# Reply to the Comments of Yves Plusquellec and Esperanza Fernández-Martínez on the paper by A. May "Micheliniidae and Cleistoporidae (Anthozoa, Tabulata) from the Devonian of Spain"

ANDREAS MAY

MAY, A. 2007. Reply to the Comments of Yves Plusquellec and Esperanza Fernández-Martínez on the paper by A. May "Micheliniidae and Cleistoporidae (Anthozoa, Tabulata) from the Devonian of Spain". *Bulletin of Geosciences 82(1)*, 90–94. Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received February 12, 2007; issued March 30, 2007. • DOI 10.3140/bull.geosci.2007.01.90

*Andreas May, Saint Louis University – Madrid campus, Avenida del Valle 34, E-28003 Madrid, Spain; maya@madrid.slu.edu*

I would first like to thank Y. Plusquellec and E. Fernández-Martínez for commenting on my paper. Their comments clearly show that many details of the systematics of these groups of tabulate corals are still under discussion. Systematically evaluating the frequency of skeletal elements is one point of discussion. For example, for Plusquellec & Fernández-Martínez, a difference expressed as little as between 'mural pores and tabulae are rare' and 'mural pores and tabulae are absent' is a significant criterion for distinguishing *Paracleistopora* Plusquellec, 1973 from *Cleistopora* Nicholson, 1888 (for more details, see below). Knowing the high variability of these and other morphological characteristics in many groups of tabulate corals (*e.g.*, Hladil 1998, May 1998, Mötus 2006), such a method is disputable. Another important point of discussion is the systematic evaluation of the observable microstructure (further discussed below). Furthermore, the comments of Plusquellec & Fernández-Martínez show that important parts of their systematics are based on an unpublished thesis by Plusquellec (2006). The fact that this thesis has not been published (and the citation does not indicate that it ever will be) somewhat discredits their criticism, as only published material can be considered as contributing to the self-improving process of science. This is particularly true for (palaeo-) zoology, where these conditions have very strict definitions.

I am very glad that Plusquellec & Fernández-Martínez obtained permission to make thin sections of the material. When I was investigating this material, such permission was not given to me. Nevertheless, it would surely have increased the validity of the comments of Plusquellec & Fernández-Martínez if they had described additional material instead of merely re-investigating that described by May (2006). In this way, they missed an opportunity to advance our knowledge on Spanish corals. To evaluate this appropriately, the introduction of May (2006, p. 163) should be read: "Knowledge of Devonian tabulate corals in Spain is very incomplete." An overview of the modern publications will be instructive in understanding why this knowledge is still so incomplete. The introduction of May (2006, p. 163) shows that the three main investigators of Spanish Devonian tabulate corals in the last 15 years are E. Fernández-Martínez, Y. Plusquellec and myself. E. Fernández-Martínez has contributed five papers and Y. Plusquellec three (see references), each of which describes one or two species. These two authors have thus described a total of nine species of Spanish tabulate corals in seven papers between 1991 and 2006 (as one paper was co-written by both authors). During the same period (1993–2005) A. May has published three papers describing 12 species of tabulate corals, while the paper of May (2006) describes 5 species.

## Answers to criticisms

### Specifics of the old museum samples

The first of the three points criticized harshly by Plusquellec and Fernández-Martínez is that "it is not productive to create new species for which the information about exact locality, stratigraphic position and age are imprecisely known." Anyone would agree with this statement. However, only one new species was erected, based on two specimens from the same locality. This species has such unusual characteristics that, despite all their criticism, Plusquellec and Fernández-Martínez accept it as a new species.

### Specific determinations

Plusquellec & Fernández-Martínez agree in two cases with the specific determination given by May (2006) and disagree in following three cases: *Pleurodictyum elisabetae* May, 2006, *Michelinia guerangeri* (Milne-Edwards & Haime, 1851) and *Cleistopora smythi* Le Maître, 1952.

*Pleurodictyum elisabetae*. – Concerning *Pleurodictyum elisabetae* May, 2006, I am very thankful to Plusquellec &

Fernández-Martínez for their documentation of the pores in the basal plate, which further clarifies the exact systematic position of this very interesting species. I agree with their assertion that *elisabetae* is better assigned to *Procteria (Granulidictyum)* Schindewolf, 1959. However, I disagree with their opinion that the comparison of *elisabetae* with *Pleurodictyum? parvum* Dubatolova, 1960 was unnecessary. In the description of a new species, references should be made to closely related or similar species. As *elisabetae* has a much smaller corallite diameter than almost all similar Micheliniidae, comparison with a species like *Pleurodictyum? parvum*, with a comparable corallite diameter, is entirely appropriate.

*Michelinia guerangeri.* – One of the reasons cited by Plusquellec & Fernández-Martínez against the assignation of the Spanish material to *Michelinia guerangeri* (Milne-Edwards & Haime, 1851) is that the "Armorican species is more or less globular in shape and apparently devoid of 'epitheca' while in the Spanish specimens there are two distinct areas with an aboral surface showing well developed growth wrinkles." In fact, this holotheca is visible in the Spanish material, as documented clearly by May (2006, p. 167, fig. 1H). However, the difficulties in observing epitheca or holotheca in the Armorican material may be due to details of the growth form or the mode of preservation. Nevertheless, possession of a holotheca is part of the definition of the subfamily Micheliniinae (*e.g.*, Birenheide 1985, p. 92), and there is no reason to assume that *guerangeri* differed in this aspect from the other members of the subfamily. Consequently, the observation of the holotheca in the Spanish material doesn't exclude it from *guerangeri.*

As another reason for excluding it from *guerangeri*, Plusquellec & Fernández-Martínez describe the shape of the Spanish coralla as "more or less flattened". This is not correct, as the Spanish coralla are "irregularly spherical" (May 2006, p. 167, fig. 1F–G). Consequently, the shape of the coralla cannot be used to exclude the Spanish material from *guerangeri.*

Furthermore, Plusquellec & Fernández-Martínez write "The diameter of the corallites seems to be smaller in the Spanish species." This statement is perplexing, as the corallite diameters match very well: The large (= mature) calices in the Spanish material have diameters between 3.8–4.5 mm (May 2006, p. 167), while the calices in the Armorican material have diameters between 3.5–4.0 mm (Lafuste & Plusquellec 1980, pp. 148–171; Birenheide 1985, p. 97).

The differences observed by Plusquellec & Fernández-Martínez between the Spanish material and the Armorican material in the development of the lamellar microstructure do not justify their separation into different taxa, because the lamellar microstructure is of diagenetic origin (discussed further below) (May 2006, pp. 166, 167).

All remaining differences between the Armorican material of *guerangeri guerangeri* and the Spanish material, which Plusquellec & Fernández-Martínez found in the examination of their newly made thin sections of the Spanish coralla, only permit separation on a subspecific level. The fact that the wall in the Spanish material contains more spines than in the subspecies *guerangeri guerangeri* cannot be used to exclude it from the species *guerangeri*, because Lafuste & Plusquellec (1980, pp. 162–171) added the Armorican *Praemichelinia guerangeri cryptospina* Lafuste & Plusquellec, 1980, with more weakly developed septal spines, to this species. In this context, it perhaps necessary to emphasize that May (2006) did not assign the Spanish material to *Michelinia guerangeri guerangeri* (Milne-Edwards & Haime, 1851), but rather declined to make a subspecific assignment (May 2006, p. 168).

Otherwise, I am very thankful to Plusquellec & Fernández-Martínez for their description and illustration of the thin sections, as they clearly show that the Spanish material belongs to *Michelinia guerangeri* (Milne-Edwards & Haime, 1851). It probably represents a new subspecies, characterized by the numerous spines in the wall.

Though the short notice from Plusquellec & Fernández-Martínez on "some small flattened colonies" collected by Soto "in the Colle section", doesn't give relevant information, as no description is given, nor is any attempt at a systematic determination made.

*Cleistopora* versus *Paracleistopora*. – Concerning the validity of *Paracleistopora* Plusquellec, 1973, it must be stated that all non-microstructural characteristics given by Plusquellec & Fernández-Martínez toward distinguishing this genus from *Cleistopora* Nicholson, 1888, are only differences in gradation:

Mural pores and tabulae are rare in *Cleistopora*, but are absent in *Paracleistopora*. Both genera have spongy tissue, though it is better developed in *Cleistopora*. The coralla of *Cleistopora* have more corallites than those of *Paracleistopora*.

Except for microstructural differences, which may be the result of diagenetic alterations, Plusquellec & Fernández-Martínez offer no discrete differences between both genera, only gradual differences. Such gradual differences would ordinarily justify only the separation into different species, but not into different genera. However, a systematic category like the genus functions not only in representing biological relatedness as exactly as possible, but also to organize the observable biological diversity into comprehensible elements. Because of this second function, it may be acceptable in the case of groups with a large amount of species to distinguish different genera based on gradual differences (Mayr 1975, pp. 214–216). However, both *Cleistopora* and *Paracleistopora* contain very few species. Thus, the separation of both genera is not supported.

It must be stated that the number of genera with one or very few species in the families Micheliniidae and Cleistoporidae has increased drastically during the past 40 years. In many cases, these genera were erected by Plusquellec, though Mayr (1975, pp. 215, 216) clearly states that a classification with a high number of monotypic taxa is not useful.

Incidentally, Birenheide (1985, p. 103) writes in his description of *Cleistopora smythi* Le Maître, 1952, that mural pores are rare and the spongy tissue is well developed. *Cleistopora smythi* is the type species of *Paracleistopora.* If the description of Birenheide (1985, p. 103) is correct, most of the distinctive characters of *Paracleistopora* given by Plusquellec & Fernández-Martínez would be invalidated.

*Cleistopora smythi*. – Plusquellec & Fernández-Martínez give the following two reasons for denying that the Spanish corallum belongs to *Cleistopora smythi* Le Maître, 1952: "1) the structure of the corallum differs from that of the known species of *Paracleistopora* in which a bilateral symmetry is easily recognizable (generally 3 or 5 corallites); and 2) the granulation of *P. smythi* is much more tiny with granules outlines not irregular."

However, the original material of *Cleistopora smythi,* figured by Le Maître (1952, pl. 3, figs 16–26) shows variability in the development of the granulation, and contains examples which are consistent with that of the Spanish corallum (May 2006, fig. 1J). The corallum of May contains nine corallites, while the majority of the coralla in the original material of *Cleistopora smythi* contains six corallites. However, Le Maître (1952, p. 86) also found coralla with up to ten corallites.

Neither the description nor the figures of *Cleistopora smythi* (Le Maître 1952, pp. 85–87, pl. 3, figs 16–26) give any hint of a bilateral symmetry. However, I cannot exclude the possibility that there may exist a *Paracleistopora* species with bilateral symmetry, because Plusquellec & Fernández-Martínez don't give any reference related to this statement. Nevertheless, the type material clearly shows that bilateral symmetry is not characteristic of *smythi*.

May (2006, p. 169) writes that "the basal part of the corallites is filled by a spongy mass of septal elements." This observation was based on the natural longitudinal section figured by May (2006, fig. 1K). Though this spongy tissue was clearly visible only in small parts, its existence in other areas could be surmised. The statements of Plusquellec & Fernández-Martínez on this topic are very ambiguous, for they deny the existence of spongy tissue, and yet they state that "this structure is spiny and exhibits some small tabulae." And in the explanations of their Fig. 3 they write about a "false spongy structure." Thus the Spanish corallum apparently contains some amount of spongy tissue. However, a clear answer on this crucial question is not yet possible, as Plusquellec & Fernández-Martínez did not publish any photographs of the thin section, and their drawings (Fig. 3) don't allow the recognition of the details of the internal structure of the corallum. For example, it is unclear from the drawing if the thick massive basal part was originally so massive, or if its upper part consists of spongy tissue that has been transformed into an apparently massive structure by diagenetic processes.

In conclusion, it must be stated that all arguments of Plusquellec & Fernández-Martínez against the assignation to *Cleistopora smythi* by May (2006) can be controverted. Furthermore, it is not possible to evaluate possible relationships of the corallum described by May (2006, p. 169, fig. 1J, K) to *Vaughaniopsis* nom. nud., because the thesis of Plusquellec, in which it is erected, is still unpublished. Consequently, there is no reason to doubt that the corallum described by May (2006, p. 169, fig. 1J, K) truly belongs to *Cleistopora smythi* Le Maître, 1952.

## Diagenesis of microstructure

Plusquellec & Fernández-Martínez make a commendable attempt to discuss the observed microstructural patterns. Their first criticism is "If the lamellae result only from diagenetic alteration, why do the fibrous trabeculae are preserved, in the same wall, with their more or less original microstructure or, at least, as rods in stereoplasm?" This generally relictic trabeculae embedded in microlamellae can be observed easily in many rugose corals, one example of which is a *Stringophyllum* figured by May (1993a, p. 78, pl. 14, fig. 3). That figure also shows that the margins of these relictic holacanthine trabeculae have been "eaten" by microlamellae (proving in this way the diagenetic origin of the microlamellae). The next figure of rugose corals from May (1993a, p. 78, pl. 14, fig. 4) provides even more instructive examples of the diagenetic origin of the (micro-) lamellar microstructure. In a *Grypophyllum,* a microlamellar microstructure overprints the original septae, and in one part, this first microlamellar microstructure and the septal elements are overprinted by another, lighter coloured microlamellar microstructure. Another example of trabeculae embedded in what are clearly diagenetic microlamellae is given by Oekentorp (2001, fig. 29).

In general, the publications of Oekentorp (1972, 1980, 2001) and Brühl & Oekentorp (1997) demonstrate many cases in which the observed (micro-) lamellar microstructure is of diagenetic origin. Furthermore, several other authors have independently arrived at similar results. The following recent examples may be given: in the case of the Devonian rugose coral *Tabulophyllum*, Sorauf (1997) demonstrated that the observed lamellar structure was the result of diagenetic alterations that were triggered by variations in the trace element composition of the calcite of the skeleton; Hladil *et al.* (1997, p. 175) used image analysis to observe the late diagenetic origin of calcite "tablets", which supports a diagenetic origin of the (micro-) lamellar microstructure in general; The investigations of Webb & Sorauf (2002) and Sorauf & Webb (2003) on the origin and significance of the zigzag microstructure clearly prove that it is of diagenetic origin and is closely related to the (micro-) lamellar microstructure; Sorauf & Webb (2003) observed that the (micro-) lamellar microstructure occurs together with the zigzag microstructure, and that this (micro-) lamellar microstructure is also of diagenetic origin.

The above cited paper of Sorauf (1997) hints at a possible explanation of the phenomenon of trabeculae preserved within a (micro-) lamellar microstructure: A trace element composition of the trabeculae which differs from that of the surrounding skeleton would easily lead to different susceptibility for diagenetic alterations.

In view of this ample evidence for the diagenetic character of the (micro-) lamellar microstructure in rugose and tabulate corals, it would be necessary to look for reasons why the same would not be the case for the Micheliniidae and Cleistoporidae as well. Furthermore, even if Plusquellec & Fernández-Martínez had given convincing reasons for the original biological character of the (micro-) lamellar microstructure in the Micheliniidae and Cleistoporidae, another serious question would remain. Discussing earlier publications of Lafuste and Plusquellec, Sorauf (1993, p. 65) writes: "This biological variation of structural type in the exoskeleton at genus level or below is not probable. Living coral animals do not change their biology radically at the subordinal level. Did the Paleozoic corals?" In other words, if recent corals do not change the microstructure within one family, why would the microstructure change from one genus to another within the Micheliniidae and Cleistoporidae?

In conclusion, Oekentorp (1972, 1980, 2001) and the other cited authors present such a strong case, that the slight treatment of their results given by Plusquellec & Fernández-Martínez is disappointing.

## Contributions to knowledge

Plusquellec & Fernández-Martínez finish their comments with the statement "the May's conclusions presented in the discussed paper does not much contribute to the knowledge of the tabulate corals in Spain." I therefore point out the weaknesses in their criticisms discussed above. However, the importance of a contribution should be measured by the increase of knowledge that it brings. It is explained above that our "knowledge of Devonian tabulate corals in Spain is very incomplete" (May 2006, p. 163). Extrapolating from the slowness with which publications on Spanish Devonian tabulate corals appear (see above), it seemed clear that there was no reasonable hope of Plusquellec & Fernández-Martínez improving our knowledge of Micheliniidae and Cleistoporidae in a timely manner. If I hadn't published my study of the material from the Museo Geominero, those fossils would have long remained outside the attention of the scientific community.

## Conclusion

Most of the points of criticism cited Plusquellec & Fernández-Martínez are shown to be unfounded. Indeed, their discussion of the possibility of a diagenetic origin of the observed microstructures is particularly insufficient. Their inappropriate use of microstructures in systematics, and their overestimation of the systematic value of some gradual morphological differences, have resulted in highly disputable taxonomical decisions.

## References

Birenheide, R. 1985. Chaetetida und tabulate Korallen des Devon. *Leitfossilien 3*, 1–249.

Brühl, D. & Oekentorp, K. 1997. Secondary microstructures in tabulate corals of the genus *Alveolites* Lamarck, 1801 from the Middle Devonian of the Dollendorf Syncline (Eifel Hills, Germany). *Boletín de la Sociedad Española de Historia Natural (Sección Geológica) 92(1–4)*, 87–97.

Fernández-Martínez, E. 1999. Heliolitidae (Cnidaria, Tabulata) del Devónico de la Cordillera Cantábrica (NW de España). *Trabajos de Geología 21 (Volumen Homenaje a J. Truyols)*, 97–110.

Fernández-Martínez, E. & Plusquellec, Y. 2006. A new species of *Praemichelinia* (Tabulata) from the Emsian (Lower Devonian) of Colle (Cantabrian Mountains, NW Spain) and the occurrence of solenia-like pores in the genus. *Revista Española de Paleontología 21(1)*, 43–59.

Fernández-Martínez, E. & Tourneur, F. 1993. El genero *Caliapora* (Tabulata) en el Devónico de la Cordillera Cantábrica (NW de España). *Revista Española de Paleontología no extraordinario*, 58–70.

Hladil, J. 1998. Evolution of intraspecific morphological variability and its relationship to environment (*Caliapora battersbyi*, Devonian). *Věstník Českého geologického ústavu 73(1)*, 61–74.

Hladil, J., Čejchan, P. & Sedlák, R. 1997. Image analysis of thin sections: Implication for calcite fabric of diagenetically changed coral skeletons. *Coral Research Bulletin 5*, 171–179.

Lafuste, J., Fernández-Martínez, E. & Tourneur, F. 1992. *Parastriatopora* (Tabulata) de las calizas del Lorito (Devónico inferior, Provincia de Córdoba): Morfología y microestructura. *Revista Española de Paleontología 7(1)*, 3–12.

Lafuste, J. & Plusquellec, Y. 1980. Les Polypiers – Tabulata, 143–173. *In* Plusquellec, Y. (ed.) *Les schistes et calcaires de l'Armorique (Devonien inférieur, Massif Armoricain),* *Mémoires de la Société géologique et minéralogique de Bretagne 23.*

LAFUSTE, J., PLUSQUELLEC, Y. & SOTO, F. 1993. Coexistence de lamelles et de microlamelles dans le sclérenchyme de "*Ligulodictyum*" Plusquellec, 1973 (Tabulata, Dévonien du Nord-Gondwana). *Courier Forschungsinstitut Senckenberg 164*, 329–337.

LE MAÎTRE, D. 1952. La faune du Dévonien inférieur et moyen de la Saoura et des abords de l'Erg el Djemel (Sud-Oranais). *Materiaux pour la carte géologique de l'Algérie, 1ère Série Paléontologie 12*, 1–171.

MAY, A. 1993a. Korallen aus dem höheren Eifelium und unteren Givetium (Devon) des nordwestlichen Sauerlandes (Rheinisches Schiefergebirge). Teil II: Rugose Korallen, Chaetetiden und spezielle Themen. *Palaeontographica, Abteilung A 228*, 1–103.

MAY, A. 1993b. *Thamnopora* und verwandte ästige tabulate Korallen aus dem Emsium bis Unter-Eifelium von Asturien (Devon; Nord-Spanien). *Geologica et Palaeontologica 27*, 73–101.

MAY, A. 1995. *Thamnopora* (Anthozoa: Tabulata) aus dem Givetium bis Frasnium von Asturien (Devon; Nord-Spanien). *Münstersche Forschungen zur Geologie und Paläontologie 77*, 479–491.

MAY, A. 1998. Statistische Untersuchungen an der tabulaten Koralle *Thamnopora* (Anthozoa; Devon). *Geologica et Palaeontologica 32*, 141–159.

MAY, A. 2005. A new *Parastriatopora s*pecies (Anthozoa, Tabulata) from the Lower Devonian of Colle (Spain, Cantabrian Mountains). *Bulletin of Geosciences 80(4)*, 287–290.

MAY, A. 2006. Micheliniidae and Cleistoporidae (Anthozoa, Tabulata) from the Devonian of Spain. *Bulletin of Geosciences 81(3)*, 163–172.

MAYR, E. 1975. *Grundlagen der zoologischen Systematik.* 370 pp. Verlag Paul Parey, Hamburg and Berlin.

MÖTUS, M.-A. 2006. Intraspecific variation in Wenlock tabulate corals from Saaremaa (Estonia) and its taxonomic implications. *Proceedings of the Estonian Academy of Sciences, Geology 55(1)*, 24–42.

OEKENTORP, K. 1972. Sekundärstrukturen bei paläozoischen Madreporaria. *Münstersche Forschungen zur Geologie und Paläontologie 24*, 35–108.

OEKENTORP, K. 1980. Aragonit und Diagenese bei jungpaläozischen Korallen. *Münstersche Forschungen zur Geologie und Paläontologie 52*, 119–239.

OEKENTORP, K. 2001. Review on diagenetic microstructures in fossil corals – a controversial discussion. *Bulletin of the Tohoku University Museum 1*, 193–209.

PLUSQUELLEC, Y. 1993. Un Tabulé pleurodictyforme "biface" *Procterodictyum* n. gen. (Emsien du Nord Gondwana). *Geologica et Palaeontologica 27*, 103–121.

SORAUF, J.E. 1993. The coral skeleton: analogy and comparisons, Scleractinia, Rugosa and Tabulata. *Courier Forschungsinstitut Senckenberg 164*, 63–70.

SORAUF, J.E. 1997. Geochemical signature of incremental growth and diagenesis of skeletal structure in *Tabulophyllum traversensis* (Winchell, 1866). *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica) 92 (1–4)*, 77–86.

SORAUF, J.E. & WEBB, G.E. 2003. The origin and significance of zigzag microstructure in Late Paleozoic *Lophophyllidium* (Anthozoa, Rugosa). *Journal of Paleontology 77*, 16–30.

TOURNEUR, F. & FERNÁNDEZ-MARTÍNEZ, E. 1991. *Parastriatopora cantabrica*, nueva especie de tabulado del Devónico inferior (Emsiense) de la Cordillera Cantábrica (NO de España). *Revista Española de Paleontología 6(1)*, 3–19.

WEBB, G.E. & SORAUF, J.E. 2002. Zigzag microstructure in rugose corals: A possible indicator of relative seawater Mg/Ca ratios. *Geology 30(5)*, 415–418.