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# HISTORY OF CONULARIID RESEARCH

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## ABSTRACT

Conulariids have been studied for more than two centuries and during that time they have been classified variously as molluscs, cnidarians or members of an extinct phylum. They have been studied by several different research schools, including the Czech, Swedish, German, Brazilian, North American and Chinese schools. Some important palaeontologists who studied conulariids were Joachim Barrande (1799-1883), Guido Sandberger (1821-1869), Gustaf Lindström (1829-1901), Karl Alfred Ritter von Zittel (1839-1904), Gerhard Holm (1853-1926), Jan Vratislav Želízko (1874-1938) and Bedřich Bouček (1904-1975). A history of conulariid research, from 1793 to the present day, is presented here. Four main stages are recognized.

**Keywords:** Conulariids, Cnidaria, History of study, Bibliographic analysis

## INTRODUCTION

Conulariids are extinct marine organisms with a worldwide distribution in the fossil record. Stratigraphically they range from the Ediacarian (Caster, 1957; He, 1984; Ivantson and Fedonkin, 2002) to the Triassic (note, however, that some authors have recorded supposed Lower Jurassic conulariids: Argéliez, 1856; Dana, 1863; Kayser, 1924; Zittel, 1924, 1927), a geological duration of more than 400 million years, and comprise 52 genera (Figure 1) and 357 described species. Conulariids have importance in stratigraphical correlation and support palaeobiogeographical reconstructions inferred from other invertebrate fossils (e.g. graptolites and trilobites) in the Palaeozoic (Sendino and Domínguez, 2006).

Conulariids have four-sided, acute pyramidal exoskeletons (Figure 2) which are usually preserved in the original calcium phosphate, or as external moulds. Their size ranges from a few millimetres up to about 50 centimetres (Kiderlen, 1937; Bouček, 1939). The exoskeleton tapers gradually and uniformly. This shape suggested to some early palaeontologists that conulariids were molluscs (Sowerby, 1821; Archiac and Verneuil, 1842; Sandberger, 1847; Rouault, 1851; McCoy, 1855; Barrande, 1867; Tromelin and Lebesconte, 1876a; Hall, 1879; Barrois, 1891; Hola, 1893; Lindström, 1884; Delgado, 1897, 1908; Miller and Gurley, 1896). However, phylogenetic studies have indicated that they are scyphozoan cnidarians (Van Iten, 1991b; Van Iten *et al.*, 1996; Van Iten *et al.*, 2006b).

In total, there are more than 2,000 bibliographical references on conulariids, from purely descriptive, to publications discussing their biological affinities, phylogeny, taphonomy and stratigraphy.

## EARLY STUDIES

Conulariids were first figured at the end of the 18th century when the Reverend David Ure illustrated (1793: pl. 20: fig. 7), without naming, a Scottish Carboniferous specimen of *Paraconularia quadrisulcata* (Sowerby, 1821) (Sendino, 2007).

During the 19th century, particularly in the first half, studies focused on taxonomic description. Kurt Osswald published the pioneering work on conulariids in 1818. A series of publications by James Sowerby (1814-1845) on *The shells of Great Britain* followed. This includes the first description of the taxon *Conularia* in the volume for 1821. The name was attributed to Mr Miller, "*of Bristol*", (sometimes written Müller or Muller). In some later references the date is given as 1820 instead of 1821 (Figure 3). The same volume describes the type species of *Conularia*, *C. quadrisulcata* Sowerby, 1821. From this date, there followed a proliferation of studies devoted to descriptions of conulariids, and the first studies on their biological affinities. Sowerby (1821) was the first to classify conulariids, regarding them as cephalopods based on the basis of Mr. Miller´s observations (*in* Sowerby, 1821: "resembling an *Orthocera*").

The first important taxonomic advances were made by Guido Sandberger (1847) who listed the species described up to that date and formulated criteria for specific distinction, which was followed by later authors such as Holm (1893) and Slater (1907). In 1849 the catalogue of molluscs compiled by John Edward Gray, then Keeper of Zoology at the *British Museum*, listed fourteen true conulariids in the collection of what is now the Natural History Museum, London.

Marie Rouault (1851) described the Armorican Massif conulariids and was the first of several women to study this group. Subsequently, Fielding Bradford Meek and Amos Henry Worthen (1865) and Samuel Almond Miller and William Frank Eugene Gurley (1896) described new North American species. Between these dates, John William Salter (1866) published his work on the fossils of North Wales, which included some new species of conulariids.

Important work on conulariids from Bohemia was published by Joachim Barrande (1867) (Figure 4). Barrande's seminal paper firstly reviews the history of research on conulariids and goes on to study their morphology in detail, finishing by describing the 27 species then recognized in Bohemia. Born in France, Barrande settled in the Czech Republic in 1833 where he worked on the construction of the railway extension from Prague to Pilsen. During this work, a multitude of invertebrate fossils were discovered and formed the basis for Barrande's huge collection, most of which was later bequethed to the *Národní Muzeum* (National Museum, Prague) (Svoboda, 1983; Horný, 1999). These fossils provided the foundation for Barrande's massive monographic work, compiled

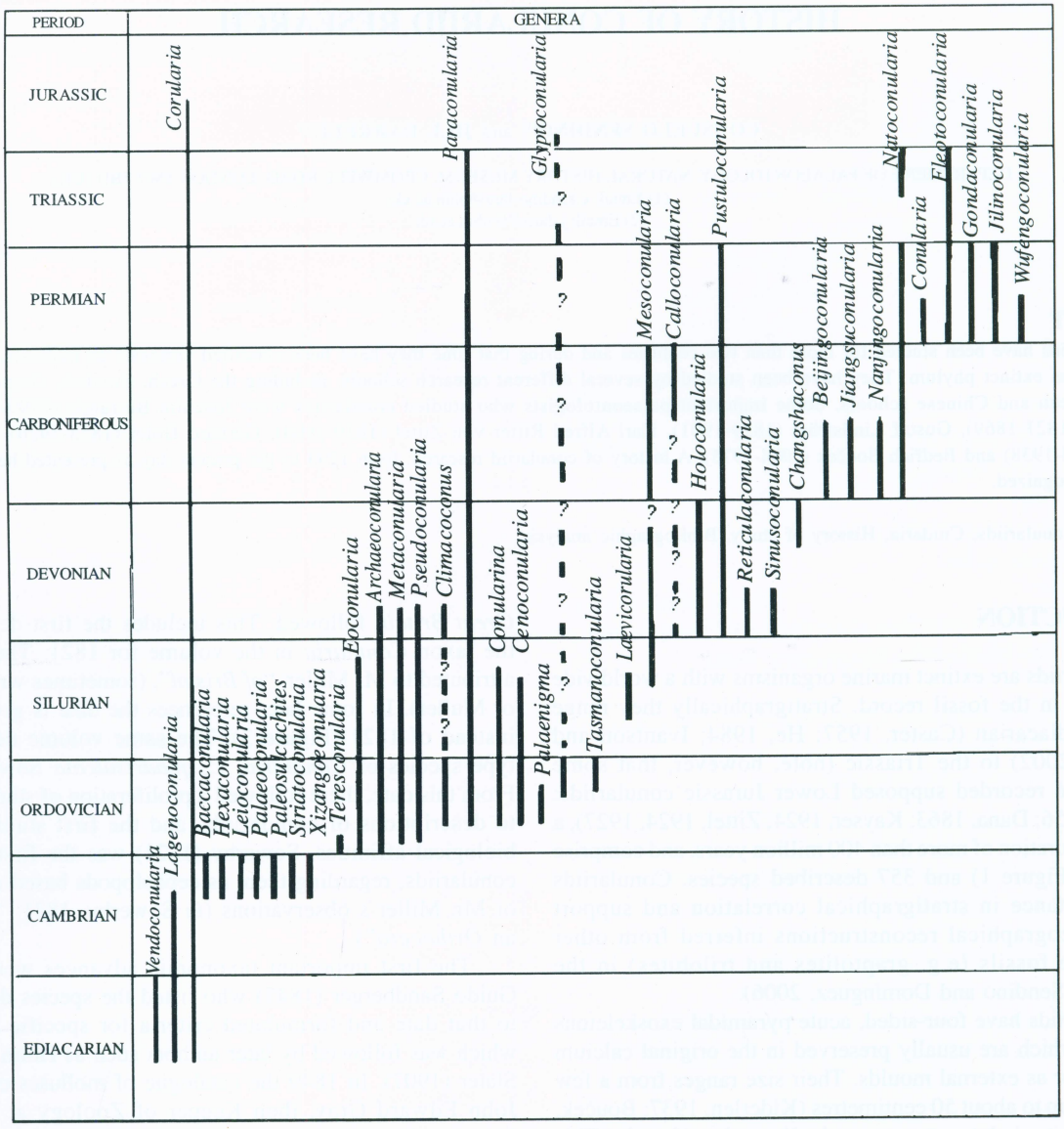


Fig. 1. Genera conulariids through the geological record

during the following 44 years, that comprised more than 6,000 pages and has been recognized as the largest scientific work written by a single author. The conulariids were described in 1867, 34 years after the beginning of the construction of the railway.

Other contributions of this type, synoptic and descriptive, but more modest in scope, are those of: Jacques Amand Eudes Deslongchamps (1825) and Gaston of Tromelin and his colleague Paul Lebesconte (1876a) on Armorican fossils; Laurent Guillaume of Koninck (1842-1844a, b) on fossils from Belgium; James Hall (1847-1879) on fossils from New York State; Frederick McCoy (1855) on British Palaeozoic fossils; Jonas Gustaf Oskar Linnarsson (1869) and Carl Wiman (1894-1908) on Swedish fossils; and Robert M. Johnston (1887-1888) on fossils from Tasmania.

The first use of conulariids as stratigraphical indicators is in the work of Henry Hicks (1875) on the Welsh Ordovician. In Spain, Lucas Mallada and Jesús Buitrago (1878) worked on conulariids from the Cantabrian Mountains; in France, it is worth highlighting the publications of Gaston de Tromelin and Paul Lebesconte (1876b, c), Henri Hermite (1878) and Charles Barrois (1891) on Ordovician conulariids; and in Portugal, those of J. F. Nery Delgado (1897, 1908), also on the Ordovician.

The first attempt to subdivide the group was made by Gustaf Lindström in 1884. Lindström recognized three groups that contain five species of *Conularia* Miller *in* Sowerby, 1821. Later, another Swedish palaeontologist, Gerhard Holm (1893), tried to devise a "natural grouping"of conulariids. However, this bears little resemblance with modern classifications. Holm's grouping established criteria that allowed species to be distinguished, besides citing every species known at the time, listing them by countries and geological period, and giving bibliographical references for all of the Swedish species. One year before, in 1892, Arnold Ulrich had considered two characters - cross sectional shape and aperture type - for the classification of conulariids from Bolivia.

At the end of the 19th century, from 1896 to 1898, Rudolf Ruedemann published on the palaeoecology of supposed

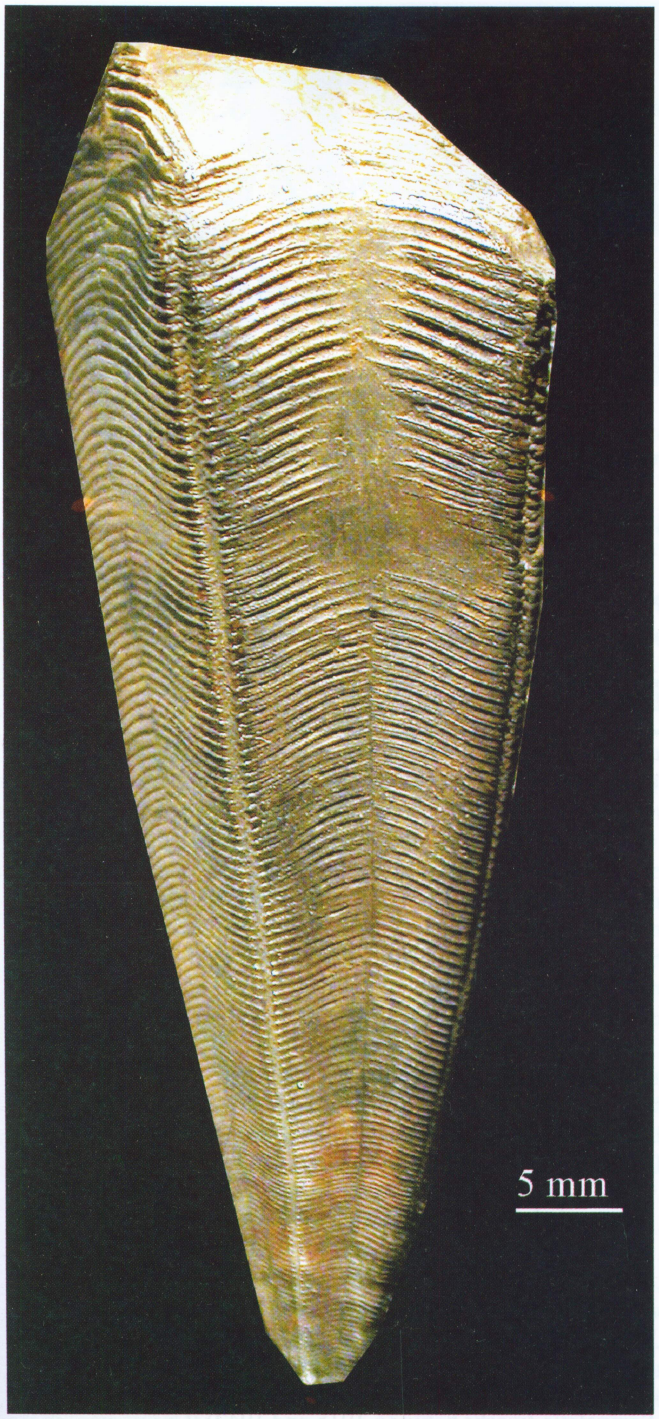


Fig. 2. Specimen of *Paraconularia quadrisulcata* (Sowerby, 1821) (NHM PG 4480).

conulariids, regarding them as sessile organisms. However, Ruedemann's study was based on material now known to belong to another group of presumed cnidarians, *Sphenothallus* Hall, 1847 (Van Iten, 1994).

## 20th CENTURY: INCREASING KNOWLEDGE OF CONULARIIDS

The first half of the 20th century included five outstanding works on conulariids: Slater (1907), Bouček (1928), Kiderlen (1937), Fletcher (1938), and Sinclair (1948a). These summarize the themes of studies at the time: (1) systematic description, (2) morphology, (3) taxonomic studies of the group, (4) biological affinities, (5) exoskeleton composition, and (6) stratigraphical studies.

Ida Slater (1907), the second woman to study conulariids, organized all known British species based on the large collections of the then British Museum (Natural History), as well as other museums including the Sedgwick Museum, University of Cambridge, the Hunterian Museum, University of Glasgow and the Geological Survey in Edinburgh. She also studied specimens borrowed from elsewhere. Slater drew the first archetypal conulariid with morphological elements that were copied by many subsequent authors. She followed Gerhard Holm's classification (1893). Her work is key to the study of the huge collection that is located in the present Natural History Museum in London, comprising almost 35% British material, including important material from the Ordovician Starfish Bed of Girvan that was collected by Mrs Elisabeth Gray. Slater became one of the outstanding figures among conulariid researchers.

Bedřich Bouček (1928) revised all of the Czech conulariids, including Barrande's (1867) material. Most of these samples are located in the Národní Muzeum, Prague, making this museum one of the most important in the world, with at least 2,135 specimens, and second after the Natural History Museum, London, in terms of the taxonomic diversity of conulariids represented, with 39 species (Sendino, 2007). Bouček (1939) later devised a new classification of conulariids, recognizing seven different groups at generic and subgeneric levels. Furthermore, he also studied, together his colleague F. Ulrich, the exoskeletal composition of conulariids (Bouček and Ulrich 1929).

In 1937, Helmut Kiderlen published one of the most influential works on conulariids - *Die Conularien* - that covers their morphology, classification and biological affinity. Kiderlen's hypothesis provided a solid beginning for future research on conulariids. For the first time the hypothesis of a scyphozoan cnidarian affinity was proposed for conulariids. Kiderlen did not stand alone at this time. His fellow American, James Brookes Knight, also published in parallel during the same year (1937) a work on scyphozoan affinity, but this study has less depth.

Harold Fletcher (1938) continued the tendency to describe species by region, began by Rouault in 1851, in this case in Australia. His work applied Holm's (1893) classification (Laeves, Longitudinal, Moniliferae and Cancellata), and dealt mainly with Permian species in contrast to the British and Czech material which is mainly Ordovician or Silurian. Fletcher (1938) corrected some mistakes made by previous authors; for example, he noted the synonymy between *Paraconularia derwentensis* and *Paraconularia tasmanica* (Johnston, 1887), and the homonomy of *Conularia quadrisulcata* with *Paraconularia quadrisulcata* (Sowerby, 1821) and *Metaconularia sowerbyi* (Verneuil, 1845).

After the Second World War, in 1948, George Winston Sinclair (1948) wrote the first thesis entirely on conulariids. This compiles previously published information on the morphology, palaeoecology, geographical and stratigraphic distributions, biological affinities and taxonomy of genera and species globally, but with emphasis on occurrences from the Laurentian microcontinent.

Additional works that appeared in the first half of the 20th century are those of Jan Vratislav Želízko (1900-1921), I.

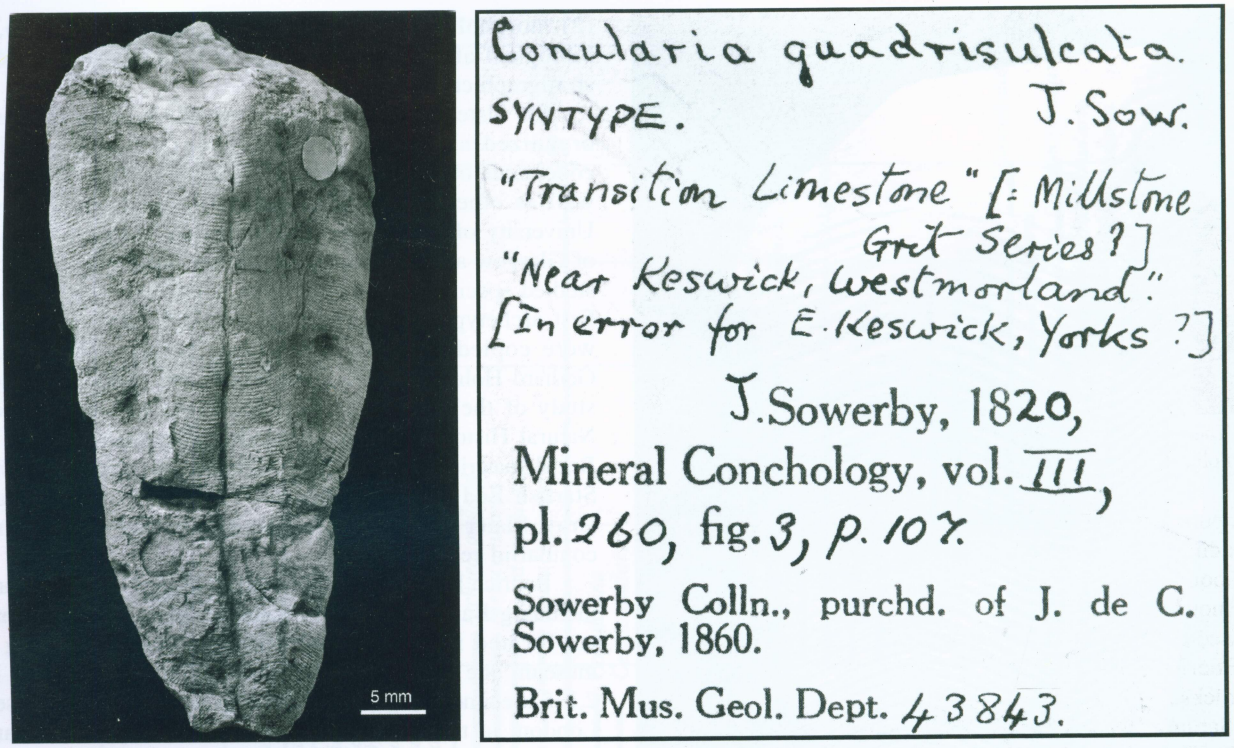


Fig. 3. A. An original Sowerby syntype of *Conularia quadrisulcata* Sowerby, 1821 (NHM 43843). B. The accompanying specimen label; note that the correct date of publication is 1821 and not 1820 as written on the label.

Hayasaka (1920a, b), Edwin Dinwiddie McKee (1935) and Ivar Hessland (1949) on specimens from Bohemia, Japan, Arizona and Sweden respectively. Other authors included descriptions of conulariids in regional studies of fossils: Alexander Fuchs (1915) on the Devonian Hunsrückschiefer of Germany; August Frederic Foerste (1928) on Ordovician of Arctic America; Marcel Thoral (1935) on Ordovician of the Montagne Noire, France; Hervey Woodburn Shimer and Robert Rakes Shrock (1944) on the Ordovician-Carboniferous of North America; and Henri Termier (1936) and Genevieve and Henri Termier (1950) on the Ordovician - Carboniferous of Morocco. There are a few studies of morphology and biological affinities, like the works of Rudolf and Emma Richter (1930) on conulariids from the Hunsrückschiefer in Germany, and J. Kowalski (1935) on Armorican conulariids (French Ordovician) with extraordinary preservation, studying for the first time the microstructure of the exoskeleton. Henri and Genevieve Termier (1947, 1949) studied the morphology and affinities of Moroccan conulariids, and Bermudo Meléndez (1950) published a study in Spanish of the biological affinities and morphological terminology of the conulariid archetype. Conulariid biostratigraphy was considered by Vicente Kindelán (1918) (Ordovician and Silurian), Pierre Comte (1937) (Silurian), and Primitive Hernández Sampelayo (works between 1915 and 1942) (Ordovician) in the Iberian Peninsula.

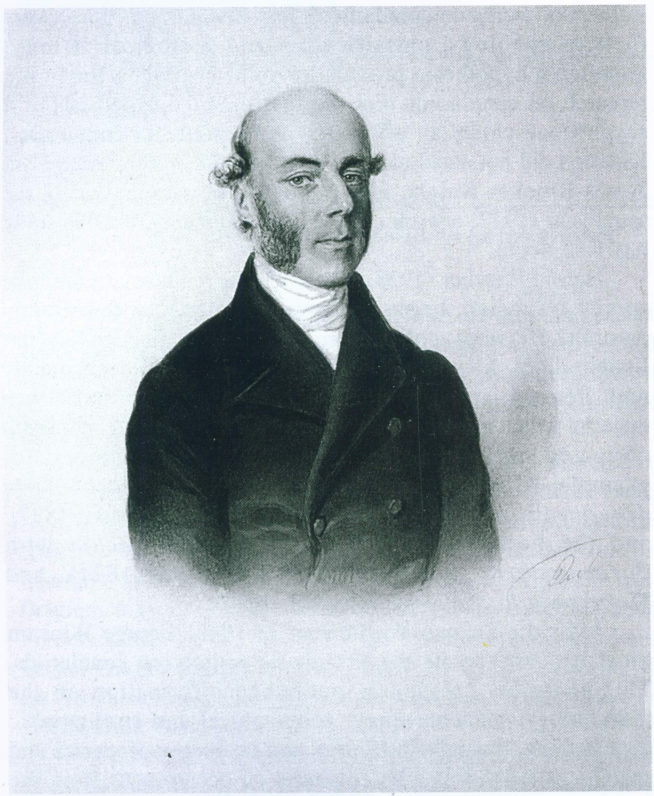

Fig. 4. The French-born palacontologist Joachim Barrande (1799-1883) (V Dvořáková *in* Horny, 1999)

In the second half of the 20th century studies on conulariids became more numerous and comprehensive, with new discoveries that helped to clarify their affinities. Publications worthy of note are those of George Winston Sinclair (1952) on the classification of conulariids, and the same author's compilation of all bibliographical references on conulariids, in collaboration with E. S. Richardson, in 1954. Raymond C. Moore and his colleague H. James Harrington (1956a, b) devoted a chapter to the class Conulata in their encyclopaedic *Treatise on Invertebrate Paleontology*, and in another chapter they investigated conulariid affinities with the Scyphozoa and also studied the composition and microstructura of the exoskeleton.

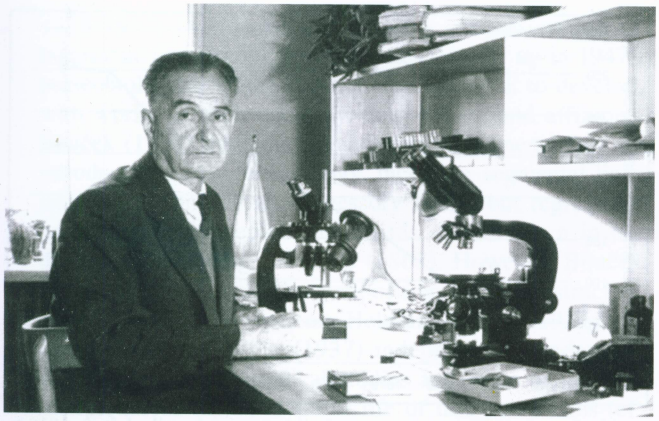

Fig.5. The palaeontologist Roman Kozlowski (1889-1977) in his study at the Polish Academy of Sciences, Warsaw (http://www.graptolie.net).

An important study is that of Robert M. Finks (1960) based on the finding of two individuals attached to the external surface of a sponge, allowing a sessile mode of life to be inferred. Other notable publications are the systematic studies of Egbert G. Driscoll (1963) on North American conulariids; Fritz Kutscher and Eberhard Kümmerle (1964) on conulariids from the Hunsrückschiefer; Enrico Serpagli on Ordovician conulariids from Sardinia; G. A. Thomas (1969) on Australian conulariids; Tom L. Harland and Ron K. Pickerill (1987) on an Ordovician conulariid from Québec, inferring its mode of life; and Andrey Yu. Ivantsov and Mikhail Aleksandrovich Fedonkin (2002) on a six-sided conulariid from the Vendian of Russia.

No account of the history of conulariid research would be complete without some mention of the works of Kozlowski (1968) and Bischoff (1978). The Polish palaeontologist Roman Kozlowski (Figure 5) published an innovative study in 1968 giving evidence that supposed conulariids had an endoskeleton. Some conulariid taxa were dedicated to Kozlowski by his Bolivian colleague Leonardo Branisa (e.g. *Conularia kozlowskii* Branisa, 1960, later regarded as a junior synonym of *Conularia quichua* Ulrich *in* Steinmann and Döderlein, 1890), in gratitude for his work as professor and director of the Department of Geological Sciences of the School of Mines of Oruro (Bolivia) from 1913 at 1921. The second author, Günther C. O. Bischoff (1978), an Australian of German origin, supported the relationship of conulariids with scyphozoans. Finally, it is necessary to mention Bernd Hergarten's (1985, 1988, 1994) contributions to conulariid systematics, describing new German genera and species; and that of Nigel C. Hughes *et al.* (2000) who studied conulariid affinities and introduced new taxa from North America. McKinney *et al.* (1995) found examples of budding, supporting a scyphozoan affinity, in conulariids from the Pyrenees. The observed buds emerged from a larger individual at an angle of 90º.

Important studies on conulariids were published by Loren E. Babcock and collaborators between 1985 and 1996. These focus on taxonomy, biological affinities (considering conulariids to be an independent phylum), and teratology and pathology. Fredrik Jerre worked between 1988 and 1994 on conulariid systematics, exoskeletal microstructure, morphology, biological affinities and stratigraphic distribution in the Silurian of Gotland, Sweden. Finally, the seminal publications of Heyo Van Iten (Figure 6) and colleagues between 1987 and 2006 considered the phylogenetic relationship of conulariids with cnidarians, systematics, microstructure of the exoskeleton, morphology, and the stratigraphical distribution of Ordovician conulariids from Minnesota, New York and Iowa states. The phylogeny of conulariids was an almost virgin field until Prof. Heyo Van Iten began his career, but between 1987 and 2006 he published a dozen papers on conuariiid phylogeny.

Outstanding theses completed in this period are of those of L. E. Babcock (1986), F. Jerre (1988) and H. Van Iten (1989).

Other publications during the second half of the 20th century deal with the biostratigraphy of conulariids. These include the works of Henri and Genevieve Termier (1950, 1959) on the Ordovician-Carboniferous of Morocco; Esteban Márquez Triguero (1962) on the *Conularia* slate bed of the Silurian of the Iberian Peninsula; Sayar (1955, 1964) in the Bosphorus; Vladimír Havlíček and J. Vanek (1966), and Petr Štorch and Michal Mergl (1989) on Bohemian Ordovician conulariids; A.J. Whiteman (1971) on the Cambro-Ordovician of Algeria; William T. Dean (1975, 1980) on the Turkish and Jordanian Ordovician *Conularia* Sandstone; Michel Robardet (1981) on the Ordovician of the Armorican Massif; Juan Carlos Gutiérrez-Marco and colleagues between 1983 and 2003 on the Ordovician of the Iberian Peninsula and the Moroccan Anti-Atlas; unpublished works of the Geologic Service of Morocco under the direction of Jacques Destombes between 1983 and 2002; a study of the Argentinean Precordillera by Juan Luis Benedetto and Zarela Angélica Herrera in 1987; and studies of the Montagne Noire by William Thornton in 1996 and José Javier Álvaro and collaborators in 2001.

At the end of 20th century there was a proliferation of publications about conulariid systematics, exemplified by the works of Jean Pillet and Gerad Beaulieu on the Armorican Ordovician in 1995 and 1998, and of Chinese authors such as

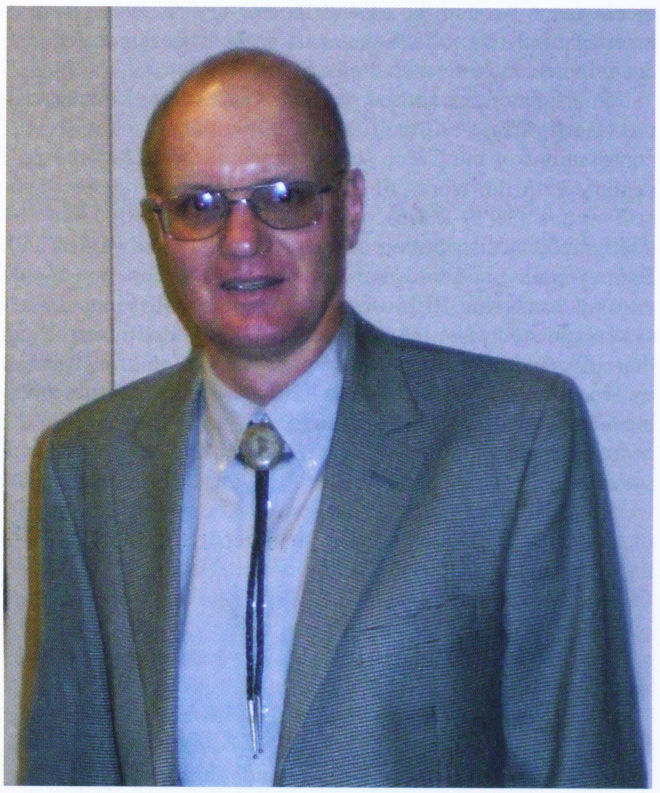

Fig. 6. Professor Heyo Van Iten (Hanover College, Indiana) (photo courtesy of H. Van Iten).

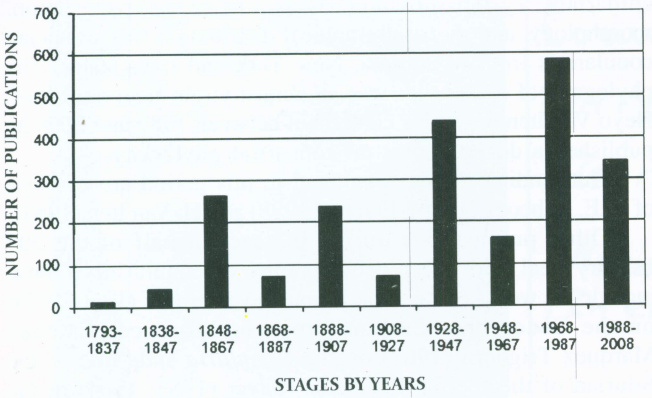


Fig. 7. Number of publications on conulariids during different historical stages

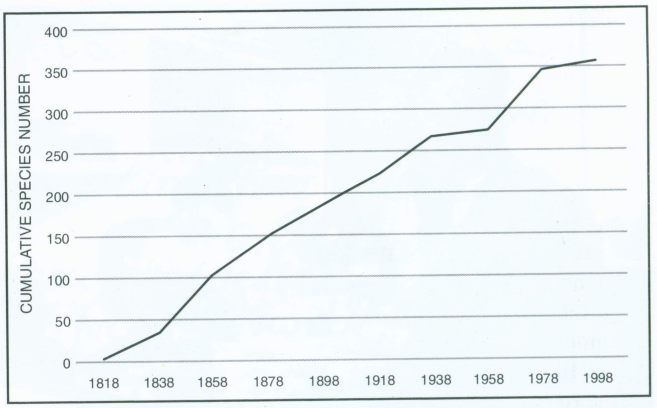


Fig. 8. Cumulative increase in conulariid species described from 1818 to 2008. The continuing upward trend in the curve implies that there are additional species yet to be described.

Zhang Shou-Xin (1977), Xu Gueiyong and Li Fenglin (1979a, b), He Tinggui (1984) and Zhu Zhi-kan (1985).

John R. Nudds and J. John Sepkoski (1993), in *The Fossil Record 2,* classified conulariids as scyphozoans, under the order ?Conulariida Miller and Gurely, 1896, recognizing five families.

The last decade of the 20th century witnessed the beginning of research on small shelly fossils related to conulariids, including those on hexangulaconulariids by Simon Conway Morris and Chen Menge in 1992; protoconulariids by Qian Yi Heyo Van Iten, Robert S. Cox, Mao-Yan Zhu and Zhuo Er-Jun in 1997; and other fossils as *Olivooides* by Stefan Bengtson and Yue Zhao in 1997 too.

## FROM THE TURN OF THE CENTURY

Conulariid research has undergone significant changes in recent years. Around the turn of the century, there has been a proliferation of publications with great importance for the development of future studies on conulariids.

Four schools are at the forefront of research on conulariids, the Czech, Chinese, Brazilian and Argentinean schools. The contributions of the Czech school began at the end of the 20th century with the works of Zdeňka Vyhlasová Brabcová and colleagues (1999-2005), contributing knowledge on the stratigraphical distribution of species in Perigondwanian and Baltic regions, and with the study of the morphology of the exoskeleton using SEM. The Chinese school, focusing on systematic studies in the 20th century, has added research on the embryonic development of phosphatic Cambrian fossils by Hua Hong and collaborators (2004). The Brazilian school includes the work of Sabrina Coelho Rodrigues and Juliana de Moraes Leme and colleagues (2003a-d) on the taphonomy and systematics of conulariids, providing evidence that conulariids were sessile. Juliana de Moraes Leme (2006) wrote a fifth thesis on conulariids that included a phylogenetic study based on the subfamilies proposed by Moore and Harrington (1956b). In Argentina Nora Sabattini's works and collaborators stand out (2001, 2004, and 2005) stand out. These concern taphonomy and new discoveries of conulariids with sessile modes of life. Another thesis was completed in 2007 by one of us, Maria Consuelo Sendino Lara, on the conulariid collections of the Natural History Museum, London. This collection was studied systematically, stratigraphically and phylogenically, and compared with other important conulariid collections.

Therefore, the study of conulariids has slowly expanded, within the areas of stratigraphical distribution as well as morphology, taphonomy and phylogeny. This has been helped by the greater ease to travel and have access to specimens in collections around the world. In addition, technical advances have also been important, such as the availability of better microscopes (including SEM) and more advanced software for phylogenetic studies.

The current century has seen a continuation of research on Precambrian and Cambrian fossils related to conulariids by Andrey Yu. Ivantsov and Mikhail Aleksandrovich Fedonkin (2002) and by Loren E. Babcock, Anne M. Grunow, Georg Robert Sadowsk and Stephen A. Leslie (2004), as well as on protoconulariids by Liu Yunhuan, Li Yong, Shao Tiequan, Wang Yaopei, Yu Bo, Han Huiping and Yang Jian (2005) and Leanne J. Pyle, Guy M. Narbonne, Godfrey S. Nowlan, Shuhai Xiao and Noel P. James (2006).

## STAGES

A bibliometric compilation shows an increase in the number of publications on conulariids, from Ure (1793) to the present day, in which it is possible to distinguish four stages (Figure 7):

1 1793-1867: Initial period that corresponds to the first descriptions of conulariid fossils (i.e. α-taxonomy of Mayr, 1969). The number of works increased progressively through time, with the first tentative suggestions of the biological affinities of conulariids based on their shape (Sowerby, 1821; Archiac and Verneuil, 1842; Sandberger, 1847). The outstanding publication of this period is the encyclopaedic work of Joaquim Barrande (1867) entitled *Système Silurien du Centre de la Bohême* where 27 species are described, a culmination of the early studies on the group.

2 1868-1927: During this stage research on the stratigraphical distribution of conulariids became important, and the first works on classification were published (Lindström, 1884). The number of publications increased up to 1907 and then slightly decreased until 1927. The monographs of Holm (1893) and Slater (1907) stand out during this period. Holm (1893) studied conulariids from the Baltic, synthesized existing knowledge about the group, with particular reference to central European and British species, and made a second attempt at classification. In contrast, the monograph of Slater (1907) is focused on British conulariids.

3 1928-1967: In this period, besides a continuation of taxonomic and stratigraphical studies (mostly up to 1947), palaeobiological studies on conulariids began to develop, with works on their anatomy, morphology and affinities. Bouček (1928) improved the anatomical nomenclature by introducing a new terminology, including segmental lines (median, secondary and accessory lines), but regrettably he continued to depict conulariids upside-down in his drawings, following Barrande (1867). However, Bouček pioneered the study of the composition and microstructure of the exoskeleton. Later on, Helmut Kiderlen (1937) and James Brookes Knight (1937) independently undertook the first modern anatomical studies and some of the first interpretations of the mode of life of true conulariids (cf. Ruedemann 1896-8 who misidentified *Sphenophallus* as a conulariid). One of the reconstructions of Kiderlen (1937) was reproduced by later authors (Bouček, 1939; Moore and Harrington, 1956a). Also worthy of note are the works of George Winston Sinclair between 1940 and 1952, including his doctoral thesis (Sinclair, 1948a), in which all aspects of conulariids are treated, including history of study, morphology, geographical and stratigraphical distributions, biological affinities, systematics, taxonomy and paleoecology. This period also saw the publication of the conulariid volume of the *Treatise on Invertebrate Paleontology* (Moore and Harrington, 1956a, b).

4 1968-2008: In this period an important increase in stratigraphical studies occurred, multiplying the number of site records for conulariids. In the few last years, taphonomic, phylogenetic and morphological studies of the group have continued. Four schools (Czech, Chinese, Brazilian and Argentinean) researching conulariids have emerged. For example, the Brazilian school has researched conulariid palaeoecology, taxonomy, taphonomy and phylogeny (Leme *et al.*, 2003a, b; Rodrigues *et al.*, 2003; Leme, 2006). It is worth highlighting: the doctoral thesis of Loren E. Babcock (1986) and later publications by Babcock and Feldmann (1986a, b, c) and Babcock *et al.* (1987a, b, c) among others; the thesis of Fredrik Jerre and subsequent papers (1988, 1989, 1991, 1993, 1994a, b) dealing with stratigraphy and functional morphology; the thesis of Heyo Van Iten (1989a) and numerous later publications which approach the study of conulariids from a modern phylogenetic perspective; the work of Juliana de Moraes Leme (2006) based fundamentally on phylogenetic studies; and the thesis of María Consuelo Sendino Lara on the NHM, London collection of conulariids. Notable new discoveries include those of Puesto La Carlota in the Argentinean Permian (Sabattini and Hlebszevitsch, 2004, 2005) and Ponta Grossa in the Brazilian Devonian (Rodrigues et *al.*, 2003a, b) showing the sessile mode of life of conulariids.

## CONCLUSIONS

Advances in the study of conulariids during the more than 200 years since the Ure (1793) first figured a conulariid are remarkable (Table 1). There has been increasing interest in conulariids during the second half of the 20th century, and new researchers continue to enter the field. Knowledge has improved considerably, not only of morphology but also of phylogeny and palaeoecology. Technological advances, including the availability of SEM, and the increase in interest bodes well for the future of research on conulariids (see Leme *et al.*, 2008).

**Table 1: Landmarks in the history of the study of conulariids**

| Year | Author | Landmark |
|---|---|---|
| 1793 | Ure | First figure of a conulariid |
| 1821 | Sowerby | Genus *Conularia* is erected |
| 1859 | Murchison | First depiction of a conulariid in original life orientation |
| 1875 | Hicks | First use in stratigraphy |
| 1884 | Lindström | First classification |
| 1896 | Ruedemann | First palaeoecological study |
| 1907 | Slater | Archetype with morphological elements |
| 1937 | Kiderlen Knight | First interpretation as a scyphozoan |
| 1948 | Sinclair | First suggested to be an extinct phylum |
| 1971 | Glaessner | First phylogenetic study (as cnidarians) |
| 1986 | Babcock and Feldmann | Phylum Conulariida proposed |
| 1991 | Van Iten | First cladistic analysis |
| 1997 | Conway Morris and Menge | First study of putative ancestors of conulariids ancestors |

Despite these advances, the fossil record of conulariids is still incompletely known. This is implied by a cumulative plot of new species descriptions through time which shows little evidence of levelling-off (Figure 8).

Of note are the studies on conulariids by women, some undertaken at times when it was socially almost unheard of for females to engage in research or geological fieldwork. In France Marie Rouault (1813 -1881) collected conulariids during the 19th century. The British women Elisabeth Gray (1831-1924), a collector of invertebrates, particularly from the Starfish Bed of Girvan, and Ida Slater (1881-1969) were active in the 19th and early 20th centuries. Other women who have worked on conulariids are Geneviève Termier (1917-2005) from France, Zdenka Vyhlasová Brabcová from the Czech Republic, Juliana de Moraes Leme from Brazil, Argentineans Sabrina Coelho Rodrigues and Nora Sabattini, and the Spaniard María Consuelo Sendino Lara.

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