Revision of the species of *Ridgeia* from northeast Pacific hydrothermal vents, with a redescription of *Ridgeia piscesae* Jones (Pogonophora: Obturata = Vestimentifera)

Eve C. Southward, Verena Tunnicliffe, and Michael Black

Abstract: Examination of vestimentiferan worms attributed to the genus *Ridgeia* from more than 50 vent sites in the northeast Pacific indicates that only one species is present. We amalgamate *Ridgeia piscesae* Jones and *R. phaeophiale* Jones under the name *R. piscesae* and include other forms previously suspected to be different species. Allozyme evidence supports the hypothesis that the populations belong to a highly plastic phenotype. The distance data indicate no substantial genetic differences among populations along Juan de Fuca Ridge and across a transform fault to the northern Gorda Ridge. Morphological data indicate that the original distinction of two species on the basis of obturacular saucer number and tube colour was based on the extremes of a continuum of characteristics that relate to animal size, levels of predation, and probably vent fluid conditions. The intriguing effect of habitat on phenotype in this abundant vent animal requires further investigation now that the taxonomy is better understood.

Résumé : L'examen des populations de vestimentifères appartenant au genre *Ridgeia* sur plus de 50 sites hydrothermaux de la dorsale du Pacifique nord-est a révélé la présence d'une seule espèce. Nous avons redécrit les espèces *Ridgeia piscesae* et *Ridgeia phaeophiale* Jones, ainsi que plusieurs formes qui pouvaient être morphologiquement considérées comme des espèces différentes, sous le nom de *R. piscesae*. L'étude du polymorphisme enzymatique appuie l'hypothèse d'une forte plasticité phénotypique chez les individus des populations étudiées. Les distances génétiques calculées ne montrent pas de différences significatives entre les populations, qu'elles soient distribuées le long de la ride de Juan de Fuca ou séparées par une faille transformante sur la ride de Gorda. Le nombre de collerettes de l'obturaculum et la couleur du tube, qui auparavant avaient servi à l'identification des 2 espèces, correspondent en fait aux extrêmes d'un continuum de caractéristiques morphologiques vraisemblablement associé à la taille de l'animal, aux taux de prédation et aux caractéristiques du fluide hydrothermal. L'effet probable de l'habitat sur le phénotype de cette espèce très abondante nécessite maintenant de nouvelles études, la taxonomie de ce complexe étant aujourd'hui mieux connue.

Introduction

Abundant vestimentiferan tube worms often dominate mature assemblages at hydrothermal vents in the eastern Pacific. Symbiosis with chemoautotrophic bacteria appears to sponsor this large biomass. The genera *Riftia*, *Tevnia*, *Oasisia*, and *Ridgeia* are described from these vents (Jones 1985), but only the last occurs on the Juan de Fuca Ridge area of the northeast Pacific (Fig. 1). Dense clusters of *Ridgeia* spp. tubes over 1 m long may cover large areas of basalt around sulphide-rich waters, while clumps of small tubes grow on high-temperature chimneys. *Ridgeia* spp. clumps provide substratum and shelter to numerous smaller organisms.

When Jones (1985) described the genus *Ridgeia* and two species, *R. piscesae* and *R. phaeophiale*, he noted that two additional species might be present in the material at hand. The existence of three other species of *Ridgeia* at Juan de Fuca and Explorer Ridge vents was suggested by de Burgh (1986), Tunnicliffe and Fontaine (1987), and Tunnicliffe (1988, 1991). According to Jones (1985, p. 154), "The two species of *Ridgeia* may be differentiated on the basis of the nature and number of saucer-like structures on the obturacular face and on the nature of the tubes; in *Ridgeia piscesae* there are one or two transparent/translucent-white saucers and the tubes are transparent/translucent-white and flexible; in *Ridgeia phaeophiale* there are up to 11 brown/golden saucer-like structures and the tubes are transparent brown and brittle." Table 1 presents the characteristics of the two species as derived from Jones' (1985) descriptions. His collections came from three Juan de Fuca Ridge sites in the early 1980s.

Subsequently, many sites on these ridges have yielded

Received June 29, 1994. Accepted October 12, 1994.

E.C. Southward. Marine Biological Association, Citadel Hill, Plymouth PL1 2PB, United Kingdom.
V. Tunnicliffe and M. Black.[1] Department of Biology, University of Victoria, Victoria, BC V8W 2Y2, Canada.

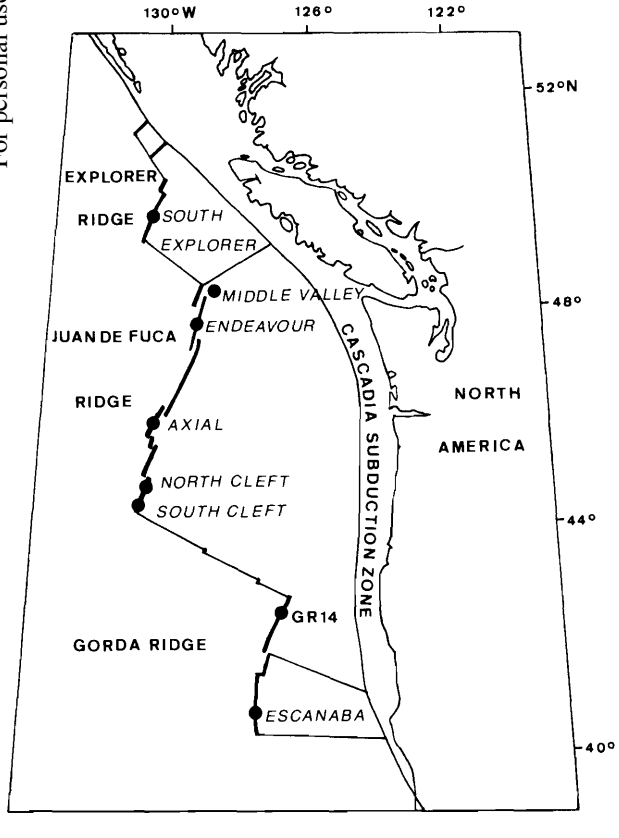
[1] Present address: Center for Theoretical and Applied Genetics, Cook College, Rutgers University, New Brunswick, NJ 08903-0231, U.S.A.

Table 1. Characters presented by Jones (1985) in his diagnoses of two vestimentiferan species of the genus *Ridgeia*.

Character	*Ridgeia piscesae*	*Ridgeia phaeophiale*
Tube		
Nature*	Transparent/translucent-white, flexible	Brown, brittle
Anterior diameter (mm)	3.5–11 (mean 8.1)	2–5 (mean 2.8)
Length (mm)	323+ to 1511	18+ to 151
Obturaculum		
Saucer number*	1 or 2	Up to 11
Saucer colour*	Transparent to whitish	Brown/golden
Number of lamellae	Up to 35 pairs	Up to 31 pairs
Filaments lacking pinnules	Up to 11 dorsal	3 dorsal and 3 ventral
Dorsal groove	Broad	Narrow
Length (mm)	14.7–41.2	3.0–17.0
Vestimentum		
Anterior margin	Short	Longer; sheath around obturaculum base
Length (mm)	12.3–36.0	3.1–13.0
Trunk		
Length (mm)	205–1376	11.0–58.5
Opisthosome		
Number of segments	Up to 62	Up to 29
Length (mm)	5.2–26.0	1.6–2.0

*Character stated by Jones (1985) to be diagnostic of the species.

Fig. 1. Location of hydrothermal vent fields where *Ridgeia* spp. populations are known. Specimens from all indicated sites were examined but material for allozyme analysis was not available from the South Explorer or Escanaba sites.



collections of *Ridgeia* showing a wide range of tube form and saucer number. We have each experienced difficulty in classifying these specimens, in both distinguishing the described species and attempting to diagnose new species using the characters defined by Jones (1985). The problem lies in the apparent morphological variation and in the lack of distinct species-specific characters. Accordingly, a study of allozyme variation was initiated to aid in species distinction. When it became clear that these genetic characters did not support the presence of more than one species, we examined both original and recent collections to determine the range of variation present and to redefine the species. The original type collections, fixed in formalin, were unsuitable for allozyme study; thus, the allozyme collections were reassessed for specimens attributable on the basis of morphology and locality to *R. piscesae* and *R. phaeophiale* as defined by Jones (1985).

These animals have been the subject of numerous studies, including studies of their reproduction and development (Jones and Gardiner 1988, 1989; Southward 1988; Southward and Coates 1989; Gardiner and Jones 1993), symbiotic bacteria (de Burgh 1986; de Burgh et al. 1989), biochemistry (De Bevoise and Taghon 1988; A.J. Southward 1991; Southward et al. 1994), behaviour (Tunnicliffe et al. 1990), and phylogeny (Williams et al. 1993). It appears important to establish the identity of the study organism. This study presents the basis on which we recommend amalgamation of the described and putative *Ridgeia* species. We document the range in variation for two reasons. First, future workers should have a better basis on which to decide the taxonomic status of further collections. Second, such a range of phenotypes is intriguing for what it may mean in terms of response to the habitat.

Methods

Material examined

A. Type specimens of *Ridgeia piscesae* and *R. phaeophiale* from the National Museum of Natural History,

Table 2. Number of collections and sample sizes of *Ridgeia* types used in allozyme analyses.

Site	Worm types present	Number of collections	Sample sizes
Middle Valley	*R. piscesae*	2	35, 35
Endeavour Segment	*R. piscesae*	2	40, 32
	R. phaeophiale	2	34, 35
Axial Seamount	*R. piscesae*	3	38, 35, 35
	R. phaeophiale	5	35, 35, 35, 35, 35
	Small type	3	25, 26, 26
	Taper type	1	35
Cleft Segment	*R. piscesae*	8	32, 20, 31, 9, 18, 22, 35, 35
	Small type	2	27, 33
	Taper type	3	26, 35, 21
	Fat type	2	40, 35

NOTE: University of Victoria collection number designations can be found in Black (1991). The "types" are descriptors we had assigned in anticipation of taxonomic descriptions.

Washington (USNM) (Jones 1985): holotype and two paratypes of each species as follows.

Ridgeia piscesae Jones 1985: Holotype: USNM 098105, from Shepherd's Vent, Axial Seamount, Juan de Fuca Ridge, 45°59′30″N, 130°03′30″W, 1599 m depth, Aug. 10, 1983, dive P1322.
R. piscesae: Paratype: USNM 098107, from Shepherd's Vent, dive P1322.
R. piscesae: Paratype: USNM 098110, Axial Seamount, Juan de Fuca Ridge, 45°56′N, 130°01′W, 1546 m depth, July 18, 1984, dive A1413.
Ridgeia phaeophiale: Holotype: USNM 098111, Endeavour Segment, Juan de Fuca Ridge, 47°57′N, 129°06′W, 2120–2090 m depth, Oct. 7, 1982, dredged by the RV *T.G. Thompson*.
R. phaeophiale: Paratype: USNM 098121, from Lamphere Chimney, Axial Seamount, Juan de Fuca Ridge, 45°59′30″N, 130°03′30″W, 1599 m depth, Aug. 10, 1983, dive P1322.
R. phaeophiale: Paratype: USNM 98122, Southern Segment, Juan de Fuca Ridge, 45°13′N, 130°09′W, 2380 m depth, July 15, 1984, dive A1410.

B. Frozen specimens used for electrophoresis were collected from Juan de Fuca Ridge in 1986, 1988, and 1990 (Table 2). Thirty-three collections came from four spreading segments of the ridge. See Black (1991) for collection location detail.

C. Preserved samples of *Ridgeia* spp. are at the University of Victoria. Southern Explorer Ridge (5 vents); Juan de Fuca Ridge: Middle Valley (2 vents), Axial Seamount (17 vents), Endeavour Segment (8 vents), and Cleft Segment (20 vents); Gorda Ridge: Escanaba Trough (2 vents). The depth range is about 1550–2400 m and latitudinal range is 49°46′–51°00′N (Fig. 1).

D. A selection from C of *Ridgeia* spp. from type localities: (*i*) that of *R. piscesae* holotype: Shepherd's Vent on Axial Seamount on Aug. 10, 1983, dive P1322, 45°59′30″N, 130°03′30″W; (*ii*) that of *R. piscesae* paratypes (near Shepherd's Vent): Taylor's Vent on Axial Seamount, collected Aug. 17, 1983, dive P1327; (*iii*) source of *R. phaeophiale* holotype: tubes dredged on Endeavour Segment, October 1982, sample 66D-153, 47°57′N, 129°05′W; and (*iv*) *R. phaeophiale* dredged near location of previous sample, October 1982, sample C58-123, 47°57′N, 129°05′W. All samples are presently stored at the University of Victoria (UVic).

Sample collection and preservation

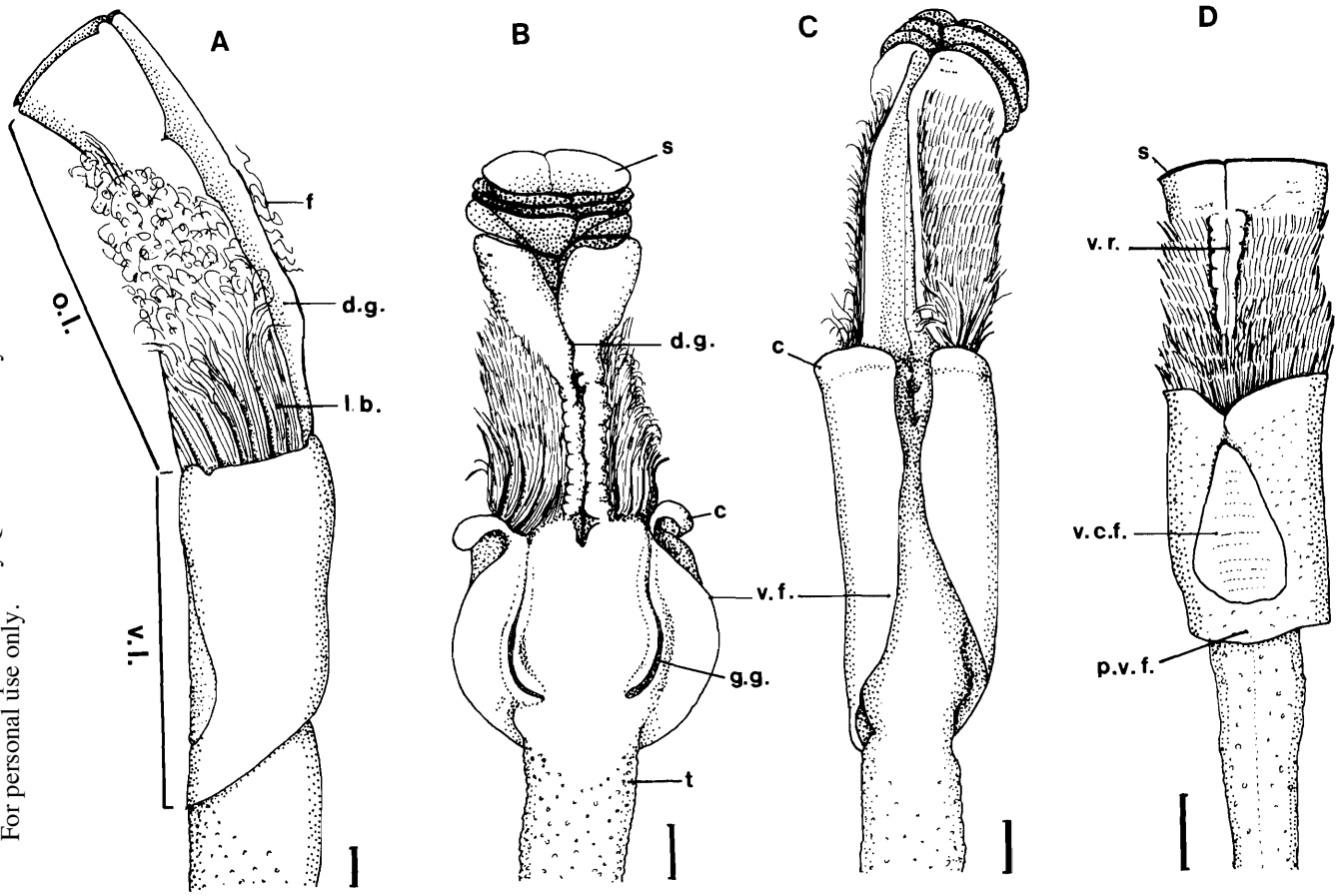
Most populations sampled were seen by one of the authors either in situ or in photographs. Descriptive notes on appearance or "type designation" were taken. The first recovery was made by dredging from the RV *T.G. Thompson*. Subsequent samples were collected by manipulator arms on the manned submersibles *Pisces IV* and *Alvin* and a few by the remote vehicle *Ropos*. Preserved specimens were placed in 10% formalin in seawater after preliminary sorting at sea (they were later transferred to 5–7% formalin). Selected small specimens were fixed in 2.5% glutaraldehyde in seawater. On land, collections were sorted and stored according to a unique collection number with site information. Material for electrophoresis was frozen as soon as possible in a −80°C freezer.

Preparation for enzyme electrophoresis

Sample sizes used for electrophoresis varied between 20 and 40 worms per collection (Table 2), for a total of 1025 individuals. Each specimen was assayed for the full suite of presumptive loci used. Individual animals were thawed in distilled water on an iceboat and obturaculum, vestimentum, and ventral ciliated field lengths were measured; obturacular saucers and opisthosomal segments were counted. The symbiont-containing trunk was removed. No tissue-specific allozyme activity was detected, so obturaculum (minus saucers) and vestimentum were combined. Specimens were ground by hand with glass pestles in a buffer of 0.05 M Tris and 20% v/v glycerol adjusted to pH 8.0 with NaOH.

Allozyme variation was assayed by standard horizontal starch gel electrophoresis, adapted from McDonald (1985), Pasteur et al. (1987), and Murphy et al. (1990). Buffer and enzyme stain recipes were adapted from these authors plus Shaw and Prasad (1970), Harris and Hopkinson (1977), and

Fig. 2. *Ridgeia piscesae*, anterior end. (A) Side view of a specimen from Shepherd's Vent (collection taken on dive P1322), showing the regions measured. (B) Dorsal view of a specimen fixed out of the tube (Endeavour Segment, A1451). (C) Dorsal view of a specimen fixed inside the tube, from same sample (A1451). (D) Ventral side of a smaller specimen from the same sample (A1451). *c*, collar; *d.g.*, dorsal groove of obturaculum; *f*, branchial filament; *g.g.*, genital groove; *l.b.*, lamella base; *o.l.*, obturaculum length; *p.v.f.*, posterior vestimental fold; *s*, saucer; *t*, trunk; *v.c.f.*, ventral ciliated field; *v.f.*, vestimental fold; *v.l.*, vestimentum length; *v.r.*, ventral ridge of obturaculum. Scale bars = 1 mm.



Aebersold et al. (1987). Full details on electrophoresis and staining conditions are available in Black (1991). Allele frequencies were computed from individual genotypes using distance measures generated by the BIOSYS-1 program (release 1.7; Swofford and Selander 1989) and GENESTAT-PC (Lewis and Whitkus 1989).

Tube and animal characters

For selected collections, tube observations included total length, anterior diameter, size and spacing of the collars (funnels circling tube), colour, and rigidity.

The vestimentiferan body comprises four regions: obturaculum with branchial filaments, vestimentum, trunk, and opisthosome (Figs. 2 and 3). Obturacular shape, number of terminal saucers, and relative lengths of obturaculum and vestimentum have been used in species discrimination (van der Land and Nørrevang 1977); part of the trunk and the attached opisthosome are often missing. On the animal body, the following length measurements were made on frozen specimens: obturaculum, dorsal vestimental region, and opisthosome when present. Obturacular saucers and opisthosome segments were counted. For preserved specimens the diameter of the obturaculum and of the vestimental region were also measured. For selected specimens, dissections of the branchial plume to separate lamellae allowed examination of branchial filaments.

Microscopy

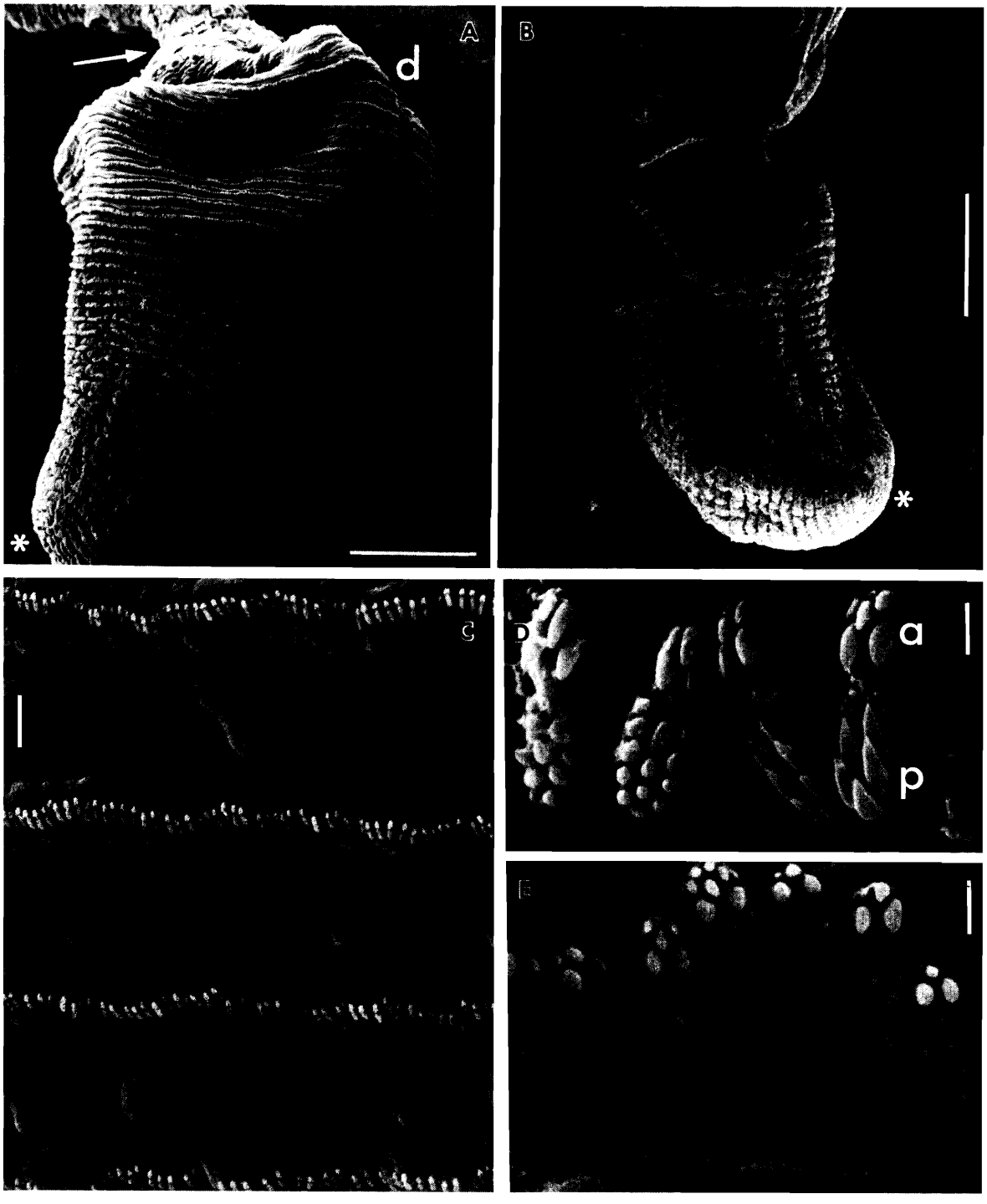
Small glutaraldehyde-fixed specimens were washed, post-fixed in 1–2% osmium tetroxide in seawater, dehydrated in an ethanol series, and embedded in Spurr's resin. Sections 0.5–1.0 μm thick were stained with toluidine blue for light microscopy and thin sections were stained with uranyl acetate and lead citrate for examination with a Philips 300 transmission electron microscope. Whole juveniles and the opisthosomes of adults were chosen from formalin- and glutaraldehyde-fixed material, washed with distilled water, critical-point dried, mounted on stubs, and coated with gold. Scanning electron micrographs were taken to show the outer surface and setae (uncini).

Results

Allozyme interpretation

Eleven enzymes yielding 15 presumptive gene loci could be confidently resolved. These enzymes were as follows (the enzyme nomenclature number is given in parentheses): L-lactate dehydrogenase (1.1.1.27), malate dehydrogenase

Fig. 3. Scanning electron micrographs of opisthosomes of *Ridgeia piscesae*. (A) Left side of a specimen from A1451 with 27 setigerous and at least 12 non-setigerous segments. (B) Ventral view of a specimen with about 14 setigerous and 15 non-setigerous segments (P1732). (C) A typical arrangement of setae (P1732). (D and E) Face view of setae (D, P1322; E, P1732) with 3–9 teeth in the anterior group (*a*) and three rows of 3 or 4 teeth (occasionally two rows) in the posterior group (*p*). *d*, mid-dorsal line; the asterisk indicates the growing region of the opisthosoma and the arrow the posterior end of the trunk. Scale bars: 100 μm for A; 250 μm for B; 20 μm for C; 2 μm for D and E.



(1.1.1.37), isocitrate dehydrogenase (1.1.1.42), aspartate aminotransferase (2.6.1.1), esterase (3.1.1.–, resolved with 4-methylumbelliferyl acetate), leucine amino peptidase (3.4.11.1), fructose(bis)phosphate aldolase (4.1.2.13), fumarate hydratase (4.2.1.2), triose-phosphate isomerase (5.3.1.1), mannose-6-phosphate isomerase (5.3.1.8), and glucose-6-phosphate isomerase (5.3.1.9).

Five loci were fixed for the same allele in all populations.

Table 3. Comparisons by geographical region and morphotype.
(A) Major collection sites.

	Middle Valley	Endeavour Segment	Axial Seamount	Cleft Segment
Middle Valley	—	0.9702	0.9644	0.9693
Endeavour Segment	0.0302	—	0.9992	0.9997
Axial Seamount	0.0363	0.0008	—	0.9996
Cleft Segment	0.0312	0.0003	0.0004	—

(B) *Ridgeia* types and putative species.

	Ridgeia piscesae	*Ridgeia phaeophiale*	Small type	Taper type	Fat type
R. piscesae	—	0.9994	0.9998	0.9984	0.9947
R. phaeophiale	0.0006	—	0.9994	0.9990	0.9904
Small type	0.0002	0.0006	—	0.9981	0.9948
Taper type	0.0016	0.0010	0.0019	—	0.9892
Fat type	0.0053	0.0097	0.0053	0.0109	—

NOTE: Nei's unbiased genetic identity (I) values are above the diagonal and genetic distance (*D*) values below the diagonal.

Standard χ^2 analysis indicated that the majority of loci met expectations of Hardy–Weinberg equilibrium; all deviations from these were as heterozygote deficiencies. Overall levels of genetic variation were high; observed heterozygosity ranged from a low of 0.073 to a high of 0.185. Mean observed heterozygosity was 0.116 (SE 0.031) and 46.7% of alleles were polymorphic ($P > 0.95$). A few individuals of two other vestimentiferan genera were run to ensure that the system could distinguish between distinct species. Specimens of the genera *Riftia* and *Tevnia* (each currently placed in families different from *Ridgeia*) each revealed different diagnostic allozymes at four loci present in *Ridgeia*. In general, the current established genera of vestimentiferans are readily differentiated by allozymes (Trivedi et al. 1994; M.B. Black, unpublished data). Controls were run to ensure that contamination by symbiont tissue had not compromised interpretation of allozyme patterns.

Unbiased measures of genetic identity (*I*) and distance (*D*) (Nei 1972, 1978) were used to compare collections, morphotypes, and sites. Among the 33 collections *D* values ranged from 0.000 to 0.088. One collection ("fat type") from the southernmost site and the two northernmost collections ("*piscesae*" type) were most distinct; otherwise, *D* values were below 0.025. Table 3 presents values computed with collections grouped by geographic region and by morphotype. Only one sample a fat type from Cleft Segment, diverged slightly from the rest: comparison with P1722 (*piscesae*) gave a *D* value of 0.035 and comparison with P1726 (*phaeophiale*) gave a *D* value of 0.058. Neither value indicates any basis for a formal taxonomic distinction between the morphotypes.

Ridgeia piscesae and *R. phaeophiale* in material used for allozyme analysis

We reexamined the preserved counterpart of collections used in the above allozyme study. To be able to say conclusively that genetic analysis did not distinguish between the two published species, those putative species must be present in the collections used. While the holotype collections could not be used, subsequent samples did come from the same vent fields as Jones' (1985) paratypes for both species.

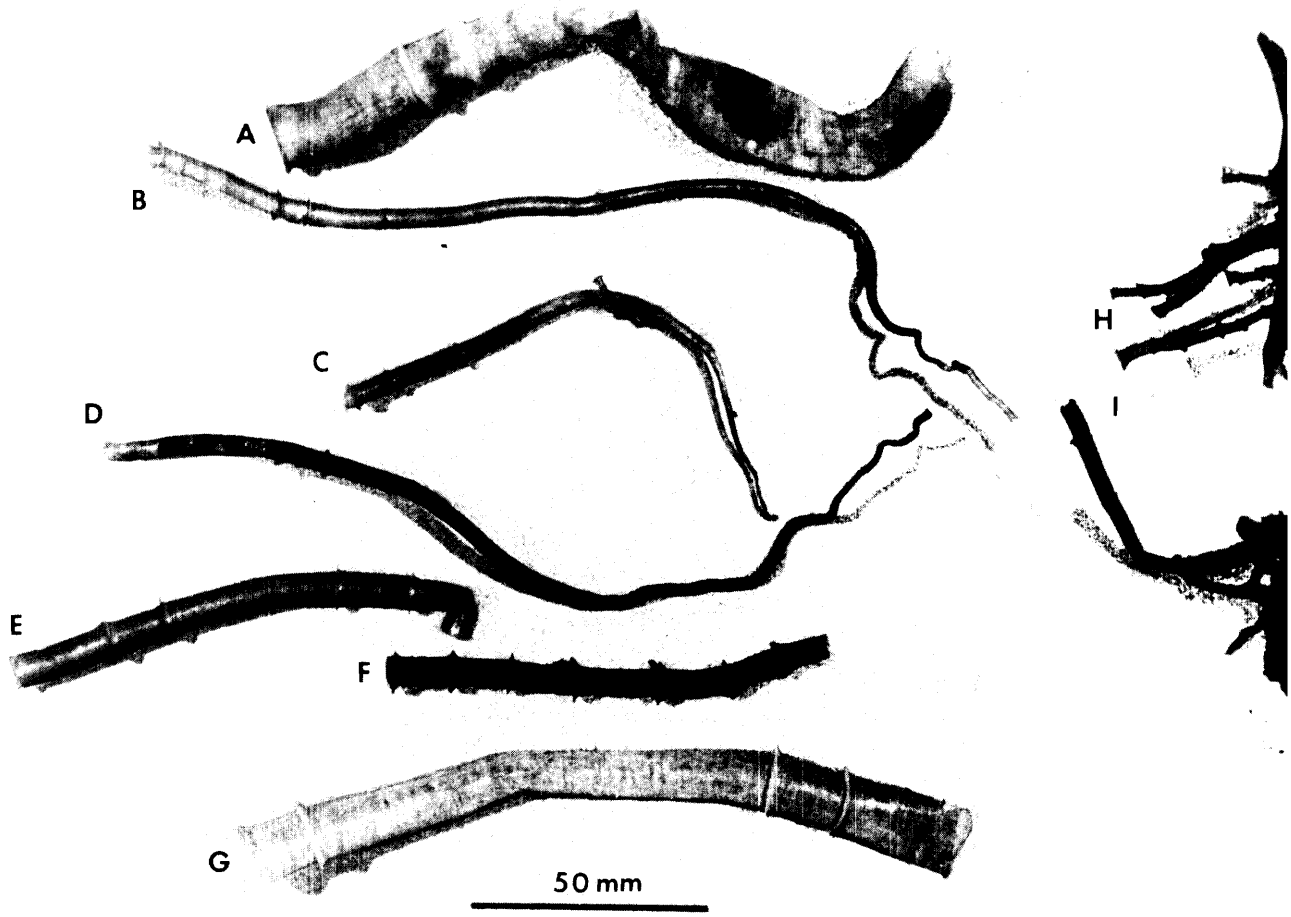
Tubes from collection P1722 (Mushroom Vent, Axial Seamount, 45°55′N, 130°03′W, July 18, 1986) matched the tube form of *R. piscesae* Jones type material from Axial Seamount. Forty specimens from P1722 were used for electrophoresis: their obturacular saucers ranged from 0 to 5 in number, only 2 specimens having more than 2 saucers. We consider this sample to be typical *R. piscesae* Jones.

Selection of a typical sample of *R. phaeophiale* from the electrophoresis collections was more difficult because of variation among the holotype and paratypes (Jones 1985). Two samples were chosen, both from Axial Seamount: P1726 Southern Area vent, 45°55′N, 130°03′W, July 27, 1986, and A2089, Hell Vent, 45°58′N, 130°03′W, Aug. 17, 1988. Both contain brownish tubes similar to some designated *R. phaeophiale* by Jones (1985). The numbers of saucers on the electrophoresis specimens were as follows: P1726 (40 specimens), range 0 (4 specimens) to 8, (21 had 3 or more); A2089 (40 specimens), range 0 (4) to 7 (24 had 3 or more). These specimens fall within the range of *R. phaeophiale* Jones. For these species "types," Nei's genetic distances (*D*) were 0.006 for P1722 (*piscesae*) compared with P1726 (*phaeophiale*) and 0.007 for P1726 (*phaeophiale*) compared with A2089 (*phaeophiale*).

Field observations

Among us, we have visited eight vent fields on Juan de Fuca Ridge; each apparently with a discrete hot water source. The *R. piscesae* type occurred at warmer vents with higher flux of clear water. (for the paratype locality see the cover of Nature, Vol. 313, No. 5999, 1985). These flexible tubes seemed to support each other in a dense mass. The *R. phaeophiale* type was common where flowing water was not evident and temperatures were low (see Fig. 2A in Normark et al. 1982). Tubes are supine or mineral accumulations give them enough stiffness to remain semi-erect. On chimneys where flow is often highly directed, the small type is most

Fig. 4. *Ridgeia piscesae* tubes of different types; for large tubes the top portion only is shown. (A) Fat, yellowish, soft (Cleft Segment, A1461). (B) Whitish, tapering (Axial Seamount, P1730). (C) Small, pale brown (Endeavour Segment, A1452). (D) Black at the base, yellow–brown at the top (Coaxial Segment, A2681). (E) *Ridgeia phaeophiale* type, brown, long sections (Axial Seamount, P1322). (F) *Ridgeia phaeophiale* type, brown, wide funnels, short sections (Endeavour Segment, A1451). (G) *Ridgeia piscesae* type, whitish, soft (Axial Seamount, P1322). (H) Small form of *R. phaeophiale* type (see F). (I) Small gold–black type (Axial Seamount, P1731).



common (see Tunnicliffe 1991, p. 337). Clumps of worms grow close to the chimney surface.

Tube

There is a remarkable variety of shapes, colours, and sizes of tubes among *Ridgeia* spp. collections. In the field, numerous colony and tube forms were seen: sparse groups formed long, straight, and low tubes, small clumps around limited vent flows comprised sinuous, intertwined tubes, while vigorous flow was colonized by dense mounds of upright tubes. Figure 4 illustrates some of the variety in collected forms. While Jones (1985) reports species distinctions in colour and rigidity of tubes, he did not have the benefit of collections from many habitats. We record these colours: translucent-white, gold, brown, grey, and black. Rigidity varies from the consistency of wet paper to very hard and brittle. Mixed-type collections were very rare but changes along tubes occur in some collections. For instance, the tube may change from a golden hard surface at the base to a whitish soft surface near the top. Genital grooves indicative of mature adults were seen on animals in tubes as small as 3 mm in diameter. The occurrence of tube collars appears to be highly variable and of little use as a specific character. Tests of collar frequency along tubes in the Shepherd's Vent type collection revealed no significant correlations within or among tubes.

Obturacular saucers

Saucers (Fig. 5) are hardened cuticular structures formed on the anterior obturacular surfaces and attached to a double stalk secreted by the median surfaces of the obturacular halves. Saucers are produced sequentially as the obturaculum grows, to form a tapering stack with the most recent at the base. They darken with age from colourless through yellow to brown. Filamentous bacteria, ciliates, polychaetes, and even young *Ridgeia* spp. may settle on the saucers. Among the 1229 animals used for allozyme electrophoresis the maximum saucer number was 15, but only 1% of the animals had more than 9, while 46% had 3–9. Figure 6A shows saucer number against obturaculum length (as an index of animal size) for 15 frozen samples (582 individuals). The frequency

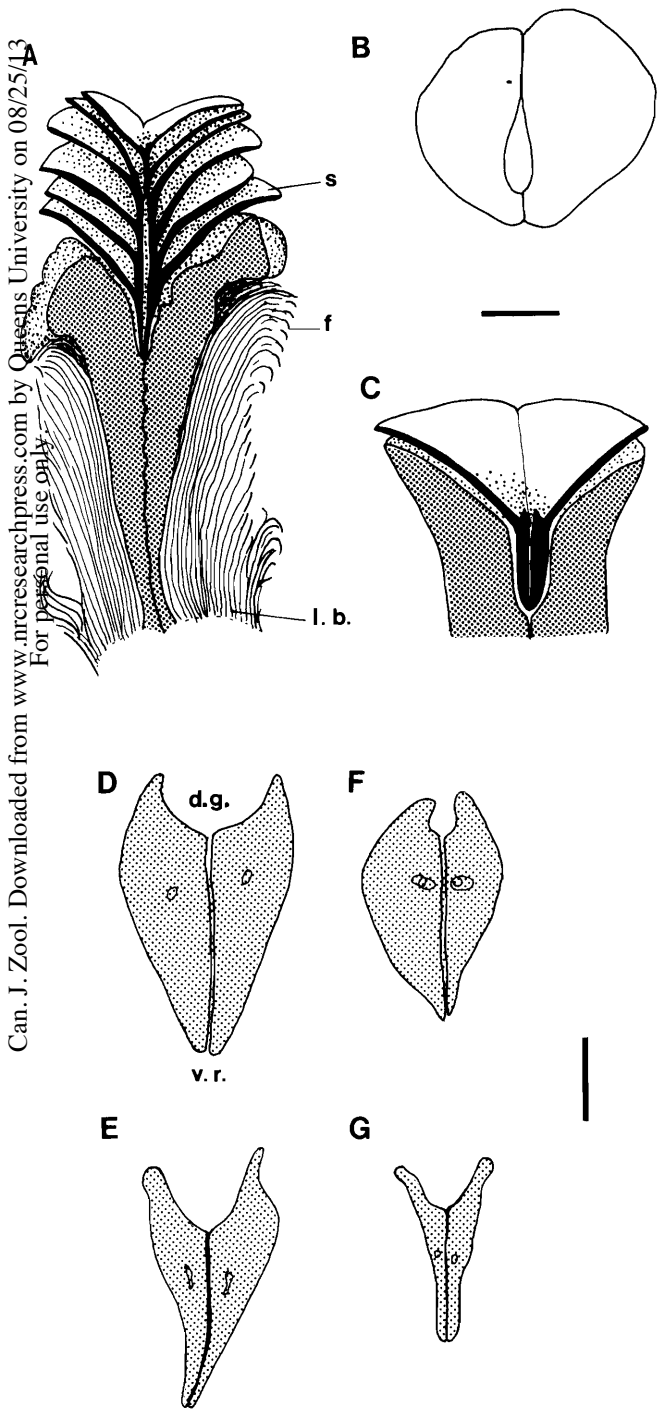


Fig. 5. (A) Ventral half of anterior end of *Ridgeia piscesae* (specimen from A1451) cut vertically to show the conical shape of the obturaculum (the cut surface is dotted) surrounded by branchial lamellae and capped by a stack of 6 saucers on a double axial rod (the cut surface is black). (B) Anterior view of a saucer (A1451). (C) Vertically sectioned obturaculum and single saucer (P1322). (D and E) Transverse sections of the obturaculum taken near the top and near the base (P1322). (F and G) Similar sections from collection A1451. *d.g.*, dorsal groove; *f*, branchial filament; *l.b.*, lamella base; *s*, saucer; *v.r.*, ventral ridge. Scale bars = 1 mm.

of occurrence appears to be consistent, from 0 to 9. There is a wide range in saucer number at most lengths: the largest have fewer saucers, presumably having lost earlier saucers. The four individuals with highest number of saucers come from the same collection, a fat type that also falls out as the most different in the allozyme analysis.

In a separate study of *R. piscesae*, the saucer numbers of 213 individuals from the paratype collection from Taylor's Vent, Axial Seamount, were related to tube diameter (Fig. 6B). Loss of saucers is apparent in larger individuals. The type specimens of *R. piscesae* from Taylor's and Shepherd's vents had no more than 2 obturacular saucers (Jones 1985), but 20% of the animals from the Taylor's Vent type collection had 3 or 4 saucers and so overlap the range reported for *R. phaeophiale* (Jones 1985).

Obturacular groove

The dorsal groove is variable in width depending, in part, on contraction during fixation (Figs. 2 and 5). No clear distinction between samples or types was evident.

Branchial crown

Branchial filament tips can reach to near the lowest saucers (Fig. 2) but are often damaged or cropped by predators. They develop in concentric rows around the obturacular base; filaments adhere side by side to form lamellae, with new lamellae forming outside the older ones. The newest one or two are single and midventral, while the remainder are paired, with a midventral gap separating the right and left lamellae. Lamellae adhere closely at their bases, but the tips of the filaments are free. Outer lamellae (up to 13 each side) form looser semicircles, overlapping one another and gradually increasing in length, lateral extent, and number of filaments (Fig. 2).

Jones (1985) describes two types of branchial filaments: most are short with pinnules near the tips, but certain dorsal filaments are longer and lack pinnules. Jones describes differences between species in filament arrangement (Table 1). We examined the crowns by removing the lamellae from the outside, one by one, in animals ranging in size from 1 to 9 mm obturaculum diameter.

Dissections of *R. piscesae* from the holotype collection (P1322) reveal variation both in filament number and type between lamellae in any one specimen and between large and small specimens. In the newest lamellae, the filaments have no pinnules, closely adhere, and are few in number. New filaments are added, one by one, at both ends of the row (dorsal and ventral) (Fig. 7). Those at the dorsal end of the row are long and tapering, without pinnules, while others are shorter with two rows of pinnules. A few intermediate-type filaments, tapering but with pinnules, may occur between the two main groups and a few short, nonpinnulate filaments are usually present at the ventral border of each lamella. Filament number per lamella thus increases as the lamella and the animal grow. A specimen 1 mm in diameter has 10–15 filaments in each of its larger lamellae, of which 1–3 are of the long, tapering type. A 2-mm specimen has 20–25 filaments, with 3–5 long-tapering. A 9-mm juvenile has 50–70 filaments with 7–9 long-tapering. *Ridgea phaeophiale*-type (sample P1733) specimens show similar variation. The

Fig. 6. (A) The number of obturacular saucers related to the length of the obturaculum for 582 individual *Ridgeia* spp. from 15 frozen samples used for allozyme electrophoresis. Black squares indicate the sample of fat type, A2259, which included the four individuals with the highest number of saucers and showed the greatest genetic distance (Table 3). (B) Saucer number (mean and range) related to grouped tube diameter for 213 individual *Ridgeia* spp. in the paratype collection of *R. piscesae* (P1327).

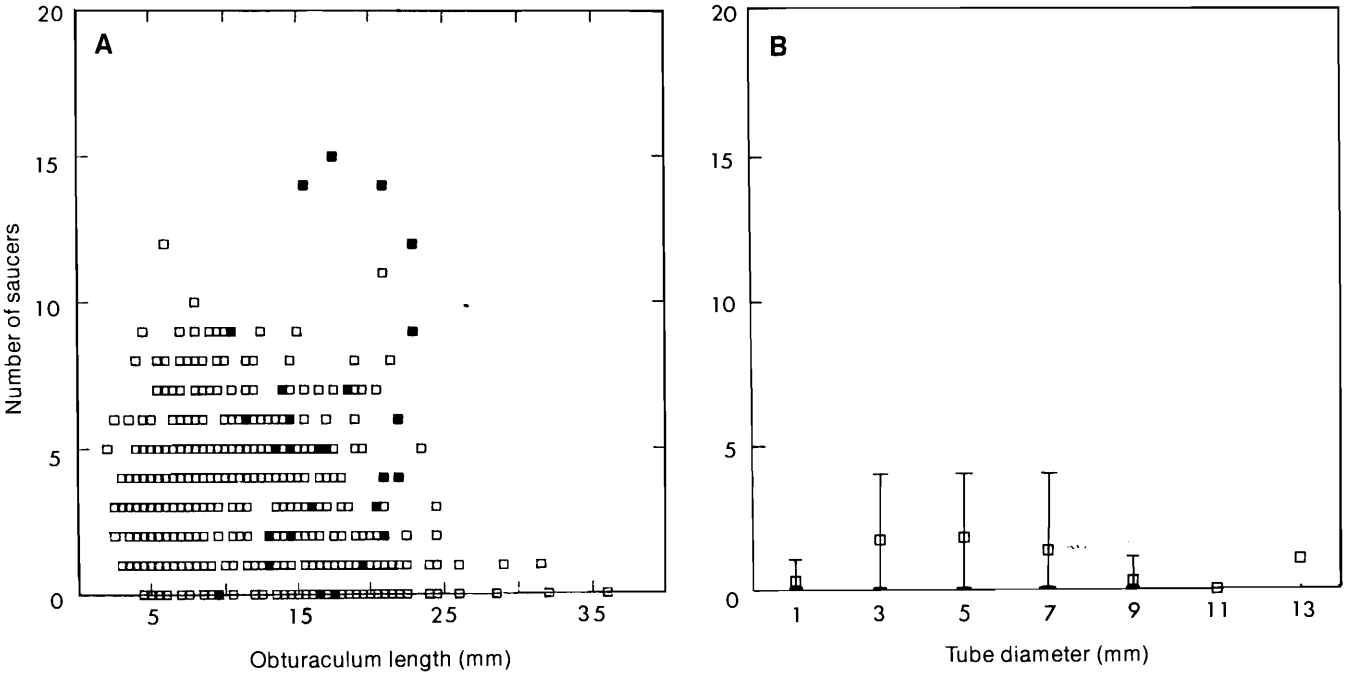


Fig. 7. Branchial filaments of *Ridgeia* spp. (A) Tip of tapered, nonpinnulate type. (B) Dorsal region of a branchial lamella, including both types. (C) Tip of a pinnulate filament. Scale bars: 0.1 mm for A and C; 1 mm for B.

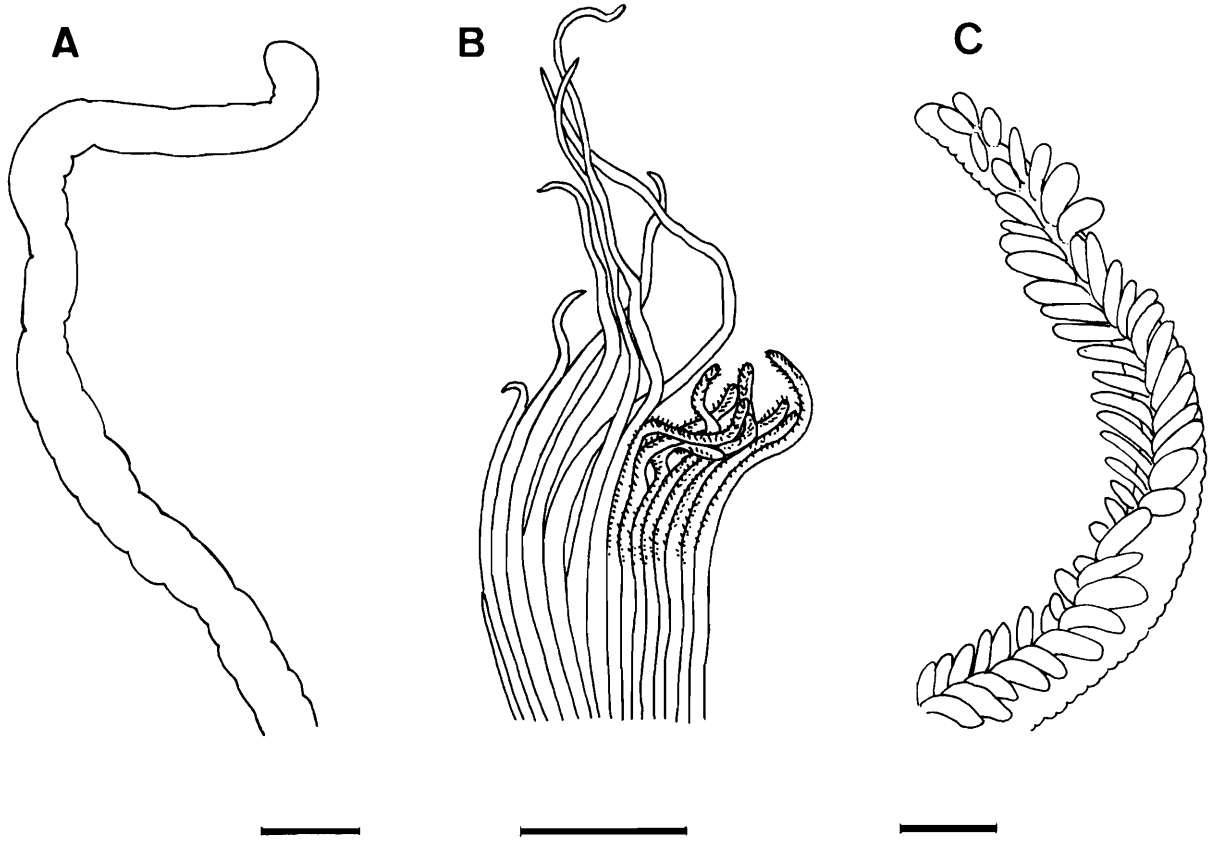
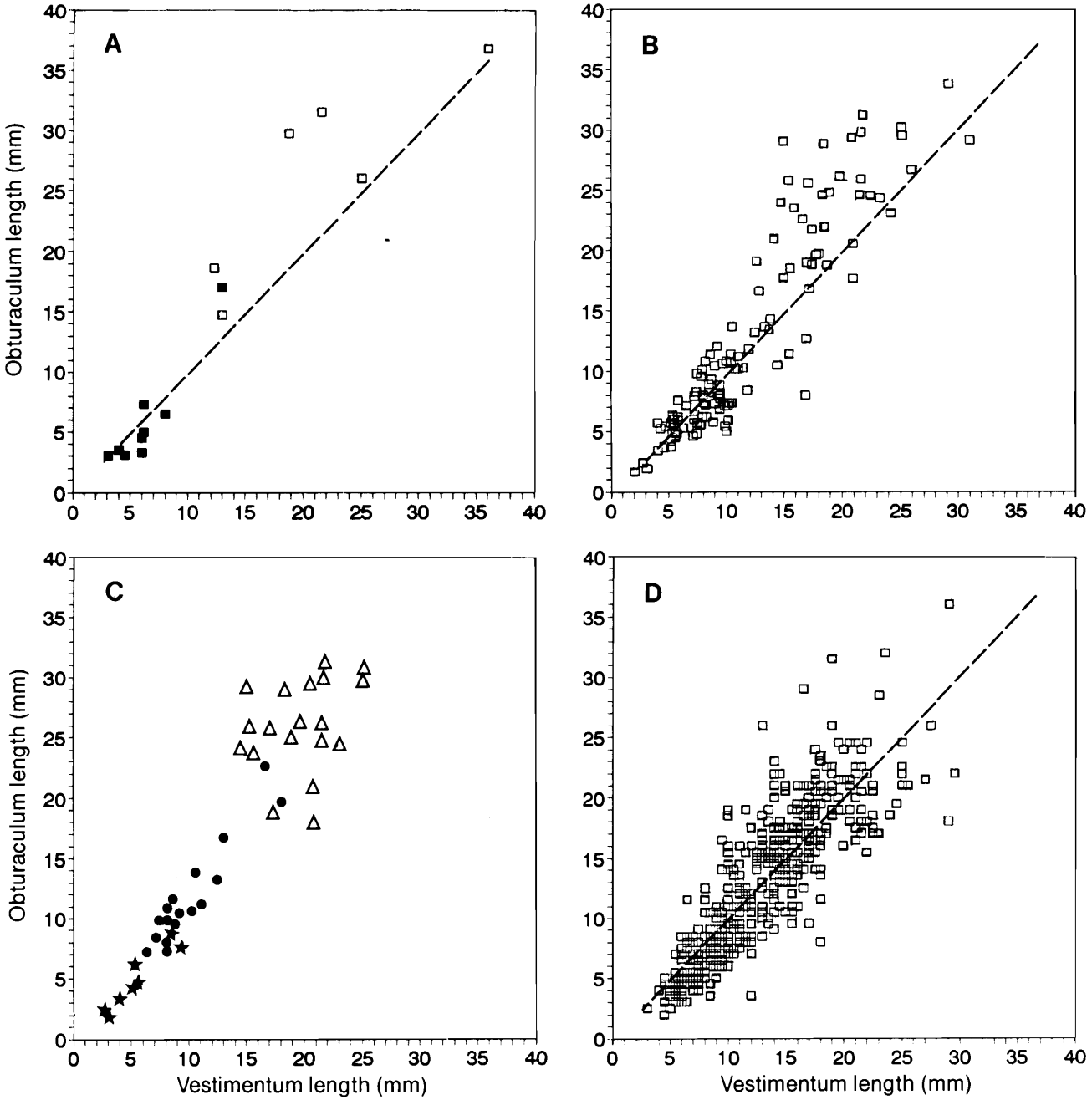


Fig. 8. Relationship between obturaculum length and vestimentum length. (A) Type specimens of *Ridgeia piscesae* Jones (□) and *R. phaeophiale* Jones (■). (B) One hundred and twenty-five specimens from 12 preserved samples chosen to span the size range. (C) Specimens from 3 of the above 12 samples to show a typical range within a sample: ★, P1323; ●, A1463; △, A1461. (D) Three hundred and fifty-three frozen specimens used for allozyme electrophoresis (15 samples selected from 33 to span the size range). The broken lines in A, B, and D indicate a 1:1 relationship.



difference between *R. piscesae* and *R. phaeophiale* noted by Jones (1985) appears to be the effect of size differences between the type specimens.

Relative obturaculum size

The measurements of obturaculum and vestimentum length given in Jones (1985) suggest a difference in relative lengths in his specimens of the two species. The ratio is greater than 1 in *R. piscesae* but near 1 in *R. phaeophiale* (Fig. 8A). However, the size differences and small number of individuals make interpretation difficult. We selected specimens from several preserved collections to span the size range. The continuum plotted (Fig. 8B) suggests that a shift to a relatively longer obturaculum may occur with increasing size. Figure 8C illustrates three of the most different of the eight collections.

Frozen specimens were measured during preparation for electrophoresis, where there was a bias toward selection of

the largest individuals from each collection for electrophoresis. ANOVA analyses could not be used to test for ratio differences among frozen collections because the condition of homogeneity of variances was not met. A modified Hochberg's GT2 multiple comparison of the collection means (Sokal and Rohlf 1981) did not detect significant differences. The regression line for the frozen group fits a 1:1 obturaculum: vestimentum ratio, with values ranging from 2:1 to 1:2. For most smaller specimens the ratio is less than 1, while for most larger specimens it is greater than 1; medium-sized specimens fall in between. There appears to be continuum in this ratio that relates to worm growth.

Opisthosome

Opisthosomes (Fig. 3) were examined on 16 preserved and 37 frozen individuals from collections attributed to several *Ridgeia* types. Opisthosomes 1–2 mm long have 20–37 segments and opisthosomes 10–15 mm long have 45–64 segments; there is wide scatter in this relationship, perhaps related to the variable state of contraction. Table 1 differentiates the type specimens in this regard but a continuum is evident in a larger sample spanning all sizes.

Redescription

Ridgeia piscesae Jones, 1985, emended

Ridgeia piscesae Jones 1985, p. 144–150, Figs. 45–48.
Ridgeia phaeophiale Jones 1985, p. 150, Figs. 49–52.

TYPE MATERIAL: The holotype is the specimen designated the holotype of *Ridgeia piscesae* by Jones 1985, p. 148, USNM 98105 (Smithsonian) from Shepherd's Vent, Juan de Fuca Ridge, *Pisces* dive P1322. The type series includes Jones' paratypes of *R. piscesae* and his holotype and paratypes of *R. phaeophiale* Jones, 1985. Selected examples representing the range of morphotypes have been added to the type series in the National Museum of Natural History, Washington, D.C.: USNM 169813 (UVic Collection No. A1461-132), USNM 169808 (A1452-154), USNM 169814 (A1451-178), USNM 169809 (P1731-192), USNM 169812 (P1730-2657), USNM 169811 (A2444-2763), and USNM 169810 (R202-2764).

TYPE LOCALITY: Shepherd's Vent, Axial Seamount, Juan de Fuca Ridge, as designated by Jones (1985) for *R. piscesae*.

DISTRIBUTION: Hydrothermal vents of Juan de Fuca Ridge and northern Gorda Ridge.

Description

Tube

Shape and size very variable, straight or serpentine, tapering from an anterior diameter of 2–13 mm to a closed posterior end less than 1 mm in diameter; maximum length 190 cm. Open anterior end usually funnel shaped; the rims of earlier funnels remain as external collars lower down the tube; the collars may be widely spaced or closer together. Colour white, grey, gold, brown, occasionally nearly black; commonly translucent. The wall may be thin or thick and the whole tube may be flexible or stiff. A colony is normally composed of tubes of similar colour and form.

Animal

The cup-shaped anterior face of the obturaculum bears 1–15 saucer-shaped structures held together by an axial rod between the obturacular halves. The saucers may be missing from some specimens, but traces of the axial structure often remain. The proximal 1 or 2 saucers are translucent-white, while the smaller distal saucers are yellow–brown.

The obturacular halves are closely adherent on the ventral side, forming a midventral ridge, but with a longitudinal groove separating them on the dorsal side; the obturaculum is Y-shaped in transverse section. Up to 35 pairs of branchial lamellae make up the branchial plume, the number being related to the diameter of the animal. A few of the ventralmost, newly formed pairs of branchial lamellae may be fused. Dorsal to these, a midventral space is usually present between the left and right blocks of lamellae.

The branchial filaments are of two types, pinnulate and nonpinnulate; the pinnulate filaments are shorter than the nonpinnulate and predominate (up to 70 filaments); one or a few at the ventral end of each lamella are short and lack pinnules because they are still developing; 3–11 filaments at the dorsal end of each lamella are longer and slightly more tapering and have no pinnules. Filament number varies with lamella position in the branchial crown and with the diameter of the animal. There may be a few intermediate pinnulate filaments, more like the nonpinnulate filaments in shape. Undamaged filaments can be as long as the obturaculum, but cropped filaments may be difficult to differentiate.

The obturaculum tapers from a broad top to a narrow base. The maximum diameter is 10 mm, the maximum length, without saucers, is 41.5 mm. The length:diameter ratio varies from 1.2:1 to 3:1 in smaller animals (diameter up to 3 mm) and from 3:1 to 5:1 in larger animals.

The vestimental region has a short collar surrounding the branchial plume base, lateral folds meeting in the mid-dorsal line, and a complete posteroventral fold behind the ciliated field. The maximum length of the vestimental region is 31 mm and the maximum diameter 10 mm; the length:diameter ratios range from 1.3:1 to 4:1, being very variable at all sizes. The obturaculum tends to be shorter than the vestimental region in smaller animals but equals or exceeds it in length in larger animals. The pear-shaped ventral ciliated field ranges from 0.53 to 0.91 of the length of the vestimentum. Genital grooves are present in both sexes but are usually shorter in females.

The trunk, in life, extends almost to the posterior end of the tube, but both tube and trunk are often broken in sampling; the greatest length found, 1376 mm, was in one of the paratypes of *R. piscesae* Jones, 1985 (USNM 98106). Cuticular plaques on the trunk papillae are oval, 60–95 μm across. The sperm head is 30–40 μm long; mature oocytes are 90–100 μm in diameter; bacterial symbionts are spherical, up to 10 μm in diameter.

The opisthosome is 1.5–18 mm long, with 24–63 segments; single rows of setae are visible on the anterior segments; the last 10–15 segments lack obvious setae. Denticulate setal heads are 8.0–9.5 μm long × 2 μm wide, with 7–13 teeth in the posterior group, typically arranged in three rows, and 3–7 in the anterior group (Figs. 3D, 3E).

Higher taxonomy

After we had studied the *Ridgeia* types closely, we concluded that there is a need to add to the diagnosis of the genus *Ridgeia*, which Jones (1985) gave as "characters of the family" (family Ridgeiidae). Important modifications are given in

italics below. Features of the musculature of the obturaculum could not be confirmed.

Diagnosis

Vestimentiferan worms in tapering tubes *with external collars*; *obturacular face bears one to many saucer-shaped structures attached to an axial rod*; *dorsal side of the obturaculum grooved longitudinally*; orientation of major branchial blood vessels basal; orientation of branchial lamellae axial and parallel to obturaculum; filaments of lamellae of two kinds, the dorsalmost 3–11 lack pinnules and are longer and more tapering than the others; *pinnules are present on most of the shorter filaments, with the exception of the ventralmost*; no peripheral lamellar sheaths; with paired external excretory pores; posteroventral margin of the vestimentum entire; setae of opisthosome in single rows side by side; most setae with 3 vertical rows of denticles in posterior group.

Discussion

The question of the number of species of *Ridgeia* is an important one because this animal provides much of the biomass and physical framework of the vent communities in the hydrothermal province of the northeast Pacific. The existence of several sympatric species would require explanation and the mechanism of differentiation would be of some interest. The present study has focused on an alternative hypothesis that the forms observed on the Juan de Fuca Ridge, at least, belong to one species whose morphology is highly variable.

The problematic nature of field identification of fresh collections of tube worms raised the question in our minds of whether we were dealing with a set of cryptic species or the expression of a highly plastic phenotype. Allozyme evidence supports the latter hypothesis. Levels of heterozygosity and polymorphism in populations of *Ridgeia* indicate considerable genetic variability within the species. In comparison with known variation (Thorpe 1983; Nei 1987; Templeton 1989), the distance data indicate no substantial genetic differences among populations along the length of the Juan de Fuca Ridge. Comparison of allozyme patterns of Gorda Ridge tube worms with those of Cleft Segment indicates that the species *Ridgeia piscesae* (emended) ranges at least as far south as the northern Gorda vent site (GR14, Fig. 1), with no significant genetic divergence across the Blanco Transform Fault (M.B. Black, unpublished data). A formal population genetic analysis of these *Ridgeia* allozyme data will be presented elsewhere.

Vestimentiferan tube worm populations, in general, display phenotypic plasticity in the absence of genetic differentiation (Black 1991; Black et al. 1994; Trivedi et al. 1994). *Riftia pachyptila* populations from the Gulf of California, East Pacific Rise, and Galapagos Rift are morphologically variable but an allozyme study of these populations indicated no genetic divergence among populations separated by many thousands of kilometres (Black et al. 1994). Local extinction and recolonization must be fairly frequent at vent sites, owing to the unstable nature of the physical environment. Nevertheless, genetic data for *Ridgeia* and *Riftia* indicate that high gene flow exists. A similar situation was recorded by France et al. (1992) for amphipod populations along a spreading segment, although genetic differentiation across transform faults was evident. With genomic comparisons, Vrijenhoek et al. (1994) find that the specimens of vesicomyid clams on Juan de Fuca from Endeavour, Axial, and Cleft segments represent the same species. Thus, the wide distribution of the same species of vent tube worm is not extraordinary.

The original described species of *Ridgeia* were distinguished on the basis of two characters (tube colour and saucer number), both exposed surfaces. We do not believe these to be valid characters. The initial impression of the existence of several species, based on the variety of tubes, receives poor support from subsequent body examinations. The tube apparently varies with habitat. A single sample comprises all the same type but, in different fluid conditions only metres away, another type will be seen. A synchronous change in tube colour and stiffness can be seen within a collection (Fig. 4D). Numbers of obturacular saucers relate to age and predation level. Polynoids are common predators of *Ridgeia* spp. (Tunnicliffe et al. 1990). Saucers are easily lost in handling, so presumably can be removed during other disturbance as well. The most "chewed" specimens had the fewest saucers. Tube colour and saucer number do seem to be related. Mineral encrustration influences tube colour (Tunnicliffe and Fontaine 1987) and may increase the robustness of saucers.

Table 1 illustrates a distinct size difference between the groups of specimens used to describe the two species. Other aspects of Jones' (1985) and our own (unpublished) "species" descriptions incorporate characters that relate to a growth series: absolute sizes of body parts, relative sizes of obturaculum/vestimentum, branchial filament arrangement, and opisthosome segment number. The measurements presented here illustrate a continuum of character states and no clear differentiation. Our measurements on extensive collections of *Ridgeia* spp. support the hypothesis that only one species is present. Thus, "species" in Table 1 represent two ends of the size spectrum of a single species.

Independent support for the single species comes from De Bevoise and Taghon (1988), who find that RNA:DNA ratios in *Ridgeia* differ with collection site, not with putative species type. De Burgh et al. (1989) find no differences in appearance of symbionts among *Ridgeia* types. They do cite minor ultrastructural differences but we believe these to be size and (or) preservational artefacts.

The extent of tube variation in *R. piscesae* (emended) appears to relate to habitat. We have only initial information on the relation of vent fluid characteristics to tube form. In general, the large white tubes are found at higher sulphide levels, while gold or black tubes are found near smokers with higher concentrations of metals in the vent fluid. We postulate that the availability of sulphide influences growth rate and thus the form of the tube. Tunnicliffe and Fontaine (1987) document the accumulation of metal complexes on gold and black tubes and abundant bacterial filaments on white tubes. The collars or funnels around the tubes may be irregular stiffening devices. Because the tube top is nearly always flared, it appears that growth episodes occur between collars. Vestimentiferan tubes are composed mostly of chitin and protein, 24% chitin in the soft tubes of *Riftia* spp. and 46% chitin in the stiff tubes of *Tevnia* spp. (Gaill et al.

1992); the composition of the soft and hard tubes of *Ridgeia piscesae* may vary.

Descriptive taxonomy in vestimentiferans is at an early stage, as only 11 species have been described; these are assigned to seven genera, four of which are monotypic (Webb 1969; Jones 1981, 1985; E.C. Southward 1991). Characters of generic importance are found mainly at the anterior end of the body, the trunk and opisthosome showing little variation except in size. Differences are described in the form and ornamentation of the obturaculum, arrangement of branchial filaments, and shape of the posterior vestimental folds.

The following species are distinguished: four in *Lamellibrachia* (Webb 1969; van der Land and Nørrevang 1975; Mañé-Garzon and Montero 1985; E.C. Southward 1991) and two each in *Escarpia* and *Ridgeia* (Jones 1985). For *Lamellibrachia*, tube characters have been used, together with the shape of the obturaculum, the ratio of obturaculum length to vestimentum length, and characters of the branchial lamellae. In *Escarpia*, the major specific difference lies in the ornamentation of the obturacular face (spike or lamina), but the published measurements show that the vestimentum is consistently relatively thinner in one species than in the other; however, the sample size is very small.

Specific separations in *Lamellibrachia* and *Escarpia* are applied to geographically separated samples, but the type localities of *R. piscesae* (sensu Jones 1985) and *R. phaeophiale* are separated by only 50 m on Axial Seamount. Such sympatric distribution continues on other segments of the Juan de Fuca Ridge. While we feel it is unlikely that another species of *Ridgeia* will be described from this region, it is possible that allopatric separation at the ends of the ridges could result in sibling species formation. The exact status of the tube worms from Explorer Ridge and Escanaba Trough of Gorda Ridge awaits genetic confirmation. We believe that genetic studies are very useful in elucidating the systematics of this group. In future, suspected new species collections should be subdivided into preserved and frozen samples to allow both morphological and genetic investigations.

Acknowledgements

Many people have helped us with collections and observations over the years: Kerry Wilson, Maureen de Burgh, Kathryn Coates, Tim Siferd, and Kristi Skebo. Alan Southward helped to prepare figures and gave advice on the manuscript. This work was funded by the Natural Sciences and Engineering Research Council of Canada. Financial assistance to E.C.S. and M.B. from the Leverhulme Trust is gratefully acknowledged.

References

Aebersold, P.B., Winans, G.A., Teel, D.J., Milner, G.B., and Utter, F.M. 1987. Manual for starch gel electrophoresis: a method for the detection of genetic variation. NOAA Tech. Rep. NMFS (Natl. Mar. Fish. Serv.) No. 61.

Black, M.B. 1991. Genetic (allozyme) variation in Vestimentifera (*Ridgeia* spp.) from hydrothermal vents of the Juan de Fuca Ridge (Northeast Pacific Ocean). M.Sc. thesis, University of Victoria, Victoria, B.C.

Black, M.B., Lutz, R.A., and Vrijenhoek, R.C. 1994. Gene flow among vestimentiferan tube worm (*Riftia pachyptila*) populations from hydrothermal vents of the eastern Pacific. Mar. Biol. (Berl.), **120**: 33–39.

De Bevoise, A.E., and Taghon, G.L. 1988. RNA:DNA ratios of the hydrothermal-vent vestimentiferans Ridgeia piscesae and *R. phaeophiale* indicate variations in growth rates over small spatial scales. Mar. Biol. (Berl.), **97**: 421–426.

De Burgh, M.E. 1986. Evidence for a physiological gradient in the vestimentiferan trophosome: size–frequency analysis of bacterial populations and trophosome chemistry. Can. J. Zool. **64**: 1095–1103.

De Burgh, M.E., Juniper, S.K., and Singla, C.L. 1989. Bacterial symbionts in northeast Pacific Vestimentifera: a TEM survey. Mar. Biol. (Berl.), **101**: 97–125.

France, S.C., Hessler, R.R., and Vrijenhoek, R.I. 1992. Genetic differentiation between spatially-disjunct populations of the deep-sea, hydrothermal vent-endemic amphipod *Ventiella sulfuris*. Mar. Biol. (Berl.), **114**: 551–559.

Gaill, F., Voss-Foucart, M.F., Gerday, C., Compere, P., and Goffinet, G. 1992. Chitin and protein contents in the tubes of vestimentiferans from hydrothermal vents. *In* Advances in chitin and chitosan. *Edited by* C.J. Brine, P.A. Sandford, J.P. Zizakis. Elsevier Applied Science, New York. pp. 232–236.

Gardiner, S.L., and Jones, M.L. 1993. Vestimentifera. *In* Microscopic anatomy of invertebrates. Vol. 12. Onychophora, Chilopoda and lesser Protostomata. *Edited by* F.W. Harrison and M.E. Rice. Wiley–Liss, New York. pp. 371–460.

Harris, H., and Hopkinson, D. 1977. Handbook of enzyme electrophoresis in human genetics. North-Holland, Amsterdam.

Jones, M.L. 1981. *Riftia pachyptila*, new genus, new species, the vestimentiferan worm from the Galapagos Rift geothermal vents (Pogonophora). Proc. Biol. Soc. Wash. **93**: 1295–1313.

Jones, M.L. 1985. On the Vestimentifera, new phylum: six species, and other taxa, from hydrothermal vents and elsewhere. Bull. Biol. Soc. Wash. No. 6. pp. 117–158.

Jones, M.L., and Gardiner, S.L. 1988. Evidence for a transient digestive tract in Vestimentifera. Proc. Biol. Soc. Wash. **101**: 423–433.

Jones, M.L., and Gardiner, S.L. 1989. On the early development of the vestimentiferan tube worm *Ridgeia* sp. and observations on the nervous system and trophosome of *Ridgeia* sp. and *Riftia pachyptila*. Biol. Bull. (Woods Hole), **177**: 254–276.

Lewis, P., and Whitkus, R. 1989. GENESTAT-PC, version 2.1. Ohio State University, Columbus.

Mañé-Garzon, F., and Montero, R. 1985. Sobre una neuva forma de verme tubicola *Lamellibrachia victori* n.sp. (Vestimentifera), proposicion de un nuevo phylum: Mesoneurophora. Rev. Biol. Urug. **8**: 1–28.

McDonald, J.H. 1985. No bad gels: starch gel electrophoresis for the masses. State University of New York, Stony Brook.

Murphy, R.W., Sites, J.W., Buth, D.G., and Haufler,

C.H. 1990. Proteins I: isozyme electrophoresis. *In* Molecular systematics. *Edited by* D.M. Hillis and C. Moritz. Sinauer Associates, Sunderland, Mass. pp. 45–126.

Nei, M. 1972. Genetic distance between populations. Am. Nat. **106**: 283–292.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics, **89**: 583–590.

Nei, M. 1987. Genetic distance and molecular phylogeny. *In* Population genetics and fishery management. *Edited by* N. Ryman and F. Utter. University of Washington Press, Seattle. pp. 193–223.

Normark, W.R., Lupton, J.E., Murray, J.W., Koski, R.A., Clague, D.A., Morton, J.L., Delaney, J.R., and Johnson, H.P. 1982. Polymetallic sulfide deposits and water-column tracers of active hydrothermal vents on the southern Juan de Fuca Ridge. Mar. Technol. Soc. **16**: 46–52.

Pasteur, N., Pasteur, G., Bonhomme, R., Gatalan, J., and Britton-Davidian, J. 1987. Manuel technique de genetiqe par électrophorèse des proteines. Lavoisier, Paris.

Shaw, C.R., and Prasad, R. 1970. Starch gel electrophoresis of enzymes—a compilation of recipes. Biochem. Genet. **4**: 297–320.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry: the principles and practice of statistics in biological research. 2nd ed. W.H. Freeman, New York.

Southward, A.J. 1991. Effect of temperature on autotrophic enzyme activity of bacteria symbiotic in clams and tube worms. Kiel. Meeresforsch. Sonderh. No. 8. pp. 245–251.

Southward, A.J., Southward, E.C., Spiro, B., Rau, G.H., and Tunnicliffe, V. 1994. $^{13}C/^{12}C$ of organisms from Juan de Fuca Ridge hydrothermal vents: a guide to carbon and food sources. J. Mar. Biol. Assoc. U.K. **74**: 265–275.

Southward, E.C. 1988. Development of the gut and segmentation of newly settled stages of *Ridgeia* (Vestimentifera): implications for relationship between Vestimentifera and Pogonophora. J. Mar. Biol. Assoc. U.K. **68**: 465–487.

Southward, E.C. 1991. Three new species of Pogonophora, including two vestimentiferans, from hydrothermal sites in the Lau Back-arc Basin (southwest Pacific Ocean). J. Nat. Hist. **25**: 859–881.

Southward, E.C., and Coates, K.A. 1989. Sperm masses and sperm transfer in a vestimentiferan, *Ridgeia piscesae* Jones, 1985 (Pogonophora: Obturata). Can. J. Zool. **67**: 2776–2781.

Swofford, D.L., and Selander, R.B. 1989. BIOSYS-1: a computer program for the analysis of allelic variation in population genetics and biochemical systematics, release 1.7. Illinois Natural History Survey, Champaign.

Templeton, A.R. 1989. The meaning of species and speciation: a genetic perspective. *In* Speciation and its consequences. *Edited by* D. Otte and J.A. Endler. Sinauer Associates, Sunderland, Mass.

Thorpe, J.P. 1983. Enzyme variation, genetic distance and evolutionary divergence in relation to levels of taxonomic separation. *In* Protein polymorphism: adaptive and taxonomic significance. *Edited by* G.S. Oxford and D. Rollinson. Systematics Association, London. pp. 131–152.

Trivedi, A.K., Black, M.B., and Vrijenhoek, R.C. 1994. Allozyme diversity within and among tube worm (Vestimentifera) species from deep-sea hydrothermal vents of the East Pacific Rise. Isozyme Bull. **27**: 59. [Abstr.]

Tunnicliffe, V. 1988. Biogeography and evolution of hydrothermal-vent fauna in the eastern Pacific Ocean. Proc. R. Soc. Lond. B Biol. Sci. **233**: 347–366.

Tunnicliffe, V. 1991. The biology of hydrothermal vents: ecology and evolution. Mar. Biol. Oceanogr. Annu. Rev. **29**: 319–407.

Tunnicliffe, V., and Fontaine, A.R. 1987. Faunal composition and organic surface encrustrations at hydrothermal vents on the southern Juan de Fuca Ridge. J. Geophys. Res. **92**: B11303–B11314.

Tunnicliffe, V., Garrett, J.F., and Johnson, H.P. 1990. Physical and biological factors affecting the behavior and mortality of hydrothermal vent tube worms (vestimentiferans). Deep-Sea Res. **37**: 103–125.

van der Land, J., and Nørrevang, A. 1975. The systematic position of *Lamellibrachia* (Annelida, Vestimentifera). Z. Zool. Syst. Evolutionsforsch. Sonderheft 1. pp. 86–101.

van der Land, J., and Nørrevang, A. 1977. Structure and relationships of *Lamellibrachia* (Annelida, Vestimentifera). K. Dan. Vidensk. Selsk. Biol. Skr. **21**(3): 1–102.

Vrijenhoek, R., Schutz, S.J., Gustafson, R.G., and Lutz, R.A. 1994. Cryptic species of deep-sea clams (Mollusca, Bivalvia, Vesicomyidae) in hydrothermal vent and cold-water seep environments. Deep-Sea Res. I, **41**: 1171–1189.

Webb, M. 1969. *Lamellibrachia barhami*, gen.nov., sp.nov. (Pogonophora), from the Northeast Pacific. Bull. Mar. Sci. **19**: 18–47.

Williams, N.A., Dixon, D.R., Southward, E.C., and Holland, P.W.H. 1993. Molecular evolution and diversification of the vestimentiferan tube worms. J. Mar. Biol. Assoc. U.K. **73**: 437–452.