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THE SYSTEM AND PHYLOGENY OF MONOGENEANS OF THE FAM. DICLIDOPHORIDAE

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The paper examines the existing systems of monogeneans of the fam. *Diclidophoridae*, proposes a new system for this family and provides a new phylogenetic scheme.

The system of monogeneans of the fam. *Diclidophoridae* proposed by S. Yamaguti in his monograph (Yamaguti, 1963) suffers, in our opinion, from some major shortcomings. Besides, the fam. *Diclidophoridae* has significantly increased in size since that book was published: a great many new species have been described, and the number of genera has increased by the factor of two. All of this makes a revision of the composition of this family and of its very system an absolute necessity.

Over the past few years the author of this paper has to one degree or another been involved in the study of monogeneans of the fam. *Diclidophoridae* and has published a number of papers on the new species and genera, on the systems and phylogeny of individual taxons, and has also presented his views on the principal characteristics of the evolution of the diclidophorids (Mamaev, Parukhin, 1970; Mamaev, 1972a, b, 1973, 1975a, b; Mamaev, Lyadov, 1975; Mamaev, Parukhin, 1975a, b).

We used for our research the vast original material gathered by various expeditions and preserved in the collections of the Laboratory for General Helminthology of the Institute of Biology and Pedology of the Far East Science Centre of the USSR Academy of Sciences. At the Institute of Zoology of the USSR Academy of Sciences we were able to study those genera that were not to be found in our collections. We believe the time has come to undertake a revision of the fam. *Diclidophoridae* in general and to propose its new system.

A Brief Overview of the fam. *Diclidophoridae* and Notes on the Systematic Position of Its Individual Genera

Works that summarize the taxonomy of a particular group of organisms usually begin with a historical overview of research that has been focussed on the given group. For example, we should proceed from the discussion of the works by Cerfontaine that were published in the last century. However, we shall take the liberty of deviating from this tradition and we shall start with the work by Sproston (Sproston, 1946), which was the first fundamental work on the taxonomy of monogeneans. It relates the whole pre-1946 history of research on the *Diclidophoridae* in a very complete though extremely concise form.

Sproston divides the fam. *Diclidophoridae* into two subfamilies —

58/

Diclidophorinae and *Choricotylinae* — according to the structure and functional characteristics of their adhesive clamps. In the first subfamily the clamp acts as a clasp or pincers, whereas in the second subfamily it functions as a reinforced sucker. The subfam. *Diclidophorinae* contains only one genus *Diclidophora* (10 valid and 3 dubious species), while *Choricotylinae* has six genera — *Choricotyle, Cyclobothrium, Diclidophoropsis, Echinopelma, Heterobothrium* and *Pedocotyle.*

Hargis in his papers (Hargis 1955, 1959) follows to the same classification. B. E. Bykhovsky (1957) shares Sproston's understanding of the size of the fam. *Diclidophoridae* and accepts her nomenclature for its genera, but he does not recognize the subdivision of the family into two subfamilies.

Yamaguti (Yamaguti, 1963) introduced some significant changes into the system of this family. In addition to the already existing subfamilies *Diclidophorinae* and *Choricotylinae,* he proposed two more: *Pedocotylinae* for the two species of *Pedocotyle* — *P. morone* (MacCallum, 1913) and *P. minima* (Hargis, 1955) — and *Eurysorchiinae* for *Eurysorchis australis* (Manter et Walling, 1958). He restored the status of the genus *Cyclocotyloides* (Price, 1943), formed for it and for the genus *Diclidophoropsis* (Gallien, 1937) a new subfamily *Diclidophoropsinae* and placed the latter in the fam. *Discocotylidae.* He removed from the fam. *Diclidophoridae* six species: *Diclidophora pollachii* (v. Beneden et Hesse, 1863), *D.*

denticulata (Olsson, 1876), *D. luscae* (v. Beneden et Hesse, 1864), *D. gadi* (Reichenbach — Klinke, 1951), *D. phycidis* (Parona et Perugia, 1889), *D. palmata* (Leuckart, 1830); he restored for the first four species the genus *Dactylocotyle* (v. Beneden et Hesse, 1863) and the subfam. *Dactylocotylinae*; for the other two he founded a new genus *Pseudodactylocotyla* and the fam. *Pseudodactylocotylinae* and placed these subfamilies into the fam. *Dactylocotylidae* (Brinkmann, 1942) restored by him. Within the subfam. *Diclidophorinae* he founded a new genus *Allodiclidophora* for *Diclidophora squillarum* (Parona et Perugia, 1889), which was regarded by many authors (see Sproston, 1946) as a synonym for *Choricotyle smaris* (Ijima in Goto, 1864), and included *Choricotyle charcoti* (Dollfus, 1922) in this new genus.. He restored the genus *Neoheterobothrium* (Price, 1943) that had not been recognized by Sproston (1946) and Bykhovsky (1957), and in addition to the previously existing *N. affine* (Linton, 1898) and *N. cynoscioni* (MacCallum, 1917), he incorporated into it *N. pugetensis* (Robinson, 1961) (=Diclidophora p.).

According to Yamaguti, the system of *Diclidophoridae* in its entirety looks as follows:

Diclidophorinae with the genera *Diclidophora, Allodiclidophora* and *Osphyobothrus.*

Choricotylinae with the genera *Choricotyle, Cyclobothrium, Echinopelma, Heterobothrium* and *Neoheterobothrium.*

Eurysorchiinae with the monotypical genus *Eurysorchis.*

Pedocotylinae with the genus *Pedocotyle.*

A considerable contribution to the taxonomy of diclidophorids has been made by Unnithan (Unnithan, 1966) who described a number of new species and genera, and by Llewellyn (Llewellyn, 1956a, 1958; Llewellyn, Tully, 1969) whose works on the functional morphology of monogeneans, their ecology and host-specificity are very important for understanding the philogeny and taxonomy of diclidophorids.

From our point of view, the simple system of *Diclidophoridae* proposed by Sproston in 1946 is essentially the most correct one: it represents the two major directions in the evolution of these monogeneans. Naturally, as time went by, this system became antiquated and needed to be updated and supplemented, taking into account the new genera described after its publication, which has been done by Yamaguti. Many systematic rearrangements he undertook are quite legitimate and should be accepted, but some of his innovations proved to be completely
59/
unfounded, and therefore the system he proposed is, on the whole, far from natural. We share Dillon and Hargis' view (Dillon, Hargis, 1965) that Yamaguti had no reasons to transfer the genera *Diclidophoropsis* and *Cyclocotyloides* from the fam. *Diclidophoridae* into *Discocotylidae,* even though identification of the subfam. *Diclidophoropsinae* was certainly justified. The removal of the six above-mentioned species of diclidophorans from the fam. *Diclidophoridae* and the restoration of a separate fam. *Dactylocotylidae* for them is totally unwarranted. Nor can we accept a distinct genus *Allodiclidophora* (the species that are included in it should belong to the genus *Choricotyle*) and a number of other systematic rearrangements in the fam. *Diclidophoridae*.

Before we commence our discussion of the issues associated with the philogeny of monogeneans of the fam. *Diclidophoridae* and propose a new system, we would like to make a few comments on the systematic status of certain genera of this family.

Diclidophora (Kroyer, 1831) is a type genus of the family and of the nominative subfamily. According to its morphological characteristics, this genus occupies a central position in the subfam. *Diclidophorinae*: all of its representatives have a well-developed chitinoid membrane in the anterior valve of their clamp, which is a typical feature of the given subfamily.

There are 12 valid species in the genus *Diclidophora* to date. They diverged significantly in their attributes and are quite distinct. Besides, the differences between some species of diclidophorans are, in our opinion, more than differences between the species. For example, *D. lotella* (Machida, 1972) differs significantly from all the others in the structure of its attachment disc; some species display considerable differences in the topography of their internal organs, while others differ in the structural details of their clamps. Thus, there are some grounds for subdividing the genus *Diclidophora* into several genera as it was done by Yamaguti. However, due to the pronounced interpenetration of specialization within this genus, it is very difficult to divide it even into subgenera. Following Sproston (1946) and Llewellyn (1958), we believe that a more sensible solution would be to preserve a single large genus *Diclidophora* parasitic on the Gadiformes and on their relatives, the Macruriformes.

The genus *Diclidophoroides* (Price, 1943) was founded by Price (1943) for a monogenean described and identified by MacCallum (MacCallum, 1917: see Price, 1943) as *Diclidophora merlangi*. The diagnostic attributes of this genus are as follows: the attachment disc is clearly separated from the body itself and the posterior pair of clamps is larger than the rest. Judging from a drawing by Price, *Diclidophoroides maccallumi* also differs significantly from the typical diclidophorans by the structure of its clamps: the basal median plate is wider, but it does not form a true membrane. If this is, indeed, the case (and not an error on

Price's part), *D. maccallumi* does merit a genus of its own. For the time being we believe it necessary to preserve this genus that was abolished by Sproston and has not been recognized by any subsequent authors.

Neoheterobothrium (Price, 1943) was regarded by Sproston (1946) as a synonym for the genus *Heterobothrium* (Cerfontaine, 1895). Her point of view was shared by Nagibina (1953) and Bykhovsky (1957). Yamaguti (1963) restores the genus *Neoheterobothrium* and includes into it *N. affine* (Linton, 1898) — a type species, *N. cynoscioni* (MacCallum, 1917), and *N. pugetensis* (Robinson, 1961). In their 1969 work Llewellyn and Tully use the name *Diclidophora pugetensis* and, consequently, do not attribute this species to the genus *Neoheterobothrium,* but whether they recognize the genus *Neoheterobothrium* as such is not mentioned in this work.

Having studied the structure of *N. pugetensis* from the materials preserved in our Laboratory, we came to the conclusion that *Neoheterobothrium* was an independent genus of the subfam. *Diclidophorinae* (and not of *Choricotylinae,* as

60/

Price and Yamaguti used to think) and that it was quite close to *Lebboia* and *Diclidophora* but rather distant phylogenetically from *Heterobothrium.* In recent years B. E. Bykhovsky, too, was inclined to subscribe to this view.

Only two species — *N. pugetensis* and *N. affine* — should be included in this genus, and the third species —*N. cynoscioni* — attributed by Yamaguti to this genus is in reality a representative of the genus *Choricotyle.*

As for the genus *Osphyobothrus,* Yamaguti (1958) finds it necessary to comment on its host contingent. Representatives of this genus are apparently parasitic only on the fishes of the genus *Saurida* (fam. *Synodontidae*). Yamaguti (1958) mentions *Parapercis pulchella* — a fish from the order of the Perciformes —

as the host for the type species *O. parapercis,* but we are convinced that this was a mistake: either Yamaguti's material (1958) was accidentally mislabelled or the monogenean in question happened to be on *Parapercis* by pure accident. Our collections contain a vast amount of material on this genus of monogeneans obtained from the saurids in eight areas of the Indo-Pacific (3 species from 4—5 species of fish). These monogeneans were not found on the fishes of the genus *Parapercis.* We (Mamaev, Parukhin, 1970, 1975a) updated the diagnosis of the genus *Osphyobothrus* in several respects.

The systematic position of the genera *Heterobothrium* (Cerfontaine, 1895), *Tagia* (Sproston, 1946) and *Gempylitrema* (Yamaguti, 1968) was examined in the paper by Bykhovsky, Mamaev and Nagibina (1976).

Cyclocotyloides (Price, 1943) is a valid genus. It is close to *Diclidophoropsis* (Gallien, 1937) and together with the latter it differs significantly from all the other diclidophorids by the presence of a twin vagina and by the primitive structure of their clamps. Separation of these genera into a distinct subfam. *Diclidophoropsinae,* as it was done by Yamaguti (1963) was quite legitimate. But as we have already mentioned above, this subfamily should belong to *Diclidophoridae* rather than to *Discocotylidae.*

Choricotyle (van Beneden et Hesse, 1863), the type genus of the subfam. *Choricotylinae,* is the largest in the diclidophoridean family. We count 15 valid species in it, as well as 4 *sp. inquerenda,* which are now very difficult to determine with greater accuracy. The recently described *Choricotyle oregonensis* (McCauley et Smoker, 1969) also needs a re-examination. It is unlikely to belong to this genus, although it undoubtedly belongs to the fam. *Choricotylinae* (Mamaev, 1975a). Genus *Choricotyle* is certainly in need of a thorough study and revision of its composition, but this can be accomplished only by studying the type specimens of the species *Choricotyle,* as well as the new original material; the published data alone are not sufficient for that purpose.

We identified the genus *Hargicotyle* (Mamaev, 1972) for the two species that had previously been attributed to the genus *Choricotyle* parasitic on the sciaenid fishes. *Hargicotyle* is characterized by the copulative organ whose structure is similar to that of *Diclidophoropsis* but with a multirow armament. In its other morphological characteristics this genus is undistinguishable from *Choricotyle,* but this similarity must be a consequence of the parallelism in the evolution of these taxons. We believe that the genus *Hargicotyle* should even be regarded as an independent subfamily.

Genus *Macruricotyle* (Mamaëv et Ljadov, 1975) should belong to the subfam. *Choricotylinae.* A mistake was made in our initial description (Mamaev, Lyadov, 1975): large excretory ducts were mistaken for the vaginal ones (see Bykhovsky, Mamaev, Nagibina, 1976 that describes the genus *Zeicotyle* gen. nov., which is closest to *Macruricotyle*).

As we know, the genus *Pedocotyle* (MacCallum, 1913) is characterized by the rudimentation of the posterior pair of attachment clamps situated on a single long stem that seems to be an extension of the worm's body. This morphological

61/

characteristic is not found in any other genus *Diclicophoridae,* for which reason Yamaguti (1963) identifies it as an independent subfam. *Pedocotylinae. Pedocotyle* is certainly an aberrant genus, but it is close to *Choricotyle* and, from our point of view, hardly merits to be identified as an independent subfamily. However, there might be other opinions on that score, therefore we believe it possible to retain the subfam. *Pedocotylinae.*

Dussumericola (Unnithan, 1966) is apparently an independent genus of the subfam. *Choricotylinae,* but it is impossible to determine accurately its position in this subfamily without a repeat study of the type material: the clamp structure in *D. dussumieri* (Unnithan, 1966) has been poorly studied and the drawings of the clamps provided by Unnithan (Unnithan, 1966) are very schematic.

Genus *Paracyclocotyla* (Dollfus, 1970), whose one and only species has been described on an unknown fish, belongs to the subfam. *Eurysorchiinae,* as it is characterized by a copulative organ with a double crown of hooks. By the structure of its attachment clamps it is very similar to the type genus of the subfam. *Eurysorchis* (Manter et Walling, 1958), but it differs significantly from it by the shape of its attachment disc and by the topography of its internal organs. In the original description (Dollfus, 1970) it was also pointed out that unlike *E. australis* (Manter et Walling, 1958), *P. cherbonnieri* possesses a vaginal system. A few specimens of *P. cherbonnieri* (ironically, they, too, were collected from an unknown fish) turned up in the material collected in 1970 in the South Pacific and obtained by us from the Pacific Research Institute of Fisheries and Oceanography (TINRO). When studying them, we established that *P. cherbonnieri* had no vaginal system and that there was an error in the original description: excretory ducts were mistaken for the vaginal ones. Dollfus has recently corrected his error. His joint paper with Euzet (Dollfus, Euzet, 1973) gives a revised description of this genus on the basis of some new material and points out the absence of the vagina. The paper also mentions the host of this monogenean: it happens to be *Alepocephalus rostratus,* a fish from the fam. *Alepocephalidae.*

For the time being we do not attribute to any subfamily the recently described genus *Tribuliphorus* (Mamaëv et Paruchin, 1975) that occupies an intermediate position between the primitive genera *Diclidophorinae* and the fam. *Anchophoridae* (Bychowsky et Nagibina, 1958). We hope that in the next few years some other similar monogeneans will be found on the fishes of the order Gadiformes or on flatfishes, so that it will be clear what place in the system should be occupied by this genus. There are three possibilities: 1) to incorporate the genus *Tribuliphorus* into *Diclidophorinae*; 2) to form a separate subfam. *Tribuliphorinae* and 3) to demote the fam. *Anchorophoridae* to the rank of subfamily (within *Diclidophoridae*) and to incorporate the genus *Tribuliphorus* into it.

The Main Morphological Characteristics of *Diclidophoridae*

The main morphological characteristic of *Diclidophoridae* is the presence of four pairs of symmetrically positioned attachment clamps whose skeleton in the type consists of eight chitinoid plates: in the anterior valve of the clamp there is a basal median plate and a pair of anterior lateral plates, while in the posterior valve there is an additional median plate, a pair of median lateral plates and a pair of posterior side plates (we use the terminology of skeletal formations proposed by Bykhovsky (1957). In many diclidophorids, these plates — particularly those in the anterior valve — may fuse together, but it is always possible to conduct a homology of these formations using the skeleton of the most primitive diclidophoridean clamp that consists of eight loose plates. This kind of clamp is found in such representatives of *Diclidophoropsinae* as *Diclidophoropsis* and *Cyclocotyloides*. It is a semispherical bowl with a regularly distributed musculature, and it exercises both pinching and

62/

sucking action, which is apparently achieved by changing the curvature of the walls. The skeleton of the clamp is symmetrical.

In the representatives of the subfam. *Diclidophorinae* the pinching as well as the sucking action of the clamp is significantly increased. This is achieved by the greater mobility of the folds and by the development of the sucker-plunger at the base of the inner section of the clamp. As Llewellyn (1958) demonstrated, the tight compression of the clamp valves in *Diclidophora* occurs mainly with the help of the sucker (Llewellyn calls it a diaphragm) that creates a negative pressure in the clamp when pulled back by the powerful extrinsic muscles. At the same time, due to the strengthening of the fixator function of the clamp, the diclidophorids develop an asymmetry of the clamp skeleton. A flat growth develops on the side of the basal median plate and projects towards the inner section of the anterior valve of the clamp. A small protuberance of this kind is already present on the median plate of the clamps in *Cyclotyloides* and *Diclidophoropsis*; a bundle of extrinsic muscles is attached to it. In diclidophorineans the primary function of this protuberance is apparently the same, but it also acts as a reinforcement of the clamp wall. As the sucker-plunger develops in the process of the evolution of diclidophorineans, and consequently, as the strain on the walls of the clamp increases, the latter function of the protuberance on the basal median plate keeps increasing and it becomes transformed into a large membrane to which the anterior lateral plates begin to fuse.

In the genus *Lebboia* the formation of the membrane through the expansion of the distal end of the basal median plate is in its initial stage: there are no signs of an emerging ring that supports the sucker, but the sucker itself exists, even though it is poorly developed. This is the most primitive genus of diclidophorineans we know, but the clamp of these monogeneans already bears the marks of narrow specialization: the posterior lateral plates are superimposed on one another as well as on the end of the additional median plate, and partly fuse together forming a characteristic "tooth" that plunges into the tissues of the gill filament of the host when the valves are closed. The distal end of one anterior lateral plate has separated, and when the folds clamp together, the separated piece of the plate, which is situated opposite the "tooth" of the posterior valve, is apparently capable of moving aside, which results in an even more vigorous clamping of the gill.

In *Diclidophoroides* this membrane is probably developed just as poorly. But as we have already mentioned, the structure of the clamp in these monogeneans has not been adequately studied.

In *Neoheterobothrium* the membrane is developed somewhat better; it comes out of the middle part of the basal median plate and, thus, with the distal end of the latter (to which the end of the anterior lateral plate is attached), it forms a half ring that supports the sucker.

In the genus *Diclidophora* the membrane is fully developed. In *D. coelorhynchi* (Robinson, 1961) it is not yet fused to the anterior lateral plate; the ring that supports the sucker is not complete. In *D. paracoelorhynchi* (Mamaëv et Paruchin, in litt.) and in *D. lotella* (Machida, 1972) the membrane is in one spot fused with the lateral plate, and the ring is closed. In *D. macruri* (Brinkmann, 1972) the lateral plate is fused to the membrane along nearly the whole length, but the ring is incomplete, since the end of the lateral plate is not fused with the base of the median plate. In all diclidophorans parasitic on the Gadidae the lateral plate is fused to the membrane along the whole length and the ring is complete.

All other *Diclidophorinae* have a complete ring around their sucker and a well-developed membrane totally fused to the lateral plate. In some diclidophorids there is a secondary reduction of the membrane on the side of the basal median plate that disappears altogether.

In *Flexophora* the basal median plate has disappeared, the membrane is significantly reduced and joined to the anterior lateral plate, which is in the process of fusing to the second lateral plate.

In *Polyipnicola* the membrane is slightly narrower in the distal part but considerably wider in the base in comparison with *Diclidophora;* the second lateral plate is wider and it is fused to the first one.

In *Myctophiphilus* the skeleton of the anterior valve of the clamp has the same structure as that of the previous genus; in the posterior valve the median lateral plates and the posterior lateral plates are fused together and form a single pair.

In *Osphyobothrus* the skeleton of the anterior valve is the same as in the two previous genera; in the posterior valve the posterior lateral plates are fused to the distal end of the additional median plate (in one of the species this kind of fusion did not occur).

In *Upenicola* the whole anterior valve is covered with a chitinoid membrane except for a small oval aperture; the posterior lateral plates are fused to the additional median plate.

In *Allotagia* the skeleton of the anterior valve has a rather distinctive structure: the membrane is well-developed and totally fused with the lateral plate, while the second lateral plate is significantly wider but is not joined to them. The posterior and the median lateral plates are fused together and form a single pair of long plates.

In the genera *Heterobothrium, Gempylitrema* and *Heterobothrioides* the membrane has been reduced and transformed into a narrow strip.

The membrane is also significantly reduced in *Absonifibula bychowskyi* (Lawler et Overstreet, 1976) that was isolated by the authors as an independent subfam. *Absonifibulinae*. The membrane of this genus has another peculiarity: it is poorly sclerotized with the exception of a narrow strip along the edges.

The clamp of *Tribuliphorus* is similar to the clamp of the primitive diclidophorins: it is of a closed type, has a small triangular membrane but no sucker or ring, and most important — its anterior and posterior lateral plates are equipped with large curved teeth. This clamp acts as a trap by plunging its teeth into the gill tissues of the fish.

In all diclidophorineans the clamps are of a closed type and their shape is generally reminiscent of a bivalve mollusc shell; in *Choricotylinae* the clamps are of an open type.

The most primitive choricotylins are *Macruricotyle, Zeicotyle* (and possibly *"Choricotyle" oregonensis* McCauley et Smoker, 1969) and, just like Diclidophoropsinae, they have symmetrical clamps with a squeezing and sucking action. In all the other choricotylineans the sucking function of the clamp strongly prevails and its skeleton is more or less asymmetrical. The whole width of the inner section of the clamp is filled with the sucker-plunger. The more developed the sucker is, the more curved the basal median plate is and the more it is shifted towards the outer section. In the most advanced in the evolutionary sense choricotylineans this plate forms a complete ring that supports a powerful sucker. According to the degree of the curvature of the basal median plate and the kind of ring it forms, the genera *Choricotylinae* and other related subfamilies can be arranged in the following order: 1) *Keralina*; 2) *Papillochoricotyle, Eurysorchis, Paracyclocotyla, Pseudoeurysorchis*; 3) *Choricotyle, Hargicotyle, Pedocotyle*; 4) *Cyclobothrium*; 5) *Echinopelma*; 6) *Bravocotyle*; 7) *Helciferus, Urocotyle.*

One should note that various species of *Choricotyle* differ significantly in the degree of the curvature of their basal median plate towards the inner section of

64/

the clamp. In the genus *Cyclobothrium* the curvature of the median plate is no greater than in the most specialized species of *Choricotyle*, but its proximal end forms, if one trusts the descriptions, a long protuberance fused with the anterior lateral plate, which results in the formation of an almost compete ring that supports the sucker. In *Echinopelma* the median plate itself forms an almost complete ring; there is a chitinoid disc on the surface of the sucker; thus, the sucker has turned into a true plunger. In *Bravocotyle* the basal median plate is closed in a ring; its ends, however, are not fused together; the whole surface of the sucker is highly sclerotized. In the genera *Helciferus* and *Urocotyle* the basal median plate has been transformed into a monolithic ring that occupies the centre of the clamp; some lateral plates are reduced.

Thus, the clamps of diclidophorids are easily arranged in rows according to the strengthening of their skeletons. Such adaptive rows of clamps of some genera of diclidophorids are represented in fig. 1 (this scheme does not include the genus *Absonifibula* and those genera whose clamps are poorly studied or do not differ significantly from those shown in the figure).

In comparison with the "multiclamp" monogeneans, the copulative apparatus of *Diclidophoridae*, as well as of most other "eight-clamp" monogeneans

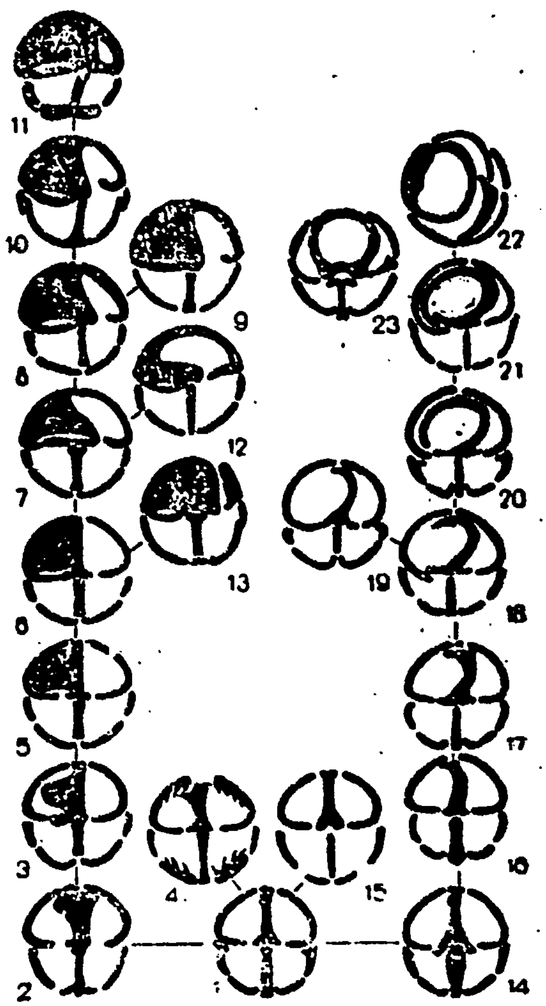

Рис. 1. Адаптивные ряды прикрепительных клапанов моногеней сем. Diclidophoridae: 1 — Diclidophoropsis, Cyclocotyloides; 2 — Lebboia; 3 — Neoheterobothrium; 4 — Tribuliphorus; 5 — Diclidophora coelorhynchi; 6 — Diclidophora minor; 7 — Flexophora; 8 — Polyipnicola; 9 — Myctophiphilus; 10 — Osphyobothrus; 11 — Upenicola; 12 — Heterobothrium, Gempylitrema; 13 — Allotagia; 14 — Macruricotyle; 15 — Zeicotyle; 16 — Keralina; 17 — Papillochoricotyle; 18 — Choricotyle; 19 — Cyclobothrium; 20 — Echinopelma; 21 — Bravocotyle; 22 — Urocotyle; 23 — Helciferus

Fig. 1. Adaptive rows of the attachment clamps of monogeneans of the fam. *Diclidophoridae*: 1 — *Diclidophoropsis, Cyclocotyloides*; 2 — *Lebboia*; 3 — *Neoheterobothrium*; 4 — *Tribuliphorus*; 5 — *Diclidophora coelorhynchi*; 6 — *Diclidophora minor*; 7 — *Flexophora*; 8 —*Polyipnicola*; 9 — *Myctophiphilus*; 10 — *Osphyobothrus*; 11 — *Upenicola*; 12 — *Heterobothrium, Gempylitrema*; 13 — *Allotagia*; 14 — *Macruricotyle*; 15 — *Zeicotyle*; 16 — *Keralina*; 17 — *Papillochoricotyle*; 18 — *Choricotyle*; 19 — *Cyclobothrium*; 20 — *Echinopelma*; 21 — *Bravocotyle*; 22 — *Urocotyle*; 23 — *Helciferus*

65/

is characterized by the relative uniformity of its structure. We examined the evolutionary aspect of this issue in our previous works (Mamaev, 1975a, b).

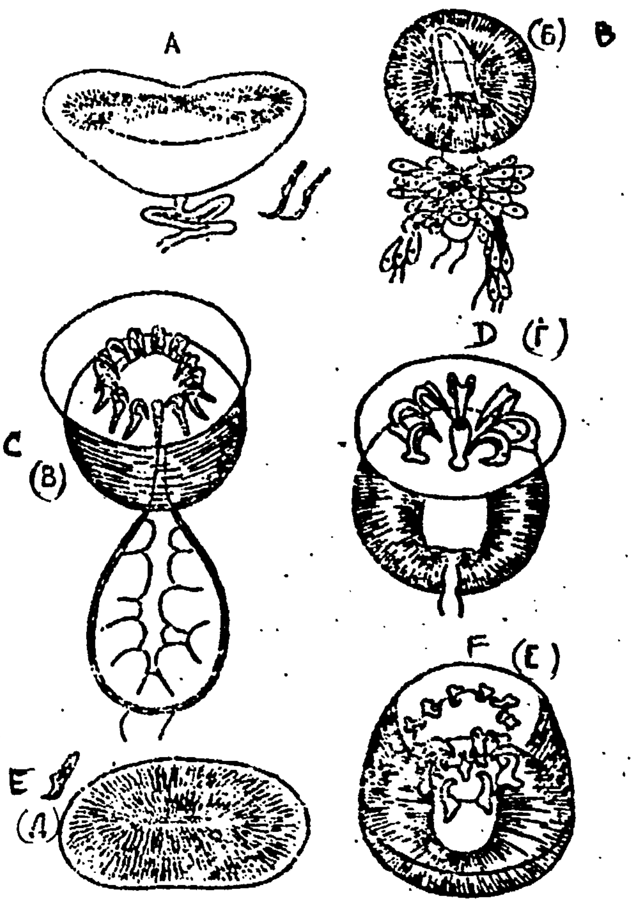

Рис. 2. Копулятивные органы Diclidophoridae: А — *Diclidophoropsis;* Б — *Cyclocotyloides;* В — *Macruricotyle;* Г — *Choricotyle;* Д — *Hargicotyle;* Е — *Eurysorchis*

Fig. 2. Copulative organs of Diclidophoridae: A (both Russian and English) — *Diclidophoropsis;* B (Russian letter Б) — *Cyclocotyloides;* C (Russian letter В) — *Macruricotyle;* D (Russian letter Г)— *Choricotyle;* E (Russian letter Д)— *Hargicotyle;* F (Russian letter Е)— *Eurysorchis*

The most primitive copulative organ is found in *Diclidophoropsis tissieri.* It is a muscular cushion with a circle of numerous, relatively straight hooks (fig. 2, A).

The copulative organ of *Hargicotyle* has a similar structure, the only difference being that there are several rows of hooks. In *Cyclocotyloides pinguis*, the closest relative of *Diclidophoropsis tissieri* (which is corroborated by the extreme similarity of their entire morphology with the exception of their copulative apparatus), the copulative organ has no hooks and is a simple muscular ring. The absence of the chitinoid armament in this genus is undoubtedly a secondary phenomenon; on the whole, the copulative organ is significantly altered compared to *Diclidophoropsis*: the ejaculatory duct is wider, it is surrounded by a muscular padding, its end protrudes in the form of a papilla, and the prostatic glands are well-developed.

In all the other diclidophorids except *Absonifibula bychowskyi* (Lawler et Overstreet, 1976) the copulative organ is a muscular bulb with a crown of identical crescent-shaped hooks (fig. 2, C[B], D[Γ]). Representatives of the subfam. *Eurysorchiinae* have a second, additional, crown of smaller hooks situated on the semispherical extension of the copulative organ (fig. 2, F[E]).

The crescent-shaped hooks of the typical "diclidophoridean" copulative organ undoubtedly evolved from the hooks of a simpler shape, such as those of *Diclidophoropsis* and *Hargicotyle*. The blade of the hook became broader and the handle shorter. It is highly significant that in one representative of choricotylineans — *Macruricotyle clavipes* — the hooks of the copulative organ still have a rather long handle (fig. 2, C[B]), whereas in *Choricotyle* (fig. 2, D[Γ]), for example, the handle is almost completely reduced. Besides, in the higher diclidophorids the number of crescent-shaped hooks on the copulative organ is, as a rule, smaller (it reaches 6) than in the more primitive ones (compare fig. 2, C[B] and D[Γ]).

The copulative organ of *Absonifibula* has the appearance of a muscular

66/

bulb with two pairs of hooks and one pair of long dagger-like spines. The hooks are reminiscent of the crescent-shaped hooks of other diclidophorids, but the blade of the hook is narrower. The dagger-like spines have a straight wide blade that even preserved a median groove typical of the crescent-shaped hooks. These spines are apparently nothing other than the straightened-out "diclidophoridean" hooks, and, consequently, the copulative organ of *Absonifibula* is a somewhat altered copulative organ of an ordinary "diclidophoridean" type.

Thus, monogeneans of the fam. *Diclidophoridae* have three basic types of copulative organs: 1) a muscular cushion with numerous slightly curved hooks — in one species of *Diclidophoropsis* and in two species of *Hargicotyle*; 2) a muscular ring without any armament and with a central papilla — in one species of *Cyclocotyloides*; 3) a muscular bulb with crescent-shaped hooks — in all the others diclidophorids.

Behind the copulative organ of most diclidophorids there is a round or pear-shaped vesicle that is usually called seminal. We consider it more appropriate to call it a prostatic vesicle, since there are some round transparent prostatic cells on its walls. In some diclidophorids it is almost completely filled with these cells. Numerous narrow ducts lead to the vesicle from the external prostatic glands situated laterally with respect to the copulative organ. Only the representatives of the subfam. *Diclidophoropsinae* (*Diclidophoropsis* and *Cyclocotyloides*) do not seem to have a prostatic vesicle. We used to believe (Mamaev, 1975a) that it was also absent in *Choricotyle*, but we have since had an opportunity to find out that the prostatic vesicle is poorly developed in the species of this genus and is therefore difficult to identify.

The genital atrium in *Diclidophoridae* is small and unarmed. The sources that mention the existence of an armed genital atrium in these monogeneans are mistaken: the hooks are situated on the copulative organ rather than on the walls of the atrium.

A more complicated issue is the presence or the absence of the vaginal system in diclidophorids. A twin vagina with pronounced vaginal ducts is found in the representatives of *Diclidophoropsinae*. We have not observed either vaginal apertures or ducts in the rest of diclidophorids, even though some sources mention the presence of the vagina in *Echinopelma bermudae* (Raecke, 1945) and in some other monogeneans (see Bychowsky, 1957). Apparently *Absonifibula* has a twin vagina. In general, one should point out that in some groups of the higher monogeneans the vaginal system is subject to dramatic changes (these changes, however, occur within certain limits and have only a few variations). Occasionally, within the same genus, some closely related species may display two variations of the structure of the vaginal system, and there is often no correlation between the structure of the copulative organ and the structure of the vaginal system (Mamaev, 1967, 1970; Mamaev, Parukhin, 1975c). The reasons for this are not understood.

Not all diclidophorids have a semen receptacle. It is absent in the representatives of the fam. *Diclidophoropsinae* (Mamaev, 1975a; Mamaev, Lyadov, 1975); the sperm is contained in the long and very wide oviduct. All the *Choricotylinae, Eurysorchiinae, Hargicotyle* and *Pedocotyle* have a semen receptacle, which is oval or slightly lobed. In some *Diclidophorinae* the absence of the semen receptacle is secondary. For example, it is not found in *Flexophora, Polyipnicola, Myctophiphilus* and *Allotagia*. There is a semen receptacle in other genera of this subfamily. It may be oval, slightly lobed (in *Diclidophora*) or strongly lobed (in

Osphyobothrus). There seems to be a secondary absence of the semen receptacle in *Absonifibula* and *Gempylitrematinae*. Instead of a semen receptacle,

67/

Heterobothrioides has some characteristic large-size tubercles connected to oviducts that fan out across the whole area of the anterior preovarian region of the body.

The main morphological attribute used for systematization (the main taxonomic attribute) of monogeneans of the fam. *Diclidophoridae* is the structure of the copulative apparatus and of the attachment clamps; the rest of the attributes — presence or absence of the vaginal system, of the semen receptacle and their structure — are of lesser importance. B. E. Bykhovsky used to emphasize that the dominant device that determines the evolutionary processes in monogeneans is the development of the attachment organs and the method of their adhesion to the hosts. Subsequent studies have provided a growing body of evidence to corroborate this point of view. The evolution of diclidophorids is primarily the evolution of their attachment clamps (Mamaev, 1975a, b). Structural characteristics of the attachment clamps are particularly important for constructing the system of *Diclidophoridae*. However, a very significant role in identifying the largest subdivisions of this family belongs to the structure of their copulative apparatus. This is a very constant attribute in *Diclidophoridae* and related families. Unlike the changes in the clamps, which were gradual and of an obviously adaptive nature, the restructuring of the copulative apparatus in diclidophorids (and other "eight-clamp" monogeneans) apparently occurred very rapidly and "suddenly", and this process was probably due to some internal causes. The nearly total absence of transitional forms between different types of the copulative apparatus in the "eight-clamp" monogeneans suggests that these changes were due to some macromutations.

As we know, for constructing a system for the class of monogeneans it is very important to take into consideration the structure of their larvae and, above all, of their attachment organs (Bykhovsky, 1937, 1957; Llewellyn, 1963, 1970). However, this criterion is, unfortunately, inapplicable to devising a system for this family and to elucidating the phylogenetic relationships within it (Mamaev, 1975a). Besides, the larvae of only six species of diclidophorids have been studied to date. For this reason we do not even examine here the structure of oncomiracidium.

The Phylogenesis of the Family *Diclidophoridae*

We examined the general features of the phylogenesis of *Diclidophoridae* in one of our previously published works (Mamaev, 1975a). However, due to the fact that the above paper was addressed to biologists at large, rather than to specialists involved in the study of monogeneans, various issues of phylogeny received a rather uneven treatment in it. Besides, while the paper was in the process of publication, there appeared some new data that enabled us to supplement the phylogenetic scheme of diclidophorids.

Hargis (1955) put forward the idea that *Diclidophoridae* had the greatest affinity with *Discocotylidae* and that they had evolved from them. Bykhovsky (1957) came to a similar conclusion. He believed that *Discocotylidae, Anthocotylidae* and *Diclidophoridae* had common ancestors and that the latter were possibly a collateral line of *Anthocotylidae*.

The diclidophoridean clamp that has eight plates undoubtedly evolved from a more primitive clamp of a discocotylidean type by developing an additional median plate. However, it is certainly unacceptable to "derive" *Diclidophoridae* directly from *Discocotylidae.* As it was demonstrated by Llewellyn and Owen (1960), the clamp in discocotylideans is already quite complicated and specialized. In *Discocotyle* a small projection that serves as a pulley-block, as it were, for the tendinous cord of the extrinsic muscle is found on the proximal end of the basal median plate. The ends of the tendinous cord are joined to the ends of the posterior

68/

lateral plates and pull them towards the anterior valve and into the interior of the clamp when the muscles contract. A similar, though somewhat improved, mechanism of clamp action is observed in *Mazocraeidae, Plectanocotylidae* and *Mazoplectidae* (Llewellyn, 1956b, 1957; Llewellyn, Owen, 1960; Mamaev, Slipchenko, 1975), but is absent in diclidophorids. This tells us that diclidophorids descended from the monogeneans that were more primitive than the present-day discocotylideans. The term we use for the common ancestors of both diclidophorids and discocotylideans is prodiscocotylideans. Their attachment clamps had one median plate and four lateral ones, and subsequently six lateral plates. Those monogeneans parasitized on the teleostean fishes (*Teleoistei*) that existed at the beginning of their main evolutionary branch called *Protacanthopterygii* (Greenwood, Rosen, Weitzman, Myers, 1966). Prodiscocotylideans were probably the original group from which descended most, if not all, higher monogeneans of the order *Mazocraidea.* Being rather primitive in the structure of their clamps and in some other structural features, *Discocotylidae (s. l.)* remained on the initially freshwater fishes of the groups *Ostariophysi* and *Salmonoidei*; the evolution of the rest of *Mazocraidea* is associated with sea fishes.

Ancestral diclidophorids (prodiclidophorids) that descended from prodiscocotylideans probably had symmetrical attachment clamps consisting of eight plates, a copulative organ in the form of a muscular cushion or a ring with a crown of numerous straight hooks or spines, and a twin vagina. All of these characteristics are observed in the present-day *Diclidophoropsinae,* and the last two features are found in most *Discocotylidae.*

Prodiclidophorids simultaneously generated several evolutionary branches. There were at least three of them.

The first short evolutionary branch led directly to the subfam. *Diclidophoropsinae* whose evolutionary development was weak and which retained nearly all of its primitive attributes; in one of the representatives of this subfamily (*Cyclocotyloides*) the copulative apparatus lost its armament.

In the second branch there remained a primitive copulative apparatus of the *Diclidophoropsis* type, but the rows of hooks on it increased in number, and the vaginal system was lost; the attachment clamps that functioned on the suction principle acquired by convergence a complete identity with the clamps of the monogeneans of the modern genus *Choricotyle.* From that evolutionary branch only one genus *Hargicotyle (Hargicotylinae subfam. nov.)* parasitic on the sciaenid fishes seems to have survived to date.

The third, main, evolutionary branch produced a copulative apparatus in the form of a bulb with crescent-shaped hooks (of an ordinary "diclidophoridean" type). Soon afterwards this branch was in turn divided into two vigorous evolutionary branches, one of which led to *Diclidophorinae* and through them to *Gempylitrematinae, Absonifibulinae, Anchorophoridae* and *Macrovalvitrematidae,* while the other led to *Choricotylinae* and, through them, to *Eurysorchiinae* and *Pedocotylinae.*

In the fishes of the order Macruriformes (*Macruriformes*) one finds the representatives of all major subfamilies of diclidophorids: both genera *Diclidophoropsinae*; the primitive *Choricotylinae* — the genus *Macruricotyle* that occupies a somewhat intermediate position between the three major subfamilies; the primitive *Diclidophorinae* — the genus *Lebboia*, and the first representatives of the true diclidophorineans — the three genera *Diclidophora*. All of this makes one presume that the splitting of diclidophorids into the main subfamilies began to occur even prior to the separation of the main evolutionary branches of fish —

69/

Paracanthopterygii and *Acanthopterygii* (Greenwood et al., 1966) — from the ancient protacanthropterygians.

The first diclidophorineans that appeared in the ancient *Paracanthopterygii* were similar in their structure to the genus *Lebboia*. A chitinoid membrane began to emerge in the clamps of these monogeneans on the projection of the basal median plate (this tubercle was well-developed in prodiclidophorids and has been preserved in the modern diclidophoropsineans). At the same time a sucker-plunger evolved at the base of the inner section of the clamp. It was primarily the squeezing action of the clamp, and then the sucking one, that was reinforced. The genera *Lebboia* and *Diclidophoroides* have probably descended directly from those original diclidophorineans and have preserved their primitive characteristics (even though, as we have mentioned above, the clamps in *Lebboia* possess certain features of narrow specialization).

The genus *Neoheterobothrium*, which parasitizes on the flatfish families *Pleuronectidae* and *Bothidae* and has a better-developed membrane and an incomplete ring that supports the sucker, descended from the primitive diclidophorineans closely related to the genus *Lebboia* and parasitic, we believe, already on the ancient Macruriformes.

The genus *Tribuliphorus* parasitic on *Moridae* and *Gadiformes* is inferior to the above diclidophorineans as far as the development of its membrane is concerned. Its sucker is completely undeveloped. In this genus of parasites the specialization of clamps assumed a different course: the clamp squeezes a gill filament and hooks onto it with the sharp curved teeth of its lateral plates. This adhesive technique does not stimulate the development of the sucker or further evolution of the membrane. As one can see in the case of the genus *Anchorophorus* (*Anchorophoridae* parasitize on the flatfish fam. *Cynoglossidae*), which undoubtedly descended from the monogeneans that were close to the genus *Tribuliphorus* (Mamaev, Parukhin 1975), the subsequent evolution of the attachment organs in these monogeneans followed the line of increasing the teeth of the clamp and transforming the plates into peculiar "anchors" that are plunged into the gills of the host. *Tribuliphorus* probably descends from the most primitive diclidophorineans that lived on the ancient Macruriformes or on even more distant ancestors of this group of fish.

It is not at all easy to explain the origins of the genus *Diclidophora*. Judging from the fact that two species of diclidophorans parasitic on the Macruridae are considerably more primitive in their morphology than the other nine (eight of which parasitize on the Gadiformes and one on the Macruridae) one may presume that they are more ancient and that it was precisely on the Macruriformes that this genus first appeared and that subsequently its individual representatives moved to the Gadiformes. However, various species of the genus *Diclidophora* differ significantly in their morphological attributes, and it is impossible to derive the more advanced in the evolutionary sense species directly from the species parasitic on the Macruriformes. We believe that this genus emerged in the process of the parallel development of a whole group of forms separated from the primitive *Diclidophora* that used to live on the common ancestors of the Macruriformes and the Gadidae, or from an even more primitive form that was close to *Lebboia.*

It was this kind of diclidophoran-type form that was the ancestor of the genus *Flexophora,* which in evolutionary terms is more advanced than *Diclidophora* and which lives on the fishes of the fam. *Ophidiidae,* as well as of at least three separate evolutionary branches leading to the following genera: 1) *Polyipnicola, Myctophiphilus* and *Osphyobothrus;* 2) *Upenicola* and 3) *Allotagia.*

Polyipnicola and *Myctophiphilus* are closely related genera; the third genus, *Osphyobothrus,* which, too, parasitizes on the fishes of the order *Myctophiformes,* stands somewhat apart. Representatives of the first two genera have no semen

70/

receptacle (they must have lost it), while in *Osphyobothrus,* it is on the contrary, hypertrophic.

Upenicola and *Allotagia* parasitize on the Perciformes (the first on *Mullidae,* and the second on *Sciaenidae*), but they seem to be in a rather distant phylogenetic relationship, since the strengthening of their clamp skeletons followed different paths. Besides, in *Upenicola* there is a large lobed semen receptacle, while in *Allotagia* it is absent.

There was another evolutionary branch that diverged from some primitive diclidophorineans; its representatives were characterized by the inverted anterior pair of clamps rotated by 180° with respect to the other three pairs. These monogeneans had a vaginal system with two apertures like in *Diclidophoropsinae,* but in some of them there subsequently occurred a simplification of their vaginal system resulting in a single median aperture, while in others the vaginal system disappeared altogether. It is not known whether they used to have a semen receptacle, since it is absent in all modern representatives of this evolutionary branch, and in *Heterobothrioides* its function is performed by some special tubercles connected to oviducts. The changes in the clamp skeleton in these monogeneans followed the same route as in the typical diclidophorineans: the membrane that covered the inner section of the clamp kept growing, and a ring was formed that supported the sucker. This process continued until it reached the stage that corresponded to the clamp of the genus *Diclidophora;* then, after the full development of the membrane and its fusion with the lateral plate, the reduction of the membrane commenced. As a result, the modern *Gempylitrematinae* has preserved only the basal part of the membrane in the form of a narrow strip; in *Absonifibulinae* the membrane has been reduced in lesser degree (but it is very poorly sclerotized). One can see an example of a partial reduction of the membrane and a complete disappearance of the traces of its basal median plate in the subfam. *Diclidophorinae* — in *Flexophora;* it is less manifest in *Polyipnicola, Myctophiphilus* and *Osphyobothrus.* Thus, until a certain stage, the evolution of the clamp skeleton in *Diclidophorinae* and in *Gempylitrematinae* — *Absonifibulinae* proceeded along parallel lines. In the former, however, the reduction of the clamp membrane only started and became clearly manifest in only one genus *Flexophora* (in all the others the area of all valvular plates continued to increase), whereas in the latter this process advanced in all its genera.

Generally, in those cases when no convincing evidence is available, one should bear in mind that affinity between taxons is a result of the successive divergent evolution and that it implies the possibility of their parallel formation. The significant role of parallelisms in the evolution of monogeneans was particularly emphasized by B. E. Bykhovsky (1957). We are in complete agreement with his views (Mamaev, 1975a) and believe that parallelisms in the evolution of the higher monogeneans are observed far more often than we have previously supposed.

There is no doubt that *Gempylitrematinae* and *Absonifibulinae* have identical origin and that initially it was a single evolutionary branch that subsequently split into two. We now know three genera in the subfam. *Gempylitrematinae*: two of them, *Gempylitrema* and *Heterobothrium* have a very close affinity with each other and differ significantly from the third one, *Heterobothrioides*, which must have split off before them. However, one cannot exclude the possibility of all three of them developing in parallel. It is worthy of note that alongside their primitive characteristic of an unfused second anterior lateral plate, the clamps of *Heterobothrioides* also display the traces of greater specialization: their membrane has undergone the highest degree of reduction. Besides, this genus parasitizes on the Perciformes, just like *Gempylitrema*, whereas *Heterobothrium* is parasitic on the Tetraodontidae.

71/

In *Gempylitrematinae* the vaginal system has disappeared, whereas in the evolutionary branch that led to *Absonifibulae* it has been preserved, although the structure of the copulative apparatus in these monogeneans has somewhat changed. The genus *Absonifibulae* occupies an intermediate position between *Diclidophoridae* and *Macrovalvitrematidae*. Naturally, it also represents an intermediate step in the evolution of these families. the genus *Pterinotrematoides* — a representative of the fam. *Macrovalvitrematidae* — undoubtedly descended from one of the forms that were close to *Absonifibulae*. Judging from the structure of the posterior pair of clamps of *Pterinotrematoides mexicanum* (they changed in a lesser degree than the anterior ones), in the process of evolution the chitinoid membrane found in *Absonifibulae* shifted into the middle of the clamp base and the skeleton acquired a secondary symmetry[1] .

One may claim that parallel to the evolutionary branch that led from the *Absonifibula*-type form to *Pterinotrematoides,* there was one branch or several branches leading from diclidophorids to other genera *Macrovalvitrematidae* with an unchanging (typically "diclidophoridean") copulative apparatus. It is very likely that in the near future such "transitional" genera of diclidophorids will be found in the Sciaenidae, which are still poorly studied as far as parasitology is concerned, and we shall have another vivid example of parallelisms in the evolution of a whole family of monogeneans.

The subfam. *Choricotylinae* together with *Pedocotylinae* and *Eurysorchiinae* appear to be a more uniform group than *Diclidophorinae.* This is probably explained by the fact that clamp morphology in this group is more uniform and that it is more difficult to restore its phylogenesis.We believe that at certain stages of the evolution of *Choricotylinae* there existed a number of individual phylogenetic lines that followed parallel paths and produced similar results.

The most primitive representatives of choricotylineans are *Macruricotyle, Zeicotyle* and *"Choricotyle" oregonensis* (McCauley et Smoker, 1969). The latter — a parasite that lives on the Moridae — has been poorly studied and it is difficult to say anything about it. We include *Macruricotyle* and *Zeicotyle* in *Choricotylinae* very provisionally: they must have separated from the line of this subfamily at the very beginning of its evolution. The attachment clamp of *Macruricotyle* (a parasite of

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[1] Some highly specialized diclidophorids with a sharply asymmetrical clamp skeleton manifest an interesting tendency towards acquiring a secondary (false) symmetry (Mamaev, 1973).

Macruriformes) is still very close to the clamp of diclidophoropsineans but is somewhat more complex. The clamp of *Zeicotyle* (a parasite of *Zeiformes*) is completely symmetrical and its basal median plate has no protuberance so characteristic of diclidophoropsineans. This complete symmetry of the clamp skeleton is an obviously secondary phenomenon, and so is the appearance of the numerous small chitinoid tubercles on the inner surface of the clamp in its basal part. The simplified hooks of the copulative organ, which almost completely lost their base, also prove that *Zeicotyle* is a more specialized genus. The evolution of this genus followed a somewhat different path than the evolution of other choricotylineans.

The genera of the true choricotylineans with asymmetrical clamps evolved later. The evolutionary branch of these monogeneans was initially unified and subsequently split into at least two branches (each of which apparently consisted of several parallel lines, so that we can speak of the two branches of choricotylineans only provisionally).

One branch of choricotylineans developed on herring-like fishes (*Clupeiformes*, according to Greenwood *et al.*, 1966), while the other lived on the

73/

Perciformes and their relatives Scorpaeniformes. Unlike B. E. Bykhovsky (1957), we believe that *Choricotylinae*, which parasitizes on the Clupeiformes, descended independently from the more primitive forms of choricotylineans, rather than migrated to the Clupeiformes from the Perciformes. This is corroborated by the parasitological data obtained in recent years, which were, naturally, inaccessible to B.E. Bykhovsky (Mamaev, 1975a). In 1957 only one species of *Choricotyle* was known to exist on the Clupeiformes, whereas nowadays another species of this genus has been found (it turned out to be close to the first one), as well as representatives of three independent genera, two of which possess some primitive characteristics and cannot possibly be derived from the genera parasitic on the Perciformes. Nor does the third, and a very distinctive, genus *Helciferus* (parasitic on *Engraulidae*) have any close relatives among the monogeneans parasitic on the Perciformes.

The central genus of this subfamily — *Choricotyle* — represents, as we have repeatedly mentioned, an obviously composite polyphyletic or, rather, paraphyletic group. The type species of this genus, *Ch. chrysopryi* (parasitic on the Sparidae), is to all appearances rather remote phylogenetically not only from the species of *Choricotyle* on the Clupeiformes, but also from some species that live on the Perciformes.

The genus *Pedocotyle* certainly descended from the choricotylineans that are close to the genus *Choricotyle,* i.e. from the species that were rather advanced in evolutionary terms. This is born out by the fact that even the posterior clamps of *Pedocotyle* that are in the reduction stage possess all the characteristics of the clamps of *Choricotyle.*

Judging from its clamp structure and from its host-specificity, the subfam. *Eurysorchiinae* characterized by a copulative organ with a double crown of hooks descended from the first true choricotylineans that lived on the Perciformes.

A phylogenetic scheme of *Diclidophoridae,* which has been devised with due regard for the progressive complication of their morphology — above all, of their clamp skeleton — and for their host-specificity, is represented on fig. 3. The genera of diclidophorids appear in the form of schematic sketches of their clamps or as circles in those cases when the clamp structure has been poorly studied or is unknown. Next to the lines that represent various branches of the phylogenetic tree there are schematic representations of the copulative organ of those monogeneans that belong to a given line.

72/

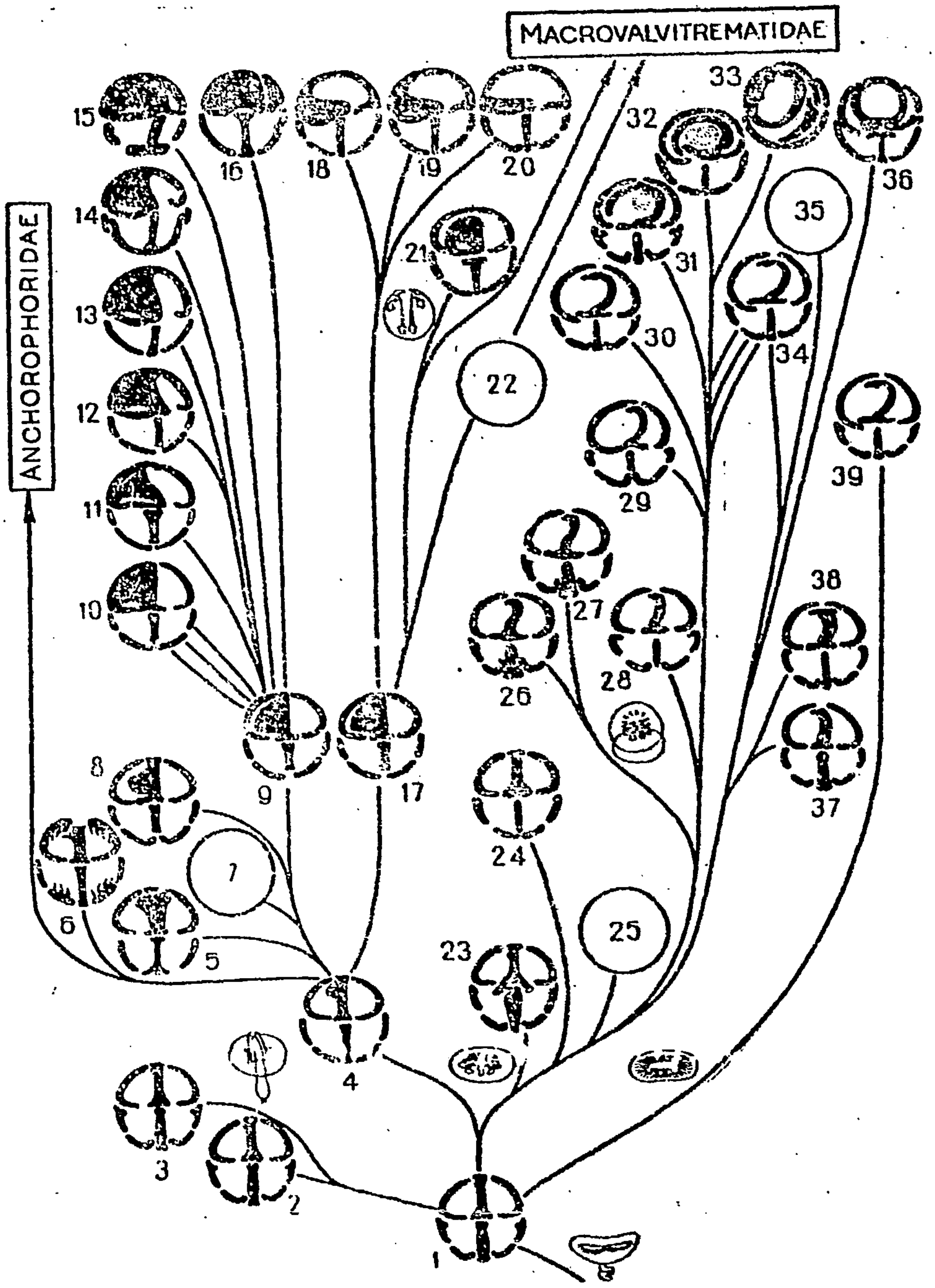

Рис. 3. Схема филогенеза сем. Diclidophoridae: 1 — гипотетические продиклидофориды. Diclidophoropsinae: 2 — *Diclidophoropsis;* 3 — *Cyclocotyloides;* 4 — гипотетическая форма, близкая к роду *Lebboia;* 6 — *Tribaliphorus.* Diclidophorinae: 5 — *Lebboia;* 7 — *Diclidophoroides;* 8 — *Neoheterobothrium;* 9 — гипотетическая форма, близкая по строению прикрепительных клапанов к *Diclidophora coelorhynchi;* 10 — *Diclidophora;* 11 — *Flexophora;* 12 — *Polyipnicola;* 13 — *Myctephiphilus;* 14 — *Osphyobothrus;* 15 — *Upenicola;* 16 — *Allotagia;* 17 — гипотетическая форма, близкая по строению прикрепительных клапанов к примитивным видам рода *Diclidophora.* Gempylitrematinae: 18 — *Heterobothrium;* 19 — *Gempylitrema;* 20 — *Heterobothrioides.* Absonifibulinae: 21 — *Absonifibula.* 22 — неизвестная форма, промежуточная между [illegible] родами (например, *Macrovalvitrema*) Macrovalvitrematidae. Choricotylinae: 23 — *Macruricotyle;* 24 — *Zeicotyle;* 25 — «*Choricotyle*» *oregonensis;* 28 — *Pseudoeurysorchis;* 29 — *Cyclobothrium;* 31 — *Echinopelma;* 32 — *Brezocotyle;* 33 — *Urocotyle;* 34 — *Choricotyle;* 35 — *Dussumiericola;* 36 — *Helcifera;* 37 — *Kerulina;* 38 — *Papillochoricotyle.* Pedocotylinae: 30 — *Pedocotyle.* Euryso[illegible]nae: 26 — *Eurysorchis.* 27 — *Paracyclocotyla.* Hargicotylinae: 39 — [illegible]rgicotyle (Объяснение в тексте)

Fig. 3. The phylogenetic scheme of the fam. Diclidophoridae: 1 — hypothetical prodiclidophorids. Diclidophoropsinae: 2 — *Diclidophoropsis*; 3 — *Cyclocotyloides*; 4 — a hypothetical form close to the genus *Lebboia*; 6 — *Tribuliphorus*. Diclidophorinae: 5 — *Lebboia*; 7 — *Diclidophoroides*; 8 — *Neoheterobothrium*; 9 — a hypothetical form close to *Diclidophora coelorhynchi* in the structure of its attachment clamps; 10 — *Diclidophora*; 11 — *Flexophora*; 12 — *Polyipnicola*; 13 — *Myctophiphilus*; 14 — *Osphyobothrus*; 15 — *Upenicola*;

16 —*Allotagia*; 17 — a hypothetical form close to the primitive species of the genus *Diclidophora* in the structure of its attachment clamps. Gempylitrematinae: 18 — *Heterobothrium*; 19 — *Gempylitrema*; 20 — *Heterobothrioides*. Absonifibulinae: 21 — *Absonifibula*. 22 — an unknown form that occupies an intermediate position between Diclidophoridae and certain other genera (for example, *Macrovalvitrema*). Macrovalvitrematidae. Choricotylinae: 23 — *Macruricotyle*; 24 — *Zeicotyle*; 25 — *"Choricotyle" oregonensis*; 28 — *Pseudoeurysorchis*; 29 — *Cyclobothrium*; 31 —*Echinopelma*; 32 — *Bravocotyle*; 33 — *Urocotyle*; 34 —*Choricotyle*; 35 — *Dussumericola*; 36 — *Helciferus*; 37 — *Keralina*; 38 — *Papillochoricotyle*; Pedocotylinae: 30 — *Pedocotyle*. Eurysorchiinae: 26 — *Eurysorchis*; 27 — *Paracyclocotyla*; Hargicotylinae: 39 — *Hargicotyle*. (Explanations are given in the text)

73/

The System of the Fam. *Diclidophoridae Fuhrmann, 1928*

I. Subfam. Diclidophorinae Cerfontaine, 1895

1. Diclidophora Kroyer, 1838

* Type species: *D. merlangi* (Kuhn, in Nordm., 1832) Kroyer, 1851.

Host: *Odontogadus merlangus* (Gadidae).

* *D. coelorhynchi* Robinson, 1961.

Hosts: *Coelorhynchus australis, C. fasciatus* (Macruridae).

* *D. denticulata* (Olsson, 1876) Price, 1943.

Host: *Pollachius virens* (Gadidae).

D. esmarkii (Th. Scott, 1901) Sproston, 1946.

Host: *Trisopterus esmarkii* (Gadidae).

* *D. lotella* Machida, 1972.

Host: *Lotella maximowiczi* (Moridae, Gadiformes).

74/

D. luscae (v. Beneden et Hesse, 1863) Price, 1943.

Host: *Trisopterus luscus* (Gadidae).

D. Macruri (Brinkmann, 1942) Sproston, 1946.

Host: *Macruris rupestris* (Macruridae).

* *D. minor* (Olsson, 1868) Sproston, 1946.

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* Asterisks indicates the species we studied from actual specimens.

Hosts: *Micromesistius poutassou, M. australis* (Gadidae)

* *D. palmata* (Leuckart, 1839) Diesing 1850.

Host: *Molva molva* (Gadidae).

* *D. paracoelorhynchi* Mamaëv et Paruchin, in litt.

Host: *Coelorhynchus fasciatus* (Macruridae).

D. Phycidis (Parona et perugia, 1899) Sproston, 1946.

Host: *Phycis blennoides* (Gadidae).

D. pollachii (v. Beneden et Hesse, 1863) Price, 1843.

Host: *Pollachius pollachius* (Gadidae).

Dubious species: *D. gadi* Reichenbach — Klinke, 1951, described on *Gadus aeglefinus* is probably a synonym for *D. merlangi* (see Llewellyn, 1958). *D. morrhuae* (v. Beneden et Hesse, 1863) Sproston, 1946, described on *Gadus morrhua* is a synonym for another species. The host must have been erroneously identified, for despite a great number of examined fishes, no one has since found any species of the genus *Diclidophora* on cod (see Llewellyn and Tully, 1969).

2. Diclidophoroides Price, 1943

D. Maccallumi Price, 1943.

Host: *Urophycis chuss* (Gadidae).

3. Lebboia Mamaëv et Paruchin, 1975

* *L. striaturae* Mam. et Par., 1975.

Host: *Coryphaenoides striatura* (Macruridae).

4. Neoheterobothrium Price, 1943

Type species: *N. affine* (Linton, 1898) Price, 1943.

Hosts: *Paralychthys dentatus, P. lethostigmus* (Bothidae, Pleuronectiformes).

* *N. pugetensis* (Robinson, 1961) Yamaguti, 1963.

Hosts: *Atherestes stomias, A. evermanni* (Pleuronectidae).

5. Flexophora Prost et Euzet, 1962

F. ophidii Prost et Euzet, 1962.

Host: *Ophidium barbatum* (Ophidiidae, Gadiformes).

6. Polyipnicola Mamaëv et Paruchin, 1975

* Type species: *P. macrocarium* Mam. et Par., 1975.

Host: *Polyipnus spinosus* (Sternoptychidae, Salmoniformes).

* *P. argentinae* Mam. et Par., 1975.

Host: *Argentina elongata* (Argentinidae, Salmoniformes).

7. Myctophiphilus Mamaëv, 1976

* *M. arabicus* Mam., 1976.

Host: *Myctophum* sp. (Myctophidae).

75/

8. Osphyobothrus Yamaguti, 1958

Type species: *O. parapercis* Yam., 1958.

Host: *Parapercis pulchella* (?).

* *O. bychowskyi* Khoche et Chauhan, 1969.

Hosts: *Saurida tumbil, S. undosquamis* (Synodontidae, Myctophiformes).

* *O. multivitellatus* Mamaëv et Paruchin, 1970.

Host: *Saurida gracilis.*

* *O. sagittula* Mam. et Par., 1975.

Host: *Saurida undosquamis.*

9. Upenicola Unnithan, 1966

* Type species: *U. upeneoides* Unn., 1966.

Hosts: *Upeneus vittatus, Upeneus* sp. (Mullidae, Perciformes).

* *U. capheni* Mamaëv, 1972.

Host: *Upeneus* sp.

* *U. digitata* Mam., 1972.

Host: *Upeneus* sp.

10. Allotagia Dillon et Hargis, 1965

* *A. otolithis* (Yamaguti, 1953) Dillon et Hargis, 1965.

Hosts: *Otolithis* sp., *Argyrosomus dussumieri* (Sciaenidae, Perciformes).

II. Subfam. Gempylitrematinae Yamaguti, 1968

1. Gempylitrema Yamaguti, 1968

* Type species: *G. longipedunculatum* Yam., 1968.

Host: *Prometheichthys prometheus (Gempylidae, Perciformes).*

* *G. gempylli* (Dillon et Hargis, 1965) Yam. 1968.

Hosts: *Rexea solandri, Epinnula orientalis (Gempylidae).*

2. Heterobothrium Cerfontaine, 1895

* Type species: *H. tetrodonis* (Goto, 1894) Cerf., 1895.

Hosts: *Tetraodon* spp., *Spheroides alboplumbeus, Spheroides* sp. *(Tetraodontidae, Tetraodontiformes).*

* *H. ecuadori* Mezerve, 1938.

Hosts: *Spheroides annularis, Spheroides* sp.

* *H. praerorchis* Bychowsky, Mamaëv et Nagibina, 1076.

Hosts: *Spheroides alboplumbeus, S. vermicularis, Spheroides* sp.

* *H. tonkinensis* Bych., Mam. et Nagibina, 1976.

Hosts: *Spheroides vermicularis, Spheroides* sp., *Lagocephalus sceleratus.*

* *H. sp.* (= *H. tetrodonis,* sensu Yamaguti, 1968).

Host: *Spheroides xanthopterus.*

3. Heterobothrioides Mamaëv et Paruchin, 1975

* *H. psenesi* Mam. et Par., 1975.

Host: *Psenes indicus (Nomeidae, Perciformes).*

76/

III. Subfam. Absonifibulinae Lawler et Overstreet, 1976

Absonifibula Lawler et Overstreet, 1976

* *A. bychowskyi* Law. et Ov., 1976.

Host: *Micropogon undulatus (Sciaenidae).*

IV. Subfam. Diclidophoropsinae Yamaguti, 1963

1. Diclidophoropsis Gallien, 1937

* *D. tissieri* Gallien, 1937.

Host: *Macrurus laevis (Macruridae).*

2. Cyclocotyloides Price, 1943

* *C. pinguis* (Linton, 1940) Price, 1943.

Hosts: *Albatrossia pectoralis, Coryphaenoides acrolepis, Coryphaenoides* sp. *(Macruridae).*

V. *Subfam. Choricotylinae Sproston, 1946*

1. Choricotyle v. Beneden et Hesse, 1863

* Type species: *Ch. chrysophryi* v. Ben. et Hesse, 1863 [syn. *Ch. pagelli* (Gallien, 1937)].

Hosts: *Chrysophrys auratus* (syn. *Pagrosomus auratus, Sparus auratus*), *Pagellus centrodontus, Pagrus pagrus (Sparidae).*

Ch. aspinachorda Hargis, 1955.

Host: *Orthropristis chrysopterus (Pomadasyidae, Perciformes)*, as well as on the Isopoda *Cymothoa.*

Ch. caudalis (Koratha, 1955) Hargis, 1959.

Host: *Leisotomus xanthurus (Sciaenidae).*

Ch. caulolotili (Meserve, 1938) Sproston, 1946.

Hosts: *Caulolatilus princeps (Latilidae), Trachurops crumenophthalma (Carangidae, Perciformes).* Another species probably parasitizes on the Carangidae.

Ch. cynoscioni (MacCallum, 1917) Llewellyn, 1941.

Host: *Cynoscion ragalis (Sciaenidae).*

Ch. elongata (Goto, 1894) Llewellyn, 1941.

Hosts: *Pagrus tumiforous, Pagrosomus unicolor (Sparidae)*, as well as on the Isopoda *Cymothoa, Meinertia.*

Ch. hysteroncha (Fujii, 1944) Sproston, 1946.

Hosts: *Bathystoma striatum, Brachygenys chrysargyreus, Haemulon flavolineatum (Pomadasyidae).*

Ch. labracis (Cerfontaine, 1895) Llewellyn, 1941.

Hosts: *Labrax lupus, Morone labrax (Serranidae, Perciformes).*

Ch. multaetesticulae (Chauhan, 1945) Sproston, 1946.

Host: *Pellona sp. (Clupeidae).*

Ch. pellonae Kritsky et Bilquees, 1973.

Host: *Pellona elongata* (syn. *Ilisha elongata*). (In Mamaev's work of 1972 this species was called *Ch. clupeiphila sp. nov.*, but since no description was provided, this name should be regarded as *nomen nudum*).

* *Ch. polynemi* Mamaëv, 1972.

Host: *Polynemus sextarius (Polynemidae).*

77/

Ch. prionoti (MacCallum, 1917) Llewellyn, 1941.

Hosts: *Prionotus carolinus, P. scitulus (Triglidae, Scorpeniformes).*

* *Ch. simplex* Mamaëv, 1976.

Host: *Plagiogeneion macrolepis (Emmelichthyidae, Perciformes).*

Ch. smaris (Goto, 1894) Llewellyn, 1941 {syn. *Ch. squillarum* (Par. et Per., 1889)].

Host: *Smaris vulgaris (Maenidae, Perciformes),* as well as on the Isopoda *Cymothoa.*

Ch. sonorensis Caballero et Bravo-Hollis, 1962.

Host: *Microlepidotus inornatus (Pomadasyidae)* sp. inq.

Ch. charcoti (Dollfus, 1922) Llewellyn, 1941.

Host: *Trachurus trachurus (Carangidae),* as well as on the Isopoda *Cymothoa.*

Ch. marionis St. Loup, 1885.

Host: *Maena vulgaris (Maenidae).*

Ch. squillarum (Parona et Perugia, 1889).

Host: *Bopyrus squillarum.*

Ch. tachenbergii (Par. et Per., 1889).

Host: *Sargus rondeletii (Sparidae)* sp. inc. sed.

"Choricotyle" oregonensis McCauley et Smoker, 1969.

Host: *Antimora rostrata (Moridae).*

2. Macruricotyle Mamaëv et Ljadov, 1975

* *M. clavipes* Mam. et Ljad., 1975.

Host: *Macrurus* sp.

3. Zeicotyle Mamaëv, 1976

Z. magna Mam., 1976

Host: *Allocyttus verrucosus (Zeidae, Zeiformes).*

4. Keralina Unnithan, 1966

K. opisthopterus Unn., 1966

Host: *Opisthopterus turdoore (Clupeidae).*

5. Papillochoricotyle Mamaëv, 1975

* *P. ilishae* Mam., 1975

Host: *Ilisha elongata (Clupeidae).*

6. Pseudoeurysorchis Caballero et Bravo-Hollis, 1962

P. travassosi Caball. et Br.-Hollis, 1962.

Host: *Microlepidotus inornatus (Pomadasyidae).*

7. Cyclobothrium Cerfontaine, 1895

Type species: *C. sessile* (Goto, 1894) Cerf., 1895.

Hosts: *Choerops japonicus, Semicossyphus reticulatus* (Labridae).

C. iniistii Yamaguti, 1937.

Host: *Iniistius dea (Coridae, Perciformes).*

C. semicossyphi Yamaguti, 1938.

Host: *Semicossyphus reticulatus.*

78/

8. Echinopelma Raecke, 1945

Type species: *E. bermudae* Raecke, 1945.

Host: *Haemulon album* (?) *(Pomadasyidae).*

E. neomaenis (MacCallum, 1917) Raecke, 1945.

Host: *Neomaenis analis (Lutianidae, Perciformes).*

9. Bravocotyle Lamoth-Argumedo, 1867

B. sanblasensis Lam.-Arg., 1967.

Host: Cynoscion xanthulus (Sciaenidae).

10. Dussumericola Unnithan, 1966

D. *dussumeria* Unn., 1966.

Host: *Dussumeria hasselti (Clupeidae).*

11. Helciferus Mamaëv, 1973

* *H. tenuis* Mam., 1973.

Hosts: *Coilia mystus, Coilia sp. (Engraulidae, Clupeiformes).*

12. Urocotyle Unnithan, 1966

Type species: *U. pristipoma Unn.,* 1966.

Host: *Pristipoma guoraca (Pomadasyidae).*

* *U. anellus* Mamaëv, 1972.

Host: *Sciaena dussumieri, Sciaenidae gen. sp.*

VI. Subfam. Pedocotylinae Yamaguti, 1963

Pedocotyle MacCallum, 1913

Type species: P. *morone* (MacCallum, 1913) MacCallum, 1913.

Host: *Morone americana (Serranidae).*

P. *minima* Hargis, 1955.

Host: *Bairdiella chrysura (Sciaenidae).*

VII. Hargicotylinae Mamaëv, subfam. nov.[2]

Hargicotyle Mamaëv, 1972

Type species: *H. louisianensis* (Hargis, 1955) Mamaëv, 1972.

Host: *Menticirrhus americanum (Sciaenidae).*

H. pacifica (Bravo-Hollis, 1967) Mamaëv, 1972.

Host: *Umbrina sinaloae (Sciaenidae).*

VIII. Subfam. Eurysorchiinae Yamaguti, 1963

1. Eurysorchis Manter et Walling, 1958

* Type species: *E. australis* Manter et Walling, 1958.

Host: *Seriolella brama (Nomeidae, Perciformes).*

* *E. manteri* Mamaëv, 1976.

Host: *Seriolella maculata, Seriolella sp.*

79/

2. Paracyclocotyla Dollfus, 1970

* *P. cherbonnieri* Dollfus, 1970.

Host: *Alepocephalus rostratus (Alepocephalidae, Perciformes).*

A genus provisionally not included in any of the subfam. *Diclidophoridae*

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[2] The diagnosis of this subfamily corresponds to the diagnosis of the genus *Hargicotyle.*

Tribuliphorus Mamaëv et Paruchin, 1975

* *T. salilotae* Mam. et Par., 1975.

Host: *Salilota australis (Moridae).*

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THE SYSTEM AND PHYLOGENY OF MONOGENEANS OF THE FAM. DICLIDOPHORIDAE

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SUMMARY

A new system and scheme of phylogeny have been suggested for the fam. Diclidophoridae. The family comprises eight subfamilies: Diclidophorinae, Gempylitrematinae, Absonifibulinae, Diclidophoropsinae, Choricotylinae, Pedocotylinae, Hargicotylinae subfam. n., Eurysorchiinae. Diclidophoridae and Discocotylidae undoubtedly had common ancestors. These monogeneans, which we name prodiscocotylids, parasitized in Teleostei at the beginning of the evolutionary branch of Protacanthopterigii. Ancient diclidophorids gave at least three evolutionary branches to Diclidophoropsinae, to Hargicotylinae, and to other subfamilies.