BRITISH ANTHOZOA

(Coelenterata: Octocorallia & Hexacorallia)

Keys and notes for the identification of the species

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A Synopsis of the British Anthozoa

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Introduction

The Anthozoa is a subphylum of predominantly sessile marine animals belonging to the phylum Cnidaria (Coelenterata). Both solitary and colonial forms occur, including such creatures as the sea anemones, corals, sea-fans and sea-pens, and the aptly named "Dead men's fingers". Geographical distribution of the group is worldwide and some 6500 living species are known, occurring in most habitats throughout the marine environment, from the upper shore to the depths of the deepest oceans. A few species are found in brackish-water or lagunar habitats but none has overcome the problems of a freshwater existence.

The importance of anthozoans as major components of marine ecosystems is probably underrated, with the exception of the vast coral reef formations of the tropics which are still, in spite of man's efforts, the largest animal productions on this planet. Such reefs support a wonderfully diverse and largely dependent fauna, including many other anthozoans. On a more modest scale the sea anemones and soft corals found on the British coasts often occur locally in large numbers and in such localities their influence on the ecology must be considerable.

Anthozoans, due to their frequently brilliant coloration and variety of form were a favourite subject of the Victorian naturalists, at that time being classified amongst the Zoophyta—animal plants—a heterogeneous assemblage of many unrelated sessile animals. The foremost student of the group in those times was undoubtedly Phillip Henry Gosse, whose gift for observation and description of minute detail was second to none in this field. During the years 1853–1860 he produced numerous articles and books popularizing the subject, culminating in his classic *History of the British Sea Anemones and Corals* (1860). No less than 10 genera and 14 species originally described by Gosse are included in this *Synopsis*.

A second milestone in the study of British anthozoans was the publication of Stephenson's beautifully illustrated monograph on *The British Sea Anemones* (1928, 1935). Anemones have generally received greater attention in this country than other anthozoans as they are by far the most numerous members of the group and often the only anthozoans encountered on the shore. Indeed one class, the Octocorallia, has not been revised in any worthwhile systematic manner since Johnston's *History of the British Zoophytes* (1847).

Present-day research on anthozoans is centred mainly on various aspects of their behaviour and physiology; they are ideal subjects for electrophysiological study of simple nervous systems and work in this field is very much a major current interest; see Shelton (1981) for a review of present knowledge. It may seem surprising that such apparently simple creatures as anthozoans are capable of exhibiting complicated behaviour patterns; nevertheless, recent studies on aggression in several anemone species suggest considerable scope in this field and anthozoans of some other groups have also been found to show such behaviour.

In recent years the popularity of skin diving, using SCUBA gear, has led to an increased awareness of and interest in the marine environment. Anthozoans, being prominent and colourful inhabitants of the clear inshore waters favoured by divers, have naturally attracted much attention. Much of the new information on distribution and occurrence of species in British waters provided in the following pages is due to the efforts of diving enthusiasts. Several species hitherto unknown in Britain have recently been discovered and the known ranges of many others have been extended. In addition, the numerous excellent underwater colour photographs which have generously been lent have contributed much to knowledge of habitats and other details of the biology of this fascinating group of animals.

Anthozoans are soft-bodied, highly contractile animals whose shape and movement are governed by a hydrostatic skeleton antagonized by various sheets and blocks of muscle. Because of this, many subjective but strongly characteristic features can only be observed in living specimens. Experience has shown that many species, particularly the solitary forms lacking any sort of hard skeleton, may be extremely difficult to identify in the preserved state—such identification usually involves tedious histological study and measurement of nematocysts. Compared to its living counterpart a pickled anemone is a miserable and singularly unattractive object. Therefore the main aim of this *Synopsis* is to facilitate the identification of living specimens, although anatomical definitions of taxa at genus level and above are also provided. Fortunately, most anthozoans are of manageable size and are hardy in captivity; given reasonable care and attention they will live and expand under laboratory conditions, where they can be studied in detail; but it is hoped that, in most cases at least, the descriptions and illustrations will enable accurate identification in the field without the need to collect specimens.

Large numbers of anthozoan species occur in the deep oceanic waters off the Continental Shelf to the west of the British Isles. Most of these have a generally north Atlantic distribution and barely qualify as British, therefore they are considered beyond the scope of this *Synopsis*. The majority of species included are those which habitually occur within the 100 m depth contour around British coasts; this does not exclude those which also occur beyond this limit. A few exceptions to this rule, such as the coral *Lophelia*, are included as they are relatively well-known members of the British fauna.

General Structure

Individual anthozoans are known as **polyps**; they are **solitary** in some species, **colonial** in others. Anthozoan colonies consist of a number of polyps which are permanently connected by some form of common basal tissue and often reinforced by various skeletal structures.

The two classes of the Anthozoa—Octocorallia and Hexacorallia—have exploited the possibilities of a sessile existence by two basically different strategies. Octocorals are invariably colonial, the polyps generally being small and of remarkably uniform and relatively simple structure throughout the group, although polymorphism occurs in some groups. The polyps within an octocoral colony are, to a greater or lesser degree, mutually interdependent. On the other hand hexacoral polyps, which may be solitary or colonial, are usually large in comparison to octocoral polyps and attain a higher level of structural complexity. Polyps in hexacoral colonies are generally less interdependent and polymorphism never occurs.
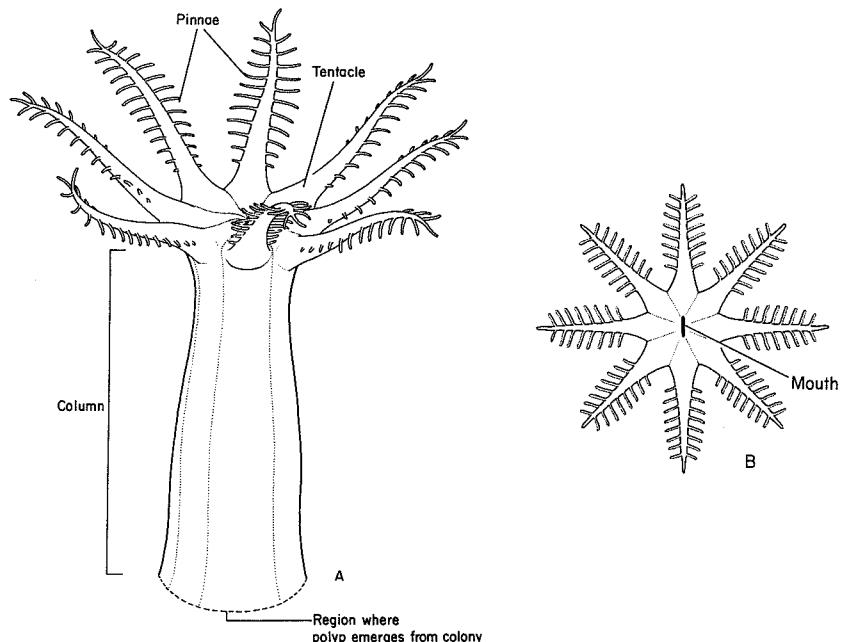
FIG. 1. A typical octocoral polyp showing general anthozoan structure. A, External view of whole polyp. B, View from above showing oral disc. C, Diagrammatic view of whole polyp bisected longitudinally, to show gross internal features, with cross-sections at two levels. Mesenteric insertions on external surfaces are shown as dotted lines. The pinnae on the tentacles and just eight mesenteries, all perfect, are characteristic of the Octocorallia but not of Anthozoa in general.

Actinopharynx

Mesentery

Mesenteric insertion

Column wall

Mesenteric filament

Siphonoglyph
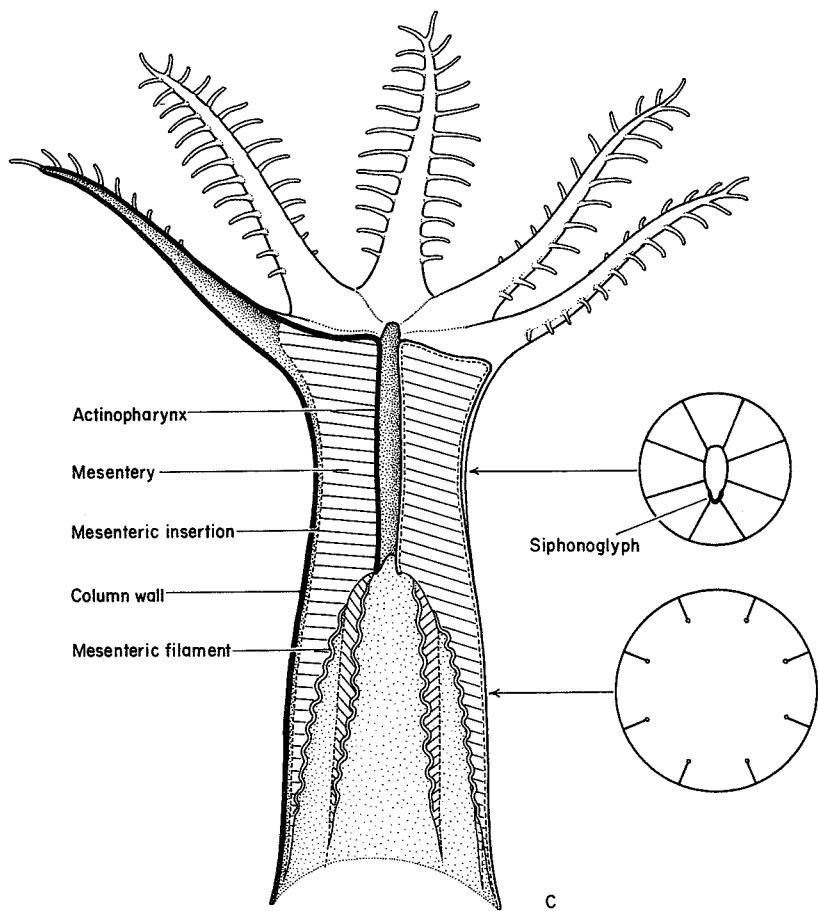
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The relatively simple polyp of an octocoral (Fig. 1) provides a good example of basic anthozoan structure. Details of the structure of various anatomical features, mainly of importance in hexacoral classification, will be described subsequently.

The hollow, cylindrical body of a polyp is the **column,** which terminates at its upper, oral end in a transverse **oral disc** (or just **disc**). At the centre of the disc is the slit-like **mouth** from which a flattened tube, the **actinopharynx,** leads into the body cavity or **coelenteron.** The internal surface of the folded edge of the actinopharynx is formed into a densely ciliated groove, the **siphonoglyph,** which

directs a water current into the coelenteron. This water current is used both for respiratory purposes and to inflate the polyp by hydrostatic pressure. The octocorals possess only one siphonoglyph, the opposite fold of the acti-nopharynx being unspecialized, but in the Hexacorallia one, two, or exceptionally more siphonoglyphs may be present.

The coelenteron is divided into a series of alcoves, or **chambers**, by radially arranged walls of tissue, the **mesenteries**.* These are attached to the interior surfaces of the column and disc and at least some of them reach the acti-nopharynx. Mesenteries which reach and attach to the actinopharynx are termed **perfect**, those that do not are **imperfect**. Their lines of attachment to the column wall and disc, which are often externally visible, are called **mesenteric insertions**. The triangular interspaces between the mesenteric insertions on the disc are known as **radii**, from each of which arises a single hollow **tentacle**, whose cavity is continuous with the coelenteron; in some hexacorals more than one tentacle arises from each radius. Each tentacle of an octocoral bears two opposing lateral rows of small offshoots, **pinnae**; these do not occur in the Hexacorallia.

The mesenteries are complex and variable in structure as they bear the organs of digestion and reproduction and various muscles; these will be described in detail later (pp. 8, 11). In all anthozoans the free, inner edge of most mesenteries is formed into a thread-like, more or less convoluted, **mesenteric filament.**

The lower, **basal** or **aboral** end of an anthozoan polyp is variable in form: in most colonial species it is imbedded in a common tissue mass, the **coenenchyme,** or it may bud directly from the wall of another polyp. In the solitary hexacorals the base may either form a transverse **basal** or **pedal disc**, which adheres to the substratum, or a rounded extremity which usually correlates with a burrowing mode of life.

Most anthozoan polyps are able to retract their oral parts—disc, tentacles and the upper part of the column—into the coelenteron, for protection. Retraction is accomplished by shortening the longitudinal muscles on the mesenteries and contracting the parts being retracted. The terms **contraction** and **retraction** should not be confused, some anthozoans being incapable of retraction although still very **contractile.**

Various hard skeletal elements, usually of calcareous material, occur in many anthozoans. Most octocorals possess **sclerites (spicules)**, tiny calcareous deposits of variable form imbedded in the flesh; additionally the sea-pens and sea-fans (orders Pennatulacea and Gorgonacea) are supported by an internal axial rod, or **axis**, of horny or calcareous substance. The best-known anthozoan skeletons are, of course, those of the stony corals (Scleractinia) whose aggregated **coralla** (sing. **corallum**), calcareous cups into which the polyps can retreat, form the coral reefs of tropical regions.

*Terminology: Many publications on general zoology use terms different from those described above, in spite of specialists accepting as standard the terms defined by Stephenson (1928) and Carlgren (1949). Three potentially confusing examples are:
Septa, an incorrect alternative to mesentery; this term should only be used to define the radial skeletal plates of the Scleractinia;
Sulcus, an antiquated alternative to siphonoglyph which has never gained acceptance; the same applies to *stomodaeum* (actinopharynx).

Detailed Structure of General Features

Body wall: As in other Cnidaria this consists of three layers, an external cellular **ectoderm**, a collagenous middle layer of elastic connective tissue, the **mesogloea**, and an internal cellular **endoderm** (gastrodermis). The mesogloea is variable in thickness, sometimes being very thick and cartilaginous in texture, although always more or less flexible and elastic.

Musculature: Muscle cells in the Anthozoa occur as a single layer of fibres attached along their length to the surface of the mesogloea. Generally the fibres are aligned in a circular direction on the endodermal surfaces of the column wall and longitudinally on the ectodermal surfaces, becoming radial on the oral disc. This basic arrangement is frequently modified to suit different functions.
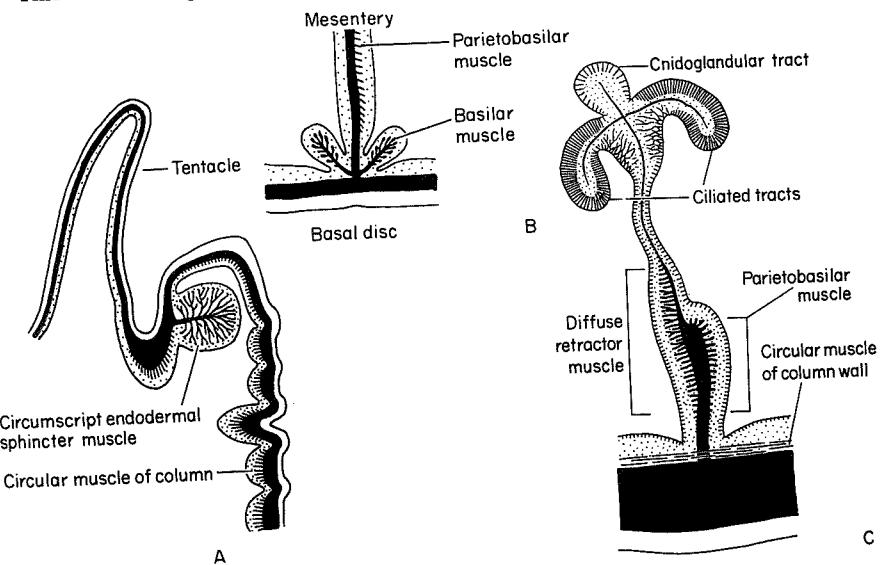
Fig. 2. Diagrammatic sections through muscles and other structures. A, Longitudinal section through the distal part of the column of *Urticina felina* showing the circumscript sphincter muscle, undifferentiated circular muscle, and a tentacle. The small elevations on the external surface, which cause irregularities in the circular muscle, are verrucae (see p. 98). B, Vertical section through the insertion of a mesentery into the basal disc of *Urticina felina* showing basilar muscles and part of the parietobasilar muscle. C, Transverse section through a small, imperfect mesentery of *Calliactis parasitica* showing the parietobasilar muscle, a weak, diffuse retractor muscle, and the trifid part of the mesenteric filament with cnidoglandular and ciliated tracts. Ectoderm unshaded, endoderm stippled, mesogloea black.

The simplest modification involves the raising of the mesogloea into a number of narrow parallel ridges or **processes** to accommodate a greater number of muscle fibres. Figure 2A shows the typical appearance of the circular muscle of

the column wall in diagrammatic cross-section, the muscle processes appearing like the teeth of a comb. Where still stronger, localized contraction is required discrete blocks of muscle are built up by broadening and subdividing the processes. The longitudinal **retractor muscles** and oblique **parietobasilar muscles** of the mesenteries, the radial **basilar muscles** and circular **sphincter muscles** are formed in this way. Figure 2 shows sections through these various muscles.

The occurrence, structure, and position of the discrete musculature forms the basis of conventional classification within the Hexacorallia. The sphincter, if present, may be **mesogloeal**—embedded within the thickness of the mesogloea (Fig. 3) or **endodermal** (Fig. 2A). All other discrete muscles are endodermal. Such a muscle is **diffuse** if it consists of a number of separate processes arising from the mesogloeal surface (Fig. 2C), or **circumscript** if supported above the level of the mesogloea by a single, thickened process terminating in numerous branches and sub-branches (Fig. 2A). An intermediate condition, **circumscript-diffuse**, is also recognized but this is really only a very strong diffuse muscle.

Only in some Actiniaria is a complete complement of discrete muscles present, as shown in Fig. 3. In all other orders, except the Ceriantharia, retractor muscles are present, located on one face of each mesentery, the remainder of this mesenteric surface bearing a layer of weak, undifferentiated longitudinal muscle. The orientation of the retractors indicates the affinities of the mesenteries—see below. Parietobasilar muscles, if present, occur on the opposite face of the mesentery from the retractors and run obliquely from column wall to basal disc; this side of the mesentery also bears a layer of weak, undifferentiated transverse muscle (Fig. 3). Basilar muscles, present only in combination with parietobasilar muscles, occupy both angles formed by the attachment of the mesentery to the base (Fig. 2B). The muscular base of such species is capable of creeping along the substratum to which it is attached.

The sphincter muscle, which occurs in the order Zoantharia and many genera of the Actiniaria, closes the aperture at the top of the column when the disc and tentacles have been retracted. It is a common fallacy, perpetuated in many text-books, that the sphincter (often incorrectly termed oral sphincter and even illustrated encircling the actinopharynx) is responsible for retraction, this is of course impossible.

Arrangement of mesenteries and tentacles: In all anthozoans the mesenteries are arranged in a bilaterally symmetrical manner on either side of a plane of symmetry, the **directive axis**, which is defined by the elongation of the actinopharynx and passes through the siphonoglyph(s). The plan of this mesenterial arrangement, and consequently that of the tentacles, is character-istic of the different anthozoan groups. Many of the external features employed in the keys are related to these arrangements and therefore a clear understanding of them is important. Such arrangements are conventionally illustrated as a diagrammatic, cross-sectional plan (Fig. 4), a typical **hexamerous** (six-rayed) sea anemone being given as an example. Typical plans for other groups are illustrated in the introduction to each group.
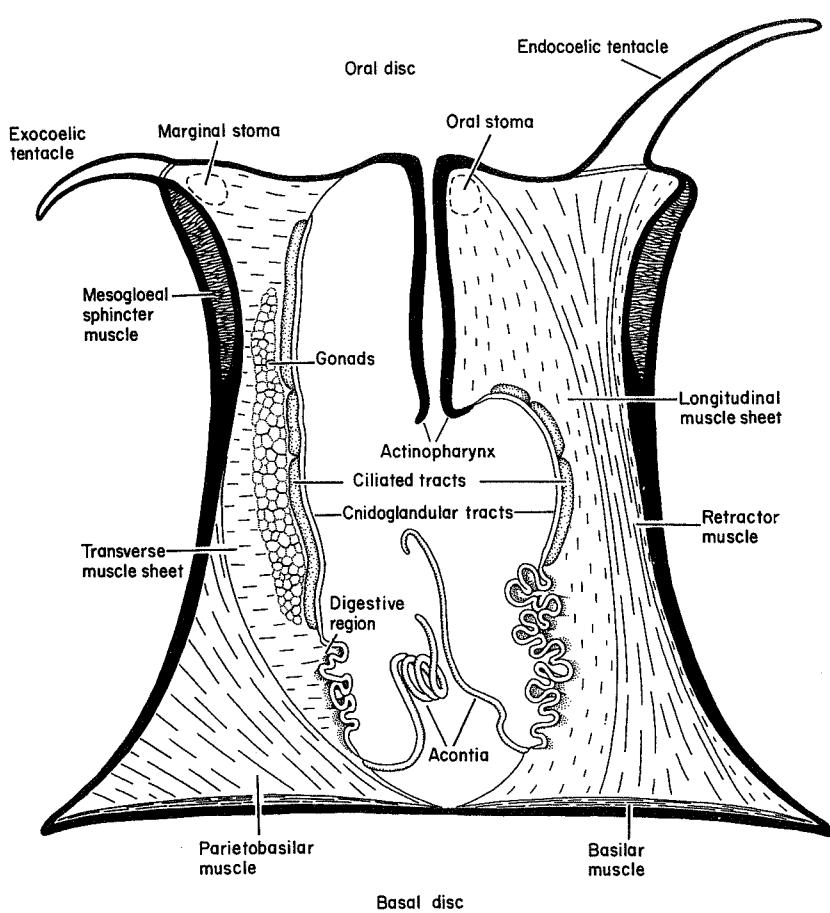
Fig. 3. Diagrammatic longitudinal section through the sea anemone *Calliactis parasitica* showing the musculature of the endocoelic face of a perfect mesentery (right) and the exocoelic face of a large imperfect mesentery. The imperfect mesentery is fertile—with gonads—the perfect one is not. Various other features described in the text are shown; the tracts of the mesenteric filaments and the acontia are exaggerated in thickness, and the actinopharynx is shortened, for clarity. *Calliactis* does not possess mesenteric stomata, the approximate position of which is shown by broken lines.

Mesenteries may be arranged in adjacent **pairs** in which the sides bearing the retractor muscles face each other, except for the **directive pair**, or pairs, which straddle the directive axis and have their retractors facing outward. Directive mesenteries are usually perfect and associated with a siphonoglyph. Pairs of mesenteries are usually arranged in **cycles**, members of a cycle being at a similar level of development. In Fig. 4B the first (**primary** or **oldest**) cycle consists of six pairs of perfect mesenteries (hence **hexamerous**), the **secondary** cycle consists of six pairs of large imperfect mesenteries, the **tertiary** cycle of 12 pairs of smaller imperfect mesenteries, and the **quaternary** cycle (**youngest** in this instance) of 24 pairs of tiny imperfect mesenteries. The youngest mesenteries may be very small, as in the figure, and do not necessarily extend the whole length of the column. The **chamber** enclosed by a pair of mesenteries is an **endocoel**, that between adjacent pairs being an **exocoel**. Generally the primary cycle of mesenteries is the first to appear during development, with mesenteries of subsequent cycles arising in the exocoels between these; Fig. 4A shows an early stage of development in which only six pairs of mesenteries are present.

Mesenteries do not necessarily form pairs but are almost invariably **coupled**, two mesenteries occurring in equivalent positions on opposite sides of the directive axis forming a **couple**. Some groups, such as the Ceriantharia (p. 62), have their mesenteries arranged exclusively in couples, never being paired, although of course in paired arrangements couples also occur.

A single tentacle, rarely more, arises from each endocoelic and exocoelic radius on the oral disc. These are arranged in concentric **cycles** directly related to the mesenteric cycles and termed accordingly. The primary tentacles form the **inner cycle,** nearest the mouth, and are generally the largest; tentacles of subsequent cycles occur progressively further out with those of the outermost (exocoelic) cycle situated at the margin of the disc. Generally tentacles of succeeding cycles diminish in size but occasionally the reverse is true. As the tentacles of the outermost cycle arise from the exocoels the number of tentacles is usually double the number of mesentery-pairs, with one more cycle of tentacles than mesenteries occurring. The arrangement of tentacles is conventionally expressed as a formula; thus the formula for Fig. 4B is $6 + 6 + 12 + 24 + 48 = 96$. Minor irregularities are frequent, the outer cycles often being incomplete, or the whole arrangement may be secondarily irregular as a consequence of asexual reproduction by fission, see p. 18.

Although the hexamerous plan illustrated is typical of many Actiniaria and Scleractinia, arrangements based on other numbers of primary tentacles occur, such as *Urticina* where the plan is **decamerous** (10 primaries). More than one cycle of mesenteries, sometimes all of them, may be perfect, imperfect mesenteries of younger cycles eventually growing to be perfect. Sometimes perfect mesenteries pair with imperfect ones, as in *Edwardsia*, and this can produce a different type of plan which is very distinctive. Typically the number of tentacles and mesenteries in successive cycles doubles after the second cycle, with the primaries and secondaries being equal in number, but in *Stomphia* the secondary tentacles are greater in number than the primaries, providing yet another distinctive arrangement.
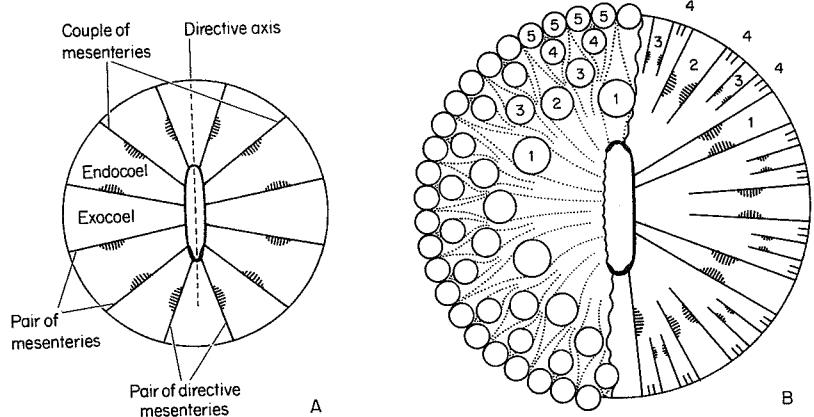
FIG. 4. Diagrams showing the arrangement of mesenteries and tentacles in a regularly hexamerous sea anemone (Actiniaria). A, Transverse section through the actinopharynx region of a young stage in which only the six pairs of mesenteries belonging to the first cycle are developed, demonstrating the terminology. B, A much more advanced stage with four cycles of mesenteries and five cycles of tentacles. The left-hand side of the diagram is a view of the oral disc with the position of the tentacles shown as small circles, and the mesenteric insertions as dotted lines; notice how the latter are distorted around the tentacle bases. The right-hand side shows a cross-section in the actinopharynx region. Retractor muscles are indicated by shaded semi-circles and siphonoglyphs by thickenings of the actinopharynx. Numbers indicate cycles of tentacles and mesenteries.

If, as occurs in several groups, only a single siphonoglyph is present this is termed **ventral**, a term which probably has no ontogenetic significance but does allow exact definition of various elements within the overall plan, hence **dorso-lateral primary endocoel**, etc. In the Ceriantharia, a perverse group, the single siphonoglyph is generally considered to be **dorsal**, although no satisfactory justification for this inversion exists.

Structure of the mesenteries: Mesenteries are formed as inward projections from the mesogloea of the body wall and thus are covered on both surfaces with endoderm. In certain regions the surface is differentiated into organs concerned with reproduction, digestion, and water circulation; and as already described the mesenteries also bear most of the important discrete musculature. In some Actiniaria the distal regions of the mesenteries are pierced by oral or marginal **stomata**; these are small holes which allow the passage of water between adjacent chambers. Figure 3 shows the general layout of the organs in a typical sea anemone.

The position of the gonads is variable within the region between the retractor muscle and the mesenteric filament; in some groups their location and distribution on mesenteries of different cycles is of systematic importance.

The mesenteric filament forms a thickened, thread-like rim, rounded in cross-section, running along the free inner edge of most mesenteries, from the lower edge of the actinopharynx almost to the base. It is greatly convoluted along most of its length, particularly in the proximal **digestive region,** where the endoderm of the adjacent mesentery surfaces is thickened and bears numerous gland cells which produce digestive enzymes.

In the Zoantharia and most Actiniaria the upper part of the filament, usually above the digestive region, bears an additional strand running parallel along each side, so that in cross-section it appears trifid (Fig. 2C). These two lateral strands are the **cilated tracts** (the main, central strand usually being called the **cnidoglandular tract**) which probably contribute to water circulation within the coelenteron. They are transversely corrugated (not shown in Fig. 2C) and may be interrupted at irregular intervals (**discontinuous**). In fresh, dissected specimens the cilated tracts may not be easily observed, as they are often translucent, but in fixed or sectioned material these and other details of mesenteric anatomy are more easily seen.

Acontia: Some anemones possess **acontia**, each acontium being a slender thread attached by one end to the lower edge of the mesentery. Superficially they resemble the simple mesenteric filament but are usually slightly stouter and never attached by their edges. Acontia possess a core of mesogloea bearing a few muscle fibres and are densely armed with nematocysts. Their function is probably two-fold: to help subdue active prey that has been swallowed, and for defence. When alarmed the anemone contracts strongly, forcing water out of pores (**cinclides**) in the body wall, or the mouth, which carries the free ends of the acontia with it. The acontia may extend for many centimetres beyond the column wall and can later be withdrawn by muscular and/or ciliary action. Undoubtedly this sudden emission of the nematocyst-laden acontia helps to deter would-be predators and is particularly well demonstrated in the two hermit crab commensals *Adamsia* and *Calliactis*, which readily emit acontia when their host crab becomes agitated. Some Ceriantharia possess acontia-like organs, **acontioids**, whose function is unknown.

Mouth and actinopharynx: The form of the mouth does not vary much; sometimes it is raised on a rounded or conical elevation of the disc, the **hypostome.** The actinopharynx is fairly thick-walled, usually with pronounced longitudinal ridges opposite the insertions of the perfect mesenteries. In unhealthy specimens it may be protruded through the mouth in a series of inflated lobes. One or two siphonoglyphs may be present, exceptionally more in irregular, asexually produced polyps. In some forms the siphonoglyph is only weakly differentiated from the rest of the actinopharynx, in others it is very strongly marked, forming a deep groove with a thick endodermal lining. In most living specimens the entrance to the siphonoglyph is visible as a slight dilation at the corner of the mouth.

Tentacles: These are more or less conical but in some species they have knobbed tips, **acrospheres**, laden with numerous large nematocysts; in *Aureliania* they are very short, terminating in variably shaped vesicular swellings. Tentacles are usually very contractile and in some species are capable of turning inside-out when the polyp is retracted, although it is difficult to understand how this is achieved.

Coenenchyme: This is a general term for the common basal tissue mass of an anthozoan colony—tissue which cannot be attributed to any individual polyp. Coenenchyme consists largely of mesogloea which spreads from the basal regions of the polyps comprising the colony. It is usually penetrated by a system of endodermal canals and tubules which circulate water throughout the colony and also serve to inflate it. In the Octocorallia the mesogloea of the coenenchyme contains numerous sclerites, which add rigidity and probably help to deter predators. In colonial Scleractinia the tissue which connects the polyps is derived from the column wall of individual polyps and spreads over the surface of the calcareous skeleton; such tissue, which is somewhat different in nature from the coenenchyme of other anthozoans, is known as **coenosarc.**

Periderm: Many anthozoans secrete a flexible cuticular covering which adheres firmly to the body wall, **periderm**. This varies considerably in texture; it may be thin and chitinous, resembling a layer of corneus skin, as in *Cornularia* and *Phellia*, or thicker, softer, and more felt-like, as in *Edwardsia* and *Cataphellia*. Often the periderm layer incorporates foreign material—sand grains, diatoms, etc., and in *Phellia* may even serve as a substratum for encrusting Bryozoa or Algae.

Some anemones, such as actiniids and sagartiids, secrete a loose layer of mucus around the lower part of the column, this is never adherent and may be removed without damage to the anemone. Such mucus layers do not constitute true periderm.

In addition to the major features of anthozoan anatomy described above numerous minor structural modifications, significant at the family level or below, occur, particularly in the Actiniaria. These will be described in the relevant introductory passages to these groups.

Remarks on form and size: The anthozoan polyp when fully expanded and relaxed assumes a more or less definite shape maintained by internal hydrostatic pressure. Otherwise, an individual may vary its size, shape, and proportions at will, due to the great elasticity of its tissues and localized muscle contraction. Hexacoral polyps are more variable in this respect than octocorals. Only in full expansion is the shape or posture of a species truly characteristic, although in some species various conditions of contraction or retraction are fairly typical; therefore most of the illustrations in this *Synopsis* show well expanded specimens. It is important to understand that a specimen under observation may not necessarily resemble the shape or form shown in the figures. A freshly collected specimen rarely expands to its fullest extent until it has had time to acclimatize

to the new conditions. However, with a little experience it is possible to assess subjectively the potential expanded form of a specimen. Observations made in the field will naturally be of great assistance in this respect.

Size is also a very variable factor and the measurements given serve only as an approximate guide. The proportional length of the tentacles in a reasonably expanded specimen is given according to the following scale: short—less than half disc diameter; moderate—less than disc diameter; long—more than disc diameter; very long—more than twice disc diameter. These proportions, although only approximate, should prove more useful than absolute measurement.

Cnidae (Nematocysts)

Cnidae are the single most important feature of the Cnidaria, being largely responsible for the success, and even the existence, of the phylum. They occur in most tissues of the ectoderm and endoderm and are produced by special cells called **nematocytes**. A cnida is a microscopic, hollow capsule provided with a hollow, evertible **tube** whose wall is continuous with that of the capsule. Before use the tube lies within the capsule; in response to various tactile or chemical stimuli the tube is everted with considerable force, usually sufficient to penetrate the tissues of any organism within range. At least some kinds of cnidae can inject a toxic substance into the victim and in some species, few of them British, this may be harmful to man. Other kinds are not penetrative but entangle or adhere to the victim. Cnidae thus serve three basic functions: prey capture, defence, and in some cases adhesion to a substratum. The functional significance of their structure is, however, poorly understood.

Many types of cnida occur; in the Anthozoa the distribution of different categories and their size ranges in certain tissues are important as an aid to classification. The full complement of cnidae present in an anthozoan taxon is known as the **cnidom**. Two major categories of cnidae occur:

Spirocysts (Fig. 5A): These are unique to the Hexacorallia, where they occur mostly in the tentacles. The tube lacks spines and is not penetrative; when discharged it is entwined by a left-hand spiral of a glutinous substance which soon decomposes to a network of irregular strands. Under the light microscope the capsule wall does not stand out sharply, being poorly refractile, but the tube is clearly visible. Measurements of spirocysts have little systematic value as, in most species, they fall within a similar size range.

Nematocysts (Fig. 5B–K): These occur in all Anthozoa and other Cnidaria and are found in most tissues, including the tentacles. The tube usually bears an armament of spines which are arranged in three right-hand spirals, and is usually penetrative. The capsule walls are usually highly refractile and thus are easily observed, and measured, under the light microscope. Measurements of undischarged nematocysts, usually expressed as size ranges or means for each category in each separate tissue or organ, are of great systematic value, particularly for defining closely related species. At higher taxonomic levels the occurrence of different categories is usually significant.
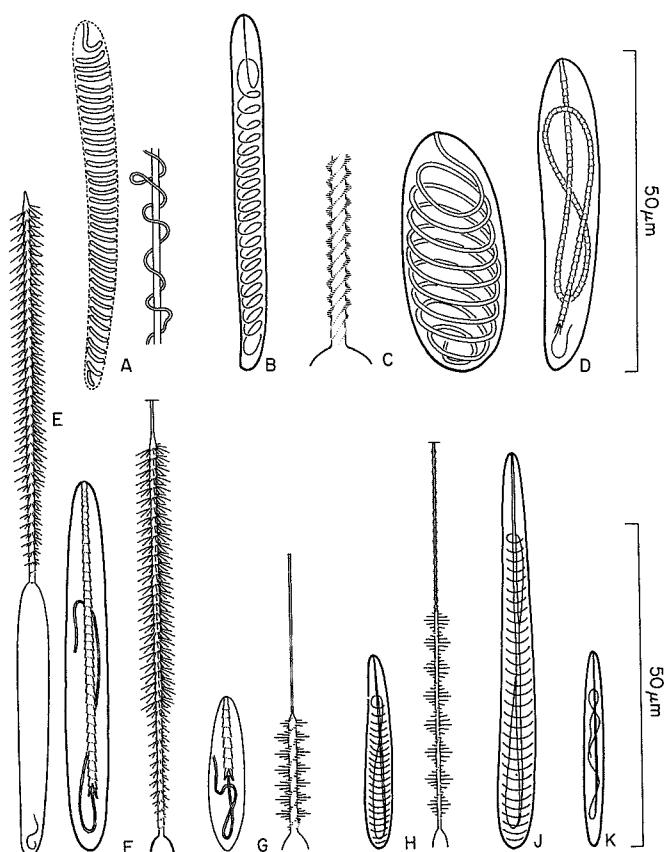
FIG. 5. A representative selection of anthozoan cnidae, showing undischarged capsules and some everted tubes, in semi-diagrammatic form. A, Spirocyst. B, Holotrich, acrorhagus of *Actinia equina*. C, Holotrich, filaments of *Corynactis viridis*. D, Macrobasic *p*-mastigophore, tentacle of *Diadumene cincta*. E, *P*-mastigophore (amastigophore), acontium of *Cereus pedunculatus*. F, *P*-mastigophore, acontium of *Aiptasiogeton pellucidus*. G, *P*-mastigophore, filament of *Urticina felina*. H, *B*-mastigophore (basitrich), acontium of *Sagartia elegans*. J, *B*-mastigophore, nemathybome of *Edwardsia timida*. K, Special *b*-mastigophore, acontium of *Aiptasia mutabilis* var. *couchii*. The scale is only approximate.

Many different categories have been described in the Cnidaria as a whole but only four main types occur in the Anthozoa: all of these have tubes with open tips (**stomocnidae**). The standard nomenclature is that of Weill (1934) which has since undergone several modifications. The system described below is based on the work of Carlgren (1940) and Schmidt (1969, 1972, 1974), the latter having employed electron microscopy to elucidate many fundamental but previously misunderstood characters.

Simplified classification of anthozoan nematocysts

Haplonemes: Tube, and its armament of spines if present, not differentiated into regions; any change in diameter of the tube or the size of its spines is gradual and even throughout its whole length. Haplonemes may be devoid of spines (**atrichs**), or they may possess an armament of spines throughout their whole length (**holotrichs**, Fig. 5C). Some types formerly called atrichs, principally those occurring in the acrorhagi (aggressive organs, see p. 98) of certain Actiniidae, have been shown to possess spines that are too small to be observed under the light microscope, these are now termed **holotrichs.**

Heteronemes: Tube always possessing spines and always differentiated into regions; basal part of the tube forming a **shaft** differentiated from the distal **thread** either by its greater diameter, its possession of larger spines, or both. The change of diameter or spine size is always more or less abrupt. Heteronemes, due to their great variability, are systematically the most important group of nematocysts in the Anthozoa. Two major categories occur:

P-mastigophores: Shaft always greater in diameter than thread, with a short, conical junction between the two. In undischarged p-mastigophores the junction exhibits a distinct "**V-notch**", in reality a cone formed by the final turn of large spines on the shaft. P-mastigophores may be either **macrobasic** (Fig. 5D), rare in British species, in which the shaft before discharge is much longer than the capsule and hence is folded within it, or **microbasic** (Fig. 5F), in which the shaft is shorter than the capsule before discharge and lies straight within it. The thread of p-mastigophores varies considerably: it may be long or short, it may possess or lack spines, it may break off at discharge and remain inside the capsule (**amastigophore**), or, in some types the spines may strip off the shaft at discharge, remaining stuck together to form a detached "dart" (**q-mastigophores**), but the latter occurrence is erratic.

B-mastigophores: Shaft not necessarily greater in diameter than thread, the latter always with spines, spines of shaft always larger than those of thread, V-notch in undischarged condition always absent. Before discharge the shaft lies straight within the capsule and usually the thread is coiled in even turns around it; in the acontia of the Aiptasiidae the thread is relatively short and does not form regular coils (Fig. 5K). The category **basitrich**, formerly regarded as a distinct type, is now considered to be a synonym of b-mastigophore.

The above terminology, although simplified, may still appear to be formidable but for present purposes only the categories holotrich, atrich, p-mastigophore and b-mastigophore need be understood. These are not difficult to determine under the light microscope (see p. 24 for methods). Cnidae appear to be of little value in classifying Octocorallia but in the Hexacorallia they are very important. In this *Synopsis* their use is restricted to the definitions of higher taxa, to determine species where no alternative method is available, and as an additional aid in identifying species within a difficult group, e.g. the acontiate anemones. Schmidt (1969, 1972) defined and illustrated many sub-categories and described their distribution in the Anthozoa (1974); his term rhabdoid is equivalent to mastigophore as used above.

Reproduction

Anthozoans reproduce both sexually and asexually, the latter taking place in several different ways.

Sexually produced individuals develop direct from a ciliated **planula larva**. In colonial forms the larva, usually after a short free-swimming period, settles and develops into an **ancestral polyp**, which gives rise to the colony by asexual budding. Fertilization may be external or internal, with the larvae classified according to their habits: feeding—planktotrophic, detritotrophic; parasitic or non-feeding (lecithotrophic)—planktonic or demersal. Internal fertilization may involve a brooding period within the parental coelenteron resulting in the eventual release of larvae (**larviparity**) or fully formed young (**viviparity**). "Viviparous" young are often produced by freshly collected specimens and this process may be frequently observed in the common anemones *Actinia equina* and *Cereus pedunculatus*.

Two British forms produce larvae which appear seasonally in the plankton. Larvae of *Peachia cylindrica* are obligatory parasites of various hydromedusae, which serve as both food and transport. The free-swimming larvae of ceriantharians, known as **arachnactis**, are planktonic carnivores.

Asexual reproduction occurs in all major groups of the Anthozoa except the Ceriantharia and may be divided broadly into four methods.

(1) *Budding:* In the Octocorallia new polyps bud from the **solenia** (tubular connections between existing polyps) or new polyps may bud directly from the walls of others. Budding in the Hexacorallia occurs in the colonial Scleractinia and Zoantharia. Buds arise from existing polyp walls or extensions of these, the **edge-zone** in Scleractinia (this form of asexual reproduction in this group being known as **extratentacular budding**) and **basal coenenchyme** in Zoantharia. A second form of "budding" occurring in some colonial Scleractinia is **intratentacular budding**; this is, in effect, a version of longitudinal fission (see (2)) with the new individuals remaining connected as part of the colony.

(2) *Longitudinal fission:* This occurs in some Actiniaria and Corallimorpharia, and (in a modified form) in some Scleractinia. Initially the polyp stretches itself by elongation of the base, usually along the directive axis; fission then proceeds as a tearing process across the plane of stretching, resulting in two daughter individuals of approximately equal size. This process is usually rapid, taking no more than a few hours, and the torn surfaces heal quickly to ensure a minimal loss of functional activity.

(3) *Transverse fission:* This is relatively rare in anthozoans; only four British species are definitely known to employ this method, of which three different variations occur. In *Aiptasia mutabilis* and *Nematostella vectensis* a circular constriction appears on the lower part of the column, which is eventually pinched off. A new disc, actinopharynx and tentacles are regenerated fairly rapidly by the separated lower part whilst the upper part grows a new base, usually rather more slowly.

Gonactinia prolifera grows a ring of new tentacles around the lower or middle part of its column and a second actinopharynx develops at the same level before the two new individuals separate (Fig. 31B). In this species a second fission may begin before completion of the first, resulting in a short chain of differentiated but connected individuals, reminiscent of strobilation in the Scyphozoa.

The tiny coral *Sphenotrochus andrewianus*, which lives unattached, develops a second calyx, complete with disc, tentacles and actinopharynx, at its aboral end. The two individuals then divide along a predetermined transverse plane.

(4) *Basal laceration:* In some anemones small fragments of tissue separate from the limbus region (junction of column and basal disc) by constriction or tearing; these regenerate into tiny anemones. Some species are very prolific, the adult anemone creeping along the substrate leaving a trail of developing fragments in its wake.

Consequences of asexual reproduction: The method of asexual reproduction employed in the Actiniaria is often characteristic of a species (Stephenson, 1929) and therefore may be used as a guide to identification. Although the occurrence of asexual reproduction may not be immediately obvious the signs of subsequent regeneration are often unmistakable. In regenerating after a fission the polyp almost invariably loses its basic biradial symmetry, development of new tentacles and mesenteries proceeding in an irregular manner. The number of these in each cycle will usually be variable and may not increase from cycle to cycle in a regular progression. As an example, a specimen of *Sagartia* may be found in which the tentacle formula is $9 + 7 + 15 + 26 + 52 = 109$. As *S. elegans* habitually reproduces asexually (by basal laceration) but *S. troglodytes* does not, this specimen could be assigned to the former species with reasonable confidence. The reverse, that all regularly hexamerous specimens of *Sagartia* must therefore be *S. troglodytes*, is however, not necessarily correct. Sexually produced specimens of *S. elegans* are regularly hexamerous, only those produced from basal lacerations being likely to develop irregularly. Specimens of this species exhibiting regular hexamery are admittedly rare but, nevertheless, their possible occurrence should not be dismissed.

Ecology and Distribution

Anthozoans are common in most marine habitats and there are few benthic niches which they have not exploited. Many species live on the shore (the **littoral** region) and are well adapted to life in this demanding environment, with its unpredictable wave turbulence, extremes of temperature and problems of desiccation. Most shore-dwelling species extend into the shallow **sublittoral** (a term used here in its broadest sense to describe all depths below low water mark), down to about 25 m depth.

The majority of anthozoans attach themselves to hard substrata, being either permanently fixed, as in most colonial species, or temporarily attached by an adhesive basal disc, like the sea anemones. Many colonial species are exclusively sublittoral in occurrence as they have little or no tolerance to the stresses imposed by wave turbulence; such species also tend to prefer dimly lit or even totally dark habitats and thus usually inhabit deep clefts and crevices, caves and undercuts, which offer both shade and shelter. Two permanently fixed species, *Alcyonium digitatum* and *Caryophyllia smithii*, thrive in more turbulent conditions, being found on the lower shore or in relatively exposed locations in the sublittoral. Forms such as sea-fans live where current flow is predictable, projecting across the currents that bring their food. They are able to flex in a restricted plane, to cope with surges in the current, but cannot survive in turbulent conditions where they may be stressed in awkward directions.

On rocky shores sea anemones are the dominant anthozoans. They occur in most available niches and, although most species prefer slightly sheltered sites, several thrive in places exposed to the full force of the surf. Favourite abodes are deep pools and gullies, especially where the sides are undercut to form shaded caves and overhangs; crevices and holes (sedimentary rocks that are riddled with piddock holes often contain enormous populations of anemones); beneath boulders or imbedded stones; and in the tangles of kelp holdfasts. Some anemones are often found attached to the bedrock beneath a layer of mud or gravel at the bottoms of pools and gullies. These often stick a layer of gravel to their columns, probably as a defence against abrasion as individuals of the same species occurring in the sublittoral usually lack this gravel coating.

Although most anthozoans occur on hard substrata, a surprisingly large number are adapted to life in mud, sand, or gravel. The sea-pens (Pennatulacea) are the only free-living octocorals; they live with their stalks embedded in mud or sand in sheltered localities, such as sea lochs, or in deep water. Most other soft-substratum inhabiting anthozoans are solitary forms. Cerianthids live in long tubes buried in the substratum and thus are restricted to a fixed location, although capable of burrowing in again and constructing a new tube if dug up. The burrowing anemones (Athenaria) do not build tubes and therefore, to a greater or lesser extent, are able to shift their position. This has obvious advantages but does require that the substratum be fairly stable: cerianthids can exist in relatively unstable substrata. Burrowing anemones are mainly sublittoral in occurrence but in a few sheltered areas, where the substratum is rarely disturbed by strong water movement, they may be found on the lower shore. In

the past, beds of eel-grass (*Zostera*) on the lower shore and in the shallow sublittoral provided the necessary stable substratum for these burrowers, but since the disappearance of the grass from many areas, due to an epidemic of disease in the 1930s, the topography of these shores has altered drastically, to the detriment of the associated fauna. Although the *Zostera* has recovered in some regions it has not yet regained its former glory and the associated fauna, including the burrowing anemones, has not reappeared in many localities.

Probably all anemones, including species with adherent basal discs, are able to dig into soft substrata. Many of these are found in mud or gravel, usually attached to a buried stone or shell; this habit is termed **burying**, to distinguish it from the activities of the true burrowers.

A few anemones are able to tolerate wide ranges of salinity and may be encountered in brackish-water estuaries, marshland creeks, or even isolated lagoons where great extremes of salinity and temperature may occur.

The British Isles benefit from being on the fringe of several zoogeographical regions. On the south and west coasts much of the fauna originates from the warm-temperate, south-west European *Lusitanian* region. Many Lusitanian species reach their northernmost limits in Britain: some extend no further than Cornwall, Devon, or South Wales; others may reach western Scotland, and *Caryophyllia smithii* even occurs around northern Scotland and in the North Sea.

A few *Boreal-Arctic* species, which range from the north polar regions to most of northern Europe, reach the east coast of Britain. These usually occur no further south than the North Sea but in the past one or two have been recorded in the English Channel.

Some anthozoans are widespread throughout the cold-temperate region of the north Atlantic: various sea-pens, *Alcyonium digitatum*, some zoanthids, and anemones such as *Metridium*, *Urticina*, and *Stomphia*. One anemone, *Halcampoides purpurea*, occurs in most regions of both hemispheres, whilst the little orange-striped anemone, *Haliplanella*, has in recent times migrated throughout most of the northern hemisphere.

Numerous fauna lists, covering specific areas of the British Isles and northern France, have been compiled. The following are devoted to or include anthozoans: Scilly Isles (Robins, 1969), Lundy (Hiscock, 1974), South Pembrokeshire (Dyfed) (Crothers, 1966), Isle of Man (Bruce *et al.*, 1963), Strangford Lough, Northern Ireland (Williams, 1954), St Andrews, Berwickshire (Laverack and Blackler, 1974), Cullercoats, N. Shields (Bull, 1939; Evans, 1978), Norfolk (Hamond and Williams, 1977), Plymouth district (M.B.A., 1957), Roscoff, Britanny (Teissier, 1965), Isles Glénans, West Britanny (Lafargue, 1970). Stephens (1909) published a list of deep-water Octocorallia and Scleractinia occurring off the Irish coasts and Picton (1985) has up-dated this. A set of photographs, mostly in colour, illustrating nearly all the known British anthozoans has recently been published (Manuel, 1983) and should be used in conjunction with the descriptions in this *Synopsis*.

Predators and Other Enemies

Due to the efficiency of their cnidae as a means of defence, anthozoans do not figure prominently on the menu of many predatory animals. The nudibranch molluscs—sea slugs and their relatives—are one of the few animal groups to have overcome this problem successfully and, in British waters at least, are probably the only anthozoan predators of any significance.

Aeolidia papillosa and several species of *Aeolidiella* are large sea slugs that are known to feed on a variety of anemones, including *Actinia, Anemonia, Sagartia, Cereus, Sagartiogeton* and *Metridium*. Other nudibranch species are more selective, many of them feeding exclusively on one anthozoan species: *Tritonia hombergi* and *T. plebia* graze on *Alcyonium digitatum, T. odhneri* on *Eunicella verrucosa*, and the rare *Arminia loveni* preys on the sea-pen *Virgularia mirabilis*. For descriptions of these molluscs see *Synopsis No. 8, British Opisthobranch Molluscs* by Thompson and Brown (1976).

Some prosobranch molluscs also eat anthozoans and possibly predation by these is more common than generally realised. *Simnia patula* feeds largely on *Alcyonium digitatum* but has also been found on *A. glomeratum* and *Eunicella* (Hiscock, 1974). Mr B. Picton (personal communication) has observed a large unidentified species of *Clathrus* (wentletrap) feeding suctorially on *Anemonia sulcata* in western Ireland. Another correspondent, Mr F. R. Moore, reported the alga-browsing top shell *Calliostoma zizyphinum* eating *Anemonia* in aquaria; this was presumably an exceptional instance, possibly caused by a lack of its normal food.

The sea spider *Pycnogonum littorale* is sometimes found clinging tenaciously to the columns or discs of various anemones: it has been recorded on *Actinia, Urticina, Sagartiogeton* and *Peachia*, and also on *Alcyonium digitatum. Pycnogonum* feeds suctorially, sucking up the juices through its proboscis; it appears to cause little damage to its host and is probably better regarded as an ectoparasite than a predator. Another pycnogonid, *Nymphon gracile*, has been observed, possibly feeding, on *Actinia equina*.

A number of highly specialized, endoparasitic copepods are known to occur in various anthozoans. Several species belonging to the families Asterocheridae, Lichomolgidae, Lamippidae and Xarifiidae have been found in European octocorals (*Sarcodictyon, Alcyonium, Parerythropodium, Eunicella* and *Pennatula*) and anemones (*Actinia, Anemonia, Bolocera* and *Corynactis*); Bouligand (1966) reviewed this subject in detail and provided excellent illustrations. Few records exist of copepod parasites in anthozoans in Britain but Haddon and Shackleton (1891) found an unidentified copepod in *Epizoanthus macintoshi*.

Anemones and other anthozoans are often found amongst the stomach contents of fishes but whether they constitute a regular item of diet is uncertain. According to McIntosh (in Stephenson, 1928) anemones are a favourite food of certain gadids and the same observer frequently found flounders whose stomachs were distended with edwardsias. Most specimens of the sea-pen *Virgularia* lack the uppermost portion of the colony and this has frequently been ascribed to nibbling by fishes.

A barnacle, *Boscia (Pyrgoma) anglica*, is a common epizooic of *Caryophyllia smithii* and other corals, usually being attached to the corallum near its upper margin. The exact nature of this relationship is unknown; the barnacle may cause irregular septal growth of the coral which otherwise appears to suffer little inconvenience.

The activities of man are injurious to many species, particularly permanently attached, erect forms such as octocorals. Constant scouring of the sea bed by trawls, oyster dredges and other fishing gear must wreak havoc amongst aggregations of sea-fans, sea-pens, alcyonarians, and probably many anemones. On the shore amateur crab and lobster hunters scrape out all likely crevices and gullies where, in addition to their quarry, there are numerous anthozoans which have no defence against iron crab-hooks. Neither is the tourist trade blameless and many fine colonies of *Eunicella*, which may have taken many years to grow, are dried out and sold as souvenirs. The Anthozoa as a whole, though, probably suffer less from this trade than some other marine animals, such as echinoderms and molluscs.

Practical Methods

Collecting anthozoans is rarely the simple task it may appear to be. A few anemone species adhere to the open rock and may carefully be peeled away using a blunt knife or some suitable natural object such as a mussel shell, but the majority are less easily accessible. Most species live with their bases inserted into a hole or crevice into which they can withdraw when disturbed. In such situations careful work with a hammer and *sharp* cold chisel may be necessary. A heavy hammer (a 2½ lb block hammer is ideal) will prove more controllable in most circumstances as wild swipes with a lighter weapon are likely to cause damage to specimen and collector alike. Anemones in deep holes may prove difficult to extract without damage and it is usually best to search for another, similar specimen that can more readily be obtained. If a specimen is damaged during collection it is best left where it is; providing it is still at least partly attached its chances of survival are good. A damaged specimen will be of little value as it is unlikely to expand in captivity and may thus be unidentifiable.

Permanently attached forms, such as octocorals, zoanthids, and scleractinian corals must be removed together with the portion of substrate to which they are attached, for this the hammer and chisel are essential.

In sandy or muddy areas anemones are often found attached to stones or shells buried in the substrate. Once these are found collection poses few problems and a small trowel is all that is needed. True burrowing anemones are usually discovered by accident while digging for other animals but if you are fortunate enough to find one with its disc expanded at the surface do not be misled by its apparently small size. Most burrowers, including the relatively small edwardsiids, become greatly attenuated when buried and the aboral end of the column may be as much as 30 cm below the surface of the substrate. Failure to dig deeply enough inevitably results in damage. The best plan is to dig a hole alongside the specimen allowing the substrate to fall away until it is exposed. The same method should be used for cerianthids but in this case the final digging should be carried out with the fingers, feeling along the tube until the animal itself is felt, then pinching off the tube below it, finally removing animal and tube together.

Specimens are best transported in plastic buckets with lids; before leaving the shore refill each container with fresh, *cool* sea-water (water in pools may be warmed by the sun). Polythene bags do not provide much protection for soft-bodied animals and are likely to be punctured by pieces of substrate but they may be used inside buckets to keep loose specimens separate. Rocks etc. with specimens attached may be buried in a layer of gravel in the bucket to prevent them rolling around and damaging the specimens. Loose anemones of different species must be kept separate as they may eat each other; most actiniids will eat other anemones, even specimens of similar size.

Before collecting consider: is a specimen really required? Can an identification be carried out on the spot? Many species are readily identified in the field and unless specimens are needed for a definite purpose they are best left in peace. *Collecting an animal just because it is there is unforgivable.*

Field photography is a good alternative to specimen collecting and in calm weather is not difficult. A single-lens reflex camera, equipped with extension

tubes and a small flash gun, is suitable equipment. Anemones in pools are often well expanded and provided the flash gun is carefully positioned to avoid reflection an excellent, permanent record of the species in its natural surroundings may be obtained.

Laboratory identification requires little special equipment, most anthozoans being a convenient size to handle. Many of the external features used in the keys can be determined with the naked eye but for some characters a good magnifying glass, or better still, a low-power stereo dissecting microscope, will be required. Freshly collected specimens should be allowed to settle in containers of fresh sea-water, preferably in a cool dark place. Glass desiccating dishes or transparent plastic "lunch packs" are suitable containers. Most anemones will expand fairly readily if left for a few hours. Many of the internal features in an expanded specimen can be seen by transmitted light through the translucent body walls and careful use of the available illumination is important. Burrowing anemones will rarely expand fully unless buried but if left undisturbed the tentacles will usually appear, when they can be counted, although they rarely attain their full length in these conditions. Octocorals and scleractinians do not need to be expanded for identification and in the latter group the important structure of the corallum can only be observed in living specimens if the polyp is tightly contracted.

Calcareous skeletal elements—sclerites and coralla—can be isolated and cleaned of flesh by macerating in a solution of caustic soda, sodium hypochlorite, or domestic bleach. A representative selection of octocoral sclerites for any given species is obtained by macerating a whole polyp together with a portion of the coenenchyme. Cleaned sclerites can be stored as a dry powder or, more conveniently, rinsed in fresh water, dehydrated in absolute alcohol (or dried in air) and mounted on a microscope slide in Canada Balsam.

Study of nematocysts: Simple, temporary preparations are easily made from fresh, unfixed material. A tiny piece of tissue—1 mm square is sufficient—should be dissected from the specimen, taking care to avoid contamination from other tissues. Acontia can usually be obtained by prodding the anemone until they are emitted, short lengths being pinched off with fine forceps. The sample is placed on a glass slide in a drop of sea water and mashed using fine mounted needles. The preparation is then gently compressed under a cover-slip, using a piece of blotting paper as a buffer and to soak up surplus liquid. The nematocysts can now be examined immediately under the microscope, using an oil immersion objective if necessary; phase-contrast illumination is helpful but not essential.

Preserved material may require a short period of maceration in 10% KOH solution before a satisfactory "squash" can be achieved. Measurements should be made using a graduated eyepiece calibrated with a stage micrometer. By scanning the preparation before measurements are taken, a subjective estimate of the size ranges present can be obtained. Measurement of about 20 capsules (undischarged) is usually sufficient to provide an absolute size range. In some cases it is only necessary to determine which categories are present. No satisfactory method of permanently mounting nematocysts for study under the light microscope is known, photomicrography of temporary preparations being the only means of obtaining a permanent record.

Preservation: Anthozoans are not easy to fix in an expanded condition due to their highly contractile nature. However, with a little practice satisfactory results may be obtained using an aqueous 7·5% solution of $MgCl_2$ in fresh water to relax the musculature.

Allow the specimen to expand in a small quantity of sea water, attached to its substrate where appropriate, then gently add an equal quantity of the $MgCl_2$ solution of similar temperature or lower. Uncooperative specimens may often be induced to expand by feeding them, by placing them in darkness, or in shore animals by flooding them with cool, well-aerated fresh sea-water. Leave the specimen undisturbed, ideally in a cool dark place for 4–6 hours then test its reactions by gentle prodding. If slight contraction or any other voluntary movement occurs wait until even a relatively violent stimulus fails to produce any response, before proceeding with fixation. An advantage of this method is that if a specimen contracts before it is thoroughly relaxed it will recover if returned to fresh sea-water.

Formalin is an excellent general fixative; add a sufficient quantity of commercial formaldehyde solution to the fluid containing the specimen to make a 7–10% solution. This should be thoroughly mixed by pipetting. If possible inject some of the resulting solution into the coelenteron of the specimen by pipetting through the mouth, taking care not to introduce air bubbles which may cause difficulties later on. With a little care the specimen may also be slightly inflated by this means. After fixation—allow 24 hours—the specimen can be removed to 5% formalin in sea water for storage. Formalin is preferable to other commonly used fixatives, such as alcohol, as these may harden the tissues unduly and also may cause a massive discharge of nematocysts. Discharged nematocysts in preserved specimens cannot usually be identified accurately and thus a valuable aid to identification may be lost.

For subsequent histological study Bouin's picro-formalin is a good fixative. Relaxed specimens should be transferred carefully to the fixative and some should also be injected into the coelenteron. If specimens are too small for injection to be practical they can be cut in two transversely. After fixation specimens should be stored in 70% alcohol. As Bouin's fluid causes nematocyst discharge do not use it to the exclusion of formalin. A few well-relaxed specimens fixed in each will make an adequate series for later study. Also, being an acid solution, Bouin's fluid will dissolve away any calcareous structures present, such as sclerites or coral skeletons, and this effect should be taken into consideration.

Anthozoans are excellent subjects for microtome sectioning and for this the standard paraffin wax embedding technique works well. A good general stain is Masson's trichrome (Sumner and Sumner, 1969) which dyes the mesogloea deep green in contrast to the cellular regions. Preparation of sections is an essential requirement in identifying preserved specimens of most groups as it offers the only method of determining the structure and position of the musculature.

The coloration of preserved specimens disappears soon after fixation so it is always useful, if possible, to photograph the specimen before it is preserved. Good colour photographs improve the value of a collection of preserved specimens and will, of course, aid subsequent recognition of the species. Anthozoans are attractive and colourful animals and time and effort used in producing good photographs will never be wasted.

Classification of the Anthozoa

The higher classification of the Cnidaria was recently revised by Petersen (1979): he raised the Anthozoa from its previous status as a class to a subphylum and proposed a new subphylum, Medusozoa, to include the remaining cnidarian classes—Hydrozoa, Scyphozoa, Cubozoa and the extinct Conulata. Medusozoa are cnidarians in which, with a few exceptions, the sexually reproducing "adult" stage is a free-swimming **medusa** (jelly-fish) and the polyp generally an asexually reproducing, sessile phase. No medusoid stage ever occurs in the Anthozoa, which are exclusively polypoid in form. Anthozoan polyps are distinguished from those of the Medusozoa by the possession of such characters as mesenteries and actinopharynx, and differences in the cnidom.

Subphylum ANTHOZOA Ehrenberg, 1834

Cnidaria of exclusively polypoid form, no medusoid stage ever occurring. The body of an individual polyp consists of a hollow column whose cavity or coelenteron is divided into chambers by radially arranged mesenteries. A transverse oral disc terminates the distal end of the column and from the mouth at its centre a tubular, throat-like actinopharynx leads into the coelenteron. A number of hollow tentacles arise from the oral disc, their cavities being continuous with the coelenteron. The basal part of the polyp varies in structure according to its function. Colonial and solitary forms occur, with or without various hard skeletal elements. The cnidom includes spirocysts, atrichs, holotrichs, *b*- and *p*-mastigophores, in various combinations in different taxa.

The Anthozoa is divided into two classes:

OCTOCORALLIA   Colonial; polyps usually small, each with eight pinnate tentacles and eight perfect mesenteries. Sclerites usually present and a rod-like, internal axial skeleton may also occur. Cnidom consists of small nematocysts resembling *b*-mastigophores, all other categories being absent (p. 31).

HEXACORALLIA   Colonial or solitary; polyps small to large, never with just eight pinnate tentacles and eight perfect mesenteries—tentacles and mesenteries usually numerous. Sclerites never present but other skeletal structures may occur. Cnidom includes spirocysts, which are characteristic of the class, and all categories of anthozoan nematocysts (p. 60).

Phylum CNIDARIA
Subphylum ANTHOZOA
Class OCTOCORALLIA
  Order STOLONIFERA
     Family Cornulariidae
         Cornularia cornucopiae (Pallas)
     Family Clavulariidae
         Sarcodictyon roseum (Philippi)
  Order ALCYONACEA
     Family Alcyoniidae
         Alcyonium digitatum Linnaeus
         Alcyonium glomeratum (Hassall)
         Parerythropodium coralloides (Pallas)
  Order GORGONACEA
     Family Paramuriceidae
         Swiftia pallida Madsen
     Family Plexauridae
         Eunicella verrucosa (Pallas)
  Order PENNATULACEA
     Family Funiculinidae
         Funiculina quadrangularis (Pallas)
     Family Virgulariidae
         Virgularia mirabilis (Muller)
         Balticina christii (Koren & Danielssen)
     Family Pennatulidae
         Pennatula phosphorea Linnaeus
Class HEXACORALLIA
  Order CERIANTHARIA
    Suborder Spirularia
     Family Cerianthidae
         Cerianthus lloydii Gosse
         Pachycerianthus multiplicatus Carlgren
    Suborder Penicillaria
     Family Arachnactidae
         Arachnactis albida Sars
  Order ZOANTHARIA
     Family Epizoanthidae
         Epizoanthus incrustatus (Duben & Koren)
         Epizoanthus couchii (Johnston)
         Epizoanthus macintoshi Haddon & Shackleton
         Epizoanthus paguriphilus Verrill
     Family Parazoanthidae
         Parazoanthus axinellae (Schmidt)
         Parazoanthus anguicomus (Norman)
         Isozoanthus sulcatus (Gosse)
    incertae sedis:
         Zoanthus alderi Gosse

Order ACTINIARIA
  Suborder Protantheae
    Family Gonactiniidae
        Gonactinia prolifera (Sars)
        Protanthea simplex Carlgren
  Suborder Nynantheae
    Tribe Thenaria
      Subtribe Endomyaria
    Family Actiniidae
        Actinia equina (Linnaeus)
        Actinia fragacea Tugwell
        Anemonia viridis (Forskal)
        Bolocera tuediae (Johnston)
        Urticina felina (Linnaeus)
        Urticina eques (Gosse)
        Bunodactis verrucosa (Pennant)
        Anthopleura ballii (Cocks)
        Anthopleura thallia (Gosse)
    Family Aurelianiidae
        Aureliania heterocera (Thompson)
      Subtribe Mesomyaria
    Family Actinostolidae
        Stomphia coccinea (Muller)
      Subtribe Acontiaria
    Family Aiptasiidae
        Aiptasia mutabilis (Gravenhorst)
        Aiptasiogeton pellucidus (Hollard)
    Family Diadumenidae
        Diadumene cincta Stephenson
        Haliplanella lineata (Verrill)
    Family Metridiidae
        Metridium senile (Linnaeus)
    Family Sagartiidae
        Sagartia elegans (Dalyell)
        Sagartia troglodytes (Price)
        Cereus pedunculatus (Pennant)
        Actinothoe sphyrodeta (Gosse)
        Sagartiogeton laceratus (Dalyell)
        Sagartiogeton undatus (Muller)
        Phellia gausapata Gosse

Family Hormathiidae
    Hormathia digitata (Muller)
    Hormathia coronata (Gosse)
    Cataphellia brodricii (Gosse)
    Paraphellia expansa (Haddon)
    Actinauge richardi (Marion)
    Calliactis parasitica (Couch)
    Adamsia carciniopados (Otto)
    Amphianthus dohrnii (Von Koch)
  Tribe Athenaria
Family Halcampoididae
    Halcampoides purpurea (Studer)
Family Haloclavidae
    Anemonactis mazeli (Jourdan)
    Peachia cylindrica (Reid)
    Mesacmaea mitchellii (Gosse)
Family Halcampidae
    Halcampa chrysanthellum (Peach)
Family Edwardsiidae
    Nematostella vectensis Stephenson
    Edwardsiella carnea (Gosse)
    Edwardsia claparedii (Panceri)
    Edwardsia ivelli Manuel
    Edwardsia delapiae Carlgren & Stephenson
    Edwardsia timida Quatrefages
    Scolanthus callimorphus Gosse
Order CORALLIMORPHARIA
  Family Corallimorphidae
    Corynactis viridis Allman
Order SCLERACTINIA
  Family Caryophylliidae
    Subfamily Caryophylliinae
      Caryophyllia smithii Stokes & Broderip
    Subfamily Turbinoliinae
      Sphenotrochus andrewianus Milne-Edwards & Haime
    Subfamily Desmophylliinae
      Hoplangia durotrix Gosse
      Lophelia pertusa (Linnaeus)
  Family Dendrophylliidae
    Balanophyllia regia Gosse
    Leptopsammia pruvoti Lacaze-Duthiers

Use of the Keys to the British Anthozoa

Due to the wide range of structural variability in the Anthozoa, with each group having its own peculiar terminology, it is not practical to construct a single large key to all forms. Within each class, keys to the orders are provided, whole orders, or groups of manageable size within these orders, being keyed direct to species. These keys, as has already been emphasized, are intended mainly for use with living specimens as many of the external characters used are not always evident in preserved material.

It is not, of course, necessary to possess a comprehensive knowledge of internal anatomy in order to use the keys, but it is important that most of the external features and their attendant terminology be understood. These features are described either in the introduction to general structure or, if of a more specialized nature, in the introductory passage to each group. A good general grasp of the nature of the animals and how they function will also aid the use of the keys.

Keys to genera are not given as these are mostly defined by internal characters and many contain only one British species, but brief definitions of genera and higher taxa are provided and these will serve to identify preserved specimens to genus level. Identification of preserved specimens at the species level may cause problems, particularly in the Actiniaria, and measurement of the nematocysts in certain tissues may be the only means of distinguishing them. In such cases size ranges of these nematocysts are given; these ranges are not, of course, absolute, but used with discretion should give a reliable identification.

Order ZOANTHARIA Gray, 1870

Colonial (rarely solitary) Hexacorallia; colonies consist of numerous polyps arising from an encrusting coenenchymatous mass, polyps and coenenchyme usually encrusted with sand or other particulate matter. Tentacles arranged in two equal cycles, only one arising from each radius of the disc. Mesenteries arranged in couples and pairs; those subsequent to the first six couples arising serially in the ventro-lateral exocoels (Fig. 23A). Filaments with ciliated tracts present on all perfect mesenteries. Siphonoglyph single, ventral, and clearly differentiated. The cnidom consists of spirocysts, holotrichs, p- and b-mastigophores.

All the British species of this order are colonial. The form of the basal coenenchyme varies from a thin, creeping stolon to a thick, encrusting fleshy mass; occasionally it is reduced or absent. Some species live commensally on hermit crabs, forming a **carcinoecium** on the gastropod shell inhabited by the crab. In mature carcinoecia the mollusc shell is often completely dissolved away and replaced by the zoanthid colony.

Individual zoanthid polyps are remarkably uniform in their structure. The disc is a little wider than the column, concave, with the mouth on a rounded hypostome. A wide tentacle-free area surrounds the mouth, the tentacles being arranged in two distinct neat cycles at the edge of the disc. The column consists of a long cylindrical **scapus** terminating above in a definite rim or **parapet** which encloses a shallow groove, the **fosse**. The upper part of the scapus bears a number of longitudinal **scapular ridges**, each of which terminates on the parapet as a **marginal tooth**. In all British species except *Isozoanthus sulcatus* scapular ridges occur only on the endocoels, thus the marginal teeth correspond to the tentacles of the inner cycle.

The mesogloea of the scapus is often thick and usually contains isolated cells, or groups of cells, known as **cell-islets**. In some genera a system of canals, communicating with the ectoderm, forms a network within the mesogloea. This canal system may form a distinct **ring-sinus** in the upper part of the scapus, running just below the endodermal surface of the mesogloea, or parts of it may be separated as isolated **lacunae** (Fig. 23C). A sphincter muscle is always present in the parapet region; this may be mesogloeal (Fig. 23B) or endodermal (Fig. 23C). Sections cut through an endodermal sphincter can be confusing: where the muscle passes through a mesentery it may give a false impression of being mesogloeal. Usually the ectoderm of the scapus and coenenchyme is encrusted with sand grains, sponge spicules, foraminiferan shells, etc., many of which may become deeply embedded in the mesogloea. A layer of periderm may also occur amongst this incrustation.

The mesenteries are arranged as shown in Fig. 23A. Two pairs of directives are present, the ventrals being perfect and the dorsals imperfect. The lateral mesenteries form pairs, each pair (apart from those including the macrocnemic mesenteries) consisting of a perfect and an imperfect mesentery, each with a weak retractor muscle on the endocoelic face. New mesenteries arise as couples, eventually forming pairs, in the ventro-lateral exocoels. The mesenteries of the fifth couple (Fig. 23A) may be perfect—the **macrocnemic** condition found in all

Macrocnemic mesentery

Ventro-lateral exocoel

A

Mesogloeal
sphincter

B

Endodermal
sphincter

Ectodermal
canal
(ring sinus)

C
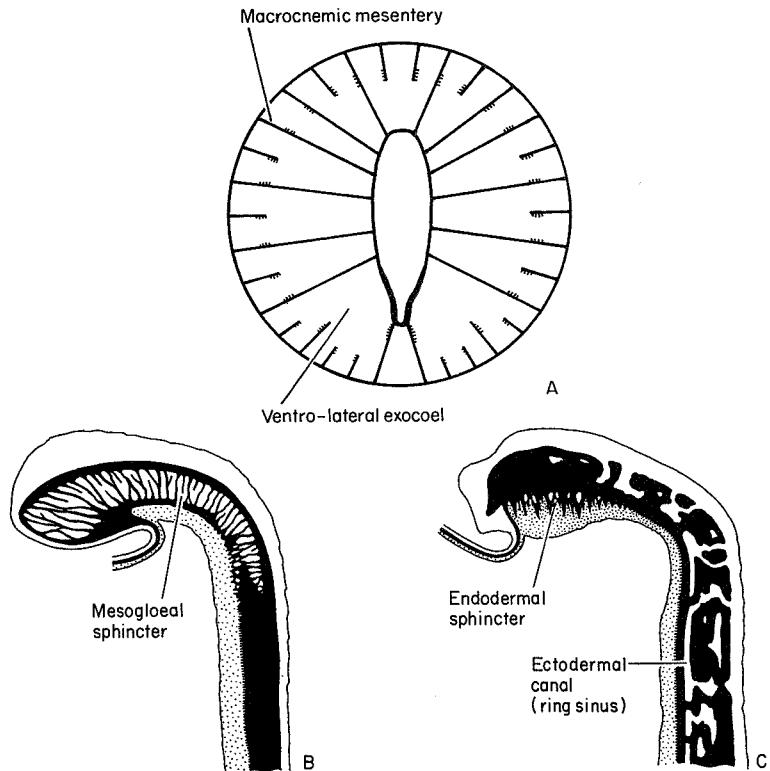
FIG. 23. Anatomy of the Zoantharia. A, Diagram of the mesentery plan of a macrocnemic zoanthid. B, *Epizoanthus couchii*, longitudinal section through the column wall in the parapet region, showing the form of the mesogloeal sphincter muscle. C, *Parazoanthus anguicomus*, similar section to B showing the endodermal sphincter and the mesogloeal canal system.

British species, or imperfect (**brachycnemic**). Although the retractor muscles are weak the tentacles are always fully retractile.

The British species of Zoantharia are little known, largely because they are inconspicuous animals of mostly sublittoral occurrence and cryptic habits. The only systematic work on the British species is the monograph by Haddon and Shackleton (1891). Some of the systematic characters used by these authors, such as the height:diameter ratio in preserved specimens, are no longer considered to be of value.

Despite most generic and specific characters being internal, the British zoanthids are not too difficult to distinguish in life, although identification is not eased by their nervous disposition—they will retract at the slightest disturbance.

Key to the British species of Zoantharia in life

Epizoanthus macintoshi is omitted as its appearance in life is unknown.

1. Polyps very small, up to 2 mm diameter; not more than 22 tentacles **7**

   Mature polyps larger than 2 mm diameter; usually more than 22 tentacles ..**2**

2. Colonies associated with hermit crabs, forming carcinoecia **3**

   Colonies encrusting substrata other than hermit crabs, or free **4**

3. Polyps very large, up to 30 mm tall and 15 mm diameter
   Epizoanthus paguriphilus (p. 77)

   Polyps not very large, not exceeding 15 mm tall and 6 mm diameter
   Epizoanthus incrustatus (p. 73)

4. Colony free, basal coenenchyme reduced or lacking
   Epizoanthus incrustatus (free form) (p. 74)

   Colony attached and encrusting, basal coenenchyme present **5**

5. Tentacles long in expansion, transparent, tipped with tiny but conspicuous white knobs ....*Epizoanthus couchii* (p. 75)

   Tentacles moderate to long in expansion, not transparent, terminal knob absent or inconspicuous **6**

6. Mean number of tentacles 30–32 (range 26–34), polyps yellow or orange, rarely whitish ....*Parazoanthus axinellae* (p. 78)

   Mean number of tentacles 40–42 (range 34–44), polyps whitish
   Parazoanthus anguicomus (p. 80)

7. Polyps brown .... *Isozoanthus sulcatus* (p. 82)

   Polyps white .... *Zoanthus alderi* (p. 83)

Family EPIZOANTHIDAE*

Macrocnemic Zoantharia possessing a mesogloeal sphincter muscle (Fig. 23C). Colonies may be encrusting, free, or forming carcinoecia.

Genus EPIZOANTHUS Gray, 1867

Epizoanthidae lacking a canal system and lacunae in the mesogloea of the column, cell-islets present.

Type-species: *E. incrustatus.*

Epizoanthus incrustatus (Duben and Koren)

10mm
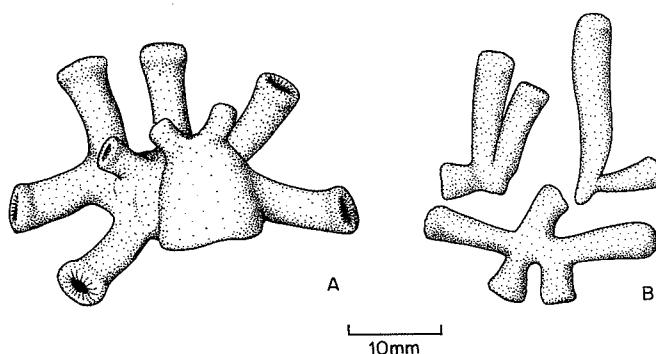
FIG. 24. *Epizoanthus incrustatus.* A, Preserved carcinoecium. B, Preserved examples of the free form.

Mammillifera incrustata Duben and Koren, 1847 p. 268

Zoanthus couchii: Gosse, 1860 p. 297 (part)

?Zoanthus rubricornis Holdsworth, 1861 p. 99; Haddon and Shackleton, 1891 p. 652

Epizoanthus americanus Verrill, 1864 p. 34

Epizoanthus incrustatus: Haddon and Shackleton, 1891 p. 636

This species occurs in two forms; as a carcinoecium or as a free colony.

Carcinoecium: Usually formed on gastropod shells (*Natica* spp. and others) inhabited by the hermit crab *Anapagurus laevis* (Bell), although other species may be involved, particularly outside Britain. The mollusc shell becomes entirely replaced by the basal coenenchyme of the colony, which is up to 40 mm long including polyps. Up to 20 polyps occur in a single colony and these are variably arranged, with the anterior one usually the largest. In preserved specimens the polyps are up to 15 mm tall and 6 mm diameter, with 15–24

*Despite an extensive search through the literature I have been unable to find the original authority for this family or the Parazoanthidae.

marginal teeth. The encrustation of sand grains is usually very dense.

Free form: Distinct basal coenenchyme is absent; polyps radiate from a common central point or bud from the walls of others. In preserved specimens the polyps measure up to 25 mm tall and 6 mm diameter.

Habitat: Both forms are found mainly on sand or gravel bottoms in depths of 20–200 m.

Distribution: Formerly frequent in many localities around British coasts but there are no recent records; further information is very desirable. Elsewhere it is known throughout the North Atlantic, including the east coast of North America, as far north as the Arctic Circle.

Remarks: The above description is based on preserved material as the appearance of this species in life is unknown. The polyps probably resemble those of *E. couchii.*

Zoanthus rubricornis was described from a single, unattached colony from Plymouth sound. The polyps were up to 25 mm tall with red tentacles. Nothing in its description suggests that *Z. rubricornis* is distinct from the present species and as similar colonies (of unknown colour in life), undoubtedly belonging to *E. incrustatus* have been taken in the same locality, *Z. rubricornis* is included as a probable synonym of *E. incrustatus.*
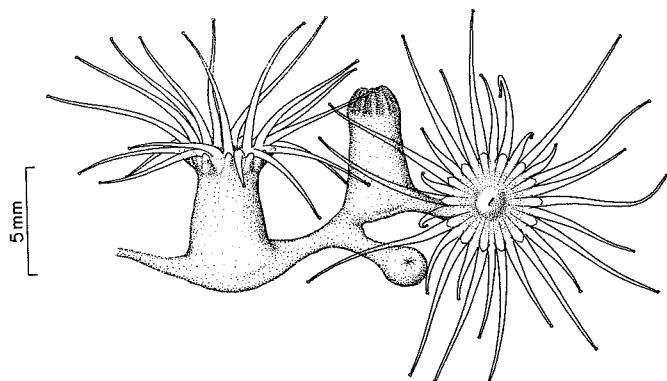
FIG. 25. *Epizoanthus couchii.* Part of a living colony with two expanded polyps.

Zoanthus couchii Johnston, in Couch, 1844 p. 73; Gosse, 1860 p. 297 (part)
Epizoanthus couchii: Haddon and Shackleton, 1891 p. 644
Epizoanthus wrightii Haddon and Shackleton, 1891 p. 651

Basal coenenchyme forming a thin stolon-like band with the polyps arising at irregular intervals, occasionally with small lateral expansions giving rise to a cluster of polyps. The polyps are very variable in size, up to 12 mm tall and 4 mm diameter. There are 12–16 well-defined marginal teeth, the body wall between them being very thin, almost membranous in texture. Tentacles: 24–32, typically 28; they are very long in expansion and taper evenly to their tips, each of which bears a tiny but distinct terminal knob. A thin encrustation of fine sand grains, often incorporated into a brownish periderm, covers the stolon and lower parts of the column, extending upward along the marginal teeth. Coenenchyme and column whitish, buff or pink, becoming translucent in extension. Disc and tentacles colourless and transparent, sometimes freckled with white, with the tips of the marginal teeth, lips of the actinopharynx and tentacle knobs opaque white, often very conspicuous in full expansion (Plate 1C).

Habitat: Colonies encrusting on rocks, stones, and shells, from around LWST to at least 100 m depth. The low, inconspicuous stolon is often overgrown by other encrusting organisms so that the colony may easily be overlooked unless the polyps are expanded.

Distribution: Common in many localities on the western and southern coasts of the British Isles, and in north France; not recorded from the North Sea. Its further distribution is unknown.

Remarks: Epizoanthus wrightii was described by Haddon and Shackleton (1891) as possessing the following characters: Coenenchyme broad, flat, irregular; polyps with 16 marginal teeth and 32 tentacles; colouration whitish or orange-pink, disc speckled with white, tentacles with white tips. Locality: Dublin Bay, on rocks between tide-marks. An examination of the type-specimens of *E. wrightii*, including measurements of the few nematocysts that could be found, strongly suggests that this species is not distinct from *E. couchii*. As its appearance in life is also identical *E. wrightii* is included as a synonym of *E. couchii*.

Epizoanthus macintoshi Haddon and Shackleton

(not illustrated)

Epizoanthus macintoshi Haddon and Shackleton, 1891 p. 649

Little is known of this species, of which only the original, type-specimen exists. This consists of a preserved colony of three tightly contracted polyps, densely incrusted with foraminiferan shells, arising from a narrow band of coenenchyme. The largest polyp has 18 scapular ridges and measures 7 mm tall and 6 mm diameter; presumably in expansion this size would be considerably exceeded but no record of the appearance in life exists. Further examination of the specimen, which was dredged from an unknown depth off Shetland, has confirmed that *E. macintoshi* is distinct from other British species of *Epizoanthus* but its relationship to species from outside British waters is unknown.

Epizoanthus paguriphilus Verrill
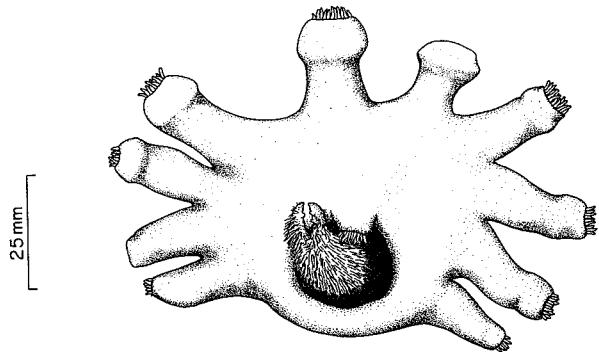
FIG. 26. *Epizoanthus paguriphilus*. A preserved carcinoecium, complete with crab.

Epizoanthus paguriphilus Verrill, 1882 pp. 137, 316; Haddon and Shackleton, 1891 p. 641

This species forms large carcinoecia inhabited by the hermit crab *Parapagurus pilosimanus* Smith. As in *E. incrustatus* the original gastropod shell, usually a large whelk, *Buccinum*, etc., is replaced by coenenchyme, which in *E. paguriphilus* is very thick and cartilaginous in texture with a sparse incrustation of sand and foraminiferan shells. The polyps are large, up to 30 mm tall and 15 mm diameter in preserved specimens, with indistinct scapular ridges and up to 70 long tentacles. Each colony consists of up to twelve polyps arranged in a single longitudinal row with a further, relatively short polyp adjacent to the aperture of the carcinoecium, the whole carcinoecium being up to 100 mm long. In life the tentacles are orange, the coenenchyme and polyp walls greyish.

Habitat and distribution: A deep-water species usually found in depths greater than 500 m. It occurs throughout the North Atlantic from western Europe to eastern North America and has often been recorded off South-west Ireland in depths of 600–800 m.

Family PARAZOANTHIDAE (see footnote to Epizoanthidae)

Macrocnemic Zoantharia possessing an endodermal sphincter muscle. One genus, the non-British *Gerardia*, secretes a horny axial skeleton.

Genus PARAZOANTHUS Haddon and Shackleton, 1891

Parazoanthidae with a well-developed canal system in the body-wall mesogloea forming a distinct ring-sinus (Fig. 23C); lacunae and cell-islets may also be present. Horny axial skeleton absent.
Type-species: *P. axinellae.*

Parazoanthus axinellae (Schmidt)

(Fig. 27A, B)

Palythoa axinellae Schmidt, 1862 p. 61
Parazoanthus axinellae: Haddon and Shackleton, 1891 p. 654
Parazoanthus dixoni: Hiscock, 1974 p. 28; Campbell, 1976 p. 86 (not *P. dixoni* Haddon and Shackleton, 1891 p. 658)

Colonies encrusting, the growth form varying considerably according to the substratum. The basal coenenchyme may form broad, irregular expansions or narrow stolons which branch and anastomose. Occasionally thick spongy masses are formed where luxuriant growth occurs on a limited substratum. The polyps are usually set close together, so that the expanded tentacles overlap, but may be more spaced out on stolons. Coenenchyme and column encrusted with sand grains and sponge spicules. Polyps up to 15 mm tall and 5 mm diameter, with moderate to long tentacles which taper to fine points. There are 26–34 tentacles, typically 30 or 32. Colour of coenenchyme and column walls yellow, rarely whitish, disc and tentacles bright yellow shading to orange around the mouth. A plain white form is also known.

Habitat: Mainly on organic substrata—sponges, shells, worm tubes, dead gorgonians, etc.—but also on rocks, in depths of 6–100 m.

Distribution: Extreme south-west coasts of the British Isles, around south-west Europe to the Mediterranean, where it is common and well known.

Remarks: This species has previously been confused with *P. dixoni* (see *P. anguicomus*) and several recent records of *P. dixoni* (Hiscock, 1974; Campbell, 1976; and probably others) are misidentifications of *P. axinellae.*

P. axinellae can only be positively distinguished from *P. anguicomus* by the number of tentacles present and the sizes of the holotrich nematocysts found in the ectoderm of the column, including the canals (Fig. 27B). In the present species these measure $23–33 \times 12–15 \ \mu m$ and occur in only one size range.
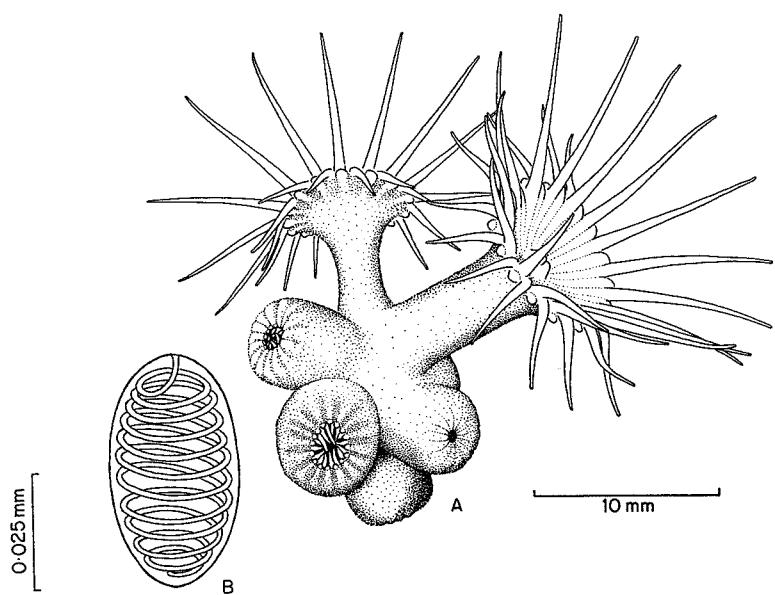
FIG. 27. *Parazoanthus axinellae*. A, A small colony with two expanded polyps. B, Holotrich nematocyst from the ectoderm of the column.

Parazoanthus anguicomus (Norman)

(Figs 23C, 28)

Zoanthus anguicoma Norman, 1868 p. 319

Parazoanthus anguicomus: Haddon and Shackleton, 1891 p. 656

Parazoanthus dixoni Haddon and Shackleton, 1891 p. 658

?Parazoanthus haddoni Carlgren, 1913, p. 55

Form of colonies and their variations similar to *P. axinellae*; polyps generally larger, up to 25 mm tall and 8 mm diameter. Tentacles proportionately shorter than in *P. axinellae*, 34–44, typically 40–42. The encrustation of sand grains, sponge spicules, and foraminiferan shells is variable in extent; where encrustation is sparse the texture of the column is grainy, resembling the skin of an orange. Colouration of whole colony whitish, sometimes tinted with buff or pink, the latter due to ripe gonads. Preserved specimens often become yellowish or reddish brown. The holotrich nematocysts of the ectoderm occur in two size ranges: $40–53 \times 19–25 \ \mu m$ and $23–35 \times 13–19 \ \mu m$.

Habitat: This species has been recorded encrusting sponges, worm tubes, corals (*Lophelia*) and stones. Generally occurring in deep water down to at least 400 m but also found in shallow coastal waters, *c.* 20 m.

Distribution: Occurs in many parts of the north-east Atlantic, probably widespread in deep water off the continental shelf; recorded in British waters from western Ireland, western and northern Scotland.

Remarks: P. dixoni Haddon and Shackleton, 1891 is regarded as a junior subjective synonym of *P. anguicomus* (Norman, 1868) as the original description of *P. dixoni* agrees well with recently examined specimens of *P. anguicomus*. Unfortunately an examination of the type-specimens of *P. dixoni* failed to provide confirmatory evidence as at some time the specimens had become dried out and no nematocysts could be found. Observation of a large number of living specimens of *P. anguicomus* from Rockall suggests that *P. haddoni* Carlgren, 1913 was merely a growth form of this species, therefore *P. haddoni* is included as a possible synonym of *P. anguicomus*.
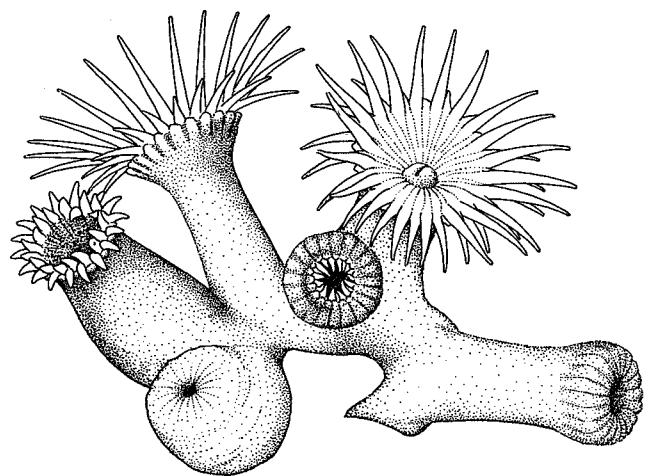
FIG. 28. *Parazoanthus anguicomus*. A small colony with polyps in various states of expansion, none of them fully extended.

Genus ISOZOANTHUS Carlgren, 1905

Parazoanthidae with a poorly developed canal system which does not form a ring-sinus; lacunae and cell-islets may be present. Horny axial skeleton absent.
Type-species: *I. arborescens* (Danielssen, 1890).

Isozoanthus sulcatus (Gosse)
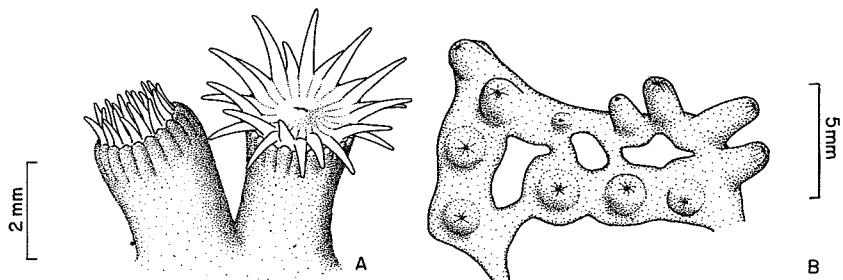
FIG. 29. *Isozoanthus sulcatus*. A, Two polyps in different states of expansion, the tentacles may become longer than this. B, Part of a contracted colony.

Zoanthus sulcatus Gosse, 1860 p. 303; Haddon and Shackleton, 1891 p. 660
Isozoanthus danicus Carlgren, 1913 p. 48
Parazoanthus sulcatus: Teissier, 1965 p. 46
Isozoanthus sulcatus: Manuel, 1979 p. 395

The coenenchyme forms an irregular basal band or network, with occasional broad expansions. Polyps small, up to 2 mm diameter and 4 mm tall; arising from the coenenchyme at irregular intervals or in small clusters. Each polyp has 19–22 tentacles, which are short or moderate in length, and an equal number of scapular ridges. The coenenchyme and walls of the polyps are encrusted with fine sand. Polyps vary in colour from dull olive to rich purplish brown, with whitish tips on the tentacles and marginal teeth and occasionally with white streaks on the disc.

This is the only European zoanthid known to possess zooxanthellae, which occur in profusion on all endodermal surfaces. Their presence may be confirmed by microscopic examination of a squash preparation; the zooxanthellae are visible as spherical brownish cells about 10 μm in diameter.

Habitat: In pools on the shore, encrusting the rock surface amongst calcareous algae or detritus, or on stones or shells in shallow coastal waters down to about 25 m. Due to its small size, cryptic habits, and readiness to contract at the slightest disturbance this species is easily overlooked and may be more common and widespread than present records indicate.

Distribution: Recorded in British waters from several localities in south Devon and south Wales; elsewhere from Denmark and the Channel and Atlantic coasts of north France.

Species *incertae sedis:*

Zoanthus alderi Gosse

(not illustrated)

Zoanthus alderi Gosse, 1860 p. 305; Haddon and Shackleton, 1891 p. 662

Coenenchyme forming a narrow basal stolon. Polyps small, up to 4 mm tall and 1 mm diameter, inversely conical, with no encrustation and about 20 scapular ridges; opaque white in colour.

The generic position of this species, known only from a single colony found growing beneath a stone on the shore at Cullercoats, Northumberland, is uncertain; it is unlikely to be a member of the genus *Zoanthus* Cuvier, as this is exclusively tropical. It is even uncertain whether *Z. alderi* was a zoanthid at all as the original description was very incomplete. Possibly it was a specimen of *Isozoanthus sulcatus* which, due to its situation beneath a stone out of the light, had lost its zooxanthellae and hence was colourless.