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Scaphopod mollusks (Scaphopoda)

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Abstract

The tusk shells (~500 sp.) are grouped into 14 families and two orders within the molluscan Class Scaphopoda. Only two molecular studies have focused on phylogenetic relationships within scaphopods. Estimates of divergence times among families are estimated here. The initial divergence among scaphopods, separating Gadilida and Dentaliida, is estimated to have occurred near the Devonian–Carboniferous boundary, ~359 million years ago (Ma), with the Fustiariidae, Rhabdidae, and Dentaliidae diverging in the Carboniferous (359–299 Ma). In contrast, the families included in the study from the Order Gadilida were estimated to have diverged from one another in the Cretaceous, 139–96 Ma.

The scaphopods (Phylum Mollusca, Class Scaphopoda) are known as tusk shells because of their curved shape (resembling elephant tusks), open at both ends (Fig. 1). They are relatively small, usually 3–6 cm in length. Scaphopods burrow into sediments with the wider (anterior) end of the shell oriented downward. Both the head and foot (used for burrowing) have an anterior location, whereas the viscera are posterior. There are ~500 valid species of recent scaphopods and about 800 valid fossil species. There is some argument as to when the lineage originated. Scaphopod fossils have been described from the Ordovician, Silurian, and Devonian, but many of these specimens have been reclassified as belonging to other groups. Yochelson (1) and others have suggested that scaphopods most likely evolved in the early Carboniferous. Here we review the evolutionary relationships and divergence times of the members of the Class Scaphopoda.

The Class Scaphopoda consists of 14 families and two orders. Two of the families contain only fossil genera

(Baltodentaliidae and Prodentaliidae), whereas four others contain at least one fossil genus each, along with genera containing living species (Dentaliidae, Gadilinae, Laevidentaliidae, and Gadilidae). The orders of Scaphopoda differ in the shape of the foot. The dentaliids have a conical foot whereas gadilidans have a worm-shaped foot with a terminal disk capable of expansion. Additional distinguishing features are provided by Steiner (2). The monophyly of the two orders has been supported by morphological data (3) and by molecular analyses based on the nuclear gene for *18S ribosomal RNA (rRNA)* (4) and the mitochondrial *cytochrome oxidase I gene (COI)* (5).

The Order Gadilida comprises four recent families. Entalinidae is placed within the Suborder Entalimorpha, distinguished by a ribbed shell and by a smooth rachis in the radula. The remaining three families—Pulsellidae, Wemersoniellidae, and Gadilidae—are placed within the Suborder Gadilimorpha, distinguished by a smooth shell and by a cuspid rachis. Support for these suborders has been provided by morphological data (3, 6–9) and by molecular analyses based on *18S rRNA* (4), although molecular analyses based on *COI* have suggested that the Gadilimorpha is paraphyletic (5). Analyses using *18S rRNA* did not support the monophyly of the Gadilidae (4).



Fig. 1 Two scaphopod shells (*Pictodentalium vermedei*) from Taiwan (right) and two shells of an undescribed species (*Pictodentalium* sp.) from Broome, Australia. Credit: B. Sahlmann.

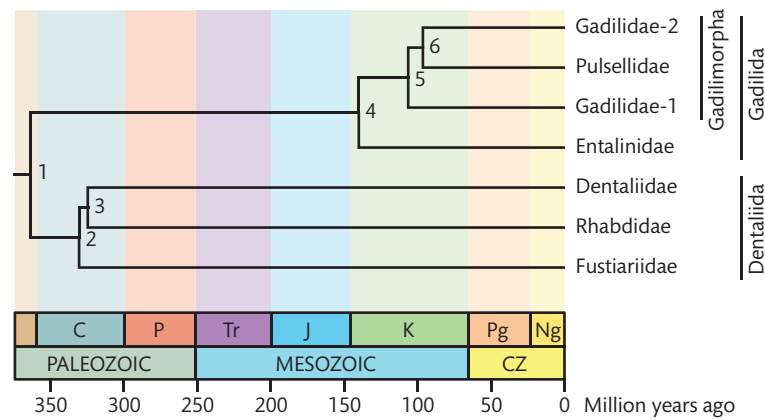


Fig. 2 A timetree of Scaphopoda. Divergence times are shown in Table 1. Gadilidae-1 contains the Subfamily Siphonodentaliinae and Gadilidae-2 contains the Subfamily Gadilinae of the classical Gadilidae. *Abbreviations:* C (Carboniferous), CZ (Cenozoic), J (Jurassic), K (Cretaceous), Ng (Neogene), P (Permian), Pg (Paleogene), and Tr (Triassic).

The Order Dentaliida comprises eight recent families whose interrelationships are not well resolved. Different taxon sampling within morphological studies makes comparisons difficult, and authors have expressed preferences for different character sets which have yielded conflicting results. Taxon sampling within molecular studies is particularly poor. Representatives from three dentaliid families were sequenced for *18S rRNA* (4). Fustiariidae was basal to a clade composed of Dentaliidae and Rhabdidae. The monophyly of Dentaliidae was not supported because of *Rhabdus* (Rhabdidae) falling within a clade containing *Antalis*, *Fustiaria*, *Dentalium*, and *Fissidentalium* (Dentaliidae). A study based on *COI* (5) suggested Dentaliidae to be paraphyletic. In this case, *Rhabdus* grouped with *Fissidentalium*, which was closest to a clade containing *Antalis* and *Dentalium*.

There are no previous published studies estimating divergence times among scaphopod families. We have therefore taken the nuclear *18S rRNA* sequences from GenBank (4) and applied a penalized likelihood method of Sanderson (10) in the program “r8s” to estimate these divergence times. Cross-validation scores were examined over a range of smoothing parameters to find the optimal smoothing parameter for the analysis. Confidence intervals were estimated using a bootstrap approach.

We selected only those (minimum) fossil constraints whose validity has not been questioned to date. For example, many authors (1, 4, 11–13) reject claims that *Rhytidentalium kentuckyensis* and other early fossils showing “scaphopodization” are true scaphopods (12). So, we have not used them. Yet, we have made an attempt to select the earliest fossil representatives for

each relevant taxon. We included the following fossils: *Prodontalium fredericae*, *Dentalium acutoides*, *Antalis torquatus*, *Fissidentalium pukaea*, *Fustiaria glabellum*, *Rhabdus paralelum*, *Entalina curvum*, *Cadulus groenlandicus*, *Polyschides arnoensis*, and *Pulsellum infundibulum*. Where the specific age of a fossil was not given, the midpoint of the epoch/age of the fossil was used as a minimum constraint. Fossil dates used for calibration are as follows: minimum of 329 Ma for the divergence of Dentalida and Gadilida, minimum of 322 Ma for the diversification of Dentalidae (*Dentalium* v. *Antalis*), minimum 172.5 Ma for the divergence of Rhabdidae and Dentalidae, minimum of 123 Ma for the divergence of Entalinidae and Gadilidae, minimum of 28.3 Ma for the divergence of Fustiariidae and Dentalidae, minimum of 18 Ma for the divergence of Gadilidae and Pulsellidae (*Cadulus* vs. *Pulsellum*), a minimum of 88 Ma for the diversification of Gadilinae (Gadilidae; *Cadulus* vs. *Cadulus*), and a minimum of 45 Ma for the diversification of Siphonodentaliinae (Gadilidae: *Siphonodentalium* vs. *Polyschides*).

A variety of conflicting hypotheses has been proposed as to which molluscan crown groups are closest to the Scaphopoda. However, recent molecular evidence has supported a close relationship between Cephalopoda and Scaphopoda (4, 14). We have therefore rooted the tree with the four cephalopod species used in the previous study (4). Given that potential scaphopod fossil species have been described from as early as the Ordovician (although many are admittedly controversial), we have again taken a conservative approach and placed a maximum age constraint of 488 Ma on the divergence of

Table 1. Divergence times (Ma) and their confidence/credibility intervals (CI) among tusk shell mollusks based on analyses reported here.

Timetree		
Node	Time	CI
1	363.3	367–359
2	329.9	354–306
3	324.0	345–303
4	139.5	154–124
5	106.2	121–91
6	96.0	110–82

Note: Estimates are based on a penalized likelihood analysis of the nuclear 18S rRNA sequences.

the cephalopods and scaphopods at the Cambrian–Ordovician border.

The resulting timetree is shown in Fig. 2. The initial divergence among scaphopods, separating Gadilida and Dentaliida, is estimated to have occurred ~363 Ma, with the Fustiariidae, Rhabdidae, and Dentaliidae diverging in the Carboniferous (359–299 Ma). In contrast, the families included in the study from the Order Gadilida were estimated to have diverged from one another in the Cretaceous, 139–96 Ma. The most basal family, the Entalinidae, was estimated to have diverged close to the Jurassic–Cretaceous border, 145 Ma. Steiner and Dreyer's (4) sequence data imply the polyphyly of the Gadilidae (see earlier). The Subfamily Gadilinae (Gadilidae-2, Fig. 2) was estimated to have diverged from the Family Pulsellidae in the Middle Cretaceous (110–82 Ma). Together this clade diverged from the Subfamily Siphonodentaliinae (Gadilidae-1, Fig. 2) slightly earlier in the Cretaceous. Whilst the dates proposed for the divergence of groups within the Dentaliida show close affiliation with dates from the fossil record, our timetree suggests that divergences within the Gadilida occurred a little earlier than is suggested by the fossil record (15).

The fossil record of scaphopods is extensive and is well suited to a molecular dating analysis by taking into account the abundance and distribution of fossil scaphopods. However, such an endeavor awaits further progress in molecular sequencing of the Scaphopoda. Additional sequencing of more scaphopod families and a greater number of genes would undoubtedly improve the resolution and information that could be gained from such an analysis.

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