

Shell Morphometrics and Systematics: A Revision of the Slender, Shallow-Water *Cadulus* of the Northeastern Pacific (Scaphopoda: Gadilida)

by

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Abstract. The shell morphologies of 15 populations of eastern Pacific *Cadulus* species with slender shells were quantitatively examined and compared. Indices of shell shape were constructed relating total shell length to length from the dorsal aperture to the maximum width (LI), and maximum shell diameter to apertural diameter (WI). Using these indices, and Ws, the rate of whorl expansion, *Cadulus fusiformis*, *C. hepburni*, and *C. nitentior* were determined to be junior synonyms of *C. aberrans*. The indices were shown to be replicable and useful in distinguishing between shells of very similar shape.

Cadulus aberrans is redescribed using the above indices, including measures of the variability of shell shape, and ecological characteristics.

The shell shape of these slender scaphopods likely arose to facilitate escape from predators. Some aspects of scaphopod shell shapes, particularly dorsal apertural lobation, and secondary shell tubes are likely too variable to be useful as generic-group characters.

INTRODUCTION

Four nominal species of slender scaphopod mollusks of the genus *Cadulus* are synonymized as a result of the construction and comparison of indices based on shell morphology. The indices were constructed from measurements taken of two large samples collected from different northern populations and from smaller samples of several southern populations. One purpose of this paper is to assess variability of several measures of shell morphology. Secondly, I use these indices in conjunction with the examination of type material to determine synonymies within this group of nominal species, and to redescribe the species occurring north of central California. Where possible, and when relevant, I present data on other aspects of the morphology of these species.

I have defined the slender *Cadulus* (Figure 1) as those scaphopods with a polished shell, a total length of less than 15 mm, and an anterior or oral (anatomically ventral) aperture that is from 0.8 to 1.0 times the maximal shell diameter. If the maximal width of the shell is located posterior (anatomically dorsal) to the ventral aperture, it

is in the anterior third of the shell. Although curved, with the concave portion of the curve on the dorsal (anatomically anterior) side of the animal, the curve is not pronounced. In the northeastern Pacific the nominal taxa of *Cadulus* with these characters are *C. aberrans*, *C. hepburni*, *C. fusiformis*, *C. nitentior*, *C. perpusillus* (PILSBRY & SHARP, 1897-1898; GRANT & GALE, 1931; KEEN, 1971; ABBOTT, 1974; EMERSON, 1971; BAXTER, 1987). The more typical *Cadulus* forms, represented in this area by several species, particularly *C. tolmiei* and *C. californicus*, differ from the slender species in that they have a pronounced narrowing at the ventral aperture, and the widest part of the shell, often twice or more the width of the aperture, is located in the middle third of the shell.

All these species were described prior to 1910 utilizing only the most basic shell characteristics; the original descriptions were generally qualitative and uniformly brief, and little or no effort was devoted to determination or mention of variability (WHITEAVES, 1887; DALL, 1897; PILSBRY & SHARP, 1898; ARNOLD, 1903). Additionally, relatively few consistent shell measurements were made; thus, construction of various discriminatory indices has been difficult. As the various malacologists and major collections of the period were scattered, and comparison between the collections apparently uncommon, and as spec-

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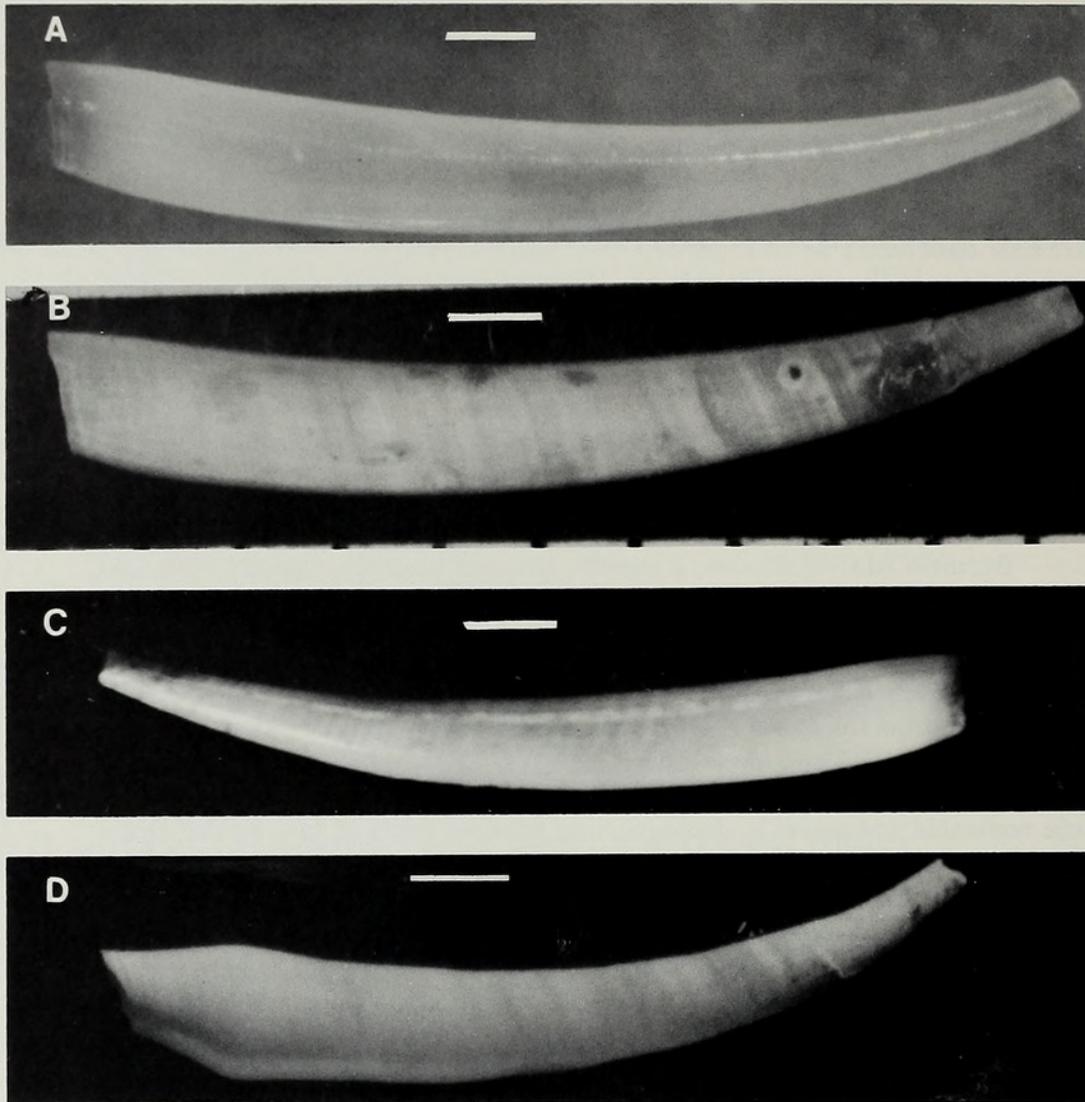


Figure 1

Cadulus types and specimens. Scale bar = 1 mm. A. *C. aberrans* Whiteaves, 1887, largest syntype. National Museums of Canada No. 555. B. *C. hepburni* Dall, 1897, figured type. USNM No. 107612. C. *C. fusiformis* Pilsbry & Sharp, 1898, lectotype. USNM No. 133809. D. *C. perpusillus* (Sowerby, 1832). Typical specimen from population LACM8, 31.12°N.

imens were collected relatively infrequently, several descriptions of small slender scaphopods assignable to *Cadulus* were published (WHITEAVES, 1887; DALL, 1897; PILSBRY & SHARP, 1897–1898; ARNOLD, 1903).

These small scaphopods, often common in the subtidal soft-sediment habitats of the Pacific Coast of North America (SHIMEK, 1988), are seldom found at depths less than 20 m, but are frequently collected from deeper areas, and some species appear to be widespread (ABBOTT, 1974; BAXTER, 1987).

During a study of the ecological interactions of a multi-species scaphopod assemblage found in the Barkley Sound region of Vancouver Island, British Columbia (Shimek, in prep.), I collected large numbers of scaphopods, including several hundred small *Cadulus* assignable to at least three species.

With this large sample from one region as a basis, I have made a detailed examination of shell morphology

utilizing several replicable measurements. These measurements allow the construction of reliable indices that can be used not only to describe and discriminate among the species in question, but also to quantitatively examine shell morphological variation within and between populations.

Finally, the relationship of some supra-specific characters within the class Scaphopoda are briefly discussed. Some of the presently accepted taxonomic characters within the class are spurious and have been used because of insufficient knowledge of the living animals.

SYSTEMATIC ACCOUNT

Cadulus aberrans WHITEAVES, 1887:124, fig. 2. Type locality: Quatsino Sound, Vancouver Island, British Columbia, in 30–50 fm (55–92 m).

Cadulus hepburni DALL, 1897:12, pl. 1, fig. 13. Type locality:

Near Victoria, Vancouver Island, British Columbia, in 60 fm (110 m).

Cadulus fusiformis PILSBRY & SHARP, 1898:193, pl. 35, fig. 14. Type locality: San Pedro, California, at 150 foot (46 m) depth. Also known, as a fossil, from San Diego, California.

Cadulus nitentior ARNOLD, 1903:187, pl. 8, fig. 13. Type locality: Pleistocene, Deadman Island, San Pedro bluffs, California.

REDESCRIPTION OF *Cadulus aberrans*

External Anatomy

Shell: Shell slender, length to maximum width ratio = 0.13 ± 0.02 , slightly curved, $\ln(Ws) = 6.076 \pm 1.231$ (Ws = whorl expansion rate = 1344 ± 4607); highly polished, lustrous, translucent white; minute growth lines present (visible with magnification only); ventral (=oral or anterior) aperture oblique, round; dorsal (=anal, or posterior) aperture round, not lobed. No dorsal secondary apertural tube (such as found in *Dentalium*). Juvenile specimens, to about 10 mm in total length, without constriction of ventral aperture. Adult size determinate, total length to about 13 mm; adult specimens with slightly constricted aperture ($WI = \text{Width Index} = \ln(\text{Ap}W + 1)/\ln(\text{Wm} + 1) = 0.852 \pm 0.063$). Maximal width near anterior end ($LI = \text{Length Index} = \ln(\text{LWm} + 1)/\ln(\text{LTot}) = 0.513 \pm 0.055$). Shell lip thin and sharp.

Soft part morphology: The mantle is generally dull white, except for a golden ring at area of outer mantle fold. When extended out of the ventral aperture, the mantle has a triradiate fold. The foot extends through the center of this triradiate area. The mantle may protrude about 1 mm beyond the dorsal aperture in an adult (shell length > 10 mm). There are no consistent sexual differences in the shape of the "pavilion," or tube formed from the dorsal mantle edge, in living animals.

The foot is extendable to the length of the shell, caduliform, with a terminal disk, and papillate laterally; sometimes one or two small papillae are visible on the distal face of the terminal disk.

Captacula are numerous, over 100 in adults, and extendable to 2–3 mm; the terminal bulb is densely ciliated, and stalk cilia are limited to tufts arranged linearly (SHIMEK, 1988).

Visible internal morphology: The radula is visible through the shell, brownish, and highly mineralized, with most highly mineralized areas being black; the radular formula is 1·1·1·1·1; the marginal teeth are large and platelike; the lateral teeth are hooked, with two cusps, and the central tooth is small. All teeth are mineralized with iron and calcium salts.

The cerebral ganglia are visible through the shell ventral (=anterior) to radular mass, and are pinkish.

The digestive gland is dark brown to black, prominent, and visible through the shell.

The gonads are visible through the adult shells. The

gonads are brilliant white in males and brown in females; ova are brown.

Ecological Characteristics—British Columbia Specimens

Specimens are found in clean, well-sorted sand; the depth distribution is 20–100 m, and the population density 6–10/m². The animal is a predator on small (maximal dimension generally <0.300 mm) live foraminiferans; it prefers *Rosalina* cf. *columbiana* (Cushman, 1925), *Cribrononion lene* (Cushman & McCulloch, 1940), rejects (eats fewer than would be expected) *Florilus basispinatus* (Cushman & Moyer, 1930), and eats *Elphidiella hannai* (Cushman & Grant, 1927) as encountered. The most abundant minor prey species are *Buliminella elegantissima* (d'Orbigny, 1839) and *B. exilis* (H. B. Brady, 1884); other foraminiferan species are occasionally taken. Prey are maintained in a buccal pouch (=proboscis) prior to maceration, and individuals may have up to 125 foraminiferans in the pouch.

Geographical Range

Southern California through Prince William Sound, Alaska.

Lectotypes

I here designate the following specimens as lectotypes of *Cadulus aberrans* Whiteaves, 1887:

Cadulus hepburni Dall, 1897, USNM No. 107612;

Cadulus fusiformis Pilsbry & Sharp, 1898, USNM No. 133809;

Cadulus nitentior Arnold, 1903, USNM No. 23729.

MATERIALS AND METHODS

Type or Reference Specimens Examined

The following *Cadulus* type or reference specimens were examined: *C. aberrans* Whiteaves, 1887, National Museums of Canada catalogue number 555, 5 specimens, all syntypes; *C. hepburni* Dall, 1897, United States National Museum of Natural History (USNM) catalogue number 107612, 1 specimen, a paratype, the figured type; *C. fusiformis* Pilsbry & Sharp, 1898, USNM number 133809, a lectotype, designated by Pilsbry & Sharp, 1898; *C. nitentior* Arnold, 1903, ex Carpenter MS, USNM number 23729 (not type); *C. perpusillus* Sowerby, 1832, photo of lectotype, USNM number 96570, designated by EMERSON (1971:fig. 1); *C. californicus* Pilsbry & Sharp, 1898, USNM number 107698, a lectotype; *C. tolmiei* Dall, 1897, USNM number 107613, figured paratype.

The types, reference specimens, or photographs listed above were examined and measured (Figure 1, Table 1). I was not able to physically examine the types of *Siphonodentalium quadrifissatum* (Pilsbry & Sharp, 1898) and *Ca-*

Table 1

Measurements taken of *Cadulus* type and reference specimens examined. See the text for the appropriate transformation.

Species of <i>Cadulus</i>	Transformed measurements				Derived indices		
	lnLTot	lnApW1	lnWm1	lnLWm1	LI	WI	Ws
<i>aberrans</i>							
1	2.41	0.77	0.86	1.10	0.46	0.90	395
2	2.40	0.82	0.92	0.82	0.34	0.89	107
3	2.49	0.75	0.85	0.85	0.34	0.88	323
4	2.54	0.88	0.97	1.15	0.45	0.91	135
5	2.43	0.78	0.85	0.94	0.39	0.93	477
<i>californicus</i>	2.69	1.13	1.40	1.58	0.59	0.81	343
<i>fusiformis</i>	2.26	0.63	0.78	0.65	0.29	0.80	2601
<i>hepburni</i>	2.33	0.80	0.88	0.80	0.34	0.91	1396
<i>nitentior</i>	2.16	0.72	0.81	1.23	0.57	0.88	100
<i>perpusillus</i>	1.96	0.49	0.66	0.54	0.27	0.85	255
<i>tolmiei</i>	2.43	1.02	1.19	1.55	0.64	0.86	261

dulus perpusillus; however, measurements of the latter were made from published illustrations of the lectotype designated by EMERSON (1971:fig. 1). Although I did not examine the figured type of *C. nitentior*, I examined Carpenter's specimen from the U.S. National Museum of Natural History that was used in Arnold's determination of this species (ARNOLD, 1903). The figured individual was a different, more eroded, individual than that used in the description.

Experimental Material Examined

In addition to the types, I examined specimens of slender *Cadulus* collected at 15 localities along the west coast of North America from 24°N to about 50°N and from a considerable depth range. Collection data from the 15 localities are as follows: population LACM1, from 23.52°N, 109.00°W, collection depth 9 m, 27 individuals, none were juveniles; population LACM2, from 24.18°N, 111.35°W, collection depth 69–87 m, 10 individuals, no juveniles; population LACM3, from 24.23°N, 110.03°W, collection depth 250–400 m, 5 individuals, 1 juvenile; population LACM4, from 27.21°N, 114.53°W, collection depth 107–129 m, 11 individuals; population LACM5, from 27.69°N, 115.09°W, collection depth, 89 m, 13 individuals, 4 juveniles; population LACM6, from 27.95°N, 115.13°W, collection depth 31–36 m, 40 individuals, 1 juvenile; population LACM7, from 29°N, 113°W, collection depth 18–36 m, 6 individuals, 1 juvenile; population LACM8, from 31.12°N, 114.82°W, collection depth 7–11 m, 133 individuals, no juveniles; population LACM9, from 33°N, 118°W, collection depth 25 m, 6 individuals, no juveniles; population LACM10, from 33.47°N, 118.48°W, collection depth 82–91 m, 2 individuals, no juveniles; population LACM11, from 33.58°N, 118.42°W, collection depth 14 m, 6 individuals, no juveniles; population LACM12, from 36.63°N, 121.90°W, collection depth 36 m, 101 individuals, 20 juveniles; population LACM13, from 48.41°N, 126.10°W,

collection depth 274 m, 9 individuals, no juveniles; population DS, from 48.43°N, 125.50°W, collection depth 100–150 m, 92 individuals, 31 juveniles; population T, from 48.83°N, 125.18°W, collection depth 18–91 m, 334 individuals, 101 juveniles. Thus a total of 794 individuals were examined, of which 159 or 20.03% exhibited the juvenile shell morphology.

For outgroup comparisons I examined *Dentalium rectius* Carpenter, 1864, *Pulsellum salishorum* Marshall, 1981, and *C. tolmiei* Dall, 1897, a more typical *Cadulus* species. All were collected from Barkley Sound, on the southwest side of Vancouver Island. Thirty specimens of *C. tolmiei* were collected from a depth of 150–350 m at Sarita Bay, 48.89°N, 125.05°W. *Dentalium rectius* and *P. salishorum* were collected from three localities: Mayne Bay, 48.98°N, 125.33°W, collection depth 35–40 m; Imperial Eagle Channel, 48.88°N, 125.19°W, collection depth 75–80 m; and Trevor Channel, 48.83°N, 125.18°W, collection depth 30–110 m. Collections from the above sites were pooled, yielding for comparison 483 individuals of *D. rectius* and 283 individuals of *P. salishorum*.

Measurements

For all the specimens, unless otherwise noted, I measured total length (LTot), length from the most anterior position of the ventral aperture of the shell to the widest portion of the shell (LWm), length from the ventral aperture to the place of maximum arc (Larc), the interior ventral aperture width (ApW), the maximum width (Wm), and the maximum arc (arc). As the measurement orientation is important for replication, the exact orientation of the measurements is indicated (Figure 2). All measurements, unless otherwise noted, were taken using a stereo dissection microscope with a calibrated ocular micrometer at magnifications of 10 (*Dentalium rectius*) to 40 diameters (*Cadulus* spp. and *Pulsellum* sp.). The lobes around the dorsal aperture were counted. All linear measurements

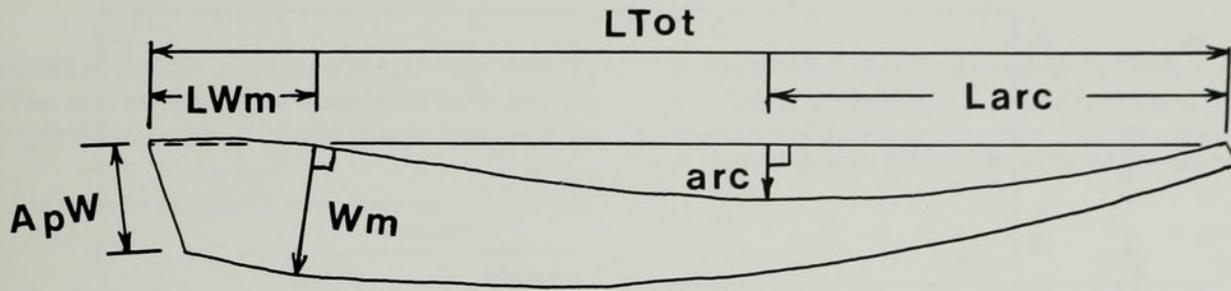


Figure 2

Measurements taken of all specimens; all orientations labeled anatomically; *i.e.*, the foot is ventral. Abbreviations: ApW = interior width of the ventral aperture, measured perpendicular to the anteriormost shell surface; arc = maximum perpendicular distance from a line connecting the anteriormost margin of the dorsal aperture to the anterior surface of the shell to the anterior margin of the ventral aperture; Larc = distance from the anteriormost margin of the dorsal aperture to the point where the arc was measured; LTot = total length, from anteriormost margin of the dorsal aperture to the anteriormost margin of the ventral aperture; LWm = length to point of maximum width, from the anteriormost margin of the ventral aperture to the anteriormost point of the widest part of the shell; Wm = maximum shell diameter, measured perpendicular to the anteriormost surface of the shell at that point.

were converted to their natural logarithms to minimize problems of size scale for comparison. As index calculations involving LWm, ApW, and Wm might result in terms less than or equal to zero, resulting in the natural logarithms being either negative or undefined, one (1) was added to each of these terms for calculation purposes.

Derivation of Indices

From these measurements, the following indices were defined. LI = ln(LWm + 1)/ln(LTot); WI = ln(ApW + 1)/ln(Wm + 1). The whorl expansion rate (Ws) (RAUP, 1966) was also calculated. Scaphopods never complete one entire whorl; however, the index could be derived from the measurements taken of the scaphopod shells.

$$\text{Whorl expansion rate} = Wa^{\frac{\theta}{2\pi}} = \frac{R_i}{R_0} \quad (\text{RAUP, 1966})$$

$$\text{Let } R_i = \text{LTot}, \text{ and } R_0 = \sqrt{(\text{LTot} - \text{Larc})^2 + (\text{arc})^2}.$$

$$\text{Then } Wa^{\frac{\theta}{2\pi}} = \frac{\text{LTot}}{\sqrt{(\text{LTot} - \text{Larc})^2 + (\text{arc})^2}}$$

$$\text{And } Ws = Wa^{\left(\frac{1}{\frac{\theta}{2\pi}}\right)} = Wa^{\frac{2\pi}{\theta}}$$

$$\text{And } \frac{\theta}{2\pi} = \text{atan} \frac{\text{arc}}{\text{LTot} - \text{Larc}}$$

Thus Ws

$$= \frac{\text{LTot}}{(\sqrt{(\text{LTot} - \text{Larc})^2 + (\text{arc})^2})^{\left(\frac{1}{\text{atan}\left(\frac{\text{arc}}{\text{LTot} - \text{Larc}}\right)}\right)}$$

For comparisons between populations, I used the natural logarithm of the population median values of Ws. The medians were less sensitive to extreme values and, thus, were better indicators of central tendency. The use

of the logarithms eliminated some of the problems caused by comparisons over several orders of magnitude.

For morphometric comparisons, except for *Cadulus tolmiei*, I used shells with clearly adult morphology. Where necessary, I eliminated from the comparison specimens missing one or more of the measurements. Various measurements might be unreliable owing to breakage or changes in curvature resulting from healed fractures. I used the largest possible data set for each test and/or comparison. Consequently, differing comparisons of the same population sometimes varied slightly in the total number of individuals. No more than 10 specimens were ever removed from any comparison by this arbitrary method.

Buccal content analyses were done using methods described in BILYARD (1974) and SHIMEK (1988).

RESULTS

Determination of Mature Individuals

A number of individuals from some populations did not have the typical *Cadulus aberrans* shape (with the widest part of the shell one-third or less the distance from the ventral to the dorsal aperture); instead the widest part of the shell was at the ventral aperture. Although these animals tended to be smaller in total length than those with the normal morphology, in the northern populations particularly, many were relatively large and apparently sexually mature (Figure 3).

I found no shells intermediate between these "non-bulging" and the more typical "bulging" *Cadulus aberrans* shapes (Figure 3). Thus it was possible that these two morphologies represented two distinctly different species with similar, but subtly different shell shapes.

I did buccal content analyses of specimens of both shapes collected from area T, 48.83°N, from June to December 1984. The variety and proportion of dietary items from both sets of specimens were similar, and the dietary over-

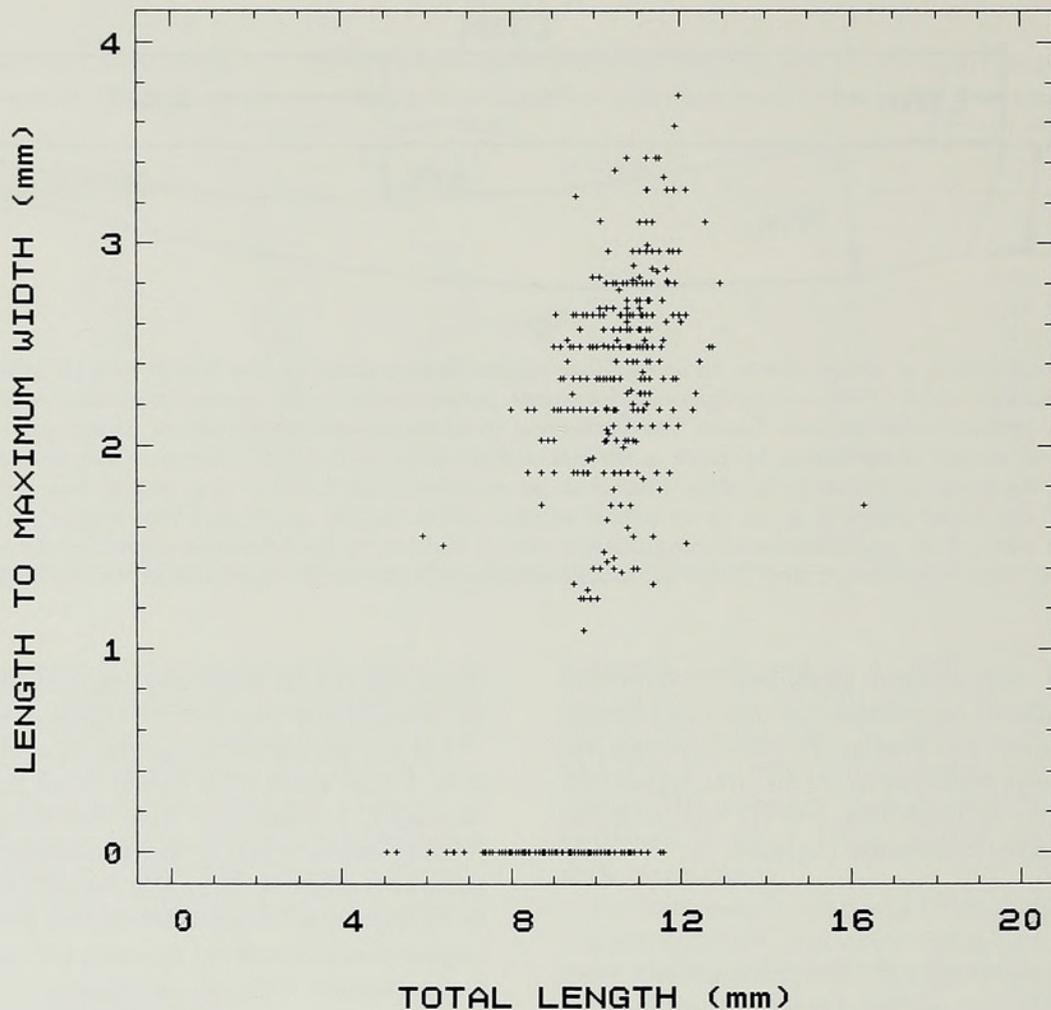


Figure 3

Adult and juvenile *Cadulus aberrans* from pooled populations DS and T. Ordinate = length from the ventral aperture to the point of maximum width; Abscissa = total shell length. Upper cluster of points ($n = 294$) is animals with the typical adult morphology (*i.e.*, a constricted ventral aperture). The lower line ($n = 132$) represents those animals without a ventral apertural constriction, *i.e.*, juveniles.

lap, as measured by the least common percentage index (D) (SCHOENER, 1968), was high (Table 2). Nevertheless, the mean dietary foraminiferan size from the animals with the "bulging" morphology was significantly larger (Table 3). There were, however, no statistically significant differences in either the sizes or distributions of the other buccal contents (Table 3). *Cadulus aberrans* is a specialist predator on foraminiferans (SHIMEK, 1988). Consequently, the predominance of foraminiferans meant that the average item in the pooled buccal contents from the bulging animals was significantly larger than that from the contents of the "non-bulging" animals (Table 3).

No single foraminiferan species, however, accounted for this difference in prey size, and, in fact, none of the major prey species was found to be significantly larger in the buccal contents of the "bulging" morphology (Table 4). Rather, the aggregate total distributions are statistically and distinctly different, owing to the larger sample size (Tables 3, 4).

Anatomical examination indicated no distinct difference between those animals with the "bulging" and "non-bulging"

morphologies except in the degree of sexual maturity. Some of these "non-bulging" animals appeared to be sexually mature, judging by the visual estimation of the gonadal development. Although I did not note these animals particularly at the time of collection, I estimated them to account for no more than 10% of the "non-bulging" animals. The remainder of the "non-bulging" animals lacked gonads visible through the shell. Although in a few cases the brown pigmentation characteristic of mature females was present in a thin tissue strand lateral to the pedal retractor muscles, gender was indeterminate for most of the "non-bulging" forms; the gonads were simply too small for adequate visual determination through the shell. The adult normal sex ratio is 1:1, but only 28 of the 101 "non-bulging" individuals from area T were clearly female; thus, some individuals were too immature to be sexually differentiated. Consequently, because of the close dietary correspondence, I concluded that these "non-bulging" animals were juveniles or recently sexually mature individuals rather than a different species of similar shape. Thus the data from these individuals could be treated with the remainder

Table 2

Buccal contents of *Cadulus aberrans* collected from area T, 48.83°N. The two morphologies considered here are the "bulging" and "non-bulging" morphologies indicated in the text.

Item	Morphology			
	Bulging (LI > 0)		Non-Bulging (LI = 0)	
	n	Pro- portion	n	Pro- portion
Foraminiferans:	507	0.746	137	0.753
<i>Cribronion lene</i>	178	0.262	48	0.264
<i>Florilus basispinatus</i>	126	0.185	22	0.121
<i>Elphidiella hannai</i>	53	0.078	15	0.082
<i>Buliminella exilis</i>	49	0.072	17	0.093
<i>Rosalina cf. columbiana</i>	32	0.047	11	0.060
Others (11 spp.)	62	0.132	24	0.175
Unidentified foraminiferans	6	0.009	5	0.027
Foraminiferan tests:	55	0.081	24	0.132
<i>Rosalina cf. columbiana</i>	21	0.031	10	0.055
<i>Florilus basispinatus</i>	10	0.015	2	0.011
<i>Buliminella elegantissima</i>	8	0.012	2	0.011
<i>Cribronion lene</i>	6	0.009	7	0.038
Others (6 spp.)	10	0.013	3	0.016
Foraminiferan fragments	101	0.149	13	0.071
Diatom tests	2	0.003	2	0.011
Mineral grains	14	0.021	6	0.033
Sediment bolus	1	0.001	0	—
Total	680	1.000	182	1.000

Dietary overlap between adults and juveniles = $D = 0.810$.

of the *Cadulus aberrans* data, particularly in the calculation of whorl expansion rate.

Determination of Population Parameters

Cluster analyses of the mean population values for LI and WI and the median population values for Ws gave three distinct groupings containing animals of similar shapes (Figure 4): a northern group and two southern groups, here concluded to be *Cadulus aberrans*, *C. perpusillus*, and *Siphonodentalium quadrifissatum* respectively.

The samples and the determined species follow, along with the disposition of the specimens. Determined to be *Cadulus aberrans* were the individuals in population LACM6, Los Angeles County Natural History Museum (LACM) accession number 71-158, populations LACM9 through 13, LACM accession numbers 122873, 70-115, 65-1, 60-23, and 72-140 respectively, population DS, deposited at the Institute of Ocean Sciences (Canada), Patricia Bay, British Columbia, and population T, deposited in the author's personal collection. *Cadulus perpusillus* was represented by those individuals from the following stations: populations LACM2 through 5, LACM accession numbers 71-16, 69-59, 71-176, and 71-168 respectively,

Table 3

A comparison of buccal contents of "bulging" and "non-bulging" (adult and juvenile) *Cadulus aberrans*.

A. Size of Buccal Content Items in Micrometers (Mean \pm 1 SD).

	Adult		Juvenile	
	Mean \pm 1 SD	n	Mean \pm 1 SD	n
All foraminiferans	153 \pm 93	506	126 \pm 89	137
Foram. tests	125 \pm 68	55	118 \pm 55	24
Foram. fragments	87 \pm 33	101	100 \pm 34	13
All other items*	78 \pm 34	17	87 \pm 48	8
All others*	139 \pm 87	679	121 \pm 81	182

* Sediment bolus excluded.

B. Mann-Whitney Pairs Tests Comparing Adult and Juvenile Diets.

	Large sample z statistic	Probability of equalling or exceeding z	n
All foraminiferans	3.850	0.0001	643
Foram. tests	0.171	0.864	79
Foram. fragments	1.286	0.198	114
All other items	0.119	0.906	25
All items	2.847	0.004	861

and population LACM8, LACM accession number 68-33. Finally *Siphonodentalium quadrifissatum* was represented by those individuals from populations LACM1 and 7, LACM accession numbers 71-22 and 65-43.

Pair-wise comparisons of the indices (Tables 5-7) clearly indicate the two *Cadulus* populations are significantly different in all three indices. The northern (*C. aberrans*) individuals tapered much more gradually from the widest part of the shell to the aperture (LI was greater) (Tables 5, 6), and the aperture was relatively larger than that of southern (*C. perpusillus*) individuals (WI was greater) (Tables 5, 6). Furthermore, the median whorl expansion rates calculated from the southern populations were generally less than those calculated from the northern ones, indicating a more pronounced shell curvature (Table 6).

The indices showed that *Siphonodentalium quadrifissatum* narrowed more abruptly to the aperture than either *Cadulus* population, while the ratio of apertural width to maximum width was intermediate between the *Cadulus* populations. The rates of whorl expansion were significantly different from the northern *Cadulus* populations, but similar to those of the southern ones (Tables 5-7).

Adult northern *Cadulus* (*C. aberrans*) were longer and had a wider aperture than the southern ones (*C. perpusillus*), but the maximum width was similar. The distance to the maximum width was much greater in northern specimens than in southern ones. Specimens from the population of *Siphonodentalium quadrifissatum* were intermediate between the northern and southern *Cadulus* species

Table 4

Comparison of the buccal content foraminiferans from adult (bulging) and juvenile (non-bulging) *Cadulus aberrans* collected from population T, 48.83°N.

Foraminiferan species	Morphology						<i>t</i> -test on difference of the mean sizes	
	Adult			Juvenile				
	Eaten		Size (μm)	Eaten		Size (μm)	Value	<i>P</i>
Number	Percent	(Mean ± 1 SD)	Number	Percent	(Mean ± 1 SD)			
<i>Cribrononion lene</i>	178	35.18	111 ± 38	48	35.04	103 ± 42	1.59	0.113
<i>Florilus basispinatus</i>	126	24.90	233 ± 98	22	16.06	216 ± 100	0.83	0.831
<i>Elphidiella hannai</i>	53	10.67	211 ± 97	15	10.95	165 ± 115	1.55	0.126
<i>Buliminella exilis</i>	49	9.68	60 ± 22	17	12.41	52 ± 16	1.31	0.193
<i>Rosalina cf. columbiana</i>	32	6.32	156 ± 49	11	8.03	141 ± 49	0.84	0.403
Others	68	13.24		24	17.52			
All major species	438	86.75	157 ± 93	113	82.48	129 ± 86	2.88	0.004
Total	506	99.99		137	100.01			
Number examined	39			8				

in length, and smaller than either in the other measurements.

Thus the three population groupings differ unambiguously from one another. Furthermore, the within-pop-

ulation variance is relatively small and consistent. My examination was based on samples taken from 23.52°N to 48.83°N. Unfortunately, the samples were not evenly distributed throughout that large geographical range. None-

Table 5

Comparison of the derived indices for the determined species and outgroups. Only the adult morphologies were used in the calculation of the indices except for *Cadulus tolmiei*; see text for explanation. *t*-tests of comparison of the means for each species were calculated from all the specimens of the indicated species as determined by previous analyses. The probability of both means being independently drawn from the same population is given below the unit diagonal, the level of significance is given above it.

Index		Species					
		<i>C. aber.</i>	<i>C. per.</i>	<i>S. qua.</i>	<i>C. tol.</i>	<i>P. sal.</i>	<i>D. rec.</i>
LI	<i>Cadulus aberrans</i>						
	<i>Cadulus perpusillus</i>	—	***	***	**	***	***
	<i>Siphonodentalium</i>	<0.001	—	***	***	***	***
	<i>quadrifissatum</i>	<0.001	<0.001	—	n.s.	***	***
	<i>Cadulus tolmiei</i>	<0.001	<0.001	0.686	—	***	***
	<i>Pulsellum salishorum</i>	<0.001	<0.001	<0.001	<0.001	—	n.s.
	<i>Dentalium rectius</i>	<0.001	<0.001	<0.001	<0.001	1	—
WI	<i>Cadulus aberrans</i>						
	<i>Cadulus perpusillus</i>	—	***	n.s.	n.s.	***	***
	<i>Siphonodentalium</i>	<0.001	—	***	***	***	***
	<i>quadrifissatum</i>	0.420	<0.001	—	n.s.	***	***
	<i>Cadulus tolmiei</i>	0.105	<0.001	0.685	—	***	***
	<i>Pulsellum salishorum</i>	<0.001	<0.001	<0.001	<0.001	—	***
	<i>Dentalium rectius</i>	<0.001	<0.001	<0.001	<0.001	1	—
lnWs	<i>Cadulus aberrans</i>						
	<i>Cadulus perpusillus</i>	—	***	**	n.s.	***	***
	<i>Siphonodentalium</i>	<0.001	—	n.s.	***	***	***
	<i>quadrifissatum</i>	0.041	0.681	—	***	***	***
	<i>Cadulus tolmiei</i>	0.046	<0.001	<0.001	—	***	***
	<i>Pulsellum salishorum</i>	<0.001	<0.001	<0.001	<0.001	—	***
	<i>Dentalium rectius</i>	<0.001	<0.001	<0.001	<0.001	<0.001	—

n.s., not significant at $\alpha = 0.05$; **, significant at $\alpha = 0.05$; ***, significant at $\alpha = 0.001$.

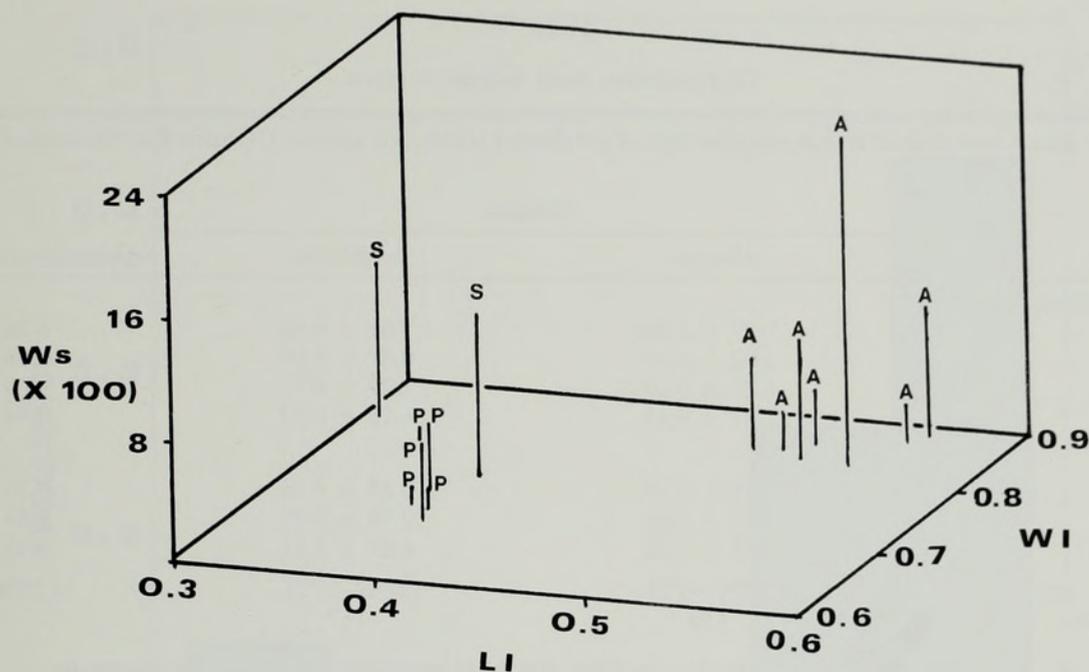


Figure 4

Population clusters generated by the LI, WI, and W indices, calculated for animals with adult morphologies. The LI and WI values used were the mean values for the populations, the Ws value was the population median. A = *Cadulus aberrans*, P = *C. perpusillus*, S = *Siphonodentalium quadrifissatum*. Compare with Tables 5-7.

theless, it is evident that the northern *Cadulus* species has a southern limit at about 28°N, while the southern one extends north to about 31°N. Consequently, there was a zone of overlap. Interestingly, the samples examined showed few signs of having individuals of both species; the estimates of variance for all measurements from populations within the bordering or overlapping areas were no greater than within the more distant ones, and there was no clear geographical pattern in the variation of the mean measurements (Table 6).

DISCUSSION

The relatively constant maximum sizes for the slender *Cadulus* and *Siphonodentalium* species indicate they have a determinate growth pattern. Apparently, once the apertural narrowing occurs, growth in length effectively ceases, although repair of fractures is possible. The large variance in the measurements of *C. tolmiei* seems (Table 7) to argue against a similar growth pattern in this species, but in fact, the pattern is likely the same; a number of juvenile *C.*

Table 6

Derived index values for adults from each of the examined populations.

Popula- tion	Latitude	n	LI		WI		Ws	
			Median	Mean (± 1 SE)	Median	Mean (± 1 SE)	Median	Mean (± 1 SE)
LACM1	23.52°	27	0.30	0.31 \pm 0.01	0.85	0.85 \pm 0.01	962	2173 \pm 570
LACM2	24.18°	10	0.40	0.39 \pm 0.01	0.68	0.69 \pm 0.01	501	1961 \pm 1328
LACM3	24.23°	4	0.37	0.37 \pm 0.02	0.76	0.73 \pm 0.06	57	58 \pm 13
LACM4	27.21°	11	0.37	0.37 \pm 0.02	0.72	0.74 \pm 0.02	419	728 \pm 210
LACM5	27.69°	9	0.39	0.40 \pm 0.03	0.73	0.71 \pm 0.03	133	862 \pm 454
LACM6	27.95°	39	0.50	0.50 \pm 0.01	0.85	0.84 \pm 0.01	269	560 \pm 136
LACM7	29°	5	0.36	0.34 \pm 0.02	0.82	0.81 \pm 0.02	57	153 \pm 69
LACM8	31.12°	133	0.39	0.38 \pm 0.00	0.77	0.77 \pm 0.00	1038	2832 \pm 449
LACM9	33°	6	0.51	0.49 \pm 0.01	0.83	0.83 \pm 0.02	593	660 \pm 192
LACM10	33.47°	2	0.56	0.56 \pm 0.05	0.89	0.89 \pm 0.03	853	853 \pm 369
LACM11	33.58°	6	0.54	0.54 \pm 0.01	0.84	0.83 \pm 0.01	2129	5659 \pm 3900
LACM12	36.63°	81	0.51	0.51 \pm 0.01	0.84	0.84 \pm 0.01	736	4186 \pm 1074
LACM13	48.41°	9	0.56	0.55 \pm 0.02	0.87	0.87 \pm 0.01	254	887 \pm 541
DS	48.43°	61	0.52	0.51 \pm 0.01	0.86	0.83 \pm 0.01	451	2533 \pm 863
T	48.83°	233	0.52	0.52 \pm 0.00	0.86	0.86 \pm 0.00	330	540 \pm 46

Table 7
Comparative shell morphometrics.

A. Mean (± 1 SD) parameters of shell morphology for each of the slender scaphopod species. Calculated on the basis of adult morphology only.

	<i>Cadulus</i>		
	<i>aberrans</i>	<i>perpusillus</i>	<i>Siphonodentalium quadrifissatum</i>
Measurements (mm)			
LTot	9.97 \pm 1.46	7.61 \pm 0.98	8.36 \pm 0.99
ApW	1.02 \pm 0.15	0.87 \pm 0.09	0.86 \pm 0.07
Wm	1.28 \pm 0.19	1.29 \pm 0.17	1.09 \pm 0.10
LWm	2.27 \pm 0.49	1.18 \pm 0.22	0.94 \pm 0.23
Indices			
LI	0.51 \pm 0.06	0.38 \pm 0.05	0.31 \pm 0.05
WI	0.85 \pm 0.06	0.76 \pm 0.05	0.84 \pm 0.04
ln(Ws)	7.08 \pm 1.23	6.67 \pm 1.57	6.55 \pm 1.51
Latitude range	28°N–49°N>	<24°N–31°N	<23°N–29°N
n examined	430	167	32

B. Comparison of the shell morphology parameters for the other species of scaphopods examined as outgroups.

	<i>Cadulus tolmiei</i>	<i>Dentalium rectius</i>	<i>Pulsellum salishorum</i>
Measurements (mm)			
LTot	7.97 \pm 2.10	27.60 \pm 8.79	7.46 \pm 1.35
ApW	1.66 \pm 0.24	2.03 \pm 0.44	1.10 \pm 0.11
Wm	1.89 \pm 0.30	=ApW	=ApW
LWm	1.33 \pm 1.31	0	0
Indices			
LI	0.29 \pm 0.28	0	0
WI	0.83 \pm 0.22	1	1
ln(Ws)	5.61 \pm 1.03*	14.86 \pm 7.00	4.63 \pm 0.99
Number examined	30	483	283

* Includes juveniles; see text.

tolmiei without the apertural narrowing were measured to increase the sample size for the index derivation. *Pulsellum salishorum* may also have a defined adult size, although this is less clear (Table 7).

For the *Dentalium* and *Pulsellum* specimens, LWm = 0, and Wm = ApW + 2(shell thickness). These values alone separate these individuals from the adult *Cadulus* specimens, although as discussed above, juvenile *Cadulus aberrans* also show the same values.

Dentalium rectius, on the other hand, obviously grows in an indeterminate manner. The large variance in the total length measurements confirms this, as does the substantial number of healed fractures at various points along the shell (unpublished observations).

The shell morphology indices used here are consistent and useful as objective measures of shape. Coupled with clustering analysis they allow the discrimination of subtle adult shell shape differences. Even the very similar morphologies of the slender Gadilida are separated. Consequently, I conclude that these measurements show the morphological limits to four species of slender gadilid scaphopods (Table 7).

Pulsellum salishorum was obviously the easiest of the northeastern Pacific Gadilida to discriminate. There was never any apertural narrowing, and the shell surface texture was decidedly different, being unpolished and similar to that of *Dentalium*.

The other gadilid species are similar in shell surface texture and general shape. Nonetheless, use of the length (LI) and width (WI) indices and the rate of whorl expansion (Ws) can adequately separate them. The length and width indices are usually significantly different among these species and show quite small within-species variances even though the populations examined might be geographically distant. The whorl expansion rate is more variable, and consequently less useful on its own as a discriminating agent. This variability is likely due to the animals' small size and the resultant measurement errors. These errors, although individually minute, are magnified in the calculation process, producing substantial index variations. Similarly, because of the calculation methods for Ws, slight variations in the initial curvature of the shell will introduce large variations in this index. Even so, use of Ws alone is sufficient to discriminate among some of the species. The

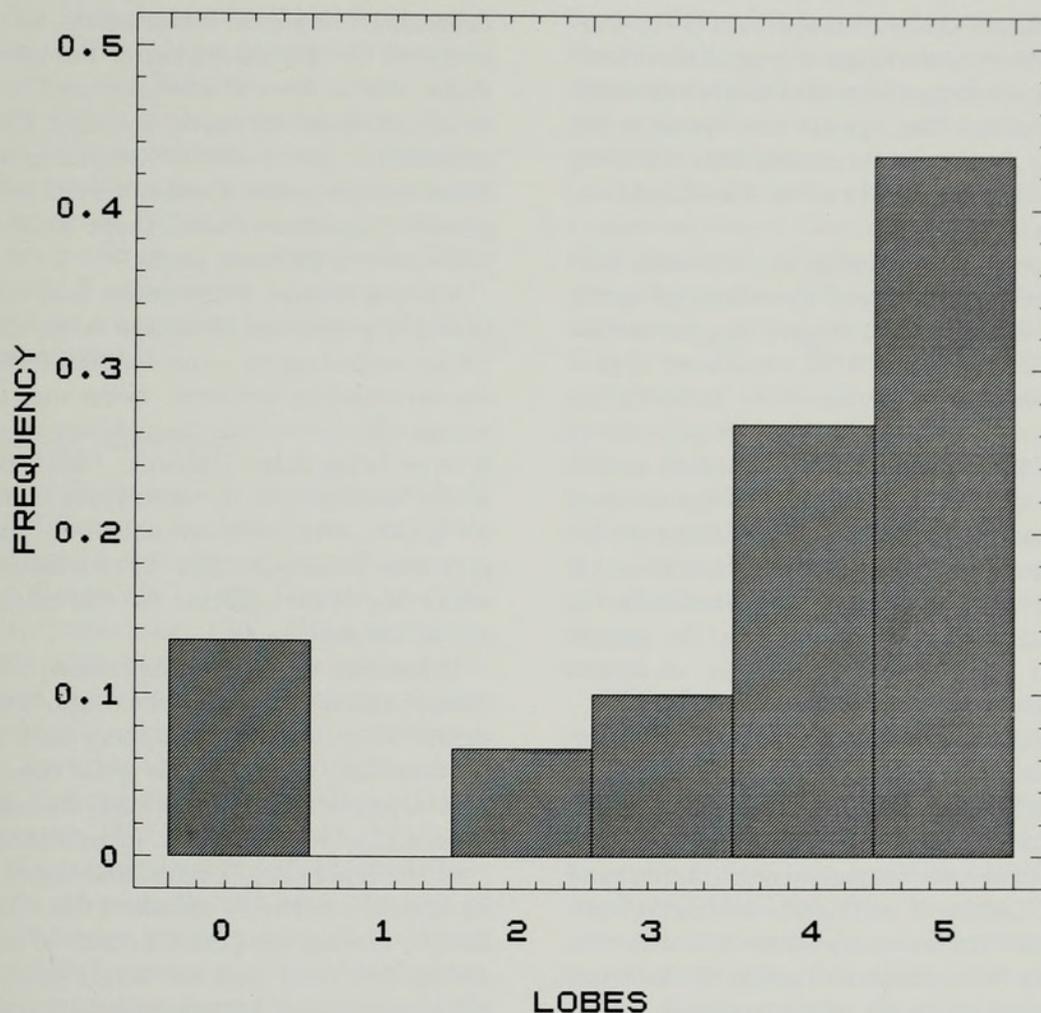


Figure 5

Cadulus tolmiei dorsal apertural lobes. $n = 30$. All specimens collected from 48.89°N, 125.05°W, 150–350 m depth.

three indices together allowed the determination of three superficially similar species of slender gadilid scaphopods from within the pool of specimens examined.

Because the measurements leading to these indices are simple, replicable, and unambiguous, the use of the indices in comparative studies can allow rapid separation of similar shell morphologies in animals such as scaphopods where only subtle shell shape differences separate distinct species. In the case of an unknown shell similar to the species examined here, the comparison of the calculated length and width indices with the ranges published here would tell whether that shell was of similar shape. Examination of the other meristic data (*i.e.*, length, width, maximal arc) would confirm or deny the existence of shape congruity. For fossils, these data might be sufficient to identify the shell. Other aspects of the biology of the living animals should certainly be examined before the identification was confirmed, but the removal of the ambiguity in the description of shell shape should certainly assist in the identification process.

The smallest of the three inferred groupings, containing those animals collected from 23.52°N and 29°N, was con-

cluded to be *Siphonodentalium quadrifissatum* (Pilsbry & Sharp, 1898). This group often showed more overlap with the southern populations of *Cadulus* than the northern ones; nevertheless, the differences in the index means were significant. Although none of the five animals from the 29°N population possessed the lobulation of the narrow aperture characteristic of this species, virtually all specimens examined from the 23.52°N population had these apertural lobes and all specimens were similar in other characteristics. The lobulation of the posterior aperture was quite variable in *Cadulus tolmiei* (Figure 5), and I suspect the lack of the lobulation in the sample from the 29°N population simply reflected the small sample size. Although I did not examine the type of *S. quadrifissatum*, the shells examined here closely match the original descriptions of that species (PILSBRY & SHARP, 1897–1898).

The other species were superficially similar in general morphology: they were small, seldom more than 13 mm long, slender, and rarely over 1.5 mm wide; they lacked lobes around the dorsal aperture, and were slightly curved. They differed, however, in the distance from the ventral aperture to the point of greatest width (LI), and in the

amount of constriction of the ventral aperture (WI). Furthermore, although there was a range of geographical overlap, the different morphologies remained distinct throughout the range of overlap. One species was found in the northeastern Pacific, and its southernmost limit was from central to southern California. The other was found from the same latitudinal area south.

This southern species is concluded to be *Cadulus perpusillus*. The general morphology of the examined specimens is similar to descriptions and photographs of that species (KEEN, 1971; EMERSON, 1971); however, a photograph of the lectotype (EMERSON, 1971) yielded measurements and indices somewhat different from those in the populations studied herein (Table 1). *Cadulus perpusillus* has a range extending substantially to the south of the populations I examined (EMERSON, 1971; KEEN, 1971), and the type is from these more southern populations. It is certainly possible that the examined specimens from the northern populations were less variable than the species as a whole, or that their measurements were skewed in some manner relative to the rest of the species.

The northern species was first described by WHITEAVES in 1887, from specimens collected in Quatsino Sound on the northwestern edge of Vancouver Island (Table 1). Several other similar nominal species were subsequently described. Examination and measurement of the types of *Cadulus fusiformis*, *C. hepburni*, and *C. nitentior* show, however, that these species are junior synonyms of *C. aberrans*. The analyses herein show conclusively that *C. fusiformis* has a shell morphology consistent with *C. aberrans*, and is thus a junior synonym of that species (Table 1). The similar close correspondence in the shapes for the type specimens also shows that *C. hepburni* is also a junior synonym and confirms the opinion (GRANT & GALE, 1931) that *C. nitentior* is too (Table 1).

Interestingly, none of the described types is a "typical" *Cadulus aberrans*, if "typical" is defined as having the average characteristics of the species. The indices derived from measurements of all of the types are displaced substantially from the centers of the distributions of any of the indices. Nonetheless, they are clearly within the range of variation of those species.

The indices also differentiated more distinctly different *Cadulus* species, for example, *C. tolmiei*. Although the variances around the index means were greater for this species than those around the means for any of the slender species, the indices together still served to delimit them all (Table 7). Insignificant differences among the various parameters point out some hitherto undiscerned correspondences in shape, however, such as the relative degree of aperture narrowing that is similar in *C. tolmiei* and *Siphonodentalium*.

Functionality of Shape

All *Cadulus* are narrower around the ventral aperture than around the middle portion of the shell. Indeed, this characteristic is the major morphological shell character

delimiting this genus. Nevertheless, no function has been proposed for the narrowing of the aperture. This study shows that at least *C. aberrans* (and *C. tolmiei*) juveniles do not have the narrowed aperture. Consequently, these animals are clearly able to live and grow having two different morphologies. Indeed, a strict interpretation of the generic characters of shell shape alone would assign the juveniles to a different genus.

Natural history observations may allow the determination of a selective advantage to the narrowed aperture. These animals prey upon foraminiferans collected from the surrounding sediment. Items that may be eaten are brought into the mantle cavity where they are manipulated prior to being eaten (SHIMEK, 1988). Both juveniles and adults, however, eat the same types of prey. Furthermore, the adults, even with the narrowed aperture, eat larger prey than do the juveniles. Thus it seems unlikely that the narrowing of the aperture has any relation to the kind or size of the prey eaten.

In addition to narrowed apertures, all live, and recently dead, *Cadulus* that I examined also had highly polished shells. They were very slippery and difficult to grasp. Furthermore, *C. aberrans* is quite capable of rapid locomotion (up to 1 cm/sec) through the sediment in which it is normally found (Shimek, unpublished observations).

In the laboratory, I have maintained *Cadulus aberrans* for several months in sediment taken from their natural habitat. During this period I observed them regularly, and seldom saw them with the dorsal aperture extended into the water column. In many cases I watched them through the sides of their glass or transparent plastic containers. Contrary to the information normally given about scaphopods, these animals seldom got closer to the surface than 6–8 cm and were commonly found buried as deeply as 30 cm. During reproduction, however, they must be close enough to the surface to be able to liberate their gametes directly into the water. During this period, sexually mature adult *C. aberrans* would be subject to predation by epibenthic predators.

Although I lack direct evidence, I suspect that adult *Cadulus aberrans* individuals with a narrowed aperture can burrow faster than juveniles of the same length. I suggest that the narrowing of the aperture of *Cadulus* species has evolved, together with the highly polished shell, in part to permit rapid, efficient, burrowing to escape predation. As a corollary to this, it follows that juveniles would tend to be found deeper in the sediments than the adults, which would account for their relative rarity in collections. The highly polished shell may also make it difficult for a predator to seize a *Cadulus* individual.

Dentalium rectius and *Pulsellum salishorum* are often sympatric with *Cadulus aberrans* or *C. tolmiei*, and both of the former species often show healed shell fractures (Shimek, unpublished data), presumably caused by attempted predation. Such healed fractures are rare on *C. aberrans*, indicating little unsuccessful predation, and perhaps indicating success by the scaphopod at escaping predation.

In the Barkley Sound region, the major predators on

scaphopods are ratfish, *Hydrolagus colliei* (Shimek, in prep.). During examination of *H. colliei* gut contents I commonly found *Dentalium rectius* and *Pulsellum salishorum*, while *Cadulus* species were seldom noted, even though the fishes were collected from habitats where *Cadulus* is common. Similarly, longsnout pricklebacks, *Lumpenella longirostra*, which live below depths of 250 m in some soft-sediment Alaskan habitats, are predators on small mollusks. Their guts often contain only *P. salishorum* even though both *P. salishorum* and *C. tolmiei* are common in those areas (Baxter, personal communication).

Shell Character Sets in Scaphopods

Species and generic determinations in scaphopods have been dominated by differences in shell shapes with little or secondary regard to the morphology of the body secreting the shell (PILSBRY & SHARP, 1897–1898; LUDBROOK, 1960; HABE, 1963, 1964; SHIMANSKY, 1963; STAROBOGATOV, 1974; PALMER, 1974; CHISTIKOV, 1975; EMERSON, 1952, 1962, 1978). In some cases, these shell characters appear to have been applied arbitrarily, without any consideration of variability, and have been used to erect higher-level systematic groupings that therefore may be spurious (DALL, 1897; PILSBRY & SHARP, 1897–1898; CARTER, 1983).

The reasons for the uncritical use of variable shell characters in scaphopods are probably related to the lack of easily defined shell character sets within the class. At first glance, the scaphopod shell seems featureless, and the need to discriminate between perceived species has fostered the use of minute, subjective, and variable shell characters. This study indicates that quantification and manipulation of only a few measurements can be used to assess variability and accurately determine similar shell shapes. Thus the use of variable characters is unnecessary; in effect, the shell is not as featureless as it may seem.

Additionally, the lack of population and ecological information has contributed to the use of characters that are simply either expressions of variability within the population or phenotypic responses to ecological events. For example, *Dentalium rectius* collected from Barkley Sound often has the tip of the dorsal aperture broken off. This occurs as the result of breakage or attempted predation by the ratfish, *Hydrolagus colliei*, which nips the tip off (if it does not eat the whole animal). As a result, during subsequent shell repair, a secondary tube is secreted from the dorsal aperture. This tube is effectively identical with those illustrated by EMERSON (1962) and PALMER (1974) as a character for the genus *Episiphon* Pilsbry & Sharp, 1897, although EMERSON (1962) also illustrates several other genera with a similar tube. The growth of this tube in *D. rectius* is rapid; I have measured tubes of 10 mm or more in length secreted by an adult within 2–3 weeks in the laboratory. This particular morphology, at least within *D. rectius*, indicates nothing other than shell repair. I suggest that similar morphologies in other species indicate similar processes of either shell repair or growth. Unless these changes in shape can be shown to be correlated with dif-

ferences in internal morphology distinct from other populations lacking the morphological attribute in question, they certainly should not be used for generic discrimination, although they may be useful as indicators of potential predation pressure.

The lobation of the dorsal aperture also deserves particular mention as it has been used as the primary character to discriminate subgeneric (or, more recently, generic) groupings within *Cadulus* Philippi, 1844 (PALMER, 1974; SCARABINO, 1979; CARTER, 1983). The data presented on *C. tolmiei* (Figure 5) clearly show this character to be variable within a single well-defined population of a geographically widespread species. The genera *Polyschides* Pilsbry & Sharp, 1898, and *Platyschides* Henderson, 1920, have been defined, in part, on the basis of the number of slits between the lobes and their relative depth even though the latter likely depends upon relative growth rates. Without addressing the variability, both within and between species, uncritical acceptance of these genera is not warranted.

Critical examination of the variability of shell characters may validate existing subgeneric groupings as well. These slender *Cadulus* can be or have been placed in the subgenus *Gadila* Gray, 1847. If examination of other aspects of the anatomy indicates that this is a natural group distinct from the more typical *Cadulus*, then generic status would be warranted. Until that time it seems prudent to maintain these species within *Cadulus*. Interestingly, given the ambiguity concerning the validity of *Polyschides* and *Platyschides*, *Gadila* may be the only presently named valid subgeneric unit in *Cadulus*. Elaboration of these indices might present a way to subdivide critically this genus on the basis of shell shape; corroborative studies of the other aspects of the anatomy could then be used to confirm these subdivisions.

One major reason for the subdivision of *Cadulus* into several genera seems to be the impression that a large genus is somehow unwieldy and not useful (PALMER, 1974). On the contrary, if a given morphology is successful and becomes widespread, then maintaining similar, and obviously closely related, species of common descent together in one natural genus allows a reasonable evaluation of the factors contributing to the success of that body plan. Examination of closely related, similar morphologies has been used to advantage within many of the larger genera of mollusks, i.e., *Buccinum*, *Conus*, *Macoma*, *Murex*, *Octopus*, *Oenopota*, and *Terebra*, and certainly could be used within this relatively small class.

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