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BIODIVERSITY AND SYSTEMATICS IN CEPHALOPODS: UNRESOLVED PROBLEMS REQUIRE AN INTEGRATED APPROACH

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Some problems of cephalopod biodiversity are discussed. Many squid species are represented by 2–4 intraspecies groupings that may be wholly or partly sympatric, but differ in spawning season and size at maturity. They may be genetically distinct stock units, but their taxonomic status remains unresolved. Discovery of a biochemical or molecular key to distinguish between intra- and interspecific differences may help to solve the problem of subspecific taxa in cephalopods, as stated by G. L. Voss in 1977. Electrophoretic study of allozyme differentiation is a good method for clearing up relationships between taxa within a family, but this method cannot be used in situations when the concept of subgenus or subfamily is necessary. The problem of suprafamilial taxa needs urgent attention. However, restructuring only one family or group of families leaving others unrevised may lead to skewing the entire system. Examples are splitting the Enoploteuthidae into three families (as proposed by M. R. Clarke in 1988) and raising the rank of the Sepiidae and the Sepiolidae to ordinal, a proposal by P. Fioroni in 1981. In such cases the method of common level should be applied: subdivisions in a large taxon shall be separated by approximately similar characters. Many attempts to select natural groups of families, for example in the Oegopsida, failed primarily because they were based on analysis of a single organ or system of organs when study of other organs/systems may lead to different natural groupings. The use of molecular techniques in cephalopod phylogeny may be profitable, but initial attempts have led to results that are not easily interpretable. The evolution of Recent Cephalopoda has probably proceeded with such large variations in rates among different clades that it is impossible to construct a non-contradictory system based on any single organ or system. No single organ/system-of-organs nor single methodology currently exists that will solve every problem in taxonomy. An integrated approach, based on analysis of as many organs and different taxa as possible, is necessary to construct an accurate picture and not a mosaic of dispersed random pieces.

Biodiversity has been a “fashionable” word during the last decade. However, what does it mean? According to the Convention on Biological Diversity, it is “the variability among living organisms from all sources, including diversity within species, between species and of ecosystems”. The aim of biodiversity studies is the measurement, protection and management of biological diversity at all levels from local populations of a species up to communities and ecosystems. Diversity within species includes all expressions of genetic variation. Bearing in mind that all individuals in non-clonal species are genetically distinct, to measure, monitor and protect biodiversity as a whole is the same as to count and protect each individual separately (Parin and Nesis 1994). This is clearly a *reductum ad absurdum*. The definition makes it clear that this discipline belongs to applied rather than fundamental sciences. Its goal is to prevent loss of any species or other category of organisms. However, it is not an easy task to exterminate a species of cephalopod. The inhabitants of the open ocean are protected by nature, by vastness of the habitat, much more effectively than terrestrial or freshwater organisms. To the author’s knowledge, there is no published and proven report of a species of any marine fish or invertebrate becoming extinct during the past hundred years for direct anthropogenic reasons. Therefore, what really is biodiversity? “Is it just a new linguistic bottle for the wine of old ideas – a changed fashion label designed to attract funding – or does it refer to new and fundamental questions in science?” (Harper and Hawksworth 1994, p. 5). There may well be some truth in the statement that biodiversity is “an element of a game, a part of technology devoted to obtaining additional funding” (Ghilarov 1996, p. 503), at least in dealing with marine, as opposed to freshwater or terrestrial, animals.

Another face of the biodiversity problem must be examined: how many species and other taxonomic categories constitute the class Cephalopoda in general (in the world’s oceans or in a given area), and why is this number so big or so small? This is a fundamental, not an applied, problem. The first part of the question belongs to the discipline of taxonomy, the second to the disciplines of ecology and biogeography. Only the taxonomic aspect is discussed here.

The difficulties in estimation of species numbers, either for a particular group or for a particular place, are well known (May 1994). The difficulties are even greater in estimating numbers within categories

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below and above the species level. Therefore, this paper studiously avoids discussing the number of species and other taxa among cephalopods, but concentrates on current problems of their estimation and on some pitfalls along the way. The way of thinking about this subject is critical and the view presented is that of a sceptic. The most urgent task in cephalopod taxonomy was, is and will be the need to discover and describe new species, particularly in poorly studied areas such as the tropics and the depths of the ocean, and to resolve taxonomically such "catch-all" genera as *Octopus*, *Sepia* and *Loligo s.l.* However, there is also a need to outline and discuss some taxonomic problems concerning biodiversity that arose or became urgent during the last decade or so.

INTRASPECIES GROUPINGS

During the past two decades, many large active squid (Loliginidae, Ommastrephidae, some Gonatidae) and some species of *Sepia* and *Octopus* have been found to consist of some 2-4 partly or wholly sympatric intraspecies groupings differing only in the size at maturity (early- and late-maturing groupings) and/or spawning season (Nesis 1977, 1985, 1993, 1995, Shevtsov 1978, O'Dor 1983, Okutani 1983, Hatanaka *et al.* 1985, Zuev *et al.* 1985, Natsukari *et al.* 1988, Nigmatullin 1989, Hatfield and Rodhouse 1991, Arkhipkin 1993, Nesis and Nezlin 1993, Arkhipkin *et al.* 1996, and many others). Almost all commercially important squid demonstrate such a differentiation.

Spatio-temporal stability of the pattern of differentiation of squid into intraspecies groupings, in spite of protracted spawning and broad range of sizes at maturation (characteristic of squid), is well known and may indicate at least some degree of genetic separation. Each grouping may represent a separate stock unit of population or suprapopulation rank. Are these groupings in fact genetically different and, if so, what is their taxonomic status? Study of this problem using electrophoretic allozyme methods seems to be an appropriate approach.

Such methods found that geographically separate populations of *Illex argentinus* from the Patagonia-Falklands area, supposedly belonging to the spring-summer-spawning shelf grouping and winter-spawning slope grouping, are as different as separate species (Tsygankov 1988, Carvalho *et al.* 1992, Carvalho and Nigmatullin 1993). However, no stable differences have been found between seasonal groupings in *Loligo patagonica* (= *L. gahi*) from the Falklands (Carvalho and Pitcher 1989), nor between the Japanese warm-season- and coldseason-spawning *Photololigo edulis*, previously treated as belonging to different subspecies (or even species) *P. e. kensaki* and *P. e. budo* (Natsukari *et al.* 1988, Natsukari and Tashiro 1991). Further, no unambiguous differences were found between summer-, autumn- and winter-spawning *Todarodes pacificus* from south-eastern Korea, despite clear differences in morphological characters (Kim 1993, Kang *et al.* 1996). The last two papers considered them as three separate ecological populations which maintain genetic exchange. Similarly, no substantial differences have been found between seasonal groups in *Berryteuthis magister* (Katugin 1993, 1995).

Cryptic speciation, as evidenced by allozyme frequencies, is known in both the Loliginidae (*Photololigo*, Yeatman and Benzie 1994) and the Ommastrephidae (*Martialia*, Brierley *et al.* 1993). It is a pity that, among so many papers devoted to the study of allozyme polymorphism in cephalopods, only a few compare squid from different intraspecies groupings. Study of such groupings may bring something interesting to light. The commercial importance of such investigations is obvious, because each stock unit should be managed separately.

GEOGRAPHIC SUBSPECIES

More than 20 years ago, Voss (1977, p. 58) wrote: "So far in systematics we have been dealing mainly with species as separate entities .... Some cephalopod systematists refuse to use subspecies .... In my opinion ... some of the species complexes ... would be clarified using subspecies instead of ... allopatric species". Unfortunately, little has changed since this statement was published. In this paper, some examples of the successful use of the subspecies concept for geographically separated populations and of those cases when it may be useful are presented.

The geographic range of *Loligo vulgaris* consists of two large isolated areas: Faeroe Islands and southern Norway to Senegal, including the Mediterranean Sea, and Angola to East London; it is absent off tropical West Africa. The supposition (Nesis 1982a, 1987) that northern and southern populations belong to different subspecies (not species, as they had commonly been treated), *L. v. vulgaris* Cuvier and *L. v. reynaudii* d'Orbigny, was confirmed by thorough morphological and genetic biochemical analysis (Augustyn and Grant 1988), and recently supported by gene sequence comparison (Bonnaud *et al.* 1996).

The situation is similar for *Loligo forbesii* Steenstrup, which has a seemingly uninterrupted range from central Norway to Cap Blanc (including the Meditterranean Sea) and an isolated population of giants (largest size among all loliginids) around the Azores. Study of genetic variation shows that the European (Faeroes – Lisbon) and Azorean populations belong to different subspecies (Brierley *et al*. 1995), although they remain unnamed.

The small-sized but large-egged Japan Sea population of *Berryteuthis magister* (Berry) is isolated geographically (by shallow straits) and well separated biologically from the homogeneous main population, inhabiting the Okhotsk and Bering seas and the northern North Pacific (Nesis 1989, Kubodera 1992). Separation of the Japan Sea population into a different subspecies was recently validated using both morphological (Katugin 1997) and genetic-biochemical criteria (Katugin 1993, 1995, 1997); formal description of the new subspecies awaits publication.

The vast distribution range of the large, common and economically important neon flying squid *Ommastrephes bartramii* (LeSueur) consists of three completely isolated parts: one in the North Atlantic, one in the North Pacific, and one in the southern hemisphere (Nesis 1985, 1987). A long time ago, morphological, parasitological (Gaevskaya and Nigmatullin 1976) and biochemical (Shevtsova *et al.* 1977, 1979) data proved that squid from all three parts belong to the same species but to three different subspecies, of which the southern one is closer to that in the North Pacific than to the one in the North Atlantic (Shevtsova *et al*. 1979). At present, these subspecies have not been formally described.

A similar situation is known for the giant squid *Architeuthis*, whose distribution also consists of three parts, embracing the North Atlantic, the North Pacific and the Southern Ocean (Nesis 1985, 1987). Many species have been described in this genus. The search for characters which could be used for their identification continued for decades without an acceptable result. Supposed differences do exist, but they are smaller than those usually found between squid species, so the *Architeuthis* taxa remain sibling species or subspecies (Nesis *et al*. 1985, Roeleveld and Lipinski 1991). Valid names for them were selected from the pool of existing formal species names (Nesis *et al*. 1985): *Architeuthis* (*dux*) *dux* Steenstrup (North Atlantic), *A.* (*dux*) *martensi* (Hilgendorf) (North Pacific), and *A.* (*dux*) *sanctipauli* (Vélain) (southern hemisphere). The situation remains unresolved, and in almost all recent papers giant squid are named only *Architeuthis* sp.

The isolated tropical population of *Todarodes pacificus* Steenstrup (type locality: North Australia) was described as a separate subspecies *T. s. pusillus* Dunning by Dunning (1988). Similarly, the range of a related species *Todarodes angolensis* Adam from the southern hemisphere consists of groups in isolated areas: the South-East Atlantic off Namibia and western South Africa; the Tasman Sea and areas around New Zealand. Recently, the species was found between these areas, off Kerguelen Island, by Cherel and Weimerskirch (1995). It is definitely absent from both the South-East Pacific and the South-West Atlantic. It may well be represented by some vicariant subspecies, but a genetic difference has not been found between *T. angolensis* from off Namibia and in the Tasman Sea (Shevtsova 1988).

Many epi- and mesopelagic circumtropical species are widely distributed in the Atlantic and Indo- or Indo-West Pacific, but there is no gene flow between the Atlantic and Indo-Pacific parts of their ranges around South Africa (Nesis 1985). Some species are represented by a series of local forms inhabiting different macrocirculation systems, particularly in such genera as *Abraliopsis*, *Pyroteuthis* and *Pterygioteuthis* (Nesis 1987). In such cases one can also predict the occurrence of geographic subspecies, one in the Atlantic and another in the Indo(West)-Pacific. A disjunct range is also known for *Spirula spirula*, *Octopus* “*vulgaris*” and other species. Voss (1977) believed that use of the subspecies concept in such cases would far better describe relationships between isolated populations and superpopulations than only using species. The present author agrees. It would be important to find a biochemical or molecular key to distinguish between intra- and interspecific differences. The substrate-specific properties of optic ganglia cholinesterases may be such a key (Shevtsova *et al.* 1977, 1979).

GROUPING ABOVE SPECIES LEVEL: ELECTROPHORETIC EVIDENCE

The most speciose cephalopod genera, *Sepia*, *Loligo* and *Octopus*, are almost certainly heterogeneous and the task to resolve them and to revise the respective families, Sepiidae, Loliginidae and Octopodidae, at the generic level has immediate importance. Many attempts to perform this have been made during recent years using conventional morphological methods (Roeleveld 1972, Khromov 1990, Alexeyev 1991, Hochberg *et al.* 1992, Voight 1993, Anderson 1996a, and others). Electrophoretic study of allozymes is an appropriate method for such a task, and it has also been used repeatedly. Unfortunately, the number of species investigated was sometimes limited: in two cases only three species were compared. Common sense indicates that if three species are randomly selected from a large group, it may be expected that two are closer to one another than to the third. Thus, a tree of two branches would be found, one with two species and another with one. This was indeed all that was obtained in such studies.

Perez-Losada *et al.* (1996) and Sanjuan *et al.* (1996) found that *Sepia* (*Rhombosepion*) *orbignyana* and *S.* (*R.*) *elegans* are closer to each other than to *Sepia* (*Sepia*) *officinalis* (nomenclature after Khromov 1990). *Sepia* s. str. and *Rhombosepion* were considered in one paper (Perez-Losada *et al.* 1996) as subgenera, in accordance with Khromov (1990), but in another (Sanjuan *et al.* 1996) as full genera.

Brierley and Thorpe (1994) found that *Loligo vulgaris vulgaris* and *L. forbesi* are closer to each other than either is to *L. gahi.* The last species was considered earlier as a member of the separate genus *Amerigo* Brakoniecki (Brakoniecki 1986, Alexeyev 1991). Addition of two more species *L. edulis* and *L. chinensis*, both with rectal photophores, absent in the three former species, resulted (Brierley *et al.* 1996) in the appearance of a third branch, corresponding to *Photololigo* Natsukari. However, a thorough cladistic analysis of 40 loliginid species based on morphological data (Anderson 1996a) supported the validity of *Photololigo* (as well as *Nipponololigo*, but not *Amerigo*), but demonstrated a much more complex pattern of relationships among loliginid taxa than that derived from limited genetic-biochemical data.

These examples give rise to the following conclusions. Electrophoretic investigation of allozyme frequencies cannot be considered as a "super-method" that leads to results preferable to those derived from conventional morphological analysis; rather, both complement one another. The calculation of Nei's Genetic Distance (*D*) and the construction of respective dendrograms is a good method to clarify taxonomic relationships between species in a family, but it is hardly suitable for determining the taxonomic rank of a branch, because the hierarchy of *D* values is simpler than that resulting from a morphological investigation. Unlike the standard for the calculation of *D* (species, genus and family), more than three levels are used in routine morphological analysis, including some intermediate levels (subgenus, subfamily, etc), and these are unresolvable when using *D*. Morphological analysis will more exactly reflect the complex relations between taxa in nature. The usefulness of the analysis is dependent on the number of species in a genus or family. The last statement seems trivial, but these examples show that the set of species under investigation may be determined not by selection of those species necessary and sufficient to solve the problem, but only of those available for study. The present author knows only one genetic-biochemical investigation treating a family (Ommastrephidae) as a whole, using 9 genera and 16 species (Yokawa 1994). The resulting tree showed clearly the complexity of relationships among taxa in this family and is rather like that resulting from morphological analysis (Ch. M. Nigmatullin, AtlantNIRO, Kaliningrad, pers. comm.).

FAMILIES AND ORDERS: MORPHOLOGICAL EVIDENCE

The classification of modern cephalopods was formulated in general terms many decades ago, before the Second World War, and is outdated (Nesis 1982b). During the past 10 or 15 years many attempts have been made to revise it and particularly to incorporate the classification of extant cephalopods into the system of extinct ones (for a review, see Nesis 1996). In most of these attempts, the characters of one system of organs was used, e.g. skeleton (sepion, gladius). Such changes in classification have not been widely accepted. Nesis (1996) attempted to show that a system based on features of the skeleton disagrees with one based on other organs (in that paper the reproductive system was used). Two attempts at partially improving the classification, based on features of many organs, and almost universally accepted soon after publication, are discussed herein. Such novelties, although seemingly reasonable, in the opinion of the current author, distort the existing system rather than improving it.

Clarke (1988b) elevated the rank of three traditionally adopted subfamilies of the family Enoploteuthidae (Enoploteuthinae, Ancistrocheirinae and Pyroteuthinae) to families. He based this conclusion on features of the gladius, the beaks, the statoliths, the tentacular hooks, on structure and distribution of photophores, on the form of body and fins, the mode of swimming and buoyancy mechanisms. According to Clarke (1988b, p. 337), these subfamilies differ as much as many families differ from one another. To this list two more features, unique among squid, may be added: the absence of nidamental glands in the Enoploteuthinae and the absence/reduction of one oviduct in the Pyroteuthinae. However, many of these differences, such as the presence/absence and position of photophores, the presence, structure and position of hooks, the structure of the statoliths, beaks and gladius, the form of body, fins and buoyancy mechanisms are found commonly between genera in other families (Sepiolidae, Loliginidae, Gonatidae, Onychoteuthidae, Neoteuthidae, Ommastrephidae, Chiroteuthidae, Mastigoteuthidae, Cranchiidae) – see Voight *et al.* (1994) and Nesis (1996). The differences between three subfamilies, although clear and evident, are not greater than between subfamilies in the Sepiolidae, Lycoteuthidae and Cranchiidae. The characters recognized as familial in the former Enoploteuthidae are comparable to subfamilial characters in these families.

Fioroni (1981) had elevated the family Sepiolidae into a separate order. He used the ordinal names Sepioidea and Sepioloidea. (Both are poor choices because the International Code of Zoological Nomenclature recommends [Recommendation 29A] the ending *-oidea* for superfamilies. Clarke and Trueman [1988] and Clarke [1988a] used better names, Sepiida and Sepiolida). The Sepiidae and Sepiolidae are undoubtedly sufficiently distant from one another, and this was confirmed recently by molecular and immunological data (Bonnaud *et al.* 1994, 1996, 1997, Boucher-Rodoni *et al.* 1995). Nevertheless, the former order Sepiida had contained three other families, the Spirulidae, Sepiadariidae and Idiosepiidae. Fioroni (1981) had included the Spirulidae in the order Sepioidea, but the positions of the Sepiadariidae and the Idiosepiidae were unclear. Subsequent authors placed these families in either of the two orders (see Nesis 1996 for review). However, the Idiosepiidae have some unique characters that preclude their grouping with either the Sepiidae or the Sepiolidae, such as the presence of a pelagic paralarval stage (Boletzky 1996), the absence of tentacles in hatchlings (Natsukari 1970), and the supposed absence of accessory nidamental glands (Lewis and Choat 1993). It should, however, be noted that Hylleberg and Nateewathana (1991a, b) indicate the presence of accessory nidamental glands in *Idiosepius pygmaeus* and *I. biserialis*. Based on molecular data, *Idiosepius* is grouped with oegopsid squids (Bonnaud *et al.* 1996, 1997). The Sepiadariidae are characterized by a set of characters different from all other families. *Spirula spirula*, one of the most unusual of all Recent cephalopods, with its unique chambered shell, its super-osmotic buoyancy mechanism, unique “tail” photophore, oegopsid eye, absence of a radula and other features, is more distant morphologically from any other family of the former Sepiida than these families are from each other. Therefore, if the Sepiidae and the Sepiolidae are separated into different orders, it would be necessary to separate the Sepiadariidae and the Idiosepiidae into two more orders, and the rank of the Spirulidae cannot be lower than that of superorder. Moreover, the differences between these two superorders and five orders are really no higher than the differences between families of the suborder Oegopsida. The structure of the reproductive system in *Spirula* is typical for the Sepiida (Nesis 1996).

In such cases as the Enoploteuthidae or Sepiida, and lacking information on phylogeny, the method of “common level” (Scarlato and Starobogatov 1974) may be applied: subdivisions of a large taxon (e.g. Sepiida or Teuthida) could be separated by approximately similar characters. Of course, the value of this method, as of any other, should not be overestimated. Nevertheless, classification of the Coleoidea with one segment restructured (Enoploteuthidae or Sepiida) and the others left unchanged reminds one of a large old apartment house with one flat rebuilt into a palace!

FAMILIES AND ORDERS: MOLECULAR EVIDENCE

In recent years, technical advances have permitted study of the phylogeny of classification of Recent Cephalopoda by the investigation of nucleotide sequences. This method provides more consistently meaningful results than electrophoretic investigation of allozymes at the levels above genus. First, partial mitochondrial 16S rDNA sequences were studied (Bonnaud *et al.* 1994, Boucher-Rodoni and Bonnaud 1996). They were soon complemented by sequences of other mitochondrial genes, cytochrome oxidase subunits I and III (Anderson 1996c, Bonnaud *et al.* 1996, 1997). Nucleotide sequence is an integrated character uniting many events in molecular evolution of a taxon and, in this sense, it may be termed a super-character.

The first results of applying sequence comparison to the phylogeny of the Cephalopoda (Bonnaud *et al.* 1994, 1996, 1997, Boucher-Rodoni and Bonnaud 1996) were not encouraging. In fact, the only clear result relevant to classification was the separation of the Sepiidae from the Sepiolidae, although *Spirula* and *Idiosepius* remained grouped with teuthis squid. In general, phylogeny at the suprafamilial level remains unresolved. One, and probably the most important, cause of this may be, as Bonnaud *et al.* (1994, 1997) supposed, that the evolution of Recent Cephalopoda was very rapid and proceeded with unequal rate in different branches. However, morphological, allozymic and DNA sequences may diverge at different rates in the same taxon (Davis 1994). If the evolutionary pattern in cephalopods caused the lack of phylogenetic resolution in the cited studies, then the nucleotide sequencing of these genes cannot be a crucial method for determination of sister taxa in coleoid cephalopods. It should be stressed that different nucleotide sequences can have a different evolutionary history and are useful for resolving relationships at different evolutionary levels. Because the samples of sequencing of DNA can be fixed in alcohol and even sun-dried (Anderson 1996b), a rapid increase in the number of studied taxa would be expected.

One of the most thorough studies of cephalopod phylogeny was recently published by Young and Vecchione (1996). It was based on a detailed investigation of 50 morphological and anatomical characters in 17 cephalopod families. It showed that the Decapoda and the Octopoda + Vampyromorpha are sister groups, as are the Cirrata and the Incirrata. However, all the cuttlefish (Spirulidae, Sepiidae and Sepiolidae), the Loliginidae and six oegopsid families, including the controversial Thysanoteuthidae, are grouped into one cluster, clearly indicating, first, the monophyly of the Decapoda, and second, the inability of the morphological and anatomical characters they investigated to split it unambiguously into subordinate, suprafamilial taxa. Among oegopsid squid, there are clearly different evolutionary lines, each including one or more families (Clarke 1988b, Young 1991, Anderson 1996a, Nesis 1996), but all attempts to identify them unequivocally remain unsuccessful up to now. This may be an indication that the evolution of Recent cephalopods was more fan-like than tree-like.

CONCLUSIONS

An attempt to compare the classifications of living cephalopods based on characters of the skeleton and reproductive organs showed the incompatibility of these inferred relationships (Nesis 1996). Data based on both systems are also hardly compatible with cladogams based on characters of the beaks, statoliths, hooks, buoyancy mechanisms and locomotion (Clarke 1988a, b, Clarke and Maddock 1988a, b, Engeser and Clarke 1988). This may indicate that the evolution of different systems in Recent Cephalopoda proceeded at an unequal rate and that most (if not all) taxa combine both primitive and advanced characters (Nesis 1985). This point of view is further supported by the results of comparative morpho-anatomical studies at the level of the family (Anderson 1996a) and class (Young and Vecchione 1996). Construction of a non-contradictory system based on any single organ or system of organs, whether skeleton, reproductive organs or any other, is virtually impossible. When attempting to divide taxa at family or higher rank into a set of subordinate ones, it is dangerous to call attention to obvious differences between taxa while ignoring the common characters that unite them. If evolution of the Recent Cephalopoda was quick and at an unequal rate among clades, then nucleotide sequencing could not solve all major taxonomic problems in the group. Clearly, no single system nor any single methodology can open every door and solve every problem in taxonomy. The only solution would be to use as many taxa and characters as possible and to control one methodology (e.g. allozyme analysis or nucleotide sequencing) by another, independent one (e.g. morphological and anatomical). Only such an integrated approach will permit construction of the correct and entire picture, rather than a mosaic of dispersed, random pieces.

To understand the real extent of cephalopod biodiversity, besides the obvious task of discovering new species and higher taxa, three problems should be addressed:

(i) the taxonomic status (if any) of intraspecies groupings differing in spawning time and/or size at maturity;
(ii) a proper description of the status (supposedly subspecific) of populations in isolated parts of disjunct species ranges;
(iii) resolution of the complex and confusing classification of three large families, the Sepiidae, the Loliginidae and the Octopodidae.

To solve these problems, biochemical-genetic, morphological and biological approaches should be combined. The number of genera and species will increase substantially as a result of these investigations, probably including the number of sibling species that may be identifiable only by biochemical or molecular methods, an obvious headache for field-workers obliged to identify cephalopods to species level on a ship's deck.

However, irrespective of the extent to which the numbers of cephalopod species, genera or families increases, they will remain far fewer than those of fish. Operationally, cephalopods are fish (Packard 1966, 1972), but the biodiversity of fish exceeds that of cephalopods by almost an order of magnitude, whether all species are compared or only those inhabiting the open ocean (Parin 1984, Nesis 1985). This difference may be attributed to the youth of Recent Cephalopoda as a whole. Evolution of the class Cephalopoda began in the Upper Cambrian, earlier than that of fish, which first appeared in the Silurian, but the evolutionary explosion of teleostean fish was in the Lower Cretaceous. The time of radiation of modern cephalopods is disputable, but it was probably not earlier than the Palaeocene, i.e. much more recent than that of fish, and the current pattern of cephalopod biodiversity was probably not formed before the Miocene (Nesis 1985). If this statement is true, cephalopods simply have not had enough time to diversify to the extent of fish. Cephalopod ascendancy is yet ahead!

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