THE GENUS *Tesseropora* (CIRRIPIEDIA:TETRACLITIDAE) FROM SÃO MIGUEL, AZORES

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The barnacle *Tesseropora* was considered as primarily an insular Indo-Pacific genus until *Tesseropora atlantica* was described from Bermuda and the Azores (S. Jorge). *T. atlantica* has also been recorded from Saint Paul’s rocks (equatorial Atlantic), confirming its link with isolated oceanic islands. Recently, another *Tesseropora*, *Tesseropora arnoldi*, was described as an Azorean endemic, but as there is some doubt as to the validity of this species, we continue to refer to *Azores Tesseropora* as *T. atlantica*. Little is known of the biology of this ancient genus recorded from the Italian Oligocene. In this paper, we report on the habitat, distribution and several population parameters (relative abundance, density and size structure) of *Tesseropora atlantica* from a boulder beach at Cerco da Caloura, S. Miguel. On this shore, *Tesseropora* has a patchy distribution and is found below the upper limit of *Chlamys stellatus*. Clump densities of *T. atlantica* varied between 37-66, however, nearest neighbour values indicated a rather random distribution within each patch. In addition, the morphology of external plates, examined using scanning electron microscopy, showed some differences compared with published illustrations for the two Atlantic species.

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INTRODUCTION

The genus *Tesseropora* has a long lineage being known from Italian Oligocene fossils (*T. isseli*) (Newman & Ross 1977). Primarily insular, *Tesseropora* was thought to be restricted to the Indo-Pacific region until *Tesseropora atlantica* was described from specimens collected mainly from Bermuda but also referring to Azorean material (Newman & Ross 1977). Following Newman & Ross (1977), therefore, subsequent *Tesseropora* collected from the Atlantic were assumed to be *T. atlantica*. The distribution of *T. atlantica* was extended to other Azorean islands (including S. Miguel) down to Saint Paul’s Rocks in the equatorial Atlantic (Edwards & Lubbock 1983a, b). This distribution being quite remarkable for a species lacking a planktonic larval phase. Recently, Young (1998) described a new species of *Tesseropora* (*T. arnoldi*), endemic to the Azores, casting doubt on the earlier records of *T. atlantica* from the Azores and St. Paul’s Rocks. However, Southward (1998), who has examined museum material from the Azores and Bermuda (including paratypes and new material), is of the opinion that most of the characters used by Young (1998) to separate *T. arnoldi* are invalid and that, in particular, the differences in the labrum appear to be the result of damage to the Bermuda type used to illustrate the description by Newman & Ross (1977). Furthermore, Southward (1998) states that the differences in the interior of the scutum are not obvious when valves of the actual type material are examined, in contrast to published drawings, as much depends on the angle of illumination used to examine them. Southward (1998) continues to refer to the Azorean *Tesseropora* as *T. atlantica* until the
completion of a projected molecular biological study. In view of the uncertainty of the new species, we follow SOUTHWARD (1998) and refer to Azores Tesseropora as T. atlantica. Little is known of the biology of Tesseropora. In the current paper we report on aspects of the ecology and morphology of T. atlantica found on a boulder shore at Cerco da Caloura, S. Miguel.

METHODS

FIELD OBSERVATIONS

All fieldwork was carried out at Cerco da Caloura, a sheltered, gently-sloping cobble bay on the south coast of São Miguel, the largest island of the archipelago of the Azores (Fig. 1). The Azorean coastline, consisting mainly of high cliffs, rocky platforms, and boulder and cobble beaches resulting from erosion of volcanic rocks, is narrow and has limited littoral habitats (MORTON et al. 1998). The maximum tidal range for São Miguel is 1.89 m, and mean tidal ranges for neap and spring tides are 0.65 m and 1.44 m respectively (INSTITUTO Hidrografia 1981). Two transects were established (16th and 17th February 1998), each perpendicular to the sea edge, and extending from the highest point of littorinid occurrence to the lowest water level. For each transect, shore profiles were obtained using two graduated poles, each of 2 m, with an attached spirit level. These were placed at right angles at the shore position to be levelled, and the horizontal distance between the two points was read from the horizontal pole and the elevation was read from the vertical pole (EMERY 1961). The heights were related to Chart Datum (Azores) using the position of the water's edge at the time of predicted low water. Taking into account the presence of residual swell and the methods used, shore heights are approximate (+0.1 m). At each sampling site along the transect (17 sites used per transect), a note was made of the macrofauna and flora, with no attempt to quantify surface cover or densities.

Having established the vertical distribution of T. atlantica, density and Nearest Neighbour measurements were taken. The presence of boulders made quantitative sampling very difficult and random density counts of barnacle abundance were not attempted. Instead, density counts (taken in July 1997, and February and May 1998) were based upon positioning a 10 x 10 cm quadrat on different rocks with Tesseropora. Hence, our density measures varied depending on the presence of other sessile animals (Spirorbis sp. & Chthamalus stellatus), and gave indications of the maximum abundances for Tesseropora. At the same time as the densities were recorded, the lengths of all T. atlantica on each rock were measured using hand-held vernier calipers;
Barnacles, attached to their original rocks, were transported from Cerco da Caloura (July 1997) to the laboratory in seawater. In the laboratory, they were removed from the rock using a scalpel blade, fixed in 4% seawater formalin and dissected from their shells. Entire animals, together with the shell plates, were dehydrated in a series of increasing alcohol concentrations (10 min in each of 30%, 65% and two changes in 100% alcohol). Following dehydration, the shells and barnacles were placed (10 min in each mixture) in 50% acetone followed by two changes of 65% and two changes in 100% alcohol. The shells and barnacles were placed for 20 mins in a 98% solution of hexamethyldisilane. The material was mounted on specimen stubs, coated with carbon and gold-palladium (60:40%) and viewed with a JEOL SEM (JSM 400) and Nearest Neighbour (NN) analysis (JSM 5410).

RESULTS AND DISCUSSION

HABITAT OF Tesseropora

At Cerco da Caloura, the boulders tend to mask zonation patterns but three general "zones" may be distinguished. At the lowest level, the rocks are covered with a red algal turf comprising Corallina officinalis L. and Gigartina acicularis (Roth). The middle "zone" is characterised by tufts of the green alga Ulva rigida Agardh and the third, uppermost level, is devoid of macroalgae. On each transect, T. atlantica was found within the lower region of the "Ulva zone", generally below Chthamalus stellatus, although the distribution of the two species does overlap (Fig. 2). This zonation confirms the observations of SOUTHWARD (1998) who found T. atlantica on the outer steps of the breakwater at Ponta Delgada (São Miguel) and in the algal turf below C. stellatus at Porto Pim (Faial). At Cerco da Caloura and Ponta da Queimada (Agua d'Alto), T. atlantica is always found in crevices, on the shaded aspects of boulders and on the underside of cobbles. On these shores, individuals found towards the lower level were larger than those seen at the upper distributional limits. In the Ulva zone, limpets (Patella candei) and chitons were also found on the rocks colonized by T. atlantica. The underside of cobbles, where T. atlantica was found, was also covered with sponges and serpulid polychaetes. In Ponta da Queimada (Agua d'Alto), not only could we find T. atlantica and Chthamalus on the same cobble, but also Verruca spengleri was frequently encountered. Interestingly, at Porto Pim, T. atlantica formed contiguous clusters in the holes formed by small individuals of the sea urchin Paracentrotus lividus (SOUTHWARD 1998). Earlier records from the Azores indicate that Tesseropora sp. was locally abundant at one site in Urzelina (S. Jorge) where it was found in 1 m of water (BAKER 1967). Although the data are sparse, it appears that T. atlantica is intolerant to water loss despite the presence of a calcareous basis, generally regarded as an adaptation to reduce desiccation stress (NEWMAN & ROSS 1977). YOUNG (1998) reported T. arnoldi extending from the intertidal to about 25 m depth, usually attached to Megabalanus azoricus and mollusc shells.

The distribution of Tesseropora atlantica at Cerco da Caloura was patchy and clump densities (numbers of barnacles in 10 x 10 cm quadrats) varied between 37 and 66. Nearest Neighbour values (ca. 1.6) indicated a more random than clumped distribution within each patch.

SIZE-FREQUENCY DISTRIBUTIONS

The maximum size of Tesseropora atlantica from Cerco da Caloura was 4.5 mm, with a mean of 2.6 mm (Fig. 3); these are the smallest sizes reported for Tesseropora. Although NEWMAN & ROSS (1977) do not give extensive measurements, they state that the largest basal diameter for T. atlantica was 10 mm (compared with maxima of 30 mm for T. rosea and 40 mm for T. viridis). SOUTHWARD (1998) gives a size range of 1.5-6.5
mm with a mode around 3.5 mm for the animals he collected in the Azores, and reported a maturity size of 4 mm shell length. YOUNG (1998) refers to a carino-rostral diameter of about 5 mm for T. arnoldi and only one specimen measured 7 mm.

**BIOLOGY OF Tesseropora**

Both *Tesseropora atlantica* and *T. arnoldi* have suppressed development with the nauplius being retained in the mantle cavity (SOUTHWARD 1998; YOUNG 1998). The same was reported for *T. wireni* (NEWMAN & ROSS 1877). SOUTHWARD (1998) observed that, within 24 h of release, the cyprids (carapace length of 0.63 mm) of *T. atlantica* underwent searching behaviour which continued for a further 24 h although no settlement or metamorphosis was seen. Lack of a dispersal phase in the life cycle of barnacles occupying isolated oceanic islands is interpreted as an adaptation for maintaining insular populations (NEWMAN & ROSS 1977). For example, the risk of loss of propagules from donor populations is removed. Such species will also have restricted genetic pools and it is to be anticipated that they will show high levels of endemism.

**SPECIES OF Tesseropora**

Currently, four extant species of *Tesseropora* are described, *T. rosea*, *T. wireni*, *T. atlantica* and *T. arnoldi*. *T. rosea* is restricted to the southern hemisphere, and has been recorded from the southern tip of South Africa, New South Wales (Australia), the Kermadec Islands and New Caledonia. The other species are distributed mainly in the northern hemisphere. *T. wireni* is found from Dar-es-Salaam east, and from Chagos Bank to Wake. Specimens of *T. wireni* from Hawaii do not appear to be typical for this species and may be a new species (NEWMAN & ROSS 1977). *T. atlantica*, believed to be a relict species surviving from the Sea of Tethys (NEWMAN & ROSS 1977), occurs in Bermuda (type locality).
and has been reported from the Azores (NEWMAN & ROSS 1977; SOUTHWARD 1998) and from Saint Paul's Rocks (equatorial Atlantic) (EDWARDS & LUBBOCK 1983). Since the description of T. arnoldi, however, there remains a question mark over these last two records. Finally, T. arnoldi, endemic to the Azores, has been found on two islands (Faial and S. Miguel) (BAKER 1967; YOUNG 1998).

**MORPHOLOGY OF Tesseropora**

NEWMAN & ROSS (1977) listed the distinguishing features of extant species of Tesseropora, some of which are shown in Figure 4 together with the corresponding plates for the new species, T. arnoldi (YOUNG 1998). The most obvious difference between T. atlantica and the other non-Atlantic species is the differential alignment of the scutal adductor ridge with the articular ridge. In T. atlantica, the adductor ridge is in line, and nearly continuous, with the articular ridge whereas in the other species it overlaps the articular ridge. In T. arnoldi, the adductor ridge is separated from the articular ridge (YOUNG 1998). Another distinguishing feature relates to the parietal pores (Fig. 4). In T. atlantica and T. arnoldi the pores are in a single row as they are in T. rosea, however, the very different geographical distributions of this latter species prevents confusion. The parietal pores of T. wireni, on the other hand, are divided into secondary and tertiary rows leading to a dendritic pattern. All the other Tesseropora species have only one row of parietal pores (NEWMAN & ROSS 1977; YOUNG 1998). T. arnoldi can also be distinguished from Pacific Tesseropora (T. rosea and T. wireni) by the colour of the sheath, the development of the radii and the parietal tubes, and the structure of the cirri (NEWMAN & ROSS 1977; YOUNG 1998). Distinctions of T. arnoldi from T. atlantica reported by YOUNG (1998) include the well developed ribs from the basis to the sheath, intercalated by numerous fine ribs instead of only small numerous fine ribs; the position of the adductor ridge of the scutum in relation to the articular ridge; and the presence of conspicuous teeth on the crest.

Despite the erection of T. arnoldi as an Azorean endemic, there are clear differences in the morphology of the opercular and lateral plates of Tesseropora atlantica from Cerco da Caloura (Fig. 5) and those of T. arnoldi described by YOUNG (1998) from the Azores (Fig. 4). More detailed descriptions of the critical distinguishing features (labrum, opercular plate, cirri) are required before concluding whether there are two species of Tesseropora endemic to the Azores or whether there is a high degree of polymorphism in Azorean Tesseropora. In the light of our findings, it is clear that a comprehensive review of the genus is required.

**CONCLUSIONS**

The taxonomy of genus Tesseropora requires careful re-appraisal in the light of the recent description of T. arnoldi, one of the limited number of littoral marine invertebrate Azorean endemics. Moreover, the doubts raised by SOUTHWARD (1998) and the current work demand a very careful study of the morphology of the critical distinguishing features of these barnacles.

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**REFERENCES**

Fig. 5. Scanning Electron Microscopy (SEM) pictures of *Tessaropora atlantica* from Cerco Caloura. A, B Calcareous basis; C, D Internal view of opercular plates; E, F Internal view of lateral plate.


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