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*l'épidémiologie humaine - ou animale.*

*Danemark*

## *Ployploid hosts: strange attractors for parasites?*

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While a major force in higher plant evolution (Stebbins 1971, 1977), polyploidy is largely restricted among animals to lower vertebrates such as fish, amphibians and reptiles (Ohno 1970, Bogart 1980, Schultz 1980). Interestingly, many polyploid fish species occur in the African cyprinid family (Oellerman and Skelton 1990, Golubtsov and Krysanov 1993, Doadrio 1994, Guégan et al. 1995). Although cases of host-parasite associations in polyploid host species are absent in the literature, they are of interest because they permit comparative study of host-parasite adaptation. We aim to show here that polyploid host species may harbour higher parasite species richness than their diploid relatives, and in this context, studies of polyploids and their associated parasites may considerably help evolutionary ecologists and parasitologists to better understand host-parasite interactions.

We have studied monogenean ectoparasites of North and West African freshwater fishes. The occurrence of monogenean host specificity is attributed to independent specialisation which has evolved for reasons other than interspecific competition that can include host-parasite coevolution (Klassen and Beverley-Burton 1989, Guégan and Agnèse 1991, Van Every and Kritsky 1992), enhancement of mating by congeners (Rohde 1989), or avoidance of hybridisation (Euzet and Combes 1980). Patterns in monogenean community richness and organisation among host species have been explained by host body size and age (Guégan et al. 1992), host geographical range and latitudinal gradients (Rohde 1989), host diversity (Rohde 1989, Guégan and Kennedy 1993), or host phylogeny (Guégan and Kennedy 1993). We used the infracommunity species richness observed on the richest host individual (richness values are ranked from 0 to 13 across host species), for 29 African cyprinid fish species and a total of 618 collected specimens, and this data were regressed against the 6 independent variables: host species body size, geographical range, host diversity defined as the number of species per fish genus, host species phy-

logeny, latitudinal gradients (West and North Africa), and host species ploidy level (threefold levels of ploidy were found:  $2n = 50$ ,  $2n = 100$ ,  $2n = 150$ ).

To address the question of whether the parasite species richness is correlated with some traits of their hosts, we applied both simple and multiple regression procedures (Sokal and Rohlf 1981). Generally, closely related host species are more likely to exhibit similar development than distant species (Felsenstein 1985, Pagel and Harvey 1988), and they cannot be treated as statistically independent points. For instance, a relationship between parasites and host ploidy level across all fish species may be a result of phylogenetic history since fish species that share common descent are likely to be subject to similar evolutionary constraints and are likely to exhibit similar ploidy level. Comparative methods have recently been proposed to take this non-independence into account, considering phylogeny fixed and controlling for its effect on regressions (Harvey and Pagel 1991). Here, we used the independent comparisons method (Pagel 1992, Purvis and Rambault 1994, 1995) to identify a set of independently evolved comparisons within fish taxa. The host phylogeny was obtained from morphological data together with molecular data. We made a second control for sampling effort (defined as the number of collected specimens per fish species), as uneven sampling bias affects richness estimates (Gregory 1990, Walther et al. 1995). For all regressions, host body size, host geographical range and host diversity logarithmic values were used (Harvey 1982). Parasite species richness values were  $\log(x + 1)$  transformed.

Across species of cyprinid fishes, the number of parasite species observed correlates positively, in decreasing order of significance, with host body size ( $r = 0.53$ ,  $p = 0.001$ ), host diversity ( $r = 0.45$ ,  $p = 0.001$ ), host phylogeny ( $r = 0.35$ ,  $p = 0.001$ ) and host ploidy level ( $r = 0.21$ ,  $p = 0.005$ ). The number of parasite species a fish species harbours does not correlate significantly with neither host latitude ( $r = 0.06$ ,  $p = 0.186$ )



nor host range ( $r = 0.04$ ,  $p = 0.195$ ). Across these taxa, there is no relationship between parasite richness and sampling effort (Kendall's test rank,  $p = 0.075$ , Spearman's rank correlation,  $p = 0.536$ ), and between parasite richness and host range ( $p = 0.099$  and  $p = 0.106$ , respectively). The possibility that the contribution of independent variables on parasite richness values may be confounded by the effect of host phylogeny is assessed by the significant relationships observed between phylogeny and host body size ( $r = 0.64$ ,  $p = 0.001$ ), and between phylogeny and host diversity ( $r = 0.83$ ,  $p = 0.001$ ).

Multiple regression procedures using the backward elimination procedure yielded results which retain both host body size and host ploidy level to account for a significant proportion of the variance ( $r = 0.56$ ,  $p = 0.001$ ,  $n = 29$ ) in number of parasite species richness across host species. The two predictor variables retained by the analysis have positive coefficients which are significantly different from zero in both cases. Examination of standard partial coefficients shows that host body size (std.  $b = 0.52$ ,  $p = 0.001$ ) is the major factor for explaining the variation in parasite species richness, and an additional proportion (std.  $b = 0.175$ ,  $p = 0.007$ ) is covered by the ploidy level variable.

The independent comparisons method yielded results which show that host species with higher ploidy level may have evolved higher parasite species richness (Fig. 1). Calculating differences between each pair of host species at the tips of the phylogeny, and between the higher nodes of major chromosomal transitions ( $2n = 50$ ,  $2n = 100$ ,  $2n = 150$ ), we found a set of 24 mutually independent contrasts in the host phylogeny. We obtained  $Y = 0.34X$  ( $r = 0.42$ ,  $F$ -test = 5.02,  $p = 0.035$ ).

Until now, no attention has been paid to parasite species variability across different levels of ploidy in host species in comparison with that observed in diploid taxa, and nothing is known about how these interactions between parasites and polyploid hosts evolved. What matters for the relationship between host species ploidy level and parasite species number is the number of ploidy levels found among taxa: three-fold levels of ploidy were only encountered in African fishes. Perhaps more appropriately, using taxonomic groups with more ploidy series (more than the actual three-fold series analysed in this work), the correlations would become more robust, but higher ploidy series are rarely found among organisms. Consequently, we are absolutely conscious of a certain "natural" weakness of these findings. The significant results emerging from our analysis after strong mathematical controls have been made on covarying factors could possibly change as new data become available, but our work provides a way of testing new ideas about how parasite species may interact with host genome characteristics, and more specifically those like chromosome numbers.

Perhaps the most surprising result of this work is the effect of ploidy level on parasite species richness, when the effects of both host body size and phylogenetic relationships between host taxa have been controlled for by regressions. One explanation is that the positive relationship observed is a consequence of both ploidy level and parasite richness values being correlated with a third unidentified variable. Furthermore, at least five different kinds of explanations can be proposed, all based upon the assumption that there is a causal relationship between the two variables.

In one version, the polyploidisation event could be relatively recent in time. Polyploids would not have had enough time to develop resistance against parasite attacks, and they may be subjected to more infestations by a large range of parasite species. An objection to this scenario is that polyploidisation could probably have occurred over 50 Myr ago (Ferris and Whitt 1979) before the dichotomy between cyprinid and catostomid fish taxa.

In a second version, the polyploidisation event might have caused some unbalanced physiological problems in fish, and disturbance in hosts could have led to ample opportunities for parasite invasions.

In a third version, polyploid fish species could be more susceptible to parasite invasions because they are (allopolyploid) hybrid forms. Heavy parasite loads (Sage et al. 1986, Moulia et al. 1991) and higher parasite species richness (Dupont and Crivelli 1988) have been reported in (true) hybrids.

In a fourth version, the increased biochemical diversity observed in polyploids could provide more opportunities for interactions between hosts and parasites. For instance, the chromosome number and DNA content in tetraploid North American catostomid fishes have been proved to be approximately twice those of related diploid cypriniform taxa (Uyeno and Smith 1972, Ferris and Whitt 1979, Ferris 1984).

In a fifth version, polyploid taxa may express a significantly higher number of locus enzyme systems than their diploid relatives, and more specifically those conferring resistance to parasites, even if the ratio of gene duplication by tetraploidisation is not on a strictly two-for-one basis due to extinction of some genes (Ferris and Whitt 1977, 1979, Allendorf and Thorgaard 1984, Ferris 1984).

Of these five versions, there is still no consensus on the conditions under which higher ploidy level may favour the installation of a greater parasite diversity. The two first versions imply that virulence should have considerably affected the local survival of novel combinations of polyploid hosts and their parasites. In contrast, the relative evolutionary success of polyploid cyprinid taxa on the African continent (at least 50% of tetraploid and hexaploid cyprinid species occur in North Africa, which is a well documented area, out of 32 native fish species) stands in contrast to the observa-

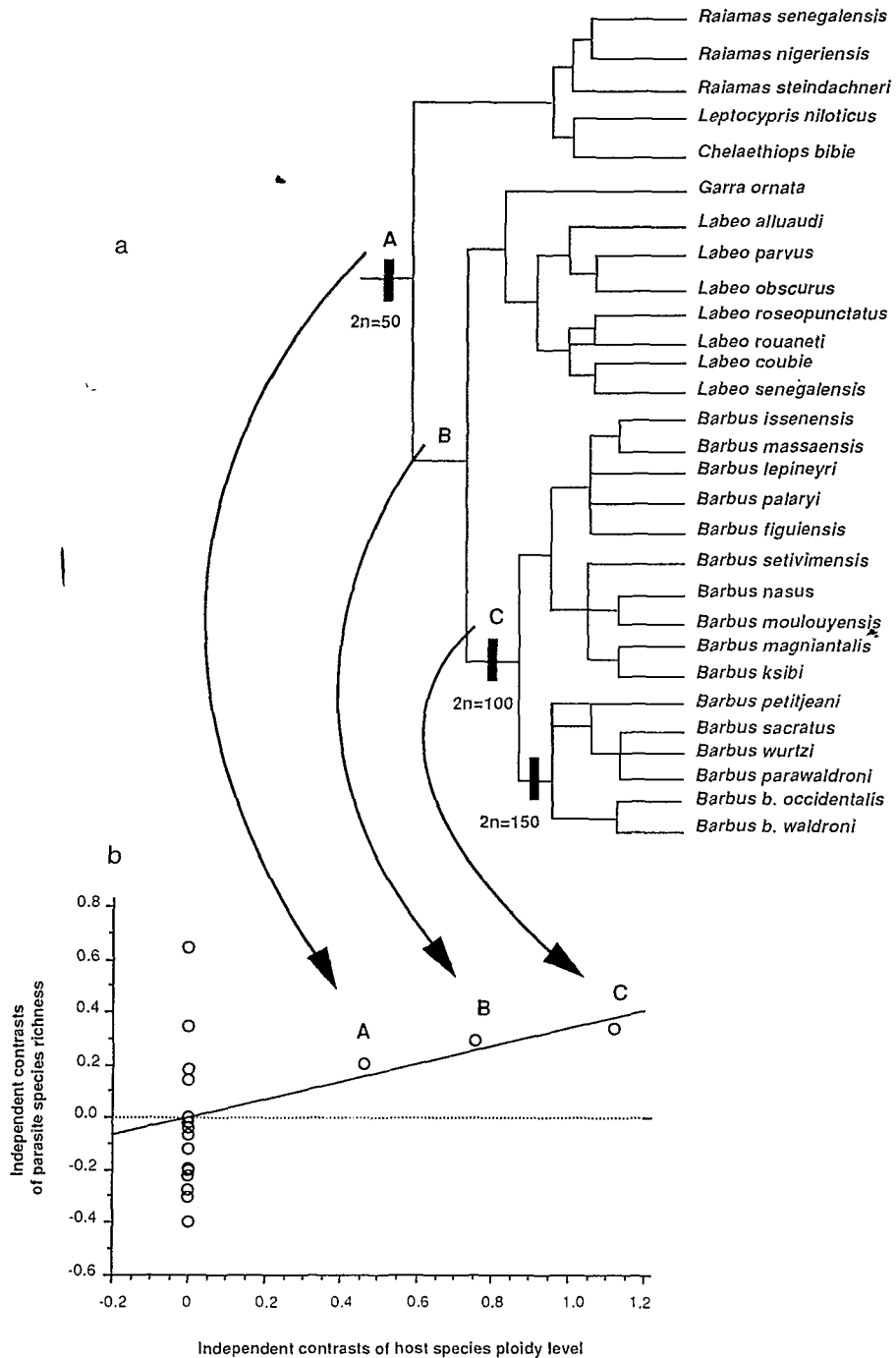


Fig. 1. (a) Phylogenetic tree of 29 African cyprinid fish species and their major chromosomal number transitions ( $2n = 50$ ,  $2n = 100$  and  $2n = 150$ ). Independent contrasts are estimated in calculating the ploidy value difference between pairs of host species within each of the lowest clades of the branching phylogeny, and then again at the next highest nodes of the tree. Letters corresponding to nodes of major ploidy level transitions (A, B and C) represent independent contrasts illustrated in Fig. 1b. Working phylogeny drawn from many sources (Agnès et al. 1990, Guégan 1990, Guégan and Agnès 1991, Doadrio 1994). (b) Parasite species richness contrasts plotted against ploidy level contrasts for cyprinid fish species. The regression analysis (Ordinary Least Square through the origin) of changes in parasite richness on to changes in host ploidy level provided by Comparative Analysis using Independent Contrast is significant ( $Y = 0.34X$ ,  $r = 0.42$ ,  $F = 5.02$ ,  $n = 24$ ,  $p = 0.035$ ). The letters (A, B and C) designate the nodes in Fig. 1a. See Purvis and Rambault (1995) for further details on the method.

tions made above. The third version involves a difference in the manner a tetra(poly)ploidisation event has occurred in fish through hybridisation of two parental species (allopolyploidy) or through formation of multivalents during meiosis (autopolyploidy). However, this seems unlikely to account for these African fish taxa for which the genome was probably multiplied via intracellular divisions of an ancestral diploid origin (Guégan et al. 1995). Of the two final versions, the last one is probably the more seductive. The proliferation of genetic material in polyploid taxa, with the evolution of many efficient specific enzymes from a set of ancestral low-efficiency enzymes found in diploid taxa, could provide more opportunities for host-parasite interactions. Chromosome numbers and other associated host characteristics may have been more often associated with host parasite species diversity in that they could be interpreted in terms of an advantage of a division of labour (Szathmary and Maynard Smith 1995) against multiple parasite species assaults. Polyploidy in hosts, and the subsequent duplication of specific resistance genes, could be an essential part of combating parasite attacks!

In summary, this study, in taking into account the non-independent branching structure of host phylogeny, shows a positive relationship between host species ploidy level and corresponding parasite species richness. An immense amount of work, however, still needs to be done to test this relationship and to understand the exact causal interaction between these two variables. There are three or four areas of research that we think will be the most fruitful in the future when developing studies on polyploid host taxa-parasite associations: plants and their pathogens such as Gramineae and their pests, other aquatic animals such as many molluscs and some fishes and frogs.

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