

In defence of invertebrate fossil taxonomy

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ABSTRACT:

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Starting from a subjective viewpoint on the decreasing interest in invertebrate fossil taxonomy, this essay discusses its importance in palaeobiological studies exemplified with cases from the palaeobiogeography and palaeoecology of rugose corals, and aims at provoking a discussion on the topic. The possible causes of this negative declining trend include inherent problems of palaeontological taxonomy, and changing systems in science and higher education.

Key words: Taxonomy; Invertebrates; Palaeobiology; Palaeobiogeography; Palaeoecology.

INTRODUCTION

Comparison of the Earth to a book is trivial but nothing better comes to my mind in order to illustrate the enormous amount of information hidden in the rocks. The Earth's book, as any other book can be read with understanding only by a person knowing the language it is written in. In the case of the palaeobiological chapter of the Earth's book, the taxonomy of fossils forms a kind of linguistic fundamental.

The better we know the language, the more mysteries hidden in the rock pages of the Earth's book become readable and understood. Why did we recently reduce the language to a few basic words instead of trying to develop it? A professional taxonomist, i.e., a person eligible to follow the requirements of a complete taxonomic study should have undertaken broad courses in geology and palaeontology supervised by an experienced teacher and should be given time adequate to become acquainted with all details important for the group of animals or plants he/she wants to investigate. Is this possible in our days?

Fossil taxonomy flourished during the 18th and 19th centuries and has been respected during most of the past century, but then, has gradually become a ne-

glected field of study. Beyond any doubt, however, invertebrate taxonomic palaeontology, intimately confined to evolutionary endeavours, is crucial in various aspects of palaeobiological considerations. Without its further development, such studies will soon collapse to a blind and illiterate level.

This essay demonstrates the potential of well-grounded taxonomic knowledge and the need for careful taxonomic work in palaeobiological studies, exemplified here with palaeobiogeographic and palaeoecological analyses. The examples given here are based on the rugose corals, the group of fossils which have been the main focus of my studies for decades. Nonetheless, similar examples can be found in almost any selected invertebrate clade.

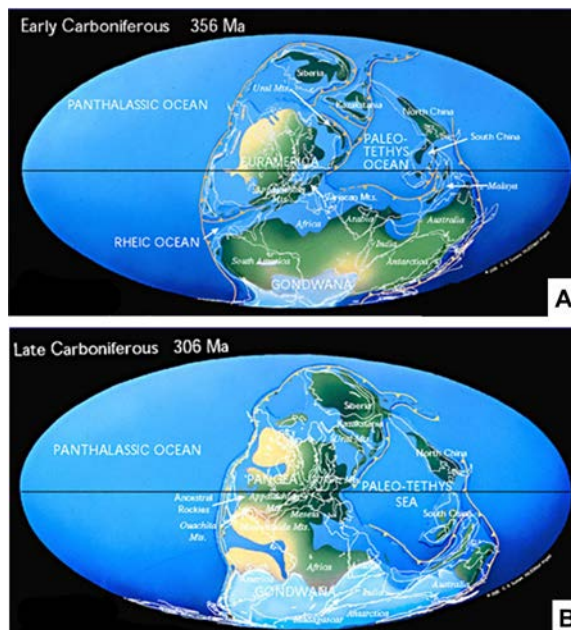
With this text I hope to provoke a discussion that may help to stop the declining trend in taxonomic studies, which is dangerous for the field of invertebrate palaeobiology as a whole.

TAXONOMY AND PALAEBIOGEOGRAPHY

The intimate inter-relationship between the taxonomy of extant plants and animals and their geographical distribution has been obvious since A. v.

Humboldt travelled to the Americas (e.g., Humboldt and Bonpland 1805–1829). However, the reasons governing why fossil taxa found in currently distant areas had potentially close relationships, while certain taxa present in adjacent regions were quite evolutionarily distinct, remained mysterious for over a century. The Carboniferous and Permian Rugosa illustrate well the mutual effect of precise taxonomy on correctly reconstructed palaeogeography, and *vice versa*. For instance, let's consider the two papers of Minato and Kato (1965a, b) as an example. The recognition by those authors of the clinotabulae (i.e., a very specialised skeletal detail) in the Waagenophyllidae Wang, 1950, and the absence of such skeletal structures in the Durhaminidae Minato and Kato, 1965b, constitutes one of the fundamental differences between these families of Permian colonial Rugosa. However, the reconstructions by those authors of the palaeogeographic distribution of the coral families mentioned created questions rather than offered solutions. It is worth reminding the reader that the theory of plate tectonics has been widely accepted only since the mid-1960's. In this pre-plate tectonics era, Minato and Kato (1965a, figs 112–125; 1965b, fig. 1) did not have the chance of implementing that then-nascent notion of continental wandering into their reconstructions of the distribution of the Waagenophyllidae and Durhaminidae.

Only the theory of plate tectonic enables a reliable explanation of these major palaeobiogeographic questions. The distribution of the Waagenophyllidae and Durhaminidae during the Cisuralian, mysterious when maps by Minato and Kato (1965a, b) are considered, becomes quite comprehensible after Pangea is reconstructed, based on global tectonics (Text-fig. 1A, B). Representatives of the Waagenophyllidae dwelled in the areas restricted to the Palaeotethys: the eastern shelves of Pangea to the west (e.g., the recent Carnic Alps and Sicily), and the Chinese and the Indochinese microcontinents to the east. By contrast, the Durhaminidae appear to have been restricted to the north-western and western shelves of Pangea, occupying the long belt from the recent Urals through Svalbard and the Canadian Arctic Archipelago, the Cordillera and the Andes to Peru (Fedorowski *et al.* 2007). Thus, precise rugosan taxonomy, when combined with the proper reconstruction of Cisuralian palaeogeography, easily explains why the rugose corals from the Urals have nothing in common with contemporaneous corals from the Carnic Alps and China, in spite of being located at present between those two areas. Those recognitions, in turn, lead to the distinction of two main late Carboniferous and Permian



Text-fig. 1. Reconstructions of the palaeogeography of the world. A – early Carboniferous, B – late Carboniferous (after Scotese 2001).

rugosan realms (Fedorowski 1986; Fedorowski *et al.* 2007). The stratigraphic ranges of particular rugosan clades developing in those two realms led to a conclusion that their late Permian extinction was diachronous (Fedorowski 1997). The rugose coral dwellers of the Tethys Realm continued to the latest, although not to the end, of the Changhsingian, whereas those developing in the Cordillera-Arctic-Uralian Realm disappeared from the stratigraphic record either near the end of the Wuchiapingian or in the early Changhsingian.

The stratigraphic ranges of taxa, superimposed on the sequence of palaeogeographic changes, is yet another character that must be considered in phylogenetic reconstructions. The main Carboniferous and Permian Rugosa clades offer a handsome example. The family Kepingophyllidae Wu and Zhou, 1982 appeared either shortly after the closing of a passage between the Uralian and the Palaeotethys seas, or after that connection became impassable for corals. Thus, that family is unknown from the Cordillera-Arctic-Uralian Realm, but gave rise to the Permian family Waagenophyllidae in the Palaeotethys. In contrast, the families Durhaminidae and Kleopatriniidae Fedorowski, Bamber, and Stevens, 2007 are restricted to the Cordillera-Arctic-Uralian Realm. The simplest representatives of the Kepingophyllidae,

Durhaminidae, and Kleopatrionidae bear some characters pointing to the Family Lithostrotionidae d'Orbigny, 1852 as ancestral. The Lithostrotionidae were globally distributed during the Mississippian and early Pennsylvanian (Text-fig. 1A), prior to the formation of Pangea. These examples clearly suggest that phylogenetic reconstructions in general, and taxa identifications in detail, must take into account the palaeobiogeographic distribution in time, if a monophyletic taxonomic approach is followed.

However, the creation of distinctive palaeobiogeographic realms is not restricted to the activity of large-scale geographical barriers, like Pangea. Indeed, obstacles on smaller scales can create effective barriers and result in significant endemism. For instance, the huge eastern Laurussian peninsula that appeared following the Caledonian orogeny illustrates the bearing of small-scale geographic configuration on endemism. Precise taxonomy of the ancient dwellers of the sea behind that peninsula allowed Oliver (1976, fig. 1) and Oliver and Pedder (1979, figs 3–7) to separate those faunas from the cosmopolitan Early and Middle Devonian rugose coral faunas and thereby confirm an endemic Eastern Americas Realm.

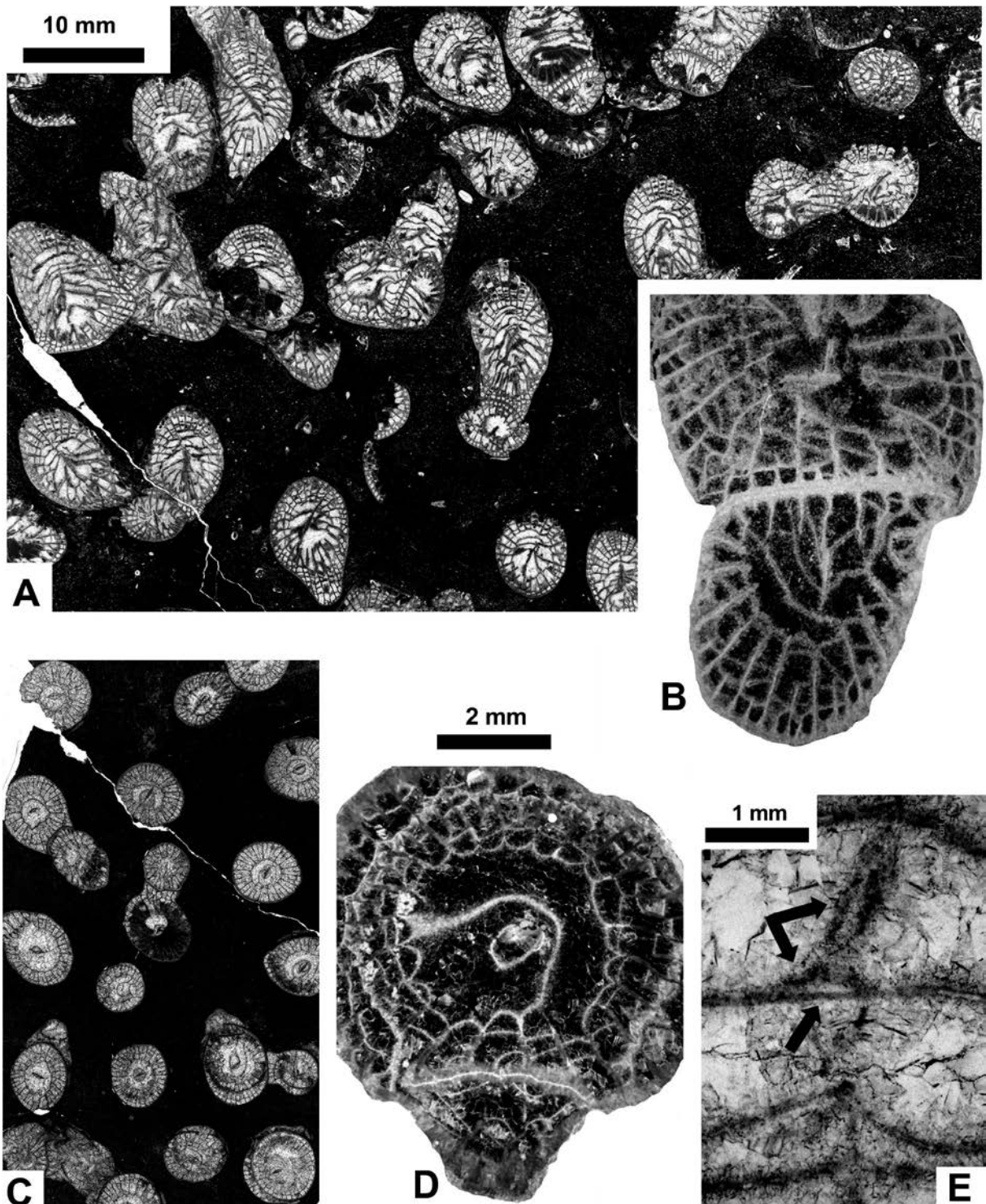
An absence of the environmental conditions requisite for the larvae of sessile organisms to settle, metamorphose, and propagate is the next, and least recognized, reason for partial or advanced endemism. The Mississippian Lithostrotionidae of western North America and Europe can serve as an example. The occurrence in North America of the genera *Diphyphyllum* Lonsdale, 1845 and *Siphonodendron* McCoy, 1849 during the latest Tournaisian to middle Viséan was previously questioned by Fedorowski and Bamber (2007) in an introductory study. Their recent study on corals from the Liard Basin of the Canadian Northwest Territories (Fedorowski *et al.* 2019) confirms that position based on substantial differences in blastogeny, which is in stark contrast to the morphological similarities of lithostrotionids from both areas (Text-fig. 2A–E). Indeed, Bamber *et al.* (2017) support the notion that true *Siphonodendron*, derived from European species, invaded North America in the late Viséan, several million years later than previously suspected. This example is introduced here in order to point out both the value of identifying the environmental conditions that preclude the widespread distribution of larvae and the value of hystero-ontogenetic – i.e., blastogenetic – studies as a taxonomic tool. The Laurussian shelves (Text-fig. 1A) apparently allowed migration in either a clockwise or counter clockwise direction. However, siliciclastic deposits shed from the Ellesmerian, Caledonian, and

Variscan orogens (Ziegler 1988) created depositional environments impassable for larvae of some rugose coral species until the late Viséan.

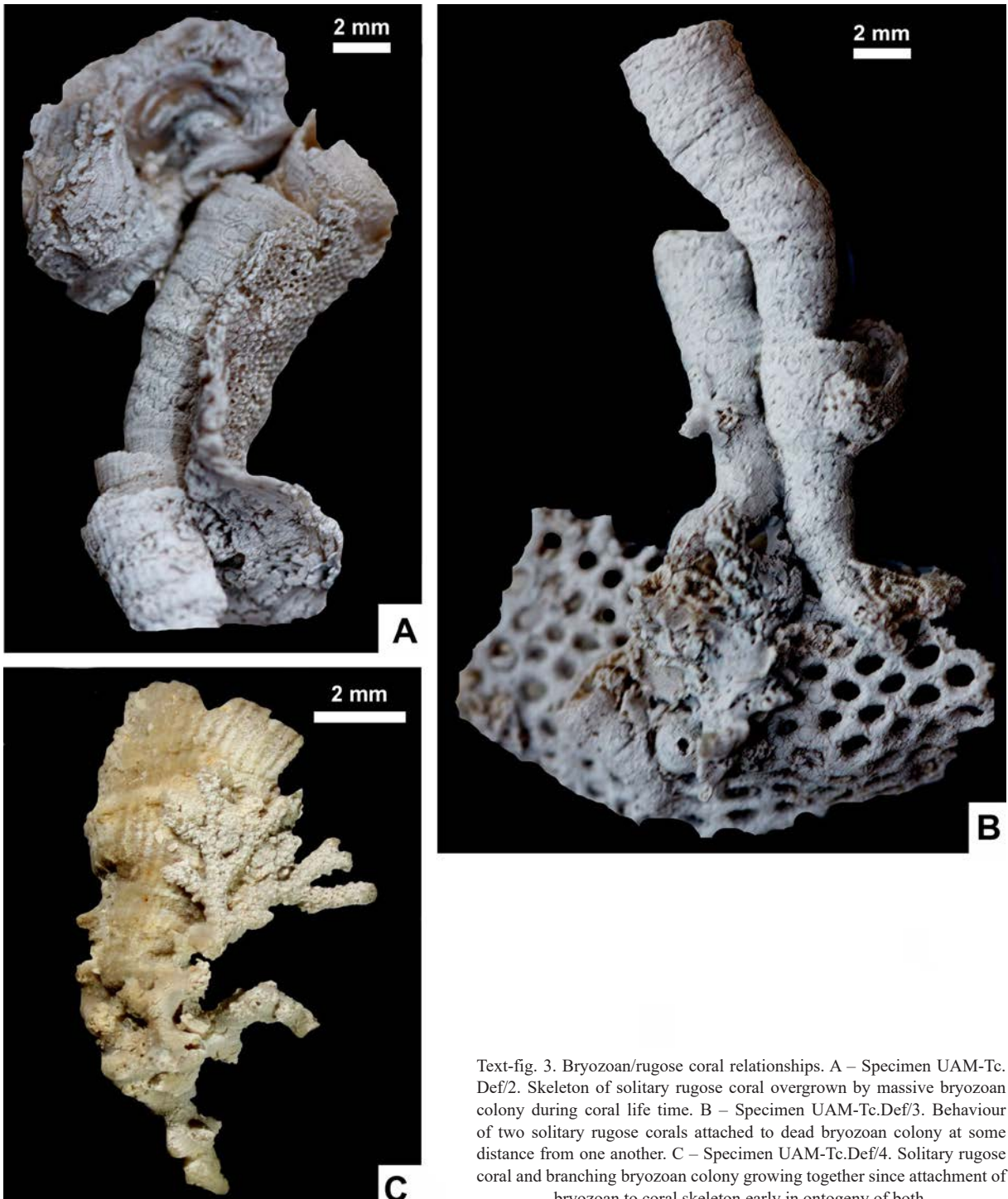
Not only a disregard of the plate tectonic data for the palaeobiogeography, but also a disregard of palaeontological data in tectonic reconstructions may cause crucial consequences. The book by Torsvik and Cocks (2017) is certainly a very comprehensive contribution combining an enormous amount of data derived from the physical part of a widely understood geology, but the palaeobiological data incorporated in the book are very limited. A small detail, the physical geology data contrasting with palaeobiological data, concerns the time of closing of the inlet between the Gondwana and the Laurussia landmasses through northern Iberia, i.e., the recent Cantabrian Mountains. Both maps (Torsvik and Cocks 2017, figs 9.1c and 9.7) show the closing of that inlet in the middle Moscovian, whereas many papers devoted to Pennsylvanian fossils document marine deposits rich with fossils, developing at least up to the Kasimovian (e.g., de Groot 1963; Rodríguez 1984; Rodríguez and Kullmann 1999). The Moscovian rugose corals from the Cantabrian Mountains display a close relationship to those from south-eastern Laurussia, i.e., the recent Donets Basin in the Ukraine, but differ to a large extent from the contemporaneous corals of south-western Laurussia, now found in Texas, Oklahoma and Kansas. Thus, the corals demonstrate to some extent difficulties in the direct connection between those two areas in the Moscovian, open at least till the Bashkirian inclusively (Fedorowski 2019). However the Spanish Moscovian rugose coral taxa disprove the siting of northern Iberia within a chain of the Variscan landmass as illustrated by Torsvik and Cocks (2017, fig. 9.7). Garcia-Bellido and Rodríguez (2005) suggested the occurrence of an Iberian inlet connecting the Panthalassa with the Palaeotethys Ocean during the Moscovian.

TAXONOMY AND PALAEOECOLOGY

Reconstructions of the living conditions and mutual relationships of extinct taxa is one of the most fascinating topics in palaeontology. Papers dealing with corals, other animals, and algae can serve as examples (e.g., Gómez-Herguedas and Rodríguez 2009; Said *et al.* 2011; Sorauf and Kissling 2012; Berkowski and Zapalski 2018). The value of such studies, however, depends on the degree of species identification. Only solid taxonomy can establish a robust framework upon which palaeoecological reconstructions



Text-fig. 2. Offsetting as a taxonomic tool. Transverse thin sections unless stated otherwise. **A, B** – *Siphonodendron martini* (Milne Edwards and Haime, 1851), specimen UAM-Tc.Def/1, from the upper Viséan of Kamionki Village, Sudetes, Poland. **A** – fragment of colony, **B** – offset. **C–E** – “*Diphyphyllum*” *mutabile* Kelly, 1942. **C, D** – Specimen C-413008 from the middle Viséan of the Liard Basin, Northwest Territories, Canada. **C** – fragment of colony; **D** – offset. **E** – Specimen C-7349 from the Rundle Group of east-central British Columbia, Canada. Longitudinal thin section. Pseudocolumella (upper arrows) created on tabula surface (lower arrow) and tabulae/pseudocolumella relationships in lower part of picture (See Fedorowski and Bamber 2007, p. 251, for blastogeny). Scale bar above **A** corresponds to **A** and **C**. Scale bar above **D** corresponds to **B** and **D**.



Text-fig. 3. Bryozoan/rugose coral relationships. A – Specimen UAM-Tc.Def/2. Skeleton of solitary rugose coral overgrown by massive bryozoan colony during coral life time. B – Specimen UAM-Tc.Def/3. Behaviour of two solitary rugose corals attached to dead bryozoan colony at some distance from one another. C – Specimen UAM-Tc.Def/4. Solitary rugose coral and branching bryozoan colony growing together since attachment of bryozoan to coral skeleton early in ontogeny of both.

can be constructed, whereas the utility of the resultant reconstructions diminishes parallel to the decreasing precision of taxonomic identification. The examples that follow illustrate that notion.

The well-preserved, partly to intensely silicified fossils (Text-fig. 3A–C) etched out from the Permian

deposits of the Glass Mountains (Texas, USA) document the poverty of the conclusions which can be reached in the absence of taxonomic support. The rugose coral/bryozoan relationships illustrated here document three different bryozoan taxa. Their differentiated colonial growth form and some external char-

acters are sufficient for a preliminary identification, but perhaps not closer than at family level, or questionably to genus level. In contrast to the bryozoans, however, an equivalent level of taxonomic precision is completely unattainable from the external characters of the rugose corals. The deep septal ribbing of one of the three specimens (Text-fig. 3C) allows for its probable distinction from the other two. However, the true relationship of those corals will remain unknown until they are sectioned and investigated in detail.

In the case of Text-fig. 3A, either the parallel growth of the solitary rugose coral and the bryozoan colony, or an overgrowth by that colony on a dead coral skeleton deposited on the sea floor, seems possible. A closer examination of both organisms suggests the first option. The shape and size of the bryozoan colony suggests its expansion towards objects adjacent to the coral. Those objects, most probably calcitic, disappeared during the etching process. The manner of attachment of the bryozoan colony to both the coral and those lost objects (Text-fig. 3A, upper left and lower right), the extension of that colony beyond the limit of the coral skeleton along the line of disconnection, and the lack of any traces of erosion or corrosion in skeletons of both animals suggest that both organisms are preserved in life position. The state of preservation of both organisms in the second example (Text-fig. 3C) suggests their parallel growth since the early post-larval growth stage of the coral, and that both remained in their life positions. Thus, the reconstruction based on that example is quite similar to that of the first, despite their obviously different systematics. These very limited reconstructions, however, can only be completed by comprehensive studies and taxonomic identifications of both the bryozoans and rugose corals.

In contrast to the first two examples, the bryozoan skeleton constituted a *post mortem* basis for larval settlement: in this situation, growth of two rugose corals (Text-fig. 3B). The similarity in the external characters of those corals may suggest a conspecific relationship. However, external characters are extremely misleading when considering rugose corals. They can be applied, at most, as auxiliary characters for species identification. Thus, the systematic position of both those specimens is unknown. The following can be stated: the specimen on the left tended toward the right one, and died shortly after reaching its partner. The specimen on the right changed its growth direction when met by the attaching specimen. From that, we can suggest the following: the specimen on the left may have been looking for support against strong water movements. Furthermore, it may have died from

starvation because the specimen on the right shadowed its calice, drastically reducing the food supply to its polyp. That rather trivial conclusion, the most possible without proper species identification of both specimens, leaves many important questions untouched. These include, but are not limited to: inter- vs. intra-specific competition; potential aggression of a somehow stronger specimen of the same species, as opposed to one of a different species; and the absence of rejuvenation traces in the smaller specimen, which are typical for rugosans in a strongly stressed environment. Furthermore, there are examples of rugosan inter-relationships beyond simple attachment. The two corals discussed may not only meet one another, but unite as well. Indeed, corals from the same area and age (Glass Mountains, Permian), of a similar shape and size, and that meet in a similar manner demonstrate that possibility (Fedorowski 1980, pl. 27, fig. 1a, b). They have lost their external skeletal walls in their meeting sector, and their polyp bodies have united for a considerable growth distance, suggesting their relationship was close enough to break their immunological barriers. To summarise: in all three examples illustrated, excellent material brought about a minimum of meaningful information in spite of the lack of systematic identifications.

Vinn and Mõtus (2014) could be cited as representing an advancement relative to the trivial examples discussed above. Unfortunately, this is only apparent. The stromatoporoids discussed by these authors are identified to species level, while the rugose corals are included in the genus *Palaeophyllum* Billings, 1858, but left in open nomenclature. Such an unequal level of taxonomic identification results in bias that leads to overly interpretative, and thus only possible conclusions. The Stromatoporoidea has always been distinct from my interests: thus, I accept the identification of the stromatoporoid as correct. However, the generic identification of the rugose corals can be contested upon several grounds. *Palaeophyllum* is diagnosed as a phaceloid colonial genus with long major septa, reduced minor septa, an absent dissepimentarium, and a wide stereozone present on the periphery (Hill 1981, p. F138). Only one of those characters, the reduced minor septa can be observed in the specimens of Vinn and Mõtus (2014). The most important diagnostic character, a phaceloid colonial growth form, is not suggested by the authors and cannot be attributed to their illustrated specimens. The solitary growth forms of these specimens are reflected in: 1) the absence of offsetting specimens, despite many mature corallites being sectioned in the transverse, longitudinal, and

oblique directions; 2) sections of very young specimens located discretely away from the mature ones, at distances excluding their connection not only by offsetting but also by attachment; 3) the growth directions of neighbouring corallites excluding their direct connection by offsetting. Moreover, either an incomplete dissepimentarium or concave tabularium occurs in Vinn and Môtus' (2014, fig. 6) specimens, i.e., the very characters lacking in *Palaeophyllum*. Thus, not only are taxa of different taxonomic levels compared by Vinn and Môtus (2014), but one of these taxa almost certainly belongs to a genus different from that assigned. Together, these facts render incorrect the assertion that "Endobiotic *Palaeophyllum* sp. has been described from *Plectostroma intermedium* from [the] Ludlow of Gotland." Thus the statement that "*Palaeophyllum*, but probably a different species, also inhabited other stromatoporoid species" (Vinn and Môtus 2014, p. 6) is completely unsupported upon taxonomic grounds.

I will not discuss in detail the methodological errors made by Vinn and Môtus (2014), such as using the diameters of specimens taken at different growth stages for a mean value of the species, or using six randomly polished sections, instead of well-oriented thin sections, as the basis for their conclusions. That error results in making several of their interpretations utterly groundless. For instance: "Some of the embedded tubes (Figures 3–4) with small diameters appear to lack septa, but they also belong to rugosans." (Vinn and Môtus 2014, p. 2). Those specimens not only "belong to rugosans", but are most likely early growth stages of the same species as the large corallites. "It's possible [*sic*] that some apparently truncated corallites actually underwent lateral budding and survived, but we did not find any evidence for that." One cannot leave the most important diagnostic character of a taxon unidentified and expect any acceptance of their conclusions.

The critical remarks given above are not intended to specifically target the authors of that paper. Indeed, I would like only to elevate the taxonomic standard that must become unquestionable for acceptable palaeoecological studies. The experience of the authors in that fundamental field must be quite limited, judging by the fact that they acknowledge their old colleagues for the identification of both corals and stromatoporoids. Also, I want to point out the further potential offered by material as good as that studied by Vinn and Môtus (2014). Some of the questions left untouched by the authors are: How could the rugose coral larvae have attached to the skeletons of a living stromatoporoid? What are the structures

located almost parallel to the growth directions of the stromatoporoid? How, when, and why did the stromatoporoid overgrow the calices of some rugose corals, while it did not overgrow those of the others (Vinn and Môtus 2014, fig. 5)?

I may only suspect that the errors, misinterpretations, and omissions pointed out above resulted from a 'publish or perish' situation, especially dramatic for young scientists. Nevertheless, papers like Vinn and Môtus (2014) can be characterised as follows: the editor(s) are happy because the impact factor of their journal increases; the authors(s) are happy because their H-index grows. *But what about the science?*

The paper by Berkowski and Zapalski (2018) can be cited as an example of a study complete in both taxonomic and palaeoecological aspects. Both authors are well-trained taxonomists and neither of them is under considerable time pressure – that is to say, subjected to the 'publish or perish' regime. As a result, the reader receives a complete description of the general environmental conditions that allowed the well-known tabulate coral species *Halysites catenularius* (Linnæus, 1767) to build a biohermal framework that created conditions suitable for hosting the rugose coral *Cystiphyllum visbyense* Wedekind, 1927. In contrast to *H. catenularius*, *C. visbyense* provoked several doubts with regards to its intraspecific variability, early ontogeny, and attachment to the substrate. Thus, it was redescribed in those aspects, including a recapitulation of rhizoid formation. The latter structures allowed *C. visbyense* to attach to the colonies of *H. catenularius* (most commonly) and to other objects, and to colonize empty rooms within *H. catenularius* chains. All of these data presented made the documentation of their chapter 'Syn-vivo interactions between *Halysites catenularius* and *Cystiphyllum visbyense*' complete, and so the authors' general conclusions fully acceptable.

CONCLUSIONS

Why has interest in taxonomy collapsed? My answer to the above question is subjective, but that interest in taxonomy has dramatically decreased more recently is an objective fact and should be at least pointed out with the hope for a discussion and hopefully a break in this trend. The decreasing number of well-documented papers dealing with taxonomy of invertebrate fossil animals may end with the impossibility of returning to their investigation if this unfortunate trend is not stopped. Museums are already full of collections hopelessly waiting for inves-

tigation. The reasons making up this negative trend in fossil invertebrate taxonomy represent (i) inherent problems of this branch of palaeontological studies, (ii) changing systems in higher education and science in general and (iii) difficulties in the publication of purely taxonomic papers.

(i) The main inherent problem of taxonomic study of palaeontological material is to what extent do the morphological characteristics, which are the basis of its identification, reveal its actual taxonomic relationships. This issue can widely be tested in neontological material, however, it is not simple (?possible) at all in fossils. Let me comment on the subject again by a reference to corals. Undoubtedly, the taxonomy of corals is undergoing a major revision (e.g., Kitahara *et al.* 2016; Cowman *et al.* 2020), and in certain groups of corals the species clearly cannot be delineated using classical morphological criteria (e.g., *Oxypora* Saville Kent, 1871 and *Euphyllia* Dana, 1846 in Arrigoni *et al.* 2016; or in acroporids, see Cowman *et al.* 2020). Extreme cases include representatives of *Pocillopora* Lamarck, 1816, where a colony can shift from the morphology of one 'species' to that of another over months (Paz-Garcia *et al.* 2015). It seems, however, that the traditional morphological taxonomy may still be reliable and useful in certain groups. An example of reliable morphospecies may be the one of the scleractinian azooxanthellate genus *Coenocyathus* Milne Edwards and Haime, 1848, where species delineation based upon the skeletal features is supported by differences seen in a molecular study (Kitahara *et al.* 2020). Another example of clear morphological delineation is that of *Cyphastrea salae* Baird, Hoogenboom and Huang, 2017, where the number of septa delineates it clearly from other representatives of the genus (Baird *et al.* 2017).

(ii) The reasons which appear to result from changes in the system of higher education and science are less straightforward. They all can, however, be ascribed to a time-pressure imposed on scientists, and on new students, to demonstrate the results of their study as fast as they can. And a truly important taxonomic paper requires time. The students and newcomers, supervised by an experienced tutor, need a broad education to accumulate a knowledge specific for a given clade. Only a well-trained specialist is able to get the exact meaning of specific details in fossil skeletons, important for the correct taxonomic evaluation. Only a correctly identified taxon, superimposed on the palaeogeographic map of its location allows the distinction between close relationship and homeomorphy (homeomorphies, however, can occur in contemporary environments also on a small, sub-

regional scale). And *vice versa*, correctly studied and named fossils allow one to omit inaccuracies in some details of the palaeogeography reconstructed on the basis of purely physical data. Palaeoecological reconstructions based on unnamed or incorrectly identified taxa leading to either incomplete and superficial or even to false deductions, can be recognized exclusively by a well-trained taxonomist. Only well-trained taxonomists are fully qualified to produce well-documented taxonomic papers which can create a basis for correct conclusions in palaeobiogeography and palaeoecology.

(iii) There seems to be a restricted number of journals readily accepting purely taxonomic papers, sometimes under a condition of their special value for a given group of fossils. Thus, there is always a risk of not finding a journal ready to publish a purely taxonomic paper resulting from many months of arduous investigations. Not many young scientists, living under the 'publish or perish' pressure are ready to take such a decision. Easy access to publishing in important palaeontological journals will most probably increase the interest of young scientists in purely taxonomic studies.

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