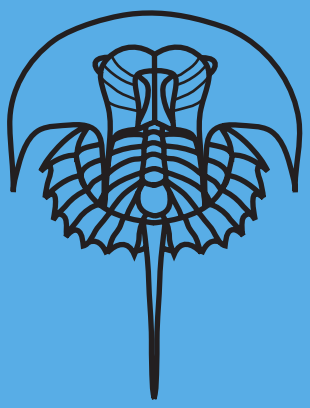

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D. T. Donovan and Dirk Fuchs

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PART M, CHAPTER 14: HISTORY OF HIGHER CLASSIFICATION OF COLEOIDEA

D. T. Donovan and Dirk Fuchs

[University College London, desmond.donovan@virgin.net; Freie Universität Berlin, drig@zedat.fu-berlin.de]

MAJOR SUBDIVISIONS OF CEPHALOPODA

LINNAEUS AND SCHNEIDER

Carl Linnaeus (1707–1778) is justly famous as the founder of modern classification of plants and animals. In the tenth edition of his *Systema naturae* (Linnaeus, 1758), the invertebrate animals comprised two classes: Insecta (i.e., all arthropods) and Vermes (worms), which included everything else, not only wormlike animals but also jellyfish, corals, and echinoderms, among other things. Class Vermes was divided into five orders: Intestina, Mollusca, Testacea, Lithophyta, and Zoophyta. The internal anatomy of invertebrates was poorly known, and, consequently, the animals today grouped in Mollusca were split up according to whether they possessed an external shell (Testacea), or not (Mollusca). Later research, initiated by Cuvier (from 1769 to 1832), showed that this was an artificial criterion.

Accordingly, Linnaeus (1758) listed *Sepia* under Mollusca with the species *S. officinalis* and *S. media, S. Octopodia, S. Loligo,* and *S. Sepiola.* The two other cephalopod genera included were *Argonauta* and *Nautilus,* both in Testacea. Affinity of these with the cuttlefish was evidently recognized, however, for Linnaeus (1758) wrote *Animal Sepia,* with a "?" in the case of *Nautilus.* In *Nautilus,* Linnaeus (1758) included *Spirula,* fossil *Orthocera,* and noncephalopodan entities now placed in Foraminifera, all these groups being united on account of their chambered shells.

The German polymath Johann Gottlob Schneider (1750–1822) was the first to recognize cephalopods as a distinct group and offer a logical classification. He called them Octopodia, a term which had been used by Scopoli (1772). Schneider has been credited with originating the term cephalopod (e.g., Mangold & Portmann, 1989), but the word does not occur in his work.

Schneider (1784, p. 109, 116) divided Octopodia into two classes, which he did not name:

Classis I. Pedes octoni breves, promuscides binae; venter pinnatus, ossiculum dorsi.

Classis II. Pedes octoni longi basi palmati, absque promuscidibus, pinnis et osse dorsali.

He thus made the distinction between Decapoda and Octopoda, although these were not named until 1817. Classis I included *Sepia, Loligo, Teuthis,* and *Sepiola.* In Classis II, he included *Polypus, Moschites, Nautilus,* and *Pompilus*. These were referred to as *Arten,* a word now used for species but used in a more general sense by earlier German writers. Hemming (1954) concluded that *Octopodia* was a generic name and that the eight subdivisions were species. The International Commission on Zoological Nomenclature suppressed *Octopodia* (as a genus) and the other eight names (whether as genera or species) in ICZN Opinion 233 (1954).

The earliest generic name to be proposed for a fossil coleoid was *Belemnites,* which in a formal sense is held to date from Lamarck (1799) (Doyle & Riegraf, 1986). Several authors employed more or less formal versions of this word, including family Belemnitidae (Owen, 1836). The genus *Belemnites* was suppressed by ICZN Opinion 1721 in 1993, and the family name Belemnitidae was ruled to be unavailable at the same time.

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CUVIER AND LAMARCK

The beginning of modern classification is to be found in the work of the French biologist Georges Cuvier (1769–1832). Cuvier spent the years 1788 to 1794 as tutor to a family in Normandy, making observations on marine and terrestrial natural history and publishing papers on limpets, woodlice, and Diptera. Moving to Paris early in 1795, he was ready to make major improvements to the Linnaean classification. In the spring of that year, he read several papers to the Société d'Histoire naturelle. After disposing of a new classification of mammals on 20 April, he turned his attention on 10 May to the Insecta and Vermes of Linnaeus, replacing the two old classes with six: Mollusques, Crustacés, Insectes, Vers, Échinodermes, and Zoophytes (Cuvier, 1795a). Thus, he united Linnaeus's Mollusca and Testacea, separated the former Insecta into the primarily marine crustaceans and the primarily terrestrial insects, and rescued the echinoderms from submergence in Vermes: Mollusca.

At the meeting on 30 May, Cuvier (1795b) examined the mollusks in detail and subdivided them into three new orders: céphalopodes, gastéropodes, and acéphales. Throughout this revolution in classification, Cuvier stressed the importance of dissection and internal anatomy, and he was thus able to improve on earlier work based essentially on external appearance. Inevitably, mistakes occurred at first; Acéphales included brachiopods, barnacles, and tunicates, as well as the modern Bivalvia. These mistakes were gradually corrected as more animals were dissected.

Céphalopodes were defined as mollusks with a free head supporting an arm crown, and included "les seiches, que je divise en seiches [i.e., cuttlefish] et en poulpes [i.e., octopus]." (Cuvier, 1795b, p. 448). The term céphalopode (Greek κεφαλη, head, ποδος, foot) was coined because of the use of the arms for locomotion (". . . grands tentacules sur lequels ils marchent," Cuvier, 1795b, p. 447), presumably referring to octopods.

Céphalopodes originally included only the subdivision later named Dibranchiata (Owen, 1832). Cuvier (1797) extended the scope of the group to include ectocochleate forms: *Nautilus,* the fossil ammonites, and orthoceratites. He also included Foraminifera, or at least those with chambered shells, possibly following Linnaeus, who had included some of them in *Nautilus* (1758, p. 709).

French authors of this period habitually used vernacular names. The formal term Cephalopoda was first used in the English translation (1802) of Cuvier's lectures on comparative anatomy.

While Cuvier's classification of the Mollusca was founded primarily on the soft parts, a different approach was followed by Jean-Baptiste de Monet de Lamarck (1744–1829). He had devoted his earlier biological work to botany but in 1793 was appointed "Professeur d'Histoire Naturelle des Insectes et de Vers" (i.e., the invertebrates of Linnaeus) at the Paris Natural History Museum. Lamarck at that time had much more experience with taxonomy than his junior Cuvier. In 1792, he had published a paper on some of the "vers testacés" in which he remarked, perhaps with a touch of irony, that a classification founded on the animals rather than on their shells would render collections of shells almost useless, but, in any case, was at that time impossible as the inhabitants of many shells were still unknown. In his "Nouvelle classification des coquilles" (Lamarck, 1799), the octopod *Argonauta* was placed in Coquilles univalves uniloculaires, while *Nautilus* and *Spirula,* along with *Belemnites* and several more fossil genera, were Coquilles univalves multiloculaires. Lamarck did not then use the term céphalopodes.

Two years later, Lamarck (1801) included the endocochleate genera in Mollusques céphalés (i.e., cephalopods and gastropods), dividing these into Mollusques céphalés nus, which included *Sepia, Loligo,* and *Octopus*

and some opisthobranch gastropods, and Mollusques céphalés conchilifères, which included the ectocochleate cephalopods and most of the shell-bearing gastropods. LAMARCK's classifications of 1799 and 1801 were patently artificial in the light of CUVIER's work. They were meant to be applicable to both Recent and fossil shells.

It may be stressed at this point that the variety of living cephalopods then known was very limited: essentially *Nautilus* and *Spirula* (shells only), cuttlefish (*Sepia*), a few squids (*Loligo*), and octopus. They were much less diverse than gastropods or bivalves. In the early classifications, higher taxa were almost as numerous as genera. Fossil forms did not add much to this diversity. All then recognized had chambered shells, and ammonites and belemnites were each still regarded as a single genus. The great variety of fossil nautiloids was yet to be discovered. Hence, there was little argument about the bases of classification, compared, for example, with the situation in Bivalvia (NEWELL, 1969). Differences between schemes largely involved names rather than principles.

Returning to LAMARCK, however, soon the logic of CUVIER's work became compelling. A classification based solely on shells, however useful for the proud owners of cabinets, could not be applied to animals that did not have them. Accordingly, LAMARCK (1804, p. 97) adopted CUVIER's mollusques céphalopodes as a division of his Mollusques céphalés. There were three subdivisions: Céphalopodes nus (cuttlefish, squids, and octopus), Céphalopodes à coquille uniloculaire (argonauts and carinaires), and Céphalopodes à coquille multiloculaire (*Nautilus, Spirula,* ammonites, orbulites, nummulites).

The first to propose formal suprageneric names for CUVIER's *poulpes* (octopods) and *seiches* (decapods) was another Frenchman, the brilliant Constantine RAFINESQUE (1783–1840). His peripatetic career and excessive zeal for nomenclature fortunately need not concern us here. In his *Analyse de la nature* (1815), privately printed in Palermo, Sicily, the order Cephalopodia (*sic*) contained the suborders Antepedia and Polarnaxia. Antepedia included families Octopia, Sephinia, and Argonautea. Polarnaxia contained the ectocochleate cephalopods and also *Spirula* and the nummulites. These terms remained unnoticed until they were resuscitated by GRAY (1849). RAFINESQUE had the merit of correctly grouping *Argonauta* with the octopods, whereas in LAMARCK's systems, it had been placed with gastropods, scaphopods, and even nummulites.

LEACH AND GRAY

Meanwhile, in Britain, an important classification of living forms was published, without comment, by William Elford LEACH (1790–1836), "perhaps one of the more brilliant minds to enter science in the [British] Museum" (GUNTHER, 1980, p. 49). LEACH admired CUVIER and, like him, realized that the Linnaean classes, still used by many British authors at the time, were outdated and inadequate. LEACH was not the first to make the distinction between cephalopods with eight and ten arms, but he introduced the terms Octopoda and Decapoda, perhaps the most widely used of several pairs of names for these subdivisions. The term Decapoda was, as LEACH must have known, identical with Decapoda LATREILLE (1801–1802, p. 20), a subdivision of the Crustacea. The full classification (LEACH, 1817, p. 137) was:

Class Cephalopoda
- Ordo I. Octopoda.
  - [no subdivision into families]
  - Genera:
    1. *Eledone.*
    2. *Polypus.*
    3. *Ocythoe.*
- Ordo II. Decapoda
  - Fam. I. Sepiolidea.
    - Genera:
      4. *Sepiola.*
      5. *Cranchia.*
  - Fam. II. Sepiidea.
    - Genera:
      6. *Sepia.*
      7. *Loligo.*

The classification was published again in France (LEACH, 1818) and in Germany. This classification had no place for the pearly nautilus. LESUEUR (1821, p. 87) objected to the fact that LEACH included *Sepia* and *Loligo* in the same family and placed them in separate families, Loligoidea (new) and Sepiidea.

LEACH's terms Decapoda and Octopoda were quickly adopted, e.g., by A. É. J. P. J. F. d'Audebard DE FÉRUSSAC (1821), who accommodated *Nautilus* and the fossils by the simple expedient of including them all in Decapoda:

1st Order: Les Décapodes
- 1st Family: Les Ammonées
- 2nd Family: Les Hippurites
- 3rd Family: Les Bélemnites
- 4th Family: Les Orthocères
- 5th Family: Les Lituites
- 6th Family: Les Discorbes
- 7th Family: Les Nautiles
- 8th Family: Les Camérines
- 9th Family: Les Milioles
- 10th Family: Les Seiches

2nd Order: Les Octopodes
- Family: Les Poulpes

A near contemporary of LEACH was John Edward GRAY (1800–1875), who became Keeper of Zoology (1840–1874) at the British Museum. GRAY had assisted LEACH with the Mollusca at the Museum and escorted CUVIER around London during his visit in 1818. In July 1820, LEACH left the Museum on sick leave, never to return, and in March 1821, a month after GRAY's 21st birthday, his "Natural arrangement of Mollusca" was published (GRAY, 1821). Notwithstanding his indebtedness to LEACH and his knowledge of the French authors, GRAY introduced another set of new terms. CUVIER's Cephalopoda became the class Antlio-Brachiophora, with three orders: Anosteophora for the Octopoda, Sepiœphora for *Sepia* and *Sepiola,* and Nautilophora for *Nautilus, Spirula,* and the fossil chambered shells, including some Foraminifera. Squids were not mentioned. This was the first reasonably logical threefold subdivision of cephalopods.

FRENCH AND BRITISH AUTHORS 1825–1850

Most of the research on cephalopods during the early 19th century was still being done in France. BLAINVILLE in his *Manuel de Malacologie* (BLAINVILLE, 1825, p. 364–366, 368, 375) proposed yet another new set of names:

Class Cephalophora
- Order I. Cryptodibranchiata
  - Family Octocera
  - Family Decacera
- Order II. Cellulacea
- Order III. Polythalamacea
  - (7 families)

The term Cryptodibranches had been invented by BLAINVILLE (1814) as a substitute for CUVIER's Cephalopoda. For BLAINVILLE (1818), it included both naked cephalopods and those with shells. In his 1825 classification, it was restricted to the naked genera: LAMARCK's "Céphalopodes nus;" Cellulacea were the naked Foraminifera. Polythalamacea were the chambered shells, with some families including a mixture of Foraminifera and cephalopods. BLAINVILLE probably did not know of RAFINESQUE's classification, though he must have known of LEACH's.

The most indefatigable French worker on cephalopods, both living and fossil, was A. C. V. Dessalines D'ORBIGNY (1802–1857). Like other great naturalists of the time, including Charles DARWIN and T. H. HUXLEY, he served his apprenticeship on an expedition, working in South America at the same time as DARWIN. Collaborating with his senior d'Audebard DE FÉRUSSAC (1786–1836) on a major monograph, he also undertook on his own numerous ambitious synoptic works, including *Mollusques vivantes et fossiles* (1845–1846) and the *Paléontologie française,* which are bibliographically complicated and were never completed.

In 1826, D'ORBIGNY published a "Tableau méthodique de la classe des Céphalopodes,"

whose three orders were essentially those of Blainville. Cryptodibranches now included Leach's Octopoda and Decapoda; but new terms were introduced for the other two orders: *Siphonifères* for the forms with chambered shells and a siphuncle, and *Foraminifères* for the (mainly) microscopic chambered shells lacking a siphuncle. Foraminifera were now segregated, though still included in Cephalopoda.

In the 1820s, de Férussac was planning a series of monographs to cover all Mollusca, only parts of which were published. D'Orbigny collaborated on the part on the cephalopods (de Férussac & d'Orbigny, 1835–1848). De Férussac himself wrote the introduction to the cephalopods (de Férussac, 1834), in which d'Orbigny's three orders were retained. Another new term was used, however: "céphalopodes acétabulifères" (literally cup- or socket-bearing, i.e., sucker-bearing) (d'Orbigny 1840 in de Férussac & d'Orbigny, 1835–1848) in place of Blainville's cryptodibranches. The term Acetabulifera was in common use for Recent coleoids by French authors in the 19th century.

Félix Dujardin (1801–1860) examined the soft parts of Foraminifera and showed that they had nothing to do with mollusks (Dujardin, 1835), as had already been suspected by Deshayes (1830, p. 227). In d'Orbigny's later schemes (d'Orbigny, 1845–1847), they were excluded, at last, from Cephalopoda.

The famous British comparative anatomist Richard Owen (1804–1892) was the first to make the distinction between the naked and shell-bearing cephalopods on the basis of their anatomy. Following his dissection of the first *Nautilus* animal to reach Europe (Owen, 1832), which revealed that *Nautilus* possessed two pairs of gills, he divided the class Cephalopoda into the orders Tetrabranchiata and Dibranchiata for forms with four and two gills respectively. Dibranchiata was listed by Owen (1836) as including Leach's Octopoda and Decapoda. Owen's terms were widely used for the next century and more.

The last of the early subdivisions of living coleoids, which are still in use today, was made by d'Orbigny (1845 in 1845–1847) in his *Mollusques vivants et fossiles,* which despite its title never got farther than the cephalopods. This was the distinction between myopsids and oigopsids. d'Orbigny's definitions were as follows:

DECAPODA MYOPSIDÆ. Yeux sans contact immédiat avec l'eau extérieure, libres dans une cavité orbitaire et recouverts, en dehors, par une continuité du derme qui devient toujours transparente sur une surface ovale longitudinale, égale au diamètre de l'iris. Une paupière inférieure aux yeux (d'Orbigny, 1845 in 1845–1849, p. 237).

DECAPODA OIGOPSIDÆ. Caractérisés par leurs yeux ouverts en dehors, en contact immédiat avec l'eau (d'Orbigny, 1845 in 1845–1849, p. 367).

His use of the terms was different from those more recently current. Myopsida included not only *Loligo* and *Sepia* and their close relatives but also *Cranchia* and *Spirula* and the fossil genera *Beloptera, Beloteuthis, Geoteuthis, Leptoteuthis, Teudopsis,* and *Spirulirostra.* Oigopsida included the other living dibranchiate forms then known and the fossils *Belemnites, Belemnitella, Celaeno* (*sic*), and *Conoteuthis.*

Early 19th century classifications had placed *Spirula* with the ectocochleate chambered shells because the animal was unknown. It was now possible to classify it correctly with the dibranchiates. Belemnites were also now included in the dibranchiates, previous authors up to Owen (1832) having included them in Tetrabranchiata.

Louis Agassiz (1846), for the purposes of his *Nomenclator Zoologicus,* divided Cephalopoda into five groups of equal (unstated) status:

Octocera
Decacera (Peristolata)
Spirulacea
Nautilea
Ammonitea

He followed d'Orbigny in placing belemnites in his Decacera.

Gray (1849) silently ignored his youthful excesses of 1821, reverting to Cuvier's class Cephalopoda, but resurrected Rafinesque's (1815) subordinate taxa, presumably on the grounds of priority. He was not followed by other specialists. He also employed three suborders of the Decapoda: Chondrophora (new) for the squids, Sepiaphora (Sepiœphora Gray, 1821), and Belemnophora (new) for *Lituus* (=*Spirula*) and fossil coleoids with chambered shells. He was followed, e.g., by Fischer (1882), who replaced Belemnophora with Phragmophora, and by the *Cambridge Natural History* (Cooke, 1895).

LATER 19TH CENTURY

Owen's subdivisions of Cephalopoda based on number of gills were generally adopted throughout the 19th century, Dibranchiata being divided into Leach's Octopoda and Decapoda, the latter with d'Orbigny's subdivisions Myopsidœ and Oigopsidœ. This was the case with such midcentury authors as Woodward (1851) and Keferstein (1866 in 1862–1866), with some variation in the names favored for the subdivisions; for example, Jeffreys (1869), in his survey of British conchology, favored Blainville's Decacera and Octocera. The ammonites were generally included in Tetrabranchiata, on account of their having coiled, chambered shells, but Owen's two subdivisions became increasingly difficult to apply as the diversity of fossil forms became known.

Yet another attempt to replace the term Cephalopoda was made by E. Ray Lankester (1877), who invented the term Siphonopoda. This has been adopted by Salvini-Plawen (1980; and Salvini-Plawen & Steiner, 1996) but has not otherwise found favor.

PHYLOGENETIC CLASSIFICATIONS

Ernst Haeckel (1834–1919), Darwin's great German follower, was the first author after the publication of Darwin's *On the Origin of Species* (1859) to present a phylogenetic tree of the Mollusca (Fig. 1; Haeckel, 1866, pl. VI). His classification of Cephalopoda was conservative, retaining subclasses Tetrabranchia and Dibranchia (*sic*), the latter with orders Decabrachia and Octobrachia, yet another pair of new names for long-recognized subdivisions. The phylogenetic tree shows Tetrabranchia as (in modern terms) a paraphyletic group branching off the stem that later gave rise to Dibranchia. Thirty years later, Haeckel presented a more detailed classification, which is discussed below.

THREEFOLD SUBDIVISIONS OF CEPHALOPODA

One who was no longer satisfied with the assignment of ammonoids to the Tetrabranchiata was the great German paleontologist Wilhelm Heinrich Waagen (1841–1900). In his monograph on fossils from the Salt Range (Punjab, India) (Waagen, 1879, p. 21), he excluded ammonites from Tetrabranchiata and used a heading "Order ?/Family Ammonitidae." Three years later, in a major systematic work on Mollusca, the *Manuel de Conchyliologie* (1880–1887), Paul Fischer (1882) recognized a separate order, Ammonea (formalized from Lamarck's *Ammonées*), of being equal status with Tetrabranchiata and Dibranchiata. Fischer put the belemnoids in Decapoda, and therefore in Dibranchiata, like d'Orbigny (1845 in 1845–1847), in contrast to earlier systems that had tended to include them in Tetrabranchiata on account of their chambered shells.

Fischer's system was adopted by Karl von Zittel (1839–1904), himself a student of fossil cephalopods, in his influential *Handbuch der Palæontologie* (1881–1885), which ran to several revised editions in several languages.

Francis Arthur Bather (1863–1934) was a paleontologist who became Keeper of Geology at the British Museum (Natural History). He is better remembered for his work on echinoderms, but in his earlier days, he took an interest in the shell structure and classification of cephalopods. With contemporary authors such as Alpheus

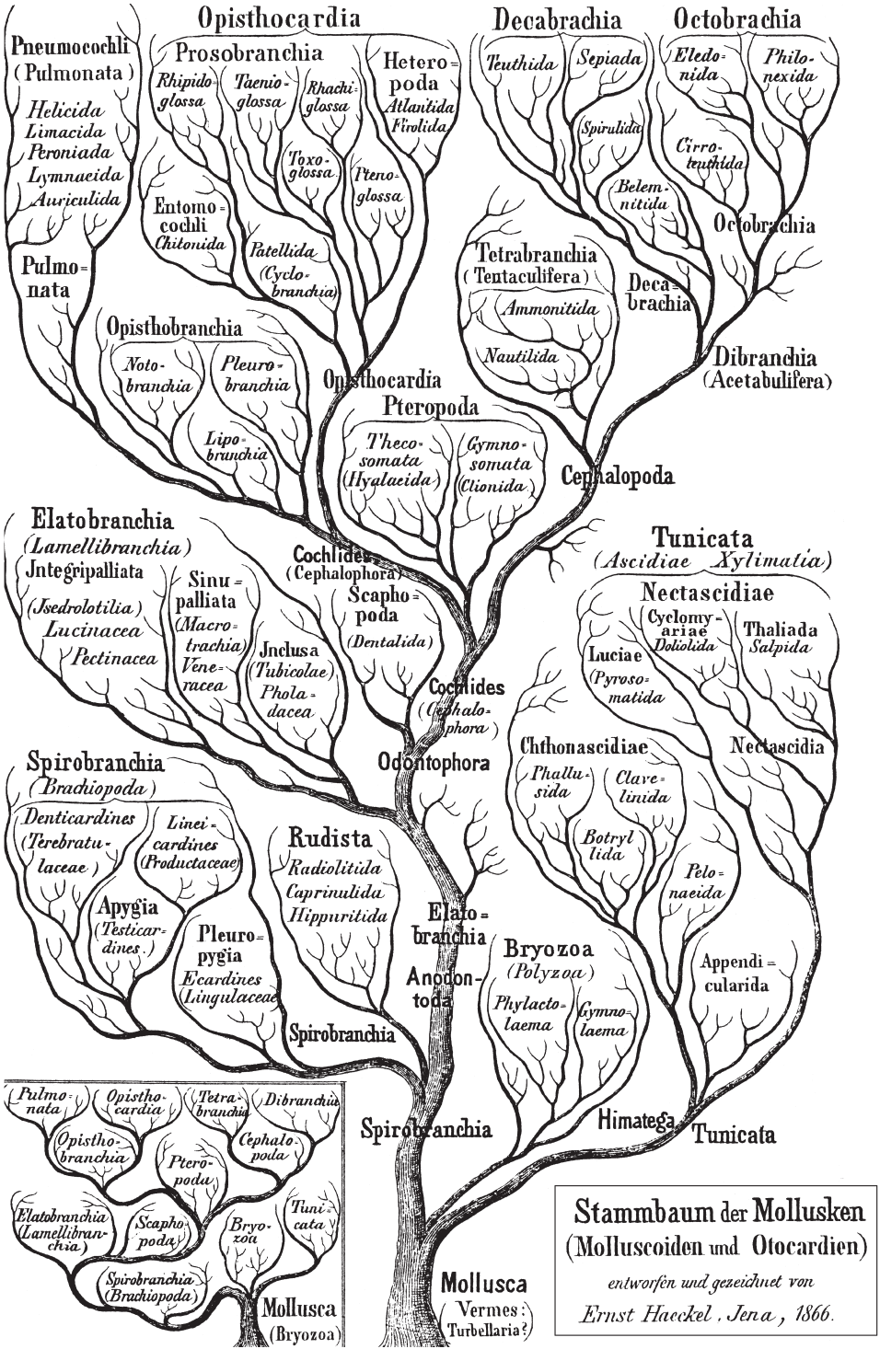

FIG. 1. Phylogeny of the mollusks (Haeckel, 1866).

Hyatt and C. W. F. Branco, he believed the protoconch to be an important character in primary classification. Like Haeckel, he regarded phylogeny as the proper basis of classification and recognized three main lines of descent: Nautiloidea, Ammonoidea, and "The straight forms in which the protoconch is protected by a sheath (*Aulacoceras*, *Belemnites*, &c.) [which] form another genetic series parallel with the Ammonoidea, for which I propose the name Coleoidea" (from Greek κολεός, sheath) (Bather, 1888a, p. 302). Later the same year (Bather, 1888b, p. 423–424), he gave the following definitions:

Nautiloidea, Cephalopoda in which the protoconch is not preserved, although coiling takes place.

Ammonoidea, Cephalopoda in which the protoconch is preserved by shell-coiling and comes to be affected thereby.

Coleoidea, Cephalopoda in which the protoconch is typically preserved by an external sheath deposited by the mantle; the shell comes to be enveloped by the mantle, and may partly, even wholly, disappear.

Thus, Fischer's threefold subdivision was formalized.

Soon after this, Bather gave a lecture, which was not published, to the Geologists' Association in London, in which he used a basic twofold subdivision of cephalopods: Lipoprotoconchia (for Nautiloidea) and Sosiprotoconchia (for Ammonoidea plus Coleoidea), new terms reflecting the different situation as regards the protoconch. These new names were published by J. F. Blake (1892, p. 294); happily, they were not taken up by other workers. Bather (1892) abandoned them himself and subdivided Coleoidea as follows:

Osteophora (new)
- Aulacoceratidae
- Xiphoteuthidae
- Belemnitidae
- Belopteridae
- Spirulidae
- Sepiadae

Chondrophora (Gray, 1849)
- (Myopsid)
- Beloteuthidae
- Teuthidae
- Belemnoteuthidae
- Loligidae
- Sepiolidae
- (Oigopsid)
- Octopodidae
- Philonexidae
- Cirrhoteuthidae

The interpretation of the oigopsids as comprising the octopods is inexplicable, unless something was left out by the printer.

Bather (1888a, 1888b) regarded ammonoids as the sister group of coleoids. A different view, that octopods were descended from ammonoids, was popular in the late 19th century. Ernest Hubert Lewis Schwarz (1873–1928), in his only paper on Cephalopoda, written at age 21 (Schwarz, 1894), adopted this idea, and he believed that the Dibranchiata included two components of different origin: belemnoids and living Decapoda, descended directly from Nautiloidea, and Octopoda from Ammonoidea. He proposed the new terms Ectocochlia and Endocochlia:

Ectocochlia: Nautiloidea, Ammonoidea, Octopoda

Endocochlia: Belemnitidae, Sepiadae, Teuthidae, Spirulidae

His classification, apparently artificial, was thus intended to be phylogenetic. Ectocochlia and Endocochlia have not been widely adopted, though Lehmann (1976) used them as infraclasses. The terms ectocochleate and endocochleate have been found to be convenient terms for forms with external and internal shells.

Bather's threefold classification was not immediately adopted either. The taxon Dibranchiata continued to be used well into the 20th century by such authorities as Pelseneer (1906), Naef (1922), and Thiele (1926), and in works of reference such as the *Cambridge Natural History* (Cooke, 1895) and the *Encyclopœdia Britannica* (Cunningham, 1910). Grimpe (1922) also perpetuated a twofold subdivision, merely substituting the new terms Protocephalopoda

and Metacephalopoda for Tetrabranchiata and Dibranchiata. Ammonoidea were placed in Protocephalopoda as they had been placed in Tetrabranchiata by 19th century authors.

Paleontologists tended to adopt the threefold system, because they had to accommodate the Ammonoidea, while authors dealing solely with Recent forms could refer to Tetrabranchiata and Dibranchiata without making any problems for themselves. Even so, the paleontologist Jean ROGER (1952) retained Dibranchiata for the living and fossil coleoids.

In 1890, the learned Reverend Canon NORMAN published his *Revision of British Mollusca.* He reviewed classifications of Cephalopoda and discussed phylogeny, noting the likelihood of parallel evolution and the difficulty of expressing phylogeny through taxonomy. He thought that hectocotylization was an important character for classifying Recent coleoids, and, on this basis, he proposed the suborders Opistharsenia and Prostharsenia, the latter with sections Anoprostharsenia and Katoprostharsenia. Perhaps fortunately, these terms do not seem to have been adopted by anyone else.

ERNST HAECKEL: TWOFOLD SUBDIVISION AGAIN

HAECKEL's phylogenetic studies culminated in a three-volume work that presented classifications for all plant and animal groups, taking account of embryology, ontogeny, and phylogeny. The second volume (1896) dealt with the invertebrates. Unlike many authors, HAECKEL suspected that the tetrabranchiate state in *Nautilus* was derived and restricted to one evolutionary branch (Fig. 2), and the dibranchiate state was primitive, on account of the generally dibranchiate condition in other Mollusca. Like SCHWARZ (1894), whose paper he almost certainly had not seen, HAECKEL argued (1896, p. 582) that Tetrabranchiata and Dibranchiata must be abandoned as primary divisions. His new classification was:

Classis VI Cephalopoda
Subclassis TOMOCHONIA (Funnaperta)
Ordo I: Archolenae = Proteuthodes
Ordo II: Teutholenae = Palateuthyes
Ordo III: Nautolenae = Nautilades
Subclassis GAMOCHONIA (Funnoclausa)
Ordo IV: Octolenae = Octopodales
IVA: Ammonitaria
IVB: Octopodaria
Ordo V: Decolenae = Decapodales
VA: Belemnaria
VB: Spirularia
VC: Sepiaria
VD: Loligaria

Order I was a hypothetical ancestral stock, which did not have a siphuncle and would be excluded from Cephalopoda by most authors. Orders II and III comprised the Nautiloidea. The classification of Coleoidea ["Gamochonia;" HAECKEL may not have known of BATHER's (1888a, 1888b) papers] looks unfamiliar because HAECKEL invented new names for the major groups. Like SCHWARZ, HAECKEL followed STEINMANN (1888) in deriving the octopods from the ammonoids or at least from early ammonoid stock (Fig. 2), hence the inclusion of Ammonitaria (goniatites plus ammonites) in Octolenae.

Buried in HAECKEL's comprehensive survey, his classification appears to have been overlooked, or at least ignored, by everyone, even by such other German workers as GRIMPE and THIELE.

The German zoologist Georg GRIMPE (1889–1936), in several short papers between 1916 and 1922, introduced a number of new higher taxa. GRIMPE (1916, p. 353) subdivided the order Octopoda LEACH into the now familiar suborders Cirrata and Incirrata, Cirrata having fins and bearing cirri on the arms, while Incirrata lack both these structures.

MULTIPLICATION OF TERMS

Kir N. NESIS (1982) has pointed out that a number of more or less equivalent pairs of names were based on different characters:

Gills: Tetrabranchiata, Dibranchiata (OWEN, 1832)
Suckers present or absent: Tentaculifera, Acetabulifera (FÉRUSSAC & D'ORBIGNY, 1835 in 1835–1848)

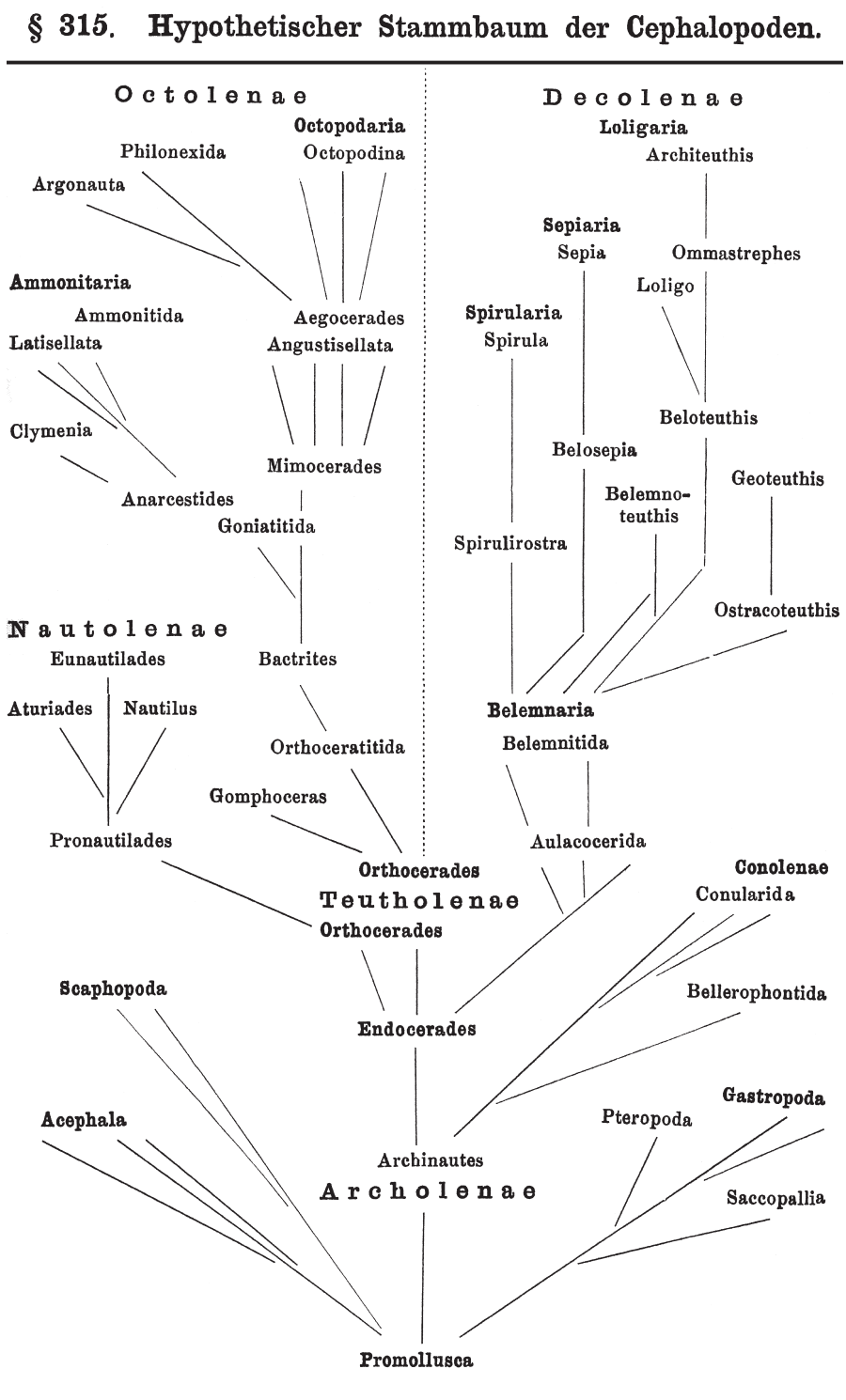

FIG. 2. Hypothetical phylogeny of the cephalopods (Haeckel, 1896).

Shell and supposed phylogeny: Ectocochlia, Endocochlia (Schwarz, 1894)
Funnel structure: Tomochonia, Hamochonia (Haeckel, 1896)
Supposed primitiveness or advancement: Protocephalopoda, Metacephalopoda (Grimpe, 1922)

Few other schemes need be noticed. Ulrich Lehmann (1967), following his discovery of the fossilized radula of ammonoids, coined the terms Lateradulata for nautiloids, with more elements in the radula than Angusteradulata, which included Ammonoidea and Coleoidea. In the German edition of his book on ammonoids, Lehmann (1976) employed a conventional classification of cephalopods, but, in the English edition (Lehmann, 1981), he introduced the new terms for the same subdivisions: Palcephalopoda, essentially the Nautiloidea of authors, and Neocephalopoda, comprising Bactritida, Ammonoidea, and Coleoidea.

Mangold-Wirz and Fioroni (1970), in a detailed review of the anatomy, embryology, and ontogeny of Cephalopoda, concluded that it should be regarded as a subphylum of Mollusca rather than a class. Nevertheless, the volume of Grassé's *Traité,* edited by Mangold-Wirz (as Mangold) (Mangold & Portmann, 1989), reverted to a class Cephalopoda. Finally, Serafinski and Strzelec (1984) tried to detach Cephalopoda from the phylum Mollusca altogether, concluding that they should be a separate phylum and including a phylogenetic diagram showing their derivation independently from Mollusca.

SUBDIVISION OF COLEOIDEA

Leach's (1817) subdivisions Octopoda and Decapoda with various different names (see Nesis, 1982) served for practical classification for about 100 years after they were invented. This simplicity was destroyed soon after Joubin (1912) described paired filaments, lying between arm pairs I and II, in his new genus *Melanoteuthis.* This genus was placed in the Cirrata, and its unusual feature attracted little attention until Grimpe (1917, p. 326) separated *Melanoteuthis* and several other genera from other cirrates as Eurytreta (=Vampyromorphae). Robson (1929) promoted this to be his suborder Vampyromorpha: Octopoda was now divided into three suborders. Finally, the British zoologist Grace E. Pickford (1902–1986) showed (1936) that *Melanoteuthis* and several other genera were synonyms of the monotypic genus *Vampyroteuthis* (Chun, 1903), thus emphasizing the isolated position of Vampyromorpha, which she raised to ordinal status, of equal rank with Octopoda and Decapoda. This position has been widely accepted, though the affinities of *Vampyroteuthis* have been much debated.

The Upper Cretaceous *Palaeoctopus* was included in Incirrata, e.g., by Grimpe (1916), but Naef (1921a, 1921b) classified it in a third suborder of Octopoda, the Palaeoctopoda.

ADOLF NAEF

The Swiss zoologist Adolf Naef (1916; and see History of Study of Fossil Coleoidea, *Treatise Online,* Part M, Chapter 13) divided Decapoda into three suborders: Belemnoidea, the new Teuthoidea (divided into T. myopsida and T. oegopsida), and Sepioidea. His classification was an important influence on subsequent ones in two ways.

First, the new suborder Teuthoidea [Haeckel (1896) had introduced an order Teutholenae that had remained unnoticed] was a significant innovation. Owen (1836) had used a family Teuthidae for the squids, so the idea was not new, but, following Naef, most authors have classified the Recent squids in Teuthoidea, with trivial variations of spelling (Teuthomorpha: Kretzoi, 1942; Teuthidida: Sweet, 1964; Teuthida: Jeletzky, 1965, 1966; Sweeney & Roper, 1998).

The second concerns the scope of Sepioidea. Squids and cuttlefish had long been put into different genera (Lamarck, 1799) and then families (Rafinesque, 1815). Taxon names based on *Sepia* had been used during most of the 19th century to cover all the Decapoda. Many authors since Gray (1821),

however, had placed Sepiidae and Spirulidae, the two Recent groups with chambered shells, into different orders or suborders. NAEF placed less emphasis on the differences between them and reduced them to families of the same suborder Sepioidea. He was followed by several authors, and it was not until much later in the century that zoologists again regarded the differences as meriting ordinal rank (FIORONI, 1981), while paleontologists had tended to keep them in separate orders or suborders (e.g., KRETZOI, 1942).

A few years later, NAEF (1921a, 1921b) made more radical changes, proposing three new higher taxa within Dibranchiata: Prototeuthoidea, Mesoteuthoidea, and Metateuthoidea.

Prototeuthoidea was diagnosed as a fossil teuthoid with a well-calcified gladius in which the median field is usually delimited by asymptotes, with a blunt anterior end, without a median keel. These were mainly Jurassic families that NAEF (1922, p. 303) believed had become extinct before the end of the Mesozoic.

Mesoteuthoidea was diagnosed as having a gladius with a rounded or pointed anterior end, a median keel forming a ventral groove, and a large cone flag (Conusfahne). It included Late Jurassic and Cretaceous families that had also become extinct but which probably gave rise to the Metateuthoidea. Metateuthoidea included only Recent genera of squids.

Samuel Stillman BERRY (1887–1984), a distinguished American authority on Recent Coleoidea, regarded the group Teuthoidea as "not altogether satisfactory" (BERRY, 1920, p. 145) and did not use it, instead grouping the squids into six new superfamilies, a taxonomic rank that has not been much used by coleoid workers. Most later workers seem to have evaded the challenge of grouping the Recent squid families (27 at the latest count) into higher units.

M. KRETZOI is a vertebrate paleontologist who made one excursion into invertebrates when he described (1942) a fossil gladius from the Oligocene of Hungary. In the same paper, he revised the classification of Dibranchiata. The Decacera (=Decapoda) was divided into three suborders with new names: Spirulomorpha, Sepiomorpha, and Teuthomorpha. A number of new family-group taxa were included, most of which appear to be invalid under ICZN Article 13 (1999), because no definitions were given.

GILBERT VOSS

Since World War II, a leading researcher on Recent coleoids has been Gilbert L. VOSS (1918–1989). In 1964, he contributed the article Cephalopoda to the 14th edition of the *Encyclopœdia Britannica* (VOSS, 1964). After reviewing the classifications of NAEF (1921) and GRIMPE (1917, 1922), he offered:

Class Cephalopoda
- Subclass Nautiloidea
- Subclass Ammonoidea
- Subclass Coleoidea
  - Order Belemnoidea
  - Order Sepioidea
  - Order Teuthoidea
    - Suborder Myopsida
    - Suborder Oegopsida
  - Order Vampyromorpha
  - Order Octopoda
    - Suborder Palaeoctopoda
    - Suborder Cirrata
    - Suborder Incirrata

These are essentially BATHER's orders promoted to subclasses, with subdivisions for the Recent forms.

In the same year, Walter C. SWEET (1964), in the introduction to Part K of *Treatise on Invertebrate Paleontology,* divided class Cephalopoda into six subclasses (four of them extinct), subclass Coleoidea comprising the orders Belemnitida, Phragmoteuthidida (new), Teuthidida, Sepiida, and Octopodida.

JURIJ A. JELETZKY

JELETZKY (1965, 1966) (see History of Study of Fossil Coleoidea, *Treatise Online,* Part M, Chapter 13), in his preparatory study for the *Treatise on Invertebrate Paleontology,* Part M, was the first author since NAEF to put forward a classification that attempted to accommodate both living and fossil forms

in some detail. Apart from matters of rank (Naef's suborders become orders), the chief difference from Naef's classification is that Aulacocerida and Phragmoteuthida were removed from Belemnitida as independent orders, in consequence of Jeletzky's phylogenetic conclusion that these three groups had originated independently. Vampyromorphina were, unusually, placed as a suborder of Teuthida following a detailed discussion (Jeletzky, 1966, p. 46–50) of the affinities of *Vampyroteuthis.* Jeletzky's classification was:

Order †Aulacocerida Stolley, 1919
Order †Phragmoteuthida Jeletzky in Sweet, 1964
Order Octopida [new name]
  Suborder Cirromorphina
  Suborder Incirratina
Order Teuthida Naef, 1916
  Suborder †Loligosepiina Jeletzky, 1965
  Suborder †Prototeuthina Naef, 1921a, 1921b
  Suborder †Mesoteuthina Naef, 1921a, 1921b
  Suborder Vampyromorphina Robson, 1929
  Suborder Oegopseina d'Orbigny, 1839, =Architeuthacea Thiele, 1935
  Suborder Myopseina d'Orbigny, 1839 [*sic* 1845], =Loliginacea Thiele, 1935
Order Sepiida Zittel, 1895 em. Naef, 1916
Order †Belemnitida Zittel, 1895
  Suborder †Belemnitina Zittel, 1895
  Suborder †Belemnopseina Jeletzky, 1965
  Suborder †Diplobelina Jeletzky, 1965

Taxa marked † are exclusively fossil. Jeletzky regarded *Palaeoctopus* as a probable cirromorphine (1966, p. 52) and did not adopt the Palaeoctopoda of Naef. The reference of Oegopseina and Myopseina to d'Orbigny (1839) is an error.

Classifications published in recent years have ranged from the conventional (Jeletzky, 1966; Nesis, 1982; Clarke & Trueman, 1988) to the innovative, the latter especially resulting from the application of phylogenetic systematics to the Cephalopoda.

The Russian authority on Recent Coleoidea, Kir N. Nesis (1934–2003), after a critical review of the problem (Nesis, 1982), followed Voss fairly closely. He did not accept Fioroni's separation of Sepiolida at ordinal level, retaining them in Sepiida. He agreed with Voss in abandoning Decapoda, replacing them with Sepiida and Teuthida. As far as fossil groups were concerned, he accommodated them as follows:

Subclass Coleoidea
  Order †Phragmoteuthida
  Order †Aulacocerida
  Order †Belemnitida
  Order Sepiida
    Suborders Spirulina, Sepiina
  Order Teuthida
    Suborders †Loligosepiina, †Prototeuthina, †Mesoteuthina, Myopsida, Oegopsida
  Order Vampyromorpha
  Order Octopoda
  Suborders †Palaeoctopoda, Cirrata, Incirrata

Another Russian worker, Ya. I. Starobogatov (1983), published a detailed classification of all Cephalopoda. The part relevant to the Coleoidea is as follows. It appears to be unfamiliar partly because Starobogatov has adopted strict priority, and partly because of the unusual endings used for the ordinal-rank taxa.

Subclass Octopodiones Schneider, 1784
  Superorder Sepiiformii Gray, 1821
    Order Aulacoceratiformes Stolley, 1919
    Order Belemnoteuthidiformes Stolley, 1919
      Suborder Phragmoteuthidoidei Jeletzky in Sweet, 1964
      Suborder Belemnoteuthidoidei Stolley, 1919
      Suborder Diplobeloidei Jeletzky, 1965
    Order Spiruliformes *nov.*
      Suborder Belemnosoidei *nov.*
      Suborder Spiruloidei (new rank)
    Order Sepiiformes Gray, 1821
      Suborder Sepioidei Gray, 1821
      Suborder Sepioloidei Fioroni, 1981

- Order Vampyroteuthidiformes Grimpe, 1917
  - Suborder Vampyroteuthidoidei Grimpe, 1917
  - Suborder Kelaenoidei *nov.*
- Order Belemnitiformes Gray, 1849
  - Suborder Belemnitoidei Gray, 1849
  - Suborder Belemnopsoidei Jeletzky, 1965
- Order Loliginiformes Lesueur, 1821
  - Suborder Loligosepioidei Jeletzky, 1965
  - Suborder Teudopsoidei *nov.* (=Mesoteuthoidea Naef, *partim*)
  - Suborder Enoploteuthidoidei *nov.*
  - Suborder Loliginoidei Leseur, 1821 (=Myopsida d'Orb.)
- Order Architeuthidiformes *nov.*
  - Suborder Architeuthidoidei (new rank) (=Prototeuthoidea Naef, *partim*)
  - Suborder Cranchioidei *nov.*
- Order Cirroteuthidiformes Berry, 1920
  - Suborder Palaeoctopodoidei Naef, 1921a
  - Suborder Cirroteuthidoidei Berry, 1920

Superorder Octopodoidei Leach, 1818 [*sic* 1817]

- Order Octopodiformes Leach, 1818 [*sic* 1817]
  - Suborder Octopodoidei Leach, 1818 [*sic* 1817]
  - Suborder Bolitaenioidei *nom. nov.* (=Ctenoglossa Naef)

In raising Spiruliformes to ordinal rank, Starobogatov reverted to the classification used before Naef's work (1916). Cirroteuthids and vampyromorphs are included in Sepiiformii rather than in Octopodoidei. The suborders of Loliginiformes recall the superfamilies into which the squids were divided by Berry (1920).

Grimpe's Cirrata were generally regarded as suborders of the order Octopoda, with some variation in names and ranks [superfamily Cirroteuthoidea Berry, 1920; suborder Cirroteuthoidea Naef, 1921a; suborder Cirromorpha Robson, 1929, p. 484 (replacing Cirrata)]. J. Z. Young (1989, p. 202), however, felt that the cirrate octopods were so different from the incirrate ones that they should be an order, of equal rank with a restricted Octopoda (=Incirrata of Grimpe):

Class Coleoidea
- Infraclass Octobrachia
  - Order Cirroctopoda [new]
  - Order Octopoda
    - Suborder Benthoctopoda [new] (*Octopus, Eledone*)
    - Suborder Epipelagoctopoda [new] (*Argonauta*)
    - Suborder Bathypelagoctopoda [new] (*Japetella*)
- Infraclass Decabrachia
  - Order Teuthida
  - Order Sepiida
  - Order Sepiolida
  - Order Spirulida
- Infraclass Vampyromorpha

No discussion of the new suborders was included.

Guerra (1992) adopted a similar system, with a new taxon *Pseudoctobrachia* for the vampyromorphs and different ranks:

Subclass Coleoidea
- Superorder Octobrachia Fioroni, 1981
  - Order Cirroctopoda J. Z. Young, 1989
  - Order Octopoda
- Superorder Decabrachia (*non sensu* Fioroni, 1981)
  - Order Teuthoidea
  - Order Sepiida (including Spirulidae)
  - Order Sepiolida
  - Order Idiosepioidea *nov.* (Boletzky MS)
- Superorder Pseudoctobrachia *nov.*
  - Order Vampyromorpha

Mary Wade (1988) reverted to a subclass Dibranchia, in which she included superorders Ammonoidea, Coleoidea, and the supposed ancestral stock Bactritoidea.

Another Russian worker, D. N. Khromov, a specialist on sepiids, proposed (1990) dividing subclass Coleoidea into two superorders: Camerophora for the forms with phragmocone, and Incamerophora for those

with gladii. These are essentially Bather's Osteophora and Chondrophora with new names.

Winfried Haas (1997, p. 64) presented a phylogeny of living Decabrachia and proposed the subdivisions Palaecoleoidea for "Aulacoceratida," Belemnitida, Phragmoteuthida, and Belemnoteutida (*sic*) (=Belemnoidea and Phragmoteuthidida of Doyle, Donovan, & Nixon, 1994), and Neocoleoidea for, presumably, the remaining groups. The term Neocoleoidea was independently introduced by Young, Vecchione, and Donovan (1999, p. 394) for "the sister group to the Belemnoidea," nearly the same meaning as that of Haas.

A major review of the classification of Recent cephalopods was made by Sweeney and Roper (1998). Their higher classification is:

Superorder Decabrachia Boettger, 1952
- Order Spirulida Stolley, 1919
- Order Sepiida Zittel, 1895
- Order Sepiolida Fioroni, 1981
- Order Teuthida Naef, 1916
  - Suborder Myopsina d'Orbigny, 1841 [in Férussac & d'Orbigny, 1835–1848]
  - Suborder Oegopsina d'Orbigny, 1845 in 1845–1847

Superorder Octobrachia Fioroni, 1981
- Order Octopodida Leach, 1818 [*sic* 1817]
  - Suborder Cirrina Grimpe, 1916
  - Suborder Incirrina Grimpe, 1916
- Order Vampyromorphida Pickford, 1939 [*sic* 1936]

This classification is important because it is complete down to species level, indicating type species of genera and the repositories where type specimens of each species are to be found.

Riegraf, Janssen, and Schmitt-Riegraf (1998) presented a classification similar to that of many 20th century workers. Their classification additionally provided a fundamental array of taxonomic information (including synonymy lists).

PHYLOGENETIC SYSTEMATICS

Most, if not all, recent classifications are avowedly founded on phylogeny. A phylogenetic classification, of course, is only as good as the phylogeny on which it is based, and lack of unanimity reflects the fact that the branching order of the major living groups of Coleoidea is still uncertain. While Recent forms can be reasonably classified on their own, attribution of fossil groups is not always easy. Most recent classifications, such as those of Jeletzky (1966) and Starobogatov (1983), if interpreted in phylogenetic terms, imply unresolved polyfurcations.

Phylogenetic systematics (cladistics) claims to formalize the inferral of phylogeny through character analysis and to erect classifications in which taxonomic rank depends on the order of the successive evolutionary bifurcations that produced the taxa that are being classified (i.e., "sister groups [should] be co-ordinate, and thus have the same absolute rank," Hennig, 1979, p. 155). This procedure, strictly followed, has been criticized as producing an inconveniently large number of taxonomic ranks, since there are usually a large number of successive bifurcations.

Berthold and Engeser (1987) adopted Lehmann's Angustiradulata, containing the sister groups Ammonoidea and Coleoidea. Within Coleoidea, like most other workers, they regarded Belemnoidea and the remaining coleoids as sister groups (Neocoleoidea of Young, Vecchione, & Donovan, 1999). They did not assign taxonomic ranks; there are four taxonomic levels between Coleoidea and family-group taxa. Berthold and Engeser (1987) introduced the new terms Octopodiformes for vampyromorphs plus octopods [Starobogatov (1983) had used Octopodoformii in a more restricted sense], and Uniductia for spirulids plus myopsids.

Engeser and Bandel's (1988) classification was also based on phylogenetic analysis.

Subclass Coleoidea Bather, 1888a
  Superorder Belemnoidea Gray, 1849
    Order Aulacocerida Stolley, 1919
    Order Phragmoteuthida Jeletzky in Sweet, 1964
    Order Belemnitida Gray, 1849
    Order Diplobelida Jeletzky, 1965
  Superorder Vampyromorphoidea *nov.* [Berthold & Engeser, 1987]
    Order Octopoda Leach, 1818 [*sic* 1817]
      Suborder Cirrata Grimpe, 1916
      Suborder Incirrata Grimpe, 1916
    Order Vampyromorpha Robson, 1929
    Order Prototeuthida Naef, 1921a, 1921b
      Suborder Prototeuthina Naef, 1921a, 1921b
      Suborder Mesoteuthina Naef, 1921a, 1921b
  Superorder Decapoda Leach, 1818 [*sic* 1817]
    Order Spirulida Stolley, 1919
    Order "higher decapoda"
      Suborder Teuthina Naef, 1916
      Suborder Sepiina Zittel, 1895

Vampyroteuthis and its supposed fossil relatives (Prototeuthida) were placed closer to Octopoda, as opposed to Jeletzky's (1966) scheme, where they were classified in Teuthida. Apart from the fact that grouping into three superorders was new, the classification of fossil gladius-bearing coleoids (so-called fossil teuthids) as octopods had a striking impact on previous phylogenies, since unambiguous teuthids are unknown from the Mesozoic fossil record, according to this classification.

Engeser (1990) essayed a further analysis of the Coleoidea in greater detail, resulting in some changes to the ordering and several new names. This useful paper includes critical analyses of a number of problem taxa.

Doyle, Donovan, and Nixon (1994), Haas (2002), and Bizikov (2004) partly accepted the concept of Engeser (1990) and classified Mesozoic gladius-bearing coleoids (Loligosepiina, Teudopsidina) as octopods. In Doyle, Donovan, and Nixon (1994), only the Prototeuthidina (=Plesioteuthididae therein) remained as teuthids.

Although some doubts still exist today, both the soft tissue morphology of Mesozoic gladius-bearing coleoids and the common view that the octopod and cirroctopod gladius vestiges (paired or unpaired) evolved from a Mesozoic gladius support Engeser's phylogenetic classification (Haas, 2002; Bizikov, 2004; Fuchs, 2006, 2009).

A cladogram (most parsimonious tree) for major divisions only of Cephalopoda, based on 73 characters, was published by Salvini-Plawen and Steiner (1996). Translated into a hierarchical classification this produces:

Subclass Nautiloidea
Subclass Coleoidea
  [Octobrachia]
    Vampyromorpha
    Octopoda
      Incirrata
      Cirrata
  [Decabrachia]
    Oegopsida
    Uniductia
      Spirulida
      Myopsida
        Sepioloidea
        Sepioidea
        Loliginoidea

In general, phylogenetic approaches largely confirmed previous divisions of the eight-armed coleoids (Young & Vecchione, 1996, table 1; Strugnell, North, & others, 2005; Strugnell, Jackson, & others, 2006). However, a consequent phylogenetic classification of ten-armed coleoids is still hampered by unresolved polytomies at higher levels (Young & Vecchione, 1996; Lindgren, Giribet, & Nishiguchi, 2004; Strugnell, North, & others, 2005).

A difficulty that is encountered in trying to apply phylogenetic systematics to the

Coleoidea is the very restricted number of characters that can be used for both fossil and living species. It may be preferable to restrict cladistic analyses to living forms (YOUNG & VECCHIONE, 1996) and use the fossils to try to interpret the resulting phylogenies.

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