Historical perspective: 140 years of Mesozoic radiolarian taxonomy

Luis O'DOGHERTY
Facultad de Ciencias del Mar, Universidad de Cádiz,
E-11510 Puerto Real (Spain)
lodogher@uca.es

Patrick DE WEVER
Muséum national d'Histoire naturelle, Département Histoire de la Terre,
case postale 48, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
dewever@mnhn.fr

Špela GORIČAN
Paleontoloski Institut Ivana Rakovca ZRC SAZU,
Novi trg 2, SL-1000 Ljubljana (Slovenia)
spela@zrc-sazu.si

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ABSTRACT
This paper summarises quantitatively the progress made on the taxonomy of Mesozoic radiolarians over the last 140 years and it provides an overview over 170 years of radiolarian literature. The dataset consists of radiolarian genera and species described as new since 1876. These collections contain 915 genera and 6296 species described in 449 publications. The analysis focuses mainly on a descriptive statistics of the genera collection, ensuing the review carried out by the Mesozoic Working Group of InterRad. Twelve diagrams are presented. They illustrate the yearly production of new species and radiolarian publications since 1834, and the number of new species per Mesozoic period, per radiolarian order, and per most prolific authors. A special attention is given to the quantitative analysis of valid vs. invalid genera (synonyms, homonyms, *nomina dubia*), that are also related to the age of radiolarians, research period and authors.

KEY WORDS
Radiolaria,
Triassic,
Jurassic,
Cretaceous.

RÉSUMÉ
Perspective historique : 140 ans de taxonomie des radiolaires mésozoïques.
Cer article résume 140 ans de taxonomie des radiolaires et 170 ans de bibliographie sur ces mêmes organismes. Le jeu de données concerne tous les genres et espèces de radiolaires décrits comme nouveaux depuis 1876 soit 915 noms de genres et 6296 espèces décrits dans 449 publications. L'analyse a été focalisée sur les genres, en cohérence avec le travail mené par le groupe de travail Mésozoïque d'InterRad. Douze diagrammes illustrent les résultats. Ils représentent la production annuelle de nouvelles espèces, le nombre de publications depuis 1834, le nombre de nouvelles espèces par période du Mésozoïque, par ordre de radiolaires, et par auteur. Une attention particulière a été portée sur les noms de genres valides/invalides (synonymes, homonymes, *nomina dubia*), en fonction des âges, des époques d'étude et des auteurs.

MOTS CLÉS
Radiolaires,
Trias,
Jurassique,
Crétacé.

INTRODUCTION

Study of radiolarians is relatively recent. The first account of a living radiolarian dates from 1834 when Meyen described the first colonial radiolarian from the China Sea. Ehrenberg described the first fossil in 1838 from the Eocene-Oligocene of Barbados. Haeckel first used the informal word "radiolarians" in 1860. Our knowledge made a significant jump in 1881 and 1887 when he published an extensive description of living and fossil radiolarians in the Report of the H.M.S. *Challenger* expedition. More than 1200 genera and 2790 species were introduced. His classification was based on the geometry of the shell, the number of segments or the concentric shells, the presence of latticed or spongy shells, the presence or absence of a terminal aperture. Haeckel himself admitted in 1887 the artificial character of his taxonomic classification, but his classification system remained in use until very recently although criticised by many authors as early as 1889 (Bütschli). The first modern revision of Haeckel's classification was done by Campbell (1954) but his effort resulted in further complication than clarity. Applying mechanically the guidelines of the *International Code of Zoological Nomenclature* (ICZN 1999) he designated type species for all radiolarian genera that were described by Haeckel on the basis of Cenozoic specimens. Unfortunately, many of these type species had never been illustrated by Haeckel, or had been previously described by Rüst (1885, 1888, 1892, 1898) from thin sections of Mesozoic rocks, and named following Haeckelian taxonomy. Thus, Campbell made many genera unrecognisable or changed completely the meaning of some of Haeckel's genera and families. Several radiolarists recognised these great defects of Campbell's work and tried, without success, to have it placed in the Official Index of Rejected Works in Zoology. The Haeckelian system had a two-sided effect on the development of the understanding of radiolarians. On the positive side, it has provided a comprehensive, simple, geometric framework within which to record most of the radiolarians encountered in all the sedimentary record. On the negative side this purely geometric classification inhibited for a long time the development of any alternative, probably more natural system. A recent proposition has been made by Dumitrica using the inner structure which has been exposed in De Wever *et al.* (2001).

Calcareous plankton such as foraminifers and coccoliths are far more abundant and widespread in sedimentary rocks than siliceous microfossils. They were thus preferred by micropaleontologists in the early 1960s. Three decades later, our knowledge is such that radiolarians are useful tools for stratigraphic studies, paleobiology, and palaeoenvironmental reconstructions. Therefore a need rose at the end

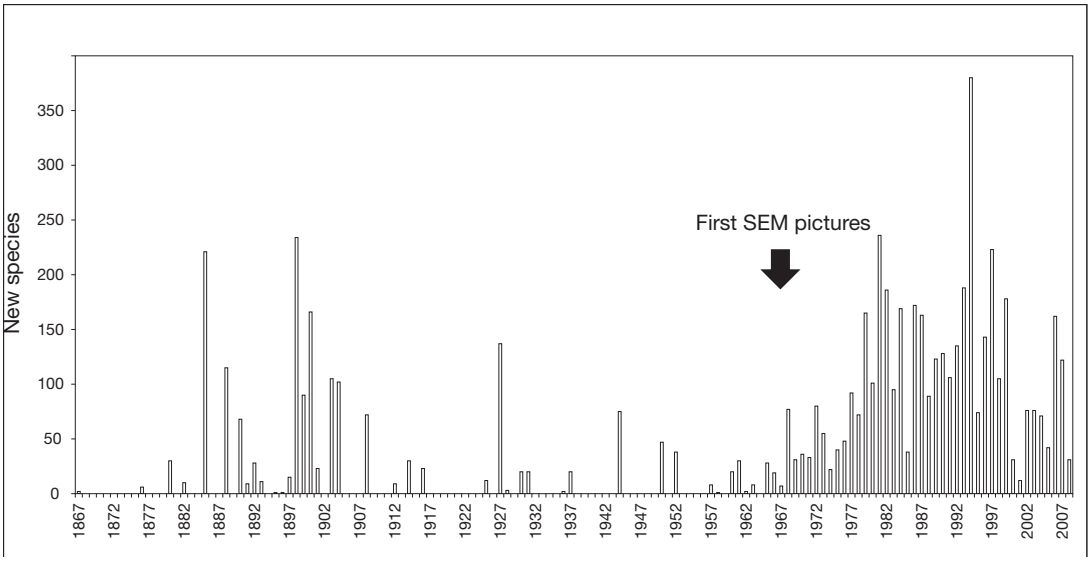

FIG. 1. — New species of Mesozoic radiolarians published between 1867 and 2008.

of the 20th century to work out a comprehensive synthesis including a general review at the family level (De Wever *et al.* 2001). Following this stage we felt the need to synthesise the information of the stratigraphic range still at the family level (De Wever *et al.* 2003, 2006). Having, in the present work, revised all the Mesozoic genera, it is now interesting to have a look at the general evolution of Mesozoic radiolarian studies since the beginning.

MESOZOIC SPECIES

The complete dataset of generic and species names being unavailable, a taxonomic review for the whole Mesozoic was not possible up to now. With the present work we are able to present the distribution of data after the information given in the original species description. The data analyzed come from the master list of Mesozoic species prepared by O'Dogherty (2009, this volume) and encompass the period between 1867 and 2008.

For a long time it was thought that the German author Zittel (1876) was the first to report a Mesozoic radiolarian: the Cretaceous species *Dictyomitra multicostata* Zittel, 1876. However Dumitrica & De Wever (1991) discovered that, paradoxically, the first Mesozoic radiolarian species was in fact described some years earlier by Karrer (1867) but erroneously attributed to a benthic Foraminifera (*Lagena dianae* Karrer, 1867). During the two last decades of the 19th century and the first half of the 20th, the research on Mesozoic radiolarians experienced a prolific period. Unfortunately the foundation of a true Mesozoic radiolarian stratigraphy and taxonomy were established much later.

As previously stressed by De Wever (1997) and De Wever *et al.* (1994, 2001) the history of research on radiolarians can be divided in two main stages (*discovering* and *recovering*) separated by a quiet interval of abandon of researches.

The Figure 1 shows the distribution of newly described Mesozoic species throughout time. It is clearly observed a bimodal distribution between 1867-1959 and 1960-2008. The recovery stage starts with the applications of the Scanning Electron Microscope (SEM) to the study of radiolarians in the 1970s, when it became clear that the taxonomic system of Mesozoic radiolarians would have to be reconsidered. Simultaneously, the first edition of the *International Code of Zoological Nomenclature* was published in 1961. At the same time a new international venture in oceanographic exploration began with the first international scientific ocean drilling program: the Deep Sea Drilling Project (DSDP). Between August and September 1968,

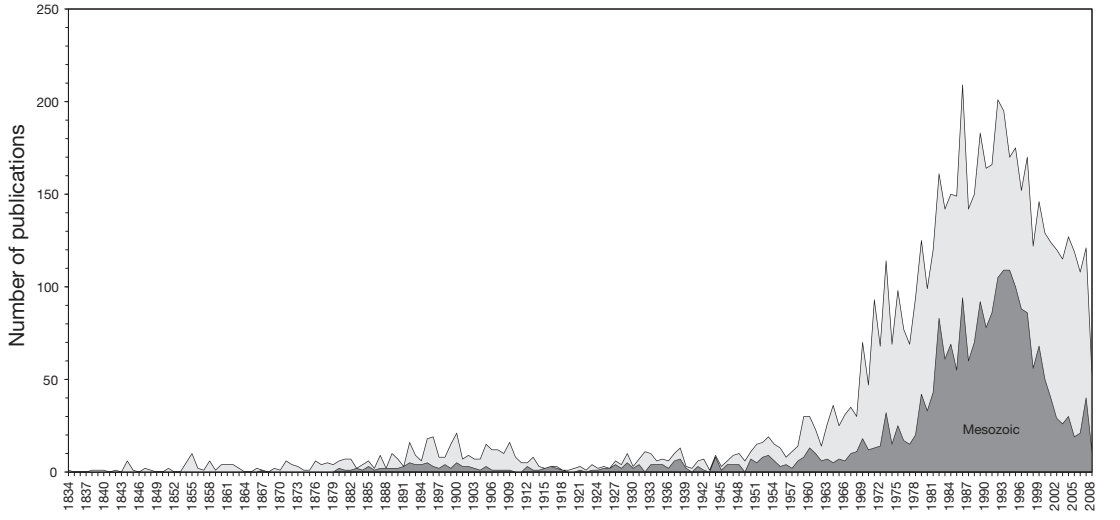

FIG. 2. — Area diagram showing the distribution of papers published on radiolarians (6100 publications) with indication of Mesozoic (2333 publications) between 1834 and 2008.

the Leg 1 of the D/V *Glomar Challenger* was coring sediments from which the first Mesozoic (Pessagno 1969) and Cenozoic radiolarians (Riedel & Hays 1968) were reported.

Similarly, a bimodal distribution is also observed in the history of published papers concerning radiolarians (Fig. 2). The history of discoveries on radiolarians tends to point out the main inputs in the knowledge of the radiolarians. They deal with the impact of research. Another scope is to have a look on the number of publications which refer more to the efforts of a community and somehow also to the efficiency of research. Our review dealt with the 6100 papers published from 1834 up to winter 2008, that is to say more than 170 years of research.

Publications on radiolarians began in the first part of the 19th century. One of the earliest papers was that of Meyen in 1834 describing low-latitude Cenozoic radiolarians from the Atlantic Ocean. Papers dealing with Mesozoic appeared in the later part of the 19th century. Zittel (1876) described the first Cretaceous genera and species from northern Germany. The study of Mediterranean Mesozoic radiolarians began some years later with Pantanelli (1880) who first described some species from Tuscany (Italy). Soon after, Rüst (1885, 1889) and Parona (1890) described and illustrated numerous Neocomian species from different Alpine locations in Italy, Switzerland and Austria.

Interests of early researchers were not confined to radiolarians but dealt with all fossil groups and Recent micro-organisms. Several monographs concerning Radiolaria were published during the late 19th century. The most extensive was that by Haeckel (1887) documenting the specimens collected during the voyage of H.M.S. *Challenger* (1873 to 1876). At that time, research was mainly carried out by men of independent means who, judging by the volume of work produced, regarded their studies with great enthusiasm.

Although the early scientists did not have the technology to recover the specimens as free elements, to record them or store the data as efficiently as present workers, the value of these early works should not be underestimated. In many cases, it is easier to improve an established work than to initiate it. As said elsewhere, these early studies were mainly done on thin-sections preparations, which only allow to describe part of the entire shape.

Prior to the development or availability of adequate photographic techniques, many of the earlier illustrations were hand-drawn and without any scale.

Even so, drawings are still valuable now, as they have the advantage of emphasising morphological features considered important which may not be noticed on a photographic illustration. An excellent more recent example of the use of hand-drawn illustrations is a paper published by Dumitrica in 1970 or the 465 drawings of radiolarians to illustrate families in the book published in 2001 by De Wever *et al.*

International communication was weak during the early years of radiolarian study and there was no international rules to regulate the way of creating new names (the first edition of the *International Code of Zoological Nomenclature* appeared only in 1961). Many species were described and, more importantly, named by two or more different authors with, as a result, taxonomic confusion. Such problems were only recently resolved and taxonomic clarity also is the main goal of the present work.

The Haeckel's monumental work on the *Challenger* material represented a period of discovery. It was followed by a period of depletion, mainly corresponding with the First World War, up the end of the Second World War. With the advent of the use of microfossils for oil exploration, around the mid 20th century, more people became interested in micropaleontology and this is reflected in the number of publications concerned with Radiolaria (see Fig. 2).

By the early 1970s, the international programme of ocean drilling (DSDP) provided a new impetus reinforced by the wide availability of the scanning electron microscope which made study of microfossil morphology easier and more complete. Indeed, in 1968, the first voyage of the *Glomar Challenger* for the Deep Sea Drilling Project (Leg 1) marked the start of an extensive exploration programme of the ocean basins and margins for purely scientific reasons. This programme has made available for study numerous sections which were previously inaccessible. The organization of the DSDP/ODP/IODP projects, and the co-operation of different nations, has resulted in a large inter- and multidisciplinary dataset in such fields as sedimentology, geochemistry and biostratigraphy. These data are available in a comprehensive, accessible form to non-specialists of these disciplines. The integration of this multi-disciplinary information provided a very good opportunity to constrain more accurately new interpretations.

Recorded occurrences of Mesozoic radiolarians both from DSDP/IPOD/ODP/IODP and land-based sections show that the distribution of these fossils is global on present geography and that they have been identified from a wide variety of host sediments. The bloom of their studies began in the 1980s. Their success is largely due to their unique ability to date the sediments associated with the basalts of the opening oceans. Therefore the number of publications increased up to a maximum of more than 100 publications per year. The flourishing period is between 1986 and 1997. More particularly four years (1992-1995) recorded the maximum of activity: reaching 100 and 109 publications in 1993 and 1994 respectively. Since then, the number of publications has decreased to reach the level of the 1970s, while the number of publications dealing with other eras seems to be more constant (around 80 to 100) since the 1970s. The reason of this decrease in Mesozoic research is uncertain but we can put forward two hypotheses. Firstly, the geological community may have lost its interest in radiolarians, because new spectacular discoveries are no more expected in this research field. The taxonomy is now considered to be relatively stable and the zonations for most of the Mesozoic are developed to a point that allows sufficiently precise radiolarian dating for general geological studies. Most siliceous sediments (in ophiolite complexes and others) have now been satisfactorily dated. This hypothesis, however, fails to explain why vast territories (e.g., the entire South America) remain largely unexplored (out of 2333 publications on Mesozoic radiolarians only 12 focus on South America). Secondly, the decrease in number of publications can be related to a general decrease of interest in paleontology by geologists who hope to replace it by geochemistry and geophysics. If such is the case, one can only predict a return to paleontology since it remains the cheapest, relatively rapid and certainly the most reliable way to obtain datings on rocks and sediments.

The history of Mesozoic research shows that the number of new species published during the 1st

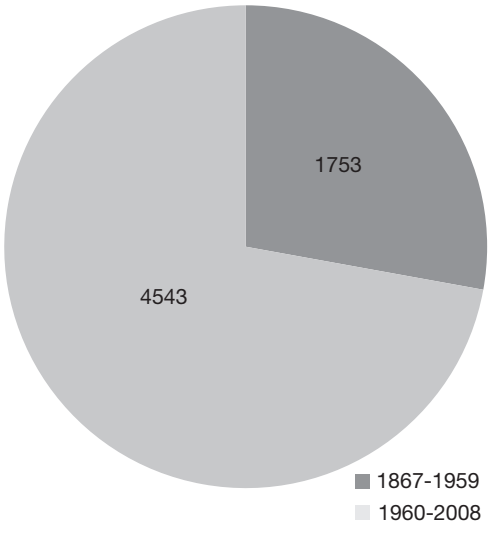

FIG. 3. — Pie diagram showing the number of new species across the two main historic stages of researches.

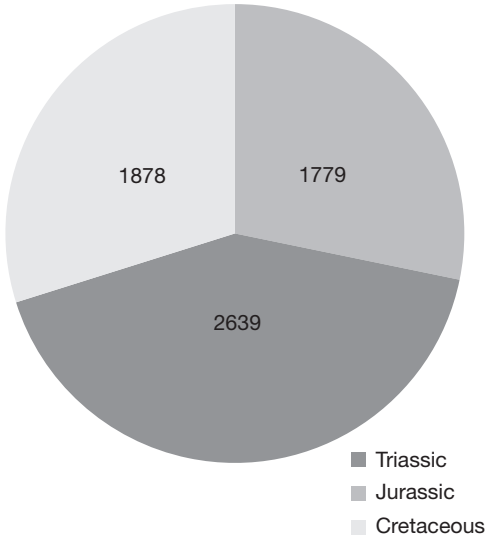

FIG. 4. — Pie diagram showing distribution of new radiolarian species across the Mesozoic Periods.

stage of radiolarian research is significantly high (Fig. 3) according to modern standards, if one considers the constraints and difficulties of study at that time. These pioneering paleontological descriptions were based exclusively on observations with optical microscopes. The inadequacy of laboratory techniques, the imprecise age-assignment of many taxa, the artificial character of the taxonomy at the genus and family levels founded by Haeckel in 1887 and the use of Cenozoic genera for Mesozoic species led to an inaccurate taxonomic system. For a long time the Mesozoic taxonomy was based on the Haeckelian system of classification in the belief that radiolarians did not change very much over time. The way to biostratigraphic progress was only opened in 1970 with the discovering of the HF method to extract radiolarians (Dumitrica 1970, Pessagno & Newport 1972). This method enabled a detailed description of the radiolarian fauna isolated from hard siliceous rocks.

An account of all new species described across the main Periods of the Mesozoic (Fig. 4) clearly shows that they are not equally distributed. Moreover, the number of species for the Jurassic and Cretaceous is amplified by the large amount of taxa described during the 1st Period (1867-1958), most of which should be unfortunately considered as *nomina dubia.* As stressed before, during the first period of research the taxonomy was implemented upon thin sections, therefore the holotypes remain quite imprecise. Moreover, some are based on fragmentary material which amplifies the doubtful definition. Besides these negative conditions several original collections are nowadays difficult or impossible to retrieve.

Among the six radiolarian orders occurring in Paleozoic-Mesozoic deposits (De Wever *et al.* 2001), three were strongly affected at the Late Paleozoic crisis (Albaillellaria, Archaeospicularia and Latentefistularia). Only one order (Entactinaria) crossed clearly the event, and some rare representative of two (Nassellaria, Spumellaria) occured before this limit, but clearly increase in diversity after the crisis (De Wever *et al.* 2006). The analysis of species across main orders of radiolarians has shown (Fig. 5) that most of the Mesozoic species (about 93%) have been described either as Nassellarians or Spumellarians. The low number recorded for Entactinaria may be somewhat artificial due to the poor knowledge on the initial structure of most of them. As a matter of fact, many Mesozoic species are described from poorly preserved material or, in some cases of well-

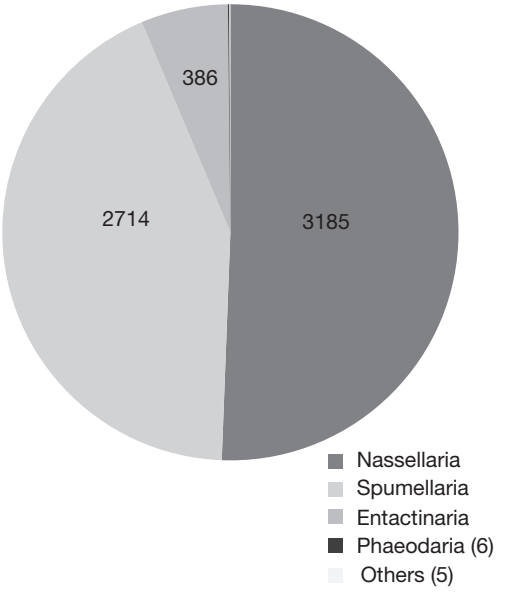

FIG. 5. — Pie diagram showing distribution of Mesozoic species across the main orders of radiolarians. Since the order's assignments are probably not accurate, this diagram is of weak meaning.

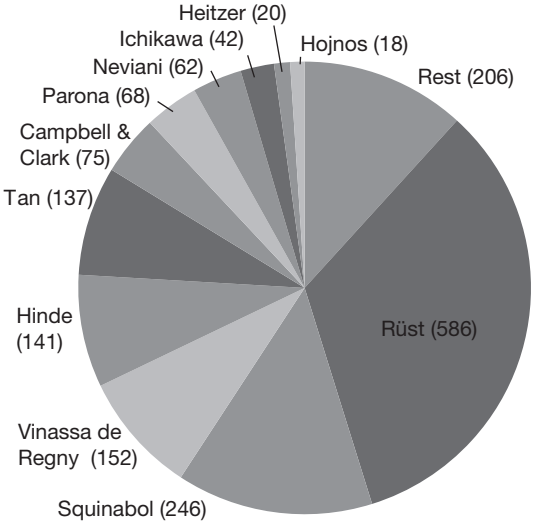

FIG. 6. — Pie diagram showing distribution of Mesozoic species across their authorship for the 1st period of research (1867-1959). Number of species in brackets.

preserved specimens, only external characters were used for their descriptions.

SPECIES AUTHORSHIP

More than 150 authors have contributed to the taxonomy of Mesozoic radiolarians, either creating new species or genera. The Figure 6 illustrates the authorship of new Mesozoic species during the first stage of research. The authorship in these years is localized in only few radiolarists but having a large scientific production. As stressed before, unfortunately most of these species should be considered as *nomina dubia* because their descriptions are based on thin sections. This impressive number reflects, in part, the influence of a Haeckelian taxonomy especially in earlier research on Jurassic-Cretaceous faunas prior to the application of SEM techniques. Another problem is that the species described during this period lack precise informations about the stratigraphic provenance or locality.

The distribution of Mesozoic species across their authorship for the second stage of research is plotted in Figure 7. In this diagram we have included those authors having authority on more than 45 genera against the rest of authors. That implies that

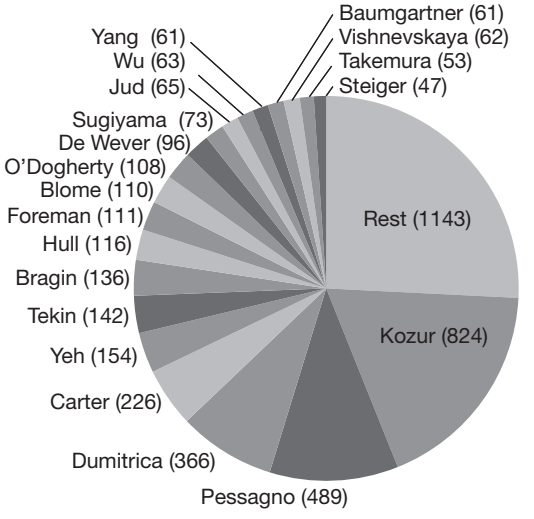

FIG. 7. — Pie diagram showing distribution of Mesozoic species across their authorship for the 2nd period of research (1960-2008). Number of species in brackets.

TABLE 1. — Number of genera by current status category with indication of the number of survivors of the Triassic/Jurassic (T/J) boundary. *, These homonyms are provisionally included in valid names in other chapters of this volume.

	Mesozoic	Triassic	Jurassic-Cretaceous	T/J survivors
Valid genera	584	281	332	29
Nomina dubia	136	14	128	6
Nomina dubia and homonyms	3	–	3	–
Synonyms	151	72	89	10
Synonyms and homonyms	4	1	3	–
Homonyms (replaced)	24	10	14	–
Homonyms (not yet replaced)*	9	1	9	1
Invalid	2	–	2	–
Invalid and synonyms	1	1	–	–
Invalid, synonyms and homonyms	1	1	–	–
Total	**915**	**381**	**580**	**46**

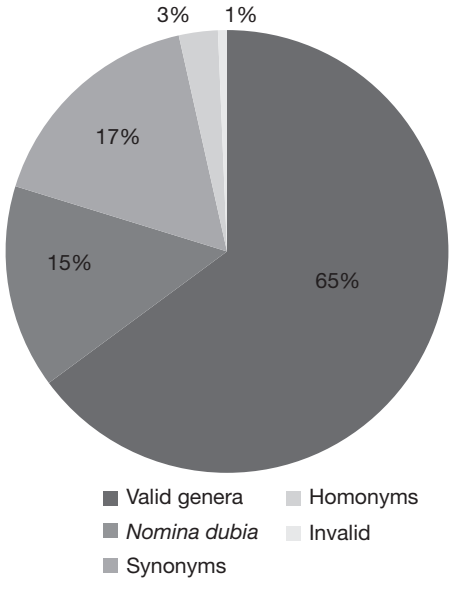

FIG. 8. — Pie diagram showing the percentage distribution of Mesozoic genera across their current taxonomic status.

¾ of the species are erected by 20 contributors of a whole of 150. However a more interesting aspect in the pie diagram is that ⅓ of the species were erected only by three authors during the second stage of research (Dumitrica, Kozur, Pessagno), which correspond with the main contributors at generic level too (see Fig. 12). One positive aspect of this achievement is that the basis of the Mesozoic taxonomy (defining species and genera) follows homogeneous guidelines.

MESOZOIC GENERA

Under the auspices of the International Association of Radiolarian Paleontologists (InterRad) the Mesozoic Working Group has carefully reviewed and reexamined the taxonomy of all available genera for the Mesozoic Era. The prime objective of their discussion was to agree on the systematics of genera and to achieve a taxonomic consensus of all contributors. The current status category of Mesozoic genera is summarized in Table 1 and it represents, in terms of numbers of taxa, the final result achieved by this revision.

The most interesting aspect in this table is the low number of genera crossing the Triassic-Jurassic boundary which reflects the significant change in morphologic patterns and faunal composition that occurred in the latest Triassic (Carter 1993; Carter & Hori 2005; Longridge *et al.* 2007). A similar pattern, however, is not found at the Jurassic-Cretaceous boundary, where the faunal assemblages do not display any perceptible change.

The distribution of Mesozoic genera across their current taxonomic status is presented in Figure 8 and summarizes the revision work settled by the Mesozoic Working Group through three years of intense collaborative research in Mesozoic genera.

Nomina dubia

The pie diagram in Figure 9 shows the distribution of genera of doubtful application (*nomen dubium*) plotted according to the present catalogues (Triassic against Jurassic-Cretaceous). It is quite evident that the Triassic period is marked by a very low occurrence of *nomina dubia*.

The Triassic has only a few *nomina dubia* (four genera), because the taxonomy is developed exclusively during the 2nd period of researches, especially since 1970, with a good illustration of the type species for most genera.

The distribution of *nomina dubia* across the main periods of research is presented in Figure 10. A high percentage of *nomina dubia* are assignable to Haeckel during the 1st period of research, but mostly because of the way they were used by Rüst from 1885-1989. Rüst described 586 Mesozoic species following the artificial systematics created by Haeckel in his famous *Prodromus* (1881). In this way he defined numerous new species much earlier than Haeckel himself (1887) might have designated the type species to be included in his own genera. By this act, up to 55 Rüst's species are first reported to the syntypical genera of Haeckel. In the *Treatise on Invertebrate Paleontology*, Campbell (1954) subsequently designated and fixed the type species. This action created an exasperating nomenclatorial problem because the new species of Rüst (as well as the majority of species created by his contemporaries) were based on broadly defined holotypes and in most cases the illustrations are either fragmentary or lack important diagnostic features allowing a precise identification of the species. In short, many species are unrecognizable and their use as type species entails a considerable degree of uncertainty. Following the ICZN guidelines, and with the purpose to stop this endless confusion, the Mesozoic Working Group has treated all these taxa as *nomina dubia*.

Inexplicably, during the 2nd period, a substantial proliferation of *nomina dubia* is recorded in spite of the new extracting techniques developed in the 1970s (Dumitrica 1970). The majority of these taxa (up to 36 genera) were published by Tikhomirova (1975, 1983, 1986, 1987a, b, 1989, 1990) based on extremely poor thin section photographic images.

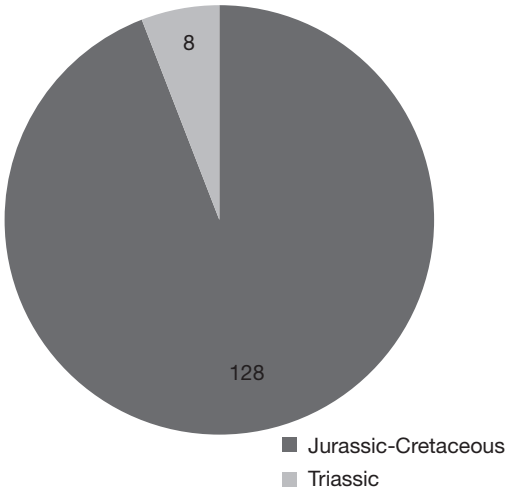

Fig. 9. — Pie diagram showing the distribution of *nomina dubia*.

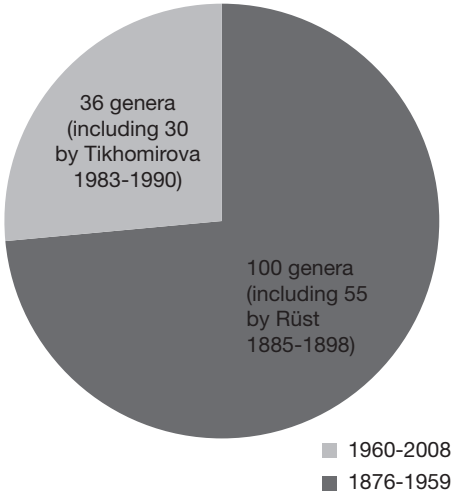

Fig. 10. — Pie diagram showing the distribution of *nomina dubia* genera for the Mesozoic Era plotted by stages of radiolarian researches.

Authorship of genera and synonyms

The authorship of genera is distributed in the Mesozoic across 80 radiolarists, who have contributed with the creation of 915 new genera in 140 years of research. However a reduced group of only 20 authors have been in charge for 80% of authorship (see Figs 11; 12).

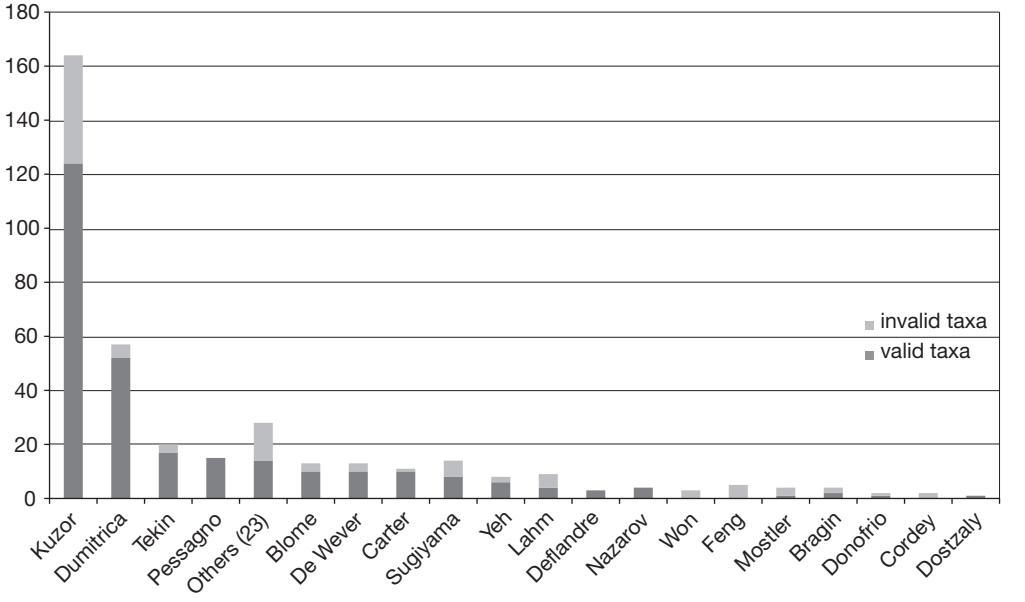

FIG. 11. — Bar diagram showing the distribution of invalid genera (mostly synonyms) for the Triassic period.

The genera revision project has shown that most synonyms were created since the explosion of modern research based on SEM studies. The systematic revision has declared 151 Mesozoic genera as synonyms with a similar number of synonyms in the Triassic (72) as in the Jurassic-Cretaceous period (89). Between 1867 and 1959 (prior to SEM), only eight cases of synonymy were recognized, whereas the number grows up to 145 for the second stage of research. The reason of this rapid increase in synonyms is very likely a consequence of a vast proliferation of new generic names in scattered publications in only two decades.

Undoubtedly the most prolific author in the Mesozoic has been Heinz W. Kozur, having the authority of 824 species, more than 200 genera and around 70 families. Figure 11 shows that Kozur has become the most prolific author for the Triassic, but also the most splitter, making an impressive number of synonyms.

The advantage of his taxonomic approach is a great number of illustrations providing detailed information on all observed combinations of morphologic characters defining the range of variability of species or genera (see for example the 14 different species of *Steigerispongus* described by Kozur & Mostler in 1996 from a single Longobardian sample).

For the Jurassic-Cretaceous Pessagno and coworkers are the most splitter team at species and generic levels. The highly-split taxonomy used by the aforementioned authors is based on slight morphologic differences that are generally too narrowly defined to be successfully applicable for stratigraphic correlations.

CONCLUSIONS

Through the 1970s investigators have continued to replace parts of the artificial Haeckelian taxonomy by new genera and families reflecting in this way more natural phylogenetic relationships. This was only possible thanks to the application of radiolarians in the sedimentary successions with the basic purpose of age determination. Undoubtedly, the stratigraphic record has provided the only support on which the phylogenetic relationships are based (Riedel & Sanfilippo 1986; Sanfilippo &

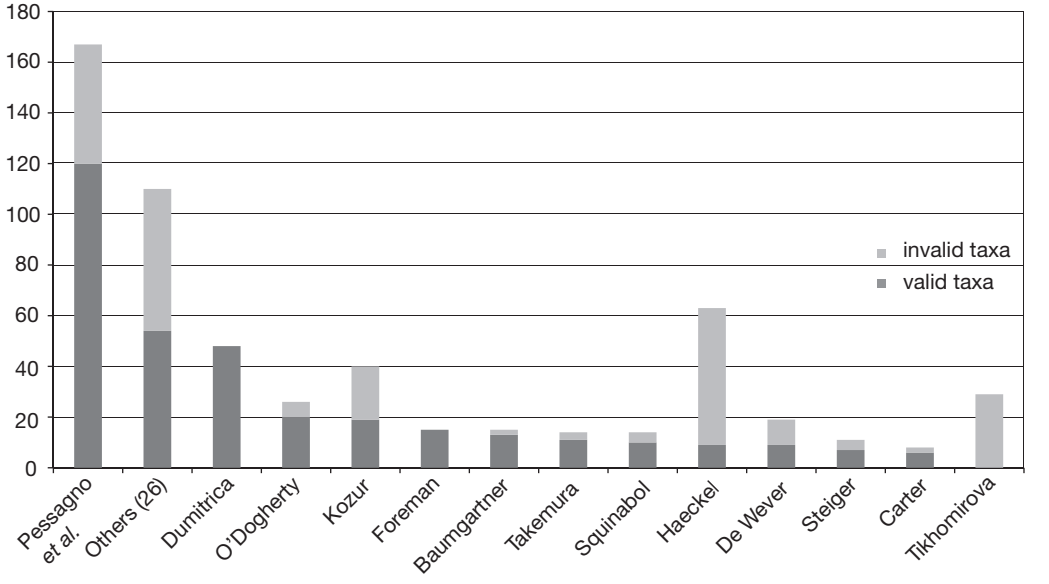

FIG. 12. — Bar diagram showing the distribution of synonymous genera for the Jurassic-Cretaceous period.

Riedel 1992; Dumitrica & Dumitrica-Jud 1995; Dumitrica & Hungerbühler 2007). In this manner the taxonomy has become more natural and as a consequence, a finer stratigraphic resolution has been attained (Baumgartner 1984; Pessagno *et al.* 1987; Jud 1994; Goričan 1994; O'Dogherty 1994; Baumgartner *et al.* 1995; Carter *et al*. 1998; Gorican *et al.* 2006).

An important goal attained by the Mesozoic revision of genera is to declare a large number of generic names as *nomina dubia*, because these genera inevitably have poorly defined type species. This line of reasoning led us to reject most of the Haeckel's generic names that were so far often used for the Mesozoic. We believe that by choosing recently described genera (or even by erecting new generic names) radiolarian taxonomy is better accommodated to the needs of future research, which will be preferentially oriented in phylogeny and high-resolution biochronology. The principal advantage of this course of action is that subsequent generations of authors will have a standard of reference for the type species.

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