

Morphological Variability during Longitudinal Fission of the Intertidal Sea Anemone, *Anthopleura elegantissima* (Brandt)¹

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ABSTRACT: The sea anemone *Anthopleura elegantissima* forms clonal aggregations on rocky shores along the Pacific Coast of North America by a process of longitudinal fission. Fission can occur by lateral stretching of the column and separation of the two halves followed by internal regeneration of parts of the actinopharynx and of the column. Two new directive mesenteries, one siphonoglyph, and several pairs of mesenteries flanking the directives also form. Alternatively, large individuals appear to form new directive mesenteries and siphonoglyphs well in advance of division.

THE MOST COMPLETELY DESCRIBED cases of longitudinal fission and clone formation in sea anemones are those of *Haliplanella luciae* (Verrill) and *Anthopleura elegantissima* (Brandt). *Haliplanella luciae* divides rapidly and continuously when fed (Minasian 1976, 1979, 1982; Minasian and Mariscal 1979; Shick and Lamb 1977), forming dispersed clones covering large areas of intertidal rock (Uchida 1932, 1936; Kiener 1971; Williams 1973, 1975; Shick 1976; Shick and Lamb 1977) on shores around much of the northern and southern hemispheres. Its rate of division and size at division are strongly temperature dependent (Miyawaki 1952, Johnson and Shick 1977, Minasian 1979) as are those of *A. elegantissima* (see Sebens 1980).

Anthopleura elegantissima divides once or less per year (Sebens 1979, 1980, 1982a) and forms dense aggregated clones (Hand 1955; Francis 1973a, 1979; Fredericks 1976; Sebens 1977, 1981a,b, 1982b, in press) in the intertidal zone of rocky shores along the west coast of North America. Unlike *Haliplanella luciae*, fission is inhibited when *A. elegantissima* is fed (Sebens 1980). Fission thus occurs primarily during the fall, winter, and early spring when the anemones are capturing the least amount

of food. Both species use specialized organs for agonistic behavior against other anemones and other clones of the same species [acrorhagi in *Anthopleura* (see Francis 1973b, 1976), catch-tentacles in *Haliplanella* (see Williams 1975)]. *Anthopleura elegantissima* is dioecious and reproduces sexually each year (Sebens 1981b), but it is less clear that *H. luciae* reproduces sexually regularly, if at all (Shick 1976).

The ecological and physiological aspects of longitudinal fission are better understood than are the morphological rearrangements necessary to effect division. Several studies have described the fission of *Haliplanella luciae* (Davis 1919; Atoda 1954, 1976), which tears itself in two and subsequently regenerates the missing parts. Such rearrangement and regeneration have also been described for anemones that reproduce asexually by other methods including pedal laceration (Torrey and Mery 1904, Hammat 1906, Cary 1911, Stephenson 1929) and transverse fission (Schmidt 1970). The present study is the first description of the morphology of longitudinal fission in *Anthopleura elegantissima* and points out the apparent occurrence of two distinct mechanisms of fission.

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METHODS

Serial sections of individuals at various stages of division were prepared to investigate the morphological reorganization that must

occur in order to effect longitudinal fission in *Anthopleura elegantissima*. Anemones were collected (during 1973–1977 and 1982) at Tatoosh Island (48°24' N, 129°48' W), Iceberg Point (48°25' N, 122°53' W) on Lopez Island, and Cattle Point (48°27' N, 122°57' W) on San Juan Island, Washington. Specimens appearing to be in some stage of fission were immediately pinned to slabs of paraffin in as close to the natural posture as possible with the pedal disc against the paraffin. If not so restrained, the tension between the two halves caused them to curl so that the oral surface became very concave, indicating that tension was greater along this surface than along the pedal disc. Pinned anemones were relaxed in a 1 : 1 mixture of 7.5 percent $MgCl_2$ and sea water at 5°C for 24 hr, then fixed in Bouin's solution.

Specimens were embedded in paraffin or, if very large, in Parlodion (see method in Sebens 1981*b*). Sections of Parlodion-embedded specimens, 25 and 50 μm thick, were collected in groups of five and stained, with each group in a separate jar so that a serial array was maintained. Sections were stained with Heidenhain's Azan or Azan modified for Parlodion. A total of 63 anemones was fixed and embedded, 42 of which were used in this study. Six additional specimens were dissected after relaxation, and many more were observed and photographed alive in the field at all stages of division.

Two hundred anemones, collected at Cattle Point in June and July 1974, were dissected to determine the incidence in the population of siphonoglyph numerical abnormalities. Two siphonoglyphs each supported by a pair of directive mesenteries (diglyphy) is the most common arrangement, but monoglyphic and triglyphic individuals do occur. Several dividing anemones in the sectioned material had four siphonoglyphs and four sets of directive mesenteries (tetraglyphy), which could occur if a second pair had formed just prior to or during division. Alternatively, tetraglyphic states may represent division of a normally tetraglyphic polyp. The second case might be expected if some percentage of the non-dividing population were found to be tetraglyphic.

RESULTS

The pedal disc is normally approximately circular. It is not uncommon, however, to observe individuals with the longest dimension of the pedal disc several times that of the shortest. This posture is assumed when an individual conforms to a very thin crack in a rock surface, or when squeezing between obstacles in its path. It also occurs when the anemone is in motion, the axis of elongation being the same as the direction of locomotion, in which case the pedal disc is not very far from circular. Elongation is often followed by a return to the circular pedal disc. Such elongated postures, which superficially resemble the first stage of longitudinal fission (Figures 1, 2*B*), differ in the shape of the oral aperture, which is rounded or slightly oval in an individual not undergoing fission. In anemones commencing fission, the two ends of the pedal disc are actively moving apart and may show a partial inflation of the edges as is common during locomotion. The adhesive verrucae of the column are arranged in closely packed vertical rows at opposite ends of the column along the long axis and are spread wide apart along the short axis (Figure 2*D*). The latter area is stretched by the movement of the two ends of the pedal disc. The entire oral disc is elongated, and the tentacles are more sparse in the area under tension. The siphonoglyphs lie at the two extreme ends of the actinopharynx along the long axis at the beginning of the elongation. Later, if the development of a second set of siphonoglyphs occurs, the original ones may be shifted somewhat away from the ends of the long axis.

Division of the column commences aborally and continues in an oral direction followed immediately by closure of the column wall where separation occurs. The initial elongation progresses as the pedal disc divides into two separate portions which continue to move apart. The anemone is now free of the substratum underneath the central portion, although the entire body is often pulled flat against the substratum. At this point a probe can be passed underneath the center of the dividing anemone without dislodging either of the two pedal disc halves. Finally, the two

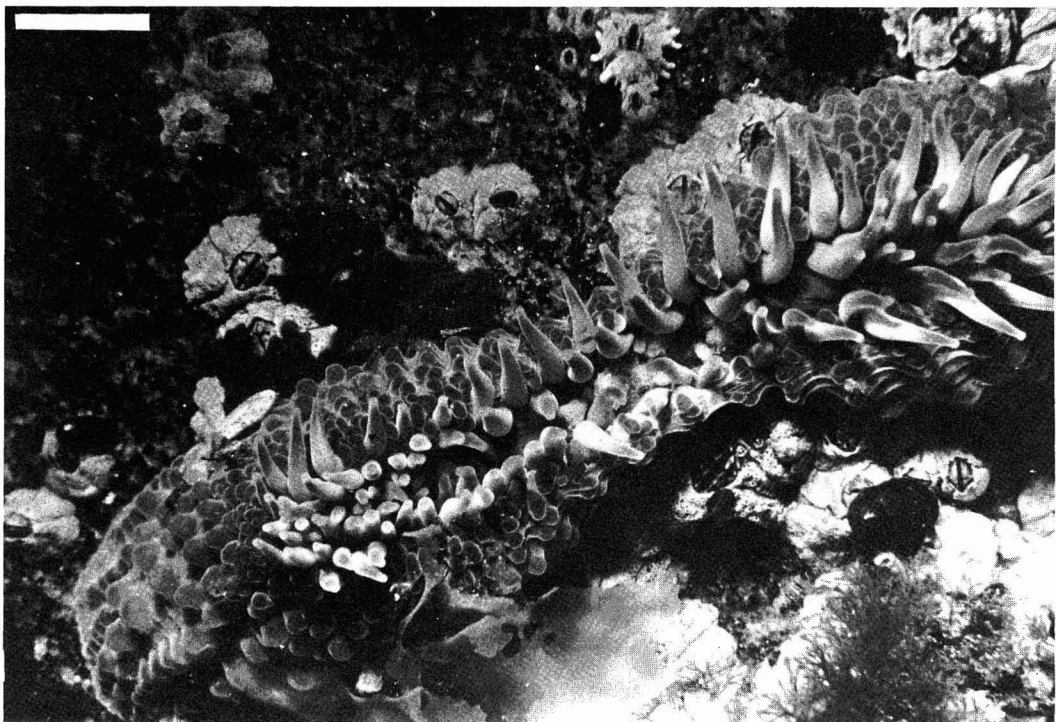


FIGURE 1. An elongated individual of *Anthopleura elegantissima* in the process of longitudinal fission. The anemone has probably already divided the actinopharynx and is still attached by the oral disc and the column. Limekiln Lighthouse Point, San Juan Island, Washington, July 1982 (scale bar = 0.5 cm).

halves are held together only by the oral disc and by the marginal sphincter muscle. The actinopharynx can be seen through the open oral aperture as having divided although still connected along its oral rim. Separation of the actinopharynx and oral disc occurs next, and the two halves are then connected only by the marginal sphincter (Figure 2F), which appears as two thin bands of tissue stretched between the halves. These bands eventually give way, one at a time, resulting in complete separation.

The broken ends of the upper column and sphincter then roll inward and fuse, completing the formation of two separate individuals (Figure 2H). At this stage, a strip of smooth light-colored tissue is visible running vertically from the pedal disc to the parapet where closure of the column wall has been effected. The actinopharynx is not yet complete orally and has two free edges facing the axis of division. There is a conspicuous lack of

tentacles in the region above the strip of light-colored tissue. Eventually, the actinopharynx is completed and the two siphonoglyphs are positioned at opposite ends of the actinopharynx as new mesenteries and body-wall tissue are added. If the division results in monoglyphic halves, a new siphonoglyph arises from the scarred area in each daughter individual.

The timespan of division is highly variable. In newly collected anemones, longitudinal fission has been completed in as short a time as 5 days. In other individuals the process has proceeded over 6 to 8 wk. The first stage of elongation lasts the longest, with the actual separation occurring in a period of a few days or less. The new individuals produced retain the light-colored strip of tissue for at least 1 mo and as long as several months (Sebens 1980, 1982a), although the pharynx is complete and centralized approximately 1 to 2 wk after division. At the early stages the column

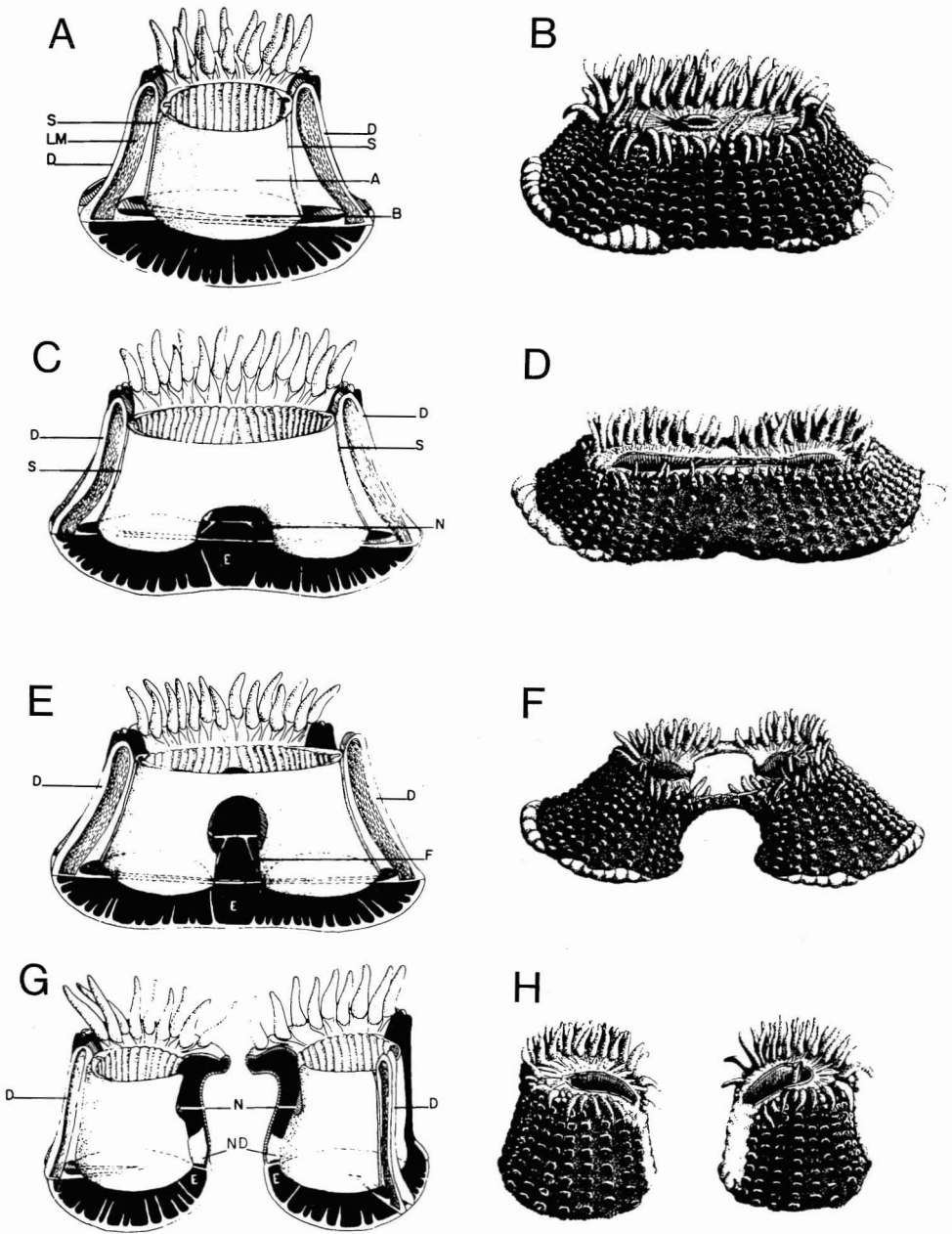


FIGURE 2. Longitudinal fission of *Anthopleura elegantissima* (originally diglyphic type). *A*, *C*, *E*, and *G* are internal views; *B*, *D*, *F*, and *H* are external. *A*, *B*: A diglyphic nondividing individual or one just prior to division. Note the circular oral aperture. Siphonglyph (*S*), longitudinal retractor muscle (*M*) of directive mesentery (*D*), actinopharynx (*A*), basal extension of directive mesentery (*B*). *C*, *D*: Beginning of division. Elongation of the oral aperture, basal notch (*N*) formation in the actinopharynx and widening of complete mesenterial endocoels (*E*) perpendicular to axis of division. Note that the pedal disc in *D* is partially inflated in the direction of movement of each half and that the vertical rows of verrucae are separated where division will occur. *E*, *F*: Late division stage. The actinopharynx division is almost complete, and the two daughter actinopharynxes have not yet fused at their basal ends (*F*). The individual in *F* is slightly further along toward separation than that in *E*. The body wall has divided and the two new individuals are held together only by the marginal sphincter and upper body wall. The oral disc is held close to the substratum but has been raised in this diagram to show the lower column. *G*, *H*: Postdivision daughter individuals. When the separation has been effected, the upper portion of the actinopharynx has yet to fuse. New directive (*ND*) mesenteries and other mesentery pairs will form opposite the old. Note the white division scars in *H*.

TABLE 1

SIPHONOGLYPH ARRANGEMENT IN A POPULATION *Anthopleura elegantissima* COMPARED TO THAT IN DIVIDING AND RECENTLY DIVIDED INDIVIDUALS

| SIPHONOGLYPH ARRANGEMENT | FIELD POPULATION | | DIVIDERS | | POSTDIVISION |
|-----------------------------|------------------|-------------------------|----------|-------------------------|--------------|
| | <i>N</i> | DIAMETER (cm ± s.d.) | <i>N</i> | DIAMETER (cm ± s.d.) | <i>N</i> |
| Monoglyphic | 5 | 1.0 ± 0.1 | 0 | 0 | 6 |
| Diglyphic | 187 | 1.4 ± 0.5 | 19 | 1.2 ± 0.5 | 3 |
| Triglyphic | 8 | 1.7 ± 0.3 | 0 | 0 | 0 |
| Tetraglyphic | 0 | 0 | 6 | 1.5 ± 0.6 | 0 |
| Total | 200 | 1.4 ± 0.5 | 25 | 1.3 ± 0.5 | 9 |

NOTE: Diameter of dividers is the average of longest and narrowest diameter; that of postdividers was not taken.

is very elongated horizontally as is the oral aperture. However, internal reorganization has hardly begun at this point. For this reason, many of the specimens sectioned show little more than the beginnings of actinopharyngeal division and widening of the spaces between mesenteries perpendicular to the axis of elongation. In fact, several of the anemones collected either were in the very early stages of longitudinal fission or were simply elongated and probably not dividing at all.

The earliest modification of the actinopharynx in the process of longitudinal fission is a division of the aboral rim (Figure 2B). This occurs along the plane of division at approximately the same site as the widest separation between mesenteries (Figure 3D), perpendicular to the directive axis. The longest mesenteries in this area do not connect to the actinopharynx at this level. There must be a separation of the mesenteries from the actinopharynx in this region, as well as the formation of a notch at opposite sides of the aboral rim (Figure 2C). Later stages show that division of the actinopharynx (Figure 3B) progresses toward the oral end with a concurrent infolding of the aboral free lateral edges. The final result of this infolding is the fusion of the free edges (Figure 3D) to form two complete actinopharynxes aborally while division continues orally. This produces an inverted U-shaped structure as in Figure 2C. The fusion of the free edges of the divided actinopharynx does not usually begin before final

separation of the whole anemone. Rather, final division of the actinopharynx is just prior to that of the oral disc, immediately preceding separation of the collar and marginal sphincter. Fusion of the oral margin of the actinopharynx occurs some time after separation of the two halves of the anemone.

Of the 25 anemones showing division to the stage of actinopharynx division, 6 were tetraglyphic while the other 19 were diglyphic (Table 1). The tetraglyphic state (Figure 3A) probably arises just prior to or during division. Of the 200 anemones sampled in the field, 187 were diglyphic, while 5 were monoglyphic and 8 triglyphic. The monoglyphic polyps averaged 1.0 ± 0.1 cm s.d. diameter (fixed) while the triglyphic averaged 1.7 ± 0.3 cm s.d. diameter. Neither the triglyphic nor the monoglyphic polyps were significantly different in size from the diglyphic ones (1.4 ± 0.5 cm s.d.), although the triglyphic ones were larger than the monoglyphic ($P < 0.05$, Analysis of Variance and Student-Newman-Keuls test, $F = 3.17$, method of Sokal and Rohlf 1969). Evidently, tetraglyphy is an uncommon state among nondividing anemones while not at all uncommon during division. It is quite possible that division of tetraglyphic polyps could result in either two diglyphic or one monoglyphic and one triglyphic individual. Alternatively, triglyphic individuals may be a developmental stage leading to the tetraglyphic condition. Their large size and the lack of postdivision triglyphic in-

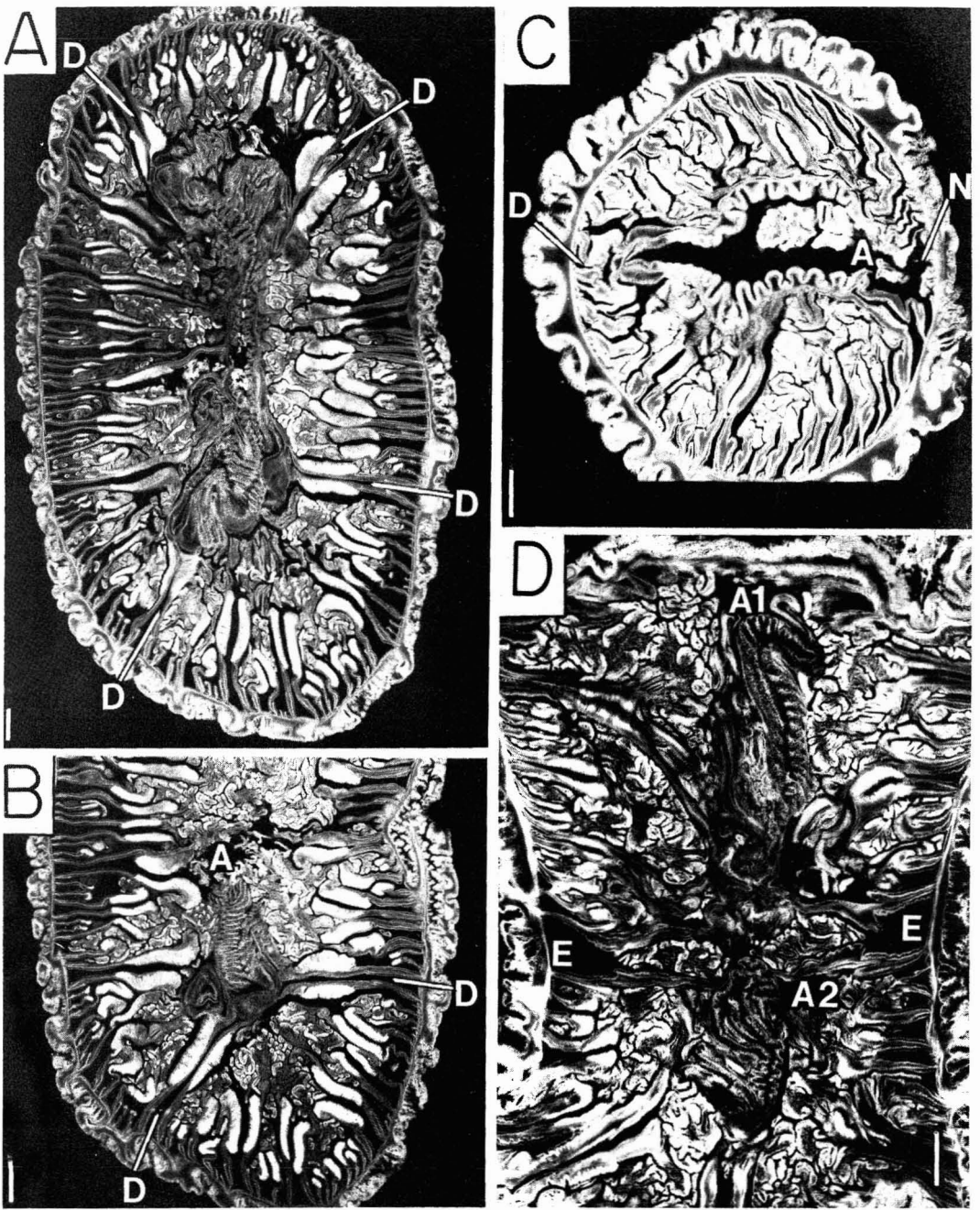


FIGURE 3. Sections of *Anthopleura elegantissima* during longitudinal fission (scale bar = 1 mm). *A*: a tetraglyphic individual in division. Note the four directive pairs (D) and the complete actinopharynx. Section taken at mid-actinopharynx level. *B*: A tetraglyphic individual in division showing the separation of the actinopharynx (A) as in Figure 2C. Same individual as in *A* with section taken at lower level of actinopharynx. *C*: A daughter individual resulting from division of a diglyphic anemone. Note the single directive pair (D), the incomplete actinopharynx (A), and the formation of new mesenteries (N) in the division scar area as in Figure 2G. Section taken at mid-actinopharynx level. *D*: Division of diglyphic individual showing the separation of the actinopharynx and fusion to form two actinopharynxes (A1, A2) and the widening of the complete mesenterial endocoels (E) as in Figure 2E. Section at lower level of actinopharynx. Photographs printed by placing sections in enlarger (no negative).

dividuals support this interpretation. Division of diglyphic polyps almost always results in two monoglyphic individuals. This explains the field population that consists of mostly diglyphic individuals with a few monoglyphic and triglyphic individuals. Tetraglyphic polyps in division (1.5 ± 0.6 cm s.d.) were only slightly larger than diglyphic ones (1.2 ± 0.5 cm s.d.) (not significantly different by ANOVA). It may be that internal rearrangement of larger polyps takes so long that it must be begun before division occurs.

Sections of daughter individuals showed that they can be either monoglyphic or diglyphic (no triglyphic ones were observed) (Table 1). In the monoglyphic division products, new directive pairs arise from the body wall in the division scar area and grow inward to meet the actinopharynx. The process proceeds from the aboral to the oral end, and a new siphonoglyph forms where the directive mesenteries meet the actinopharynx. Diglyphic daughter individuals have the two siphonoglyphs situated approximately 60° apart. There must be substantial mesenterial rearrangement if such individuals are to return to symmetry, involving production of new mesenteries opposite the division scar. None of the sections showed a definite example of such rearrangement, and it may be that the asymmetry persists for a long time after division since it should not impair function.

The division scar area is the center of reorganization where new mesentery pairs arise from the body wall, from the aboral to the oral end. Several of the sections showed such rearrangement (Figure 3C) involving production of up to six new mesentery pairs within the first few weeks after division. Externally the division scar begins to develop verrucae within a month or less after fission. The new scar is probably indistinguishable after 2 to 4 mo.

DISCUSSION

Asexual reproduction of sea anemones occurs by four distinctly different processes. The first of these, longitudinal fission, has been described for *Bunodosoma* (= *Actinia*)

cavernosa by McCrady (1859), for *Metridium senile* (= *M. fimbriatum*) by Torrey (1898), and by Parker (1899), and for *Haliplanella* (= *Sagartia*) *luciae*, *Anemonia sulcata*, and *Anthopleura thallia* by Stephenson (1929). It has also been reported in several other genera, including *Anthopleura elegantissima* (see Hand 1955; Davis 1962; Francis 1973a, b, 1976, 1979), although no details of the process have been given. Fission is similar in all such species and results in the production of two equal or slightly unequal individuals following a division of the body in the longitudinal plane (Francis 1976).

Transverse fission, the second distinct asexual method, has been described for *Gonactinia prolifera* and *Aiptasia couchii* by Stephenson (1929), for *Anthopleura stellula* by Schmidt (1970), and for *Fagesia lineata* by Crowell and Oates (1980). In this method, division is in the transverse plane and superficially resembles the process of strobilization in the Scyphozoa. Of the three asexual methods, transverse fission is the rarest and has been studied the least.

Basal fragmentation or pedal laceration, the third method, has been differentiated as two distinct types (Stephenson 1929). Tearing basal fragmentation occurs in *Sagartia elegans* and *Diadumene cincta*. Small portions of the pedal disc are separated by a tearing process as the anemone moves and these develop directly into individual anemones. Basal fragmentation by constriction occurs in *S. lacerata* (Stephenson 1929) where portions of the pedal disc form lobes that separate from the main individual by constriction. Such fragments then develop similarly to those resulting from tearing fragmentation. Cary (1911) described the process of pedal laceration in *Aiptasia pallida*, *Aiptasia tagetes*, *Bartholomea annulata*, and *Cylista leucolea*, and Rawlinson (1934) did so for *Metridium senile*. Torrey and Mery (1904), Hammat (1906), and others have described the internal development and regeneration of naturally produced basal fragments and those produced by experimental separation of portions of the pedal disc (see reviews in Stephenson 1929, Chia 1976). The phenomenon of budding, common among the hydroids, has never been described in

the Actiniaria although incomplete basal fragmentation or the formation of a second oral disc as a result of injury or developmental accident (e.g., in *Metridium senile* as shown by Torrey 1898, and by Parker 1899 may give the appearance of budding.

Longitudinal fission is widely distributed taxonomically among actinarians, but its description has usually been superficial and external. Only the studies of Torrey (1898), Parker (1899), Walton (1918), Davis (1919), and Atoda (1954, 1976) have given serious consideration to the internal events. The very complete study by Davis (1919) described both the process of fission and the course of regeneration in the resulting individuals using serial sections from *Haliplanella luciae* at many stages of division. Torrey (1898) and Parker (1899) both dealt with a very few specimens of *Metridium senile*, a species in which specimens with two oral discs are only rarely observed. Asexual reproduction of *Metridium* is accomplished by pedal laceration (Hoffmann 1976, Shick and Hoffmann 1980, Purcell and Kitting 1982); in fact, there has been no subsequent evidence that longitudinal fission actually occurs in this species. Walton's (1918) study of *Actinia bermudensis* also involved few individuals; the species normally reproduces sexually (dioecious) and broods the juveniles. Again, Walton's specimens may have been developmental abnormalities. In a study of the population dynamics of *Anthopleura xanthogrammica* in Washington (Sebens 1977, in press), I observed one individual with two fully formed oral discs in a population of greater than 500 mapped individuals. This individual (8 × 10 cm basal diameter) survived at least the 3 yr of the study. Such individuals are thus very rare but viable even in the field.

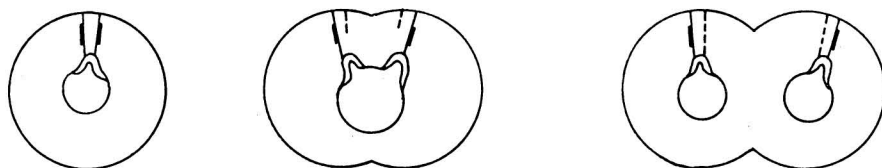
There appear to be two distinct modes of longitudinal fission in *Anthopleura elegantissima* differing as to the timing of production of new directive mesentery pairs and siphonoglyphs (Figure 4). Either the diglyphic polyp tears itself in half with no prior internal rearrangement (as in *Haliplanella luciae* studied by Davis 1919 and Atoda 1954), leaving each half monoglyphic, or it first becomes tetraglyphic and then divides to form two usually

diglyphic individuals. The three-dimensional conformation of the actinopharynx during division of *A. elegantissima* (Type II) is strikingly different from any previously described. Division is externally similar to that of *H. luciae*, but actinopharynx division is concurrent with column division in *H. luciae* so that closure of the actinopharynx must occur after separation of the two halves. Two complete actinopharynxes are never seen in sections of *H. luciae* during division. In *Metridium senile* and *Actinia bermudensis* division was thought to proceed from the oral to the aboral end as did division of the actinopharynx, which was seen as two complete tubes in the upper portion of the anemone (Torrey 1898, Parker 1899, Walton 1918). It is thus similar to *A. elegantissima* in conformation but with the polarity reversed. These examples are probably developmental abnormalities that do not continue to divide the entire animal. New directive mesenteries arise from the division scar area in daughter individuals of *H. luciae*. Old directive pairs divide in both *M. senile* and *A. bermudensis*. Division is thus through at least one directive endocoel while it occurs through the endocoels of complete mesenteries perpendicular to the directives in *A. elegantissima*.

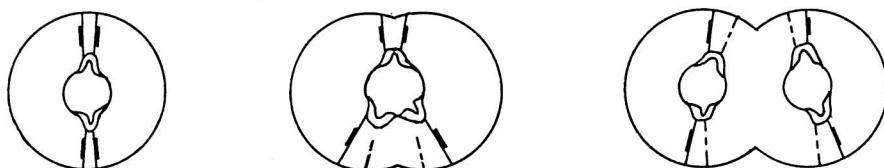
The less common form of longitudinal division in *Anthopleura elegantissima* (tetraglyphy, Type II) is a complex process in which most of the major internal reorganization is carried out prior to division of the body wall. When the separation finally occurs, the two daughter individuals have almost complete actinopharynxes, complete body walls, a fused sphincter muscle, and two siphonoglyphs (in symmetric division). There is less rearrangement necessary to return them to their former symmetry than in Type I division. This may be important in larger individuals where rearrangement and regeneration could take longer. It is still possible that the tetraglyphic condition is not preparatory for division. The large fraction of apparently dividing individuals that were tetraglyphic (24 percent, Table 1), when none were found in samples from the field population, argues that it is, in fact, associated with fission.

The more common form of division in

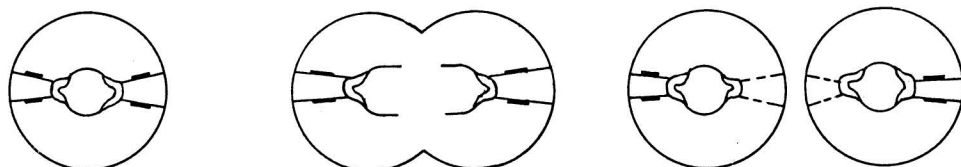
METRIDIDIUM SENILE



ACTINIA BERMUDENSIS



HALIPLANELLA LUCIAE , A. ELEGANTISSIMA



ANTHOPLEURA ELEGANTISSIMA TYPE II

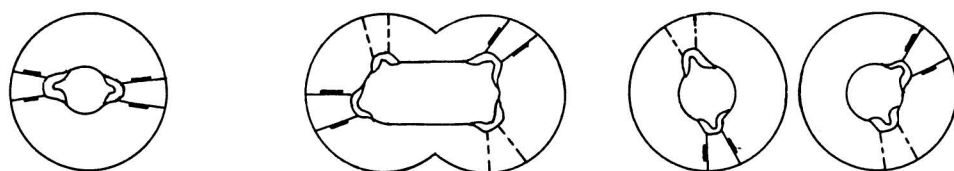


FIGURE 4. Rearrangement during longitudinal fission of three sea anemones. Partial division of a monoglyphic *Metridium senile* (Torrey 1898) occurs with separation of the directive mesenteries and formation of a new member of each pair (dotted lines). Such abnormalities divide the oral disc and upper column but probably never go on to divide the entire anemone. In *Actinia bermudensis* (Walton 1918), a diglyphic individual divides with a similar separation of each pair of directives and formation of new members for the pairs. Division of both species occurs oral to aboral. *Haliplanella luciae* (Davis 1919) and *Anthopleura elegantissima* divide perpendicular to the directive pairs and new pairs are formed in each daughter rather than new members for each pair (Figure 2). In the second type of division of *Anthopleura elegantissima*, a new pair of directives arises in each half prior to division such that the polyp is tetraglyphic while it is dividing (Figure 3A, B). Division of the latter two species occurs aboral to oral. Only the directive mesenteries and new directives (dotted lines) are shown. Other new mesenteries also arise in the area of the new directives.

Anthopleura elegantissima is identical with that of *Haliplanella luciae* in most respects. The latter divides rapidly and must then spend a considerable amount of time in reorganization during which its normal behavior is impaired. Since the major internal structures of the Actiniaria are similar for most species, it is surprising to find such a diversity in the process of splitting in two. However, natural selection may work differently on such factors as the length of time involved in division, the length of the regenerative period, and the postural condition of the anemones during fission. Since the anemones studied to date live in very different habitat types, it is not surprising that the problem of division has been solved in several different ways. The two modes of division in *A. elegantissima* may be characteristic of different habitats, seasons, energetic states, or simply initial individual size; these possibilities will be explored in future studies.

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LITERATURE CITED

- ATODA, K. 1954. The development of the sea anemone, *Diadumene luciae*, reproduced by the pedal laceration. Sci. Rep. Tohoku Univ., Ser. IV Biol. 20:123-129.
- . 1976. Development of the sea anemone *Haliplanella luciae*. V. Longitudinal fission and the origin of mono-, di-, and tri-glyphic individuals. Bull. Biol. Stat. Asamushi 15:133-146.
- CARY, L. R. 1911. A study of pedal laceration in Actinians. Biol. Bull. Woods Hole 20:81-108.
- CHIA, F. S. 1976. Sea anemone reproduction: Patterns and adaptive radiations. Pages 261-270 in G. O. Mackie, ed. Coelenterate ecology and behavior. Plenum Press, New York.
- CROWELL, S., and S. OATES. 1980. Metamorphosis and reproduction by transverse fission in an edwardsiid anemone. Pages 139-142 in P. Tardent and R. Tardent, eds. Developmental and cellular biology of coelenterates. Elsevier/North Holland Biomedical Press, New York.
- DAVIS, C. 1962. One equals two: A sea anemone achieves its plurality in singular fashion. Nat. Hist. 71:61-63.
- DAVIS, D. W. 1919. Asexual multiplication and regeneration in *Sagartia luciae* Verrill. J. Exp. Zool. 28:161-263.
- FRANCIS, L. 1973a. Clone specific segregation in the sea anemone *Anthopleura elegantissima*. Biol. Bull. 144:64-72.
- . 1973b. Intraspecific aggression and its effect on the distribution of *Anthopleura elegantissima* and some related sea anemones. Biol. Bull. 144:73-92.
- . 1976. Social organization within clones of the sea anemone *Anthopleura elegantissima*. Biol. Bull. 150:361-376.
- . 1979. Contrast between solitary and clonal lifestyles in the sea anemone *Anthopleura elegantissima*. Amer. Zool. 19:669-681.
- FREDERICKS, C. A. 1976. Oxygen as a limiting factor in phototaxis and in intracolonial spacing of the sea anemone *Anthopleura elegantissima*. Mar. Biol. 38:25-28.
- HAMMAT, M. L. 1906. Reproduction of *Metridium marginatum* by fragmental fission. Amer. Nat. Boston 40:583-591.
- HAND, C. 1955. The sea anemones of central California. Part II. The endomyarian and mesomyarian anemones. Wasmann J. Biol. 13:37-99.
- HOFFMANN, R. J. 1976. Genetics and asexual reproduction of the sea anemone *Metridium senile*. Biol. Bull. 151:478-488.
- JOHNSON, L. L., and J. M. SHICK. 1977. Effects of fluctuating temperature and immersion on asexual reproduction in the intertidal sea anemone *Haliplanella luciae* (Verrill) in laboratory culture. J. Exp. Mar. Biol. Ecol. 28:141-149.

- KIENER, A. 1971. Contribution à l'écologie, la physiologie et l'éthologie de l'actinie *Diadumene luciae* (Verrill). Bull. Soc. Zool. France 1971: 581–603.
- MCCRADY, J. 1859. Instance of incomplete longitudinal fission in *Actinia cavernosa*. Pages 275–278 in Vol. I of Proc. Elliot. Soc. Nat. Hist., Charleston, S. C.
- MINASIAN, L. L., Jr. 1976. Characteristics of asexual reproduction in the sea anemone, *Haliplanella luciae* (Verrill), reared in the laboratory. Pages 289–298 in G. O. Mackie, ed. Coelenterate ecology and behavior. Plenum Press, New York.
- . 1979. The effect of exogenous factors on morphology and asexual reproduction in laboratory cultures of the intertidal sea anemone, *Haliplanella luciae* (Anthozoa: Actiniaria) from the coast of Delaware. J. Exp. Mar. Biol. Ecol. 40: 235–246.
- . 1982. The relationship of size and biomass to fission rate in a clone of the sea anemone *Haliplanella luciae* (Verrill). J. Exp. Mar. Biol. Ecol. 58: 151–162.
- MINASIAN, L. L., JR., and R. N. MARISCAL. 1979. Characteristics and regulation of fission activity in clonal cultures of the cosmopolitan sea anemone *Haliplanella luciae* (Verrill). Biol. Bull. 157: 478–493.
- MIYAWAKI, M. 1952. Temperature as a factor influencing upon fission in the orange-striped sea anemone, *Diadumene luciae*. J. Fac. Sci. Hokkaido Univ., Ser. IV, Zool. 11: 77–80.
- PARKER, G. H. 1899. Longitudinal fission in *Metridium marginatum* Milne-Edwards. Bull. Mus. Comp. Zool. Harvard 35: 901–919.
- PURCELL, J. E., and C. L. KITTING. 1982. Intraspecific aggression and population distribution of the sea anemone *Metridium senile*. Biol. Bull. 162: 345–359.
- RAWLINSON, R. 1934. A comparative study of *Metridium senile* L. var. *dianthus* (Ellis) and a dwarf variety of this species occurring in the River Mersey, with a discussion on the systematic position of the genus *Metridium*. J. Mar. Biol. Assoc. U.K. 19: 901–919.
- SCHMIDT, H. 1970. *Anthopleura stellula* (Actiniaria: Actiniidae) and its reproduction by transverse fission. Mar. Biol. 5: 245–255.
- SEBENS, K. P. 1977. Habitat selection, reproductive ecology, and the control of body size in two intertidal sea anemone populations, *Anthopleura xanthogrammica* and *A. elegantissima*. Ph.D. Thesis, University of Washington, Seattle.
- . 1979. The energetics of asexual reproduction and colony formation in benthic marine invertebrates. Amer. Zool. 19: 683–697.
- . 1980. The control of body size and longitudinal fission in the sea anemone *Anthopleura elegantissima* (Brandt). Biol. Bull. 158: 370–382.
- . 1981a. The allometry of feeding, energetics, and body size in three sea anemone species. Biol. Bull. 161: 152–171.
- . 1981b. Reproductive ecology of the intertidal sea anemones *Anthopleura xanthogrammica* (Brandt) and *Anthopleura elegantissima* (Brandt): Body size, habitat, and sexual reproduction. J. Exp. Mar. Biol. Ecol. 54: 225–250.
- . 1982a. Asexual reproduction in *Anthopleura elegantissima* (Brandt) (Anthozoa: Actiniaria): Seasonality and spatial extent of clones. Ecology 63: 434–444.
- . 1982b. Recruitment and habitat selection in the intertidal sea anemones *Anthopleura elegantissima* and *A. xanthogrammica*. J. Exp. Mar. Biol. Ecol. 59: 103–124.
- . In press. Population dynamics and habitat suitability of the intertidal sea anemones *Anthopleura elegantissima* (Brandt) and *A. xanthogrammica* (Brandt). Ecol. Monogr.
- SHICK, J. M. 1976. Ecological physiology and genetics of the colonizing actinian *Haliplanella luciae*. Pages 137–146 in G. O. Mackie, ed. Coelenterate ecology and behavior. Plenum Press, New York.
- SHICK, J. M., and R. J. HOFFMANN. 1980. Effects of the trophic and physical environments on asexual reproduction and body size in the sea anemone *Metridium senile*. Pages 211–216 in P. Tardent and R. Tardent, eds. Developmental and cellular biology of coelenterates. Elsevier/North Holland Biomedical Press, New York.
- SHICK, J. M., and A. N. LAMB. 1977. Asexual

- reproduction and genetic population structure in the colonizing sea anemone *Haliplanella luciae*. Biol. Bull. 153:604-617.
- SMITH, N., and H. M. LENHOFF. 1976. Regulation of frequency of pedal laceration in a sea anemone. Pages 117-126 in G. O. Mackie, ed. Coelenterate ecology and behavior. Plenum Press, New York.
- SOKAL, R. R., and F. J. ROHLF. 1969. Biometry: The principles and practice of statistics in biological research. W. H. Freeman and Company, San Francisco. 776 pp.
- STEPHENSON, T. A. 1929. On methods of reproduction as specific characters. J. Mar. Biol. Assoc. U.K. 16:131-172.
- TORREY, H. B. 1898. Observations on monogenesis in *Metridium*. Proc. Calif. Acad. Sci., Ser. 3, Zool. 1:345-360.
- TORREY, H. B., and J. R. MERY. 1904. Regeneration and non-sexual reproduction in *Sagartia davisii*. Univ. Calif. Publ. Zool. 1:211-226.
- UCHIDA, T. 1932. Occurrence in Japan of *Diadumene luciae*, a remarkable actinian of rapid dispersal. J. Fac. Sci. Hokkaido Univ., Ser. VI Zool. 2:69-82.
- . 1936. Influence of the currents upon the distribution of races and frequency of asexual reproduction in the actinian, *Diadumene luciae*. Zool. Mag. Tokyo 48:895-906.
- WALTON, A. C. 1918. Longitudinal fission in *Actinia bermudensis* Verrill. J. Morph. 31:391-406.
- WILLIAMS, R. B. 1973. Are there physiological races of the sea anemone *Diadumene luciae*? Mar. Biol. 21:327-330.
- . 1975. Catch-tentacles in sea anemones: Occurrence in *Haliplanella luciae* (Verrill) and a review of current knowledge. J. Nat. Hist. 9:241-248.