J. Moll. Stud. (1999), **65**, 151–161

A NEW GENUS AND SPECIES OF THE FAMILY ANULIDENTALIIDAE (SCAPHOPODA: DENTALIIDA) AND ITS SYSTEMATIC IMPLICATIONS

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(Received 16 March 1998; accepted 1 June 1998)

ABSTRACT

Shell, radula, and anatomy of *Epirhabdoides ivanovi* new genus and species are described from a sample of the Russian Vitjaz Expedition from the Japan Trench. It is distinguished from the similar *Laevidentalium sominium* by shell morphometrics and radula morphology. The radula is almost identical with that of *Anulidentalium bambusa* (Anulidentaliidae). The anatomy of the mantle margins, however, including dorsolateral slits at the anterior mantle margin and a connective tissue bolster at the posterior mantle opening is that of the family Rhabdidae. In a parsimony analysis *Epirhabdoides ivanovi* takes an intermediate position between a basal grade of Gadilinidae and the remaining Dentaliida implying convergent evolution of mantle characters. An alternative but less parsimonious tree with *E. ivanovi* as sister taxon to *Rhabdus* requires convergences in radula characters. This is the first documented case of convergent anatomical features among Scaphopoda and enhances the need of radula and soft part investigation of the conchologically little informative, smooth-shelled dentaliid groups.

INTRODUCTION

Smooth shelled dentaliid Scaphopoda pose great difficulties for classification because shell sculpture is one of the most important (and easiest assessable) characters for species and genus identification. The great variety of patterns of longitudinal ribbing are especially useful. Left without soft body and with a smooth shell the remaining characters, shell shape, shell cross section and apical features, often provide insufficient information for correct identification. Apical characters like slits or pipes may help with the generic assignment but are not always developed in all specimens due to the dynamics of the posterior mantle edge (Steiner, 1991, 1992b; Reynolds, 1992). Moreover, the fragile pipes of *Episiphon* break easily in the process of collection, sorting and examination. Five genera of five different family-rank taxa, namely *Calliodentalium, Laevidentalium, Rhabdus, Fustiaria*, and *Episiphon*, are predominantly or exclusively comprised of smooth shelled species (Scarabino, 1995, for generic diagnoses). In addition, some species of the genera *Antalis* and *Fissidentalium* may have smooth shells. *Calliodentalium* and *Fustiaria* can be more reliably identified due to their shell shape (medium or strong curvature, more rapidly expanding). Most species of the genera *Laevidentalium, Rhabdus* and *Episiphon*, however, have weakly curved and slender, slowly expanding shells with circular or laterally compressed cross sections.

The Russian Vitjaz Expedition collected smooth shelled scaphopods from the Japan Trench that resemble *Laevidentalium sominium* (Okutani 1964. Light- and electron microscopical examination of the radula and the mantle, however, revealed considerable differences not only from the types of *L. sominium* but also to the characters diagnostic for the genus *Laevidentalium* and all other dentaliid genera.

MATERIAL AND METHODS

The specimens examined were collected by the Russian Vitjaz Expedition and loaned from the collection of the Zoological Museum, Moscow (ZMM). Types of *Laevidentalium sominium* Okutani 1964 were loaned from the National Science Museum Tokyo (Holotype Mo.69572, 47 paratypes Mo.69573) for comparative purposes. Type specimens designated in this study are deposited in the Zoological Museum Moscow, Muséum national d'Histoire naturelle, Paris (MNHN), and the Natural History Museum, London (BMNH).

Shell morphometry: Measurements were taken according to Shimek (1989) including length (L),

the anterior shell diameter (Da), the apical diameter (Dp), maximum curvature (arc), and the distance of the point of maximum curvature from the apex (darc) (Fig. 1). Mean values, standard deviation, minima and maxima are listed in Table 1.

SEM preparation: Radulae were extracted from the soft parts, cleaned in 10% KOH and by ultrasonic treatment and mounted while air-drying. This prevents the radula ribbon from rolling up on itself at least to some degree. Specimens were sputter coated with gold and examined on a Jeol JMS 09 or on a Phillips XL20.

Histological preparation: Soft parts were extracted from the shells, post-fixed and decalcified in Bouin's fluid, dehydrated in graded series of ethanol and embedded in synthetic paraffin (Histocomp). Transverse serial sections, 7 μm thick, of three specimens were stained with Kernechtrot and Picroindigocarmine.

Phylogenetic analysis: The species-level data matrix of Steiner (1998) was modified as discussed below (for matrix, characters, and character coding see Appendix) and submitted to PAUP 3.1 (Swofford, 1993) for parsimony analysis. All characters were equally weighted and character states unordered. Multistate entries were treated as polymorphisms. Heuristic searches with 50 random input sequences and TBR branch swapping were performed. Tree lengths, consistency index (CI) and rescaled consistency index (RC) were calculated.

SYSTEMATIC DESCRIPTIONS

Class Scaphopoda Bronn, 1862
Order Dentaliida Da Costa, 1776
Family Anulidentaliidae Chistikov, 1975

Diagnosis (modified from Chistikov, 1975): Shell up to 52 mm long, slender to needle-like, slightly curved to straight, thin, polished, translucent to white. Sculpture of bamboo-like annular swellings or smooth. Apex simple. Shell cross section circular or laterally compressed. Central tooth of radula with three medial columnar cusps on the superior border. Lateral teeth with pronounced head and a strong primary cusp similar to that in the Gadilinidae.

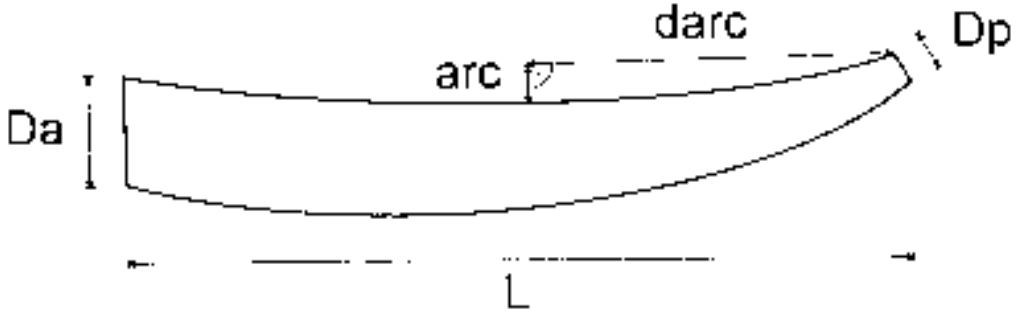

Figure 1. Shell morphometric parameters taken in this study. L, length; Da, anterior diameter; Dp, apical diameter; arc, maximum curvature; darc, distance of the point of maximum curvature from the apex.

Table 1. Shell morphometric parameters with mean values, standard deviation (SD), maxima (max) and minima (min) for the type series of *Epirhabdoides ivanovi and Laevidentalium sominium*. L, length; Da, anterior shell diameter; Dp, posterior shell diameter; arc, maximum curvature; darc, distance of point of maximum curvature from apex. Asterisks mark parameters significantly different between species at $p < 0.01$ (Mann-Whitney-U Test).

	Epirhabdoides ivanovi				Laevidentalium sominium			
	Mean	SD	max	min	Mean	SD	max	min
L*	27,4	6,1	40,2	15,6	34,2	6,7	45,0	14,6
Da*	1,7	0,2	2,1	1,2	1,9	0,2	2,2	1,1
Dp	0,5	0,1	0,6	0,3	0,5	0,1	0,8	0,2
arc	1,4	0,4	2,2	0,8	1,3	0,5	2,6	0,1
darc*	12,8	3,2	17,5	6,5	15,9	3,8	23,0	6,5
L : Da	16,1	2,0	19,1	12,7	18,2	2,1	22,6	13,2
darc : arc*	9,1	1,9	13,8	6,9	14,9	13,4	98,0	6,3

Marginal teeth slightly sinusoidal. Anterior mantle edge with one pair of dorsolateral slits. Posterior mantle opening with a ventral bolster of connective tissue as in Dentaliidae.

Epirhabdoides new genus

Type species: Epirhabdoides ivanovi new species.

Diagnosis: Shell thin and translucent, slightly curved, slender, expanding in diameter very slowly. Sculpture of irregular growth lines only forming slight undulations but not regular swellings. Apex simple or irregularly broken. Shell section circular throughout. Central rooth of radula of the dentaliid type with three median columnar cusps on the superior border flanked by finely serrated ridges. Lateral teeth with pronounced head, a strong and pointed primary cusp, anterior of which one smaller secondary denticle and a shallow nodulose ridge are developed. One low posterior secondary denticle. Marginal teeth weakly sinusoidal. Anterior mantle edge with two dorsolateral slits. Valve organ of posterior mantle edge with conspicuous ventral bolster.

Remarks: The radula of the type species closely resembles that of *Anulidentalium bambusa* Chistikov 1975. However, the shell of *Epirhabdoides ivanovi* is larger and not compressed but circular in section. Instead of the typical bamboo-like annulations of *A. bambusa* there are only very slight and irregular swellings. These differences justify the placement in a genus separate from *Anulidentalium*. Although radula morphology suggests assignment of *Anulidentalium* and *Epirhabdoides* to the family Gadilinidae, subfamily Anulidentalinae, the anatomical data of the mantle edges presented here place them close to the family Rhabdidae. Because of this intermediate position between the families Gadilinidae and Rhabdidae the Anulidentaliidae are treated as a family level taxon here.

Epirhabdoides ivanovi new species

Type material: holotype ZMM Lb-23, paratypes ZMM Lb-24 (2), Lb-25(4); MNHN Paris (2), BMNH 1996379 (2).
Type locality: Vitjaz stn. 24-3578, 38°35′–142°53′E, Japan Trench; 1641 m.

Etymology: named after Dimitry L. Ivanov, curator at the Moscow Zoological Museum, who provided the specimens for description.

Description:

Shell: very thin, translucent to transparent, slightly curved and slender, expanding very gradually (Figs, 2, 3A). Shell surface smooth except for somewhat irregular growth lines becoming more irregular in the anterior part of the shell where they may even produce slight undulations. Where worn, the shell has a chalky appearance. Apex is simple or irregularly broken. Shell cross section circular.

Measurements (mm): L 15.6–40.2; Da 1.2–2.1; Dp 0.3–0.6; arc 0.8–2.2; darc 6.5–17.5 (Table 1).

Radula: Rhachidian with three central projections of the superior border (Figs. 3B, 4A and B) resembling that of *Anulidentalium bambusa* (see Scarabino, 1995, p. 290, fig 95g). The projections seem to become eroded quickly and are absent in the anterior rows. Laterals with pronounced head bearing a prominent primary cusp, one low posterior and one sharp anterior secondary denticle, the latter being followed by a short nodulose ridge (Fig. 4C). Marginals weakly sinusoidal, the outer border wider than the border adjacent to the laterals (Fig. 4D).

Mantle edges: The anterior mantle edge has two short, longitudinal slits positioned dorsolaterally (Figs 5A and B). They lead posteriorly from the frontal epithelium of the mantle edge and close to form a short tube. There are remnants of dense ciliation in the slits (Fig. 5C), but cilia are detached from the epithelium. Thus, preservation is insufficient to infer ciliation patterns. The posterior mantle edge forms a valve apparatus with a ventral bolster of connective tissue (Fig. 5D) similar to that in the Dentaliidae, Rhabdidae, Laevidentaliidae, and Calliodentaliidae known for their anatomy (Steiner, 1991, 1998). A ring of large cells with long cilia is situated just outside of the valve apparatus (Fig. 5F).

A ligament of two to three fibres originates from between the statocysts and extends posteriorly to attach at the buccal septum (Fig. 6A). It has been reported from all Dentaliida investigated so far except for the genus *Rhabdus* (Steiner, 1992a, 1998). There are two pairs of dorsoventral muscles in the abdominal region (Fig. 6B), a large inner pair and a smaller outer pair. Although two pairs of dorsoventral muscles is the most common situation in the Dentaliida, Steiner (1998) reported four species with only a single pair, *Laevidentalium* (?) *martyi, Episiphon kiachowwanense, Gadilina insolita* and *G. pachypleura*.

Figure 2. *Epirhabdoides ivanovi*. **A.** Holotype (ZMM Lb-23); **B.** and **C.** paratypes (BMNH 1996379). Scale bar = 5 mm.

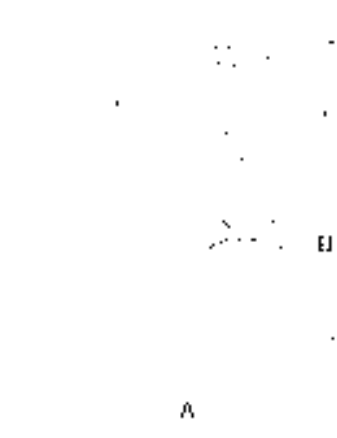

Figure 3. *Epirhabdoides ivanovi*. **A.** Shell and detail of the apex; **B.** Radula: rhachis, lateral tooth in dorsal and posterior view, marginal tooth,

Remarks: This species is very similar to and hardly distinguishable from *Laevidentalium sominium* Okutani 1964. Principal Component Analysis of shell measurements of the present material and the type series of *L. sominium* (Fig. 7) reveals significant differences ($p < 0.001$) only on the third axis. A discriminant analysis, however, classifies 87% of the cases correctly (data not shown). *Epirhabdoides ivanovi* is slightly more expanding and slightly more arched. This is reflected in significantly smaller ratios of L : Da ($p < 0.05$) and darc : arc ($p < 0.001$). As noted by Okutani (1964) the shell of *Laevidentalium sominium*, and thus also that of *Epirhabdoides ivanovi*, resembles that of *Rhabdus toyamaense* (Kuroda & Kikuchi, 1933) but is more slender and smaller. In the present material no traces of brownish accrementions were apparent.

Radula morphology provides a more reliable

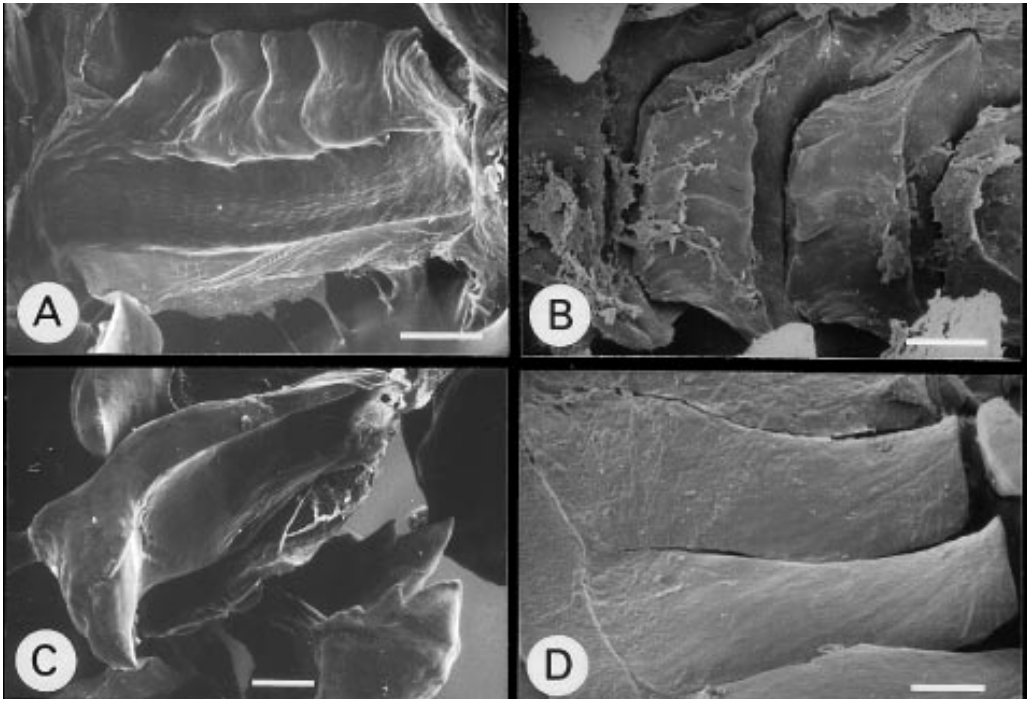

Figure 4. *Epirhabdoides ivanovi* radula. **A.** Rhachis tooth, not eroded; **B.** two rhachis teeth moderately eroded; **C.** lateral teeth; **D.** marginal teeth. Scale bars = 25 μm.

distinction between *Laevidentalium sominium* and *Epirhabdoides ivanovi* than shell features. *Laevidentalium sominium* (Fig. 8) has a rhachis tooth most similar to *Episiphon virgula* Hedley 1903 (Scarabino, 1979, p. 100, fig. 100) (subsequently synonymised with *E. subrectum* together with *E. carneum* and *E. makiyamai* in Scarabino, 1995): the superior border has a platform with three small denticles arranged in a flat triangle. This is not only clearly distinct from the three central columns of *Epirhabdoides ivanovi*, but has not been reported from *Laevidentalium* species at all. Radula morphology, thus, suggests assigning *sominium* to *Episiphon* rather than *Laevidentalium*, but it will be kept in the original genus *Laevidentalium* in this paper. The lateral teeth are also distinct having a broad and very prominent primary cusp in *Epirhabdoides ivanovi* as is typical for *Episiphon, Gadilina* and *Anulidentalium*, but in *L. sominium* having a series of anterior secondary denticles being almost as strong as the primary cusp. The entire lateral tooth in *L. sominium* is much shorter relative to the other radula elements than in *Epirhabdoides ivanovi*. Finally, the marginal teeth are weakly sinusoidal in *Epirhabdoides ivanovi* but almost straight and more slender in their proportions in *L. sominium*. The radulae of *Epirhabdoides ivanovi* and *Anulidentalium bambusa* are almost identical. Radula morphology, thus, places *Epirhabdoides ivanovi* well within the Gadilinidae *sensu* Scarabino (1995).

In contradiction to radula morphology, the organisation of the anterior mantle edge of *Epirhabdoides ivanovi* is very similar to that of *Rhabdus rectius* and *Rh. perceptum* (Steiner, 1991 and 1998): both have a pair of deep dorsolateral slits interrupting the outer gland region. This has also been illustrated for *Anulidentalium bambusa* (Chistikov, 1979, p. 110, fig. 4b). A detailed comparison of ciliation patterns inside the slits is not possible because of the poor preservation of these epithelia in the present material. The organisation of the valve appartus of the posterior mantle opening with its ventral connective tissue bolster also corresponds to that of the Rhabdidae, but also to that of the Dentaliidae, Laevidentaliidae and Calliodentaliidae. Mantle morphology, as far as can be said from this material, groups *Epirhabdoides ivanovi* with the Rhabdidae.

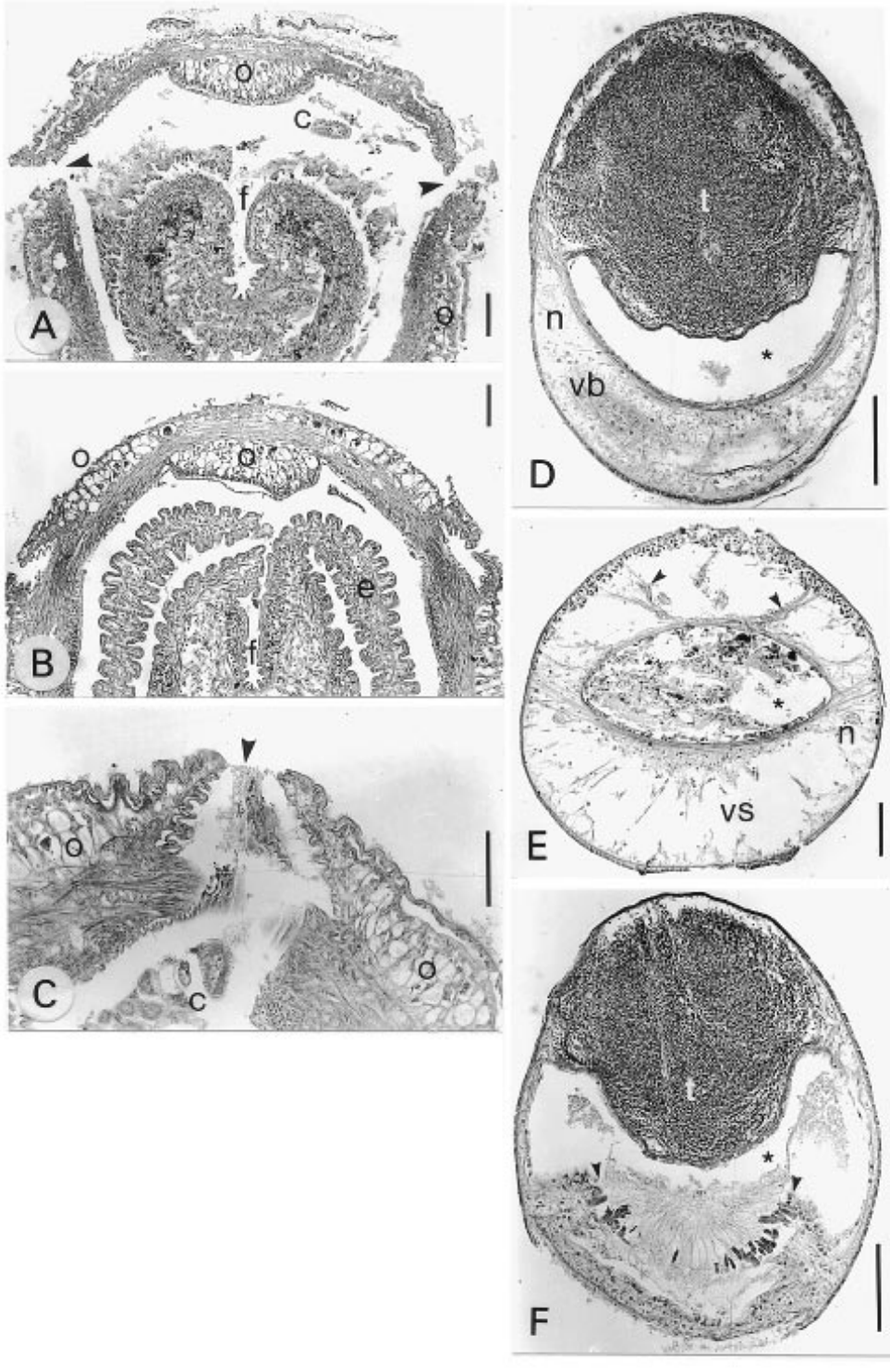
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Figure 5. *Epirhabdoides ivanovi.* A. – C. Anterior mantle edge in transverse section. **A.** Dorsolateral slits (arrowheads) open; **B.** posterior of A., dorsolateral slits closed towards mantle cavity; **C.** dorsolateral slit near closure towards mantle cavity, arrowheads indicate remnants of ciliation; D. – F. Posterior mantle opening and valve apparatus in transverse section. **D.** Ventral bolster of connective tissue; **E.** ventral sinus proximal to connective tissue bolster, scarcely delimited from dorsal sinus of the dorsal flap; arrowheads indicate retractor muscles of dorsal flap; **F.** ventral part of ring of ciliated cells (arrowheads) outside valve appartus. c, captaculum; e, epipodial collar; f, foot; n, pavillon nerve; o, subepithelial gland cells of outer gland region of anterior mantle edge; vb, ventral bolster of connective tissue; vs, ventral sinus proximal to ventral bolster; asterisk, mantle cavity. Scale bars = 100 μm.

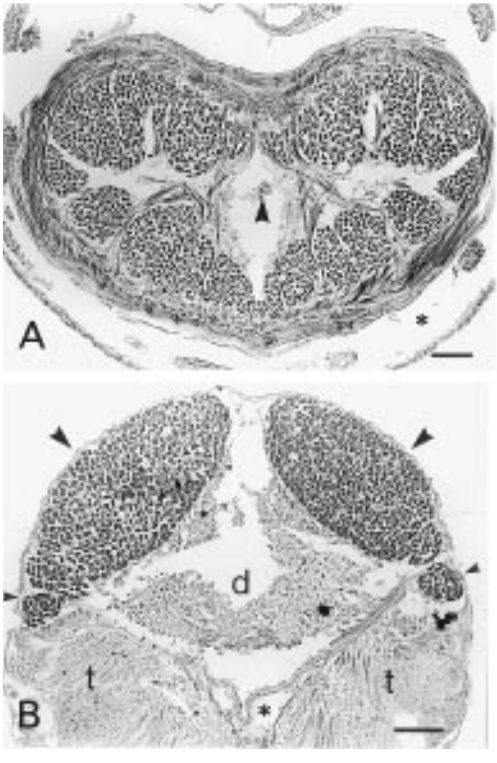

Figure 6. *Epirhabdoides ivanovi.* **A.** Foot in transverse section. Ligament (arrowhead) connecting statocysts and buccal septum in pedal sinus. **B.** Abdominal region in transverse section with a large inner pair (large arrowheads) and a small outer pair (small arrowheads) of dorsoventral musculature. d, remnants of posterior diverticulum of digestive gland in abdominal sinus; t, testis; asterisk, mantle cavity. Scale bars = 50 μm.

SYSTEMATIC AND PHYLOGENETIC IMPLICATIONS

A phylogenetic analysis based on the species-level data matrix of Steiner (1998) was made to determine the systematic position of *Epirhabdoides ivanovi* among the Dentaliida. This data set codes for characters states found in particular species. Only when two or more species of the same genus or family are identical in their character states, the supraspecific taxon is used. The original data matrix was modified by:

1) using only the dentaliid taxa and *Entalina* (Gadilida) and Tryblidiida as outgroups; the dentaliid genus *Omniglypta* was excluded for the lack of anatomical data; *Laevidentalium sominium* was also not included because anatomical data are not available;
2) eliminating non-informative characters for the present set of taxa;
3) adding two characters for the lateral teeth of the radula. Character #8 codes for the presence or absence of a well developed head of the lateral teeth. Character #9 classifies the denticulation of the lateral teeth as *Dentalium*-like (4 or more denticles with the posterior one strongest), *Gadilina*-like (3 to 4 denticles, the central one being a broad triangular cusp), *Rhabdus*-like (2 to 3 unevenly spaced small denticles or wrinkles and a prominent conical denticle), and *Entalina*-like (seven to nine denticles including 2 lateral larger cusps (Scarabino, 1995)). Excellent illustrations of radulae typical for these genera are given by Scarabino (1995). Detailed accounts of the other characters and character states are given in Steiner (1992b, 1998). The resulting data matrix contains 11 characters for 13 taxa including *Epirhabdoides ivanovi.*

The heuristic search produced 6 most parsimonious trees of length 30 (consistency index = 0.767, rescaled consistency index = 0.575). One of these is identical with the majority-rule consensus tree (Fig. 9A) placing *Epirhabdoides ivanovi* between the paraphyletic family Gadilinidae (genera *Gadilina* and *Episiphon*) and *Fustiaria*. The remaining variation among the 6 most parsimonious trees concerns the collapse of the branches between *Episiphon* sp. and *Epirhabdoides*, and between *Fustiaria* and Dentaliidae. The position of *Epirhabdoides* permits a non-homoplastic reconstruction of three radula characters #8–#10. To overrule the radula characters in favour of the two mantle

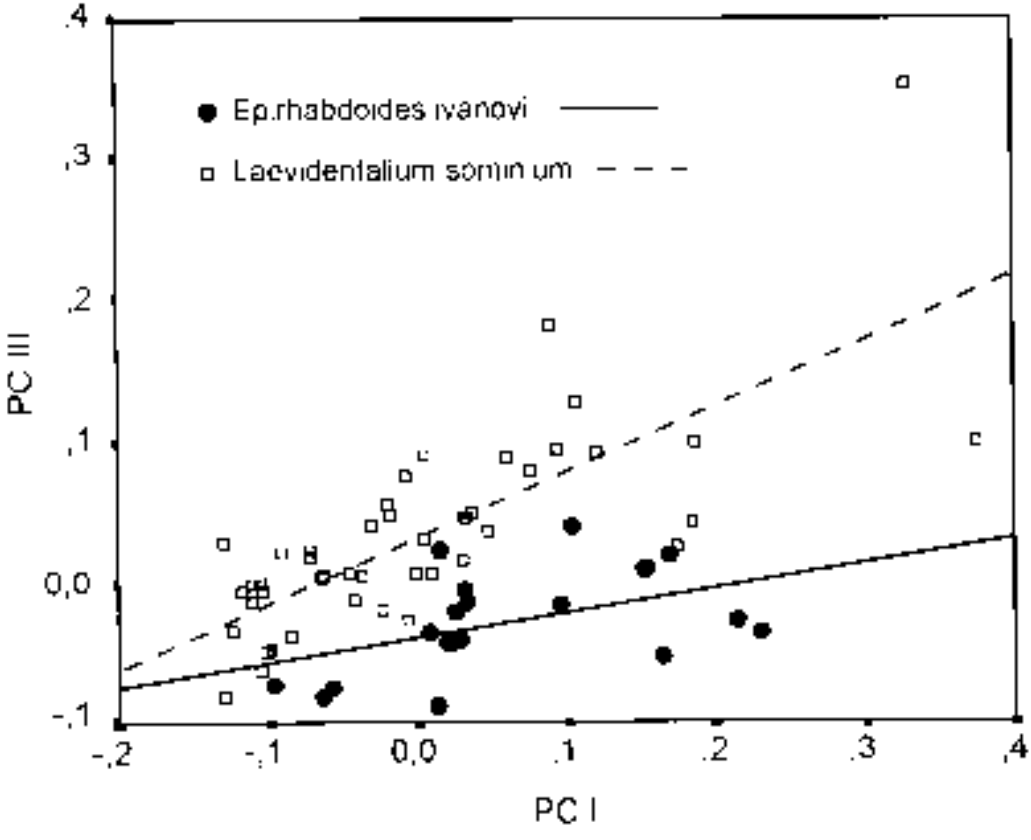

Figure 7. Principle Component Analysis of shell parameters of *Epirhabdoides ivanovi* and the type series of *Laevidentalium sominium*. Scatterplot of PC I and PC III with linear regression calculated for each species. The first 3 axes describe 95.3% of the variance. PC I: size axis as all parameters strongly positive loaded, dominated by L, Da, and darc; PC II: dominated by positive load of Dp and negative load of darc; PC III: dominated by positive loads of arc and Dp and negative load of darc. Significant differences ($p > 0.001$, Mann-Whitney-U test) of values between species are limited to the third axis.

characters, #3 and #4, these were arbitrarily given the weight 5. This yields 4 shortest trees of length 33 (CI = 0.697, RC = 0.448), the majority-rule and strict consensus tree (Fig. 9B) being one step longer (L = 34, CI = 0.676, RC = 0.411). As expected, mantle characters #3 and #4 show no homoplasy under this topology, but three to four reversals or convergences are necessary in the radula characters.

Thus, the organisation of *Epirhabdoides ivanovi* confronts us with the first obvious case of convergent evolution in scaphopod phylogeny. *Epirhabdoides* and, thus, the Anulidentaliidae represent a morphological link between the Gadilinidae and the Rhabdidae. They share radula features (general shape of the rhachis tooth with a central elaboration of the superior border, lateral teeth with triangular cusp) with the former and the anatomy of mantle openings (dorsolateral slits, ventral bolster) with the latter. At present, the decision whether mantle or radula characters are convergent is not possible, although parsimony prefers solutions where the more numerous radula characters are non-homoplastic. There are well documented cases of convergent radula teeth morphology in gastropods being caused by similar diets (e.g. Shimek & Kohn, 1981; Hickman, 1984; Jensen, 1993) and individual adaptation of tooth shape to different food availability (Padilla, 1998). However, without detailed information on dietary preferences of the scaphopod

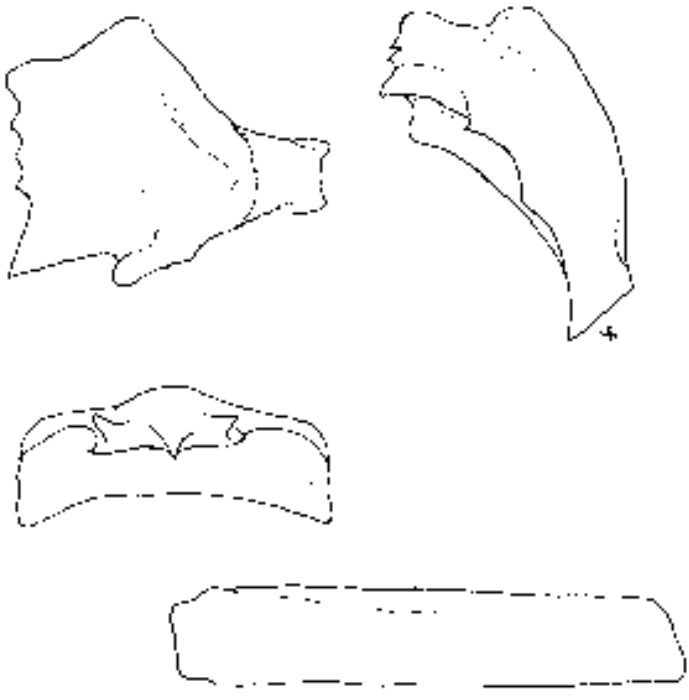

Figure 8. *Laevidentalium sominium*, radula: rhachis, lateral and marginal tooth.

species in question this argument remains speculative. Independent acquisition of a ventral connective tissue bolster in the posterior mantle opening seems not too unlikely. The correlation with the dorsoventral slits in the anterior mantle margin, on the other hand, renders such a convergence less likely. A phylogenetically straight forward solution deriving the group of Rhabdidae + Laevidentaliidae + Calliodentaliidae directly from the gadilinid grade with the Anulidentaliidae as stem group is not possible because of the intermediate position of the Fustiariidae having the gadilinid mantle organisation (without dorsolateral slits) but a radula similar to the Dentaliidae.

The present contribution points towards a greater variety of character combinations among the smooth-shelled dentaliid Scaphopoda than previously recognised. There is urgent need for studies of both radula and anatomical features of members of the Gadilinidae, Rhabdidae, Laevidentaliidae and Anulidentaliidae to assess this variation. These additional data will most likely lead to considerable changes and refinement of dentaliid systematics and will increase our understanding of scaphopod phylogeny.

ACKNOWLEDGEMENTS

I am greatly indepted to Dr. Dimitry L. Ivanov for the opportunity to work on the Vitjatz material and to Dr. Saito, National Science Museum Tokyo, for supplying the types of *Laevidentalium sominium*.

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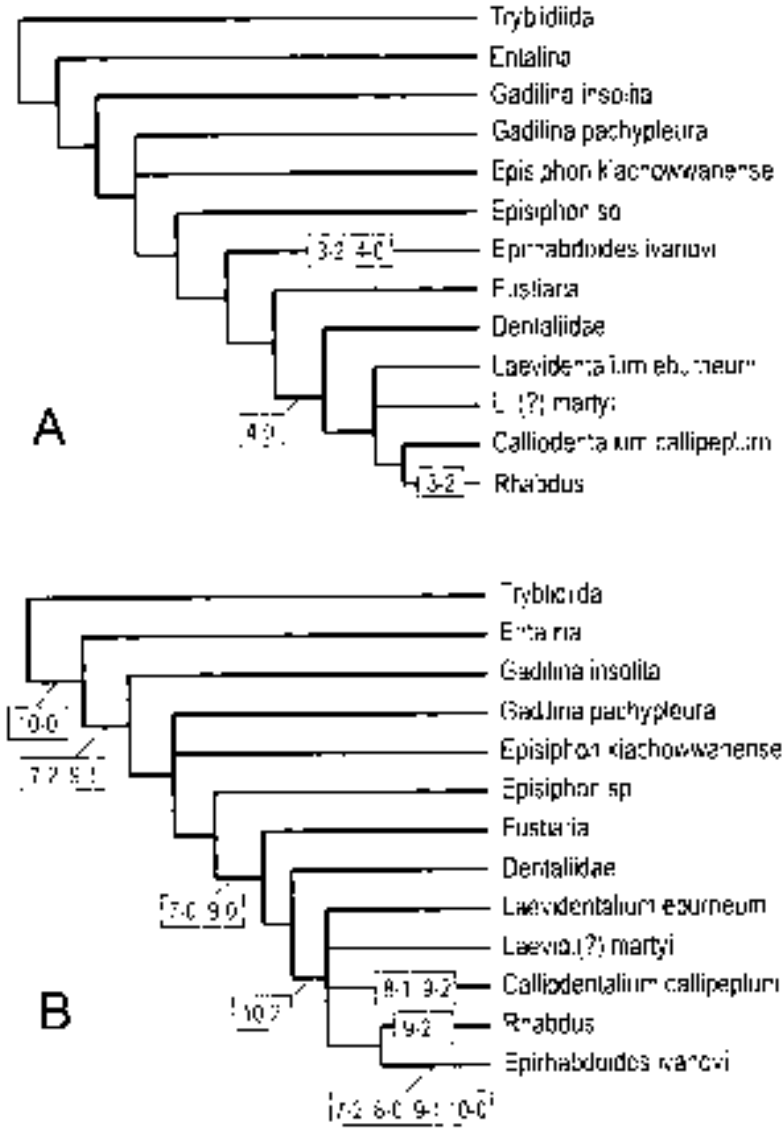

Figure 9. Majority-rule consensus tree of 6 most parsimonious trees with equally weighted characters (L = 30, CI = 0.767, RC = 0.575). **B.** Majority-rule consensus tree of 4 most parsimonious trees with weight 5 (see text) assigned to characters #3 and #4 (L = 34, CI = 0.676, RC = 0.411). Homoplastic character state transitions (character—state) are indicated in boxes at the respective branches.

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APPENDIX

a. *Characters, states and codes*

No.	Character	codes
1	shell sculpture	0 longitudinal, 1 smooth, 2 annulated
2	shell curvature	0 medium, 1 strong, 2 straight
3	ciliary organ (anterior mantle margin)	0 absent, 1 annular, 2 dorsolateral slits
4	valve apparatus	0 dorsal flap + ventral bolster, 1 dorsal flap only, 2 clasp
5	pavillon gland cells (post. mantle margin)	0 absent, 1 present, 2 abundant
6	rhachis tooth—shape	0 wider than high, 1 not wider than high
7	rhachis tooth—border	0 smooth, 1 trilobed, 2 tricuspidate, 3 monocuspidate
8	lateral tooth—head	0 elaborate, 1 little differentiated
9	lateral tooth cusps	0 *Dentalium*-like, 1 *Episiphon*-like, 2 *Rhabdus*-like, 3 *Entalina*-like
10	marginal tooth—shape	0 sinusoid, 1 curved, 2 straight
11	no. of dorsoventral muscles	0 more than two, 1 two, 2 one

b. *Data matrix*

? = missing or inapplicable, c = {123}, d = {12}

Dentaliidae	00101	00000 1
Fustiaria	10112	00000 1
Rhabdus	12201	01122 1
Laevidentalium eburneum	10101	01002 1
L. (?) martyi	d0101	00002 2
Calliodentalium callipeplum	11101	00122 1
Gadilina insolita	0111?	02011 2
Gadilina pachypleura	1011?	??01? 2
Episiphon kiachowwanense	10110	02010 2
Episiphon sp.	10110	02010 1
Epirhabdoides ivanovi	10200	02010 1
Entalina	00020	10030 2
Tryblidiida	c????	1???? 0