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IV ВСЕРОССИЙСКОЙ ШКОЛЫ
ПО ТЕОРЕТИЧЕСКОЙ
И МОРСКОЙ ПАРАЗИТОЛОГИИ**

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В сборнике представлены краткие сообщения, посвященные актуальным проблемам теоретической, экологической и морской паразитологии. В них освещены современные вопросы становления теоретической, экологической и морской паразитологии; морфологии, систематики, эволюции и фауны паразитических животных; теории жизненных циклов и результаты их изучения в различных группах паразитов; структуры и функционирования паразитарных систем; взаимоотношения паразит – хозяин на индивидуальном и популяционном уровнях; популяционной биологии паразитов и о паразитах как биологических метках при исследовании различных сторон экологии хозяев и экологической структуры сообществ.

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**PROCEEDINGS
OF THE IV ALL-RUSSIAN WORKSHOP
ON THEORETHICAL
AND MARINE PARASITOLOGY**

***Kaliningrad (Lesnoye Settlement)
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The collection of short papers on the actual problems of theorethical, ecological and marine parasitology has been presented. There are described the modern problems of making of theorethical, ecological and marine parasitology; morphology, taxonomy, evolution and fauna of parasites; theory of parasite life cycles and results of their study in different groups of parasite animals; structure and functioning of parasitic systems; parasite-host relations on individual and population levels; population biology of parasites and attempts of data on parasites as biological tags in the ecological studies of different aspects of host ecology and community ecology.

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ЭВОЛЮЦИЯ ПАРАЗИТИЗМА В ОКЕАНЕ

THE CONCEPT OF CUMULATIVE PARASITE EVOLUTION IN MARINE FISH PARASITES

The Ocean is the largest ecosystem on earth, accounting for a large part of global biodiversity. Though it is generally understood that the tropical Ocean with its extensive coral reefs is at the centre of marine biodiversity, also other systems such as the deep sea are highly diverse. Besides regular invertebrate and vertebrate life, a large number of more «primitive» life forms ranging from viruses and fungi to bacteria and also parasites inhabit the sea. Parasitism is one of the most successful modes of life displayed by living organisms (Poulin, Morand, 2000), and the parasitic life in the Oceans exceeds that of ordinary organisms. There are more parasitic than non-parasitic life forms on earth (Price,

1980; Schmidt, Roberts 1989; Windsor, 1998), with all organisms becoming attacked or even victim of diseases and parasites at least during one phase of its life time (Marcogliese, Price, 1997). Parasites and other pathogens significantly contribute to the natural mortality of any aquatic organism.

The evolution of host-parasite diversity is a matter of central interest. Host-parasite checklists have demonstrated that the number of fish parasites exceeds that of their hosts. Rohde (2002) estimated more than 100,000 species of protozoan and metazoan parasites of fish, and Klimpel et al. (2001), considering the occurrence of 13,500 known fish species in marine and brackish water habitats, estimated a total of 20,250-43,200 metazoan parasite species. Hardy (1959) already recognized that there are at least 2 or 3 species of parasites per host, and Palm et al. (1999) calculated 3.1 metazoan fish parasites per host species in German coastal waters. Even in the deep sea, where only a fraction of the fish species have been studied for parasites, a worldwide average of 1.5 parasite species per fish host is known to science (Kimpel et al. 2001). Fish parasite communities cannot be assumed to be saturated in the sense that further species cannot be added over evolutionary time, and Rohde (1998) stated that there are still a large number of free ecological niches that might be used by fish parasites in future.

The present paper presents the concept of cumulative parasite evolution that was introduced by Palm (2004). Host switching of generalistic parasites with the exploration of new hosts and habitats is responsible for the new parasite species development in the marine system. The high parasite diversity is suggested to be the result of steadily increasing parasite numbers per host species, where the established generalists can be considered to be the driving force behind the evolution of parasite species diversity (Palm, Klimpel, 2007).

In terms of species diversity, ectoparasitic monogeneans with direct life cycles and crustaceans are the most species rich fish parasites, with many of them being considered host specific. Of the known endoparasitic helminths, marine acanthocephalans, nematodes and cestodes are transferred through the marine food web to complete their life cycles. They involve several intermediate hosts before they can reach the final hosts (heteroxenous). Of these, trypanorhynch cestodes were used as a model taxon, where larval and adult distribution patterns can give insight into the evolutionary processes that are involved into species diversification (Palm, Klimpel, 2007).

Trypanorhynch cestodes are an ancient group of marine tapeworms that infest elasmobranchs. They are characterized by a scolex with 2-4 bothria (Fig. 1a) and a tentacular apparatus, consisting of four retractile tentacles as extensions of tentacle sheaths that are attached to four bulbs (Palm 2004). Antagonistic bulbs and retractor muscles enable evagination and retraction of these flexible structures that serve as holdfasts while the bothria are used for movement. The tentacles are adorned with hooks or hooklets in complex arrangements (Fig. 1b-f). Trypanorhynchs follow 3 or 4 host life cycles, where invertebrates and teleosts serve as intermediate hosts before reaching the final host. More than 260 species are known from the 1000 elasmobranchs today (Palm 2004; Beveridge, Campbell, 2005; Beveridge, Justine, 2006), and more species are added year by year. A new classification of trypanorhynchs with the analysis of 3945 host records revealed the surprising result that these cestodes, though being highly divers, seem to be relatively low host specific in the intermediate and final host (Palm 2004), or generalistic in the sense of Parker et al. (2003). Low host specificity or generalism is advantageous for successful metazoan fish parasites to explore new host species and habitats (Palm, Klimpel, 2007). Because most helminth life cycles follow a basic scheme and often include 3 or max. 4 hosts (as in the case of the trypanorhynchs), Parker et al. (2003) suggested that the incorporation of new hosts into the life cycle must have occurred long time ago. This suggests that new life cycle patterns mainly evolve by exploring new host species, however, not adding to but changing already existing intermediate and final

host species.

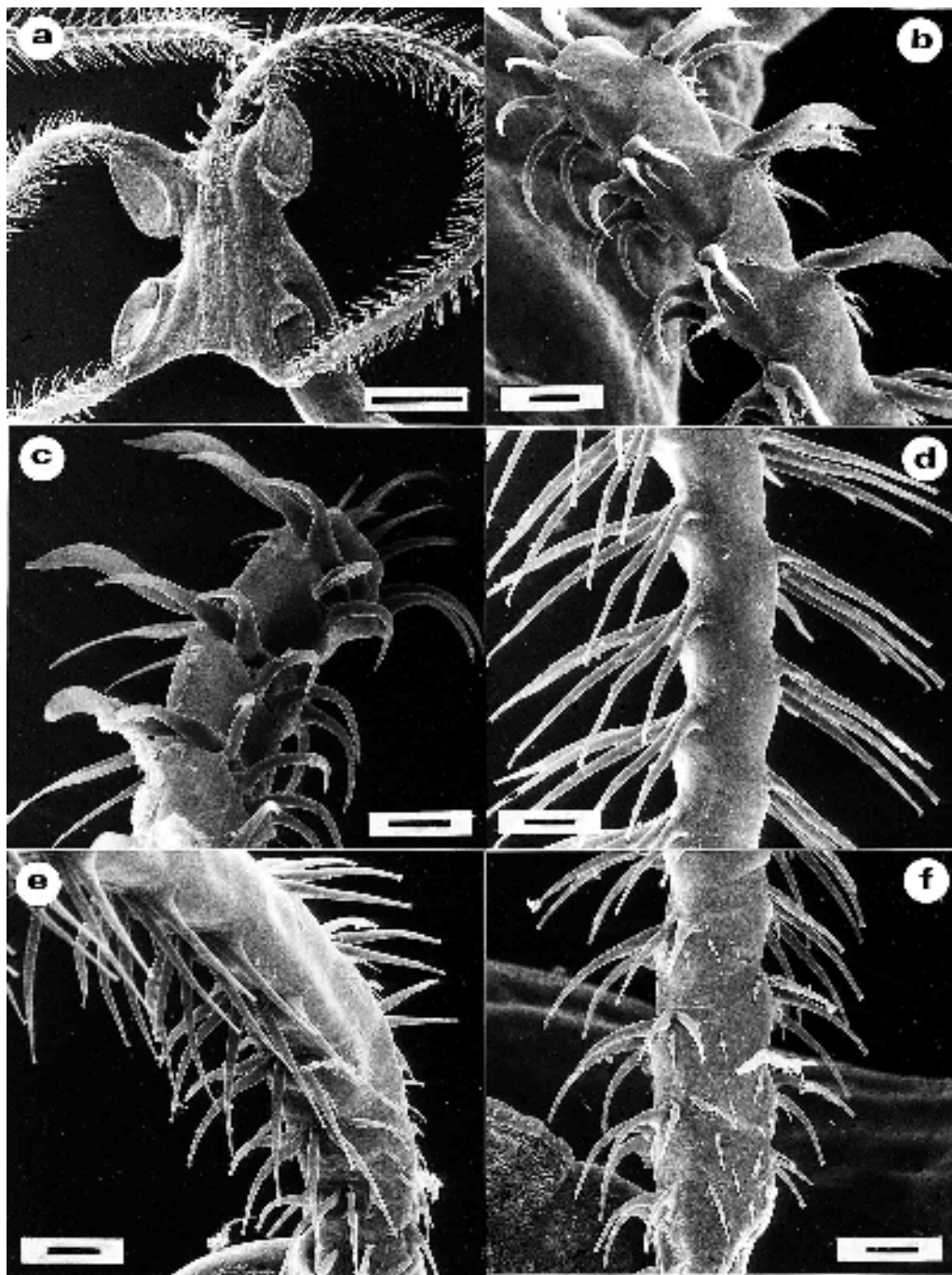


Fig. 1. Scolex morphology of *Pterobothrium acanthotruncatum*. a.-d. External surface, metabasal armature. Note the 5 elongated hooks on each tentacle side. e.-f. Bothrial surface, basal armature. f. Bothrial surface, basal armature. Note the additional intercalary hooks and single hooks on the external surface. Scale bars: a, 200; b-f, 20 (Palm 2004).

The evolution of the Trypanorhyncha can be described as follows (Palm 2004). The development of a primary trypanorhynch lineage with a successful life cycle that has established first intermediate host(s) can lead to a species radiation within that trypanorhynch group 1 and within host group A (Fig. 2). Beyond that stage, all parasites

can use similar intermediate and final hosts. The most successful variation with the most successful character combination remains the core species within a respective host species A1. Driven by relatively low host specificity, the core species remains capable of infesting less suitable hosts A2-A.... Similarly, variations (siblings or species) within the trypanorhynch group 1 remain capable of infesting host A1. Less suitable hosts might be unfavorable for the parasite in terms of anatomical, physiological or immunological conditions, thus failing to provide a suitable microhabitat. They might be phylogenetically more distantly related to host A1, or simply might not share the same biotope as the parasite, making successful transmission less likely.

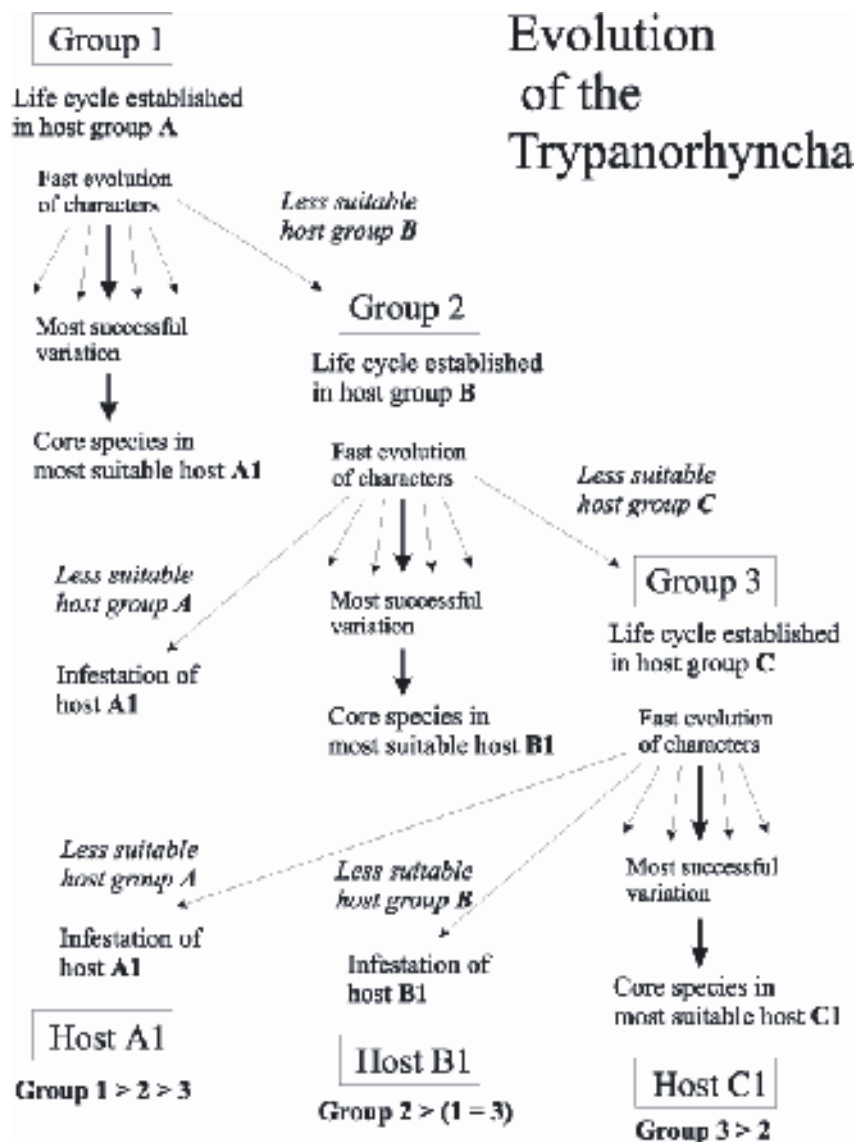


Fig. 2. **Evolution of the Trypanorhyncha.** Cumulative evolution of 2 trypanorhynch taxa (groups 2 and 3) out of group 1. Trypanorhynch group 1 are most present and diverse in host group A, with the single hosts A1-A... being infested with many trypanorhynch species of group 1, some of group 2 and few of group 3 (Group 1 > 2 > 3). Group 2 are most present and diverse in host group B, with the single hosts B1-B... being infested with many trypanorhynch species of group 2, and some of group 1 and 3 (Group 2 > (1 = 3)). Group 3 are most present and diverse in host group C, with the single hosts C1-C... being infested with many trypanorhynch species of group 3, and some of group 2 (Group 3 > 2) (Palm 2004).

Some variations of trypanorhynch group 1 are able to invade new intermediate and final hosts (also new host taxa in terms of phylogenetic development) simply by utilizing

the marine food web. This necessitates an actual niche overlap between the existing and the new host, and requires generalistic parasites (Parker et al. 2003). Such transmission could take place accidentally, though host switching seems to be common phenomenon in trypanorhynch cestodes as well as in other marine fish parasites. As the new hosts pursue a different feeding ecology and distribution within the marine environment than originally followed by the hosts of trypanorhynch group 1, new pathways including other first intermediate hosts become established until a new life cycle is established. Separation of two species can happen in continuous sympatry of the hosts. Due to originally relatively low host specificity, variants of the new species group 2 may either reinvade the hosts that are utilized by the original species group 1, or discover new hosts, which then enable the establishment of a further life cycle pattern in group 3. As illustrated in Fig. 2, trypanorhynch species group 1 would be most present and diverse in host group A, with the single hosts A1-A... being infested with many trypanorhynch species of group 1, some of group 2 and a few of group 3. Trypanorhynch group 2 would be most present and diverse in host group B, with the single hosts B1-B... being infested with many trypanorhynch species of group 2, and some of group 1 and 3. Trypanorhynch group 3 would be most present and diverse in host group C, with the single hosts C1-C... being infested with many trypanorhynch species of group 3, and some of group 2. Species of the original group 1, however, might not infest these hosts, if the new group 3 pursues a specific life cycle that enables it to reach host group C due to a completely different feeding ecology of the hosts, or possibly because it lives in a different habitat such as the deep sea.

As a consequence of the process described above, more and more trypanorhynch species develop and accumulate over time within the marine environment (cumulative evolution, Palm, 2004). Considering the trypanorhynchs as a model taxon for fish parasitic helminths that utilize solely the marine food web for transmission, a similar process can be expected also for other parasitic taxa. Maintaining generalists that speciate into specialists and further radiate will lead to a mixture of highly specific or non-specific parasites within the different parasite taxa. The process of a parasite taxon development is schematically illustrated in fig. 3, where the species number of a potential host taxon is set to 100 (Fig. 3, point of time A) and a single parasite species infests one of these potential hosts (Fig. 3, point of time B). Under the assumption of the Ocean being a stable environment at an evolutionary scale, potential host species numbers within a specific taxon either develop stable, increase or decrease (Fig. 3, point of time C). With a successful new infestation by a generalistic parasite, after discovery of a first suitable intermediate host (Fig. 3 point of time B) and under the assumption that the evolution of the parasites follows that of their hosts, the number of parasite species within each successful taxon will increase under stable, multiplied and even reduced host species number scenarios (Fig. 3, point of time C-E). Because this process happens simultaneously in different parasite taxa by utilizing different hosts and habitats, this must result in continuously increasing parasite species numbers within an evolutionary time frame. Though upwards (new final host) and downwards (new intermediate host) incorporation of new hosts (Parker et al., 2003) in the first place led to a variety of different life cycles and parasitic taxa that nowadays exist in the world oceans, the lateral incorporation (new host exploration or host switching) by generalistic parasites as the second step followed by further specialization according to their principal life cycle as the third step is responsible for the actual high diversity of marine fish parasites (Palm, Klimpel, 2007). This can also explain the co-existence of generalists and specialists within the marine fish parasite taxa. Obviously, generalism costs are sufficiently small even for larger marine fish parasitic taxa, to maintain generalism over long evolutionary time, and the maintaining generalists can be considered as the driving force of parasite species diversity evolution (Palm, Klimpel, 2007).

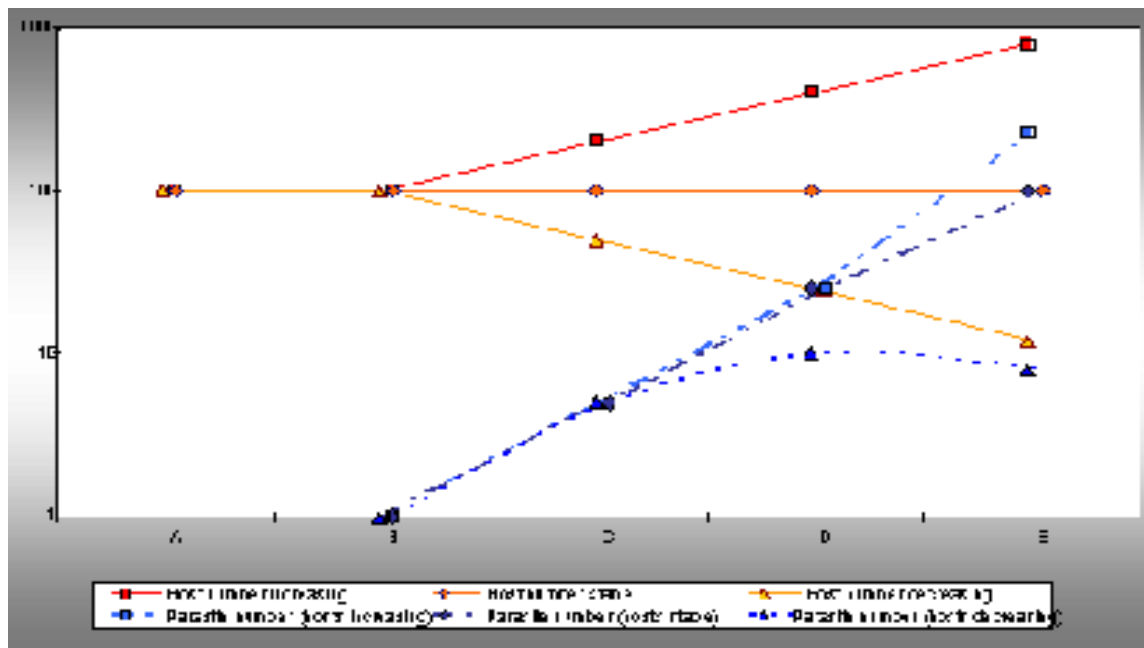


Fig. 3. **Schematic illustration of the concept of cumulative parasite evolution.** Increasing parasite numbers over time (point of time A, before infestation; B, new parasite infestation; C-E, three time steps) under increasing ($\times 8$), decreasing ($/ 8$) and stable host species number development. It is exemplified that after the first successful exploration of a new host group (lateral incorporation) by a generalistic parasite, the number of parasites is developing with the factor 5 until reaching one parasite per host species. Each newly established life cycle will follow a similar process, resulting in steadily increasing parasite-host ratios in the Ocean over evolutionary time

It can be suggested that the high parasite diversity of marine fish is the result of a process of cumulative evolution of parasitic life forms over time (Palm, 2004; Palm, Klimpel, 2007). Consequently, the general parasite number in comparison to its hosts is continuously increasing, resulting in a process of increasing host-parasite ratios over time. Any successful mutant surviving in an extra host spreads and fixates, maintaining generalism in the arising taxon. This also suggests that generalism proceeds specialism in marine fish parasite evolution. Windsor (1998) stated that «Most of the species on Earth are parasites». Interestingly, the theory above supports Windsor's view on the driving factor of host-parasite co-evolution. Originally, hosts evolve to survive in the biosphere and parasites evolve just to be able to ride along with their hosts. However, under the concept of cumulative parasite diversity, all non-parasitic host organisms must cope with a continuously increasing number of parasites and pathogens that finally outnumbers them and challenges their immunological and ecological abilities. Because many parasites and their life cycles develop wide ranges of distribution involving as many as possible potential intermediate and final hosts, host organisms can seek to prevent infestation or damage by physiological or ecological (Mouritsen, Poulin, 2003) adaptations, linked with changes in behavior or exploration of new habitats. Another solution is adaptation towards increasing natural parasite loads to the benefit of both, thus ensuring the survival of the parasite and increasing fitness in the host. In both cases, parasites have reached the stage of becoming true engines of evolution.

Thus, the concept of cumulative parasite evolution suggests that the number of

marine fish parasite species per host species is continuously increasing at an evolutionary time scale. Host switching of generalistic parasites with the exploration of new hosts and habitats is responsible for the new parasite species development in the marine system. The established generalists can be considered to be the driving force behind the evolution of marine fish parasite species diversity.

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