The history of Mesozoic coral research after 1940

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Abstract: About 260 palaeontological papers on Mesozoic corals published since 1940 have been quantitatively analysed. New higher taxa such as genera, subfamilies, families, superfamilies and suborders are introduced. Systematic differences in the approaches of various authors and the role of some important new morphological terms are discussed. An extensive bibliography is furnished separately.

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THE INCREASE in geological research after World War II was accompanied by extensive palaeontological studies. Fossil corals which occur less frequently due to their ecological restriction, were investigated in greater detail. This made new concepts of palaeogeography necessary. Descriptions of fossils of this group and of new localities from the past fifty years are available in relatively large numbers from all over the world.

We therefore decided to compile in a data bank all the literature on Mesozoic corals (stratigraphy, occurrence, palaeoecology, morphology, systematics) published in the years from 1940 to 1990. A partial printout of this data bank is already available. All these publications were classified according to their content. In addition, some 260 of these were specially evaluated in an attempt to define their contribution to the systematics of corals. Some publications could not be obtained, which means that this data bank is not quite complete.

After reviewing almost all the literature of Mesozoic corals we became increasingly aware of past and present problems of coral research. We tried to pinpoint the reasons for the disproportionate development of coral research in the past and drew conclusions for future work.

Evaluation of the literature

The bibliography is based on data banks compiled by several colleagues and comprises most of the literature on Mesozoic corals published over the last fifty years.

As becomes evident from the accompanying diagram (Fig. 1), there has been an increase in publications in the period under review but also a change in subjects.

Before 1940 there was no continuous development: up to that time researchers followed the principles of systematics proposed by MILNE-EDWARDS & HAIME (1857/60), which were revised in part by KOBY (1880/89) and OGILVIE (1897).

Major investigations were resumed about fifty years ago: they were carried out, on one hand, by the founders of the American school (VAUGHAN & WELLS, 1943; WELLS, 1956) and, on the other, by the acknowledged master of the French school (ALLOITEAU, 1952, 1957). The systematic revisions made by both reserach groups were accompanied by a development of research methods and resulted in a complete renewal of systematics and in a flood of new taxa. These works revolutionized the study of corals, highlighted the backwardness of this field and led to an increased interest in Mesozoic corals worldwide.

Publications of the following twenty years were for the most part descriptions of corals. In addition to France and the USA, they were mainly from Great Britain, Hungary, Spain, Japan, the Soviet Union, Yugoslavia and Germany, to name only some of the countries. After 1960 studies were also carried out in Poland, Bulgaria, China and Czechoslovakia, whereas in Spain and Germany the interest grew less. The development was accelerated by worldwide improvements in telecommunication as well as in library and postal services, with improved facilities for exchange of literature and prompt availability of papers.

The contents of the publications changed: Whereas up to 1975 they consisted primarily of descriptions of fossil corals with details of their geological occurrence, subsequent publications dealt increasingly with aspects of palaeoecology, palaeogeography and morphology. Coral research, no longer a solely descriptive science, acquired a new quality: systematic investigations made it possible to formulate causal relations to explain the distribution patterns of Mesozoic corals. Also, phylogenetic conclusions were no longer based solely on observations of macroscopic features; microstructures received

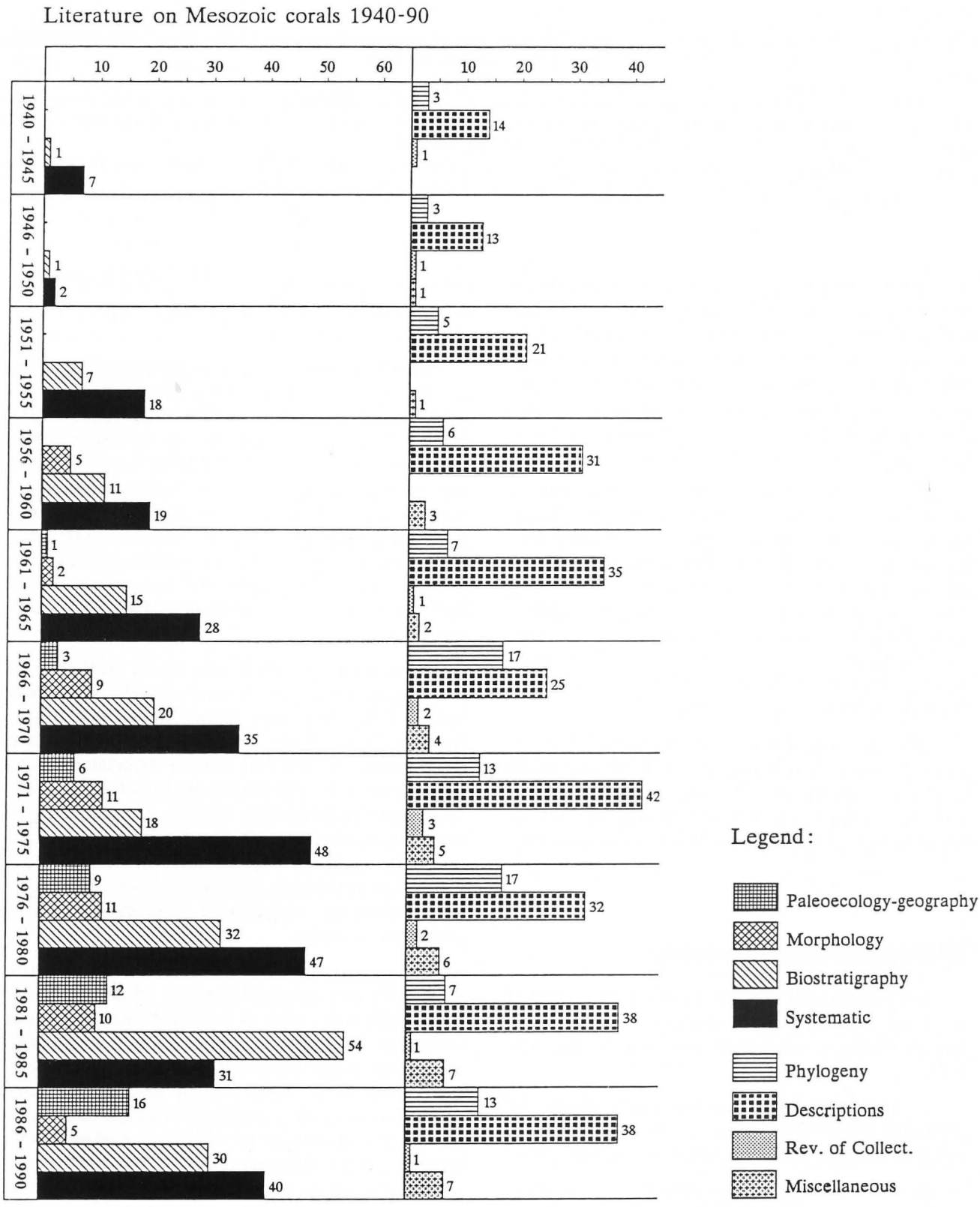

Figure 1. Number of palaeontological papers dealing with Mesozoic corals published after 1940; in 5 year intervals ("Systematic" covers in addition these papers which were analysed separately).

increasing attention. Revisions of many old collections (DEFRANCE, KOBY, GREGORY, D'ORBIGNY, MICHELIN, QUENSTEDT, MILNE-EDWARDS & HAIME, REUSS, OPPENHEIM) contributed to the development of taxonomy.

However, compared with the literature on index fossils such as ammonites or foraminifers, the number of publications dealing with Mesozoic corals is rather small. Some 800 papers published over the past fifty years mark this group of animals as a marginal one.

Systematics of Mesozoic corals

Basic characteristics of the system after 1940

The time after 1940 was a specially independent period for systematization of corals. The whole system underwent two large revisions, one by ALLOITEAU (1952) and one by WELLS (1956) (based on VAUGHAN & WELLS, 1943). There are undoubtedly differences in designating some taxa but both revisions are unique in the level and value of the systematic categories.

The same concept of higher categories continues to the present time with difference however, that new names have been added to the same systematic levels with new findings of corals and/or with the discovery of new structural elements.

An integrated approach to the systematics of Mesozoic corals after both ALLOITEAU and WELLS was given by BEAUVAIS (1981). She combined the results of all previous investigators adding her own observations. All other studies dealt with partial systems. They were largely confined to stratigraphical and regional investigations.

The Triassic corals were treated systematically by CUIF (1972, 1974, 1975a, b, 1976, 1977), MELNIKOVA (1975, 1983, 1984), MONTANARO-GALLITELLI (1975), KRISTAN-TOLLMANN, TOLLMANN & HAMEDANI (1984), DENG & KONG (1984), XIA & LIAO (1986), RONIEWICZ (1989) and others.

The systematics of Jurassic corals can be traced in the works of GEYER (1954, 1955a, b), GILL (1967, 1977, 1981), LAMBELET (1968), KRASNOV (1970), BABAEV (1973), BEAUVAIS (1964, 1981), ELIASOVA (1976, 1981), RONIEWICZ (1966, 1976), LIAO & LI (1980), BENDUKIDZE (1982), ROSENDAHL (1985), KHUSANOV (1987), ERRENST (1987) and others.

Systematics of Cretaceous corals were studied by MORYCOWA (1964, 1971), ZLATARSKI (1968), L. & M. BEAUVAIS (1975), SIKHARULIDZE (1979, 1985), TURNSEK & MIHAJLOVIC (1981), TSCHECHMEDJIEWA (1985), LÖSER (1989), and especially by M. BEAUVAIS (1982).

Data base of systematic studies

To get a review of all systematic categories of corals used during the past 50 years we set up a data bank comprised of 275 publications ("Systematic" in Fig. 1), dealing with descriptions and systematic work on corals. This data base contains about 750 nominal genera with author and year, and their attribution to subfamilies, families, superfamilies, suborders and orders. The source of literature and the stratigraphical age are added as well. In this way, we gained insight into similarities or differences of the systems used. It enabled us to analyse all the systems quantitatively and to draw comparisons between several systems.

We also compiled data of all the new taxa decribed between 1940 and 1990: species, genera, subfamilies, families, superfamilies, suborders and orders. Figure 2 shows the numerical frequency of these taxa per five year interval.

Unfortunately, some publications were not available to us, therefore the analysis is not complete.

Nomenclatoral inconsistencies

Some nomenclatoral errors and inconsistencies are repeated up until the present times:

a) Different spelling of names: ***ea-aea*** (*Actinastr**ea/aea***); ***cae-coe*** (*Heliocae**/coe/**nia*)
b) Different suffixes of higher taxa: **ina-ida**, **oidae-icae**; (Fungi**oidae**-Fungi**icae**)
c) Different years of introduction of a particular taxon: (*Aulosmilia, Columnocoenia* ALLOITEAU 1949, 1951, 1952, 1957)
d) Attribution of the same taxon to different authors: (Distichophylliidae CUIF 1977, BEAUVAIS 1981)

Analyses of systematic categories

Order

The highest systematic category of stony corals commonly used during this period is the order. ALLOITEAU (1952) used the name "Madreporaria", WELLS (1956) prefered "Scleractinia". Both authors attributed all the Mesozoic stony corals to a single order.

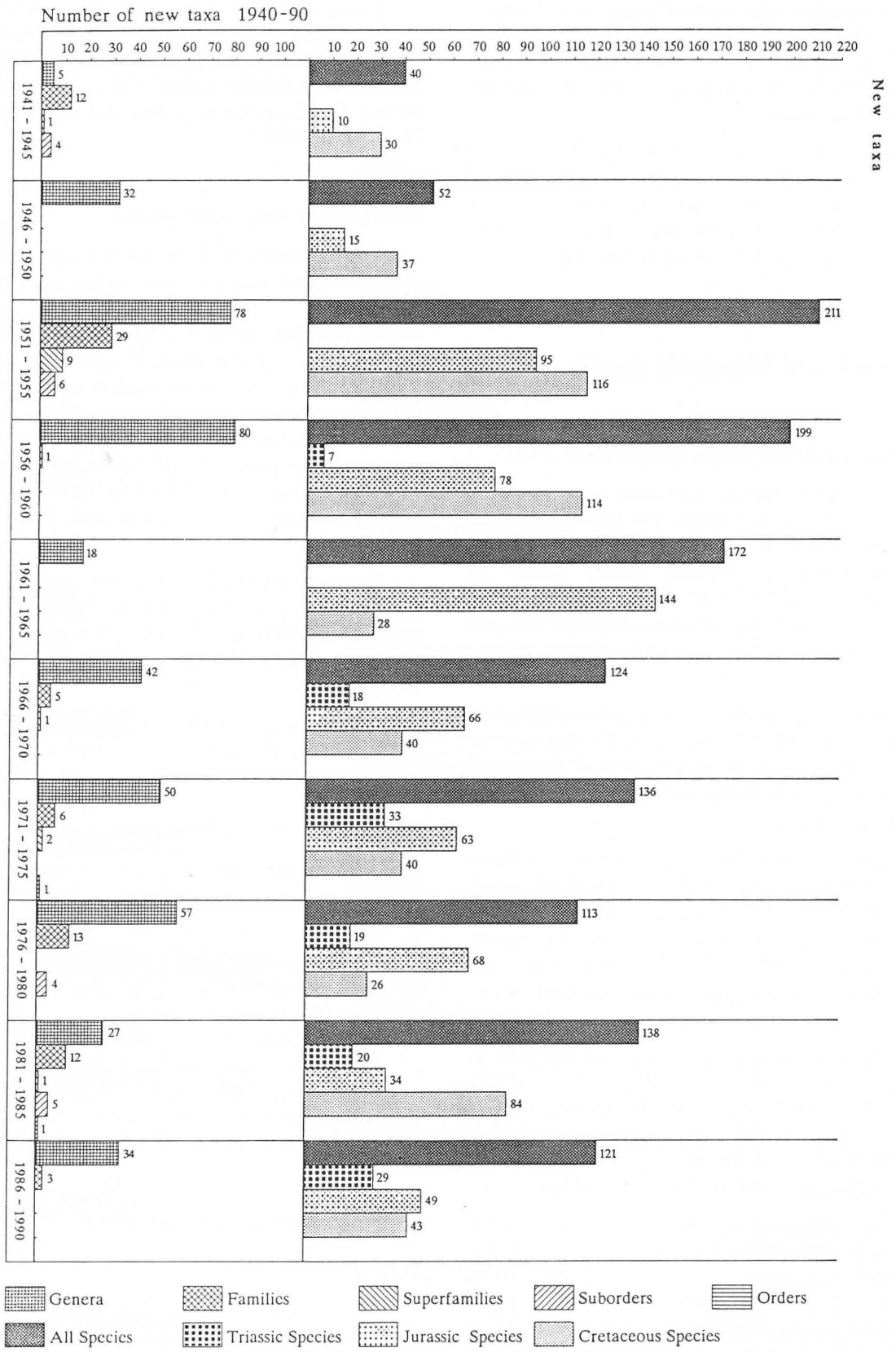

Figure 2. Number of new higher taxa of Mesozoic corals described in the period between 1940 and 1990; in 5 year intervals. The higher taxa from orders to genera are shown on the left; the diagrams on the right show the species (total and according to formations).

Both names have approximately the same number of followers. In 1975 MONTANARO-GALLITELLI introduced the new order Hexanthiniaria, based on a special wall structure. This has often been followed in recent years. There were made efforts to introduce some other names of orders as well: KRASNOV (1970) proposed three suborders, two of them (Montlivaltiida and Pinacophyllida) are new; MELNIKOVA (1984) proposed the new order Archaeocoeniina. Due to similar names of suborders and because of the insufficient differences and incomplete descriptions, such taxa have not been well accepted.

Suborder

The subdivision of the Scleractinia into suborders by ALLOITEAU and WELLS is essentially the same. The main criteria are: 1. synapticulae and porosity of septa; 2. septal structure and ornamentation; 3. microstructure (trabeculae, sclerodermites); and 4. endotheca.

VAUGHAN & WELLS (1943) and WELLS (1956) introduced four new suborders, to which ALLOITEAU (1952) added another six, using criteria such as manner of budding and symmetry of the septal apparatus, dimensions of trabeculae, and more precise data of ornamentation of the septa. Thus ALLOITEAU split the suborder Astrocoeniina, as used by VAUGHAN & WELLS, into the Archaeocoeniina and Stylinina; instead of Faviina he used the name Astraeoina and added the Meandriina and the Amphiastraeina; he emended the Dendrophylliina and renamed them Eupsammina; for the Fungiina and Caryophylliina both authors used the same names. Only the old name of the suborder Fungiina remained as already used before.

Very schematic comparisons of the suborders in VAUGHAN & WELLS (1943) and WELLS (1956) with those of ALLOITEAU (1952) are given below:

VAUGHAN & WELLS (1943) WELLS (1956)	ALLOITEAU (1952)
Astrocoeniina V. & W., 1943	- Archaeocoeniina ALL., 1952
	- Stylinina ALL., 1952
Faviina V. & W., 1943	- Astraeoina ALL., 1952
	- Meandriina ALL., 1952
	- Amphiastraeina ALL., 1952
Dendrophylliina V. & W., 1943	- Eupsammina ALL., 1952
Caryophylliina V. & W., 1943	- Caryophylliina V. & W., 1943
Fungiina VERRILL, 1865	- Fungiina DUNCAN, 1884

Later investigators followed one or the other of the systems. However, more authors continued to adhere to ALLOITEAU's names. To all the suborders mentioned nine new names were added, based on a more precise investigation of the microstructure. These suborders are the following: Carolastreaina (ELIASOVA, 1976), Pachythecalina (ELIASOVA, 1976), Rhipidogyrina (RONIEWICZ, 1976), Heterocoeniina (M. BEAUVAIS, 1977), Distichophylliina (L. BEAUVAIS, 1981), Stylophyllina (L. BEAUVAIS, 1981), Cuifastraeina (MELNIKOVA, 1984) and Protoheterastraeina (MELNIKOVA, 1984). Their main microstructural characteristics are listed below. Note the very unclear definitions for some suborders.

Subordo	Main microstructural characteristics
Carolastraeina ELIASOVA, 1976	archaeotheca of two parts 1. internal: concentric lamellae 2. external: septal fibres
Pachythecalina ELIASOVA, 1976	wall of centred fibres, radially oriented
Rhipidogyrina RONIEWICZ, 1976	costosepta of small trabeculae septal apophyses, lonsdaleoid, ornamentation granular
Heterocoeniina M. BEAUVAIS, 1977	simple trabeculae, normal to the face of skeleton
Archaeofungiina L. BEAUVAIS, 1981	trabeculae simple, arranged in series, synapticulae
Distichophyllina L. BEAUVAIS, 1981	non trabecular, median line present
Stylophyllina L. BEAUVAIS, 1981	non trabecular, median line absent
Cuifastraeina MELNIKOVA, 1984	"zernistie menniani" (granular menianae)
Protoheterastraeina MELNIKOVA, 1984	?

Superfamily, Family, Subfamily

All higher taxa mentioned above have variably been used. Thus a complete analysis is practically impossible. Since 1940, 58 new subfamilies, 81 new families, and 14 new superfamilies have been established (see appendix). All these taxa are based on different characteristics and sometimes even taxa of one and the same level can hardly be compared. Most distinct is the definition of the superfamily Pennulacea GILL (1967), based on the pennulae. In spite of that, it has not been followed, perhaps because of conflicts with the suborder Fungiina.

Genus

All genera, treated and described after 1940, amount to 750 of which 425 are new (the genera listed by WELLS, 1986, are not included in the following analysis).

To reach a better insight into the frequency and regional distribution of the genera and the appearance of

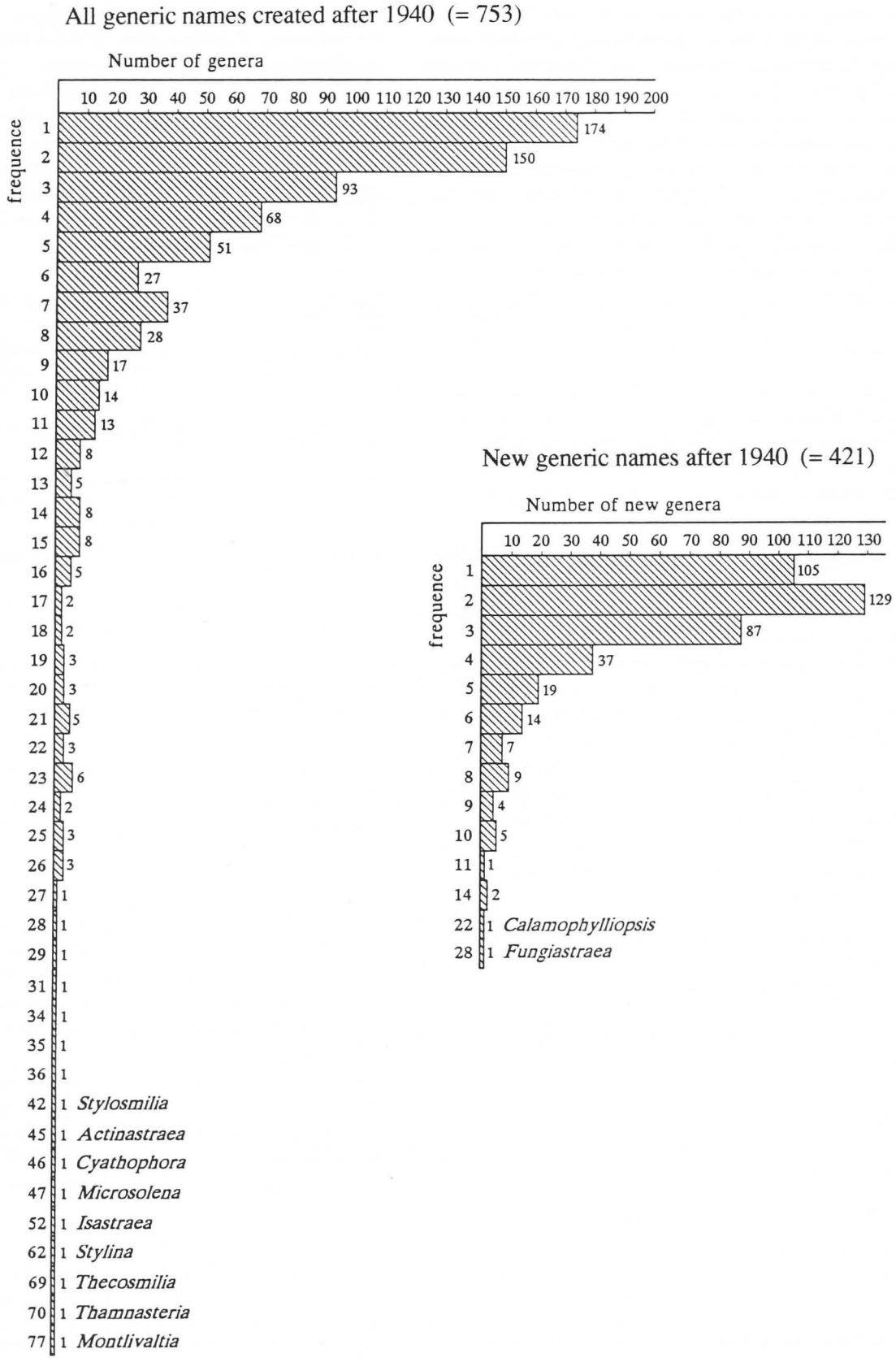

Figure 3. Frequency of the citation respectively using of Mesozoic coral generic names (total and new ones) in the literature from 1940-1990.

their names in palaeontological literatures was analysed. It turned out that most frequent were genera, that were mentioned only once (174). More than 600 generic names were used less than five times. This corresponds to more than 80% of all generic names. Nine generic names were mentioned more than 40 times, among them prevail *Stylina* (62 x), *Thecosmilia* (69 x), *Thamnasteria* (70 x) and *Montlivaltia* (77 x). Approximately the same ratio show newly established genera. 105 of them were mentioned only once, even 90% less than five times. Only *Calamophylliopsis* (22 x) and *Fungiastraea* (28 x) appear more than 20 times in the literature (see Fig. 3).

Further analysis dealt with the systematics of genera. For this reason a data bank, based on the assignment of the genera to subfamilies, families, superfamilies, and suborders in several papers, was set up. Here again the unique system prevails, which shows that more than 50% of the genera are grouped in the same higher category. Nevertheless, there is a large number of other genera which are ascribed to two, three, or even more different higher systematic categories, e.g., 59 genera were assigned to three different families, 14 genera to four, seven genera to five, and even three genera to six different families. Great differences were recognized concerning attribution to the suborder. Forty-eight genera were ascribed to three different suborders, 23 to four, three genera to five, and even two genera to six different suborders. An extreme example is with the genera *Latusastraea* and *Tiaradendron*. The latter genus was assigned to the suborders Astrocoeniina, Stylinina, Archaeocoeniina, Distichophylliina, Heterocoeniina, and Rhipidogyrina (Fig. 4).

Such heterogeneous approaches to systematics can be explained both by the establishment of new higher taxa and by different interpretations of structural elements, or by the acceptance or non-acceptance of such elements as distinguishing traits. The analysis of suborders has already shown that criteria for individual higher categories are based on slight structural differences which do not represent any real basis for systematics.

New morphological elements

Since ALLOITEAU (1952) and WELLS (1956), precise investigations of structural elements were carried out by several researchers. These studies mainly comprise detailed investigations of elements already known, although some authors introduced new elements or new names for structural details.

GILL: pennulae, menianae (1967), auriculae (1977), fulturae (1981).

MORYCOWA, 1971: trabeculae uniform, subsegmented, segmented, axis discontinuous, fibres in discordance (= ?sclerodermites) (partly after ALLOITEAU, 1952, 1957)

CUIF, 1977 (compilation): trabecular microstructure - median line ondulated, straight, continuous and divergent, forming lateral axes, fibres perpendicular, oblique, bundled, fasciculated ...

L. BEAUVAIS, 1981: trabecular septa, nontrabecular septa, continuous, and discontinuous trabeculae, axis lateral

M. BEAUVAIS, 1982: "collines septales, collines biseptales", wall trabecular, microstructure crystalline

RONIEWICZ, 1982, 1989: adaxial trabeculae, multiaxial septal trabeculae, trabeculae branched, pennular, granular, neorhipidacean, adtrabecular bars, intertrabecular sutures, trabecular apophyses, primary trabeculae, vepreculae, pellicula, coarse and fine fibred trabeculae, minitrabeculae, median size trabeculae, large trabeculae, wall bilaminar, palisaded, pellicular

MELNIKOVA, 1983: "zernistie menniani" (granular menianae)

From such terms it can be seen, that some older terms, from which the newer terms were derived, have lost their original meaning. Let us examine the terms "trabecula" and "sclerodermite":

ALLOITEAU, 1952, 1957: ... sclerodermite consists of very fine elongated crystals. A trabecula is a fine tuft (baguette) of sclerenchyme or a system of fine crystals. A trabecular structure can be recognized by the presence of centres of calcification or a median dark line, to which crystalline elements converge.

WELLS, 1956: ... sclerodermite is a center of calcification and surrounding cluster of calcareous fibres. A trabecula is a pillar of radiating calcareous fibres. A simple trabecula is composed of a series of single sclerodermites. A compound trabecula is composed of bundles of sclerodermites.

Thus it can be demonstrated that in subsequent literature the term sclerodermite has lost its meaning. The elementary skeletal unit, the trabecula, has no precise definition.

The median dark line as a part of a trabecula can be observed only in an oriented longitudinal section and only if it transects the centre of the trabecula. In the horizontal (transverse) section of a septum, the median line appears as a series of calcification centres with only lateral fibres. In this case the trabecula cannot be defined as a bundle of fibres. In modern literature, the median line in transverse sections is understood even as a non-trabecular structure (e.g. L. BEAUVAIS, 1981).

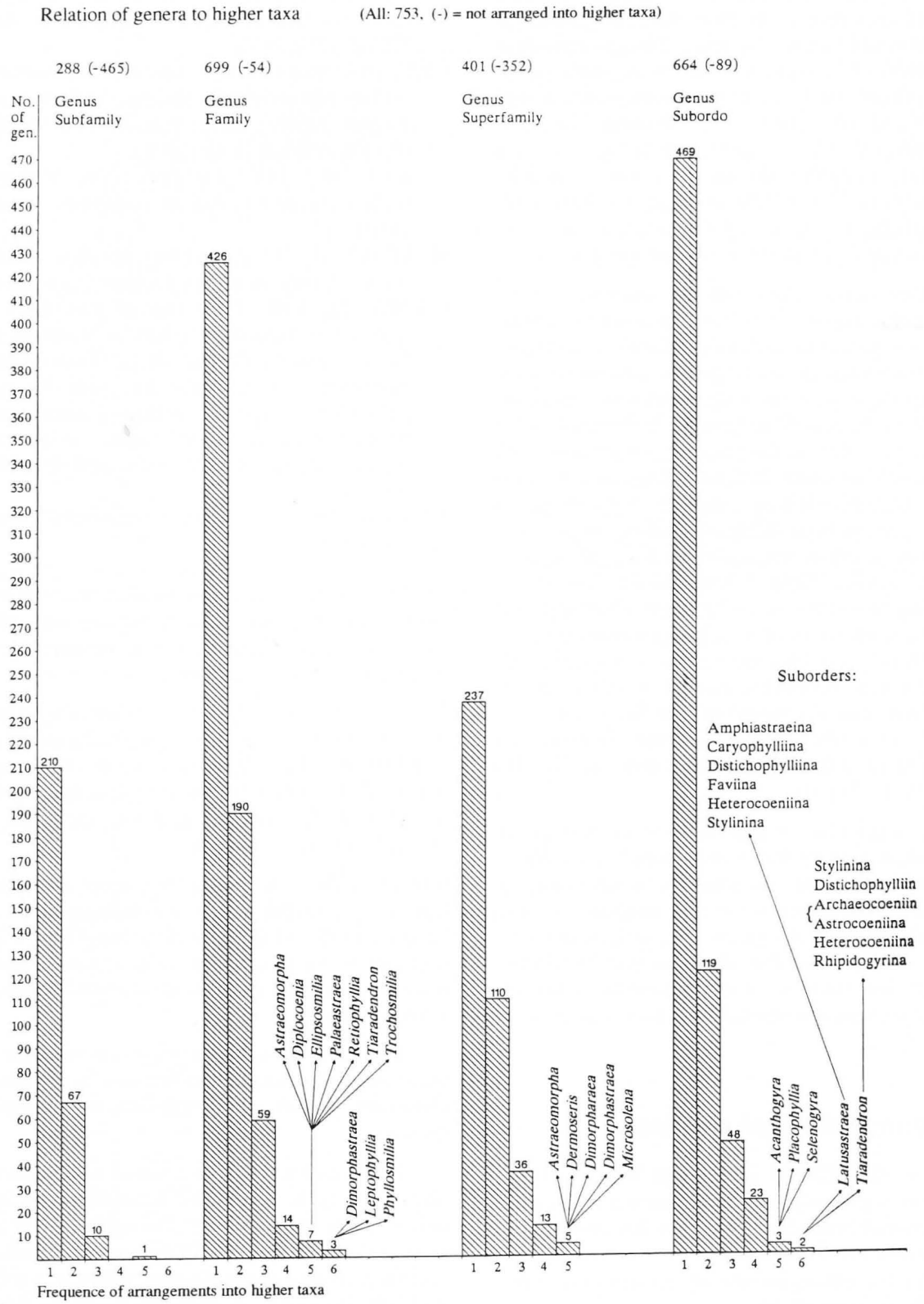

Figure 4. Numerical summary of Mesozoic coral genera (in the literature from 1940-1990) attributed to the different higher systematic categories.

Features such as segmented and non-segmented trabeculae, continuous and non-continuous trabeculae, undulated and straight median line: all can be the result of the orientation of the section relative to the skeletal elements.

Such subtleties are of great importance, because many times they have been proposed as characteristics for new taxa, including higher taxa such as superfamilies, suborders or orders. If they are described insufficiently or on the basis of unoriented sections, they cannot be accepted. Trabecula must be described precisely. Thus we propose that microstructure must always be observed in the same oriented section or in combination with more oblique sections. Such a standardized method was proposed by RONIEWICZ (1989: 8) for measuring the diametre of trabeculae along the calicular radius.

Conclusions

Taxonomy as the basis of research

Taxonomy as the science of classification of organisms, is the basis of palaeontological research. A comparison of findings would not be possible without classification. Palaeogeographical and palaeoecological conclusions could not be achieved without comparisons. Ironically, while the interest in problems of taxonomy is decreasing, there has been a steady increase in new taxa (genera, species). Revision of systematics cannot keep pace with this development.

Three reasons can be given to account for this unsatisfactory state of systematics:

- The concept of the taxa is ill-defined. Opinions differ widely concerning the significance of morphological characteristics and their relevance in distinguishing one group from another. Although a specimen rarely shows all the characteristics of the species it belongs to, the description of new taxa on the basis of populations has not yet gained general acceptance.

- Nomenclature rules stipulate the priority of type specimens. But many collections have been lost or may not be studied in sections. Collecting topotypical material is difficult since many type localities are no longer accessible.

- With so many taxa an overview is hardly possible. The systematic position of many taxa is uncertain. Grouping lower taxa into higher ones is difficult because of the above-mentioned disagreement on the relevance of certain morphological characters. Before the debate on causal relations concerning the occurrence of fossil corals can be profitably continued, it seems necessary to turn more attention to taxonomic questions.

Analyses of literature

The relatively low rate of publications (110 papers during the past five years, which is just over 20 publications a year) permits an overview of recent publications. An increasing number of papers deal with the occurrence and mode of life of fossil corals; taxonomic studies and revisions are decreasing. Today's taxonomic literature is of varying quality with regard to illustrations, descriptions and systematic conclusions. The quality of a publication probably depends on whether the latest literature is available to the author or not or on other factors such as differences in technical equipment and in the state of preservation of the material (e.g., microstructures are rarely preserved). Language barriers (inadequate understanding of arguments put forward in foreign languages) and inaccurate application of nomenclatural rules also affect the quality of publications to a considerable extent.

The literature on palaeogeography and palaeoecology is getting increasingly of doubtful status, dealing simply with the occurrence of "corals", lacking much systematic studies. The benefits which such work can bring, e.g. the characterization of certain groups of corals as indicators of particular ecological conditions or as quasi-index forms within narrowly defined stratigraphic limits, should be based on systematic research.

Recent publications dealing with morphology have demonstrated methods for determining the relationship of corals. There is the risk that all characteristics found are classified as phylogenetically relevant, with undue emphasis on microstructures and ultra-microstructures. Since there is very little material that shows these structures, such conclusions are not very helpful. Morphological findings should therefore be examined from the point of view of their suitability for grouping corals into all levels of taxa.

Recommendations

Our studies and the conclusions drawn from them indicate the need for increased cooperation in various fields. It is essential to reach an agreement in basic questions of taxonomy and to develop generally valid and applicable principles of systematics. We recommend working out a morphology standard in which each morphological element is precisely defined, depicted and explained, drawing a clear line between primary and secondary characteristics. Further revisions of original

collections and the compilation of indices (where can which original be found?) are very important for settling outstanding questions of taxonomy and nomenclature. Agreement on a standard regulating the exact mode of description of new taxa would also be useful. Central data banks on taxa and literature with common data interfaces will provide a better overview of known species as well as serving as a means for the development of conclusive principles of classification and nomenclature.

We think it is necessary for researchers to concentrate on smaller groups of the Scleractinia and to pay more attention to systematic works within these groups, since the field as a whole has become too vast to be conveniently handled by a single scientist. Some of the above recommendations have already been implemented in part or are in the process of being put into practice, while others are still awaiting implementation, probably also within the framework of the IASFCP.

Ackowledgements

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Appendix

The following data banks compiled in connection with this project and relating to the period under review (1940-1990) are available as separate printouts:

- literature published during this period (Generals/Triassic/Jurassic/Cretaceous), published in the Fossil Cnidaria Newsletter and also available as computer data bank (in dBase format for IBM compatible personal computers XT/AT)
- list of newly described species (Triassic/Jurassic/Cretaceous)
- list of newly described higher taxa (subfamilies, families, superfamilies, suborders, orders)
- index of quotations of genera from 260 selected papers and their attribution to higher systematic categories.

All who are interested are requested to contact H. LÖSER.