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## A Re-description of *Ditrupa gracillima* Grube, 1878 (Polychaeta, Serpulidae) from the Indo-Pacific, with a Discussion of the Genus

HARRY A. ten HOVE<sup>1</sup> & RICHARD S. SMITH<sup>2</sup>

<sup>1</sup>Instituut voor Taxonomische Zoölogie,  
Postbus 4766, 1009 AT Amsterdam.

<sup>2</sup>Australian Broadcasting Corporation, TV Science Unit,  
GPO Box 9994, Sydney, NSW 2001, Australia

**ABSTRACT.** Like so many other serpulid genera, *Ditrupa* has a history of taxonomic confusion, even to the extent that the worm tubes have been included in the Mollusca by some workers. In recent publications, most authors follow Fauvel (e.g. 1953) and recognise a single species, *Ditrupa arietina* O.F. Müller, 1776, worldwide, despite the fact that descriptions of this species were based on European and Atlantic material. A re-examination of type specimens and study of a broad range of samples from the Indo-Pacific now justifies the recognition of a separate species, *Ditrupa gracillima* Grube, 1878, from this region. It shows extreme variation, at least partly related to depth: from 100 m downwards an ecophenotype prevails, previously described as *D. arietina* var. *monilifera*.

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*Ditrupa* Berkeley, 1835 is a genus of serpulid polychaete found living unattached in soft sediment marine environments around the world. The worms are clearly recognisable from other serpulids by their anatomy, behaviour and distinctive tusk-shaped tubes. Despite this, most descriptions are poor, having been based solely on dredged calcareous tubes, most often devoid of the polychaete. The worms and their tubes can form a significant component of the muddy benthic community. In the Atlantic, *Ditrupa* is sometimes found in populations of over 1000/m<sup>2</sup> (Dyer *et al.*, 1982:310) and may account for more than 50% of the biogenic carbonate sediments

(Wilson, 1979:M87). Fossil *Ditrupa* may be so abundant that they are used as key beds for geological field work, and to deduce the direction of prevalent palaeocurrents (Cheng, 1974). Although a number of Recent species has been erected in the past, most authors currently follow Fauvel (e.g. 1953:470), who recognises only a single species, *Ditrupa arietina*, worldwide.

There has always been considerable confusion in the classification of *Ditrupa* (sometimes spelled *Ditrypa*). In the 18th and 19th centuries particularly, as well as more recently, species were misidentified as the scaphopod genus *Dentalium* Linnaeus, 1758 and vice versa. For

example, *Dentalium perpusillus* Sowerby, 1832 had been placed in *Ditrupa* by Mörch (1863:427), but is correctly referred to *Cadulus (Gadila) perpusilla* by Emerson (1971:77; material studied BMNH 1950.10.10.1-5). Moreover, *Dentalium*'s have frequently been mistaken for *Ditrupa*, for example by Fauvel & Rullier (1959:196). In view of this, in future all possible synonyms given below should be checked against the material, if it is still in existence. As another example, Fauvel's 1932 record from a depth of 1,500 m is suspect as it exceeds the known depth limit for living specimens (650 m, reported herein) by 850 m.

No wonder that in fossil literature the confusion is worse. Even authors who tried to base fossil upon Recent taxonomy by using Recent material for comparative purposes, sometimes misinterpreted the genus *Ditrupa* completely. Lommerzheim (1979:143-145, pl.15 figs 1-4) attributes three species with a fixed, generally triangular apical tube-part to *Ditrupa*, while Recent representatives are free-living and even the youngest tube-parts are always circular in diameter, without a trace of an adnascent part. In our opinion it is unlikely that the many fossil species with angular tubes attributed to *Ditrupa* really belong to this genus — for instance, *D. canteriata* (Hagenow, 1840), *D. retusa* and other species by Regenhardt (1961) and *D. tricostata* (Goldfuss, 1841). "*Ditrupa*" *mosae* (Bronn, 1837) already has been referred to the genus *Sclerostyla* by Cupedo (1980).

In this paper, attention is focused on *Ditrupa* from the Indo-Pacific region. Though commonly found, *Ditrupa* is not well known from these waters. Examination of Recent northern Australian specimens with variable tube appearance suggested to us the possibility of one or more species co-existing in the area. Certainly, the worms did not appear to fit within *D. arietina* of the Atlantic, of which a diagnosis is given for comparative purposes. The examination of type material of *Dentalium laevis* Brazier, 1877 in the collections of the Australian Museum and of *Ditrypa gracillima* Grube, 1878 in the Museums of Wrocław and Berlin, coupled with the availability of a large amount of new and much unworked material, has made a partial revision of this confusing genus possible.

## Materials and Methods

Material studied existed in several forms. Empty tubes were examined from either dry or wet collections. Where entire animals were preserved in wet collections, it was found that specimens could be pushed from their tubes by inserting a horse hair gently into the apex (i.e. the narrow posterior end). In this way, breaking the tube into fragments could be avoided. The live material examined was maintained for several weeks in a closed aquarium system.

Ten Hove & Jansen-Jacobs (1984) proposed a standard method which seeks to avoid data from juveniles influencing the descriptions of the adult worms. Essentially their method is used in this paper.

The following parameters were noted for each worm: length and width of animal, length of radioles, termination of

thoracic membranes, number of both thoracic and abdominal setigers, number of radioles on left and right side of body, point of insertion of peduncle, length and width of operculum, and the shape of setae in first setiger. The mean and standard deviations have been computed from non-juvenile specimens with a thoracic width of at least 50% of the maximum observed width. For example, the notation (30)32-36.8-40 (SD=2.3, n=10) means that the number of abdominal segments observed is 30-40, but that SD and mean (36.8) have been computed over ten non-juvenile specimens in which the range was 32-40.

An attempt was made to discern populations from their tubes. For this purpose eight measurements were taken in the large samples of Tadjourah, Oga (Stn M), Shimoda (Stn N) and Darnley Island (type series of *Dentalium laevis* Brazier; "rough" and "smooth" tubes analysed separately); interior and exterior diameters of tube mouth (orifice) and apex, maximal width, length (measured in straight line between apex and orifice), length from apical width of 0.8 mm to orifice (to avoid effects of missing apices), and from height (defined as the widest distance between inner curve of tube and the straight line between apex and orifice). Various ratios have been computed, notably the arcuation (height: length  $\times$  100, c.f. Palmer, 1979:739). The data were filtered for evidently incomplete tubes, and for tubes with a maximal width of less than 50% of the largest specimen from the sample. In some localities only larger tubes were measured, in this case unfiltered and filtered data are the same. After analysis of the results of these four samples only length, maximal width and height were noted for the tubes of the remaining samples.

The following abbreviations have been used in the text: AM — Australian Museum, Sydney; BMNH — British Museum (Natural History), London; ITZ — Instituut voor Taxonomische Zoölogie, Amsterdam; MNHN — Muséum National d'Histoire Naturelle, Paris; MPW — Muzeum Przyrodnicze, Wrocław; NSMT — National Science Museum, Tokyo; RMNH — Rijksmuseum van Natuurlijke Historie, Leiden; tH — collection number in ZMA; W — short for collection number AM W; ZMA — Zoölogisch Museum, Instituut voor Taxonomische Zoölogie, Amsterdam; ZMB — Zoölogisches Museum, Berlin; ZMK — Zoologisk Museum, Kjobenhavn; ZSI — Zoological Survey of India, Calcutta.

## Taxonomic Account

### *Ditrupa* Berkeley, 1835

**Type species.** *Dentalium subulatum* Deshayes, 1825 = *Dentalium arietinum* O.F. Müller, 1776; designated by Bush, 1905 (following synonymy of Saint-Joseph, 1898).

**Diagnosis** (emended). Tube free, not attached to substratum, elongated curved fusiform, circular in cross-section. Tube open at both sides, broadening anteriorly though exterior tapers just prior to tube mouth. Tube wall consisting of variably hyaline outer and opaque

inner layer. Operculum hemispherical with chitinous end-plate. Peduncle positioned as first radiole; smooth. No pseudo-operculum. Branchial radioles arranged in two half circles, inserted on pectinate basis. Pair of filiform mouthpalps adjacent to dorsal lip. Large entire collar continuous with thoracic membranes, ending at first setiger. Six thoracic setigers, all with setae and uncini. Thoracic setae limbate and capillary, first setiger sometimes with special setae. Uncini saw/rasp-shaped (Fig. 61) or rasp-shaped (Fig. 60) with bifurcate peg; 20–30 teeth visible in profile. Abdominal setae geniculate; uncini rasp-shaped, with up to 8 rows of teeth, 20–25 in profile.

**Remarks.** *Genus.* *Ditrupa* was proposed as a new genus by Berkeley (1835:425–426) for two species he identified as *Dentalium subulatum* Deshayes, 1825 and *Dentalium gadus* Montagu (= *Dentalium coarctatum* Lamarck). No type species was designated.

The type locality of *Dentalium subulatum* is not known. Berkeley's Irish material, also figured by Chenu (1842–1845, Livr. 7, pl.6 fig.25; Livr. 8, pl.7 fig.13, was considered a synonym of *Ditrupa arietina* (= *Dentalium arietinum* O.F. Müller, 1776) by Sars (1851:204). This synonymy was subsequently accepted by, for instance, Saint-Joseph (1898:444) and Bush (1905:223), the latter first designated *Ditrupa arietina* (= *Dentalium subulatum*) as the type species of the genus *Ditrupa*.

Lommerzheim (1979:143) considers that the earliest name for the type species is *Dentalium corneum* Linnaeus, 1767 but the status of that name and the species it applies to is unclear, as fully discussed later in this paper.

Berkeley included *Dentalium gadus* Montagu (= *Dentalium coarctatum* Lamarck) in *Ditrupa* as well. Both names have a confused and confusing history. Montagu (1803:496) mentions *Dentalium gadus* from "...many parts of the British channel...known to mariners by the name of Hake's tooth..." Although the description and figure evidently apply to the scaphopod *Cadulus* (*Gadila*) *gadus* (Montagu, 1803), Jeffreys (1877:157) had already surmised from the locality and common name that Montagu's material at least partly belonged to the serpulid *Ditrupa arietina* O.F. Müller, 1776. As for *Dentalium coarctatum*, the name was used first by Brocchi (1814:264, pl.1 fig.4) for a fossil from south Italy with is considered to belong to *Ditrupa* by, for instance, Pilsbry & Sharp (1898:242), Wrigley (1951:191) and Ronchetti (1952:5). However, *Dentalium coarctatum* :Lamarck (1818:346) was referred to the scaphopod *Dischides bifissus* by Jeffreys (1877:157), correctly so judging from the figures by Chenu (1842–1845:livr.7, pl.6 figs 26, 36). *Dentalium coarctatum* :Philippi (1844:208) and :Costa (1850:38–39) are considered to be scaphopods of the genus *Cadulus* by Pilsbry & Sharp (1898:144,237).

**Thorax.** In almost all Sabellida the first setiger has only collar setae, all other thoracic setigers have setae and uncini. It would appear that uncini secondarily are lost in the collar segment, "setae + uncini" being the normal character state (the biramous condition occurs in both the Polychaeta and Oligochaeta). The fact that the first setiger in *Ditrupa* shows setae + uncini might thus be explained as a plesiomorphic character. However, it is generally assumed

in the literature (e.g. Saint-Joseph, 1898:445; Zibrowius, 1868a:170; Bianchi, 1981:123–124) that this is not the case, but that the collar setae have become lost in *Ditrupa*. Reasons for this assumption are not given in the literature. Probably they are implicit: a pair of excretory organs are depicted anterior to the first setiger by Saint-Joseph (1898:445, fig.251). Since these occur along with collar setae in the first segment of other serpulids, he may have assumed that the collar setae are lost. Even in tiny specimens (2–4 mm), Zibrowius (1968b:384) was unable to find traces of collar setae. Nevertheless, secondary loss of collar setae, reported to occur incidentally in *Pomatoceros*, *Spirobranchus* and *Sclerostyla* (ten Hove, 1970:221; 1973:4,10) is the most likely explanation for the characteristic arrangement of the first setiger in *Ditrupa*. Thus *Ditrupa* would be apomorphic on two counts: first, loss of collar setae and, second, takeover of their function by the second setiger. In the other examples given, loss of collar setae is not accompanied by visible compensatory changes. *Placostegus*, also without collar setae, shows a belt of eyespots in the first segment; its broadly rasp-shaped thoracic uncini and short geniculate abdominal setae differ greatly from those of *Ditrupa*. Moreover, the tube structure, though hyaline, is completely different (ten Hove & Zibrowius, 1986:fig.5; Zibrowius & ten Hove, 1987:fig.3).

**Relations with other genera.** The relation of *Ditrupa* to other serpulid genera is very unclear. Grube (1862:63) placed it in *Placostegus* Philippi, 1844, solely upon the similarity in operculum. Mörch's (1863:424) literature based discussions concentrated upon the question whether the branchial radioles have one or two rows of pinnulae, and on the large collar of *Ditrupa*. However, all serpulids have two rows of pinnules, and the extent of the collar varies according to species. Mörch also alluded to a variety of *Placostegus*, which would indicate that one and the same species can live both in adnascent and free tubes ("...en Antydning til et en og samme Art kan leve baade fastheftet og frit.") Although *Placostegus* species indeed tend to grow perpendicular to the substrate, and break off easily, free living specimens have never since been mentioned in the literature. It certainly cannot be used to infer a relation with *Ditrupa*. All three arguments are moot.

*Serpula crenata* (Ehlers, 1908), widely differing in morphology from *Ditrupa*, is reported to also have curved free tubes, though angular in cross-section. *Hyalopomatus*, also occurring in bathyal environments, very often shows a small area of attachment before growing away from the substrate. It is likely that *S. crenata* starts similarly, becoming detached in later life. It seems probably that curved tubes are an adaption to a soft sediment existence and, therefore, convergent amongst these three genera. This is probably also the case for the fossil subgenera *Triditrupa*, *Tetraditrupa* and *Pentaditrupa* as discerned by Regenhardt (1961:72–75), which do not appear to be related to *Ditrupa* at all, but more likely to a secondarily free living form like *S. crenata*.

*Ditrupa* associates, either artificially or by implication, with a number of genera in keys. Bush's (1905:221–223) key links *Ditrupa* with *Vermiliopsis* s.l. on the basis of its

operculum with chitinous endplate and the erroneous assumption that *Ditrupa* should have limbate collar setae. A chitinous endplate is widely spread in serpulids, and cannot be used for phylogenetic decisions on this level. In the keys of Southward (1963:585–587) and Fauchald (1977: 141–142), *Ditrupa* associates with *Bonhourella* (see synonymy), *Placostegus* (see above), *Sclerostyla* Mörch, 1863 (those missing collar setae only), *Dasyneuma* Saint-Joseph, 1894 (on the mistake that this genus lacks collar setae) and *Marifugia* Absolon & Hrabe, 1930. *Marifugia* indeed shows a superficial resemblance (no collar setae, limbate thoracic setae, uncini with gouged peg), however, it has an adnascent tube and occurs in freshwater caves. Moreover, *Marifugia* has only eight teeth per thoracic uncinus and long abdominal setae which are geniculate like those in *Vermiliopsis* s.l. (ten Hove, unpublished).

In the present state of knowledge it is not possible to attribute *Ditrupa* to one of the recognised groups such as *Pomatoceros*/*Spirobranchus* or *Serpula*/*Crucigera*/*Hydroides*.

*Ditrupa arietina* (O.F. Müller, 1776)

*Dentalium arietinum* O.F. Müller, 1776: 236. Diagnosis – Denmark and/or Norway.

*Dentalium corneum* (non Linnaeus) Lamarck, 1818: 345. Diagnosis – material studied.

p.p. *Dentalium strangulatum* Deshayes, 1825: 372–373. Diagnosis – one syntype studied, see nomenclature of *Ditrupa gracillima*.

*Dentalium subulatum* Deshayes, 1825: 373, pl.16 fig.29. Diagnosis – unknown locality.

*Ditrupa subulata*.—Berkeley, 1835: 424, pl.19 fig.2. Diagnosis – Ireland.—Chenu, 1842–1845: livr.7, pl.6 fig.25; livr.8, pl.7 fig.13. Diagnosis – Ireland.

*Serpula libera* Sars, 1835: 52–54, pl.12 fig.33. Description – Norway.

*Ditrupa arietina*.—Sars, 1851: 204. Name only.—Saint-Joseph, 1898: 443–447, pl.23 figs 249–254. Description – Gulf of Biscay.—Fauvel & Rullier, 1959: 196 (in part; their specimen from Rio de Oro is *D. arietina*, the other two specimens are scaphopods. Material studied MHNH; also fide Zibrowius, 1973:78–79).—Zibrowius, 1968a: 169–171, pl.9 figs 8–13. Description – Mediterranean Sea.—Zibrowius, 1968b: 383–385. Diagnosis – material studied.—Bianchi, 1981: 124–125, fig.47. Diagnosis – Italy.

*Dentalium goreanum* Clessin, 1896: 42, pl.10 figs 9–10. Description of tube – Senegal.

*Ditrypa arietina*.—Bush, 1905: 223. Name only.—McIntosh, 1923: 380–383, pl.122 figs 5–6, pl.132 fig.1. Description, discussion – U.K., Azores, Mediterranean.

**Material studied.** ICELAND – off south Iceland, coll. R.E. Stobbs (1 tube, AM W201218). NORWAY – Bergen (3 mounted tubes, older label *Serpula libera* Sars. UNITED KINGDOM – off Flamborough Head, UK 68, 29 Jan. 1987 (1 specimen, private collection E. de Wit). FRANCE – “*Travailleur* stn 111, 9 Aug. 1882, 100 m” (33 tubes, MHNH; label not conform list of localities of the “*Travailleur* according to note by Zibrowius); Mediterranean, Baie de Cavalaire, coll. Bodoy, 1980,

40–50 m (50 tubes, ZMA tH 500). MOROCCO – Atlantic, 33°30'N, 08°24'W, stn 56, *Vanneau*, 24 June 1924 (32 specimens, MNHN). MADEIRA – Lapa Island, stn 10 *Jean Charcot*, 12 July 1966 (10 specimens ZMA tH 69); Funchal, coll. Sjorensen (2 tubes, ZMK); west of Deserta Grande, 32°29'N, 16°31'–32'W, stn 19, 21 *Onversaagd*, 8 Mar. 1976 (2 specimens from 30 m, 100 tubes from 240 m, ZMA tH 560/1). CANARY ISLANDS – south-west off Palma 28°39'N, 17°58'W, stn 4.148 RV *Tydemann*, 3 June 1980, 60–80 m (10 specimens, 100 tubes, ZMA tH 559). RIO DE ORO – Cap Blanc, 21°05'N, 17°14'W, stn 1, *Calypso*, 10 May 1956 (1 tube, MNHN).

**Diagnosis.** *Tube.* The tube (Figs 19–21,23) is tusk-shaped and slender, open at both ends, with a length of up to 34 mm (usually 25–32 mm). Generally tubes appear to be whitish, mottled with brown even after 150 years in collection; however, this colouration of the inner tube layer may vary according to population. The outer tube layer is hyaline, unless it is opaque by abrasion. Irregularities in tube wall thickness may cause ‘annuli’ (e.g. figs 9–10 of *Dentalium goreanum* Clessin, 1896: 42; Fig.23). However, these annuli never are so abruptly and regularly elevated as in the “monilifera” forms of *Ditrupa gracillima*.

	Maximum tube width	Arcuation index
Cavalaire	1.9-2.32-2.7 (SD = 0.24)	10.5-12.8-15.0 (SD = 1.7)
all material	1.5-2.16-2.8 (SD = 0.33)	10.5-13.5-17.1 (SD=2.0)

For explanation see *D. gracillima*.

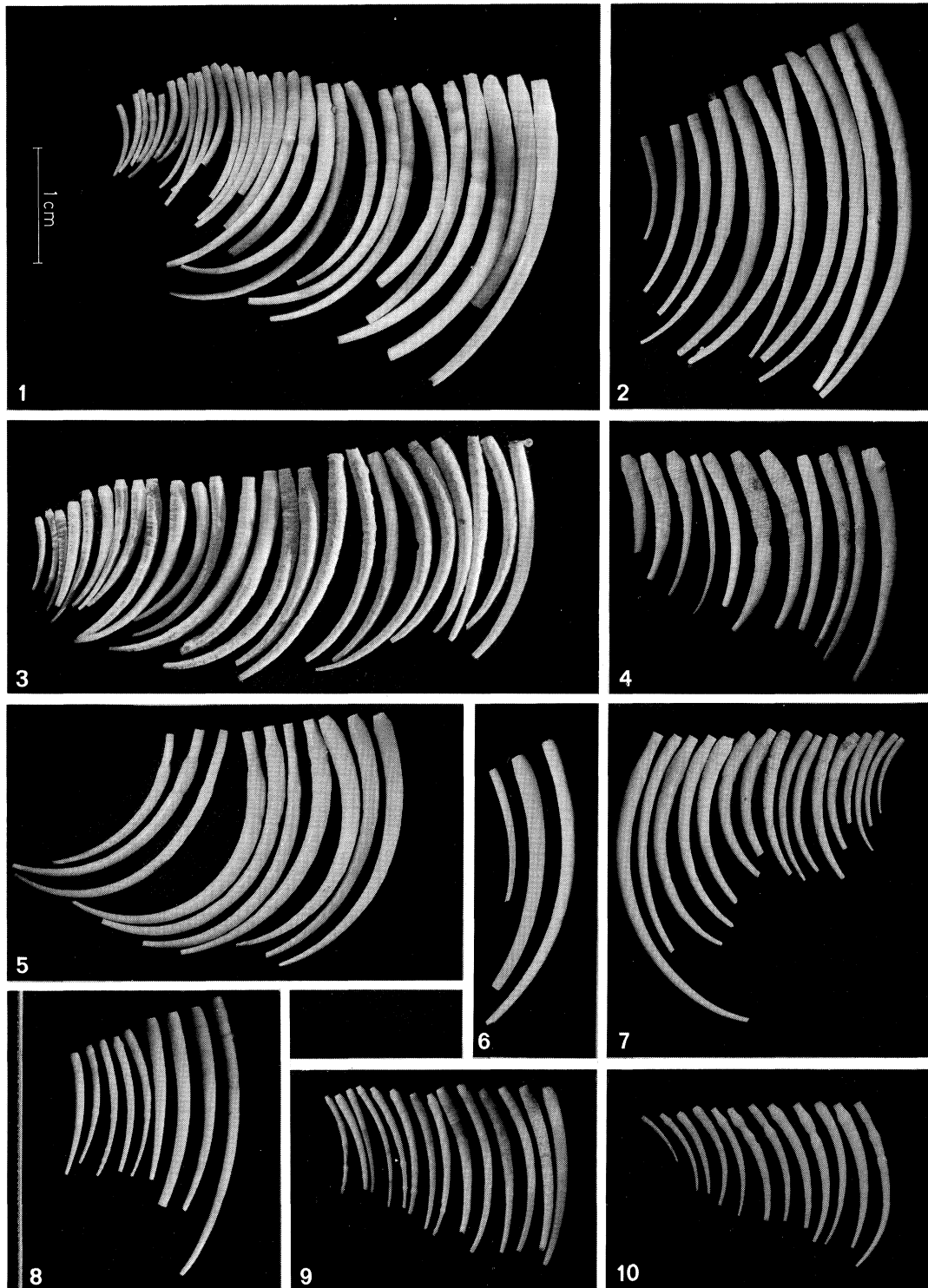
*Branchiae and peduncle.* Generally 10–12 pairs of branchial radioles. See further *D. gracillima*.

*Operculum.* Globular, with a distal chitinous endplate. Endplate flat and circular, usually featureless. Rarely a small central spine, surrounded by a few concentric growth-rings. Globular ampulla has form of an inverted cone. We have not been able to find a talon to the opercular plate, as figured by Nelson-Smith & Gee (1966:fig.13B). At most there is a faint depression of the chitinous endplate. Diameter of operculum up to 1.2 mm, length of ampulla up to 1.3 mm.

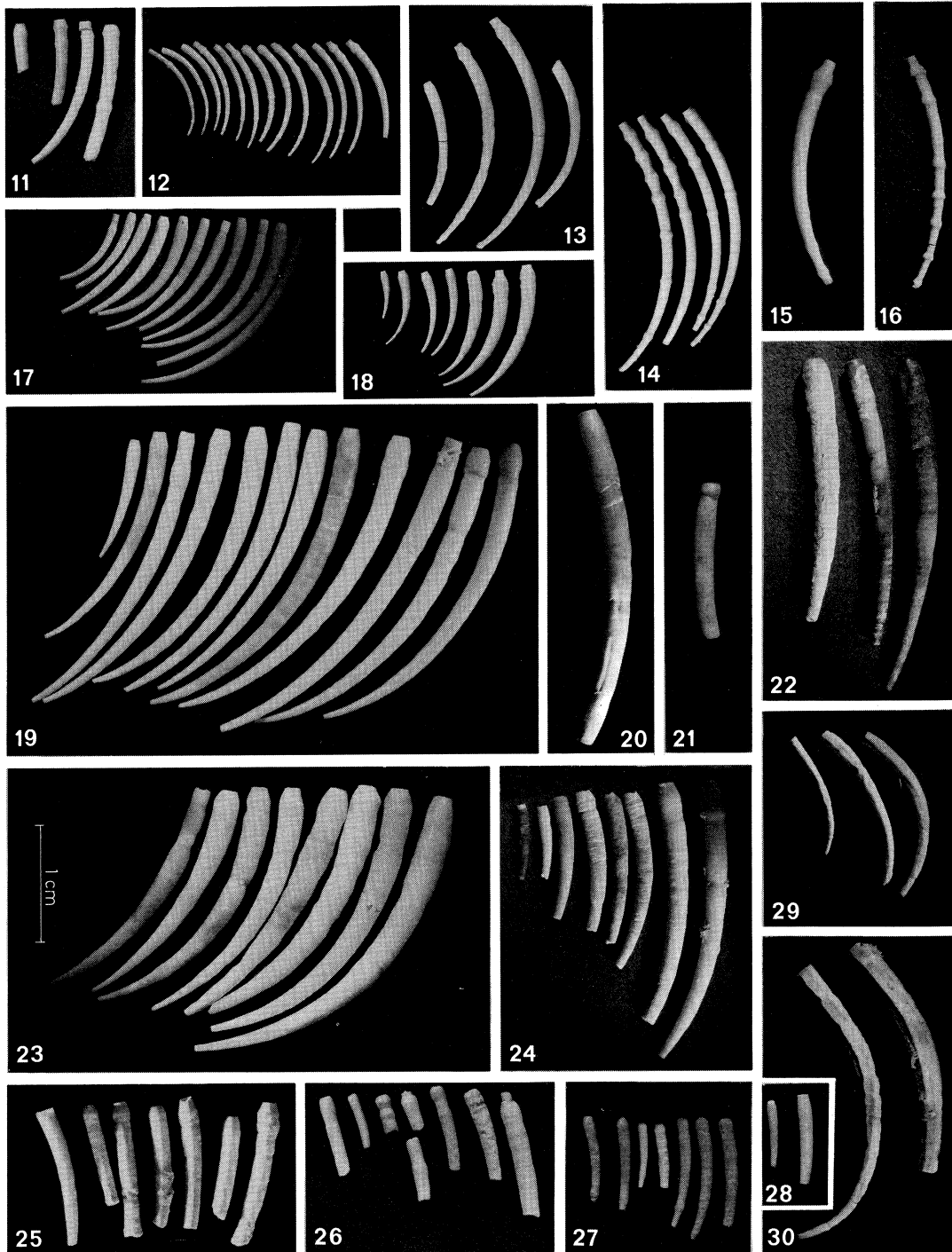
*Collar and thoracic membranes.* Collar well developed, with entire edge. Bianchi (1981:123–124) mistook the slightly swollen sides of the thorax for a continuation of the thoracic membranes. Contrary to his opinion and fig.47b, there is no apron across the abdomen, but thoracic membranes end just anterior to the first setiger.

*Setation.* Thorax has only 6 setigers, rather than the 7 usual in other serpulids, and all are uncinigerous. Collar setae absent. First setiger occupies a place similar to that of collar setiger in other serpulids, is widely spaced from remaining 5 setigers. All thoracic setae, including those of first setiger, are limbate and of two sizes (checked in 25 specimens from 3 localities). Uncini along entire thorax saw- to rasp-shaped for their greater parts but with 2 or 3 rows of 2–3 teeth just above anterior fang. Up to 22 teeth can be seen in profile.

The up to 55 abdominal setigers have all rasp-shaped uncini. The posterior 20–25 setigers may have a few almost capillary setae as well, with faintly geniculate tips.



**Figs 1—10.** For full details of localities see text. *Ditrupa gracillima* — 1: Queensland, Darnley Island, smooth tubes; lectotype of *Dentalium laeve* Brazier is 20th specimen from left; juvenile tubes with up to 4 annuli; 2: Japan, Shimoda, tubes 3,6 and 8 are rough or smooth to rough; 3: Queensland, Darnley Island, rough and smooth to rough (6,13,14 from left) tubes; 4: La Réunion (170–225 m), variation in roughness and expansion rate; 5: Gulf of Tadjoura, variation in expansion rate and arc, extended orifices; 6: syntypes of *D. gracillima*; 7: Papua, Manubada, tubes 4 and 7 are rough-smooth-rough; 8: La Réunion (45 m), up to 4 annuli; 9: La Réunion (75–90 m), smooth and rough tubes, up to 5 annuli; 10: Western Australia, Bunbury, irregular growth patterns but no real annuli. All approximately (10% error) to same scale.



**Figs 11—30.** For full details of localities see text. *Ditrupa gracillima* — 11: New South Wales, Sydney, up to 3 annuli; 12: Western Australia, Dampier, monilifera-forms, but also 1 tube with a single annulus; 13: Iranian Gulf, Patrick Stewart Bank, up to 3 annuli; 14: Solomon Islands, monilifera-forms with 4–7 annuli; 15: New South Wales, Cape Three Points; 16: Indonesia, Great Kei, monilifera-form; 17: Red Sea, Menar Aba Samra, smooth to/and rough tubes; 18: Indonesia, Kalimantan, high expansion rate. *Ditrupa arietina* — 19: Marseille; 20: off South Iceland, with abnormal longitudinal depression; 21: syntypes of *Dentalium strangulatum*; 23: France, stn 111. *Ditrupa aff. arietina* — 22: Pleistocene, Italy, Torrente Stirone (W 201219); 24: Pliocene, Italy, Bodognano (W 201238). *Ditrupa strangulata* — 25: Eocene, France, Basin of Paris, Belleu (ZMA tH 115). *Ditrupa gracillima* — 26: Miocene, Victoria, Rutledge Creek; 27: Miocene, Victoria, Hamilton, some tubes with annulus; 28: Miocene, New Zealand. *Serpula crenata* — 29,30: New South Wales, off Eden (W 201245). All approximately (10% error) to same scale.



*Ecology.* Although tubes have been collected from depths down to 530 m, specimens are known only to a depth of 150m.

**Remarks.** Sars (1835) described the animal as a new species *Serpula libera*, since *Dentalium arietinum* Müller was based on an empty shell only. In 1851 he placed his own species into the synonymy of *Ditrupa arietina*, the older available name. A full revision of the species, which has been mentioned in the literature well over a hundred times under at least ten specific names falls outside the scope of present paper.

**Distribution.** Boreal to subtropical: East Atlantic from Iceland to Azores, Canary Islands and Senegal; Mediterranean and ?Black Sea.

### *Ditrupa gracillima* Grube, 1878

?p.p. *Dentalium strangulatum* Deshayes, 1825 (1826?): 372–373, pl.16 fig.28. Diagnosis – not the fossils from Europe, but the recent material from “Terres Australes”, see Nomenclature.

?p.p. *Ditrupa strangulata*.—Mörch, 1863: 426. Diagnosis – Terres Australes.

*Dentalium laeve* (non Turton, nec Schlotheim) Brazier, 1877: 59. Diagnosis – north-east Australia, material studied, AM A 93, i-iii, C.7523, a, C.2528.—Ponder & Stanbury, 1972: 53. Lectotype in Macleay Museum, presently deposited in the AM. See Nomenclature.

*Ditrupa gracillima* Grube, 1878: 279–280. Description – Philippines.—Wiktor, 1980: 281. Type in MPW, nr.272.

*Cadulus laevis*.—Pilsbry & Sharp, 1898: 195. No new data, although they doubt if the species is a scaphopod.—Hedley, 1900: 499, pl.26 figs 8–10. Diagnosis after types.—Boissevain, 1906: 75–76, pl.3 fig.43. No new data.—?Cotton & Godfrey, 1933: 149. Diagnosis – south-west of Neptune Islands, SA.

*Bonhourella insignis* Gravier, 1905: 448–451. Description – Djibouti, Golfe de Tadjourah, 20 m.—Gravier, 1906: 115 (name only).—Gravier, 1906–1908: 134–138, figs 493–495, pl.8 figs 301–302. Description – Djibouti, Golfe de Tadjourah, 20 m. See Remarks.

*Ditrupa arietina* (non Müller) Gravier, 1906: 113 (Name only). Djibouti, 15–20 m, material studied MNHN.—Gravier, 1906–1908: 124–125. Description – Djibouti, 15–20 m, material studied MNHN.—Fauvel, 1932: 247. Description – Andaman Sea, 1500 m; see Introduction.—Fauvel, 1933a: 80 (name only). Gulf of Eilat, Suez.—Fauvel, 1933b (name only). Gulf of Eilat, Suez.—Monro, 1937: 319 (name only, but referring to var. *monilifera* for Aden material). Red Sea, South Arabian Coast, 26–38 m, Gulf of Aden, 655–732 m, material partly studied.—Mesnil & Fauvel, 1939: 36 (name only). Salibabu Island, material studied, ZMA V Pol 1639.—Wesenberg-Lund, 1949: 358 (name only). Iranian Gulf, 50–60 m, material studied ZMK.—Fauvel, 1953: 470, figs 246a–g. Andaman Sea, 1500 m. [N.B. The figures are a copy of Fauvel, 1927 and referring to Mediterranean material].—p.p. Zibrowius, 1973: 78 (name only). Malagasy, Djibouti, material from last

locality studied, MNHN.—Imajima, 1978: 69 (name only). Izu Islands, Japan, up to 85 m.—Imajima, 1979 (name only). Honshu, Japan, part of material studied, ZMA tH 383.—Imajima, 1982: 53 (name only). Palau Islands, 5 m, part of material studied, ZMA tH 458.—Soota, Misra & Chakraborty, 1980: 69. Material studied, ZSI.—Hong, 1984: 42–46, fig.4a–m. Description – South Korea.—Vine & Bailey-Brock, 1984: 146 (name only). Red Sea, 75–80 m.

?*Ditrupa australia* Bretnall, 1921: 156, fig.2. Description – holotype not found in AM in 1986.—Dew, 1959: 47, fig.18A. Diagnosis – Queensland, New South Wales, 2–20 m. Material not found in AM.—Straughan, 1967: 248 (no new data). see Remarks.

*Ditrupa brazieri* Bretnall, 1921: 156, fig.1. New name for *Dentalium laeve* Brazier, of which the holotype is in the Macleay Museum, University of Sydney.

*Ditrupa arietina* var. *monilifera* Fauvel, 1932: 247, fig.12. Diagnosis – Andaman Sea, 642 m, material studied ZSI.—Mesnil & Fauvel, 1939: 36. Diagnosis – Kei Island, material studied ZMA V Pol 1634.—Fauvel, 1953: 470, fig.246h. Andaman Sea, 642 m, material studied ZSI.—Soota, Misra & Chakraborty, 1980: 69. Material studied ZSI.

not *Ditrupa crenata* (Ehlers).—Mesnil & Fauvel, 1939: 36. Indonesia. This species belongs to the genus *Serpula* s.l., material studied ZMA V Pol 1640, 1739. It also is known as *Dentalium tiwhana* Dell (1953: 48, figs 17–22; 1957: 564, figs 17–19, pl.39 figs 6–7) part of material studied, AM W 201251.

*Ditrupa amphora* Dew, 1959: 48, fig.18D. Diagnosis – Queensland, 150 m; material not found in AM.

*Ditrupa laeve*.—Dew, 1959: 47, figs 18B,C. Diagnosis – Queensland, 100 m, material not found in AM.

*Ditrupa arietina monilifera*.—Hartman, 1974: 200 (name only). Bay of Bengal off Kakinada, 37 m.

**Material studied** (unless stated otherwise the tubes are “smooth”; “monilifera” forms are indicated by \*). LA RÉUNION — 19°44′–21°20′S, 54°08′–55°52′E, *Marion Dufresne* campagne MD32, 12 Aug. 1982 - 2 Sept. 1982, 40–980 m, stn DC 1, 3, 10, 41, 56, 86\* (75–90 m), 124, 126\* (110 m), 128, 176, FA 39, DR 90, 154 (altogether 500 tubes of which 40 “rough”, 7 specimens: MNHN, ZMA tH 617, 618, W 202505/6, USNM 104939/40). MADAGASCAR — south-west Madagascar, région de Tuléar: Andetoky, S.Grand Récif, Ankarandara, Lagon de Tuléar, coll. B.Thomassin, J.Picard *et al.* – stn 222, 29 Sept. 1969, 24 m (1 spec., 1 rough and 1 smooth tube); 227, 2 Oct. 1969, 27 m (1 spec., 7 tubes); 231, 236, 240, 3–8 Oct. 1969, 15–36 m (1 spec., 13 tubes of which 8 rough); 617, 621, 622, 623, 9–11 Apr. 1972 (2 specs, 24 tubes of which 11 rough); 658, 28 Oct. 1971, 112 m (8 tubes); 726, 730, 734, 737, 738, 741, 20–25 May 1972, 12 m (64 tubes, of which 12 rough); 1305, 1307, 1316, 1321, 1330, 1340, 1341, 1351, 1352, 1354, 28 Aug. 1963 - 25 Sept. 1963, 10–77 m (4 specs, 50 tubes of which 6 rough); 1336, 12 Sept. 1963, 280 m (1 tube). Most specimens MNHN; some ZMA tH 619, W 202504 and USNM 104938. COMORES — Campagne BENTHEDI Mayotte, Sud îlot Gombé Doumé, 12°45′S, 45°15.9′E, stn 18S, 22 Mar. 1977, 15 m (2 specs, MNHN); W de la Grande Passe de l’Ouest, 12°46′S, 44°57.6′E, stn 62DS, 29 Mar. 1977, 530–535 m (59 tubes\*, some living, MNHN, ZMA tH 613); Sud Banc de la Zélée, 12°25.6′S, 46°16.2′E, stn 110S, 10 Apr. 1977, 24m (1 tube, MNHN). GULF OF TADJOURA — between



- Pingouin and Météore Reefs, coll. Gravier, 26 Feb. 1904 - 22 Mar. 1904, 15-20 m (30 specs, 80 tubes, MNHN and ZMA tH 598). RED SEA — stn. MB 1d, coll. John Murray Expedition, 17 Sept. 1933, 26 m (1 spec., 2 rough tubes, BMNH ZK 1937.9.2.582); Gulf of Aqaba - stn. 38, coll. R.Ph. Dolfuss, 1 Feb. 1929 (7 tubes, MNHN); Nuweiba, coll. J. Levy, Apr. 1977, coral sand, 18 m (1 tube, W 201228); off West Murach, stn. 36, 9 Oct. 1976, 73-82 m (15 tubes, W 201258); off Nuweiba el Tarabin, stn 34, 8 Oct. 1969, 137-146 m (2 tubes, W 201248); off Menar Aba Samra, stn 3, 6 Oct. 1969, 46-49 m (75 rough and smooth tubes, W 201296); off Mersat Abu Samra (north), stn 4, 6 Oct. 1969, 51-53 m (35 rough and smooth tubes, W 201254); same (centre), stn 5, 6 Oct. 1969, 49-55 m (13 rough and smooth tubes, W 201294); Eilat, stn 8, coll. C. Lewinsohn, 7 Sept. 1966, 60-80 m (10 tubes, W 201304); marine station, stn AQ4, coll. B.A. Thomassin, 17 Apr. 1981, 10 m (1 spec., MNHN). SOUTH ARABIAN COAST — stn 43, 45, coll. John Murray Expedition, 28-29 Oct. 1933, 40-83 m (3 incomplete specs, 16 rough and smooth tubes, BMNH ZK 1937.9.2.581, 585-589). GULF OF OMAN — stn 72, coll. John Murray Expedition, 26 Nov. 1933, 75 m (40 tubes, BMNH ZK 1937.9.2.590). IRANIAN GULF — 7 miles east-north-east of Patrick Stewart Bank, *Ingolf* stn 71D, coll. G. Thorson, 19 Apr. 1937, 69 m (3 tubes, ZMK); 29°04'N, 49°56'E, *Ingolf* stn 23D, coll. G. Thorson, 13 Mar. 1937, 50 m (1 tube, ZMK); 26°33'N, 56°42'E, stn 94, coll. Blegvad, 28 Mar. 1938 (1 tube, ZMK). ANDAMAN SEA — 11°26'30"N, 92°53'45"E, *Investigator* stn 322, 378 fms (1 specimen\*, TYPE of var. *monilifera*, ZSI). SRI LANKA — north of Trincomalee, 8°54.5'N, 81°05.5'E, stn 260, coll. M.V. *Survey*, 12 Aug. 1921, 29 m (6 tubes of which one rough, W 201259); 9°16'N, 79°28.5'E, stn 390, coll. M.V. *Survey*, 19 Sept. 1921, 13 m (1 tube, W 201250), Palk Strait, 9°57.5'N, 79°46'E, stn 358, coll. M.V. *Survey*, 16 Sept. 1929, 13 m (1 tube, W 201234); 12 miles south of Galle, stn 187a, 27 Dec. 1920, 91 m (1 tube, W 201285). SINGAPORE — east of Singapore, 1°45'N, 106°40'E, coll. Andréa, 1869, 63 m (2 tubes, ZMK). THAILAND — Gulf of Thailand, off Koh Mok, Koh Kut and Koh Chuen, coll. Th. Mortensen, Jan. - Mar. 1900, 18-36 m (4 tubes, ZMK). HONG KONG — east side of Mirs Bay, south-east of Ping Chau Island, coll. A.J. Brandt & W.F. Ponder, 12 Nov. 1973, sand deposits from dredging, to 8 m (10 tubes, W 201231). KOREAN STRAITS — west of Goto Islands, 33°02.5'N, 128°48.5'E, stn 11, HMS *Sylvia*, coll. Capt. St. John, 1876, 40 m (2 specs in smooth tubes, 1 rough tube BMNH ZH 1878.10.25.2); 33°14'N, 128°55'E, probably stn 17, HMS *Sylvia*, coll. Capt. St. John, May 1876, with *Spirobranchus laticapus* (Marenzeller, 1885), 72 m (1 tube, BMNH ZB 1977.102). JAPAN — Sea of Japan, 130 m (2 dried out specs in rough and smooth tube, BMNH ZK 1921.5.1.4513); Honshu, Sea of Japan, off Oga, 13 localities between 39°48'-40°06'N and 139°41'-53'E, 31-101 m (200+ specimens); off Akita, 39°47'N, 139°51'E, 60 m (1 spec.). Honshu, Pacific Ocean, Sagami Nada, 35°09'N, 139°23'E, 500 m (1 spec.); Suno-Saki, coll. Th. Mortensen, 12 June 1914, 36-144 m (3 tubes, ZMK); off Shimoda, 18 localities between 34°37'-45'N and 138°56'-139°02'E, 39-120 m (150+ specimens). All specimens (except ZMK) ident. M. Imajima, *D. arietina*, NSMT, ZMA tH 608, 609; off Kushimoto, coll. M. Imajima, July 1978, 58-60 m (2 specs, rough tubes, ZMA tH 383). PALAU ISLANDS — Arumonogui, coll. M. Imajima, July 1980 (2 specs, ZMA tH 458). PHILIPPINES — Pandanon, coll. Semper (SYNTYPES, 1 incomplete, partly macerated specimen and 3 tubes, MPW 272; 2 incomplete specimens with tubes, ZMB 1560); 11°42.6'N, 122°34.5'E, stn 140, campagne MUSORSTOM 3, 6 June 1985, 99-93 m (3 tubes, MNHN); off Jolo, coll. Th. Mortensen, 20 Mar. 1914, 38 m (1 spec., ZMK). INDONESIA — Kalimantan (=Borneo; 7 tubes, W 201226); off Java, 8°S, 114°E, stns 6, 9, coll. Th. Mortensen, 5-6 Apr. 1929 (30 tubes, ZMK); Salibabu Island, anchorage off Lirung, Siboga stn 133, 25/27 July, 1899, mud and hard sand, to 36 m (1 rough tube, ZMA V. Pol. 1639); Ambon Bay, off Kota Ambon, 3°42'S, 128°10'E, Snellius II Expedition, stn 4.008, 4 Apr. 1984, sandy, 105 m (1 tube, RMNH 18173); Amboina, leg. Semon (2 tubes, ZMB F412); Kei Island, off Toeal, stn 19, coll. Th. Mortensen, 14 Apr. 1922, 20 m (1 rough tube, ZMK); west of Great Kei Island, 5°53.8'S, 132°48.8'E, *Siboga* stn 262, 18 Dec. 1899, solid bluish grey mud, 560 m (1 tube\*, ZMA V. Pol. 1634). PAPUA — off Port Moresby, on sheltered north-west side of Manubada (Local) Island, coll. W.F. Ponder & P.H. Colman, 21 June 1970, in sticky sandy mud, 23 m (1 rough to smooth tube, W 201275); same, west end of Manubada (Local) Island, coll. W.F. Ponder & P.H. Colman, 24 June 1970, just inside outer reef, sticky muddy sand, 18-22 m (180 tubes of which 35 rough or partly rough, W 201220, ZMA tH 607); south-west Port Moresby, off west side of Lolorua Island, coll. W.F. Ponder & P.H. Colman, 21 June 1970, 13-18 m (9 rough tubes, W 201263); off Cape Possession, near Yule Island, Gulf of Papua, coll. P.H. Colman, 12 Nov. 1970, 27 m (1 tube, W 201242). NEW CALEDONIA — 21°35.8'S, 166°29'E, stn DW106, campagne BIOCAL, 8 Sept. 1985, 650-625 m (2 specs\*, MNHN, ZMA tH 612). SOLOMON ISLANDS — west coast Malaita Island, off Laulesi, coll. P.H. Colman, 27 Aug. 1973, olive-grey mud and stones, 366 m (4 tubes\* with dry specimens inside, W 201290). AUSTRALIA — Western Australia: east of Hood Point, CSIRO, stn G2/109/62, HMAS *Gascoyne*, 82 m (8 tubes, W 201269); east off Cheyne Bay, 34°55'S, 119°00'E, CSIRO, stn G3/150/62, HMAS *Gascoyne*, 7 Aug. 1962, 75 m (6 tubes, W 201267); between Port Augusta and Cape Leeuwin, 34°40'-32'S, 114°56'-115°02'E, stn G3/170-171/62, HMAS *Gascoyne*, 9 Aug. 1962, 66-130 m (1 tube, W 201298); south-west of Cape Naturaliste 33°44.5'S, 114°26.1'E, stn 21, HMAS *Diamantina*, 16 Mar. 1972, 238-183 m (1 tube, W 201222); west of Bunbury, 33°03'S, 114°44'E, CSIRO, stn G3/175/62, HMAS *Gascoyne*, 10 Aug. 1962, 156 m (150 tubes, W 201207, ZMA tH 608); Houtman's Abrolhos, south of Pelsart Island, 29°06.7'-07.5'S, 113°58.5'-114°00'E, stn 33m, M.V. *Sprightly*, 91.4 m (1 rough tube, W 201230); 50 miles north of Boolbarly, 23°28'S, 113°28'E, CSIRO, 18 Nov. 1948, cone dredge, 91.5 m (2 tubes, W 201293); 170 miles west of Port Hedland, 19°29'S, 116°01'E, BMR stn E68-743, M.V. *Espirito Santo*, 1 Dec. 1968, 137 m (4 tubes\* W 201266); 72 miles north-north-west of Dampier, 19°28.9'-29.0'S, 116°29.4'-0'E, stn 26-18, FRV *Soela*, coll. B.W. Jenkins, 26 Oct. 1983, 110 m (30 tubes\*, W 201236); 120 miles north of Port Hedland, 18°42'S, 118°02'E, BMR stn E68-708, M.V. *Espirito Santo*, 25 Nov. 1968, 161 m (5 tubes, W 201221); 200 miles west of Roebuck Bay, 18°33'S, 119°08'E, BMR stn E68-554, M.V. *Espirito Santo*, 128 m (4 tubes, W 201252); 280 miles west of Roebuck Bay, 18°30'S, 118°03'E, BMR stn E68-576, M.V. *Espirito Santo*, 11 Oct. 1968, 238 m (5 tubes\*, W 201278). Northern Territories: Darwin, off Emery Point, coll. P.H. Colman, 25 Oct. 1969 on sandbar (1 tube, W 201284); 200 km north of Melville Island, 9°23'S, 131°22'E, BMR P69-1186, M.V. *San Pedro Sound*, coll. P.H. Colman, 15 Nov. 1969,

clayey sand, 215 m (1 tube, W 201223); 250 km north of Melville Island, 9°09'S, 131°35.5'E, BMR-1176, M.V. *San Pedro Sound*, coll. P.H. Colman, 14 Nov. 1969 (1 tube, W 201209); 91 km north of Goulburn Island, 10°42'S, 133°36'E, BMR stn 1065, M.V. *San Pedro Sound*, coll. P.H. Colman, 31 Oct. 1969, clayey sand, 58 m (2 tubes, W 201282); 210 miles north-east of Croker Island, 8°18'S, 133°58'E, M.V. *San Pedro Sound*, coll. P.H. Colman, 3 Nov. 1969, 132 m (1 tube, W 201271); 420 km north of Melville Island, 8°18'S, 134°11'E, BMR stn 1091, M.V. *San Pedro Sound*, coll. P.H. Colman, 3 Nov. 1969, sand, 141 m (1 tube\*, W 201206); 365 km north of Milingimbi Island, Arnhem Land, 8°48'S, 134°58'E, BMR stn 985, M.V. *San Pedro Sound*, coll. P.H. Colman, 18 Oct. 1969, clayey sand, 100 m (5 tubes, W 201261). Queensland: coll. E.J. Gabriel (1 rough tube, BMNH ZK 1965.31.77); Gulf of Carpentaria, south of Sweers Island, coll. D.F. McMichael & party, 7/9 Dec. 1963, 9-12 m (1 tube, W 201249); Torres Strait, Darnley Island, York Island, Chevert Exp. 1875, 5-30 fms (235 tubes of which 100 rough, AM A93, A93i, C7523, C7523a, C7528); off Murray Island, 9°56'S, 144°04'E, coll. C. Hedley, 30 Aug. - 3 Oct. 1907, 9-15 m (4 smooth and rough tubes, W 201239); Cape Grenville, Chevert Expedition 1875, 20 fms (1 tube fragment, AM A93iii); Princess Charlotte Bay, Chevert Expedition 1875 and coll. C. Hedley, 24 m (16 smooth and rough tubes, AM A93ii, W 201205); Low Isles, near Port Douglas, British Great Barrier Reef Expedition, coll. Iredale, McNeill & Livingstone, Oct. - Nov. 1928 (1 tube, W 201306); off Endeavour Reef, 20 fms (25 tubes of which 23 rough, AM); off Cairns, 16°51'36"-00"S, 146°01'12"-04'E, stn C23, HMAS *Kimbla*, coll. W.F. Ponder & I. Loch, 14 Oct. 1981, sandy mud/shell, 33-35 m (4 smooth and rough tubes, W 201262); off Townsville, soft sediment bottoms, 12-36 m (numerous, W 202429/30, ZMA tH 621); same, 18°49'S, 146°58'E, stn 938, R.V. *James Kirby*, 12 Jan. 1982, 34-35 m (3 rough tubes, W 201300); west of Hayman Island, 20°03'S, 148°50'E, stn 11, HMAS *Kimbla*, coll. P.H. Colman & F. Rowe, 19 Nov. 1977, grey, muddy sand, 33 m (7 tubes, W 201229, 201255); off Mackay, 21°03'S, 149°39.2'E, stn 15, HMAS *Kimbla*, coll. W.F. Ponder, I. Loch & P. Terrill, 13 Dec. 1977, thick, fine grey mud, 37 m (1 tube, W 201265); east of Broad Sound, 21°58.5'S, 150°45'E, stn 6, HMAS *Kimbla*, coll. P.H. Colman & F. Rowe, 18 Nov. 1977, coarse to fine sandy mud and shell, 57 m (3 tubes, W 201276); east of Broad Sound, 22°06'S, 150°49'E, stn 18, HMAS *Kimbla*, coll. W.F. Ponder, I. Loch & P. Terrill, 13 Dec. 1977, coarse shell, 53 m (1 tube, W 201243); 2 miles north-east of west side of Gillett Cay, Swains Reef, Australian Museum Party, 17-19 Oct. 1962, 63-72 m (50 rough tubes, W 201235); south-east of Swains Reef, 22°31'-32'S, 152°33'-42'E, stns 8, 9, HMAS *Kimbla*, coll. P.H. Colman, 5 July 1984, 78 m (3 tubes, W 201233, +17 tubes AM); 24.5 miles east of Lady Musgrave Island, 23°33.7'S, 152°37'E, stn 3, HMAS *Kimbla*, coll. P.H. Colman & F. Rowe, 17 Nov. 1977, yellow/grey mud, 348-339 m (1 tube\*, W 201232); Hervey Bay, coll. J. Voorwinde (1 tube, W 201204). New South Wales: east of Cape Three Points, 33°28'-29'S, 151°52'E, stn K79-20-08, FRV *Kapala*, coll. K.J. Graham, 5 Dec. 1979, 457-476 m (1 tube, W 201224); Port Stephens, HMS *Herald* circumnavigation, coll. Rayner & McDonald, Apr. 1857, 135-144 m (1 tube, BMNH ZH 1859.1.14.6); east of Sydney, CSIRO, HMAS *Gascoyne*, stn G2/55-57/62, 18 July 1962, 75-150 m (4 tubes, W 201286); 1.5 km south-east of Long Bay, shelf benthic survey, 20 July 1972 (2

tubes, AM).

**Fossil.** AUSTRALIA — Victoria: Warrambyne Creek, beside road bridge, about 3 miles south-west of Interleigh, coll. P. Rodda. Middle Miocene, Bairnsdalian or younger (25 tube fragments, W 201253); Rutledge Creek, to east of Port Campbell, coll. W.F. Ponder, T.A. Darragh & E.K. Yoo, 6 Mar. 1977. Middle Miocene, Bairnsdalian, Rutledges Creek. Member, Port Campbell Limestone (1000 tubefragments, W 201308/9, ZMA tH 558); Hamilton, Muddy Creek, north behind Yulecart Hall, coll. W.F. Ponder & E.K. Yoo, 3 Mar. 1977. Lower Miocene, Batesfordian, in Muddy Creek Marl, Lower Beds, just below base of Upper Beds (15 tubes partly rough, W 201227); same, south-west below Clifton Homestead, in McDonalds Bank, coll. W.F. Ponder & E.K. Yoo, 4 Mar. 1977. Pliocene, Kalimnan, Grange Burn 'Coquina', Upper Beds (1 tube, W 201288); Portland, rocky shore below Whalers Bluff, coll. W.F. Ponder & E.K. Yoo, 4 Mar. 1977. Miocene, Upper Portland Member (20 broken tubes of which 5 with orifice, W 201246). NEW ZEALAND — South Island: Pareora, south of Timaru, 1904, pres. C. Hedley, Lower Miocene (2 tubes, W 201247).

**Description.** *Tube.* The tube (Figs 1-18, 26-28, 31-37) is tusk-shaped and slender, open at both ends, with length of up to 33.7 mm (usually 20-25 mm). Although the tube surface is usually clean and bright white in living animals, there are three ways — "smooth", "rough" and "monilifera" — in which its appearance may vary. "Smooth" tubes (Figs 1, 10) are characterised by a highly polished porcellaneous finish. "Monilifera" forms (Figs 14, 16) share this but also feature irregularly spaced annular thickenings along their length (they are so-called from the first specimens collected with this feature — var. *monilifera* Fauvel, 1932). Generally the outer tube layer is somewhat translucent, while the inner layer is opaque. The translucent layer is not as hyaline as in *D. arietina*, though it is very similar in ultrastructure (compare Figs 31, 34 with Zibrowius & ten Hove, 1987, fig. 3). About one quarter of the tubes have a surface classified as "rough" (Figs 3, 4). In these, the outer layer is chalky and opaque. A fine honeycomb structure (Fig. 32) gives these tubes a somewhat coral-like appearance. Intermediates with a partly rough, partly smooth surface occur (Fig. 2, 3, 7). See Remarks for discussion.

Tubes broaden very gradually from posterior apex, which is entire, towards orifice. Minimal measured internal diameter of apex is 0.16 mm, which presumably is the width of a newly metamorphosed larva. Internal diameter of orifice is 0.35-1.1 mm, generally about 0.9 mm. Just before orifice, tubes narrow at a gentle angle, forming conical shoulder (Fig. 35) up to 2.4 mm in width (generally less than 2 mm, see below). In few cases part between shoulder and orifice concavely extended, like the neck of a bottle (Fig. 5). The rim of the tube mouth is circular, smooth and entire. A pronounced thickening is absent, except in a few juvenile tubes with a "monilifera" appearance (Fig. 1). Rarely a thickened orifice shows an irregular pattern of shallow indentations (Fig. 36, see Ecology).

Giving reliable statistics of tubes is extremely difficult since the apex is often missing for an indeterminable distance. Not knowing the expansion rate, which appears to

be variable anyway (compare for instance Figs 12 and 18), it is impossible to guess what length is missing. When the apex breaks off during life, the animal may block the increased posterior access to its tube by the formation of a tabula with 6 foramina (compare ten Hove, 1973:19; Bandel, 1986:68). We have observed this phenomenon only once, in a tube from off Oga (stn M).

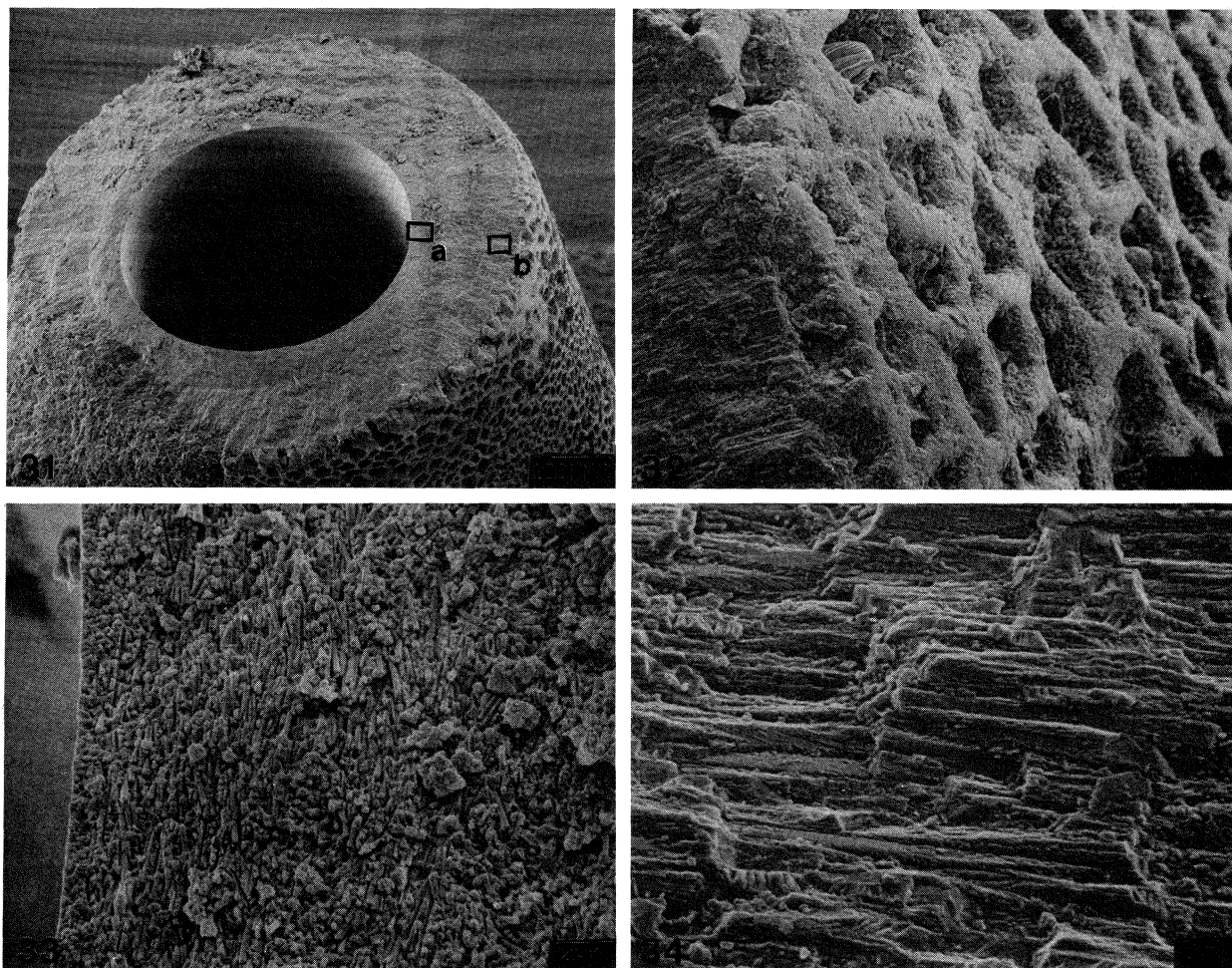
Although there is a wide overlap in the tube measurements between different populations, the arcuation (arc, see below) and maximal width of the tube may give statistical differences. For instance, the following figures are derived from a series of at least ten tubes from four different locations:

	Maximum tube width	Arcuation index
Tadjourah	1.2- <b>1.63</b> -1.9 (SD = 0.28)	18.4- <b>25.4</b> -35.7 (SD = 5.9)
Shimoda	1.1- <b>1.43</b> -1.7 (SD = 0.18)	11.9- <b>15.5</b> -21.7 (SD = 3.7)
Oga	1.15- <b>1.30</b> -1.4	12.5- <b>16.0</b> -19.6

	(SD = 0.08)	(SD = 2.0)
Reunion	1.2- <b>1.55</b> -2.0 (SD = 0.05)	6.0- <b>11.9</b> -18.4 (SD = 3.5)

The arc of the tube (height of inner curve/length  $\times$  100) varies considerably (e.g. Fig. 5), from almost straight in a juvenile (6.0) to 35.7 in the most curved one (50 is the arc of a half circle). In a series of 14 rough and 10 smooth tubes, all entire (i.e. which started with an apex of about 0.16 mm) from Darnley Island (Figs 1,3), most had an arcuation index of about 17 and no statistical difference could be detected. Most samples had insufficient intact tubes for this kind of analysis, though the overall impression is that differences as given above are a result of geographic rather than bathymetric variation.

*Branchiae.* Up to 14 (generally 12) branchial radioles on each side, arranged pectinately, and not connected by a branchial membrane. The first left and first right normal radiole have about twice the diameter of the following ones. Pinnules increase in length distally, where they are about three to four times as long as the rhachis is wide;



**Figs 31—34.** *Ditrupa gracillima*. Scanning electron micrographs of transversely fractured rough tube. Japan, off Kushimoto. 31: low magnification to show location of detail photographs: a = 33, b = 34; 32: detail of rough outer surface of tube, and of large prismatic crystals in outer part of wall; 33: high power magnification of inner criss-cross layer; 34: high power magnification of outer prismatic layer.

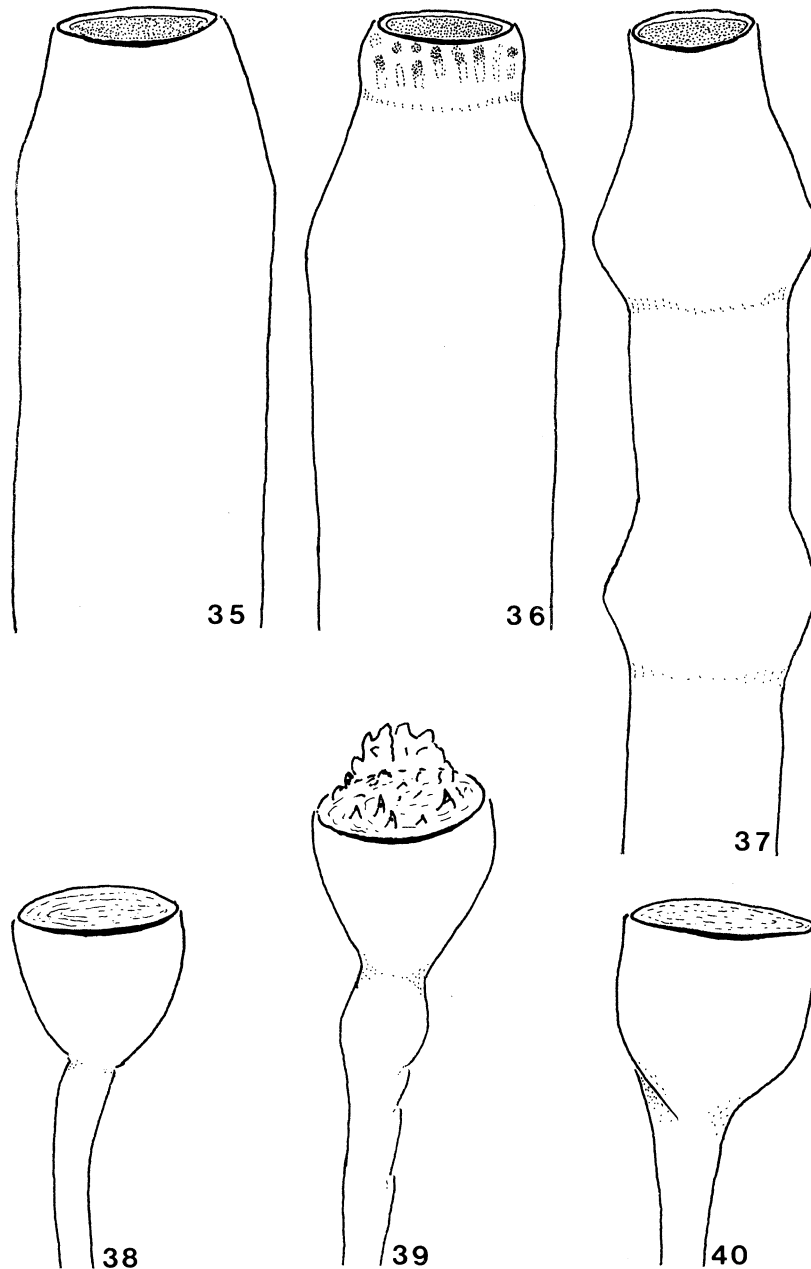
terminal filament not especially developed, but may be up to twice as thick as a normal pinnule. Branchial eyes and stylodes are absent.

*Peduncle.* Smooth and circular in cross-section. Its insertion precedes the first radiole on the left side, but is displaced inward from the half circle of normal radioles. There is no pseudo-operculum. A lost operculum is regenerated from the rudiment of the peduncle. Distally, there is a smooth transition as the peduncle swells to become the opercular bulb (Fig. 40).

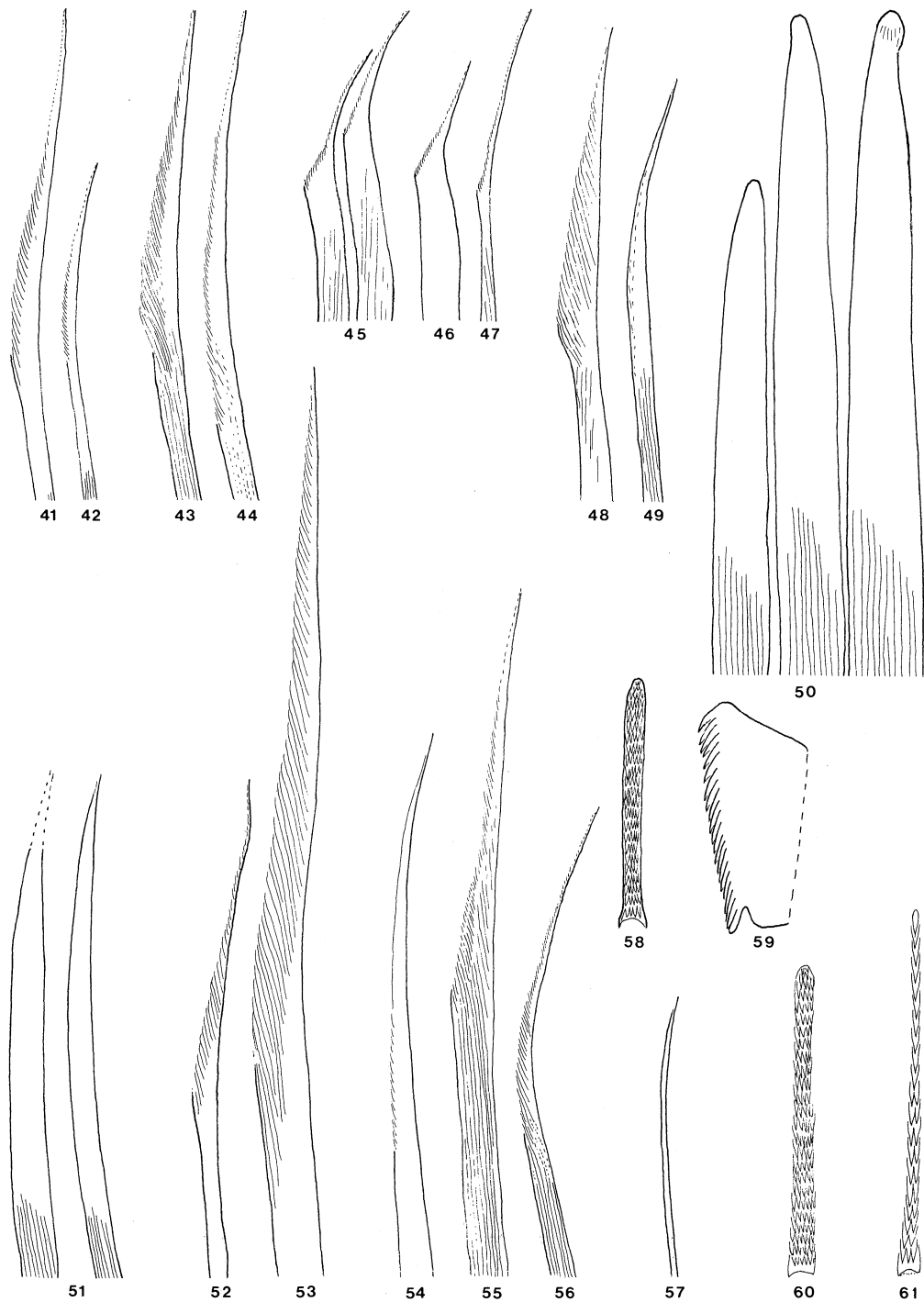
*Operculum.* Globular, with a distal chitinous endplate.

The endplate is flat and circular, lacking both ornamentation (Fig. 38) and talon. The globular ampulla has the form of an inverted cone with convex walls. (In a small number of animals from north Queensland, these walls were slightly concave). The endplate is sometimes overgrown by athecate hydroids (Fig. 39). Diameter of operculum up to 1 mm, length of ampulla up to 1.2 mm; both varying according to population.

*Collar and thoracic membranes.* Generally the collar is high, with an entire edge. The margin sometimes looks serrated, if fixed when closely pressed against the radioles.



**Figs 35—40.** *Ditrupa gracillima* — 35: anterior tube part, common form, Townsville; 36: anterior tube part, thickened orifice with indentations, possibly caused by epibionths, La Réunion; 37: anterior tube part, monilifera-form, Indonesia; 38—39: opercula, Tadjourah, 39: operculum, covered by athecate hydroids; 40: operculum, Red Sea.



**Figs 41—61.** *Ditrupa gracillima* — 41–42: thoracic setae, first setiger, Tadjourah; 43–44: thoracic setae, fourth setiger, Tadjourah; 45: almost geniculate setae, first setiger, smooth tubed specimen, Palau Island; 47: almost capillary seta, first setiger, smooth tubed specimen, Palau Island; 48–49: fourth setiger, smooth tubed specimen, Palau Island; 46: Kushimoto, rough tubed specimen, almost geniculate seta, first setiger. 50–51: first setiger, acicular and capillary setae, Oga; 52–53: fourth setiger, Oga. *Ditrupa arietina* — 54: first setiger, setae and uncinus. South-west off Palma, Canary Islands (ZMA tH 559); 55–56: fourth setiger, setae and uncinus. South-west off Palma, Canary Islands (ZMA tH 559); 57: abdominal capillary, setae and uncinus. South-west off Palma, Canary Islands (ZMA tH 559); 61: edge view of thoracic uncinus, setae and uncinus. South-west off Palma, Canary Islands (ZMA tH 559). Not to scale. *Ditrupa gracillima* — 58–59: uncini, first setiger, edge and side view, Oga; 60: thoracic uncinus, syntype, edge view. Not to scale.

The collar is continuous with the thoracic membranes, and without any lateral incisions. The thoracic membranes end just anterior to the first setiger.

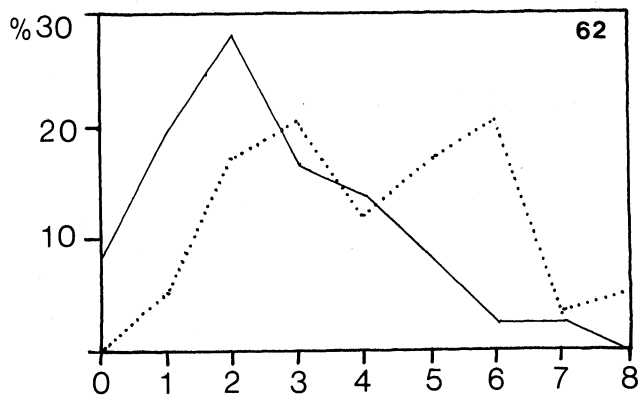
**Thorax.** The thorax has only 6 setigers, all uncinigerous. Collar setae are absent. The first setiger occupies a place similar to that of the collar setiger in other serpulids and is widely spaced from the remaining 5 setigers. All thoracic setae are limbate and of 2 sizes (e.g. Figs 41–44). In the populations from south Japan and the Palau Islands, the first setiger has more or less geniculate setae as well (Figs 45–47). Worms from the Sea of Japan and Korean Straits show acicular setae (Fig. 50), as mentioned by Hong (1984, fig.4h). *Apomatus*-setae are absent. Uncini along the entire thorax are rasp-shaped, with about 30 rows of 3–5 curved teeth, the most anterior apparently bifurcate (Figs 58–60). A pair of prostomial eyes of up to eight pigmented spots is situated within the tissue at the base of the branchial lobes.

**Abdomen.** Up to 55 abdominal segments, though this number varies according to population (Tadjourah: 44–48.4–55, SD=3.8, n=10; Shimoda: (40)42–46–53, SD=4.1, n=5; Oga (30)32–36.8–40, SD=2.3, n=10). Uncini are rasp-shaped, with about 25 rows of 4–6 teeth (this number increases slightly towards the pygidium). All setae are capillary (Fig. 57). The pygidium is bilobed. There is no posterior glandular pad.

**Size.** Length up to 25 mm, generally about 16 mm. Width of thorax up to 1 mm. Branchiae and operculum account for one third to one fifth of the entire length.

**Colour.** Branchial radioles are transparent with red-brown pigment bands.

**Ecology.** i) Distribution with depth. Although present records indicate that tubes of *D. gracillima* have been collected to a depth of approximately 1,000 m, the bulk of living specimens occur only above 130 m. Of live material collected, only “monilifera” forms (i.e. with four to ten annular thickenings in the tube) have been observed from greater depths (75–650 m). Between one and three such annuli may occur in juvenile tubeparts of almost any shallow population. Often the annuli are positioned near the apex, though occasionally the first and only annulus occurs near the orifice. Moreover, the incidence of occurrence as well as the number of annuli apparently



**Fig.62.** Monilifera-form, number of annuli (horizontal axis) in populations from different depth. Vertical axis: % of occurrence. Continuous line: La Réunion, 75-90 m (n = 36); dotted line: the Comores, 530-535 m (n = 59).

increases with depth (Fig. 62). In larger samples of the “monilifera” form it proved to be impossible to find an obvious ratio between size of tube and number of annuli. Annuli are irregularly spaced and variable in thickness. Exceptionally a tube may score four annuli when first measured, yet score six on a subsequent examination. In view of this, and since the material is scanty, the “monilifera” form is regarded as an ecophenotypic variation.

ii) Behaviour. Most authors agree that *Ditrupa* can move around. Sips (personal communication) mentions that when placed on top of the substrate, *D. arietina* can come out of its tube for the greater part of its length. Shifting its weight around, it can turn over its tube from lying on the right side to lying on its convex side or even its left side.

Some preliminary behavioural observations are available for “smooth” and “rough” specimens from Townsville. When placed in dishes with fine muddy sediment taken from their natural habitat, smooth tubed specimens use their branchial crown to burrow actively. Both whorls of radioles are flexed outwards proximally but held inwards distally and used as limbs for excavating a depression in the sediment. This is then used as an anchoring point from which the rest of the worm and tube is drawn forwards into the sediment by muscular flexion of the partially extended thorax. (At times during this process the entire thorax may extend from the tube). This procedure is repeated until the anterior portion of the tube reappears above the sediment at an angle of about 45° and the posterior apex is just exposed at the other end. The branchial crown is expanded into a small depression which it forms at the surface of the sediment when the tube re-emerges. This is likely to be the natural posture of this species in the environment. Worms thus positioned are able to continue filter feeding while remaining almost indiscernable against the sediment background.

This posture appears to conform more or less to Bandel’s (1986:73) observations on *D. arietina*, but differs from Gambi’s (1986:19) deductions. It is also in partial disagreement with Wilson’s (1976:294) observations. From the relative abundance of tubes with solitary corals attached to the concave side, he supposed that the normal orientation of *D. arietina* is in a plane more or less vertical to the surface, with the convex side of the tube upwards, and the apex slightly buried. Given the angled posturing observed in the aquarium, however, it would be quite feasible for corals to settle on the anterior section of the tube and particularly on the concave side.

Also, the epibiotic relation between *D. arietina* and *Hydroides norvegica* Gunnerus, 1768, as figured by Gambi (1986), is unlikely to have developed in an orientation almost parallel to the surface. A similar epibiosis involving *H. multispinosa* Marenzeller, 1885 and *Spirobranchus laticapus* (Marenzeller, 1885) was noticed in the material from the Sea of Japan, off Java respectively. Yet another, so far unidentified, epibiosis has been observed: in about 15 tubes, all with at least one “monilifera” annulus, there is a slightly raised brim around the orifice, ornamented with an irregular pattern of shallow indentations (Fig. 36). This has been observed in fossil



tubes as well.

Two interpretations are possible for these epibioses: in the environment the worms either orient their tubes at an angle above the sediment surface (enabling other organisms to use it as a safe anchoring place), or settled organisms prevent the worms to maintain the normal position, a hypothesis favoured by Wilson (1976).

Interestingly, we were unable to induce rough-tubed specimens to burrow in the aquarium, although they used the same technique as the smooth-tubed forms to manoeuvre over the sediment surface and flip the tube from side to side. When a more sandy sediment was provided, neither "rough" nor "smooth" specimens could be induced to burrow.

iii) feeding. Hong (1984:45) assumes that the genus may be a surface deposit feeder, and in a position more or less parallel to the surface, it would be possible for the worms to exploit this food source. However, filter-feeding was the only feeding strategy we observed in our aquarium specimens, even in those worms that lay flat on the sediment surface. Bandel (1968: 73) probably is correct in his observation that filter feeding is the main method to collect food.

**Nomenclature.** Despite the extensive synonymy, the oldest available name is *Ditrypa gracillima* Grube, 1878. Fortunately Grube's description is based not only on empty tubes but on specimens as well. Hence, by elimination we propose the specific designation *gracillima* for this Indo-Pacific *Ditrypa*.

The name *laeve* or *laevis* has a confused and confusing history. *Dentalium laeve* Turton (1819:256) was proposed as a new name for the preoccupied *Dentalium politum* (non Linnaeus, 1767) Turton (1819:38–39, Torbay, U.K.), both of which are most likely scaphopods judging from the descriptions.

*Dentalites laeve* Schlotheim (1820:93–94) is a primary junior homonym of *Dentalium laeve* Turton. Figured by Chenu (1842–1855, livr.7, pl.7 fig.8a,b), it appears to be a fairly large serpulid or scaphopod.

*Dentalium laeve* (non Turton, nec Schlotheim) Brazier, 1877 (Figs 1,3) is a junior primary homonym of *Dentalium laeve* Turton. It must, therefore, be permanently rejected (International Code of Zoological Nomenclature, article 57b) as suggested by the first reviser Bretnall (1921: 155–156). However, the new name proposed by Bretnall, *Ditrypa brazieri*, is a junior synonym of *Ditrypa gracillima*. According to Bretnall (1921:155), Hilgard & Hopkins (1878) also used the name *Dentalium laeve* for a fossil from the USA.

*Serpula laeve* Montagu (1803:524), also mentioned by Pennant (1812:364) and Turton (1819:157) belongs to the Foraminifera. The fossil *Serpula laevis* Goldfuss (1826–1833:236; 1834–1840:pl.70 fig.3) and *S. laevis*: Geinitz (1873:285, pl.63 figs 13–14) have triangular adnascent tubes, and were referred to two different species of *Parsimonia* by Regenhardt (1961:38) and Lommerzheim (1979:140).

The next oldest name for Indo-Pacific material appears to be *Dentalium strangulatum* Deshayes (1825:372–373, pl.16 fig.28), referred to *Ditrypa* by Mörch (1863:426).

However, this is also very confused. A syntype of *Dentalium strangulatum* (Fig. 21; MNHN, Paris) is labelled "Voyage aux terres australes, Péron et Les. 1803", and also bears a crossed out label "Dentalium cornée". It is the specimen figured by Deshayes (1825: pl.16 fig.28). However, neither label nor Deshayes' text give a proper locality, both simply state that the specimen was brought back by the expedition. Vain attempts have been made to find reference to *Dentalium* in Péron's voluminous reports (1807, 1816). The expedition under captain Baudin left Australia in 1803, returning to Europe via Africa. According to Lamarck (1818:345) *Dentalium corneum* "Habite les mers d'Afrique", and his material (MNHN, Paris) is labelled "Péron et Leseur, Expédition du Cap. Baudin, 1803". It may be inferred from this that Lamarck's material, at least, was collected in Africa. His fragmentary tubes, with a width of 2.1–3.0 mm and faint arcuation, definitely belong to the Atlantic species *Ditrypa arietina*. The syntype of *Dentalium strangulatum* has a width of 2.2 mm, but the fragment is only 14.5 mm long. Deshayes mentions a length of 30 mm. Except for a slight difference in colour, it would fit nicely in the series of Lamarck's *Dentalium corneum*. In all of the hundreds of Indo-Pacific tubes now studied, only two tubes are over 2.1 mm in width and 30 mm in length. Conversely, these dimensions are quite normal for *Ditrypa arietina*. On its outward voyage, the expedition spent some weeks collecting around the island of Tenerife after dropping anchor in Santa Cruz (Canary Islands). *Ditrypa arietina* can be found here by the thousand (ten Hove, unpublished). In view of this, it is far more likely that the syntype was collected in the Atlantic, than in the Indo-Pacific.

It would appear that Deshayes mainly referred to fossil material from Europe in his description of *Dentalium strangulatum*. He included *Dentalium incrassatum* Sowerby (1815:180, pl.79 figs 3–4; figured by Chenu, 1842–1855, Livr.7, pl.7 fig.19) from the U.K. Eocene, and *Dentalium coarctatum* Brocchi (1814:264, pl.1 fig.4; mentioned in Pilsbry & Sharp, 1898:242) from the Italian Pliocene. Consequently *Ditrypa strangulata* has been used more often for European fossils (e.g. Wrigley, 1951:191). More recently, Zibrowius & ten Hove (1987:fig.3; Fig.25 herein) have shown that these fossil tubes are extremely similar to those of the Recent *Ditrypa arietina* O.F. Müller, 1776 at an ultrastructural level. Fossil Italian Pliocene material in the AM (Figs 22,24; W 201219, 201238, 201302) confirms this opinion, these tubes can hardly be distinguished from Recent material of *Ditrypa arietina*. Other Recent material included in *Dentalium strangulatum* by Deshayes is *Dentalium corneum* as described by Lamarck (1818:345) from Africa (though not the material of Linnaeus, 1767:1263 which, if Deshayes may be believed, is an insect larva). Unfortunately, no original material of Linnaeus could be found in the collections of the Linnean Society, London nor in Uppsala. As stated above, *Dentalium corneum*: Lamarck is synonymous with *Ditrypa arietina*. To complicate matters, *Ditrypa cornea* (L.) has been used for Eocene Hungarian material by Bohnné Havas (1981) in her study of the ultrastructure of the tube wall. The material figured as *Dentalium strangulatum* var. by Chenu (1842–1855, Livr.7, pl.6 figs 24, 24a,b) looks similar



to the rough tubes (24), smooth tubes (24b) and “monilifera” forms (24a) described herein. Without access to all the actual material, it is not possible to evaluate the full implications of Deshayes’ taxon and it evidently is a mix of several forms and a *nomen dubium*.

**Distribution.** Mostly tropical: Indo-west Pacific.

### Remarks

The description of *Bonhourella insignis* Gravier, 1905 (and 1906–1908, figs 301–302), particularly the unique arrangement of the first thoracic setiger in relation to the remaining ones, point to a synonymy with *Ditrupa*, the more so since Gravier mentions *D. arietina* from the same station. The latter material has been studied and belongs to *D. gracillima*. The holotype (MNHN) was examined by Zibrowius in 1971, and he confirms this suspicion (*in litteris*).

With regard to *Ditrupa australis*, as figured by Dew (1959, fig. 18A), the original description indeed points to a [juvenile] specimen of *Ditrupa*: “The walls of the posterior [Brettnall errs here, he refers to anterior] opening are thickened and slightly contracting in perfect specimens”. However, both Brettnall and Dew’s figures appear to be of either damaged tubes or a scaphopod.

The figure of *Ditrupa amphora* Dew (1959:48, fig. 18D), with a distinct “shoulder” anteriorly, is extremely similar to some juvenile tubeparts for example in the type series of *Dentalium laeve* Brazier. Some of those juvenile parts even show three more or less annular “shoulders”, just like the ones in the form described as var. *monilifera* by Fauvel (1932:fig. 12), before giving way to the normal bright white and gradually broadening tube of an adult worm.

The tube surface was researched in some detail to determine the nature of those with a rough appearance. It has not been possible to show an epibiotic origin. Colleagues familiar with calcareous algae, bryozoans and sponges could not recognise the structure. Examined optically in a geological thin section, there is no clear boundary between the central transparent and the outer rough layer. There is room for doubt, though, as scanning electron micrographs suggest a discontinuity in this region. However, the mineralogy of the inner opaque and outer rough layer is the same. Both are purely calcitic, as checked both optically and by x-ray diffraction. Some tubes start smooth, and halfway their lengths switch gradually to rough or vice-versa. A couple of specimens even start with a rough tube part, change to smooth, and back again to rough around the orifice. Smooth and rough tubes co-exist in many localities over the entire distribution of the species. We are of the opinion that the rough surface, rather than caused by some unknown epibiont, is a property of the animal. The 1:3 occurrence of rough:smooth tubes points to a Mendelian heredity, perhaps influenced by environment. On first sight, rough tubes are more massive in proportion than the smooth ones. Up to a length of 19 mm, rough tubes are 10 to 35% wider than smooth tubes. However, the effect is lost in tubes over 20 mm. We have

not been able to find other differences between rough and smooth tubes in an extensively measured series of 40 from Darnley Island, except that smooth tubes reach a larger size (30.4 mm, width 2.0 mm against 22.4 mm, 1.7 mm) in this sample.

A similar rough surface structure is mentioned for the fossil *Sclerostyla polyforata* Jäger (1983:87–88, pl. 10 figs 10–12), and for *Dentalium entalis* as figured by Chenu (1842, Livr. 7, pl. 3 fig. 2). We also found it in tubes of *Protula* specimens from Java (8°26’S, 114°29’E, stn 6, coll. Th. Mortensen, 5 Apr. 1929, 70 m; ZMK).

Although Cheng is mistaken in his remark that the inner layer of the tube is of organic material (it is calcareous as well, cf. Bohnné Havas, 1981:pl. 6; Zibrowius & ten Hove, 1987:fig. 3), the chevron structures mentioned by him are indeed visible in thin sections. By comparing these with the orientation of the crystals in the outer transparent layer of the tube (these face diagonally outward and slightly forward), it is indeed possible to infer the posterior apex of the tube in paleontological material.

It is remarkable that the first setiger (apparently second segment) has taken over place and function of the collar setae of other serpulids. Limbate setae are the plesiomorphic character-state, since they occur in other thoracic segments too and are the most common type in all serpulids. Two populations (Sea of Japan and Korean Straits on the one hand, south Japan and Palau Island on the other) are characterised by a unique apomorphy: special setae in the first setiger. All other material (*D. arietina* from Marseille and Madeira, syntypes of *D. gracillima*, rough and smooth tubed specimens from La Réunion, Madagascar, Comores, Red Sea, South Arabia, Townsville and the “monilifera” form from south Japan) has limbate setae only. However, we were unable to find a consistent difference in any of the other characters checked. For instance, although tubes from the Sea of Japan are invariably smooth, while those from south Japan are rough and/or smooth, the measurements for these populations are more similar to each other than to the population from Tadjourah. On the other hand there is an almost complete overlap in number of abdominal setigers between Tadjourah and south Japan, while the mean and maximum are considerably lower in the Sea of Japan. We therefore decided not to attribute a specific rank upon this single apomorphy. In view of the chorology of the forms with aberrant first setigers, it is possible that speciation is about to occur.

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