FOLIA PARASITOLOGICA (PRAHA) 25: 131–136, 1978.

SOME ASPECTS OF MONOGENEAN EXISTENCE

B. I. LEBEDEV

Institute of Biology and Pedology, Far East Science Center, USSR Academy of Sciences, Vladivostok

Abstract. This paper deals with some ecology and evolution problems of monogeneans — gill parasites of fishes, such as congeneric simultaneous doublets, spatial distribution of species on the gills, interspecific restrictions of biotopes etc. The author proves competitive character of site selection in monogeneans. The role of hermaphroditism in the evolution and biology of monogeneans, and morphological adaptations (mainly androgynous) directed to increasing of mating chance are discussed. The author concentrates on analyzing the cases of monoxenous distribution and speciation and also on examining the concept of symxenity and alloxenity. He attaches great importance to ecological and evolutionary investigations of Monogenoidea.

Recently, numerous data have appeared pertaining to interesting synecological and evolutionary aspects of monogenean existence, in particular questions of joint simultaneous parasitism of two species of one monogenean genus on a single host specimen. Works of Euzet (1972), Ktari (1975), Lambert and Maillard (1975), and Oliver (1976) contain information about thirty-four species of lower monogeneans (Polyonchoinea), forming "doublets congénériques simultanés" (Oliver 1974). Only lately Rohde (1976a, b) gave two examples of similar doublets for the higher monogeneans (Oligonchoinea). One of them (*Pseudothoracocotyla indica* + *Pseudothoracocotyla gigantica*) does not seem to us to be irreproachable since the validity of synonymization of *Dawesia* and *Pseudothoracocotyla* (and after Rohde 1976 problematically even *Thoracocotyle*) has not yet been proved at all. Similar examples were known to us (Lebedev 1972, 1977).

These interesting cases of joint parasitism have been recorded as follows: *Bilaterocotyloides carangis* and *B. madrasensis* (fam. Protomicrocotylidae) on gills of *Megalaspis cordyla* (= *Caranx rottleri*) from the Southern coast of India (three fishes); *Upenicola digitata* and *U. upeneoides* (fam. Diclidophoridae) on gills of *Upeneus sulphureus* from the Southern coast of India (two fishes); *Paramazocraes vicinus* and *P. trissocles* (fam. Mazocraeidae) on *Thrissocles* sp. from South China Sea (two fishes); and *Pseudaxinoides bychowskyi* and *P. caballeroi*, (fam. Gastrocotylidae) on three host-species from four regions in six cases (see Table).

Characterizing the known examples of this phenomenon Euzet (1972) writes: "Ce parasitisme particulier est difficile à expliquer. En écologie une règle assez générale veut que deux espèces congénériques ne puissent occuper la même niche écologique. Si cela se produit il y a compétition et élimination de l'espèce la moins adaptée" (p. 77). Following Euzet his adherents consider that the analyzed material testifies to an existence of more than one ecological niche on fish gills and show that there are preferential microbiotopes on gills for every species. Lambert and Maillard (1975) assume that the distribution of species along preferential microenvironments is not the result of an interspecific competition. Lambert and Maillard (1975) and Oliver (1976) emphasize that some differences in spatial distribution of certain monogenean species on gills depend upon their centrifugal migration on

Table 1. Doublets congeneric simultaneous among higher monogeneans

No.	Doublets: pair of monogenean species (family)	Host (family)	Locality	Author, remarks
1	*Pseudothoracocotyla indica* + *Pseudothoracocotyla gigantica* (Gastrocotylidae)	*Scomberomorus commersoni* (Cybiidae)	east coast of Australia	Rohde (1976)*)
2	*Gotocotyla bivaginalis* + *Gotocotyla secunda* (Gotocotylidae)	*Scomberomorus commersoni* (Cybiidae)	east coast of Australia	Rohde (1976) (there are in our material also)
3	*Bilaterocotyloides carangis* + *Bilaterocotyloides madrasensis* (Protomicrocotylidae)	*Megalaspis cordyla* (Carangidae)	south coast of India	Lebedev (1972)
4	*Upenicola upeneoides* + *Upenicola digitata* (Diclidophoridae)	*Upeneus sulphurens* (Mullidae)	south coast of India	our data
5	*Paramazocraes thrissocles* + *Paramazocraes vicinus* (Mazocraeidae)	*Thrissocles* sp. (Engraulidae)	South-China Sea	our data
6	*Pseudaxinoides bychowskyi* + *Pseudaxinoides caballeroi* (Gastrocotylidae)	*Caranx* (*Atule*) *djedaba* *Caranx* (*Atule*) *kalla* *Caranx* sp. *Caranx* (*Atule*) *djedaba*	Masirah Isl. Sofala (Mozambique strait) Masirah Isl. Masirah Isl. Hainan Isl. (South China Sea)	Lebedev (1977)

*) Taxonomical position is not clear

gill arches. On the contrary, Molnar (1971) thinks that site selection in *Dactylogyrus lamellatus* depends upon the fish age rather than upon the age of the parasite. In addition, such an important factor of environmental distribution of parasites on gills as a hydrodynamic one (Fernando and Hanek 1976) should be taken into consideration (see also Wootten 1974).

Strong and variable directed "microstreams" (which are turbulent in certain parts of gill cavity) certainly must greatly influence the distribution of parasites. Perhaps, just these effects may considerably account for the site diversification of monogeneans on gills in "monoparasitic" case.

But Rohde (1976a, b) considers that "niche restriction" in Monogenea develops on the non-competitive basis: "It is not necessary to postulate either competition or reinforcement of reproductive barriers to account for separation of sympatric species. Random selection of habitats alone... may lead to the separation of sympatric species, although competition and/or reinforcement may be the most important factors in certain cases or may at least have the secondary effect of increasing interspecific separation." (pp. 67—68). This conclusion is being drawn on account of an existence of niche restriction not only in tropical aquatories where gill biotopes are saturated but also in the temperate and cold regions, where there is usually a single species of monogeneans parasitizing fishes (non-saturated gill biotopes). Rohde (1976b) writes: "Increase in the change of mating may be the most important mechanism leading to habitat restriction — more significant than competition and reinforcement of reproductive barriers..." (pp. 479—480).

Not denying, in principle, a possibility of non-competitive site diversification we are apt to consider Rohde's evidences to be not satisfactory, mainly according to the following reasons. An increase in chance of mating, to our mind, is not quite the mechanism of process (Rohde 1976b) but the result of its acting, since success or failure of vital functions in populations is finally expressed as a reproductive success. Facts given by Rohde in papers cited testify rather in favour of competition existence as the main motive force of site selection and the subsequent segregation of species divided ecologically. An increase in chance of mating and reduction of competition degree among species in the case considered will be a consequence of site selection but not its reason (see also spatial segregation of species in gill biotopes mentioned in the papers by Euzet and Ktari 1971, Ktari 1971, Llewellyn 1956 and others).

Lawlor and Maynard Smith (1976) showed mathematically in general that coevolution of the competitive consumers in the "coarse-grained" (i.e. heterogenous, unstable etc.) environment was possible in the direction of stabilization of isolation only. In the "fine-grained" environment two consumers may well coevolve but diverging under the influence of competition. Further, a coevolution of consumers naturally leads to their divergence by means of random selection and, that is essential to emphasize, to reduction of a degree of competition among them.

Conditions of monogenean existence on gills may, in principle, be regarded as stable; Oliver (1974) emphasizes the ecological monotony of gills. We think that the pattern of Lawlor and Maynard Smith (1976) in its particular fine-grained variant is applicable to monogeneans. Clearly that in case of selection affecting the efficiency of the employment of sources in relatively stable environmental conditions ("K — selection") the most intensive competition is reflected leading ultimately to specialization. That is why we consider that coevolution of related species in high density biotopes follows the way of competitive niche diversification. Holmes (1973) showed in the more general case (joint parasitism of any close species in one biotope) that niche diversification appears as a result of interactive relationships between competitors and leads to site segregation with subsequent arising of specificity to these microbiotopes. In all cases the alternative of this will be elimination of less adaptive species.

Increasing of reproductive potential in monogenean population is undoubtedly achieved by an increase in chance of mating in narrow environment. Ktari (1971) put more emphasis on the importance of concentration of specimens on certain part of gills for successful cross-fertilization since selfing and self-fertilization are excluded for more monogeneans. This concentration is the primary consequence of the effect of site selection. It should be also borne in mind that simultaneous hermaphroditism enabling cross-interfertilization, is essential in increasing the chance of mating. Simultaneous hermaphroditism, according to our observations, does not eliminate the presence of protandry in juvenile part of population and similar forms of consequent or alternative hermaphroditism, and it must not be opposed against them. Alternative hermaphroditism in population, surely, approximated it to gonochoric type. Simultaneous hermaphroditism of monogeneans does not necessarily lead to self-fertilization. Cross-fertilization prevails as a rule (Bykhovsky 1957, Ktari 1971 and others) though some polystomatids are sometimes self-fertilized.

Development of androgynous adaptation of terminal parts of male and female reproductive system, finding their greatest expression for example in heteraxinid monogenean *Gonoplasius longirostris* Robinson, 1961 (see Lebedev 1968) and diplectanid *Telegamatrix pellonae* Ramalingam, 1955 evidences to phylogenetic domination of cross-fertilization. Similar androgynous adaptations can arise only in groups with the constant (in the evolutionary aspect) predominated cross-fertilization. In addition there are high specialized species with complicated copulative organ and reduced vagina among Oligonchoinea (e.g. *Gastrocotyle* spp., see Lebedev 1975); fertilization takes a course of intrahypodermal injection of sperm into parenchyma of the specimen-mate (Macdon'ald and Caley 1975).

This instance (as well as an existence of the fam. Diplozoonidae) allows to ascertain that reproductive selection in monogeneans was as a rule vectored towards cross-fertilization.

Therefore it is necessary to note that it is impossible to consider that simultaneous hermaphroditism must surely lead to self-fertilization, with the result that "offspring of simultaneous hermaphroditic specimen always turns out to be isogenic population" (Logachev 1976, p. 147). As it was shown by us a premise in this suggestion is not correct.

Euzet (1972) analyzing the known examples of simultaneous congeneric doublets, writes about their presence: "Il existerait donc sur les branchies des poissons deux ou plusiers niches écologiques distinctes chacune étant occupées par une espèce de Monopisthocotylea" (p. 77). This inference is not convincing since if it is permissible to speak about niche segregation or niche restricition one could never subdivided fish gills (for monogeneans), or, for example, tree crown (for insects) into certain numbers of niches. It is impossible to put sign of equality between a biotope and niche as well as in the notion of niche to interpret only its spatial aspect.

Modern omnispective interpretation of the niche concept does not unlikely identify it with the concept of species. It is generally accepted that ecological niche is a "profession" of species, its functional role in community, its trophical status, position relative to gradients of external factors etc. Erosion of the boundary between the niche and species is especially evident in numerous cases of presumable absence of competitive exclusion in a niche (i.e., the principle of Gause-Chardin) when to explain the absence of competition, the niche concept receives more detailed characteristics, attributed not to environment, but to a species. Generally it is environmental niche that is kept in mind; niche-habitat, niche-biotope, i.e., biotopes are always concerned but not niche. The omnispective niche could not be treated only environmentally, it must be interpreted to a considerable extent in the specific aspect.

Phenomenon of congeneric simultaneous doublets is very interesting from the viewpoint of speciation. Manter (1963) noted the importance of registration of similar parasitic species of helminths on one host species though in contiguous regions.

Doublets considered above are mostly the species separated recently. It is difficult to assume and explain the allopatric formation and secondarity of transition to joint parasitism.

The concept of allopatric (geographical) and sympatric (ecological) speciation advanced by Mayr in the forties was from the very beginning not quite distinct in definition and contradictory in corollaries thus producing numerous specifications later on. It was suggested to distinguish such notions as syntopic and allotopic (Rivas 1964). This author reinterpreted notions of allopatric and sympatric, considering those species to be sympatric which have the same or overlapping distribution regardless of wheter or not they occupy the same microhabitat. Species which occupy the same microhabitat are regarded to be syntopic. Naturally, when one considers parasitic organisms as the obligate attribute having host, it is necessary to detail the notion concerned introducing "xenous" — parameter.

Eichler (1966) suggested to distinguish among parasites the synhospitalic and allohospitalic species (i.e. species occurring on the same host or on different hosts). We consider to be more preferable the terms with the same sense but formed from Greek roots, namely, symxenous and alloxenous. It is necessary to our mind to distinguish the notion monoxenous distribution (i.e. distribution in the same specimen of host) in addition to the notion symxenous, implying only the presence of the same species of host.

The other system of terms (Schults and Gvozdev 1972) when localisation of helminths is characterized by terms of locus and loculus is more preferential, in our opinion, for autecological approach.

О НЕКОТОРЫХ АСПЕКТАХ СУЩЕСТВОВАНИЯ МОНОГЕНОИДЕЙ

Б. И. Лебедев

Резюме. Рассмотрены некоторые проблемы существования моногеноидей на жабрах рыб: наличие однородовых симультанных дублетов, пространственное распространение видов на жабрах, межвидовая рестрикция биотопов. Доказывается конкурентный характер позиционного отбора у моногеней. Рассмотрена роль гермафродитизма в эволюции и биологии моногеней, морфологических адаптаций, направленных на увеличение шанцов спаривания. Анализируются случаи моноксенного распространения и видообразования, а также понятия симксенности и аллоксенности. Подчеркивается большое значение экологических и эволюционных исследований моногеноидей.

REFERENCES

BYKHOVSKY B. E., Monogeneticheskie sosalshchiki, ich sistema i filogenia. (Monogenetic flukes, their systematics and phylogeny). Izd. AN SSSR, Leningrad, 1—509, 1957. (In Russian).

EICHLER W., Two new evolutionary terms for speciation in parasitic animals. Syst. Zool. 15: 216—218, 1966.

EUZET L., Parasitisme branchial simultané par deux espèces congénériques de monogènes Monopisthocotylea. Comp. Rend., 1-r Multicolloq. europ. de parasitol, Rennes, 76—77, 1972.

—, KTARI M. H., *Aspinatrium gallieni* n. sp. (Monogenea: Polyopisthocotylea) parasite de *Strongylura acus* Lacépede, 1803 en Mediterranée. Bull. Soc. Zool. France 96, 509–517, 1971.

FERNANDO C. H., HANEK G., Gills. In: Ecological aspects of parasitology. North-Holland Publ. Co, Amsterdam: 209–226, 1976.

HOLMES J. C., Site selection by parasitic helminths: interspecific interactions, site segregation, and their importance to the development of helminth communities. Canad. J. Zool. 51: 333–347, 1973.

KTARI M. H., Recherches sur la reproduction et le développement de quelques monogènes (Polyopisthocotylea) parasites de poissons marins. Univ. sci. natur. et techniq., Languedoc, Montpellier: 1–327, 1971.

—, The occurrence of two congeneric species of Monogenea on the gills of *Echeneis naucrates* L. (Pisces — Teleostei) collected in Tunisia. 2nd europ. Multicolloq. parasitol., Trogir, 93–94, 1975.

LAMBERT A., MAILLARD CL., Répartition branchiale de deux monogènes: *Diplectanum aequans* (Wagener, 1857) Diesing, 1858 et *Diplectanum laubieri* Lambert et Maillard, 1974 (Monogenea, Monopisthocotylea) parasites simultanés de *Dicentrarchus labrax* (téléostéen). An. Parasitol. hum. comp. 50: 691–699, 1975.

LAWLOR L. R., MAYNARD SMITH J., The coevolution and stability of competing species. Amer. Natur. 110: 79–99, 1976.

LEBEDEV B. I., Monogeneans of food fishes from the Pacific bassin. Fam. Heteraxinidae Price, 1962. In: Helminths of animals from the Pacific ocean. Nauka, Moscow, 38–45, 1968. (In Russian).

—, The taxonomy of monogeneans of suborder Gastrocotylinea. In: Investigations on the fauna, systematics and biochemistry of helminths in the Far East. Proc. Inst. Biol. and Pedol., new ser., 11 (114), Vladivostok, 121–145, 1972. (In Russian).

—, A taxonomic survey of the genus *Gastrocotyle* (Monogenoidea: Gastrocotylinea). In: Helminthological investigations of animals and plants. Proc. Inst. Biol. and Pedol., New ser., 26 (129), Vladivostok, 73–96, 1975. (In Russian).

—, Two new species of monogeneans from fishes of Indo-Pacific waters and notes concerning the genera *Pseudaxine* and *Pseudaxinoides*. Univ. Nat. Auton. de México, Exc. Parasitol. en Mem. del Dr. Ed. Caballero Publ. espec. 4: 69–78, 1977.

LLEWELLYN J., The host-specificity, micro-ecology, adhesive attitudes and comparative morphology of some trematode gill parasites. Journ. Mar. Biol. Ass. U. K. 35: 113–127, 1956.

LOGACHEV E. D., Importance of stabilizing selection in evolution of biological systems „parasite — host“. In: Problems of exper. morphophysiol. and genetics. Kemerovo, 139–149, 1976.

MACDONALD S., CALEY J., Sexual reproduction in the monogenean *Diclidophora merlangi*: tissue penetration by sperm. Z. Parasitenk. 45: 323–344, 1975.

MANTER H. W., The zoogeographical affinities of trematodes of South American freshwater fishes. System. Zool. 12: 45–70, 1963.

MOLNAR K., Studies on gill parasitosis of the grass carp (*Ctenopharyngodon idella*) caused by *Dactylogyrus lamellatus* Achmerow, 1952. Acta Vet. Acad. Sci. Hung. 21: 361–375, 1971.

OLIVER G., Nouveaux aspects du parasitisme des Diplectanidae Bychowsky, 1957 (Monogenea, Monopisthocotylea) chez les téléostéens perciformes des côtes de France. C. R. Acad. Sci. D 279: 803–805, 1974.

—, New observations on biology and ecology of some Diplectanidae (Monogenea, Monopisthocotylea). In: Studies on the monogeneans Proc. Inst. Biol. and Pedol. New ser. v. 34/137 Vladivostok, 104–109, 1976. (In Russian).

RIVAS L. R., A reinterpretation of the concept "sympatric" and "allopatric" with proposal of the additional terms "syntopic" and "allotopic". System. Zool. 13: 42–43, 1964.

ROHDE K., Monogenean gill parasites of *Scomberomorus commersoni* Lacepède and other mackerel on the Australian east coast. Z. Parasitenk. 51: 49–69, 1976a.

—, Marine parasitology in Australia. Search 7: 477–482, 1976b.

SCHULTS R. S., GVOZDEV E. V., Osnovy gelmintologii. (Principles of helminthology). Nauka, Moscow, 2: 1–515, 1972. (In Russian).

WOOTTEN R., The spatial distribution of *Dactylogyrus amphibothrium* on the gills of ruffe *Gymnocephalus cernus* and its relation to the relative amounts of water passing over the parts of the gills. J. Helminthol. 48: 167–174, 1974.

Received 30 August 1977.

B. L., Institute of Biology and Pedology, Far East Science Center, USSR Academy of Sciences,
690 022 Vladivostok, U.S.S.R.