William Healey Dall:

A Neo-Lamarckian View of Molluscan Evolution

by

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Abstract. Throughout his career William H. Dall attempted to reflect evolutionary relationships in his molluscan classifications. From 1865 to 1877 Dall's evolutionary scenarios were built almost exclusively around heterochronic processes (primarily peramorphosis). Biogeographic congruence and natural selection were also invoked. The patterns Dall saw and the processes he inferred were probably derived from the training he received from L. Agassiz and others at the Museum of Comparative Zoology, Harvard University. By 1882 Dall had formalized his heterochronic arguments in terms of Edward Cope and Alpheus Hyatt's patterns of acceleration and retardation. Variation and *de novo* structures appeared through the interaction of physical forces with the organism, and were past on to progeny by the inheritance of acquired characters. By 1882 Dall was an active participant in the Neo-Lamarckian movement in America. Dall's evolutionary models determined how he evaluated character state polarities, transformations, and their import. In his monographs and revisions he ordered his species and higher taxa from "primitive" to "derived," reflecting his best interpretation of their "natural order." The recognition of Dall's intent and the rules by which he interpreted history requires us to carefully consider the implications of using his classifications today.

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INTRODUCTION

William Healey Dall (1845-1927) was one of the great, late 19th and early 20th century American naturalists. Like many naturalists of his time his expertise spanned a broad array of taxa, geologic epochs and biological thought. His contributions are to a variety of fields, including physical and cultural anthropology, oceanography, paleontology, and invertebrate and vertebrate zoology. He published over 1600 papers, reviews and commentaries in many of the most prestigious journals of his day, such as *Nature*, *Science*, *American Naturalist*, *Proceedings of the National Academy of Sciences*, and various publication series of the Smithsonian Institution (Bartsch *et al*., 1946). His expedition and field work centered in Alaska, but he also conducted field studies in Nicaragua and along both the east and west coasts of the United States. He was an elected member of numerous American societies, including the American Association for the Advancement of Science, National Academy of Sciences, National Geographic Society, Philosophical Society of Washington, as well as numerous European societies with whom he met during his travels abroad.

Although Dall was an expert in many areas of natural history, his greatest scientific contributions were in the field of malacology. As a malacologist working on both fossil (Tertiary) and living mollusks, W. H. Dall described over 5300 species (Boss *et al*., 1968). Many of his publications were short taxonomic papers, but several were comprehensive monographs, including anatomical descriptions and phylogenies of the taxa under consideration. Unlike most other pioneer American malacologists Dall was interested in the evolutionary relationships of the taxa with which he worked. In two papers on the phylogeny of Docoglossa (= Patellogastropoda) published in 1871 and 1876 we get a glimpse of his evolutionary thinking. Like many biologists of his day, Dall accepted evolution but thought Darwin's theory did not fully explain its causes. In this early work he used terminal addition of characters, combined with biogeographical patterns to construct evolutionary scenarios (Dall, 1876).

My purpose is to examine Dall's evolutionary thinking as demonstrated in his published papers, addresses, reviews, and personal correspondence. My interest was stimulated by the fact that we both have worked on the same group of gastropods – namely the Patellogastropoda (Dall's Docoglossa). However, our respective hypotheses of relationships are diametrically opposed (Figure 2). And although both of our approaches are evolutionary in intent and argument, the discrepancy in our respective results begs explanation. Moreover, insights into Dall's evolutionary philosophy may help us evaluate his other systematic work and taxonomic groupings, many of which remain in use today.

W. H. DALL THE EVOLUTIONIST

In Dall's (1877a) first strictly evolutionary paper he moved closer to fully embracing Darwin's theory of natural selection than he did in his earlier taxonomic papers mentioned above. He began by proposing a hypothesis to account for "missing links in the chain of development," a pattern that he regarded as the "chief weapon of all opponents" of natural selection (Dall, 1877a:1). This defense of a theory that he had regarded as "plausible but highly unsatisfactory…" only six years earlier marks Dall's closest encounter with pure Darwinian evolution. Dall, aware of the absence of intermediate types in the fossil record, had been seeking a mechanism that would produce "leaps, gaps, saltations…for some years…" He termed his new mode of evolution "saltatory evolution."

Dall began with a paradox outlined by Edward Cope (1868) in his paper "On the Origin of Genera." Cope had distinguished two distinct evolutionary engines. The laws of acceleration and retardation (see Gould, 1977:85) guided the origin of genera, while the origin of species was determined by natural selection. These engines operated independently of one another. Thus, in Cope's view it was possible "that at times *the change of generic type has taken place more rapidly than that of specific, and that one and the same species … has, in the natural succession, existed in more than one genus*" (Cope, 1868:272). This rapid change or leap would leave no intermediate forms and this is what Dall sought to explain and he concluded that saltations were "perfectly in accordance with the view that all change is by minute differences gradually accumulated in response to the environment…" (pp. 2). This is in marked contrast to Cope's assertion that the mechanisms that would produce such leaps (acceleration and retardation) were independent of natural selection. In today's idiom, Dall sought a model to explain a macroevolutionary pattern that did not negate microevolutionary processes.

Dall's paper also contained some other seemingly modern components. For example, Dall recognized aspects of stasis in the fossil record and the rapidity in which character change would take place, aspects of evolution that would much later fall under the rubric of punctuated equilibrium (Eldredge & Gould, 1972). He also began his hypothesis with a clearly stated species concept, "... similar individual organisms in which for the time being the majority of characters are in a condition of more or less stable equilibrium; and which have the power to transmit these characters to their progeny with a tendency to maintain this equilibrium." (Dall, 1877a: 136).

Dall's hypothesis required this tendency to maintain equilibrium be strong enough to resist gradual changes in the environment until a point where a critical threshold was achieved and there was a massive reorganization within the animal followed again by stasis. Dall likened this phenomenon to the damming of water behind debris in a gutter that ultimately would break through the dam only to reform and repeat the event behind additional debris farther downstream. However, the dam was never completely watertight and small continuous trickles existed between these events.

This variation and differential transmission of the tendency to maintain character states would produce a divergence within a species, one population accumulating character state changes as it tracked the environment while the other remained relatively unchanged until a punctuated event. The populations that tracked the environmental changes on the microevolutionary level would be better adapted and "able to persist" across this event. While those populations in stasis undoubtedly had a "broader base" [*i.e.*, less specialized] and were "less injuriously affected by *adverse* circumstances and consequently might still endure" across the event as well. Intermediate individuals would be the "least fitted to persist" and would be "rapidly eliminated." Through this model Dall envisioned "a parallel series of species in two or more genera, existing simultaneously." Dall closed his paper with a call for the study of stasis ("inherited tendency to equilibrium") pointing out that the "inherited tendency to vary" was receiving all the attention.

It is likely that Dall first noted examples of Cope's paradox while working on brachiopods rather than mollusks. Dall (1877b) discussed brachiopod species pairs that had identical specific characters, but belonged to two genera – *Terebratella* and *Magasella*. Dall noted that the similarity between these species pairs was "usually only remarkable when the *young* of the latter is compared with the *adult Magasella*" (pp. 164). After discussing the taxa and their distributions Dall stated that three criteria must be met to confirm that "the relations of the one to the other in development should be in harmony with the development of the group as a whole in geological time and organic differentiation."

1. The distribution of any two species so related to each other should absolutely coincide.

2. The young should all be *Magasellae*; the adults (barring dwarfs), all the “companion genus”
3. Actual study of the embryology and young stages should be able to trace the edentueous stage into the *Magasellae* stage, and that into the final “companion” stage.

Dall presented observations falsifying all three criteria and thought that “another hypothesis will explain them, if not equally well, yet in greater harmony with the analogy of the case, and … with greater probability of accuracy.” Dall concluded that this subject would provide the key to some important generalizations. And although he thought he had identified transformations through three genera “in the life of one individual,” Dall discounted Cope and Hyatt’s progressive evolution as the mechanism.

Dall’s first excursion into evolutionary thought generated an unfavorable response from his friend and colleague Alpheus Hyatt at the Boston Society of Natural History. Hyatt and Dall had undoubtedly met when both were students of Louis Agassiz at the Museum of Comparative Zoology at Harvard University in 1862 (see below). Hyatt (1877a) thought Dall’s paper on saltatory evolution to “misquote Cope and entirely skipped your humble servant who’s specialty happens to be and has been for 16 years just the point you allude to.” Hyatt went on to accuse Dall of not reading his [Hyatt’s] “little pamphlets, which I so trustingly send you from time to time…" and of not acknowledging Herbert Spencer. Hyatt closed his letter with pleasantries, but still maintained that Dall had overstated his contribution.

It is difficult to understand Hyatt’s criticism of Dall’s hypothesis. Dall did not follow Cope’s reasoning for the origin of genera and species, and his reference to Cope’s paper is limited to proposing an alternative hypothesis to explain Cope’s one species, two genera paradox. Moreover, Dall does not mention any acceleration or retardation mechanism, and to the contrary, argues that natural selection alone is sufficient to produce the paradox. Since Hyatt’s “little pamphlets” also primarily dealt with Hyatt’s insights into the role of acceleration and retardation in evolution, it is likewise hard to understand how Hyatt’s work related to Dall’s hypothesis. Whatever the source of Hyatt’s irritation with Dall’s saltatory evolution it apparently was soon smoothed over by a letter from Dall to Hyatt, because in less than 9 days’ time Hyatt had written Dall a second letter apologizing for his hasty conclusions and promising to re-read Dall’s paper with greater deliberation (Hyatt, 3the American Association for the Advancement of Science meeting in Montreal, Quebec, Dall (1882) used the opportunity to state his view of evolution and the role of natural selection. Dall began by focusing on the state of malacology in America. He paid homage to Cuvier and the "immortal Lamarck" who reformed the Linnean classification and "created a science of Malacology" (Dall, 1882:4). He also recalled the resistance that he and other workers experienced when they first began to propose classifications that reflected phylogeny – "The early students, seeking to know the relations of the animals which were huddled in a few heterogeneous genera by Linné, were the subject of no little opprobrium from the conchologists of that day, and were very generally looked upon as dangerous radicals and unsafe guides.”[1] Dall continued with a summary of the state-of-our-knowledge of North American molluscan faunas by habitat, and a review of potential research programs in the field. Highlighted study areas included biogeography, the deep-sea faunas, and molluscan development and behavior (all still worthy topics today). The last study area that Dall addressed was “the subject, of which the methods applied to other forms of animal life have occupied a very large portion of the thought and activity of the scientific world for

[1] It is noteworthy that similar distrust of phylogenetic classifications and the workers who advocate and produce them still exists in the field of malacology today.

more than twenty years." Dall was speaking of "modification of organic life" and in a curious way acknowledged Darwin without ever mentioning him by name. He did this by acknowledging that the results of those studies "have revolutionized science and justly immortalized the remarkable naturalist who led the way" (pp. 10).

In contrast to his earlier paper (1877a), and unlike his treatment of Darwin, Dall acknowledged the American Neo-Lamarckian leaders by name and clearly aligned himself with them – "The labors of Cope, Hyatt, Ryder, Morse and others *among us* [emphasis added], are no less fruitful than suggestive in these directions" (pp. 11). Dall echoed Cope's and Hyatt's arguments that the characteristics on which natural selection worked were produced by dynamical evolution and "the *rhythm* of development as shown by periodic acceleration and retardation…." (pp. 11). Dall even venerated Herbert Spencer. Dall's praise exactly corresponds to Hyatt's criticism of Dall's earlier paper and its lack of acknowledgments.

After these acknowledgements, Dall returned to his earlier theme of uniformity of character states between taxa and expanded it to ask the question why there were so few basic body plans, given the profusion of variation in the natural world. For Dall (1877b:12), the answer to this "mystery lies in the direct physical action of the environment, by ways and methods few of which are yet understood…."

Dall returned to the molluscan message of his address and revisited a topic first broached in 1871 where he noted that natural selection apparently was important in the evolution of plants, insects, and birds, but had no appreciable effect in the evolution of the Mollusca. Whereas Cope had created a dichotomy where natural selection was relegated to acting only at the species level, while the laws of acceleration and retardation worked at higher levels, Dall suggested a dichotomy based on mental and physical prowess.

Dall considered the actions of natural and especially sexual selection, to be far more pronounced and their effects far more important among organisms of "high mental and physical rank" interacting with each other or on "lower" organisms with which "higher forms" interact. As one example of this latter case he suggested bees and wasps interacting with plants. Dall thought simple organisms were much less subject to the actions of natural selection. "It is only when advanced to a comparatively high stage of differentiation that organisms can offer, as it were, a handle for natural selection to take hold of." (pp. 11).

Dall viewed mollusks as an intermediate group between higher organisms (where natural selection is active) and lower animals (where it is inefficient) and therefore concluded that mollusks would make excellent exemplars for evolutionary studies.

Within the mollusks natural selection was strongest in terrestrial snails because they interacted with higher organisms (smarter enemies) such as birds and mammals. Color patterns could be strongly selected by sighted predators. In contrast, the struggle in the sea was less violent than on land owing to the more uniform conditions of the sea, the more abundant food sources, and the less intelligent predators (mainly fishes and other mollusks). Because natural selection was not as strong here marine species showed more variation in form, external sculpture and coloration than terrestrial species. Protoconch sculpture and the bright colors of tropical pulmonates were under the control of some unknown evolutionary force.

However, even in marine species natural selection could still operate albeit in a secondary role to physical causes. Dall noted that Alaskan littorine snails exposed to heavy surf were modified with low spires, enlarged apertures, and reduced shell sculpture. Dall concluded that individuals not so modified would be removed by wave action, and thought this example "one of the most obvious instances I have observed of the action of selection among marine mollusca." (pp. 14). Dall concluded his address with a discussion of carrier shells (Xenophoridae) that have the habit of cementing bottom debris to their shells. He considered their behavior to represent an unexplainable acquisition of a valuable habit that was perpetuated by natural selection in some species, while in others it continued to persist although it was no longer useful.

This address clearly aligned William H. Dall with the Neo-Lamarckians. His earlier attempt (Dall, 1877a) to attribute both large- and small-scale morphological change to natural selection was abandoned, and the Neo-Lamarckian duet of dynamic evolution and acceleration and retardation were prominent in his world view. Although the perplexing pattern of morphological uniformity, first noted in 1877, still concerned him, another earlier theme – different evolutionary processes for "lower" and "higher" animals – resurfaced here as well. Because of Dall's international reputation in the malacological community, the influence of his evolutionary ideas was not limited to America and a translated extract of his address appeared within two months in Germany (Anonymous, 1882).

In his last principal paper on evolution Dall (1890) laid out his view of dynamical evolution and argued its primary role in evolution. Dall again returned to the argument that natural selection does not produce variation and contends that the physical forces and mechanical stresses placed on the organism by the environment are the sources of variation, and that these acquired characters are then inherited. Because no two individuals are ever exposed to identical environmental conditions, variation is an inescapable outcome. Dall also revisited his correlation between intelligence and the strength of the role of selection with natural, and especially sexual, selection being more important and often more rapid in those organisms with higher "mental qualities." As before he pointed out that only one of any pair of interacting organisms need "possess intelligence of a certain grade," but his terrestrial-snail-being-eaten-by-birds-and-mammals example was replaced by an insect/orchid example.

Dall next considered Weismann's (1882) attack on the evidence in support of the inheritance of acquired characters. Dall attempted to negate one of Weismann's points by arguing against the inheritance of mutilations and pathological characters. He chose as his example bivalve mollusks that settled in the empty burrows of rock boring taxa such as *Lithophagus* [=*Lithophaga]* and pholads. He pointed out that although they grew to conform to the "antecedent borer," he predicted that their progeny "would probably exhibit no traces of their parents' deformity." This position was contrary to Hyatt's view of the potential of pathological characters to be inherited and form a "degradational series of individuals, species and genera" (Jackson, 1890b). Dall then discussed his earlier paper on the development of the bivalve hinge structure (Dall, 1889) and a forthcoming paper on the development of the columellar folds of gastropods (Dall, 1894), both of which he considered excellent examples of the dynamic influences of the environments of organisms (see below).

In a note added after his paper was read before the Biological Society of Washington, Dall reported that the Darwinians (and strong critics of dynamical evolution) Lankester and Weismann had recently suffered serious setbacks in their championing of natural selection over Neo-Lamarckism. Dall's satisfaction with this state of affairs is expressed in his addendum:

> "In fact these and other signs indicate that the most able of those who have through haste or conservatism been disposed to ignore dynamical influences in evolution, will before long join in the procession, and lend their undoubted abilities to the perfection and elaboration of the only theory yet propounded which fully and efficiently supplements that of Natural Selection and closes the too

> obvious gaps which have hitherto existed in the intellectual structure of the modern theory of organic evolution" (1890:10).

Osborne (1890) made the same argument in a similar response to the apparent weakening of Weismann's position.

In a review of Dall's paper Jackson (1890a) credited Dall with providing a new way to understand the relationship between dynamic influences and natural selection. Rather than there being two separate forces in evolution, natural selection acted "in harmony with, and as a natural outcome of dynamic influences." According to Jackson, Dall had melded the engine of variation (dynamic influences) with natural selection.

Dall published two other papers that dealt with dynamical influences in molluscan evolution. In the first Dall (1889) addressed the higher classification of the Pelecypoda (Bivalvia). He considered earlier attempts unsuccessful because the characters on which such work had been based were "not fundamental in the evolutionary history of the minor groups" (Dall, 1889:445). For Dall the characters of adductor muscles, gills and siphons were too variable because they were intimately associated with the "mechanics" of the group. Dall then provided examples to illustrate his point and included a discussion of the role that convergence would play in confusing relationships. Dall regarded the then current classification based on hinge structures as suspect, but he felt it could be resolved if interpreted in the context of dynamical influences as Cope and Ryder had done in their studies of the development of the mammalian foot and tooth.

Dall's "archetypal form of bivalve" was small, with symmetrical, equilateral valves, a short, central ligament, and a smooth hinge area, and noted that this was the case in the larval shells of many taxa. He argued for initial small size of bivalves based on the fossil record. Dall also allowed that this condition "in the adult state" was likely due to "degeneration." Thus, as long as the taxa remained small and symmetrical there was no mechanical selection on the hinge structure. However with size increase and/or asymmetry, the forces were no longer trivial and changes in the ligament and hinge plate structure would be compulsory to compensate for the new mechanical conditions – "Nature, through natural selection and physical stresses, has developed these cardinal processes which are known as teeth" (pp. 452).

Based on his understanding of the evolution of the bivalve hinge structure Dall proposed three orders. These were the Anomalodesmacea, Priondodesmacea, and Teleodesmacea, the last taxon having the "highest and evolutionarily the most perfect type of hinge." Moreover, "prionodont traces" remained in most members of this latter group – a clear indication of the direction of evolution in the group. Dall also correlated the presence of nacre with these tooth types showing it common in the Anomalodesmacea, but absent in the Teleodesmacea. The remainder of the paper discussed groupings within these orders and the derivation of their hinge structures. As in his dynamical influences paper (Dall, 1890), he used a supplementary note at the end to again drive home the importance of physical forces in evolution and its implications for reconstructing molluscan evolution. Citing unnamed workers who considered the molluscan shell to be nothing more than a secretion of the mantle, Dall conceded that the "original theoretic protoconch" may have been so, but once it existed it came under the influences of physical forces that influenced the growth and structure of the viscera. Dall saw molluscan anatomy molded by the shell as much as the shell was secreted by a portion of that anatomy. In this view the physical factors that produced the shell acted through the shell to constrain the anatomy. Thus, it was Dall's conclusion that when "intelligently studied and properly appreciated" the relationships of the Mollusca are discernible solely through shell characters. The idea that the shell mechanically constrained the viscera was to be revisited in his second paper considering dynamical influences.

In this work Dall (1894) addressed the mechanical causes of folds in gastropod apertures. Dall began with the observation that among fusiform rachiglossate taxa the attachment points for the adductor muscle lie deeper within the shell in those taxa with columellar folds than in those without folds. He then formulated a model in which the gastropod animal consisted of a thin, loose, cone-shaped mantle epidermis in which the relatively solid body cone resided. The adductor muscle attached this dual cone complex to the shell columella. Dall envisioned that when the animal retracted into its shell "the natural diameter" of the mantle cone would exceed the shell volume and the mantle epidermis would therefore wrinkle longitudinally. The strongest folds would be along the columella because "the attachment of the adductor prevents freedom in wrinkling, and the groove of the canal will mechanically induce the first fold in that vicinity." Repeated extension and contraction of the wrinkled surface over the shell would produce plications on the columella and either lirae or teeth on the outer lip of the aperture.

Dall then returned to his earlier observation of the correlation that the attachment points for the adductor muscle lie deeper within the shell in those taxa with columellar folds than in those without folds. Dall explained that taxa with the adductor muscle closer to the aperture would experience less compression of the body complex and therefore fewer wrinkles of the mantle would be produced. The deeper the adductor attachment point, the more compression of the body and more wrinkling, thereby producing more plications. Dall considered this explanation to have "marvelous precision with the results called for … based on the dynamical status of the bodies concerned, their motions and secretions" (pp. 913). Moreover, the exceptions were readily clarified. For example, species with extensive mantles typically had lirate apertures (*e.g.*, *Oliva* spp., *Cypraea* spp.). Those with extensive mantles but no lirae do not entirely withdraw into their shells (*Harpa* spp., Opistobranchia).

Unlike his earlier hinge structure paper, this article made no reference to the usefulness of these characters in understanding the evolutionary history of the rachiglossate taxa in which they were expressed. Instead, Dall seemed to view them as constructional artifacts; features that are present only because of the interaction between tissues and coiled shell. It is interesting that nowhere in this paper does Dall use the term "natural selection." In Dall's evolutionary model natural selection acted "in harmony with, and as a natural outcome of dynamic influences." Although these particular characters were the products of dynamic influences, they remained neutral and were not selected for, most likely because they were too intimately associated with the "mechanics" of the group.

NEO-LAMARCKIANISM IN MOLLUSCAN CLASSIFICATION

In 1871 Dall published his first "natural" (= evolutionary) classification of a molluscan taxon, treating the Docoglossa (*i.e.*, Patellogastropoda of Lindberg, 1986); the classification had been read before the Boston Society of Natural History on 19 October 1870. For the next 50 years this arrangement of taxa would remain virtually unchanged in Dall's publications and serves as one of the best examples of Dall's evolutionary reconstructions. Dall had not previously stated any evolutionary philosophy, so the arguments he marshaled in favor of his 1871 patellogastropod classification (and in subsequent papers in 1876 and 1893), combined with the three evolutionary articles discussed above are used here to examine his approach to reconstructing molluscan relationships during the second half of the 19th century.

In the "General Remarks" section, Dall (1871) made several statements that underscored parts of his evolutionary perspective at that time. He considered the group to have a "peculiar persistency of immaturity, when compared with other groups of gasteropods [sic]"; for him this trend was especially evident in the shell, radula, and gills. Dall (1871:233) also found "a certain geographical agreement in regard to generic characters which favors the hypothesis of a development of the various forms from a few more simple and more closely allied ancestors." That concept would be more fully developed in 1876, and although Dall believed that this pattern was the result of evolution, he could not attribute it "to the very plausible but highly unsatisfactory doctrine of 'natural selection.'"

Dall's (1876) second paper on docoglossan phylogeny began with a comment on Lankester's (1867) mistaken identification of the patellogastropod "wart organs" as gonopores. The anatomical observations that he made to refute Lankester, combined with his acquisition of additional specimens, provided Dall with the opportunity to further resolve and expand upon his earlier phylogeny.

Dall viewed the northwest coast of America as the center of origin of the Docoglossa. From there they had migrated south and east where they "changed or added to their original characters" (Dall, 1876: 40) (Figure 1). This pattern required three components to support it: (1) the "maximum development of the lower or parent forms" in the North Pacific, (2) "a local abundance and radiating distribution of the next higher genera," and (3) the presence of the most specialized taxa in the nearest "favorable" region. The importance of the proximity of the "favorable" region was a suspected correlation of time with specialization. Thus, the sooner the ancestral taxon could get to a new area, the more time there would be for subsequent specialization to occur. In the Docoglossans "this is exactly the real state of the case."

Dall considered radula, gills, sensory structures, and body size to be key characters for reading this pattern, and all supported his model. The supposedly most primitive docoglossans – the lepetids – are found subtidally in the Arctic and boreal North Pacific and Atlantic oceans. They are small limpets without eyes, gills, and lateral teeth and are "sluggish in their motions." Given their obviously inferior condition, Dall concluded that they were "protected by the uniform conditions of their deep water station."

Dall suggested that the Acmaeidae evolved from the lepetids by developing the radula (perhaps by "natural selection") and acquiring eyes and gills; a general size increase was also present. "Strong in the possession of their new organs" they invaded the intertidal zone (*Collisella*) although a "few smaller and weaker forms" remained in the subtidal. Traveling westward from their North Pacific center the Acmaeidae reached Japan (*Collisella*) and migrated down the western Pacific margin to Australia (*Collisellina*). Conditions were less favorable eastward through the Bering Strait and over Arctic Canada, and this accounts for the fact that only two species occur in northern Europe. Lottia, with its large size (>100 mm) and the addition of a secondary gill, represented the next step in acmaeid evolution. Completion of the secondary gill along the anteriormost mantle margin in Scurria of South America marked the "highest stage of development" in the family.

For Dall the next step in the development of the Docoglossa was the transition from the Acmaeidae to the Patellidae (Figure 1). This was accomplished by: (1) loss of the gill from the nuchal cavity ("rejection of useless parts"), (2) development of the muzzle frill into tactile papillae, (3) development of a "rhachidian [sic] tooth of properly proportioned size," and (4) development of the "abortive uncini of the Acmaeidae" into functional teeth. Moreover, it is in this last group that "the highest development of total bulk known to the order, is added to the greatest known specialization of the other characters."

For Dall there was complete agreement of character polarities and transformations in four distinct character groups of eleven taxa, as well as complete biogeographic congruence between their distributions and relationships as well as aspects of their ecology. These latter two augmentations of character polarization would be formalized as the criterion of "chronological progression" (Hennig, 1966). Dall (1876:40) was so confident of his phylogeny that he argued, "In many cases their paths have become dry land, and the track must be followed rather by organic relations than contiguity in distribution." Modern practitioners of vicariance biogeography share Dall's confidence in biological relationships as a guide to reconstructing earth history. Dall knew that "Greater knowledge would doubtless increase the complications" for his phylogeny, but he still allowed that "without verging greatly on the speculative, we may construct a genealogical tree, which cannot greatly differ from the following scheme" (Figure 1).

Dall's first two papers on docoglossan phylogeny were published only 5 years apart, but it was 17 years until the third paper appeared. In the interim all three of Dall's evolutionary theory papers appeared. Dall (1893) wrote the third phylogeny paper as a response to Thiele (1891) who Dall felt had misinterpreted his conclusions regarding the most primitive members of the Docoglossa. Dall's arguments are similar to his earlier points and there are no obvious references to dynamical evolution. The only element in this paper that may reflect Dall's acceptance of Neo-Lamarckian principles is used as a disclaimer for the phylogeny he was defending. Dall (1893:285) confessed that he attached "little importance to speculations of this kind, which can only be placed on firm footing by extended embryological researches…"

After this caveat Dall stated that "we find therefore in Lepetidae the greatest number of archaic characters (somewhat masked by degeneration of other organs) which remain in any of the three groups..." (Dall, 1893:285). To the earlier characters he now added protoconch morphology, and reiterated the patterns of the 1876 phylogeny, starting in the cold north where the simple forms first appear and subsequently migrate into the temperate and ultimately tropical regions of the world where they become larger and more complex in their character states.

The most interesting portion of this paper is Dall's (1893:287) cautionary remarks about convergence in limpet-like shell morphologies and a prediction about monoplacophoran affinities. A series of discoveries of distinct radular types in deep-sea limpets with virtually identical shells had impressed on Dall the strong convergence that was possible in limpet-like species. If such convergence were possible in living species, fossil taxa would likely be present similar problems. Moreover, determinations in the fossil record would be even more dubious, the deeper the time and the more unfamiliar the taxa. He singled out the similarity of shells of Silurian *Tryblidium* with Recent patellid taxa and warned that it was dangerous to conclude that *Tryblidium* anatomy would have been similar to living patellids – "it is almost inconceivable that the Silurian form should have any closely allied recent representative." Moreover, the symmetry of the adductor scars of the monoplacophoran fossils suggested to Dall "a peculiar disposition of the organs which might, indeed, have paralleled in some particulars the organization of some of the *Chitons* of that ancient time." It would be 45 years until the same argument was repeated by Wenz (1938) (see Knight, 1952), and another 19 years before the recovery of living monoplacophorans confirmed Dall's insight into the non-torted state of these animals (Knight & Yochelson, 1958).

In summary, the overall direction of Dall's evolutionary trends in the patellogastropods was the addition of characters; this resulted in an increase in both complexity and size in descendant taxa. Dall's polarity determinations were based on ingroup comparisons. However, by 1893 he thought that the ultimate test of his phylogeny would be made by extended embryological research.

Cladistic analysis (Lindberg & Hedgeaard, 1996) (using many of the same characters that Dall used) produces a hypothesis of relationships that reverses Dall's evolutionary trends and argues that the derived taxa exhibit mostly paedomorphic, not peramorphic, character transformations (Lindberg, 1988a, 1988b) (*cf*. Figures 2a & b). The diametrically opposed nature of our respective phylogenies results from our different assumptions regarding character polarity and transformations. Dall's model assumed strictly progressive evolution going from simple to complex forms by terminal addition. In contrast, the alternative phylogeny of Lindberg & Hedegaard (1996) is based on a parsimony analysis, with the determination of character polarity and transformations based on outgroup analysis.

Dall's work on bivalve taxa in the late 1890's and early 1900's also contains terminology and scenarios indicative of Neo-Lamarkian thought. Many of these scenarios contain terms that make them appear mainstream from today's perspective, but dynamic evolutionary thought is clearly present. Dall (1901) considered the shell sculpture of the Lucinacea, which showed virtually no change from the Cretaceous to Recent, to be an example of "neutral selection." Dall argued that the sculpture originally resulted from "trifling mutations of the armature of the mantle edge…" but were not "essentials in the lives of these animals…" Therefore, once they were acquired "natural selection has little or no influence upon them, and therefore rarely sets up any tendency to change" (Dall, 1901:780).

Dall's (1899) synopsis of the bivalve group "Leptonacea" (= Galeommatacea) well illustrates his evolutionary views at the end of the 19th century. He saw in this group the general effects of degeneration overlain by modifications for specific habitats. Dall considered this group to have members representative of "teleodont" ancestors. However, this similarity was only superficial because groups that represented true starting points for taxa are "notable for their tendency to vary and interchange characters." In the Leptonacea the evolution of commensalism and parasitism produced paedomorphic characters "accompanied by a revival of atavistic primary characters" (Dall, 1899:873). Dental features of the hinge plates of the Leptonacea resulted from degeneration and had produced indistinct and amorphous dentition. Bernard (1897) had used positional information to argue homology of bivalve hinge plate structures, but Dall cautioned that:

> The dynamic reactions of the teeth upon each other are, I am confident, of the utmost importance in the development of the hinge. As in the vertebrate skeleton, pressure and friction in localized areas will produce directly a response in facets and buttresses. In fact, to the eye trained to take such matters into account, *every hinge* [emphasis added] shows more or less evidence of the mutability of hinge structure and its responses to stress as well as to inherited tendencies of form" (Dall, 1899:874).

Moreover, of all the bivalve groups Dall thought this mechanism was most obvious in the Leptonacea. Thus, from a reduced and simplified starting point "trifling modifications" resulting from dynamical evolution produced all states seen in the taxon."

Although the overall pattern was from simple to complex forms by the addition of structures to the hinge at the pressure points, further degeneration also could occur.

Five of the 17 characters used by Bieler & Mikkelsen (1992) in their phylogenetic analysis of the leptonacean taxon Galeommatidae were based on hinge structures and all were subsequently discovered to be synapomorphies of clades. Like the patellogastropod example discussed above, most of the transformations in these characters involved reduction or loss (lateral hinge teeth, cardinal teeth), not the simple-to-complex pattern Dall saw in his scheme. Bieler & Mikkelsen also concluded that hinge teeth states were difficult to interpret and score. Unlike Dall, but in agreement with Bernard, they suggested that ontogentic studies would be required to resolve hinge teeth homologies. These and other examples suggest that it was not Dall's eye that was trained to see the natural arrangement of the taxa he studied, it was an unqualified belief in Neo-Lamarckian principles that found its support in every bivalve hinge he examined.

DISCUSSION

William H. Dall's early training in "natural classifications" as well as clandestine exposure to evolutionary theory began at the Museum of Comparative Zoology (MCZ), Harvard University in 1862. Dall's father, a graduate of Harvard and Harvard Divinity School, took the 17 year old William to meet Louis Agassiz in 1862. Dall subsequently left high school in his final year to begin studies with Agassiz. Although Dall always referred to himself as a "pupil of Agassiz", there is little evidence to indicate that the feeling was mutual. Winsor (1991) does not list Dall as one of Agassiz's students or associates nor does he appear on unpublished lists of students (Winsor, personal communication). Dall's (1908) listing of his fellow students at the MCZ includes J. A. Allen, H. Hagen, C. F. Hartt, F. W. Putnam, S. H. Scudder, and A. E. Verrill and corresponds well with Winsor's student chronology with two notable exceptions. The first is Dall's omission of A. Hyatt who was in residence at MCZ from 1858-1864; the second is Dall's listing of H. Hagen, who did not arrive at Harvard until 1867, four years after Dall had left Harvard (Dall, 1908; Winsor, 1991). Dall did not receive a doctorate degree until 1904 when the University of Pennsylvania conferred an honorary degree of Doctor of Science (Dall, 1908).

The absence of W. H. Dall's name from the student rosters likely resulted from the introduction his father provided to Agassiz. The elder Dall was a Unitarian missionary to India and he had hoped to see the younger Dall enter the tea trade in Assam, India. According to Bartsch, *et al*. (1946), Agassiz and his colleagues recognized the potential of having a MCZ collector in India and gave the young Dall intensive training in collecting and natural history. Thus, Dall may have had a different curriculum and status at MCZ than his contemporaries. Dall (1908) recounts that his year or so at the MCZ consisted of training in zoology under Agassiz, training in anatomy and medicine under Wyman, and geology from Agassiz's lectures. It is also likely that Dall was exposed to discussions of Darwinian evolution which first began among Agassiz's students (including Morse, Verrill and Hyatt) in 1860 (Wayman, 1942; Winsor, 1991).

Further zoological training, and especially exposure to evolutionary thinking, were probably limited after Dall left Harvard and the MCZ in 1863. Upon leaving Harvard, Dall did garrison duty at the Watertown Arsenal, then worked on the India Wharf as an office boy for the firm of Deshon & Yarrington (West African Traders), and later that year went to Chicago where he found work in the land office of the Illinois Central Railroad (Dall, 1908). In early 1864 Col. J. W. Foster aware of Dall's training with Agassiz, asked Dall to serve as his assistant surveying iron deposits in northern Michigan during the summer of 1864. Upon his return from the field Dall spent the fall and winter preparing field reports and working on the chemistry of iron and steel. In late 1864 and early 1865 Dall volunteered evenings at the Chicago Academy of Sciences (directed by Robert Kennicott) and studied anatomy and medicine under the direction of Daniel Brainard and N. S. Davis (Dall, 1908).

In early 1865 Kennicott asked him to join the Alaska Survey Party for the Russian-American Telegraph Company. He left for Alaska in March 1865 and did not return to the East Coast until October of 1868. Scientific interactions during this time were limited to an 8-month stay in San Francisco between November 1865 and July 1866.

Dall took up residence at the Smithsonian Institution in December 1868 and began working on his collections from Alaska. He had completed his studies for the natural classification of the Patellogastropoda by October 1870. In July 1871 he was again sailing to Alaska, this time in the employment of the U. S. Coast Survey and charged with surveying the Alaskan coastline; he returned to the Smithsonian in the winter of 1874 (Woodring, 1958).

After his return he may have discussed some aspects of evolutionary theory with A. Hyatt. In a letter to Dall dated 21 October 1873, Hyatt wrote of the "little successes" Hyatt had experienced on his recent trip to Europe. Hyatt confided to Dall that his "theoretical views with regard to the evolution of forms etc. must undergo great changes but that in the main they are correct." Hyatt did not go into detail in his letter but promised Dall "all sorts of discussions" when he visited Hyatt in Cambridge the following spring (Hyatt, 1873); there is no record of what they may have discussed. Within three years of his return Dall published his paper on saltatory evolution.

The above chronology suggests that Dall had few opportunities to discuss and interact with colleagues engaged in evolutionary studies after he left Harvard until he returned to the Smithsonian in late 1874. Possible exceptions include the time he spent at the California Academy of Sciences and the three years at the Smithsonian between 1868 and 1871.

The importance of Dall's contributions to Neo-Lamarckian theory are difficult to gauge. Jackson (1890a) favorably reviewed Dall's paper on dynamical influences in the *American Naturalist* and cited his contributions to molluscan evolution in his work on bivalve phylogeny (Jackson, 1890b). Hyatt (1894) acknowledged Dall only for loaning ammonites to him in his1894 tome on the *Phylogeny of an Acquired Characteristic.* In contrast, the work and contributions of Cope, Jackson, and Beecher were widely cited by Hyatt. Cope (1896) listed Dall second in research featuring the inheritance of mechanically acquired characters in the Mollusca [Hyatt, Dall, Jackson, and Beecher] and he cited Dall's work a total of four times. Kellogg (1908) presented Dall's (1877a) theory of sudden species changes in his chapter on "Other theories of species-forming."

Pfeifer (1965), who considered Dall a lesser figure in the American Neo-Lamarckian school, also cited Dall's (1877a) paper, finding in it the Neo-Lamarckian disposition to view evolution as a struggle between the forces of change and those of equilibrium, but there are no other clues here that Dall was writing from a Neo-Lamarckian perspective. To the contrary, he evoked only natural selection as a process, and did not spare his praise of "Mr. Darwin, whom nothing escapes…" This paper contains no reference to the inheritance of acquired characters or the source of variation. Instead he attempts to explain stasis in the fossil record and argues the equal importance of the "inherited tendency to equilibrium" with the "inherited tendency to vary."

Hyatt's (1877a) accusatory letter that Dall had failed to cite pertinent literature suggests that Dall was not fully immersed in the Neo-Lamarckian literature at that time, and there is evidence that Cope *et al*. did not consider him one of their own either. Cope's (1896:528) "List of Papers by American Authors who have Contributed to the Evidence Used in this Book" lists Dall's evolutionary papers beginning in 1889. The only reference to an earlier paper is Cope's mention of Dall's (1877b) brachiopod work in which Dall rejected progressive evolution as an evolutionary mechanism in the formation of species pairs, an uncharacteristic action for a supposed Neo-Lamarckian. Lastly, Dall's (1877a) own footnote states that he did not have a copy of Cope's (1868) paper and had not read it since its publication. It had been published 9 years earlier and most likely came out during his 8 month association with the California Academy of Sciences between Alaskan cruises. This suggests Dall was not fully familiar with the literature on evolutionary theory. However, by 1882 there is no doubt of Dall's knowledge of, and allegiance to the Neo-Lamarckian school.

Dall’s account of his formal training combined with his opportunity to interact with colleagues in the Neo-Lamarckian movement and the above analyses of the evolutionary scenarios in his papers, suggests two stages in Dall’s evolutionary thinking. Before 1877 Dall’s views were built exclusively around heterochronic processes and often incorporated biogeography into his patterns (*e.g.*, Figure 1). While there were some gestures to the role of natural selection, they were never developed and no alternative evolutionary modes were proposed or discussed. By 1882 Dall had formalized his heterochronic arguments with the patterns of acceleration and retardation espoused by Cope and Hyatt. This is also when examples and arguments in favor of the origination of structures by physical forces and the inheritance of acquired characters first appear in his writings. Dall’s first stage required nothing more than the training he received from Agassiz or reading Agassiz’s (1857) “Essay on Classification” (see Winsor, 1991 on the training of Agassiz’s students). While the influences for the second stage of Dall’s evolutionary views most likely came from Hyatt and Cope and developed after Dall returned to the Smithsonian in the late 1870’s. Perhaps this was spurred, in part, by Hyatt’s review of Dall’s (1877a) first evolutionary paper. Interestingly, that paper is primarily Darwinian and therefore anomalous to both stages.

It is likely that Dall's role and involvement in the American Neo-Lamarckian movement has not been widely recognized in malacological circles because his prodigious publication record has caused the few primarily evolutionary articles to be lost among the hundreds of papers on other topics. Moreover, most of his biographers have been malacologists who have focused on his contributions to molluscan systematics rather than his views on evolution. For example, Woodring (1958) in a biography for the National Academy of Sciences listed Dall's "principal contributions to science", but not a single publication on evolution is listed. I think there is little doubt that if dynamical evolution had not been rejected as an evolutionary hypothesis, Dall’s contributions in this area would have been prominently listed here. Dall bet on the wrong horse, and although his evolutionary philosophy has tremendous implications for his systematics and ultimately the classifications he produced, it has been previously ignored because of a paradigm shift.

It is both unfair and inappropriate to judge Dall's evolutionary thinking in terms of today's theories and assumptions of evolutionary processes and models. For their time Dall's evolutionary arguments are both plausible and internally consistent. With the rediscovery of Mendel's work in the early 20th century and the emergence of a new model for the passing of characters between generations and the origin of variation, the Neo-Lamarckian model was no longer viable and its advocates were soon quiet.

Although criticism of Dall's evolutionary theories is untimely, the legacy of his immense contribution to North American molluscan classification *based on those theories* remains like a skeleton in the closet. Because of the nomenclatural status of his work, and because nomenclature and taxonomy are not decoupled, it cannot be swept away or ignored as a silly idea of the past. Dall's evolutionary model determined how he evaluated character state polarities, transformations, and their import. In his monographs and revisions he ordered his species and higher taxa from “primitive” to “derived” reflecting his best interpretation of their "natural order." The recognition of Dall's intent and the rules by which he interpreted history requires us to carefully consider the implications of following his classifications today. The necessity of using phylogenies in biological or paleontological studies that purport to draw evolutionary conclusions is well documented (*e.g.*, Lauder, 1990; Brooks & McLennan, 1991; Wenzel, 1992; Padian *et al.*, 1994). While criticizing Dall may be inappropriate, workers who continue to use his classifications in evolutionary studies without first rigorously testing his phylogenies do not share his exemption.

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Table 1
Synonyms and equivalents of Dall's (1871) taxa (Figure 1) used for cladogram construction in Figure 2.

Figure 1. Dall (1871)	Figure 2. Lindberg (1988a, In press)
Cryptobranchia	Included in *Lepeta*
Pilidium	*Propilidium*
Lepeta	*Lepeta*
Collisella	*Lottia*
Collisellina	*Patelloida*
Acmaea	*Acmaea*
Lottia	*Lottia*
Scurria	*Scurria*
Patella	*Patella*
Nacella	*Nacella*
Patinella	*Nacella*
Patina	*Helcion*
Helcion	*Helcion*
Helcioniscus	*Cellana*
Ancistromesus	*Scutellastra*

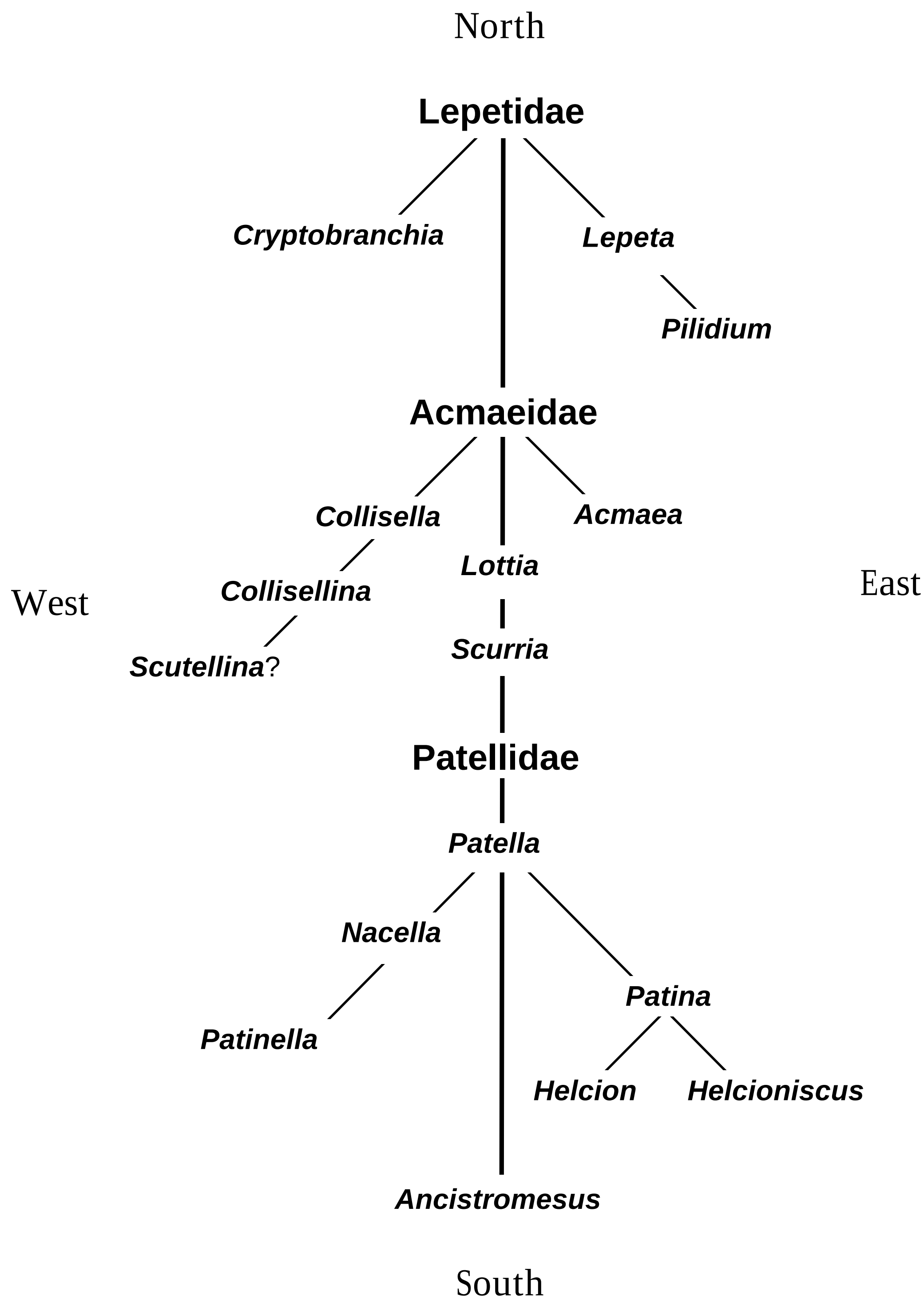

Figure 1
"Genealogical tree" of the Patellogastropoda redrawn from Dall (1876). Note the incorporation of biogeography into Dall's scheme.

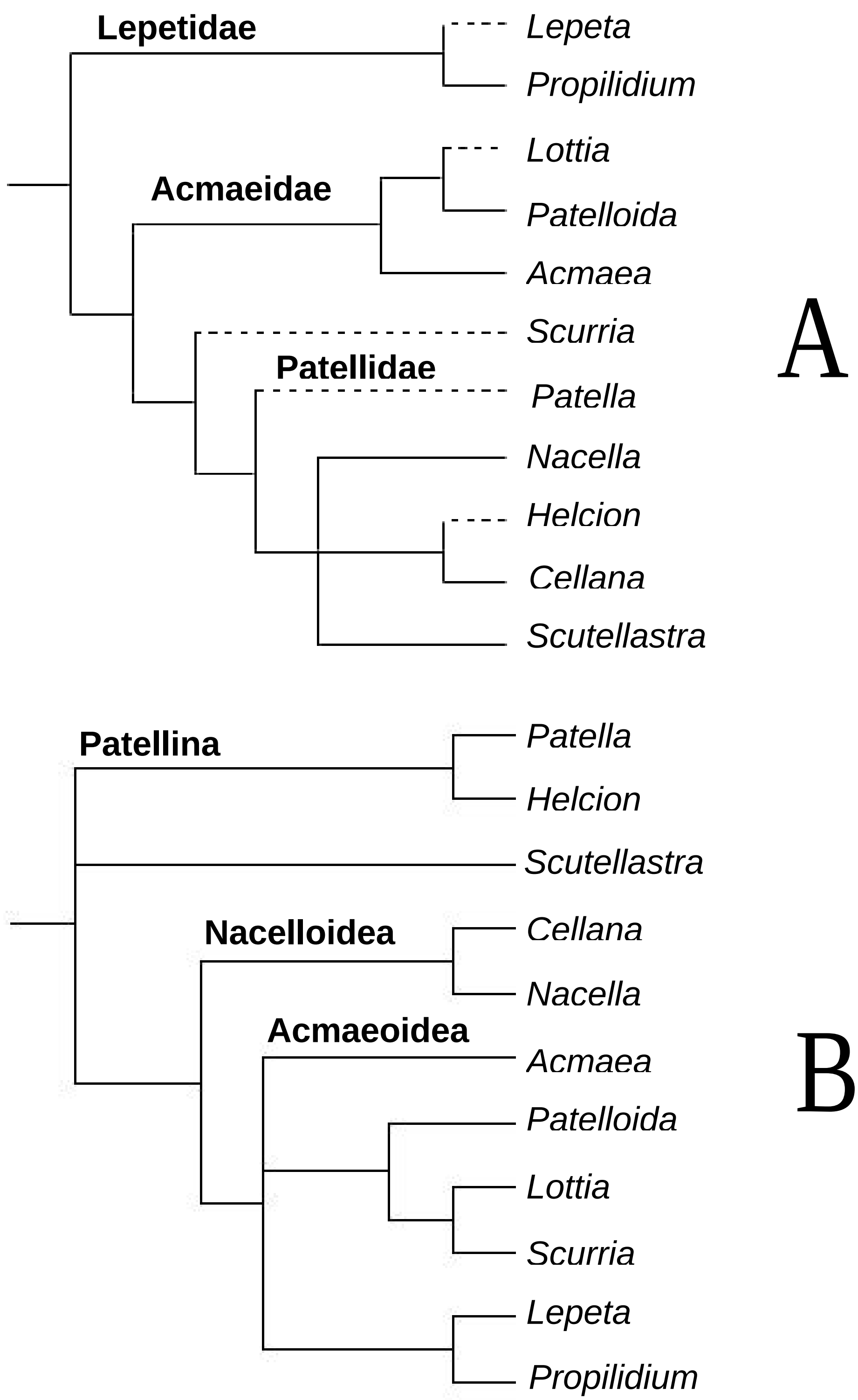

Figure 2
Phylogenetic relationships among the Patellogastropoda. A. Dall's (1876) genealogical tree (Figure 1) redrawn as a cladogram; stippled branches have 0 length. B. Cladogram based on parsimony analysis of the Patellogastropoda [redrawn from Lindberg & Hedegaard (1996)]. See Table 2 for synonyms and equivalent taxon names.