The anatomy, terminology, and homology of acrorhagi and pseudoacrorhagi in sea anemones

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The morphology of the column margin is an especially important feature in the taxonomy and biology of members of the sea anemone family Actiniidae. Despite the importance of marginal structures, their anatomy and the terminology describing them is poorly delimited. Consequently, homologies of the components of the marginal structures are poorly understood and taxonomies that depend on the presence, absence, or particular manifestation of marginal structures are confused. I review and synthesize anatomical descriptions of the marginal structures and find that they consist of two parts: a projection of the column and a holotrich-dense pad (= acrorhagus) that is histologically differentiated from the surrounding tissues. Although acrorhagi are functionally similar to the catch tentacles of some Actiniaria and to the capitate tentacles of Corallimorpharia and Scleractinia, as structures of the column, acrorhagi are not homologous to them.

Introduction

Nematocyst-dense swellings at the junction of the oral disc and column (= margin) are crucial to actiniarian taxonomy and biology. The presence and arrangement of these structures is of great taxonomic importance in Actiniidae, where they are a primary character for distinguishing the genera (Carlgren, 1949). Because these structures are prominent in so many actiniids, their function was the topic of much early research (e.g., Hollard, 1851; Duncan, 1874; Korotneff, 1876; Abel, 1954). Even after their function in intraspecific defense became known, marginal structures remained an active focus of research because the specificity and variability of the behaviours involved in their use indicated a surprising degree of biochemical, immunological, and behavioural complexity (e.g., Bonnin, 1964; Francis, 1973, 1976, 1988; Bigger, 1976, 1980; Ayre, 1982; Ayre & Grosberg, 1995; Zeh & Zeh, 1997). Despite the importance of marginal structures, their anatomy and the terminology describing them is poorly delimited. Consequently, homologies of the components of the marginal structures are poorly understood, and taxonomies that depend on the presence, absence, or particular manifestation of marginal structures are confused.

Marginal structures have been considered to belong to one of two categories: acrorhagi and pseudoacrorhagi. An acrorhagus is a swelling in the fosse or on the margin that contains holotrichous nematocysts. Following contact with the tentacles or column of member of the same or different species, an acrorhagus will expand, lengthening towards the nearby actiniarian. Contact between an acrorhagus and the targeted actiniarian results in the ectoderm of the acrorhagus adhering to the ectoderm of the target, causing necrosis around the acrorhagial "peel" (Abel, 1954; Bon-

nin, 1964). In response, the targeted actiniarian typically moves out of reach or dies. The acrorhagial reaction depends on specific ectodermal anatomy and on the presence of holotrichous nematocysts, which help the peel adhere to the victim (Bigger, 1982). Pseudoacrorhagi, being swellings in the fosse or on the margin, resemble acrorhagi in gross anatomy, but contain only basitrichs (Stephenson, 1918a, 1928; Carlgren, 1949; Bigger, 1982; Riemann-Zürneck & Gallardo, 1990). The function of pseudoacrorhagi is not known (Bigger, 1982).

The distinction between acrorhagi and pseudoacrorhagi is at the heart of the confusion over the identity of the marginal structures. Structures described initially as acrorhagi were found, upon closer examination, to be pseudoacrorhagi (e.g., McMurrich, 1889); species thought to have pseudoacrorhagi were later shown to have acrorhagi (e.g., Stephenson, 1918b). Many species placed in genera now characterized as bearing (or lacking) acrorhagi prior to the characterization of acrorhagi as containing holotrichs have not been re-examined or studied in detail. This has compromised the practical value of acrorhagi as a taxonomic feature, and may contribute to erroneous interpretations of the anatomy and cnidom of constituent species based on the characteristics of the genus. For example, *Anthopleura* is characterized as having holotrichous acrorhagi; this feature distinguishes its members from those of *Aulactinia, Bunodactis*, or *Gyractis*. However, the cnidom is not reported for several species currently placed in *Anthopleura*, including *A. listeri* (Johnson, 1861) and *A. rosea* (Stuckey & Walton, 1910); these species should not be assumed to have acrorhagi. Furthermore, because the feature upon which generic placement rests is unknown for these species, their generic assignment is dubious.

England (1987) suggested that both acrorhagi and pseudoacrorhagi be renamed to make the distinction between the two more explicit. He recommended that marginal structures be simply called "marginal spherules", and that spherules be differentiated based on their cnidom. In his parlance, acrorhagi are holotrichous marginal spherules, and pseudoacrorhagi are basitrichous marginal spherules (England, 1987). Although Riemann-Zürneck & Gallardo (1990) agreed with England that the distinction between an acrorhagus and a pseudoacrorhagus required clarification, they recommended retaining existing terminology because the term "acrorhagus" is widely used, and conveys functional and biological information. Riemann-Zürneck & Gallardo (1990: 455) redefined acrorhagi as "blunt, hollow structures that are developed in connection with the top of the column (margin) beneath the outermost cycle of tentacles (on the parapet or fosse). They are armed with special nematocysts and are concerned with aggression."

Neither of the proposed solutions completely resolves the ambiguity and confusion over the identity of acrorhagi and pseudoacrorhagi. Riemann-Zürneck & Gallardo (1990) were not explicit about which types of nematocysts are found in an acrorhagus. Their proposed definition includes a functional component that is impossible to evaluate with preserved specimens. The solution proposed by England (1987) introduces yet more terms into the discussion, and fails to differentiate between the terminal verruca in an endocoelic row and a pseudoacrorhagus. Neither England (1987) nor Riemann-Zürneck & Gallardo (1990) distinguished between the nematocyst-dense pad and the projection of the column that may bear it.

Distinguishing between the marginal projection and the nematocyst-dense pad is

important for several reasons. These structures are anatomically distinct and show independent morphological variation. For example, in members of *Isoaulactinia stelloides* (McMurrich, 1889), the marginal projection lacks a nematocyst pad; in members of *Actinia equina* (Linnaeus, 1758), the nematocyst-dense pad lies in the fosse rather than on a marginal projection. Some species have both marginal projections with acrorhagi and marginal projections without acrorhagi (e.g., *Anemonia alicemartinae* Häussermann & Försterra, 2001). The marginal projection may be simple, as in *Anthopleura krebsi* Duchassaing de Fonbressin & Michelotti, 1860, or frondose, as in *Saccactis coliumensis* Riemann-Zürneck & Gallardo, 1990. Given this variability, simply stating that marginal spherules are present or absent is insufficient, and obscures the similarities and differences among marginal structures. Because the nematocyst-dense pad and the marginal projection are functionally distinct, failure to differentiate adequately between them may have consequences for understanding the biology of an animal. Finally, recognizing and incorporating the full extent of anatomical variability among members of the Actiniidae may clarify taxonomy and phylogeny of the genera.

In order to resolve the confusion over the marginal projections, acrorhagi, and pseudoacrorhagi, I review and synthesize anatomical descriptions of them, exploring the terminological, anatomical, and systematic implications of various definitions. I find that the marginal structures consist of one or both of two elements: a marginal projection of the column and a holotrich-dense pad (acrorhagus) that is histologically differentiated from the surrounding tissues. The acrorhagus is situated either on the oral surface of the projection or in the fosse, and may protrude during the acrorhagial reaction. Many, if not all, structures previously called a pseudoacrorhagus are not different from the rest of the marginal projection or fosse tissue in terms of anatomy or cnidom. Based on their position and histology, I conclude that neither a marginal projection nor an acrorhagus should be considered a highly modified tentacle.

Terminology

Most of the published terms for the marginal structure do not distinguish between the nematocyst-dense swelling used in the acrorhagial reaction and the projection of the column margin that may bear it. The terms "bourses marginales" (Hollard, 1851), "tubercles calicinaux" (Milne-Edwards, 1851), "marginal spherules" (Gosse, 1860), and "Randsäckchen" (Hertwig & Hertwig, 1879) apply to the entire structure. In contrast, Duncan (1874) applied the term "bourse chromatophore" to only the nematocyst-dense pad. Andres (1883) suggested the term acrorhagus, which he coined from the Greek for "spherules on the edge", to supplant other terms, but was not explicit about whether he intended this term to include both the projection and the nematocyst-dense pad. Most authors followed Andres, and the term acrorhagus supplanted all others except marginal spherule, which persisted in a few, albeit important, works (e.g., Carlgren 1921, 1949).

Andres (1883) recommended a standard term because the proliferation of names threatened to obscure similarities among the marginal structures of actiniids. The acrorhagi of *Actinia*, *Anemonia, Anthopleura, Bunodosoma*, and *Phymactis* share the function of intra-and inter-specific aggression (e.g., Abel, 1954; Bonnin, 1964; Francis, 1973; 1988; Brace, 1981; Bigger, 1982). Furthermore, the behavioural and anatomical elements of the acrorhagial reaction are identical among members of these genera.
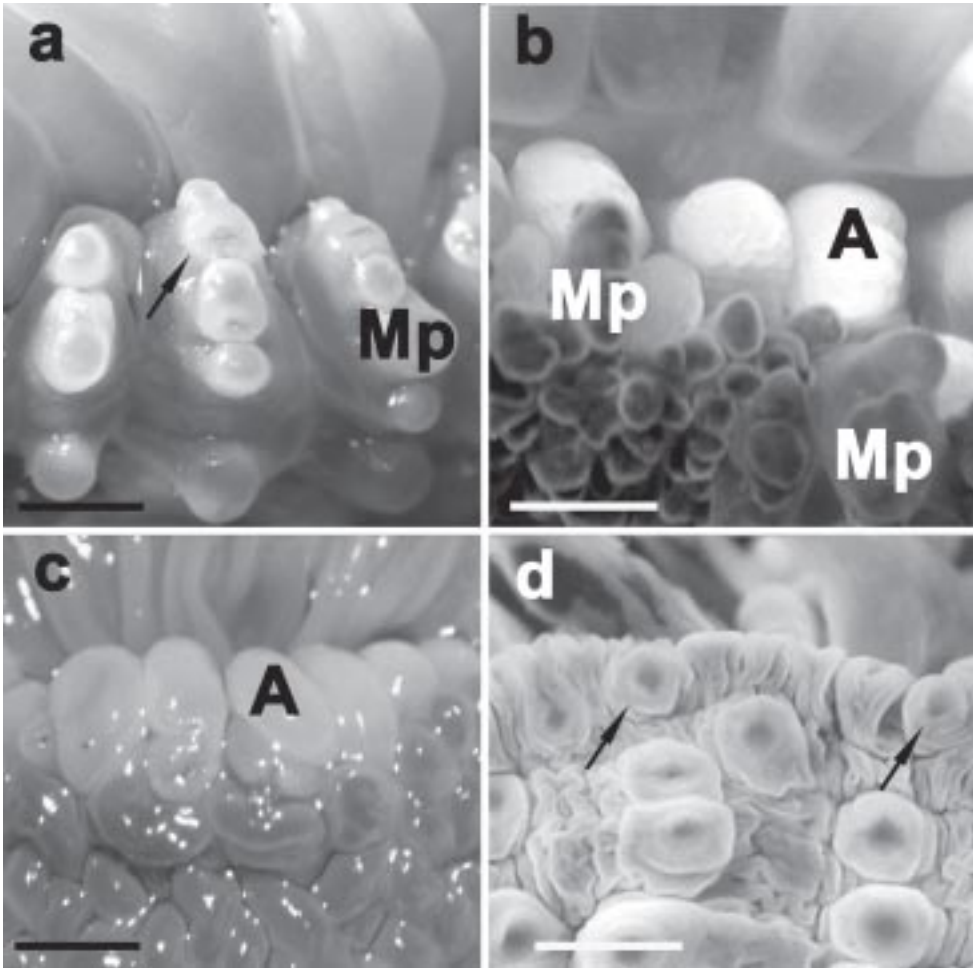
Fig. 1. External anatomy of margin. Scale = 2 mm a. Margin of *Anthopleura dowii*. Prominent, simple, conical marginal projections (Mp) with verrucae (arrow) obscure acrorhagi, which are located on oral side of projection. b. Margin of *Bunodosma cavernata*. Note contrast between dark, papillose marginal projections (Mp) and pale, pedunculate acrorhagi (A). The non-adhesive vesicles of the marginal projection are identical to those of the column. c. Margin of *Phymactis clematis*. Acrorhagi (A) located in fosse; margin without projections. d. Margin of *Heteractis* sp. Margin without projections or acrorhagi; compare to figs. 1a-c. Distal-most verrucae (arrows) easily distinguished from marginal projections (e.g., figs. 1a, b).

The description of structures that are superficially similar to acrorhagi but that are histologically and functionally distinct introduced a second confounding element into the discussion of actiniarian anatomy and taxonomy. Pseudoacrorhagi have been described erroneously as containing no nematocysts (e.g., Stephenson, 1918a); the cnidom of pseudoacrorhagi are recognized as having basitrichs and sometimes spirocysts, but not holotrichs.

Nine currently recognized genera in Actiniidae are described as having pseudo-acrohagi (Table 1). Pseudoacrorhagi are much less important taxonomic characters than acrorhagi, descriptions of many genera indicate that these structures differ among species of a genus (e.g., Carlgren, 1949; Dunn et al., 1980). Existing definitions and descriptions of pseudoacrorhagi are insufficient to discriminate between marginal projections and pseudoacrorhagi because marginal projections, like the distal column in general, contain only basitrichs.

Table 1. Currently valid genera in Actiniidae described as having acrorhagi or pseudoacrorhagi.

Acrorhagi	Pseudoacrorhagi
Actinia Linnaeus, 1758	*Aulactinia* Verrill, 1864
Anemonia Risso, 1826	*Bunodactis* Verrill, 1869
Anthopleura Duchassaing & Michelotti, 1860	*Cribrinopsis* Carlgren, 1921
Anthostella Carlgren, 1938	*Gyractis* Boveri, 1893
Bunodosoma Verrill, 1899	*Isotealia* Carlgren, 1899
Mesactinia England 1987	*Paracondylactis* Carlgren, 1934
Oulactis Milne-Edwards & Haime, 1851	*Phyllactis* Milne-Edwards & Haime, 1851
Phymactis Milne-Edwards & Haime, 1851	*Tealianthus* Carlgren, 1927
Pseudactinia Carlgren, 1928	*Telactinia* England, 1987
Saccactis Lager, 1911	

Anatomy

Gosse (1860) described the margin of the genus *Bunodes* as "denticulate," a condition he recognized as distinct from having conspicuous marginal spherules. In species Gosse referred to *Bunodes,* the spherules, when present, are obscured by finger-like extensions of the column (figs 1a, b). The small protrusion of the distal most verruca or vesicle (e.g., fig. 1d) is easily distinguished from the permanent, fingerlike projections of the margin of members of *Anthopleura, Bunodosoma*, and *Bunodactis*, each of which bears multiple verrucae or vesicles. Marginal projections vary in shape: in *Anthopleura dowii* Verrill 1869, the marginal projections are simple and conical (fig 1a), with two or three verrucae on the outer surface of each projection; in *Saccactis coliumensis*, the marginal structures are frondose and divided into several verrucae-studded branches (Riemann-Zürneck & Gallardo, 1990). The coelenteric space of a marginal projection may communicate with either an endocoelic or an excoelic space (e.g., Belém & Pinto, 1990; Haüsermann & Försterra, 2001).

The structure and cnidom of a marginal projection resembles that of the column. If the column bears adhesive verrucae, the projection does too (e.g., members of *Anthopleura*; fig. 1a); if the column bears non-adhesive vesicles, the marginal projection also bears them (e.g., members of *Bunodosoma;* fig. 1b). The histology and cnidom of the marginal projection is identical to that of the column (fig. 2a).

The marginal projection serves no known function. Even in members of species whose column contains holotrichs, the holotrichs on the outer surface of the projection are not used in agonistic interactions (Bigger, 1982). The outer surface of the projection may bear adhesive verrucae, which hold small stones and shell fragments, and may retard water loss during low tide (Hart & Crowe, 1977). The verrucae or the projection itself (e.g., Dunn, 1974) may be perforate, and thus facilitate the expulsion of water during contraction.
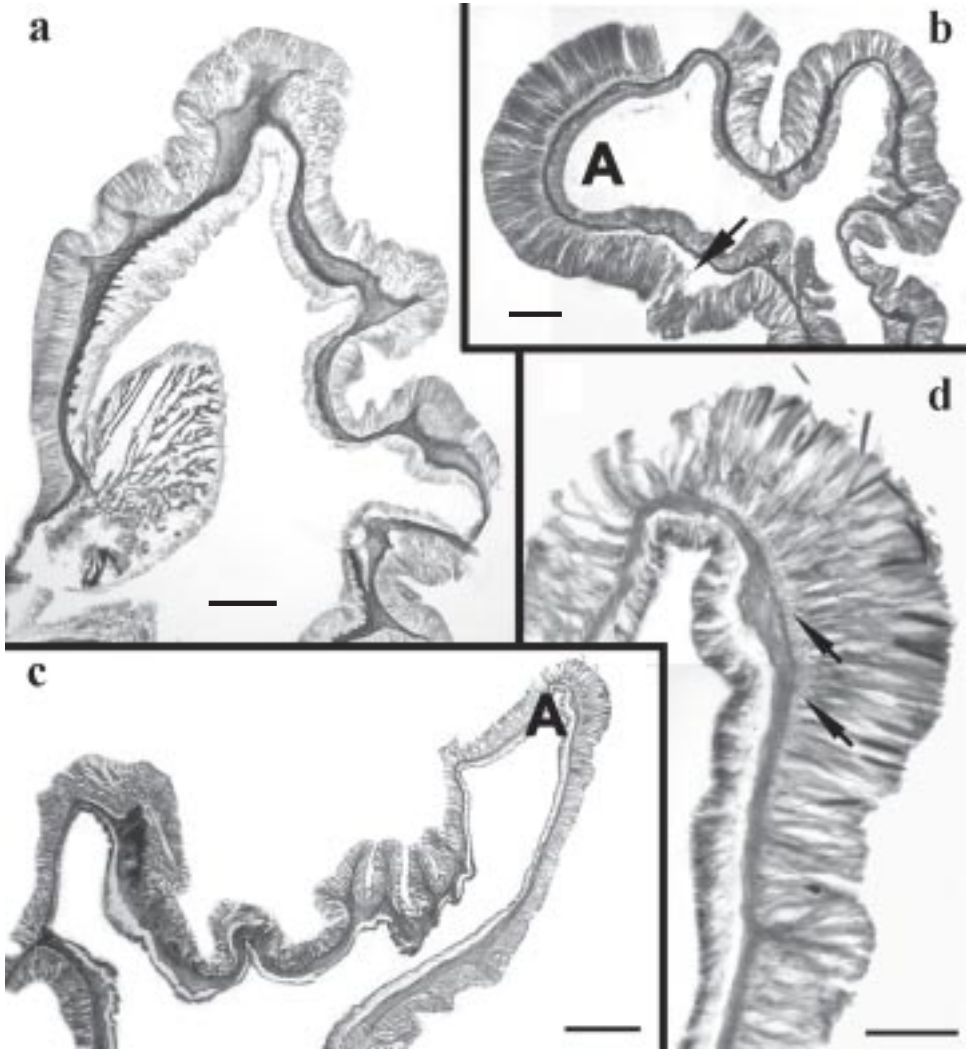
Fig. 2. Internal anatomy of margin (longitudinal section). All specimens oriented so that the left-hand side of the page is orad. a. Margin of *Isoaulactinia stelloides*. Oral surface of projection not differentiated from adoral surface. Scale = 60 μm. b. Margin of *Anthopleura pallida*. Acrorhagus (A) on oral surface of projection distinguishable from surrounding tissue by its dense pad of holotrichs and darkly staining granular gland cells. Note ectoderm peeling away from mesoglea (arrow). Scale = 60 μm. c. Margin of *Phymanthea pluvia*. Acrorhagus (A) at distal tip of projection. Scale = 1 mm. d. Enlarged view of the acrorhagus of *Phymanthea pluvia*. Note bilayered ectoderm (arrows), in which the epitheliomuscular cells have vacuolated bases. Holotrichs less dense than in acrorhaus of *A. pallida* (fig. 2b). Scale = 60 μm.

An acrorhagus lies either in the fosse or on the oral side of the marginal projection. The border between the acrorhagus and the marginal projection or fosse is sharply defined (Bonnin, 1964; Doumenc, 1972; Bigger, 1982), and the two structures may differ in colour (e.g., Doumenc, 1972; Bigger, 1982) (fig. 1b). The size of an acrorhagus varies among species, from relatively large (fig. 2a), given the size of the animal, to relatively small (fig. 2c). In contrast to marginal projections, acrorhagi are exclusively endocoelic.

The ectodermal epitheliomuscular cells of the acrorhagus appear more densely packed, compared to the surrounding tissue (figs 2b, d). The acrorhagus bears ciliary cones, which are sensory structures associated with the acrorhagial reaction (Bigger, 1976, 1980), and has abundant holotrichs and granular gland cells (fig. 2b), whereas the surrounding tissues lack ciliary cones and holotrichs and have mucous gland cells (Doumenc, 1972). The bases of the ectodermal epithelial cells of an acrorhagus are enlarged and highly vacuolated (Doumenc, 1972) (figs 2b, d), which may facilitate the separation of the ectoderm during the acrorhagial reaction. The ectoderm of the acrorhagus is not anchored to the mesoglea by hemidesmosomes or other cell junctions (Doumenc, 1972; Bigger, 1982). Because of its fragility, the acrorhagial ectoderm may slough off when specimens are handled (Hand, 1955; see fig. 2b), making acrorhagi difficult to detect.

Although an acrorhagus can be identified based on its microanatomy, the most conspicuous and oft-used diagnostic feature of an acrorhagus is its cnidom. The holotrichs of an acrorhagus may be of two morphologies (Hand, 1955; England, 1987, 1992; Pearse & Francis, 2000): a relatively thick, barrel-shaped holotrich and a more slender, tapering holotrich (= heterotrich of England, 1987, 1992). Both of these differ from the holotrichs found in the column. Spirocysts are approximately four times less common in the acrorhagus, compared to the tentacles (Bigger, 1982). Because the acrorhagus is bordered by tissue containing basitrichs, the cnidom of an acrorhagus is frequently characterized as including basitrichs (e.g., Carlgren, 1952; Dunn, 1978; England, 1987). Whether the acrorhagus itself contains basitrichs varies among taxa: although Bigger (1982) found that basitrichs are rare or absent in the acrorhagus of species of *Anemonia, Anthopleura,* and *Bunodosoma*, the acrorhagi of specimens of *Phymactis clematis* (Drayton in Dana, 1846) contain rod-like basitrichs not seen in the surrounding ectoderm (Carlgren, 1945).

The holotrichs of the acrorhagus are typically more numerous and more closely packed than the basitrichs of the surrounding column tissue (fig. 2a). However, the relative density of holotrichs varies with both species and specimen, in part because the size of the holotrichs varies among species. In *Phymanthea pluvia* (Drayton in Dana, 1846; figs 2c, d), the acrorhagus is relatively small, and contains qualitatively fewer holotrichs than the acrorhagus of *Anthopleura pallida* Duchassaing & Michelotti, 1864, in terms of both absolute number and density (c.f. figs 2b, c, d).

Acrorhagi also vary within species. For example, the percent of endocoelic compartments bearing acrorhagi varies from zero to 100% among individuals of at least some species (e.g., Hand, 1955; Francis, 1976; Bigger, 1982; pers. obs.). This may reflect differences in ecology: in the well-studied aggregation-forming species *Anthopleura elegantissima* (Brandt, 1835), individuals on the periphery of an aggregation have more acrorhagi than those in the center (Francis, 1976). The size of acrorhagi and the density of holotrichs within acrorhagi vary among conspecifics as well, and

may vary among acrorhagi in the same specimen (Francis, 1976; pers. obs.).

Most of the structures previously described as pseudoacrorhagi do not differ in anatomy or cnidom from the column or fosse. In his investigation of the structure of the pseudoacrorhagi of *Bunodactis texaensis* (Carlgren & Hedgpeth, 1952), Bigger (1982) found that the oral surface of the marginal projection is not anatomically differentiated from the adoral surface. Furthermore, the basitrichs are patchily distributed, rather than clustered into a dense pad as in acrorhagi, and spirocysts are lacking (Bigger, 1982). The pseudoacrorhagi of members of *Bunodactis hermaphroditica* (McMurrich, 1904), also cannot be distinguished from the marginal projection based on anatomy or cnidom; this may be the case for all species in this genus. England (1987: fig. 34) depicted the oral and adoral surface of the marginal structure of *Telactinia citrina* (Haddon & Shackleton, 1893), as identical in structure; however his figure is diagrammatic and may not accurately reflect the anatomy of *T. citrina*. In these instances, the structures that have been called pseudoacrorhagi are simply marginal projections.

Recommendations and Implications

Terminology

The term acrorhagus has referred to both the holotrich-dense pad and a compound structure consisting of a marginal projection and holotrich-dense pad. However, despite this confusion, the term acrorhagus has been reserved for structures with holotrichs. Because of its generally consistent application, and because it conveys functional, behavioural, and anatomical information that is lacking from newly coined descriptive phrases like "holotrichous marginal spherules," the term acrorhagus should be retained. The term acrorhagus refers to an endocoelic structure outside the tentacle crown and adoral to the marginal sphincter (further away from the mouth) in which the ectoderm contains holotrichous nematocysts and epitheliomuscular cells that are vacuolated at their bases.

This redefinition emphasizes the distinction between an acrorhagus and a marginal projection of the column, and retains the historical, anatomical, behavioural, and functional information already associated with the term acrorhagus. Including ectodermal structure in the definition of an acrorhagus excludes columnar structures such as verrucae that contain holotrichs in some species but that are never used in agonistic interaction.

Describing and defining pseudoacrorhagi is more complex. Most structures termed pseudoacrorhagi are actually endocoelic projections of the column, here termed marginal projections. Although most structures previously termed pseudoacrorhagi are actually marginal projections, some actiniid genera characterized as having pseudoacrorhagi may have marginal structures distinct from both acrorhagi and marginal projections. For example, the marginal structures of some species belonging to *Gyractis* may qualify as true pseudoacrorhagi; in *Gyractis excavata* Boveri, 1893 (= *Actinogeton sesere* (Haddon & Shackleton, 1893)) the marginal projection sometimes bears a swelling (e.g., Dunn, 1974; England, 1987; pers. obs). In this species, the oral surface of the projection is distinguished from the rest of the marginal projection in having thinner mesoglea and thinner, more closely packed ectodermal epitheliomuscular cells.

Homology

The inference of homology is based on recognition of the shared historical origin of structures following rigorous phylogenetic analysis (Patterson, 1982). Topology, connectivity, and detailed structural similarity are guides that lead to the initial proposition of homology between structures (see review in Rieppel & Kearney, 2002). The aim of this review is to redefine anatomical elements so that structures given the same name are similar in position and anatomy. Despite findings of similarity, homology remains conjectural, contingent on the discovery of shared ancestry. Based on preliminary phylogenetic analyses of Actiniidae (McCommas, 1991; Solé-Cava et al., 1994), I infer that the acrorhagus is homologous at least among members of *Actinia*, *Anemonia*, *Anthopleura*, and *Bunodosoma*, despite the fact that an acrorhagus of a member of *Anthopleura* or of *Bunodosoma* is borne on a marginal projection and an acrorhagus of a member of *Actinia* or *Anemonia* is not.

The more critical question of acrorhagi homology has been that of homology between acrorhagi and other structures in non-acrorhagi bearing taxa. Hand (1966) suggested that acrorhagi may be homologous to the capitate tentacles of corals and corallimorpharians; Williams (1975) suggested that acrorhagi may be homologous to the catch tentacles of acontiarian sea anemones. Like acrorhagi, both capitate tentacles and catch tentacles contain holotrichs. An acrorhagus resemble a capitate tentacle of a coral or corallimorpharian in its general morphology, as both are short, with a rounded tip (Hand, 1966). An acrorhagus resembles a catch tentacle in function rather than in morphology, as both are used in agonistic interactions with other actiniarians (Williams, 1975; Purcell, 1977): in an antagonistic encounter, the tip of a catch tentacle is applied to the ectoderm of the targeted actiniarian, resulting in necrosis (Williams, 1975; Purcell, 1977).

Despite these similarities, neither capitate tentacles nor catch tentacles are good candidates for homology with acrorhagi, as acrorhagi are topologically and anatomically distinct from both. The anatomical similarity between an acrorhagus and a capitate tentacle is superficial, as the ectoderm of capitate tentacles lacks the specializations seen in the ectoderm of acrorhagi (Bigger, 1982). Although the cnidae characteristic of acrorhagi, catch tentacles, and capitate tentacles are of the same general type, the holotrichs in acrorhagi are dissimilar from those of catch tentacles and of capitate tentacles in terms of microstructure (Schmidt, 1974; Bigger, 1982; pers. obs.). Furthermore, both capitate tentacles and catch tentacles differ from acrorhagi in their relative position: relative to the marginal sphincter, capitate tentacles and catch tentacles are orad (located closer to the mouth), whereas acrorhagi are adorad (Hand 1955, 1956; Williams, 1975).

Williams (1975) suggested that acrorhagi might be highly modified verrucae; Carlgren (1938) implied homology between acrorhagi and verrucae when he described acrorhagi, pseudoacrorhagi, verrucae, and vesicles as different types of columnar spherules. Verrucae are serially repeated, with several verrucae arranged in a longitudinal band in an endocoelic or exocoelic compartment. In contrast, a single acrorhagus crowns an endocoelic space.

After examining the ultrastructure of acrorhagi and verrucae, Bigger (1982) concluded that they were unlikely to be homologous. Verrucae are distinguishable from

acrorhagi (or pseudoacrorhagi) in having many secretory cells and few cnidae (Carl-gren, 1938; Bigger, 1982; den Hartog, 1987), having ectoderm anchored to the mesoglea with hemidesmosomes (Bigger, 1982), and lacking ciliary cones (Bigger, 1982). How-ever, verrucae and acrorhagi are similar in position, and are found in many of the same taxa, suggesting that their evolutionary histories may be closely tied. A hypothe-sis of homology between acrorhagi and verrucae entails specialization and transfor-mation of the distal-most verruca of the endocoelic compartments or entails serial rep-etition of transformed acrorhagi along the column. The direction of any transforma-tion between acrorhagi and pseudoacrorhagi (as in *Gyractis excavata*) is unclear: com-pared to acrorhagi, pseudoacrorhagi may be an evolutionary intermediate, a sec-ondary reduction or transformation, or novel structures. Existing hypotheses of rela-tionship for Actiniidae are inadequate for addressing the historical relationship between pseudoacrorhagi, acrorhagi, and verrucae: future studies need to examine these questions in detail.

Taxonomy

The possession of acrorhagi is used to diagnose and differentiate genera within Actiniidae (e.g., Stephenson, 1935; Carlgren, 1949; Manuel, 1981; Dunn, 1982; England, 1987). Although the presence of acrorhagi seems to be a good taxonomic feature, because these structures are fragile, and may be transient in some species, acrorhagi are not always recognized and therefore may not be a consistently applied taxonomic criterion. Imprecision in the definition and application of the terms acrorhagus and pseudoacrorhagus has led to instability and confusion over generic placement. For example, many species have been transferred between *Anthopleura* and *Bunodactis* (e.g., Stephenson, 1922; 1928; Carlgren, 1949, 1952), genera that are distinguished by the presence of acrorhagi in members of *Anthopleura* (see Carlgren, 1949; Dunn et al., 1980; England, 1987). Furthermore, because marginal projections and acrorhagi have sometimes been considered synonymous (e.g., Stephenson, 1922), the intention of many original descriptions is unclear.

Recognition of the diversity and variability of marginal structures is a necessary step in rectifying genus-level taxonomy in Actiniidae. The separation of acrorhagi and pseudoacrorhagi from marginal projections increases the number of characters available for classification. Distinguishing between marginal projections of the column and the nematocyst-dense pad eliminates some of the ambiguity and confusion surrounding acrorhagi as a taxonomic character. The type specimens of genera currently character-ized as having acrorhagi or pseudoacrorhagi (Table 1) should be reexamined before generic definitions are altered to ensure that anatomy corresponds to taxonomy.

Acknowledgements

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