Bayer's Corrections

1981 b,c,d,e

STATUS OF KNOWLEDGE OF OCTOCORALS OF WORLD SEAS

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One day many years ago, the Assistant Secretary of the Smithsonian Institution telephoned me at the annual budget time and asked: "What good are the animals that you study?" My reply to that question was: "Dr. Keddy, if you must justify my position on the practical importance of the animals I study, it is not possible." My position was not abolished, and I continued to study Octocorallia. Nevertheless, the incident posed a question that you may share with that former Assistant Secretary: Why study octocorals?

I think it unnecessary to make any apology for pure research to a group of scientists such as this. The octocorals are a widespread group of marine organisms, commonly occurring in dense populations, from littoral waters down to the deep-sea abysses, and from Arctic to Antarctic. A study of their systematics tells us as much about phylogeny, evolution, zoogeography, animal diversity and variations, as does the study of any other group of animals or plants. However, the value of the purely systematic results of research on octorals is enhanced by practical applications of several kinds. For example, most gorgonian corals are especially intolerant of temperature, salinity, and siltation beyond their normal ranges, hence they may be useful indicators of changes in these environmental factors. Octocorals are a conspicuous component of reef communities in the tropical regions of the world, providing support, concealment, and sustenance to a wide variety of invertebrate as well as vertebrate reef-dwellers. Therefore, they offer a rich field for research by ecologists and by behaviorists concerned with commensal, symbiotic, parasitic, and predatory relationships.

Often overlooked is the fact that the precious red coral, *Corallium,* is really a gorgonian. This gives the octocorals a prominent economic importance, as raw coral of good size and color may sell for about 900 dollars per kilogram. The example of the Mediterranean coral fishery, which has been depleted seriously, has stimulated the United States Government to support an intensive investigation into the

ecology and life history of the precious red corals of Hawaii. Without controls, commercial exploitation could deplete the stock and destroy the 11-million-dollar-a-year industry (as of 1975) that now exists in Hawaii. The situation is much more complex in Hawaii than it is in the Mediterranean, because several *Corallium* species occur there instead of one, and they are part of an octocoral community of more than 100 species. Its taxonomic problems are complex, and a study of its ecology is extremely difficult, because this community lives at a depth of 500-1000 meters. However, enough information has been obtained to permit the establishment of fishery controls and quotas.

Octocorals may be commercially important on yet another front, as shown by the case of *Plexaura homomalla,* a Caribbean gorgonian species that was found to produce large amounts of the chemicals called prostaglandins (950, 1410, 1412). As these substances are involved in many physiological processes and have important pharmaceutical applications, knowledge of the systematics and ecology of *Plexaura* became intensely interesting to the pharmaceutical industry. The biochemistry of octocorals is at present being investigated by several commercial and research organizations in the search for other medically important compounds, so systematic information about octocorals in general is in greater demand than usual.

In addition to the professional and personal satisfaction derived from research on octocorals, I might mention also the esthetic rewards of studying these beautiful animals. Not only are their forms graceful and attractive, but their sclerites – which provide a primary taxonomic character – display an almost infinite array of complex forms and delicate colors that are among the most beautiful art-forms found in nature.

The beginnings of our knowledge of the octocorals lie in the works of ancient writers, among them Pliny the elder (954) in the first century A.D., and even in mythology. Ovid, in the Metamorphoses, and Orpheus of Thrace, tell the story of how the goddess Minerva endowed the red coral with magic properties that protect travelers from danger. Many authors of the late Renaissance and following years, for example, Gesner (303, 304) L'Obel (745), Clusius (201), Cerutus & Chiocco (186), and Olearius (897), included the red coral and other gorgonians in their works on botany and descriptions of private museums.

However, the foundations of scientific knowledge about octocorals date from the middle and late 18th Century and are to be found in the works of John Ellis (166), Linnaeus (743, 744), Pallas (901), Ellis & Solander (274), Gmelin (309), and Esper (275). In their works are described the classic nucleus of octocoral species, distributed among the genera *Alcyonium, Gorgonia, Isis, Pennatula* and *Tubipora.*

In the first part of the 19th Century, scientists such as Lamouroux (709-711), Lamarck (705-707), Ehrenberg (261), Dana (218), and Valenciennes (1314), with increasing powers of discrimination, added many genera and species to the list of known octocorals and began to recognize narrower family groupings.

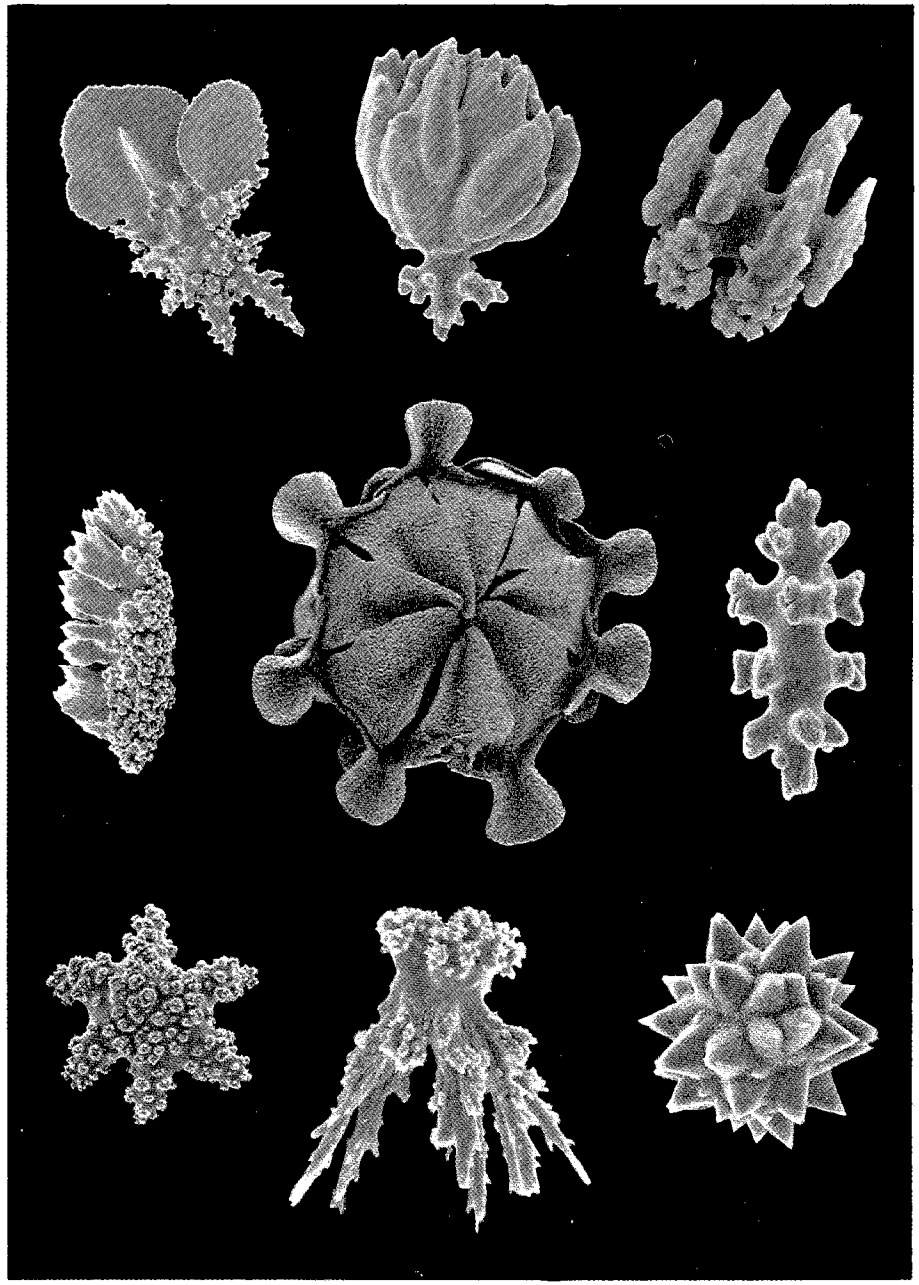

Fig. 1 – Oral view of octocoral polyp with sclerites in place, surrounded by isolated sclerites of various species showing diversity of form. Various magnifications. S.E.M. micrographs by W.R. Brown, Smithsonian Institution.

Probably the greatest single contribution to the classification of octocorals was the discovery of the importance of calcareous sclerites as a taxonomic character. This was first reported by Valenciennes (1314) in a preliminary extract of a monograph that never was published in full. Using the principles set forth by Valenciennes, Kölliker (603) ten years later published a still brief but nevertheless more detailed classification of octocorals illustrated with beautifully executed drawings of sclerites, thus becoming the father of our present method of classification.

The second half of the 19th Century produced authors, among them Duchassaing & Michelotti, J.E. Gray, Koren & Danielssen, A.E. Verrill, and Wright & Studer, who added scores of genera and species to the existing classification. It also saw the beginning of the prolific work of Willy Kükenthal, who probably was the most productive and influential of all students of octocorals. The work of these scientists certainly opens up the modern period of research on octocorals.

The large number of investigators publishing works on octocorals in the first part of the 20th Century precludes mentioning them in detail. Elisabeth Deichmann and C.C. Nutting in the United States; Sidney J. Hickson and J. Arthur Thomson in Britain; J. Versluys and Gustav Stiasny in Holland; Willy Kükenthal in Germany; Hjalmar Broch in Norway; Kumao Kinoshita and Kamakichi Kishinouye in Japan are among the authors who contributed substantially to our knowledge of the octocorals around the world.

The second half of the 20th Century has seen the emergence of a new generation of workers with relatively few ties with those who preceded World War II. Whereas workers before the war were largely dominated by Kükenthal and Hickson, those who came after were mostly independent. In the United States, Deichmann, who was not trained by Verrill or by any of the contemporary European specialists, continued to publish, infrequently, up to 1960. Tixier-Durivault in France has published prolifically upon Alcyonacea up to the time of her retirement. In Japan, Huzio Utinomi made extensive contributions to the knowledge of the Alcyonacea, especially Nephtheidae, from 1950 to the present. Ferinand Pax in Germany, often in collaboration with Ingeborg Müller, contributed to our knowledge of the Mediterranean and West African faunas.

Most of the papers by the authors I have just mentioned deal with collections from expeditions to limited geographical regions, or with a small number of species from specific localities. Some of the early authors, for example Pallas and Esper, dealt with all the species then known and tried to organize their synonymies. In the 18th Century, that task was comparatively easy. Pallas (900) included 31 species of *Gorgonia,* 4 of *Isis,* 4 of *Alcyonium,* 1 of *Tubipora* and 11 of *Pennatula* in his *Elenchus Zoophytorum* – 51 species of octocorals known from the whole world. Today, I estimate there are about 2000 species described, and perhaps one thousand to two thousand more awaiting discovery.

There is no comprehensive monograph of the world fauna. In 1915, Willy Kükenthal published his volume on Pennatulacea in *Das Tierreich* (671). That

volume is a complete review, with keys and synonymies, of all the sea pens known at that time. In 1924, he published a companion volume on Gorgonacea (681). Both of these works were refinements and condensations of earlier reports on the collections of the German Deep-sea Expedition aboard the Valdivia (683, 677), and remain to this day the only guides to the world fauna of any of the orders of Octocorallia.

As I have said, the geographical coverage of the literature on octocorals is extremely scattered. Some regions are moderately well known through the reports on collecting expeditions, such as the *Siboga* Expedition in Indonesia (478, 485, 886-891, 1094, 1098, 1199, 1395, 1398), the *Investigator* in the Indian Ocean (1205, 1213), and the *Blake* and the *Albatross* in the Caribbean (231), but even these reports are far from complete because the collections on which they are based were very inadequate. For example, very few of the *Blake* and *Albatross* stations in the western Atlantic were shallower than about 100 meters, so the rich fauna living on the reefs and reef slopes was for the most part not sampled. Similarly, the *Siboga* and the *Investigator* worked chiefly by dredging and obtained only a fragmentary sampling of the rich fauna living between low tide and 50-100 meters.

With these circumstances in mind, we can review the present status of knowledge of octocorals in the major geographical regions of the world. They can be distributed among four broad levels of taxonomic knowledge, as follows:

1. Essentially complete: where there is a rich literature, and most of the species have been adequately described. The major problems remaining are refinements in taxonomy, details of distribution and ecology, and experimental research on biological aspects.
2. Moderately well-known: where there is extensive literature, but many more species remain to be described and taxonomic problems to be solved, and the major patterns of distribution must yet be worked out. Much descriptive work remains to be done before ecological and experimental studies can proceed at an effective level.
3. Poorly known: where the literature is sparse and incomplete. Here the major part of the fauna remains to be described and a large number of species will inevitably be new to science. The major faunal relationships can be deduced, but distributional patterns are not clearly understood.
4. Minimally known: where the literature consists of scattered taxonomic descriptions and isolated distributional records, many of them inadequately substantiated. Most of the basic descriptive work remains to be done.

We can now consider the major geographical regions of the world in regard to these categories of systematic knowledge about octocorals.

To the first category, the most complete, belong only the Mediterranean Sea and the waters of western Europe. Here the work of Johnson (533-538A), Johnston (540), von Koch (586-588, 592, 595, 601), Studer (1163), and Thomson (1196) are classic, and modern investigators including Carpine (172, 173, 174), Grasshoff (338-344), Theodor (1177, 1183) and Weinberg (1408, 1409) are

refining the details. Even so, a complete synthesis is not available yet, though Grasshoff is working toward that goal.

To the second category, moderately well-known, belong several regions.

(1) The tropical and temperate northwestern Atlantic Ocean where the foundation was laid down by Elisabeth Deichmann (231), Duchassaing & Michelotti (251, 252), Kükenthal and collaborators (674, 688, 689, 998, 1264), and A.E. Verrill (1326, 1344, 1345-1348, 1350, 1352, 1354-1364).

(2) The boreal North Atlantic, Arctic and Scandinavian waters, known through the works of Broch (121-128, 131-133, 141, 142), Danielssen (225-227), Grieg (399-406), Jungersen (542, 545-549), Koren & Danielssen (614-619), Madsen (762-764, 766), Molander (810), and others.

(3) South Africa in the vicinity of the Cape of Good Hope studied first by Hickson (465, 468) and J. Stuart Thomson (1214, 1215, 1217-1221), later by Broch (137), Stiasny (1122), Tixier-Durivault (1243, 1250, 1250A), and Velimirov (1318).

(4) The Red Sea in papers by Ehrenberg (261), Gohar (312-315), Hickson (500), Klunzinger (581), Kükenthal (641, 666), Stiasny (1108, 1123), Tixier-Durivault (1244), and Verseveldt (1373, 1380, 1381, 1388).

(5) The Japanese islands and northwestern Pacific Ocean in the works of Kinoshita (561-572), Kükenthal (646), Kükenthal & Gorzawski (684, 685), Nutting (892), and Utinomi (1272 et seq.).

(6) Central Indonesia, especially the Celebes, Flores, Molucca and Banda seas around the island of Celebes through the collection made by the Siboga Expedition reported upon by Hickson (478, 485), Nutting (886-891), Stiasny (1094, 1098), J. Arthur Thomson & Laura Dean (1199), and Versluys (1395, 1397).

To the third category, poorly known, belong the following:

(1) The coast of South America from Trinidad to Rio de la Plata. In spite of the fact the Brazilian fauna undoubtedly is closely related to the better-known West Indian fauna, few papers dealing specifically with it have appeared – notably those of Verrill (1333, 1364), da Costa Belem & de Figueiredo Alvarenga (75), Tixier-Durivault (1256), and Tommasi (1265). In 1912, Verrill reported 24 species and varieties, only 19 of them definitely, from Brasil (1364). Deichmann (236) reported 16 species, omitting the plexaurids for which she cited Kükenthal's book of 1924 (681). In 1961, I included everything I could find recorded from Brazil, amounting to 19 species, not including synonymies (64). In 1959, I reported 7 species new to the Brazilian fauna and listed a total of 44 species from eastern South America (62). Then, material from Brazil sent to me by Dr. Marc Kempf for identification provisionally includes at least 38 species, which is probably about one-quarter of the fauna living in Brazilian waters.

(2) The eastern Atlantic Ocean from the Azores south as far as South African waters known chiefly by the collections made by the Prince of Monaco and reported by Studer (1163) and J. Arthur Thomson (1196), together with several papers by Gustav Stiasny (1096, 1097, 1101-1103, 1110, 1112-1114, 1116, 1118), Tixier-Durivault (1245, 1251, 1258), and Pax & Müller (932).

(3) The east coast of Africa and Madagascar, where the soft corals have been studied by Stiasny (1117), Tixier-Durivault (1254, 1257, 1259) and Verseveldt (1376, 1378, 1382, 1384, 1385) in some detail but the gorgonaceans scarcely at all, principally those of Zanzibar by Thomson & Henderson (1202).

(4) The coasts of India and the adjacent waters of the Indian Ocean in papers by Hickson (467), Pratt (967, 968), Thomson & Crane (1197, 1198), Thomson & Henderson (1205), and Thomson & Simpson (1213).

(5) The Malay Archipelago in reports on the collection of the Snellius Expedition by Stiasny (1124) and Verseveldt (1370, 1374).

(6) Australia with its rich fauna described in papers by Briggs (117), Broch (120, 129), Burchardt (164, 165), Hickson (495), Kükenthal (661), Ridley (996), Thomson & Mackinnon (1207), Thorpe (1222), Tixier-Durivault (1253), Utinomi (1304, 1305, 1307, 1311), and Verseveldt (1392).

(7) New Zealand in papers by Benham (78-80), Brewin (115) and Grant (334).

(8) New Caledonia in papers by Tixier-Durivault (1256A) and Verseveldt (1387).

(9) The Philippine Islands in papers by S.F. Light (729-733), Francis Mai-Bao-Thu & Domantay (768, 769), Toxas (1025, 1026) and Stiasny (1119, 1132).

(10) The Hawaiian Islands in a paper by Nutting (884) partly revised by Bayer (47, 55) and now under active study by K. Muzik.

(11) The western coast of the Americas south of the Gulf of Panama in papers by Hickson (489), Kükenthal (665), Nutting (885), Stiasny (1136) and Verrill (1334).

(12) The Canadian Arctic reported by Verrill (1365).

(13) The Antarctic in papers by Broch (146), Gravier (354, 355, 357), Hickson (476), Jungersen (546A), Kükenthal (663), May (788), Molander (815), Roule (1016, 1019, 1020), J. Arthur Thomson & J. Ritchie (1211), and several others.

In the fourth category, the octocorals of vast areas of the Indian and Pacific Oceans, with their numerous islands, are known only from isolated reports of a few species from widely separated localities. The same holds true for Malaysia and parts of Indonesia not surveyed by expeditions, for the isolated islands of the South Atlantic, and the west coast of South America as well as the extreme southern part of the east coast. An important reason for these gaps in knowledge is the lack of collections, though in some cases existing collections have not been studied even after many years. We have no information whatever about the octocoral fauna from enormous areas of open ocean and countless oceanic islands, and with the escalating cost of seagoing operations, it is very unlikely that this information will be forthcoming in the foreseeable future.

Knowledge of the biology of octocorals lags behind that of the systematics. In this general field, the anatomy probably has been more thoroughly studied than other subjects such as physiology, life histories, and behavior.

Anatomical works in a modern sense go back to that of Kölliker in 1865, who illustrated axial structure and some general anatomy as well as the form of sclerites (603). Nearly half a century later, Neumann (869) and A. Schneider (1051) also studied axial structure. European forms such as *Alcyonium digitatum* and *Isidella elongata* were studied by Pouchet & Myevre (962), S.J. Hickson (463), and G. von Koch (586), and exotic species such as *Tubipora musica* by Hickson (458) and von Koch (585), and *Helipora*, the Blue Coral, by Moseley (842). In the United States, C.C. Nutting (882) produced an early account of the anatomy of gorgonians, W.M. Chester (191) published a detailed study of *Pseudoplexaura crassa* (now properly called *Pseudoplexaura porosa*), and more recently, I investigated *Plexaura homomalla* (68). Using the transmission electron microscope, S. Kawaguti in Japan examined the polyps and sclerites of the gorgonian *Euplexaura erecta* (554) and the soft coral *Heteroxenia elisabethae* (555). Furthermore, there is a substantial amount of anatomical information scattered through the descriptions in taxonomic works, which is therefore not accessible except through patient search. For example, Kölliker procuded an exhaustive systematic treatment of the Pennatulacea (607), in which he described the anatomy of many species in detail. A great many smaller papers also contain important information of this kind.

Ecology and behavior of a few species of sea-pens have been studied by Birkeland (87), Honjo (515), and Magnus (767). G.H. Parker (912-914) investigated the physiological and behavioral interrelation of the polyps in a few species of gorgonians and in the sea-pansy, *Renilla.* The ecology of Mediterranean *Eunicella* species, and their adaptations to water currents, were studied by Theodor (1177, 1187) and Velimirov (1320, 1322), orientation of *Gorgonia* by Wainwright & Dillon (1405), orientation and growth of *Muricea* in California by Grigg (409), adaptations to water movements in *Acabaria* in the Red Sea by Schuhmacher (1053), ecology of West Indian gorgonians by Cary (178), Birkeland (86), and Opresko (898, 899), and zonation of Jamaican gorgonians by Kinzie (574).

Papers describing various physiological aspects of octocorals include the neuromuscular system of *Heteroxenia* in the Red Sea by Gohar & Roushdy (318), and of *Cavernularia* in Japan by Honjo (515), photosynthesis of symbiotic zooxanthellae by Burkholder & Burkholder (166), and respiration in various gorgonians at the Tortugas in Florida by Cary (181).

Embryology and development of octocorals have been studied by Lacaze-Duthiers (692), Kowalevsky (623), Kowalevsky & Marion (624, 625), von Koch (592), Wilson (1420-1422, 1424, 1425), Gohar (314), Gohar & Roushdy (319), and others.

Because of the small size and location of calcareous sclerites in the mesogloea of octocorals, study of the mechanism of calcium deposition is very difficult, but some work has been done by Bourne (110), Dunkelberger & Watabe (256A), and

Woodland (1428, 1429). The crystalline nature of the sclerites of *Briareum* was studied by W.J. Schmidt (1047, 1048) and the ultrastructure and chemistry of *Tubipora* by Spiro (1078).

The chemistry of many octocorals has been studied by members of the department of Chemistry at the University of Oklahoma, including Leon Ciereszko (194, 195), A.J. Weinheimer (1410-1412), F.J. Schmitz (1049) and others, and by David Anderson (988) and colleagues at the University of Miami. Walter Goldberg also at the University of Miami, studied the chemistry of the gorgonian axis (321), and Flores & Huacuja (284) investigated the chemistry of the coenenchyme and the occurrence of trace elements in gorgonians of the Gulf of Mexico.

Many octocorals, especially reef-dwelling species, have brightly colored sclerites, but the pigments of these colored skeletons have not been studied extensively. Among the few are investigations by Ranson & Durivault (980), Rudiger *et al.* (1072), and Tixier (1227) on the blue coral *Heliopora*, and by Fox *et al.* (193) on the orange-colored gorgonian *Eugorgia ampla.*

In conclusion, I think that the foregoing remarks clearly demonstrate the inadequacy of world knowledge of the octocorals, pointing to a need for continuing basic descriptive research leading eventually to a world-wide synthesis. Knowledge of the biology of octocorals is based on studies of only a few of the 2000-4000 species, and cannot safely be assumed to apply to all. Accordingly, the need for further experimental work is very great, but is dependent upon a better knowledge of the systematics on a world scale.

In regard to Brazil in particular, there remains a need for a more complete faunal inventory based upon wide sampling in all habitats both shallow and deep. This will clarify the southern distribution of the Caribbean species whose ranges extend into Brazilian waters and more clearly emphasize the purely endemic elements of the fauna. Such basic information will facilitate further experimental studies on these interesting animals.