AN OVERVIEW OF CEPHALOPOD SYSTEMATICS: STATUS, PROBLEMS AND RECOMMENDATIONS

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Abstract

This paper reviews the current status of systematics of Recent cephalopods (squids, cuttlefishes, octopuses and nautiluses) on a world-wide basis. It includes lists of recent revisionary publications (1960-1981), and revisions in progress. Problems that impede progress in cephalopod systematics are discussed, including the taxonomic and geographic complexity of the group, lack of comprehensive collections and well preserved specimens, scarcity of classical studies, scattered literature, and lack of funding for research and education. The situation in Australia is cited as an example of the status of cephalopod systematics in most other regions of the world. A list of Australian species in four major families (Sepiidae, Loliginidae, Ommastrephidae, Octopodidae) is presented, as is a bibliography of the cephalopod biological literature of the Australian region.

Recommendations are given in an effort to improve the status of cephalopod systematics and consequently to provide information required in other fields (e.g., biomedical research, behavior, ecology, parasitology, fisheries biology): (1) recognition of need for research and education and for increased funding to support them; (2) training and development of regional (geographic) specialists as well as taxon-oriented (world-wide) specialists; (3) support and production of keys to identification, catalogues of important collections, and revisions and monographs; (4) establishment of national, regional, and world-wide authoritative reference collections; (5) designations of four major families of cephalopods in critical need of comprehensive systematic revision (Sepiidae, Loliginidae, Ommastrephidae, Octopodidae).

Introduction

Voss (1977) presented an historical account of major systematic works and pointed out reasons for the comparatively primitive state of our knowledge concerning cephalopod systematics. The present review deals with the broader aspects of systematics and morphology in the context of the theme of the International Workshop on the Biology and Resource Potential of Cephalopods (Melbourne, Australia, March, 1981). The topics discussed include the current status of systematics in cephalopods, problems that impede the progress of cephalopod systematics, the status of systematics of Australian cephalopods, and recommendations for enhancing systematic programs in cephalopods that will aid fisheries scientists as well as advance general systematic knowledge.

The term “systematics” (taxonomy) is used here in its broadest sense to cover all aspects from descriptions of taxa, classification, phylogeny, zoogeography, taxonomic life history, population analysis, and comparative and functional morphology. The basis of all modern systematics, of course, is morphology.

Ideally, a thorough knowledge of the systematics of a species is the required foundation upon which all other biological and resource management studies must be based, because the biology of each species is different. This ideal, however, is seldom realized for a variety of reasons. Comprehensive collections, time, and trained specialists, to mention only a few, are the necessary requirements for thorough systematic studies.

Several examples of the lack of systematic knowledge about cephalopods exist in reference to fisheries. Several years ago a vigorous fishery developed for squid in New Zealand waters, based on the single known species in the area, Nototodarus sloani (Gray, 1849), which is restricted to those waters. As biological information accumulated for support of the fishery and for development of a management scheme, significant inconsistencies in occurrence and distribution became apparent. Requested systematic studies then confirmed the presence of a second species, Todarodes filippovae Adam, 1975, which subsequently has been recorded circum-globally in the southern regions of all three oceans. More recently, detailed biological studies have demonstrated the existence of several distinct populations of the two known species, as well as the presence
of a third, undescribed species (Smith, Roberts & Hurst, 1981).

In the Gulf of Campeche, Mexico, a traditional fishery was based on Octopus vulgaris Lamarck, 1798, a ubiquitous octopus of broad distribution. In the absence of local studies, knowledge about the biology of O. vulgaris from other seas was applied to the Campeche octopus for fishery statistics and management purposes. The discovery that the octopus was indeed a new species, described as O. maya Voss and Solis, 1966, with a very different life history, explained the problems that had plagued biologists assigned to study the fishery and develop recommendations.

More recently, an expanding fishery has developed in Australia based on the ommastrephid squid, Nototodarus gouldi (McCoy, 1888). Australian fisheries agencies are interested in accumulating sufficient knowledge in order to formulate management plans before the population becomes too severely impacted by the fishery, a most commendable goal. However, the recent discovery of another species of Nototodarus sympatric in the northern range of N. gouldi, as well as Todaropsis eblanae (C. C. Lu, pers comm., 1982), dictates a very cautious and detailed approach. The existence of seven additional species of ommastrephid squids (M. Dunning and C. C. Lu, pers. comm.) now known to inhabit Australian waters graphically demonstrates the need for immediate, intensive systematic studies.

These examples vividly demonstrate that we must have sound systematic knowledge about species and populations if we are to approach the truth about the biology, ecology, behavior, and fisheries of these forms. But frequently scientists in these disciplines cannot wait for systematic revisions to be completed. Often, the best that can be hoped for is an identification of the species being studied or fished based on the most recent revision, which may, in fact, be decades old and not comprehensive in geographical coverage, life stages, etc. Clearly this does not solve the problems.

**Current Status**

*General Review.*—The status of cephalopod systematics perhaps can be reviewed best by listing the revisions published during the last two decades, the "recent era" (Table 1). I have interpreted the term revision rather broadly, so that researchers interested in a particular group will have a starting point; therefore, several works listed are not true revisions in the strict systematic sense. Further, it is interesting that most of the works deal with families and genera with (1) small numbers of species, (2) oceanic or deep-sea forms, or (3) small-sized animals. While some of these studies may be very important to cephalopod systematics and phylogeny in general, they are of little help to fisheries biologists or others who need systematically

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<th>Year</th>
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sound information. Curiously, the families most in need of comprehensive, systematic revisions are those that are of greatest importance to fisheries on a world-wide basis. These include:

Sepiidae, the cuttlefishes; *Sepia*, *Sepiella*
Loliginidae, the inshore, neritic, myopsid squids; *Loligo*, *Doryteuthis*, *Lolliguncula*, *Loliotus*, *Sepioteuthis*, *Alloteuthis*, *Urotulethis*, *Lolipopsi*

Ommastrephidae, the neritic and upper pelagic oceanic squids; *Illex*, *Todarodes*, *Todaropsis*, *Nototodarus*, *Ommastrephes*, *Dosidicus*, *Ornithoteuthis*, *Symplectoteuthis*, *Martialia*

Octopodidae, the inshore, benthic octopuses; *Octopus*, *Cistopus*, *Hapalochlaena* etc.

Species of these four families sustain approximately 90% of the world’s fisheries catch. (Species of the Gonatidae and Onychoteuthidae are emerging as exploited stocks but their contribution to the total catch currently is small; certainly they require systematic treatment as well.)

Table 2 lists the groups (families or genera) of cephalopods known to be under revision currently. Here again most of these revisions are on groups that have little direct application to fisheries, with the exception of the ommastrephids, loliginids, and possibly the gonatids and octopods. There is, of course, important indirect application of these revisions as well as those already published, in that most of these cephalopods form an extremely significant part in the diets of many fishes and toothed whales of commercial importance. Other marine mammals and pelagic birds prey extensively on cephalopods as well, so systematic knowledge of all groups indeed is valuable to biologists studying other marine organisms.

**Problems.**—The large families, so important as fisheries resources, largely have been ignored insofar as their systematics are concerned. Their importance is universally recognized, not only in fisheries but in prey-predator, behavioral and biomedical research, and yet they seem to remain untouched. Why? Some of the reasons are linked to the problems that we face in systematics in general and these are

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<th>Table 2</th>
<th>Revisions of Cephalopod Groups Known to be in Progress.*</th>
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<td>Burgess—Central Pacific <em>Abralia</em> and <em>Abraliopsis</em>; <em>Enoploteuthis</em> (1982)</td>
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<td>Roper and Sweeney—Brachoteuthidae</td>
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<td>Voss, G.—<em>Enoploteuthinae</em>, <em>Abralia</em> and <em>Abraliopsis</em></td>
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<td>Voss, G.—<em>Cirrata</em>, deep-sea octopods</td>
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<td>Voss, N.—<em>Cranchidae</em></td>
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* Please consult with individual authors concerning the status of these revisions; addresses are provided in Appendix 1.

compounded by a few specific problems, such as large numbers of poorly known species. The four major families mentioned above comprise about 50% of the known species of cephalopods. Estimates indicate that there are over 100 species of octopodids, about 100 species of sepids, 40 to 50 species of ommastrephids, and 60 to 80 species of loliginids; so the largest, most speciose families of cephalopods must be dealt with. As most of the genera at least are world-wide in distribution, systematic collections are grossly inadequate. Also the literature is widely scattered, in many different languages and journals, and of widely varying quality. Furthermore, often it is difficult to get the literature, particularly the older, obscure, but nonetheless important works. Another reason is that the type specimens, the specimens upon which species names are based and which are so vital for comparative studies, no longer exist in many cases and no lectotypes have been established. Because of the soft-bodied nature of cephalopods, they require special attention for initial fixation and long-term preservation. Many older specimens lacked that attention, and were allowed to dry out or are in such poor condition that the important systematic characters are no longer distinguishable. It is very discouraging for a systematist to visit an old museum with great anticipation which
quickly dissolves to disappointment when the holotype turns out to be a bit of sludge or slurry in the bottom of the jar. Poor fixation and preservation are not limited by any means to the old collections. While it is not universally true, very frequently if a systematist wants to have good systematic-quality specimens, properly fixed and preserved material, he must collect and prepare them himself, or at least instruct others on proper techniques of fixation. (Guidelines to techniques of preservation are published elsewhere in these proceedings (Roper & Sweeney, 1983)).

Samples taken during fisheries surveys or non-systematically oriented collecting programs frequently are most conveniently frozen. Thawed specimens or those casually fixed after freezing, however, do not make adequate material for systematic analysis. For example, many characters, such as the viscera and the hectocotylus, become soft, flacid, and amorphous; sucker rings, often of such great taxonomic value, become dislodged from the suckers and lost. Fixation of at least a portion of the fresh sample in 8-10% buffered formalin will ensure that important taxonomic characters are preserved; fixed material should contain both males and females as well as specimens from the whole range of sizes available.

Octopuses fixed in formalin (or other fixative) while still alive are extremely difficult if not impossible to work with, because they contract so vigorously that their arms become tightly coiled, immeasurable coil springs, the mantle a solid lump, and the viscera, a congealed, half-rotted mass, untouched by fixative that could not penetrate rapidly enough through the contracted mantle muscle and closed-off mantle opening. To avoid these problems, octopuses must be narcotized or killed in fresh water, then fixed while the arms are kept straight. No cephalopod, squid, cuttlefish or octopus, should ever be fixed in a container shorter than the total length (less tentacles of squids and cuttlefishes) of the specimen. The soft-bodied creatures become permanently molded in the position they initially are fixed in, whether they be squeezed into a jar or laid out in a tray. (Of course, if no selection of containers exists, a specimen may be carefully folded at the neck and fixed, rather than have no specimen.)

Another hindrance to major systematic studies on cephalopods is the problem of adequate samples. Too frequently the collections are poorly preserved, from widely scattered localities, inadequate in numbers, and lack various life stages. The life stages of very few species are known. In fact, in many of the oceanic species only the larvae and juveniles have been described. Moreover, specimens of large species, e.g., of Architeuthis, Moroteuthis, ommastrephids often are not preserved. Only in the last decade or so with the use of very large mid-water trawls and examination of predator gut contents have we begun to acquire adults of many forms (Clarke, 1977, 1980; Roper, 1977). Cephalopods frequently are extremely difficult to catch; because they are very perceptive, and very fast swimmers, they are able to avoid the nets. Capturing adequate samples is so difficult, in fact, that those of us who sample oceanic and midwater groups insist that we catch only the slow, the sick and the stupid. A recent workshop on problems of assessing populations of macronekton addressed this problem (Wormuth and Roper, 1983). With cephalopods recognized as a extremely frustrating group for biologists, how can we begin to assess populations when we catch only two or three specimens? Adequate samples for purposes of identification and systematic study should consist of specimens of both sexes from the full range of sizes available and from as broad a geographic range as possible.

Still another problem in the systematics of cephalopods is related to the nature of their structure and morphology. Because cephalopods are soft-bodied, lack an external shell (except Nautilus), have no fin rays, no bones, and no spines, an element of frustration and difficulty is introduced. That is not to say that no taxonomic characters exist, but it does mean that systematics must search extremely diligently for taxonomic characters, some of which may be obscure and/or minute. Cephalopods, in general, don't have the type of meristic characters that occur in crustaceans, fishes and
shelled mollusks, for example. Furthermore, we still are at a very primitive stage in knowledge about the characters themselves. Until very recently, there seemed to be a lack of recognition and definition of new characters or character states. As yet, we don't know the range of variability of characters across the geographical range of most species, and we don't know how this range of variation applies to species, sub-species and populations. In part, this lack of knowledge is a result of the lack of adequate collections.

A further problem is that in general there is a lack of comparative systematic studies. Currently no internationally established standards exist for descriptions of cephalopods, so a wide variety in the quality of descriptions exists. The strong recommendation for the establishment of minimum standards for descriptions of cephalopod species was made during this workshop and has resulted in its implementation and publication in these proceedings (Roper & Voss, 1983). Each description of every new species of cephalopod published hereafter should follow these guidelines, so that all necessary characters are described. The botanists have very standardized techniques for describing species, as do many entomologists and crustacean taxonomists. Oftentimes authors describe only a few of the characters, only the most obvious ones, or only the positive characters, so that when more than the original specimen are examined, they are unidentifiable. We have claimed that no problem exists in the systematics of cephalopods as long as only one specimen is present, but as soon as a second is at hand, problems arise, because variation rears its Hydra-head and we simply do not know enough about variation in cephalopod characters and character states. We must increase our knowledge of all of the characters in cephalopods, positive and negative, so that we can conduct the detailed comparisons with other closely related species so necessary for a more thorough understanding of their biology.

Illustrations play a vital role in the descriptions of cephalopods, but currently as broad a range of variation exists in the quality of illustrations as in descriptions. Illustrations often are poorly rendered, lack detail, are absent altogether, or they appear as photographs. While a photograph may be adequate for the general habitus of a cephalopod, it is extremely difficult to show the fine details of characters of squids and other cephalopods (photomicrographs and SEM photos excepted). Lists of illustrations accompany the standards for descriptions mentioned above. Certain characters always should be illustrated and those required illustrations should be of a high standard. Standards of descriptions and illustrations will help form the basis for modern comparative morphological studies that lead to an understanding of the systematics and phylogeny of the group.

An attitudinal problem also exists. Because systematics often is looked upon as an archaic, unexciting science, it is difficult to attract students, researchers and science administrators to an appreciation of the necessity for systematic research. Part of the problem lies with systematists themselves who often have failed to promote their science. When personal attitudes and the archaic image are changed, systematics will attract more students and the field will advance. In fact, the field now seems to be enjoying a resurgence of "popularity" due largely to the application of new technology (e.g., scanning and transmission electron microscopy) and "new" analytical approaches, such as cladistics. Application of these techniques should be boldly encouraged and tested as tools to aid modern systematic research.

The lack of funding for systematic research is the last problem I shall discuss. Part of this problem is related to the attitudinal problem—systematics is not particularly trendy or flashy and that affects the thinking of funding agencies and administrators. Modern systematists require more support than the magnifying lenses and green eye shades of their predecessors of past centuries. As much money is required to support comprehensive, modern systematic research as for many other kinds of research. For example, if collections of marine organisms must be made, the cost of ship time alone can be very significant. Until additional funding is directed toward systematic research on cephalopods, the field will advance too slowly and too sporadically to meet the
demands for systematic information (identifications, fishery management, relationships, zoogeographic distributions, etc.).

Regional Example: Australia. — A bit of history concerning the systematics of cephalopods in Australia will serve as an example of the status of systematics in general. Perhaps Australian cephalopod history goes back to the days of Captain Cook. Certainly, Captain Cook was greeted by stranded cuttlebones, as well as goannas (lizards) when he landed on Lizard Island in search of an escape route through the Great Barrier Reef. The Dutch and French were among the first to have made collections during their early exploring expeditions; the Astrolabe and the Geographie, for example, collected species that were described by Quoy and Gaimard in 1832. Gray described several Australian species in 1849 from material brought back by the British explorers. The major contributor to Australian cephalopod systematics in the 19th Century was W. E. Hoyle who in 1875 described the material from the Challenger Expedition that went up through the Coral Sea and the Arafura Sea. But, in general, the status of systematics of cephalopods in Australia largely has remained at a primitive level, primarily because no specialist in cephalopods has worked in Australia. T. Iredale did describe a large number of species and genera of cuttlefish based on cuttlebones, but all those taxa must be questioned until verified with specimens. (See Appendix 2 for a bibliography of Australian cephalopod literature).

The Australian state museums have collected cephalopod material and maintain collections. Reports of their holdings are included as papers in this volume (Lu, 1983; Rudman, 1983; Slack-Smith, 1983; Zeidler, 1983). Just as the four major families, Sepiidae, Loliginidae, Ommastrephidae and Octopodidae are considered in critical need of systematic revision on a world-wide basis, they are equally in need of revisionary studies in Australia. In Australia, members of these families are the most accessible, the most abundant, and the most important for active and potential fisheries. The species in these families are listed in Table 3 as an indication of their importance in Australian waters. These are species recorded or described from Australia but the validity of many must be verified by further investigation.

Table 3
Nominal species of Sepiidae, Loliginidae, Ommastrephidae and Octopodidae described or reported from Australian waters.

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<th>A. Sepiidae</th>
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<td>Sepia</td>
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<tr>
<td>apama Gray, 1849</td>
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<td>bdependens Adam, 1938</td>
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<td>bartletti (Iredale, 1954)</td>
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<td>pefferi Hoyle, 1885</td>
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<tr>
<td>pharaonis Ehrenberg, 1831</td>
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<td>plagion Gray, 1849</td>
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<tr>
<td>reesi Adam, 1979</td>
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<tr>
<td>rex (Iredale, 1929)</td>
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<td>rhoda (Iredale, 1929)</td>
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<td>rosettata (Iredale, 1926)</td>
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<tr>
<td>smithii Hoyle, 1885</td>
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<td>subantennata (Iredale, 1926)</td>
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<td>treba (Iredale, 1954)</td>
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<tr>
<td>perco Adam, 1979</td>
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<td>versuta (Iredale, 1926)</td>
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<td>whiteleyana (Iredale, 1926)</td>
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<th>B. Loliginidae</th>
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<tr>
<td>Loligo</td>
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<tr>
<td>chinensis Gray, 1849</td>
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<td>etheridgii Berry, 1918</td>
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<td>edulis Hoyle, 1885</td>
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<tr>
<td>Doryteuthis</td>
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<td>sibogae Adam, 1954</td>
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<td>singhbiensis (Ortmann, 1891)</td>
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Financial support is urgently needed for maintenance of collections and data; for hiring assistants and, especially, illustrators; for costs of publication; for modern equipment, e.g., histological instruments and microscopes; for training students; and for hiring and supporting trained systematists. An impetus to train students, for example, would be recognition by quality universities that systematics is a legitimate science worthy of sustaining advanced degree research. There are major universities in many countries at which theses in systematic topics are not allowed for a doctoral dissertation. Recognition and support by various funding agencies, both basic and applied, as well as a concerted and coordinated effort by existing systematists and by the users or beneficiaries of systematic research, will (or should) provide the persuasion for universities and institutes to offer programs and curricula in systematics. Furthermore, fishery biologists and administrators must recognize that cephalopods represent an exploitable resource with immense potential on a world-wide basis. Cephalopods must be studied in the same manner that all other major fisheries species are studied: the systematics, the whole animal biology, and the populations.

2. Another recommendation concerns the types of specialization required for cephalopod systematics. Training and encouragement are required to develop these specialists.

a. One type is the regional specialist, a scientist who is knowledgeable about the systematics of all species that occur within a region, e.g., Australia, or the Indo-west Pacific. These systematists are necessary to define the fauna that exists within the region, as well as to respond to the requirements of fisheries biologists or biomedical researchers, for example.

b. The other type of specialist is one who studies the systematics of cephalopods at the taxon level but on a world-wide basis. Not only is this approach necessary for the basic science itself, but also it is important to be able to respond on a world-wide basis to the needs of non-specialists with information about particular taxa.
3. A number of useful services or products can be rendered by cephalopod systematists, particularly in the form of publications.

a. Some of the most useful publications, certainly to those who are not authorities in cephalopods, are keys to the identification of species. Fisheries biologists, or biologists who study predators of cephalopods, e.g. marine mammals, pelagic birds, pelagic fishes, must know the identity of the species involved in the fishery or as prey organisms. So the recommendation cannot be too strongly made that identification keys be produced as soon as a regional fauna or a taxonomic group is sufficiently known to accurately support such aids.

b. Another aid, to be strongly recommended particularly to systematists themselves, is the catalogue that lists the type material or important historical collections that are housed in a particular museum. These are especially important for museums that have large, historically, nomenclaturally important collections, e.g. the British Museum of Natural History and the Museum de Histoire Natural in Paris. While a few catalogues have been prepared (Smith, 1974, California Academy of Sciences; Roper & Sweeney, 1978, National Museum of Natural History, Smithsonian Institution; Zeidler & MacPhail, 1978, South Australian Museum) and one is in preparation for the Zoological Museum, Copenhagen (Knudsen & Kristensen, pers. comm.); catalogues are lacking for all other major collections of the world. Catalogues are extremely useful not only to specialists but to other biologists who may wish to refer to the collections.

c. Finally, publications in the form of thorough systematic revisions and monographs are the ultimate product of the systematist. Not only do these consist of keys, catalogues, and illustrations, but they should represent the most complete analysis possible concerning the classification, nomenclature, phylogeny, zoogeography, life history, morphology, populations, etc. of the taxonomic group. Because of the breadth of biological topics of a modern systematic monograph, the very strongest recommenda-

tion is given for their support and encouragement.

4. A strong need exists to build up authoritative reference collections, particularly in areas where traditionally no sustained cephalopods studies have been conducted, e.g., Australia and South America. Such collections now are needed to support the systematic studies that are increasingly required by fisheries or biomedical researchers, for example. In addition, reference collections should be initiated to encourage deposition of material derived from regional exploratory surveys and local fisheries in order to have available material for the future systematic studies that certainly will be necessary. An example of this type of collection is the Australian Museum in Sydney where for years the need for a reference collection of cephalopods has been recognized and such a collection has been built up, largely as a result of fisheries explorations. Now, with the rapidly developing Australian squid fisheries, much important comparative material is available for the systematic studies that are necessary. Such authoritative reference collections are necessary on national, regional, and world-wide levels.

5. A strong recommendation is given to designate four major families of cephalopods that are in critical need of modern, comprehensive systematic revisions. These are the Sepiidae, Loliginidae, Ommastrephidae, and Octopodidae. They are critical families in that (1) they contain the largest numbers of species that occur in the greatest abundance, primarily in neritic, benthic, or epipelagic habitats; (2) they comprise the great majority of the fishery resource (at least 90%), both currently exploited and potentially; (3) they comprise the species that support biomedical, ecological and other biological research; (4) they are among the most poorly known cephalopods so far as their world-wide systematics is concerned. Researchers, educators, administrators, and funding agencies are urged to recognize the critical status of these families and to encourage and develop the research, educational and financial climate necessary to ensure that these important cephalopods receive the attention re-

quired to improve our knowledge and under-
standing. (The Gonatidae and Onychoteuthidae might be added to this list as they are quite speciose and have a potential of significant development in the future).

In view of the status of the world-wide economy it may seem unrealistic to make recommendations that can be carried out primarily through financial commitment. But financial support alone will not advance the science or the development of the resources. Progress in both the scientific and the commercial realms will be achieved only with the combination of financial support and attitudinal commitments. Cephalopods are too valuable a resource for basic and applied purposes for us not to make these firm commitments now for both immediate and future considerations.

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Appendix 2: Bibliography of Cephalopod Biology of the Australian-New Zealand Region


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TECHNIQUES FOR FIXATION, PRESERVATION, AND CURATION OF CEPHALOPODS

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