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Phylum Echinodermata*

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*In: Zhang, Z.-Q. & Shear, W.A. (Eds) (2007) Linnaeus Tercentenary: Progress in Invertebrate Taxonomy. Zootaxa, 1668, 1–766.

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"...this highly diverse, successful, and ancient phylum." (Littlewood et al., 1997)

Introduction

The Phylum Echinodermata, comprising approximately 7,000 living species, and 13,000 fossil species, is epitomized by the familiar sea star, a universal symbol of the marine realm. This distinctive group of animals may be briefly defined as possessing a skeleton of calcium carbonate in the form of calcite; a unique water-vascular system which mediates feeding, locomotion, and other functions; and a more or less conspicuous five-part radial symmetry. A closer look at some extant echinoderms will show that some taxa of sea cucum-

bers lack calcite in their body walls, some taxa of sea stars have "outgrown" five-part symmetry and may have 50 or more arms, and many echinoderms show a more or less conspicuous bilateral symmetry superimposed upon a radial pattern. Fossil echinoderms can be even more puzzling, for some are decidedly asymmetrical, and others may lack evidence of a water-vascular system. Perhaps the only truly reliable taxonomic character of the phylum is that its members today are restricted to the marine realm.

Despite, or perhaps because of, their distinctive appearance and characteristics, the echinoderms continue to be of great interest to specialists studying higher levels of classification of invertebrates. The history of the phylum is fraught with misconceptions. Linnaeus (1758) did not recognize the echinoderms as a separate group, and placed the echinoderms that were known to him in his "Mollusca", a subdivision of "Vermes". Bruguière (1791) revived Klein's (1734) name Echinodermata—a short-lived independence for the group, for Lamarck (1801) referred the echinoderms to his "Radiata", where they stayed for several decades until finally Leuckart (1854) successfully established the Echinodermata as a distinct phylum. Over the past 160 years, progress on the higher classification of the extant and fossil echinoderms has been fairly steady, with such authors as Ludwig (1889–1907), Bather (1900), Cuénot (1948), and Hyman (1955) providing authoritative summaries of classification history. Given today's formidable flow of publications on higher classification of echinoderms, a one-volume summary *a la* Hyman's would be a monumental task for a single author!

The numerous authors who contributed to the Echinodermata volumes of the Treatise on Invertebrate Paleontology (Moore, 1966–1978) grasped the opportunity provided by the Editor, Raymond C. Moore, to revise the groups for which they were responsible, so that the 1960's became an era of great change in our knowledge of the phylum. At times, new and innovative classifications displaced the old, while for certain taxa the old arrangements won out, but not before exchanges of many letters among the experts had taken place. I was but a minor participant in the Treatise Echinodermata volumes (Pawson, 1966; Fell & Pawson, 1966a, 1966b), but my file of correspondence with Raymond Moore on various problems in the Echinoidea and Holothuroidea is very thick!

Publication of the Treatise volumes stimulated much research work, particularly on fossil groups. New and exciting approaches to taxonomy have resulted in a reassessment of most major groups of fossil and living echinoderms. Cladistic analyses of extant and fossil groups helped to reshape some major classifications, and Mooi and David's (2000 *et. al.*) extraxial-axial theory (EAT) provided a new framework for study of interrelationships. Within the past couple of decades, molecular analyses are offering powerful tools, especially in combination with morphology, with which to address long-standing problems. Thus, the past 40 years have witnessed upheavals in classification at the family, order, and even class level. In the past decade numerous important volumes have been published on the echinoderms, living and fossil. Some of the most comprehensive include: Candia Carnevali & Bonasoro (1999), Mooi & Telford (1998), Barker (2001), Jangoux & Lawrence (2001), Féral & David (2001), Kasyanov (2001), Heinzeller & Nebelsick (2004), Matranga (2005).

Despite the increasing attention received by to this phylum, there remain many major uncertainties and unresolved problems. I am not qualified to suggest solutions to higher classification problems. Rather, in the present paper I hope to highlight some recent research developments in extant and fossil classes. The references cited are not intended to be exhaustive; rather, it is hoped that they will lead the reader into the extensive relevant literature.

Echinodermata as Deuterostomes

The extant Deuterostomia ("second mouth") are usually defined as animals in which the mouth develops from a second opening in the embryo, opposite to the initial opening, the blastopore, of the rudimentary gut. In addition the coelom develops by enterocoely, or pouching from the primitive gut. Smith (2004b) noted that

there was fossil evidence to show that the major deuterostome groups were established by about 520 million years ago (see below under "Other extinct classes of echinoderms"). Composition of the extant Deuterostomia has changed in recent years. At present, it is usually regarded as comprising the phyla Chordata, Hemichordata, and Echinodermata (Cameron *et al.*, 2000), as well as the recently-defined phylum Xenoturbella (Bourlat *et al.*, 2006). In echinoderms with planktotrophic larval stages, the deuterostome affinities of the group are evident. Fell (1948) and others have pointed out that in a significant percentage of echinoderms 1) the coelom develops from a splitting in mesoderm and not from pouching, and 2) the larval mouth becomes the adult mouth. Pawson and Kerr (2001) reported presence of chitin in one species of sea cucumber. Chitin is usually unknown in deuterostomes, but it has been reported from a blenniid fish (Wagner *et al.*, 1993). These various exceptions to the deuterostome "norm" are believed to be relatively minor, and the echinoderms are regarded as fully qualified members of the Deuterostomia.

Interrelationships among Classes

Five extant classes of echinoderms are universally recognized: Asteroidea, Ophiuroidea, Echinoidea, Holothuroidea, and Crinoidea. A sixth class, Concentricycloidea, was described 21 years ago (Baker *et al.*, 1986), and the weight of opinion today seems to favor assignment of the concentricycloids to the Asteroidea (see below). The relationships between the extant classes of echinoderms continue to be a fruitful field for discussion, and the relatively new tools of molecular taxonomy, especially when used in combination with morphology, and evidence from fossils, can provide powerful and persuasive evolutionary scenarios. The several books mentioned above, most of them being the proceedings of international meetings and symposia, include numerous publications discussing relationships at the class level. It may be useful here to mention a small selection of additional publications.

Smith (1988a), in a phylogenetic analysis of fossil evidence, suggested times of divergence of the five (then) modern classes at 450–590 million years ago (Figure 1). Smith noted that the long subsequent history for each class allowed for introduction of a great deal of "noise" via mutations. The surge in molecular taxonomy occurred at around this time. For example, Wada & Satoh (1994) analyzed one species from each class, and concluded that phylogenetic relationships among extant classes matched those deduced from the fossil record. Then, Littlewood (1995) discussed molecular and morphological data sets, noting that poor phylogenetic resolution arose from inconsistent morphological data sets, and inadequate molecular data, based upon a small representation of taxa. Soon thereafter, Littlewood *et al.* (1997) combined more comprehensive morphological, molecular, and stratigraphic data, and arrived at three competing phylogenetic solutions, of which two appeared to be the most plausible. Their study demonstrated that frustrating pitfalls can appear even when data sets are fairly detailed.

Smith (1997) reaffirmed what many previous authors had noted, that larval morphology of echinoderms has evolved independently of adult morphology, and that larval morphology, when taken alone, cannot inform the phylogeny of adult echinoderms.

Janies (2001), providing additional sequence data, especially for the refractory ophiuroids and asteroids, concluded that echinoids and holothuroids "are related", and crinoids are the sister taxon to the remaining extant echinoderm classes. The relationship between asteroids and ophiuroids was more difficult to address, but Janies found strong support for monophyly of each of these two classes. McEdward & Miner (2001) comprehensively summarize what is known about larval development in echinoderms, and construct phylogenies for the extant classes based upon patterns of development.

As more molecular data become available, and more comprehensive and refined morphological databases are produced. It seems likely that additional support will be found for the classical "echinoids + holothuroids, asteroids + ophiuroids, crinoids" arrangement of extant classes. The various supra-class names that have been

applied to groupings of echinoderms – Echinozoa, Asterozoa, Crinozoa, Pelmatozoa, Eleutherozoa – are occasionally used in the formal sense, but for the most part they are used as informal and convenient adjectives in describing life habits, body form, feeding propensities, and the like.



FIGURE 1. Phylogram for the five classes of echinoderms, with stratigraphic ranges (solid bars), and ranges of proposed stem group taxa. Divergence times for major groups shown by stars. From Smith (1988a), q.v. Published with permission.

Concentricycloids—enigmatic, or not?

Since the first concentricycloid was described (Baker, Rowe and Clark, 1986), numerous authors have investigated and discussed the status of these small (usually <1 cm diameter), discoidal echinoderms with the mouth frame in the form of a ring, and a ring of tube feet. The only known habitat is deep-sea wood, either naturally occurring waterlogged wood, or wood that has been placed at depth by submersibles for extended periods of time. Baker *et al.* (1986) referred these extraordinary animals to a new class Concentricycloidea. Three species are now known: *Xyloplax medusiformis* Baker, Rowe and Clark, 1986; *X. turnerae* Rowe, Baker and Clark, 1988; *X. janetae* Mah, 2006. In the 21 years since description of the first species, numerous authors have voiced their opinions about the status of these strange echinoderms. Smith (1988a), Belyaev (1990), Janies & Mooi (1999), Janies (2001), argued for placement of the concentricycloids within the Class Asteroidea, perhaps near the caymanostellids. Rowe, Baker & Clark (1988), Pearse & Pearse (1994), Mooi *et al.*(1998), Baker (2003) and others have been a little more cautious in their assignment of the group. In a detailed recent summary, Mah (2006), having examined the morphological, cladistic, and molecular evidence, placed the concentricycloids within the Asteroidea (Figure 2), where they comprise the monotypic Infraclass Concentricycloidea of the Subclass Ambuloasteroidea (*sensu* Blake & Hagdorn, 2003).



FIGURE 2. Character distribution applied to crown-group asteroids and concentricycloids. Note Infraclasses Neoasteroidea and Concentricycloidea. From Mah (2006) *q.v.* Published with permission.

Class Asteroidea (sea stars, starfish)

Extant asteroids

Today's oceans are graced by 2100 species of sea stars. In their magisterial monograph of Atlantic sea stars, Clark and Downey (1992) noted that the status of the entire group—whether it should be referred to a Class or a Subclass—was 'controversial" and they declined to discuss the topic. At the ordinal level, they elected to follow the classification proposed by Blake (1987, 1989), and recognized seven orders: Paxillosida Perrier, 1884; Notomyotida Ludwig, 1910; Valvatida Perrier, 1884; Velatida Perrier, 1893; Spinulosida Perrier, 1893; Forcipulatida Perrier, 1893; Brisingida Fisher, 1928. Clark and Downey chose to ignore, or did not accept, the three Superorders proposed by Blake (1987). Gale (1987) proposed a new Subclass, Neoasteroidea for the post-Paleozoic crown group asteroids, and he differed from Blake in naming just four orders: Paxillosida, Notomyotida, Valvatida (including the velatids and spinulosids), and Forcipulatida (including the brisingids).

Subsequent to the Blake and Gale papers, Lafay et al (1995) made a combined morphological and molecular study of nine sea star species, in an attempt to provide a broader framework for discussion of the differing classifications. Papers published following a symposium on evolution of starfishes (see Blake, 2000; Blake *et al.*, 2000; Mooi & David, 2000; Hotchkiss, 2000; Vickery and McClintock, 2000; Hrincevich *et al.*, 2000; Mah, 2000; Knott & Wray, 2000) offered possibilities for resolution of some differences in morphology-based phylogenies by the addition of more comprehensive molecular data. The consensus of opinion seemed to be that molecular/morphological studies are very necessary and desirable, especially for resolving problems at the family-level and below (see, for example, Hrincevich et al, 2000; Knott & Wray, 2000; O'Loughlin & Waters, 2004; Mah, 2007). Refractory ordinal-level problems may eventually yield to the cumulative effect of studies at lower levels of classification. For example, Matsubara *et al.* (2005) found that comparisons of genome structure were "uninformative for the purposes of asteroid phylogeny, but that phylogenetic analyses based upon nucleotide and amino acid sequences indicated that paxillosidan characters are secondarily derived, and perhaps the paxillosids are specialized rather than primitive asteroids".

Extinct asteroids

In a comprehensive paper describing the Ordovician to recent history of the Asteroidea, Blake & Hagdorn (2003) diagnosed a new Subclass Ambuloasteroidea, to reflect their findings and those of Mooi & David (2000 *et al.*) on their extraxial/axial theory; see above) in regard to the axial skeleton of Paleozoic and post-Paleozoic asteroids. Blake & Elliott (2003) found that axial skeletal characters could be compared across stem- and crown-groups of asteroids. The Ambuloasteroidea embrace two infraclasses, one "Unknown" which includes the late Paleozoic Families Calliasterellidae Schöndorf 1910, and Compsasteridae Schuchert 1914, the other Gale's (1987) Infraclass (formerly Subclass) Neoasteroidea. The Neoasteroidea embraces the remaining post-Paleozoic asteroids.

Shackleton (2005) comprehensively reviewed Ordovician stem-group asterozoans (asteroids plus ophiuroids) and proposed a revised classification. A new Plesion (Order) Eopentaroida was proposed to accommodate three distinctive Silurian genera.

It was noted that the asteroid and ophiuroid body plans, already established in the Ordovician, indicated that these groups had a considerable, but unknown, pre-Ordovician history. In this context, Herringshaw *et al.* (2007) established that the Silurian *Lepidaster grayi* was the earliest-known multiradiate sea star, so that the multiradiate body plan was also established early. Blake & Hotchkiss (2004) characterized the post-Paleozoic asteroid crown group, identifying apomorphies of crown-group diversification.

Class Ophiuroidea (brittle stars, serpent stars, basket stars)

Extant ophiuroids

The 2,000 species of ophiuroids are traditionally assigned to two orders, as follows: Order Euryalida Lamarck, 1816; Order Ophiurida Müller & Troschel, 1840. Smith, Paterson & Lafay (1995) summarized the state of knowledge of ophiuroid classification after a cladistic analysis based upon morphological characters. Their molecular data were equivocal, and did not help to resolve some problems arising from the morphological analyses. Smith & Paterson assigned the mysterious *Ophiocanops fugiens* (see Fell, 1962, 1963) to Subclass Oegophiuridea Matsumoto, 1915, and referred all other ophiuroids to Subclass Ophiuridea Gray, 1840. However, Pearse *et al.* (1998), with access to new material of *Ophiocanops*, demonstrated that this genus belonged in the Family Ophiomyxidae. These findings, coupled with those of Hotchkiss (1977) have resulted in the disappearance of the Oegophiuridea as a subclass of ophiuroids.

Cisternas *et al.* (2004) studied development patterns in 23 species, suggested some evolutionary pathways, and noted that good molecular phylogenies would help to refine their hypotheses.

Extinct ophiuroids

The puzzling Ordovician stelleroid *Stenaster* was studied in detail by Dean (1999), who concluded, after a cladistic analysis of early asteroids, somasteroids, and ophiuroids, that this asteroid-like animal was in fact an ophiuroid, converging secondarily with asteroids.

Kroh (2004) reported on the first fossil record of a euryalid ophiuroid from the Miocene of the Mediterranean. Jagt (1999) found a rich fauna of ophiuroids in the Cretaceous of the Maastrichtian Stage. Hotchkiss (1993 *et al.*) has described several Ordovician and Devonian ophiuroids from North America, and commented extensively on origins and relationships of skeletal features.

Class Echinoidea (sea urchins, sand dollars, heart urchins)

Extant and fossil echinoids

The 800 species of echinoids alive today, coupled with the wonderful fossil record, make the echinoids excellent candidates for a great variety of studies, from reproductive biology to evolution. Echinoids are also of commercial importance; Yokota *et al.* (2002) cover biology and aquaculture of sea urchins, and Lawrence (2001, 2006) deals with biology, ecology, and aquaculture of edible sea urchins worldwide.

Extant echinoids are informally divided into "regular" forms with obvious radial symmetry, spherical bodies and uniformly long spines, and "irregular" forms – bilaterally symmetrical urchins, including sand dollars and heart urchins. Echinoids are typically classified into two subclasses and 12 orders, as listed by Smith (1984), and modified slightly by Littlewood & Smith (1995). Subclass Cidaroidea Claus, 1880 comprises the Order Cidaroida Claus, 1880. Subclass Euechinoidea Bronn, 1860 includes all other echinoids: Order Echinothurioida Claus, 1880; Order Diadematoida Duncan, 1889; Order Pedinoida Mortensen, 1939; Order Calycina Gregory, 1900; Order Arbacioida Gregory, 1900; Order Phymosomatoida Mortensen, 1904; Order Temnopleuroida Mortensen, 1941; Order Echinoida Claus, 1876; Order Cassiduloida Claus, 1880; Order Clypeasteroida Agassiz, 1872; Order Spatangoida Claus, 1876. All of the above orders except the last three are regular echinoids; the last three comprise the irregular echinoids. Most fossil echinoids can be assigned to the orders listed above; there are some exceptions, and the reader is referred to the papers cited below for further information.

Phylogenetic relationships of the echinoid higher taxa have been studied by several authors, using morphological data (test and spine morphology, structure of teeth, pedicellariae, structure of larvae) and molecular sequences. Some of the more comprehensive studies include Smith (1988b), Smith *et al.* (1992), Littlewood & Smith (1995), Lee (2003), Stockley *et al.* (2005), Smith *et al.* (2006) and Smith (2007). In many cases the fossil record was involved, peripherally or primarily, in the discussions as well. Most of the regular echinoids seem to have diverged relatively recently, between 65 and 35 million years ago. Solovjev & Markov (2004) studied earliest divergence of irregular echinoids, and selected 15 binary characters for cladistic analysis. They agreed in general with the conclusions of Smith (1984) and Rose & Olver (1988) but differed in some details.

Class Holothuroidea (sea cucumbers, beche de mer)

Extant holothuroids

The approximately 1400 species of holothurians, in particular the tropical shallow-water forms, are receiving increasing attention from specialists, and substantial changes in classification below the family level are expected to occur over the next decade. Above the family level, the classification has been fairly stable for many years. The orders Aspidochirotida Grube, 1840; Elasipodida Théel, 1882; Molpadiida Haeckel, 1896; and Apodida Brandt, 1835 remain well-characterized. The distinction between the Dendrochirotida Grube, 1840 and Dactylochirotida Pawson & Fell, 1965 is less well-defined. At some points the alleged morphological differences between these two groups are less well defined, but at the molecular level, the distinctions are more robust (Kerr & Kim, 2001). The three subclasses introduced by Pawson & Fell (1965) - Apodacea, Aspidochirotacea, and Dendrochirotacea—as a convenient grouping of the orders have essentially been abandoned over the years, and Kerr & Kim (2001) convincingly demonstrate their impracticality.

The interrelationships between extant holothurians at the family level and above were rather neglected until the 1990's, when a few authors used morphological and molecular approaches to investigate relationships. The publications by Kerr & Kim (1999, 2001) and Kerr (2001) were pioneering efforts, and they surely stimulated the surge in popularity of holothurians as research subjects at all levels of classification! Lacey *et al.* (2005) found cause to disagree in some areas with Kerr & Kim's conclusions, but all of these authors agreed with several earlier authors in suggesting a basal position for the Apodida.

Smirnov (1998) revised the classification of the Order Apodida, using morphological characters. Phylogenetic studies of family-level and lower groups are burgeoning (for example, Kerr *et al.* 2005) and certainly these studies will materially affect the higher classification in the near future.

Extinct holothuroids

The fossil record of holothurians has long been regarded as poor, an opinion disputed by Kerr & Kim (1999). Since the attempts by Pawson (1966, 1980) to integrate the higher-level classifications of fossil and recent holothuroids, the study of fossil groups has burgeoned, largely under the leadership of Gilliland (1992, 1993) and Reich (2002, 2004 *et al.*). Gilliland (1993) provides a comprehensive summary of the state of knowledge of fossil holothurians, and identifies areas where more research is required. In several publications, Reich reviews European and other fossil holothurians. Gilliland and Reich, and Smirnov (1999), suggest divergence times for the major holothurian taxa, and their conclusions are discussed by Kerr & Kim (1999, 2001), and others.

Class Crinoidea (sea lilies, feather stars)

Extant crinoids

The 650 species of extant crinoids, represented by 100 stalked crinoids and 550 feather stars, have received considerable attention from specialists, partly because of their intrinsic interest, and partly because these extant animals can throw some light on the living habits of the fossil crinoids. The living crinoids are all referred to the Subclass Articulata Zittel, 1879. Most authors regard the feather stars as comprising a single order, Comatulida A.H. Clark, 1908. Messing (1997) notes that Simms (1988) reduced the comatulids to an infraorder, Comatulidia. Rasmussen & Sieverts-Doreck (1978) recognized seven superfamilies in the order Comatulida. Further details are provided by Messing (1997). The extant stalked crinoids are assigned to four orders: Millericrinida Sieverts-Doreck, 1952; Cyrtocrinida Sieverts-Doreck, 1952; Bourgueticrinida Sieverts-Doreck, 1952.

In a recent review of the comatulids, Messing (1997) covers classification, ecology, and taphonomy, among other topics. For the stalked crinoids Roux *et al.* (2002) provide keys and checklists to the genera. Comprehensive and detailed revisions, such as David *et al.* (2006) of the stalked crinoid genus *Endoxocrinus* are regrettably rare, as are regional studies such as Messing (2007). The emphasis on morphology is gradually being complemented (supplanted eventually?) by molecular approaches, some producing astonishing results. For example, Cohen *et al.* (2004) found that a clade containing the genera *Caledonecrinus, Gymnocrinus, Holopus,* and *Proisocrinus,* and also possibly *Cyathidium* raises many intriguing questions about the taxonomic placement of these entities. Future molecular investigations should reveal further major surprises in the extant crinoids.

Extinct crinoids

More than 6,000 species of fossil crinoids are known, and revisionary work, usually below the order level, is proceeding apace. The current classification of the class Crinoidea, in the opinion of Ausich (1998) recognizes six subclasses: Aethocrinea Ausich 1998; Cladida Moore & Laudon, 1943; Camerata Wachsmuth & Springer, 1885; Flexibilia Zittel, 1895; Articulata Zittel, 1879; Disparida Moore & Laudon, 1943. Hess *et al.*

(2003) describe assemblages of crinoids from the Ordovician to the Tertiary, and they study form and function, evolutionary history, classification, among other topics. Ausich (1999) discussed the origin of crinoids in light of the re-interpretation of the Cambrian *Echmatocrinus* as an octocoral. Ausich suggests an early Ordovician origin for the crinoids from primitive rhombiferans via paedomorphosis. Ausich & Kammer (2001), emphasizing mostly fossils, comment on the status of research on crinoids, and identify areas for future research.

Other Extinct Classes of Echinoderms

A useful and comprehensive classification of fossil echinoderm groups is provided by Simms *et al.* (1993). Mooi (2001) discussed (Figure 3) and critically assessed publications on fossil echinoderms for the period 1980-2000. Ausich and Webster (in press) undoubtedly contains comprehensive summaries of the status of most fossil echinoderm groups, along with an extensive list of references.



FIGURE 3. Phylogenetic hypothesis of fossil and extant echinoderms. From Mooi (2001), *q.v.* Published with permission.

Loven's law and ray homologies are described in echinoids, ophiuroids, edrioasteroids, and an ophiocistioid by Hotchkiss (1995). In a related study with broad implications, Sumrall & Wray (2007) discuss pentamerous symmetry and its origin in the 30 Cambrian-Ordovician clades of echinoderms.

Shu *et al.* (2004) describe, and Smith (2004b) comments on, what are believed to be ancestral echinoderms ("velulocystids") from the Lower Cambrian of China (Figure 4). The vetulocystids have a globose theca and a tail. Smith (2004a) studied phylogeny of deuterostomes, and anatomy of carpoids, and concluded that early deuterostomes with a stereom skeleton and gill slits may have existed, but it is not likely that sterom and a notochord co-occurred. These conclusions support in part (gill slits), and disagree in part (notochord) with the ideas of Jefferies *et al.* (1996). David *et al.* (1999), applying the extraxial/axial theory, regard the four non-pentamerous classes comprising the homalozoans as early echinoderms, but not indicative of the plesiomorphic morphology of the phylum. Further, the Homalozoa is not a monophyletic assemblage. Lefebvre (2007) studied in detail the palaeobiogeography and palaeoecology of cornutes and mitrates. Parsley (1999), using a cladistic approach, determined that the Cincta (Homostelea) are blastozoans.

Ophiocistioids have been reviewed by Haude (2004), and Reich & Haude (2004).

Dominguez-Alonso (1999) presented new data on the structure of ctenocystoids and proposed a new approach to the early evolution of echinoderms.



FIGURE 4. Phylogeny of early deuterostomes. From Shu et al. (2004), q.v. Published with permission.

Some New Horizons

Molecular analyses are transforming our view of the echinoderms at all taxonomic levels. Such analyses cannot solve all problems, and may merely add "noise" to equivocal morphological results. But some recent research results are startling indeed, and point to exciting future approaches. Here are just two examples: Wilson *et al.* (2007) found that the Antarctic comatulid previously known as the single widely distributed species *Promachocrinus kerguelensis* may in fact embrace at least five species-level clades. Further work is indicated! And, while it appears that molecular analyses in ophiuroids can produce some equivocal results, in the case of the cosmopolitan "species" *Amphipholis squamata*, analysis of 16s mitochondrial DNA allowed successful identification of several allopatric clades (Le Gac *et al.*, 2004).

It would be foolish to ignore the internet in this review article. Forey *et al.* (2004) have noted that "webbased taxonomy is the way forward, having the advantage of speed and currency of information dissemination..." Scientific literature is becoming readily available on the web, and on-line specialized library and literature searches, and database searches, will soon be a matter of convenient routine to biologists world-wide. In addition, exchange of scientific information can occur with extreme rapidity and with great benefit to all involved. For example, a group of about 30 holothurian experts led by Gustav Paulay at the University of Florida and Alexander Kerr at the University of Guam is currently studying aspidochirotids (mostly tropical *Holothuria* and *Stichopus* and their relatives). Digital images of interesting specimens found in the field or in a museum collection are sent to participants for comment, and morphological and molecular studies can be completed within a few days. Investigators in the field, laboratory, and museum bring their varied expertise and experience to bear on complex problems. New taxa are characterized; localities, populations, museum specimens, are scheduled for further study, and comprehensive databases are being constructed. Authoritative revisions of tropical holothurian groups are under way. Colleagues are mystified over the fact that these tropical sea cucumbers, the "ugly sisters" of the splendiferous sea stars, can create such excitement in a group of cynical marine biologists!

Acknowledgements

I thank my research collaborator, Doris J. Vance, for kindly reading a draft of this paper.

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