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Functional Morphology and Zonation of Three Species of Sea Anemones from Rocky Shores in Southern Chile

W.B. Stotz

Instituto de Zoologia, Universidad Austral de Chile; Valdivia, Chile

Abstract

Three species of sea anemones, clearly exhibiting zonation on the shore, are grouped into intertidal [*Phymactis clematis* (Drayton, 1846), *Anthothoe chilensis* (Lesson, 1830)] and infralittoral [*Antholoba achates* (Drayton, 1846)] forms. A series of observations revealed that intertidal forms have the ability to retain water in the coelenteron during exposure to air, while the infralittoral form cannot do so. This different behaviour is attributed to morphological characteristics, such as the specific body shape and the structure of the sphincter and retractor muscles. These features, in combination with specific abiotic factors of the various habitats under consideration, determine the upper limits of distribution of each species, while zonation below these limits seems to be affected in addition by biological interactions.

Introduction

Intertidal animals are regularly exposed to air, and are subjected during such periods to a number of stresses which are absent when they are covered by water (Barnes *et al.*, 1963). A primary stress due to exposure arises from loss of water by evaporation, which may ultimately lead to desiccation. Physiological, morphological and behavioural adaptations to prevent desiccation will enable particular species to occupy a certain level in the intertidal environment. Broekhuysen (1941) showed a definite correlation between zonal distribution and resistance to desiccation among 5 of 6 gastropod species in False Bay, South Africa. Dayton (1971) points out that the wider distribution pattern across desiccation gradients of sessile animals compared with algae suggests that the distribution patterns of these animals are less likely to be determined by physiological stresses than those of the algae. The major exception to the communities studied by Dayton (1971) is the sea anemone *Anthopleura elegantissima*, because its distribution seems to be limited partially by desiccatory stresses. This species is very similar to the Chilean sea anemone *Phymactis clematis*.

The present study aims mainly to investigate if there is any relation between the vertical distribution within the midlittoral and infralittoral zone and the morphological structures or behavioural features of the following species of sea anemones: *Phymactis clematis* (Drayton, 1846), *Anthothoe chilensis* (Lesson, 1830), and *Antholoba achates* (Drayton, 1846).

Materials and Methods

The present study was carried out on the rocky shores of Maiquillahue Bay (Province of Valdivia, Southern Chile; 39°25' S, 73°14'W). The vertical distribution and behaviour of the macrofauna was directly observed in the field, measuring some heights and observing the limits between the population of the different organisms. The structure of the sea anemones was investigated by histological sections of 6 to 10 µm, stained with fast red and picro-indigocarmine according to the method described by Adam and Czihak (1964; see also Stotz, in press). Climatological data were obtained from the Meteorological Station of the Institute of Geology, Universidad Austral de Chile, located in the study area. The classification of the zones in the intertidal area given by Stephenson and Stephenson (1949) was followed.

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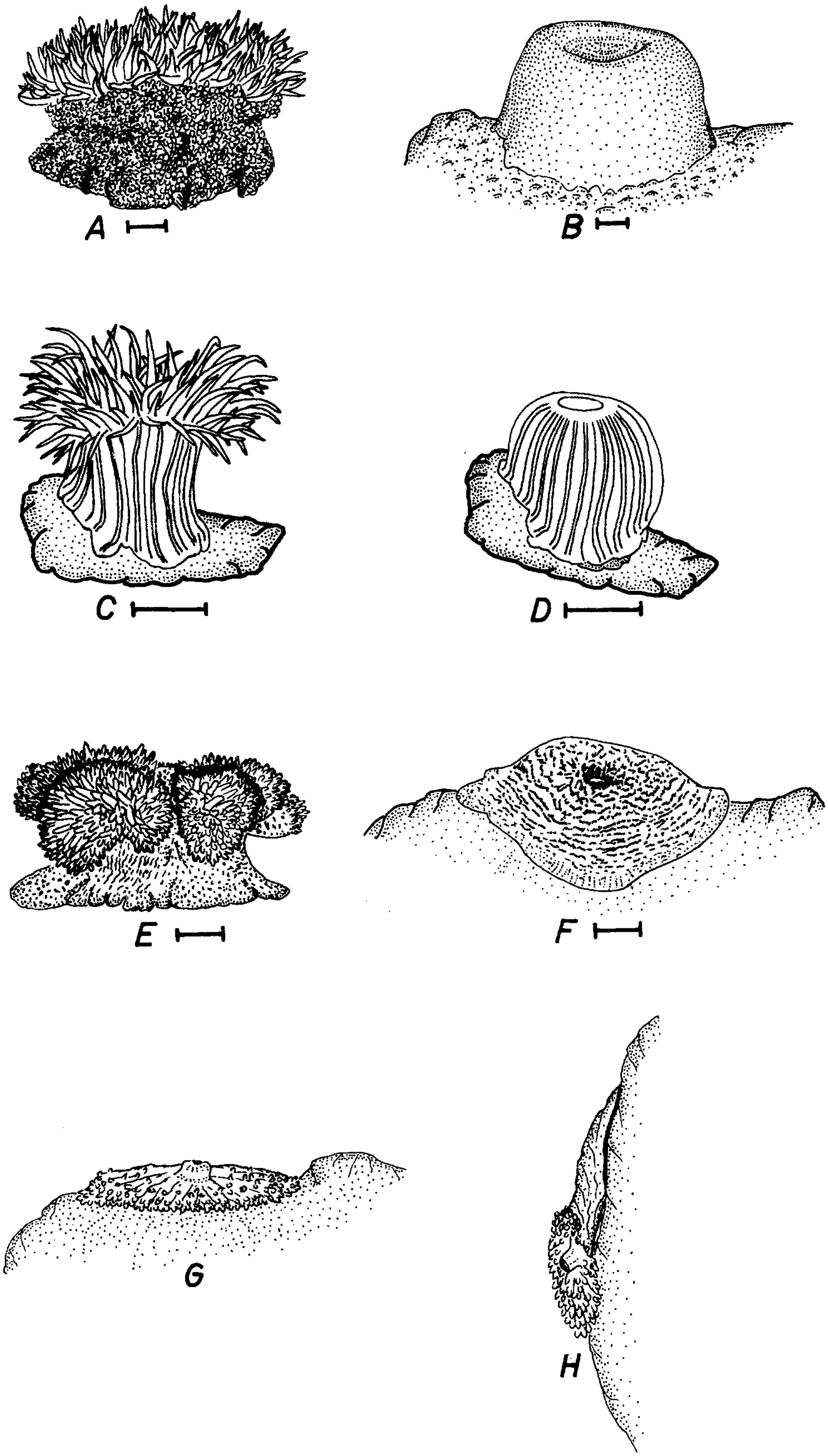


Fig. 1. Expanded and contracted sea anemones. (A), (B) *Phymactis clematis*; (C), (D) *Anthothoe chilensis*; (E), (F), (G), (H) *Antholoba achates*. All scale bars = 1 cm

Results and Discussion

Research Area and General Distribution

The rocky shores of Maiquillahue Bay are mostly broken, formed of large boulders of 1 to 6 or more m in diameter. This feature gives rise to habitats with marked gradients of wave action, wind exposure, and sun and rain intensity.

The 3 sea anemones, *Phymactis clematis*, *Anthothoe chilensis*, and *Antholoba achates* (Fig. 1) are not present in areas exposed directly to wind, waves and rain, but in places protected against rain, e.g. under overhanging boulders or, mostly, on vertical walls which are occupied at a higher intertidal level by *Perumytilus purpuratus* populations. Furthermore, *Anthothoe chilensis* and *Antholoba achates* are not present in places exposed to the sun, whereas *Phymactis clematis* can be found in areas directly exposed to the sun. Viviani (1969) states that this species is more affected by rain than by sun. Rain, therefore, can be considered an important limiting factor to distribution of sea anemones in this bay. The total annual rainfall in the research area amounts to 1,460 mm, 60% of which occurs from May to August; during these 4 months, the mean rainfall is 11.8 mm day^{-1}, ranging from 9.5 to 13.2 mm (averages for the last 10 years).

In general, the 3 sea anemones occur in steep rocky places, just below the *Perumytilus purpuratus* belt. This region is the research area considered here; its vertical extension averages 1.5 m. The highest zone of this area is occupied by *Phymactis clematis*, the middle by *Anthothoe chilensis*, and the lowest by *Antholoba achates* (Fig. 2).

Measurements of temperature, relative humidity, wind velocity and intensity of sun radiation revealed no significant differences at the various levels at which the sea anemones are located. Length of exposure to air seems to be the only factor controlling their different distributions. It is obvious that the higher the distribution of a species, the longer the time of exposure to air and the greater the probability of water loss due to evaporation. *Phymactis clematis*, therefore, would seem to be more affected by evaporation than *Anthothoe chilensis* and this species more than *Antholoba achates*.

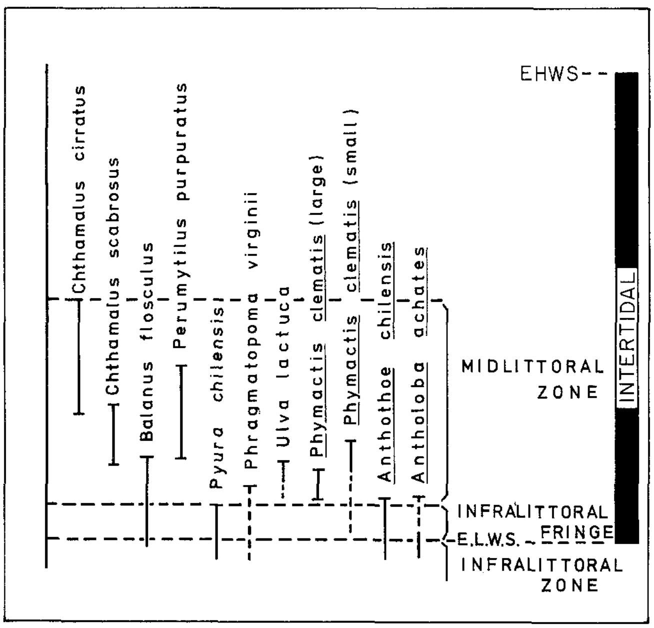


Fig. 2. Zonation of most common organisms in areas occupied by all 3 species of sea anemones. Dashed bars represent isolated specimens. Black bar on right represents what is considered "intertidal" in this work (see text). The 3 species of sea anemones are underlined. EHWS: extreme high-water spring tides; ELWS: extreme low-water spring tides

Analysis of Vertical Distribution

Different size classes of *Phymactis clematis* have different vertical distributions. The smallest individuals (column diameter <0.5 cm) principally inhabit the interstices of the *Perumytilus purpuratus* belt or small crevices of the rock, mostly covered by *Ulva lactuca*, both of which are highly humid microhabitats. Their vertical distribution within the *P. purpuratus* belt, however, is related to seasonal changes. In summer, immediately after spatfall, small individuals occur along the entire belt; in late autumn they are restricted to the lower part of the belt, probably because of rainfall, and remain here the rest of the year. Medium-sized individuals (column diameter between 0.5 and 2 cm) occupy a narrow zone immediately below the *P. purpuratus* belt; they form very dense aggregations which greatly reduce the danger of evaporation (cf. Francis, 1973). Large individuals (column diameter >2 cm) occur further below the *P. purpuratus* belt until they are replaced by *Anthothoe chilensis* at about the upper limit of the infralittoral fringe (Fig. 2). The boundary line between the populations of *Phymactis clematis* and *A. chilensis* is very precise and with no overlap (Fig. 3). Further down (about 30 to 50 cm from the upper limit of the distribution of *A. chilensis*), among individuals of *A. chilensis* in the infralittoral zone, appear the

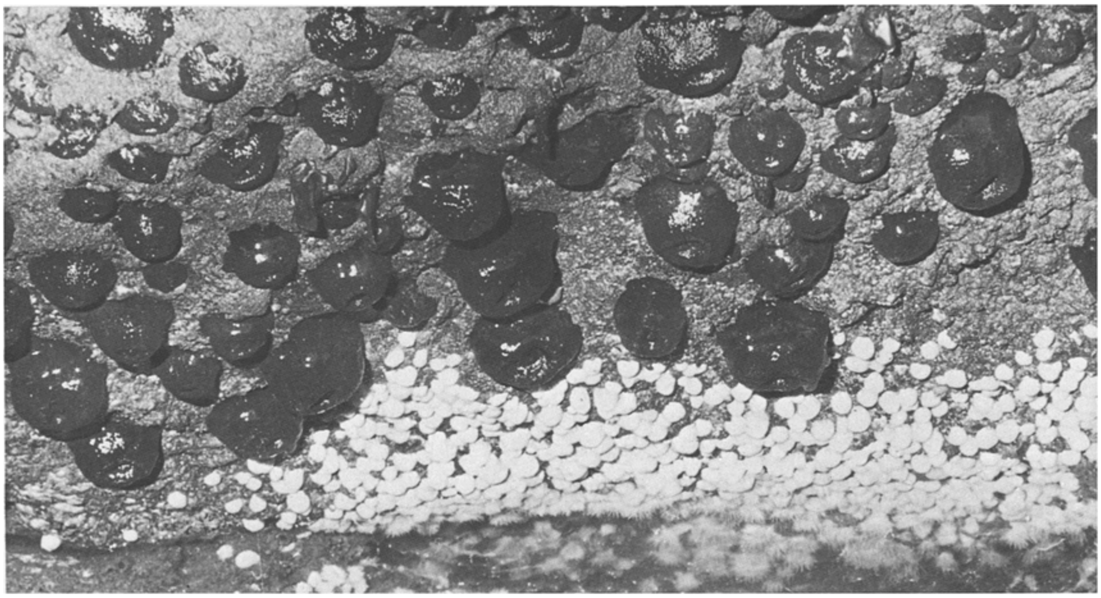


Fig. 3. Aggregations of dark *Phymactis clematis* and white *Anthothoe chilensis*

first isolated specimens of *Antholoba achates*. Dense aggregations of the latter species, however, are restricted to an area 0.5 to 1 m below the level of extreme low water at spring tides. Apart from this typical distribution of *A. achates*, some isolated individuals may occur even at the highest levels reached by *Anthothoe chilensis*, but only in well-shaded, wind-protected places.

According to zonation, *Phymactis clematis* and *Anthothoe chilensis* can be considered to be intertidal species. In this paper, the term "intertidal" is equivalent to the term "littoral", in the sense used by Stephenson and Stephenson (1949) (see also Fig. 2 of present paper). The presence of *Antholoba achates* in the intertidal area must be considered exceptional or accidental.

Functional Morphology and Zonation

The two intertidal species, although of different subtribes, have in common the following behavioural characteristic, which is less developed or wanting in *Antholoba achates*: When they are exposed to air, only the upper part of the column contracts; it covers the tentacles and partially or completely covers the oral disc, forming a small dome (Fig. 1 B, D). In this way the intertidal species are able to retain a relatively large volume of water in the coelenteron, which amounts to 10-15 ml of water in an individual *Phymactis clematis* with a base diameter of 6 to 8 cm. Furthermore, the dome-like contraction reduces the body surface. *A. achates* is also able to adopt this body shape; however, after a short period it contracts totally, resulting in a flat dome (Fig. 1 F), and consequently, nearly all the water is expelled from the coelenteron. Another behaviour typical of *A. achates* is to expand its oral disc while relaxing the column and lying or hanging in a flaccid manner (Fig. 1 G, H), thus also losing most of the water from the gastral cavity. The behaviour described here for the two intertidal forms, was also observed by Dayton (1971) investigating the intertidal *Anthopleura elegantissima* from the California (USA) coast. Dayton stated that the retention of a certain amount of water in the coelenteron could be considered a protection against desiccation.

The relation between the diameter of the oral disc and that of the column, together with the structure of the sphincter, are important for the contraction of only the upper part of the body. In both intertidal species, the oral disc is of almost the same diameter as the column (Fig. 1 A, C), and the sphincter is located in the upper part of the body (Fig. 4 A, C). In contrast, *Antholoba achates* has an oral disc which is much wider than its column (Fig. 1 E), and the sphincter is very elongated, extending over almost the entire length of the column (Fig. 4 E).

A comparable situation is found in the retractor muscles, which are very compact in the intertidal species *Phymactis clematis* and *Anthothoe chilensis* (Fig. 5

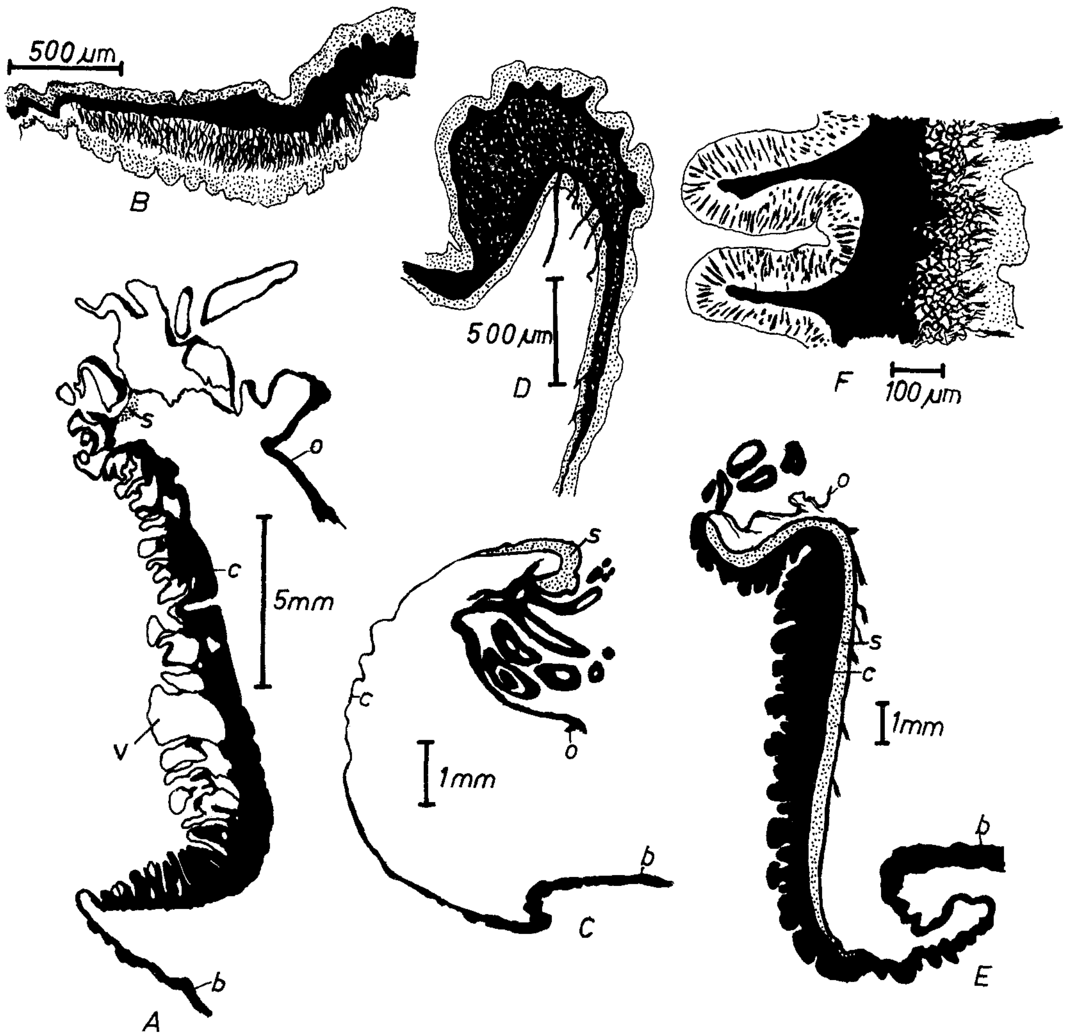
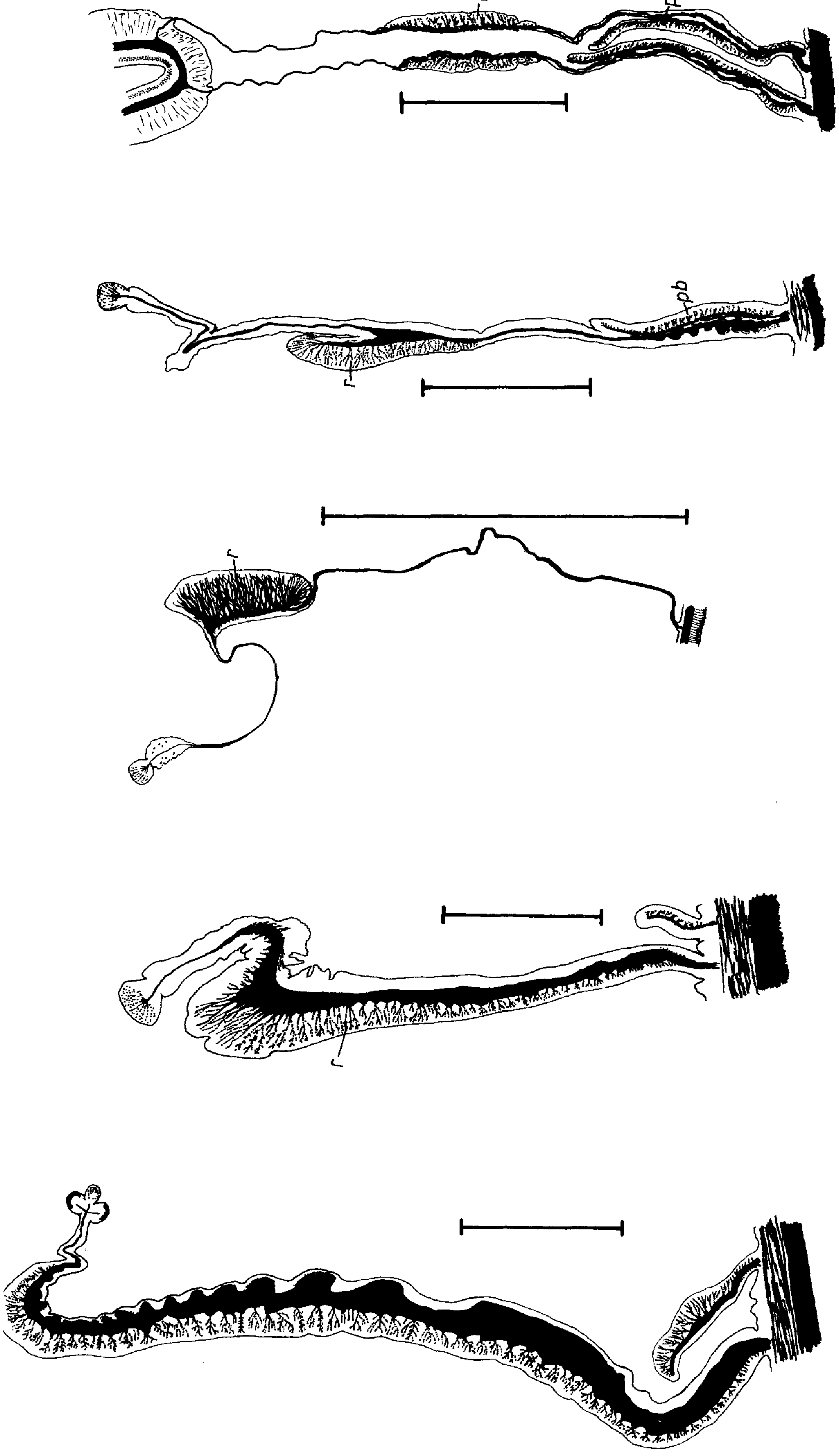


Fig. 4. Location and structure of sphincter in longitudinal sections of the 3 sea anemones. (A), (B) *Phymactis clematis*; (A) column wall; (B) sphincter. (C), (D) *Anthothoe chilensis*; (C) column wall; (D) sphincter. (E), (F) *Antholoba achates*; (E) column wall; (F) part of column, showing structure of sphincter. b: Base; c: column; o: oral disc; s: sphincter, presented as dotted area; v: vesicles

A, B, C), but extend over the full breadth of the mesentery (Fig. 5 D, E) in the infralittoral species *Antholoba achates*. Furthermore, *P. clematis* has not only a strong retractor muscle but also a well-developed parietobasilar muscle on the mesentery (Fig. 5 A, B).

The muscular system with concentrated bundles (in the intertidal forms) seems to play an important role in allowing a better control of the body shape during exposure to air. The lack of such a muscular system in *Antholoba achates* and the presence of a wide oral disc which hardly can be covered by the column, are responsible for the inability of this species to maintain the dome-like contraction for longer periods of time and to retain a larger amount of water in the coelenteron. Consequently, the distribution of *A. achates* in the intertidal area is restricted to well-shaded places wherein stress by desiccation is highly reduced. The highest-living species, *Phymactis clematis*, has by far the thickest column wall, which in contrast to that of the two other sea anemones, is covered with small vesicles (Fig. 4 A) which may play a further important role in reducing danger of evaporation. When *P. clematis* is exposed to air, the vesicles collapse to a certain degree and adhere to each other, forming a continuous layer without increasing the exposed surface. Thus, during exposure to air the vesicles as a whole represent a capillary system enclosing many little drops of water. Evaporation of this wa-



A

B

C

D

E

ter layer seems to be reduced by cohesion and by the capillary force which, in turn, will become more effective with any further increase in salinity caused by evaporation. Furthermore, the exterior of the column is covered by a layer of mucus which probably also helps to reduce evaporation.

In regard to heating-up and evaporation, the white colour of *Anthothoe chilensis* may be a great advantage in contrast to the dark colours of *Phymactis clematis* (green, brownish-red, blue). For the green sea anemone *Anthopleura elegantissima* for example, Dayton (1971) demonstrated a difference in temperature of 13.3 C^{o} between the interior of the sea anemone and the surrounding air. In *P. clematis*, which colonizes sun-exposed sites, pigmentation is of fundamental importance. The danger of heating-up, which is necessarily combined with pigmentation, may be overcome in *P. clematis* by the vesicle system already mentioned above. From longitudinal sections (Fig. 4 A) it can be seen that the vesicles have very thin walls in contrast to the thick wall of the column, and that the lumina of the vesicles are connected by narrow ducts with the coelenteron. Furthermore, the walls of the ducts are well-equipped with muscle fibres so that the quantity of water inside the vesicles can be controlled by opening and closing these ducts. Thus, the vesicle system also seems to represent a well controllable evaporation or cooling system.

Until now, zonation has been described and discussed as a result of physiological stress resulting from physical environment. However, biological interactions may also have some influence. For example, the very precise limit between the populations of *Phymactis clematis* and *Anthothoe chilensis* (Fig. 3) could be considered, according to Daubenmire (1969; *in* Dayton, 1971) to result from competitive interaction. When *A. chilensis* is not present, *P. clematis* extends its distribution a little further down the shore. It seems that *A. chilensis* controls to some extent the lower distributional limit of *P. clematis* when both species occur together (however, except for this observation, no direct evidence of competition between these two species exists). Biological interaction is also indicated by the patchy distribution of these actinians in the intertidal zone, since there seem to be more places with appropriate physical conditions than are occupied by sea anemones.

These two observations, together with the general vertical distribution of the species, show that physiological stress determines only the highest limit reached by the population of each species of sea anemone on the shore. *Antholoba achates* has been found in the infralittoral zone to a depth of 162 m (Carlgren, 1949), while *Anthothoe chilensis* has been observed to a depth of 4 to 5 m (own observations in the Maiquillahue Bay). *Phymactis clematis* constitutes an exception; it seldom occurs in the infralittoral zone and, when found, is represented by only small and isolated individuals. The statement by Lewis (1964, p. 229) that "the emersion is not simply a transient inconvenience but in some way has become essential for their (its) well-being" seems to apply for this species.

Conclusions

The intertidal species (*Phymactis clematis* and *Anthothoe chilensis*) are characterized by the dome-like contraction of their body, which makes it possible to retain a relatively large volume of water in the coelenteron. This ability, which enables the intertidal species to withstand exposure to air for a longer period of time, is less developed or lacking in the infralittoral species *Antholoba achates*. The dome-like contraction is made possible by means of (i) an oral disc not wider than the column, (ii) a sphincter concentrated distally and (iii) a strong retractor muscle located in the middle of the mesentery. Loss of water due to evaporation also depends upon the thickness and structure of the column wall.

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Fig. 5. Cross-sections of mesenteries in the 3 sea anemones, showing location of retractors. (A), (B) *Phymactis clematis*; (C) *Anthothoe chilensis*; (D), (E) *Antholoba achates*. r: Retractor; pb: parietobasilar muscle. All scale bars = 1 mm

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Wolfgang B. Stotz
Instituto de Zoologia
Universidad Austral de Chile
Casilla 567
Valdivia
Chile

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