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THE PARACLADISTIC APPROACH TO PHYLOGENETIC TAXONOMY

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ABSTRACT

The inclusion of some paraphyletic groups in a temporally and taxonomically comprehensive phylogenetic classification is inevitable because cladistic methodology is incapable of excluding the possibility that a structurally (i.e., based on the branching pattern of a given cladogram) monophyletic group contains the ancestor of another group, i.e., that it is historically paraphyletic. Paracladistics is proposed as a pragmatic synthesis of phylogenetic and evolutionary taxonomy in which true monophyly is distinguished from structural monophyly with historical paraphyly, some structurally paraphyletic groups are retained in the interest of nomenclatorial continuity and stability, and both unranked and suprageneric ranked taxon names are defined phylogenetically. Ancestral groups are structurally paraphyletic or structurally monophyletic but historically paraphyletic sets of species that are believed to contain the ancestor for the most recent common ancestor of a descendent group. Historical paraphyly is determined by considering evidence of nesting in cladistic analyses, timing of first appearances in the fossil record, polarity in character evolution, and taxa that are morphologically intermediate between groups of species. The decision to name an ancestral group is based on the same criteria as the decision to name a clade. Ancestral groups are defined in the same manner as clades, except that their descendent group(s) are designated as external specifiers. Recognizing that two supposedly monophyletic, cladistically defined sister taxa can represent ancestral and descendent groups has implications for inferring their times of origination. To illustrate the advantages of the paracladistic approach to phylogenetic taxonomy, alternative paracladistic and phylogenetic classifications of the crown group families of Nuculanoidea (Mollusca, Bivalvia) are presented.

Keywords: ancestry, cladistics, paracladistics, paraphyly, phylogenetics

INTRODUCTION

Phylogenetic taxonomy, pioneered by Hennig (1950, 1966, 1969), and with clade nomenclature standardized by the *PhyloCode* (Cantino & de Queiroz, 2010), requires all taxa to be monophyletic. The *PhyloCode* defines monophyly as a set consisting of an ancestor and all of its descendants. However, phylogenetic taxonomy distinguishes monophyly solely on the basis of a phylogenetic tree's branching pattern as derived from parsimony, likelihood, Bayesian, or other cladistic analyses of molecular and/or non-molecular data. Further, phylogenetic tree topology is constrained by the assumption that sister taxa are monophyletic and originated simultaneously from a common ancestral species (Altaba, 2009). Non-cladistic evidence to test whether cladistic sister taxa originated simultaneously, or whether one cladistic sister taxon contains the ancestor of the other, i.e., that

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it might be historically paraphyletic, is excluded from consideration. Phylogenetic taxonomy maintains its restricted, topological application of the term monophyly by limiting the concept of ancestry to a definitely identified organism, breeding pair, population, or species in a monotypic genus. Thus, a group, that is believed to contain the ancestor for the most recent common ancestor of another group, is regarded as monophyletic as long as the former ancestor remains unidentified at the species level. Because species-level ancestry is virtually impossible to verify, phylogenetic taxonomy effectively eliminates the concept of ancestry, including the concept of group ancestry, from taxonomy.

Historical paraphyly can be concealed by a cladistic analysis when one or more synapomorphies are lost in a descendent group. For example, the presence of a radula is a synapomorphy in the phylum Mollusca, but this structure was lost in its class Bivalvia. A cladistic analysis of the Mollusca might, therefore, resolve the Bivalvia as a sister group to the remainder of Mollusca. However, paleontological evidence indicates that the radulate molluscan class Monoplacophora contains the ancestor of Bivalvia, and is therefore historically paraphyletic with respect to the Bivalvia (Runnegar & Pojeta, 1974; Carter, Campbell, & Campbell, 2000; Vendrasco, 2012). It is similarly possible for one or more molecular synapomorphies to become lost or unrecognizable in a descendent group, as exemplified by the phenomenon of long-branch attraction. Structural monophyly can also conceal historical paraphyly when a stem group is excluded from a cladistic analysis. For example, González and Giribet (2014) concluded, on the basis of molecular phylogenetic evidence, that the bivalve family Astartidae is monophyletic, yet paleontological evidence indicates that its extinct subfamily Opinae contains the ancestor of Crassatellidae (Morris, 1978).

Carter and others (2011) recognized that a truly monophyletic, temporally and taxonomically comprehensive, phylogenetic classification is unachievable because every truly monophyletic group must have a corresponding ancestral group, i.e., a structurally paraphyletic or structurally monophyletic but historically paraphyletic group, that contains the ancestor for its most recent common ancestor. In their classification of extant and extinct Bivalvia, they minimized structural paraphyly by designating paraplesions, i.e., extinct members of a group that are removed to make the group monophyletic, or to reduce the extent of paraphyly. However, they retained some structurally paraphyletic groups in the interest of nomenclatorial continuity and stability. Carter and others (2012) called this approach to taxonomy "paracladistic systematics". It is presently called the paracladistic approach to phylogenetic taxonomy, or just paracladistics.

Paracladistics is presently proposed as a pragmatic synthesis of phylogenetic and evolutionary taxonomy in which true monophyly is distinguished from structural monophyly with historical paraphyly, some structurally paraphyletic groups are retained in the interest of nomenclatorial continuity and stability, and both unranked and suprageneric ranked taxon names are defined phylogenetically. To illustrate the advantages of the paracladistic approach to phylogenetic taxonomy, alternative paracladistic and phylogenetic classifications of the crown group families of Nuculanoidea (Mollusca, Bivalvia) are presented.

THE PARACLADISTIC APPROACH

Unlike phylogenetic taxonomy, paracladistics differentiates between true monophyly and structural monophyly with historical paraphyly. It identifies historical paraphyly by considering nesting in cladistic analyses, as well as evidence independent of cladistic analyses, such as timing of first appearances in the fossil record, polarity in character evolution, and taxa that are believed to be morphologically transitional between groups of species. Also unlike phylogenetic taxonomy, paracladistics has the option of retaining widely used, structurally paraphyletic groups (ancestral groups) in the interest of nomenclatorial continuity and stability. The paracladistic concept of ancestral groups is not to be confused with the invalid concept of group ancestry, if the latter is interpreted to mean that a species is derived from a group of species rather than from a single species, population, or individual organism (see discussion of ancestry in phylogenetic taxonomy by Wiley & Lieberman, 2011, p. 241). Ancestral groups are defined phylogenetically in the same manner as clades, except that their descendent group(s) are designated as excluded, external specifiers.

Paracladistics allows for the use of both unranked and rank-based names, and both descriptive (e.g., Bivalvia) and typified (generic-based) names (e.g., Hominidae). However, other than genera and species, all taxon names are defined in phylogenetic terms. Rules for naming rank-based taxa follow the rank-based taxonomic codes, such as the ICZN (1999) and ICBN (2006), whereas rules for naming unranked taxa follow the *PhyloCode*. To maximize compatibility between typified, rank-based names and typified, unranked names, the *PhyloCode* convention is adopted that definitions of typified names include, as an internal specifier, the type species of the nominal genus, and, if it is questionable whether the type species is part of the group to be named, the genus should not be used as the basis for the name. Paracladistics strives for concordance between phylogenetic hierarchy and categorical ranks. However, some discordance might be unavoidable due to a large number of phylogenetic levels and a limited number of categorical ranks. Categorical ranks are used merely as a shorthand indication of inclusivity and degree of morphologic and/or temporal divergence (Stys & Kerzhner, 1975; Starobogatov, 1991), without other theoretical connotations.

Paracladistics follows the *PhyloCode* (Article 9.2) convention that a new clade name derived from a preexisting name must be identified by "converted clade name" or "*nomen cladi conversum*" (*nom. cl. conv.*), whereas a new clade name *not* derived from a preexisting name must be identified by "new clade name" or "*nomen cladi novum*" (*nom. cl. nov.*). In paracladistics, a new ancestral group name derived from a preexisting name must be identified by "converted ancestral group name" or "*nomen patrius conversum*" (*nom. patr. conv.*), whereas a new ancestral group name *not* derived from a preexisting name must be identified by "new ancestral group name" or "*nomen patrius novum*" (*nom. patr. nov.*). Ancestral group names are further identified by an exclamation mark "!" after their name.

For classifications using both unranked and rank-based names, the *PhyloCode* recommends placing "[P]" (for phylogenetic) or "[R]" (for rank-based) after the name, e.g., "Chordata[P]" for an unranked name as opposed to "Hominidae[R]" for a rank-based name. Alternatively, one may write "clade Chordata" as opposed to "family Hominidae" (*PhyloCode*, Rec. 6.1B). The latter option is favored for its simplicity, but with the addition of the category of "ancestral group" for paraphyletic taxa. Widely used, rank-based typified names of the family-group (subtribe through superfamily) are preferentially retained as clade or ancestral group names to minimize the proliferation of new names, and to retain the advantages of the rank-based codes of taxonomic nomenclature. The *PhyloCode* recommends that all scientific taxon names should be italicized. This convention is not presently adopted for all zoological names, for which the ICZN Code mandates that only genus and species names should be italicized.

The following phylogenetic and paracladistic classifications of the crown group families of the superfamily Nuculanoidea illustrate the advantages of paracladistics when compelling evidence exists for ancestor-descendant group relationships. Both classifications utilize the positional number system of Hull (1966), Hennig (1969), and Ereshefsky (1994) to indicate the phylogenetic hierarchy. By this method, a taxon's degree of inclusiveness is indicated by the number of digits in its identifier: the fewer the digits, the more inclusive the taxon. As recommended by Wiley and Lieberman (2011, p. 243), the name of an ancestral species is placed on the same line in the phylogenetic hierarchy as the supraspecific taxon of which its descendants are parts. Paracladistics applies this convention also to ancestral group names. Thus, each line in a phylogenetic hierarchy represents the origination of a clade, ancestral group, and/or ancestral species. To avoid unintended implications of temporal or phylogenetic sequence among members of a polytomy, the nominotypical taxon is listed first, followed by the remaining taxa in alphabetical order.

The superfamily Nuculanoidea contains six extant and two extinct families (Carter & others, 2011, presently emended). The extinct family Polidevciidae is presently used as an outgroup to polarize the evolution of morphological characters for the paracladistic classification. The monogeneric, Jurassic–Paleocene family Isoarcidae Keen, 1969, has no bearing on the present classification and is excluded from consideration. Morphologic diagnoses for the nuculanoidean families are summarized below, along with their known geologic time ranges. These are traditional diagnoses and not lists of synapomorphies. Priority author/date, based on ICZN (1999) rules, is indicated in parentheses after the nominal family author/date in cases where these differ:

I. Family Nuculanidae Adams & Adams, 1858 in 1853–1858 (Gray, 1854) (Late Triassic?, Early Jurassic?, Early Cretaceous–Holocene). External ligament weakly mineralized, not prominent; resilium prominent and shallowly to deeply submarginal; hinge teeth palaeotaxodont; shells porcelaneous, not nacreous; shells generally posteriorly extended; solid-walled, posterior excurrent siphon well developed; functional posterior incurrent siphon present; gut not penetrating deeply into foot; foot lacking strong posterior projection from its heel; no permanent dorsoposterior shell gape.

II. Family Malletiidae Adams & Adams, 1858 in 1853–1858 (d'Orbigny, 1846 in 1835–1847) (Early Triassic–Holocene). External ligament prominent, strongly mineralized; resilium absent to small and shallowly to moderately submarginal; hinge teeth palaeotaxodont; shells porcelaneous, not nacreous; shells generally posteriorly extended; well-developed, solid-walled, posterior excurrent siphon present; functional posterior incurrent siphon present; gut not penetrating deeply into foot; foot lacking strong posterior projection from its heel; no permanent dorsoposterior shell gape.

III. Family Phaseolidae Scarlato & Starobogatov, 1971 (Pliocene–Holocene). External ligament greatly reduced; resilium deeply submarginal and internal; hinge teeth partially to entirely imbricate lamellar; shells porcelaneous, not nacreous; shells slightly posteriorly extended; well-developed, solid-walled, posterior excurrent siphon present; functional posterior incurrent siphon present; gut not penetrating deeply into foot; foot with strong posterior projection from its heel; shells not gaping or permanently gaping dorsoposteriorly.

IV. Family Polidevciidae Kumpera, Prantl, & Růžička, 1960 (Ordovician–Late Jurassic). External ligament prominent, strongly mineralized; resilium small to moderately well developed, shallowly to deeply submarginal; hinge teeth palaeotaxodont; shells nacreous, not porcelaneous; shells posteriorly extended; posterior excurrent siphon absent or minimally developed, based on absence of a pallial sinus; presence or absence of functional posterior incurrent siphon unknown; anatomy of gut and foot unknown; no permanent dorsoposterior shell gape.

V. Family Siliculidae Allen & Sanders, 1973 (Late Cretaceous–Holocene). External ligament greatly reduced, resilium deeply submarginal to slightly internal; hinge teeth rarely entirely palaeotaxodont, more commonly transitional palaeotaxodont/imbricate lamellar or entirely imbricate lamellar; shells porcelaneous, not nacreous; shells slightly to greatly posteriorly extended; well-developed, solid-walled, posterior excurrent siphon present; functional posterior incurrent siphon absent; gut penetrating deeply into foot; foot lacking strong posterior projection from its heel; shells not gaping or permanently gaping dorsoposteriorly.

VI. Family Tindariidae Verrill & Bush, 1897 (Late Cretaceous–Holocene). External ligament prominent, well mineralized; resilium absent to minute and shallowly submarginal; hinge teeth palaeotaxodont; shells porcelaneous, not nacreous; posterior part of shell extended or reduced; posterior, excurrent siphon well-developed to reduced; functional posterior incurrent siphon absent or present; gut penetrating deeply into foot; foot lacking strong posterior projection from its heel; no permanent dorsoposterior shell gape.

VII. Family Zealedidae Scarlato & Starobogatov, 1979 (Paleocene–Holocene). External ligament reduced, non-mineralized; resilium small, shallowly submerged; hinge teeth palaeotaxodont; shells porcelaneous, not nacreous; shells posteriorly slightly to moderately extended; posterior, excurrent siphon present, with hollow walls; functional posterior incurrent siphon present; gut not penetrating deeply into foot; foot lacking strong posterior projection from its heel; no permanent dorsoposterior shell gape.

The alternative phylogenetic and paracladistic classifications utilize three molecular phylogenetic analyses for the subclass Protobranchia from Sharma and others (2013). The Nuculanoidea portion of one of these analyses (maximum-parsimony based on direct optimization) is reproduced in Figure 1, with colors added to highlight the distribution of the traditional families. The other two molecular phylogenetic analyses, based on maximum likelihood and Bayesian inference, are not presently illustrated. They both differ from Figure 1 in resolving

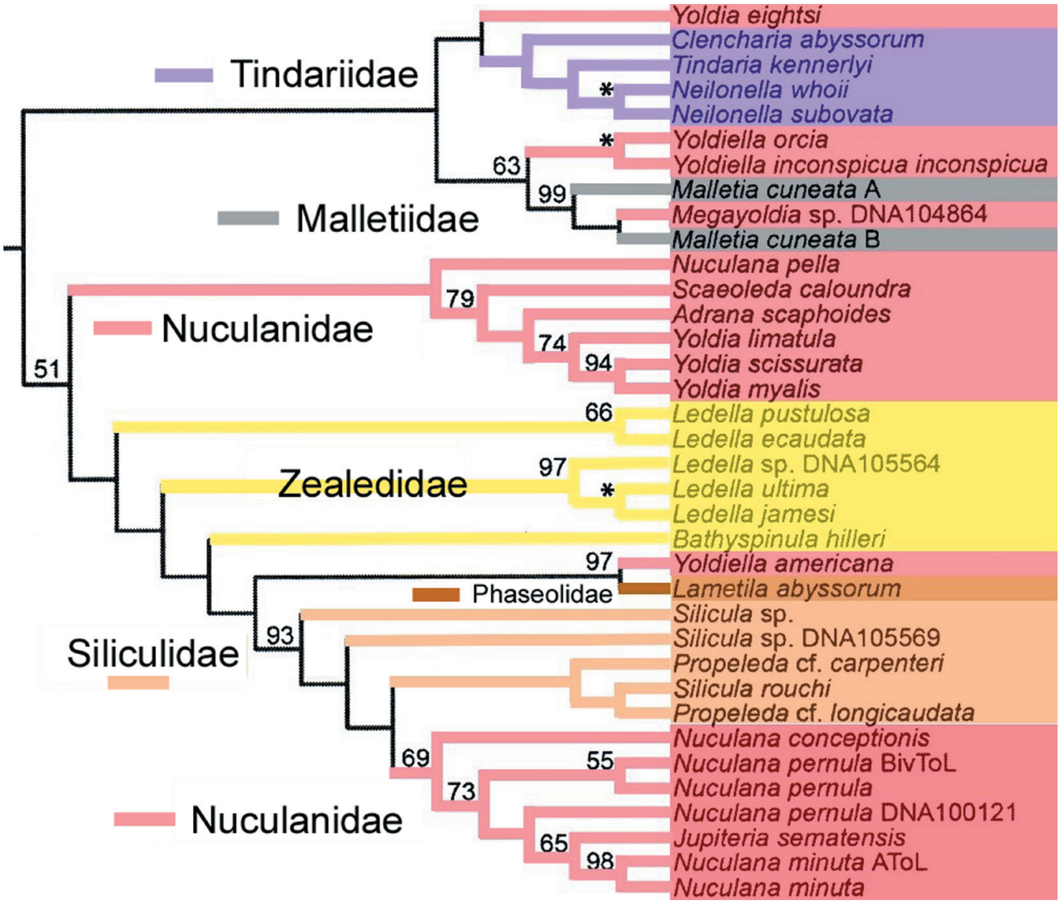

Figure 1. Parsimony analysis under direct optimization of five genes (numbers on nodes indicate jackknife resampling frequencies (>50%, with '*' indicating 100%) for the Nuculanoidea, one of four molecular phylogenetic topologies in Sharma and others (2013: fig. 4). Colors indicate family assignment prior to the present taxonomic revision and correspond to the color coding applied to the family names. Note that the species of *Jupiteria* is now assigned to the genus *Nuculana*.

the Zealedidae and Malletiidae as monophyletic, in resolving the Tindariidae as polyphyletic, and in placing the sareptoidean family Pristiglomidae within the clade of Nuculanoidea. Pristiglomidae does not appear in Figure 1 because in this molecular phylogenetic analysis it was resolved as a sister group to Nuculanoidea. All three molecular phylogenetic analyses resolved the family Nuculanidae as paraphyletic, and populated its members across two clades. One clade also contains the Malletiidae and most or all Tindariidae; the other clade also contains the Zealedidae, Siliculidae, Phaseolidae, and, in the two molecular analyses not presently illustrated, the tindariid *Clencharia abyssorum* (Verrill & Bush, 1898).

We begin the phylogenetic classification by naming the two major clades in Figure 1 the Malletiiformes and Nuculaniformes (Fig. 2). Neither clade corresponds to a traditional taxonomic grouping, nor has an apparent morphological synapomorphy. Within the Malletiiformes, subclades Malletiidae and Tindariidae, both also lacking an apparent morphological synapomorphy, can be defined as monophyletic groups on the basis of at least one of the three molecular phylogenetic analyses. The Nuculaniformes shows two subclades, one smaller and one much larger, in all three molecular phylogenetic analyses. However, all three molecular analyses place *Nuculana pella* (Linnaeus, 1767) in the smaller subclade, apart from other members of its genus, and two of the molecular analyses (not Fig. 1) resolve the tindariid *Clencharia abyssorum* in the smaller subclade rather than with other members of Tindariidae in the Malletiiformes. We choose not to name these two Nuculaniformes subclades because of their variable taxonomic composition and because neither subclade would have an apparent morphological synapomorphy.

The clade Nuculaniformes contains all analyzed members of the families Zealedidae, Phaseolidae, and Siliculidae, as well as most of the Nuculanidae, including *Nuculana pernula* (O. F. Müller, 1779), the type species for its genus. The Zealedidae was resolved as monophyletic in two of the three molecular phylogenetic analyses (not Figure 1). Its hollow siphon walls provide the grounds for an apomorphy-based clade definition. The Phaseolidae was represented in the molecular phylogenetic analyses by only one species, *Lametila abyssorum* Allen and Sanders, 1973. However, a clade Phaseolidae can be defined on the basis of this species and *Phaseolus ovatus* Monterosato, 1875, the type species for its nominal genus. The Siliculidae was resolved as paraphyletic in all three molecular phylogenetic analyses, and it has no apparent morphological synapomorphies. Siliculidae cannot presently be restricted to a monopyletic subset of

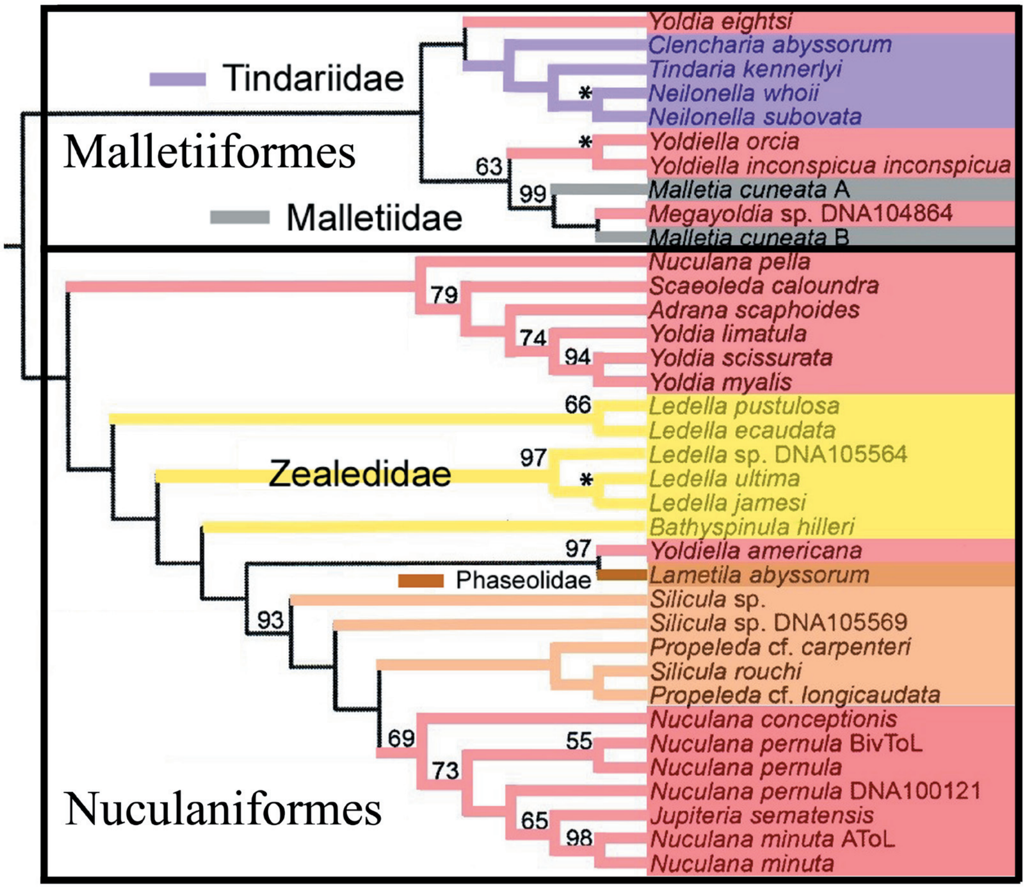

Figure 2. Same as Figure 1, but with the superimposed phylogenetic classification. Clades Malletiiformes and Nuculaniformes each contain two families plus several traditional members of the Nuculanidae, or Nuculanidae and Siliculidae, respectively, that are not assigned to a family.

its traditional members because the type species of *Silicula* was not included in the molecular phylogenetic analyses, so its phylogenetic position relative to the analyzed siliculids is unknown (*PhyloCode* Recommendation 11.7A). We elect not to restrict the family Nuculanidae to the small clade of *Nuculana pernula*, *Nuculana conceptionis* (Dall, 1896), *Nuculana minuta* (O. F. Müller, 1776), and *Jupiteria sematensis* (Suzuki & Ishizuka, 1943) (= *Nuculana* according to World Register of Marine Species, 2015), because such restriction would limit Nuculanidae to a subset of the genus *Nuculana*.

The present phylogenetic classification of Nuculanoidea is illustrated in Figure 2 and summarized below, using the positional number system to indicate phylogenetic hierarchy. The classification follows the *PhyloCode* convention of listing after a clade name the nominal author/date followed, in square brackets "[ ]", by the definitional author/date. The nominal author/date indicates the first publication of a taxon name with the spelling adopted as the clade name, regardless whether it was phylogenetically defined. The definitional author/date indicates the first publication of a phylogenetic definition for a name, either the original definition or an emended one. As required by the *PhyloCode*, definitions of clade names converted from typified names include the type species of the nominal genus as an internal specifier. Note that the clade Malletiiformes contains four traditional members of Nuculanidae, not assigned to a subclade. Also, the clade Nuculaniformes contains several traditional members of Nuculanidae and all traditional members of Siliculidae, also not assigned to a subclade.

1. Clade Malletiiformes [*nom. cl. nov.*]. The most recent common ancestor of *Malletia cuneata* (Jeffreys, 1876), *Malletia chilensis* Des Moulins, 1832 (the type species of *Malletia*), and *Tindaria kennerlyi* (Dall, 1897) that is not also an ancestor of *Nuculana pernula* (O. F. Müller, 1779), plus all descendants of that common ancestor.

1.1. Clade Malletiidae Nevesskaja & others, 1971. [*nom. cl. conv.*]. The clade originating with the most recent common ancestor of *Malletia cuneata* (Jeffreys, 1876) and *Malletia chilensis* Des Moulins, 1832 (the type species of *Malletia*).

1.2. Clade Tindariidae Scarlato and Starobogatov, 1971 [*nom. cl. conv.*]. The clade originating with the most recent common ancestor of *Tindaria kennerlyi* (Dall, 1897), *Tindaria arata* Bellardi, 1875 (the type species of *Tindaria*), and *Clencharia abyssorum* (Verrill & Bush, 1898).

2. Clade Nuculaniformes [*nom. clad. nov.*]. The most recent common ancestor of *Nuculana pernula* (O. F. Müller, 1779) (the type species of *Nuculana*) that is not also an ancestor of *Malletia cuneata* (Jeffreys, 1876), plus all descendants of that common ancestor.

2.1. Clade Phaseolidae Scarlato & Starobogatov, 1971 [*nom. cl. conv.*]. The most recent common ancestor of *Phaseolus ovatus*

Monterosato, 1875 (the type species of *Phaseolus*) and *Lametila abyssorum* Allen & Sanders, 1973, that is not also an ancestor of *Yoldiella americana* Allen, Sanders & Hannah, 1995, plus all descendants of that common ancestor.

2.2. Family Zealedidae Scarlato & Starobogatov, 1979 [*nom. cl. conv.*]. The clade originating with the first species to possess hollow siphon walls as inherited by *Ledella pustulosa* (Jeffreys, 1876), *Bathyspinula hilleri* (Allen & Sanders, 1982), and *Zealeda hamata* Marwick, 1924 (the type species of *Zealeda*).

We turn now to the paracladistic classification of crown group Nuculanoidea. The paracladistic classification differs from the phylogenetic alternative in retaining the family Nuculanidae as a paraphyletic, ancestral group, thereby making the names Malletiiformes and Nuculaniformes obsolete. All three molecular phylogenetic analyses resolved some members of Nuculanidae basal to all members of Malletiidae, Tindariidae, Zealedidae, Phaseolidae, and Siliculidae. This is compatible with the hypothesis that Nuculanidae contains the direct or indirect ancestor(s) for these five groups. The most ancient nuculanoidean family, the Polidevciidae, is characterized by nacreous (mother-of-pearl) shells, non-gaping, dorsoposterior shell margins, and palaeotaxodont hinge teeth, i.e., chevron-like hinge teeth with non-lamellar shapes. In contrast, all extant nuculanoideans have non-nacreous, porcelaneous shells. Of the extant nuculanoidean families with only palaeotaxodont hinge teeth, the Nuculanidae and Malletiidae appeared first in the fossil record. The Malletiidae might have predated the Nuculanidae, but this is uncertain. Both families were present by the Early Cretaceous, before all other extant nuculanoidean families. However, nuculanid and malletiid shells are externally similar, and the two families are differentiated largely on the basis of ligament structure, which is poorly known for many early Mesozoic putative members. Until the first appearance of Nuculanidae is better known, and until more molecular data become available for Malletiidae, we tentatively accept the molecular phylogenetic evidence that Nuculanidae contains the ancestor of Malletiidae. The Nuculanidae can therefore be defined as the ancestral group originating with the first species to possess porcelaneous, non-nacreous shells, as inherited by *Nuculana pernula* (O. F. Müller, 1779) (the type species of *Nuculana*), with the exclusion of its directly or indirectly descendent families, which are designated as external specifiers.

Malletiidae and Tindariidae both resemble Polidevciidae and differ from Nuculanidae in having a prominent, external ligament, and the molecular evidence suggests that Malletiidae and Tindariidae are very closely related. However, a Malletiidae + Tindariidae clade would have no apparent morphological synapomorphies, and the molecular evidence does not justify excluding traditional nuculanids from such a clade. These two families are therefore inferred to have been derived independently from separate ancestors in Nuculanidae. The molecular phylogenetic evidence is also compatible with the hypothesis that Nuculanidae is directly ancestral to Zealedidae, which was resolved as monophyletic in two of the three molecular phylogenetic analyses (but not in Fig. 1).

None of the molecular phylogenetic analyses resolved the grouping Siliculidae + Phaseolidae as monophyletic, but one analysis (Fig. 1) placed the one analyzed phaseolid, *Lametila abyssorum*, in an adjacent position to Siliculidae. Most members of Siliculidae and all members of Phaseolidae differ from all the other nuculanoidean families in replacing the plesiomorphic palaeotaxodont hinge teeth with at least partially imbricate lamellar hinge teeth, and most members of both families also have a distinctive, permanent, dorsoposterior shell gape. The siliculid *Propeleda* Iredale, 1924, resembles many nuculanids in its posteriorly elongate, rostrate shell shape, submarginal, non-internal ligamental resilium, distinct commarginal sculpture, and single, faint, anterior radial rib in each valve. Further, *Propeleda louiseae* (Clarke, 1961) has transitional palaeotaxodont/imbricate lamellar hinge teeth (Allen & Sanders, 1996, fig. 43). Phaseolids are more derived than siliculids in terms of their more internally positioned resilium and presence of a functional, posterior incurrent siphon. These features, and the earlier appearance of Siliculidae than Phaseolidae in the fossil record, suggest that Siliculidae was derived from an ancestor in Nuculanidae, and that it contains the ancestor of Phaseolidae. This inference can be represented in the paracladistic classification by emending the family Phaseolidae to contain the basal, paraphyletic subfamily Siliculinae and its descendent subfamily Phaseolinae. The use of Phaseolidae (instead of Siliculidae) for the family name is required by priority and the ICZN principle of coordination of family-group names.

In the following summary of the paracladistic classification, Siliculinae is placed at the same level in the phylogenetic hierarchy as its family Phaseolidae because they represent the same origination event. The paraphyletic nature of Nuculanidae and Siliculinae is indicated by the exclamation mark after their name. As in the phylogenetic classification, clade names that are converted from typified names include, as an internal specifier, the type species of the nominal genus. Authorship and dates of publication conform to ICZN rules because, in this classification, all clade and ancestral group names are typified, family-group names. Priority author/date for family-group names is indicated in parentheses "( )" after the nominal author/date in cases where these differ. Note that the paracladistic classification preserves all of the traditional nuculanoidean families except for Siliculidae, which is reduced in rank to a subfamily of Phaseolidae.

1. Family Nuculanidae! Adams & Adams, 1858 in 1853–1858 (Gray, 1854). The ancestral group originating with the first species to possess porcelaneous, non-nacreous shells, as inherited by *Nuculana pernula* (O. F. Müller, 1779) (the type species of *Nuculana*), excluding the descendent families Tindariidae, Malletiidae, Zealedidae, and Siliculidae.

1.1. Family Malletiidae Adams & Adams, 1858 in 1853–1858 (d'Orbigny, 1846 in 1835–1847). The clade originating with the most recent common ancestor of *Malletia cuneata* (Jeffreys, 1876) and *Malletia chilensis* Des Moulins, 1832 (the type species of *Malletia*).

1.2. Family Phaseolidae Scarlato, & Starobogatov, 1971. The clade originating with the most recent common ancestor of *Phaseolus ovatus* Monterosato, 1875 (the type species of *Phaseolus*), *Lametila abyssorum* Allen & Sanders, 1973, *Silicula fragilis* Jeffreys, 1879 (the type species of *Silicula*), and *Propeleda louiseae* (Clarke, 1961). **Subfamily Siliculinae! Allen & Sanders, 1973.** The clade originating with the most recent common ancestor of *Silicula fragilis* Jeffreys, 1879 (the type species of *Silicula*), and *Propeleda louiseae* (Clarke, 1961), excluding the descendent subfamily Phaseolinae.

1.2.1. Subfamily Phaseolinae Scarlato & Starobogatov, 1971. The clade originating with the most recent common ancestor of *Phaseolus ovatus* Monterosato, 1875 (the type species of *Phaseolus*) and *Lametila abyssorum* Allen & Sanders, 1973.

1.3. Family Tindariidae Verrill & Bush, 1897. The clade originating with the most recent common ancestor of *Tindaria kennerlyi* (Dall, 1897), *Tindaria arata* Bellardi, 1875 (the type species of *Tindaria*), and *Clencharia abyssorum* (Verrill & Bush, 1898).

1.4. Family Zealedidae Scarlato & Starobogatov, 1979. The clade originating with the first species to possess hollow siphon walls, as inherited by *Ledella pustulosa* (Jeffreys, 1876), *Bathyspinula hilleri* (Allen & Sanders, 1982), and *Zealeda hamata* Marwick, 1924 (the type species of *Zealeda*).

DISCUSSION

It is the goal of phylogenetic taxonomy to discover and diagnose monophyletic groups, yet its cladistic methodology is incapable of distinguishing between true monophyly and structural monophyly with historical paraphyly. Further, the inclusion of some historically paraphyletic groups is unavoidable in any temporally and taxonomically comprehensive phylogenetic classification. The paracladistic approach differs from the strictly phylogenetic approach in distinguishing between true monophyly and structural monophyly with historical paraphyly, and in accepting some widely used, structurally paraphyletic groups. These differences promote nomenclatorial stability as well as continuity with traditional taxonomy, while also adding an evolutionary dimension to phylogenetic taxonomy. The decision to name a structurally paraphyletic group is based on the same criteria as those for naming a clade. According to the *PhyloCode*, these include, but are not restricted to, level of support, phenotypic distinctiveness, economic importance, and whether the clade (or in this case paraphyletic group) has historically been named.

Dias, Assis, and Udulutsch (2005) have argued that accepting [structurally] paraphyletic groups will result in taxonomic chaos, or groups that contain no phylogenetic information. To the contrary, the present paracladistic classification of the Nuculanoidea demonstrates that structurally paraphyletic groups, such as the Nuculanidae, can be phylogenetically defined with the same rigor as clades, and that they can convey useful phylogenetic and evolutionary information. The paracladistic classification is compatible with the molecular phylogenetic data in Sharma and others (2013), except for its recognition of a Siliculidae + Phaseolidae clade, based on non-cladistic evidence.

Recognizing the difference between true monophyly and structural monophyly with historical paraphyly has implications for inferring time of origination of cladistically defined sister taxa. For example, molecular phylogenetic analyses of extant bivalves resolve the order Unionida as a sister group to the order Trigoniida, thereby implying a ghost lineage for Unionida of about 130 Ma (Bieler & others, 2014, fig. S2; Gonzales & Giribet, 2014, fig. 3; Gonzales & others, 2015, fig. 2). The morphological phylogenetic analysis of extant and extinct bivalves by Carter, Campbell, and Campbell (2006) resolved the Unionida as a sister group to the Trigoniida family Trigonodidae, implying a ghost lineage for Unionida of 5–10 Ma. In contrast, non-cladistic, paleontological evidence suggests that both inferences of timing are incorrect, and that Unionida was derived from a contemporaneous, Late Triassic member of Trigonodidae (Newell & Boyd, 1975, p. 136; Carter, Campbell & Campbell, 2006). In a second example, phylogenetic taxonomy regards the sister subtribes Hominina Gray, 1825, and Australopithecina Gregory and Hellman, 1939, as derived simultaneously from a most recent common ancestor 3.9 – 4.2 million years ago (Haviland & others, 2008, p. 134). This contradicts paleontological evidence that Hominina dates from only about 2.8 million years ago (Villmoare & others, 2015). From the paracladistic perspective, Hominina was derived either from a most recent common ancestor with Australopithecina, or from one of its members (Cela-Conde & Altaba, 2002; Cela-Conde & Ayala, 2003). These examples illustrate that the paracladistic approach to phylogenetic taxonomy can be more heuristic and evolutionarily more accurate than strictly cladistic phylogenetics.

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