Parasite evolutionary events inferred from host phylogeny: the case of *Labeo* species (Teleostei, Cyprinidae) and their dactylogyrid parasites (Monogenea, Dactylogyridae)

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Independent phylogenies of West African *Labeo* (Teleostei, Cyprinidae) and their gill parasites of the genus *Dactylogyrus* (Monogenea, Dactylogyridae) are proposed. The phylogeny of *Labeo* is based on allele characters, whereas the phylogeny of the parasites is based on morphometric features. The comparison of host and parasite phylogenies did not correlate completely with predictions made by using Fahrenholz's rule. Parasites encountered on *L. coubie* and *L. senegalensis* seem to have evolved in parallel with their host, or by sequential colonizations between these two related hosts. Whatever the host–parasite evolutionary events between *L. coubie* and *L. senegalensis* and their specific dactylogyrids, two hypotheses of host switching on *L. parvus* and *L. roseopunctatus* are probable, reflecting a close ecological relationship between the various host taxa. *Dactylogyrus brevicirrus* and *D. nathaliae*, found on the gills of *L. parvus* and *L. roseopunctatus*, respectively, are each the sister-species of a living parasite on *L. coubie*. The notions of parallel evolution (or coevolution in a broader sense) and host switching with speciation are discussed. Finally, Fahrenholz's rule is analyzed as a forecasting tool that can be used in systematics.

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Deux phylogénies élaborées de manière indépendante, l'une concernant des poissons, l'autre leurs ectoparasites branchiaux, sont proposées. La première phylogénie réalisée à partir de caractères alléliques intéresse des poissons africains du genre *Labeo* (Teleostei, Cyprinidae). La seconde, établie sur la base de caractères morpho-anatomiques, illustre les relations des Monogènes du genre *Dactylogyrus* (Monogenea, Dactylogyridae) spécifiques de leur taxon-hôte. La comparaison des phylogénies hôtes et parasites ne semble pas totalement répondre aux prédictions faites en fonction de la règle de Fahrenholz. Les parasites rencontrés chez *L. coubie* et chez *L. senegalensis* semblent résulter à la fois d'un processus d'évolution parallèle hôte–parasite ainsi que de multiples séquences de colonisations entre ces deux espèces hôtes parentes. Cependant, quel que soit le type de relation retenu entre *L. coubie* – *L. senegalensis* et leurs parasites spécifiques. *Dactylogyrus brevicirrus*, parasite spécifique de *L. parvus*, et *D. nathaliae*, parasite spécifique de *L. roseopunctatus*, résultent d'un phénomène de capture parasitaire et de spéciation sur un nouvel hôte. *Dactylogyrus brevicirrus* et *D. nathaliae* forment chacun l'espèce-soeur de parasites vivant chez *L. coubie*. Ces possibilités de capture reflètent une association écologique étroite entre les divers taxons hôtes. Les notions d'évolution parallèle (ou co-évolution dans un sens plus large) et de transfert d'hôte avec spéciation sont discutées. Enfin, la règle de Fahrenholz est analysée en tant qu'outil prédictif pouvant servir à la systématique.

Introduction

A feature of parasites is that they live in a biotope formed by a living organism, their host. The biology and evolution of parasites are thus connected to a greater or lesser extent with those of the host. Euzet and Combes (1980) defined three types of specificity: strict or oioxenic when a parasite species can only live in a single host species, close or stenoxenic when a species parasitizes different, phylogenetically related species, and broad or euryxenic when the parasite is found in numerous hosts whose similarity is more ecological than phylogenetic.

Parasite dependence on a particular host has led a number of parasitologists to postulate the existence of coevolution between parasites and their hosts. The term coevolution was created by Ehrlich and Raven (1964) in the context of relationships between phytophagous insects and the specific plant that forms their food. Janzen (1980) gave a more precise definition of coevolution in which a character of species A evolves in response to the action of a character of species B which itself evolved in response to the action of a character of species A. In

other words, and in a more general manner, each of the pair must continuously adapt to avoid being eliminated (Van Valen 1973).

In the case of oioxenic parasites, coevolution leads to hypothesizing perfect agreement between host and parasite phylogenies. This is known in parasitology as Fahrenholz's rule: *parasite phylogeny mirrors host phylogeny*. Numerous examples have been proposed to illustrate this (Eichler 1940; Brooks 1979, 1988; Mitter and Brooks 1983; Timm 1983; Beveridge 1986; Hafner and Nadler 1988). Lyal (1986) criticized the use of this rule and questioned its value in explaining all the relationships in host–parasite assemblages. Thus, the contradictory examples accepted in the literature are mostly cases of host switching to phylogenetically distant hosts. Hoberg (1986) proposed that the most parsimonious explanation of the distribution of eight species of *Alcataenia* (Cyclophyllidea, Dilepididae) in the bird family Alcidae was host switching between the parasites. Renaud (1988) conceived the possibility of switching and then isolation of a new population of *Bothriocephalus* (Cestoda, Pseudophyllidea) specific to *Ciliata mustella* (Teleostei, Gadidae) in the Atlantic Ocean.

To gain a better understanding of evolutionary relationships between host and parasite, we used two independent methods to

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TABLE 1. Host specificity of *Dactylogyrus* parasitizing four sympatric species of *Labeo* in West Africa (after Guégan *et al.* 1988)

Host	Labeo parvus	Labeo roseopuncatus	Labeo coubie	Labeo senegalensis
D. digitalis			x	
D. decaspirus			x	
D. oligospirophallus			x	
D. retroversus			x	
D. titus			x	
D. falcilocus			x	
D. jaculus			x	
D. cyclocirrus				x
D. senegalensis				x
D. labeous				x
D. rastellus				x
D. tubarius				x
D. nathaliae		x		
D. brevicirrus	x			

study gill monogeneans and their fish hosts (polymorphism of enzymatic proteins in fish, morphometric characters in parasites). Monogeneans with a direct life cycle, i.e., one that takes place in a single host, frequently display strict host specificity. They are usually good biological markers of host species (Euzet *et al.* 1988; Paugy *et al.* 1990). These specific ectoparasites are thus of value as sources of information on the taxonomic level of the host to which they are closely adapted.

In this paper we show the phylogenetic relationships between 14 species of *Dactylogyrus* (Monogenea, Dactylogyridae) and their 5 host species of the genus *Labeo* (Teleostei, Cyprinidae). Agreements and disagreements between the phylogenies of the hosts and their parasites are examined. The use of Fahrenholz's rule is evaluated with regard to showing evolutionary relationships between hosts and parasites. Finally, the idea of coevolution of fish ectoparasites is discussed.

Materials and methods

Hosts and parasites

Five species of *Labeo* and their *Dactylogyrus* parasites were studied in West Africa. The species and numbers of fish studied were as follows: *L. coubie* Rüppell, 1832, 16 specimens from Niger River; *L. senegalensis* Valenciennes, 1842, 10 and 7 specimens from the Baoulé and Niger rivers, respectively; *L. parvus* Boulenger, 1902, 10 and 5 specimens from the Niger and Cavally rivers, respectively; *L. roseopunctatus* (Paugy *et al.* 1990), 14 specimens from the Baoulé River; *L. alluaudi* Pellerin, 1933, 4 specimens from the Nipoué (Cess) River. The first four Cyprinidae, the only ones known in the large Sahel and Sudan basins in West Africa (Paugy *et al.* 1990), were collected in an area of sympatric species in the Baoulé River at Missira (Senegal basin) and in the Niger River at Bamako, Mali. *Labeo alluaudi* has been found in two West African coastal basins, the Cavally and the Nipoué (Liberia and Ivory Coast), where it is endemic.

The parasites were described or redescribed in earlier work (Guégan *et al.* 1988). These monogeneans are characterized by oioxenic specificity and were distributed as follows: seven different species were found only in *L. coubie* and five others only in *L. senegalensis*, whereas *L. roseopunctatus* and *L. parvus* both displayed monospecific parasitism (Table 1). No *Dactylogyrus* were found on the gills of *L. alluaudi* populations in the Nipoué and the Cavally.

Genetic study of the fish hosts

Pieces of skeletal muscle were excised from each fish and stored in liquid nitrogen in the field. The extracts were frozen at −30°C in the laboratory.

Starch-gel electrophoresis was conducted on crushed muscle protein

by means of the techniques described by Pasteur *et al.* (1987). Two buffer systems were used for the gels: (*i*) TC 6.7 was used to separate aspartate transaminase (Aat; EC 2.6.1.2), adenylate kinase (Ak; EC 2.7.4.3), lactate dehydrogenase (Ldh; EC 1.1.1.27), malate dehydrogenase (Mdh; EC 1.1.1.37), phosphogluconate dehydrogenase (Pgd; EC 1.1.1.44) and nonspecific protein (Pt); (*ii*) TM 6.9 was used to analyze esterase (ES; EC 4.2.1.11), glyoxalase (Glo; EC 2.6.1.1), and malic enzyme (Me; EC 1.1.1.40).

Morphometric study of monogeneans

Phylogenies of the parasites were reconstructed using morphometric data from their descriptions or redescriptions (Guégan *et al.* 1988). The original descriptions by Paperna (1969, 1973, 1979) were expanded for species that had already been reported. The procedure was inspired by the work of Klassen and Beverley-Burton (1987, 1988) on monogeneans in North American fish.

Seven morphometric characters consisting of 22 character states were selected for the study.

Character 1: shape of haptor. Distinctions were made between three character states: 1:1, width of haptor equal to body width; 1:2, haptor broader than body, swollen and disk- shaped; 1:3, haptor broader than body and formed by lateral digitations.

Character 2: shape of hamuli. Two character states: 2:1, hamuli with long thin shaft, strongly developed inner root in comparison with the outer root; 2:2, sort thick hamuli with a short inner root.

Character 3: shape and hooklet arrangement. Two character states: 3:1, hooklets all the same size; 3:2, hooklets I and II more developed than the short lateral hooklets.

Character 4: number of transverse bars. Two character states: 4:1, two transverse bars, one dorsal and the other ventral; 4:2, single dorsal transverse bar.

Character 5: shape of vagina. Four character states: 5:1, nonsclerotized vagina; 5:2, vagina sclerotized only at vaginal pore; 5:3, sclerotized vagina forming a straight, very short tube; 5:4, sclerotized tubular vagina, long and curved.

Character 6: shape of penis. Five character states: 6:1, hollow, very broad tube; 6:2, rigid narrow tube; 6:3, curved, very fine tube from insertion in the basal ampulla; 6:4, fine, more or less curved fine tube; 6:5, spiral tube, very fine from base onwards.

Character 7: shape of accessory piece. Five character states: 7:1, nonsclerotized; 7:2, slightly sclerotized, forming a loose sheath directly attached to the basal ampulla; 7:3, bifid, sclerotized, and stem connected to the basal ampulla; 7:4, in the shape of a narrow gutter, stem connected to the basal ampulla.

Methods of phylogenetic analysis

Two independent hypotheses concerning the evolutionary relationships of hosts with their parasites were constructed using Hennigian argumentation (Hennig 1966; Wiley 1981; Felsenstein 1983) and tested with PENNY (PHYLIP inference package by J. Felsenstein, Washington University, Seattle), a branch and bound algorithm. With regard to the study of monogeneans, the evolutionary trend of the different character states was determined using the outgroup method (Watrous and Wheeler 1981). The outgroup selected for our analysis was a species of *Dactylogyrus*, *D. archaeopenis* (Guégan and Lambert 1990), parasitizing three West Africa cyprinids of the genus *Barbus*: *B. sacratus*, *B. petitjeani* and *B. parawaldroni* (Guégan and Lambert 1990a).

Results

The fish hosts

No significant different in allele frequencies was found between samples of *L. senegalensis* (Niger and Baoulé rivers) and *L. parvus* (Niger and Cavally rivers) from the different basins. Consequently, all individuals of the same species were grouped in this analysis. The allele frequencies observed are shown in Table 2. Frequencies of genotypes with polymorphic loci did not diverge significantly from the frequencies forecast by Hardy–Weinberg's law.

Host phylogeny was obtained from a matrix of presence

TABLE 2. Allele frequencies observed at 13 loci for five species of *Labeo* from West Africa

Locus	Allele	Labeo senegalensis	Labeo coubie	Labeo roseopuncatus	Labeo parvus	Labeo alluaudi
Aat	80					0.25
	90				0.79	0.25
	100				0.21	0.50
	110			1.00		
	120	1.00	1.00			
Ak	100			1.00	1.00	
	110	1.00	1.00			1.00
Es	100	1.00	1.00	1.00	1.00	1.00
Glo	80				1.00	1.00
	100	1.00	0.50			
	120		0.50	1.00		
Ldh-1	100	1.00	1.00	1.00	1.00	1.00
Ldh-2	50				1.00	1.00
	100	1.00	0.88	1.00		
	105		0.12			
Mdh-1	100	1.00	1.00	1.00	1.00	1.00
Mdh-2	100	1.00	1.00	1.00	1.00	
	101					1.00
Me	90	1.00			1.00	
	100		1.00	1.00		1.00
6-Pgd	90					1.00
	95	1.00	1.00	0.50		
	100			0.50	0.75	
	105				0.25	
Pt-1	80			1.00	1.00	
	90					1.00
	100		1.00			
	110	1.00				
Pt-2	100	1.00	1.00	1.00	1.00	1.00
Sod	90	·		1.00		
	100				1.00	
	110	1.00	1.00			1.00

absence of alleles processed by PENNY to find all most parsimonious trees. This algorithm offers the greatest assurance of finding the shortest trees (Hendy and Penny 1982); it is the most effective because it is consistent with the parsimony criterion for minimizing the number of character state changes during analysis. In the absence of an outgroup, it is not possible to find the root of this network. Nevertheless, it was observed that the nonhomoplaseous characters (characters that are present only once in the network) were almost always appearances of alleles (except for *Mdh-2* 100). Indeed, it is less probable that two species acquired two alleles independently than that they lost the same allele independently (Bonhomme *et al*. 1984). Thus, the common possession of one allele gives more information than the common absence of an allele in two taxa. As a result, the hypothetical root must lie at a place in the network where disappearance events are minimized. This hypothetical root determines two monophyletic groups: the *L. alluaudi* – *L. parvus* group and the *L. roseopunctatus* – *L. coubie* – *L. senegalensis* group (Fig. 1). The resulting most parsimonious tree requires a total of 36 steps (CI = 0, 78). Our data are well supported by ichthyologists' conceptions of the affinities of African *Labeo*. Morphological and biometrical data on fishes support the idea that we are dealing with two host groups; *L.*

coubie and *L. senegalensis* form one monophyletic group and *L. parvus* and *L. alluaudi* another in West Africa (Reid 1985). In our study, the new species *L. roseopunctatus* shares a common ancestor with the *L. coubie* – *L. senegalensis* group that it does not share with the *L. parvus* – *L. alluaudi* group.

The parasites
The different character states (Table 3) were arranged one by one on the basis of their degree of similarity (Ax 1987) and polarized in comparison with a functional outgroup. Each sequence is a reflection of successive stages of evolution of the characters, and the series of characters becomes a series of transformations, or morphocline (Maslin 1952). Each transformation series (Fig. 2) was then coded using the additive binary coding system developed by Farris (1970). The method consists of replacing one transformation series by several binary characters which conserve all the initial data (Table 4). The coded characters are sometimes also referred to as binary factors.

The cladogram depicting phylogenetic relationships of monogeneans was obtained using the same algorithm, PENNY. Owing to the presence of unique states (autapomorphies) and redundant taxa, multiple solutions (or cladograms) with small
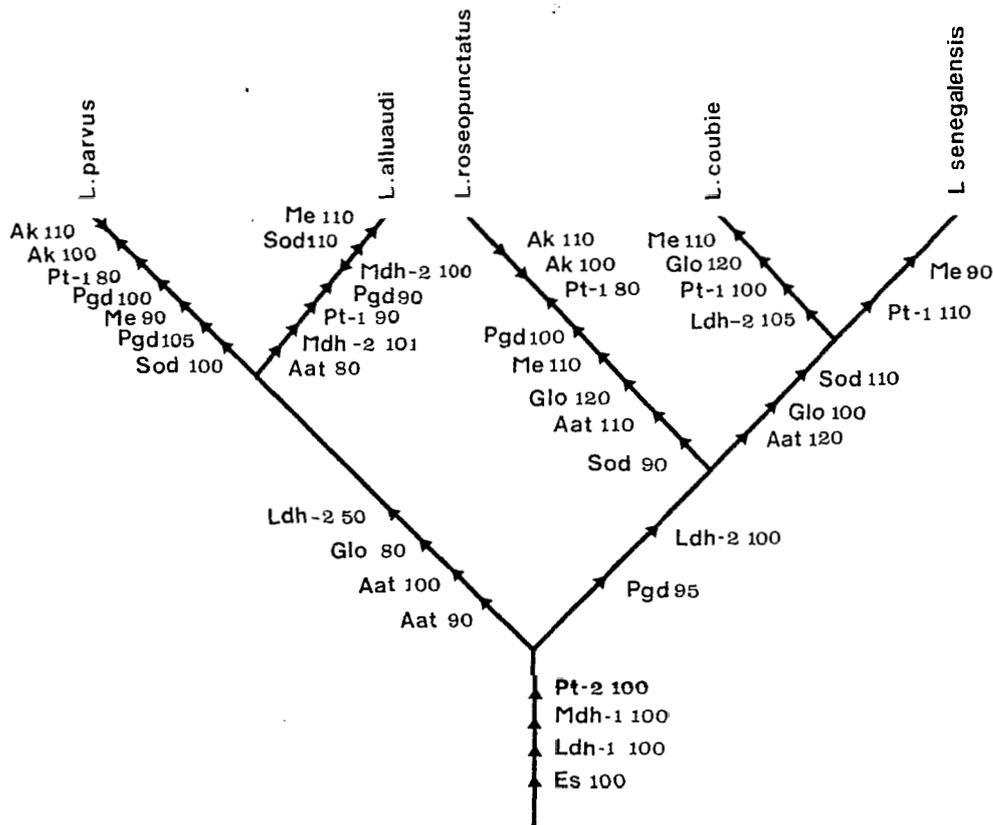
FIG. 1. Cladogram illustrating the relationships between five species of *Labeo* from West Africa. The network was constructed using the program PENNY (PHYLIP package), using an allele presence/absence matrix. The hypothetical ancestor was positioned in such a way as to minimize the disappearance of alleles.

structural differences (zero branch lengths) were obtained. Polytomies obtained by means of the absence of real apomorphies resulting from the coding matrix were resolved using the morphological affinities of the copulatory apparatus in each polytomy. These are discussed in detail in the descriptions of the individual monophyletic groups. Parasite relationships are well supported by our previous observations (Guégan *et al.* 1988). This cladogram requires a total of 15 coding steps (CI = 1, 00). The outgroup that enabled us to define the root of our network was the only one to possess the character state 4:1. The 14 other *Dactylogyrus* species forming the ingroup shared character state 4:2, and are distributed in different monophyletic groups as follows:

Group I: *D. digitalis*, *D. nathaliae*, *D. cyclocirrus*
Group II: *D. tubarius*, *D. titus*, *D. retroversus*, *D. rastellus*
Group III: *D. labeous*, *D. brevicirrus*, *D. jaculus*, *D. falcilocus*
Group IV: *D. oligospirophallus*, *D. decaspirus*, *D. senegalensis*

Monophyletic group I is characterized by character states 1:2, 2:2, and 3:2. In this group, *D. digitalis* and *D. nathaliae* have a common ancestor that they do not share with *D. cyclocirrus*.

Monophyletic group II–III–IV is defined by character states 6:2 and 7:3. Subgroup II is characterized by internal apomorphic modalities: 7:3:1, bifid accessory piece with two equal branches; 7:3:2, bifid accessory piece with two equal, well-developed branches which are not as long as the stem; 7:3:3, bifid accessory piece with two equal, well-developed branches which are as long as the stem.

The monophyletic group III–IV is characterized by character states 5:2 and 6:3. Subgroup III is defined by internal apomor-

TABLE 3. Distribution of character states (present/absent) for 14 species of *Dactylogyrus* on *Labeo* from West Africa; the outgroup was defined from a systematic study of Dactylogyridae on Cyprinidae, genus *Barbus* (see text)

Character:	1	2	3	4	5	6	7
Character state:	123	12	12	1	1234	12345	1234
Outgroup	100	10	10	0	1000	10000	1000
D. senegalensis	100	10	10	1	0001	00001	0001
D. cyclocirrus	010	01	01	1	1000	10000	1000
D. labeous	100	10	10	1	0100	00010	0010
D. rastellus	100	10	10	1	1000	01000	0010
D. tubarius	100	10	10	1	1000	01000	0010
D. digitalis	001	01	01	1	1000	10000	0100
D. decaspirus	100	10	10	1	0001	00001	0001
D. jaculus	100	10	10	1	0100	00100	0010
D. retroversus	100	10	10	1	1000	01000	0010
D. falcilocus	100	10	10	1	0010	00100	0010
D. oligospirophallus	100	10	10	1	0001	00001	0001
D. titus	100	10	10	1	1000	01000	0010
D. nathaliae	010	01	01	1	1000	10000	0100
D. brevicirrus	100	10	10	1	0100	00100	0010

phic modalities: 7:3:4, bifid accessory piece with two unequal branches, one of them well-developed, the other reduced; 7:3:5, bifid accessory piece with two unequal branches, one well developed and turned round the stem; 7:3:6, trifid accessory piece with unequal branches, two well developed, the other reduced.
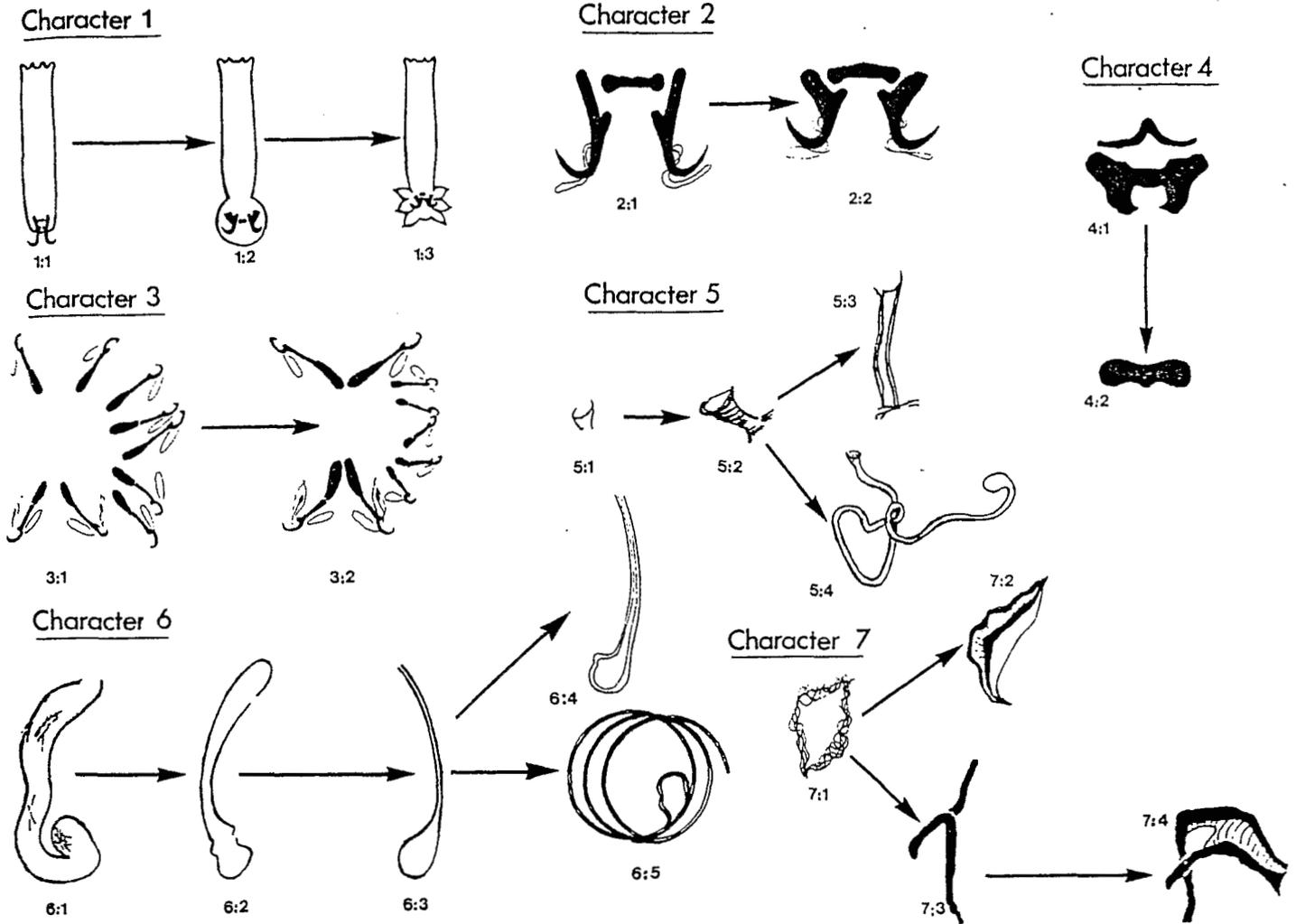
FIG. 2. Stylized representation of 7 characters and 22 character states used to reconstruct the phylogeny of 14 species of *Dactylogyrus* parasitizing five species of *Labeo* from West Africa. The numbers below each diagram denote character states. Arrows indicate the direction of transformation for each series. Character 1 is haptor shape; character 2 is shape of the hamuli; character 3 is arrangement of the hooklets; character 4 is number of transverse bars; character 5 is vagina shape; character 6 is penis shape; character 7 is shape of the accessory piece.

Finally, subgroup IV can be distinguished by the appearance of character states 5:4, 6:5, and 7:4. The internal apomorphic modality is 6:5:1, a spiral penis with more than four turns (Fig. 3).

Discussion

The preferential presence of parasite forms on *L. coubie* and *L. senegalensis* displays the close phylogenetic affinities between these two cyprinids. *Labeo roseopunctatus* and *L. parvus* are both characterized by monospecific parasitism. *Labeo alluaudi* does not possess *Dactylogyrus* in the Cavally and Nipoué rivers.

Labeo coubie and *L. senegalensis* possess at least one species of parasite belonging to the four groups and subgroups of monogeneans revealed by phylogenetic analysis (I, II, III, and IV). Since the phylogeny of the hosts is known, a hypothesis can be put forward to account for the current distribution of parasite species on *L. coubie* and *L. senegalensis*.

Four ancestral species of *Dactylogyrus* parasitized the common ancestor of *L. coubie* and *L. senegalensis*. Two populations of each ancestral species of *Dactylogyrus* were isolated

TABLE 4. Coding of character states for 14 species of *Dactylogyrus* forming the ingroup according to the method proposed by Farris (1970); the outgroup was established from a systematic study of Dactylogyridae on cyprinids belonging to the genus *Barbus*

| Character:	1	2	3	4	5	6	7
Outgroup	00	0	0	0	000	0000	000
D. senegalensis	00	0	0	1	101	1101	011
D. cyclocirrus	10	1	1	1	000	0000	000
D. labeous	00	0	0	1	100	1110	010
D. rastellus	00	0	0	1	000	1000	010
D. tubarius	00	0	0	1	000	1000	010
D. digitalis	11	1	1	1	000	0000	100
D. decaspirus	00	0	0	1	101	1101	011
D. jaculus	00	0	0	1	100	1100	010
D. retroversus	00	0	0	1_	000	1000	010
D. falcilocus	00	0	0	1	110	1100	010
D. oligospirophallus	00	0	0	1	101	1101	011
D. titus	00	0	0	1	000	1000	010
D. nathaliae	10	1	1	1	000	0000	100
D. brevicirrus	00	0	0	1	100	1100	010

PARASITE GROUP HOST
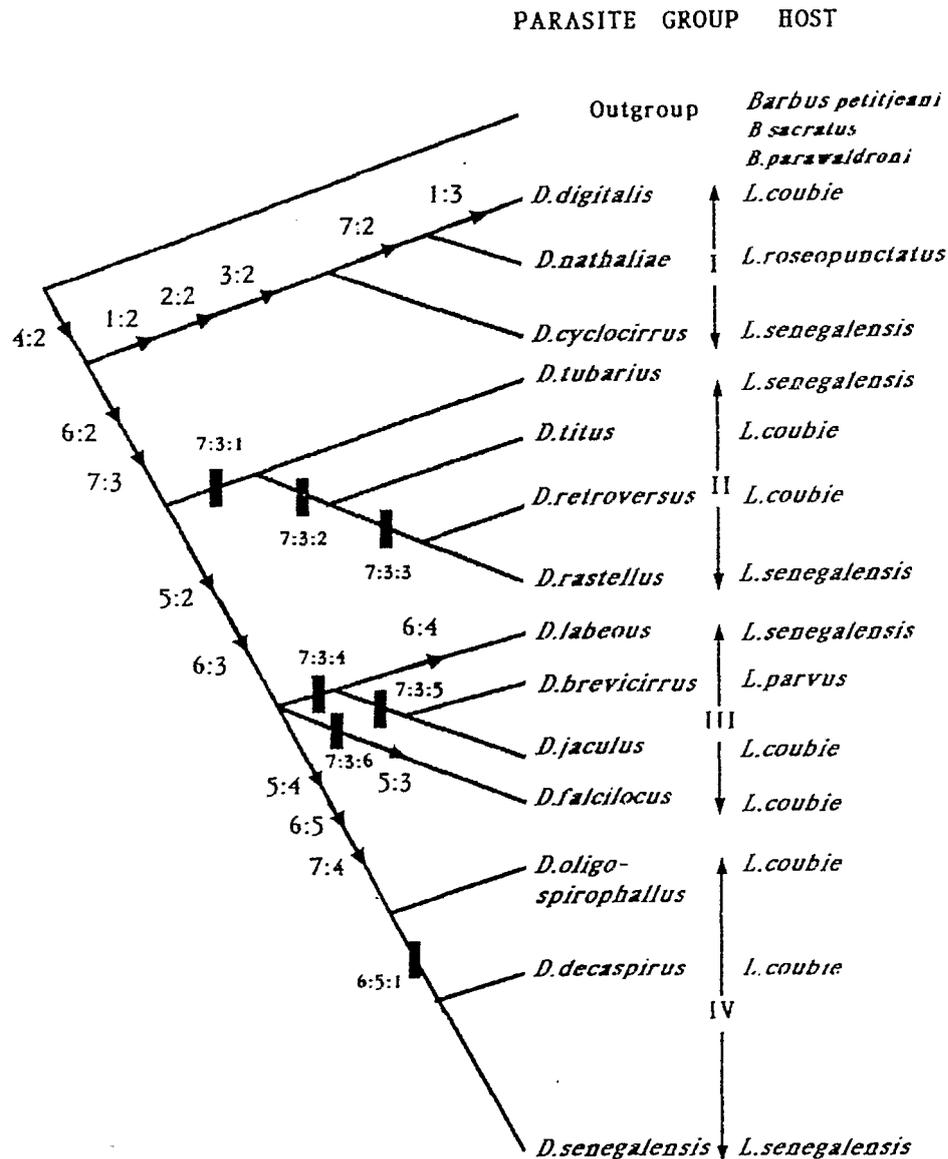
FIG. 3. Cladogram illustrating the relationships between 14 species of *Dactylogyrus* on West African *Labeo*. The code at each step represents the character and then the character state used in data processing. In each monophyletic group, black rectangles represent steps added by hand in accordance with the concept put forward by the authors. Roman numerals denote the groups of parasites determined by analysis. Each host species is opposite its parasite(s).

during speciation of the hosts. Each of these parasite populations also evolved independently until it achieved species status (Fig. 4). The diversity of *Dactylogyrus* doubled at first because of this parallel speciation, still referred to as phylogenetic speciation (Euzet and Combes 1980). Thus, certain *Dactylogyrus* found on *L. coubie* correspond to a similar species on *L. senegalensis*, as follows; group I, *D. cyclocirrus* on *L. senegalensis*, *D. digitalis* on *L. coubie*; group II, *D. tubarius* on *L. senegalensis*, *D. titus* on *L. coubie*; group III, *D. labeous* on *L. senegalensis*, *D. jaculus* on *L. coubie*; group IV, *D. senegalensis* on *L. senegalensis*, *D. decaspirus* on *L. coubie*. *Dactylogyrus falcilocus* (group III) found on *L. coubie* does not correspond to a similar species on *L. senegalensis*. This may have disappeared or have never existed (fig. 4). The presence of sister species of *Dactylogyrus* on the same host, i.e., *D. decaspirus – D. oligospirophallus* (group IV) on *L. coubie*, could be explained by hypothesizing that certain parasite populations have speciated into two species on the same host species (synxenic speciation sensu Euzet and Combes 1980).

It should be noted that this parallel speciation of host and parasite taxa, if it could be verified, indicates cospeciation but not necessarily coevolution. In no case is the long evolutionary history of such a system necessarily proof of coevolution, even if it results in topologically congruent phylogenies (Holmes 1983). The term coevolution should be used more restrictively (Janzen 1980; Van Valen 1973) when reciprocal selective pressures have been demonstrated. With regard to monogenean ectoparasites of fish, we accept the more accurate terms dependent evolution or concomitant evolution, i.e., evolution of the parasite population depends on evolution of the host population, and the selective pressure exerted by the parasites, if it exists, is difficult to evaluate.

Another scenario can be proposed concerning parasites that have not cospeciated on *L. coubie* and *L. senegalensis*. Some monogenean species inhabiting *L. coubie* and *L. senegalensis* could be the product of multiple sequential colonizations between sympatric sister-species of hosts, and might not have involved Fahrenholz's rule and cospeciation. This should be the
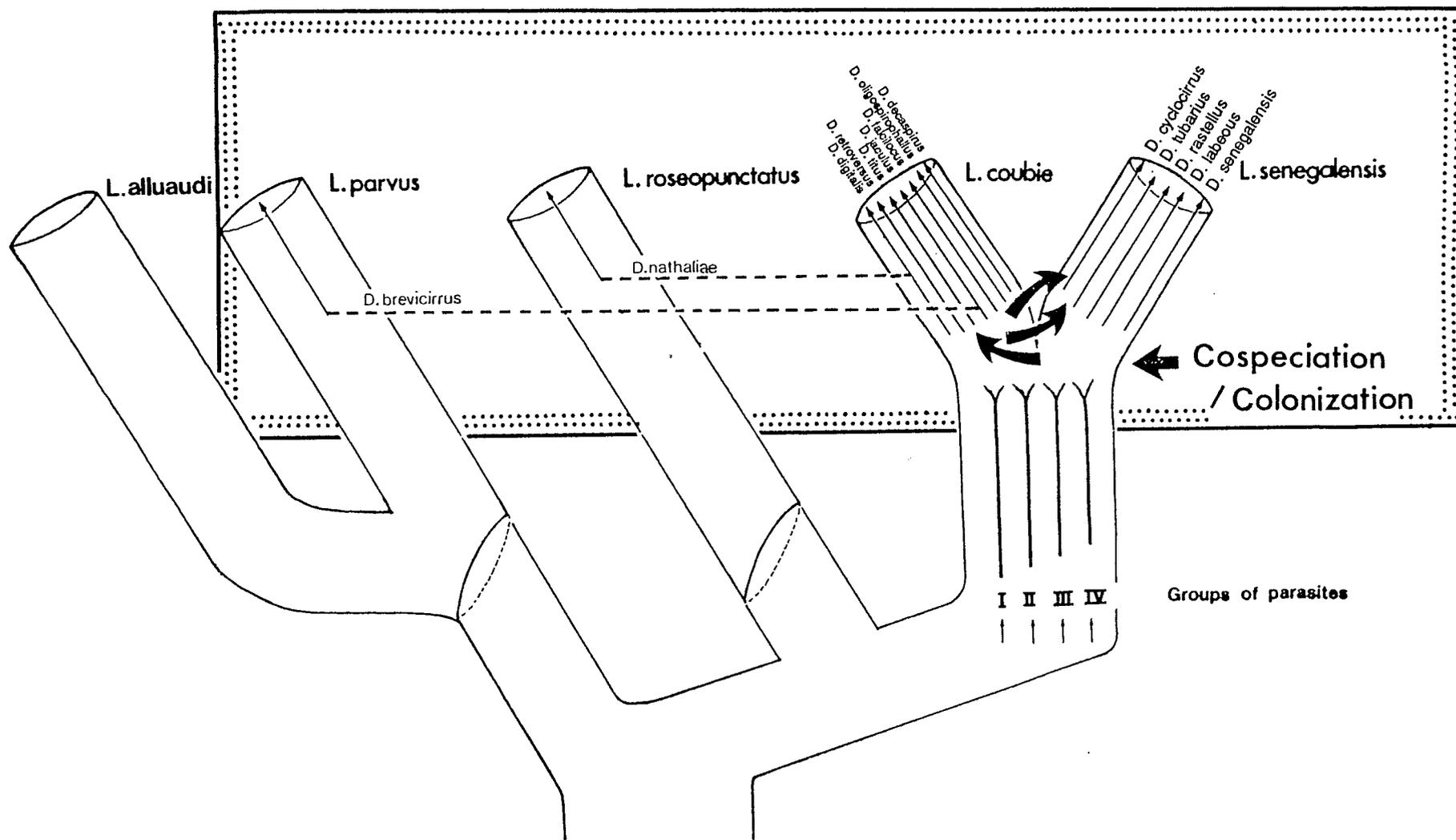
FIG. 4. Diagram showing the phylogenetic relationships between 14 species of *Dactylogyrus* and five hosts (genus *Labeo*) in West Africa. Host taxa are represented by large connected columns. Within the columns, each fine arrow represents a parasite taxon. The large arrows indicate sequential colonizations. Broken lines indicate host switching. The frame symbolizes the conditions that allow host switching in our study.

case for *D. rastellus* on *L. senegalensis* and *D. retroversus* on *L. coubie* (groupe II) which are very close.

The evolution of all parasites found on the gills of *L. coubie* and *L. senegalensis* appears to be the result of a variety of coevolutionary / sequential colonization phenomena between those two related hosts.

In this study, the parasite reflected close affinities between *L. coubie* and *L. senegalensis* (Fig. 4). Nevertheless, the phylogenetic relationships between the 14 *Dactylogyrus* studied were not a perfect reproduction of the relationships between the hosts. Whatever the host–parasite relationships between *L. coubie* – *L. senegalensis* and their parasites (cospeciation and (or) colonization), the monogeneans of *L. roseopunctatus* and *L. parvus* are phylogenetically close (sister-species) to some parasites of *L. coubie* (Fig. 3).

Two hypotheses may account for the partial disagreement between the phylogeny of the parasites and that of their hosts: (*i*) parallelism between the different evolutionary lines of the parasites; (*ii*) host switching.

The possibility of two instances of parallelism (hypothesis 1) between *D. brevicirrus* on *L. parvus* and all the monogeneans of *L. coubie* and *L. senegalensis* on the one hand, and *D. nathaliae* on *L. roseopunctatus* and all the monogeneans of *L. coubie* and *L. senegalensis* on the other, is eliminated by the absence of homoplasy, which leads to the supposition that parallelism was rare in this study.

The second hypothesis, involving switching from one host species to another, most likely accounts for the observations. The monospecific parasitism observed in *L. parvus* and *L. roseopunctatus* may result from switching of parasites present on *L. coubie*: *D. brevicirrus* (specific to *L. parvus*) and *D. jaculus* (specific to *L. coubie*) may have a common ancestor; *D. nathaliae* (specific to *L. roseopunctatus*) and *D. digitalis* (specific to *L. coubie*) may likewise have a common origin in a parasite on *L. coubie* (Fig. 4). This hypothesis of host switching is partially supported by biogeographical data. *Dactylogyrus brevicirrus* parasitizes *L. parvus* populations in the Sahel and Sudan basins where we find *L. coubie* (Guégan et al. 1988). However, this monogenean species does not parasitize *L. parvus* populations in short West African coastal rivers in Guinea, Sierra Leone, and Liberia (Guégan and Lambert 1990*b*), where *L. coubie* is not present (Lévêque and Daget 1984). In West Africa, coastal rivers form an isolated hydrographical system (Grove 1985). Fish and their parasite communities are relicts and have not been affected by the extinction – host switching processes (Guégan and Lambert 1990*b*).

Colonization of a new host appears to be frequent in numerous parasites with both a heteroxenous (indirect; e.g., Cestoda, Trematoda) or holoxenous (direct; e.g., Monogenea) life cycle. Klassen and Beverley-Burton (1987) suggested that the ancyrocephalid monogeneans of the genus *Ligictaluridus* may have resulted from transfer from a fish of the family Centrarchidae to one of the Ictaluridae in North America. Lyal (1986) put forward the host-switching hypothesis for lice (Phthiraptera) on birds. Change to a new host and then speciation ("capture" sensu Chabaud 1965; "host switching" according to Mitter and Brooks 1983) constitute nonphylogenetic evolution or evolution that is horizontal in time (Llewellyn and Tully 1969; Quentin 1971; Mayr 1978; Euzet and Combes 1980; Renaud et al. 1984).

A number of studies have shown perfect agreement between the phylogenetic relationships of hosts and their parasites (Mitter and Brooks 1983; Hafner and Nadler 1988). The present work shows that the phylogenies of *Dactylogyrus* species and their

Labeo hosts do not obey Fahrenholz's rule perfectly. The disagreement between the two phylogenies is apparently mainly the result of colonization and host switching. In the present case, this disagreement was all the more marked because the only *Dactylogyrus* species occurring on *L. parvus* and *L. roseopunctatus* should have resulted from host switching.

The ancestral taxa of the two cyprinid species mentioned above may have lost their parasite faunas as they evolved, at least in the zone studied. Zeddam et al. (1988) put forward the same hypothesis for the distribution of ectoparasite copepods of flatfish. They reported the presence of an individual population of *Lepeophtheirus europaensis* (Copepoda, Caligidae) on the flounder *Platichthys flesus* (Teleostei, Pleuronectidae) in the Mediterranean, whereas this parasite is generally specific to the brill, *Scophthalmus rhombus* (Teleostei, Scophthalmidae), along the coastline of Europe. These authors proposed that *L. pectoralis* specific to the flounder in the Atlantic disappeared when the host populations entered the Mediterranean. The capture of a copepod and then the beginning of speciation were probably due to a combination of two factors: the absence of parasites in the flounder and contact with other parasitized flatfish. Extinction of the parasites also conflicts with Fahrenholz's rule (Lyal 1986).

It is considered that monogenean host switching is all the more probable because a parasite-free species of fish was in contact with one or more parasitized, phylogenetically close species (Kuris et al. 1980; Klassen and Beverley-Burton 1987). The absence of monogeneans on *L. alluaudi* populations in the Nipoué and Cavally might be accounted for by the lack of contact between this host species, which lives in small rapids, and other cyprinids likely to "spread" their parasites.

Conclusion

The respective proportions of phylogenetic evolution (Fahrenholz's rule) and nonphylogenetic evolution (colonization, host switching) are always difficult to evaluate in a complex of parasite species. In the present example both types of evolution were apparently displayed: evolution by descent and sequential colonizations (*L. coubie* – *L. senegalensis* and their monogeneans) and evolution by host switching (*L. parvus* and *L. roseopunctatus* and their monogeneans). Biogeographical data provide a phylogenetic argument to support host switching.

Ax, P. 1987. The phylogenetic system: the systematization of organisms on the basis of their phylogenesis. J. Wiley & Sons, Chichester, New York, Brisbane, Toronto, Singapore.

BEVERIDGE, I. 1986. Coevolutionary relationships of the helminth parasites of Australian marsupials. *In* Coevolution and systematics. *Edited by* A. R. Stone, and D. L. Hawksworth. Clarendon Press, Oxford. pp. 93–116.

BONHOMME, F., CATALAN, J., BRITTON-DAVIDIAN, J., CHAPMAN, V. M., MORIWAKI, D., NEVO, E., and THALER, L. 1984. Biochemical diversity and evolution in the genus *Mus*. Biochem. Genet. **22**: 275–303.

BROOKS, D. R. 1979. Testing hypothesis of evolutionary relationships among parasites: the digeneans of crocodiles. Am. Zool. **19**: 1225–1238.

——— 1988. Macroevolutionary comparisons of host and parasite phylogenies. Annu. Rev. Ecol. Syst. **19**: 235–259.

CHABAUD, A. G. 1965. Particularités physiologiques des Nématodes : spécificité parasitaire. Traité Zool. **4**: 548–557.

EHRLICH, P. R., and RAVEN, P. H. 1964. Butterflies and plants: a study in coevolution. Evolution, **18**: 586–608.

EICHLER, W. 1940. Wirtsspezifität und stammesgeschichtliche Gleichläufigkeit (Fahrenholzsche Regel) bei Parasiten im allgemeinen und bei Mallophagen im besonderen. Zool. Anz. **132**: 254–262.

EUZET, L., and COMBES, C. 1980. Les problèmes de l'espèce chez les animaux parasites. Mém. Soc. Zool. Fr. **3**: 239–285.

EUZET, L., AGNÈSE, J.-F., and LAMBERT, A. 1988. Valeur des Monogènes parasites comme critère spécifique : démonstration par une double approche parasitologique et génétique des Poissons hôtes. C. R. Acad. Sci. Paris, **308**: 385–388.

FARRIS, J. S. 1970. Methods for computing Wagner trees. Syst. Zool. **19**: 83–92.

FELSENSTEIN, J. 1983. Parsimony in systematics: biological and statistical issues. Annu. Rev. Ecol. Syst. **14**: 313–333.

GROVE, A. T. 1985. The physical evolution of the river basins. *In* The Niger and its neighbours: environmental history and hydrobiology, human use and health hazards of the major West African rivers. *Edited by* A. T. Grove. A. A. Balkema Publishers, The Netherlands. pp. 21–61.

GUÉGAN, J.-F., and LAMBERT, A. 1990a. Dactylogyrids (Platyhelminthes, Monogenea) of West African barbels (Teleostei, Cyprinidae) with some biogeographic implications. Syst. Parasitol. **17**: 153–181.

——— 1990b. Dactylogyrids (Platyhelminthes, Monogenea) of *Labeo* (Teleostei, Cyrpinidae) from West African rivers: implications of host isolation on their branchial parasitofauna. J. Helminthol. Soc. Wash. **58**: 85–99.

GUÉGAN, J.-F., LAMBERT, A., and EUZET, L. 1988. Étude des Monogènes de Cyprinidae du genre *Labeo* en Afrique de l'Ouest. I. Genre *Dactylogyrus* Diesing, 1850. Rev. Hydrobiol. Trop. **21**: 135–151.

HAFNER, M. S., and NADLER, S. A. 1988. Phylogenetic trees support the coevolution of parasites and their hosts. Nature (London), **332**: 258–259.

HENDY, M. D., and PENNY, D. 1982. Branch and bound algorithms to determine minimal evolutionary trees. Math. Biosci. **59**: 277–290.

HENNIG, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana.

HOBERG, E. P. 1986. Evolution and historical biogeography of a parasite–host assemblage: *Alcataenia* spp. (Cyclophyllidea, Dilepididae) in Alcidae (Charadriiformes). Can. J. Zool. **64**: 2576–2589.

HOLMES, J. C. 1983. Evolutionary relationships between parasitic helminths and their hosts. *In* Coevolution. *Edited by* D. J. Futuyama, and M. Slatkin. Sinauer Associates Inc., Sunderland. pp. 161–185.

JANZEN, D. H. 1980. When is it coevolution? Evolution, **34**: 611–612.

KLASSEN, G. J., and BEVERLEY-BURTON, M. 1987. Phylogenetic relationships of *Ligictaluridus* spp. (Monogenea, Ancyrocephalidae) and their ictalurid (Siluriformes) hosts: an hypothesis. Proc. Helminthol. Soc. Wash. **54**: 84–90.

——— 1988. North American freshwater ancyrocephalids (Monogenea) with articulating haptoral bars: phylogeny reconstruction. Syst. Parasitol. **11**: 49–57.

KURIS, A. M., BLAUSTEIN, A. R., and ALIO, J. J. 1980. Hosts as islands. Am. Nat. **116**: 570–586.

LÉVÊQUE, C., and DAGET, J. 1984. Cyprinidae. *In* Check-list of the freshwater fishes of Africa. *Edited by* J. Daget, J. P. Gosse, and Th. van den Audenaerde. M.R.A.C.-RSTOM, Paris. pp. 217–341.

LLEWELLYN, J., and TULLY, C. M. 1969. A comparison of speciation in diclidophorinean monogenean gill parasites and in their fish host. J. Fish. Res. Board Can. **26**: 1063–1074.

LYAL, C. H. C. 1986. Coevolutionary relationships of lice and their hosts: a test of Fahrenholz's rule. *In* Coevolution and systematics. *Edited by* A. R. Stone, and D. L. Hawksworth. Clarendon Press, Oxford. pp. 77–91.

MASLIN, T. P. 1952. Morphological criteria of phyletic relationships. Syst. Zool. **1**: 49–70.

MAYR, E. 1978. L'Évolution. Pour la Science, No. 13. pp. 15–24.

MITTER, C., and BROOKS, D. R. 1983. Phylogenetic aspects of coevolution. *In* Coevolution. *Edited by* D. J. Futuyama and M. Slatkin. Sinauer Associates Inc., Sunderland. pp. 65–98.

PAPERNA, I. 1969. Monogenetic trematodes of the fish of the Volta basin and south Ghana. Bull. Inst. Fr. Afr. Noire, **31**: 840–880.

——— 1973. New species of Monogenea (Vermes from African freshwater fish: a preliminary report. Rev. Zool. Bot. Afr. **87**: 505–518.

——— 1979. Monogenea of inland water fish in Africa. Ann. Mus. R. Afr. Cent. Sér. 8 Zool. **226**: 1–131.

PASTEUR, N., PASTEUR, G., BONHOMME, F., CATALAN, J., and BRITTON-DAVIDIAN, J. 1987. Manuel technique de génétique par électrophorèse des protéines. *Edited by* Lavoisier. Techniques et Documentation, Paris.

PAUGY, D., GUÉGAN, J.-F., and AGNÈSE, J.-F. 1990. Three simultaneous and independent approaches to the characterization of a new species of *Labeo* (Teleostei, Cyprinidae) from West Africa. Can. J. Zool. **68**: 1124–1131.

QUENTIN, J. C. 1971. Sur les modalités d'évolution chez quelques lignées d'Helminthes de Rongeurs Muroidea. Cah. ORSTOM Ser. Entomol. Med. Parasitol. **9**: 103–178.

REID, G. M. 1985. A revision of African species of *Labeo* (Pisces, Cyprinidae) and a re-definition of the genus. Thesis Zoologicae. Vol. 6. Verlag J. Cramer, Branschweig.

RENAUD, F. 1988. Biologie et évolution des populations d'Helminthes parasites: le modèle Helminthes–Téléostéens. Thèse d'État, Université des Sciences et Techniques du Languedoc, Montpellier.

RENAUD, F., GABRION, C., and ROMESTAND, B. 184. Le complexe *Bothriocephalus scorpii* (Mueller, 1776). Différenciation des espèces parasites du Turbot (*Psetta maxima*) et de la Barbue (*Scophthalmus rhombus*): étude des fractions protéiques et des complex antigéniques. Ann. Parasitol. Hum. Comp. **59**: 143–149.

TIMM, R. M. 1983. Fahrenholz's rule and resource tracking: a study of host–parasite coevolution. *In* Coevolution. *Edited by* M. H. Nitecki. University of Chicago Press, Chicago. pp. 225–265.

VAN VALEN, L. 1973. A new evolutionary law. Evol. Theory, **1**: 1–30.

WATROUS, L. E., and WHEELER, Q. D. 1981. The out-group comparison method of character analysis. Syst. Zool. **30**: 1–11.

WILEY, E. O. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley and Sons, New York.

ZEDDAM, J. L., BERREBI, P., RENAUD, F., RAIBAUT, A., and GABRION, C. 1988. Characterization of two species of *Lepeophtheirus* (Copepoda, Caligidae) from flatfishes: description of *Lepeophtheirus europaensis* sp. nov. Parasitology, **96**: 129–144.