

Fact, Theory and Tradition in the Study of Molluscan Origins

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Discussions of phylogenetic relationships and origins often use figures called “archetypes,” or “reconstructed common ancestors.” Here we discuss one such creature, the hypothetical ancestral mollusc or HAM. HAM first appeared 150 years ago as T.H. Huxley’s archetypal mollusc and has speciated often since then. Radiations have occurred within both fossil and Recent taxa (from the paleontological and neontological literature, respectively). Eight species have appeared in the last 30 years alone and at least six species remain extant today.

We performed both phenetic and cladistic analyses of the character states present in these figures. Our best approximation of the phylogeny of HAM (based on known ancestor-descendant relationships and stratigraphy) requires 53 more steps than the most parsimonious tree found by cladistic analysis. Phenetic trees based on neighbor joining and UPGMA analyses require two and twelve more steps, respectively than the most parsimonious trees. The evolution of HAM exhibits all the typical processes and developmental heterochronies thought to encompass organic morphological evolution, and both phenetic analysis and cladistic analyses have problems relating paedomorphic taxa.

HAM has not aided evolutionary biologists or paleontologists in solving problems, but it has often had the opposite effect, by requiring that theories be treated within its framework. Moreover, real data have ended up being “tested” against a hypothetical anatomy to determine whether a hypothesis should be accepted or rejected. It has been argued that HAM serves a valuable role as a pedagogical teaching aid. Unfortunately, these imaginary animals do not come clearly labeled with warnings about the harm that they might do if mistaken for real organisms.

Key words: Mollusca; hypothetical ancestors; phylogeny; archetypes; typology; conceptual evolution.

According to the current evolutionary ontology, species, lineages, and many other things are individuals, not classes (Ghiselin 1974, 1997; Hull 1976). This suggests that at least some of those “other things” might be studied from an evolutionary point of view. Among the candidates have been sport cars (Rowland 1968), literary genres (Ghiselin 1980), cladists (Carpenter 1987), and scientific theories (Hull 1988). The list could be greatly expanded. One intriguing possibility is lineages of diagrams in the scientific literature. Griesemer and Wimsatt (1989) examine the diagrams that illustrate the Weismannian concept of the continuity of the germ plasm and discuss the study of such diagrams in considerable depth. As they point out, such diagrams can be dated precisely,

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are a very convenient focus of attention, and the analogy between a given diagram and an organism that forms part of a lineage is captivating.

Here we consider some diagrams that depict something even more strongly analogous (and perhaps in a certain sense homologous) to organisms: pictures of hypothetical ancestral molluscs that adorn (one might prefer to say disfigure) the pages of the scientific literature. Our study differs from that of Griesemer and Wimsatt by incorporating phenetic and cladistic analyses to estimate the relationships and character transformations of the images. Furthermore, we direct our commentary primarily to comparative biologists and paleobiologists like ourselves, though we hope that historians and philosophers of science will find it useful as well.

Discussions of phylogenetic problems often use figures called “archetypes,” “*Baupläne*,” or “reconstructed common ancestors.” There is some disagreement as to what such diagrams are supposed to mean. Idealistic morphologists, such as Remane (1952) have asserted that they are just diagrams of the relative position of parts, designed, perhaps, to look like animals. Others, such as Beklemishev (1969), have claimed that, if done properly, they really do represent the common ancestor. From the point of view of taxonomy, we might consider them “pictorial diagnoses”—summaries of the features common to all the organisms in a taxon. From the point of view of phylogenetics, we might consider them hypotheses about a common ancestor—illustrating what was inferred to be present in the last common ancestor of the group. These interpretations are not mutually exclusive.

Systematists often treat hypotheses about common ancestors as results, rather than as starting points, of investigations. To do so makes sense only in terms of a naive inductionism that does no justice to the subtleties of scientific reasoning. Hypotheses are conjectures that are tested by reference to evidence, perhaps by refuting them, as suggested by the title of a well-known book by Popper (1962). Whether one is a “refutationist” (who would deny that hypotheses can be verified) or not, a hypothesis remains a hypothesis irrespective of whether one has gathered any evidence that might lead one to prefer it or some alternative.

Hypotheses are tested by means of experiments, or by comparative methods that are of the same basic logical form as experiments. When a hypothesis explains a variety of empirical data and withstands serious attempts at refutation, it is preferable to one that explains less or generates false predictions about the material universe. With respect to hypothetical ancestral models, this means that at the very least they should have the properties that biologists find among living organisms in general. But the mere plausibility of such a model is no reason to prefer it to some alternative that is equally plausible, or perhaps even more so.

Nonetheless, hypotheses often remain viable in spite of contradictory evidence. There may be some conditions under which it is scientifically legitimate not to falsify a particular hypothesis even when it seems to have been refuted. For example, the test may refute, not the hypothesis itself, but another premise in the system, for example, a “fact” that turns out to be an inaccurate measurement. However, when the hypothesis is simply taken for granted, and contradictory data are ignored or explained away, something is wrong. In this case we are dealing with something that functions not as a hypothesis, but as an assumption being treated as if it were fact. Non-algorithmic phylogenetic hypotheses are often treated this way, but so are many others. The reasons for this are not to be sought in pure logic. Scientists are not alone in accepting what everybody around them takes for granted. They believe what they read in textbooks and what they were told by their teachers. What they accept becomes an integral part of a body of knowledge, in which fact and conjecture are not clearly distinguished. The data then become selectively gathered in a way that tends to “confirm” the assumptions. If unaware of the premises, scientists may be unable to recognize the circularity of their own reasoning. Thus, we get covert assumptions that are better called “tradi-

tions” than “hypotheses,” but that are treated as “facts” by their proponents. Only by going back to fundamentals, identifying the premises, and distinguishing fact from theory, can we hope to get outside the circle. The initial premises must be conjectural and open to revision. The notion that one can start out with unbiased data is a preposterous myth.

Traditions, like species, are individuals: they originate, vary, compete with one another, evolve, and, ultimately, become extinct. To come to grips with them, we must deal with them as historical entities, see where they came from, and what forces have maintained them in their environments. Herein we discuss one such creature, Huxley’s Archetypal Mollusc — HAM for short. Kept in an artificial, polemic environment, it has flourished and persisted in spite of its teratological character, an animal that never existed except in the fancy of theoreticians.

MATERIALS AND METHODS

TAXA STUDIED.— Our study lineage dates from Huxley (1853) who referred to his special creation as the “archetypal molluscous form” and cautioned that he was not proposing any idealized form. Instead, Huxley viewed his archetype as a starting point on which the “the known laws of development” might act to modify it into “the different secondary types.” Thirty years later Lankester (1883) referred to his modification of Huxley’s diagram as the “schematic mollusc” in the figure caption. However, within the text Lankester allowed for the possibility that the schematic mollusc might, in fact, represent the “original Mollusc or archi-Mollusc (more correctly Archimalakion).” For consistency we here select Huxley’s use of the phrase “archetypal molluscous form” as the first designation, and because of the lack of rules of nomenclature for common names, and as first revisers of HAM nomenclature (neither of which matters), transmute this to “Huxley’s Archetypal Mollusc” or HAM, and designate it as the type species and the common ancestor of all taxa placed in the imaginary genus *Hamus*.

Specimens collected in academic libraries provided clear evidence that HAM has speciated often since 1853. At least eight species have appeared in the last 30 years alone and more than six species remain extant today. These species include both fossil and Recent taxa (from the paleontological and neontological literature respectively). Twenty-two taxa were included in the initial analyses; the outgroup taxon and 21 ingroup taxa (Table 1 and Appendix). These taxa were chosen because they represented both neontological and paleontological lineages, and are mostly found in textbooks.

Six additional “Cambrian” species were included in a second analysis. These species have a first occurrence in Pojeta and Runnegar (1976: Figs. 9a-f), and have had a very important role in the discussion of monoplacophoran and gastropod relationships (e.g., Peel 1991; Geyer 1986; Parkhaev 2001). We included them here in a second analysis because fossils can often be extremely important in phylogenetic reconstruction (Donoghue et al. 1989).

EXCLUDED TAXA. — We restrict our analysis of taxa primarily to the Anglo-American subclade *Hamus* s.s. Other taxa, belonging to separate intellectual traditions (i.e., lineages) have evolved in relative isolation to the Anglo-American fauna. For example, many of the German language taxa are clearly distinct, the language barrier inducing a certain amount of endemism and reduced opportunities for outbreeding and hybridization although there is some evidence of limited outcrossing on the continent. For example, Haszprunar (1992) published a HAM in an Italian journal and Salvini-Plawen and Steiner (1995) published in an English book (we include *Hamus salvini-teinerorum* in our analysis because of its prominent Anglo habitat). Also see remarks on the relationships of *Hamus pelseneeri*, *Hamus (Jambonus) portmanni* and *Hamus (Schinkenus) naefi* below.

Other taxa such as the peculiar *Protohamus verrilli* developed by Verrill (1896) and

Protohamus yongi (Yonge 1960) have been excluded from our analysis. Verrill's species was a larva or "veliger-like form"; an enviable hopeful monster, evidently produced through complete progenetic loss of all adult structures. *P. yongi* is similar to Verrill's creation, although Yonge's later special creations are clearly referable to the genus *Hamus*.

OUTGROUP AND CHARACTER SELECTION.— The data available for the study of the evolution of *Hamus* are unique. We possess an almost perfect fossil record for the taxon, preserved in dated textbooks and other publications (Fig. 1; Table 1). We also have the actual common ancestor in its natural environment. The characters are limited to the anatomical features that each author penned into their creature, and the character transformations fixed by our possession of most of the actual phylogeny of the group, often indicated by such expressions as "After . . .", or "Redrawn from . . ." in the caption of the figure. In tracing the various derived forms from their known origin, we can readily observe the character transformations, evolutionary trends and divergences. Moreover, we have an excellent opportunity to test phylogenetic hypotheses (e.g., phenograms and cladograms) with the actual history of the group.

HAM did not arise without antecedents. Traces of its early beginnings can be found in the writings of von Baer (1828:pl. 3, fig. 12). However, as a clearly recognizable entity (i.e., an individual), from which the others were derived, it takes its origin from a drawing by T.H. Huxley (1853) (Fig. 2). Therefore, *Hamus huxleyi* is the consummate sister taxon and outgroup.

The ancestral condition exhibited by *Hamus huxleyi* provides the plesiomorphic states for characters used in our analysis (Fig. 2; Appendix). These character states include a body with clearly differentiated head and foot, cephalic and optic tentacles, and a dorsal visceral mass covered by a mantle. Surprisingly, a shell is absent. The viscera consist of a straight digestive tract with a style sac, a heart with an anterior aorta, and paired kidneys. Gills are present on the postero-dorsal surface of the animal. It is important to note that in the ancestral condition the gills are not located in a posterior mantle cavity. The *H. huxleyi* nervous system consists of four major pairs of ganglia (cerebral, pleural, pedal, and buccal). Obviously Huxley had a rather snail-like ancestor in mind — a sort of untorted limpet without a shell. It stands to reason that when one thinks typologically one will associate "the mollusc" with the most familiar examples, rather than with creatures that are more exotic such as chitons or scaphopods.

ANALYSIS.— The character matrix and analysis (see Appendix) describes the 36 characters used in our analyses and their states. We performed both phenetic and cladistic analyses of the data using PAUP* Ver. 4.0b10 (Swofford 1998). The UPGMA and neighbor joining options in PAUP*

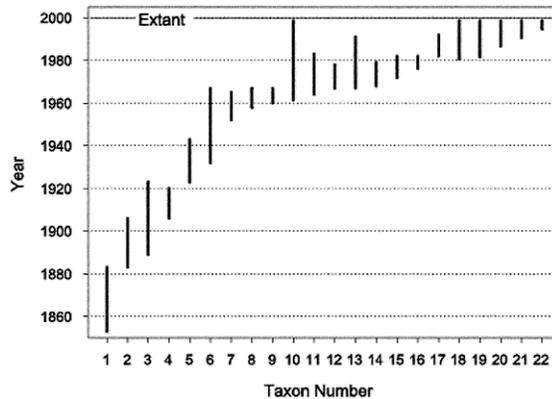


FIGURE 1. Stratigraphic distribution of *Hamus* species treated herein. Taxa 10 and 18–22 are currently extant. Taxon numbers are referenced to Table 1.

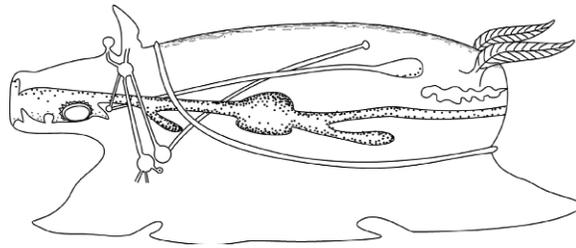


FIGURE 2. *Hamus huxleyi*. T.H. Huxley's Archetype of the Cephalous Mollusca. Redrawn from Huxley (1853).

TABLE 1. Data for *Hamus* species analyzed here. Citations for figured specimens consists of Author(s) + First columns. Data present below are also graphically represented in Figure 1 (First and Last occurrences) and Figure 8a (Duration).

Taxon No.	Taxon	Author(s)	First	Last (to 2000)	Duration	Paleo	Textbooks	Insular
1	<i>H. huxleyi</i>	Huxley	1853	1883	30			√
2	<i>H. lankesteri</i>	Lankester	1883	1906	23			√
3	<i>H. nicholsoni</i>	Nicholson & Lydekker,	1889	1923	34	√	√	√
4	<i>H. pelseeneeri</i>	Pelseeneer	1906	1920	14		√	√
5	<i>H. swinnertoni</i>	Swinnerton	1923	1943	20	√	√	√
6	<i>H. borrapottorum</i>	Borradale & Potts	1932	1967	35		√	√
7	<i>H. moolafisherorum</i>	Moore, Lalicker & Fisher	1952	1965	13	√	√	
8	<i>H. mortoni</i>	Morton	1958	1967	9			√
9	<i>H. eastoni</i>	Easton	1960	1967	7	√	√	
10	<i>H. barnesi</i>	Barnes	1963	—	37		√	
11	<i>H. mortonyongorum</i>	Morton & Yonge	1964	1983	19			√
12	<i>H. hickmani</i>	Hickman	1967	1978	11		√	
13	<i>H. meglitschi</i>	Meglitsch	1967	1991	24		√	
14	<i>H. russellhunteri</i>	Russell-Hunter	1968	1979	11		√	
15	<i>H. staseki</i>	Stasek	1972	1982	10			
16	<i>H. yongethompsonorum</i>	Yonge & Thompson	1976	1982	6			√
17	<i>H. barthbrosonorum</i>	Barth & Broshears	1982	1992	10		√	
18	<i>H. bossi</i>	Boss	1982	—	18			
19	<i>H. seedi</i>	Seed	1983	—	17			√
20	<i>H. barcalolivorum</i>	Barnes, Calow & Olive	1988	—	12		√	√
21	<i>H. ravenjohnsonorum</i>	Raven & Johnson	1992	—	8		√	
22	<i>H. salvinisteinerorum</i>	Salvini-Plawen & Steiner	1996	—	4			

were used to calculate phenetic trees based on distance matrix of mean character differences. In both phenetic analyses ties were broken randomly. The data matrix was also subjected to heuristic searches under maximum parsimony with *H. huxleyi* serving as the outgroup. All characters were equally weighted and unordered, and were assumed to show accelerated character transformation. Strict and majority rule (50%) consensus trees were calculated.

RESULTS

The single tree from the UPGMA analysis is presented in Fig. 3a; it contains two distinct groupings. The first group is made up of the early HAM taxa + paedomorphic taxa + flatworm-like

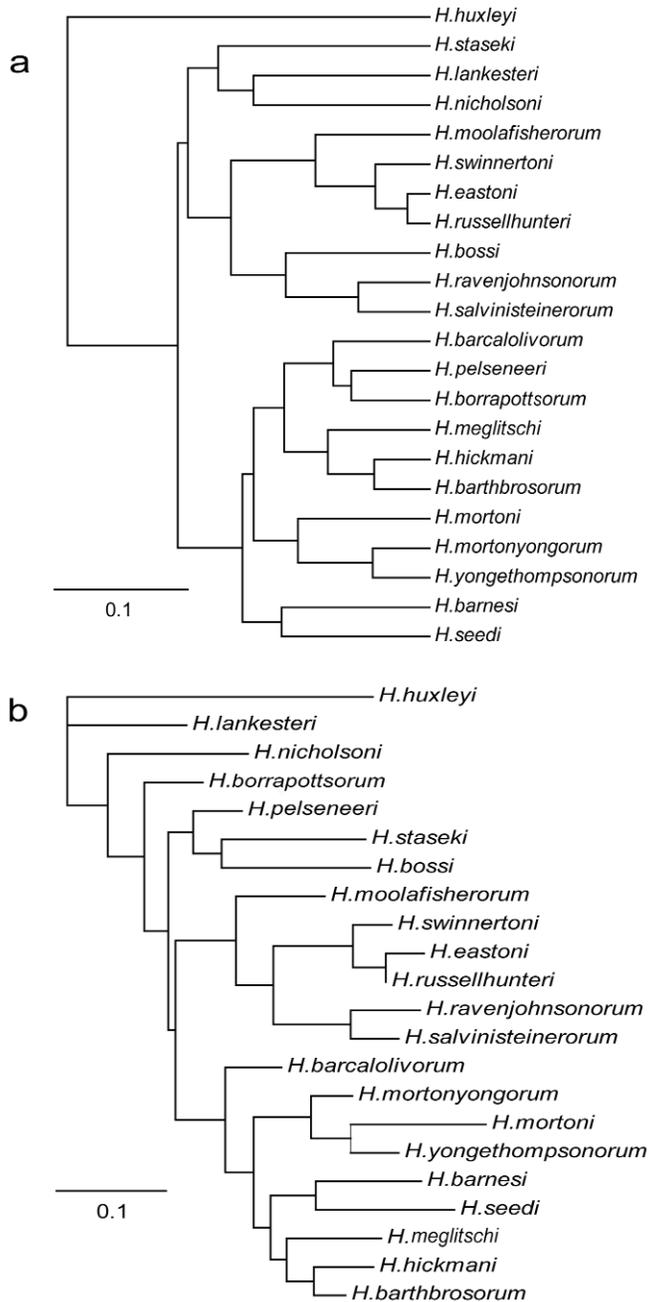


FIGURE 3. Phenetic trees from analysis of distance matrix of mean character differences. a. UPGMA and b. neighbor joining analysis. (See Appendix for data matrix.)

consensus tree (Fig. 4b) is virtually identical to the neighbor joining solution; they differ primarily in the placement of *Hamus mortonyongorum* and *Hamus borrapottorum*. Half of the resolved branches appear in 80% or more of the most parsimonious trees (Fig. 4b).

taxa. Although the paedomorphs + flatworm-like taxa are clearly delimited in the analysis, the disjunct stratigraphic record of these taxa suggests that this cluster is better attributed to convergence rather than common ancestry. The second cluster consists primarily of textbook HAMs + the insular (*i.e.*, British) HAMs. Unlike the first cluster, the textbook and insular HAMs do not form unique groups, but instead are mixed within the cluster. The topology of the UPGMA tree requires 108 steps.

The single tree from the neighbor joining analysis is presented in Fig. 3b. In the neighbor joining analysis, the flatworm-like taxa group with the textbook and insular HAMs with the paedomorph group as its sister taxon. *Hamus lankesteri* and *Hamus nicholsoni* are outside of these three groups in both phenetic analyses. The topology of the neighbor joining tree requires 98 steps.

Maximum parsimony analysis found 76 trees with 96 character steps. Strict and majority rule consensus trees for these trees are presented in Fig. 4. In the strict consensus tree, four subclades are present (Fig. 4a). These are: (1) *Hamus mortoni* and *Hamus yongethompsonorum*, (2) *Hamus pelseneeri* and the flat worm-like HAMs, (3) the paedomorph group, and (4) HAMs from four American invertebrate zoology textbooks and the single insular species *Hamus seedi*. The majority rule

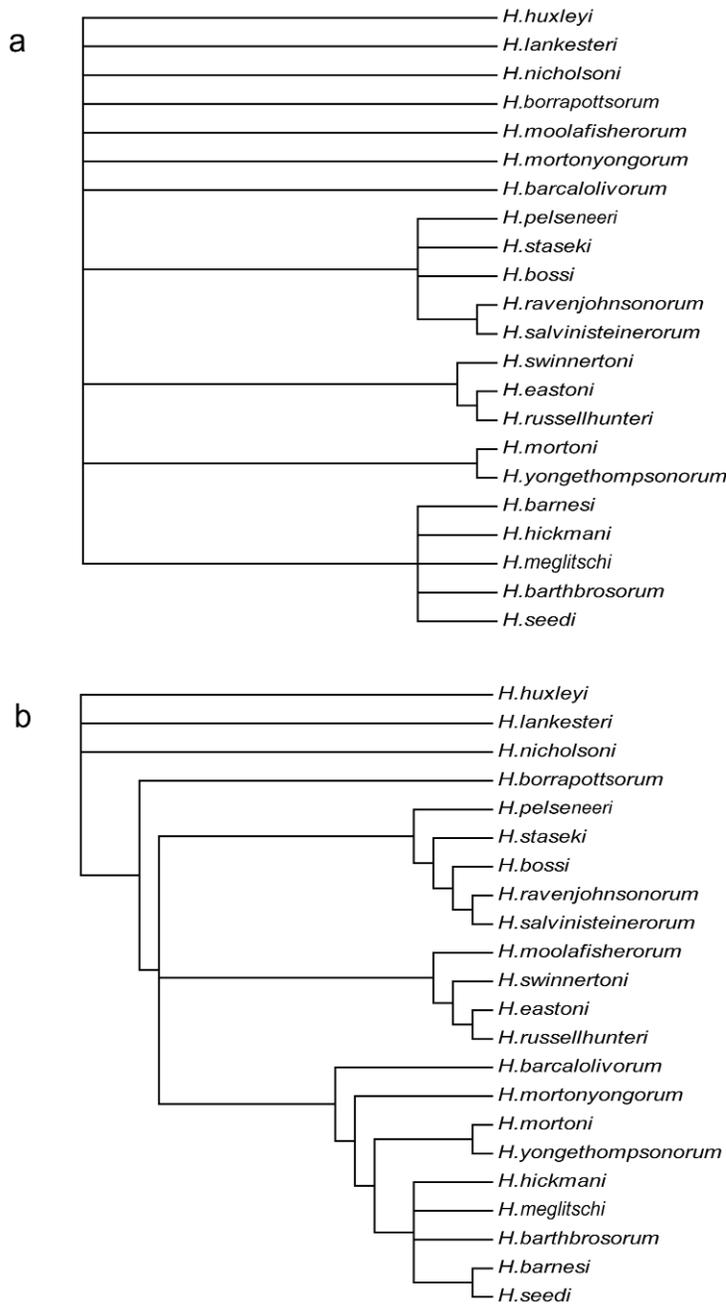


FIGURE 4. Consensus cladograms of 76 most parsimonious trees found by PAUP* analyses of the 22 HAM taxa listed in Table 1. CI and RI for randomly selected tree (No. 127) = 0.4725 and 0.6000, respectively. a. Strict and b. majority rule consensus trees. (See Appendix for data matrix.)

pojetarunnegarorum taxon groups. The remaining members of the complex form their sister taxon. The overall effect of the addition of fossils to our analysis is to intermingle members of the flat-

In the final cladistic analysis, the “Cambrian” species complex *Hamus pojetarunnegarorum*, comprising six taxa, was added to the data matrix. *Hamus pojetarunnegarorum* taxa are well known in the Cambrian literature (e.g., Pojeta and Runnegar 1976) where they are typically used to differentiate between untorted and torted molluscs. Because of their association with some of the oldest molluscan fossils, they have some of the highest number of unknown character states in the analysis, being surpassed only by some of the paedomorphic taxa (see Appendix). The addition of these taxa to the data matrix produced 4875 trees of 1034 character steps. In the strict consensus tree, the addition of these taxa produces a large unresolved polytomy at the base of the tree while the only remaining subclades are *Hamus mortoni* and *Hamus yongethompsonorum* and the HAMs from four American invertebrate zoology textbooks + the single insular species *Hamus seedi* (Fig. 5a). In the majority rule consensus tree (Fig. 5b), the complex is situated in a subclade consisting primarily of paedomorphs with the exception of the flat-worm-like *Hamus ravenjohnsonorum* with which *H.*

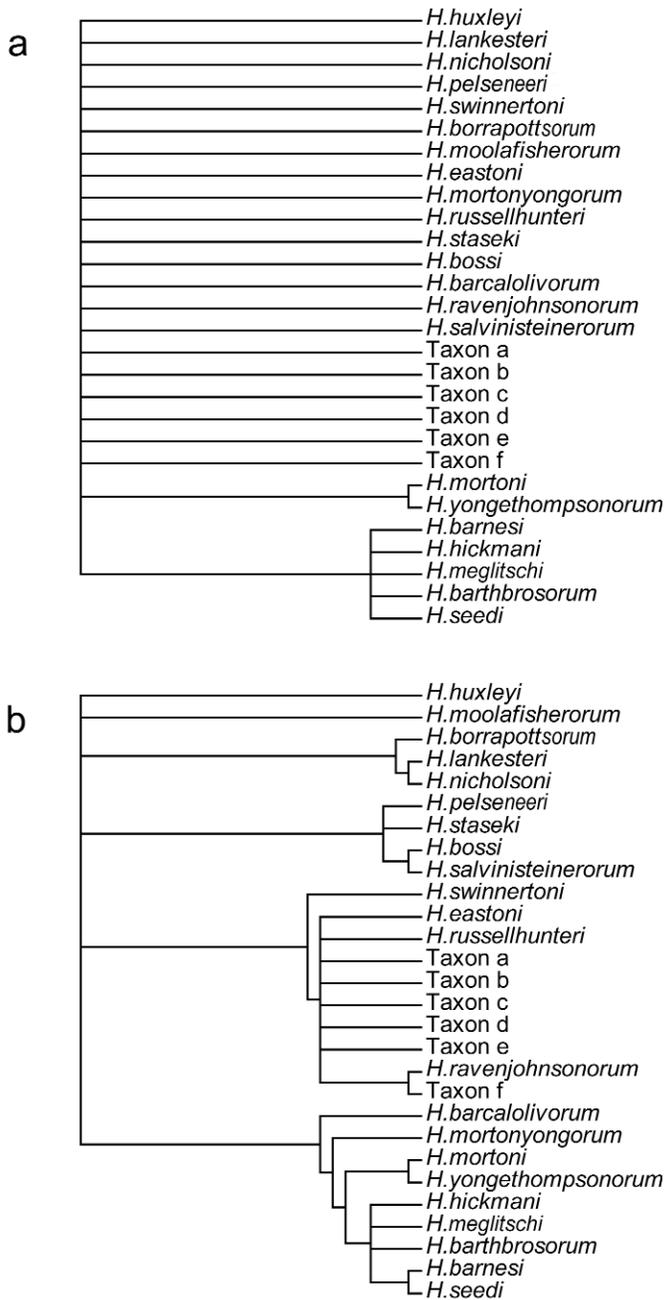


FIGURE 5. Consensus cladograms of 4875 most parsimonious trees found by PAUP* analyses of the 22 HAM taxa listed in Table 1 plus six taxa of the "Cambrian" species complex *Hamus pojetarunnegarorum*. CI and RI for randomly selected tree (No. 356) = 0.4757 and 0.6932, respectively. a. Strict and b. majority rule consensus trees. (See Appendix for data matrix.)

worm-like and paedomorph groups and reduce overall resolution of these groups. In contrast, occurrence of the subclade consisting of *Hamus mortonyongorum*, *Hamus barcalolivorum*, *Hamus mortoni*, *Hamus yongethompsonorum*, the four American invertebrate zoology textbook HAMs and *Hamus seedi* increases from 68% to 97% at three nodes because of the addition of the fossils (*cf.* Figs. 4b and 5b).

Our best approximation of the actual phylogeny of HAM based on known ancestor-descent relationships and stratigraphy (Fig. 6) requires 53 more steps than the most parsimonious trees. Three distinctive clades are present in this phylogeny (Fig. 6):

1. **Lankester group.**— an early group (1883) of mostly fossil species tracing their ancestry to *Hamus lankesteri*. A single pair of paedomorphs represents the most "derived" taxa within this clade.
2. **Morton group.**— a large, comb-like group whose members trace their ancestry to *Hamus mortoni* (1958). This group consists of intermingled insular and textbook *Hamus* species. A second pair of paedomorphs is nested within this clade.
3. **Stasek group.**— the sister taxon of the Morton group, and although it shares the same minimum age of divergence (1958) with the Morton group, the earliest known members date from 1972 (*Hamus staseki*). Half of the extant *Hamus* species are members of this group. The continental taxon *H. salvinisteinerorum* is arbitrarily placed in this clade because of its recurrent sister taxon relationship with *H. ravenjohnsonorum* in all analyses with the exception of the addition of the Cambrian taxa.

Two of these groups were

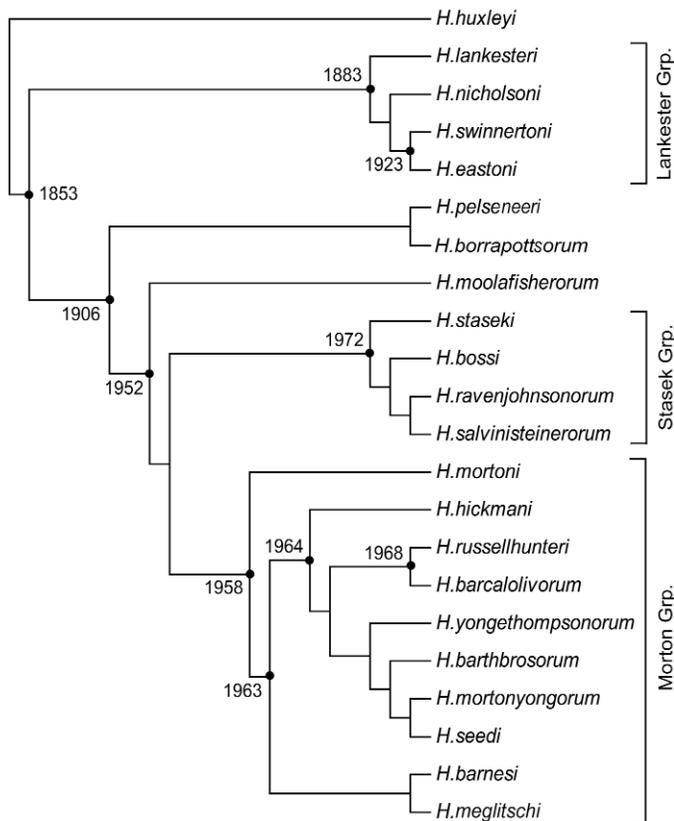


FIGURE 6. Best approximation of the actual relationships of *Hamus* species based on known ancestor-descent relationships and stratigraphy. Dates at nodes indicate minimum divergence times for sister taxa. Consistency index = 0.2986, retention index = 0.1583.

and their anatomies have converged on each other as well as with the fossil taxa (Fig. 5b). However, there is a 45 year difference in the time of origination of the first and most recent of these groups and any suggested relationship is likely to be spurious. The universal occurrence of this group in our analyses shows that whether real organisms or cartoons, paedomorphs are difficult taxa to relate in phylogenetic reconstructions.

STRATIGRAPHY.— Fossil HAMs appear earlier in the record than the majority of zoological ones (Fig. 1, Table 1). However, not one fossil HAM has originated in a textbook environment since 1964. In contrast, 76% of zoological HAMs have originated since 1960 and all six of the extant HAMs (*i.e.*, texts and monographs not out of print) are zoological species (Table 1). Before 1960, the ratio between fossil and zoological *Hamus* species was about 1:1 (Table 1).

Following Norell and Novacek (1992) we compared the known stratigraphic ranges with divergence patterns based on our cladistic and phenetic analyses. Testing the fossil record against cladistic phylogenies typically determines how complete the record probably is, and therefore how useful the taxon might be for stratigraphic purposes (Padian et al. 1994). However in our unique situation, the stratigraphy is certain and therefore can be used to evaluate the reconstructed divergence patterns (Fig. 7).

When the number of branch nodes between *Hamus huxleyi* and the taxa on the true tree are

present to varying degrees in our analyses (*cf.* Figs. 3–6). Components of the Morton group are present in the UPGMA and neighbor joining trees, and in both the strict and majority rule consensus cladograms. The Stasek group was represented by the flatworm-like taxa in the UPGMA and neighbor joining analyses, and in the majority rule consensus cladograms. In the UPGMA analysis the Stasek group was the sister taxon of the paedomorph group (Fig. 3a), while in the majority rule consensus cladogram, the neighbor joining tree, and the true phylogeny, this group is the sister taxon of the Morton group (*cf.* Figs. 3b, 4b, and 6).

The “Paedomorph group” which is present in some form in all of our analysis is polyphyletic and represents two separate events, one in the Lankester group and the other within the Morton group. We regard these taxa as paedomorphs because of their degenerated morphology,

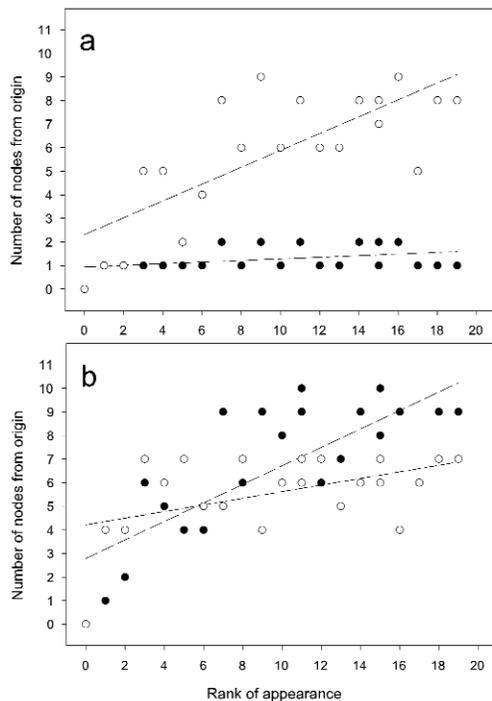


FIGURE 7. Scatterplots of the relationship between rank of appearance (as measured by absolute age) and the number of branch nodes between origin and taxon on tree. a. Results plotted from cladistic analyses. Solid circles from strict consensus cladogram ($r^2 = 0.1312$, slope = 0.0335); open circles from majority rule consensus cladogram ($r^2 = 0.5710$, slope = 0.3571); b. Results plotted from phenetic analyses. Solid circles from neighbor joining tree ($r^2 = 0.5900$, slope = 0.3920); open circles from UPGMA phenogram ($r^2 = 0.2299$, slope = 0.1400).

shell, pedal nerve cords, gonads, the movement of the gills into the mantle cavity, and the loss of a differentiated foot, style sac, radula, jaws, aorta, statocysts, epipodium, buccal ganglia, optic tentacles, and buccal mass. This grade in the evolution of *Hamus* (which is generally retained through *Hamus moolafisherorum*) represents a sort of “average” mollusc, with emphasis upon the more “primitive” forms. The basic body plan was arrived at by assuming that characters present in the “most primitive” members of each (extant) class were also present in a common ancestor, and all (extant) classes could be derived from it (see Huxley 1853). Thus, many early *Hamus* species were intended to encompass the characters of the five molluscan classes then known. The discovery of other taxa (such as the fossil *Rostraconchia* and the still extant *Monoplacophora*) has done surprisingly little to induce serious rethinking of this original structure (see below).

The only apomorphy of the Lankester group is the appearance of both a posterior and anterior aorta. The HAM of Nicholson and Lydekker (1889) traces its ancestry directly from *Hamus lankesteri*, but shows little of the anatomical retrogression seen in *Hamus swinnertoni* and *Hamus eastoni*. The lack of a radula and gonad in *Hamus nicholsoni* suggests a possible common ancestor, but the lack of tentacles and the cap-shaped shell also suggests a spurious relationship with *Hamus pelseneeri*, which would not make an appearance for another 17 years. A peculiar autapo-

plotted on the rank of appearance of the taxa, the resulting r^2 of the regression equals 0.6746 and the slope equals 0.4223. This is not significantly different from the majority rule consensus tree (Fig. 7a) or the phenetic UPGMA tree (Fig. 7b) (pairwise t -test, $p > 0.05$). However, it is significantly different ($p = 0.0012$) from the neighbor joining tree regression (Fig. 7b). The strict consensus tree has virtually no stratigraphic signal with a slope of 0.0345 (Fig. 7a).

Origination rates remained below 0.15 species/year for the first 80 years of Hamman history, however between 1960 and 1980 origination rates skyrocketed to over 0.40 species/year and have since begun to decline (Fig. 8a). Extinction rates have typically been lower, but follow a similar trend (Fig. 8a). The consequence of the difference between these two rates is a roughly exponential species diversity curve through time (Fig. 8b). Although species diversity was ≤ 2 for over 100 years, the substantially higher origination rates have maintained a relatively stable diversity of five or more HAMS for the last 30 years (Fig. 8b). Lastly, mean duration for individual *Hamus* species is 16.8 ± 9.4 years and the relative frequency of species durations is skewed towards shorter durations (Fig. 8a).

RELATIONSHIPS AND EVOLUTIONARY SCENARIO.—Members of the ingroup are derived from *Hamus huxleyi* by the acquisition of a

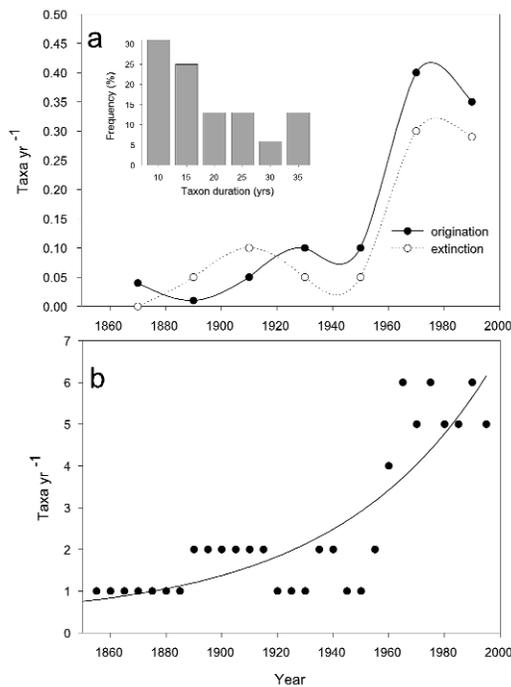


FIGURE 8. Macroevolutionary data for *Hamus*. a. extinction and origination rates, and species duration; b. species diversity.

loss of eyes. This basic body plan was arrived at by assuming that the characters are present in most of the remaining taxa with the exception of members of the Stasek group. Something analogous to “species selection” may help to explain why Pelseener’s HAM had such a strong influence on Anglo-American HAM speciation. Pelseener was a Belgian and wrote mostly in French, but *H. pelseeneri* appeared in a very influential textbook in English in 1906. Actually, this was a punctational event in a marginal habitat — Pelseener (1897) published an earlier version in French. Pelseener’s HAM species also had an important dispersal episode. Pelseener (1885) remarks that he worked in Lankester’s laboratory during the winter of 1884–1885, thereby allowing us to document not only direct ancestry, but perhaps the original dispersal event between England and the continent as well. The HAM of Moore, Lalicker, and Fischer (1952) (*Hamus moolafisherorum*) is diagnosed by ventral digestive glands, and the loss of the pericardium, gonads and pedal nerve cords.

The remaining HAMs are divided into two distinct subclades, and it is this divergence between 1952 and 1958 that marks the beginning of the modern *Hamus* radiation (Fig. 6). Before this branching point, the phylogeny of HAM was primarily comb-like (Fig. 6), the earlier HAMs forming a grade of evolution. The synapomorphies that united these two subclades are the presence of the osphradium and radula. Three synapomorphies diagnose the Morton group; all are typical gastropod characters. They include the presence of a style and gastric shield, osphradium, and afferent gill membrane. The five synapomorphies that diagnose the Stasek group are the reappearance of gonoducts, osphradium positioned on dorsal surface of pallial cavity, multiple shell attachment muscles, and the loss of cephalic tentacles and the digestive gland.

Like *Hamus swinnertoni* (Fig. 9a) the HAMs of Russell-Hunter (1968) (Fig. 9c) and Barnes,

morphology characterizes *Hamus nicholsoni* — the anterior mantle cavity with its single branchia (Fig. 10b). This untorted mollusc with an anterior mantle cavity would be a “hopeful monster” in anyone’s phylogeny, and although it might have served as a novel preadaptation for the Gastropoda, it never produced any descendants. The HAM illustrated by Swinnerton (1923) is directly descended from *H. lankesteri* (“after Lankester”) and is the first instance of pedomorphosis in the taxon *Hamus*. *Hamus swinnertoni* (Fig. 9a) has lost numerous organs, including the radula, gonad, heart, pericardium, kidneys, and the entire nervous system. Moreover, the shell of this species is conical rather than cap-shaped, and the overt morphology is distinctively gastropod-like, in spite of its degenerate viscera. *Hamus eastoni* is the sister taxon of *H. swinnertoni* and is even more degenerate (Fig. 9b).

The common ancestor of *Hamus pelseeneri* and *Hamus borrapottorum* is further characterized by the movement of the digestive gland from the ventral to dorsal position,

gonads opening into the pericardium, and the

Calow and Olive (1993) are undoubtedly products of paedomorphic processes that have beset these species, and as with so many cases of degenerative evolution, we have at least two cases of convergence amongst four taxa. While the known phylogeny of *H. swinnerton* allows us to identify its ancestry, we have no indisputable evidence for the determination of the relationships of the remaining three species. However, mentorship distribution and stratigraphy provide insights into their relationships (see discussion of the Morton group below).

The HAMs of Stasek (1972), Boss (1982), Raven and Johnson (1992) (Fig. 9d) and Salvini-Plawen and Steiner (1996) are all flatworm-like. In addition, the solid shell is lost and replaced by a spicule-studded integument in *Hamus bossi*, *Hamus ravenjohnsonorum*, and *Hamus salvini-steinerorum*.

The appearance of the Morton Group marks a major evolutionary event within the genus (Fig. 6). Members of the Morton group have the most complicated anatomies of any of the *Hamus* species, emphasize gastropod features, and mark a clear departure from previous HAM lineages. This increasing convergence with the Gastropoda is clearly illustrated by the sequence a→b→c→d in Fig. 10 (see also Haszprunar 1992).

Hamus mortoni is diagnosed by six autapomorphies (jaws, two digestive glands, epipodial tentacles, salivary glands, esophageal glands, and spherical kidneys), all of which further emphasize gastropod features. Many features present in the gastropod-like *H. mortoni* are absent in the Morton and Yonge (1964) HAM. *Hamus mortonyongorum* has lost the osphradium, afferent gill membrane and eyes. The nervous system is also condensed, and only a single ganglion remains.

Two American HAMs are basal members of the Morton group — *Hamus barnesi* (Barnes 1963) and *Hamus meglitschi* (Meglitsch 1967). Synapomorphies include the presence of the osphradium on the efferent membrane of the gill and the loss of the hypobranchial gland. The most unusual feature in this subclade is the knobs on the tentacles of *H. meglitschi* — evidently the parallel selection pressure toward gastropod structure in North America has turned it into somewhat of a pulmonate gastropod!

Two more paedomorphs, *Hamus russellhunteri* and *Hamus barcalolivorum*, are treated here as members of the Morton group. This placement is congruent with stratigraphic data and makes sense considering the academic parentage of their creators.

Several non-Anglo-American HAMs often superficially resemble or are erroneously attributed to insular *Hamus* species. For example, the South American HAM (Camacho 1966) resembles both *Hamus mortoni* and *Hamus mortonyongorum*. However, this similarity is entirely due to convergence. Camacho's HAM was copied with virtually no changes from Portmann (1960: fig. 1470). This, in turn, was a modification of a figure by Naef (1924), which, however, represented the ancestral conchiferan, not the ancestral mollusc. Naef derived the molluscs from the annelids, and Portmann reduced the gills from two pairs to one. There is also Dechaseaux's (1952) HAM species, which claims its ancestry as "after Lankester," but is in fact identical to the paleo-paedomorph *H. swinnerton*.

DISCUSSION

A major feature in Hammian evolution has been the expansion and enlargement of the posterior mantle cavity and the migration of gills into it (Fig. 10). It is significant that the posterior mantle cavity, with its paired gills and associated structures and orifices, is not an ancestral, but a derived condition. The canalization of HAM morphology also deserves special mention. In spite of new discoveries in the field of malacology, such as the discovery of living Monoplacophora in the 1950s or the recognition of the Rostroconchia in the late 1970s, the general morphology of *Hamus* species has remained little modified. Lineages that respond to changes in the environment tend to be short-lived and quickly go extinct. This phenomenon is particularly well documented in the

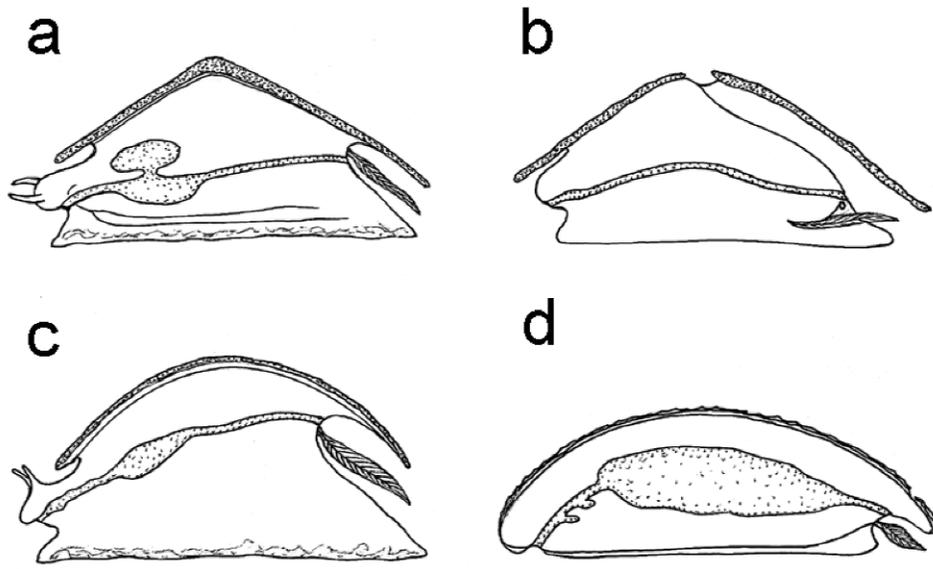


FIGURE 9. Pedomorphic and flatworm-like *Hamus* species. Pedomorphs include a. *H. swinnertoni*, b. *H. eastoni*, c. *H. russellhunteri*, and the flatworm-like d. *H. ravenjohnsonorum*. Note virtual lack of mesodermal structures (e.g., kidneys, heart, gonads). Redrawn from Swinnerton (1923), Easton (1960), Russell-Hunter (1968), and Raven and Johnson (1992), respectively.

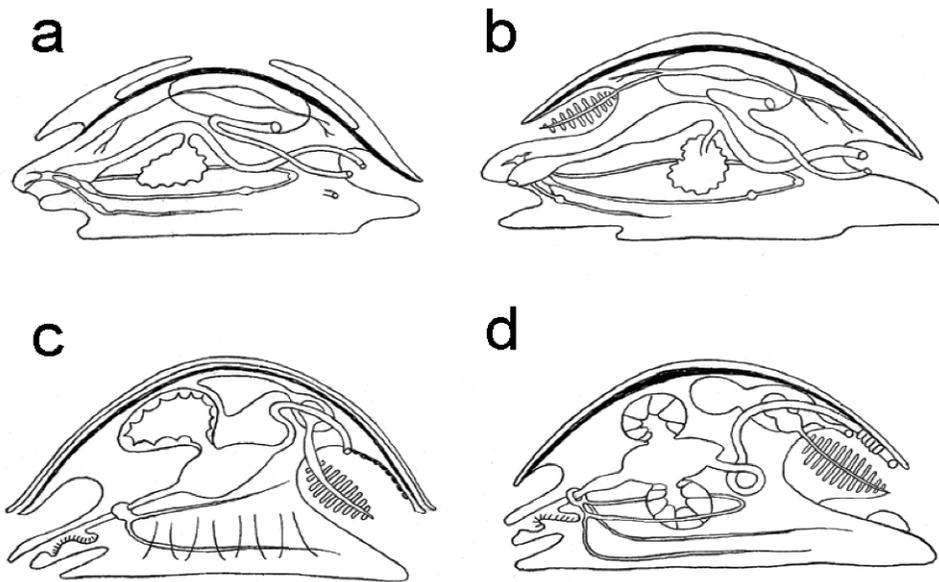


FIGURE 10. Generalized HAMs showing major trends in Hamnian evolution over the last 150 years. Note increasing complexity and number of organs in transition from a→d, and the teratological *Hamus nicholsoni* (b) with its anterior mantle cavity, and yet untorted nervous system and alimentary tract. a. after Lankester (1883), b. after Nicholson and Lydekker (1889), c. after Barnes (1963), and d. after Seed (1983) (from Hickman and Lindberg 1985).

Morton lineage by *Hamus mortonyongorum*, *Hamus barnesi*, and *Hamus yongethompsonorum*. All three of these species have serial pedal muscles, reflecting the discovery of the monoplacophoran *Neopilina*. However, not one species that has originated since 1976 shows any segmentation whatsoever and only *H. barnesi* remains extant. HAM's normal environment is a sort of pedagogical refugium, in which degenerative reversions are quite common. Strong stabilizing selection may also have helped to keep HAM on a maladaptive peak.

The Morton group is convergent with the Gastropoda in many aspects of its anatomy. One wonders if some kind of mimicry is perhaps involved, though something more like lateral gene transfer is perhaps a better way to put it. Neontological and paleontological HAMs are interspersed throughout the early history of the group and have no intrinsic characters that distinguish them.

The evolution of HAM exhibits all the typical processes and developmental heterochronies thought to encompass organic morphological evolution, and therefore both phenetic and cladistic analyses have problems with paedomorphic taxa. Loss of organs and other features, particularly the radula and gonads, is a major process in HAM evolution (there are no data on how HAMs that lack gonads reproduce, but for modern species photocopying is a distinct possibility). Metamerism, or the duplication of structures, occurs in the pedal musculature, gills, digestive glands, and is — surprisingly — a derived rather than ancestral feature within the group. In many *Hamus* species, organs appear in the juvenile condition, although the animal as a whole is represented as an adult. Such paedomorphosis is seen in the various degrees of development of the nervous system. Loss of the gonads is perhaps a case of progenesis, these being the last mesodermal structures formed, but it is hard to see how such a change could not be a "lethal" mutation in terms of Darwinian fitness. The most extreme form of heterochrony in *Hamus* species appears in *Hamus swinnertoni*, *Hamus eastoni*, and *Hamus russellhunteri*. In these species only endoderm- and ectoderm-derived structures are present. Mesoderm derivatives fail to develop, and the degenerative anatomy of these species is readily apparent (Fig. 9).

THE INFLUENCE OF HAM ON MOLLUSCAN STUDIES

HAM's fitness depends upon a symbiotic relationship with its pedagogical environment. It has not aided evolutionary biologists in solving problems, but it has often had the opposite effect, by requiring that theories be treated in the context of HAM. HAM has functioned as a Procrustean bed in molluscan phylogenetics because its advocates have presupposed as an answer what ought to have been the question. Namely, they have taken a phylogenetic hypothesis to be a fact, instead of testing its merit relative to some alternative. With the advent and implementation of molecular techniques over the last 10 years, many of the questions that HAM was inappropriately used to address have diminished in their import. Here we examine two previous uses of HAM in evolutionary debate — (1) determination of the sister taxa of the Mollusca, and (2) the anatomy and classification of Cambrian univalve molluscs. While the question of the sister taxon has moved from the morphological to the molecular arena, HAM's presence in the paleontological literature remains problematic. And regardless of the state-of-our-knowledge, both examples provide valuable insights into the risks associated with hypothetical ancestors and their uncritical 'evolution' as described above.

FLATWORMS OR ANNELIDS?—Prior to molecular data there were two major competing hypotheses about molluscan origins: (1) molluscs are modified flatworms, (2) molluscs are modified annelids. Ghiselin (1988) and Winnepeninckx et al. (1994, 1995) provide some of the earliest analyses of small subunit ribosomal DNA (18S) to address this question. These studies, and others, including Field et al. (1988), Lake (1990), Turbeville et al. (1991, 1992), have served as the

basis for many molluscan sister taxon comparisons, and they have consistently placed the Mollusca among the lophotrochozoan taxa (molluscs, annelids, brachiopods, bryozoans, and phoronids). However, the relative branching pattern for these taxa has yet to be resolved (Halanych et al. 1995). For example, Zrzavy (1998), using a combined analysis of 18S data and morphology, suggested that the sipunculids were the sister taxon of the molluscs. However, Boore and Staton (2002), using partial mitochondrial gene order data, suggested the sipunculids are actually more closely related to annelids rather than molluscs. Mallat and Winchell (2001), based on a 28S data set, suggested that brachiopods and/or phoronids may be the molluscan sister group. In no case have the flatworms been supported as the sister taxa of the Mollusca, so why was the prior debate so persistent? Was the morphological data so homoplastic and perplexing that previous workers were unable to resolve relationships?

In making phylogenetic statements based on morphology (or molecules) one should proceed as follows, compare the organisms, homologize as fully as possible, and treat the organisms sharing the most synapomorphies as sister-groups. One might also want to use additional techniques, but most people agree that we should at least do these things. If we do, it is clear that molluscs and flatworms share many symplesiomorphies — *e.g.*, spiral cleavage — which annelids also possess. But molluscs and annelids also share many synapomorphies not present in flatworms — an anus, a coelom, a particular larval type, just to mention a few. On this evidence, one has to conclude that the molluscs share a more recent common ancestor with annelids than they do with flatworms. To refute this line of reasoning, one must show that there are flatworm-mollusc synapomorphies not shared with annelids. Historically, the only ones worth mentioning are some alleged features of the pedal musculature, and hermaphroditism — the former evidently convergent and the latter demonstrably so. Alternatively, one has to disestablish the mollusc-annelid synapomorphies.

These arguments were readily available decades before molecular data, but because the flatworm theory and its implications, including the unsegmented HAM, had been presupposed, the annelid theory was widely dismissed. The arguments brought in to bolster an unsegmented HAM and the flatworm theory have been a veritable museum of fallacious logic. We give eight examples.

(1) We have the logical fallacy of basing an argument upon negative evidence. Lack of evidence that X occurred is taken as evidence that Y occurred. We are told that annelidan conditions are not recapitulated, as in certain aspects of the development of *Chiton* (Hammersten and Runnström 1925). There are plenty of examples of non-recapitulation, for instance chicken-teeth. When something is recapitulated, it is a fact to be explained, and nothing more.

(2) We have the formal fallacy of irrelevant conclusion. Russell-Hunter and Brown (1965) assert that *Neopilina*'s structure does not fit Hyman's definition of "metamerism." The question is not whether how somebody uses a word applies, but rather what has happened. The issue is not whether molluscs "are" segmented, but what their ancestors were, and what their relationships are.

(3) We have rampant *ad hoc* hypothesizing. Many authors have been able to imagine reasons why, say, *Nautilus* needs more gills (Hoffmann 1937), but they need additional *ad hoc* hypotheses to explain away the multiple kidneys, and coelomoducts.

(4) We find a habit of treating the relational property "primitive" as if it were, like "spiny," an intrinsic one, to be read off without comparison. Korschelt and Heider (1900) argue, in so many words, as follows: Cephalopods are advanced; *Nautilus* is a cephalopod; *Nautilus* has four gills; therefore, having four gills is an advanced trait. It is curious that among the cephalopods *Nautilus* is considered "primitive" — except in precisely those features in which it contradicts HAM and the flatworm theory.

(5) We get a conflation of historical relationships and what we see in extant forms. Clark (1980) claimed to have discovered the perfect example of metamerism in oligochaetous annelids.

Molluscs, he said, are different, and therefore are not derived from annelids. This amounts to belief in a physiological essence. Segmentation, like all sorts of other things, has evolved. There is no reason to believe that the physiologically ideal state represents the ancestral one, and even if it did, it would not show a lack of descent.

(6) We find the *possibility* of an event having occurred treated as if it *had in fact* occurred. Clark, again, shows that metamerism has evolved independently among tapeworms, chordates, and the annelid stock. If not three times, why not any number at all? The opposite conclusion accords with the principles without which it is impossible to infer relationships at all.

(7) We have circular reasoning, or begging the question, in which attempts to support the flatworm model presuppose that the flatworm theory is true. Particularly in the works of Stasek (1972), we find it asserted that molluscs are “pseudometamorous.” Why not “vestigially metamorous?”

(8) And, finally, we have an abuse of scenarios. There is some healthy controversy as to what role scenarios ought to play in phylogenetic research. But if one is to use them, one ought to do so logically. A logically legitimate role that they can play is in testing hypotheses. If a theory implies the existence of hypothetical organisms that would not have been viable, that theory is false. But it is the logical fallacy of denying the antecedent in a conditional statement, to “confirm” hypotheses by showing that they do not contradict particular theses. Thus, both Stasek (1972) and Salvini-Plawen (1980) provide us with a long account of what happened physiologically as flatworms were transformed into molluscs — never considering the obvious fact that the annelid theory can accomplish the same end, without the long list of imaginary intermediates and numerous convergences that the flatworm theory and HAM demand.

Of course, there is no real evidence that HAM ever existed. Indeed, the non-conchiferan molluscs (aplacophorans and chitons) have been treated as “non-molluscs” by some authors because they lack the “defining characters” found in HAM (*e.g.*, Odhner 1919), and the lack of an HAM stage in the ontogeny of any extant mollusc was first noted by Verrill (1896).

Today, the “flatworm versus annelid” controversy is being argued in somewhat different terms. Some authors argue that body ‘segmentation,’ upon which the supposed relationship of the molluscs, annelids, and arthropods was largely based, is actually convergent. In parallel, our understanding of fine structure, development, and “segmentation” of both molluscs and annelids has also markedly increased with the application of modern imaging and developmental techniques as well as detailed anatomical studies of basal molluscan groups (*e.g.*, Salvini-Plawen and Bartolomaeus 1995; Haszprunar and Schaefer 1997; Wanninger and Haszprunar 2002). Others, however, maintain very much the opposite thesis, namely that segmentation has been secondarily reduced not only in molluscs but in many other groups and may even go back as far as the bilaterian common ancestor (Balavoine and Adoutte 2003). Part of the evidence comes from molecular trees, which show that some animals with no obvious trace of segmentation are closely related to those with it. In some of these, such as echiurans, there are morphological traces of segmentation as well (Hessling 2002). The mechanisms that control the morphogenesis of segments in all animals have been widely homologized as well. There may, however, have been a considerable amount of parallelism involved, so that the seriality was not as widely expressed as it is, for example, in modern arthropods and annelids. At the very least, given that molluscs and annelids are more closely related to each other than to arthropods, the kind of segmentation that has been hypothesized to have been present in the common ancestor of annelids and arthropods must either be convergent or have been secondarily reduced in Lophotrochozoa. Two theoretical points are worth mentioning in this connection. In the first place, the notion that evolution always proceeds from simple to complex was very common in the nineteenth century, and it is about time that it no longer be presupposed in efforts at phylogenetic reconstruction. Second, there are good theoretical reasons for thinking

that it is easier for parts to be lost than gained. Our views on such matters may profoundly affect our conclusions, but they are rarely made explicit. Although the ultimate outcome of the “segmented common ancestor” question for the Mollusca remains elusive, we need to proceed with care and rigor in testing alternative hypotheses and not rely on imaginary creatures to parse and test data as in the past.

USE AND ABUSE OF FOSSIL HAMS.—Paleontologists often try to stuff HAM into shells as if they were dishing out escargot. Following a tradition that goes back at least as far as Knight (1952), Peel (1974, 1991) and others have loaded large bellerophon shells onto tiny HAMS. The alternative that at least some bellerophon shells were slugs was well argued by McLean (1984). Others, such as Knight (1952), Pojeta and Runnegar (1976), and Peel (1990, 1991), tested alternative morphologies (*i.e.*, torted or non-torted) for extinct Paleozoic molluscs, based on the fit of fossil conchs, resplendent with holes, tubes, slits, and trails, on HAM’s anatomical body plan. Here we have real data being “tested” against a hypothetical anatomy to determine whether the hypothesis shall be accepted or rejected on the grounds of which reconstruction “looks comfortable.” Paleontologists may claim to base their inferences on the fossil record and the structure of extant organisms. But in the case of molluscs, their procedure all too often has been to use an imaginary organism — HAM — as a Procrustean bed, to which the soft parts of fossils are fitted by adding features here, lopping off others there, and stretching the data wherever they fall short of the desired effect.

Because of the use of HAM to distinguish untorted molluscs from torted gastropods, it has surreptitiously become a linchpin in some torsion scenarios. Ghiselin (1966) suggested a possible scenario for the non-saltatory origins of gastropod torsion. Batten, Rollins and Gould (1967) countered with claims based upon unpublished results. These results, subsequently published by Rollins and Batten (1968), employed HAM to justify the non-torted nature of the mollusc used to argue against Ghiselin’s scenario. And, although Harper and Rollins (1982) ultimately retracted their claims, the damage had already been done, and this episode has been used to discredit functional thinking.

Sanitation issues are often evoked in torsion scenarios because many of the holes, tubes, slits, and trails of the fossil conchs are frequently linked with hypothetical water circulation patterns in the HAM anatomy so that waste products will be removed from the mantle cavity. It is interesting to note that Pelseneer (1894), who first discussed the sanitation problems that molluscs face with the anus and gills in close proximity, also was the first to pen a HAM with the gills located *within* the mantle cavity! Sanitation problems for *Hamus* species were intensified in 1952 when a new character state appeared in the common ancestor of *Hamus moolafisherorum* and the Morton/Easton groups (Fig. 5). This synapomorphy was the placement of the anus **above** the gills rather than below them (*i.e.*, downstream) (Appendix, character 20); so much for intelligent design. Although potential outgroups such as chitons and monoplacophorans have the anus and gills separate and the anus located below the gills, *Hamus* evolution has not converged with these functioning anatomies and, instead, has been directed towards an ever increasingly maladaptive state. Because of its more problematic nature, these maladaptive characters in the HAM phylogeny provide a much larger arena for speculation and interpretation and are vastly more interesting than the character states found in real organisms.

SUMMARY

The difficulties associated with reconstructing relationships, hypothetical taxonomic units, fossil anatomies, and incorporating fossil taxa into evolutionary scenarios by no means implies that we should give up. Rather, we should try alternatives, especially alternatives to HAM. Many of our colleagues have argued that HAM should be allowed to exist as a sort of pedagogical fairy tale, justified as a means of teaching molluscan anatomy. They acknowledge that no such creature ever

existed and that any evolutionary scenario deriving molluscan taxa from it represents misinformation. Such arguments remind us of ones given in favor of paraphyletic taxa. Unfortunately, neither the imaginary animals nor the misleading groups come clearly labeled with warnings about the harm that they might do if mistaken for real organisms or monophyletic units.

It is our conclusion that HAM is a pest being preserved in a textbook refugium, and science needs a better basis for determining the structure, relationships, and classification of organisms than an expedient of didactics and pedagogy. The sooner all *Hamus* species become extinct the better.

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LITERATURE CITED

- BAER, K.E. VON. 1828. *Über Entwicklungsgeschichte der Thiere. Beobachtung und Reflexion*. Gebrüder Bornträger, Königsberg.
- BALAVOINE, G. AND A. ADOUTTE. 2003. The segmented Urbilateria: a testable hypothesis. *Integrative and Comparative Biology* 43:137–147.
- BARNES, R.D. 1963. *Invertebrate Zoology*. W.B. Saunders Company, Philadelphia.
- BARNES, R.S.K., P. CALOW, P., AND P.J.W. OLIVE. 1988. *The Invertebrates: A New Synthesis*. Blackwell Scientific Publications, Oxford.
- BARTH, H.H., AND R.E. BROSHEARS. 1982. *The Invertebrate World*. CBS College Publishing, New York.
- BATTEN, E.L., H.B. ROLLINS, AND S.J. GOULD. 1967. Comments on “the adaptive significance of gastropod torsion.” *Evolution* 21:405–406.
- BEKLEMISCHW, W.N. 1969. *Principles of Comparative Anatomy of Invertebrates*, 3rd ed. University of Chicago Press, Chicago.
- BOORE, J.L., AND J.L. STATON. 2002. The mitochondrial genome of the sipunculid *Phascolopsis gouldii* supports its association with Annelida rather than Mollusca. *Molecular Biology and Evolution* 19:127–137.
- BORRADAILE, L.A. AND F.A. POTTS. 1932. *The Invertebrata*. Cambridge University Press, Cambridge.
- BOSS, K.J.J. 1982. Mollusca. Pages 945–1166 in S.P. Parker, ed., *Synopsis and Classification of Living Organisms*. McGraw-Hill Book Company, New York.
- CAMACHO, H.H. 1966. *Invertebrados Fósiles*. Editorial Universidad de Buenos Aires, Buenos Aires.
- CARPENTER, J.M. 1987. Cladistics of cladists. *Cladistics* 3:363–375.
- CLARK, R.B. 1980. Natur und Entstehung der metameren Segmentierung. *Zoologische Jahrbücher. Abteilung für Anatomie* 103:169–195.
- DECHASEAUX, C. 1952. Généralités sur les Mollusques. *Traité de Paleontologie* 2:205–209.
- DONOGHUE, M.J., J.A. DOYLE, J. GAUTHIER, A. KLUGE AND T. ROWE. 1989. The importance of fossils in phylogeny reconstruction. *Annual Review of Ecology and Systematics* 20:431–460.
- EASTON, W.H. 1960. *Invertebrate Paleontology*. Harper and Brothers, New York.
- FIELD, K.G., G.J. OLSEN, D.J. LANE, S.J. GIOVANNONI, M.T. GHISELIN, E.C. RAFF, N.R. PACE, AND R.A. RAFF. 1988. Molecular phylogeny of the animal kingdom. *Science* 239:748–753.
- GEYER, G. 1986. Mittelkambrische Mollusken aus Marokko und Spanien. *Senckenbergiana Lethaea* 67: 55–118.
- GHISELIN, M.T. 1966. The adaptive significance of gastropod torsion. *Evolution* 20:337–348.
- GHISELIN, M.T. 1974. A radical solution to the species problem. *Systematic Zoology* 23:536–544.
- GHISELIN, M.T. 1980. Natural kinds and literary accomplishments. *Michigan Quarterly Review* 19:73–88.

- GHISELIN, M.T. 1988. The origin of molluscs in the light of molecular evidence. *Oxford Survey of Evolutionary Biology* 5:66–95.
- GHISELIN, M.T. 1997. *Metaphysics and the Origin of Species*. State University of New York Press, Albany.
- GRIESEMER, J.R., AND W.C. WIMSATT. 1989. Picturing Weismannism: A case study of conceptual evolution. Pages 75–137 in M. Ruse, ed., *What the Philosophy of Biology Is*. Kluwer Academic Press, Dordrecht.
- HALANYCH, K.M., J.D. BACHELLER, A.M.A. AGUINALDO, S.M. LIVA, D.M. HILLS, AND J.A. LAKE. 1995. Evidence from 18S ribosomal DNA that the lophophorates are protostome animals. *Science* 267:1641–1643.
- HAMMERSTEN, O.D. AND J. RUNNSTRÖM. 1925. Zur Embryologie van *Acanthochiton discrepans* Brown. *Zoologische Jahrbücher. Abteilung für Anatomie* 47:261–318.
- HARPER, J.A AND H.B. ROLLINS. 1982. Recognition of Monoplacophora and Gastropoda in the fossil record: a functional morphological look at the bellerophont controversy. Pages 227–232 in B. Mamet and M.J. Copeland, eds., *Proceedings of the Third North American Paleontological Convention*, vol. 1. Geological Survey of Canada, Ottawa.
- HASZPRUNAR, G. 1992. The first molluscs — small animals. *Bollettino di Zoologia* 59:1–16.
- HASZPRUNAR, G., AND K. SCHAEFER. 1997. Anatomy and phylogenetic significance of *Micropilina arntzi* (Mollusca, Monoplacophora, Micropilinidae Fam. Nov.). *Acta Zoologica* 77:315–334.
- HESSLING, R. 2002. Metameric organisation of the nervous system in developmental stages of *Urechis caupo* (Echiura) and its phylogenetic implications. *Zoomorphology* 121:221–234.
- HICKMAN, C.P. 1967. *Biology of Invertebrates*. C.V. Mosby Company, Saint Louis.
- HICKMAN, C.S. AND D.R. LINDBERG. 1985. Pages 13–16 in T.W. Broadhead, ed., *Perspectives on Molluscan Phylogeny. Notes for a Short Course*. University of Tennessee, Department of Geological Sciences, Studies in Geology.
- HOFFMANN, H. 1937. Über die Stammesgeschichte der Weichtiere. *Verhandlungen der deutschen zoologischen Gesellschaft* 39:33–69.
- HULL, D.L. 1976. Are species really individuals? *Systematic Zoology* 25:174–191.
- HULL, D.L. 1988. *Science as a Process*. University of Chicago Press, Chicago.
- HUXLEY, T.H. 1853. On the morphology of the cephalous Mollusca, as illustrated by the anatomy of certain Heteropoda and Pteropoda collected during the voyage of H.M.S. Rattlesnake in 1846–1850. *Philosophical Transactions of the Royal Society* 143:29–66.
- KNIGHT, J.B. 1952. Primitive fossil gastropods and their bearing on gastropod classification. *Smithsonian Miscellaneous Collections* 17:1–56.
- KORSCHULT, E., AND K. HEIDER. 1900. *Text-Book of the Embryology of Invertebrates*, vol. 4. Macmillan, New York.
- LAKE, J.A. 1990. Origin of the Metazoa. *Proceedings of the National Academy of Sciences, U.S.A.* 87:763–766.
- LANKESTER, E.R. 1883. Mollusca. Pages 632–695 in *Encyclopaedia Britannica*, 9th ed., vol. 16. Henry G. Allen, New York.
- MALLATT, J.M. AND C.J. WINCHELL. 2001. Use of combined large-subunit and small-subunit ribosomal RNA sequences to classify the protostomes and deuterostomes. *American Zoologist* 41:1512–1513.
- MCLEAN, J.H. 1984. A case for derivation of the Fissurellidae from the Bellerophontacea. *Malacologia* 25: 3–20.
- MEGLITSCH, P.A. 1967. *Invertebrate Zoology*. Oxford University Press, London.
- MOORE, R.C., C.G. LALICKER, AND A.G. FISHER. 1952. *Invertebrate Fossils*. McGraw-Hill, New York.
- MORTON, J.E. 1958. *Molluscs*. Hutchinson University Library, London.
- MORTON, J.E. AND C.M. YONGE. 1964. Classification and structure of the Mollusca. Pages 1–58 in K.M. Wilbur and C.M. Yonge, eds., *Physiology of Mollusca*, vol. 1. Academic Press, New York.
- NAEF, A. 1924. Studien zur generellen Morphologie der Mollusken 3. Teil: die typischen Beziehungen der Weichtierklassen untereinander und das Verhältnis ihrer Urformen zu anderen Cölomaten. *Ergebnisse und Fortschritte Zoologie* 6:28–124.
- NICHOLSON, H.A. AND R. LYDEKKER. 1889. *Manual of Paleontology*, 3rd ed. William Blackwood and Sons, Edinburgh.

- NORELL, M.A., AND M.J. NOVACEK. 1992. Congruence between superpositional and phylogenetic patterns – comparing cladistic patterns with fossil records. *Cladistics* 8:319–337.
- ODHNER, N.H. 1919. Norwegian solenogastres. Bergens Museum. *Aarbok Naturvidenskabelig Raekke* 3:1–86.
- PADIAN, K., D.R. LINDBERG, AND P.D. POLLY. 1994. Cladistics and the fossil record: The uses of history. *Annual Review of Earth and Planetary Sciences* 22:63–91.
- PARKHAEV, P. YU. 2001. The functional morphology of the Cambrian univalved mollusks — Helcionellids. *Paleontological Journal* 35:470–475.
- PEEL, J.S. 1974. Systematics, ontogeny and functional morphology of Silurian trilobed bellerophonacean gastropods. *Bulletin of the Geological Society of Denmark* 23:231–264.
- PEEL, J.S. 1990. Functional morphology of the class Helcionelloida nov., and the early evolution of the Mollusca. Pages 157–177 in A. Simonetta and S. Conway Morris, eds., *The Early Evolution of Metazoa and the Significance of Problematic Taxa*. Cambridge University Press, Cambridge.
- PEEL, J.S. 1991. Functional morphology, evolution and systematics of early Palaeozoic univalved molluscs. *Grønlands Geologiske Undersøgelse, Bulletin* 161:1–116.
- PELSENEER, P. 1885. The cephalic appendages of the gymnosomatous pteropoda, and especially Clione. *Quarterly Journal of Microscopical Sciences* (New Series) 25:491–509.
- PELSENEER, P. 1894. Recherches sur divers opisthobranches. *Mémoires couronnés et Mémoires des Savants étrangers publiés par l'Académie Royale des Sciences des Lettres et des Beaux-Arts de Belgique* 53:1–157.
- PELSENEER, P. 1897. Mollusques – Mollusca. Pages 1–187 in R. Blanchard, ed., *Traité de Zoologie*, vol. 16. Rueff et Cie, Paris.
- PELSENEER, P. 1906. Mollusca. Pages 1–354 in E.R. Lankester, ed., *A Treatise on Zoology*, vol. 5. Adam and Charles Black, London.
- POJETA, J., JR., AND B. RUNNEGAR. 1976. *The paleontology of rostroconch mollusks and the early history of the phylum Mollusca*. U.S. Geological Survey Professional Paper no. 98. 88 pp.
- POPPER, K.R. 1962. *Conjectures and Refutations*. Basic Books, New York.
- PORTMANN, A. 1960. Généralités sur les Mollusques. Pages 1625–1654 in P.P. Grassé, ed., *Traité de Zoologie*, vol. 5. Masson et Cie, Paris.
- RAVEN, P.H., AND G.B. JOHNSON. 1992. *Biology*, 3rd ed. Mosby Year Book, St. Louis.
- REMANE, A. 1952. *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik*. Geest and Portig, Leipzig.
- ROLLINS, H.B., AND R.L. BATTEN. 1968. A sinus-bearing monoplacophoran and its role in the classification of primitive molluscs. *Palaeontology* 11:132–140.
- ROWLAND, R.W. 1968. Evolution of the MG. *Nature* 217:240–242.
- RUSSELL-HUNTER, W. 1968. *A Biology of Lower Invertebrates*. Macmillan Company, New York.
- RUSSELL-HUNTER, W., AND S.C. BROWN. 1965. Ctenidial number in relation to size in certain chitons, with a discussion of its phylogenetic significance. *Biological Bulletin* 128:508–521.
- SALVINI-PLAWEN, L. VON. 1980. Phylogenetischer Status und Bedeutung der mesenchymaten Bilateria. *Zoologische Jahrbücher. Abteilung für Anatomie* 103:354–373.
- SALVINI-PLAWEN, L. VON, AND T. BARTOLOMAEUS 1995. Mollusca: Mesenchymata with a “coelom.” Pages 75–92 in G. Lanzavecchia, R. Valvassori, M.D. Candia Carnevali, eds., *Body Cavities: Function and Phylogeny*. Mucchi Editore, Modena.
- SALVINI-PLAWEN, L. VON, AND G. STEINER. 1996. Synapomorphies and pleisomorphies in higher classification of Mollusca. Pages 29–51 in J. Taylor, ed., *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press, Oxford.
- SEED, R. 1983. Structural organization, adaptive radiation, and classification of molluscs. Pages 1–54 in P.W. Hochachka, ed., *The Mollusca*, vol. 1. Academic Press, New York.
- STASEK, C.R. 1972. The molluscan framework. Pages 1–44 in M. Florkin and B.T. Scheer, eds., *Chemical Zoology*, vol. 7. Academic Press, New York.
- SWINNERTON, H.H. 1923. *Outlines of Palaeontology*. E. Arnold and Company, London.
- SWOFFORD, D.L. 1998. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates, Sunderland, MA.

- TURBEVILLE, J.M., D.M. PFEIFER, K.G. FIELD, AND R.A. RAFF. 1991. The phylogenetic status of arthropods, as inferred from 18S rRNA sequences. *Molecular Biology and Evolution* 8:669–686.
- TURBEVILLE, J.M., K.G. FIELD, AND R.A. RAFF. 1992. Phylogenetic position of phylum Nemertini, inferred from 18S rRNA sequences — Molecular data as a test of morphological character homology. *Molecular Biology and Evolution* 9:235–249.
- VERRILL, A.E. 1896. The molluscan archetype considered as a veliger-like form, with discussions of certain points in molluscan morphology. *American Journal of Science* 2:91–98.
- WANNINGER, A., AND G. HASZPRUNAR. 2002. *Chiton myogenesis*: Perspectives for the development and evolution of larval and adult muscle systems in molluscs. *Journal of Morphology*. 251:103–113.
- WINNEPENINCKX, B., T. BACKELJAU, AND R. DE WACHTER. 1994. Small ribosomal subunit RNA and the phylogeny of Mollusca. *Nautilus* 108 (Suppl. 2):98–110.
- WINNEPENINCKX, B., T. BACKELJAU, AND R. DE WACHTER. 1995. Phylogeny of protostome worms derived from 18S rRNA sequences. *Molecular Biology and Evolution* 12:641–649.
- YONGE, C.M. 1960. General characters of Mollusca. Pages I3–I36 in R.C. Moore, ed., *Treatise on Invertebrate Paleontology*. Part I. *Mollusca* 1. Geological Society of America, Inc. and University of Kansas Press, Lawrence.
- YONGE, C.M., AND T.E. THOMPSON. 1976. *Living Marine Molluscs*. Collins, London.
- ZRZAVY, J., S. MIHULKA, P. KEPKA, A. BEZDEK, AND D. TIETZ. 1998. Phylogeny of the Metazoa based on morphological and 18S ribosomal DNA evidence. *Cladistics* 14:249–285

Appendix

DATA MATRIX FOR *HAMUS* SPECIES

Taxon	Character Number			
	000000000 123456789	111111111 0123456789	222222222 0123456789	3333333 0123456
<i>H. huxleyi</i>	?0?000000	00000000?0	0000?00000	0?00000
<i>H. lankesteri</i>	010010000	0111000002	0021000010	0?11100
<i>H. nicholsoni</i>	111000110	0111000002	0030?01110	0?11100
<i>H. pelseeneeri</i>	111010100	01100001?2	0011101110	0?21100
<i>H. swinnertoni</i>	111010100	0111000012	02?0??0110	0?14011
<i>H. borrapottorum</i>	111010100	0111000012	0021100110	0?21100
<i>H. moolafisherorum</i>	111010100	0111000002	1110??0110	0?24000
<i>H. mortoni</i>	111010100	1010110021	1011110121	1024100
<i>H. eastoni</i>	110010100	01110001?2	12?0??0110	0?14011
<i>H. barnesi</i>	111111101	1110001011	1021101110	1124100
<i>H. mortonyongorum</i>	111110100	0110000011	1011110111	0?24100
<i>H. hickmani</i>	111010100	1110001012	1021100111	1014100
<i>H. meglitschi</i>	111010100	1111101012	1021100110	1124100
<i>H. russellhunteri</i>	111010100	01110001?2	12?0??0110	0??4011
<i>H. staseki</i>	111111000	01100001?2	00110?1110	0?1410?
<i>H. yongethompsonorum</i>	111110100	1110100011	1011110111	1124100
<i>H. barthbrosorum</i>	111010100	0110001012	1021100111	1021100
<i>H. bossi</i>	?2?110100	01100001?2	1021001110	1222100
<i>H. seedi</i>	111010101	1100001021	1011001111	1024100
<i>H. barcalolivorum</i>	111010100	0110000011	1011100110	0?23100
<i>H. ravenjohnsonorum</i>	?2??10100	01100001?2	12?0??1110	0?24011
<i>H. salvinisteinerorum</i>	?2?110100	01100001?2	1011101110	1224011
“Cambrian” taxa				
<i>H. pojetarunnegarorum</i> species complex:				
Taxon a	111010110	01110001?2	0210??0110	0?24011
Taxon b	111010120	01110001?2	0210??0110	0?24011
Taxon c	110010110	01110001?2	0210??0110	0?24011
Taxon d	110010120	01110001?2	0210??0110	0?24011
Taxon e	110010110	01110001?2	1210??0110	0?24011
Taxon f	110010120	01110001?2	1210??1110	0?24011

CHARACTER ANALYSIS

Integument

1. Shell enveloped by mantle. The plesiomorphic state is equivocal as the outgroup lacks a shell. States — shell enveloped by mantle = 0, shell not enveloped by mantle = 1.
2. Exoskeleton. Shell absent is the plesiomorphic state. States — shell absent = 0, shell present = 1, integument with spicules = 2.
3. Shell with opening. The presence of an opening in the shell is equivocal. States — shell opening present = 0, shell without openings = 1.
4. Shell attachment muscles. The absence of multiple muscles is plesiomorphic. States — multiple muscles absent = 0, multiple muscles present = 1.

Foot

5. Foot divided into propodium, mesopodium and metapodium = 0, foot not differentiated = 1.

Gills

6. Number of gills. A single pair of gills is plesiomorphic. States — single pair of gills = 0, multiple gills = 1.
7. Gills enclosed in a mantle cavity (internal) or extending beyond body (external). External gills are plesiomorphic. States — external gills = 0, internal gills = 1.
8. Gill position on body. Gills situated on the posterior portion of the body are plesiomorphic. States — posterior placement of gills = 0, anterior placement of gills = 1, lateral placement of gills = 2.
9. Efferent membrane. The absence of an efferent membrane from the gill to the roof of the mantle cavity is plesiomorphic. States — gill without efferent membrane = 0, gill with efferent membrane = 1.
10. Afferent membrane. The absence of an afferent membrane from the gill to the floor of the mantle cavity is plesiomorphic. States — gill without afferent membrane = 0, gill with afferent membrane = 1.

Digestive System

11. Jaws. The presence of jaws in the buccal cavity is plesiomorphic. States — jaws present = 0, jaws absent = 1.
12. Buccal mass. The presence of a buccal mass is plesiomorphic. States — buccal mass present = 0, buccal mass absent = 1.
13. Radula present in oral cavity. The presence of a radula is plesiomorphic. States — radula present = 0, radula absent = 1.
14. Salivary glands. The absence of salivary glands is plesiomorphic. States — salivary glands absent = 0, salivary glands present = 1.
15. Esophageal glands. The absence of esophageal glands is plesiomorphic. States — esophageal glands absent = 0, esophageal glands present = 1.
16. Configuration of intestinal tract. A straight, non-looped intestinal tract is plesiomorphic. States — intestinal tract straight = 0, intestinal tract looped = 1.
17. Digestive gland. The presence of a digestive gland is plesiomorphic. States — digestive gland present = 0, digestive gland absent = 1.
18. Position of digestive gland relative to the stomach. A ventral digestive gland is plesiomorphic. States — digestive gland ventral = 0, digestive gland dorsal = 1, both dorsal and ventral digestive glands = 2.
19. Style. The presence of a style sac without a style is plesiomorphic. States — sac without style present = 0, style present in stomach = 1, both sac and style absent = 2.
20. Anus position. An anus opening below the gill is primitive. States — anus positioned below the gill = 0, anus positioned above the gill = 1.

Coleomic structures

21. Heart and pericardium. The presence of a heart is plesiomorphic. States — heart present = 0, heart and pericardium present = 1, heart absent = 2.
22. Aorta. The presence of an anterior aortic branch is plesiomorphic. States — anterior aorta only = 0, aorta absent = 1, anterior and posterior aorta = 2, posterior aorta only = 3.
23. Gonads. The absence of gonads is plesiomorphic. States — gonads absent = 0, gonads present = 1.
24. Gonoducts. Separate gonoducts are plesiomorphic. States — separate gonoducts = 0, gonads opening into pericardium = 1.
25. Kidney morphology. Tubular kidneys are plesiomorphic. States — kidneys tubular = 0, kidneys spherical = 1.

Sensory structures

26. Cephalic tentacles. The presence of cephalic tentacles is plesiomorphic. States — cephalic tentacles present = 0, cephalic tentacles absent = 1.
27. Statocysts. The presence of statocysts is plesiomorphic. States — statocysts present = 0, statocysts absent = 1.
28. Epipodium and tentacles. The presence of an epipodium without tentacles is plesiomorphic. States — epipodium present = 0, epipodium absent = 1, epipodial tentacles present = 2.
29. Hypobranchial gland. The absence of a hypobranchial gland is plesiomorphic. States — hypobranchial gland absent = 0, hypobranchial gland present = 1.
30. Osphradium. The absence of an osphradium is plesiomorphic. States — osphradium absent = 0, osphradium present = 1.
31. Osphradium position. The position of an osphradium on dorsal surface of foot is plesiomorphic. States — osphradium on dorsal surface of foot = 0, osphradium present on efferent membrane = 1, osphradium present on dorsal surface of pallial cavity = 2.
32. Eyes. The presence of stalked eyes is plesiomorphic. States — stalked eyes = 0, non-stalked eyes = 1, eyes absent = 2.

Nervous system

33. Ganglia. The presence of four pairs of ganglia (cerebral, pedal, parietal, buccal) is plesiomorphic. States — all four pairs of ganglia present = 0, three pairs present (cerebral, pedal, parietal) = 1, cerebral only = 2, cerebral + pedal = 3, ganglia absent = 4.
34. Pedal nerve. The absence of pedal nerve cords is plesiomorphic. States — pedal nerve absent cords = 0, pedal nerve cords present = 1.
35. Visceral nerve loop. The presence of a visceral nerve loop is plesiomorphic. States — visceral nerve loop present = 0, visceral nerve loop absent = 1.
36. Nerve ring. The presence of a nerve ring around the pharynx is plesiomorphic. States — nerve ring around the pharynx = 0, absence of nerve ring around the pharynx = 1.