

Tropical Epizoic Echinoderms and their Distribution¹

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Although the newly metamorphosed young of many species of echinoderms are frequently epizoic transitorily on larger sessile or sedentary animals, it is only among the comatulid crinoids and the ophiuroids that a significant number of species, particularly suspension feeders, extend such associations throughout their lives. Where crinoids are concerned, the choice of perch for rheophilic (current-loving) species is limited by purely physical factors and it may be either animate or inanimate but for some ophiuroids an animate host is clearly preferred and the association is to some extent obligatory and can be termed commensal (or, in the case of *Ophiomaza*, even parasitic). It is noticeable that whereas the relict fauna of recent crinoids shows very limited adaptations to special circumstances, the apparently more plastic ophiuroids have evolved several unusual modifications correlated to some extent at least with the epizoic habit.

The cirri of comatulid crinoids, smooth, segmented, circular in cross-section and jointed to curl vertically downwards, are well adapted for clinging to projections of the substrate or to animate hosts and this form is paralleled to some extent by the euryalid ophiuroids, including the large arborescent basket-stars and their smaller, simple-armed relatives such as *Asteromorpha perplexum* (Koehler) (Fig. 1). These members of the suborder Euryalina are characterized primarily by the vertical articulations of their arm joints, allowing flexure downwards from the horizontal, by the very inconspicuous arm spines and by the absence of superficial segmental dorsal arm plates. *Asteromorpha*, like many of its relatives, is regularly associated with gorgonians, which form a steady support clear of the substrate, spanning any food-carrying current.

Superficially similar to *Asteromorpha* are species such as *Ophiothela tigris* Lyman (Fig. 2), also with vertically-coiling arms, diminutive arm spines and no obvious dorsal arm plates. However, *Ophiothela* is not a euryalid but belongs to the order Ophiurida (brittle-stars), characterised by having the arms normally more flexible in the horizontal plane, though its family allegiance is to the Ophiotrichidae in which the juvenile vertical flexure is retained to a greater extent than usual in the adult, even in *Ophiothrix*, the least modified in this way. *Ophiothela tigris* entwines itself in the interstices of branching corals but its congener, *Ophiothela danae* Verrill (Fig. 3) is again an associate of gorgonians.

A comparison of these two species reveals several other differences. Most

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noticeably *Ophiothela danae* has six arms rather than the usual ophiuroid five (a character shared also by *Asteromorpha perplexum*). This is correlated with the fact that it is fissiparous, commonly reproducing asexually by fission across the disc, each half regenerating the lost part of the disc and the remaining arms. For reasons about which we can at present only speculate (but most likely to do with the stability of the pentaradiate form), this phenomenon is almost invariably correlated with an arm number greater than five. The capacity for it is widespread among the asterozoan echinoderms, since it occurs in at least nine of the sixteen extant families of ophiuroids as well as in two of the thirty asteroid families (where the arm number in fissiparous individuals is commonly seven or eight rather than six). Where ophiuroids are concerned it appears to be regularly correlated with an epizoic or even commensal habit, though the reverse is not so. A second difference between *Ophiothela danae* and *O. tigris* is the much smaller size of the fissiparous species, disc diameter rarely exceeding 3 mm., whereas in *O. tigris* it is often 7–8 mm. Thirdly *O. danae* is remarkably variable, not only in the armament of the upper side of the disc and arms, which may be completely naked or covered more or less continuously with thorny granules, but also in its basic colour. Where two or more sympatric, differently-coloured gorgonians are found with associated *Ophiothelas* clinging to them, the predominant colour of the ophiuroids almost (but not quite) invariably matches the ground colour of the host.

Because of these variations in armament and colour, a number of specific names have been given to fissiparous *Ophiothelas* from various parts of the Indo-West Pacific. However, taxonomic revisions have resulted in rejection of specific distinctions for most of the different morphological and colour forms and lumping together so that *O. danae* is now treated as extending through the Indo-West Pacific area from south-east Africa eastwards to Fiji. (Although in 1971 I left Australian records separate as *Ophiothela hadra* H. L. Clark—originally described from a holotype with disc diameter less than 2 mm.—there appears to be no good reason why these should be specifically distinguished; specimens from Australia are as variable as any others from the Indo-West Pacific). Even a comparison with *Ophiothela mirabilis* Verrill from the Pacific coast of Panama I think may yield no way of distinguishing it. (Unfortunately no good samples of *O. mirabilis* are at present available to me.) In contrast, *Ophiothela tigris* is restricted geographically to the east coast of Africa in the vicinity of Zanzibar and Kenya and to the off-lying Seychelles Islands.

No species of *Ophiothela* are found in the Caribbean area, whereas the best-known fissiparous ophiuroid—the ophiactid *Ophiactis savignyi* (Müller & Troschel) (Fig. 4), coloured green with darker markings, is common there as well as on the opposite Atlantic shores of Africa, throughout the Indo-West Pacific and the East Pacific—a truly tropicopolitan species. It lives usually in sponges but also in any available crevice or cavity. As with *Ophiothela danae*, original discoveries of *Ophiactis savignyi* from different parts of its range were given separate specific names but taxonomists have for many years recognised these as (at least morphologically)

indistinguishable. There are several other nominal species of *Ophiactis* which are also fissiparous, including the bluish-green *Ophiactis maculosa* von Martens and *O. modesta* Brock, both from the Indo-West Pacific and *O. muelleri* Lütken, from the Caribbean, which are morphologically very similar to each other, possibly even conspecific, though in this case they are not linked geographically in East Pacific waters. (*Ophiactis simplex* Le Conte, the fissiparous *Ophiactis* found in the East Pacific, besides *O. savignyi*, differs in the smaller radial shields and more rectangular dorsal arm plates, judging from published illustrations).

There are also some small fissiparous members of the family Ophiocomidae, again tending to associate with sponges, and here too we have a chain of nominal species throughout the tropical reef areas, this time including the East Pacific (though excluding West Africa, where no proper reefs exist). These have had a particularly chequered taxonomic history, having been described under various specific names in the families Ophiacanthidae and Amphiuroidae as well as Ophiocomidae. In reporting on the echinoderms of the presidential cruise of 1938, A. H. Clark (1939) established a new nominal genus *Ophiocomella* for six-armed fissiparous ophiocomids, of which he described two new species, *O. caribbaea* from the West Indies and *O. schmitti* from the Galapagos Islands and also named specimens from Clipperton Island, well to the west of Mexico, as *O. parva* (H. L. Clark), referred from *Ophiocoma*, with the provisional name *Ophiocomella clippertoni* should they prove specifically distinct from material from northern Australia, the type locality of *O. parva*. Subsequently (1941) he decided that *O. clippertoni* is justified and extends to the Hawaiian Islands but also described a fifth *Ophiocomella*, *O. schultzi* from Canton Island, well to the south of the Hawaiian Islands. After examination of the type material of all these nominal species, I could find no reliable morphological differences between them not attributable to growth changes and individual variation (1963, in Parslow & Clark). All are antedated by *Ophiocnida sexradia* Duncan, 1887, which specific name I used for Indo-West Pacific Ophiocomellas in 1971. A photograph of *Ophiocomella sexradia* from the Cook Islands, Polynesia, is given here (Fig. 5) as well as one of a caribbean specimen (Fig. 6) which may still be called *O. ophiactoides* (H. L. Clark) (a senior synonym of *O. caribbaea*) pending further study. In the growth of *Ophiocomella* there is a progressive increase in the density of the disc armament, which is at first almost spiniform but becomes progressively squatter. In *Ophiocoma* species the disc armament also increases in density in young specimens, only becoming continuous in most species at a disc diameter of 7 or 8 mm and in the group of species which includes *Ophiocoma pumila* Lütken, *O. alexandri* Lyman and *O. valenciae* Müller & Troschel the armament is elongated into short papillae rather than the usual granules, especially around the periphery of the disc. The resemblance in everything but the arm number of smaller specimens of these three species and the fissiparous Ophiocomellas which are sympatric with them in the West Indies, East Pacific and western Indian Ocean respectively is very close, though Devaney (1970) has found minor differences in arm spine number and jaw structure. I think it doubtful that these warrant a generic distinction but

this point should be clarified by Devaney's projected further studies. He has pointed out that five-armed individuals of *Ophiocomella* may occur though the majority of any population is fissiparous. The fact that no *Ophiocoma* species of the *pumila*-group occurs in the Bay of Bengal and the western Pacific to match the fissiparous specimens and conversely no fissiparous specimens have been recorded from West Africa although *O. pumila* does occur there, supports the morphological evidence in indicating that they are at least specifically distinct.

However, in the case of the fissiparous species of *Ophiactis*, a proportion of the specimens, averaging 5–10% but varying in different populations is found to be five-armed and not subject to fission and regeneration. Most of these individuals are larger than the fissiparous ones and some taxonomists have assumed that they are the adults whereas the multiradiate specimens represent the young form, presumably transforming by regenerating only two arms rather than the usual three. Others, including myself, maintain that the five-armed individuals are those which have never undergone fission at all. This problem can only be properly resolved by ontogenetic studies of the post-metamorphic history to try and discover if the number of arms is genetically determined and the sixth arm appears at the end of metamorphosis within two or three days after the rudiments of the five primordial arms (as in the starfish *Leptasterias hexactis*) or whether its development must be preceded by fission.

The main difficulty in trying to determine the relationships of fissiparous ophiuroids is their relatively small size, the characters they exhibit in comparison to their larger relatives being mostly immature and convergent ones. Possibly the apparently wide distribution shown by many fissiparous species is illusory and due to inadequacies in taxonomic treatment failing to reveal genuine distinctions. However, providing we are alert to this possibility there seems little point in trying to maintain nominal species for which we have no morphological justification as distinct. The consequence of this is that most fissiparous species are found to have geographical ranges as wide as or even wider than the majority of their five-armed relatives. Where ophiuroids are concerned it certainly appears that all fissiparous species have a strong tendency to adopt an epizoic or even commensal habit, though of course the converse is not the case, there being an even larger number of non-fissiparous epizoic species.

One ophiuroid genus which carries association with other animal hosts to an extent which has been termed parasitism is *Ophiomaza* (Fig. 7), which lives on crinoids, clinging usually to the disc and stealing the food from the upturned open ambulacral grooves as it passes from the arms to the mouth. Like *Ophiothela*, *Ophiomaza* belongs to the family Ophiotrichidae but it has well developed dorsal arm plates and less flexible arms, only the distal parts flexing downwards to any great extent. *Ophiomaza cacaotica* Lyman is known to range from East Africa to New Caledonia, though the two other species of *Ophiomaza* are more restricted. So far we know little about the extent of host specificity.

A rather similar case of parasitism occurs in yet another group of epizoic ophiu-

roids, those which have developed sexual dimorphism, the male of the species being dwarfed and living a dependent existence clinging to the underside of the female, mouth to mouth. So far three species have been described in which this occurs, *Amphilycus scripta* (Koehler) (Fig. 8) of the Amphiuroidae, *Ophiodaphne materna* Koehler (misnamed following misapprehension about the nature of the relationship) and *Ophiosphaera insignis* Brock, both currently included in the related family Ophiactidae (see Mortensen, 1933). Not only are the females of all three of these species themselves epizoic but also in each case the host is another echinoderm—an echinoid in fact—respectively the sand-dollars *Echinodiscus* and *Clypeaster* and for *Ophiosphaera* the sea-urchin *Tripneustes* (also sometimes *Diadema*). Records of all these ophiuroids are few and far between, in fact widely scattered geographically, so they are probably rare or else easily overlooked by collectors. *Ophiosphaera insignis*, for instance, has been recorded from two places in the East Indies and once each from the Philippines, Zanzibar and Madagascar, though its hosts *Tripneustes gratilla* and *Diadema setosum* and *savignyi* are common right through the Indo-West Pacific from Natal to the Pacific islands. [A fourth sexually dimorphic ophiuroid species is known from the Southern Ocean, *Astrochlammys bruneus*, a euryalid. In this case the dwarf male is found on the back of some females (in one example two males to one female) and the only recorded host is a gorgonian, *Primnoella*.]

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Plate

- Fig. 1. *Asteromorpha perplexum* (Koehler) from Mauritius.
Fig. 2. *Ophiothela tigris* Lyman from the Seychelles Is.
Fig. 3. *Ophiothela danae* Verrill, six specimens from the Sinai Peninsula on white (left) and red hosts.
Fig. 4. *Ophiactis savignyi* (Müller & Troschel) from Gorgona, Panama.
Fig. 5. *Ophiocomella sexradia* (Duncan), two specimens from the Cook Is.
Fig. 6. *Ophiocomella ophiactoides* (H. L. Clark) from St. Martin, West Indies.
Fig. 7. *Ophiomaza cacaotica* Lyman from Torres Strait.
Fig. 8. *Amphilycus scripta* (Koehler) from Zanzibar.

(The scale in millimeters)

