NEW OBSERVATIONS ON BARNACLES (CRUSTACEA: CIRRIPEDIA) OF THE AZORES REGION

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Additions and revisions are made to the list of Cirripedia recorded from the Azores, including samples taken near hydrothermal vents and in the intertidal zone. Observations are reported on the distribution and breeding of *Tesseropora atlantica*, a relict oceanic species, not found on the continents, that incubates its larvae to the short-lived cypris stage. The degree of endemicity of Azorean barnacles is currently being revised, but most species reported from the Azores are widely distributed in the Atlantic and the Mediterranean. The diversity of the shallow water group is low.

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São feitas actualizações adições e revisões à lista de cirrípedes (Cirripedia) registados para os Açores, incluindo amostras obtidas em fontes hidrotermais e na zona intertidal. São descritas observações na distribuição e reprodução da espécie *Tesseropora atlantica*, uma espécie oceânica relíquia, não descrita nos continentes, que incuba as larvas até à breve fase larvar de cypris. O grau de endemicidade das cracas dos Açores está a ser actualmente registada, mas a maioria das espécies identificadas nos Açores estão amplamente distribuídas no Atlântico e Mediterrâneo. A diversidade das espécies costeiras é reduzida.

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INTRODUCTION

In compiling a bibliography of references to the marine fauna and flora of the Azores, MARTINS (1990) noted the scattered nature of the literature and the difficulty of locating some reports. The cirripedes are not as difficult as some other groups, since many of the species listed for the Azores come from the Monaco expeditions which were focussed on the region, with results published in the well-known reports. In contrast, the results of work by other specific expeditions to the Azores and by expeditions in transit are difficult to find. Not all expeditions have published or fully reported upon their results, and ecological data are often lacking.

In view of the unique position of the islands well out in the Atlantic far from continental Europe, and the typical sessile barnacle life cycle, there is a great need for an *ad hoc* study of Azorean barnacles. Barnacles are mostly cross-fertilising hermaphrodites, many incapable of self impregnation, and their extended planktotrophic larval phase might be expected to cause difficulties in maintaining insular populations. However some barnacle species, notably the scalpellids, have dwarf males that settle on adults and thus can overcome the fertilisation problem for isolated individuals. Other species reduce the risk of over-dispersal of larvae by incubating the eggs to the short-lived, non-feeding cypris stage that can settle almost immediately.

MATERIAL AND METHODS

This report is based on: published literature; residence in Faial; a brief visit to Ponta Delgada; material collected during cruises of the Department of Oceanography and Fisheries (DOP) ships; and examination at Plymouth and in the Natural History Museum, London, of material collected by expeditions to the Azores. The nomenclature follows NEWMAN & ROSS (1976), NEWMAN (1980) and ZEVINA (1981, 1982) with later emendations. The term "Azores Region" as used here comprises the whole archipelago and the surrounding EEZ of 200 nautical miles. This includes much deep-water, and the northernmost known hydrothermal vents of the Mid-Atlantic Ridge (MAR) called Lucky Strike and Menez Gwen.

The first records of barnacles of the Azores were by DROUËT (1858) and BARROIS (1888). These authors are quoted by NOBRE (1930), who visited the Azores in 1919 and made comparable observations in Madeira and Porto Santo in 1927. NOBRE (1930) does not mention the records of Azorean barnacles published by GRUVEL (1920) in the Monaco series; although many of these records were of deep-sea species, there are several from the intertidal zone or shallow depths. There had been earlier reports on deep-water barnacles that included some records for the Azores; by AURIVILLIUS (1898) based on Monaco collections, and by GRUVEL (1900a, 1900b, 1902a) on material from the 'Travailleur et Talisman' expeditions. Two London University expeditions investigated the fauna and flora of the Azores, one from Queen Mary College in 1954 (CHAPMAN 1954) and the second from Chelsea College in 1965 (BAKER 1967). In 1989 there was a joint investigation of the shallow water fauna by the University of Liverpool and the University of the Azores DOP (MARTINS et al. 1992), but parts of the invertebrate collections have not yet been reported upon. In addition to his other reports, GRUVEL (1909) reported on a collection made by the passing German South Polar Expedition. PILSBRY (1916) included some Azorean species in his monograph on the Cirripedia in the collections of the U.S. National Museum, as did HENRY & MCLAUGHLIN (1986). The most recent expedition report is that by YOUNG (1998) who studied the extensive collections made by the R.V. "Jean Charcot" in 1971; he has taken the opportunity to revise the Verrucidae.

Species reported from all these sources and my own collecting and examination of samples provided by others are listed in Table 1, substantially based on the tables in GRUVEL (1920) and YOUNG (1998).

Table 1

Species of Cirripedia reported from the Azores and nearby deep water

genus	species	authority	Depth range (m)	reference	original name if different	geographical distribution
HETERALEPADIDAE						
Heteralepas	*microstoma*	(Gruvel)	269-623	GRUVEL 1902b; YOUNG 1998; this report	*Alepas microstoma*	Azores, Madeira, Gt. Meteor Bk.
OXYNASPIDIDAE						
Oxynaspis	*celata*	Darwin	35-1425	YOUNG 1998		cosmopolitan
	patens	Aurivillius	358-406	YOUNG 1998		north Atlantic
POECILASMATIDAE						
Dichelapsis	*sessilis*	Hoek		HOEK 1883		Azores
Glyptelasma	*hamatum*	Calman	1069-1235	YOUNG 1998		circumtropical
	carinatum	(Hoek)	1250-4261	GRUVEL 1920	*Poecilasma carinatum*	circumtropical
Poecilasma	*aurantia*	Darwin	195-1386	GRUVEL 1920; YOUNG 1998; this report	includes *P. kaempferi*	eastern Atlantic
	crassum	Gray	195-1386	GRUVEL 1920; this report		circumtropical
LEPADIDAE						
Lepas	*fascicularis*	Ellis et Solander	0	GRUVEL 1920		cosmopolitan
	anserifera	L.	0	GRUVEL 1920		cosmopolitan
	pectinata	Spengler	0	GRUVEL 1920		cosmopolitan
	anatifera	L.	0	GRUVEL 1920; YOUNG 1998; this report		cosmopolitan
	hilli	Leach	0	GRUVEL 1920		cosmopolitan
Conchoderma	*virgatum*	Spengler	0	GRUVEL 1920		cosmopolitan
CALANTICIDAE						
Smilium	*acutum*	(Hoek)	1590-1740	HOEK 1883; GRUVEL 1920; YOUNG 1998	*Scalpellum acutum*	cosmopolitan
Aurivillialepas	*calyculus*	(Aurivillius)	845-880	AURIVILLIUS 1898; GRUVEL 1920	*Scalpellum calyculus*	Azores
	falcata	(Aurivillius)	454	AURIVILLIUS 1898; GRUVEL 1920	*Scalpellum falcatum*	Azores, Gt. Meteor Bk.
Scillaelepas	*grimaldii*	(Aurivillius)	845-1250	AURIVILLIUS 1898: GRUVEL 1920	*Scalpellum grimaldii*	Azores

Bk. - Bank; Gr. - Great.

Table 1 (continued)
Species of Cirripedia reported from the Azores and nearby deep water

genus	species	authority	depth Range (m)	Reference	original name	geographical distribution
SCALPELLIDAE						
Scalpellum	*scalpellum*	(L.)	63-2000	GRUVEL 1920	*Scalpellum vulgare*	north-east Atlantic
Amigdoscalpellum	*mamillatum*	(Aurivillius)	4020-4261	AURIVILLIUS 1898; GRUVEL 1920	*Scalpellum mamillatum*	Azores
	rigidum	(Aurivillius)	2440-4360	AURIVILLIUS 1898 (GRUVEL 1905 & 1920 as *Scalpellum striatum)* (ZEVINA 1976 as *Scalpellum vitreum*)		north-east Atlantic
Arcoscalpellum	*michelottianum*	(Seguenza)	1098-1458	ZEVINA 1976; YOUNG 1998 (GRUVEL 1920 as *Scalpellum velutinum)* (AURIVILLIUS 1898 as *Scalpellum erectum)*	*Scalpellum michelottianum*	cosmopolitan
	tritonis	Young	1225-1260	YOUNG 1998		north-east Atlantic
Catherinum	*recurvitergum*	(Gruvel)	3175	GRUVEL 1900a & 1905; YOUNG 1998	*Scalpellum recurvitergum*	Azores, Indian Ocean?
Neoscalpellum	*debile*	(Aurivillius)	2120	AURIVILLIUS 1898; GRUVEL 1920; YOUNG 1998 (GRUVEL 1900a & 1902a as *Scalpellum edwardsii*) (GRUVEL 1920 as *Scalpellum alboranense)*	*Scalpellum debile*	north Atlantic
Planoscalpellum	*limpidus*	Zevina	5001-5580	ZEVINA 1976; YOUNG 1998		north-east Atlantic, sub Antarctic
Teloscalpellum	*anceps*	(Aurivillius)	2900-4260	AURIVILLIUS 1898; GRUVEL 1920	*Scalpellum anceps*	Azores
	atlanticum	(Gruvel)	960-1241	GRUVEL 1900a, 1902a & 1920		
	gracile	(Gruvel)	1250	GRUVEL 1920	*Scalpellum gracile*	north-east Atlantic
	incisum	(Aurivillius)	1022	AURIVILLIUS 1898; GRUVEL 1920	*Scalpellum incisum*	Azores
	luteum	(Gruvel)	3000-3056	GRUVEL 1900a & 1902a; YOUNG 1998	*Scalpellum luteum*	Azores
Triangulosalpellum	*regium*	(Thomson)	2779-4020	GRUVEL 1900a & 1902a	*Scalpellum regium*	north Atlantic
	ovale	(Hoek)	4620-4690	GRUVEL 1905, as *Scalpellum gigas*		north Atlantic
Weltnerium	*pusillum*	(Aurivillius)	2000	AURIVILLIUS 1898; GRUVEL 1920	*Scalpellum pusillum*	Azores, north-west Atlantic

Table 1 (continued)
Species of Cirripedia reported from the Azores and nearby deep water

genus	species	authority	depth range (m)	reference	original name	geographical distribution
VERRUCIDAE						
Altiverruca	*costata*	(Aurivillius)	454-1200	AURIVILLIUS 1898; GRUVEL 1920	*Verruca costata*	north Atlantic
	crenata	(Aurivillius)	845	GRUVEL 1920	*Verruca crenata*	Azores
	erecta	(Gruvel)	3175	GRUVEL 1900b & 1902a	*Verruca erecta*	Azores
	gibbosa	(Hoek)	510-1385	YOUNG 1998		cosmopolitan
	inermis	(Aurivillius)	1022-1187	AURIVILLIUS 1898; GRUVEL 1920	*Verruca inermis*	Azores
Costatoverruca	*cornuta*	(Aurivillius)	523-1143	GRUVEL 1920	*Verruca cornuta*	Azores, Gt. Meteor Bk.
Metaverruca	*aequalis*	(Aurivillius)	1022-1385	AURIVILLIUS 1898; GRUVEL 1920	*Verruca aequalis*	Azores
	recta	(Aurivillius)	454-1385	GRUVEL 1920 (AURIVILLIUS 1898; GRUVEL 1920 as *Verruca sculpta*) (AURIVILLIUS 1898; GRUVEL 1920 as *Verruca linearis*)	*Verruca recta*	cosmopolitan
	trisulcata	(Gruvel)	1022-1143	GRUVEL 1900b, 1902a & 1920; YOUNG 1998	*Verruca trisulcata*	Azores
Verruca	*spengleri*	Darwin	0-130	GRUVEL 1920; BAKER 1967; YOUNG 1998; this report		Azores, Madeira, Mediterranean
	stromia	(O.F. Muller)		GRUVEL, 1902a & 1920	mistaken identification?	boreo-arctic
CHTHAMALIDAE						
Chthamalus	*stellatus*	(Poli)	0	GRUVEL 1920; BAKER 1967; YOUNG 1998; this report		eastern Atlantic
TETRACLITIDAE						
Tesseropora	*atlanticum*	Newman et Ross	0-40	NEWMAN & ROSS 1977; this report (BAKER 1967 as *Tetraclita squamosa elegans* Darwin) (YOUNG 1998 as *Tesseropora arnoldi*)		Azores, Bermuda, St. Paul Rocks

Bk. - Bank; Gr. - Great.

Table 1 (continued)
Species of Cirripedia reported from the Azores and nearby deep water

genus	species	authority	depth range (m)	Reference	original name	geographical distribution
ARCHAEOBALANIDAE						
Semibalanus	*balanoides**	(L)		NOBRE 1930, as *Balanus balanoides*	mistaken identification	boreo-arctic
Elminius	*crystallinus**	Gruvel		GRUVEL 1909	mistaken identification	Azores
CORONULIDAE						
Xenobalanus	*globicipitis*	Steenstrup	0	GRUVEL 1920 (on *Pseudorca crassidens*)		
BATHYLASMATIDAE						
Bathylasma	*hirsutum*	(Hoek)	570-1630	GRUVEL 1920; YOUNG 1998; this report	*Balanus hirsutus*	eastern Atlantic
BALANIDAE						
Balanus	*amphitrite*	Darwin	10	GRUVEL 1920		now cosmopolitan
	spongicola	Brown	15-100	GRUVEL 1920		Atlantic
	trigonus	Darwin	0-100	GRUVEL 1920; BAKER 1967		now cosmopolitan
	eburneus	Gould	0	this report		western Atlantic, Pacific, Europe
	*crenatus**	Bruguière	845-1165	GRUVEL 1920		boreo-arctic
Megabalanus	*azoricus*	(Pilsbry)	0 to 40	GRUVEL 1920, as *Balanus tintinnabulum* PILSBRY 1916, as var. *azoricus* BAKER 1967; this report		Azores, St. Helena, Madeira ?

RESULTS

Notes on certain groups and individual species selected from Table 1 follow. These notes cover the most frequently encountered species in the region and others that may have been erroneously attributed to the Azores by previous authors, here indicated by parentheses.

HETERALEPADIDAE

Heteralepas microstoma (Gruvel)
This group of stalked barnacles characteristically lacks shell plates. If the cirri are not protruding they might well be regarded as ascidians. *Heteralepas microstoma* is reported by YOUNG (1998) to be common around the Azores and Madeira archipelagoes at 269 to 623 m, occurring on octocorals. A clump of five were collected by Dr H. Martins, attached to octocoral in 548 m depth, from the MV "Mar de Fortuna" on 28 July 1986 over the south end of the Princess Alice Bank (Fig. 1). The largest was 50 mm. total length, capitulum 22 mm.

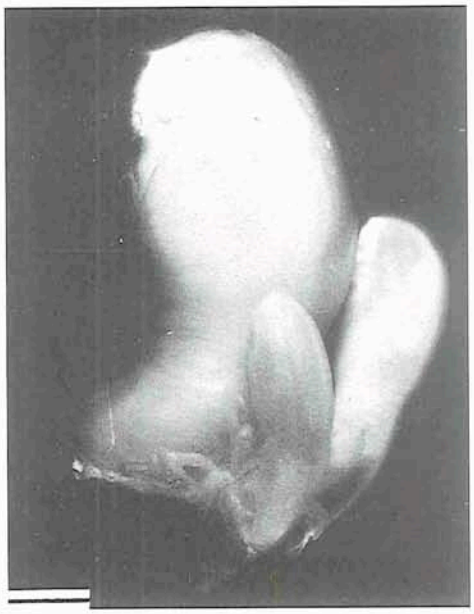

Fig. 1. Group of *Heteralepas microstoma,* from the Princess Alice Bank. Scale bar 10 mm.

POECILASMATIDAE

This group lives attached to crustaceans and sea-urchins.

Poecilasma aurantia Darwin
I am following YOUNG (1998) in assigning to this taxon the Atlantic specimens previously assigned to *P. kaemfperi*, which appears to be a Pacific species, but with reservations that molecular biological comparisons are needed, in view of the variability of the morphological characters. *P. aurantia* was common on *Chaceon affinis* trapped near the hydrothermal site at Menez Gwen, though slightly less abundant than *P. crassa* (Fig. 2). Additional specimens were taken at 900 m. depth south of Pico on 25/08/97, haul 38, on spines of *Cidaris*. Another specimen from the same location was growing on *Paramola cuiveri.*

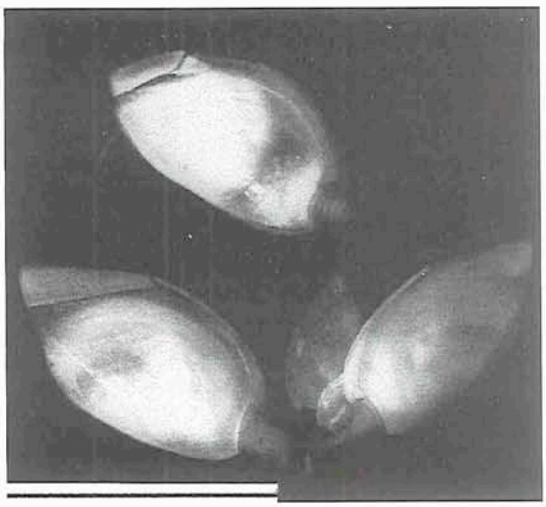

Fig. 2. Group and solitary individual of *Poecilasma aurantia* removed from the geryonid crab *Chaceon affinis* collected in traps at Lucky Strike. Scale bar 10 mm.

Poecilasma crassa Gruvel
This form was also common on *Chaceon affinis* from Menez Gwen, together with *P. aurantia*, being perhaps more abundant on the telson than on the limbs (Fig. 3).

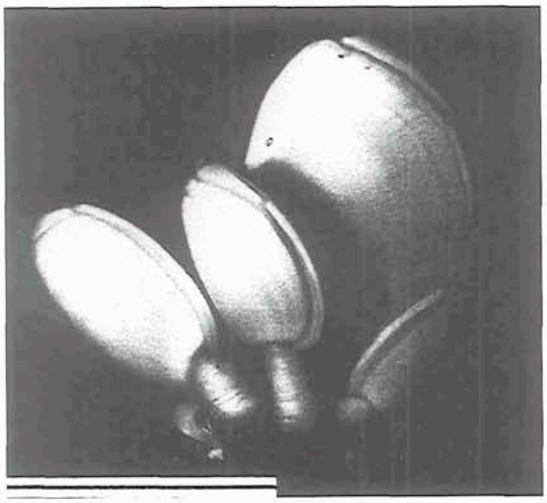

Fig. 3. Cluster of *Poecilasma crassa,* also from *Chaceon affinis* collected at Lucky Strike. Scale bar 10 mm.

Table 2 lists the records of *Poecilasma* from crabs caught in baited traps close to the hydrothermal site at Menez Gwen. These records do not imply any direct relationship between the barnacles and the hydrothermal vents. *Chaceon* appears to be an opportunist visitor to the vents and carries the barnacles with it.

Table 2
Records of epifaunal barnacles on *Chaceon affinis* taken in traps at Menez Gwen hydrothermal site

date	set	depth	*Poecilasma aurantia*	*Poecilasma crassa*
29/06/97	24	800	12	7
28/08/97	42	900	12	18
28/08/97	43	800	2	1
11/11/97	58	900	3	7
11/11/97	59	800	1	30 on telson
			5	0 on claw
30/06/97	crista 1	800-900	11	3

LEPADIDAE

Lepas anatifera L.
Several records of this species are contained in the Monaco report, taken on floating objects (GRUVEL 1920). At present it is common around the Azores on floats used for moored traps and lines (personal obs.)

Conchoderma virgatum Spengler
This species was reported by GRUVEL (1920) on *Mola mola* L. collected off the Azores. There are other Monaco records from outside the area taken from sea-turtles. In the collections of the DOP there are some recent specimens (1996) of *C. virgatum* from sea turtles. YOUNG (1998) reports the related species, *C. auritum,* from the hull of the R.V. "Jean Charcot" in Ponta Delgada, São Miguel.

SCALPELLIDAE

Many of the species of scalpellids listed in Table 1 are rare, each of them collected at only a few stations (GRUVEL 1920; YOUNG 1998). Most species have 'parasitic' dwarf males and can thus live in isolation from other adult forms unlike normal hermaphrodite barnacles. This phenomenon of dwarf males was discovered by DARWIN (1851) whose observations were extended by HOEK (1884) and by GRUVEL (1902a). Recently, HOEG & KLEPAL (1992) have described details of the dwarf males in *Scalpellum scalpellum.*

Arcoscalpellum michelottianum Seguenza
This species of scalpellid was originally described from fossil material, but has now been put as the senior synonym of several other described species, notably *Scalpellum velutinum* (Table 1). It is cosmopolitan at depths down to 5000 m. Like other scalpellids it tends to occur in isolation.

It is present at the hydrothermal site called Lucky Strike in some number.

Comparable stalked barnacles were seen there in 1994 (pers. comm. Prof. P.R. Dando), but not recovered. A relatively high population density was observed on sulphide rock in 1996 and recorded on videotape (37° 17.657' N., 32° 16.977' W, pers. comm. Dr. T. Shank). The single specimen recovered during the 1996 visit belongs to this species, as confirmed by Dr. A. Ross (Fig. 4). It is best regarded as an opportunist favoured by fallout from the vent communities.

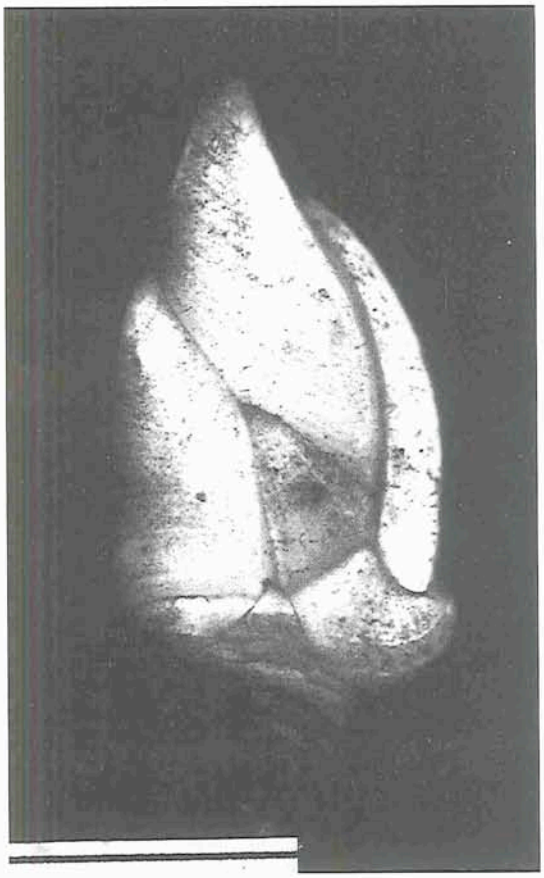

Fig. 4. *Arcoscalpellum michelottianum* collected from sulphide rock at Lucky Strike. Scale bar 10 mm.

An isolated scalpellid dredged to the north of the hydrothermal sites in 1997 (1300 m) may belong to the same species as reported for Lucky Strike, but shows slight differences in internal shell structure.

VERRUCIDAE

Verruca spengleri Darwin

This relatively shallow water species of *Verruca* was originally described by DARWIN (1851) from Madeira, but it is also found in the Mediterranean. It is abundantly distributed at low intertidal to sublittoral, under stones and in crevices (Fig. 5). I have seen specimens from Ponta Delgada (São Miguel); and from Horta and Porto Pim (Faial). It is reported by GRUVEL (1920) down to 130 m and by YOUNG (1998) down to 103 m.

Fig. 5. *Verruca spengleri* collected just below the water at low tide in the marina at Horta. Scale bar 10 mm.

The deep-water verrucids listed by GRUVEL (1920) and YOUNG (1998), tend to be uncommon and collected only at a few stations. The most frequently encountered deep-water species off the Azores are also found elsewhere; these are *Altiverruca costata*, *Metaverruca recta* and *Costatoverruca cornuta*, taken at 5 or more stations. Of these, *M. recta* is widespread along the continental slope in the north-east Atlantic, as I can confirm from my own dredgings.

CHTHAMALIDAE

Chthamalus stellatus (Poli)

The most abundant intertidal barnacle of the Azores is the true *C. stellatus* of Poli, 1794 (Fig. 6). *C. stellatus* was reported by GRUVEL (1920) from Horta (Faial) and Formigas. It was collected by both University of London expeditions and was reported (pers. comm. S.J. Hawkins) from the 1989 expedition (MARTINS et al. 1992).

YOUNG (1998) adds further records from Santa Maria and Faial. It is present on all but the most sand-scoured rocky shores, forming a zone occupying the upper half of the midlittoral, usually about 0.5 to 1 m vertically on the shores I have visited. HAWKINS et al. (1990) describe a more extensive *Chthamalus* zone on the southern shores of São Miguel. I have seen specimens collected by the two London University expeditions. I have checked the species on the shore in Ponta Delgada (São Miguel); and Porto da Praia do Almoxarife, Varadouro, Porto Pim and in the Horta yacht marina (Faial). There is no trace in the Azores of the other European species of *Chthamalus, C. montagui* Southward, which just reaches the easternmost Canary Islands (CRISP et al. 1981), but which does not reach Madeira (personal obs.).

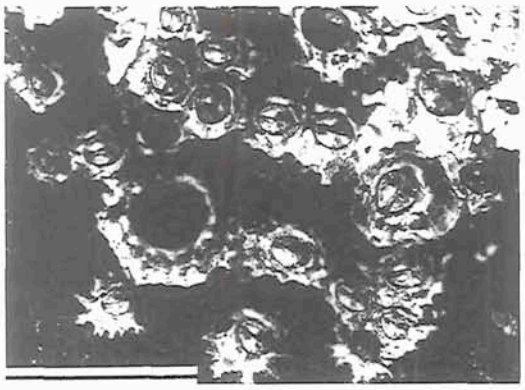

Fig. 6. *Chthamalus stellatus* from Porto da Praia do Almoxarife, north of Horta. Scale bar 10 mm.

BATHYLASMATIDAE

Bathylasma hirsutum Hoek

This species was reported by GRUVEL (1920) from a submarine cable off Faial and from dredgings on rocks at 845 m. YOUNG (1998) reports it from three stations, ranging from 570 to 1235 m, and from three other stations outside the Azores region at 810 to 960 m. It is found quite frequently on steep faces along the continental margins, where the rocks are exposed by water currents. I have also seen it taken from cables in the Bay of Biscay (SOUTHWARD & SOUTHWARD 1958). During geological dredging conducted by Professor J.R. Cann, from R.V. "Atlantis" in July 1997, several hundred separated shell compartments of this species were taken, together with larger masses of dead coral, *Lophelia prolifera*, in a haul up the slope from 1630 to 1250 m on a steep scarp on the western side of the central valley of the Mid-Atlantic Ridge (MAR), 37º17.2' N., 32º 24.3' W. to 37º17.21' N, 32º24.68' W. Both the coral and the barnacle shells were black with manganese coating. I had previously seen dead shells at several locations along the continental slope between northern Spain and south-west Ireland, but never more than one or two in each dredge haul. It appears that at a previous epoch this barnacle must have been abundant along the MAR. Possibly there was at one time a more productive surface ecosystem providing organic fall-out to the bottom, or there may have been enrichment from hydrothermal sources. Alternatively, and less likely, the shells may have been aggregated by strong along-slope currents. NEWMAN & ROSS (1971, 1976) have record similar masses of dead shells of bathylasmatids in the southern oceans.

TETRACLITIDAE

Tesseropora atlantica Newman & Ross

This is a comparatively recently described barnacle for the Azores, previously mistaken for another species. In 1965 I was sent barnacles from the Chelsea College Azores Expedition and identified some of them as *Tetraclita squamosa* var. *elegans*, not then being acquainted with the genus *Tesseropora*. This record was reported as *Tetraclita* by BAKER (1967). In 1976 I was sent specimens of another small tetraclitid collected at Bermuda, which were at first thought to be the same as the *Tetraclita squamosa stalactifera* reported by HENRY (1958). However, the shell structure seemed wrong so I sent the Bermuda specimens to Dr W.A. Newman, who promptly realised they were a species of *Tesseropora* related to the Pacific form, *T. wireni* (NEWMAN & ROSS 1977), previously known in the Atlantic as fossils. This alerted me to the Azorean specimens that I had mistakenly identified as *Tetraclita*,

which were similar to the Bermudan specimens. NEWMAN & ROSS (1977) included the Azorean specimens in their description of *T. atlantica.* The Bermudan records are from wave-swept outer reefs, partly submerged, and the Chelsea College specimens from the Azores came from the sublittoral, apparently explaining why the species had not been more widely reported.

YOUNG (1998) has now redescribed the Azorean *Tesseropora* as a new species, *T. arnoldi,* and indicates his belief that the original description of *T. atlantica* by Newman and Ross was based only on the Bermudan material. I have therefore examined the paratypes of *T. atlantica* deposited in the Natural History Museum, London, and the sample from São Jorge that I had seen earlier (BAKER 1967). In addition I have dissected several specimens from Faial collected personally and several specimens from Bermuda collected there in 1990 by M. Thomas (on a boiler, 1.5 n. miles NE of Blue Cat Light). Unfortunately, the morphological characters listed by YOUNG (1998) for separating the Azorean and Bermudan forms are not reliable. The 1990 Bermudan specimens do have teeth on the labrum, and the apparent absence of such teeth in the types examined by NEWMAN & ROSS (1977) is obviously an artefact; the labrum of the paratype not only lacks teeth but also is without setae, indicating damage. The number of setae on the intermediate joints of cirrus VI is given by Young as 4 in the Azorean specimens and 5 in the description of the Bermudan specimens; yet one in five of the 1990 Bermudan specimens has only 4 setae and one in five of the Azorean specimens has 5 setae. The supposed differences in the mandible and the shell are also unsatisfactory. It is quite possible that the populations of this barnacle on the isolated Atlantic islands may have diverged to specific level, but we must await results of proposed molecular biological investigations to be certain.

In 1996 Professor Malcolm Jones, University of Plymouth, sent me some small specimens of *T. atlantica* from the intertidal zone at Cerco de Caloura, east of Ponta Delgada, São Miguel, where this barnacle is quite abundant in the low intertidal there. In July 1997 I inspected the breakwater or mole at Ponta Delgada, searching for a four-plated species reported from this site by GRUVEL (1909) as *Elminius*, which was considered as possibly a *Tesseropora.* At the outer steps there were some crevices in the wall, and under a piece of rock were several specimens of *Tesseropora atlantica*, accompanied by *Verruca spengleri* and *Chthamalus stellatus.* Having thus located *Tesseropora*, I investigated cryptic habitats in the lower part of the intertidal zone on Faial. At Porto Pim, by the steps of the outer ruined whale factory on Monte de Guia (near T10 of MARTINS et al. 1992), *T. atlantica* was found in some numbers in the zone of algal turf, below the *Chthamalus* zone (Fig. 7).

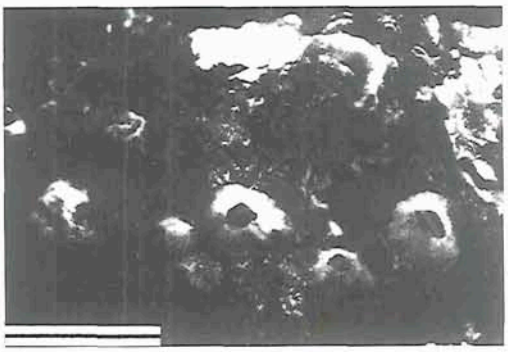

Fig. 7. *Tesseropora atlanticum* from inside rock crevices excavated by sea-urchins, low water level, Porto Pim. Scale bar 10 mm.

They were living in holes that had been excavated by sea-urchins, but in which there were few living urchins, at the upper limit of the urchin zone. The sea-urchins responsible for the holes were mostly small *Paracentrotus lividus,* but some small *Arbacia lixula* may have been present. The *Tesseropora* were on the undersides and sides of the excavations, and often formed clusters of contiguous individuals (Fig. 8).

It was thought worthwhile to inspect a number of specimens of *T. atlantica* for retention of larvae in the mantle cavity. By analogy with *Tesseropora wireni* in the Pacific, Newman and Ross had predicted the Atlantic form might incubate its embryos through the nauplius stage and liberate them at the cypris stage. YOUNG (1998) stated that all the specimens he dissected were incubating nauplii. The specimens I examined were of a wide range of sizes, and not all incubating nauplii, but the prediction by

NEWMAN & ROSS (1977) was confirmed. The naupliar stages I found in the mantle cavity of some individuals were of non-feeding form, full of lipid reserves, and one individual was found incubating viable cyprid stages. Length frequency distribution of the barnacles and data on breeding are given in Table 3. It is evident that, in this rather small barnacle, breeding begins at only 4 mm shell length.

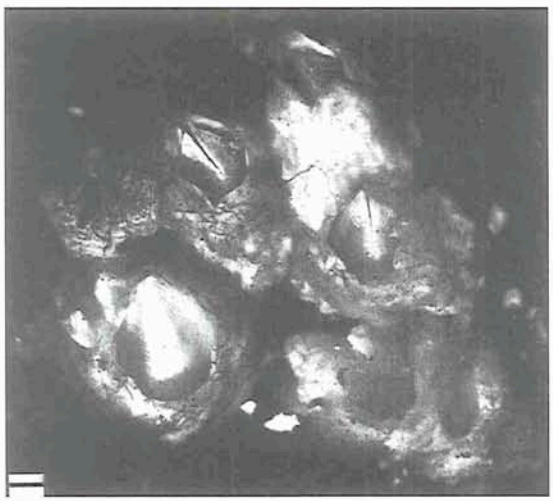

Fig. 8. Contiguous group of *Tesseropora atlanticum* from crevices Porto Pim, shells covered by filamentous red algae. Scale bar 1 mm.

The live cyprids were cultured, and within 24 h of release were actively 'searching' the substratum with their antennules (Fig. 9; see review of cyprid behaviour by WALKER et al. 1987). This searching behaviour was continued for another 24 h, but no settlement or metamorphosis was obtained, so the remaining cyprids were fixed for measurement. The average length of the cyprid carapace was 0.63 mm.

ARCHAEOBALANIDAE

[*Semibalanus balanoides* (L).]

This species was first reported by DROUËT (1858) as *Balanus semiplicatus*, and then recorded by BARROIS (1888) and NOBRE (1930) as *Balanus balanoides*. The Azores is listed as a location for *S. balanoides* by NILSSON-CANTELL (1978), presumably on the basis of these records. The Drouët record was made at a time when the monographs by DARWIN (1851, 1854) had not yet reached all European conchologists, and intertidal barnacles were often confused. The occurrence of *S. balanoides* in such a fully oceanic position, considerably further south than its known continental limits, the rias of Galicia, north-western Spain (FISCHER-PIETTE & PRENANT 1956) seems unlikely. The probable explanation of this record is that the three authors misidentified the intertidally abundant *Chthamalus stellatus*, which has a membranous basis, like *S. balanoides*.

Table 3
Length frequency of *Tesseropora atlantica* and data on breeding, Porto Pim (21-24 July, 1997)

length (mm)	total without larvae or eggs	with oocytes	with embryos	with cyprids
1				
1.5	2			
2	6			
2.5	9			
3	10			
3.5	12			
4	15			
4.5	6		1	1
5	7			
5.5	1	1	2	
6	4	1		
6.5	1		1	
damaged	6	3		
total	79	5	4	1

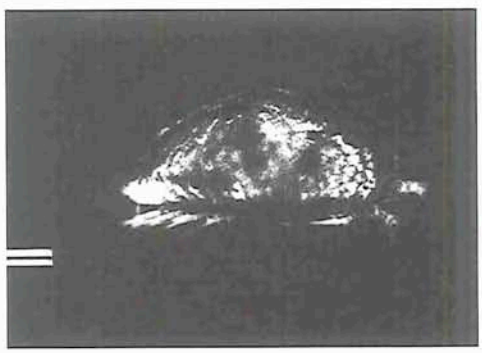

Fig. 9. Living specimen of cypris larvae of *Tesseropora atlanticum* showing the antennules used to explore the substratum. Scale bar 100 µm.

[Elminius cristallinus Gruvel]
This is a tantalising record of a genus that was when G. recorded it restricted to the southern oceans. *Elminius modestus* from New Zealand was spread by shipping to NW Europe during World War II, but has not so far colonised the Azores. The record appears to be based on a single individual barnacle collected on the breakwater at Ponta Delgada by the German South Polar expedition in 1903 (GRUVEL 1909). From the four-plated condition it at first seemed possible that Gruvel might have had a juvenile form of *Tesseropora atlantica,* but examination of a series of sizes of the latter from 6 mm to 2 mm shell length, shows that the porous shell plates are always recognisable, though the calcareous basis may be thin and fragile in the smallest sizes; *Elminius* has non-porous parietes and a membraneous basis. However, Gruvel's specimen was almost 6 mm long, a size at which *Tesseropora* is mature. So the Gruvel description cannot refer to *Tesseropora.* Both the illustration and the description are rather sketchy, but a possible explanation is that Gruvel was examining an individual of *Chthamalus stellatus* from a cryptic situation, that had some abnormal fusion of the compartments. The valves he illustrated look quite like valves of cryptic *Chthamalus stellatus* from the breakwater at Ponta Delgada. A less likely possibility is that Gruvel had a specimen of a *Tetrachthamalus*, hitherto only recorded from the Indian Ocean (NEWMAN 1967) and China (REN 1980).

BALANIDAE

Balanus trigonus Darwin
Monaco reports, intertidal from Faial, and at 54 m off San Antonio, Terceira (GRUVEL 1920); at 1 m, Urzelina, São Jorge (BAKER1967); at 1 m, Monte de Guia, Faial, T2 of the 1989 survey (MARTINS et al 1992). This species is sometimes recorded from intertidal situations, but is commoner in the sub-littoral. It is now found all over the tropical oceans and penetrates into temperate regions (NEWMAN & ROSS 1976). ZULLO (1992) adduces evidence of it being a recent introduction to the Atlantic, possibly brought to the Azores by whaling ships. YOUNG (1998) reports it intertidally from Terceira; from Faial at 0 to 18m; São Miguel, 7 to 20 m; Graciosa, 2 to 8 m; São Jorge, 27-45 m; Santa Maria, 12 to 25 m; and João de Castro Bank, 25 to 35 m. This species has the usual planktotrophic larva, and like Chthamalus stellatus, is evidently able to maintain an abundant population among the islands.

Balanus amphitrite Darwin
Monaco reports, intertidal, from Faial (GRUVEL 1920). I cannot confirm this record; it was not seen in the Horta yacht marina, though expected to be present there. YOUNG (1998) doubts the record. This species is not a recent introduction from North America or the Pacific as sometimes thought. I have examined isolated shell compartments and valves excavated by archaeologists from the site of the Carthaginian naval base near Tunis, so it has been present in the Mediterranean for over 2000 years. It has evidently been a fouling species for a long time, and might well have reached the Azores from the Mediterranean.

Balanus eburneus Gould
A large barnacle was reported to me, by Dr Filipe Porteiro, as being present in the estuary at the north end of Horta Bay. In July we found small numbers present on a vertical north face at the waterline of stagnant pools in the nearly dried-out estuary, opposite the Fayal Sport Club, not more than one or two per linear metre.

On examination in the laboratory these proved to be *B. eburneus*, a species endemic to the east coast of USA, and ranging from the Caribbean to Massachusetts. *B. eburneus* is a typical fouling species and was introduced to Europe about 100 years ago and has recently reached sites in the Pacific prior to World War II. It is well-established in waters of reduced salinity in the Mediterranean and in the southern Bay of Biscay (RELINI 1980; SOUTHWARD 1962). I hypothesise that *B. eburneus* was introduced by whaling ships from New England. However, it is difficult to understand how a population of such low density as that in Horta can maintain itself, suggesting there are colonies in other sheltered sites or brackish water regions of the Azores that form a breeding population.

[*Balanus crenatus* Bruguière]
Monaco reports, from 845 and 1165 m (GRUVEL, 1920). This report is well south of the accepted southern limit of this arctic-boreal species, which does not normally extend to great depths. It is possibly a mistaken identification of a juvenile Bathylasma hirsutum, adults of which were taken in similar depths.

Megabalanus azoricus (Pilsbry)
This is the third most common shallow water barnacle of the Azores, and the largest. It is collected for food in the Azores islands, and may be in danger of over-exploitation (SANTOS et al. 1995) it was reported as *Balanus tintinnabulum* by GRUVEL (1920) in the Monaco collections from off Faial and Pico. The description by PILSBRY (1916) is based on specimens from Terceira. YOUNG (1998) saw specimens from Faial, São Miguel and off Santa Maria, and BAKER (1967) reports it from São Jorge. I have seen specimens collected by divers at from 1 to 5 m off Horta (Faial), and a small one from a crevice in the breakwater at Ponta Delgada (São Miguel). *Megabalanus* forms a distinct zone at about 1 m below the water line (Dr. P. Wirtz, pers. comm.) in places with wave action. HENRY & MCLAUGHLIN (1986) confirm the specific nature of the Azores material and report a closely similar form from Saint Helena. It remains to be determined how the Azores species differs from the *Megabalanus* that occurs in Madeira; the specimens I have seen, collected by Dr. P. Wirtz, closely resemble the Azorean specimens, and I have seen comparable examples growing on the hull of U.K. research vessels in drydock at Plymouth after working off Madeira and the Azores. This ability to grow on floating objects may explain the number of dead shells recovered from deep water by the Monaco expeditions and by the "Jean Charcot" as reported by GRUVEL (1920) and YOUNG (1998), and indicates the species is capable of dispersal by this means.

CHELONIBIIDAE

Chelonibia caretta (Spengler)
I place in this species specimens recovered from the carapace of the local turtles that are being studied by DOP.

DISCUSSION

The majority of the barnacles listed in Table 1 are deep-sea species that are generally distributed along the continental slope in the North Atlantic, or else are common at the sea surface on floating objects. Some of the deep water scalpellids and verrucids have been reported only from the Azores region, but we lack detailed records from other parts of the Atlantic, comparable to the collecting carried out by the Prince of Monaco and Paris Museum, so it is not possible to be certain they are all endemic. If the deep-sea species are ignored, the Azorean barnacles show a rather low diversity, which might reflect the insular position, though more investigation is also desirable on these species. There are nine listed intertidal and shallow water cirripedes of the Azores, but two are probably mistaken identifications (*Elminius cristallinus*, *Semibalanus balanoides*). Two others, *Balanus amphitrite* and *B. eburneus* are probably fairly recent immigrant species, carried on ships. The species of *Megabalanus* can also be carried by ships, so caution is needed when they are named as endemics (PILSBRY 1916); the report of occurrence of *Megabalanus azoricus* at St. Helena and from ships suggests a wider distribution. *Verruca spengleri* can occur to considerable depths as can *B. trigonus* and *B. spongicola,* so these species might not need so many emerged island stepping stones to spread as do the purely intertidal species. That leaves us with just two common shallow water barnacles existing as isolated populations in the islands, *Chthamalus stellatus* and *Tesseropora atlantica.* One of these, *C. stellatus*, has the usual pelagic larval phases, and has a comparatively long planktonic life (BURROWS 1988), while the other, *Tesseropora*, is believed to be a relict species surviving from the Sea of Tethys (NEWMAN & ROSS 1977). As shown here, it incubates its larvae to the non-feeding cypris stage. *Chthamalus stellatus* is distributed from Scotland to West Africa, including the Mediterranean (CRISP et al. 1981), whereas *Tesseropora* is presently restricted to isolated islands in the Atlantic (Bermuda, Azores, and St. Paul rocks in the South Atlantic; NEWMAN & ROSS 1977;

EDWARDS & LUBBOCK 1983). Thus, excluding the immigrant fouling species, the Azorean cirripede fauna has no links with the mainland of the Americas. Yet, as noted by BAKER (1967), the European links are not strong either; for example, the islands have not been colonised by the common low tide barnacle of Europe, *Balanus perforatus* Bruguière, whose habitat is probably occupied by *Megabalanus*.

NEWMAN & ROSS (1977) have discussed the implications of elimination of planktotrophic stages in the life history of invertebrate species occurring on isolated islands. This has advantages in reducing loss of larvae by overdispersal, but also restricts the means of colonising other island groups. Species without the long-living planktonic phase must rely on 'rafting' to colonise new areas. However, this has not restricted the oceanwide tropical distribution of *Tetraclitella divisa,* which also incubates to the cypris stage. But on the other hand, the presence of long-lived planktotrophic nauplius stages in *Chthamalus stellatus* has not prevented the maintenance of a high population density of this species in the Azores islands. The barnacle fauna of the Azores is much less diverse than that of the Hawaiian Islands in the Pacific (NEWMAN 1986); possible reasons include the younger age and smaller size of the Azores and the less diverse fauna of the Atlantic compared with the Indo-Pacific.

A question still to be answered is how long have the Azores been colonised by *C. stellatus*, and if it is a comparatively recent immigrant, possibly assisted by maritime trade? If the record of DROUËT (1858) refers to this species, then it has been present for nearly 150 years at least. The distance of 1200 km from the continent of Europe is well beyond the lifetime of the larval stage, so that any natural spread would demand 'rafting' or the existence of island 'stepping stones' now vanished.

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