Key Publications (with abstracts)

Models and non-linear dynamics:

Simulation of geographical trends in Chowdhury ecosystem model

Rohde, K, and Stauffer, D.

Advances in Complex Systems (2005) 8, 1-14.

Abstract:

A computer simulation based on individual births and deaths gives a biodiversity increasing from cold to warm climates, in agreement with reality. Complexity of foodwebs increases with time and at a higher rate at low latitudes, and there is a higher rate of species creation at low latitudes. Keeping many niches empty makes the results correspond more closely to natural gradients. All these findings are in good agreement with theoretical predictions and empirical findings, demonstrating that the Chowdhury model used for our simulations realistically reflects these.

Fuzzy chaos: reduced chaos in the combined dynamics of several independently chaotic populations.

Rohde, K. and Rohde, P.P.

American Naturalist 158 (2001) 553-556

(Previous studies using non-linear modelling treated populations as homogeneous entities with single dynamics and growth rates. However, there is increasing evidence that many populations (metapopulations) consist of local subpopulations with largely independent dynamics and different growth rates. In some studies, supposedly homogeneous subpopulations may in fact have been metapopulations. We examine, for the first time, the effect such confusion may have on the demonstration of chaotic behaviour. We show that the use of ranges of population growth rates leads to bifurcation diagrams that are dramatically different from that for single subpopulations, with implications for the possibility of long-term predictions: the length of the equilibrium component is not constant, bifurcations collapse repeatedly, and the chaotic field contracts to a narrow band depending on the parameters used, with a much reduced extent of chaos. This may explain the lack of unambiguous evidence for chaos in natural populations. Our findings suggest that a re-appraisal of studies using chaotic models is necessary: empirical studies must give the answer as to whether chaos is responsible for certain patterns or not, and whether single or multiple subpopulations are involved. The fact that models based on chaos may explain a pattern is not sufficient in itself. We also suggest application of fuzzy-chaos modelling to other biological systems.)

Zoogeography:

Oceanic barriers as indicated by scombrid fishes and their parasites

K.Rohde and C.J. Hayward

International Journal for Parasitology 30 (2000) 579-583

Abstract:

Four genera of scombrid fishes (26 species) and their copepod (32 species) and monogenean ectoparasites (25 species) were used to test the hypothesis that the East Pacific Barrier is responsible for the most pronounced break in the circum-tropical warm water fauna of the continental shelves, and not the New World Barrier. Analysis at the species level showed that there is a primary centre of diversity in the West Pacific, and a secondary centre in the West Atlantic. The former, almost entirely, shares its species of the largely coastal *Scomberomorus* and *Grammatorcynus* and their parasites with seas located to the west. Only four parasites (all copepods) are shared by the East and West Pacific, and they are circum-tropical. In contrast, the West Pacific shares species of the more pelagic *Scomber* and their parasites with seas both to the east and west, although at the genus level, only two circum-tropical monogenean genera are shared by the E and W Pacific. We conclude that the East Pacific Barrier has been a 100% or almost 100% effective barrier to dispersal of species of *Scomberomorus*, *Grammatorcynus* and their parasites, whereas for species of *Scomber* and their parasites, the East Pacific has been a less effective barrier.

Keywords: zoogeography; parasites; Scombridae; Monogenea; Copepoda; East Pacific barrier; vonIhering method

Latitudinal gradients in species diversity and Rapoportʼs rule revisited; a review of recent work and what can parasites teach us about the causes of the gradients?

Klaus Rohde

ECOGRAPHY 22: 593-613, Copenhagen 1999

Abstract:

A review is given of recent work on latitudinal gradients in species diversity and their explanations, including Rapoportʼs rule. Energy input, measured by temperature or potential evapotranspiration, correlates best with the gradients. However, such a correlation does not "explain" them. It merely suggests explanations, which may be either different ceilings to diversity set by different energy levels under equilibrium conditions, recent historical events, or a gradient in effective evolutionary time (determined by speed of evolution directly driven by temperature, and by relative constancy of conditions over evolutionary time) under non-equilibrium conditions. Marine parasites are used to show that equilibrium conditions are the exception rather than the rule among animals. It is concluded that latitudinal gradients in species diversity result from a gradient in effective evolutionary time modulated by several other factors. Dispersal abilities of many marine invertebrates are likely to be greater at low than at high latitudes, suggesting an opposite Rapoport effect.

This is an invited Minireview on the occasion of the 50th anniversary of the Nordic Ecological Society Oikos.

Latitudinal differences in species and community richness and in community structure of metazoan endo- and ectoparasites of marine teleost fish.

Klaus Rohde and Maureen Heap

International Journal for Parasitology 28:461-474, 1998.

Abstract:

Relative species diversity of gastrointestinal helminths of 55 teleost fish species did not differ significantly at different latitudes, whereas relative species diversity of metazoan ectoparasites on the heads and gills of 108 teleost fish species showed a significant increase with decreasing latitude and from deep to surface waters. Abundance of endoparasites also was the same at all latitudes, whereas abundance of ectoparasites increased with decreasing latitude and from deep to shallow waters. A comparative analysis using phylogenetically independent contrasts supported these conclusions. Possible reasons for the differences between endo- and ectoparasites are discussed. A detailed analysis of the community structure of gastrointestinal helminths of five Antarctic and three tropical teleosts and of metazoan ectoparasites on the heads and gills of five Antarctic and seven tropical fish species showed the following: abundance and prevalence of infection of endoparasites are similar in Antarctic and tropical fish, but are much greater for tropical than for Antarctic ectoparasites. Relative species diversity of endoparasites is similar for Antarctic and tropical endoparasites, but much greater for tropical than Antarctic ectoparasites. In both Antarctic and tropical fish, different fish of the same species may have different dominant species of endo- and ectoparasites, although there is a greater range of dominant species of tropical ectoparasites, a consequence of the greater species pool available. The most dominant parasite (irrespective of species) represented 80 to 99 % of all endoparasites of Antarctic, and about 50 to 80 % of all endoparasites of tropical fish. The most dominant parasites (irrespective of species) represented about 90 to 100 % of all ectoparasites of Antarctic, and about 20 to 70 % of all ectoparasites of tropical fish, the difference a consequence of the greater species pool of tropical ectoparasites available. The data suggest that both endo- and ectoparasites live in assemblages not structured by interspecific competition.

(We dedicate this paper to Leo Margolis, who has done so much for marine parasitology)

Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness

Rohde K. Heap M. Heap D.

American Naturalist 142(1):1-16, 1993 July.

ISSN 0003-0147

Abstract:

Two methods are used to analyze latitudinal ranges of fish species: means of ranges of all species with a midpoint in the same 5-degrees latitude band plotted against latitude, and means of ranges of all species occurring in the same 5-degrees latitude band plotted against latitude. Application of the first method to data on 894 teleost species from the Indo-Pacific and Atlantic oceans showed that species with midpoints of latitudinal ranges near the equator have, on the average, much greater latitudinal ranges than species with midpoints at higher latitudes. Ranges of species were more or less the same when the second method was used, because of larger ranges and greater species numbers of low-latitude species. Rapoport's rule, according to which high-latitude species have greater latitudinal range than low-latitude species, therefore does not generally apply to marine teleosts. In contrast, the rule applies to North American (720 species) and North European (61 species) freshwater fish above a latitude of approximately 40-degrees-N as demonstrated by both methods. The rule has not been shown to apply to any group of organisms below a latitude of approximately 25-degrees-35-degrees-N. Attempts to explain greater species numbers of tropical species by narrower environmental tolerances of tropical species, as indicated by Rapoport's rule, are therefore premature, and such an explanation does not hold for marine teleosts. [References: 36]

Latitudinal gradients in species diversity: the search for the primary cause.

K. Rohde

Oikos 65: 514-527. Copenhagen,1992.

Abstract:

Hypotheses that attempt to explain latitudinal gradients in species diversity are reviewed. Some hypotheses are circular, i.e. they are based on the assumption that some taxa have greater diversity in the tropics. These include explanations assuming different degrees of competition, mutualism, predation, epiphyte load, epidemics, biotic spatial heterogeneity, host diversity, population size, niche width, population growth rate, environmental harshness, and patchiness at different latitudes. Other explanations are not supported by sufficient evidence, i.e. there is no consistent correlation between species diversity and environmental stability, environmental predictability, productivity, abiotic rarefaction, physical heterogeneity, latitudinal decrease in the angle of the sun above the horizon, area, aridity, seasonality, number of habitats, and latitudinal ranges. The ecological and evolutionary time hypotheses, as usually understood, also cannot explain the gradients, nor does the temperature dependence of chemical reactions permit predictions on species richness. Only differences in solar energy are consistently correlated with diversity gradients along latitude, altitude and perhaps depth. It is concluded that greater species diversity is due to greater "effective" evolutionary time (evolutionary speed) in the tropics, probably as the result of shorter generation times, faster mutation rates, and faster selection at greater temperatures. There is an urgent need for experimental studies of temperature effects on speed of selection.

Increased viviparity of marine parasites at high latitudes

K.Rohde

Hydrobiologia 127, 197-201 (1985)

Abstract:

For the first time, Thorson's rule, that non-pelagic development increases with latitude, is shown to apply to a group of marine parasites. Relative and absolute numbers of species of viviparous Monogenea, gill parasites of fish, increase with increasing latitude. The gradient can be explained by the inability, in cold waters, of (a) free larvae to locate suitable habitats (hosts) and/or (b) small invertebrates to produce pelagic larvae in sufficient numbers. Viviparous Monogenea are also more common in cold than in warm freshwater, but have not been found in the deep sea.

Latitudinal Differences in Host-Specificity of Marine Monogenea and Digenea

K. Rohde

Marine Biology 47, 125-134 (1978)

Abstract:

Data from 15 surveys of marine trematodes (average of 91 trematode species and more than 80 fish species per survey) and from 12 surveys of marine Monogenea (average of 52 Monogenea species and more than 49 fish species per survey) show that the degree of host specificity of marine digenetic trematodes increases from cold to warm seas; Monogenea do not show such a trend, and the trend is probably reversed in the Pacific Ocean.

The difference between the two groups is explained in terms of r- and k-strategy. Monogenea tend to follow a k-strategy (great complexity of adult, few offspring), which results in a high degree of host- and site-specificity to facilitate mating in low-density populations. Only one or e few related host species can be infected, and as more related host species are present in the warm Pacific, host-specificity there is reduced. Digenea tend to follow an r-strategy (simple structure of adult, many offspring), part of which is to infect many ecologically suitable hosts. Host-specificity in cold-temperate seas is reduced because of the less patchy and ecologically less restricted distribution of hosts.

Ecology:

Ecology and Biogeography of Marine Parasites

Rohde K.

Advances in Marine Biology 43 (2002) 1-86

A review is given of (mainly recent) work on the biodiversity, ecology, biogeography and practical importance of marine parasites. Problems in estimating species numbers have been thoroughly discussed for free-living species, and the main points of these discussions are reviewed here. Even rough estimates of the richness of most parasite groups in the oceans are premature for the following reasons: species numbers of host groups, in particular in the deep sea and the meiofauna, are not known; most host groups have been examined only insufficiently for parasites or not at all; even in some of the best known groups, latitudinal, longitudinal and depth gradients in species richness are only poorly understood or not known at all; effects of hosts on parasite morphology and geographical variation have been studied only in a few cases; there are few studies using techniques of molecular biology to distinguish sibling species. Estimates of species richness in the best known groups, trematodes, monogeneans and copepods of marine fishes, are given. Parasites are found in almost all taxa of eukaryotes, but most parasitic species are concentrated in a few taxa.

Important aspects of the ecology of marine parasites are discussed. It is emphasized that host specificity and host ranges should be distinguished, and a index that permits calculation of host specificity is discussed. The same index can be applied to measure site specificity. Central problems in ecology are the importance of interspecific competition and whether equilibrium or non-equilibrium conditions prevail. Marine parasites are among the few groups of organisms that have been extensively examined in this regard. A holistic approach, ie., application of many methods, has unambiguously shown that metazoan ecto- (and probably endo-) parasites of marine fish live in largely non- saturated niche space under non-equilibrium conditions, ie., they live in assemblages rather than in communities structured by competition. Nestedness occurs in such assemblages, but it can be explained by characteristics of the species themselves. There is little agreement on which other factors are involved in structuring parasite assemblages. Few studies on metapopulations of marine parasites have been made. A new approach, that of fuzzy chaos modelling, is discussed. It is likely that marine parasites are commonly found in metapopulations consisting of many subpopulations, and they are ideally suited to test the predictions of fuzzy chaos. Some recent studies on functional ecology and morphology, especially with regard to host, site and mate finding, are discussed, and attention is drawn to the amazing variety of sensory receptors in some marine parasites. Effects of parasites on hosts, and some studies on the evolution and speciation of marine parasites are discussed as well.

A detailed overview of biogeographical studies is given, with respect to latitudinal gradients in species diversity, reproductive strategies, and host ranges/specificity. Studies of marine parasites have contributed significantly to giving a non-equilibrium explanation for latitudinal diversity gradients. Recent studies on longitudinal and depth gradients are discussed, as well as parasites in brackish water, parasites as indicators of zoogeographical regions and barriers, and parasites as biological tags.

The practical importance of marine parasites in mariculture, as monitors of pollution, agents of human disease, the use of parasites for controlling introduced marine pests, and some related aspects, are discussed as well.

Co-occurrence of ectoparasites of marine fishes: a null-model analysis

Nicholas J. Gotelli and Klaus Rohde

Ecology Letters 5: 86-94, 2002

Abstract

We used null model analysis to test for nonrandomness in the structure of metazoan ectoparasite communities of 45 species of marine fish. Host species consistently supported fewer parasite species combinations than expected by chance, even in analyses that incorporated empty sites. However, for most analyses, the null hypothesis was not rejected, and co-occurrence patterns could not be distinguished from those that might arise by random colonization and extinction. We compared our results to analyses of presence-absence matrices for vertebrate taxa, and found support for the hypothesis that there is an ecological continuum of community organization. Presence-absence matrices for small-bodied taxa with low vagility and/or small populations (marine ectoparasites, herps) were mostly random, whereas presence-absence matrices for large-bodied taxa with high vagility and/or large populations (birds, mammals) were highly structured. Metazoan ectoparasites of marine fishes fall near the low end of the continuum, with little evidence for non-random species co-occurrence patterns.

Nestedness in assemblages of metazoan ecto- and endoparasites of marine fish

Rohde, K., Worthen, W., Heap, M., Hugueny, B. and Guegan, J.-F.

International Journal for Parasitology 28: 543-549, 1998.

Abstract

Assemblages of metazoan ectoparasites of 79 species and gastrointestinal helminths of eight species of marine fishes were analysed to examine whether nestedness is related to sample size, abundance, species richness, and prevalence of infection, and whether the use of z-scores or Monte Carlo simulations yields different results. No significant differences in the number of nested assemblages were found with the two methods, and neither sample size nor abundance, but prevalence of infection of ectoparasites was correlated with nestedness. Species richness was significantly correlated with nestedness only when fish species with fewer than three parasite species were not excluded. Differential colonisation probabilities are the most likely cause of nestedness.

Is there a fixed number of niches for endoparasites of fish?

Rohde K.

International Journal for Parasitology. 28: 1861-1865, 1998

Author Keywords: Endoparasites. Niche. Infracommunity. Community richness. Fish.

Abstract:

Kennedy and Guegan, based on Cornell and Lawton (1992), found a "curvilinear" relationship (the "fundamental form" of the relationship for parasite communities) between infracommunity and component community richness and interpreted this as meaning that only processes acting within the infracommunities can explain the limitation in the number of parasite species in a given host. The research described here shows that an asymptotic relationship is the consequence of the differential likelihoods of parasite species to appear in an infracommunity as determined by transmission rates and intrinsic life spans. Processes operating at the infracommunity level are not necessary to explain the curvilinear relationship. Even much richer communities than those found in European freshwater fishes cannot be assumed to be "saturated" in the sense that further species cannot be added over evolutionary time.

Niche restriction in parasites - proximate and ultimate causes

Rohde K.

Parasitology. 109(Suppl S):S 69-S 84, 1994.

ISSN 0031-1820

Author Keywords: Niche. Competition. Reinforcement of reproductive barriers. Vacant niches. Marine parasites.

Abstract:

Hutchinson's (1957) definition of an ecological niche as a multidimensional hypervolume determined by a number of physical and biotic variables is adopted. The number of niche dimensions is very great, but as a working hypothesis it is assumed that a few are sufficient to characterize the niche of a parasite species to a high degree of accuracy. They are host species, microhabitat(s), macrohabitat(s), geographical range, sex and age of host, season, food and hyperparasites. Methods to measure niche width, in particular specificity indices, are discussed, and some examples of niche restriction are described. Proximate and ultimate causes of niche restriction are discussed, mainly using marine parasites as examples. Among proximate causes of one niche dimension, host specificity, are ecological factors restricting exposure to infection to certain host species; host-specific chemical factors that induce hatching, direct infective stages to a host and bring about settlement of a parasite; factors that lead to mortality in or on the wrong host; morphological adaptations that guarantee survival in or on the 'correct' host; and availability of suitable hosts. Many factors are likely to be responsible for microhabitat specificity, but have been little studied, except for some physiological and morphological adaptations to particular microhabitats. Macrohabitats and geographical range may be determined by the distribution of intermediate hosts and certain food items, and by a variety of chemical and physical factors. Hosts of different sexes may differ in feeding habits and the composition of the skin, and thus acquire parasites differentially. Hosts of different age may be differentially infected due to accumulation of parasites with age, loss of parasites due to developing resistance (or immunity), and different size and feeding habits. Among ultimate causes of niche restriction and segregation are avoidance of competition, predation and hyperparasites; facilitation of mating; reinforcement of reproductive barriers; and adaptations to environmental complexity. Few studies permit a decision on which factor or factors are responsible in particular cases. Interspecific competition may play a greater role in helminth communities of some host groups than of others, but it seems that, overall, its role has been exaggerated at least for marine parasites. Some 'classical' examples of microhabitat segregation explained by interspecific competition can also be explained by reinforcement of reproductive barriers. There is evidence for the importance of facilitation of mating in microhabitat restriction, and the availability of many vacant niches indicates that competition, overall, is not of great importance. [References: 93]

Intra- and interspecific interactions in low density populations in resource-rich habitats.

K. Rohde.

Oikos 60: 91-104. Copenhagen, 1991.

<u>Abstract</u>:

Parasites on the gills of marine fish are used to study intra- and interspecific interactions. The model has several advantages: there are many replicas, habitats are small and can be easily examined, ectoparasite numbers vary from none to hundreds of more than 15 species, data can be quantitatively evaluated, fish are easily available in large numbers, all but one or few environmental parameters can be kept constant in "natural" experiments, in *marine* habitats uncontrolled variability can be largely excluded, only space for attachment is in limited supply. Evidence is provided that many niches are not utilized. The observations that vacant niches are available, that some fish species have many congeneric parasite species whereas others have few or none, and that there are insignificant effects of potentially competing species on microhabitats and on infection intensities do not support the view that interspecific competition has great ecological/evolutionary importance.

Morphological evidence for interspecific competition is ambiguous. Expansion of microhabitats at great infection intensities indicates intraspecific competition. The observations that microhabitat restriction leads to increased intraspecific contact, that adult stages often have more restricted sites than larval or asexual reproductive stages, that sessile and rare species have more restricted sites than mobile and common ones, and that sites may become narrower at the time of mating, provide evidence that an important function of niche restriction is enhancement of the chances to mate. Differences in microhabitat overlap between congeners compared to that between non-congeners, and differences in the structure of copulatory organs between spatially segregated and non-segregated congeners suggest that an important function of niche segregation is reinforcement of reproductive barriers. Evidence is given that most animal species are likely to occur at low densities in resource-rich habitats, and that conclusions based on the study of gill parasites can be applied to them. In particular, a discussion of a diversification equation modelled on the logistic equation for population growth shows that there is a vast number of vacant niches. The general conclusion is that the major problem for most animals is not to avoid competition but to find suitable sites for feeding and mating.

A Critical Evaluation Of Intrinsic And Extrinsic Factors Responsible For Niche Restriction In Parasites.

Klaus Rohde

The American Naturalist 114, 648-671 November 1979

Summary

Intrinsic and extrinsic factors responsible for niche restriction in parasites and particularly in Monogenea of fish are discussed. Interspecific competition may result in competitive exclusion of one or several species, or it may lead to a change in the microhabitat of one or all co-occurring species (interactive site segregation), but there is no evidence that such effects lead to evolutionary changes and avoidance of competition, i.e., to selective site

segregation. That extrinsic factors, particularly competition, are not of such great evolutionary significance among parasites as is usually assumed, is indicated by the following observations.

Most effects of competitive exclusion may also be caused by intraspecific crowding. Interspecific effects may also be positive, enhancing the chances of species co-occurring. Host-mediated effects are usually more harmful to the species evoking them than to competing species. Parasite species with coinciding or overlapping microhabitats often show no interactions. Related species commonly have widely overlapping niches. Only a small proportion of the niches available to ectoparasites of fish is filled. Species with mouthparts of different sizes may use the same food in the same habitat, i.e., such differences do not necessarily indicate segregation.

Evidence for the effect of species intrinsic factors is that in many cases microhabitats are extremely restricted, even though competing species do not exist and cannot have existed in the past, for instance in fish species at high latitudes with only one species of ectoparasite. Circumstantial evidence shows that an important factor responsible for niche restriction in parasites is selection to increase intraspecific contact and thus mating. Niche diversification is self-augmenting, and in a continuously expanding niche space populations would be diluted to such a degree that mating would become impossible without the counteracting selection for niche restriction. The probability that two species show complete niche coincidence is infinitesimally small even without competition, and it is therefore not permissible to use niche differences as proof for competition.

A Non-Competitive Mechanism Responsible For Restricting Niches

Klaus Rohde

Zoologischer Anzeiger 199:164-172, 1977.

Abstract:

Examples are given which show that all parts of the gills of tropical marine fish may be inhabited by monogenean and copepod ectoparasites; many of these parasites have strictly restricted microhabitats on the gills. Gill parasites of fish from cold-temperate seas have similarly restricted microhabitats, but most fish species have none or only one or two species of gill parasites and large parts of the gills are therefore empty; it is concluded that because of the absence of competing or potentially interbreeding species, neither competition nor reinforcement of reproductive barriers to prevent hybridization, can be responsible for restricting habitats; evidence is given that restriction of habitats leads to increased intraspecific contact and, thus, facilitates mating. Selection to increase intraspecific contact may be the most important mechanism responsible for restricting niches. Segregation of sympatric species may be due to random selection of niches. [With 2 Figures and 6 Tables.]

Parasitology:

Parasitism.

K. Rohde

In S.Levin (Ed.). Encyclopedia of Biodiversity. Vol. I, Academic Press, New York, pp. 463-484, 2001.

Contents: Definition of parasitism Related phenomena (commensalism; phoresis; mutualism; symbiosis) Types of parasites (ecto- and endoparasites; obligatory and facultative parasites; larval and adult parasites; temporary and permanent parasites; hyperparasites) Adaptations to parasitism (size of parasites; increase in reproductive capacity; reduction and increase in complexity; mechanisms of dispersal; mechanisms of infection; aggregation; hermaphroditism, parthenogenesis and asexual reproduction; host specificity; some physiological adaptations; simple and complex life cycles) Origins of parasitism (transitions to parasitism; origins of complex life cycles; the evolution of virulence; coevolution of hosts and parasites) Host-parasite interactions (cleaning symbiosis; immunity and tissue reactions; effects on host populations) The ecological niches of parasites (the niche concept; niche dimensions of parasites; saturation of niches with parasites; proximate and ultimate causes of niche restriction) The structure of parasite communities (concepts of community ecology; evolution of parasite communities; parasite communities as general ecological models) Parasite population dynamics The diversity of parasites (distribution of parasites in the animal and plant kingdoms) Zoogeography of parasites (latitudinal gradients in species diversity, in frequencies and intensities of infection, in niche width and reproductive strategies; parasites as biological markers) Economic and hygienic importance of parasites (some examples and a discussion of control measures)

The Larvae of Monogenea (Platyhelminthes)

Ian D. Whittington, Leslie A. Chisholm and Klaus Rohde

Advances in Parasitology 44: 139-232, 2000.

Abstract

There has been no comprehensive review of the infective larval stage (oncomiracidium) in the direct life-cycle of monogeneans since Llewellyn (1963, 1968). In the last 30 years, knowledge of the general anatomy and morphology of oncomiracidia has increased significantly as has information on swimming behaviour and egg-hatching strategies that may enhance chances of host infection. Nevertheless, oncomiracidia are known for only a small proportion of monogenean species described. This review consolidates established, and summarizes new knowledge since Llewellyn's work and integrates light- and electron-microscopy studies including unpublished data. Currently there is considerable debate, fuelled largely by phylogenetic studies using molecular techniques, about whether or not the class Monogenea (comprising subclasses Monopisthocotylea and Polyopisthocotylea) is monophyletic. This challenges established views that Monopisthocotylea and Polyopisthocotylea form a single clade based on two larval characters: two pairs of rhabdomeric eyes; three bands of ciliated cells. In an attempt to reveal further synapomorphies for the entire Monogenea (or provide evidence against the monophyly) or possibly for the Monopistocotylea and Polyopisthocotylea only, we review the following larval features: haptoral sclerites; ciliated cells; epidermis; terminal globule; gland, protonephridial and nervous systems; sense organs, digestive tract; parenchyma; and behaviour. Conclusions are equivocal but indicate that further larval studies, especially ultrastructural, are necessary to assess: the presence or absence of 'false' vertical rootlets of epidermal cilia; tapering epidermal cilia; the protonephridial system; the presence or absence of terminal globule; glands and their secretions; and the morphology and chemical composition of haptoral sclerites. Future integration of light- and electron-microscopy studies are likely to be particularly informative.

The origins of parasitism in the Platyhelminthes [review]

Rohde K.

International Journal for Parasitology. 24(8):1099-1115, 1994 Dec.

ISSN 0020-7519

Author Keywords: Platyhelminthes. Parasitism, evolution. Phylogeny. Aspidogastrea. Turbellaria. Fecampiidae. Horizontal gene transfer. DNA.

Abstract

Symbiotic associations have arisen independently in several groups of the largely free-living turbellarians. Morphological adaptations of turbellarians to a symbiotic way of life include suckers and adhesive glands for attachment, elaborate systems of microvilli and other epidermal structures for absorption of food, glands for the formation of cysts, cocoons and cement material, and lack of a pharynx and intestine in some species. However, many species closely resemble their free-living relatives. Egg production is greatly increased at least in some species, and life cycles are always direct. Food of symbiotic turbellarians consists of host food and/or host tissue. Ectosymbiotes show fewer physiological adaptations than entosymbiotes. The major groups of parasitic Platyhelminthes (Trematoda Aspidogastrea, Trematoda Digenea, Monogenea, Udonellidea, Cestoda including Gyrocotylidea, Amphilinidea and Eucestoda), form one monophylum, the Neodermata, characterized by a neodermis (tegument) replacing the larval epidermis, epidermal cilia with a single horizontal rootlet, sensory receptors with electron-dense collars, spermatozoa with axonemes incorporated in the sperm body by proximodistal fusion, and protonephridial flame bulbs formed by two cells each contributing a row of longitudinal ribs to the filtration apparatus. The sister group of the Neodermata is unknown but is likely to be a large taxon including the Proseriata and some other turbellarian groups. Among the Neodermata, the Aspidogastrea is likely to be the most archaic group, as indicated by DNA studies, morphology, life cycles and physiology. Aspidogastreans can survive for many days or even weeks outside a host in simple media, they

show little host specificity, and have an astonishingly complex nervous system and many types of sensory receptors, both in the larva and the adult. It is suggested that Aspidogastrea were originally parasites of molluscs (and possibly arthropods and other invertebrates) and that they are archaic forms which have remained al a stage where vertebrates represent facultative hosts or obligatory final hosts into which only the very last stages of the life cycle (maturation of the gonads) have been transferred. The complex life cycles of Digenea have evolved from the simple aspidogastrean ones by intercalation of multiplicative larval stages (sporocysts, rediae) in the mollusc host, and of cercarial stages ensuring dispersal to the now obligatory final host. Monogenea may have lost the molluscan host or evolved before the early neodermatans had acquired it. Cestoda either replaced the original molluscan with an arthropod host, retained an original arthropod host or evolved from an early neodermatan before molluscan hosts had been acquired, newly acquiring an arthropod host. Horizontal gene transfer and implications for mosaic evolution in the Platyhelminthes are discussed. [References: 109]

The minor groups of parasitic Platyhelminthes.

K. Rohde

In Baker, J.R. and Muller, R. (Eds) Advances in Parasitology 33, Academic Press, London, pp: 145-234, 1994.

ISBN: 0-12-031733-8

Contents:

Fine structure of the Monogenea, especially *Polystomoides* Ward.

K. Rohde

In Baker, J.R. and Muller, R. (Eds) Advances in Parasitology 13, Academic Press, London, pp: 1-33, 1975.

ISBN: 0-12-0317133

Contents:

The Aspidogastrea, especially *Multicotyle purvisi* Dawes, 1941.

K. Rohde

In Baker, J.R. and Muller, R. (Eds) Advances in Parasitology 10, Academic Press, London and New York, pp: 77-151, 1972

ISBN: 0-12-031710-9

Contents:

Ultrastructure and Phylogeny:

The Aspidogastrea, an archaic group of Platyhelminthes.

K. Rohde

In D.T.J. Littlewood and R.A.Bray (Eds.). Interrelationships of the Platyhelminthes. Taylor & Francis, London and New York, pp. 159-167, 2001.

(Morphological, ultrastructural and biological characteristics of larval and adult Aspidogastrea are described and illustrated, and used for a phylogenetic analysis. Combined DNA and morphological evidence has shown that the Aspidogastrea is the sister group of the Digenea, both constituting the class Trematoda. Very likely, the trematodes is the sister group of the other Neodermata. Because the Neodermata (possibly jointly with some parasitic turbellarian groups: fecampiids, Urastoma Ichthyophaga and perhaps some others) have evolved from free-living turbellarians very early in evolutionary history, the Aspidogastrea must be considered a very ancient group, which may have retained some archaic characters. These characters include a possible rudimentary spiral cleavage, "pseudosegmentation" which is not only external but extends to the glandular and nervous systems, an extraordinary variety of sensory receptors in some species, a very complex nervous system, and (in some digeneans) a pulsating circulatory system with cellular inclusions. These characters support the suggestion based on comparisons of hox genes, that platyhelminths are secondarily simplified coelomates.The life cycle is simple, including an intermediate mollusc and final vertebrate host, although some species can mature in the mollusc host. It is likely that the much more complex life cycles of digenean trematodes have evolved from that of the Aspidogastrea. Morphological and host characteristics on their own do not resolve phylogenetic relationships between aspidogastrean genera, although it is likely that the three families Rugogastridae, Stichocotylidae and Multicalycidae form one, and the Aspidogastridae another clade. Combined

DNA and morphological data may resolve phylogenetic relationships between genera.)

Protonephridia as phylogenetic characters.

K. Rohde

In D.T.J. Littlewood and R.A.Bray (Eds.). Interrelationships of the Platyhelminthes. Taylor & Francis, London and New York, pp. 203-216, 2001.

(The ultrastructure of flame bulbs and protonephridial capillaries of the major groups of Platyhelminthes is decribed and illustrated by diagrams. It is concluded that protonephridial ultrastructure is a useful phylogenetic tool in the Platyhelminthes, but is insufficient to resolve many of the phylogenetic relationships between taxa on its own.)

The interrelationships of all major groups of Platyhelminthes: phylogenetic evidence from morphology and molecules.

D. T. J. LITTLEWOOD [1,2*], FLS, K. ROHDE [3] and K. A. CLOUGH [1]

Biological Journal of the Linnean Society (1999) 66: 75-114. With 7 Figures.

<u>Abstract</u>

We used a data matrix of 65 morphological characters from 25 ingroup and 6 outgroup taxa, and an alignment comprising complete 18S rDNA sequences from 82 species of parasitic and free-living Platyhelminthes and from 19 species of lower invertebrates to analyse phylogenetic relationships of various platyhelminth taxa. Of the 1358 unambiguously alignable molecular positions, 995 were variable and 757 were phylogenetically informative (parsimony criterion); complete 18S rDNA sequences ranged in length from 1755 to 2873 bp. Main conclusions are: Neodermata are monophyletic, and the Trematoda, Monogenea and Cestoda within them are monophyletic as well. The sister group of the Neodermata is all the other Neoophora; the Kalyptorhynchia, Typhloplanida, Dalyelliida and Temnocephalida from one clade, and the last three another. Monophyly of the Seriata is rejected, but Polycladida/Macrostomida/Haplopharyngida are monophyletic, as are the last two taxa. As a consequence, validity of the taxon Trepaxonemata is rejected. Further studies must show the correct position of the Acoela and Nemertodermatida. It is stressed that morphological and molecular data in some respects lead to contradictory results, for instance concerning the position of the Fecampiidae/*Urastoma/Ichthyophaga* and the relative position of the Lecithoepitheliata. Denser sampling of taxa for molecular data, complementary sequences from independent genes, and inclusion of additional morphological data are necessary to resolve these contradictions.

Robust phylogenies and adaptive radiations - a critical examination of methods used to identify key innovations

K. Rohde

American Naturalist. 148(3):481-500, 1996 Sep.

ISSN 0003-0147

<u>Abstract</u>

A critical examination of a recent article by Brooks and McLennan has led to the conclusion that their phylogeny of parasitic Platyhelminthes is based on "synapomorphies" that are clearly wrong or superficial similarities whose homology is unlikely. Using characters likely to be homologous and DNA analyses, it has been shown that Temnocephalida is not the sister group of the parasitic Platyhelminthes (Neodermata), Udonellidea is unlikely to be the sister group of the other Neodermata, the sister group of the Neodermata is unknown but likely to be a large taxon comprising several turbellarian groups, no evidence indicates that the Arthropoda are the original hosts of the parasitic Platyhelminthes, the possibility cannot be ruled out that species poverty of some groups of parasitic Platyhelminthes is an artifact, and "key innovations" supposedly explaining the great species richness of the parasitic Platyhelminthes and some taxa within them are based on insufficient or faulty evidence. Based on an examination of the recent literature, I suggest the following steps to identify key innovations: first, establish phylogenetic trees using characters likely to be homologous on the basis of established homology criteria; second, examine whether trees are "significantly" unbalanced using null models; finally, use multiple testing to tentatively identify putative key innovations. Retrospective studies of processes that have led to radiations in the past will in many cases be impossible, and the best one can hope for is a tentative identification of putative key innovations by multiple testing. if multiple testing cannot be done, then even a tentative identification is impossible, and one is left with a "plausible suggestion." Concerning the practice of phylogenetic systematics, it is emphasized that phylogenetic analyses using a few characters whose homology has been made likely by careful assessment are more likely to reveal phylogenetic relationships than analyses using large numbers of unassessed characters. [References: 88]

Sperm and spermiogenesis of the ʻTurbellariaʼ and implications for the phylogeny of the phylum Platyhelminthes

Watson, N.A. and Rohde, K.

Advances in Spermatozoal Phylogeny and Taxonomy. Eds. B.G.M. Jamieson, J. Ausio and J .-L. Justine. Memoires du Museum National dʼHistoire Naturelle 166, 37-54, 1995.

Abstract

This chapter reviews recent ultrastructural investigations of sperm and spermiogenesis in turbellarian platyhelminths (Catenulida, Nemertodermatida, Acoela, Macrostonmida and Trepaxonemata including

Polycladida, Lecithoepitheliata, Prolecithophora, Proseriata, Tricladida, and Rhabdocoela, including Typhloplanida, Kalyptorhynchia, Dalyelliida, Temnocephalida and Fecampiida). Some distinctive characteristics of the differentiating spermatid especially in the zone of differentiation may be useful for phylogenetic considerations. Spermiogenetic and mature sperm features including axonemal or flagellar characteristics, dense bodies, nuclear components, mitochondria and microtubule arrangements are documented for each of the major taxa. It is concluded that more investigations are needed and they must be comprehensive to build a solid data base for a cladistic analysis of the phylum based on sperm and spermiogenetic characteristics.

Ultrastructure of Sperm and Spermiogenesis of two Species of the Tricladida (Platyhelminthes) - *Romankenkius libidinosus* (Paludicola) and an unidentified species of the Maricola

Rohde K. Watson NA.

Invertebrate Reproduction & Development. 27(3):181-196, 1995 Jul.

ISSN 0168-8170

Author Keywords: Tricladida. Romankenkius. Sperm. Spermiogenesis. Ultrastructure. Phylogeny.

Abstract

Sperm of the paludicolan triclad *Romankenkius libidinosus* consist of a distal process and a main body, and of two free flagella arising from the zone between both. Flagella are fused for a short distance and their tips are split into long "microvilli" containing microtubules. The single long mitochondrion extends from the distal process to close to the tip of the main body. The nucleus, consisting of lucent and dense components coiled screw-like around each other, does not extend into the distal process. A peripheral row of microtubules consists of about 37-39 microtubules in the middle parts of sperm, decreasing towards both ends. A short row of three inner microtubules extends along most of the main sperm body. Surface ornamentations are present at both ends but not in the middle parts. In early spermatids, joined by cytophores, a row of microtubules forms beneath the plasma membrane in the zone of differentiation and close to it an intercentriolar body with several dense bands connected by filaments. Many nuclear pores are prominent in the region of the nucleus close to the zone of differentiation, and an apical layer of dense nucleoplasm develops. Two flagella appear, facing in opposite directions and then rotating to lie parallel with each other. Rotation is probably brought about by contraction of microtubules inserted in the basal bodies and "dense plates" around them. Striated rootlets ("basal complexes") between basal bodies and the nucleus may support the flagella during rotation. The intercentriolar body splits into two, each half remaining at the base of a basal body, but parts of the central band are left behind. A cytoplasmic process grows out, the mitochondria fuse, and the nucleus elongates. In outgrowing spermatids, inner microtubules are not present. An unidentified maricolan triclad has similar sperm and spermiogenesis. Triclads resemble other platyhelminths in a number of characteristics of sperm and spermiogenesis, but ultrastructure of sperm and spermiogenesis does not permit a conclusion as to whether they are more closely related to the proseriates or rhabdocoels. [References: 29]

Aspects of the phylogeny of Platyhelminthes based on 18s ribosomal DNA and protonephridial ultrastructure

Rohde K. Johnson AM. Baverstock PR. Watson NA.

Hydrobiologia. 305(1-3):27-35, 1995 Jun 2.

ISSN 0018-8158

Author Keywords:
Platyhelminthes. Phylogeny. DNA. Ultrastructure. Protonephridia.

Abstract:

DNA studies of 23 taxa (20 platyhelminths, 1 nemertean, Home and Artemia) and electron-microscopic studies of the protonephridia of many platyhelminths (supported by some additional ultrastructural data) have led to the following conclusions: the Neodermata are monophyletic; Temnocephalida and Dalyelliida form one clade and are not the 'primitive' sister group of the Neodermata; Gyrocotylidea, Amphilinidea and Eucestoda form one monophylum; Pterastericolidae and Umagillidae are dalyelliids and not the sister group of the Neodermata; and Proseriata are unlikely to be closely related with the Tricladida. A large taxon consisting of the Proseriata and some other 'turbellarians' may represent the sister group of the Neodermata. [References: 41]

The evolution of protonephridia of the Platyhelminthes.

K. Rohde

in Turbellarian Biology. S. Tyler ed. pp: 315-321. Kluwer Academic Publishers, Belgium. 1991.

Author Keywords:
Protonephridia. Platyhelminthes. Ultrastructure. Evolution. Phylogeny.

Abstract:

Three types of flame bulbs are distinguished in the Platyhelminthes : type 1 has two cilia arising from a terminal cell and rootlets extending along the weir; type 2 has many cilia arising from a terminal cell and the proximal canal cell closely aligned with it; and type 3 has a non-terminal perikaryon forming many flame bulbs, each with many cilia and a single row of longitudinal ribs. Each type appears in various structural forms. Type 1 is found in the Catenulida; type 2 in the Macrostomida, Polycladida, Prolecithophora, Proseriata, Tricladida, Fecampiidae, and Neodermata; and type 3 in the Rhabdocoela and Lecithoepitheliata. The most likely evolutionary sequence is that type 3 is derived from type 2 and, perhaps, that type 2 is derived from type 1. Characters of the protonephridia show that Rhabdocoela and the Neodermata form separate phylogenetic lineages; other similarities between these taxa are due to convergent evolution (or horizontal gene transfer?).

Fine structure of sensory receptors and nervous system of flatworms:

At Least Eight Types of Sense Receptors in an Endoparasitic Flatworm: a Counter-trend to Sacculinization.

K. Rohde

Naturwissenschaften 76, 383-385 (1989)

SENSE RECEPTORS IN *LOBATOSTOMA MANTERI* (TREMATODA, ASPIDOGASTREA)

K. Rohde and N. Watson

International Journal for Parasitology 19, 847-858, 1989

Abstract:

Sense receptors of the juvenile aspidogastrid *Lobatostoma manteri* infecting the digestive gland of the prosobranch snail *Cerithium moniliferum* were examined by transmission electron microscopy. At least eight types of presumptive sense receptors, some ciliate and some non-ciliate, are described. Some of the receptors occur in thousands. This is the greatest variety of receptors ever described from a parasitic stage of a platyhelminth by electron microscopy.

Untersuchungen an *Multicotyle purvisi* DAWES, 1941

(Trematoda: Aspidogastrea)

III. Licht- und elektronenmikroskopischer Bau des Nervensystems

Von KLAUS ROHDE

Mit 29 Abbildungen

Zool. Jb. Anat. Bd. **88**, S. 320-363 (1971)

Abstract:

The nervous systems of the adult and free larva of *Multicotyle purvisi* were reconstructed from serial sections impregnated with silver. In the adult, the anterior portion of the nervous system consists of internal circumoral commissures around the mouth cavity and external circumoral commissures below the integument. The former connect the longitudinal Nervi mediales and N. ventrales interni, the latter the N. dorsales anteriores, N. dorsolaterales anteriores, N. laterales and N. ventrales anteriores externi. Between the internal and external circumoral commissures and their longitudinal nerves, there is located the Nervus mediodorsalis with its Rami lateralis, intermedius and medialis. The commissures and connectives have numerous additional transverse connections. Anteriorly, the larger longitudinal nerves communicate by means of a Commissura terminalis anterus in the dorsal lip. The cerebral commissure corresponds to the dorsal part of an internal circumoral commissure. Posterior nerves are the N. pharyngealis, which runs along the phayrnx and enters it from behind, the N. dorsalis posterior, N. dorsolateralis posterior and N. ventralis posterior. Of the numerous commissures at the level of the pharynx, the ventral part of a commissure at the anterior margin of the pharynx is best developed (Commissura infrapharyngealis majus). Behind it is the N. genitalis which

innervates the genital opening. The posterior ventral nerve is best developed; is splits a short distance behind the brain into a dorsal and ventral branch which soon reunite and split a second time. Both branches penetrate the septum, the ventral one branching into a Ramus ventralis anterior and a R. ventr. posterior. The former enters the adhesive disk between the 2nd and 3rd transverse rows of alveoles and gives rise to a rather regular pattern of connectives and commissures in the alveolar walls. These intraplantar nerves communicate by means of numerous connections with similarly arranged extraplantar nerves above the adhesive disk. Dorsal and posterior ventral branches of the posterior ventral nerve unite again at the level in front of the ovary. As a rule, each transverse row of alveoles corresponds to a complete commissural ring, also in the dorsal part of the body. The posterior ventral nerve splits near the posterior end of the body into a Ramus terminalis dorsalis and ventralis. Septum, intestine, pharynx, preparhynx, cirrus pouch, uterus, genital- and excretory openings are innervated by plexuses. The intestinal plexus is connected to the pharyngeal and posterior dorsal nerves. The internal and external circumoral commissures and the postcerebral connectives and commissures in the dorsal part of the body also tend to form plexuses.

The free larva has the same anterior nerves as the adult, but a lesser number of commissures, as in the posterior part of the body. Best developed is a dorsal commissure in front of the acetabulum, which possibly corresponds to the Ramus terminalis dorsalis of the posterior ventral nerve of the adult. Intestinal and pharyngeal nerves are sometimes separated, and there are additional posterior internal and external ventral nerves. In the acetabulum, there are a commissure running around the lumen and two posteriorly communicating connectives in its dorsal part.

The lack of oligomerisation of the nervous system is considered to be further evidence for the primitive phylogenetic status of the Aspidogastrea.

Electron-microscopically, in addition to the structures already known from other platyhelminths, a multi-layered sheath around portions of the posterior ventral nerve and cells in the periphery of nerves containing secretory grana, were shown. Clusters of paraldehydfuchsin-positive cells were found at the crossings of extraplantar connectives and commissures and at the lateral extraplantar nerves.

SENSE RECEPTORS OF *Multicotyle purvisi* DAWES, 1941 (TREMATODA, ASPIDOBOTHRIA)

KLAUS ROHDE

Nature 211 (5051) 820-822 (1966)

Life cycles

STRUCTURE AND DEVELOPMENT OF *AUSTRAMPHILINA ELONGATA* JOHNSTON, 1931 (CESTODARIA: AMPHILINIDEA)

K. ROHDE AND M. GEORGI

International Journal for Parasitology 13: 273-287 (1983)

Structure and development of *Austramphilina elongata* Johnston, 1931 (Cestodaria: Amphilinidea). *International Journal for Parasitology* 13: 273-287. The life cycle and structure of the larvae of *Austramphilina elongata* using light-microscopy, scanning and transmission electron microscopy are described. Eggs are round and non-operculate. Larvae hatch in freshwater and penetrate through the cuticle of juvenile crayfish, *Cherax destructor*, and of freshwater shrimps, *Paratya australiensis* and *Atya* (= *Atyoida*) sp., shedding their ciliated epidermis. In the last two hosts, development to the infective stage does not occur. In crayfish, larvae grow and reach the infective stage. Turtles, *Chelodina longicollis*, become infected by eating infected crayfish. Larvae penetrate through the oesophageal wall of the turtle and migrate toward the coelom, where maturation occurs. The free-swimming larva has a syncytial epidermis which covers most of the body except for the posterior region bearing the hooks. It is loosely attached to a thin underlying tegument, which is connected to 'insunk' nucleated cell bodies. It forms a thick surface layer in the posterior region. There are no lateral flames. The weir apparatus of the flame cell has the structure typical of parasitic platyhelminths. The smaller capillaries have a smooth surface, that of the terminal ducts is covered by numerous microvilli. Three types of penetration glands open anteriorly. There are five pairs of hooks; one median ʻnormalʼ, two submedian halberd-shaped, and two lateral serrate. Hook are not lost, they are arranged around the gonopore of the adult. Frontal glands opening into the proboscis were found in the anterior part of the body in all stages examined. Infective stages in crayfish have developing reproductive organs and ducts. The tegument of the adult has many microvilli.

INDEX KEY WORDS: Platyhelminthes; Cestodaria; Amphilinidea, *Austramphilina elongata*; ultrastructure; life cycle; dvelopment; protonephridia; tegument; penetration glands.

Structure and development of *Lobatostoma manteri* sp. nov. Trematoda: Aspidogastrea) from the Great Barrier Reef, Australia

KLAUS ROHDE

Parasitology (1973), **66**, 63-83

Abstract

Lobatostoma manteri sp. nov. is described. It differs from other species of this genus in the number of marginal alveoli (usually 56-62), the location of the testis near the posterior end and the large size of the cirrus pouch. Mature worms occur in the intestine of the fish *Trachinotus blochi.* Eggs containing fully developed larvae are laid. The eggs are eaten by snails and hatch in the stomach. Larvae have an oral sucker, pharynx, simple caecum, ventro-terminal acetabulum, two dorsal excretory bladder cells in front of the acetabulum, and a caudal appendage. They migrate into the digestive gland and differentiate to pre-adults with fully developed genital organs and the full number of alveoli on the adhesive disk; young spermatozoa and egg cells develop but do not mature. Pre-adults have a minimum number of 8500 sensory papillae on the surface. The worms are usually found in a cavity

formed by enlargement of the main duct and one or more (?) side ducts of the digestive gland near the stomach in *Cerithium moniliferum*, or in the stomach and main ducts of the digestive gland of *Peristernia australiensis*. They may creep from the ducts into the stomach and back into the ducts. Fish become infected by eating snails. Worms from fish die soon after transfer into sea water but can be kept alive for up to 13 days in frog's Ringer solution or dilute sea water (1:5), in which they lay eggs containing larvae infective to snails. Worms from snails remain alive in sea water, dilute sea water, frog's Ringer or Tyrode solution. Eggs of worms from single infections have the haploid chromosome number of 7; there is normally no self-fertilization and development does not reach the blastula stage. The life-cycle of *Lobatostoma manteri* is the simples two-host cycle of trematodes known. Reasons are given why it must be considered the most primitive one, of a type from which digenean life-cycles have evolved.