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Phylogenetic relationships among families of the Scaphopoda (Mollusca)

PATRICK D. REYNOLDS[1] AND AKIKO OKUSU[2]

Biology Department, Hamilton College, Clinton, NY 13323, U.S.A.

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Phylogenetic relationships among families in the molluscan class Scaphopoda were analysed using morphological characters and cladistic parsimony methods. A maximum parsimony analysis of 34 discrete characters, treated as unordered and equally weighted, from nine ingroup terminal taxa produced a single most parsimonious tree; supplementary analyses of tree length frequency distribution and Bremer support indices indicate a strong phylogenetic signal from the data and moderate to minimally supported clades. The traditional major division of the class, the orders Dentaliida and Gadilida, is supported as both taxa are confirmed as monophyletic clades. Within the Dentaliida, two clades are recognized, the first comprised of the families Dentaliidae and Fustiariidae, the second of the Rhabdidae and Calliodentaliidae; together, these groups comprise a third clade, which has the Gadilinidae as sister. Within the Gadilida, a nested series of relationships is found among [Entalinidae, [Pulsellidae, [Wemersoniellidae, Gadilidae]]]. These results lend cladistic support to earlier hypotheses of shared common ancestry for some families, but are at variance with other previous hypotheses of evolution in the Scaphopoda. Furthermore, analysis of constituent Gadilinidae representatives provide evidence for paraphyly of this family. The relationships supported here provide a working hypothesis that the development of new characters and greater breadth of taxonomic sampling can test, with a suggested primary goal of establishing monophyly at the family level.

ADDITIONAL KEYWORDS:—Dentaliida – Gadilida – *Dentalium* – *Cadulus* – systematics – cladistics – evolution – *Episiphon* – *Gadilina* – *Calliodentalium.*

CONTENTS

[1] Corresponding author: Email: preynold@hamilton.edu
[2] Current address: Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, U.S.A.

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INTRODUCTION

The Scaphopoda is a class of exclusively marine, benthic infaunal molluscs which are characterized by a univalve, tusk-shaped shell open at both ends. A protrusible burrowing foot extends from the larger, anterior end; the mantle cavity extends along the ventral side of the animal to the smaller, posterior aperture, through which respiratory currents pass. Scaphopods are world-wide in distribution, with approximately 1000 described species dating from the Ordovician to the present; there are an estimated 500 extant species known (Scarabino, 1994), currently placed in 44 genera (Scarabino, 1995). The Class Scaphopoda is divided into two subtaxa—the orders Dentaliida da Costa, 1776 and Gadilida Starobogatov, 1974. The Dentaliida precede the Gadilida in the fossil record with the appearance of *Rhytiodentalium kentuckyensis* Pojeta & Runnegar 1979, dating from the late Middle Ordovician (Pojeta & Runnegar, 1979); the first gadilid fossils date from the Permian (Pojeta & Runnegar, 1985).

Literature dealing with scaphopod phylogeny is limited. Emerson (1962) reviewed scaphopod classification and discussed evolution within the group, using shell shape and sculpture as the primary characters in the identification of generic evolutionary lineages; Chistikov (1975, 1978, 1979, 1984) discussed scaphopod relationships based on additional data from several radular and soft-part anatomical characters. Steiner (1992b) was the first to attempt a cladistic analysis of scaphopod phylogeny at the family level; Dentaliida and Gadilida monophyly, a [Dentaliidae, Fustiariidae] clade, and full resolution within the Gadilida ([Entalinidae, [Pulsellidae, [Wemersoniellidae, Gadilidae]]]) were indicated on a preferred tree. Based upon these results, two suborders were erected, the Entalimorpha Steiner, 1992 and the Gadilimorpha Steiner, 1992. However, several methodological problems with the study, including rejection of most parsimonious trees supporting Dentaliida paraphyly (Steiner, 1996), prompted a cladistic reanalysis of the Steiner (1992b) data matrix which produced less resolution of scaphopod relationships (Reynolds, 1997). In this reanalysis, while monophyly of the newly erected suborder taxa was supported, monophyly of the Dentaliida, [Dentaliidae, Fastiariidae] and [Wemersoniellidae, Gadilidae] clades were not (Reynolds, 1997). Contributing to this lack of resolution was the unavailability to Steiner (1992b) of data for several characters of the dentaliid families Gadilinidae, Omniglyptidae, and Laevidentaliidae. More recently, Reynolds *et al.* (1995) reported an analysis of scaphopod family relationships with a more complete data matrix; while yielding considerably fewer equally parsimonious trees of scaphopod family relationships, the topology of scaphopod relationships was similarly unresolved.

It is apparent that phylogenetic resolution of scaphopods based on cladistic methods is poor, with paraphyly of the order Dentaliida a strong possibility. A

severe limitation in the analysis of scaphopod phylogeny is the paucity of wet-preserved specimens on which to base scoring of morphological characters. The present study improves taxonomic sampling over previous analyses, and presents several new characters to improve resolution among families in the class Scaphopoda. The analyses performed here not only examine relationships among currently recognized families, but test the assumption of monophyly in one family, the Gadilinidae.

MATERIAL AND METHODS

Ingroup

There are currently 11 scaphopod family-level taxa (Scarabino, 1995). While representative specimens for shell characters (Ch. 1–7) were readily available for scoring, the remaining soft-part anatomical characters could be scored only from wet-preserved museum or live-collected material on which histology or scanning electron microscopy (SEM) could be performed. As a result, choice of terminal representatives was driven by availability of wet-preserved museum material in which the shell contained the animal. Wet-preserved specimens were not available for the Laevidentaliidae, Omniglyptidae, Fustiariidae, Wemersoniellidae, and Entalinidae (museums visited or contacted: Academy of Natural Sciences, Philadelphia; California Academy of Sciences; Harbor Branch Oceanographic Museum; Los Angeles County Museum of Natural History; Zoological Museum, Moscow Lomonosov State University; American Museum of Natural History; Museum of Comparative Zoology; Muséum National d'Histoire Naturelle, Paris; Natural History Museum, London; National Museum of Natural History, Smithsonian Institution), although data on soft part morphology for representative species of the latter three families were located in the literature. Therefore, nine ingroup terminal families were included in the analysis. Character scoring for the Gadilinidae was based on specimens of *Gadilina insolita* and *Episiphon subtorquatum*, the latter species having recently been moved from the genus *Plagioglypta*, family Omniglyptidae, by Scarabino (1995). For several terminals, different species contributed to the shell and soft-part character scores. A list of species examined for character scoring is given in Appendix 1; literature sources consulted for each character are cited in the 'Characters' section below.

Outgroup

The class possibly had its origins in the ribeiriid or conocardid lineages of the extinct class Rostroconchia (Pojeta & Runnegar, 1979, 1985; Morris, 1990; Engeser & Riedel, 1996; Wagner, 1997), and a rostroconch or Bivalvia sister group relationship has most commonly been suggested (Steiner, 1992b; Runnegar, 1996; Salvini-Plawen & Steiner, 1996). An alternative hypothesis suggests the bullet-shaped toxeumorphorid Xenoconchia (now placed in the Hyolitha; Peel & Yochelson, 1984) as the scaphopod sister group (Starobogatov, 1974; Chistikov, 1984), although Emerson (1978) and Pojeta & Runnegar (1979) consider the evidence for such a

relationship unconvincing. Scaphopods also share many morphological features with other conchiferans to the exclusion of Bivalvia (e.g. radula, univalve shell) (see also Plate, 1891, 1892; Edlinger, 1991), and a closer relationship with the Gastropoda, rather than Bivalvia, has been argued (Waller, in press). As pointed out by Nixon & Carpenter (1993), sister group relationships need not be established for outgroup choice, but the inclusion of multiple outgroups based on more inclusive synapomorphies contributes to phylogenetic inference. For this analysis, both gastropod (*Littorina littorea* Linnaeus 1758) and bivalve (*Nucula proxima* Say 1822) outgroups were used.

Characters

Thirty-four discrete characters, 24 binary and 10 multistate, were scored from both shell and soft part morphological features of all terminal taxa. Appendix 2 lists the characters and character states scored for all terminals. While most of the characters have been modified from previous scaphopod systematics studies (Ch. 1–3, 8–34), four characters are newly developed for this analysis (Ch. 4–7). Several characters used in the Steiner (1992b) cladistic analysis were omitted here for reasons discussed in Reynolds (1997).

1–3, Shell shape

1. Shell sculpture: 0 = smooth, 1 = longitudinal ribs or striae, 2 = annulated.

Shell sculpture has long been used as a taxonomic character in scaphopods. Smooth shells are found in most representatives examined for this analysis, the exception being the annular sculpture of *Episiphon subtorquatum*, recently moved from the Omniglyptidae (Scarabino, 1995), itself a family characterized by annular sculpture (Habe, 1953) but not represented in this analysis. A great variety of longitudinal sculpture has been described in the Dentaliidae (e.g. Palmer, 1974); this may be a source for informative multistate characters in future analyses of dentaliid relationships. Scores were taken from observations on the representatives listed in Appendix 1, and from Scarabino (1986) for the Wemersoniellidae.

2. Maximum shell diameter: 0 = at anterior aperture, 1 = not at anterior aperture.

An attenuation of the anterior shell is present in *Cadulus aberrans*, *Polyschides dalli* v. *antarcticus*, and *Platyschides agassizi*, all members of the subfamily Gadilinae, family Gadilidae. The only other member of the Gadilidae in this analysis, *Siphonodentalium quadrifissatum*, like other scaphopods does not have this attenuation, and belongs to the subfamily Siphonodentaliinae. Scores were taken from observations on the representatives listed in Appendix 1, and from Scarabino (1986) for the Wemersoniellidae.

3. Apical shell callus: 0 = absent, 1 = present.

The occurrence of an internal ridge in the posterior shell of order Gadilida scaphopods was documented by Scarabino (1979, 1995), which are the sources for the families in this analysis.

4–7, Shell microstructure

The microstructure of scaphopod shells has been examined by Bøggild (1930), Haas (1972), and Alzuria (1984, 1985a, b), and reviewed in Carter & Hall (1990),

although few species were examined in these studies. The characters used in this analysis are based upon a survey of shell microstructure of the species listed in Appendix 1, with the exception of *Antalis entalis*. Shells of all species were fractured at anterior (first fifth), mid (third fifth) and posterior (last fifth) regions to expose cross sections, and examined using SEM. For those species with a 'secondary' shell secreted by the posterior mantle (see Reynolds, 1992a), scores were based only on the primary shell, with an accretionary edge at the anterior mantle. Homology of shell layers was based upon the consistency of microstructure within a specimen when traced from anterior to posterior, the identity of position and microstructural detail of the second to outermost regular crossed lamellar shell layer among all species examined, and the appearance and microstructural distinction of the inner, third shell layer, traceable from the mid- to posterior region in many species. Shell layer number, therefore, has two character states: two shell layers, and three shell layers (Fig. 1). The shell microstructure of the first (outer), second and third shell layers were scored to represent first order variability among examined scaphopods: prismatic (Fig. 2A), regular crossed lamellar (Fig. 2B), and irregular crossed lamellar (Fig. 2C); the latter two are distinguished by the clear alignment, and longer and larger bundles, of lamellae of the former compared to the latter (Fig. 2B, C). When a third shell layer was not present, shell microstructure for character 7 was scored as '?', as were scores for the Wemersoniellidae, representatives of which were not available. A more descriptive account of shell microstructure data will be presented in a forthcoming, separate paper (Reynolds & Okusu, in prep.). Outgroups were scored from Carter (1990, *Nucula proxima*) and Taylor & Reid (1990, *Littorina littorea*).

4. Shell layer number: 0 = two, 1 = three.

Within the Rhabdidae, *Rhabdus rectius* possessed three shell layers, whereas *R. dalli* and *R. perceptum* had only two.

5. Shell microstructure, layer 1 (outer): 0 = prismatic, 1 = irregular crossed lamellar.

6. Shell microstructure, layer 2 (middle or inner): 0 = regular crossed lamellar, 1 = nacreous.

7. Shell microstructure, layer 3 (innermost, when present): 0 = prismatic, 1 = regular crossed lamellar, 2 = irregular crossed lamellar, 3 = nacreous.

8–11, Radula

As with the external shell characters, the radula has been used extensively in taxonomy of the group. Chistikov (1984) first used radular characteristics in phylogenetic estimation, while Scarabino (1979, 1995) systematically incorporated this variability into taxonomic treatises. In addition to the four characters used here, Steiner (1992b) used two additional radular characters, the shape of the rachidian tooth superior border and lateral tooth denticle number. These two characters were excluded from this analysis due to the difficulty in partitioning reported variability among states (see Reynolds, 1997); further documentation of the variability in these characters may lead to their profitable use in future phylogenetic analyses, especially at the genus and species level. In this analysis, characters were scored for the species listed in Appendix 1 from observation under a dissecting microscope ($\leq 140\times$); scores for *Gadilina insolita, Calliodentalium callipeplum*, and *Entalina tetragonum* were obtained from Scarabino (1979, 1995), for Wemersoniellidae from Scarabino (1986), and for *Pulsellum salishorum* from Marshall (1980).

8. Rachidian tooth shape: 0 = wider than high, 1 = higher than wide.

9. Lateral tooth base: 0 = narrow, 1 = broad.

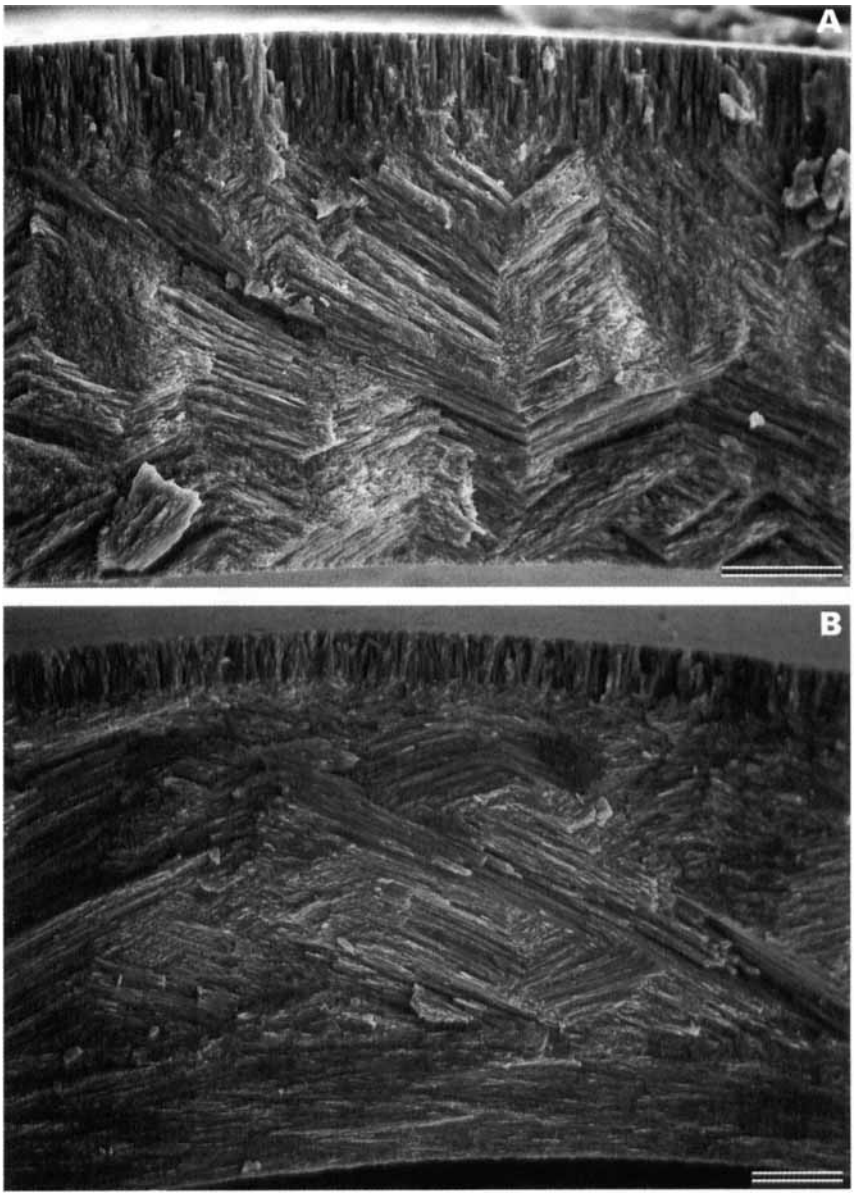


Figure 1. Character states for character 4, number of shell microstructure layers (see Appendix 2). A, two shell layers (*Polyschides dalli* v. *antarcticus*); scale bar = 20 μm. B, three shell layers (*Gadilina insolita*); scale bar = 20 μm.

10. Marginal tooth keel: 0 = absent, 1 = present.
11. Marginal tooth curvature: 0 = straight, 1 = curved, 2 = s-shaped.

12–16, Anterior mantle morphology

Documentation of anterior mantle morphology is found in Stasek & McWilliams (1973) and Steiner (1991); the latter report illustrates all character states used here,

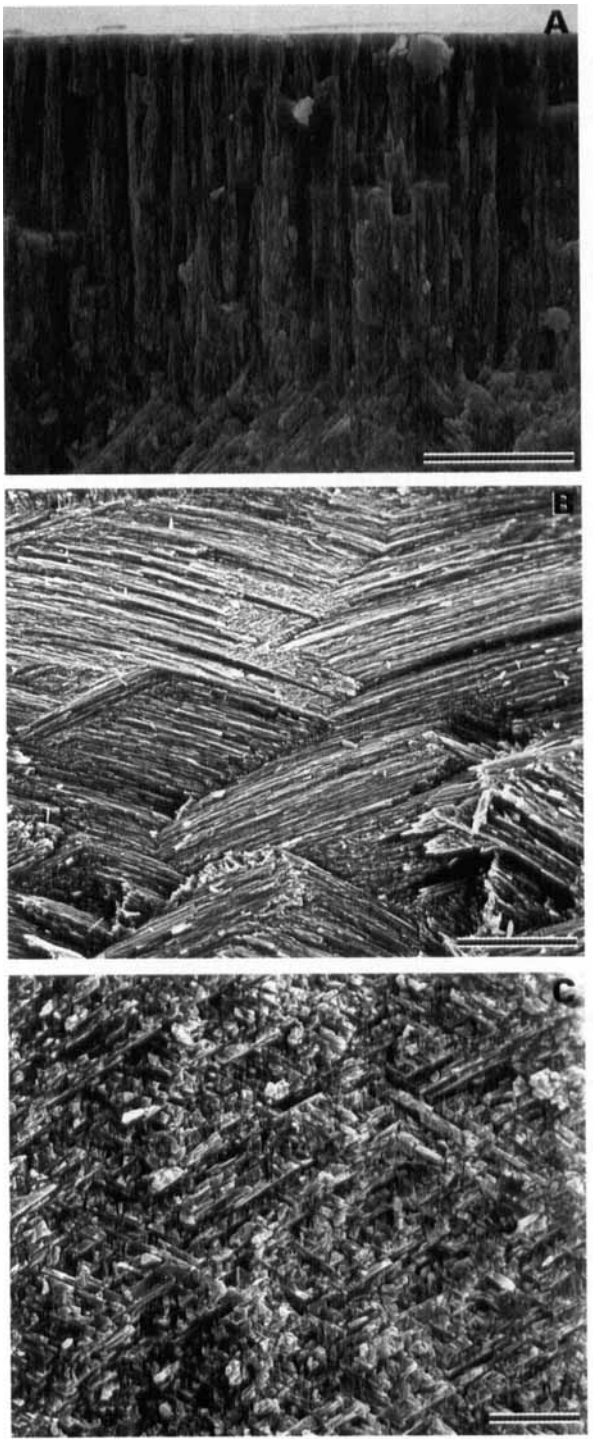


Figure 2. Character states for characters 5–7, shell microstructure type (see Appendix 2). A, Prismatic shell microstructure (*Polyschides dalli v. antarcticus*); scale bar = 10 μm. B, Regular crossed lamellar microstructure (*Fissidentalium floridense*); scale bar = 40 μm. C, Irregular crossed lamellar microstructure (*Calliodentalium callipeplum*); scale bar = 10 μm.

although some are modified as described and illustrated below. Steiner (1992b) used one character not employed here: anterior mantle sensory cell ultrastructure was excluded as class-wide variability is not yet documented; in addition, the ciliary organ character states in Steiner (1992b) are here separated between characters for the ciliary organ proper (Ch. 15) and the anterior mantle slits (Ch. 16) on the basis of independence and non-homology of these structures (Reynolds, 1997). Unless otherwise stated, all scores are based upon serial histological sections and, where informative, SEM of specimens listed in Appendix 1, with the exception of Fustiariidae, Entalinidae, and Wemersoniellidae. The latter three terminal taxa were scored from Steiner (1991,1992b).

12. Frontal glands: 0 = absent, 1 = present.

13. Anterior mantle circum-lateral glands: 0 = absent, 1 = epithelial, 2 = subepithelial and epithelial.

The character states for 12 and 13 were described well in Steiner (1991) as the outer and inner gland regions respectively; the presence or absence of the glandular regions is very discrete in the examined specimens. The state 'absent' here (and in Ch. 20) may include rare, isolated gland cells, but is clearly distinct from a region of continuous glandular tissue.

14. Frontal papillae: 0 = absent, 1 = scarce, 2 = numerous.

The singular pattern of dense papillae found on the frontal anterior mantle surface in some gadilids was described by Steiner (1991).

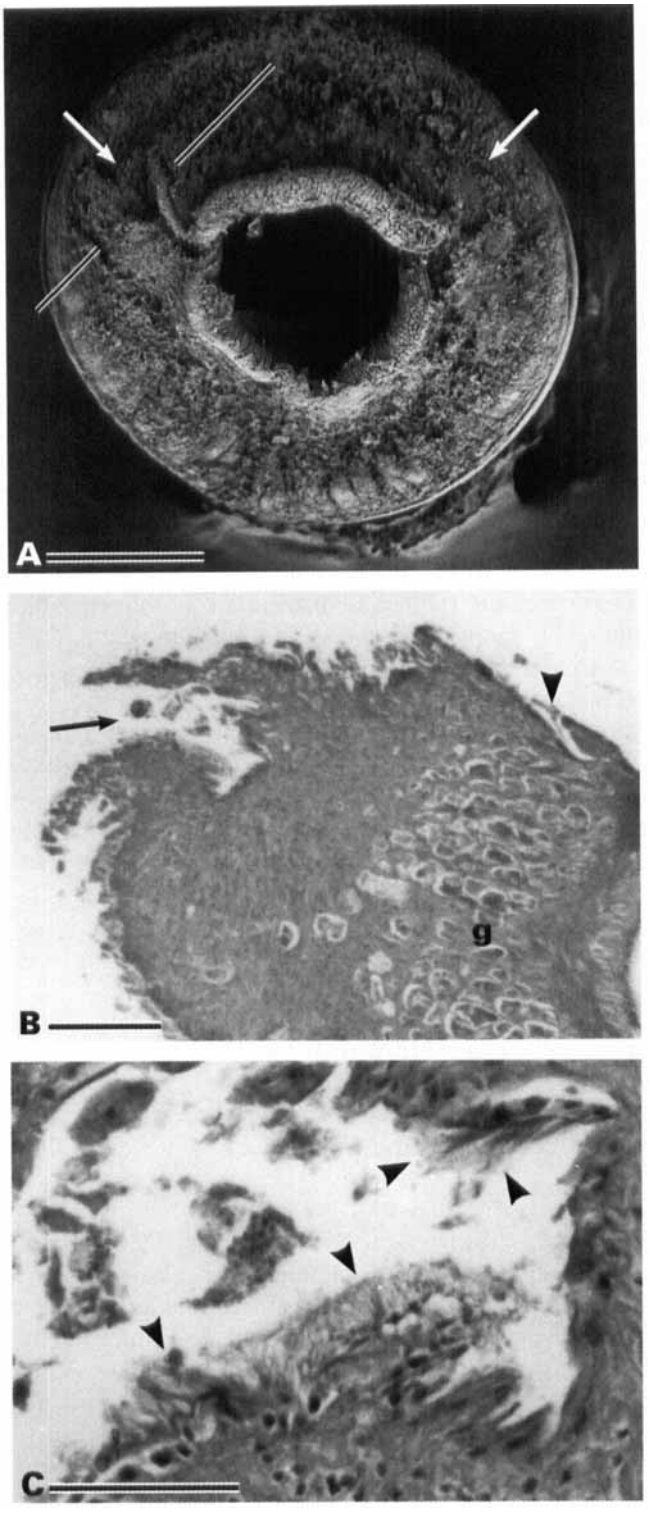
15. Apertural annular ciliary band: 0 = absent, 1 = present.

A ciliary band lining the anterior mantle aperture was reported by Steiner (1991) to occur in all Dentaliida examined except *Rhabdus rectius*, and was illustrated in that study for *Fustiaria rubescens* and *Antalis occidentalis*, using SEM and transmission electron microscopy (TEM), respectively. In this study, only serial histological sections and SEM were used to assess this character; while a ciliary organ was clearly observed in *Episiphon subtorquatum* (not examined in Steiner [1991]), it could not be confirmed for other Dentaliida listed in Appendix 1, including three species also examined by Steiner (1991), *D. laquaetum*, *A. entalis*, and *C. callipeplum*. It may be that this character is observable in most species only through TEM, or that its presence is variable within species; further comparative TEM data will help clarify the nature of this character. For this analysis, it was assumed that TEM is required to observe the ciliary band; data were therefore taken from Steiner (1991) for most family terminal taxa, and histological and SEM observations for *E. subtorquatum*. *Gadilina insolita*, neither examined by TEM in this study nor in Steiner (1991), was scored as '?'

16. Apertural ciliated slits, 0 = absent, 1 = present

Steiner (1991) described ciliated epithelial invaginations (termed 'slits') extending dorsolaterally from the anterior mantle aperture in *Rhabdus rectius*, and similar ciliated

Figure 3. Character 16, anterior mantle aperture ciliated slits (see Appendix 2). A, frontal view of the mantle of *Calliodentalium callipeplum*, SEM. Note the dorsolateral position where dorsal and ventral lips of the aperture meet, and where the epithelial invaginations, or slits (arrows), are found. Thin oblique line indicates approximate plane of section of B and C. Scale bar = 1 mm. B, ciliated slit of *Gadilina insolita*, light micrograph. g, frontal glands; arrow, ciliated slit; arrowhead, periostracal groove. Scale bar = 0.3 mm. C, ciliated slit of *Gadilina insolita*, light micrograph, magnification of B. Note two ciliated bands on lateral walls of the slit (arrowheads). Scale bar = 0.1 mm.


A
g
B
C

invaginations occur in the other two species of *Rhabdus* examined here. In all Dentaliida examined in this study, the dorsal and ventral lips of the anterior mantle aperture meet at acute angles, located dorsolaterally (Fig. 3A). In *Rhabdus* species examined to date, the invaginations extend from this meeting point through most of the distance of the frontal mantle region towards the edge of the frontal mantle surface (for illustration, see Steiner, 1991). Ciliated invaginations, of varying width but in an identical position to those observed in *Rhabdus* species, were also found in *Calliodentalium callipeplum* and *Gadilina insolita* (Fig. 3) using serial histological sections. Close examination reveals two lateral bands of cilia within each slit (Fig. 3C), as found in *Rhabdus* species (this study; Steiner, 1991). While variation exists among the ciliated invaginations of the three genera (e.g. those of examined *C. callipeplum* are wider and shorter than *Rhabdus* species, *G. insolita* narrower), available evidence indicates that on the basis of positional identity, similarity of structural detail, and continuity of form afforded by intermediates, these structures are homologous and are therefore scored as present for the character. Steiner (1991, 1992b) scored the dorsolateral invaginations as absent in *C. callipeplum*, which may reflect a narrower character state definition, restricted to the longer slits of *R. rectius*. Further comparative data for dentaliid genera and species may provide a greater range of variation in the form of this character, and multistate distribution of that variability may provide phylogenetic signal at the genus and species level in future analyses.

17–20, Posterior mantle morphology

These structures are described and illustrated in Steiner (1991) and Reynolds (1992b; Ch. 17–19 only), and used as characters in Steiner (1992b). State names have been modified from Steiner (1992b) to better reflect the morphological variability observed through serial histological sections or SEM for species listed in Appendix 1; data for Fustiariidae, Entalinidae, and Wemersoniellidae were scored from Steiner (1991, 1992b).

17. Posterior mantle aperture: 0 = lateral slit, 1 = vertical slit.

18. Posterior mantle valve components: 0 = dorsal only, 1 = dorsal and ventral, 2 = lateral only.

The morphology of the mantle valve was described by Steiner (1991); the components here refer to ingrowth of tissue that significantly narrows the mantle aperture (for illustration, see Steiner, 1991; Reynolds, 1992b). The character states are modified from that used in Steiner (1992b) in order to describe the position of the contributing parts of the aperture, rather than tissue composition or functional role of the components.

19. Mantle pavilion ledges: 0 = not ciliated, 1 = ciliated.

20. Pavilion subepithelial glands: 0 = absent, 1 = numerous. These character states differ from those used by Steiner (1992b) (not abundant, abundant) in order to more clearly distinguish between the most discrete differences among the species listed in Appendix 1. Of the species examined, the glands are numerous in all Dentaliidae and absent in all other species, although within the Dentaliidae, *Fissidentalium floridense* possessed fewer glands than the other dentaliid species examined; the numerous glands of the Fustiariidae and Wemersoniellidae are scored from Steiner (1991). Steiner (1992b) scored the Dentaliidae glands as not abundant, although as Steiner (1991) reports the glands to be 'scarce, few' and 'present' for a variety of genera, this discrepency is considered here to be a reflection of different character state definitions.

21–26, Foot morphology and associated musculature.

These characters are derived from the comparative description of pedal musculature in Steiner (1992a); character states are clearly described in Steiner (1992a, b). Data are from serial histological sections and dissection of species listed in Appendix 1, while scores for Fustiariidae, Entalinidae, and Wemersoniellidae are from Steiner (1992a,b).

21. Foot retraction: 0 = contractile, 1 = inversible.

22. Anchoring structure: 0 = lateral lobes, 1 = epipodial lobes, 2 = epipodial lobes and central filament, 3 = epipodial lobes, central filament and mucoid tissue.

23. Pedal retractor muscles: 0 = all associated with pedal wall, 1 = two originating at pedal wall, 2 = two inserting at pedal wall, 3 = four to six originating at pedal wall.

24. Transverse foot muscles: 0 = absent, 1 = present.

25. Pedal ganglion support: 0 = longitudinal muscle only, 1 = transverse and longitudinal muscle, 2 = ligament and longitudinal muscle, 3 = buccal septum and longitudinal muscle.

26. Dorsoventral muscles: 0 = one pair, 1 = two pairs, 2 = more than two pairs.

27–34, Other characters

27. Midgut gland: 0 = paired, 1 = unpaired.

All Dentaliida possess a paired midgut (digestive) gland, whereas all Gadilida possess a single gland.

28. Captacula: 0 = absent, 1 = present.

The feeding tentacles of scaphopods are unique to the class. While variability in the number of longitudinal muscles has been reported and used in phylogenetic analysis (Steiner, 1992b), sufficient comparative data are not yet available to use these as characters in this analysis (see Reynolds, 1997). Further comparative data may lead to more characters or states that are informative at the genus or species level in scaphopod analyses.

29. Ctenidia and auricles: 0 = absent, 1 = present.

Ctenidia and auricles are absent from all Scaphopoda examined to date.

30. Shell valves: 0 = univalve, 1 = bivalve.

31. Gut shape: 0 = straight, 1 = U-shaped.

32. Dominant body axis: 0 = dorso-ventral, 1 = anterio-posterior.

Scaphopoda are considered here to possess a main body axis in a dorso-ventral orientation, in common with the gastropod outgroup taxon, *Littorina littorea.*

33. Radula: 0 = absent, 1 = present.

34. Lateral mantle lobes: 0 = absent, 1 = present.

Scaphopods possess lateral mantle lobes, which later fuse ventrally. This and other plesiomorphic scaphopod characters are discussed in Steiner (1992b).

Parsimony analysis

The data matrix of characters and terminals is presented in Table 1. Taxa that did not possess the character (e.g. Fustiariidae and Gadilidae, Ch. 7), or for which the character state was unknown (e.g. Wemersoniellidae, Ch. 4–7), were scored as '?', and treated as missing data. An unconstrained, simultaneous maximum parsimony analysis of all family terminals and characters, treated as unordered and equally

TABLE 1. Data matrix used for analysis; the constituent representatives of the Gadilinidae are partitioned by dotted lines. Key: a=0&1; b=0&2

	1									2										3												
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4
INGROUP																																		
Dentaliidae	1	0	0	1	0	0	2	0	0	0	2	1	1	0	1	0	0	1	0	1	0	1	0	1	2	1	0	1	0	0	1	0	1	1
Fustiariidae	0	0	0	0	1	0	?	0	0	0	2	1	1	0	1	0	0	0	0	1	0	1	0	1	2	1	0	1	0	0	1	0	1	1
Rhabdidae	0	0	0	a	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	1	0	1	0	1	0	1	0	0	1	1
Calliodentaliidae	0	0	0	1	0	0	2	0	0	0	0	1	1	0	1	1	0	1	0	0	0	1	0	1	2	1	0	1	0	0	1	0	1	1
Gadilinidae	b	0	0	a	a	0	2	0	0	0	1	1	1	0	1	a	0	1	0	0	0	1	0	1	2	0	0	1	0	0	1	0	1	1
G. insolita	0	0	0	1	0	0	2	0	0	0	1	1	1	0	?	1	0	1	0	0	0	1	0	1	2	0	0	1	0	0	1	0	1	1
E. subtorquatum	2	0	0	0	1	0	?	0	0	0	1	1	1	0	1	0	0	1	0	0	0	1	0	1	2	0	0	1	0	0	1	0	1	1
Entalinidae	1	0	1	1	0	0	2	1	1	0	1	0	2	2	0	0	1	2	1	0	1	2	3	0	3	0	1	1	0	0	1	0	1	1
Pulsellidae	0	0	1	1	0	0	0	1	1	1	0	0	2	2	0	0	1	2	1	0	1	3	1	0	3	0	1	1	0	0	1	0	1	1
Wemersoniellidae	0	0	1	?	?	?	?	1	1	1	0	0	2	1	0	0	1	2	1	1	1	3	2	0	3	0	1	1	0	0	1	0	1	1
Gadilidae	0	a	1	0	0	0	?	1	1	1	0	0	2	1	0	0	1	2	1	0	1	3	1	0	3	0	1	1	0	0	1	0	1	1
OUTGROUP																																		
Littorina	1	0	0	1	0	0	1	1	1	0	2	0	0	0	0	0	?	?	?	?	0	0	0	1	1	0	1	0	1	0	1	0	1	0
Nucula	0	?	0	1	0	1	3	?	?	?	?	0	0	0	0	0	?	?	?	?	0	0	0	1	1	2	0	0	1	1	0	1	0	1

weighted, was performed using PAUP 3.1.1 (Swofford, 1993). A branch and bound search was conducted using the following options: multistate taxa were treated as polymorphisms, zero-length branches were collapsed, all minimal length trees were kept (MULPARS), the initial upper bound was computed via stepwise addition, and the furthest addition sequence was used. The resulting single most parsimonious tree (MPT) was rooted between the ingroup and the specified paraphyletic outgroup taxa *a posteriori* (Nixon & Carpenter, 1993), and confirmed support for monophyly of the Scaphopoda. Tree length, consistency index (CI) and rescaled consistency index (RC) were calculated using PAUP 3.1.1 (Swofford, 1993) after uninformative characters were excluded. In all analyses, characters were treated as unordered, unpolarized, and equally weighted. Bremer support indices (Bremer, 1988,1994; Donoghue *et al.*, 1992) were calculated for indication of relative support among ingroup clades. The g^1 statistic, reflecting skewness in frequency distributions of tree length, has been shown by Hillis & Huelsenbeck (1992) to be useful in discerning phylogenetic signal from random noise in molecular sequence data sets, and has been applied to morphological data sets (Anderson, 1996). This statistic was also applied here, calculated from 10 000 random trees generated from the data matrix by PAUP 3.1.1 (Table 1).

A separate analysis was run with *Gadilina insolita* and *Episiphon subtorquatum* treated independently, replacing the Gadilinidae terminal taxon, as a complete set of character data was available for these two species. This was followed by an analysis with a topological constraint for Gadilinidae monophyly, and the lengths and fit measures for the results of the two analyses were calculated as for the original analysis.

RESULTS

The single MPT resulting from analysis of all family terminals is presented in Figure 4 (length = 61; CI = 0.83, RC = 0.72; uninformative characters: 2, 6,

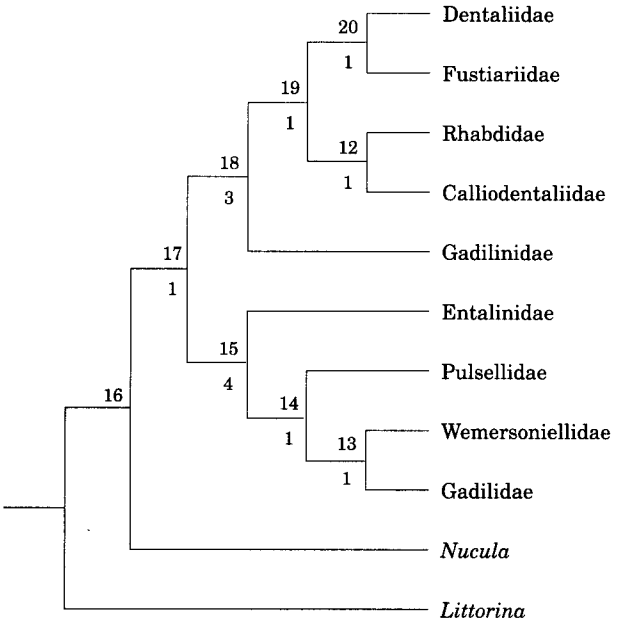


Figure 4. Single most parsimonious tree (length = 61; CI = 0.83, RC = 0.72) of scaphopod families. Numbers above horizontal bars indicate nodes/clades referred to in text; numbers below horizontal bars represent Bremer support indices.

30–34). Bremer support indices for the clades range from one to four (Fig. 4). Tree length frequency distribution was significantly skewed ($g^1 = -0.659$), well within the 95% confidence intervals calculated by Hills & Huelsenbeck (1992) for binary and four state characters from random matrices. Therefore, the single MPT is very likely a result of a strong phylogenetic signal, rather than the product of random noise from the data.

A list of all apomorphies for the identified clades, distinguishing between unambiguous changes that occur on all reconstructions and those that occur on only some, is presented in Appendix 3. Based on the simultaneous analysis of the characters scored and taxa examined in this analysis, and considering unambiguous changes only, two synapomorphies define the Scaphopoda (node 17, Fig. 4): the presence of captacula, and absence of ctenidia and auricles. The orders Dentaliida and Gadilida are both supported as monophyletic clades. The Dentaliida (node 18, Fig.4) are defined by four synapomorphies: a wider than high rachidian tooth, a narrow lateral tooth base, the presence of a frontal mantle gland region, and an apertural ciliated band. The Gadilida (node 15, Fig. 4) are defined by the presence of an apical shell callus, numerous frontal mantle papillae, inversible foot retraction, and the absence of transverse foot muscles.

Within the Dentaliida, three clades are identified. Clade 19, [[Dentaliidae, Fustiariidae], [Rhabdidae, Calliodentaliidae]] (Fig. 4) possesses one unambiguous synapomorphy, two pairs of dorsoventral muscles. The Gadilinidae is sister to this clade. The [Dentaliidae, Fustiariidae] clade (node 20, Fig. 4) is defined by one

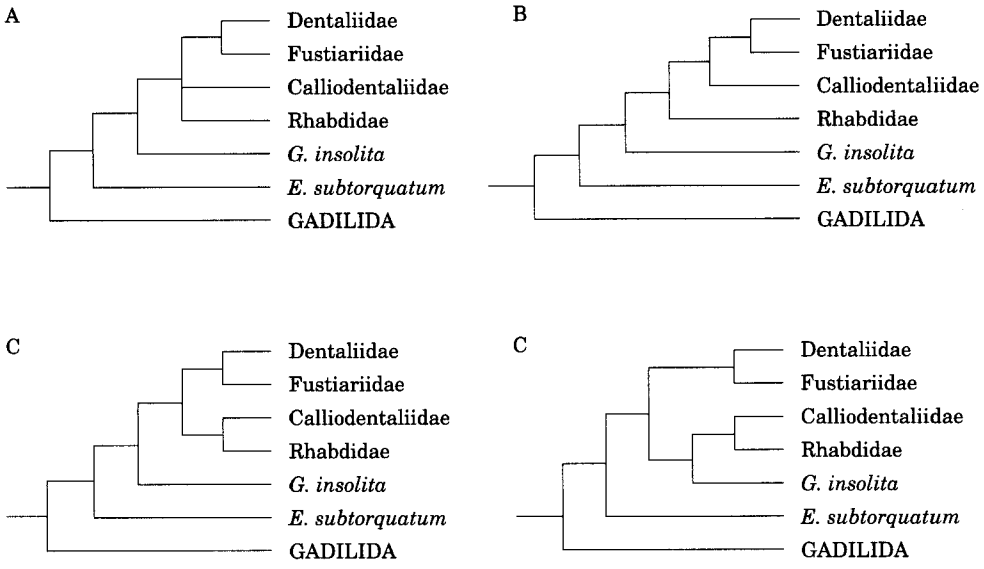


Figure 5. Four most parsimonious trees (length = 61; CI = 0.78, RC = 0.65) of scaphopod families, with Gadilinidae representatives, *Episiphon subtorquatum* and *Gadilina insolita*, analysed separately. When the constraint of Gadilinidae monophyly is imposed, the single MPT topology is identical to Figure 4 (length = 62; CI = 0.76, RC = 0.63).

unambiguous synapomorphy, numerous pavilion subepithelial glands. Clade 12 (Fig. 4), comprised of [Rhabdidae, Calliodentaliidae], is defined by a single synapomorphy, the presence of apertural ciliated slits.

The four families of the Gadilida form three nested clades. Clade 14 (Fig. 4) is composed of the [[Pulsellidae, [Wemersoniellidae, Gadilidae]], with a single unambiguous change, the presence of a marginal tooth keel; the Entalinidae is sister to this clade. The [Wemersoniellidae, Gadilidae] clade (node 13, Fig. 4) is also defined by a single unambiguous synapomorphy, the presence of scarce frontal mantle papillae.

Ingroup changes by character are presented in Appendix 4; consistency, homoplasy, retention, and rescaled consistency indices for each character are given in Appendix 5.

Analysis of the data matrix that excludes the 'Gadilinidae' terminal, replacing it with the two constituent representatives *Gadilina insolita* and *Episiphon subtorquatum*, resulted in four MPTs (length = 61; CI = 0.78, RC = 0.65). Differences from the phylogeny with a Gadilinidae composite terminal were restricted to within the Dentaliida; the four subtrees are presented in Figure 5. In all four reconstructions, *G. insolita* and *E. subtorquatum* do not fall within a monophyletic Gadilinidae clade, but rather *G. insolita* falls within a clade with the other Dentaliida families, to which *E. subtorquatum* is sister taxon. Therefore, monophyly of the Gadilinidae is not supported. When the monophyly of the Gadilinidae is constrained, with these species analysed independently, a single MPT results with topology identical to that in Figure 4, but with one extra step (length = 62; CI = 0.76, RC = 0.63).

DISCUSSION

Emerson (1962) suggested that the primary division among scaphopod species, currently the orders Dentaliida and Gadilida, probably evolved from a common stock, and that *Entalina*, the earliest known genus of the Order Gadilida, may be a link between the two groups as it combines the gadilid foot with the shell characteristics of the Dentaliida. Chistikov (1984) also considered both scaphopod orders to be independent lineages, evolved from ancestral Plagioglyptida (*Plagioglypta*). In Steiner (1992b), the first attempt at cladistic analysis of scaphopod relationships, monophyly of the Dentaliida and Gadilida was argued, although most parsimonious hypotheses supported paraphyly of the Dentaliida (Steiner, 1996) as did reanalysis of the Steiner datamatrix (Reynolds, 1997). The results presented here confirm previous hypotheses of Dentaliida and Gadilida monophyly, and provide the first support, based on simultaneous maximum parsimony analysis of morphological characters, for a phylogenetic basis to the traditional major division of the Scaphopoda.

With regard to phylogenetic relationships within the Dentaliida, Emerson (1962) identified two major evolutionary lineages, each consisting of several subgenera since elevated to full generic status by Palmer (1974): *Prodentalium/Dentalium* [*Dentalium, Coccodentalium, Antalis, Fissidentalium*] and *Plagioglypta/Fustiaria* [*Fustiaria, Rhabdus, Gadilina, Laevidentalium, Episiphon*]. The results of the current analysis (Fig. 4) indicate that *Fustiaria* is more closely related to the *Dentalium* subgenera than to the other subgenera of the *Plagioglypta/Fustiaria* lineage recognized by Emerson (1962). Chistikov (1984) described three taxa of the order Dentaliida, the Dentaliinae, Laevidentaliinae, and Episiphonidae, as a 'morphological row', with the Rhabdoidea (*Rhabdus*) as early offshoots. The results presented here differ substantially from this hypothesis of dentaliid relationships, with a sister group relationship between Rhabdidae (Rhabdoidea) and the Calliodentaliidae (represented by *Calliodentalium callipeplum*, formerly assigned to the Laevidentaliinae); both are more closely related to the [Dentaliidae, Fustiariidae] clade than to the Gadilinidae (represented in part by *Episiphon subtorquatum*) (Fig. 4). Steiner (1992b) presented only a [Dentaliidae, Fustiariidae] clade within an otherwise unresolved Dentaliida in a preferred tree; while not supported by reanalysis (Reynolds, 1997), with the addition of characters and taxa, a [Dentaliidae, Fustiariidae] clade is supported here (Fig. 4).

The analysis described above and all phylogenetic analyses of Scaphopoda to date have assumed that families are monophyletic. The paraphyly of the Gadilinidae indicated by the separate analysis of *Gadilina insolita* and *Episiphon subtorquatum* suggests that this assumption is not valid and must be tested throughout the class. In this case, the paraphyly of the Gadilinidae is a result of the recent assignment of *Dentalium subtorquatum* Fischer, 1871 from the genus *Plagioglypta* (family Omniglyptidae) to *Episiphon* (family Gadilinidae) (Scarabino, 1995). Clearly, more taxonomic sampling, at least to genus level representatives, is necessary to test family monophyly in the Scaphopoda.

Within the Gadilida, Emerson (1962) identified two main lineages, *Entalina/Pulsellum* and the current family Gadilidae. The hypothesis of relationships presented here supports a *Pulsellum/* Gadilidae lineage, to which *Entalina* is sister. Chistikov (1984) described the Entalinidae as the ancestral lineage to all other gadilids, which may be considered consistent with the support for Entalinidae as the earliest gadilid lineage in this analysis. Steiner (1992b) presented fully resolved relationships within the Gadilida [Entalinidae, [Pulsellidae, [Wemersoniellidae, Gadilidae]]]. While support for this

topology was ambiguous on reanalysis (Reynolds, 1997), the results presented here provide support for the gadilimorph relationships proposed by Steiner (1992b).

The phylogeny presented here should be treated as a working hypothesis, the best estimate of phylogenetic relationships available at this time based on the availability of specimens and application of parsimony criteria. While the g^1 statistic of Hillis & Huelsenbeck (1992) indicates a strong phylogenetic signal, Bremer support indices indicate moderately strong support for the clades corresponding to the orders Dentaliida and Gadilida, and minimal support for the clades within the orders. The development of further characters that are informative at the family level will test the hypotheses presented here. The next step, however, in revealing scaphopod relationships is to increase taxonomic sampling to the extent of testing the monophyly of family-level taxa. Resolution at the genus level will also require the development of new characters; several organ systems that have been shown to be phylogenetically informative in other molluscan groups, such as sperm ultrastructure (Healy, 1995; Hodgson, 1995) and stomach morphology (Strong, pers. comm.), may provide informative characters for further analyses of scaphopod relationships. Several characters currently identified as synapomorphic for the Scaphopoda may contribute to resolution among genera when intraspecific variation is explored further (e.g. captacular ciliation, Shimek, 1988; intestinal looping patterns, Steiner, 1994). Similarly, a finer differentiation of variation within shell microstructure and radular characters than used here may also be informative at lower taxonomic levels. The development of phylogenetically informative characters, molecular as well as morphological, with deeper taxonomic sampling and analysed under rigorous cladistic methods will in time contribute to better supported phylogenetic hypotheses; these can then be used to compile a more stable classification of the Scaphopoda based on well-supported monophyletic groups. Until some further progress in this direction is made, assignment of new taxon names between the familial and ordinal levels is unwarranted, and may not contribute in the long term to stability in scaphopod systematics. Similarly, analysis of character evolution on the basis of family-level relationships that have an uncertain foundation at lower taxonomic levels is premature. Only with a robust phylogenetic hypothesis supporting systematics in the class can we begin to address issues of character evolution and historical biogeography in the Scaphopoda.

NOTE ADDED IN PROOF

Readers are directed to Steiner (1998), which discusses issues raised in Reynolds (1997), presents additional data and analysis of scaphopod relationships, and raises the question of Gadilinidae paraphyly.

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APPENDIX 1

Material examined for character scoring. Sources: AMNH = American Museum of Natural History, CAS = California Academy of Sciences, NHML = The Natural History Museum, London, NMNH = National Museum of Natural History, Smithsonian Institution; PDR = Reynolds collection.

Family	Genus/species	Authority	Source/catalogue no.
Dentaliidae	*Dentalium laquaetum*	Verrill, 1885	NMNH 765274
	Fissidentalium floridense	Henderson, 1920	NMNH 765425
	Antalis entalis	(Linné, 1758)	NMNH 767337
	Coccodentalium carduum (shell only)	Dall, 1889	NMNH 765442
Fustiariidae	*Fustiaria* sp. (shell only)	Stoliczka, 1868	NMNH 277557
Rhabdidae	*Rhabdus rectius*	(Carpenter, 1865)	PDR (123.55°N, 41.3°W)
	R. perceptum	(Mabille & Rochebrune, 1889)	NMNH USARP Hero (uncat.)
	R. dalli	Pilsbry & Sharp, 1898	CAS 098721
Calliodentaliidae	*Calliodentalium callipeplum*	(Dall, 1889)	NMNH (uncat.; "Johnson-Smithsonian Exp., sta. 23, 4 Feb 1933, 18°32′00″N, 66°21′15″W"; see Emerson, 1952: p4)
Gadilinidae	*Gadilina insolita*	(Smith, 1894)	NHML (uncat.; "1952.3.25.83–93, John Murray Exp. 1933–4, St. 34, 16–10–33, det. Ludbrook"; see Ludbrook 1954: p.108)
	Episiphon subtorquatum	(Fischer, 1871)	NHML 2318
Entalinidae	*Entalina tetragonum* (shell only)	Brocchi, 1814	AMNH 146291
Pulsellidae	*Pulsellum salishorum*	Marshall, 1980	PDR (123.55°N, 41.3°W)
Gadilidae	*Siphonodentalium quadrifissatum*	Pilsbry & Sharp, 1898	CAS 059870
	Cadulus aberrans	Whiteaves, 1887	PDR (Monterey Bay, CA)
	Polyschides dalli v. antarcticus	Odhner, 1931	NMNH USARP Hero (uncat.)
	Platyschides agassizii	Dall, 1881	NMNH 832103

APPENDIX 2

Characters and character states used in the analysis.

Character: states

1. *Shell sculpture:* 0 = smooth, 1 = longitudinal ribs or striae, 2 = annulated.
2. *Maximum shell diameter:* 0 = at anterior aperture, 1 = not at anterior aperture.
3. *Apical shell callus:* 0 = absent, 1 = present.
4. *Shell layer number:* 0 = two, 1 = three.
5. *Shell microstructure, layer 1 (outer):* 0 = prismatic, 1 = irregular crossed lamellar.
6. *Shell microstructure, layer 2 (middle or inner):* 0 = regular crossed lamellar, 1 = nacreous.
7. *Shell microstructure, layer 3 (innermost, when present):* 0 = prismatic, 1 = regular crossed lamellar, 2 = irregular crossed lamellar, 3 = nacreous.
8. *Rachidian tooth shape:* 0 = wider than high, 1 = higher than wide.
9. *Lateral tooth base:* 0 = narrow, 1 = broad.
10. *Marginal tooth keel:* 0 = absent, 1 = present.
11. *Marginal tooth curvature:* 0 = straight, 1 = curved, 2 = s-shaped.
12. *Frontal glands:* 0 = absent, 1 = present.
13. *Anterior mantle circum-lateral glands:* 0 = absent, 1 = epithelial, 2 = subepithelial and epithelial.
14. *Frontal papillae:* 0 = absent, 1 = scarce, 2 = numerous.
15. *Anterior mantle aperture annular ciliary band:* 0 = absent, 1 = present.
16. *Anterior mantle aperture ciliated slits:* 0 = absent, 1 = present.
17. *Posterior mantle aperture:* 0 = lateral slit, 1 = vertical slit.
18. *Posterior mantle valve components:* 0 = dorsal only, 1 = dorsal and ventral, 2 = lateral only.
19. *Mantle pavilion ledges:* 0 = not ciliated, 1 = ciliated.
20. *Pavilion subepithelial glands:* 0 = absent, 1 = numerous.
21. *Foot retraction:* 0 = contractile, 1 = inversible.
22. *Anchoring structure:* 0 = lateral lobes, 1 = epipodial lobes, 2 = epipodial lobes and central filament, 3 = epipodial lobes, central filament and mucoid tissue.
23. *Pedal retractor muscles:* 0 = all associated with pedal wall, 1 = two originating at pedal wall, 2 = two inserting at pedal wall, 3 = four to six originating at pedal wall.
24. *Transverse foot muscles:* 0 = absent, 1 = present.
25. *Pedal ganglion support:* 0 = longitudinal muscle only, 1 = transverse and longitudinal muscle, 2 = ligament and longitudinal muscle, 3 = buccal septum and longitudinal muscle.
26. *Dorsoventral muscles:* 0 = one pair, 1 = two pairs, 2 = more than two pairs.
27. *Midgut gland:* 0 = paired, 1 = unpaired.
28. *Captacula:* 0 = absent, 1 = present.
29. *Ctenidia and auricles:* 0 = absent, 1 = present.
30. *Shell valves:* 0 = univalve, 1 = bivalve.
31. *Gut shape:* 0 = straight, 1 = U-shaped.
32. *Dominant body axis:* 0 = dorso-ventral, 1 = anterio-posterior.
33. *Radula:* 0 = absent, 1 = present.
34. *Lateral mantle lobes:* 0 = absent, 1 = present.

APPENDIX 3

Ingroup apomorphy list for family phylogeny tree (Figure 4). Key: ⇒, unambiguous change; →, change occurs under some reconstructions.

Branch	Character	Change
node 16→	node 17	
	13. Circum-lateral glands	0→1
	22. Anchoring structure	0→1
	25. Pedal ganglion support	1→2
	28. Captacula	0⇒1
	29. Ctenidia and auricles	1⇒0
node 17→	node 18	
	8. Rachidian shape	1⇒0
	9. Lateral tooth base	1⇒0
	12. Frontal glands	0⇒1
	15. Apertural ciliary band	0⇒1
node 18→	node 19	
	26. Dorsoventral muscles	0⇒1
node 19→	node 20	
	11. Marginal tooth curvature	0→2
	20. Pavilion glands	0⇒1
node 20→	Dentaliidae	
	1. Shell sculpture	0⇒1
node 20→	Fustiariidae	
	4. Shell layer number	1⇒0
	5. Shell microstructure L1	0⇒1
	18. Posterior valve	1⇒0
node 19→	node 12	
	16. Apertural ciliated slits	0⇒1
node 12→	Rhabdidae	
	7. Shell microstructure L3	2⇒0
	15. Apertural ciliary band	1⇒0
	25. Pedal ganglion support	2⇒0
node 18→	Gadilinidae	
	11. Marginal tooth curvature	0→1
node 17→	node 15	
	3. Apical shell callus	0⇒1
	13. Circum-lateral glands	1→2
	14. Frontal papillae	0⇒2
	17. Posterior aperture	0→1
	18. Posterior valve	1→2
	19. Pavilion ledges	0→1
	21. Foot retraction	0⇒1
	22. Anchoring structure	1→2
	23. Pedal retractors	0→1
	24. Transverse foot muscles	1⇒0
	25. Pedal ganglion support	2→3
	27. Midgut gland	0→1
node 15→	Entalinidae	
	1. Shell sculpture	0⇒1
	11. Marginal curvature	0→1
	23. Pedal retractors	1→3
node 15→	node 14	
	7. Shell microstructure L3	2→0
	10. Marginal tooth keel	0⇒1
	22. Anchoring structure	2→3
node 14→	node 13	
	4. Shell layer number	1→0
	14. Frontal papillae	2⇒1
node 13→	Wemersoniellidae	
	20. Pavilion glands	0⇒1
	23. Pedal retractors	1⇒2

APPENDIX 4

Ingroup character changes with respect to family phylogeny (Fig. 4); within terminal changes (due to polymorphisms) not shown. Key: ⇒, unambiguous changes; →, change occurs under some reconstructions.

Character	Changes	Character	Changes
1. Shell sculpture	node 20 0⇒1 Dentaliidae	17. Posterior aperture	node 17 0→1 node 15
	node 15 0⇒1 Entalinidae	18. Posterior valve	node 20 1⇒0 Fustiariidae
3. Apical shell callus	node 17 0⇒1 node 15		node 17 1→2 node 15
4. Shell layer number	node 20 1⇒0 Fustiariidae	19. Pavilion ledges	node 17 0→1 node 15
	node 14 1→0 node 13	20. Pavilion glands	node 19 0⇒1 node 20
5. Shell microstructure L1	node 20 0⇒1 Fustiariidae		node 13 0⇒1 Wemersoniellidae
7. Shell microstructure L3	node 12 2⇒0 Rhabdidae	21. Foot retraction	node 17 0⇒1 node 15
	node 15 2→0 node 14	22. Anchoring structure	node 16 0→1 node 17
8. Rachidian shape	node 17 1⇒0 node 18		node 17 1→2 node 15
9. Lateral tooth base	node 17 1⇒0 node 18		node 15 2→3 node 14
10. Marginal tooth keel	node 15 0⇒1 node 14	23. Pedal retractors	node 17 0→1 node 15
11. Marginal tooth curvature	node 19 0→2 node 20		node 15 1→3 Entalinidae
	node 18 0→1 Gadilinidae		node 13 1⇒2 Wemersoniellidae
	node 15 0→1 Entalinidae	24. Transverse foot muscles	node 17 1⇒0 node 15
12. Frontal glands	node 17 0⇒1 node 18	25. Pedal ganglion support	node 16 1→2 node 17
13. Circum-lateral glands	node 16 0→1 node 17		node 12 2⇒0 Rhabdidae
	node 17 1→2 node 15		node 17 2→3 node 15
14. Frontal papillae	node 17 0⇒2 node 15	26. Dorsoventral muscles	node 18 0⇒1 node 19
	node 14 2⇒1 node 13	27. Midgut gland	node 17 0→1 node 15
15. Apertural ciliary band	node 17 0⇒1 node 18	28. Captacula	node 16 0⇒1 node 17
	node 12 1⇒0 Rhabdidae	29. Ctenidia and auricles	node 16 1⇒0 node 17
16. Apertural ciliated slits	node 19 0⇒1 node 12		

APPENDIX 5

Character diagnostics table for the family phylogeny tree (Figure 4). CI, consistency index; HI, homoplasy index; RI, retention index; RC, rescaled consistency index.

Character	Minimum Steps	Tree Steps	Maximum Steps	CI	HI	RI	RC
1. Shell sculpture:	2	4	4	0.500	0.500	0.000	0.000
2. Maximum diameter:	1	1	1	1.000	0.000	0/0	0/0
3. Apical shell callus	1	1	4	1.000	0.000	1.000	1.000
4. Shell layer number	3	4	4	0.750	0.750	0.000	0.000
5. Shell microstructure L1	2	2	2	1.000	0.500	0/0	0/0
6. Shell microstructure L2	1	1	1	1.000	0.000	0/0	0/0
7. Shell microstructure L3	3	4	4	0.750	0.250	0.000	0.000
8. Rachidian shape	1	1	5	1.000	0.000	1.000	1.000
9. Lateral tooth base	1	1	5	1.000	0.000	1.000	1.000
10. Marginal tooth keel	1	1	3	1.000	0.000	1.000	1.000
11. Marginal tooth curvature	2	4	5	0.500	0.500	0.333	0.167
12. Frontal glands	1	1	5	1.000	0.000	1.000	1.000
13. Circum-lateral glands	2	2	6	1.000	0.000	1.000	1.000
14. Frontal papillae	2	2	4	1.000	0.000	1.000	1.000
15. Apertural ciliary band	1	2	4	0.500	0.500	0.667	0.333
16. Apertural ciliated slits	2	2	3	1.000	0.500	1.000	1.000
17. Posterior aperture	1	1	4	1.000	0.000	1.000	1.000
18. Posterior valve	2	2	5	1.000	0.000	1.000	1.000
19. Pavilion ledges	1	1	4	1.000	0.000	1.000	1.000
20. Pavilion glands	1	2	3	0.500	0.500	0.500	0.250
21. Foot retraction	1	1	4	1.000	0.000	1.000	1.000
22. Anchoring structure	3	3	6	1.000	0.000	1.000	1.000
23. Pedal retractors	3	3	4	1.000	0.000	1.000	1.000
24. Transverse foot muscles	1	1	4	1.000	0.000	1.000	1.000
25. Pedal ganglion support	3	3	7	1.000	0.000	1.000	1.000
26. Dorsoventral muscles	2	2	5	1.000	0.000	1.000	1.000
27. Midgut gland	1	2	5	0.500	0.500	0.750	0.375
28. Captacula	1	1	2	1.000	0.000	1.000	1.000
29. Ctenidia and auricles	1	1	2	1.000	0.000	1.000	1.000
30. Shell valves	1	1	1	1.000	0.000	0/0	0/0
31. Gut shape	1	1	1	1.000	0.000	0/0	0/0
32. Dominant body axis	1	1	1	1.000	0.000	0/0	0/0
33. Radula	1	1	1	1.000	0.000	0/0	0/0
34. Lateral mantle lobes	1	1	1	1.000	0.000	0/0	0/0