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History of the Study of Fossil Coleoidea

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PART M, CHAPTER 21: HISTORY OF THE STUDY OF FOSSIL COLEOIDEA

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INTRODUCTION

EARLY IDEAS ON BELEMNITES

Belemnites attracted early attention of human beings. They were collected by Paleolithic people in central Europe about 20,000 years BP and have been found in Bronze Age burials in Great Britain (Oakley, 1978, p. 225). In recent centuries they were known to English country people as thunderbolts. In Germany, at least forty-eight vernacular names for belemnites are known, as well as eight in Italy and Sweden; six in the Netherlands, France, and Luxembourg; three in India; and one in Madagscar and Brazil. Belemnites were also used in folk medicine.

The term belemnites, from Greek βελεμνον, a dart, is known in Latin from Georgius Agricola (1494–1555), who also spelled it *belenites* or *baptes* (Agricola, 1546, p. 266). Use of the word in English by Thomas Browne (1605–1682) is recorded a century later (Browne, 1646, p. 53).

Belemnites were mentioned and illustrated by numerous early writers on antiquities and natural history, but their affinities were not understood. In the sixteenth and seventeenth centuries, no clear distinction was made between what we would now call fossils and other objects found in the ground, such as minerals and archaeological artifacts. Because belemnites have no living representatives, they were not recognized as mollusks in the way that some fossil bivalves and gastropods could be identified as closely similar to extant forms. With their crystalline, calcitic structure, it was natural for them to be identified with the mineral rather than the animal kingdom. Hence, Imperato (1599, p. 476) compared them with stalactites, and Libau (1601, chapter 18) thought them to be a form of amber or agate. Other writers (Bajer, 1708, p. 33; Mendes da Costa, 1748) regarded them as *lusus naturae* (sports of nature) or *lapides sui generis* (stones whose resemblance to organic forms was accidental).

In 1565 the German Johannes Kenntmann (1518–1574) was the first author to refer belemnites to the animal kingdom. In the same year, Kenntmann's friend Conrad Gesner (1516–1565), the greatest naturalist of his day, published what may be the first printed figures of *Belemnitæ* (Gesner, 1565, fol. 91r) (Fig. 1). Gesner himself refrained from discussing the origin of the objects that he illustrated, planning a more detailed work that he did not live to complete. Other authors, though convinced that belemnites were of organic origin, variously identified them as corals, echinoderm spines, the teeth of reptiles or of whales (reviewed by Parkinson, 1811, p. 123; Blainville, 1827), or bivalves (Lhuyd, 1699, p. 89 in Epistola IV), while the septate phragmocone was mistaken for animal vertebrae (Volckmann, 1720).

An important advance in the understanding of fossils was made by John Woodward (1665–1728), a physician (as were many early naturalists) who studied in Gloucester, England, and was familiar with the abundant marine fossils in the Jurassic rocks of that area. Woodward (1695) proposed that fossils had belonged to

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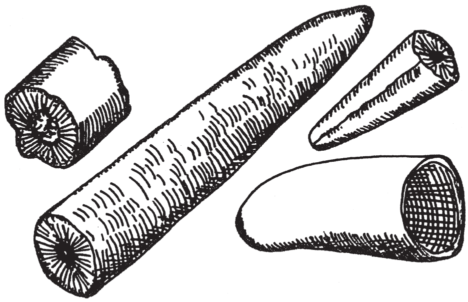

FIG. 1. Earliest printed illustration of belemnites (Gesner, 1565).

animals that lived at the time of the biblical deluge, which agitated the Earth's surface, the materials put in suspension settling out to form horizontal strata as the flood waters receded. Many fossils could thus be accepted as being of organic origin. This made it easier for fossil shells to be accepted as the remains of marine animals that had once lived.

Balthasar EHRHART (1700–1756), from Memmingen in southwestern Germany, was a medical student at Leyden in the Netherlands. Dissertations for the degree of M.D. were normally on diseases or afflictions of the human body. EHRHART's dissertation was on Swabian belemnites, though he did mention their medicinal uses in the final pages. He compared the chambered phragmocone of belemnites with the shells of *Nautilus* LINNAEUS, 1758 in 1758–1759, and ammonoids, concluding that although the latter had coiled shells, they were similar groups of animals (EHRHART, 1724, p. 18). The soft parts of *Nautilus* were not then known.

Joshua PLATT correctly understood that the belemnite rostrum was deposited on the outside of the phragmocone, the animal adding layers to the rostrum as it added chambers to the phragmocone (PLATT, 1764). He evidently did not know of the work of EHRHART.

The Genevan geologist Guillaume Antoine DELUC (1729–1812) at first thought that the belemnite was the bone of a fish. However, he later accepted that it was the internal shell of a cephalopod and discussed its composition (DELUC, 1799, 1801, 1802, 1804). LAMARCK (1799, p. 81) was probably the first to include *Belemnites* in a formal classification under *Coquilles multiloculaires.*

COLEOIDS OTHER THAN BELEMNITES

Fossil coleoids other than belemnites are generally rare because they usually lack robust skeletons. An important source of fossils of fragile or soft-bodied organisms is the lithographic limestones of the Upper Jurassic Altmühltal Formation (formerly Solnhofen Formation) of Bavaria. The remarkable fossils from these rocks were illustrated in several eighteenth-century books but not well understood. KNORR (1755, pl. 22,*2*) figured the fossil now known as *Trachyteuthis* MEYER, 1846. He compared it with fish from Italy, which were then sold preserved in vinegar. STERNBERG (1833) illustrated the hooked arm crown of the belemnoid *Acanthoteuthis* WAGNER in MÜNSTER, 1839, in a work on fossil plants, a mistake that was corrected in later editions.

THE NINETEENTH CENTURY

FRANCE

Fossil Coleoidea, apart from belemnites, began to be recognized for what they were in the second and third decades of the nineteenth century, chiefly by French paleontologists working in the Paris basin with its abundant early Tertiary fossil fauna from the Calcaire grossier (roughly equivalent to the Ypresian–Lutetian). Three Frenchmen were pioneers in understanding Mesozoic and Cenozoic coleoids.

Gerard Paul DESHAYES (1797–1875), son of a teacher of physics, was a conchologist, as was Jean Baptiste de LAMARCK (1744–1829). DESHAYES published comprehensive monographs on the early Cenozoic fossils of the Paris basin, largely at his own expense. Often in difficult straits, he achieved a professorial chair only late in life. Henri Marie Ducrotay de BLAINVILLE (1777–1850), by contrast, came from the minor nobility and survived the French Revolution to squander his patrimony in Paris. Having tried his hand at music, painting, and literature, he graduated M.D. in 1808. Only a few years younger than the famous Georges CUVIER (1769–1832), he became CUVIER's deputy and eventually, in 1832, his successor. Perhaps as brilliant as CUVIER, though less well organized, BLAINEVILLE's interests were much wider than DESHAYES's, and his *Manuel de Malacologie* (1825–1827) and *Mémoire sur les Bélemnites* (1827) were only a small part of his work. Philippe Louis VOLTZ (1785–1840), was born in Strasbourg, trained as a mining engineer, and spent his working life in that profession, becoming the French inspector-general of mines in 1836.

Though CUVIER recognized fossil cuttlebones in the Tertiary of the Paris Basin, DESHAYES was credited with inventing the name *béloptere* for these fossils, but it was BLAINVILLE who first described the new genus *Beloptera* BLAINVILLE, 1825 in 1825–1827 (p. 622), which he thought to be intermediate between *Sepia* LINNAEUS, 1758 in 1758–1759, and belemnites. VOLTZ found that different forms had been united in that genus, and separated *Beloptera saepioidea* DESHAYES as his new genus *Belosaepia* (VOLTZ, 1830). VOLTZ's chief contribution, however, was to infer the existence of the pro-ostracum of belemnites (see below, p. 6). Later in the century, DESHAYES (1864–1865) published a monograph on the fossil cephalopods from the Paris basin.

ALTMÜHLTAL (SOLNHOFEN) FORMATION

In Germany, work on fossil coleoids centered on Jurassic fossils from the Posidonienschiefer Formation (Lower Jurassic: lower Toarcian) and the Altmühltal Formation, formerly known as the Solnhofen Formation or Solnhofener Plattenkalk (Upper Jurassic: lower Tithonian). The Solnhofener Plattenkalk was becoming famous in the eighteenth century for its uniquely preserved fossils, which are now found in public and private collections throughout the world. Karl Dietrich Eberhart KÖNIG (1774–1851) was the first to correctly recognize fossil gladii from the Solnhofen Plattenkalk (KÖNIG, 1825, pl. 17,*201–203*). Eduard RÜPPELL (1794–1884) had studied and described Recent coleoids from the Red Sea (RÜPPELL & LEUCKHART, 1828). In 1829, he gave excellent illustrated descriptions of the two most common fossil coleoids, which he named *Loligo priscus* and *Sepia hastiformis*, now *Plesioteuthis prisca* (RÜPPEL, 1829) and *Trachyteuthis hastiformis* (RÜPPEL, 1829). He recognized the presence of the fossilized muscular mantle in these fossils.

In the following decades, further descriptions of the Altmühltal Formation coleoids were published, chiefly in the *Beiträge zur Petrefakten-Kunde* and the *Neues Jahrbuch,* by Georg Graf zu MÜNSTER (1776–1844) of Bayreuth and by Christian Erich Hermann von MEYER (1801–1869) of Frankfurt. MÜNSTER was a Bavarian state official who assembled a famous collection of fossils, which later formed the nucleus of the state collection in Munich. MEYER was one of the founders of the journal *Palaeontographica.*

The genera *Acanthoteuthis* and *Kelaeno* (now *Muensterella* SCHEVILL, 1950) were described, as well as numerous species. *Acanthoteuthis* was compared with the extant *Onychoteuthis* LICHTENSTEIN, 1818, because of its hook-bearing arms; although this similarity is now thought to result from independent evolution (ENGESER & CLARKE, 1988), it was a reasonable comparison at the time (see *Treatise Online,* Part M, Chapter 10). MÜNSTER, perhaps unwisely, sent some unpublished descriptions of fossil coleoids with his MS names to the French Alcide D'ORBIGNY in Paris, who published some of them (1842, 1843, 1845–1847), leading MÜNSTER to complain and causing confusion over the generic name *Kelaeno* (DONOVAN, 1994). The generic name *Trachyteuthis* was introduced by MEYER (1846), and *Plesioteuthis* by Johann Andreas WAGNER (1797–1861) in 1859. This phase of work on the

Altmühltal Formation coleoids was summarized by WAGNER (1860).

POSIDONIENSCHIEFER FORMATION

The laminated shales of the Posidonienschiefer (Jurassic: lower Toarcian) of the Holzmaden area (Württemberg, Germany), while not quite as famous as the Altmühltal Formation, also attracted paleontologists and collectors for the variety and good preservation of their fossils. C. H. von ZIETEN (1785–1846) published descriptions of gladius-like fossils (ZIETEN, 1832 in 1830–1833, pl. 25, 41), which he named *Loligo aalensis* and *L. bollensis*—both now *Loligosepia aalensis* (SCHÜBLER, 1832 in ZIETEN, 1830–1833)—and illustrated the gladius of the extant squid *Loligo* LAMARCK, 1798, on the same plate as evidence for the affinities of the fossils. MÜNSTER then (1843) described several genera and a number of species of fossil gladii. Later in the century, the principal student of Holzmaden coleoids was Friedrich August von QUENSTEDT (1809–1889), who published descriptions and magnificent lithographic illustrations (QUENSTEDT, 1849).

While the fossil coleoids described by the French in the early nineteenth century were forms with phragmocones, and therefore fairly easily recognizable as cephalopods, many of the genera from the Posidonienschiefer and the Altmühltal Formation were represented by gladii. These, for the first time, revealed the existence of a number of squidlike animals during the Jurassic. Both formations yielded specimens with ink sacs and some soft parts preserved (including arm crowns), confirming the similarity of these genera to the modern squids.

LOWER JURASSIC OF FRANCE AND ENGLAND: FOSSIL INK SACS

The English fossil collector and dealer Mary ANNING (1799–1847) of Lyme Regis (Dorset, England) was famous for her discoveries of fossil vertebrates in the Lower Jurassic (Hettangian–Toarcian). Sometime in or before 1826, she discovered fossil ink sacs, soon recognized by the English geologist and divine William BUCKLAND (1784–1856) as identical with those of extant cuttlefish. BUCKLAND described the finds to the Geological Society of London on February 6, 1829 (BUCKLAND, 1829), the same year as RÜPPELL figured (though he did not describe) ink sacs in his *Loligo priscus* and *Sepia hastiformis* from the Altmühltal Formation. BUCKLAND described the ink sacs as associated with brilliant nacre and a phragmocone like that of a belemnite, though without a rostrum. His careful description shows that the fossils then discovered were of the species later described as *Belemnoteuthis montefiorei* (BUCKMAN, 1880) and now known as *Clarkeiteuthis montefiorei* (FUCHS, DONOVAN, & KEUPP, 2013).

BUCKLAND (1836) wrote the *Bridgewater Treatise no. VI,* one of a series endowed to promote the greater glory of God, which did not deter BUCKLAND, who was in holy orders, from including a great deal of excellent paleontology. When he came to the coleoids with ink sacs from Lyme Regis, however, he described and illustrated (1836, pl. 28–29) a different form from that which he had described in 1829: these ink sacs were associated with gladii like those figured by ZIETEN (1832 in 1830–1833), rather than with phragmocones. The fossil ink sacs from Lyme, in fact, belong to two separate groups, belemnoids and loligosepiid octobrachians. This led to confusion as to the identity of the genus *Belemnosepia* AGASSIZ & BUCKLAND (ENGESER & DONOVAN, 1996), which was suppressed by the International Commission on Zoological Nomenclature (ICZN) in 1999. VOLTZ (1840) proposed specific names for several of BUCKLAND's figured specimens.

In 1832, the Swiss geologist Louis AGASSIZ (1807–1873) visited Jaques Amand EUDES-DESLONGCHAMPS (1794–1867) at Caen, Normandy, and recognized some fossils that had been found in the Toarcian of the vicinity as another type of fossil gladius, with a pointed anterior end in contrast to the common Posidonienschiefer and

Solnhofen forms. EUDES-DESLONGCHAMPS (1835) described this form as his new genus *Teudopsis.*

MIDDLE JURASSIC OF CHRISTIAN MALFORD

In 1840, a remarkably well preserved fossil assemblage of Callovian (Middle Jurassic) age was discovered at Christian Malford (Wiltshire, England) during the construction of the Great Western Railway. It quickly became famous for microconchs of the ammonite *Kosmoceras* WAAGEN, 1869, preserving the shell aperture with long lappets. The flattened but otherwise superbly preserved fossils included coleoids with ink sacs, muscular mantle, and arm crowns, the phragmocone-bearing *Belemnotheutis* PEARCE, 1842) and gladius-bearing *Mastigophora* OWEN, 1856. The locality is no longer available, but the fossils survive, distributed throughout the world's museums. Detailed description of the coleoids had to wait for another century and a half (DONOVAN, 1983; DONOVAN & CRANE, 1992; VECCHIONE & others, 1999).

The notable British comparative anatomist Richard OWEN (1804–1892) was an influential student of cephalopods, living and fossil. His contributions included the first description of the soft parts of *Nautilus* (OWEN, 1832) and the division of living forms into the orders Tetrabranchiata and Dibranchiata in the same paper. Very able but unwilling to admit that he could be wrong, OWEN misinterpreted some of the Christian Malford fossils, regarding *Belemnotheutis* (which has only a thin aragonitic rostrum) as the phragmocone of typical belemnites with calcitic rostrums and thereby entering into an unpleasant dispute with contemporary paleontologists (DONOVAN & CRANE, 1992). OWEN (1844) was, however, the first to compare the fossilized muscular mantle of *Belemnotheutis* with that of extant squids. The detailed structure has since been shown to be similar (KEAR, BRIGGS, & DONOVAN, 1995).

BELEMNOID COLEOIDS

EARLIEST COLEOIDS AND AULACOCERATIDA

Belemnite-like rostrums had been recognized in Triassic sediments from early times, but it was not until 1860 that the Austrian paleontologist Franz VON HAUER (1822–1899) distinguished some of these, characterized by a longitudinally ribbed rostrum, as the separate genus *Aulacoceras* HAUER, 1860. He was followed quickly by another student of Austrian alpine fossils, Carl Wilhelm VON GÜMBEL (1823–1898), who set up the genus *Atractites* (1861). Much later, FLOWER and GORDON (1959) described related forms from the Lower Carboniferous—*Hematities* and *Palaeoconus*—the earliest fossil Coleoidea known to date. FLOWER (1945) had described a belemnite (*Eobelemnites*) from the same strata but it is now thought to be a Jurassic specimen that had been mislabelled.

Until the middle of the twentieth century it was generally assumed that these pre-Jurassic belemnoids possessed pro-ostraca and were similar, apart from details of the rostrum, to the better-known Jurassic and Cretaceous belemnites, though Erich STOLLEY (1869–1944), a lifelong student of belemnoids, had proposed (STOLLEY, 1919) a separate Suborder, Aulacoceratidae (*sic*). Material that showed details of the pro-ostracum or conothecal growth lines, however, was hard to come by.

In 1966 JELETZKY, after carefully studying specimens of *Dictyoconites* and *Mojsisovicsteuthis*?, concluded that the apertures of these genera had a modest dorsal projection but no pro-ostracum (JELETZKY, 1966, p. 13–15). He found that these aulacoceratid genera, unlike Belemnitida, possessed a complete body chamber. He maintained that the Jurassic and Cretaceous belemnites (Belemnitida) were a distinct evolutionary development from Aulacoceratida and had not descended from the latter group as had been generally assumed. His opinion was principally based on details of the siphuncle—supposed restriction of prochoanitic septal necks to aulacoceratids—which has later been questioned (Doguzhaeva & others, 1999).

Major events in the slightly monotonous history of belemnoid systematics were the separation at ordinal level of Aulacoceratida (Stolley, 1919) and Diplobelida (Jeletzky, 1965).

PHRAGMOTEUTHIDA

Up to the middle of the nineteenth century, almost all fossil Coleoidea had been described from rocks of Jurassic, Cretaceous, and early Tertiary age. About this time, the marine faunas of the east-Alpine Triassic rocks began to be described in detail. Heinrich Georg Bronn (1800–1862) reported on the fossil flora and fauna of the Upper Triassic (Carnian) Raibler Schichten at Raibl, in the Julian Alps near Villach, Austria. In 1859, he figured and described, as *Belemnoteuthis bisinuata* (Bronn, 1859), a two-lobed structure that he correctly recognized as connected with the belemnites, though he did not understand it fully. A few years later, Eduard Suess (1831–1914) looked at better material and found that the two unequal lobes were, in fact, part of a three-lobed pro-ostracum (Suess, 1865). He referred the material to the belemnoteuthid genus *Acanthoteuthis,* previously described from the Altmühltal Formation. Both these generic assignments were probably made because the Triassic fossils bore arm hooks, which are also present in *Acanthoteuthis* and *Belemnotheutis*.

Finally, the Austrian Edmund von Mojsisovics von Mojsvár (1839–1907), a famous student of Triassic marine faunas and especially of the cephalopods, realized the distinctness of these Triassic forms and erected his new genus *Phragmoteuthis* for them, in the new family Phragmoteuthidae (Mojsisovics von Mojsvár, 1882). A Jurassic phragmoteuthid was subsequently described by Donovan (2006).

BELEMNITIDA: MORPHOLOGY

The functional morphology of belemnites received attention early in the nineteenth century. James Parkinson (1755–1824) was a London physician who was the first to describe Parkinson's disease, as well as writing the first systematic work on paleontology in English (1804–1811) and writing subversive political pamphlets under a pseudonym. Parkinson (1811, p. 124, 130) quoted from and agreed with Walch (1769–1773) that the belemnite rostrum "was originally a light substance . . . and was the float to the animal [which allowed] it to rise and fall, as the siphuncle was filled with air or with water." The buoyancy function of the shell in these fossils was thus recognized, even though the mechanism was not understood. Parkinson may have been the first to detect the organic matrix of the calcitic rostrum by dissolving the latter in very weak acid (Parkinson, 1811, p. 130).

Another early student of belemnites in Britain was John Samuel Miller (1779–1830). Born Müller in Danzig, he fled the French occupation in 1801, intending to emigrate to America, but settled in Bristol, England, where he spent the rest of his life. He may have been self taught in natural history, but he had probably been well educated in Danzig; there is some slight evidence that he collected fossils there before leaving for England. In 1817, he was elected a Fellow of the Linnean Society of London, and in 1823 he became the first curator of the Bristol Institution, forerunner of the present City Museums. On April 4, 1823, he read a paper entitled "Observations on belemnites," to the Geological Society of London (Miller, 1826a), which showed that he had both an experimental and a taxonomic approach to these fossils.

Miller correctly noted the geological range of belemnites, from the Lower Jurassic (Hettangian or Sinemurian Stage) to the Upper Cretaceous. He observed that, while the chambered part of the shell resembled that of Orthocerida, it could always be distinguished by the marginal siphuncle. He paid particular attention to the microscopic structure of the phragmocone, distinguishing between the spathose (i.e., prismatic) and nacreous layers of the shell wall, and he observed the mural parts of the septa. He was probably the first to distinguish these two basic types of shell layer. Solution of the spathose rostrum in acid showed that "animal matter intervenes in small quantity between the fibrous crystals" (Miller, 1826a, p. 49–50).

Miller observed from fossils that the phragmocone might extend far beyond the rostrum and conducted buoyancy experiments with rostrums attached to paper phragmocones, concluding that the phragmocone was capable of providing buoyancy for a spathose rostrum. Hence, in contrast to Parkinson (1811), he believed that the spathose (i.e., calcitic) nature of the rostrum was original and not the result of fossilization, initiating a controversy that has continued on and off until the present day (see Hoffmann & others, 2016). He supposed that the rostrum "acted as a counterpoise" for the buoyancy provided by the phragmocone, rather than providing the buoyancy itself as Parkinson had suggested. Miller noted that the shell was wholly covered by living tissue; he suggested that the last chamber was "like the rest, very shallow" and that "the inhabitant of the Belemnite" was "a Sepialike animal" because he believed (correctly) that buoyancy of *Sepia* was provided by the cuttlebone, though he did not understand its structure (Miller, 1826a, p. 57–58).

One further discovery was needed to understand fully the nature of belemnites. This was provided by Voltz (1830), who showed that growth lines on the conotheca could be used to reconstruct the form of the unknown aperture, and that the latter was not simple but carried a long dorsal lobe: his *région dorsale,* later named the pro-ostracum by Huxley (1864). Voltz named the hyperbolar zones in the growth lines and the asymptotes which delimit the pro-ostracum (see *Treatise Online,* Chapter 8). In 1836, he proposed homology between the *région dorsale* of the belemnite and the gladius of extant squids, recognizing hyperbolar zones in both (Voltz, 1836).

Gideon Algernon Mantell (1790–1852) was a doctor by profession and also an eminent English paleontologist (and Owen's chief opponent in the *Belemnotheutis* case). His son Reginald, a civil engineer, recognized the Christian Malford beds a few miles from the original locality, and found in them belemnites (now identified as *Cylindroteuthis* Bayle, 1878) with the phragmocone and pro-ostracum preserved. Although crushed, these showed that the phragmocone was about the same length as the rostrum and that the pro-ostracum had aragonitic lateral supports (Mantell, 1848; see, by way of comparison, Riegraf & Hauff, 1983).

Thomas Henry Huxley (1825–1895), famous English evolutionary biologist and friend of Charles Darwin, made only one contribution to fossil Cephalopoda (Huxley, 1864), but it was an important one, nevertheless. He evaluated work on belemnites up to that date in some detail and introduced the terms *conotheca* for the wall of the phragmocone and *pro-ostracum* for the *région dorsale* of Voltz. Knowledge of belemnite morphology was by then complete, until microscopic structural detail of the phragmocone and siphuncle were looked at nearly a century later by Grandjean (1910, 1911), Christensen (1925), Jeletzky (1966, 1980), Barskov (1970, 1972, 1973), and others.

BELEMNITIDA: SYSTEMATICS

Montfort (1808) used a number of names for different types of belemnite, of which only *Hibolithes,* sometimes misspelled *Hibolites,* survives as a generic name. Although a classification of belemnites was attempted in a rare pamphlet by the Frenchman J. P. J. M. Faure Biguet (1819), his work was forgotten by later authors. Miller (1826a), in the paper to Geological Society of London discussed above, described eleven species of *Belemnites,* of which eight were new. In a second paper (Miller, 1826b), he set up the new genus *Actinocamax,* which he distinguished from *Belemnites* on the mistaken assumption that, although clearly related to belemnites, it did not possess a phragmocone. He was misled by rostra, of which the anterior part with the alveolus was not preserved, apparently having been poorly calcified.

A major contribution was the *Mémoire sur les Bélemnites* of BLAINVILLE (1827). He recognized more than sixty species, of which forty-two were new, separating three of these as a new genus, *Pseudobelus.*

From the second half of the nineteenth century onward, the history of fossil coleoids is chiefly one of more and more detailed systematics of belemnites. John PHILLIPS (1800–1874), nephew of William SMITH (the Father of English Geology), became Professor of Geology at Oxford University. He commenced the first comprehensive treatise on belemnites since BLAINVILLE, with his *Monograph on British Belemnitidae* (PHILLIPS, 1865–1870, 1909), which was never completed, starting with the Lower Jurassic (Lias) and getting only as far as the Kimmeridge Clay (Jurassic: Kimmeridgian Stage in the British sense).

Although several informal groupings of species had been recognized (see JELETZKY, 1966, p. 139), PHILLIPS retained all his species in the one genus *Belemnites.* This was general practice for the first three-quarters of the nineteenth century, although a few separate genera had been named: *Actinocamax*, *Pseudobelus*, and *Belemnitella* (D'ORBIGNY, 1840 in 1840–1842). In 1878, however, Emile BAYLE (1819–1895), in a general work on French fossils (BAYLE, 1878), erected six more new genera. The subdivision of *Belemnites* now began in earnest, like that of the genus *Ammonites* at about the same time. Other new genera followed, notably from LISSAJOUS (1906, 1915), STOLLEY (1911a, 1919, 1927), and NAEF (1922).

The German malacologist Friedrich PAETEL (1875) published an alphabetical index of all known family and generic names of extant and fossil Mollusca recorded up to that date. The Family Belemnitidae dates from OWEN (1836). Karl VON ZITTEL (1884) recognized a number of informal groupings of species and separated the subfamily Belemnoteuthidae (*recte* Belemnotheutididae), but otherwise the family remained undivided for the rest of the nineteenth century. The Russian geologist and paleontologist Aleksei Petrovich PAVLOV (1854–1929) separated the families Belemnitellidae and Duvaliidae (PAVLOV, 1914). Further families and subfamilies were erected by STOLLEY (1919) and NAEF (1922).

CRETACEOUS BELEMNITE BIOSTRATIGRAPHY

Apart from the Russians A. P. PAVLOV and S. N. NIKITIN, systematic descriptions of belemnites were largely in the hands of northwestern European paleontologists. Clemens August SCHLÜTER (1835–1906), professor at the University of Bonn, Germany, was the first to demonstrate the usefulness of belemnite species for European Late Cretaceous biostratigraphy in a famous monograph (SCHLÜTER, 1876). He recognized three genera of Cretaceous belemnites: *Belemnites, Actinocamax* (MILLER, 1826b), and *Belemnitella* (D'ORBIGNY, 1840 in 1840–1842). Ernst STOLLEY (1869–1944) of Brunswick, Germany, built upon SCHLÜTER's ideas and contributed extensive monographs on the belemnite fauna of the Lower Cretaceous of northwestern Europe (STOLLEY, 1897, 1911a, 1911b, 1916, 1925a, 1925b). He also worked on Jurassic belemnites from southeastern Asia and the Arctic, developing the modern ideas of paleobiogeographic distributions of belemnites controlled by climate. STOLLEY's monographs on *Hibolithes* and *Acroteuthis* remained unpublished, and were destroyed during the Second World War, as was his large collection of belemnites.

BELEMNITE PALEOECOLOGY AND PALEOBIOGEOGRAPHY

Belemnites have generally been considered to have been pelagic animals, but until recently, there has not been too much study of their mode of life. NAEF considered it briefly (1922, p. 191–193), and GUSTOMESOV discussed paleoecology (1956,

1961) and the function of the rostrum (1956, 1961, 1974, 1978). More recently EBEL (1987) and MONKS, HARDWICK, & GALE (1996) have considered the physics of swimming.

The pioneering work of STOLLEY (1919) has already been mentioned. Since the Second World War, paleobiogeography has been an important study, with faunal provincialism being recognized in a number of groups. GUSTOMESOV (1961) studied the distribution of Upper Jurassic belemnites and proposed climatic zonation as an explanation of their provincialism. His work on the northern hemisphere has been followed up by W. K. CHRISTENSEN (1997) for the Upper Cretaceous. Graeme R. STEVENS pioneered study of the distributions of southern hemisphere belemnites (1963, 1965).

TEACHING OF THE MARBURG SCHOOL ON PHYLOGENY

During the 1930s, ideas on invertebrate phylogeny and biostratigraphy were developed at the University of Marburg, Germany, under the leadership of Rudolf WEDEKIND (1883–1961). He applied the evolution of fossil invertebrates to biostratigraphy, emphasizing orthogenesis (or unidirectional evolution), which was in fashion at the time. He maintained the idea of sudden phylogenetic explosion centers (German *phylogenetische Quellpunkte,* literally, phylogenetic source points) at certain times in evolution. WEDEKIND himself worked on foraminifers and ammonoids, among other things, and his famous family tree of the Upper Cretaceous foraminifer *Neoflabellina* (WEDEKIND, 1940) remains of worldwide importance. The belemnite papers by his pupils, however, remained more or less unknown outside Germany. For example, BURLON (1937) investigated in detail the ontogeny and phylogeny of Lower Jurassic belemnites by means of longitudinal thin sections. TRIPP (1936, 1937, 1938a, 1938b, 1940, 1941, & 1951) enlarged the field of phylogenetic study and discussed the influence of sedimentary cycles on the evolution of Lower Jurassic belemnites. Phylogenetic aspects of the Marburg teaching were applied to a revision of the Jurassic belemnite fauna of southwestern Germany by SCHWEGLER (1941, 1949, 1961, 1962a, 1962b, 1965, 1969, & 1971) and were continued and concluded by RIEGRAF (1980, 1981).

FIG. 2. Adolf NAEF (new; photo courtesy of S. von Boletzky).

THE TWENTIETH CENTURY

After the first half of the nineteenth century, little more work was done on the non-belemnoid coleoids, which had been such interesting finds from the Posidonienschiefer Formation, the Oxford Clay of Christian Malford, and the Solnhofen and Lebanon Plattenkalks. George Charles CRICK (1856–1917), in charge of fossil Cephalopoda at the British Museum (Natural History), was better known for his work on Paleozoic nautiloids, but he also published a number of

FIG. 3. J. A. JELETZKY (Tozer, 1990).

short accounts based on careful observations of fossil coleoids in the Museum.

Up to the early twentieth century, almost all work on fossil Coleoidea had been done by zoologists and paleontologists with much broader interests, and descriptions of coleoids usually formed parts of comprehensive accounts of fossil faunas. The first three-quarters of the twentieth century, in contrast, was dominated by two researchers for whom the study of cephalopods, living and fossil, was a major part of their work: Adolf NAEF and Jurij Alexeyvich JELETZKY.

ADOLF NAEF

Adolf NAEF (Fig. 2) was born on May 1, 1883, in Canton Appenzell, Switzerland. He studied biology at the University of Zürich and, finding no job in his intended profession of school teaching, continued with postgraduate studies. In 1908, he went to the Zoological Station at Naples and prepared his doctoral thesis on the development of the coelom and circulatory system of the squid (NAEF, 1909). In 1910, the director of the Station, Reinhard DOHRN, engaged him to continue the monograph on the Recent cephalopod fauna of the Bay of Naples, which had been left unfinished by the late Guiseppe JATTA. This led to exhaustive study of the living species, not only their systematics but their detailed anatomy and ontogeny.

Not content with this knowledge, which made him the best-informed worker on embryology and anatomy of living dibranchiate cephalopods, and finding himself stranded in Munich by the outbreak of the First World War, NAEF extended his studies to fossils, making use of the superb collections in German museums, especially of the material from the Altmühltal Formation, which had lain unexamined since about 1860. His book *Die fossilen Tintenfische* (NAEF, 1922; WARNKE, KEUPP, & BOLETZKY, 2004) has been a classic for workers on fossil coleoids ever since.

In 1922, NAEF became an associate professor at the medical school of the University of Zagreb, and his research henceforth was chiefly on the morphology and phylogeny of vertebrates, though the third and final part of his Naples monograph was published in 1928. In 1927, he became director of the Zoological Institute of the Egyptian University at Cairo. He hoped to return to Europe and in 1930 was shortlisted for a chair at Basel but was not appointed despite his eminence. The Second World War saw him isolated in Egypt, cut off from scientific dialogue with overseas workers. He died of a lung disease in Switzerland on May 15, 1949.

NAEF is known to cephalopod workers particularly by his monograph on the living cephalopod fauna of Naples (NAEF, 1921, 1923, 1928) and his book on fossil coleoids (1922). The thoroughness and detailed knowledge shown by these works is astonishing when one remembers that this knowledge was acquired in barely fifteen years. For most of the last 25 years of his life he worked on vertebrates. He was a fine draftsman and his books are illustrated by a large number of his own drawings.

As noted above, NAEF's knowledge of the animals was remarkable. He was also, however, a theorist, partly from his own inclination, partly through the influence of his professor at Zürich, Arnold LANG. His interest here lay in phylogeny and its relationship to embryology and morphology, and early on (NAEF, 1917), he published a critique of Ernst HAECKEL's Biogenetic Law and attempted a more rigorous statement of the relationship between ontogeny and phylogeny. He tried to bring strict logic into discussion of phylogenetic relationships, and in this, was a forerunner of, and an influence on, the more famous German Willi HENNIG.

J. A. JELETZKY

Jurij Alexeyvich JELETZKY (Fig. 3) was born J. A. ROMANOV on June 18, 1915, at Penza, about 550 km southeast of Moscow, Russia, taking the name JELETZKY from his stepfather in 1930 (TOZER, 1990). He graduated in geology at Kiev in the Ukraine in 1938 and attained his doctorate in 1941. In September of that year, Kiev fell to the Germans, being relieved by Soviet troops in 1943. JELETZKY then worked in Poland and Germany until 1948, when he was appointed to a post as a paleontologist in the Geological Survey of Canada, where he remained until his death, having officially retired in 1981. George, as he was known to his English-speaking colleagues, died in Ottawa on December 4, 1988.

JELETZKY's early interest was in Upper Cretaceous belemnites, on the morphology and taxonomy of which he published a number of meticulous papers from 1941 onward. His knowledge of these fossils led to his being invited by R. C. MOORE to undertake the present volume (*Treatise on Invertebrate Paleontology,* Part M), following the withdrawal of L. R. BAIRSTOW.

JELETZKY believed that new species should not be erected except on the basis of the most complete material, and his morphological descriptions are perhaps the most detailed of any modern writer on fossil cephalopods. Occasionally, they are difficult to follow for this reason.

Following his *Treatise* assignment, JELETZKY made extensive studies of fossil coleoid material in European museums. A result was his major pre-*Treatise* publication of 1966. Further museum studies remain unpublished but, fortunately, notes and photographs are extant. Friends and colleagues hoped that George would be able to finish the present volume before he died, but this was probably prevented by his conscientious regard for his official work, even after his retirement. JELETZKY's later official duties were largely concerned with Lower Cretaceous biostratigraphy and paleontology, and he was much involved in work in the Canadian Arctic, where he was instrumental in providing the biostratigraphical basis for correlation and subdivision of the rocks. The 1970s and 1980s saw the publication of a dozen or more major contributions to Canadian stratigraphy and paleontology as well as numerous shorter papers.

Brief mention should be made of Leslie R. BAIRSTOW (1907–1995), who was curator of fossil Coleoidea at the British Museum (Natural History) until his retirement in 1966. An immensely learned man who published nothing, he was asked to undertake the present volume in about 1950. His detailed systematic notes survive, were passed to JELETZKY, and have been used by the present authors.

END OF THE TWENTIETH CENTURY

The last two decades of the twentieth century have seen renewed interest in the anatomy and systematics of fossil coleoids other than belemnites, and the description of a number of new genera. Anatomy and mode of life have not been neglected. A study published by BANDEL & LEICH (1986) has had a sustainable impact on twenty-first century workers and thus on the systematics proposed herein (see *Treatise Online,* Chapter 21). These authors recognized that the so-called fossil teuthids never have more than eight arms and that these Mesozoic gladius-bearing coleoids, therefore, belong to the octobrachiate rather than to the decabrachiate lineage. Theo

Engeser, a passionate taxonomist, as his very useful catalog (1988) shows, corroborated this view in many subsequent articles. A notable achievement has also been the discovery by Amanda J. Kear that the muscular mantle of Jurassic coleoids had the same detailed structure as that of living species (Kear, Briggs, & Donovan, 1995). Renewed interest in fossil collecting has also played its part, especially in the discovery of new genera and species in the Altmühltal Formation.

FAKES AND FORGERIES

Fossil Coleoidea, apart from belemnites, are generally rare, and paleontologists depend to a large extent on quarrymen, professional collectors, and dealers for their material. A few paleontologists have been deceived by specimens that have been fabricated, usually by combining parts of different species. This was done to increase the monetary value of specimens rather than to promote incorrect paleontological conclusions.

Huxley was deceived by specimens in a private collection and in the British Museum, which he figured as the Lower Jurassic *Belemnites Bruguierianus* (1864, pl. 1,*1*) and *B. elongatus* (1864, pl. 1,*2*). In both these instances, a belemnite rostrum has been added to extrinsic remains, and the first-named specimen probably consists of parts of three or four different fossils. This may have led Crick (1907), although he did not himself figure faked fossils, to ascribe isolated arm crowns to belemnites. The composite nature of Huxley's specimens remained unnoticed until it was pointed out by Müller-Stoll (1936, p. 191) and later by Donovan (1977, p. 31). Phillips (1980) gave details of these specimens, and Pollard (1968, p. 383) noted a similar composite fossil in the Sedgwick Museum, Cambridge. Crick (1907) found that the arm crown of "*Belemnoteuthis montefiorei*" (Buckman, 1880) had been reoriented with respect to the body after being figured by Buckman. A consequence of these fakes is that numerous textbooks (e.g., Zittel, 1884, p. 502, fig. 686) have given erroneous reconstructions of the belemnite animal, combining a belemnoid rostrum with the arm crown of a rostrum-less belemnoid (Fuchs, Donovan, & Keupp, 2013).

In a more recent case of deception, similar combinations of belemnite rostrums with extrinsic soft parts and arms from the Posidonienschiefer Formation of southern Germany were manufactured and sold to various European museums as *Weichteilbelemniten* (belemnites with soft parts) for DM 2000 (around 1000 US dollars). The discovery was announced by Ewald Wiesenauer, an insurance agent (1976), and E. Kallenbach (a pseudonym of Wiesenauer) (1978). The fossils were published in good faith by Rietschel (1977). They were soon revealed as forgeries (Riegraf & Reitner, 1979; Riegraf & Hauff, 1983; Wolf, 1979). Real belemnites with preserved arm crowns have since been reported (Reitner & Urlichs, 1983; Riegraf & Hauff, 1983).

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