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Lessons from a Quiet Classic

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LESSONS FROM A QUIET CLASSIC

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ABSTRACT: Parasitology has a rich tradition of studies linking taxonomy, ecology, and life cycles and development. This tradition has produced an enormous amount of empirical evidence demonstrating that parasites form highly integrated reproductive–developmental–ecological systems that are highly persistent through space and time. As well, phylogenetic studies of parasites, especially of parasitic platyhelminths, represent 1 of the most progressive areas of systematic biology. Consequently, parasitologists should be at the forefront of research in evolutionary developmental biology (evo–devo) and integrative biology, and parasite systems should be model systems of choice for those research programs. Species of the digenean, *Alloglossidium*, provide a superb exemplar for such studies because we know so much about their phylogeny, population biology, ecology, and life cycles. Equally important is the recognition that *Alloglossidium* spp. is such an outstanding model system because of more than 30 yr of effort by a number of people working with little funding at small institutions, beginning with a short unassuming species description by Gerald D. Schmidt. For dedicated and creative scientists, the size of the institution and the research budget need not be an impediment to producing high-quality research. These are the people who produce the quiet classics, and they need to be recognized for their invaluable contributions.

SETTING THE STAGE

One of the most influential, and prolific, parasite taxonomists was the late Gerald D. Schmidt. Despite spending his career at an academic institution devoted more to teaching than to research, Schmidt published several hundred taxonomic papers describing a myriad of new species of eucestodes, acanthocephalans, and nematodes. Of that constellation of papers, only 1 is a description of a new species of digenean, and that was the result of pure serendipity. An undergraduate exercise in annelid biology had been highlighted by some medicinal leeches, always a student crowd-pleaser. At the end of the exercise, Schmidt decided, on a whim, to dissect some of the leeches. He was rewarded with the first adult digenean ever recorded in leeches, *Alloglossidium hirudicola* Schmidt and Chaloupka, 1969 (Schmidt and Chaloupka, 1969). The same year, Sullivan and Heard (1969) described *Macroderoides progeneticus* for gravid digeneans living in the antennary gland of the crayfish, *Procambarus spiculifer*. These findings were considered by some as simply an accidental infection (Stunkard, 1970) and by others merely a taxonomic anecdote. Within a few years, however, this anecdote became an interesting evolutionary mystery.

First, Taft and Kordyiak (1973) reported adult digeneans they identified as *A. hirudicola* living in the leeches *Haemopis* sp. and *Macrobdella decora* in Wisconsin. In rapid succession, Beckerdite and Corkum (1974) described *Alloglossidium macrobdellensis* in *Macrobdella ditetra*, and Font and Corkum (1975) described *Alloglossidium renale* in the antennary gland of freshwater shrimp, *Palaemonetes kadiakensis*, both species occurring in Louisiana. Font and Corkum (1975) also transferred *M. progeneticus* to *Alloglossidium*, providing the first hint that the adult digeneans in North American freshwater leeches and crustaceans might represent a monophyletic group. Moving north, Neumann and Vande Vusse (1976) described *Alloglossidium turnbulli* and *Alloglossidium hamrumi* in the leeches *Haemopis grandis* and in *Haemopis plumbea* and *M. decora*, respectively, from Minnesota and Iowa. In the same year, Fish and Vande Vusse (1976) described *Hirudicolatrema richardsoni* in *Haemopis marmorata, Haemopis lateromaculata*, and *H. grandis*. Shortly thereafter, Corkum and Turner (1977) described *Alloglossoides caridicola* inhabiting the crayfish, *Procambarus acutus*, from Louisiana. The 1970s ended with Timmers (1979) describing *Alloglossidium schmidti* in the leech *H. grandis* from Manitoba. In the first 2 yr of the 1980s,

Vande Vusse (1980) reported *A. schmidti* in *H. grandis* from Minnesota and reassigned *Glossidium geminum* to *Alloglossidium*, whereas Vande Vusse et al. (1981) reported that the digeneans identified by Taft and Kordyiak (1973) as *A. hirudicola* actually were specimens of *A. macrobdellensis, A. schmidti, A. turnbulli*, and *A. hamrumi*.

During this period of time, there was also considerable study of the population biology and life-cycle attributes of members of this group. Beckerdite and Corkum (1974) and Corkum and Beckerdite (1975) reported life cycle and seasonality of *A. macrobdellensis*. Font and Corkum (1975) found gravid specimens of *Alloglossidium progeneticum* free in the intestine of the ictalurid fish *Ictalurus melas* and suggested that ingestion of the crayfish host would free the gravid worms living in the antennary glands, so their eggs could be released into the environment where they could come into contact with the molluscan first intermediate host. Next, they reported seasonality of *A. renale* in *P. kadiakensis* (Font and Corkum, 1976) and then delineated the life cycle of *A. renale* and compared it with those of *Alloglossidium corti* and *A. macrobdellensis*, establishing that they were indeed different species (Font and Corkum, 1977). Vande Vusse et al. (1981), Riggs and Ulmer (1983a, 1983b), and Eaton and Font (1985) provided additional important ecological data on these digeneans, and Turner (1985) discussed the pathogenic effects of *A. caridicola* in the antennary gland of the crayfish definitive host. These studies established the specific distinctiveness of the various species, as well as important aspects of their ecologies and life histories. Taken together, there was an indication of a well-established multispecies assemblage having strong biological ties with the biology of their hosts.

On the basis of these studies, Font (1980) proposed the first hypothesis to explain the evolution of *Alloglossidium* spp. His scenario postulated an ancestral 3-host life cycle, involving a mollusc, a leech, and a fish, truncated to a mollusc and leech life cycle, followed by host switching from leeches to crustaceans. Riggs and Ulmer (1983), following an earlier proposal by Stunkard (1959) that all 3-host life cycles in digeneans were derived from 2-host cycles, proposed that the species of *Alloglossidium* evolved from an ancestral 2-host cycle in which the leech host was the definitive host, and fish hosts were added later to produce a 3-host cycle. Riggs and Ulmer (1983) did not propose explanations for the 2-host cycles involving molluscs
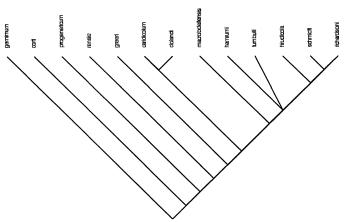
FIGURE 1.   Phylogenetic tree depicting relationships among members of the digenean *Alloglossidium* (modified slightly from Smythe and Font, 2001; for details, see Appendix 1).
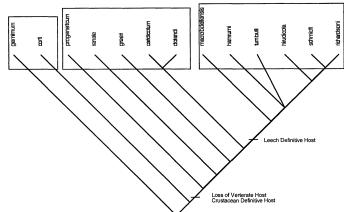

FIGURE 2.   Phylogenetic tree depicting relationships among members of *Alloglossidium*. Lines on branches indicate points of origin of changes in life-cycle pattern.

and crustaceans or for the 3-host cycles of *A. corti* and *Alloglossidium geminum*, which involve molluscs, crustaceans, and fishes.

Carney and Brooks (1990) provided the first phylogenetic systematic analysis of this group of digeneans, based on 9 species. At that time, *H. richardsoni* and *A. caridicola* were placed in their own genera, with uncertain relationships to *Alloglossidium* spp. Their study provided support for Font's (1980) hypothesis that the 3-host life cycles were ancestral and also suggested that the first 2-host life cycles in the group involved a crustacean definitive host, with leech definitive hosts arising later. The 1990s also witnessed additional taxonomic work, as Turner and McKeever (1993) described *Alloglossoides dolandi* in *Procambarus epicyrus* from Georgia, and Font (1994) described *Alloglossidium greeri* in *Cambarellus shufeldtii* from Louisiana.

Smythe and Font (2001) began the new millennium by proposing an updated phylogenetic hypothesis for the members of this group, including 2 species that had been described subsequent to their study, as well as including *H. richardsoni* and *A. caridicola* and *A. dolandi*, which they transferred to *Alloglossidium* (Fig. 1). The addition of 4 species provided additional complexity to the evolutionary story, but corroborated the basic findings of Carney and Brooks with respect to the evolution of life-cycle sequences in this group (Fig. 2). This study, however, also highlighted some additional exciting possibilities.

ALLOGLOSSIDIUM SPP. AND "EVO–DEVO"

The research program in evolutionary developmental biology called "evo–devo" (Raff, 1996) is the focus for studies of "developmental constraints" in evolution. One excellent way to go about finding general themes is the analysis of homoplasy, or the repeated evolution of similar traits in different lineages. Saether (1977, 1979a, 1979b, 1983), following Brundin (1972), suggested that "inherited" factors termed canalized evolutionary potential could also contribute to developmental constraints, particularly in the production of homoplasy. He linked this discussion with the formulations by Tuomikoski (1967), who defined the concept of "underlying synapomorphy" as a plesiomorphic capacity that made it relatively easy ("cheap") to evolve

similar traits (see also Crampton, 1929). This means that among members of a clade, and within that clade only, certain homoplasious changes occur repeatedly. The appearance of these traits conforms to a phylogenetic pattern of homoplasy, but the evolutionary capacity to produce them actually evolved only once, in the common ancestor of the clade containing all the species exhibiting the trait. It is that capacity which is named the underlying synapomorphy. Underlying synapomorphies are intriguing because macroevolutionary patterns exist that are supportive of the concept; however, the nature of, and process(es) producing, canalized evolutionary potential remains unclear. One favorite candidate is heterochrony (Raff, 1996).

Heterochrony, or changes in the timing of development that produce changes in morphology, is thought to be a source of evolutionary innovation, including homoplasy. Alberch et al. (1979) developed a general model of heterochrony [adapted for phylogenetic analysis by Fink (1982)] based on representing the development of any part of an organism with a positive trajectory having a starting point (α), an endpoint (β), and a rate of growth (k) for changes in shape (γ) or size (S). Heterochrony is determined by plotting values for α and β on the x-axis (time) and values for γ or S on the y-axis (morphology).

There are 2 general categories of heterochrony. Paedomorphosis results in the production of a descendant adult morphology that is less complex than that of the immediate ancestor. This does not necessarily imply that the descendant will have a morphology comparable to that of a juvenile or even a larval ancestor; it may resemble a less developed ancestral adult (McKinney, 1988). Paedomorphosis can be accomplished in 3 ways: growth onset can be delayed (postdisplacement), growth can be terminated earlier (progenesis), or development can proceed at a slower rate (neoteny). Paedomorphic phenomena can in some cases produce morphological changes in apomorphic traits that harken back to their plesiomorphic roots, manifested on phylogenetic trees as the form of homoplasy called evolutionary reversals. Peramorphosis, in contrast, results in the production of descendant adult morphologies that are more complex than that of the immediate ancestor. Because this produces a morphological trait in an organism that passes beyond the condition found in its ancestor, the result will be a recapitulation of the ancestral ontogeny during development. Not surprisingly,

there are 3 ways in which peramorphosis can occur: growth onset can begin earlier (predisplacement), growth can continue for a longer period (hypermorphosis), or development can proceed at a faster rate (acceleration: see also McNamara, 1986). Recurring peramorphic phenomena produce homoplasious apomorphic changes.

McNamara (1986) suggested that any modification of a developmental sequence, whether by addition or deletion of stages, may therefore be interpreted as an outcome of heterochrony. Based on this notion, he extended paedomorphosis to include a descendant passing through fewer ontogenetic stages than the ancestor and peramorphosis to include a descendant passing through more ontogenetic stages than the ancestor. For example, the plesiomorphic ontogenetic sequence for digeneans includes 3 larval stages, i.e., the miracidium, the mother sporocyst, and the cercaria. Early in the phylogeny of digeneans, a fourth stage, the redia, was intercalated between the mother sporocyst and the cercaria. This would be an example of peramorphosis. Additionally, not all descendants of the ancestral digenean in which the redia arose possess a redial stage. Many exhibit a stage termed a "daughter sporocyst" that occurs, like the redia, between the mother sporocyst and the cercaria. Both rediae and daughter sporocysts are derived from mother sporocyst germinal tissue, have a birth pore, and give rise to cercariae having (plesiomorphically and commonly) pharynges and guts. In addition, just as there is no experimentally confirmed case of a digenean lacking a mother sporocyst, there is no experimentally confirmed case in which rediae and daughter sporocysts occur in the same species. These observations lead to the hypothesis that rediae and daughter sporocysts form a homologous transformation series. Phylogenetic analysis suggests that daughter sporocysts are apomorphic, and furthermore that daughter sporocysts have evolved at least twice within Digenea (Brooks et al., 1985a, 1989; Brooks and McLennan, 1993). The difference between a redia and a daughter sporocyst is morphological; a redia has a pharynx and saccate gut, whereas a daughter sporocyst has neither. This suggests the presence of paedomorphic phenomena leading to the later than expected expression of the pharynx and gut during ontogeny in the species having daughter sporocysts (remember that cercariae have pharynges and guts). In the absence of experimental studies, we cannot say which of the 3 categories of paedomorphosis may have been involved or whether the same process was responsible for each evolutionary origin of daughter sporocysts, but we can say that daughter sporocysts appear to be rediae that are paedomorphic for the expression of the pharynx and intestine.

The phylogenetic hypothesis proposed by Smythe and Font (2001) (Fig. 1) suggests that *Alloglossidium* spp. have experienced a relatively high amount of homoplasious (convergent and parallel) evolution (26 of 56 or approximately 46% of all changes on the tree). Most of those homoplasious changes (16 of 26 or 61.5%) in *Alloglossidium* spp. are secondary changes from a derived (apomorphic) state to a more ancestral (plesiomorphic) state, called evolutionary reversals. Evolutionary reversals are often considered a phylogenetic signature of paedomorphosis. Thus, the study of Smythe and Font (2001) provided the evidence permitting us to link the phylogenetic diversification of *Alloglossidium* spp. with paedomorphic changes in development of adult morphological features.

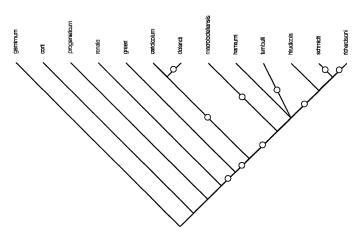At this level of analysis, we can ask 3 questions. First, do

FIGURE 3.   Phylogenetic tree depicting relationships among members of *Alloglossidium*. Circles on branches indicate occurrence of evolutionary reversals.

particular species or clades exhibit unusually high numbers of reversals? Second, do particular traits exhibit unusually high levels of reversals? Third, do any traits show correlated ("linked") reversals? Figure 3 depicts the distribution of reversals on the *Alloglossidium* spp. phylogenetic tree. Reversals do not occur on the 7 basalmost branches of the tree, but 10 of the 17 remaining branches of the tree are characterized by at least 1 reversal. Reversals occur on 5 nonterminal branches and 5 terminal branches. Reversals occur in 50% (9 of 18) of the morphological traits analyzed; characters 1 and 8 exhibit 2 reversals (1 of them a double reversal), character 2 exhibits 3 reversals (2 of them double reversals), characters 9 and 15 exhibit 2 reversals, and characters 4, 5, 11, 12, and 16 exhibit a single reversal each. Finally, on 6 of the 10 branches on which reversals occur, there are reversals in 2 characters, in the following combinations: 4 + 16, 9 + 15, 5 + 12, 2 + 8, 2 + 9, and 8 + 15. Reversals are thus a common feature of the most recently evolved 75% of the genus and involve a substantial number of characters. These reversals are not confined to particular taxa or species, some are relatively old, whereas others are relatively young, and there is little evidence to suggest that any of the reversed traits are linked.

ALLOGLOSSIDIUM SPP. AND INTEGRATIVE BIOLOGY

The research program called integrative biology seeks to provide rigorous explanations for the origin, persistence (stasis), and diversification of the very characteristics that provide the foundation for complex evolutionary systems. Wake (1991) summarized the conceptual framework for integrative biology thus: "[A]n understanding of the evolution of biological form— morphology—[is] unlikely unless one combine[s] two distinct and independent approaches: neo-Darwinian functionalism and biological structuralism, in a context of rigorous phylogenetic analysis." Stearns (1981) and McKinney (1986) were among the first contemporary evolutionary biologists to discuss the linkage between ecology and heterochrony. This has led to an understanding that evo–devo studies are incomplete as evolutionary explanations without any knowledge of the ecological context of particular developmental changes.

Parasitology with its long tradition of research combining

systematics (now augmented with phylogenetic analysis), basic ecology, and life-cycle studies has an opportunity to be at the forefront of this next major frontier in integrative biology. *Alloglossidium* spp. are outstanding models because we know so much about their population biology, ecology, and life cycles. Coupled with their high level of reversals, *Alloglossidium* spp. potentially represent a powerful system for studies in integrative biology. Using such a system will allow us to ask whether evolutionary reversals can be indicators not just of paedomorphosis in general but of paedomorphosis associated with evolutionary changes in an environmental context during development.

Are evolutionary reversals associated with changes in life-cycle structure? If not, do they occur after such a change has occurred? If we find evidence suggesting the former, we have reason to investigate how a change in life-cycle structure, the very context of reproduction, development, and evolution, can produce paedomorphosis. O'Grady (1987) demonstrated experimentally that there was a link between some cases of what is called host-induced variation and host-induced paedomorphic development. *Glypthelmins intestinalis* is a digenean inhabiting the small intestines of western spotted frogs *Rana pretiosa*. *Glypthelmins intestinalis* is distinct from other members of the group by virtue of having an extremely long hind body (so much so that it was originally placed in a separate genus, *Haplometrana*). When the western red-legged frog, *Rana aurora*, is infected with *G. intestinalis* metacercariae, the worms grow slowly, resulting in adults with short hind bodies, which is the plesiomorphic condition. If this kind of inducible phenomenon becomes heritable, the result will be seen phylogenetically as an evolutionary reversal. Alternatively, an increase in the number of reversals occurring after an evolutionary change in life-cycle structure suggests that the new ecology may have set the stage for such kinds of morphological experimentation. In either event, the implication is that a major evolutionary change in environmental context, encapsulated in the life-cycle pattern, permitted the evolving lineage to (metaphorically speaking) recapture its youth and recycle parts of ancestral morphologies in the context of newly evolving species.

Figure 4 depicts the phylogenetic tree for *Alloglossidium* spp., indicating the points at which changes in life-cycle structure emerged (patterned and black circles) and the points at which evolutionary reversals emerged (open circles). The 2 basalmost (oldest) members of the genus, *A. geminum* and *A. corti*, definitely evolved within the ancestral ecological context of a life cycle involving a mollusc first intermediate host, a crustacean second intermediate host, and a fish definitive host. Neither species exhibits any evolutionary reversals. At the other end of the phylogeny, 2 evolutionary reversals occur on the branch of the phylogenetic tree, indicating the point in evolutionary time at which a switch from a mollusc–crustacean 2-host life cycle to a mollusc–leech 2-host life cycle occurred. In addition, 5 of the 9 branches on the phylogenetic tree subsequent to that point exhibit at least 1 reversal. The most intriguing element in this story comes from assessing the remaining 5 species, all of which become gravid in crustaceans. If we place the evolutionary transition from a 3-host (mollusc, crustacean, and fish) to a 2-host (mollusc and crustacean) life cycle on the branch indicating the common ancestor of *A. progeneticum* + the remaining members of the genus, or on the branch
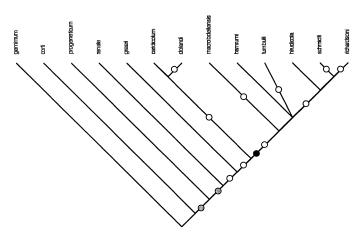

FIGURE 4.   Phylogenetic tree depicting relationships among members of *Alloglossidium*. Patterned circles indicate equally parsimonious interpretations of origin of truncated life-cycle pattern (loss of fish definitive host, sexual maturation in crustacean, which transforms from second intermediate host to definitive host); solid circle on branches indicates unambiguous change in life-cycle pattern (switch from crustacean to leech definitive host); and open circles indicate occurrence of evolutionary reversals.

indicating the common ancestor of *A. renale* + the remaining members of the genus, there is no correlation between evolutionary reversals and changes in the life-cycle pattern because neither *A. progeneticum* nor *A. renale* exhibits any reversals. Remember, however, that Font and Corkum (1976) reported finding adult *A. progeneticum* in fishes. They postulated that even though *A. progeneticum* became sexually mature in a crustacean, the fish host was necessary for liberating eggs into the environment, where they could infect the molluscan first intermediate hosts and propagate a new generation. If the same is true for *A. renale* (which can be corroborated by finding *A. renale* adults free in the intestine of fish) and if the transition from a 3-host to a true 2-host life cycle occurred in the common ancestor of *A. greeri* + the remaining members of the genus, then, just as in the case of the transition from crustacean to leech definitive host, there are 2 evolutionary reversals associated with the change in life-cycle pattern, and the 4 additional evolutionary reversals associated with *Alloglossidium* spp. using crustaceans as definitive hosts occurred after this transition.

Alloglossidium spp. are by no means the only interesting models for studying integrative biology and evo–devo using digeneans. Indeed, parasitologists have long speculated about the significance of the fact that different digenean species use different types and numbers of hosts in their life cycles. Most have assumed that the occurrence of adult digeneans in invertebrate hosts is a secondarily derived condition (e.g., Dollfus, 1932; Wisniewski, 1932; McIntosh, 1935; McMullen, 1938; Crawford, 1940; Serkhova and Bychowsky, 1940; Stunkard, 1940, 1959, 1970; Buttner, 1950a, 1950b, 1950c, 1951a, 1951b, 1951c; Peters, 1955, 1957; Biguet et al., 1956; Myers, 1956; Szidat, 1956; Freeman and Lllewellyn, 1958; Honer, 1960; Reimer, 1961; DeGiusti, 1962; Sogandares-Bernal, 1962; Allison, 1966; Jamieson, 1966; Demshin, 1968; Short and Powell, 1968; Sullivan and Heard, 1969; Nath and Pande, 1970; Macy and Basch, 1972; Deblock, 1974; Lotz and Corkum, 1975; Overstreet and Hochberg, 1975; Grabda-Kazubska, 1976; Lester and Lee, 1976; Turner and Corkum, 1977; Font, 1980). Such spec-

ulations could not be tested directly until the advent of phylogenetic systematics and modern comparative evolutionary studies (e.g., Brooks and McLennan, 1991, 1993, 2002), but current phylogenetic assessments of Digenea (e.g., Brooks et al., 1989; Brooks and McLennan, 1993; Littlewood et al., 2001) support the inference that such occurrences are indeed secondarily evolved.

Many workers have used the term progenesis for cases of putative secondary truncation of the life cycle, although Schmidt and Chaloupka (1969) referred to A. hirudicola as a neotenic parasite. As indicated above (see also Fink, 1982; Brooks and McLennan, 1993), progenesis and neoteny refer to specific aspects of ontogenetic changes in attributes of the organisms themselves, rather than to the ecological context of such changes. Heterochronic changes in ontogeny, however, can be associated with changes in the ecological context of the life cycle. For example, O'Grady's (1987) experiments with G. intestinalis resulted in paedomorphic changes in morphology within the ancestral life-cycle pattern in which cercariae emerging from the molluscan intermediate host encyst in the epidermis of an adult frog, becoming metacercariae, which are ingested by the frog with sloughed epidermis, then excysting and maturing to adulthood in the upper small intestine of the adult frog. The paedomorphic development in this case was triggered by the use of a novel definitive host rather than truncation of the number of hosts in the life cycle. In Alloglossidium spp., it appears that both truncation of the life cycle and a switch in definitive hosts may have been evolutionary stimuli for paedomorphic development in general, though not in any particular trait.

The diversity of life cycles of digeneans appears to have evolved through a complex series of elongations, truncations, and modifications of the ontogenetic trajectories, leading from egg to adult, accompanied by additions, deletions, and switches, of hosts. As a consequence, as a group, digeneans would appear to represent a rich system for assessing the relationship between fundamental ecological changes in life-history traits and the entire range of heterochronic changes in ontogeny, both paedomorphic and peramorphic. One could imagine life-cycle lengthening to be associated with the peramorphic changes, such as addition of stages in the life cycle. Alternatively, this could be associated with paedomorphic changes, such as slower rates of maturation. In a complementary way, life-cycle truncation could be associated with either peramorphic phenomena, such as accelerated rates of maturation (e.g., as suggested by McMullen, 1938), or, as appears to be the case with Alloglossidium spp., with paedomorphic phenomena.

CONCLUSIONS

Parasitology has a rich tradition of studies linking taxonomy, ecology, and life cycles and development. This tradition has produced an enormous amount of empirical evidence demonstrating that parasites form highly integrated reproductive–developmental–ecological systems that are highly persistent through space and time, i.e., evolutionary modules (Maynard Smith and Szathmary, 1995) or evolutionarily stable configurations (Wagner and Schwenk, 1999). In addition, phylogenetic studies of parasites, especially of parasitic platyhelminths, represent 1 of the most progressive areas of systematic biology

(see, e.g., contributions by Littlewood and Bray, 2001; for an online database of published phylogenies for parasitic helminths, see http://brooksweb.zoo.utoronto.ca). Consequently, parasitologists should be at the forefront of research in evo–devo and integrative biology, and parasite systems should be model systems of choice.

I hope this contribution also reminds all readers of the importance of basic research in building platforms for high-visibility studies in evolution and development. If Alloglossidium spp. become a useful model system for evo–devo and integrative biology studies, there will be a tendency to forget those whose work made that possible. Alloglossidium spp. is such an outstanding model system because of more than 30 yr of effort by many people, none of whom could have anticipated the emergence of evo–devo and integrative biology. More importantly, most of this work has been done for very little money by researchers working in small institutions lacking doctoral research programs. Jerry Schmidt worked at Northern Colorado State University; Fred Vande Vusse worked at Gustavus Adolphus College. Bill Font's contributions began when he was a graduate student at Louisiana State University, where Ken Corkum directed an inspired group of graduate students without major funding, and Font's subsequent contributions have stemmed from research at the University of Wisconsin–Eau Claire and Southeastern Louisiana State University. For dedicated and creative scientists, the size of the institution and the research budget need not be an impediment to producing high-quality research. These are the people who produce the quiet classics, and they need to be recognized for their invaluable contributions.

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APPENDIX 1—DISCUSSION OF DIFFERENCES IN PHYLOGENETIC RESULTS USED IN THIS CONTRIBUTION AND IN THOSE REPORTED BY SMYTHE AND FONT (2001)

Smythe and Font (2001) reported that their analysis produced between 9 and 244 equally parsimonious trees, depending on how certain traits were treated and whether some traits were excluded from the analysis. Their results were actually much more robust than it might appear. The large number of equally parsimonious trees, and some of the homoplasy reported, is the result of 4 technical problems.

The first 2 of these are minor. There is an apparent error in the analysis, so that reproducing their results using their published data matrix results in trees 1 step shorter than those reported by Smythe and Font (2001). If we treat character 8 as ordered when running the unordered analysis, we obtain trees 60 steps long, as reported by Smythe and Font, whereas if we treat all characters as unordered, the trees are 59 steps long. In addition, when Smythe and Font used ordered characters, they ordered characters 1, 5–8, 11, and 18. Examination of the effects of ordering these characters demonstrated that ordering characters 7 and 8 produced additional homoplasy, indicating that the ordering sequence specified by Smythe and Font was not supported by congruence with other traits.

The third problem is the use of a default option in the computer program PAUP. This is found in the menu item called Parsimony Settings. The default setting is "collapse branches

if maximum length is zero." This option gives the program permission to guess with missing data codes rather than treating them as lack of data. This is useful in analysis of nucleotide sequences, when it is not certain whether a gap in a sequence is meaningful information or only missing information. For analyses in which this is not an issue, such as morphological data, one should always choose the option "collapse branches if minimum length is zero" because this avoids creating groupings based on mutual absence of information.

The fourth problem is the use of *Glypthelmins quieta* as 1 of the outgroups. Smythe and Font (2001) reportedly used the 2 species of *Macroderoides* as primary outgroups, accepting the assessment by Carney and Brooks (1990) that *Macroderoides* is the sister group of *Alloglossidium*. They stated that they included *G. quieta* as a third outgroup because it is representative of a more generalized macroderoidid. This indicates some lack of expertise with outgroup analysis in phylogenetic systematics. Phylogenetic systematics is not analysis of taxa but of characters. For each character, or transformation series, there is a plesiomorphic state (one might mistakenly call this the generalized state, but it is more properly thought of as the ancestral condition for that trait), and that is the state occurring in the outgroups, which also occurs in at least 1 member of the ingroup (special exceptions are the traits that diagnose the monophyly of the ingroup, which, by definition, do not occur in the outgroups). There is no such thing as a plesiomorphic, or generalized, species within phylogenetic systematics. It is likely that Smythe and Font (2001) wished to add a third outgroup that represented a clade more basal to *Macroderoides + Alloglossidium*, but if so, their choice of *G. quieta* was unfortunate, for several reasons. First, we do not have a good estimate of phylogenetic relationships within the Macroderoididae (it is not certain that all genera currently included in the family form a monophyletic group: see Tkach et al., 2000, 2001), so it is possible that *Macroderoides + Alloglossidium* themselves represent the basal macroderoidids. Second, we are not certain *Glypthelmins* is monophyletic. The most recently published phylogenetic assessment of the group is highly ambiguous on this point, indicating a basal polytomy in the group; the various members of this assemblage of species may belong to 2 different families. Third, even if *Glypthelmins* is monophyletic and is, in some sense, a basal macroderoidid, *G. quieta* is unquestionably 1 of the most highly derived members of the group. Fortunately, phylogenetic systematic methods are extremely robust when multiple outgroups are used, and the inclusion of *G. quieta* as an outgroup does not change the fundamental results. It does, however, produce additional homoplasy in the results, homoplasy that is more appropriately dealt with in the context of a larger-scale phylogenetic analysis.

If we, therefore, use only the species of *Macroderoides* as outgroups, as done by Carney and Brooks (1990), if we code characters 1, 5–6, 11, and 18 as ordered, and if we use all 21 characters, the result is 3 equally parsimonious trees each with a consistency index of 54% and a retention index of 69%, rather than 9 equally parsimonious trees each with a consistency index of 48% and retention index of 68% as reported by Smythe and Font (2001). One of these 3 equally parsimonious trees has the same topology as the majority-rule consensus tree, and I have used that in my discussion in this contribution. It is also identical to preferred tree of Smythe and Font.

As indicated above, the fact that correcting these technical errors does not alter the overall results and conclusions by Smythe and Font (2001) attests to the robustness of their data and of phylogenetic systematic methods.