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THE PHYLOGENY OF THE CERCOMERIA (PLATYHELMINTHES: RHABDOCOELA) AND GENERAL EVOLUTIONARY PRINCIPLES*

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ABSTRACT: The unified theory of evolution is an expansion of Darwinian theory that asserts that evolution is driven by entropic accumulation of genetic information that is constrained and organized primarily by the genealogical effects of phylogenetic history and developmental integration, and secondarily by ecological effects, or natural selection in its classical mode. Phylogenetic systematic analysis of the 8 major groups of parasitic rhabdocoelous platyhelminths permits empirical macroevolutionary evaluation of these postulates. Of the 131 characters considered, 127 are phylogenetically constrained, and 4 show evidence of 1 case of convergence each. Data from different developmental stages are phylogenetic association of definitive hosts and parasites, and by changes in ecological components of life cycle patterns, is more conservative evolutionarily than diversification in developmental patterns, indicated by the appearance of unique larval stages, asexual proliferation of larvae, polyembryony, and heterochronic changes. These observations support the macroevolutionary postulates of the ory.

"The distinction between fundamental plesiomorphic and derived apomorphic characters is basic for any consideration of the phylogeny and systematics of any group—and especially so for a parasitic group" (Horace W. Stunkard, 1983, in litt., archives of the H. W. Manter Laboratory, Division of Parasitology, University of Nebraska State Museum).

Host-parasite systems often are considered to be interesting but unusual examples of evolutionary processes. However, Price (1980) recently argued that parasites could be good model systems for studying general evolutionary principles. A currently contentious general evolutionary principle is the unified theory of evolution (Brooks and Wiley, 1988). In this paper, I will try to show how phylogenetic analysis of a group of parasites can help examine some of the macroevolutionary postulates of the unified theory.

Price (1980) invoked a widespread view of evolution in his studies of parasite evolution when he asserted that the evolutionary "play" took place on a "stage" organized by the environment (an "ecological stage"). Under this view, phylogeny (evolutionary history) is the passive accumulation of the effects of environmental selection over time. The unified theory can be distinguished from this consensus view by expressing its major postulate as environmental se-

lection being the "play" that takes place on a "stage" whose organization is provided by "phylogenetic constraints" and "developmental constraints." Phylogenetic constraints is a synonym for persistent ancestral traits that have not evolved rapidly enough to be affected by environmental selection during any given episode of microevolutionary change. Developmental constraints is a synonym for the necessary integration of any new trait with the rest of the developmental program in order to produce a viable organism that is then potentially acted upon by environmental selection. The unified theory is not non-Darwinian because Darwin viewed evolved diversity as resulting from a combination of phylogenetic, developmental, and environmental effects, although his theories did not result in any particular expectations about the relative contributions of each of those classes of effects to overall evolutionary dynamics. Neo-Darwinian evolutionary theory has concentrated almost exclusively on the role of environmental effects, or natural selection, in evolution. The unified theory might be viewed as an expansion of neo-Darwinian theory to the extent that neo-Darwinism attempts to reduce all biological causality to environmental selection operating at the level of gene frequencies in populations. As a

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result of this narrowing of focus, research traditions that originated prior to the establishment of neo-Darwinism often incorporate less reductionist approaches. As I will show, assessing the macroevolutionary predictions of the unified theory requires a combination of systematic, developmental, and ecological data. "Classical" parasitology, with its emphasis on a combination of systematics, developmental biology, and ecology, is one such tradition. Because the unified theory attempts to integrate a variety of influences operating at different rates, and on different temporal and spatial scales, in evolution, it would seem that parasitologists should be in a strong position to offer empirical evaluations of these new ideas.

According to the unified theory, evolution results from an interaction between genealogical and ecological processes. Salthe (1985) and Eldredge (1985, 1986) have termed these the genealogical hierarchy and the ecological hierarchy. Ecological processes tend to have homeostatic effects, forcing populations into equilibrium conditions. By contrast, the genealogical processes are viewed as having developmental, nonequilibrium, or diversifying effects. The impact of phylogenetic and developmental constraints is to slow the natural entropic accumulation of genealogical diversity, providing an organized but dynamic "stage" upon which the environment can be seen as acting out the "play" of natural selection. Natural selection acts to increase the degree of organization even further. The predominant physical manifestations of the interaction between genealogical and ecological processes differ depending on the time scale chosen for observation (Brooks, 1988; Brooks and Wiley, 1988). For example, on extremely short time scales the primary manifestation is physiological loss, or the dissipation of heat due to metabolic activities. On more intermediate time scales the primary manifestation is in the accumulation and maintenance of biomass, evidenced by ontogenetic, reproductive, and successional phenomena. And on the longest time scales, the primary manifestation is the accumulation of genetic diversity. The longest time scale phenomena are responsible for phylogenetic or macroevolutionary patterns (see also Funk and Brooks, 1989). According to the unified theory, phylogenetic patterns in biology should have predictable properties. These properties occur in the form of particular correlates of phylogenetic diversification with respect to phylogenetic constraints, developmental constraints, and ecological constraints, discussed next.

PHYLOGENETIC CORRELATES OF THE UNIFIED THEORY

Genealogical hierarchy

The unified theory predicts 3 macroevolutionary aspects of genealogical processes. First, the most informative evolutionary summary of data about similarities among organisms will result from the use of analytical methods that maximize the degree of phylogenetic constraints for a given data set. Brooks et al. (1986) demonstrated that phylogenetic systematics (Hennig, 1966) is an analytical method that conforms to this prescription. Further, they presented an information theoretic measure, the D-measure, that allows one to discriminate quantitatively for a given set of data the phylogenetic tree that has the greatest information content about phylogenetic constraints.

Second, application of phylogenetic systematic methods to data derived from relatively independent sources, such as ecological, behavioral, anatomical, and biochemical characters, will result in highly concordant phylogenetic trees. This area of research is known as "congruence studies" in systematics. An excellent example of phylogenetic congruence among different data sets is the study by Hillis and Davis (1986), who demonstrated congruence among immunological, allozyme electromorph, ribosomal DNA sequencing, and morphological data for North American ranid frogs.

Finally, the necessity for developmental integration of all evolutionary innovations means that phylogenetic systematic analysis of data from different portions of the developmental program (such as larvae and adults) will result in highly concordant phylogenetic trees. This will be true even if the larvae and adults have markedly different ecologies and habitats. This has been found to be true for the relatively small number of such studies that have been performed to date (see Brooks and Wiley, 1988: 172).

Ecological hierarchy

If the ecological hierarchy exerts an organizing influence by acting as a homeostatic rather than developmental force on biological systems, the unified theory predicts that the ecological and behavioral (functional) correlates of phylogeny should be conservative relative to the morphological and developmental correlates of phylogeny. Hence, it is expected that most closely related species will be morphologically distinct from but ecologically and behaviorally similar to each other and their common ancestor. In addition, suites of ecological and behavioral traits for taxa should be congruent with the phylogenetic relationships derived from structural data, such as anatomy or macromolecules. This has also been found to be true for studies performed to date (see Brooks and Wiley [1988: 338-340] for examples of phylogenetic constraints and conservatism in ecological traits for free-living taxa; see McLennan et al. [1988] for an example of phylogenetic constraints in behavioral evolution). Among parasitic taxa, a high degree of conservatism and phylogenetic congruence in ecological life history traits has been documented for 2 groups of copepods parasitic on elasmobranchs (Deets, 1987; Deets and Ho, 1988).

Interaction of the hierarchies

The genealogical hierarchy exerts an organizing influence on biological systems through phylogenetic and developmental constraints. However, because increasing diversity and complexity is an entropic phenomenon, evolution will occur despite the various constraints on its expression. That is, the developmental "rules" of the genealogical hierarchy appear to be relatively independent of, and able to supersede, the homeostatic "rules" of the ecological hierarchy. Therefore, ecological and behavioral diversification should lag behind developmental and morphological (including macromolecular) diversification on a phylogenetic scale.

THE CERCOMERIA: A TEST CASE

During the past 5 yr, an extensive phylogenetic database for the cercomerians, a clade containing the major groups of parasitic platyhelminths, has been assembled (Brooks et al., 1985a, 1985b, 1989; Bandoni and Brooks, 1987a, 1987b; Brooks, 1989). It is my intention to show that this database, including additions and modifications to come in the future, can be used to evaluate the macroevolutionary postulates of the unified theory.

Phylogenetic constraints

Brooks et al. (1985a) performed the first phylogenetic systematic analysis of the cercomerians based on 39 anatomical characters that had been used previously by workers in major discussions

of the phylogeny of the group. The resulting phylogenetic tree had a consistency index of 95%, due to 2 postulated cases of convergent evolution. Brooks (1989) presented an updated analysis based on a total of 120 characters. The resulting tree was identical to the one presented by Brooks et al. (1985a) and had a consistency index of 96.8%, due to 4 postulated cases of convergence. That study demonstrated a high degree of phylogenetic congruence between anatomical and ultrastructural data gathered by different research groups. Brooks et al. (1985b) presented a familial-level phylogenetic systematic analysis of the Digenea, based on 158 characters with a consistency index of 73.5% (215 transformations for the 158 characters). Brooks et al. (1989) reexamined the database for the digeneans and their sister group, the aspidobothreans, and added 22 new characters, only 2 of which showed any convergence. This increased the database for the digeneans to 180 characters with a consistency index of 75% (239 transformations for the 180 characters). The topology of the phylogenetic tree presented by Brooks et al. (1985b) was not altered by the additional characters.

The study by Brooks et al. (1989) also allowed reconsideration of traits relating to the phylogenetic relationships among the major groups of cercomerians. For example, Brooks et al. (1985a) and Brooks (1989) assumed that the bifurcate condition of the gut in digeneans and in monogeneans was a convergent trait. However, Brooks et al. (1989) demonstrated that available data supported an interpretation that the bifurcate gut is also plesiomorphic for the aspidobothreans. This being the case, the phylogenetic interpretation is that the bifurcate gut originated in the ancestor that gave rise to the trematodes and the cercomeromorphs, and has been lost in more highly derived groups of aspidobothreans. This actually reduces the number of homoplasious characters postulated by Brooks (1989) from 4 to 3 at the level of the major cercomerian groups (it adds 1 homoplasy to analyses of relationships within the aspidobothreans [see Brooks et al., 1989]). In addition, the presence of elongate uteri with transversely coiled loops appears to be plesiomorphic at the same level. The presence of amphistomous juveniles discussed by Gibson (1987) and Brooks et al. (1989) is plesiomorphic for all cercomerians. The orientation of the posteroventral adhesive disc (the cercomer sensu lato) toward the ventral surface rather than posteriorly is plesiomorphic for the cercomerians, whereas

the strictly ventral orientation and relatively sessile nature of the cercomer is plesiomorphic for the trematodes. Finally, Brooks et al. (1989) presented a familial-level phylogenetic tree for the aspidobothreans. That tree included the following traits postulated to be plesiomorphic for the aspidobothreans as a group: anteriorly fused suckers, hypertrophy and linear subdivision of posterior sucker by transverse septa, and atrophy of the oral sucker. The first 2 characters replace a single character descriptor of the ventral disc of aspidobothreans used previously by Brooks et al. (1985a) and by Brooks (1989).

The current database at this level of phylogenetic resolution comprises 131 characters, 4 of which exhibit 1 instance of homoplasy each, giving a tree length of 135 for the phylogenetic hypothesis (Fig. 1 and following synoptic classification); therefore, the consistency index (CI) for this database is 97.0% (131/135). In addition, data from ultrastructural and light microscopical anatomical sources, and from life cycle studies, support the same relationships whether considered separately or in combination. These findings suggest a high degree of phylogenetic constraint in the data as a whole. If Figure 1 does not represent the phylogenetic relationships among these taxa, we must explain: (1) why the characteristics of these ecologically and developmentally diverse taxa are so well organized, and with respect to what they are organized, and (2) if 97% of the evidence suggests an incorrect pattern, how "correct" evolutionary patterns are discerned in a scientific manner. The unified theory explains such a high degree of organization by suggesting that the pattern shown in Figure 1 represents the phylogenetic relationships of the taxa and that similarities among taxa are due more to the effects of shared ancestry (phylogenetic constraints) than to the effects of individual ecologies.

A synoptic phylogenetic classification of the major groups of parasitic platyhelminths follows, modified from that given by Brooks (1989), with diagnoses based on the additions and changes to the database discussed above. The diagnoses are lists of traits that are hypothesized, on the basis of outgroup comparisons, to have characterized the ancestor of each group. Shared primitive conditions are not listed, except at the base of the tree, where the exact relationships among the members of the paraphyletic Dalyellioidea (used as a composite outgroup) are not well known. Hence, some of the traits listed at that level are



FIGURE 1. Phylogenetic tree depicting relationships among the major groups of cercomerian platyhelminths. I = Temnocephala; II = Udonellidea; III = Aspidobothrea; IV = Digenea; V = Monogenea; VI = Gyrocotylidea; VII = Amphilinidea; VIII = Eucestoda. Numbers accompanying the slash marks refer to the number of putative synapomorphies supporting each branch (refer to synoptic classification in text for identities of each synapomorphy). Each asterisk (*) represents a putative homoplasy (also indicated in synoptic classification in text).

undoubtedly symplesiomorphies for the cercomerians plus other "dalyellioids." Homoplasious characters are indicated by an asterisk (*). The total number of apomorphic traits for each group is reflected in the number accompanying the appropriate branch in Figure 1. Traits that have been modified from the condition diagnostic for each group are not listed either. Such modifications are detected by phylogenetic systematic studies at levels of greater resolution (e.g., Brooks et al., 1985b, 1989; Bandoni and Brooks, 1987a, 1987b). The nomenclature represents a compromise between that used by 2 groups of phylogeneticists (see Brooks, 1989). I believe it is compatible with nomenclatorial traditions at the ordinal level and below for most groups of parasitic platyhelminths.

Synoptic classification of the Cercomeria

Subphylum RHABDOCOELA sensu Ehlers, 1984

Infraphylum TYPHLOPLANOIDA sensu Ehlers, 1984

Infraphylum DOLIOPHARYNGOPHORA sensu Ehlers, 1984

Superclass CERCOMERIA Brooks, 1982

Diagnosis: (Doliiform pharynx and reduction of the dual-gland adhesive system indicate membership in Doliopharyngophora.) Rhabdocoelous platyhelminths lacking a vagina (1); with single ovary and paired testes (2); with paired lateral excretory vesicles (3); with doliiform pharynx (4); with saccate gut (5); with copulatory stylet (6); without locomotory cilia in adults (7); with Mehlis' gland (8); with posterior adhesive organ formed by an expansion of the parenchyma into, minimally, an external pad (cercomer sensu lato) (9); with terminal or subterminal mouth (10); with a single excretory bladder (11); with reduction of the dual-gland adhesive system (12); with amphistomous juveniles (13); with 1-host life cycles using arthropod hosts (14); with ectoparasitic mode of life* (15).

Subsuperclass TEMNOCEPHALIDEA Benham, 1901

Diagnosis: Cercomeria with cephalic tentacles (1).

Subsuperclass NEODERMATA Ehlers, 1984

Diagnosis: Genital pores in anterior half of body (1); with vagina (2); with vitellaria in adults lateral and follicular (3); without dictyosomes or endoplasmic reticulum in larval epidermis (4); with completely incorporated ciliary axoneme in sperm (5); with larval epidermis shed at end of larval stage (6); with protonephridia with 2-cell weir (7); with syncytial postlarval neodermis (8); with cilia of larval epidermis having only 1 rostrally directed rootlet (9); with epithelial sensory cells with EM-dense collars (10); with epidermal cells in larvae separated by neodermis material (11); with posterior adhesive organ shifted posteroventrally (12).

Class UDONELLIDEA Ivanov, 1952

Diagnosis: With secondary protonephridial system of canals and pores (1); with giant paranephrocytes (2); with arthropod host parasitic on vertebrate (3).

Class CERCOMERIDEA Brooks, O'Grady, and Glen, 1985

Diagnosis: With male genital pore and uterus proximate (1); with oral sucker (2); with lateral coiling of uterus (3); with bifurcate adult intestine (4); with 2-host life cycle involving an arthropod and a vertebrate (5); with endoparasitic mode of life (6).

Subclass TREMATODA Rudolphi, 1808

Diagnosis: With dorsal vagina a Laurer's canal (1); with posteroventral adhesive organ a sucker (2); without copulatory stylet* (3); with male genitalia in adults consisting of cirrus sac, pars prostatica, and internal seminal vesicle (4); with male genital pore opening into genital atrium independent of uterine opening (5); with operculate eggs usually longer than 50 μ m (6); with pharynx near oral sucker in adults (7); with lamellated walls in protonephridia (8); with posteroventral adhesive organ completely ventral, relatively sessile (9); with 2-host life cycle involving a molluscan and a vertebrate (10).

Infraclass ASPIDOBOTHREA Burmeister, 1856

Diagnosis: Without vaginal opening (1); with specialized microvilli and microtubules in neodermis (2); with oviducts divided into chambers by septa (3); with anteriorly fused suckers (4); with hypertrophy and linear subdivision of posterior sucker by transverse septa (5); with atrophy of oral sucker (6).

Infraclass DIGENEA Van Beneden, 1858

Diagnosis: With first larval stage a miracidium (1); with miracidium hatching from egg and swimming to snail host (2); with miracidium having single pair of flame cells (3); with saclike sporocyst stage ("mother sporocyst") in snail host following miracidium (4); with cercaria stage developing in snail following mother sporocyst (5); with cercariae having simple tails (6); with amphistomous cercariae (7); with anepitheliocystid cercarial excretory system (8); with stenostomatous cercarial excretory ducts (9); with secondary dorsal excretory pore in cercariae (10); with primary excretory pore at posterior end of cercarial tail (11); with cercariae remaining in sporocyst until snail host is ingested (12); with bifurcate cercarial intestine (13); with uteri in adults passing postovarian, then anteriorly to just postbifurcal (14); with paedomorphic (does not appear until redial or cercarial stage) gut development (15); with tiers of epidermal cells in miracidium (16); without evidence of endoderm in embryos* (17); with only 1 kind of electron-dense vesiculated inclusions in vitellogenic cells* (18).

Subclass CERCOMEROMORPHAE Bychowsky, 1937

Diagnosis: With posterior adhesive organ armed with hooks, called a cercomer (1); with doubled cerebral commissures (2); with doubled

posterior nervous system commissures (3); with paired lateral excretory pores (4); with 12–16 hooks on cercomer in larvae (5).

Infraclass MONOGENEA Van Beneden, 1858

Diagnosis: With paired lateral vaginae in adults (1); with 3 rows of ciliary epidermal bands in oncomiracidium larva (1 at each end, 1 in middle) (2); with 4 rhabdomeric eye-spots (3); with 1-host life cycle involving a vertebrate (loss of arthropod host) (4); with ectoparasitic mode of life* (5).

Infraclass CESTODARIA Monticelli, 1891

Diagnosis: With osmoregulatory system becoming reticulate in late ontogeny (1); without intestine (2); with posterior body invagination (3); without copulatory stylet* (4); with cercomer paedomorphic, reduced in size, and at least partially invaginated (5); with male genital pore not proximate to uterine opening (6); with vestigial oral sucker/pharynx complex (7); with follicular ovary (8); with bilobed ovary (9); with testes multiple, in 2 lateral bands (10); with 10 equal-sized hooks on cercomer in larvae (11); with syncytial larval epidermis (12); with syncytial vitelloducts (13); with neodermis not protruding to surface between epidermal cells (14); without desmosomes in the passage of the first excretory canal cells (15); without endoderm in embryos* (16); with only 1 kind of electron-dense vesiculated inclusions in vitellogenic cells* (17).

Cohort GYROCOTYLIDEA Poche, 1926

Diagnosis: With rosette at posterior end of body (1); with short funnel connecting with rosette (2); with narrow funnel (3); with anterolateral genital notch (4); with crenulate body margins (5); with body spines small over most of body, large at pharyngeal level (6); with large body spines long and narrow (7); with testes extending posteriorly only to level of metraterm (8); with vitellaria encircling entire body, extending along entire body length (9); without nuclei in larval epidermis (10); without multiciliary nervous receptors (11); without extensions of neodermis into intercellular space between epidermis and basal lamina (12).

Cohort CESTOIDEA Rudolphi, 1808

Diagnosis: With male genital pore and vagina proximate (1); with cercomer totally invaginated during ontogeny (2); with excretory system opening posteriorly in later ontogeny (3); with hooks on larval cercomer in 2 size classes (6 large and 4 small) (4); with microvilli lining protonephridial ducts (5); without subepidermal ciliary receptors with true photoreceptor functions in larvae (6); with larval protonephridia in posterior end of body (7).

Subcohort AMPHILINIDEA Poche, 1922

Diagnosis: With uterine pore and genital pores not proximate (1); with male pore at posterior end (2); with vaginal pore at posterior end (3); with irregular ridges and depressions on adult tegument (4); with "N"-shaped uterus (5); with uterine pore proximal to vestigial pharynx (6).

Subcohort EUCESTODA Southwell, 1930

Diagnosis: With body of adults polyzoic (1); with cercomer lost during ontogeny (2); with 6 hooks on larval cercomer (3); with excretory system reticulate in early ontogeny (4); with restricted medullary portion of proglottids (5); with hexacanth embryo hatching from egg, ingested in water (6); with second larval stage a procercoid (7); with third larval stage a plerocercoid (8); with protein embedments in epidermis of hexacanth (9); with tegument covered with microtriches (10); with sperm lacking mitochondria (11); with paedomorphic cerebral development, none seen in larvae (12).

Developmental constraints

There is complete congruence between larval or juvenile and adult traits for the major cercomerian groups (Fig. 1 and synoptic classification). In addition, Brooks et al. (1985b, 1989) demonstrated a high degree of phylogenetic congruence between larval/juvenile and adult traits for the digeneans at the family level, and Caira (1989) demonstrated similar congruence for a group of allocreadiid digeneans at the species level. Thus, there is evidence of a high degree of phylogenetic constraints on the evolution of developmental programs among the parasitic platyhelminths, regardless of the phylogenetic scale.



FIGURE 2. Phylogenetic distribution of general classes of major changes in developmental patterns widespread among the major groups of cercomerian platyhelminths, with some examples. Identities of taxa I-VIII as in Figure 1. 1 = unique class of larval or juvenile forms; 2 = asexual proliferation of larval stages; 3 = polyembryony; 4 = peramorphic heterochrony; 5= paedomorphic heterochrony. Aspidobothreans: (4) = accelerated development signified by sexual maturation in molluscan host in relatively highly derived species, (5) = loss of fusion of suckers in stichocotylids. Digeneans: (1) = miracidium, sporocyst, redia, cercaria; (2) = asexual proliferation of rediae, cercariae; (4)= accelerated development signified by sexual maturation in second intermediate host (transversotrematids, schistosomatoids) or in molluscan host (e.g., some gymnophallids and microphallids); (5) = paedomorphic development of gut in miracidia; same in rediae resulting in "daughter sporocysts." Monogeneans: (1) = oncomiracidium; (3) = polyembryony in gyrodactylids; (4) = hypermorphosis of cercomer, producing diverse forms of opisthaptors. Gyrocotylideans: (1) = lycophore larva. Amphilinideans: (1) = decacanth larva. Eucestodes: (1) = hexacanth larva; (5) = decelerated development signified by absence of cerebral development in hexacanth larva; loss of apical sucker in many lineages.

Despite such high degrees of phylogenetic constraint on developmental patterns, cercomerideans (trematodes plus cercomeromorphs) are notable in their diversity of specialized developmental processes. Figure 2 depicts the distribution of developmental innovations in 5 classes of developmental phenomena among the major cercomeridean groups. These include: (1) unique larval forms, (2) asexual proliferation of larval forms, (3) polyembryony, and the 2 major classes of heterochrony, (4) peramorphosis, and (5) paedomorphosis (see Fink [1982] for a discussion of phylogenetic correlates of heterochronic changes in evolution). Each number accompanying a slash mark on the phylogenetic tree in Figure 2 indicates a manifestation of the class of developmental phenomena denoted by the number that is peculiar to the taxon. Hence, all the slash marks accompanied by a "1" in Figure 2

indicate different unique larval forms. These refer to developmental innovations characteristic of the entire taxon, or a major portion of it, and do not take into consideration variations on these general themes that are manifested throughout the various groups. For example, Brooks et al. (1985b, 1989) have discussed phylogenetic correlates of heterochronic changes in early ontogeny at the familial level for digeneans. Font (1980) suggested that heterochrony had played an important role in the diversification of a group of macroderoidid digeneans. Thus, there is evidence of major contributions by developmental innovations to the morphological diversity of cercomerideans, regardless of the phylogenetic scale.

Ecological conservatism

At this very high level of phylogenetic resolution, the primary ecological correlates of evolution involve the life cycle patterns discussed above. Figure 3 depicts the distribution of data for 3 ecological components of cercomerian life cycle patterns on the phylogenetic tree from Figure 1: (1) whether they are ectoparasitic or endoparasitic as adults (top row of boxes above the tree); (2) whether they utilize a vertebrate host or not (middle row of boxes above the tree); and (3) whether they utilize an invertebrate host, and if they do whether it is an arthropod or mollusc (bottom row of boxes above the tree). The distribution of life cycle data on Figure 3 is summarized by the slash marks on the phylogenetic tree.

The analysis shown in Figure 3 supports the following inferences about the pattern of evolutionary diversification of cercomerian life cycle patterns: (1) The plesiomorphic cercomerian life cycle was a 1-host ectoparasitic cycle involving an arthropod host. This form of life cycle is seen in temnocephalideans and udonellideans. Udonellideans became associated with vertebrates when their arthropod hosts became parasitic on vertebrates, but they retain the basic 1-host ectoparasitic cycle involving an arthropod host. (2) The vertebrate/arthropod 2-host endoparasitic life cycle pattern is plesiomorphic for cercomerideans. The vertebrate host is plesiomorphic for cercomerideans, because the major trematode and cercomeromorphan groups are associated, at least primitively, with vertebrate hosts. The plesiomorphic lifestyle for cercomerideans appears to be endoparasitic, because the trematodes and 3 of the 4 cercomeromorph groups



FIGURE 3. Phylogenetic patterns of diversification of life cycle patterns among major groups of cercomerian platyhelminths. Identities of taxa I-VIII as in Figure 1. Boxes above taxa indicate distribution of traits for 3 components of life cycle patterns. Top row: light lines = adults ectoparasitic, dark lines = adults endoparasitic; middle row: open box = no vertebrate host, dark box = vertebrate host; bottom row: fine stippling = arthropod host, heavy stippling = molluscan host; 0 = no invertebrate host; ? = presence or absence, and type, of invertebrate host unknown. Slash marks on tree, and accompanying abbreviations summarize the data presented in the boxes phylogenetically. A = arthropod host acquired (primitive 1-host ectoparasitic life cycle); V = vertebrate host acquired (primitive 2-host endoparasitic life cycle); M = molluscan host acquired in exchange for arthropod host (derived 2-host life cycle); No A = arthropod host lost (derived 1-host life cycle); Ect = ectoparasitic adult; End = endoparasitic adult.

are endoparasitic. This interpretation supports theories that vertebrate hosts were added to the life cycles of parasitic platyhelminths by ingestion of infected arthropods. (3) The vertebrate/ mollusc 2-host endoparasitic life cycle is a synapomorphy for the trematodes, resulting from a shift from arthropod to mollusc intermediate hosts. (4) The vertebrate 1-host ectoparasitic life cycle is synapomorphic for the monogeneans, resulting from a loss of the arthropod intermediate host and a convergent (evolutionary reversal) shift from endo- to ectoparasitic mode of life. (5) From this phylogenetic perspective the vertebrate/arthropod 2-host endoparasitic life cycle pattern known for amphilinideans and eucestodes, and postulated for gyrocotylideans, is the most conservative life cycle pattern among the living cercomerideans.

The phylogenetic distribution of definitive host types (Fig. 4) indicates that the association between vertebrates and cercomerians began shortly after the first vertebrates evolved, probably



FIGURE 4. Phylogenetic patterns of diversification in vertebrate host group inhabited by stem groups of major groups of cercomerian platyhelminths. Identities of taxa I-VIII as in Figure 1. P = placoderms; CH = chondrichthyans; O = ostracoderms (to indicate the ancestors of all nonchondrichthyan gnathostomous vertebrates). Note association between vertebrates and cercomerians apparently early in vertebrate evolution, with extensive radiation in placoderms, due either to host-switching or sympatric speciation, and subsequent close phylogenetic association between evolutionary divergence of chondrichthyans and ostracoderms and divergence of aspidobothreans and digeneans, of gyrocotylideans and cestoideans, and possibly of various groups of monogeneans.

early in the evolution of the placoderms. It also suggests that the stem diversification of 3 major lineages of cercomerians, the trematodes, the monogeneans, and the cestodarians (gyrocotylideans, amphilinideans, and eucestodes), occurred in association with placoderm groups prior to the divergence of the chondrichthyans from the ostracoderms. The occurrence of 3 different stem groups in association with placoderms suggests a plethora of alternative evolutionary scenarios representing a continuum between 2 extremes. First, there may have been at least 2 instances of host-switching within the placoderms correlated with the emergence of these groups. Second, there may have been 2 instances of sympatric speciation within the same placoderm lineage. Following the early diversification in association with placoderms, the divergence of both the aspidobothreans from the digeneans and of the gyrocotylideans from the cestoideans (amphilinideans plus eucestodes) is correlated with the divergence of the chondrichthyans from the ostracoderm ancestor that gave rise to the rest of the gnathostomous vertebrates. If there are monogenean lineages whose basal groups distinguish taxa inhabiting chondrichthyans from taxa inhabiting other gnathostomous vertebrates, this pattern also applies to the monogeneans.

The evolutionary diversification in major



FIGURE 5. Summary of phylogenetic correlates of ontogenetic and ecological (life cycle) diversification among the major groups of cercomerian platyhelminths. Identities of taxa I-VIII as in Figure 1. Note phylogenetic constraints on both ontogenetic and ecological change, and ecological conservatism relative to developmental diversification.

modes of life cycle patterns among the major cercomerian groups has been highly conservative and phylogenetically coherent. There is evidence of longstanding and conservative association with particular vertebrate host groups in addition to the conservatism in diversification of life cycle patterns. Brooks et al. (1985b, 1989) and Shoop (1988) found a similar degree of organization in the evolutionary diversification of digenean life cycle patterns.

Interaction of the two hierarchies

Figure 5 depicts the distribution of developmental and ecological correlates of phylogeny for the major cercomerian groups. The emergence of the cercomeridean lineage is associated with the acquisition of a vertebrate host in the life cycle, an ecological correlate of phylogeny. There is no known developmental correlate of similar degree for this evolutionary change. The divergence of the trematode and the monogenean lineages also is associated with major changes in ecological correlates of phylogeny without accompanying equivalent changes in developmental patterns. Whether host-switching or sympatric speciation produced the diversity of cercomerian lineages in placoderms, such diversification may well have been facilitated by the evolution of ecological novelties in ancestral parasite groups. There is evidence of a shift in intermediate host type for the trematodes from arthropods to molluscs, coupled with hostswitching or sympatric speciation (Fig. 4). Likewise, there is evidence of a loss of the invertebrate host and return to ectoparasitic life style

in the monogeneans, also coupled with apparent host-switching or sympatric speciation (Fig. 4).

For the cercomerians as a whole, however, such ecological diversification is very conservative relative to the developmental diversification organized by phylogenetic constraints (Fig. 5). For example, the aspidobothreans and digeneans differ in diversity (estimated by total number of described species) by about 1:10. Phylogenetic systematic analyses summarized herein suggest that the molluscan/vertebrate complex life cycle characteristic of digeneans is a persistent ancestral trait that also characterized the ancestral aspidobothreans (as well as extant species). Therefore, it would appear that the differences in diversity do not reflect differences in ecological strategies. The developmental patterns exhibited by digeneans are unique to them, and serve to distinguish digeneans strongly from aspidobothreans. It is also true that the digenean developmental patterns have significant ecological and adaptive ramifications, which proximally explain the high diversity of digeneans. Therefore, I would ascribe the high diversity of digeneans relative to their sister group as being the result of a developmental revolution that had adaptive consequences. However, these adaptive consequences were manifested in an ancestral ecological context. Brooks et al. ([1985b] and the update by Brooks et al. [1989]) demonstrated a similar relationship between functional and developmental diversification at the familial level for digeneans. Once again, although the particular correlates of phylogeny depend on the phylogenetic scale investigated, similar general patterns emerge regardless of the scale.

Adaptive radiations by major groups of cercomerians appear to be triggered by developmental revolutions rather than by ecological invasions. This serves as evidence supporting the postulates of Brooks and Wiley (1988). Of course, these views also will be compatible with the views of biologists who consider themselves more traditionally minded. I would like to take this as support for the proposition that, because the unified theory is not an anti-Darwinian theory, an integration of traditional views with the results of new data and new methods of analysis is possible.

CONCLUSIONS

The database of morphological, developmental, and ecological correlates of phylogeny for the cercomerians is extensive enough to be used as an important source of tests for the macroevolutionary postulates of the unified theory of evolution, or of any alternative theory that makes explicit enough predictions for empirical testing. The data that are presently available uniformly support the predictions of the unified theory about phylogenetic correlates of morphology, development, and ecology. That is, the data considered herein show evidence of diverse ontogenies and conservative ecologies highly organized phylogenetically. It is certainly true that other parasitologists, operating in a Darwinian paradigm, have made similar conclusions about these taxa. This reinforces my assertion in the introduction that the unified theory is not a non-Darwinian theory, but an expansion of Darwinian theory.

It has been asserted that nothing surpasses parasites for adaptive plasticity and adaptive radiation (Price, 1980). If this is true, we would expect the ecological and behavioral correlates of phylogeny for nonparasitic groups to be even more conservative than those discovered for the cercomerians. That is, the studies of parasitic taxa should establish baseline expectations for the extent of adaptive evolution. It is also possible that the commonly held view has been mistaken, and parasites are actually more highly constrained in their evolution than free-living taxa. Recent work on copepod parasites of elasmobranchs cited above tends to support that possibility, but we are a long way from having a large enough database for drawing robust conclusions. In any event, the path to a clearer understanding of macroevolutionary aspects of parasite evolution, and of evolution in general, lies in generating larger phylogenetic databases for groups of parasitic and nonparasitic species. Because I expect to find more phylogenetic correlates, both ecological and developmental, as a result of ongoing phylogenetic systematic studies of the cercomerians, I hope that this group of helminths will continue to play a part in the growth of evolutionary theory and explanation.

Finally, if the pattern of ancient origins and evolutionary conservatism in ecological attributes exhibited by the cercomerians is representative of evolution in general, concerns about the ability of ecosystems (especially those in the tropics) to adapt to human timescale disruption must be heightened. Contemporary ecosystems structure may have evolved long ago and have persisted relatively unchanged for long periods of time. Boucot (1983) discussed paleontological evidence dating from the Cambrian that community ecological structure has been characterized by periods of relative stasis lasting tens of millions of years, "punctuated" by periods of what he described as "ecological chaos" lasting less than 10 million yr at a time, followed by the emergence of radically new community ecological structure. If this has been the evolutionary pattern since the Cambrian, the neontological data presented herein using the cercomerians should cast doubt on the ability of ecosystems to "heal" themselves of major disruptions on time scales important to human interests.

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