

New data on *Angustiphyllum* Altevogt, 1965, an automobile free-living rugose coral from the Eifelian of the Western Armorican Massif (France)

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ABSTRACT. The genus *Angustiphyllum* is recorded for the first time in the Armorican Massif (Rade de Brest) and two new species are erected: *A. stylophorum* and *A. vidalae*. The well preserved material shows the indisputable presence of costae on the exterior side of the corallum, which, besides the wedge-like morphology of the corallum, constitutes the main diagnostic feature of the genus. *Angustiphyllum* seems to be a good index for the Upper Eifelian of the Ibero-Armorican Domain.

KEYWORDS: Hadrophyllidae, new species, Rade de Brest, Upper Eifelian, Ibero-armorican Domain.

1. Introduction

The discovery by one of us (P.-A. J.) of numerous, well preserved specimens of *Angustiphyllum* at Saint-Fiacre in the Saint-Fiacre Formation, Rade de Brest, Western Brittany, allows the description of two new species and the presentation of new data on the structure and the morphology of the genus.

The genus *Angustiphyllum* was erected by Altevogt (1965) for wedge-like or cuneiform (sphenoid sensu Hill 1981)

solitary corals from the Eifelian of the Cantabrian Zone (North Spain). Later, Soto (1986) working on new material from the same area suggested that the axial crest was “formed by synapticalae arranged perpendicularly to the cardinal-counter plane” and described the fibrolamellar microstructure of the septa. Lastly, Plusquellec (2006) noticed the presence of costae on the proximal side of the coral and, taking into account the septal pattern, indicated affinities, not with *Combophyllum*, but with *Hadrophyllum*.

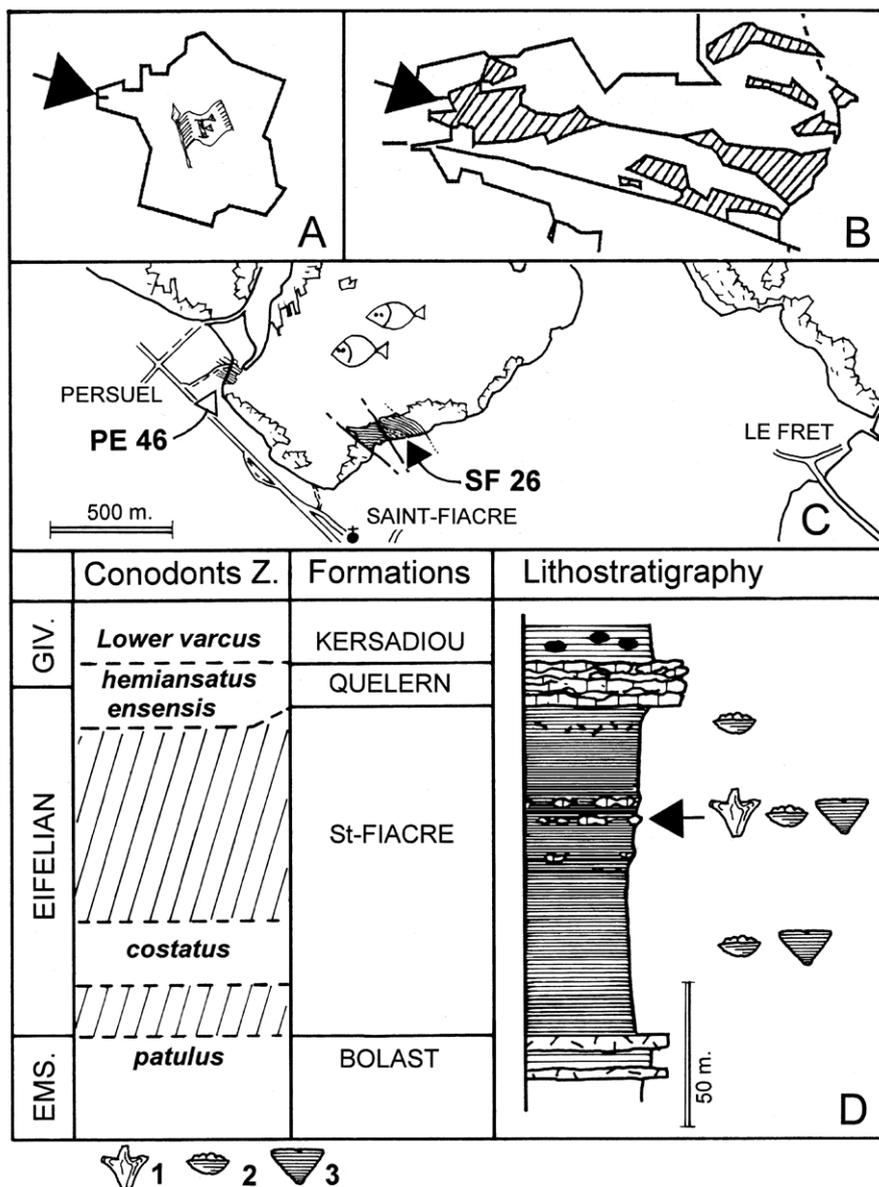


Figure 1. Saint-Fiacre, type locality of the Saint-Fiacre Formation, geographic and stratigraphic data. A-B: Location of the Palaeozoic outcrops. C: The Saint-Fiacre area with the location of the Saint-Fiacre Formation. D: The *Angustiphyllum*-bearing level in its stratigraphical context. 1: *Angustiphyllum*, 2: “*Convexocylus*”, 3: *Calceola*.

2. Lithostratigraphic, biostratigraphic and geographic data

In the Western part of the Massif Armorica the Devonian of the Châteaulin synclinorium is well exposed in the sea cliffs and on sea strands of the Rade de Brest along the southern coasts of the Plougastel Peninsula, the northern coasts of the Crozon Peninsula and on both sides of the Le Faou River.

The Palaeozoic of this area belongs to the Central-North Armorican Domain, and the Upper Emsian-Famennian time interval was carefully studied and mapped by Morzadec (1983). He recognized above the Reun ar C'hrank Formation a set of 13 lithostratigraphic units constituting the Troaon Group. Within this Group the Saint-Fiacre Formation represents the main part of the Eifelian (Fig. 1).

Outcrops of the Saint-Fiacre Formation are recorded in numerous sections along the sea side and in some places in the country in the western part of the Châteaulin synclinorium, and the level is known for yielding *Calceola sandalina* since the first report (Collin 1929). The Saint-Fiacre Formation chiefly consists of brown to dark shales with some levels of calcareous concretions and/or nodular limestones. A sedimentological/sequential study of the Lochkovian to Famennian formations of the Rade de Brest (Guillocheau 1991) shows that the maximum flooding surface occurs in the Eifelian during the deposition of the Saint-Fiacre Formation. The environment varies from lower offshore to distal upper offshore.

Two sections are of special interest. The first one is the type section exposed on the sea strand north of the little village of Saint-Fiacre, district of Crozon (see a detailed map in Morzadec 1983, fig. 14) which has yielded numerous specimens of *Angustiphyllum* and the only ones preserved in calcite. The second one is the section of Goasquellou, district of l'Hopital-Camfrout, in the eastern part of the Rade de Brest (Morzadec 1983, fig. 23), where conodonts of the *costatus costatus* Zone were recorded in the lower part of the formation (Morzadec & Weyant 1982; locality GO10 in Morzadec 1983, fig. 23), giving a "lower" Eifelian age to this level.

In the type locality of the formation, the *Angustiphyllum*-bearing level (locality SF 26 in Morzadec 1983, fig. 14) is situated in the middle part of the formation and thus a little higher in the succession than level GO10, which has provided conodonts of the *costatus costatus* Zone (Fig. 1). Unfortunately the conodonts provided by the calcareous lenses in locality SF26 are without precise biostratigraphic significance and the *partitus*, *australis* and *kockelianus* Zones are not recorded within the Saint-Fiacre Formation.

Nevertheless, the presence in the middle part of the formation (GO12, SF25-26) of *Asteropyge cantarmorica* (Morzadec and Arbizu, 1978, formerly described as *Kayserops? cantarmorica* in the Saint-Fiacre Formation and in the Huer gas Formation, Cantabrian Mountains) and of *Subanarcestes macrocephalus* Schindewolf, 1933, which is characteristic of the Upper Eifelian in Morocco (Ebbighausen et al., 2011) allow, according to Morzadec (pers. comm.), assignment of the middle and upper part of the Saint-Fiacre Formation to the Upper Eifelian, the Eifelian/Givetian boundary being placed within the overlying Quatern Formation (*ensensis-hemiansatus* Zone).

2.1. Additional data on the coral macrofauna

At Saint-Fiacre, another species of Hadrophyllidae has been collected in the formation, probably a new genus showing affinities with *Crassicyclus* Soto, 1978, *Microcyclus* Meeke & Worthen, 1868 and "new genus P" Plusquellec, 2006, but having a very well marked convex proximal side and in some cases a problematic scar at its apex. It is provisionally called *Convexocyclus* nom. nud.; the species is new. In addition, *Calceola sandalina* occurs in at least two levels of the formation at Saint-Fiacre, in its lower part in the yellow facies and in its middle part in the *Angustiphyllum* beds (Fig. 1).

Some tabulate corals are recorded in the Saint-Fiacre Formation, such as *Granulidictyum* e.g. *granuliferum* (Schlüter, 1889) in the middle part of the formation, in the section of Goasquellou (locality GO12 in Morzadec 1983) and

Kerforneidictyum kerfornei (Collin, 1912) in its upper part (in association with *Calceola sandalina* and *Convexocyclus*) on the strand of Goasquellou (locality GO27) and in the cliff SW of Squiffiec, district of Plougastel-Daoulas (locality SQ12 in Morzadec 1983, fig. 17).

Beside the corals it is interesting to note that the oldest tetrameral graptolites of *Ancyrocrinus*, *A. crozonensis* Le Menn & Jaouen, 2003 are described at Saint-Fiacre from the *Angustiphyllum*-bearing level and that pelagic elements, such as dactyloconarids, goniatites and orthoconic nautiloids, are abundant.

3. Systematic palaeontology

The material studied in this paper is housed at the Université de Bretagne Occidentale, Brest (France), Laboratoire de Paléontologie, catalogue number LPB 15 347-15 406 (Armorican material) and LPB 15 407-150413 (plastercasts from Cantabrian material). In addition, some specimens belonging to the Geologisch-Paläontologischen Institut und Museum der Universität Münster are figured (catalogue number GIM B2).

Subclass Rugosa Milne-Edwards & Haime, 1850

Order Stauriida Verill, 1865

Family Hadrophyllidae Nicholson, 1889

Subfamily Hadrophyllinae Nicholson, 1889 emend Plusquellec, 2006

Genus *Angustiphyllum* Altevogt, 1965

Type species. Angustiphyllum cuneiforme Altevogt, 1965

Comments on the diagnosis. Taking into account the succinct diagnosis of Altevogt (1965), the main features of the genus are as follows: small wedge-like solitary coral with ellipsoidal transverse section, only order I septa (= major septa) meeting along axial plane of wedge, tiny sparse tabulae, dissepiments lacking. Hill (1981) followed Altevogt but indicated "no epitheca preserved", "minor septa stunted to ?absent", "no coarse septal trabeculae observed". Soto (1986) gave nearly the same diagnosis but he added some interesting data in his description on the subject of costation "murallas..., las cuales presentan una costación grosera exértil bastante marcada".

The well preserved specimens collected in the type locality of the Saint-Fiacre Formation show that one of the main diagnostic features of the genus has either not been seen by the previous authors, or not well understood. The septal apparatus clearly shows extensions of the septa beyond the wall: the costae. Thus the radial septal structures are costosepta and the "lack of preservation" of the so-called epitheca is not due to abrasion, weathering or corrosion, but this morphological feature is basically lacking. Moreover, the presence of minor septal structures is indisputable and they are often mainly formed by their costal part. In addition, and as stated by Soto (1986), the microstructure of the septal apparatus is fibrolamellar, or mainly of this type.

It is thus necessary to add these new data in the diagnosis of the genus.

Angustiphyllum stylophorum n. sp.

(Figs 2-10; Plate 1, figs A-M)

2011 *Angustiphyllum* n. sp. 1. Plusquellec et al., p. 128, fig. 1-7.

Derivation of name. From stylus, to indicate the presence of a columella-like structure.

Holotype. Specimen LPB 15 347

Type locality and horizon. Saint-Fiacre, district of Crozon, Finistère (France), Saint-Fiacre Formation, Upper Eifelian.

Material. About 25 specimens with calcitic skeleton and 10 as natural casts; 5 thin sections, 4 acetate peels. All the specimens with their skeleton preserved come from the type locality (LPB

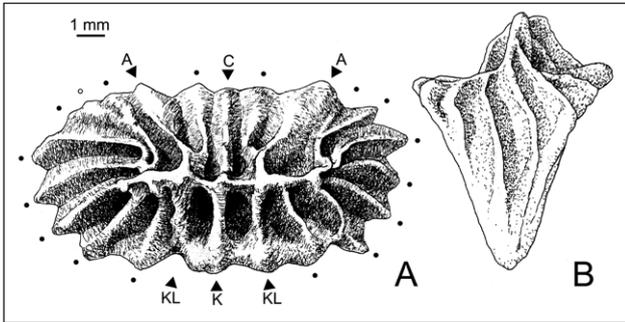


Figure 2. *Angustiphyllum stylophorum*, LPB 15 347, holotype. A: Calicinal view. B: Side view of narrow side of wedge, cardinal septum on left side. Black triangles indicates protosepta (C= cardinal [always in "North" position in calicinal view or transverse sections], K= counter, KL= counter-lateral); black circles and/or solid lines indicate major costo-septa; open circles and/or dotted lines indicate minor costo-septa; hatched lines show fossulae; broken line shows the interseptal crest (the same symbols apply for the following figures).

15 347-15 348, LPB 15 351-15 370, LPB 15 395-15 396); those in casts from 1) Le Caro, along the road between the harbour and Lannéguel, district of Plougastel-Daoulas, Finistère (LPB 15 397-15 401), 2) northern side of Le Caro cove (LPB 15 402), 3) unnamed locality along the "voie express", near Le Faou, Finistère (LPB 15 403-15 406).

Diagnosis. Large species of *Angustiphyllum* with a flat prominent columella-like structure rising in the axial part of the transversal crest and a strongly convex calicinal outline on broad side of wedge. Sides of the corallum flat to concave, commonly with a wide-mouthed outline seen from narrow side of wedge. Apical angle up to 60°-70° in large specimens. Maximum corallite diameter mainly between 6.5-14 mm and generally situated below half height. Usual number of major septa about 17-24; number of costae generally less than twice the number of septa.

Description. Form of corallum. The corallum is wedge shaped, and thus, two different outlines appear in lateral view of the exterior side. Normal to the plane of flattening (broad side of wedge) the outline shows a strongly curved calicinal margin; parallel to this

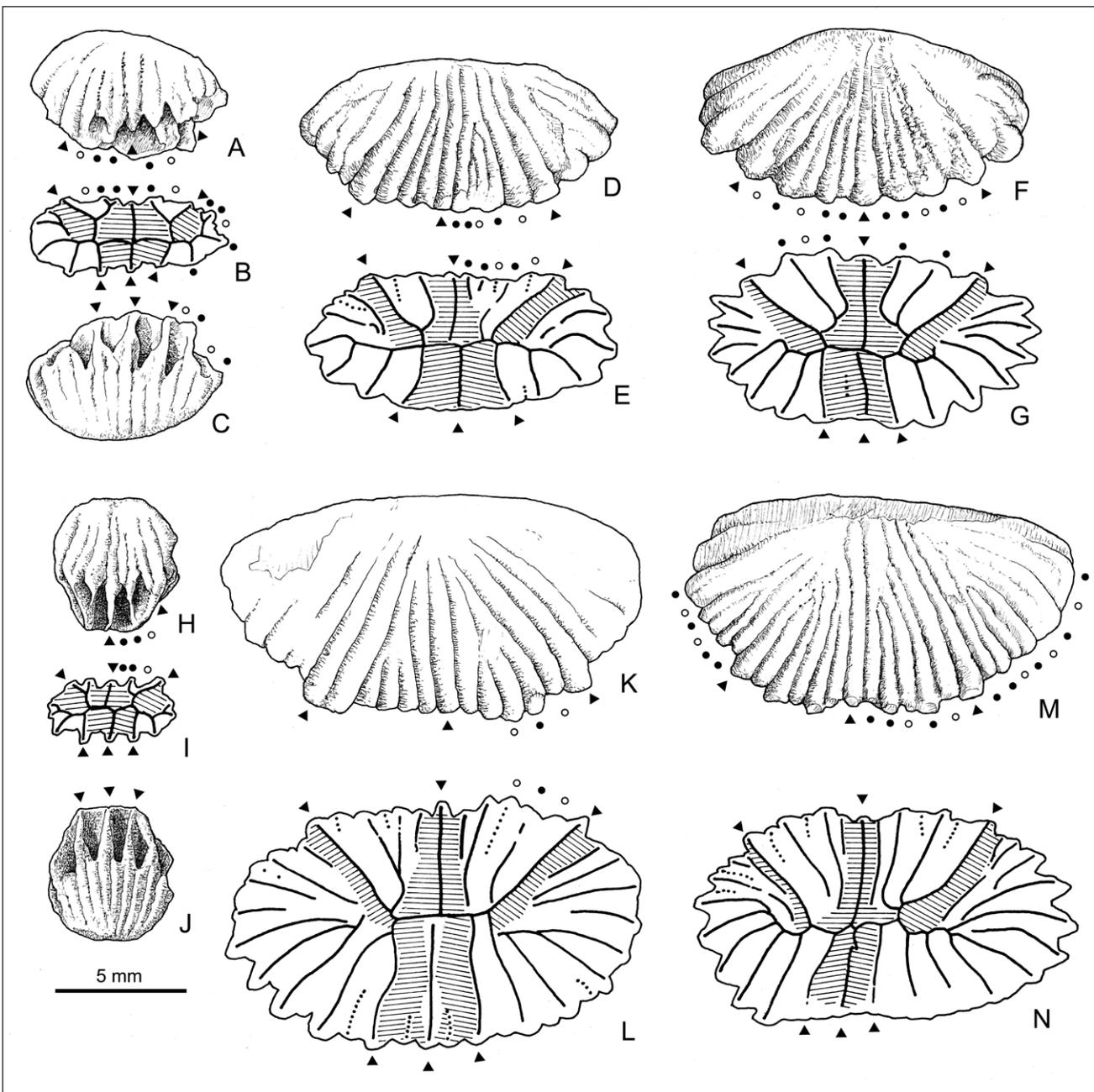


Figure 3. *Angustiphyllum stylophorum*, morphology with its interpretation. Note: for large specimens the columella is not visible on exterior views because the views are not normal to the axial plane of the corallum but to the plane of the broad side of wedge. A-C: LPB 15 368. D-E: LPB 15 361. F-G: LPB 15 360. H-J: LPB 15 348. K-L: LPB 15 358. M-N: LPB 15 355.

plane (narrow side of wedge) the sides of the corallum are flat or gently concave, and commonly in large specimens, the outline of the wedge is wide-mouthed. The maximum corallum diameter is generally situated below one-half of its height (see Table 1, $h_3/h_4 \leq 1$). In calcicular view, the outline is ellipsoidal, serrated, the long axis normal to the counter/cardinal plane.

External morphology (Figs 2-3). This exterior shows costae corresponding to major and minor septa. They are wide, smooth and separated by a narrow intercostal furrow, in some cases bearing a line of small pits. Major and minor costae generally have the same morphology; nevertheless, in some specimens the minor costae are less cambered and wider than the major ones. In young specimens the minor costae are shorter than the major ones and their distal ends are indented. In addition, the cardinal costa may be lower than the metacostae. On the counter side the costae are regularly arranged and the protocostae (K and KL) cannot be morphologically distinguished from the metacostae. On the other hand, on the cardinal side, patterns of splitting or insertion of costae are exposed in some cases, especially in large specimens. They occur on the counter side of the alar costae and on both sides of the cardinal one; these patterns are rather irregular. Following the Vollbrecht and/or the Weyer model of appearance of septa, with which we agree (Plusquellec & Semenoff-Tian-Chansky 1972; Hill 1981) it is assumed - in some cases despite appearances - that the last costoseptum arising on the counter side of each alar septum and on both sides of the cardinal one is necessarily a major costoseptum. However, whatever the model of septal insertion, the total number of costae is the same (see chapter measurements).

Calicinal morphology. The calice margin is slightly concave at the short axis of the wedge (not taking into account the columella-like structure) and convex at its long axis. The major septa exhibit a well marked bilateral symmetry and a clear pinnate pattern. The cardinal septum, opposite to the counter septum, is in middle of broad side of the wedge. The proximal parts of the six protosepta remain attached during all stages of development (Fig. 3 B young specimen and Fig. 3 L adult specimen) and thus the fossulae are closed. The cardinal fossula, with its low cardinal septum, is inverted T-shaped in adult specimens; the alar fossulae exhibit a rhopaloid outline; the counter fossula is more or less rectangular and not differentiated from adjacent interseptal loculi. The presence of retrocontrating major septa is rather usual and gives rise to inconspicuous fossuloidae described for the first time in *Hadrophyllum orbigny* Milne-Edwards & Haime, 1850 by Plusquellec (2006, fig. 9). The proximal part of the protosepta, and generally the one of the two first metasepta of the counter-lateral/alar quadrants, meet at long axial plane of wedge to form a more or less straight transverse crest. This pattern, diagnostic of *Angustiphyllum*, is in fact very similar to the one shown by the central area of some specimens of *H. orbigny* figured by Plusquellec (2006, fig. 7C-D). A prominent flat columella-like structure showing, when not worn, a protuberance at each extremity, rises from the axial part of the transverse crest of *A. stylophorum*. Remark that, following Milne-Edwards & Haime 1848, the true columella is not of septal origin, the reason why the axial boss is here called columella-like structure. The axis of the corallum (= meeting point of protosepta) is slightly eccentric, invariably towards the counter side. The metasepta are not numerous, especially in the alar/cardinal "quadrants"; see for example the holotype with only one metaseptum in this area, see also the septal formulae of other specimens (Table 1). It should be noted that the septal part (septum sensu stricto) corresponding to the most recent radial structure may be lacking in the calice while its costal part is already exposed on the exterior side. This pattern also has been mentioned in *H. orbigny* (see Plusquellec 2006, comment of fig. 10). In at least one specimen, the two youngest metasepta in the cardinal fossula show an anomalous contratingent pattern; the adaxial ends of these septa are attached to the protoseptum. The margin of the major septa is generally sharp but in some cases the counter and counter-lateral protosepta show a slightly spatulate morphology with a depressed axis (Plate 1, fig. E). This feature is reminiscent of diplosepta (Weyer 1997). The minor septa are generally not exposed in the calice, but rarely some of them are quite obvious. In specimen LPB 15 353, two narrow ridges bounding the cardinal fossula and showing their ends curved towards the protoseptum are interpreted as minor septa taking into account the unusual morphology of the exterior side of this area (Plate 1, fig. G).

Specimen	Septal formula	Nbr of major septa	Total nbr of costae-septa	∅L	∅l	Apical angle (d°)	h1	h2	h3	h4	h3/h4	h4/∅L	h3/h2
LPB 15 347	1 1 7 7	22	39	12,8	6,5	51	7,6	9,3	5,2	4,1	1,27	0,32	0,56
LPB 15 348	1 1 3 3	14	23	4,9	2,6	35	3,4	5,4	2,7	2,7	1,00	0,55	0,50
LPB 15 353	1 1 4 5	17	36	9,2	4,3	56	4,8	6,2	2,9	3,3	0,88	0,36	0,47
LPB 15 354	3 2 6 7	24	41	13,2	9,2	67	7,0	7,6	3,7	3,9	0,95	0,30	0,49
LPB 15 355	3 3 8 10	30	52	14,7	8,4	65	6,5						
LPB 15 356	3 3 7 7	26	45	16,7	12,2	72	8,0	9,3	4,2	5,1	0,82	0,31	0,45
LPB 15 357	2 2 7 7	24	42	14,8	10,0	81	6,5	7,6	3,0	4,6	0,65	0,31	0,39
LPB 15 358	3 3 8 8	28	48	15,5	9,5	67	7,6	8,8	3,2	5,6	0,57	0,36	0,36
LPB 15 359	2 2 7 7	24	42	11,7	8,0	70	6,3	6,9	2,5	4,4	0,57	0,38	0,36
LPB 15 360	2 2 6 6	22	44	12,3	6,6	62	6,0	6,8	3,3	3,5	0,94	0,28	0,49
LPB 15 361	1 3 5 5	20	36	11,7	5,3	55	5,7	6,7	3,1	3,6	0,86	0,31	0,46
LPB 15 362	2 1 6 6	21	38	13,8	8,0	57	7,6	6,7	4,1	2,6	1,58	0,19	0,61
LPB 15 363				15,9	10,2	67	7,9	9,3	3,5	5,8	0,60	0,36	0,38
LPB 15 367	1 1 5 5	18	34	7,1	2,9	37	4,6	5,6	2,9	2,7	1,07	0,38	0,52
LPB 15 368	2 1 4 4	17	27	7,6	2,8	32	4,0	5,0	2,3	2,7	0,85	0,36	0,46
LPB 15 369	1 1 2 2	12	18	4,3	1,6	35	2,2	3,6	2,2	1,4	1,57	0,33	0,61
LPB 15 370	1 1 1 1	10	16	3,4	1,5	25	2,1	2,9	1,9	1,0	1,90	0,29	0,66
Mean		20,6	36,3	11,2	6,4	54,9	5,8	6,7	3,2	3,6	1,01	0,34	0,49
Median		21,5	38,5	12,3	6,6	57,0	6,3	6,8	3,1	3,6	0,91	0,32	0,48
Standard deviation		5,6	10,4	4,3	3,4	16,5	1,9	1,9	0,8	1,4	0,39	0,07	0,09

Table 1. Biometric data for *Angustiphyllum stylophorum*.

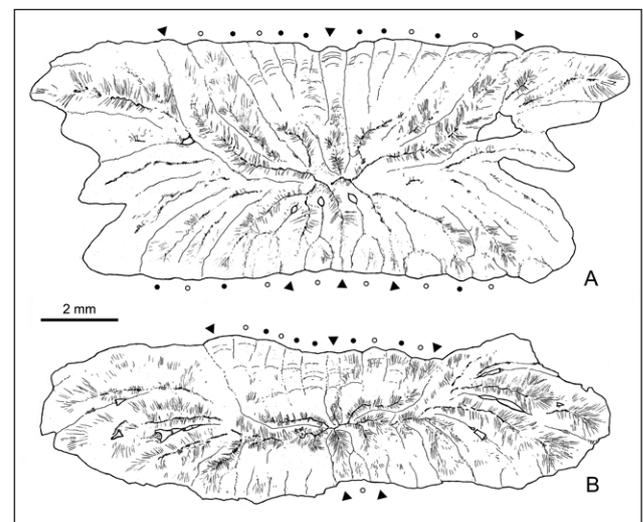


Figure 4. *Angustiphyllum stylophorum*, transverse sections of LPB 15 352, showing the structure and microstructure of the corallum. A: Rather distal section, note the small interseptal loculi between K and KL. B: More proximal section, note the lack of median line in the alar/cardinal quadrant, the interseptal loculi and tabellae at extremities of wedge.

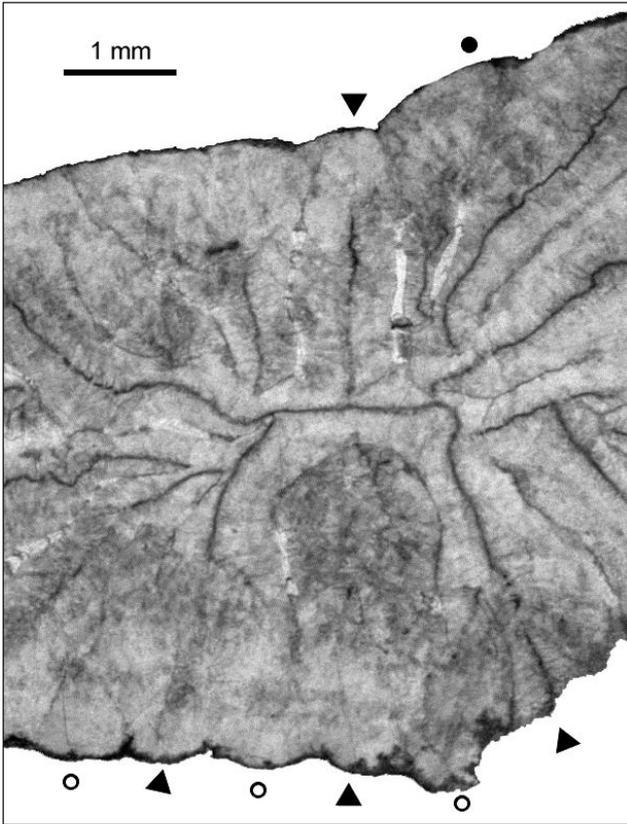


Figure 5. *Angustiphyllum stylophorum*, transverse sections in LPB 15 395, showing the development of interseptal loculi and tabellae.

Internal structure. Transverse sections have been made in four specimens and show more or less the same features. The costo-septa are almost completely contiguous, especially in the medio distal part of the corallum. However, in the proximal part of the corallum narrow interseptal loculi develop mainly in the counter-lateral/alar quadrants (Figs 4B and 5). They show sections of tabulae, or more likely tabellae, probably interstitial tabellae sensu Poty (2002); unfortunately vertical sections of these structures are not available. The area between the peripheral ends of the interseptal loculi and the costal furrows corresponds to the wall: it is of the septothecal type. In the central area of the proximal and medio-distal sections made in specimen LPB 15 352 (Fig. 4A) the protosepta and the first inserted metasepta exhibit an obvious median dark line and a contratingent pattern. The cardinal and the counter septa are not exactly opposite. In the alar/cardinal quadrants of the proximal transverse section the median line of the metasepta does not appear, and only the slightly divergence of the fibers and the concentric growth lines allow their identification (Fig. 4B). In the counter-lateral/alar “quadrants” the median line of the metasepta is better exposed

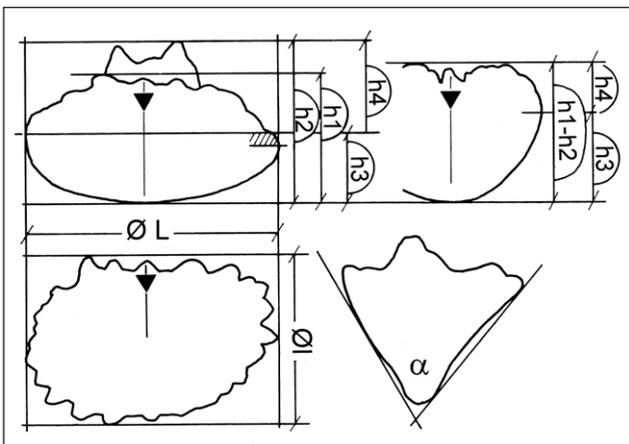


Figure 6. *Angustiphyllum*. Method of measurements. In specimens devoid of columella (*A. vidalae*, *A. cuneiforme*) h1 and h2 are amalgamated.

and they appear contratingent or contraclined. In the alar/cardinal “quadrants” of the distal transverse section it is to be noted 1) that the dark line of the first pair of major metasepta is well developed and that they are inserted by splitting of the median line of the protoseptum and 2) that the first pair of minor septa seems to be inserted not by splitting of the median line, but by appearing in fact in the fork made by the two major septa like an interpolated sheet. In the two sections, the minor costo-septa are longer in the alar/cardinal quadrants than in the counter-lateral/alar ones, and they are difficult to recognize in the extremities of wedge. In the counter/counter-lateral and the “older” part of the counter/alar quadrants the minor structures are very short and probably mainly represented by their costal part. The features described in LPB 15 352 can be recognized in the transverse sections of other specimens. The transverse sections as well as the longitudinal one do not show any structures that could be called synapticulae. In our opinion, their presence in *Angustiphyllum* as stated by Soto (1986) cannot be supported and is the result of a misinterpretation of the transverse crest.

Microstructure. In the transverse sections of *A. stylophorum* the median dark line of the septa is continuous in the axial part of the corallum, and somewhat discontinuous, even dotted, in its periphery (Fig. 4). On both sides of the midplane of the septum the fibers are slightly outwardly divergent. Thus these features show some similarities with those figured by Plusquellec & Semenoff-Tian-Chansky (1972, fig. 8-10) in *Combophyllum osismorum* where a trabecular microstructure has been recognized. However, in longitudinal sections the fibers appear to be directed at right angles to the growth lamellae and no trabecular pattern is exposed. Thus, the costo-septa belong - mainly at least - to the fibrolamellar type. A transverse section (ultra thin section) in the columella-like structure shows a microlamellar thickening and a granular nature of the median line.

Measurements. Some comments and precise details about the measurements (see Fig. 6) and the caption of Table 1 are given below.

- septal formula: the 6 protosepta are diagrammatically illustrated and the number of major metasepta indicated in each quadrant.
- number of major septa includes the 6 protosepta.
- the total number of costo-septa is counted on the exterior side of the corallum and includes all the costae corresponding to the protosepta, major metasepta and minor septa.
- the maximum diameter of the corallum at long axial plane of wedge is here called ØL, normal to this measurement is the minimum diameter Øl.
- the apical angle (narrow side of wedge) and height of the corallum are taken as shown on Figure 6.
- for each measurement the mean, the median, the standard deviation are given in the table.

In addition to Table 1, some diagrams (Figs 7-8) and box plots (Fig. 9) are provided.

Discussion. Apart from *A. stylophorum* n. sp. only two species of *Angustiphyllum* are described: the type-species *A. cuneiforme*

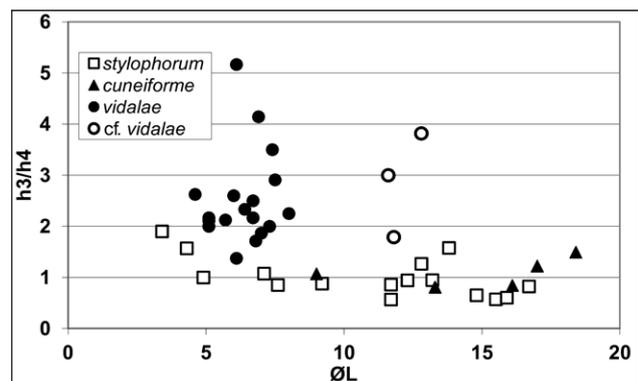


Figure 7. Diagram showing the relationships between the length of the corallum (ØL) and its height and relative curvature, represented by the ratio h3/h4 (see Fig. 6) for 3 species of *Angustiphyllum*.

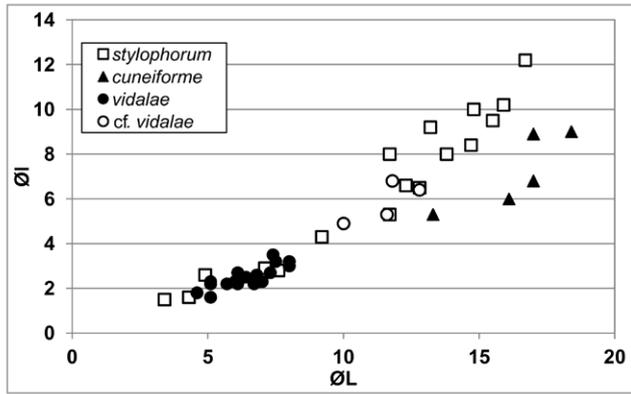


Figure 8. Relationships between length (ØL) and width (ØI) of the corallum for 3 species of *Angustiphyllum*.

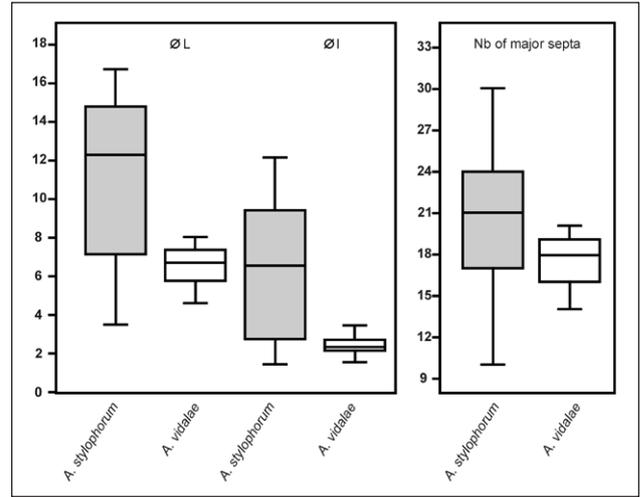


Figure 9. Boxplot representing biometric data for *Angustiphyllum stylophorum* and *Angustiphyllum vidalae*. ØL and ØI respectively length and width of the corallum.

Altevogt and *A. vidalae* n. sp. (this paper).

A. stylophorum clearly differs from these species by the presence of a flat columella-like structure, the usually wide-mouthed outline of the narrow side of wedge and by some biometric data such as the size of the corallum, the apical angle, the number of septa and the structure of the septal formula (see Tables 1-4).

In addition, the transverse crest of *A. cuneiforme* is much straighter than that of *A. stylophorum* (Figs 10A and 11A, D-E) and its wedge is flatter, with a transverse proximal section showing a slight median narrowing.

Our new species differs from *Angustiphyllum?* sp. A Soto, 1986 by its more flattened transverse outline and the shallower intercostal furrows. The interseptal loculi shown by Soto - figura 2A - are in fact opened towards the margin, especially in the counter part of figure, and thus are intercostal furrows.

***Angustiphyllum vidalae* n. sp.**
(Figs 12-13; Plate 1, figs N-W)

2011 *Angustiphyllum* n. sp. 2. Plusquellec et al., p. 128, fig. 8-13.

Derivation of name. The species is named after Dr. Muriel Vidal

(UBO, Brest).

Holotype. Specimen LPB 15 349.

Type locality and horizon. Saint-Fiacre, district of Crozon, Finistère (France), Saint-Fiacre Formation, Upper Eifelian.

Material. 25 specimens with calcitic skeleton from the type locality (LPB 15 349-15 350, LPB 15 371-15 391), of which 2 thin sections, 2 acetate peels.

Diagnosis. Small species of *Angustiphyllum* with flat to gently convex calicinal outline on broad side of wedge. Sides of the corallum flat to slightly convex on the narrow side of wedge. Apical angle mainly circa 35°. Maximum corallite diameter usually between 5.5-7.5 mm and markedly situated above half of its height. Number of major septa about 16-20; number of costae generally less than twice the number of septa.

Description. Form of corallum. On broad side of wedge, the

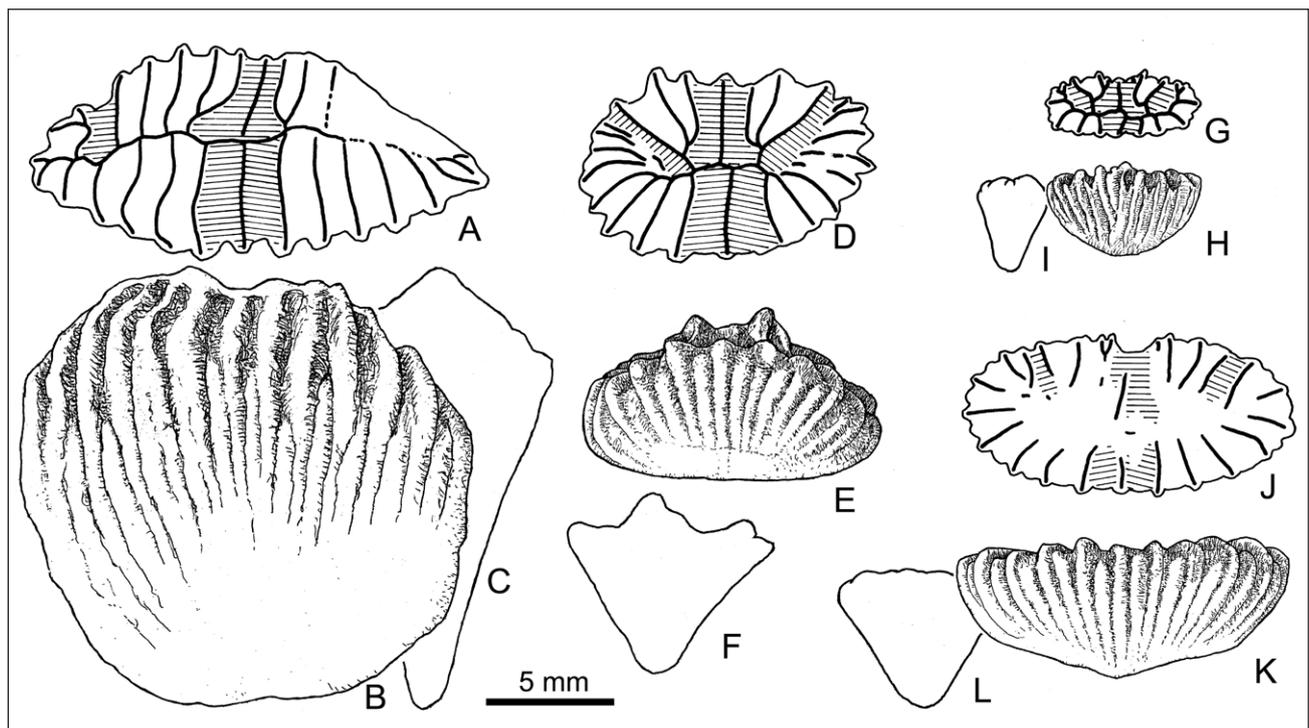


Figure 10. For comparison, the species of *Angustiphyllum* at similar magnification. Calicinal views, exterior (counter side) from broad side of wedge and outline of narrow side of wedge. A-C: *A. cuneiforme*, GIM B2. 21. 45. D-F: *A. stylophorum*, LPB 15 359. G-I: *A. vidalae*, LPB 15 380. J-L: *A. cf. vidalae*, LPB 15 392.

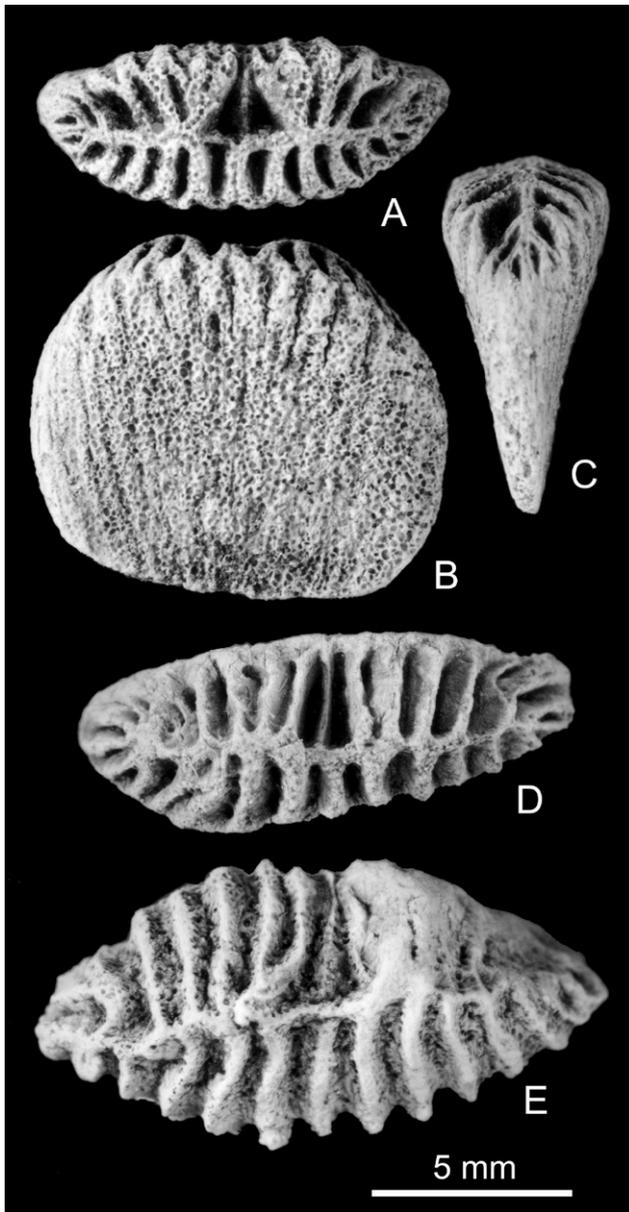


Figure 11. *Angustiphyllum cuneiforme*. A-C, GIM B2. 21. 44. A: Calicinal view. B: Side view of broad side of wedge. C: Side view of narrow side of wedge. D: DPO 11 478, calicinal view. E: GIM B2.21.45, calicinal view.

calicinal part of the outline is flat to gently convex, while its proximal part is regularly rounded (Fig. 12A, C) to wide U-shaped (Fig. 12K). The maximum corallum diameter is clearly situated above one-half height (see Table 2, h3/h4 mainly circa 2.50). On the narrow side of wedge view, the sides of the corallum are flat to slightly convex and the apical angle rather acute. In calicinal view, the broad sides of the wedge appear more flattened than in *A. stylophorum* and thus the calice of *A. vidalae* is proportionally more elongated; the indentations corresponding to the minor costae are well marked but the costae themselves are generally not very obvious.

External morphology. The costae corresponding to both major and minor septa are well marked and particularly well exposed on the broad side of the wedge. The minor costae are generally wider than the major ones and their distal part shows a strong notch (Fig. 12F and Pl. 1, fig. P). In some specimens, a row of small pits emphasizes the intercostal furrows (Fig. 12G).

Calicinal morphology. Roughly speaking, the pattern of proto- and metasepta and of fossulae is very close to that of *A. stylophorum* and, in fact, characterizes the genus *Angustiphyllum*. Nevertheless, the major septa are generally thicker and less numerous in *A. vidalae*. The presence of smooth indentations on the margin of some septa (Pl. 1, fig. T) reflects its underlying structure. This morphology is usual in corals having

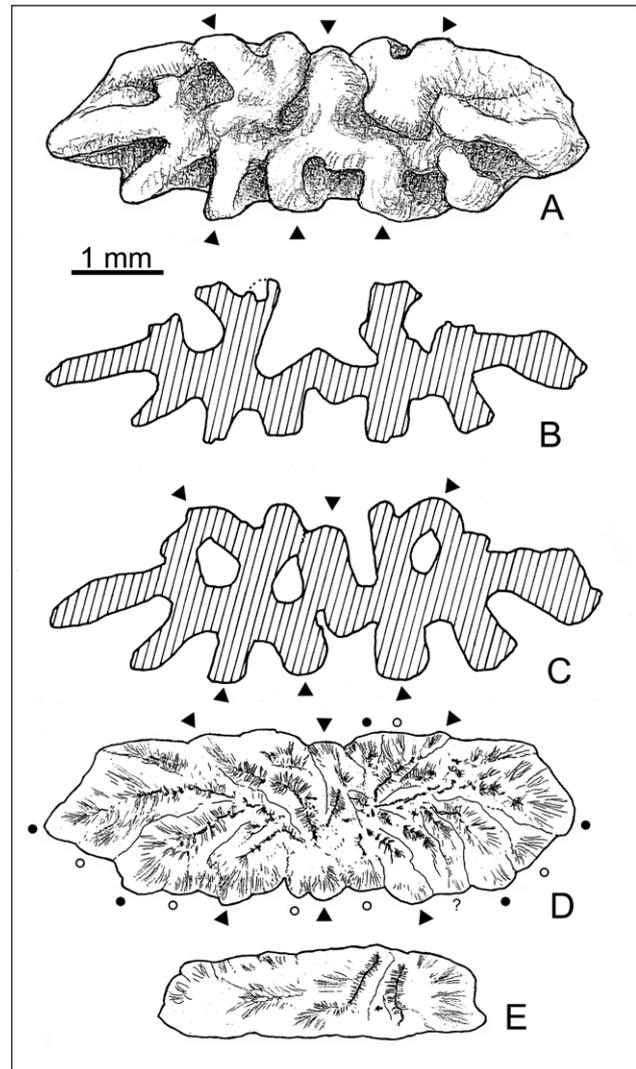


Figure 13. *Angustiphyllum vidalae*, LPB 15 350. Calicinal view of the corallum (A) and serial transverse sections, from distal part of the corallum (B) to proximal (E). B-C: Acetate peels showing the “decorative” outline of the very distal sections, but the microstructure is not visible. D: Note that the costo-septa are contiguous in the whole section; thin section Bb 964. E: See text; thin section Bb 965.

the septa composed of simple trabeculae such as *Combophyllum osismorum* (Plusquellec & Semenov-Tian-Chansky 1972); see below comments about the microstructure.

Internal structure. Two transverse sections have been made from a single specimen. In the proximal section the septa are impossible to identify, most of them being devoid of median line (Fig. 13E); in the distal section the septal units are clearly individualized but their contratingent pattern is less well expressed than in *A. stylophorum* (Fig. 13D). The fibrous microstructure of the septa and costae is indisputable but in some parts of the median plane of septa, the dotted pattern of the “dark” line is reminiscent of trabeculae. Unfortunately no longitudinal section is available.

Measurements. The biometric data are provided in Table 2 (see comments of Table 1 for captions) and diagrams (Figs 7-9).

Discussion. Apart from its small size, *A. vidalae* differs from both *A. cuneiforme* and *A. stylophorum* by its flat calicinal outline on the broad side of the wedge, by the flat to slightly convex outline of its exterior sides on the narrow side of the wedge, and by the distal position of the maximum diameter; from *A. stylophorum* by the lack of columellar structure.

Angustiphyllum cf. vidalae
(Figs 10J-L, 14)

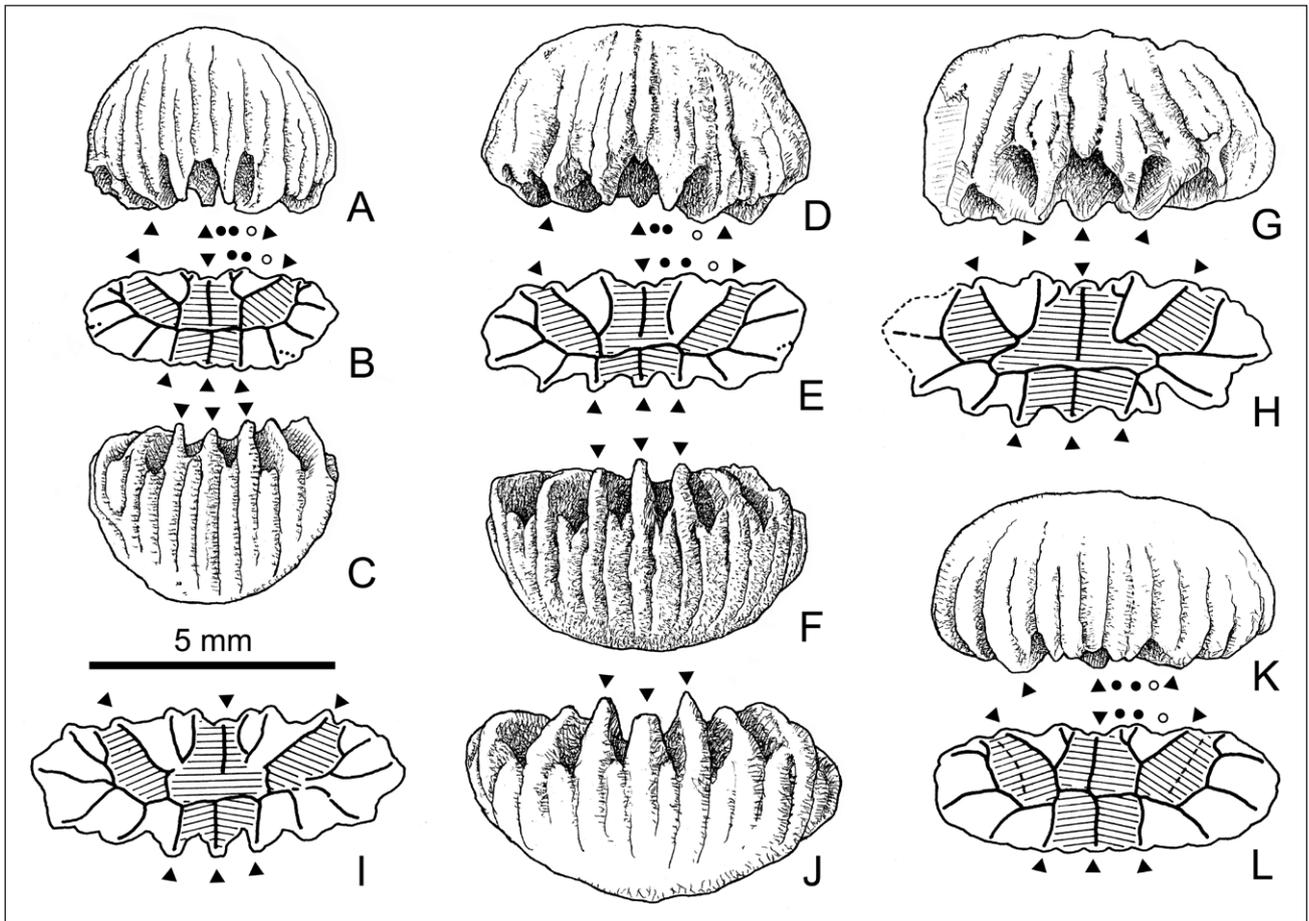


Figure 12. *Angustiphyllum vidalae*, morphology. A-C: LPB 15 388. D-F: LPB 15 349, holotype. G-H: LPB 15 374. I-J: LPB 15 391. K-L: LPB 15 375, note the presence of an interseptal crest in the alar fossulae, described for the first time in *Hadrophyllum orbigny* by Plusquellec (2006).

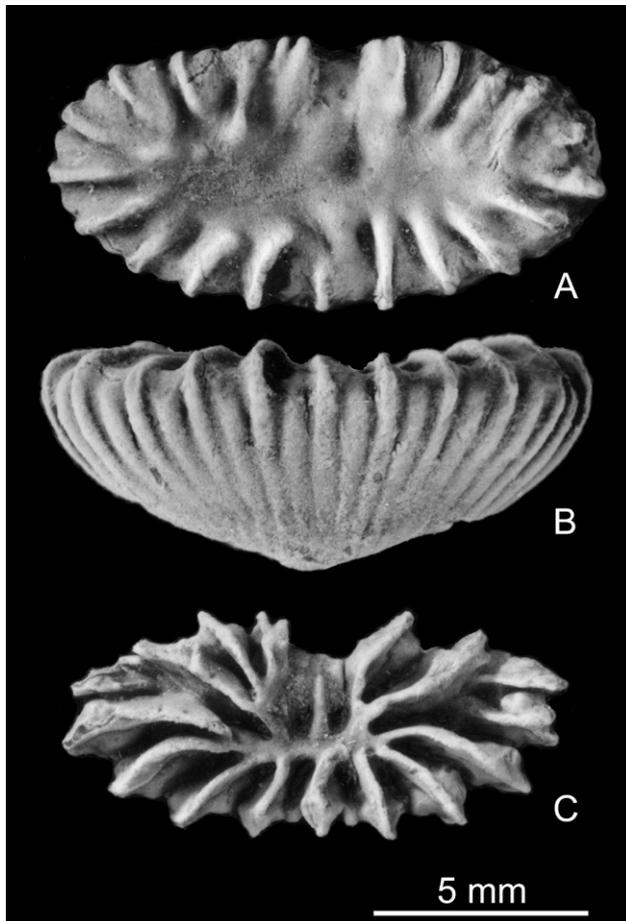


Figure 14. *Angustiphyllum* cf. *vidalae*. A-B, LPB 15 392. A: Calical view. B: Side view of broad side of wedge. C: LPB 15 394, calical view.

Material. 3 specimens with calcitic skeleton from Saint-Fiacre, district of Crozon, Finistère (France), Saint-Fiacre Formation, Upper Eifelian, same level as *A. stylophorum* and *A. vidalae*, LPB 15 392-15 394; 3 specimens in natural cast from 1) Le Caro, along the road between the harbour and Lannéguel, district of Plougastel-Daoulas, Finistère, LPB 15 414-15 415, 2) Persuel, district of Crozon, locality PE 46 in Morzadec 1983, fig. 14, LPB 15 416, Saint-Fiacre Formation, (probably Upper) Eifelian. In the localities of Le Caro and Persuel, *Angustiphyllum* is found together with *Asteropyge cantarmorica* (Morzadec, pers. comm.).

Description. *Form of corallum.* On the broad side of the wedge, the calical outline is flat and that of the proximal part more or less rounded or like a widely opened V (Fig. 14B). The height of the corallum is proportionally small and the ratio between height and maximum diameter is 1:2.2 - 3.2; the maximum diameter of the corallum is situated in its distal part as in *A. vidalae*. On the narrow side of wedge, the sides of the corallum are slightly convex and the apical angle rather significant (65° - 99°), i.e. markedly greater than that of *A. vidalae*. In calical view, the outline shows indentations corresponding to major and minor costae. The major ones exhibit a clear-cut profile, the minor ones are distinctly less marked.

External morphology. The major and minor costae are roughly of the same size in LPB 15 392, 15 393 and LPB 15 414, the minor costae clearly wider and notched in their distal part in LPB 15 594.

Calical morphology. In one of the specimens (LPB 15 394) the pattern of major septa and fossulae is close to that of *A. stylophorum*, in the other specimens the septa seem to be embedded in a kind of calical platform, the pinnate pattern is poorly or not exposed and the fossulae are not closed. The cardinal septum is invariably low as is usual in *A. vidalae*.

Measurements. The specimens are larger than those of *A. vidalae* but close to *A. stylophorum* (see Table 3).

Specimen	Septal formula	Nbr of major septa	Total nbr of costo-septa	∅L	∅I	Apical angle (d°)	h1-h2	h3	h4	h3/h4	h4/∅L	h3/h2
LPB 15 349	$\frac{1}{4} \frac{1}{5}$	17	32	6,4	2,5	35	4,0	2,8	1,2	2,33	0,19	0,70
LPB 15 350	$\frac{1}{3} \frac{1}{3}$	14	26	7,4	3,5	37	4,5	3,5	1,0	3,50	0,14	0,78
LPB 15 371	$\frac{2}{5} \frac{1}{5}$	19	32	6,7	2,2	29	3,5	2,5	1,0	2,50	0,15	0,71
LPB 15 372				8,0	3,0		3,6					
LPB 15 373	$\frac{2}{4} \frac{2}{4}$	16	28	7,3	2,7	39	4,5	3,0	1,5	2,00	0,21	0,67
LPB 15 374	$\frac{2}{4} \frac{2}{4}$	18	30	8,0	3,2	57	3,9	2,7	1,2	2,25	0,15	0,69
LPB 15 375	$\frac{2}{4} \frac{2}{4}$	18	28	6,8	2,6	28	3,8	2,4	1,4	1,71	0,21	0,63
LPB 15 376	$\frac{1}{4} \frac{1}{4}$	16	28	7,0	2,3	31	4,3	2,8	1,5	1,87	0,21	0,65
LPB 15 377	$\frac{2}{4} \frac{2}{4}$	18	28	6,7	2,3	25	3,8	2,6	1,2	2,17	0,18	0,68
LPB 15 379	$\frac{2}{4} \frac{2}{4}$	17	27	5,1	2,3	33	3,6	2,4	1,2	2,00	0,24	0,67
LPB 15 380	$\frac{2}{5} \frac{2}{5}$	20	32	6,1	2,7	40	3,7	3,1	0,6	5,17	0,10	0,84
LPB 15 382	$\frac{2}{4} \frac{2}{4}$	18	32	6,1	2,2	28	3,8	2,2	1,6	1,38	0,26	0,58
LPB 15 384	$\frac{1}{4} \frac{1}{4}$	16	28	4,6	1,8	32	2,9	2,1	0,8	2,63	0,17	0,72
LPB 15 386	$\frac{2}{5} \frac{1}{3}$	15	25	5,1	1,6	39	2,8	1,9	0,9	2,11	0,18	0,68
LPB 15 387	$\frac{2}{5} \frac{2}{5}$	20	32	6,0	2,3	32	3,6	2,6	1,0	2,60	0,17	0,72
LPB 15 388	$\frac{2}{5} \frac{2}{5}$	20	32	5,1	2,2	25	3,8	2,6	1,2	2,17	0,24	0,68
LPB 15 389		17		5,7	2,2	44	2,5	1,7	0,8	2,13	0,14	0,68
LPB 15 390	$\frac{1}{4} \frac{1}{4}$	16	30	6,9	2,3	39	3,6	2,9	0,7	4,14	0,10	0,81
LPB 15 391	$\frac{2}{5} \frac{2}{5}$	20	32	7,5	3,2	45	4,3	3,2	1,1	2,91	0,15	0,74
Mean		17,5	29,5	6,4	2,5	35,4	3,7	2,6	1,1	2,53	0,18	0,70
Median		17,5	30,0	6,7	2,3	34,0	3,8	2,6	1,2	2,21	0,18	0,69
Standard deviation		1,8	2,4	1,0	0,5	8,1	0,5	0,5	0,3	0,92	0,05	0,06

Table 2. Biometric data for *Angustiphyllum vidalae*.

Discussion. The specimens share some morphological, and above all some biometric characteristics with *A. styloporum* but the outline of broad side of wedge and especially the morphology of the calice (which is devoid of columella) show strong affinities with *A. vidalae*.

In our opinion these specimens could be gerontic forms of this species. Moreover, it should be noted that in the Cantabrian Mountains as well as in the Armorican Massif, beside the standard species there are rare specimens showing unusual morphology: *A.?* sp. A Soto, 1986 and *A. cf. vidalae*, this paper.

4. Discussions

4.1. Fossil record

The genus *Angustiphyllum* is recorded for the first time in the Armorican Massif where at least two species lived together in the same environment during Upper Eifelian time.

Owing to the number of specimens collected the representatives of this genus are not scarce and thus could be a good index for the Upper Eifelian and useful for mapping, especially in the Armorican Massif.

Specimen	Septal formula	Nbr of major septa	Total nbr of costo-septa	∅L	∅I	Apical angle (d°)	h1-h2	h3	h4	h3/h4	h4/∅L	h3/h2
LPB 15 392	$\frac{3}{7} \frac{3}{6}$	25	43	12,8	6,4	65	5,3	4,2	1,1	3,82	0,09	0,79
LPB 15 393	$\frac{2}{5} \frac{2}{5}$	20	40	11,8	6,8	77	5,3	3,4	1,9	1,79	0,16	0,64
LPB 15 394	$\frac{3}{5} \frac{1}{5}$	20	35	11,6	5,3	99	3,6	2,7	0,9	3,00	0,08	0,75
LPB 15 414	$\frac{3}{5} \frac{3}{4}$	21		10,0	4,9		4,5					
Mean		21,5	39,5	11,6	5,9	80,3	4,7	3,4	1,3	2,87	0,11	0,73
Median		20,5	40,0	11,7	5,9	77,0	4,9	3,4	1,1	3,00	0,09	0,75
Standard deviation		2,4	4,0	1,2	0,9	17,2	0,8	0,8	0,5	1,02	0,05	0,08

Table 3. Biometric data for *Angustiphyllum cf. vidalae*.

4.2. Palaeobiogeography

The genus *Angustiphyllum* is known in the (Upper) Eifelian of the Cantabrian Mountains and in the western part of the Armorican Massif, the two areas forming the Ibero-Armorican Domain situated on the north-western margin of Gondwana on the shelf of the Rheic Ocean (Fig. 15).

4.3. Mode of life

According to the morphology of the corallum, the genus *Angustiphyllum* shares numerous characteristics with 1) the Emsian Rugosa *Combophyllum* Milne-Edwards & Haime, 1850; 2) the Eocene-Recent Scleractinia *Shenotrochus* Milne-Edwards & Haime, 1848; and 3) despite the lack of costae, the Eocene-Recent *Flabellum* Lesson, 1831; thus its mode of life could be similar.

The presence of costae and consequently the lack of the so-called epitheca indicate that the polyp was fully covered with living tissue. Thus, *Angustiphyllum* belongs to the automobile free living coral group and was probably able to move (lateral migration) on the soft bottom of the Saint-Fiacre sea, or was at least capable of vertical movement to right or exhume itself (Plusquellec et al., 1999).

The presence of *Angustiphyllum* species in the rather deep environment of the Saint-Fiacre Formation (the *Angustiphyllum*-bearing level is mainly in the distal upper offshore) provides interesting data on the bathymetric distribution of the genus. Nevertheless, it would be hazardous to correlate its presence with a given depth. For example, if we refer to extant Scleractinia, the cuneiform *Sphenotrochus andrewianus* Milne-

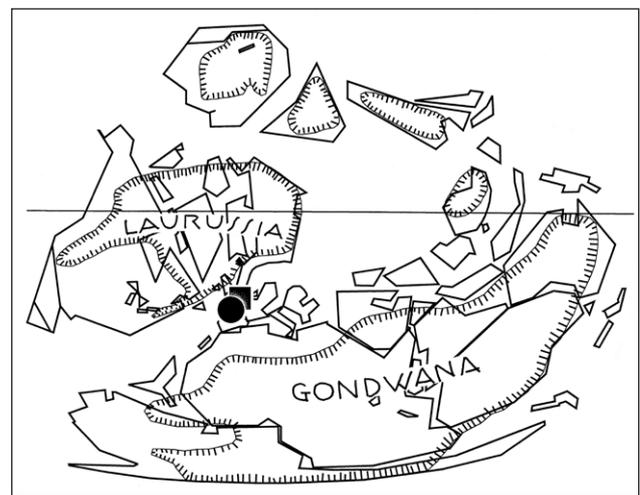


Figure 15. Paleogeographic distribution of *Angustiphyllum*. Black square for *A. styloporum*, *A. vidalae* and *A. cf. vidalae*; black circle for *A. cuneiforme*.

Specimen	Septal formula	Nbr of major septa	∅L	∅l	Apical angle (d°)	h1-h2	h3	h4	h3/h4	h4/∅L	h3/h2
Holotype		27	17,0	8,9		14,0	7,7	6,3	1,22	0,37	0,55
Fig. 11 Altev.			9,0			8,7	4,5	4,2	1,07	0,47	0,52
Fig. 8 Altev.					35						
DPO 11 478	3 3 10 9	31	16,1	6,0	27	14,0	6,4	7,6	0,84	0,47	0,46
DPO 11 479	3 3 13 10	35	17,0	6,8	34	12,0					
GIMB2,21,45	4 8		18,4	9,0	33	18,7	11,2	7,5	1,49	0,41	0,60
GIMB2,21,44	3 3 7 8	26	13,3	5,3	28	11,4	5,1	6,3	0,81	0,47	0,45
Mean		29,8	15,1	7,2	31,4	13,1	7,0	6,4	1,09	0,44	0,51
Median		29,0	16,6	6,8	33,0	13,0	6,4	6,3	1,07	0,47	0,52
Standard deviation		4,1	3,5	1,7	3,6	3,4	2,7	1,4	0,28	0,05	0,06

Table 4. Biometric data for *Angustiphyllum cuneiforme*.

Edwards & Haime, 1850 (which morphology is very similar to that of *Angustiphyllum*) lives between 15 to 105 m depending of the localities (Zibrowius, 1980).

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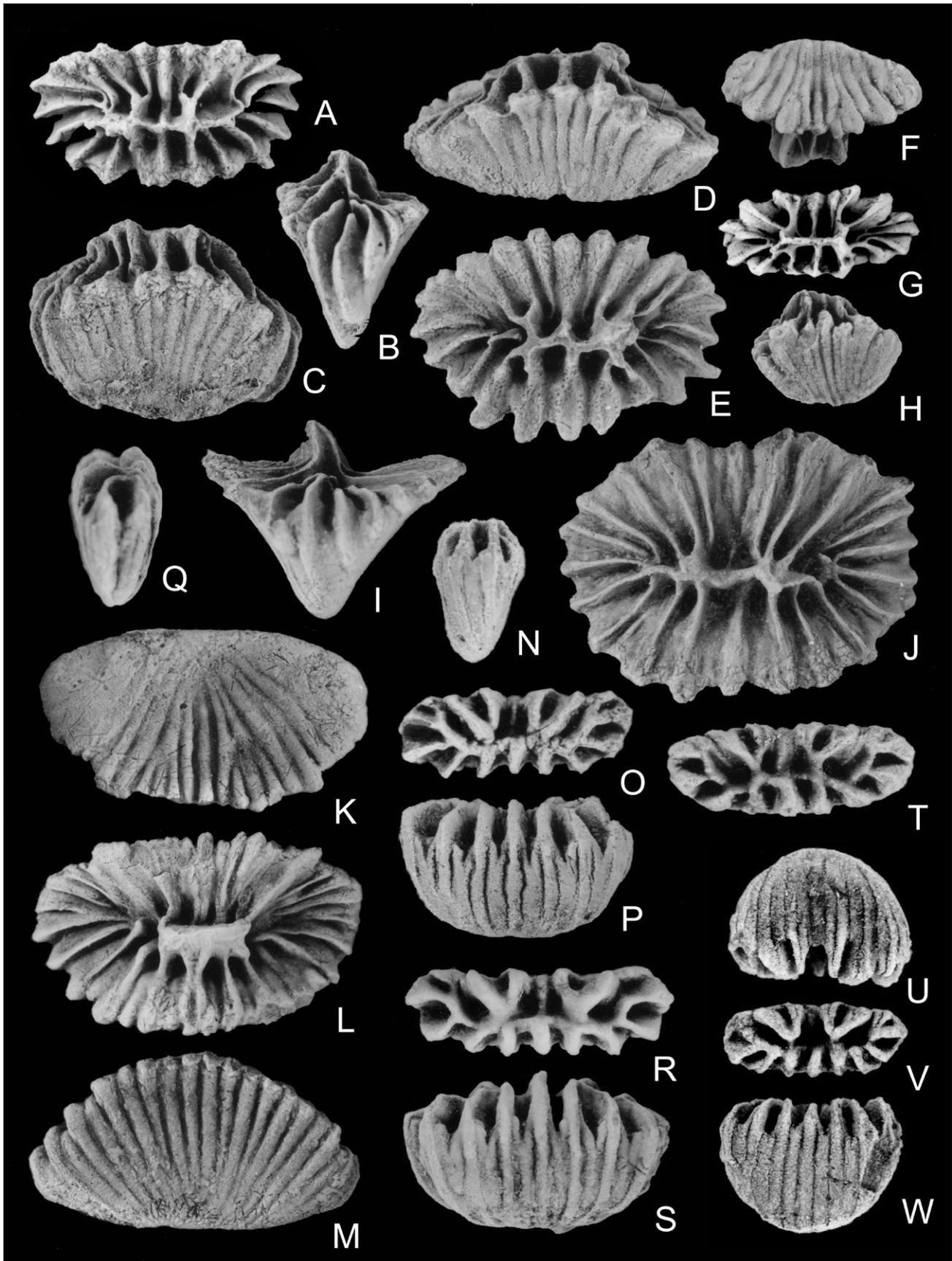


Plate 1. Morphology of *Angustiphyllum stylophorum* (A-M) and *A. vidalae* (N-W). A, G, J, L, O, R, T calicinal views, C, D, F, K, M, P, S, U, W views of broad side of wedge, B, Q, N views of narrow side of wedge. A-C: LPB 15 347, holotype, D-E: LPB 15 357, F-G: 15 353, H: LPB 15 367, I-J: LPB 15 356, K-M: LPB 15 358, N-P: LPB 15 349, holotype, Q-S: LPB 15 376, T: LPB 15 375, U-W: LPB 15 388. Magnification: *A. stylophorum* x4; *A. vidalae* x7.