Structure and microstructure of *Pachypora lamellicornis* LINDSTRÖM, 1873, a tabulate coral from the Silurian of Gotland, Sweden

Yves Plusquellec¹, Francis Tourneur², Alain Le Hérissé¹

PLUSQUELLEC, Y., TOURNEUR, F. & LE HÉRISSÉ, S., 2007: Structure and microstructure of *Pachypora lamellicornis* Lindström, 1873, a tabulate coral from the Silurian of Gotland, Sweden. – In: HUBMANN, B. & PILLER, W. E. (Eds.): Fossil Corals and Sponges. Proceedings of the 9th International Symposium on Fossil Cnidaria and Porifera. – Österr. Akad. Wiss., Schriftenr. Erdwiss. Komm. 17: 67–83, 5 Figs., 1 Pl., Wien.

Abstract: The examination of types and topotypes of the type species of *Pachypora (Pachypora lamellicornis* LINDSTRÖM, 1873), from the Upper Visby Beds, Lower Wenlock, District of Visby, Gotland (Sweden), facilitates enhanced characterization of morphology, structure and microstructure of this genus. Calices are very small, rounded or crescentic, sometimes spiny, tabulae sparse, only angle mural pores present, pore plate probably lacking, lateral increase with basal pore. Wall microstructure well preserved: median lamina built of granules in the axial zone of the branch, small plates in its margin, lacking in the peripheral zone; main layer of sclerenchyma (very thick in the peripheral zone) composed of scutellate microlamellae coated in the axial zone by a fibrous layer sometimes topped by a thin film of microlamellae. No obvious growth lamellae were noted. A comparison between *Pachypora* and *Platyaxum* is attempted.

Key words: Pachypora, Tabulata, microstructure, Silurian, Gotland

Contents

1.	Why Pachypora lamellicornis?	68
2.	Short history of the genus	68
3.	Material	69
4.	Geographic and stratigraphic data	69
5.	Additional and/or new data on the morphology, structure and microstructure of	
	P. lamellicornis	70
	5.1. Morphology and structure	70
	5.2. Wall microstructure	72

¹ Université de Bretagne occidentale, UMR 6538 "Domaines océaniques", Laboratoire de Paléontologie, Faculté des Sciences, 6 av. Le Gorgeu, F-29238 Brest cedex 3 France, e-mails: Yves.Plusquellec@univbrest.fr, alain.le.herisse@univ-brest.fr

² Impasse du Blanc Bou, 21, B-5340 Faulx-les-Tombes Belgique, e-mail: francis.tourneur@wanadoo.be

5.2.1. Observations on petrographic sections	74
5.2.2. Observations in "LFP" thin sections	74
5.3. Morphology of microlamellae	76
5.3.1. Size of microlamellae	77
6. Conclusions: Pachypora and the Pachyporidae	78
Acknowledgements	79
References	79

1. WHY PACHYPORA LAMELLICORNIS?

Pachypora lamellicornis LINDSTRÖM, 1873, type species of the genus Pachypora and type genus for the family Pachyporidae GERTH, 1921 and the superfamily Pachyporicae (cf. HILL, 1981) is a very interesting taxon. Moreover, the study of its microstructural features gave rise to various interpretations or misinterpretations, and the systematic value of the observed microstructure is controversial. Thus, in order to propose a generic and familial diagnosis established on accurate observations, it was necessary to revise the morphological, structural and microstructural characteristics of *P. lamellicornis*.

2. SHORT HISTORY OF THE GENUS

The genus Pachypora was created by LINDSTROM in 1873 for P. lamellicornis, its only branching species from the classical Silurian sections of Gotland. This species had been already described by previous naturalists, including Linnaeus, under other invalid names. The short original Latin diagnosis of LINDSTRÖM (1873, p. 14) was exactly repeated in 1876 (p. 11) and the first detailed description of the species was given in German in 1896 (p. 23-32), with an extended discussion of characters and illustrations of external and internal aspects. Interestingly, LINDSTRÖM insisted on two characters which were (and still are) grounds for discussion: the branching habits of the corallum and the microstructure of the skeleton. Both were discussed at great length by many authors, like NICHOLSON & ETHERIDGE (1877) and particularly LECOMPTE (1936). The growth form could be interpreted as an ecological feature and the thinly laminated microstructure ("strata densissima, tenuissime lamellate") as the result of diagenesis. Later, the genus was chosen as the base of the family Pachyporidae GERTH, 1921 and of the superfamily Pachyporicae HILL, 1981. It is thus both timely and appropriate to revise the species both on the classical types, and on new, freshly collected, material. Our conclusions are in agreement with those of LINDSTRÖM and LECOMPTE concerning the high systematic value of branching morphology and laminated microstructure, and we do not agree to place the genus in synonymy with either Favosites LAMARCK, 1816 or Thamnopora STEININGER, 1831, as concluded by authors like Frech (1885) or Lang, Smith & Thomas (1940).

3. MATERIAL

We have studied the following material from the type Silurian succession of Gotland:

- some original specimens of Lindström (Naturhistoriska Riksmuseet, Sektionen för Paleozoologi, Stockholm); NRM-PZ Cn. 583, 598, 600.
- one specimen figured by LECOMPTE (Institut Royal des Sciences Naturelles de Belgique); IRSNB a9827.
- 8 specimens collected by two of us (A. Le Hérissé and Y. Plusquellec); Université de Bretagne occidentale, Laboratoire de Paléontologie, Brest, France; LPB 14 205– 14 213.

All the specimens are from the Silurian of Gotland.

4. GEOGRAPHIC AND STRATIGRAPHIC DATA

The original specimens of LINDSTRÖM as well as our material comes from the Silurian of Gotland, Sweden, more precisely from some localities in the Visby district along the Northwest coast (e.g. Lundsklint 1, Ireviken1, for the material recently collected).

In his first paper, LINDSTROM (1873, p. 11) indicated that *Pachypora* "occurit ad Visby", later (1896, p. 28) he gave more geographic and stratigraphic details "Diese Art findet sich ringsum Wisby, sowohl nördlich wie südlich der Küste [...], mindestens in der Schicht d, aber auch in c".

Our specimens were collected at Ireviken 1, Visby Beds (coll. Y. Plusquellec, 1981) and Lundsklint 1, bed S151, upper part of the Visby Beds (coll. A. Le Hérissé, 1998).

The Silurian sequence of Gotland (about 500 m thick), in Sweden, is dominated by carbonate sedimentation (alternations of limestone-marls) and the repeated formation of reefs, indicative of a shallow and warm epicontinental sea environment at low latitude near the Silurian equator. Deposited on the stable Balto-Scandian Shield, the strata show only gentle folding, insignificant faulting and no deep burial. For this reason the sediment shows low grades of diagenetic alteration with excellent preservation of microfacies character and fossils (SAMTLEBEN et al., 1996).

Following the evolution of the nomenclature and stratigraphical terminology in the Silurian of Gotland, the divisions c ("younger marl-shale and sandstone") and d ("Limestone with marl-bands, or oolite in southern Gotland") of LINDSTRÖM (1896), are referred by HEDE (1921) as follows: division c is assigned to Lower and part of Upper Visby Formation; division d to upper part of Visby Formation and part of Högklint Formation.

The occurrence of *P. lamellicornis* has been clearly established at Lundsklint 1, 145 cm above the reference level of the boundary between Lower and Upper Visby beds. Because the "marly Lower Högklint" of LINDSTRÖM is now referred to the uppermost Visby Beds, it is highly probable that all the specimens of *P. lamellicornis* come mainly from the Upper Visby Beds. Thus, we consider that all specimens of the Visby district are roughly topotypes and provide indisputable data on the genus.

The Silurian Subcommission has decided to revisit the defined boundary stratotype of the Llandovery/Wenlock boundary (LOYDELL, 2001). Graptolite workers most favoured the base of the *Cyrtograptus centrifugus* Biozone. Conodont workers, with reference to Gotland, and using the Ireviken Event datum points defined by JEPPSSON (1990, 1997),

suggested datum points 2, 3, 4 or 6 as possibilities for the limit. Datum 2 seems to be the best. And for us, as correlated to the Lundsklint 1 section, the level with *Pachypora* is about four meters above datum 2, i.e. the Llandovery/Wenlock boundary (145 cm above the reference level enriched in the large solitary rugose coral *Phaulactis* sp.). Thus, the type species of *Pachypora* is very likely of Lower Wenlock even if some specimens (not known of us) are from the upper Lower Visby Beds.

The layers with *P. lamellicornis*, at least two, after LINDSTRÖM (1896), are located within a general reef bearing environment, between the *Catenipora-Favosites* biostrome (STEL, 1978) of the Lower Visby Beds (upper Llandovery) and the patch reefs of the Högklint beds (Lower Wenlock), dominated by stromatoporoids. In the Upper Visby Beds, the limestone-marl ratio gradually increases – in some localities carbonate buildups arise – and according to LINDSTRÖM (1896), the frequency of *P. lamellicornis* seems to follow this trend.

5. ADDITIONAL AND/OR NEW DATA ON THE MORPHOLOGY, STRUCTURE AND MICROSTRUCTURE OF *P. LAMELLICORNIS*

5.1. Morphology and structure

Corallum:

Specimens mainly frondescent or branching, sometimes slightly reticulate, flattened, generally of small size, rarely exceeding 5 cm (LECOMPTE, 1936, Pl. IV, Fig. 1–8). One of the larger fronds (LINDSTRÖM, 1896, Fig. without number p. 25) is unfortunately used for the genus description in numerous treatises (HILL, 1981, Fig. 385 2c; LIN et al., 1988, Fig. 215c), providing a false idea of the species.

Calices:

The calices open obliquely or perpendicularly to the exterior surface of branches. They are thick-walled, polymorphic, more or less polygonal in outline, rounded or alveolitid, generally 6- or 7-sided, less commonly 5-sided, rarely 4-sided, 3-sided not seen.

The size of calices – or more precisely of lumina or visceral chambers of calices – is very small for a tabulate coral, the diameter being mainly 0.4 to 0.5 mm (corresponding diameter of corallite about 1 mm).

On some well preserved specimens the boundary between neighbouring corallites is emphasized by a thin ridge (specimen NRM-PZ Cn. 600). We have not seen the numerous radial striae figured by LINDSTRÖM on any specimen, even on the specimen NRM-PZ Cn. 598 corresponding (?) to LINDSTRÖM'S original illustrated as Pl. V, Fig. 55 (1896). The calicinal walls bear irregular septal spines (Pl. 1, Fig. 1).

In alveolitid and slightly oblique calices a somewhat prominent lip often appears, emphasizing the crescent outline of the calice; moreover the blunted tip of the lip indicates the plane of bilateral symmetry of the calice (Pl. 1, Fig. 2). It is what LINDSTRÖM (1896) describes under the name of "Lippenzahn".

Rarely some corner mural pores can be seen in the calices, some are present especially on the little area figured by LINDSTRÖM (1896, PI. V, Fig. 60, specimen NRM-PZ Cn. 600).



Fig. 1: Pachypora lamellicornis, structure of corallum. P1 for angle pore.
A: transverse thin section showing the usual asymmetry of the branch. IRSNB a9827 (= LECOMPTE, 1936, pl. IV, Fig. 17a pars).
B, C: respectively tangential and transverse section (acetate peels). Arrow on C indicates a pore layer parallel to surface of frond. LPB 14 211, Lundsklint 151.
D: transverse section with angle pores in the axial zone. LPB 14 207, thin section B 46 968, Lundsklint 151.

In some places calices are closed by opercula (Pl. 1, Fig. 1) showing concentric growth striae very well figured by LINDSTRÖM (1896, Pl. V, Fig. 57–58, 62). The center of each operculum is occupied by a small punctiform or elongated depression.

Corallites:

In the axial part of a branch, they run parallel to the axis and turn sharply into the peripheral zone to open normal or obliquely to the surface of branch.

Walls are generally thick in the axial zone but much more so in the peripheral zone.

Pores:

There is no doubt about the presence of mural pores (see also STASINSKA, 1967), but it seems that they belong only to angle pores (=P1). These angle pores are identified in transverse section in the axial zone – moderately abundant – and in the peripheral zone too (Fig. 1D). They are large (diameter about $1/_3$ to $1/_2$ of a corallite face).

In the peripheral zone of some specimens appears an area with numerous P1 pores, located at the same level, and parallel to the surface of this frond (Fig. 1C). In tangential section the pores give a meandriform to solenid aspect to the lumina and it is probably these features that LINDSTRÖM (1896, Pl. V, Fig. 64b, section not traced) considered as burrows (Fig. 1B).

Pore plates are probably lacking.

Tabulae:

Both in the axial and peripheral zone tabulae are present; moderately spaced, thin, complete, flat, uparched or sagging, very rarely thickened.

Increase:

Some patterns of lateral increase are seen in longitudinal sections; the offset being situated on the dorsal side of the parent corallite. The basal pore, previously noticed by LECOMPTE (1936, "on observe parfois un pore à la naissance de jeunes polypiérites"), is devoid of a pore plate.

5.2. Wall microstructure

The interpretation of the microscopic features of the wall has been from the beginning a bone of contention. LECOMPTE (1936) maintained that the "structure feuilletée" of the sclerenchyma (especially in the peripheral zone) is a primary microstructure while the fibrous coating is "purement minéral" (that means in his mind probably diagenetic). Thus he agrees with LINDSTRÖM (1896) who considered the stratiform character of the wall to be diagnostic of *P. lamellicornis*.

SOKOLOV (1962) shares this opinion, but he is not very clear about the true nature of the laminar stereoplasm (platintchatoi stereoplasmy).

The opinion of HILL (1981, p. F575) is in complete contrast to this; she wrote that the "original microstructure [of Pachyporidae], when retained, shows stereozone consisting of radial fibres deposited in concentric growth lamellae".

A study of the wall microstructure by thin sections of petrographic thickness (30 μ m) and by polished ultra thin sections (the so called "LFP" of LAFUSTE, 1970; 3–5 μ m) allows very accurate observations and brings new data on the true nature (in our opinion) of the wall.

The interpretation of all the observations on microstructures in Palaeozoic corals has long been in discussion. Some scientists estimate that everything is recrystallised, owing to the original mineralogy, to the diversity of structures, supposed to be too complex for such simple organisms, and to the lack of similar microcrystals in Recent corals. A good synthesis of these opinions can be read in OEKENTORP (2001). Such hypothesis have been discussed formerly by us, and it does not seem opportune to open the debate again here. Nevertheless, a paper by NOTHDURFT & WEBB (this volume) gives interesting data about the controversal significance of the microlamellae-lamellae. They show that these microstructural units "may have analogues in scleractinian corals" and conclude that "their use in systematics may be supported".



Fig. 2: Pachypora lamellicornis, semi schematic drawings of the microstructure, margin of the axial zone. MI: median lamina – granules to "plaquettes"; Sa: inner layer of microlamellar sclerenchyma; Sb: layer of fibroids; Sc: outermost layer of microlamellar sclerenchyma. LPB 14 207, LFP thin section B 46 967, Lundsklint 151. In the axial zone the wall is built of a median lamina thickened on both sides by the peripheral stereozone (sensu SWANN, 1947).

- (1) Median lamina: It is generally a dark almost opaque and thin deep grey-lined layer (the so-called median dark line). In some places the median lamina widens and appears as a light-coloured "dark" line.
- (2) Sclerenchyma: The main layer of sclerenchyma (= LINDSTRÖM'S Endotheca, 1896, p. 27), deposited upon the median lamina, is built of small units parallel to the latter, indicating more likely a lamellar-microlamellar microstructure than growth lamellae. This inner layer (referring to the axis of the wall) can be coated by a rather homogeneous clear-appearing yellowish calcite strata: it is our outer sclerenchyma (= LINDSTRÖM'S Stereoplasma, 1896, p. 27).

In crossed nicols the outer sclerenchyma shows a radial setting of the crystalline units. This is not a layer of fibrous calcite infilling the lumen during early diagenesis because one can see the tabulae resting on this layer, not the opposite (Fig. 2, Ta). It is in fact biological thickening belonging to the wall. Nevertheless, OEKENTORP (2001, Fig. 4–10–11) presents figures trying to show that it is not an absolute criterion; it is not convincing.

The boundary between the axial and peripheral zones is marked – besides the corallites turning sharply at right angle to the surface as the stereozone widens – by the complete retrogression of the median lamina, allowing the development of continuous sclerenchyma between neighbouring corallites. The layers of this sclerenchyma, slightly wavy parallel to the surface of the branch between two neighbouring corallites, are fold down along the margins of lumina (Fig. 1A).

The yellowish outer layer is lacking (or at least rare) in the peripheral zone.

5.2.2. Observations in "LFP" thin sections

These very thin sections allow observing (and describing) the very small crystalline units of the skeleton.

(1) Median lamina: In the inner part of the axial zone, the median lamina is built of more or less isodiametric granules (Fig. 3A). Their diameter normal to the median lamina is generally between 4–11 μ m, while parallel to it is about 5–13 μ m.

In the margin of the axial zone the median lamina is built of small plates (or "plaquettes" used in English by TOURNEUR, 1986) of various size with their big axis parallel to the boundary between two adjacent corallites (Fig. 3B). Generally they correspond to the entire width of the lamina. This kind of microstructure gives rise to the broad glassy median lamina seen in petrographic thin sections. In transverse section the width of "plaquettes" is between 12–17 μ m, their length can reach more than 100 μ m! In this case it could be the result of coalescence of some units with the same orientation of the *c*-axis and according to SCHOUPPÉ & OEKENTORP (1974) we can see here a local effect of diagenesis.



Fig. 3: *Pachypora lamellicornis*, microstructure. Direction of skeletal accretion indicated by T. LPB 14 207, LFP thin section B 46 967. Lundsklint 151.

A: axial zone, transverse section in the corallite, granular median lamina (MI), microlamellar inner layer of sclerenchyma. Hatching does not represent cleavage-striae, idem for 3B. B: margin of the axial zone, transverse section in the corallite, median lamina with "plaquettes", microlamellar inner sclerenchyma.

C: peripheral zone, longitudinal section in the corallite, scutellate microlamellae of the main (inner) layer of sclerenchyma. Black triangles indicate the potential median lamina. D: margin of the axial zone, transverse section in the corallite (same location and caption as for Fig. 2).

(2) Sclerenchyma: 2a. Main layer or inner layer of sclerenchyma (Fig. 2, Sa). This thick (axial zone) or very thick (peripheral zone) layer is built of microlamellae whose morphology needs discussion (see below). They are parallel to each other and, in the axial zone, parallel to the median "dark" line in all directions of space. In the peripheral zone they are parallel to surface of skeleton (intracalicular area and "vertical" wall of calices). Nevertheless, in longitudinal section and at the boundary between two corallites, the microlamellae are oblique with distal end at bottom and are in contact along a zig-zag line, equivalent of a potential median lamina (Fig. 3C).
2b. Outer fibrous layer (Fig. 2, Sb).

This layer, generally well seen on the sections of petrographic thickness, seems to be badly preserved under the high magnification allowed by "LFP". Nevertheless, it is possible to find elongated and sinuous-outlined crystalline units normal to the microlamellar layer (Fig. 3D). Their length reaches 30 μ m for a diameter of 7 μ m. They can be assigned to embossed fibroids (perhaps recrystallisation of true fibres).

2c. Outer microlamellar layer (Fig. 2, Sc).

The layer of fibroids is sometimes coated by a very thin layer of microlamellae absolutely undetectable in petrographic sections. This allows us to maintain that the fibrous layer is not a cement.

5.3. Morphology of microlamellae

The microlamellae are flat, thin, slightly curved in the central part of their main curvature. In their peripheral part there is an accentuation of this curvature so that the margin becomes vertical. The marginal curvature is generally more pronounced on the proximal side of the microlamellae.

The microlamellae are outlined by incurvations (cupules), the concavity of which – as well as the main curvature – always faces the lumina, thus indicating the direction of skeletal accretion. On each side of the median lamina main curvature and incurvations are back to back (Fig. 3A, B).

Fig. 4:

Pachypora lamellicornis. Average sizes of the two kinds of microlamellae, top with one main curvature, bottom with two main curvatures. L: length or diameter; H: height; E: thickness; N: number of measurements.

	Ŀ	H	Ε	Ν
T T T T T T T T T T T T	26.0	7.84	5.05	19
H	32.0	8.37	5.19	19



Fig. 5: Pachypora lamellicornis. Box with whisker display, same caption as for Fig. 4. 1: microlamellae with one main curvature; 2: with two.

Within the microlamellae two morphological types can be distinguished in section:

- 1) microlamellae with one main curvature,
- 2) microlamellae with two main curvatures obvious both on proximal and distal side. These kind of units have been interpreted in *Parastriatopora sanjuanina* as the coalescence of two elements (FERNANDEZ-MARTINEZ et al., 1999).

In addition, some microlamellae exhibit a strong axial tip on their distal side without corresponding indentation on the proximal one, and in some parts of the sclerenchyma there are calcitic areas of unusual size with more than two main curvatures (probably coalescence of units).

5.3.1. Size of microlamellae

The three usual dimensions are given on Fig. 4 for microlamellae with one and two main curvatures. Generally these latter have a larger diameter but as shown on box with

whisker display (Fig. 5) the two categories are not separated. Height and thickness are roughly similar.

What kind of microlamellae is encountered in *Pachypora lamellicornis*? The flattened units of the sclerenchyma very often reach the diameter of lamellae but the outline of their main curvature, their strong cupulation, their setting with regard to the median lamina and the lack of unconformity within the layers of crystalline units, correspond to indisputable microlamellae. Taking into account their size and morphology, the microlamellae of *P. lamellicornis* are to be assigned to the "scutellate microlamellae" described by LAFUSTE (1984) in *Planalveolites fougti* MILNE-EDWARDS & HAIME, 1851. LAFUSTE indicated that they can reach "as much as 25 μ m in length" but we have noticed for the lectotype of this species (PLUSQUELLEC et al., 1997) diameters reaching 40 to 50 μ m with thickness of 5–6 μ m. So, the dimensions of the microlamellae of *P. lamellicornis* are consistent with all these data.

It is interesing to note that:

- 1) Planalveolites and Pachypora are both from the Silurian,
- 2) Pachypora is the second known genus with scutellate microlamellae, and
- 3) their scutellate microlamellae differ from the standard microlamellae of *Parastriatopora* (cupular microlamellae) which are of small diameter, thick and strongly bent.

6. CONCLUSIONS: PACHYPORA AND THE PACHYPORIDAE

If one agrees that the general arrangement of the crystalline units, their original and constant morphology, their main curvature and cupules facing the lumina in different parts of the skeleton are not due to a diagenetic process, the microlamellae (or at least their outlines) are primary or very similar to their primary shape and setting. Thus the genus *Pachypora* is basically a microlamellar tabulate coral.

As a result:

- (1) in the diagnosis of the family Pachyporidae proposed by HILL (1981) "original microstructure when retained, shows stereozone consisting of radial fibres deposited in concentric growth lamellae" has to be replaced by "microlamellar microstructure with sometimes fibrous (fibroid) outer layer".
- (2) some entirely fibrous Tabulata like the Devonian genus *Thamnopora* Steininger, 1831 (see Lecompte, 1936; Tourneur, 1986), the Carboniferous *Acaciapora* Moore & Jeffords, 1945 (see LAFUSTE & TOURNEUR, 1991), and the Permian *Gertholites* Sokolov, 1955 (see WAAGEN & WENTZEL, 1886) are to be removed from the family as defined above. In connection with that, we agree with LINDSTRÖM (1896, p. 28) who pointed out that successive and incorrect grouping of species in the same systematic unit alters its initial meaning.
- About the specimens assigned to Pachypora and allied genera we note that:
- (1) SOKOLOV (1962) following LINDSTRÖM (1896) indicates that two species belong to the genus *Pachypora*: the type species and *P. fischeri* (BILLINGS, 1860). These species from the Middle Devonian (Hamilton Group) of SW Ontario have been assigned to various genera. It was a species of *Alveolites* for BILLINGS and one of *Platyaxum* for STUMM (1950). We have not been able to see the specimen of BILLINGS; figures given by NICHOLSON (1879) are not good enough to allow us to have a definitive opinion, nevertheless it could be a *Platyaxum*.

As for the specimen of *P. fischeri* figured by DAVIS (1887, MCZ 101 678, Pl. 60, Fig. 3), who erroneously said to be the holotype following the label of the collections of the Museum of Comparative Zoology of Cambridge, Mass. (specimen studied by one of us, Y.P.), its specific assignment is difficult because little is known on the true holotype and moreover its axial zone is not well differentiated.

- (2) the genus *Platyaxum* Davis, 1887 is sometimes used as a subgenus of *Pachypora* (WERNER, 1936).
- (3) there are some similarities between the stratiform appearance (growth lamellae or lamellar/microlamellar microstructure?) of the wall in the peripheral zone of the holotype of *Platyaxum turgidum* ROMINGER, 1876 (UMMP 8 498, type species of the genus, seen by Y.P.) and that of *Pachypora*.
- (4) the main differences between the two genera are difficult to establish. They concern the morphological features (lip of calices of *Platyaxum* with two teeth) and the structure of the corallum but unfortunately more or less hidden by silicification (Plusquellec and Fernandez-Martinez, pers. observ.).
- (5) the subgenus *Parapachypora* YANG & CHOW, 1978 in YANG, KIM and CHOW seems to correspond to less flattened branches. The type species is *Thamnopora lamellosa* Yü, 1962 (not seen).
- (6) typification of *Pachypora* generally needs thin sections or peels, and this is not a truism. Within the original material of LINDSTRÖM there is an unfigured specimen with more or less anastomosing cylindrical branches (NRM-PZ Cn. 592) which is neither a *P. lamellicornis* nor a *Pachypora*. A transverse acetate peel shows a very wide peripheral zone with walls markedly thickened and bearing very numerous small septal spines inclined adaxially upwards. Another transverse acetate peel made by us in the figured specimen of *Striatopora stellulata* (LINDSTRÖM, 1896, Pl. V, Fig. 50, NRM-PZ Cn 59 302) shows the same structure. The two specimens belong to the same genus (probably new) and to the same species (*stellulata*). The provided section (LINDSTRÖM, 1896, Pl. V, Fig. 52) is not characteristic or does not belong to the species.
- (7) Pachypora gracilis YANET, 1970, from the Ludlow of the Ural could be a true Pachypora, whereas Pachypora ? crassa YANET, 1970, from the same horizon and area is, as suspected by its author himself, to be assigned to an other genus.

Acknowledgements: The authors greatly acknowledge Dr. Jonas Hagström (Naturhistoriska Riksmuseet, Stockholm) and Dr. Annie Dhondt (Institute Royal des Sciences Naturelles de Belgique, Bruxelles) for the loan of original and figured specimens. For reviewing the paper we are indebted to an anonymous reviewer and to Prof. Dr. K. Oekentorp.

References

- FRECH, F., 1885: 3. Die Korallenfauna des Oberdevons in Deutschland. Zeitschrift der Deutschen geologischen Gesellschaft, **1885**: 21–130, Berlin.
- GERTH, H., 1921: XVI. Die Anthozoen der Dyas von Timor. Paläontologie von Timor, IX: 67–147, Stuttgart.
- HEDE, J.E., 1921: Gottlands silurstratigrafi. Sveriges Geologisches Undersökning, C 305. 100 p., Stockholm.

FERNANDEZ-MARTINEZ, E., PLUSQUELLEC, Y., TOURNEUR, F. & HERRERA, Z., 1999: Nueva especie de tabulado del Devónico inferior de Argentina. – Revista Espanola de Paleontologia, 14/1: 37–57, Madrid.

- HILL, D., 1981: Part F Coelenterata, suppl. 1 Rugosa and Tabulata, vol.2. In: MOORE, R. C., ROB-INSON, R. A. & TEICHERT, C. (Eds.): Treatise on Invertebrate Paleontology. – F379 -F762, Boulder – Lawrence (The Geological Society of America, Inc. and The University of Kansas).
- JEPPSSON, L., 1990: An oceanic model for lithological and faunal changes tested on the Silurian record. Geological Society of London, Journal, **147**: 663–674, London.
- JEPPSSON, L., 1997: The anatomy of the Mid-Early Silurian Ireviken Event and a scenarion for P-S events. – In: BRETT, C.E. & BAIRD, G.C. (Eds.): Paleontological Events: Stratigraphical, Ecological and Evolutionary Implications. – 451–492, New York (Columbia University Press).
- LAFUSTE, J., 1970: Lames ultra-minces à faces ploies. Procédé et application à la microstructure des Madréporaires fossiles. Comptes rendus de l'Académie des Sciences, **270**: 679–681, Paris.
- LAFUSTE, J., 1984: Microstructure of *Planalveolites* Lang and Smith, 1939 Tabulata, Silurian). Palaeontographica Americana, **54**: 485–488, New York.
- LAFUSTE, J. & TOURNEUR, F., 1991: Microstructure du genre Acaciapora Moore & Jeffords 1945 (Tabulata; Pennsylvanien de l'Oklahoma, USA). – Geologica et Palaeontologica, 25: 99–105, Marburg.
- LANG, W.D., SMITH, S. & THOMAS, H.D., 1940: Index of Palaeozoic coral genera. 231 p., London (British Museum, Nat. Hist.).
- LIN, B., TCHI, Y., JIN, C., LI, Y. & YAN, Y. (Eds.), 1988: Tabulatomorphic corals. 450 p., Beijing (Geological Publishing House).
- LECOMPTE, M., 1936: Révision des tabulés dévoniens décrits par Goldfuss. Mémoires du Musée royal d'Histoire naturelle de Belgique. 111p., Bruxelles (Musée Royal).
- LINDSTRÖM, G., 1873: Nagra anteckningar om Anthozoa tabulata. Öfversigt af Kongl. Vetenskaps-Akademiens Föfhandlingar, **4**: 3–20, Stockholm.
- LINDSTRÖM, G., 1896: Beschreibung einiger Obersilurischer Korallen aus der Insel Gotland. Bihang till K. Svenska Vetenskaps-Akademiens Handlingar, **21** (IV/7): 1–50, Stockholm.
- LOYDEL, D.K., 2001: The Llandovery-Wenlock boundary: summary of views expressed. Silurian Times, **10**, Silurian subcommission internet report.
- NICHOLSON, H.A., 1879: On the structure and affinities of the "Tabulate corals" of the Palaeozoic period. 337 p., Edinburgh London (Blackwood & sons).
- NICHOLSON, H.A. & ETHERIDGE, R., 1877: Notes on the genus Alveolites Lamk. and some allied forms of Palaeozoic Corals. Linnean Society Journal, Zoology, XIII: 353–370, London.
- NOTHDURFT, L.D. & WEBB, G.E., 2006: "Shingle" microstructure in scleractinian corals: a possible analogue for lamellar and microlamellar microstructure in Palaeozoic tabulate corals. this volume.
- OEKENTORP, K., 2001: Review on diagenetic microstructures in fossil corals a controversial discussion. In: EZAKI, Y., MORI, K., SUGIYAMA, T. & SORAUF, E. (Eds.): Proceedings of the 8th International Symposium on Fossil Cnidaria and Porifera. Bulletin of the Tohoku University Museum, 1. 193–209, Sendai.
- PLUSQUELLEC, Y., TOURNEUR, F. & GROISARD, E., 1997: Revision of Alveolites fougti Milne-Edwards & Haime, 1851, type species of *Planalveolites* Lang & Smith, 1939 (Tabulata, Silurian of Gotland).
 Bol. R. Soc. Esp. Hist. Nat. (Sec. Geol.), 91: 205–214, Madrid.
- PLUSQUELLEC, Y., TOURNEUR, F. & LAFUSTE, J., 1995: Microstructure de Striatopora immota Moore & Jeffords 1945, Espèce-type de Parastriatoporella Tchudinova 1959 (Tabulata, Pennsylvanien).
 N. Jb. Geol. Paläont. Mh., 1995 (4): 193–204, Stuttgart.
- ROEMER, F., 1883: Lethaea geognostica, Theil 1 : Lethaea palaeozoica (Coelenterata). p. 324–543, Stuttgart (Schweizerbart).
- SAMTLEBEN, C., MUNNECKE, A., BICKERT, T. & PÄTZOLD, J., 1996: The Silurian of Gotland (Sweden): facies interpretation based on stable isotopes in brachiopod shells. – Geologische Rundschau, 85: 278–292, Heidelberg.
- SCHLUETER, C., 1889: Anthozoen des rheinischen Mittel-Devon. Abhandlungen zur geologischen Specialkarte von Preussen und den Thüringischen Staaten, VIII/4: 1–207, Berlin.

- SCHOUPPÉ, A.V. & OEKENTORP, K., 1974: Morphogenese und Bau der Tabulata. Palaeontographica A, **145**: 79–194, Stuttgart.
- SOKOLOV, B.S., 1962: Podclass Tabulata. In: ORLOV, Ju, A, (Ed.): Osnovy Paleontologii. 192–265, Moskva (Izdatelstvo Akaddemii Hauk SSSR).
- SOKOLOV, B.S., 1955: Tabuljaty paleozoya evropejskoy chasti SSSR, Vvedenie: Obshchie voprosy sistematiki i istorii razvitija tabuljat. VNIGRI **85**. 527 p., Leningrad Moskva (Gostoptekhizdat).
- STASINSKA, A., 1967: Tabulata from Norway, Sweden and from the erratic boulders of Poland. Palaeontologica Polonica, **18**: 1–112, Warszawa.
- STEL, J.H., 1978: Studies on the paleobiology of favositids. Thesis of the Rijksuniverity of Groningen. 247 p., Groningen.
- SWANN, D.H., 1947: The Favosites alpenensis lineage in the Middle Devonian Traverse Group of Michigan. – Contributions from the Museum of Paleontology, University of Michigan, (VI) 9: 235–317, Ann Arbor.
- TOURNEUR, F., 1986: Microstructure des genres *Thamnopora* Steininger, 1831 et *Lecomptopora* nov. gen., Tabulés branchus du Dévonien moyen. C. R. Acad. Sc. Paris, **303**, II, 13: 1255–1258, Paris.
- WERNER, C., 1936: Synonymy of the mid-devonian tabulate corals of the falls of Ohio. Washington university studies - New Ser. – Sciences and Technology, 9, Contribution in Geology, 88: 53–64, St. Louis, Missouri.
- YANET, F.E., 1970: Nekotorye vetvistye tabuljaty iz Siluryskikh otlojeny vostotchnogo sklona Urala. – In: Astrova, G.G. & TCHUDINOVA, I.I. (Eds.): Novye vidy Paleozoiskikh mchanok i korallov. – 87–96, Izdatelstvo "Nauka", Moskva.

Appendix

Localities: LUNDSKLINT.1. Gotland, Sweden. 2000m WNW of Lummelunda church, topographical map sheet 7J Farösund SV.NV (indicated as Lunds Klint in Edition 2, April 1973). Geological map sheet Aa 183 Visby och Lummelunda. Cliff section 500m north of Lusklint.1 (JEPPSSON, 1983). When walking along the beach towards the North from Lusklint.1, Lunds Klint.1 comprise the third protruding reef and section immediately south of it.

IREVIKEN.1. Gotland, Sweden. See description of the locality in LAUFELD (1974).

Plate 1

Pachypora lamellicornis

- Fig. 1: Calices with septal spines (top) and operculum (bottom). NRM-PZ Cn. 600; x 10.
- Fig. 2: Alveolitid calices. LPB 12 205, Lundsklint 151; x 10.
- Fig. 3: Microstructure of the peripheral zone. Open arrow for median lamina. Note the great thickness of the inner layer of microlamellar sclerenchyma on the peripheral side (top) of the corallite. LPB 12 207, Lundsklint 151, LFP thin section B 46 967, crossed nicols; x 250.
- Fig. 4: Detail of the microlamellar sclerenchyma (same location as Fig. 3); x 480.

82

