similar structures in monogeneans is not uncommon even among workers with experience and intuition. None the less, it is surprising, just like the opposite phenomenon, that of ignoring similarity in the type of adhesive organs, a salient characteristic in the evolution of the class. To unite polystomatids with higher monogeans because of the presence of bucco-oesophageal and genito-intestinal ducts (to be consistent, one would have to add to them also *Geneticoenteron* Yamaguti, 1963), is about the same as uniting diplectanids, amphidellids and monocotylids because of the characteristic coiling of the ovary around the right intestinal branch, or tristomes with chimaericolids and gyrocotylids because of the type of ovary. All would agree that these would be improper combinations. And yet, to put polystomatids in Polyopisthocotylinea (sensu Llewellyn 1970), and *Euzetrema* in capsalids, is hardly better.

Yamaguti (1963) in his classification follows, in general, Odhner's principles. He adds many new taxa at all levels and proposes some very unfortunate recombinations: he places Bothitrematidae in Dactylogyridea, *Amphibdella* in Ancyrocephalinae, makes *Salmonchus* an addition to the latter, and places *Tetraonchus* (a synonym of which *Salmonchus* becomes) in the superfamily Tetraonchoidea, to name only a few. Describing the genito-intestinal duct in *Geneticoenteron*, he makes no conclusion from this discovery, although it destroys the principle of classification that he uses. It was subjected to severe criticism by Llewellyn (1970), and cannot be given more attention here. Excellent and valuable as source of reference, Yamaguti's book contains unfortunately a number of taxonomic errors.

In summation, I must agree that the most acceptable classification of monogeneans remains so far that proposed by Bykhovsky. Many groups require revision. The position of some was nuclear to Bykhovsky and remains so. Some shifts, and establishment of new orders, subordes and families, have not so far rendered invalid its principles and its integrity. To define more precisely the position of some groups and to iron out controversial problems, intensification of work on development and morphology is needed as the first priority. It should include the study of the fine structure of dactylogyrids, acanthocotylids, microbothriids, gyrodactylids, and, particularly, polystomatids s.l. (*Euzetrema* included). Also necessary are complete detailed embryological investigations, which have been non existent for almost 80 years, and which hardly exist even now.

The rate of progress along the path leading to the solution of these problems is proportional to the accuracy and quantity of observations and data, to our ability to represent them graphically, to methodologically correct analysis and objectivity of conclusions. It is very important to the coordination of efforts of all specialists that we should organize regular all-union and international meetings, aimed at the development of uniform methods, coordination of investigations, evaluation of their results and discussion of controversial problems.

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НЕКОТОРЫЕ СПОРНЫЕ ВОПРОСЫ СИСТЕМЫ МОНОГЕНЕЙ

А. В. Гусев

Резюме. Излагаются суть возражений некоторых специалистов (Llewellyn и др.) против системы Быховского и принципы филогенетической схемы класса по Левеллину. Фактическими данными о морфологии хитиноидных образований прикрепительного диска показана ошибочность трактовки Левеллином срединных и краевых крючьев и их взаимного расположения, что положено им в основу его схемы. Последняя теряет стройность и не может быть принята. Наиболее естественной пока остается система моногеней, предложенная Быховским. Отдельные дополнения и изменения не нарушают ее принципов.

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J. Złotorzycka: Nadrodzina Philopteroidea: rodzina Philopteridae.

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The next volume from the series Keys for identification of Polish insects published by the Polish Entomological Society is devoted to the family Philopteridae. It is arranged in a similar manner as the previous parts. The introductory systematical survey of the superfamily Philopteroidea is followed by a key to its 9 families and by a systematical survey of the individual taxa of the family Philopteridae up to the level of subspecies, including the synonymy. The core of the book constitute keys for determination (pp. 15—117). They include a concise characterization of the family, key to subfamilies and, within their framework, a key to genera. The most important characters and keys to lower taxa are given for each genus. Brief data on morphology, hosts and geographical distribution of individual species are given in the key. It also comprises the species so far undetected in Poland, but possible to occur there. A total of 29 genera and 181 species and subspecies are recorded. The text is suitably complemented by numerous illustrations. At the end of the book there is a list of Latin names of parasites and hosts. In the systematical section of the book, the author adheres to her concept of small genera, which is not, however, accepted by all contemporary taxonomists dealing with this group. The publication is of high value also for other countries of central Europe and in a useful manner fills in a gap in the present determination literature.

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