

Taxon mapping exemplifies punctuated equilibrium and atavistic saltation

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Abstract Two or more exemplars of the same taxon forming a nonmonophyletic group on a molecular tree may be viewed as representing surviving populations of a deep shared ancestral taxon, and if different species of the same genus, then theoretically phenotypically static remnants of punctuated equilibrium. That taxon may be mapped on a molecular cladogram and evolutionarily resolved at the taxon level inclusive of all exemplars. The technique for mapping taxa on a molecular tree, termed here caulistics, is much like mapping traits but recovers macroevolutionary information at the taxon level. All lineages arising from the mapped taxon are its direct descendants. Mapped taxa superimposed or overlapping may reveal packaged adaptive traits. When a mapped taxon is well split by another mapped taxon on a molecular tree, atavistic saltation based on triggering an epigenetically retained trait complex is a theoretical explanation. Caulistics combines traditional taxonomy and molecular phylogenetics to reveal previously unknown aspects of the macroevolutionary past.

Keywords Caulistics · Molecular phylogenetics · Punctuated equilibrium · Saltation · Taxon mapping

Introduction

The present paper describes a means of retrieving new information on ancestor-descendant relationships of taxa. Molecular phylogenetic analysis as presently practiced instead charts the evolution of molecular traits as branching

lines of inferred trait changes (e.g., Bowler 1989, pp. 345–346; Farjon 2007; Hörandl 2006, 2007; van Wyk 2007) for exemplars (individual specimens studied) representing named terminal taxa in the cladogram. In cladistic phylogenetics, of any three taxa, two are phylogenetically more apt to share an ancestor, and that ancestor is simply represented by a tree node referred to only as an unnamed “shared ancestor” of two descendant lineages. O’Keefe and Sander (1999) discussed the inability of a cladogram to demonstrate ancestor-descendant relationships. Dayrat (2005) showed that Darwin’s discussion of a Tree of Life was based on ancestor-descendant relationships, not sister-group relationships (see also Darwin 1859, p. 95, 404), and pointed out that actually demonstrating ancestor-descendant relationships is or at least has been difficult. Brummitt (2002, 2008) and Knox (1998) have clearly shown that providing ancestors with taxonomic names immediately creates a phylogenetically unnamable paraphyletic (see “Glossary”) group. Leaving ancestors in a special unnamed category (Knox 1998) eliminates macroevolution from classification in that no identifiable ancestor-descendant transition is directly represented (see also Grant 2003; Mayr and Bock 2002; Stuessy 2009).

Geologic fossils are, of course, informative of evolution as descent with modification of taxa (Donoghue et al. 1989; Hall 2003; Novacek and Norell 1982; Jablonski 2008), and ecological niches may be inferred from expressed trait combinations, although the phylogenetic value of geologic fossils has been argued as minimal by Bateman (1996, p. 120) and Patterson (1981). Although ancestral morphological or molecular trait changes may be mapped through probabilistic or parsimonious evaluations in phylogenetic analysis and presented as sequential (Cunningham et al. 1998), this is not a satisfactory substitute for inference of evolution of taxa from other taxa (Farjon 2007; Jablonski

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2007; van Wyk 2007) because it excludes autapomorphies. Additionally, gene trees are often not the same as expected cladograms of species; the species tree problem has been well-discussed and reviewed by Doyle (1996). Attempts to infer ancestral morphological traits include parsimony, likelihood, or Bayesian mapping of traits on a molecular tree (Bollback 2006; Huelsenbeck and Bollback 2001; Maddison and Maddison 1999, 2004; Pagel 1999; Schultz and Churchill 1999), and extant phylogenetic bracketing (Witmer 1995, 1998). In this method, if a fossil lineage is surrounded in a cladogram by two lineages each sharing certain traits in their extant taxa, the fossil would be expected to also have those traits, filling out unfossilized soft parts thus completing the taxon, and features absent in the bracketing lineages would be expected to be absent in the fossil. The logic of mapping morphological traits on molecular trees is here extended to inference of a complete ancestral morphology that may be discerned at some particular taxonomic level as a kind of taxonomic uniformitarianism. In this paper, “taxon” refers to a traditional monophyletic, paraphyletic, or autophyletic taxon diagnosed by expressed traits, particularly morphology, as opposed to a taxon solely characterized by holophyly (strict phylogenetic monophyly) on a molecular tree.

The present approach assumes that a split in a molecular lineage does not necessarily signal a speciation event. Splitting of lineages followed by anagenetic change of both products into new species and pseudoextinction of the old line is required for gradualist evolution, but not for punctuationalist (Eldredge 1989; Gould 2002, p. 606; Gould and Eldredge 1993; Stanley 1981). Punctuated equilibrium leads to “budding” (Funk and Omland 2003; Robosky and Lovette 2008) and continued stasis of the ancestral taxon (Gould 2002, p. 607; Rabosky and Lovette 2008; Wagner 1998). According to Foote (1996) the latter theory predicts that half or more of extant species have ancestors that are also represented by extant populations, while up to $n - 1$ surviving ancestors are possible in cladograms. Molecular phylogenies do, however, when robust correctly infer genetic continuity (Zander 2009). The tree branches may be interpreted as isolation events. Such events can happen in phenotypically static lineages as genetically isolated descendant populations, resulting in a surviving ancestral taxon that gradually accumulates through mutations genomic changes over time, from simple point mutations in noncoding sequences to subfunctionalization involving paralogues (Kimura 1969; Koonin 2009), such as has been demonstrated for *Ginkgo* (Kuddus et al. 2002). DNA base changes may be used to track genetic continuity in both “budding” and gradualist scenarios. As pointed out by Knox (1998), Hennig (1966) acknowledged that speciation by budding was doubtless common. Patton and Smith (1994) demonstrated genetic differences in pocket gopher

populations that persisted as essentially evolutionarily independent entities over long time periods, and suggested that a “gene tree reflecting initial paraphyletic and/or polyphyletic relationships can be preserved permanently” through fixation of alternative haplotype lineages.

Identification of surviving populations of an ancestral taxon can occur in various ways: (1) A fossil associated with more recent apparently derived taxa may be found to be an extant taxon, that is, a living fossil. (2) An ancestral taxon may survive when quantum evolution may be inferred from biosystematic and cytogenetic studies (Grant 1971; Levin 2001; Lewis 1962); for example, in the event of several daughter species being all more similar to an apparent shared immediate ancestor than to each other; or peripheral isolate evolution (Hubbel and Lake 2003; Knox 1998) where founding populations are not small. (3) A surviving ancestral taxon may be singled out with a morphologically based cladogram and biogeographical information (Theriot 1992). (4) A surviving ancestral taxon is sometimes cited as represented by any exemplars that lack autapomorphies in a morphological cladogram that exhibits polytomies (Wiley and Mayden 2000, p. 157), which is problematic (Zander 1998). (5) Here, another method is discussed, that of *mapping taxa*.

Taxonomic background

Taxonomy informs all fields (Sneath 1995) requiring names for basic taxonomic units and higher natural groupings. Failures in systematics will eliminate or unnecessarily multiply scientific names that are basic to research in many fields (Szalay and Bock 1991, p. 35). Modern systematic work consists of two elements: an evolutionary analysis followed by classification. Unfortunately the evolutionary analysis is not done by specialists in evolution, but depends on computerized methods using single, across-the-board simple though mathematically nontrivial models (parsimony, maximum likelihood, and Bayesian Markov chain Monte Carlo) followed by classification using the principle of holophyly. Correcting phylogenetics by making the inferred results of evolutionary processes more accurate, more resolved, and classification more representative of the complexities of evolution is the aim of modern evolutionary systematics. Followed in this paper is Darwin’s (1859, p. 404) definition of natural taxa as based both on genealogical relationships and degree of divergence, which is essentially the position of evolutionary systematics versus the fully genealogical stance (holophyly) of phylogeneticists (Baum 1992; Stuessy 1990).

More than 250 years of thorough analysis of many thousands of specimens by a series of taxonomists have generated classifications in many fields that incorporate evolution to the greatest extent possible by identifying

conservative characters that organize more plastic traits; taking note of gaps between taxa that are left by extinctions, disruptive selection, and saltation; and further testing of such inferences in ideal cases with morphometrics, crossing experiments, geography, common garden, reciprocal transplant, cytology, chemistry, ecology, mating behaviors, and other data. The point of traditional taxonomy is to group examined specimens following concepts of species and higher taxa appropriate to the organisms and the data available, and also to minimize the potential of parallelism and convergence such that taxa should very rarely be composed of two or more totally cryptic species or genera or families. A concise description of the two present-day schools of taxonomy is given by Patton and Smith (1994), pitting process against pattern, or biological or cohesion species concepts against phylogenetic monophyly. *Phylogenetic classification* uses only those traits that are phylogenetically informative (Gould 2002, p. 605), i.e., that show sister-group relationships with other taxa, and does not reward unique evolutionary novelties with high rank, but *evolutionary systematics* recognizes in its nomenclatural hierarchies evolutionary relationships and significant new evolutionary directions. In the present paper, a molecular cladistic tree of genetic continuity provides information on ancestor-descendant relationships using traditional Linnaean classification.

Although intuition associated with personal expertise is involved in delineating the natural taxa (Buck 1986) that evince macroevolutionary ancestor-descendant relationships, the process has been clarified recently (Gigerenzer 2007; Hutchinson and Gigerenzer 2005) as an unconscious development though informal genetic algorithms of well-tested rules of thumb. Such expertise is not usually associated with explicit rules-based analysis, but the general agreement of 250 years of “subjective” Linnaean taxonomy with the results of molecular systematics demonstrates its utility. On the other hand, phylogenetic analysis names only some of the sprays of lineages associated with the principle of holophyly, and which ones are named is based on (intuitive) Linnaean analyses. All lumping and splitting associated with holophyly is artificial because macroevolution as ancestor-descendant relationships is arbitrarily eliminated from classification. The method of phylogenetic parsimony involves description of one-time events (historical narrative explanations *sensu* Bock 2004) and is quite unlike the superficially similar principle of least action in physics (Szalay and Bock 1991, p. 27), which involves universal processes (nomological deductive explanations according to Bock 2004).

A major contention in systematics is whether or not to recognize paraphyletic groups, i.e., groups of taxa of which some but not all are derived from one ancestor (De Queiroz and Gauthier 1992). Strict phylogenetic monophyly or

holophyly requires a taxon to include all exemplars sharing the same ancestor. In the present paper, it is taken as an observable fact that cladograms resulting from molecular analyses show inferred lines of genetic continuity, based mainly on noncoding DNA, but not necessarily speciation events that may inform taxonomic distinctions based on phenotype. An autophyletic taxon (a necessary word coined here) is any group that, if recognized at a rank appropriate to the evolutionary significance of its autapomorphies, renders another taxon paraphyletic. The recognition of Aves, for instance, as an autophyletic group at the same taxonomic level as Reptilia, renders Reptilia paraphyletic (Gauthier and de Queiroz 2001). Autophyletic taxa cannot be given scientific names if holophyly is used as an “absolute standard” in the sense of Williams (2009), which is simply pattern-related and quite unlike the “gold standard” of exact tests in statistics.

Insistence on holophyly commonly denies to unique evolutionary novelties their recognition at an appropriate rank (Hörandl 2007; Stuessy and König 2009), in that, e.g., one genus cannot be recognized in classification as having risen out of another genus, or a family from another family (Brummitt 2008), though two families or two genera may be sister groups. In addition, phylogenetic classifications are becoming commonly based almost solely on molecular trees with morphological traits often so shuffled that they cannot be tolerated as simply polythetic circumscriptions, e.g., according to Aigo et al. (2009), the (molecular) moss genus *Rhynchostegiella* is now morphologically “poorly defined by only a single synapomorphic change followed by reversals in half of the species” while “there is no morphological synapomorphy defining *Brachythecium*.” If one does use holophyly, then classification can be based almost entirely on cladistic relationships, resulting in a hierarchy of nested exemplars. This unfortunately minimizes perceived evolutionary novelties (autophyletic taxa) such as taxa with new, unique evolutionary features, deemed of no value for determining relative position on a cladistic tree. Holophyly is commonly described by cladists as not a theory of evolution or “dictated by the ontological structure of nature” (Knox 1998; and see Bock 2004), but a classification method or principle. Insistence on holophyly is now quite mainstream in systematics, but recently certain phylogeneticists are retaining molecularly paraphyletic and autophyletic species, e.g., a new autophyletic moss species (Sotiaux et al. 2009), and pointedly refusing to assign a species name to a molecularly different cotton population that was morphologically not distinct in a common garden (Alvarez and Wendel 2006). Classification by strict phylogenetic monophyly not only masks evolutionary information by egregious and scientifically unwarranted (1) lumping, thus suppressing the flagging of autophyletic taxa with appropriate rank, but also (2)

splitting, thus giving unique names often of high rank to molecularly somewhat isolated outliers of the same taxon.

Mapping taxa

If morphological traits can be mapped on a molecular tree (Cunningham et al. 1998; Garland et al. 1999; Wiley et al. 1991) then so can taxa. Mapping taxa immediately recovers ancestor-descendant relationships. A paraphyletic group is a mapped taxon, as is the dependent autophyletic group. If evolution is descent with modification, then both sister-group and ancestor-descendant relationships are necessary components of evolution, and the latter is a more direct inference.

When a number of exemplars of the same taxon all terminate one lineage on a molecular tree, the clear scientifically parsimonious inference is that the ancient representation of the taxon, or mapped taxon, of all exemplars is exactly that taxon, not some newly conceived ad hoc shared ancestor of unknown diagnosis. The mapped taxon may be thought of as a “virtual fossil” (Zander 2008, 2009). Cladistic insistence on unknown shared ancestors subtending every cladistic split may be based on some persisting notion of the generic cycles theory of the 19th century anatomist Robert Knox in which species evolve in four stages: vigorous spread, maximum generation of daughter species, senescent decline from competition with these, and extinction (Rehbock 1983). Although species can go extinct, there is no evidence that this manner of generation of shared ancestors is necessarily or even commonly true (Brothers 1985). Thus, a node may be a genuine shared ancestral extinct species or a series of nodes may be occupied by one ancestral taxon surviving as phenotypically intact after multiple peripheral speciation events (as “bud-dings,” see Knox 1998). If the terminal exemplars are all of specimens of one species, then the ancestor of all is that species (Fig. 1, left); if the exemplars are of different species of one genus, then the ancestral taxon may be inferred to be that genus; and if genera, then the inclusive family. On the other hand, if two clusters, each of a different taxon, are sister groups (i.e., branching from a common ancestor), then the ancestral phenotype (as opposed to just the shared traits) as a diagnosis at the same taxon level is impossible to infer (Fig. 1, right, question mark). It could be one or the other or a different extinct or unstudied taxon, perhaps of intermediate phenotype. Note that cladistics avoids naming ancestral taxa (or nodes on a tree), and Crowson (1982) criticized morphological cladistic analysis as to whether the postulated ancestral taxon is “imaginatively credible as a living species, with a definite mode of life to which its characters are well adapted?”.

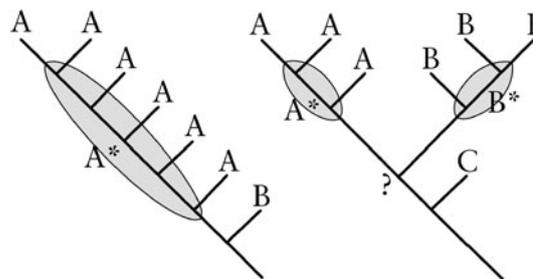


Fig. 1 *Left* Terminal clusters of exemplars of the same taxon (*A*) in one cladogram branch indicate that they are probably derived from an implied shared ancestral taxon *A** (a mapped taxon) similar in essential traits to all; that is, an ancestral taxon acceptably diagnosable as having the traits of that taxon (species, genus, family). *Right* The shared ancestral taxon (marked as ?) of two terminal clusters each of the same taxon (*A* or *B*) is not diagnosable as a named taxon

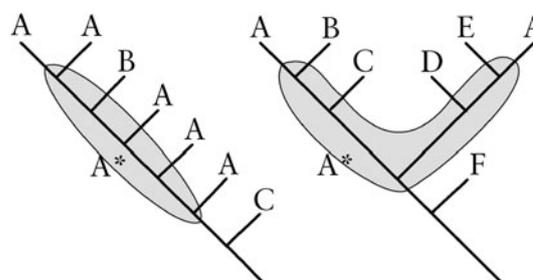


Fig. 2 *Left* A paraphyletic cluster of exemplars representing the same taxon implies a shared ancestral taxon *A** of that taxon, with the extraneous lineage (*B*) as descendant. *Right* Phylogenetic polyphyly may be simply evolutionary monophyly if the phylogenetically distant exemplars (*A*) of the same taxon are, after re-examination, definitely of that phenotypic taxon, and a deep shared ancestral taxon (*A**) is implied, with all intermediate lineages (*B*, *C*, *D*, *E*) as descendants of *A**

Mapped taxa consist of one or more concatenated ancestral nodes deep in a molecular tree. They may be identified by taxonomic name even if exemplars of the same taxon (species, genus, etc.) are separated by one or more lineages of a different taxon at the same or higher taxonomic level, as in the case of paraphyly (Fig. 2, left, where taxon *B* is a descendant of mapped taxon *A**, in addition to two exemplars of *A*) or phylogenetic polyphyly (Fig. 2, right, where taxa *B*, *C*, *D* and *E* are all descendants of *A**, in addition to two exemplars of *A*). One must examine, of course, these heterophyletic taxa for possible mistaken taxonomy, such as discovery that there are actually two taxa that were not previously distinguished until flagged by the molecular separation. On the other hand, if there is no mistake and the taxon is robust (i.e., no way of splitting the taxon is significantly better at organizing traits reflecting evolution than any other), then the exemplars of the phylogenetically split taxon offer evolutionary information.

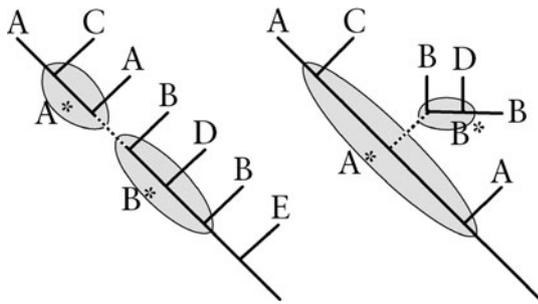


Fig. 3 Two mapped taxa, A^* implied by heterophyletic exemplars of A , and B^* implied by heterophyletic exemplars of B , may be ordered on a molecular cladogram, with A^* descending from B^* . *Left* A^* derived terminally from B^* . *Right* A^* derived from an intermediate branch out of B^* . *Dashed branch* may be short if generated by rapid burst of evolution

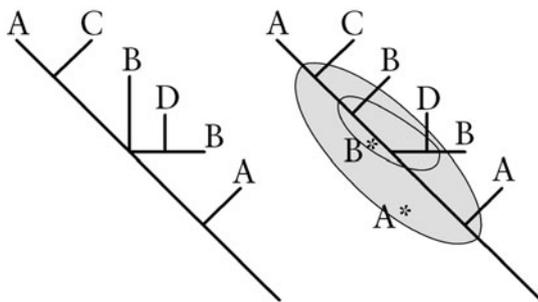


Fig. 4 Embedded mapped taxa. *Left* Same as diagram Fig. 3 (*right*) if dashed branch is too short (insufficient data) to resolve phylogenetically, resulting in a polytomy. *Right* Arbitrary analytic software resolution of the polytomy through long-branch attraction and accumulation of mutations in the tracking sequence embeds mapped taxon of B^* inside that of A^*

Cladists generally reject paraphyly (discussions of Donoghue 2005; Ebach et al. 2006; Potter and Freudenstein 2005), and thus hide the autapomorphic evolutionary information contained in classifications of traditional evolutionary taxonomy under the rubric of eliminating homoplasy (Brummitt 2008). While many individual morphological characters may be quite homoplastic (Endress 1996, p. 313), in particular confounding mosaic evolution in plants of greatly differing rates and trajectories in different organs, selection operates via the phenotype at the level of the entire genotype (Hickey 2000). Simões et al. (2008), in a laboratory study of several functional traits under selective pressure, found that the repeatability of weakly selected traits is not predictable in *Drosophila subobscura*, although the direction of key adaptations is, but that study dealt with trait changes within a species and repeatability of strongly conserved traits across speciation was not explored. An examination of evolutionary convergence between Mediterranean climate areas of Chile and California (Mooney and Cody 1977) found no evidence of convergence to total identity of originally

disparate flora and fauna in spite of considerable selective pressure as demonstrated by the development of essentially identical ecosystems. In cases of extreme similarity in morphology and birole in that study, “one-to-one correspondence, then, becomes a phenomenon maintained by closely related taxa, rather than one generated out of unrelated forms” (Cody et al. 1977, p. 187).

In the literature, exemplars representing the same taxon (particularly the same species) are occasionally pointed out as distant from each other on a molecular tree, with various explanations: (1) Molecularly heterophyletic exemplars are taken to represent multiple cryptic or sibling taxa, at least one of which requires a new taxonomic name and a molecular or at least geographic taxonomic definition (Bickford et al. 2007). These include “cryptic species” (e.g., Colborn et al. 2001; King and Hanner 1998; Stuart et al. 2006) and even cryptic genera (e.g., Brown and De Jonckheere 1999; Gontcharov and Melkonian 2005) found by molecular analysis, particularly via mitochondrial sequence barcoding (Hart et al. 2003; Hebert and Gregory 2005; Jarman and Elliott 2000; Kress et al. 2005; Kuusela et al. 2008; Lee and Foighil 2004; Molbo et al. 2003; Newmaster et al. 2006). Some may agreeably be found later to be also diagnosed by morphological or life history traits (Hebert et al. 2004; Hillis et al. 1996, p. 519). Molecular taxon crypsis is similar to that proposed in the past reflecting other methods of analysis, such as cytology and population genetics, as reviewed by Cain (1944). Competition associated with molecular cryptic diversity may explain rates and directionality of some taxa (Alizon et al. 2008). In many cases, on the other hand, the species remain fully cryptic. Elmer et al. (2007) demonstrated deep divergence and crypsis in an Amazonian frog. Shaw (2001) listed 14 cryptic or nearly cryptic species of bryophytes, while Hedenäs (2008) and Hedenäs and Eldenäs (2007) found additional moss cryptic species. Other studies uncovering mainly molecularly diagnosable cryptic species include those of Dawson and Jacobs (2001) and Zalar et al. (2005). These may be phylogenetically and geographically disjunctive populations of the same taxon surviving in phenotypic stasis perhaps through stabilizing (normalizing or purifying) selection (Koonin 2009) and habitat tracking (Eldredge 1989, p. 206). The isolated populations over time simply accumulate mutations in sequences used in molecular phylogenetic analysis. Persistence of some or even a great proportion of evolutionarily static populations or species (Eldredge et al. 2005; Guillaumet et al. 2008; Leschen et al. 2008; Shen et al. 2008), commonly of generalist phenotype (Eldredge 1989; Vrba 1984), is implied by the punctuated equilibrium theory of Gould and Lewontin (1979) and Gould and Eldredge (1993), which may be valid for many taxa (Foote and Miller 2006, p. 195; Jablonski 2007), although clear cases of gradual (Futuyma

1998, p. 114; Turner 2009) or stepwise transitions have been demonstrated (e.g., Deméré et al. 2008; Benton and Pearson 2001).

Alternatively, (2) phylogenetic distance is evidence that a heterophyletic taxon is basal or ancestral to a portion of the cladogram (Eldredge 1989, p. 175). Textbook examples of what are essentially mapped taxa as conceived here are given by Futuyma (1998, p. 456, 470), citing Moritz et al. (1992), who showed that coastal and Sierran Californian subspecies of the salamander *Ensatina eschscholtzii* apparently derived from subsp. *oregonensis*, and citing Hey and Kliman's (1993) and Kliman and Hey's (1993) analysis of the *Drosophila melanogaster* species group in which the paraphyletic *D. simulans* had at least gene copies that could be traced to a deep common ancestor.

Nelson et al. (2003) argued against Brummitt's (2002) contention that paraphyly implies an ancestral taxon. They indicated that "In practice, extinct ancestral taxa are seldom of concern, because organisms credibly representing them are seldom if ever in hand." An extensive appraisal of paraphyly and associated inferences of ancestry was given by Wiley and Mayden (2000), who agreeably asserted: "only the paraphyletic taxa of evolutionary taxonomy can be ancestors," while Graybeal (1995) discussed paraphyletic taxa as real taxa. Rieseberg and Brouillet (1994) discussed means of evolution of monophyletic descendant taxa from paraphyletic ancestral taxa through geographically local models of speciation. Assigning ancestral status to paraphyletic taxa is, thus, not new. In evolutionary systematics, evolution should be, to the extent possible, indicated by both descent and modification (Dayrat 2005; Knox 1998) of taxa (paraphyly and autophyly) rather than of traits (as in cladistic analysis).

Macroevolution

Macroevolution is here used in Jablonski's (2007) descriptive sense for evolutionary phenomena at and above the species level. Stanley (1975) pointed out that Darwin saw macroevolution as a race between evolving species. Pure chance macroevolutionary convergence or parallelism (Eldredge 1989, p. 1974) occurring to develop what is essentially the same taxon two or more times from a different ancestral taxon or taxa is here taken to be far less probable than the continued existence of populations of surviving ancestral taxa, that is, aside from orthogenesis (an internal evolutionary goal, as per Gould 2002, p. 350; McShea 2005). This is based on fundamental taxonomic study that identifies coherent groups apparently subject to stabilizing selection such that they survive through geologic time spans (Patterson 2005). Regarding the role of stasis as an explanation of the similarity of isolated groups, Gould (2002, p. 911) remarked about *Homo sapiens*, which

has experienced no directional trending in 40,000 years: "How could a new species evolve in lockstep parallelism from three ancestral populations spread over more than half the globe? Three groups, each moving in the same direction, and all still able to interbreed and constitute a single species after more than a million years of change?" Similar cases of long-isolated, but fertile when interbred, species, e.g., listed by Cain (1944), demonstrate that long isolation does not necessarily involve development of internal constraints for genetic isolation. Living examples of ancestral taxa are probably common; some survive well in extreme (Parsons 1994) and relic (Stepien et al. 2001) habitats.

Morphological trait combinations are restricted by phylogenetic constraint (limitation on swift evolution of one complex organism into another of much different complexity, see discussion of McShea 2005) or Gould's (2002, p. 901) asymmetric constraint (an apparent direction of evolution caused by purely physical limitations on direction of a drunkard's walk) and selection on some of the traits or their combinations. Conservative traits, phylogenetic constraint, and a general slow divergence of trait combinations act against fully cryptic convergence of taxa in spite of clear convergence of some traits in response to adaptation to similar environments. Here a molecular tree is taken as useful in demonstrating genetic continuity, assuming that the tree is reliable (Zander 2007a). Thus, traditional classification and molecular analysis may be syncretic in analysis of evolution, which is best modeled by descent with modification of *taxa*.

Methods

The present method uses heterophyly of traditional Linnaean taxa on a molecular tree to infer a surviving ancestral taxon (Zander 2008), or evolutionary Lazarus taxon (Zander 2007d), with interpolated lineages taken as surviving descendants. Although Cunningham et al. (1998) have pointed out that one trait at the distal of two nodes of a paraphyletic group cannot be parsimoniously decided, both nodes are assigned here to the same, ancestral taxon because a multiplicity of traits is decisive. At minimum, heterophyly involves two exemplars of one taxon with an exemplar of a different taxon as sister group to one of them on a molecular tree. The implication is that the heterophyly is due to a mapped taxon "buried" in the cladogram with those exemplars and all intermediate lineages being taxonomically identifiable descendants (Zander 2007b, c). A caulogram of diagnosable surviving ancestral taxa and extant descendants may be developed using traditional classifications that nearly obviate the chance of *total* phenotypic convergence, and the genetic continuity offered by the molecular tree.

Inferential demonstration of *two* mapped taxa is made by the presence on a molecular tree of two pairs of phylogenetically isolated identical exemplars. The implied two mapped taxa may be ordered terminally (Fig. 3, left) or from a midway branch (Fig. 3, right). Arranging these sequentially on the molecular tree creates a caulogram of mapped taxa and their descendants. Some ancestral taxa are resolvable only as the phenotypes of higher taxonomic categories, as when the mapped taxon is phenotypically diagnosable only to genus or higher.

Any nonrecent molecular heterophyly of species is evidence of punctuated equilibrium, implying ancient anagenesis and subsequent stasis of surviving populations of ancestral taxa. If punctuated equilibrium occurs, one might also expect short branches in both morphological and molecular data caused by bursts of speciation connecting mapped taxa. This is diagrammed in Fig. 3 by the dashed lines between mapped taxa A* and B*. If the lines are too short to be resolved in a molecular cladogram, the terminally ordered mapped taxon of Fig. 3 (left) might switch lineages A and B at the juncture, causing the mapped taxa to overlap. If the dashed branch is unresolved in the medially connected pair in Fig. 3 (right) then a polytomy would result (Fig. 4, left), which might be resolved through long-branch attraction (Felsenstein 1985; Lyons-Weiler and Takahashi 1999) and gradual accumulation of DNA base changes in the phylogenetic tracking sequence as one mapped taxon fully embedded in another (Fig. 4, right).

The use of traditional, phenotypic taxonomy is emphasized here because nomenclatural changes associated with molecular phylogenetic analysis (such as enforced by arbitrary strictures of phylogenetic monophyly) need to be discarded to allow inferences of macroevolution. Two kinds of ancestral taxa can be inferred for the caulogram. (1) A poorly resolved consensus taxon, which is basically the diagnosis of the next higher taxonomic category for a mixed group of taxa for which the evolutionary sequence is unknown. This is called here for want of a better term a “residuum.” (2) Surviving exemplars of ancestral taxa from which may be inferred an identical or nearly identical paraphyletic or even phylogenetically polyphyletic ancestral taxon of the same taxonomic rank (but evolutionarily monophyletic because mappable to a single taxon). Ancestral taxa are then arranged progressively following a reliable molecular tree (Zander 2007a, 2008).

The reliability of mapped taxa depends on the joint probability of the two exemplar lineages being each phylogenetically monophyletic and separated from each other by at least one internode of a different taxon (Zander 2007a). In the present paper, reliability is commonly good (with posterior probabilities of 0.95 or greater) for most mapped taxon inferences (assuming variation in gene

histories is negligible) but, because the method is new, statistical power in distinguishing evolutionary sequences is emphasized over general reliability (see discussion of statistical power by Zander 2007a).

For this study, several cladograms published by other authors were searched for sequential ancestor-descendant relationships of taxa through inference of deep caudistic ancestors using heterophyletic exemplars representing surviving populations of these putative ancestral taxa.

Results

Examination of published molecular trees and exemplars named or re-interpreted as traditional taxa often demonstrated heterophyly of exemplars of the same taxon. In the interpretative diagrams of published works figured here, mapped taxa are designated with an asterisk.

At the species and genus level, cladograms from which may be deduced simple sequential orderings of mapped taxa and their descendants are fairly common in published studies that include data on multiple exemplars of the same taxon.

The study of the angiosperm subfamily Knoxiaceae (Rubiaceae) by Kårehed and Bremer (2007) detailed well-supported heterophyly of exemplars of species of *Otomeria* (descendants being species of *Batopedina* and *Parapentas*), of *Pentansia* (descendants being species of *Neopentansia* and *Calanda*), and of *Pentas* (descendants being species of *Carphalea*, *Knoxia*, and *Placopoda*). Although the molecular tree indicated that the phylogenetic relationship of these three ancestral genera is (*Pentansia*, *Otomeria*) *Pentas*, the actual sequential evolutionary relationship is better conceived as a Besseyan cactus diagram with *Pentas* budding off both *Otomeria* and *Pentansia*. Exemplar species of *Parapentas* are quite distant on the molecular tree, separated from *Otomeria* and *Pentansia* by several genera, and if not better interpretable as two different genera, then *Parapentas* would be an intermediate on the evolutionary tree between the rather basal *Pentas* and the other two surviving ancestral genera. In another study, four well-supported mapped taxa occur at the apex of a fern phylogeny (Schuettpetz and Pryer 2007: Eupolypods 1, part 2) with mapped taxa of *Ctenopteris* and *Lelingeria* arising from that of *Terpsichore*, which itself arises from that of *Grammitis*.

A study of the Coreopsidae, Asteraceae (Mort et al. 2008) showed molecular paraphyly of *Coreopsis*, exemplars of species representing that genus appearing in scattered groups throughout the molecular cladogram, implying that this genus is the surviving ancestral morphotype for most genera of the tribe, including *Bidens*. In a molecular study (Havill et al. 2008) of the conifer *Tsuga*, *T. seiboldii* was apparently the ancestral taxon of *T. chinensis*.

Even though exemplars of *T. chinensis* appear to bracket three exemplars of *T. seiboldii*, two exemplars of *T. seiboldii* with connections much deeper in the cladogram allow a mapped taxon of *T. seiboldii* to be drawn that connects all taxa without overlap with any apparent mapped taxon of *T. chinensis*. A molecular analysis of Menyanthaceae by Tippery et al. (2008) clearly demonstrated a mapped taxon of *Villarsia* from which descended species of *Leparophyllum* and *Nymphoides*.

In an investigation of lava lizard phylogeny, Benavides et al. (2007) demonstrated phylogenetic disjunction on a nuclear DNA tree of *Microlophus quadrivittatus*, which bracketed *M. atacamensis*, which is therefore its descendant, and of *M. tigris*, which bracketed *M. peruvianus* as its descendant, although this is contradicted by the mtDNA clade. The consensus tree supported the nDNA tree, which, according to the authors, also makes better geographical sense.

Punctuated equilibrium

Evidence of punctuated equilibrium (Bokma 2008; Singh 2000, p. 571) may be interpreted from published studies in which the lineage splits are, generally, well supported. A prepunctuational phase is common in the examined publications, namely where one species (or taxon) is homophyletic (Fig. 1, left) on a molecular tree, i.e., a sequence of molecular lineages leading only to exemplars of that species, showing molecular differentiation but no phenotypic differentiation. Phenotypic stasis is easily inferred. Punctuated equilibrium is best exemplified, however, by heterophyly, i.e., an interpolated lineage or lineages of a different taxon, with rapid divergence of the new taxon and stasis of the ancestor, which is also common in the published literature as discussed above. A more complex example includes the molecular study of Setoguchi et al. (2008) of the shrub *Pieris* (Ericaceae) using *rbcL* and *matK* chloroplast sequences resulting in a well-supported molecular clade

(((*P. japonica* var. *yakushimensis*, *P. koidzumiana* exemplar 1), (*P. koidzumiana* exemplar 2, *P. taiwanensis*)), *P. japonica*)

where *P. koidzumiana* exemplars 1 and 2 are from Amami and Okinawa islands, respectively. *Pieris koidzumiana* is paraphyletic and implies a mapped taxon of the same name for the two extant island populations and for *P. taiwanensis*. *Pieris japonica* (as two varieties) is also paraphyletic but its mapped taxon, though lower in the cladogram, overlaps that of *P. koidzumiana*. This overlap implies a short and unresolved evolutionary distance between *P. japonica* and *P. koidzumiana*. If divergence times estimated on biogeographic grounds by the authors

are an indication of fossil age, then the “virtual fossil” of *P. japonica* may be dated at minimally 0.8 Mya and that of *P. koidzumiana* at 0.2 Mya.

The study of Pelser et al. (2007) of Senecioneae (Asteraceae) relationships within the subtribe Othonniae show *Othonna* to be a surviving ancestral taxon, and *Senecio* likewise in the subtribe Senecioninae. The appearance of heterophyly of certain genera (e.g., *Curio* and *Dendrophorbium*) with mapped taxa within a range of heterophyletic *Senecio* exemplar branches indicates that the molecular lineage may lack molecular data on rapid evolution of these genera, where very short branches are entirely to be expected in punctuated equilibrium. Although one might consider heterophyly as simply random convergence which may be found both outside and inside other pairs of convergences of other taxa, one must first accept the commonness of complete convergence of taxa before postulating randomness.

The same evidence of heterophyly associated with overlapping portions of ancestral tracks is found in a molecular study (Harris 2008) of the moss family Mniaceae. This showed that the heterophyletic *Plagiomnium maximoviczii* gave rise to several species including *P. cordatum*, *P. integrum*, *P. novae-zealandiae*, *P. rhynchophorum*, *P. rostratum*, and *P. vesicatum*. *Plagiomnium integrum*, however, is also heterophyletic and the track on the Harris cladogram of a mapped taxon of that species overlaps that of *P. maximoviczii*. There is apparent double convergence involving three separate lineages with the morphology of *P. maximoviczii* and two with the morphology of *P. integrum* that may be best explained instead by punctuated equilibrium among multiple surviving ancestral taxa, although another possibility is polyploidy, as discussed for other taxa by Harris (2008). Both species are attributed morphological and ecological distinctions between at least some geographically disjunct populations, but the problem warrants additional attention. This relationship may be an important evolutionary laboratory for further research.

Atavistic saltation

Saltation, here used in the broad sense or “parasaltation” of Bateman and DiMichele (2002), is a sudden change in a lineage, such as single-step speciation through point mutations in developmental genes (Theissen 2006), catastrophic selection (Lewis 1962, 1966), immediate genetic isolation by polyploidy, or macroevolution by immediate development of a major new combination of expressed traits including epigenetic reactivation of suppressed trait combinations (Armbruster 1996; Caporale 1999, 2003; Jablonka and Raz 2009; Jablonski 2005, 2007; Peterson et al. 2005; Zander 2007d), natural selection acting on a

“standing pool of genetic variation” from occasional hybridization (Schluter and Conte 2009) or reticulation (Bateman and DiMichele 2002), or (nearly) neutral mutations (Koonin 2009). It is often signaled in phylogenetics by long branches, that is, massive accumulation of shared advanced expressed traits, or by extinction or inadequate sampling (Bateman 1996). Aside from polyploidy, there is much problematic about identification of saltation, particularly in distinguishing Bateman’s “hard” long branch from one that only appears to be long because of the study’s omission of exemplar species of that lineage. Certain patterns of heterophyly may, however, identify saltation.

Shaw et al. (2008), in a study of six nuclear, plastid, and mitochondrial nucleotide sequences of 32 exemplars of the moss family Hypopterygiaceae, found that of four species of *Cyathophorum* two pairs of the species were heterophyletic, one pair near the base of the strongly supported cladogram and two well buried among 10 exemplars of the genus *Hypopterygium* (Fig. 5). Later, Bell and Newton (2006) found a similar though less well supported split in *Cyathophorum*. Shaw et al. transferred the two *Cyathophorum* species embedded in *Hypopterygium* to the latter genus to preserve phylogenetic monophyly. On the other hand, it is clear that *Cyathophorum* may also be taken as a heterophyletic genus ancestral to several descendent genera (*Arbusculohypopterygium*, *Canalohypopterygium*, *Catharomnion*, *Dendrohypopterygium*, *Hypopterygium*, *Lopidium*). Because one pair of the four *Cyathophorum* species is well embedded in *Hypopterygium*, those two species probably arose, rapidly, from a *Hypopterygium* ancestral taxon. Simple punctuated evolution cannot easily account for this heterophyly, which is apparently true evolutionary polyphyly. But is it attributable to stochastic convergence? There is no indication of over-lumping of disparate species as a bad genus on the phenotypic level.

A clear explanation is saltation, not by an inference that the phenotype of *Cyathophorum* “jumped” from a deep ancestral taxon of *Cyathophorum* to a descendent of a different ancestral taxon, *Hypopterygium*, but because gradualist re-evolution of the descendant taxa is far less probable than theoretical reversal of a major well-conserved genus-level linked trait complex (in particular anisophylly and differentiated laminal border) to that of *Cyathophorum*. This may be due perhaps to epigenetic retention and abrupt triggering of reactivation of the *Cyathophorum* trait complex as an evolutionarily well-tested, successful combination of selective advantage (Caporale 1999, 2003; Jablonski 2007; Rachootin and Thomson 1981). Of additional interest in Fig. 5 is the fact that *Lopidium* and *Hypopterygium* are apparently recently derived, given no evident heterophyly in spite of sampling from different continents in the Old and New Worlds, but

these genera do show an expected moderate internal differentiation of isolated molecular lines.

A molecular phylogeny of Iridaceae by Goldblatt et al. (2008) demonstrated a similar deep embedding of one taxon, *Calydorea*, in a mapped taxon of another, *Tigridia*, but the clade support values are rather low. If the molecular cladogram is correct, however, the fact that the *Calydorea* mapped taxon is lower in the tree than that of *Tigridia* indicates that the strongly embedded *C. mexicana* would exemplify the same atavistic saltation as described above.

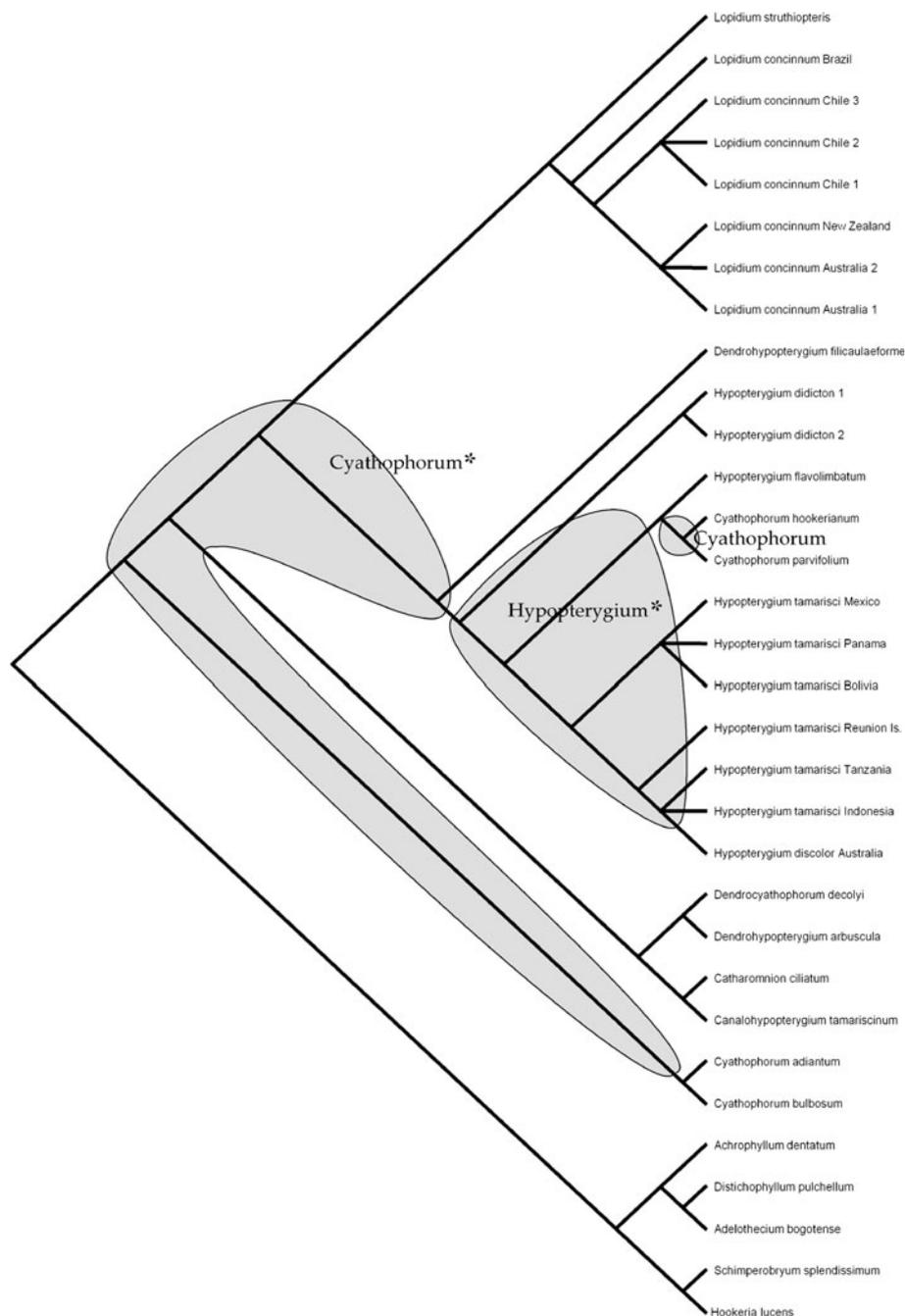
Suprageneric level heterophyly

Caulograms may also be constructed at the suprageneric level. Mapped taxa in the molecular studies of Werner et al. (2004) of the moss family Pottiaceae and Werner et al. (2005) of the Pottiaceae subfamily Trichostomoideae were identified and figured together as a “Besseyan cactus” by Zander (2008) but are here presented (Figs. 6, 7, respectively) separately, reduced to only branches at 0.95 probability or above via Zander’s (2007a) method. Shaded areas are mapped taxa.

In the Werner et al. (2004) study (Fig. 6), the most basal elements of Pottiaceae as a mapped taxon are established by the isolated pottiaceous genus *Timmiella*. The genera *Barbula* and *Pseudocrossidium*, which have apparently primitive traits (as detailed in another paper), possibly due to punctuated equilibrium and associated lack of data, and which are presently not ordered evolutionarily, directly gave rise to the subfamilies Trichostomoideae and Pottioideae. The related family Ephemeraceae, which is highly reduced morphologically and adapted to quite different, evanescent moist habitats, is derived from Trichostomoideae. The aquatic family Cinclidotaceae is derived from Pottioideae. The overall caulogram agrees to a significant extent, in spite of its poor resolution, with the morphological cladogram of the Pottiaceae by Zander (1993). Many apparent mapped taxa associated with heterophyly at the base of the cladogram (as in Fig. 5) are ignored as possibly due to poor sorting because of lack of data.

The Werner et al. (2005) study of Trichostomoideae, a subfamily of the Pottiaceae, demonstrated (Fig. 7) mapped taxa of the genera *Trichostomum* and *Weissia*, via heterophyly of species of those genera; a clear double ancestral taxon (that is, probably unresolved punctuated evolution) of *Tortella* and *Chionoloma* through overlapping heterophyly of species of those genera; the same sort of double ancestral taxon but at the species level for *Tortella tortuosa* and *T. fragilis*, and an ancestral taxon of *Trichostomum tenuirostre*. Different genera derived from mapped taxa are indicated by arrows, *Pleurochaete* derived from *Tortella*, *Pseudosymblypharis* from *Trichostomum tenuirostre*, and *Aschisma* from *Trichostomum*. In this molecular cladogram,

Fig. 5 Molecular cladogram modified from that of Shaw et al. (2008) showing inferred mapped taxa (asterisks) of *Cyathophorum* and *Hypopterygium*. A descendant pair of *Cyathophorum* species is well embedded in *Hypopterygium* and may be atavistically saltative in origin as macroevolution by rapid reversal of all diagnosable traits at the genus level

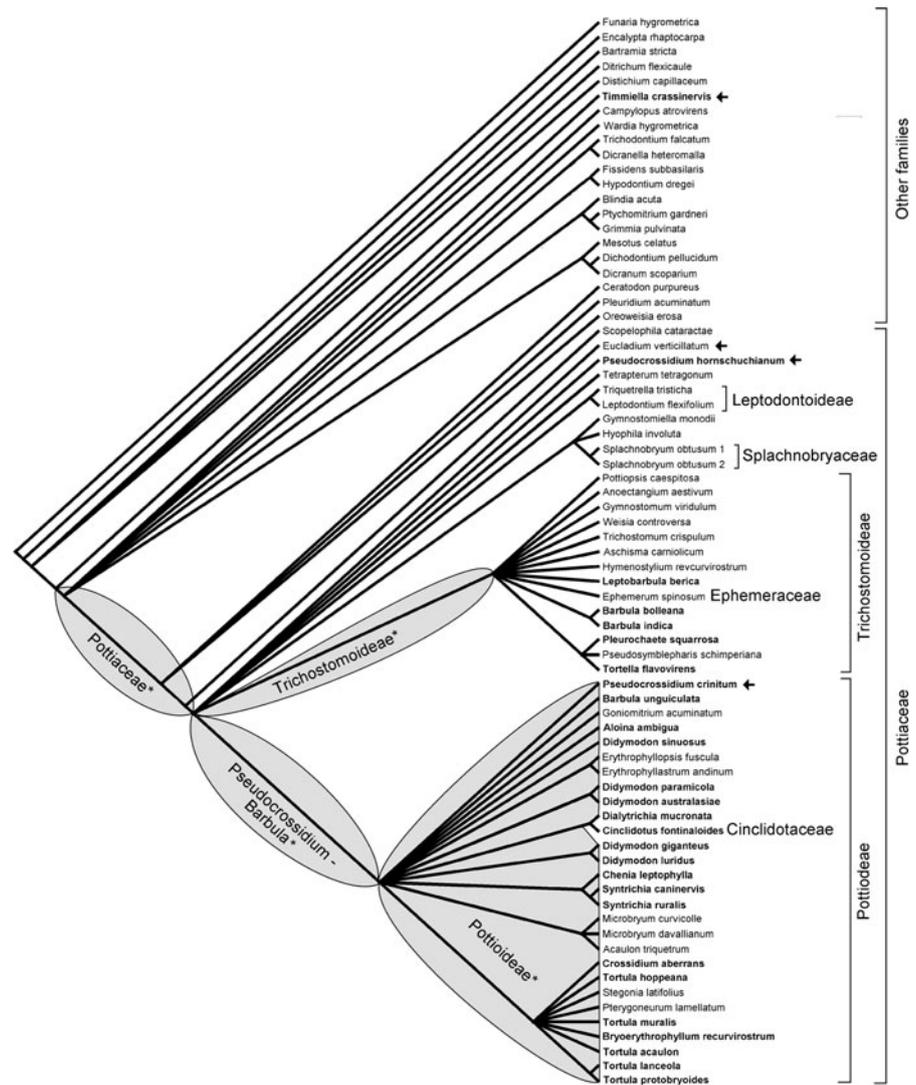


it is clear that certain taxa with exemplars sampled from geographically distant stations are probably recent in origin, namely *Tortella flavovirens* and *T. humilis*, given the well-populated clades in which they are embedded without heterophyly. Some taxa that may appear to be heterophyletic are simply unknown or unstudied taxa of relationships that need re-examination, such as *Trichostomum austrocrispum* and *Weissia ayresii*. The exemplar of *Weissia condensata* that was sampled from North America is doubtless actually *W. controversa*, as the former taxon has been taxonomically excluded from North America (Zander 2007e).

Discussion

Both Felsenstein (2000) and Koonin (2009) have called for a new synthesis beyond the “post-neo-Darwinian.” Here I propose a synthesis between evolutionary taxonomy (traditional classification reflecting paraphyletic groups) and molecular phylogenetics (lineages of genetic continuity and isolation events). There is nothing startlingly new about this, as this additional information about evolution has been staring us in the face for years, albeit masked and modified by a canonically intransigent insistence on

Fig. 6 Molecular cladogram of family Pottiaceae from Werner et al. (2004) after reliability analysis and reduction to branches supported at 0.95 probability. Inferred mapped taxa of the caulogram are shaded. *Barbula* and *Pseudocrossidium* are primitive and unordered. *Timmiella* establishes the Pottiaceae mapped taxon, and *Eucladium* the subfamily Trichostomoideae mapped taxon



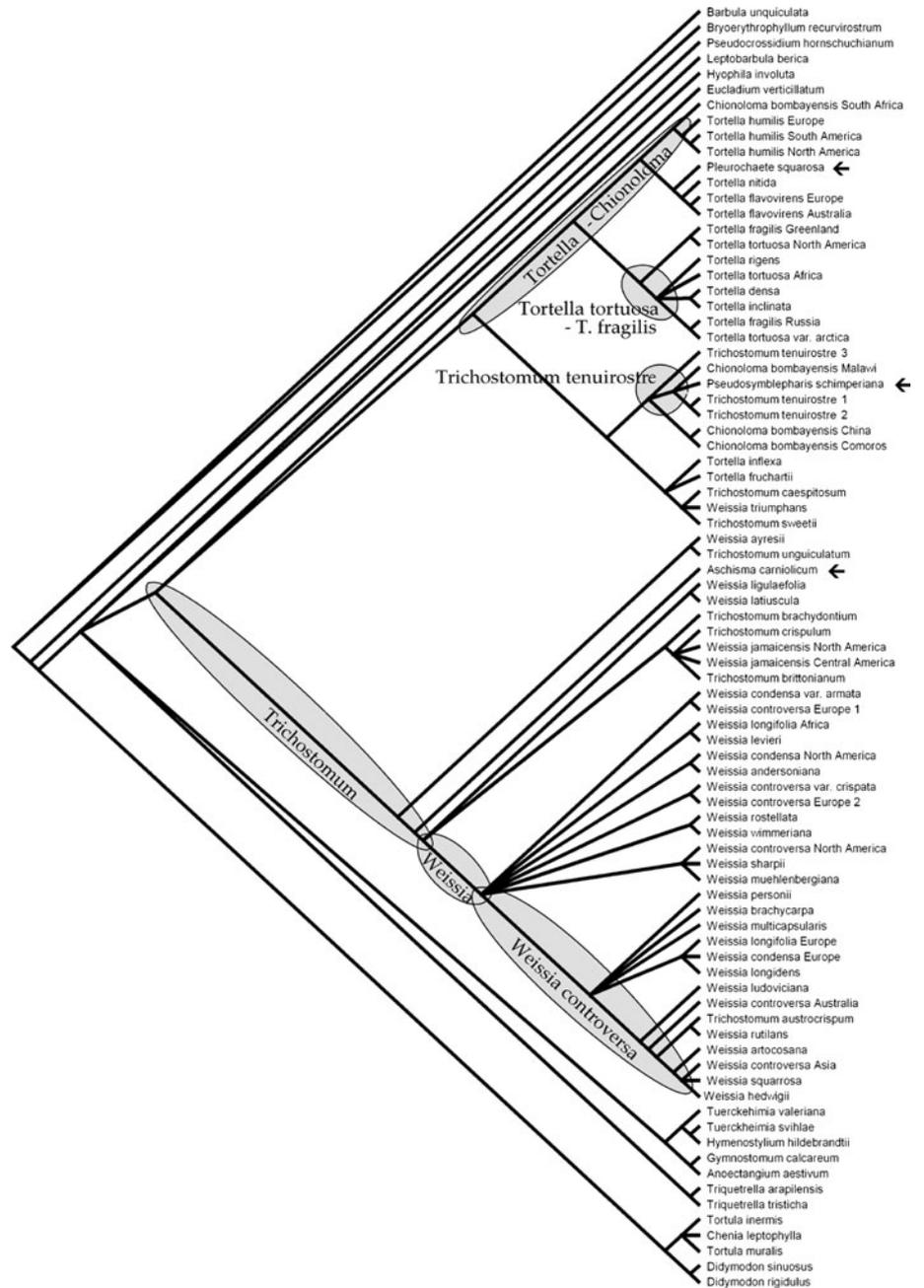
holophyly in classification. The new method introduces a scientific parsimony of ancestors, in that, given abundant evidence of surviving ancestral taxa (as the heterophyly expressed in molecular cladograms), why postulate multiple entities as Unknown Ancestors? The data, when available, are necessary and sufficient to result in a tree of named ancestral taxa and descendants.

A mapped taxon comprises two or more nodes on a molecular tree and has the same or higher taxonomic rank than that represented by its two or more extant exemplars. Phylogenetically distant exemplars of the same taxon delimit the mapped taxon lower in the tree. A caulogram is well exemplified by the oft-reprinted phyletic series chart of horse evolution by Strickberger (1990) and see discussion by Gould (1996: 62) of similar phyletic series. Phylogenetic cladograms show or map changes in traits, not taxa, and individual traits may show apparent convergence, falsely telegraphing complete convergence of an evolutionary lineage, even with complex organs generally thought not

subject to re-evolution by Dollo's Rule (Hall 2003). For instance, a master gene governing development of eye structures apparently is involved in separate evolution of the eye in 15 different lineages (Brosius 2005; Gehring and Ikeo 1999; Jablonski 2007; Pichaud and Desplan 2002; Salvini-Plawen and Mayr 1977), while, likewise, development of front and rear fangs in snakes is also governed (Vonk et al. 2008) by an evolutionary Lazarus gene. In the present study, Dollo's Rule (Hall 2003) is, however, considered applicable at the whole organismal level as a unified combination of traits as opposed to portions of the genome or traits atomized in a data set. The present method of mapping taxa infers deep evolutionary monophyly using, and not in spite of, splits in genetic continuity tracked by shared changes in molecular traits.

Parsimony in general does cluster taxa in nested groups of ancestral relationships following a simple cladogenetic model (nested hierarchies of exemplars based on shared advanced traits). Frondon and Garner (2004), however,

Fig. 7 More specialized molecular cladogram of subfamily Trichostomoideae of the Pottiaceae from Werner et al. (2005) after reliability analysis and reduction to branches supported at 0.95 probability. Inferred mapped taxa are shaded



found a theoretical abundance of preadapted, prespeciation phenotypic traits that cannot be probabilistically analyzed, while Cunningham et al. (1998) doubted the validity of the assumption of equal trait gains and reversals. Any few traits may be linked selectively or epigenetically and fixed as a unit in a new species. Of three related taxa, the pair of species sharing two adaptively or epigenetically linked traits may be no more likely to share an immediate ancestral taxon than the other two sharing only one trait.

Sometimes heterophyletic exemplars on a molecular cladogram may actually represent a misconstrued taxon (a species, genus, family, etc.) that should, after judicious

re-examination, be taxonomically separated into two. The way the included taxa are split, however, could present a multiple test or multiple comparisons problem in statistics (Zander 2007a). One should keep in mind that, e.g., a genus might be split randomly into two groups of species, and “generic descriptions” written that ostensibly describe such groups (in the main, and with some contrary phenotypic traits explained as “reversals”), but such morphology may not comprise a robust phenotypic genus with distinct autapomorphic or conservative characteristic traits more or less well gapped from related genera, commonly with a distinct evolutionary birole and habitat. Although the

importance of gaps between taxa in taxonomy is sometimes deprecated as simply relying on ignorance, particularly when geologic fossils are part of an evolutionary analysis (Gauthier and de Queiroz 2001, p. 33), an evolution-based taxonomy should mirror the present-day results of selection for a given Bauplan in a particular environment (Szalay and Bock 1991).

Punctuated equilibrium

Eldredge (1989), Lieberman and Vrba (2005), and Stanley (1975, 1979, 1981) have reviewed facts supporting punctuated equilibrium and the related quantum evolution (major change over a short time period in a small population that is usually marginal and entering a new adaptive zone), the punctuational model being supported by identification of long-lasting, little-changing lineages that contain few species at any one time. Koonin (2009) has reviewed genomic evidence in support for “big bangs” of evolution and against gradualist change. Stanley (1981) cited the bowfin fishes (family Amiidae) as classic living fossils that demonstrate little change over more than 100 million years since deposition of abundant fossils in the Cretaceous, and minor change (with no essential shift in adaptation) in the 65 million years of the Cenozoic. The lungfishes evince similar punctuational evolution in that after a burst of speciation about 300 million years ago, a few lineages have persisted to the present with little change in anatomy. The tadpole shrimp has not changed significantly since the Triassic, while other well-known living fossils include Echinoneid sea urchins, horseshoe crabs, Bairdiid ostracods, Notostracan crustaceans, sirens, New World porcupines, pangolins, American alligators, snapping turtles, coelacanths, sturgeons, garpikes, tapirs, aardvarks, dawn redwoods, and ginkgos. Stanley also gave many examples of rapid evolution, such as the four unique cichlid fish species of Lake Nabugabo, evolving after the lake formed 4,000 years ago when cut off from Lake Victoria, and several species of Hawaiian banana-feeding moths of the genus *Hedylepta* that developed only after introduction of the fruit there 1,000 years ago. According to Mayr (2001:47), nearly one-third of early fossil cyanobacteria are phenotypically identical to extant species, and nearly all are attributable to modern genera. Patterson (2005) has pointed out that we find taxonomy useful only because of stabilizing selection, which acts over hundreds of thousands or millions of years to preserve the phenotype of diagnosable species, and is thus the most common and expected form of natural selection. Punctuated evolution is criticized at length by Dawkins (1986), who asserted that speed of evolution is never fully gradual or fully punctuational. Certain evidence supporting punctuated evolution has been shown to be wrongly interpreted (Van Bocxlaer

et al. 2008), but there is abundant evidence that many lineages exhibit bursts of evolution followed by stasis (Eldredge 1989; Eldredge et al. 2005; Stanley 1981), as opposed to increasing extinction (Rabosky and Lovette 2008).

The mapped taxa described here largely pass Stanley’s test of living fossils (1979, p. 123), in which they do (1) exhibit primitive morphological traits, but they may not necessarily (2) have survived for long periods of time at low numerical diversity. The latter requirement is made obsolete by the present inference of the shared ancestry of phylogenetically distant exemplars of the same taxon without recourse to numerical diversity measures. The critical test of Gould and Eldredge (1993), that morphological change into two phenotypes does not accompany bifurcation of a lineage, is certainly demonstrated in the present analysis at various taxonomic levels by the existence of molecularly hetero-phyletic persisting ancestral taxa.

Double or superimposed ancestral taxa in otherwise well-resolved cladograms from well-populated data sets may be explained by (1) bursts of evolution and associated unresolved short phylogenetic branches coupled with long stasis of isolated populations and the confounding influence of long-branch attraction (Lyons-Weiler and Takahashi 1999) of much mutated tracking DNA sequences. Alternatively, the overlapping mapped taxa in Fig. 4 (left) might be due to (2) atavistic saltation as discussed below, or (3) parallel selection of the same traits into the same environment. Overlapping mapped taxa in all three cases suggest that adaptive, expressed traits selected for as a package may be distinguished from neutral phenotypic traits (spandrels of Gould and Lewontin 1979), with further comparative sampling of taxa and exemplars of taxa, because (1) short branches restrict anagenetic drift, (2) atavisms require a genetic “memory” of a package of probably conservative traits, and (3) fixation of identical neutral traits in isolated populations is doubtless rare. Multiple expressed traits may be linked or packaged epigenetically, pleiotropically, or through joint selection depending on a particular phenotype or Bauplan and a particular environment. Detailing the putative adaptive, packaged traits that may be involved in overlapping mapped taxa was not pursued in the present paper, but the mapping of individual adaptive traits has been discussed by Baum and Larson (1991).

There are, of course, additional explanations of one ancestral taxon being indistinguishable from other ancestral taxa on a phylogenetic tree, such as ancestral balancing selection (Schaeffer and Aguadé 2000) coupled with extinction, hybridization between recontacted long-isolated populations (Singh 2000, p. 573), or a problem with analysis of genetic continuity such as lack of data, or data-destroying extinctions. Both apparent punctuated

equilibrium and saltation may involve preadaptation or exaptation (Brosius 2005; Eldredge 1989, p. 50; Gould and Vrba 1982); frequent evocation of homologous developmental pathways as channels of constraint that yield parallelisms, not convergences (Gould 2002, p. 1134); preset channels involving linked suites of characters involved in exaptation (Vrba 2005); by selectively co-varying traits switching over a threshold to another set of selectively co-varying states as suggested by Felsenstein (2005); or by evo-devo positive and negative feedback of genomic motifs of multiple genes and regulatory elements maintaining a “criticality” that balances order and chaos around an optimal selective mode (von Dassow and Munro 1999; Fujimoto et al. 2008; Meir et al. 2002; Nochomovitz and Li 2006; Nykter et al. 2008). Such may be valid for particular instances.

Lack of data as generative of false heterophyly was demonstrated in comparing the molecular cladograms of Werner et al. (2004) and (2005), where Trichostomoideae (Bryophyta) in the former cladogram (*Oxystegus* well-buried among Pottioideae and disjunct from other members of the subfamily: Fig. 6) apparently formed a mapped taxon that conflicted with (overlapped) that of *Pseudocrossidium*, but this is resolved as no real conflict, with *Oxystegus* placed elsewhere, among the Trichostomoideae, in the Werner et al. (2005) cladogram (Fig. 7). Clearly it is early times and many problems will disappear with continuing study. The possibility of compelling explanations alternative to commonly postulated convergence, however, must be faced by phylogenetic systematists.

Atavistic saltation

Although the Shaw et al. (2008) cladogram is here taken as implying at least atavistic saltation in mosses, mechanisms of very rapid macroevolution are, however, not clear, though there are examples involving paedomorphosis, instant species through polyploidy (Masterson 1994), and reported major phenotypic saltation in otherwise conservative segment number in centipedes (Minelli et al. 2009) attributed to possible point mutations in a homeotic element specifying number of segments. Eldredge (1985) suggested that saltative theory that was not Neodarwinian (i.e., of the punctuated variant) was unscientific, while Mayr (2001) felt that all saltation theories are based on essentialism (which he opposed to gradualism). Rachootin and Thomson (1981) early on pointed out how epigenetic processes support possible mechanisms of evolutionary saltation. In the present paper, a genomic explanation, that of multi-trait silencing with later triggering of reactivation, is offered for an example that was not de novo saltation, but da capo. Such silencing is implied in Mayr’s (2001) concept of parallelophyly, the independent acquiring of the

same traits by unrelated groups because of the propensities of their shared ancestral taxa that lack such traits; he used this in explanation of similar pelvises in birds and dinosaurs as derived from thecodont archosaurians of presumably similar genotype. Vrba (1984) discussed the possibility of linked suites of characters expressed through morphogenetic rules with heterochronic variation. Such explanations should be pursued before considering, say, occasional decoupling of noncoding molecular and expressed trait evolution by an unknown mechanism.

Zander (2006a, b) tried to uncover phylogenetically ancient morphological traits in mosses (Zander 2007d) by application of various chemicals known to force expression (by opening the DNA chromatin structure) of silenced genes. It is understood that at least some gene silencing involves epigenetic effects on DNA by cytosine methylation and histone deacetylation (Yi 2007). Treatments using 5-aza-2'-deoxycytidine (a demethylation agent at micromole concentrations), sodium butyrate (a histone deacetylase inhibitor at millimole concentrations), and a combination of the two reagents on 10 common moss taxa over 4 months found no morphological abnormalities or modifications interpretable as re-expressed silenced traits. Although gene silencing doubtless occurs in mosses in light of complex differentiation of tissues and a life cycle involving radical changes in morphology, it was concluded that whatever mechanism controlled epistatic regulation in these vegetatively haploid plants was apparently not affected by these particular challenges of methylation and deacetylation.

Evidence for atavistic saltation includes genuine “hopeful monsters” (Bateman and DiMichele 1994, 2002), apparently by reactivation of groups of silenced traits, not new mutations. Stevens (1980) pointed out early discussions of “evolutionary recall” (Robson 1972), this through developmentally based violations of Dollo’s Law that complex traits do not re-evolve. Examples include apparent re-evolution of shell coiling in snails (Collin and Cipriani 2003); reactivation of wings in wingless walking sticks (Whiting et al. 2003); eye atavisms in cyclopean brine shrimp (Fryer 1999); modes of vulva formation in nematodes (Srinivasan et al. 2001); ancestral traits of the lateral lines, muscles, and gill rakers of cichlid fishes (Stiassny 1992); eye reactivation in eyeless copepods (Dingle 2003); teeth in chickens (Harris et al. 2006); and re-occurrence of a second molar in lynx (Kurtén 1963). Not all atavisms are homologous, as vestigial hips in snakes and whales have been shown to depend on quite different developmental pathways (Bejder and Hall 2002).

Macroevolution

Do supraspecific taxa evolve? Certainly Gould (Gould 2002; Hubbell 2005) and many others have thought so.

Eldredge (1985, p. 150) indicated that there is a “distinct possibility of some higher-level sorting principle in nature” that affects higher taxa, and this may be due to differential species survival (1985, p. 172), while he (1989, p. 183) also argued that “higher taxa are coherent pools of genetic information.” Vrba (1980, 1984) attributed such macroevolutionary changes not to properties of species but to attributes of organisms, particularly a cascade of specialization and short (geologic) time span in certain lineages, as the “effect hypothesis,” though this concerns trends more than punctuation itself. The phenomenon of “macroevolution lag,” in which the origination of a major group is followed by a quiet phase that itself precedes an increase in diversity (Jablonski and Bottjer 1990), implies selection-like pressures on the supraspecific taxon.

Features of macroevolution are complex, and Eldredge and Cracraft (1980) discussed trends, macroevolutionary patterns of adaptive radiation, arrested evolution, and no change. Discussions of phenotypic change at the genus level and above are given by Rensch (1960) and Stebbins (1974), while Stanley (1975) offered the mechanism of species selection, with survival favoring species with high speciation rates, a kind of natural selection operating on species in supraspecific taxa rather than individuals in populations (see also Eldredge 1989, p. 138; Gould 2002, p. 668). Gould (2002, pp. 673, 717) included stochastic processes governed by asymmetrical morphological constraint, and selection on population (or species) level emergent or aggregate properties, including change in function of pre-existing organs.

Several recent authors have pointed out that modern phylogenetic analysis does not represent macroevolution in classification (e.g., Dayrat 2005; Grant 2003; Knox 1998; Mayr and Bock 2002). In fact, unlike Darwin’s Natural System (Darwin 1859), a phylogenetic tree of life may be totally replaced by “nested parentheses of life” with no core, or caulis, of named ancestral taxa. As for the present paper, one may view mapped taxa at any taxonomic level as either simply representing populations or species evolving in the past, or as higher taxa evolving by selective extinction of certain species or by Stanley’s differential speciation rates, with results similar to balancing, directional, and disruptive selection but acting on higher taxa. I cannot see how it is possible to reject evolution at the genus level (or above) if, for example, the genus diagnosis changes because some of its species with a particular trait or trait combination disappear either through negative selection or by chance alone. No matter what the mechanism, this paper proposes that one taxon at any rank can generate another, and this may be a more useful way of diagramming evolution, when data are available, than cladistic trees requiring ad hoc hypothetical shared ancestral taxa that are unnamed and poorly characterized.

This, then, raises the question of whether genera and families are real things (discussion by Eldredge 1989, p. 12) or individuals (as per Gould 2002), or at least real categories reflecting natural processes, on the same level of investigative value as are species. Taxa in this paper are viewed following Fitzhugh’s (2005) extendible idea of species being proxies for explanatory concepts, in the present case applied to all taxa being considered as perceived real groupings in nature that can be understood by invoking various causal explanations. Certainly taxonomists have discovered the same gaps, kinds of traits (though perhaps more conservative), and specific bioroles characterizing higher taxa as they have done for species (and the same spectrum of distinctness and intergradation). Eldredge and Cracraft (1980, p. 271) averred that “species are reproductive communities,” and that “genera, orders, and so forth, do not evolve except as their component species do—that the patterns of fluctuation of diversity within taxa of higher categorical rank are a reflection of patterns of origin, survival, and the extinction of their constituent species.” Those patterns, however, can be nothing but the result of evolution through selection at the species level resulting in descent with modification of taxa.

Eldredge and Cracraft (1980, p. 282) further assert that “taxa of higher rank than species do not exist in the same way as do species,” and “cannot logically be ancestral to one another.” This, however, requires a biological species concept and a general faith in panmixis. Isolated populations of species, and also of species grouped in higher taxa, however, doubtless undergo stabilizing selection, e.g., associated with restriction to long-stable microhabitats, and this descent with nonmodification aspect of evolution is demonstrated in many publications (if here interpreted correctly). Thus, it is quite possible that a shared environment or microenvironment, as a paragenetic (Bock 2003) regulator or “envirosome,” knits together a metagenome for all species of a genus (or larger group) such that within the phyletic constraint of shared morphology, evolution is jointly affected and the genus evolves. At the genus and species level, phylogenetic nesting on the basis of molecular trait changes may be accurate, but any one ancestral species may be phylogenetically complex, e.g., the domestic cat species (Driscoll et al. 2007), pocket gophers (Patton and Smith 1994), or the *Asplenium nidus* complex (Pteridophyta) (Yatabe and Murakami 2003), and any split in a molecular lineage may involve one or more populations of a surviving ancestral taxon. Molecular lineages, however, do provide a window on genetic continuity, while there are techniques to identify hybridization, reticulation, and lateral gene transfer.

Molecular systematics does not necessarily detail lineage branching order because there may be extinct

paraphyly. Any sister group may actually be an ancestor-descendant relationship if one of the branches has an extinct line that once existed just below or above the split, while extinct lines two or more nodes below or above affect the actual branching order no matter what the support is for any particular branch. The probability of this problem for any molecular sister-group is perhaps proportional to the extent of presently available data demonstrating paraphyly or polyphyly in a particular group for a particular molecular analysis, though this may be too low as Rieseberg and Brouillet (1994) estimated that at least 50% of all plant species are products of local geographic speciation and therefore paraphyletic, and Funk and Omland (2003) found actual species-level paraphyly or polyphyly in 23% of more than 2,000 species sampled. This affects the resolution of molecular phylogenetic analysis as a whole. To increase confidence in branching order of molecular cladograms, other information is necessary, such as analysis of chromosome number, biogeography, and information on restrictions on reversals of traits (e.g., Bridgham et al. 2006).

Dating mapped taxa may use standard molecular techniques with geologic fossils as reference points in time, but ballpark estimates of minimum age can be based on the last date the two phylogenetically disjunct exemplars may have been at least sympatric. For example, at present, *Pseudocrossidium crinitum* (Fig. 5), well-distributed around the extreme Southern Hemisphere, reaches north to western North America, whereas the phylogenetically quite distant *P. hornschurchianum* is essentially European in range. The latest date the two might have at least introgressed is that of the establishment of the Atlantic Ocean, while the essentially Gondwanalandic distribution of *P. crinitum* indicates an even further, possibly pre-Tethyan genetic isolation event. Geographically distant exemplars of a taxon that are not heterophyletic on a molecular cladogram may be taken as representing a taxon of recent origin. See also examples of the use of paraphyly in biogeographic analysis by Knox (1999).

The most obvious tests of the mapped taxon method are (1) whether the interpretive results fit facts, at least as better explanations, and (2) whether the method melds well with evolutionary theory. For instance, Lammers (1999) pointed out a molecular phylogeny that showed diploid species derived from tetraploid. Although evolution is a fact, i.e., a well-documented observation, theory of mechanisms is still much argued (Gould 1983). Given that apparent surviving elements of ancestral taxa are now identifiable and available for study, it may be hoped that the additional information will prove valuable. Other tests,

such as those involving co-evolution of organisms and their parasites, pollinators, or predators (e.g., Clayton et al. 2003), of course, will occur to the evolutionist.

Cronquist (1975) maintained that parallelism of closely related taxa is no problem for taxonomy and should be ignored (see also discussion by Gould 2002:1135); and Cronquist (1987) also recognized paraphyletic (and therefore autophyletic) groups. A critique of Cronquist's paper by Donoghue and Cantino (1988) said that paraphyletic groups cannot serve as ancestors and are phylogenetically unacceptable. The present paper rejects this with a clear alternative based on fact.

Mapped taxon analysis is independent of species concept, excepting phylogenetic species concepts intolerant of the idea of a single taxon being present in two or more molecular lineages at once, or of the manner of macroevolution, such as exaptive or aggregate species selection or species sorting (as defined by Gould 2002). This includes incomplete reciprocal monophyly (Funk and Omland 2003) where the populations of differentiating species may be initially paraphyletic but assumes, sometimes wrongly, that eventual extinction of assorted genetic lines must lead to monophyly. Patton and Smith (1994) found molecularly distinct local populations of a species of pocket gopher that have long been evolutionarily independent, leading to a conclusion that a gene tree reflecting initial paraphyletic or polyphyletic relationships may be preserved permanently.

The caulistic method, by turning phylogenetic monophyly on its head and making fewer demands on credulity, infers descent with modification of taxa and suggests that punctuated equilibrium and saltation can better explain apparent massive and total convergence of taxa on cladograms, which is probably quite rare (Jardin and Sibson 1971, p. 144), while paraphyletic and polyphyletic species are probably not uncommon (Funk and Omland 2003; Rieseberg and Brouillet 1994). The method combines the best features of traditional taxonomy (maximized evolutionary classification) and molecular phylogenetics (genetic continuity and lineage isolation). Critical, however, to the method is the availability of modern classifications based on traditional methods that commonly use several techniques to accumulate and represent inferred evolutionary information about groups of organisms in nature.

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Glossary

Anagenesis	Gradual evolutionary change in a lineage	Homophyly	One taxon represented by several sequential, uninterrupted lineages on a molecular tree, with inferred molecular differentiation of lineage-tracking traits, but no change in expressed traits (e.g., Fig. 1, left)
Ancestral taxon	One or more sections of a cladogram or one section of a caulogram consisting of inferred ancestors of extant exemplars that are diagnosable together as one particular taxon	Homoplasy	Trait similarity in cladogram lineages that lead back to different ancestors, in the context of holophyly
Atavism	A reversal on a caulogram at the taxon level, e.g., two lineages of one taxon so distant on a molecular cladogram that reactivation of a suppressed cluster of traits of selective value in certain environments is a more probable explanation than parallel descent or multiple convergence at the taxon level	Macroevolution	Generation of species and higher taxa through evolutionary processes
Autapomorphy	A unique trait uninformative of sister-group relationships that may be informative of unique evolutionary status or direction	Mapped taxon	Nodes on a molecular cladogram representing inferred ancient ancestors of present-day taxa diagnosable at a particular taxonomic level through a taxonomic uniformitarianism
Autophyly	Case of an inferred descendant lineage, i.e., an interpolated lineage in a molecular tree that renders another taxon paraphyletic	Paraphyletic	A taxon cladistically including another taxon of the same rank, i.e., inferred ancestor of a taxon at the same or higher taxonomic rank in one lineage
Caulistics	Method of mapping taxa onto molecular cladograms through paraphyly and occasionally polyphyly of exemplars representing traditional Linnaean taxa, assuming one taxon may occur in two lineages through, e.g., stabilizing selection on long-isolated populations that accumulate minor molecular mutations	Phylogenetics	Analytic method of inferring sister-group (splits of lineages) relationships from morphological and molecular data
Caulogram	A sequentially organized ancestor-descendant diagram of named taxa, often superimposed on a cladogram	Polyphyly	Like paraphyly but with similar taxa more distant on a molecular tree such that it is not easy to infer a shared deep ancestor
Evolutionary systematics	Study of biodiversity through evolutionary analysis and classification, differing from phylogenetics in recognizing paraphyly and autophyly in classification as representative of ancestor-descendant relationships	Punctuated equilibrium	Speciation associated with, at first, bursts of rapid change, then long phenotypic stasis
Heterophyly	Exemplars of the same taxon distant on a molecular cladogram such that lineages of other taxa intervene by at least one node; includes both paraphyly and polyphyly	Saltation	Speciation or generation of higher ranked taxa through rapid fixation of major new traits or clusters of traits; if atavistic, than reactivation of a cluster of epigenetically suppressed adaptive traits is an explanation
Holophyly	Strict phylogenetic monophyly, or restriction of a taxonomic name to all products of one shared ancestor, i.e. any “spray” of lineages cannot include a taxon at a particular rank being derived		

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