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COLEOID CEPHALOPODS THROUGH TIME AND CYBERSPACE; USING CEPHBASE TO EXAMINE BEHAVIOR AND SELECTION

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ABSTRACT

The Coleoidea have a patchy fossil record with some groups having an extensive record and others having virtually none. These extremes are clearly shown when the Belemnoidea are compared with the Octopoda. The reason for this disparity is the lack of a calcified shell (or a shell of any kind) in the recent coleoid groups. There are also profound differences in life history, physiology, anatomy and ecology between the Coleoidea and the other extant cephalopod group, the Nautiloidea, implying that the radiation of the Coleoidea involved more than just modifying the shell. Consequently, and in contrast to the other major molluscan clades, understanding coleoid phylogeny is heavily dependent on a variety of studies of extant taxa. However, preserved material loses much unique and essential information that defines the class, such as rapid behavioral variation in appearance. Traditional methods of disseminating scientific information also limit the kinds of data that can be presented due to high publication costs. CephBase (www.cephbase.utmb.edu) offers researchers a new tool. It allows easy access to 1500 color images, 144 video clips, over 5,000 references, and predator, prey and location data for extant cephalopods.
Keywords: Database, Cephalopod, CephBase, Evolution, Bioinformatics

INTRODUCTION

The Coleoidea appeared in the Devonian and remain a diverse and widely distributed group today. From the Devonian through the end of the Cretaceous period, the majority of coleoid cephalopods had calcified shells. The fossil record of these basal groups, such as the Belemnoidea, familiarly known as "belemnites", is rich. There are hundreds of known species and they are among the most common invertebrate fossils in the Mesozoic. Many different aspects of the evolution and biology have been studied (e.g. biogeography, Stevens 1965; sexual dimorphism, Doyle 1985; mass mortalities, Doyle & Macdonald 1993; functional morphology, Monks *et al.* 1996).

In contrast, the more advanced groups, including the extant cuttlefishes, squids, and octopuses have partially decalcified shells or no shell at all. As a result, the fossil record of these groups is sparse. For example, the Octopoda are known from just two complete specimens, one Jurassic and one from the Cretaceous (Engeser & Bandel. 1988). Therefore establishing convincing phylogenetic relationships is much more difficult and consequently less certain (Jeletzky 1966, Engeser 1990, Doyle 1993, Monks & Wells 2000, Fuchs *et al.* 2003). This becomes all the more frustrating when the profound differences in life history, feeding strategies, physiology and other aspects of extant cephalopods are examined (see Boyle 1987). The fossil record is either vague or silent as far as these issues are concerned; but even a cursory comparison of the living nautilus with an extant octopus or cuttlefish shows enormous behavioral, physiological and ecological differences between them (Mather & O'Dor 1991, O'Dor *et al.* 1990, Wells & O'Dor 1991, Wells *et al.* 1992).

The fossil record can only play a secondary role in understanding the phylogeny of extant Coleoidea.

Morphological data can be collected from preserved material, but cephalopods show a remarkable degree of morphological plasticity, particularly in relation to intraspecific communication, hunting, mimicry and camouflage (Moynihan & Rodaniche 1977, Hanlon *et al.* 1999, Messenger 2001). All of these topics have the potential to provide rich phylogenetic data. However, they are completely lost during preservation. Documenting the behavior of live cephalopods in the field and laboratory by means of photography and video provides us with this kind of information.

Perhaps more than any other animal, cephalopods are able to rapidly change color, texture and shape. This ability is used to avoid predation and in inter- and intra-specific communication. These behaviors are complex and they can change rapidly. Foraging octopuses in the Pacific Ocean change their appearance on average 177 times per hour (Hanlon *et al.* 1999). Moynihan and Rodaniche (1982) were the first to describe the variety of displays used in inter and intra-specific communication in Caribbean Reef Squid (*Sepioteuthis sepioidea*). In this volume, Byrne *et al.* (2003) present the first interactive graphical model to describe the variety and complexity of these behaviors in this species.

The most obvious component of appearance is color. Cephalopods use specialized cells, chromatophores, iridophores and leucophores, to change color (Messenger 2001). They can also raise and lower papillae to change skin texture. They jet to escape threats and produce ink decoys, as the Jurassic Vampyromorphs and Belemnites possibly did (Monks & Palmer 2002). All of these components are used together to rapidly alter the animal's color, shape, posture, texture and location (Hanlon & Messenger 1996).

This information about cephalopod displays and behavior can be stored in images. Prohibitive costs of publishing color images in traditional media limits studies of the role of these displays in cephalopod evolution. Due to their size, large datasets and original data are also rarely published.

Does behavior matter in the evolution of cephalopods? Hanlon and co-workers (1999) suggest that phenotypic plasticity is used to produce an apparent rarity of any one phenotype which makes it difficult for visual predators to form an effective search image. Studies of extant cephalopods show that predation has a major effect on population density, behavior, growth and therefore selection and evolution. Octopus density is inversely correlated with teleost density (Aronson 1991) and according to Mather and O'Dor (1991) octopuses do not forage to fully maximize growth because of the risk of predation. A high fraction, 18%, of *Sepia orbignyana* cuttlebones had scars from predation attempts. Although these are from animals that lived and repaired the damage, these animals paid a price in terms of reduced growth (Bello & Paparella 2003).

The predators of cephalopods are marine mammals, birds, fish and other cephalopods; all of these groups have well developed senses and are capable of moving rapidly through the environment. CephBase contains over 500 records of ecological interactions between cephalopods and their predators. Hypotheses such as the "Packard scenario" (Packard 1972) and the "Modified Packard scenario" (Aronson 1991) feature predation from vertebrate visual predators as the major driving force of cephalopod evolution.

An additional challenge to investigating cephalopods is that much of the diversity of modern Coleoidea occurs in the deep-sea and these species are poorly studied (Wood 2000). Access to video and images to answer simple questions such as: what do they look like alive, how they swim and what behaviors are they capable of have traditionally been limited. In cases such as this, the data often exist in a laboratory where their existence is known to only a few people. Dissemination of this information is the weak link.

THE USE OF CEPHBASE

New technology allows for the inexpensive collection, storage and publication of visual data. CephBase (www.cephbase.utmb.edu), an online relational database, can help (Wood *et al.* 2000). There are over 1,500 color images of extant cephalopods that can be used to examine the range of appearance between and within species. The images are of diverse areas including external anatomy (Fig. 1 A, B), internal anatomy (Fig. 1 C, D), active behaviors (Fig. 1 E, F), camouflage (Fig. 1 G, H), reproduction (Fig. 1 I, J), hard parts (Fig. 1 K, L), life stages such as eggs (Fig. 1 M, N) and taxonomy (Fig. 1 O, P). Each image is

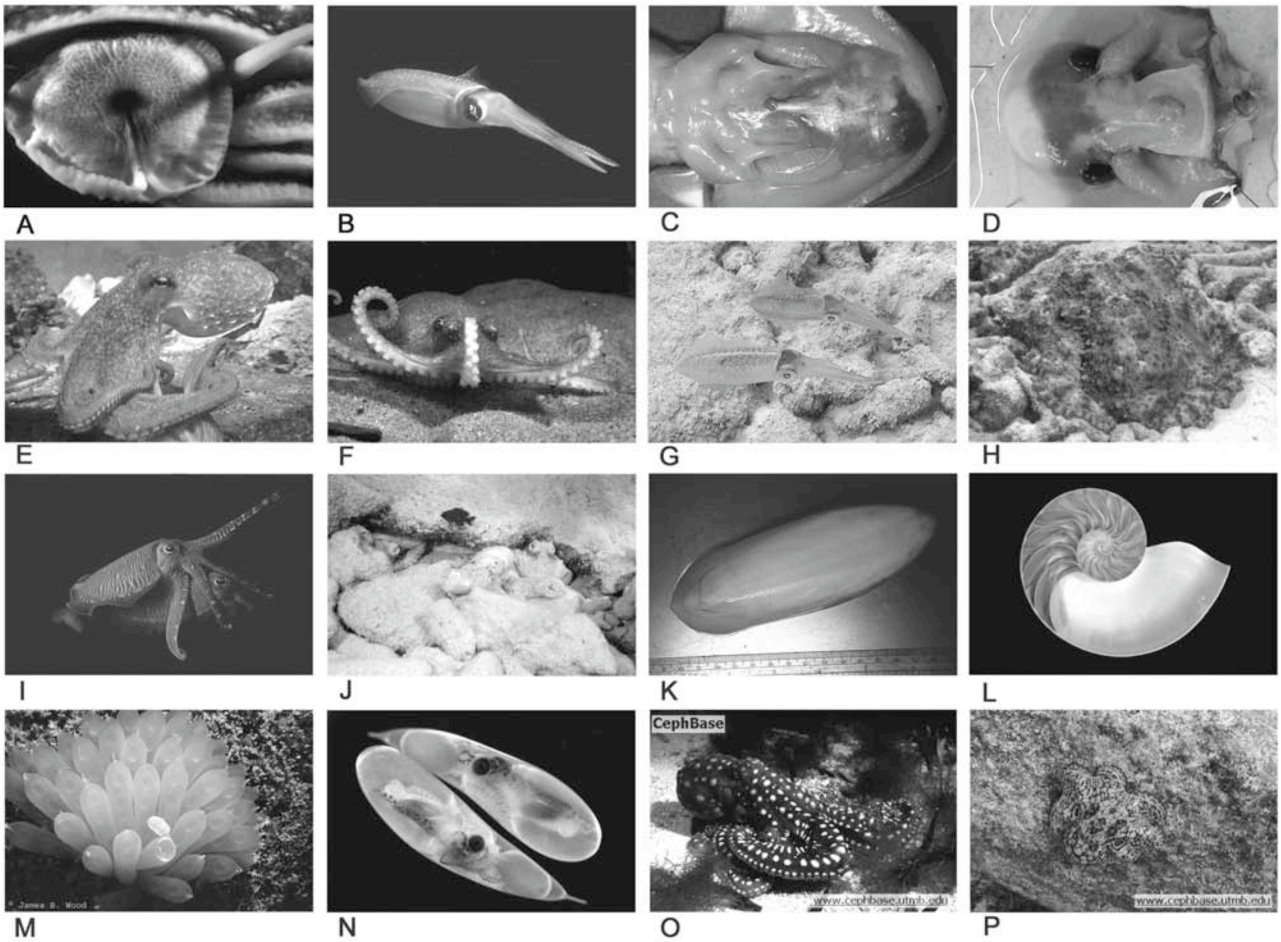

Fig. 1 Representative examples of the 1500+ images of cephalopods in CephBase. The numbers in parentheses refer to the image number in CephBase. **Anatomy, External A** . The primitive eye of *Nautilus pompilius* (1129), **B**. External morphology of the Caribbean Reef Squid, *Sepioteuthis sepioidea* (1521). **Anatomy, Internal C**. *Sepia officinalis* dissection (379), **D**. Dissection of a juvenile male *Octopus vulgaris* (1445). **Behavior, Actions E**. A visual attack of an *O. vulgaris* (1434), **F**. A deep-sea octopus, *Bathypolypus arcticus*, attacking a shrimp. **Behavior, Camouflage G**. Pale *Sepioteuthis sepioidea* (1474). **H**. This large *O. vulgaris* was out hunting during the day (1508). **Behavior, Mating I**. Mated pair of *Sepia pharaonis* (JW TBA), **J**. *O. vulgaris* mating in Bonaire (1469). **Hard Parts K**. *S. officinalis* cuttlebone (264), **L**. *N. pompilius* shell (1415). **Life Stages, Eggs M**. *S. sepioidea* eggs (642), **N**. *Octopus briareus* eggs (902) **Taxonomy O**. According to (Norman 2000) this red with white spot pattern is typical of the *Octopus macropus* species complex (1402) **P**. A Caribbean octopus with ocelli like this must be *Octopus filosus* (1464). The numbers in brackets are the CephBase images numbers. Images D, E, G, J and P by Ruth Byrne, images A, B, C, F, H, I, K, L, M, N and O by James Wood

documented with species, location, depth if known, sex, size, and a caption (Fig. 2). Data are readily accessible across geopolitical borders at any time (Wood *et al.* 2000).

At the first Coleoid Cephalopods Through Time meeting (September 17-19, 2002, Berlin, Germany), paleontologists expressed a need for more images of hard parts of extant cephalopods. For example, they demonstrated that growth, taxonomic and ecological data can be derived just from statoliths. The CephBase team is collecting beaks, pens, statoliths, cuttlebones and images thereof so that they can be documented and added to the database.

There are also currently 144 video clips that show the animal's locomotion, mating behaviors, physiology and camouflage. Many of these video clips are from the video library of collaborator Mike Vecchione of the US National Museum of Natural History. They depict rarely observed deep-sea cephalopods and are documented similarly to the images discussed above.

The repertoire of changes in appearance is species specific. However, some patterns are similar across taxa. For example, the high contrast zebra display of the common cuttlefish, *Sepia officinalis*, is very similar to the Zebra display in the Caribbean Reef Squid *Sepioteuthis sepioidea* (Fig. 3). The zebra display in

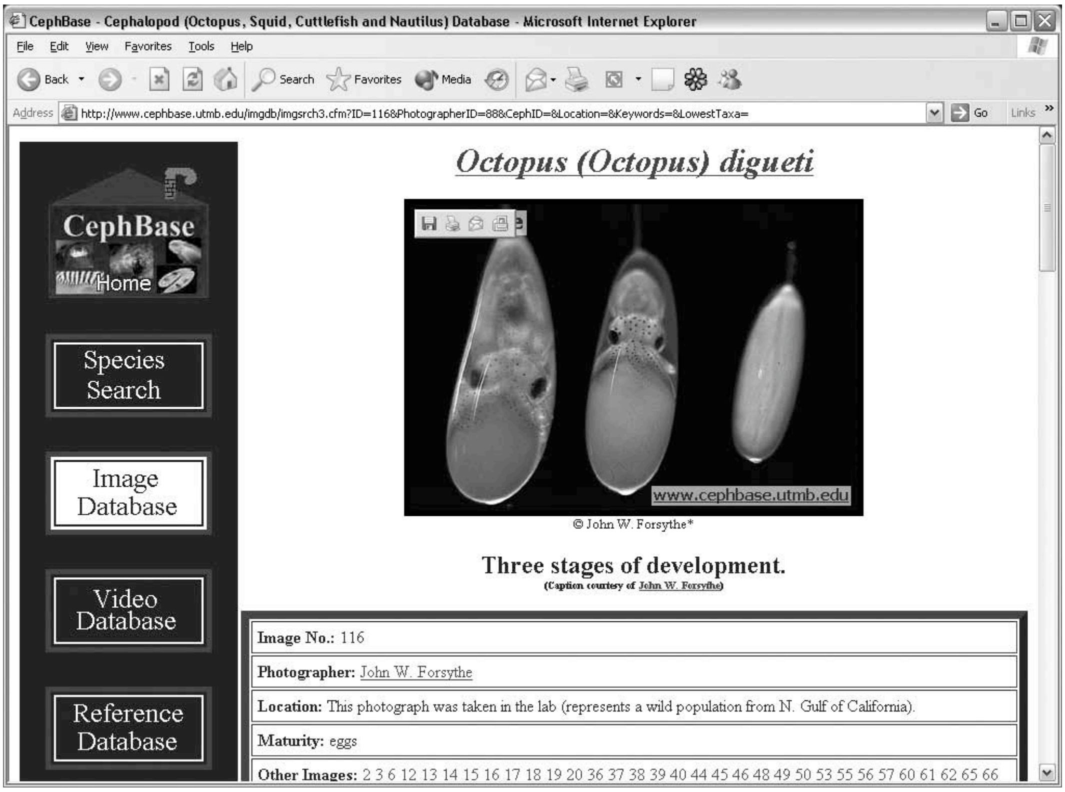

Fig. 2 Screen shot of three *O. digueti* eggs, CephBase image 116. The species name is at the top, above the image, and is linked to a page containing all the information (common names, distribution, environmental data, images, prey, type specimen details, references) that we have for this species. The photographer, John Forsythe, is clearly credited with a link to his contact information. The population these eggs were from is recorded as is their maturity stage, eggs. The cephalopods sex, size, depth observed and other details are also reported when they are known/relevant

both the cuttlefish and the squid appears to be used primarily by males in assessment contests with rival males during competition for reproductive resources. Images can be used to compare and contrast displays across species. In other words, the development of color, texture and shape components are vital for avoiding predators and competing for mates and therefore critical for evolution and natural selection.

CephBase not only contains images of a wide variety of cephalopods, but also addresses cephalopod ecology with a database of 420 predation records. Traditional publications are not able to publish large datasets such as these or the 3886 location records or the 1017 prey records found in CephBase. CephBase offers easy access to a large amount of ecological information quickly.

The data in CephBase are fully referenced; so the tools are there for scientists to verify and investigate further as they wish. For much of the location data, the references are as specific as the jar the specimen is in and the address of the repository. CephBase also contains the repository contact information of almost all of the currently existing type specimens (with modification from Sweeney & Roper 1998).

CephBase can be used to help bridge the gap between paleontologists and researchers studying modern cephalopods. The image and video clips show life history stages, color, texture, posture, movement, reproduction, swimming, hunting, camouflage and other aspects of cephalopod biology and ecology that can help generate hypotheses about extinct cephalopods. The prey database can be compared to the data from fossilized stomach contents, for example ammonites (Lehmann 1975) and the morphology of feeding structures such as beaks and radulas (see Bromley 1993 for octopus examples). Predation on modern cephalopods and their tricks to avoid it may yield clues to the evolution of both cephalopods and their predators. Additionally, the international directory of cephalopod workers helps facilitate collaboration between all cephalopod scientists.

CephBase (www.cephbase.utmb.edu) offers

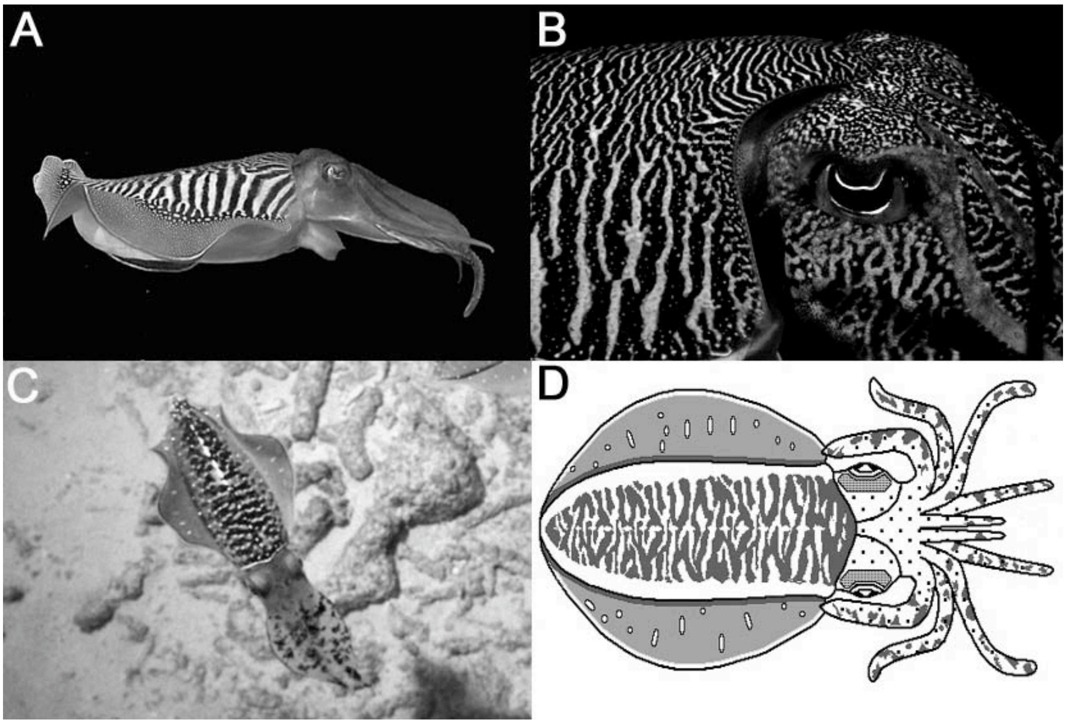

Fig. 3 Zebra display in two species of cuttlefish and a squid. **A**. *Sepia officinalis* zebra display to it's reflection in a mirror. **B**. Male *Sepia pharaonis* zebra during a challenge to another male. **C**. Medium intensity zebra display of a Caribbean Reef Squid, *Sepioteuthis sepioidea* to a rival male **D**. Graphic of a full intensity zebra display of *S. sepiodea*. These high contrast assessment displays are similar across taxa. Images A, B and C from Wood, Graphic D from Byrne *et al.* (2003)

researchers a new tool providing easy access to 1500 color images, 144 video clips, over 5,000 references, and predator, prey and location data for extant cephalopods. Comparisons between modern and extinct species are valuable: understanding the present is the key to understanding the past.

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