



Lunar and solar cycles recorded in the skeleton of a Jurassic solitary coral

Bernard LATHUILIÈRE ¹

Abstract: Regular growth increments have been identified in the epitheca of the Bathonian solitary coral *Montlivaltia* LAMOUROUX, 1821. Examination of a large population of specimens from several outcrops across Lorraine (France) shows that these cyclic patterns are recurrent and can be consistently recognized. The dimensional ratios between successive increments suggest that the observed periodicities reflect lunar cycles nested within annual growth rhythms. This interpretation allows for the estimation of coral age and provides a means to document how morphological parameters vary through ontogeny. It therefore offers a valuable alternative to the debated practice of using size as a proxy for age in evolutionary studies. Finally, the regularity of the growth cycles further supports the view that *Montlivaltia* was solitary but probably harbored zooxanthellae.

Keywords:

- Lorraine;
- Jurassic;
- coral;
- palaeoecology;
- sclerochronology;
- astronomical cycles

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Résumé : Cycles lunaires et solaires enregistrés dans le squelette d'un corail solitaire jurassique.- Des incréments de croissance réguliers ont été identifiés dans l'épithèque du corail solitaire bathonien *Montlivaltia* LAMOUROUX, 1821. L'examen d'une large population de spécimens provenant de plusieurs affleurements de Lorraine (France) montre que ces cycles de croissance sont récurrents et facilement reconnaissables. Les rapports dimensionnels entre les incréments successifs montrent que les périodicités observées reflètent des cycles lunaires imbriqués dans des rythmes de croissance annuels. Cette interprétation permet d'estimer l'âge du corail et de documenter la variation des paramètres morphologiques au cours de son ontogenèse. Elle offre ainsi une alternative intéressante à la pratique controversée consistant à utiliser la taille comme indicateur d'âge dans les études évolutives. Enfin, la régularité des cycles de croissance conforte l'hypothèse que *Montlivaltia* abritait probablement des zooxanthelles, en dépit de son caractère solitaire.

Mots-clefs :

- Lorraine ;
- Jurassique ;
- corail ;
- paléocéologie ;
- sclérochronologie ;
- cycles astronomiques

¹ Université de Lorraine, CNRS, lab. GeoRessources, UMR 7359, BP 70239, 54506, Vandoeuvre-lès-Nancy Cedex (France)

bernard.lathuiliere@univ-lorraine.fr





1. Introduction

A large body of literature in palaeoclimatic research has popularized sclerochronology as a powerful tool for reconstructing past climates from coral skeletons (for recent reviews, see HELMLE & DODGE, 2011; PEHARDA *et al.*, 2021). Classical sclerochronological studies generally rely on large, living coral colonies, which allow the reconstruction of long chronological sequences starting from the living surface that anchors the record to the present. Because the coral is still alive, diagenetic alteration of the skeleton has already begun but is minimal, and the geochemical composition is expected to accurately reflect the environmental conditions at the time of skeletal construction (GROTTOLI, 2001). The limited diagenesis and especially the preserved porosity also allows growth banding to be easily detected through radiographic analysis.

In contrast, the present study investigates the growth banding of a solitary Jurassic coral under much less favourable circumstances: its skeleton has been fully transformed from aragonite to calcite, and only the external morphology remains accessible to infer rhythmic growth patterns. Determining the age of such solitary corals opens new perspectives for evolutionary biology and provides additional tools for palaeoecological interpretation.

2. Material and methods

The study of the Bathonian coral fauna from Longuyon (LATHUILLÈRE & MICHEL, 2019; and work in progress) included the re-examination of specimens initially studied by GARDET (1947). These samples, collected from several Bathonian localities in Lorraine and originating from earlier collections, had never been illustrated. They constitute the core of this contribution, and no additional specimens are involved here. As they originated from different localities, they should be considered as a population in the statistical sense but not in the ecological acceptance of the term. Initially attributed to several nominal species (Fig. 1), they are now reassigned to *Montlivaltia caryophyllata* LAMOUREUX, 1821, based on a statistical analysis of specimens from Longuyon.

The specimens studied by GARDET are housed in the ENSG-MAN (École Nationale Supérieure de Géologie-Muséum Aquarium de Nancy) collections under catalogue numbers 2024_18 to 2024_43. Their original situation in the sediment is unknown, but, from a comparable collection in Bouvron (ZANY & LATHUILLÈRE, 2018), it is assumed that they originated from an alternation of marls with beds of argillaceous limestone. The rich macrofauna is detailed and quantified in the cited reference. They were prepared through successive mechanical and chemical treatments under a binocular microscope. Mechanical tools included a pneumatic pen, a Dremel rotary micro-brush, a manual dental file (root canal type), and finally a toothbrush with water. The chemical treatment

involved the application of diluted hydrochloric acid with a fine paintbrush, which helped reduce mechanical impacts on the skeleton and, in favourable cases, softened the matrix between septa. These methods exposed the lower surface of the skeleton in high detail, forming the basis of the present observations, which were conducted using standard optical microscopy.

I undertook a statistical characterization of the obtained set of specimens in order to minimize biological heterogeneity as much as possible. The Bathonian specimen collection was limited to a group of 150 specimens. Among these, three were excluded: one due to rejuvenescence (specimen no. 92), another (no. 90) that had clearly developed from two adjacent planulae, and a third (no. 148) that was too poorly preserved to be described. A fourth specimen (no. MAN 2024 0 44-24) deserves special mention, as it can be attributed to the genus *Kobyphyllia* BARON SZABO, 1997, which may be defined as a *Montlivaltia* with a lamellar columella. This particular specimen was retained within the analysed population.

For the remaining specimens, the large diameter (LD), small diameter (sD), and height (H) were measured for each individual. The number of septa could be determined with good confidence for 79 specimens and only approximated for an additional set of 42 specimens. It became evident that the number of septa - traditionally a key parameter in taxonomic descriptions and species diagnoses - is, in fact, difficult to determine precisely, because the observation of the smallest septa is strongly influenced by the state of preservation and the quality of sample preparation. For instance, a specimen initially estimated to have 92 septa was later corrected to 109 after further preparation.

To evaluate this uncertainty, I estimated the septal number by calculation, using measurements of diameter and septal density (see Appendix). Septal density per 3 mm (ds) was measured in 146 specimens, and trabecular density or number of trabeculae per 2 mm (dt) was reliably measured in 120 specimens. The length of the fossa (Lf), defined according to Figure 2, was confidently measured in 96 specimens.

An estimation of biological age was performed for 133 specimens. Occasionally, a certain ambiguity existed between two consecutive age values (x and $x+1$), and more rarely between x and $x+2$. In such cases, an average value was retained for calculations. Univariate analyses were performed using the maximum available sample size for each parameter, while a more restricted subset of 52 specimens - those with complete data - was used for multivariate analysis. Univariate and multivariate analyses were conducted using PAST version 4.11, and bivariate analyses were carried out with PAST and Microsoft Excel 2013. A data matrix is provided as Appendix in the supplementary material.

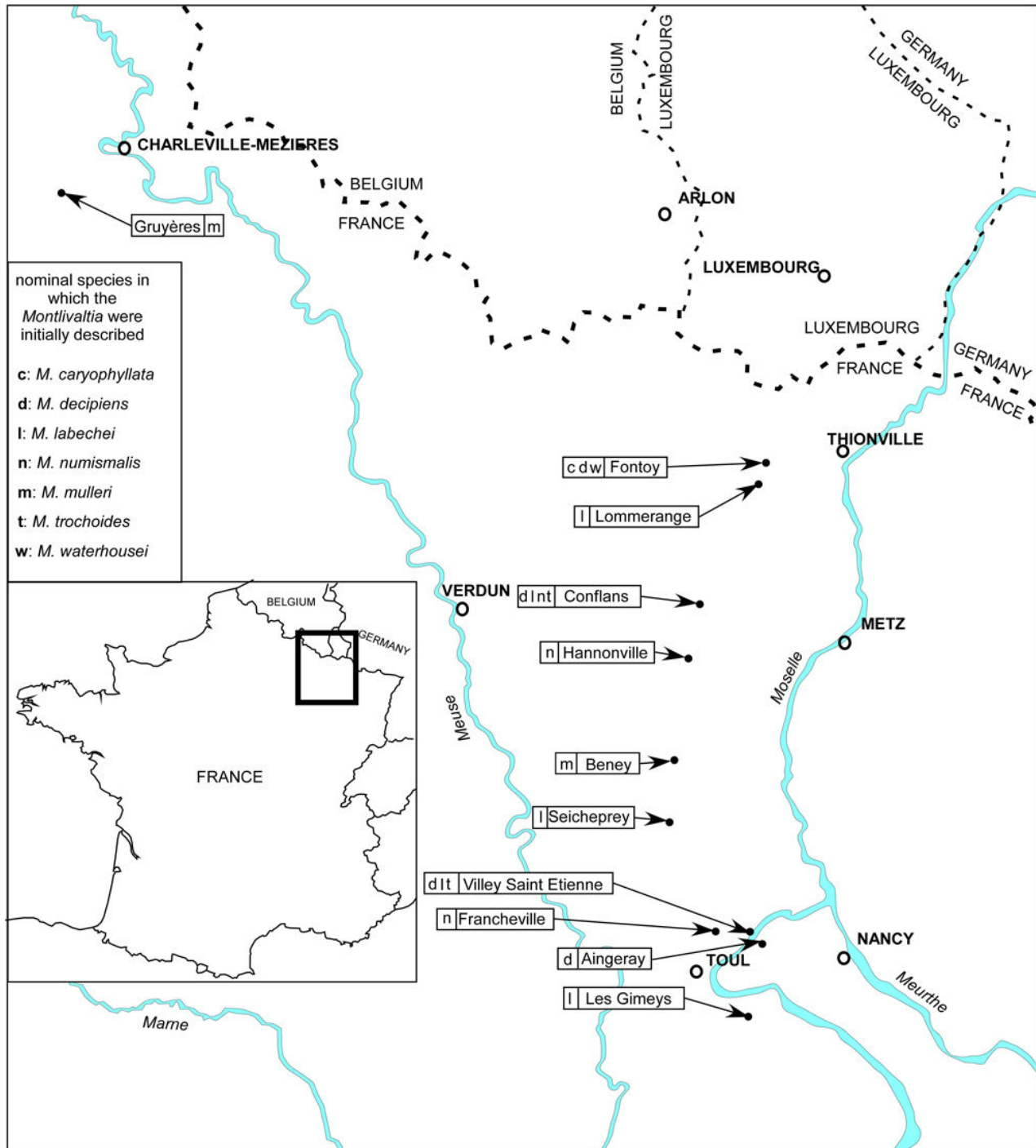


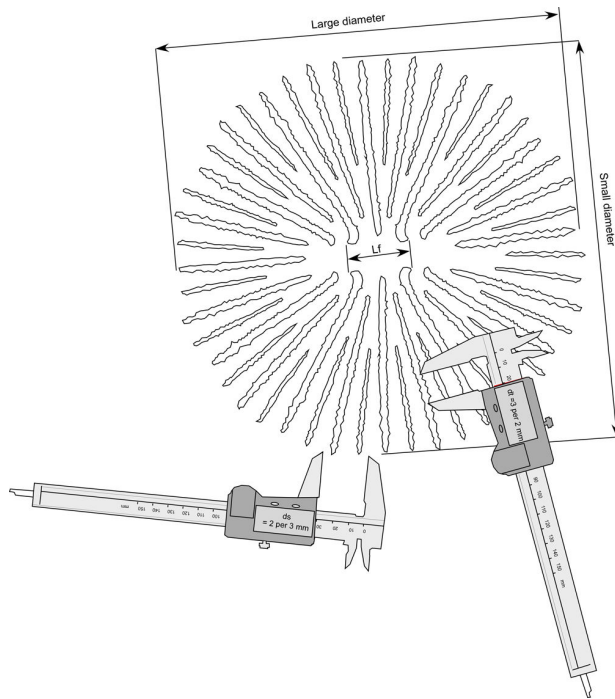
Figure 1: Location of *Montlivaltia* specimens identified by GARDET (1947) showing their original species assignments.

3. Qualitative observations

My observations focused on the distribution of growth wrinkles on the covering tissue visible on the proximal surface of the corallum. Although the exact nature of this covering tissue has not been confirmed by microstructural investigation, the distal edge of this striated layer is in some specimens raised in relief, suggesting that a true *epitheca sensu stricto* may exist in *Montlivaltia* (Fig. 3). The strict definition of "epitheca," as proposed by STOLARSKI (1995), assumes that the true epitheca (*epitheca s.s.*) grows inwardly. In contrast, earlier authors have suggested that in

Montlivaltia, the structure referred to as *epitheca sensu lato* grows outward and is formed by vesicular dissepiments covering the costae (Koby, 1889: Pl. 129, fig. 12; ALLOITEAU, 1957, p. 106).

In these two interpretations (Fig. 4) two different scenarios are implied for the basal morphology of the soft body. In Koby's model, the bottom of the soft body slopes outward, whereas in the alternative model involving a true epitheca, the bottom of the soft body lies on a concave surface, with its inner side rising on the most elevated part the endothea and its outer side extending upward on the more distal portion of the epitheca.



◀ **Figure 2:** Main measurements (subvertical calliper for trabecular density per 2mm, subhorizontal one for septal density per 3 mm. Note Lf based on the torsion of lateral S1, considered more constant and reliable than other protocols.



Figure 3: Distal view of the outer margin of *Montlivaltia* specimen Ech 2024-034 (originally identified as *M. de-labechei*), Les Gimeys Farm, Sexey-aux-Forges. Note the typical montlivaltid septal morphology and, two epithecal wrinkles with a small sulcus between the septa and the epitheca.

In the material under study, the best-preserved specimens observed in distal view show a distinct epitheca in relief, even in some with a small sulcus between the epitheca and the outer margin of the septa (Fig. 3). The outer margin of the septa is, therefore, in contact with the *epitheca* only in deeper parts, as can be seen where the *epitheca* is broken or abraded. Endothecal dissepiments emerging outward and covering the radial elements have never been observed. In one specimen, a broken surface clearly shows how the dissepiments slope downward and are externally covered by the wrinkled *epitheca* (Fig. 5). The distal relief of the epitheca is generally moderate, and septa are generally exsert, but at a variable degree, with a maximum of septal growth in vertical direction, or, also, with a significant outward component direction in some specimens.

The preservation of growth lines is made possible by the withdrawal of living tissue from the external and proximal parts of the skeleton. A persistent soft tissue covering would have obliterated these relief features, smoothing them beneath a more uniform outer layer, such as a *tectura*. A more pronounced withdrawal produces a rejuvenescence, leading to the formation of a more internal *epithec*al ring (Fig. 6).

Repeated binocular observations of epithecal growth wrinkles on the lower surface of *Montlivaltia* specimens indicate that their distribution is not random but reflects rhythmic growth pat-

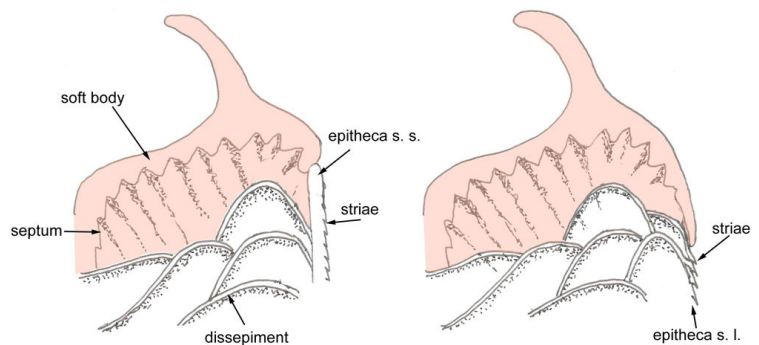


Figure 4: Two opposite models for the growth of epitheca in *Montlivaltia*. At left, a model with a true epitheca (privileged here) and at right the Kobay's model of an epitheca s.l. of dissepimental origin.



Figure 5: Skinned specimen Ech 2024-037 (originally identified as *M. trochoides* MILNE EDWARDS & HAIME, 1849a) Bathonian, Conflans. Black arrows show dissepimental vesicles covered by the wrinkled epitheca (white arrow).

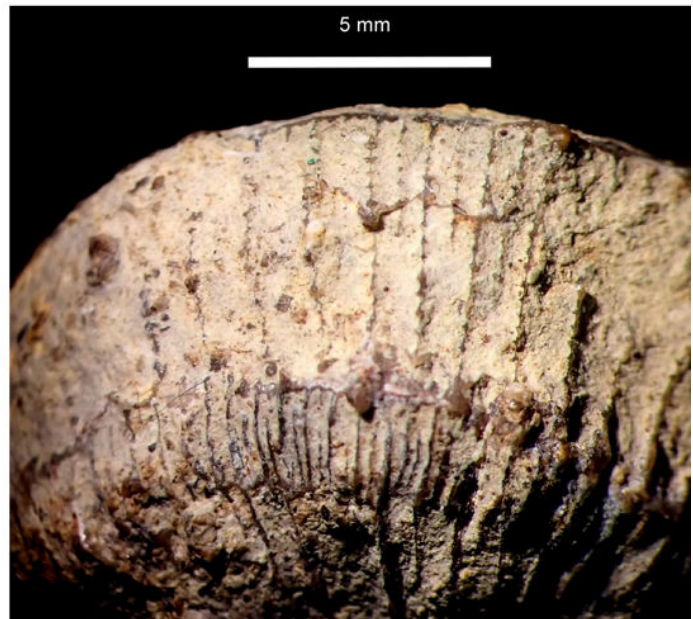


Figure 6: *Montlivaltia* Ech 2024-044-17 (originally identified as *M. labechei*) Bathonian, Fontoy. At left, rejuvenating specimen, distal view; at right enlargement of the distal surface showing septa with distal teeth and an epithecal ring due to a rejuvenescence.

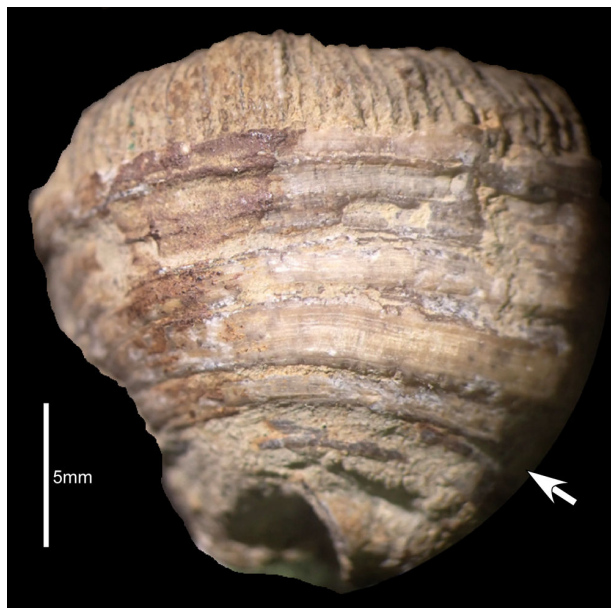


Figure 7: Lateral view of *Montlivaltia* Ech 2024-038 (originally identified as *M. decipiens*, Fontoy). Note the fairly regular annual banding and the growth wedge (white arrow), reflecting an upright reorientation of the skeleton after initial settlement. Smaller cycles can be observed.

terns. Although irregularities do occur (Fig. 7) and can sometimes complicate age determination, it is unlikely that the observed regularities result from random growth disturbances (Figs. 8-10). The periodic signal can, however, be disrupted by non-periodic events, such as the tilting of a coral within the substrate (Fig. 7).

The most evident rhythm is expressed by growth increments generally ranging between 1.5 and 3 mm. These increments correspond to alternating phases of diametric expansion and contrac-



Figure 8: Proximal view of *Montlivaltia* specimen Ech 2024-034 (originally identified as *M. delabechei*), Les Gimeys Farm, Sexey-aux-Forges, coll. GARDET. Note that the skeleton from the first year(s) is not covered by epitheca. Regular annual banding is visible over four successive years.

tion: expansion phases are represented by broad convex bands, whereas contraction phases are marked by narrower, deeper constriction lines. This fairly consistent increment size is interpreted as representing the annual growth band. Such regularity enables the estimation of the corallum's age even when certain annual records are poorly developed or irregular. Measurements are taken horizontally in discoid phenotypes and vertically in cylindroid forms.

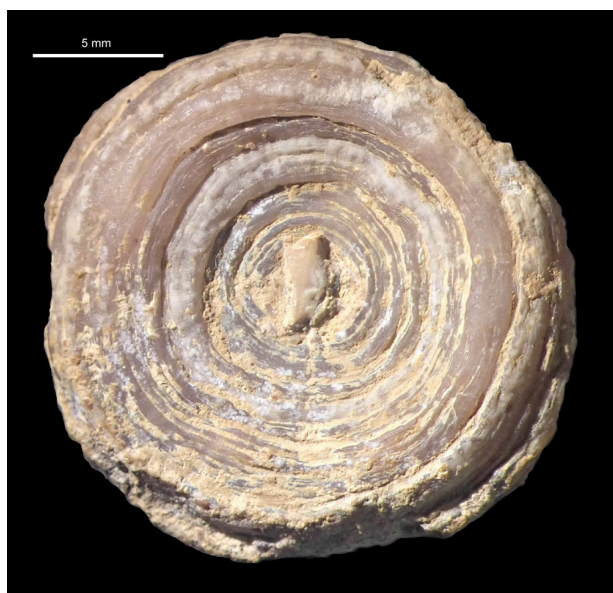


Figure 9: Proximal view of *Montlivaltia* Ech 2024 0 33, originally identified as *M. labechei*, Bathonian, Conflans, coll. GROTH.

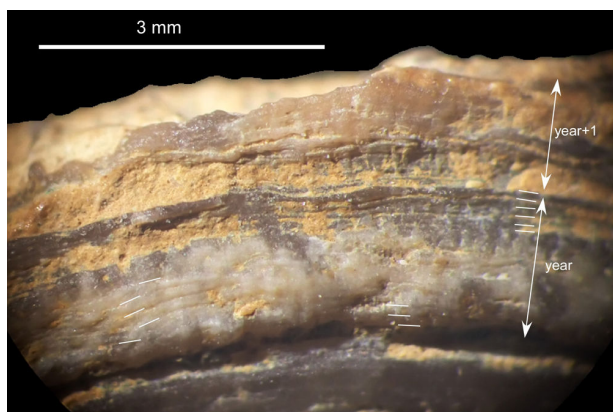


Figure 10: Epithecal growth rhythms on a *Montlivaltia* specimen Ech 2024 0 33, originally identified as *M. labechei*, Bathonian, Conflans, coll. GROTH. Note the imbrication between annual growth bands and lunar regular growth bands (highlighted by white lines).

The earliest growth stages are often not covered by epithecal tissue but instead display radiating radial elements (Fig. 8) over a small area, where growth rhythms cannot be discerned. In some specimens, the outer surface is only partially covered by epitheca, leaving radial elements visible corresponding with phases of reduced calcification.

The most distinct banding, interpreted as annual, is itself composed of smaller, subordinate increments that are locally strikingly regular. These micro-increments measure approximately 160 μm , and 12-13 of them can generally be counted within a single annual band, insofar as the annual limits can be clearly defined.



4. Quantitative results

Univariate analyses of Bathonian *Montlivaltia* from Lorraine reveal a homogeneous population, in which no species-level distinction can be inferred from the measured parameters (Fig. 11). Both large and small diameters display unimodal and symmetric distributions around their respective means. In contrast, height exhibits an almost unimodal but strongly asymmetric distribution, positively skewed, with only four specimens significantly taller than the rest.

The distribution of septal number (N_s) is approximately symmetric, but distinctly leptokurtic, and centred on a value very close to 96, the value predicted by the model of MILNE-EDWARDS and HAIME (1848), according to which septal insertion follows the formula $6S_1 + 6S_2 + 12S_3 + 24S_4 + 48S_5 = 96$ septa. Septal density, trabecular density, and fossa length all approximate normal distributions.

The estimated age-distribution is broadly unimodal, though a few exceptionally old and tall specimens may support alternative interpretations. Its positive skewness resembles that observed in the height distribution.

Several bivariate analyses are presented in Figure 12. The XY plot of large versus small diameter shows that most *Montlivaltia* specimens maintain an approximately circular outline, although a few individuals exhibit varying degrees of ellipticity. This graph does not support any subdivision of the population based on this parameter.

The XY plot of large diameter versus height indicates that most *Montlivaltia* display a low, flattened morphology, while some individuals show increased vertical growth, reflecting a wide range of ontogenetic trajectories. The plot of height as a function of age produces an elongated cloud of points, suggesting a roughly linear correlation ($R^2 = 0.6$). Exponential and logarithmic regressions yield lower coefficients of determination ($R^2 < 0.5$). The plot of number of septa (N_s) as a function of age shows no linear relation. After the age of 4 years most *Montlivaltia* reach their maximum number of septa (not far from 100) and keep it.

A multivariate analysis was performed on a smaller subset of specimens; however, the sample size remains sufficient to produce meaningful results. A Principal Component Analysis (PCA) using the correlation option in PAST (to account for parameters measured in different units) was conducted (Fig. 13). The scatter plot is primarily structured by the influence of the number of septa on the first principal component, whereas diameters and height mainly stretch the cloud along the second component. In contrast, biological age contributes little to the overall inertia of the point cloud. The scatter plot does not reveal any clear subdivision within the population. Moreover, the geographic distribution of localities does not satisfactorily explain the structure of the scatter plot, as localities with numerous specimens (Conflans and Fontoy) show substantial overlap.

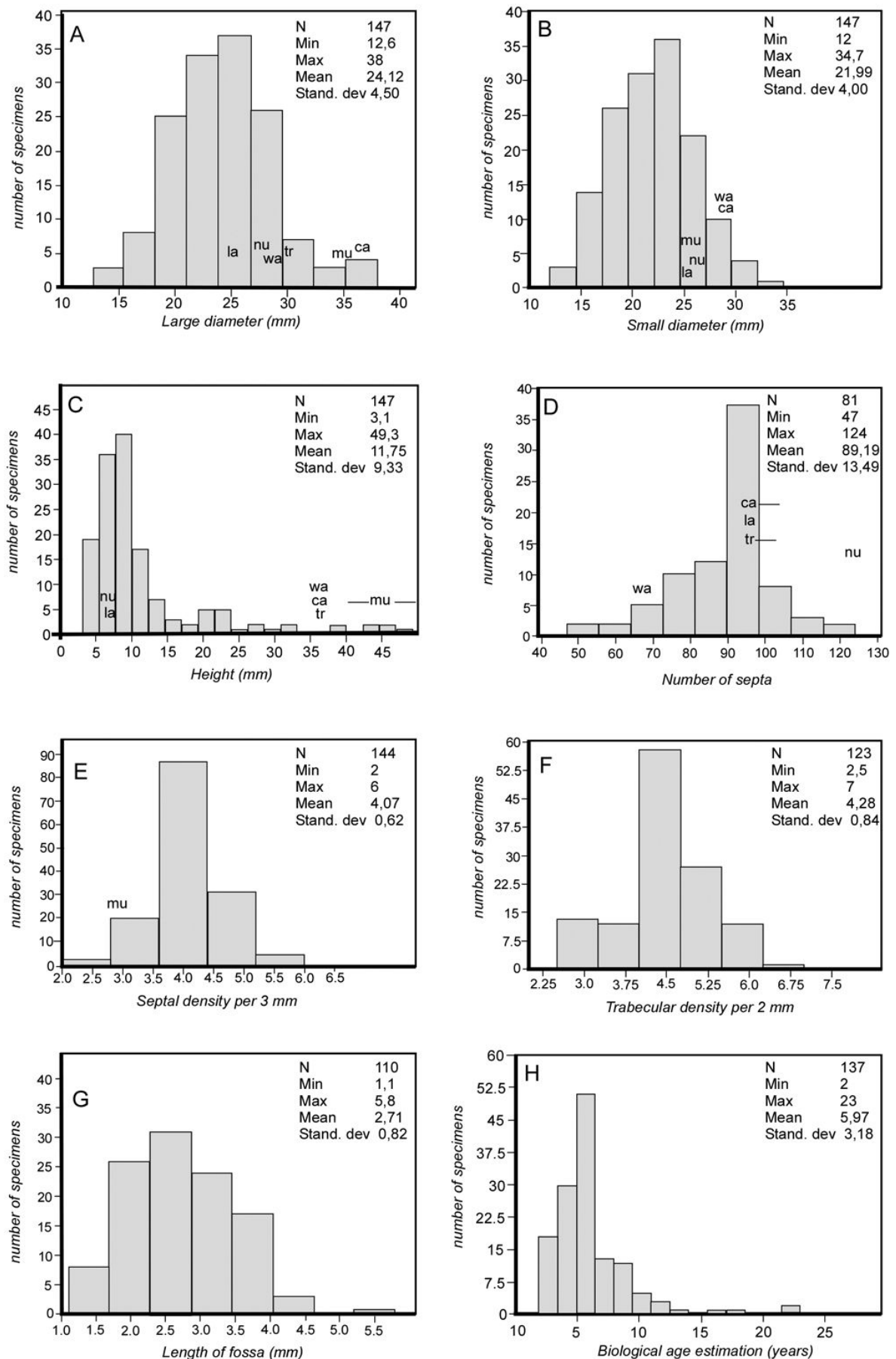


Figure 11: Univariate analyses of *Montlivaltia* from the Bathonian of Lorraine. Letters refer to the dimensions of type material of species initially identified by GARDET (1947) where available. ca = *caryophyllata*, la = *delabechei*, nu = *numismalis*, mu = *mulleri*, tr = *trochoides*, wa = *waterhousei*.



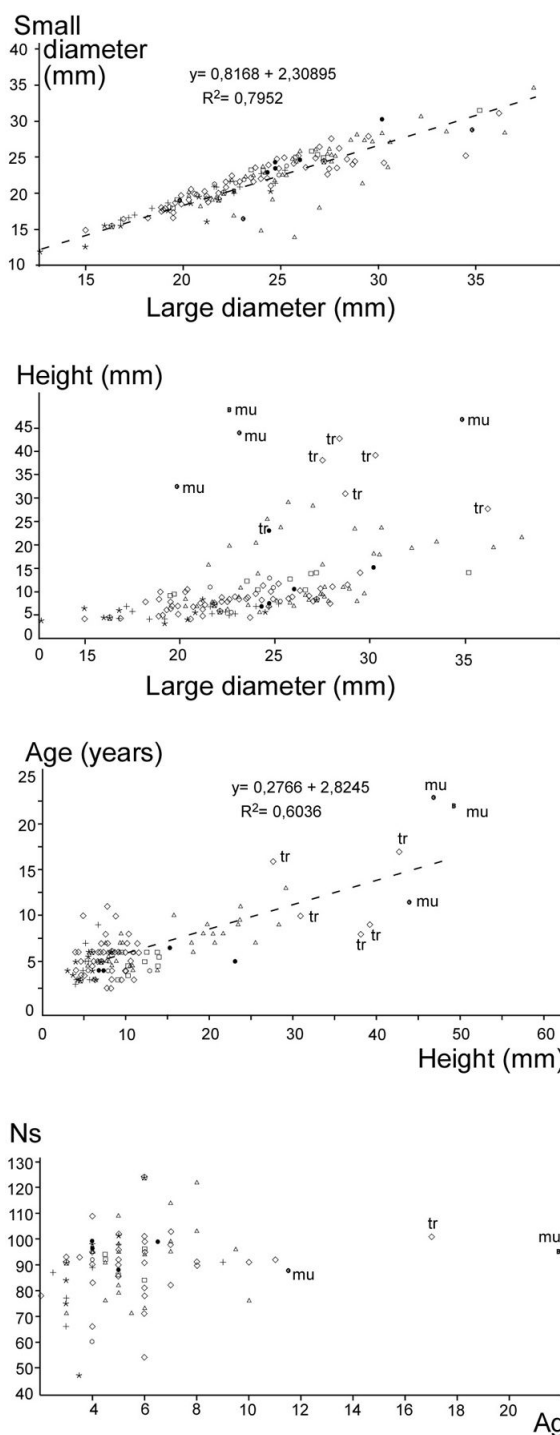
5. Discussion

Homogeneity of the population

A statistically homogeneous population does not necessarily correspond to a biologically homogeneous one. Overall, based on the combined results of univariate, bivariate, and multivariate analyses, the distribution of parameters appears relatively uniform, supporting the interpretation that the studied *Montlivaltia* specimens belong to a single species. However, several issues require careful consideration.

It is clear that the genus *Montlivaltia* has been excessively split in past taxonomic treatments. Little justification can be found for the numerous species names proposed by GARDET (1947) and other authors. GARDET (1947) did not justify his identifications, but it is assumed that he followed the traditional practice of distinguishing species based on diameter, number of septa and height as was commonly done by earlier authors (see for instance FROMENTEL & FERRY, 1865-1869). I, nevertheless, considered the authors who proposed alternative criteria for species discrimination (e.g., new parameters introduced by ALLOITEAU, 1958, or new types of graphical analyses proposed by GILL and LAFUSTE, 1971). However, as already concluded by PANDEY and FÜRSICH (2003, p. 34) after their detailed analysis of character variation, all of these additional parameters are subject to substantial intraspecific variability.

► **Figure 12:** Bivariate analyses of *Montlivaltia* from the Bathonian of Lorraine. Lettered data points correspond to GARDET's (1947) initial species identifications (mu = *muelleri*, tr = *trochoides*).



A recent population study of Middle Jurassic *Montlivaltia* from Tibet by ZHU *et al.* (2025) reached a similar conclusion, recognizing a single, morphologically variable species. Unfortunately, those authors assigned their population to the junior synonym *Montlivaltia zangbeiensis* LIAO and XIA, 1985, which closely resembles older nominal species described from Europe [*].

In cases of broad intraspecific variability encompassing several previously named taxa, interpreting specimens at the extremes of the variation range becomes problematic. The unique *Kobyphyllia* specimen (Fig. 14) is of particular interest: it occupies a central position within the quantitative distribution but differs from the others only in possessing a lamellar columella - a qualitative feature. The hypothesis that *Kobyphyllia* represents merely an individual variant of *Montlivaltia* is defensible, although no practical test currently allows verification of this idea.

[*] In the same publication, ZHU *et al.* (2025) also misassigned a species of *Adelocoenia* ORBIGNY, 1849, to the obsolete genus *Pseudocoenia* ORBIGNY, 1850 (see LA THUILLÈRE *et al.*, 2020).

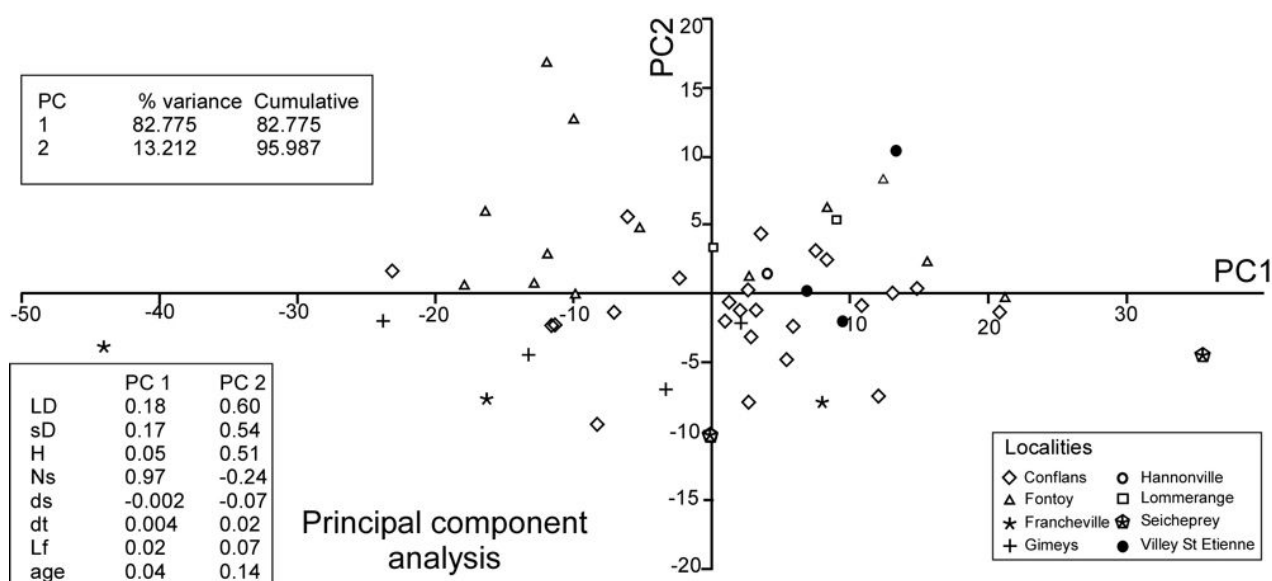


Figure 13: Multivariate analyses of *Montlivaltia* from the Bathonian of Lorraine.



Figure 14: Specimen MAN 2024 0 44-24 here identified as a *Kobayphyllia* because of its lamellar columella.

At the end of the distribution, I am not entirely convinced that the specimens originally designated as *Montlivaltia mülleri* Koby, 1884, - characterized by a markedly tall growth form - belong to the same biological unit. It remains uncertain whether this distinct morphology reflects random variation, an ecophenotypic response, or a true specific difference. This doubt is reinforced by septal microarchitectural observations that are atypical for *Montlivaltia*. These specimens are both taller and older than the others (Fig. 12) but could not be included in all analyses because trabecular density and fossa length could not be measured. An ecophenotypic interpretation is plausible: prolonged growth may have been facilitated by stable soft substrates and appropriate sedimentation rates. Notably, all previously named "*M. mülleri*" (normally corrected into *muelleri*) specimens come from distinct outcrops (Gruyère and Beney) where they represent the

only species of the genus present. Interestingly, even GOLDFUSS (1829), despite the typological framework of his time, illustrated *Montlivaltia decipiens* (then classified as *Anthophyllum*) with both discoid and cylindroid morphologies. Much later, GILL and LAFUSTE (1971) also proposed an ecophenotypic explanation. It is further possible that the weak septal ornamentation observed in older specimens reflects biological aging, involving the addition of lamellar layers that obscure the sharp relief of younger trabeculae.

Growth banding

Growth rhythms in corals may arise from various mechanisms. Some are internally regulated, reflecting compromises between the growth of soft tissues and that of the skeleton. GILL (1982) elegantly illustrated such patterns in the alternation in levels of pennulae in pennular corals, of auriculae in Stylinidae, and tabular development within and outside corallites in plocoid stylinids. In the present material, coordination between soft-tissue expansion and skeletal accretion was probably mediated by numerous vesicular dissepiments, enabling steady growth along the distal margins of the septa.

Other rhythmic patterns may record variations in growth rate linked to fluctuating environmental conditions. Since the pioneering work of MA (1933, 1934, 1937), who emphasized seasonal influences on coral growth and their palaeontological value, many studies have identified annual banding on the epitheca or within the skeleton. The annual nature of these bands has often been confirmed through geochemical analyses in Recent corals, forming the basis of sclerochronology - a key approach in palaeoclimatic reconstruction (for recent reviews, see HELMLE & DODGE, 2011; PEHARDA *et al.*, 2021). The studied population of Bathonian *Montlivaltia* is situated at a rather high palaeolatitude (not far from 30° north), which was rather favourable for the record of seasonal contrasts.



Less currently, subordinate rhythms related to lunar or circadian cycles have also been reported. Their attribution to specific periodicity is not always convincing (see for example the so-called daily growth of the Recent *Madracis* MILNE EDWARDS & HAIME, 1849b, Florida in WELLS (1970: Fig. 4) with growth increments of more than 80 micro-meters, which seem good candidates for synodic increments. Annual increments of 36-69 mm per year, calculated (and not observed) from supposed daily nested in monthly ones, for Carboniferous rugosans by JOHNSON and NUDDS (1975) seem also very high. SCRUTTON (1998) has already pointed that these results are hardly compatible with recorded growth rates in rugosan corals. SCRUTTON (1970) mentioned that daily increments are generally thinner than 50 micrometers. Lunar periodicity was described by SCRUTTON (1970) who described Devonian corals, a period in which there was 399 days in a year, and, according to the SCRUTTON's data, around 31 days in a lunar cycle. Today there are 12.4 synodic months in a year and 29.5 days per month. Lunar cycles were reported in *Lophelia pertusa* (LINNAEUS, 1758), a Recent non-zooxanthellate coral (a personal communication of S.A. WAINWRIGHT reported by SCRUTTON (1965), and by other authors in modern zooxanthellate taxa (BUDDEMEIER, 1974; WEBER *et al.*, 1975; CHEVALIER, 1987). The fine-scale increments observed within the annual growth bands of Bathonian *Montlivaltia* are interpreted as lunar in origin, based on their numerical ratio with annual bands. I see no alternative explanation and infer, as a first hypothesis, that spring-neap tidal cycles may have influenced calcification rhythms in Bathonian from Lorraine. Tidal cycles have multiple effects on environmental factors that can vary significantly in intensity according to topographical conditions. If tidal currents are channelized, they can move the water masses down to the bathyal environment (LAMBERT & ROUX, 1991), improving, for instance, oxygenation of the sea bottom, which is important for the calcification process. But lunar effects on reproductive cycles are also well established (BABBICK *et al.*, 1986; BAIRD *et al.*, 2009) and widely known through the spectacular images of mass spawning events, which occur often during specific nights each year (MERA *et al.*, 2025), and thus, cannot account for a regular monthly signal. LIN *et al.* (2021) have demonstrated that the moonrise light is synchronised with spawning in *Dipsastraea speciosa* (DANA, 1846). Eighty-percent of Recent corals are broadcasting spawner (BAIRD *et al.*, 2021) but the remaining brooders are also influenced by lunar cycles (light or tides). ATODA (1947a; 1947b; 1951a; 1951b; 1951c) has observed regular monthly production of planula larvae for the brooding coral *Pocillopora damicornis* (LINNAEUS, 1758), *Stylophora pistillata* (ESPER, 1792), *Seriatopora hystrix* DANA, 1846, *Acropora brueggemanni* (BROOK, 1891), *Galaxea aspera* QUELCH, 1886. Then, the hypothesis of *Montlivaltia caryophyllata* being a brooding species with a monthly-paced planulation controlled by an inter-

nal mechanism synchronized on astronomical rhythms is plausible as well as the direct triggering of monthly growth ridges driven by external environmental controls.

Circadian rhythms have been attributed to diurnal expansion and contraction movements of soft tissues at the colony margins (BARNES, 1972; BEAUVAIS & CHEVALIER, 1980). Such daily cycles are rarely preserved in fossils, though examples are reported from Paleozoic corals [WELLS, 1963; JOHNSON & NUDDS, 1975 (but daily increments?); GUILLAUME & SEMENOFF-TIAN-CHANSKY, 1991]. In Recent corals, daily increments (≈ 365 per year) have even been used to estimate the deceleration of Earth's rotation since the Devonian (WELLS, 1963, 1970) despite their problematic accuracy (SCRUTTON & HIPKIN, 1973). No such microincrements were detected in studied samples, likely due to the diagenetic replacement of aragonite by calcite, which increased the size of crystals and obscured very fine structures in Mesozoic corals, at least in their usual state of preservation. Assuming an annual growth increment of 1.5 mm and a Jurassic year of 380 days, the expected daily growth increments would be approximately 4 μm .

Banding and zooxanthellae

FRANKOWIAK *et al.* (2016) demonstrated that fine-scale banding within thickening deposits is regular in zooxanthellate corals and irregular in azooxanthellate ones. Unfortunately, this approach cannot be applied to the studied material, because the aragonite-calcite transformation has degraded fine-scale textures. The regularity of larger annual growth bands has also been proposed as an indicator of photosymbiosis (STANLEY & HELMLE, 2010). This observation supports the interpretation of *Montlivaltia* as a zooxanthellate coral, although the criterion requires further validation through statistical and actualistic data (see CAROSELLI *et al.*, 2017, for slow, regular growth in *Caryophyllia* LAMARCK, 1801).

Annual linear growth rates have also been used to distinguish photosymbiotic from non-photosymbiotic corals, with the former generally showing higher calcification efficiency. The Bathonian *Montlivaltia* growth rates fall within the range common to both categories. However, comparison with Kimmeridgian descendants offers additional insight. In *Montlivaltia nattheimensis* MILASCHEWITZ, 1876, illustrated by MILASCHEWITZ (1876: Pl. 44, fig. 2), an annual linear growth of 4.6 mm can be estimated - relatively high compared with solitary, non-zooxanthellate corals (*Caryophyllia*: 1.05-2.94 mm, CHEVALIER, 1987; *Leptopsammia pruvoti* LACAZE-DUTHIERS, 1897: <1 mm, CAROSELLI *et al.*, 2012).

Usage of age

Corals, like trees, are sometimes described as virtually immortal. Indeed, very old colonies do exist. CHEVALIER (1987, p. 540) reported a *Platygyra* EHRENBERG, 1834, colony 500 years old in the Red Sea and a *Pavona frondifera* (LAMARCK, 1816)



measuring 44.5×24.6 m from Shikoku Island, noting that such large colonies are composite structures regenerated by peripheral planula settlement. More recently, CUFF (2024) documented a *Pavona clavus* (DANA, 1846) colony estimated at 300 years and 32-34 m in diameter.

In colonial corals, growth generally decreases with age (CHEVALIER, 1987). In the zooxanthellate coral *Manicina areolata* (LINNAEUS, 1758), T.F. GOREAU and N.I. GOREAU (1960) demonstrated that calcification rate is inversely related to body weight (and thus size), whereas in specimens reared in darkness, growth rate remains constant. Despite the fact that both species share the trait of initial attachment to the substrate, later breaking free to live unattached within soft sediment, this statement does not parallel my observations in *Montlivaltia*, where early growth increments cover a smaller surface area.

It remains unclear whether age in these corals is biologically constrained or reflects an adaptive response to unstable, soft-bottom environments – possibly explaining their relatively short lifespans.

The regenerative capacity of corals is well known, and recent studies have begun to elucidate its mechanisms, including the discovery of adult stem cells in the colonial coral *Stylophora pistillata* (LEVANONI *et al.*, 2024). The mean age of Bathonian *Montlivaltia* population under study is six years, with the oldest specimen reaching 22 years. This individual, initially identified as *M. mülleri*, achieved its tall form through extended growth. Statistically, age (inferred from growth bands) correlates with height (Fig. 12). With a mean lifespan of six years, these corals are, of course, far from immortal and much shorter-lived than large colonial forms. Whether their death was biologically programmed or environmentally induced remains uncertain.

Finally, age estimation in fossils is of particular interest when exploring relationships between ontogeny and phylogeny in a lineage. In palaeontology, size is often used as a proxy for age – an assumption that can lead to confusion between dwarfism and progenesis, or between gigantism and hypermorphosis (ALBERCH *et al.*, 1979; DOMERGUES *et al.*, 1986). Direct age estimation, thus, provides an additional parameter for understanding size variation in the evolutionary history of the genus *Montlivaltia*. Population-based approaches will remain essential to document this lineage further.



6. Conclusions

- The studied corals of the solitary genus *Montlivaltia* from the Bathonian of Lorraine appear to represent a single homogenous population, with only minor, possibly disputable exceptions at the extremes of the variation range.
- Their epitheca displays regular growth bands organized at two hierarchical levels; the interleaving of these levels suggests control by solar and lunar cycles corresponding to annual and synodic (lunar) periodicities.
- Consequently, the biological age of these *Montlivaltia* specimens can be determined: the mean age is relatively low (≈ 6 years), while the oldest individual observed reached 23 years.
- Age determination opens a window for studying lineages and for a better understanding of evolutionary processes within the genus and comparable taxa.
- The regularity of growth further supports the hypothesis that this genus was photosymbiotic.

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Appendix

reference number used in the analyses	name in GARDET	number ENSG- MAN collection	additional number for batches of specimens	LD	sD	H	Ns	ds/3mm (measured)	ds/3mm (computed)	dt:2mm (measured)	dt:2mm (computed)	Lf (measured)	Lf (computed)	average diameter	average circumference	computed Ns (from ds and circumference)	biological age (years) (counted)	biological age (years) (computed)	geological age	Locality	collector	specimens retained for ACP	specimens retained for bivariate age/Ns	specimens retained for bivariate age/H	specimens retained for bivariate LD/H and LD/SD
1	M. labechei	2024 0 21	3	23.5	23.2	12.3	88	4	4	3	3	3.8	3.8	23.35	73.346	97.795	5	5	Upper Bathonian	Lommerange	GARDET	1	1	1	1
2	M. labechei	2024 0 21	4	35.2	31.5	14.0	circa 130	4	4	3	3	1.3	1.3	33.35	104.758	139.677	5 - 6	5.5	Upper Bathonian	Lommerange	GARDET			2	2
3	M. labechei	2024 0 21	5	25.8	25.0	12.6	?	4	4	4	4	?		25.4	79.785	106.381	6	6	Upper Bathonian	Lommerange	GARDET			3	3
4	M. labechei	2024 0 21	6	26.9	25.3	13.8	96	4	4	5	5	3.0	3.0	26.1	81.984	109.312	6	6	Upper Bathonian	Lommerange	GARDET	4	4	4	4
5	M. labechei	2024 0 21	7	26.6	25.8	10.3	circa 100	4	4	4 - 5	4.5	3.8	3.8	26.2	82.298	109.731	3 - 4	3.5	Upper Bathonian	Lommerange	GARDET			5	5
6	M. labechei	2024 0 21	8	27.2	24.9	13.9	92	4	4	5	5	?		26.05	81.827	109.103	4 - 5	4.5	Upper Bathonian	Lommerange	GARDET		6	6	6
7	M. labechei	2024 0 21	9	19.5	17.9	9.1	circa 68	3	3	6	6	2.3	2.3	18.7	58.740	58.740	3	3	Upper Bathonian	Lommerange	GARDET			7	7
8	M. labechei	2024 0 21	10	24.1	23.1	10.3	94	4	4	5	5	circa 2.0	2.0	23.6	74.131	98.842	4 - 5	4.5	Upper Bathonian	Lommerange	GARDET		8	8	8
9	M. labechei	2024 0 21	11	19.7	19.0	9.5	84	5	5	5	5	circa 3.0	3.0	19.35	60.781	101.302	6	6	Upper Bathonian	Lommerange	GARDET		9	9	9
10	M. caryophyllata	2024 0 20	1	30.6	27.1	23.7	96	3 - 4	3.5	7	7	?		28.85	90.622		9 - 10	9.5	Upper Bathonian	Fontoy	GARDET		10	10	10
11	M. caryophyllata	2024 0 20	2	36.5	28.4	19.5	circa 90	4	4	?		circa 5.8	5.8	32.45	101.931	135.908	?		Upper Bathonian	Fontoy	GARDET				11
12	M. caryophyllata	2024 0 20	3	30.5	23.6	17.9	99	3	3	3 - 4	3.5	3.8	3.8	27.05	84.968	84.968	7	7	Upper Bathonian	Fontoy	GARDET	12	12	12	12
13	M. caryophyllata	2024 0 20	4	33.5	28.6	20.7	114	4	4	4	4	circa 3.2	3.2	31.05	97.533	130.044	7	7	Upper Bathonian	Fontoy	GARDET		13	13	13
14	M. caryophyllata	2024 0 20	5	38.0	34.7	21.7	122	3	3	4	4	?		36.35	114.181	114.181	at least 8	8	Upper Bathonian	Fontoy	GARDET		14	14	14
15	M. waterhousei	2024 0 19	1	24.0	14.8	20.5	?	4	4	5	5	2.4	2.4	19.4	60.939	81.251	8	8	Upper Bathonian	Fontoy	GARDET			15	15
16	M. waterhousei	2024 0 19	2	24.6	19.1	25.6	?	4	4	4	4	?		21.85	68.634	91.513	7	7	Upper Bathonian	Fontoy	GARDET			16	16
17	M. waterhousei	2024 0 19	3	22.6	16.9	19.8	?	5	5	?		?		19.75	62.038	103.397	9	9	Upper Bathonian	Fontoy	GARDET			17	17
18	M. waterhousei	2024 0 19	4	25.7	14.0	29.2	?	5	5	?		2.6	2.6	19.85	62.352	103.920	13	13	Upper Bathonian	Fontoy	GARDET			18	18
19	M. waterhousei	2024 0 19	5	25.3	22.5	23.8	?	4	4	?		3.1	3.1	23.9	75.074	100.098	11	11	Upper Bathonian	Fontoy	GARDET			19	19
20	M. waterhousei	2024 0 19	6	29.2	21.4	23.5	?	4	4	5	5	4 ?	4.0	25.3	79.471	105.962	9	9	Upper Bathonian	Fontoy	GARDET			20	20
21	M. waterhousei	2024 0 19	7	27.0	18.0	28.4	?	4	4	4	4	2.7	2.7	22.5	70.676	94.235	9	9	Upper Bathonian	Fontoy	GARDET			21	21
22	M. decipiens	2024 0 18	1	24.9	22.5	10.9	circa 88	4	4	4	4	circa 4.0	4.0	23.7	74.445	99.261	6	6	Upper Bathonian	Aingeray, road of Fontenoy	GARDET			22	22
23	M. decipiens	2024 0 18	2	21'6	21.1	10.9	?circa 98	4 - 5	4.5	5 - 6	5.5	?					6	6	Upper Bathonian	Aingeray, road of Fontenoy	GARDET			23	23
24	M. decipiens	2024 0 18	3	24.7	23.7	12.9	60	4	4	5 - 6	5.5	circa 2.7	2.7	24.2	76.016	101.355	4	4	Upper Bathonian	Aingeray, road of Fontenoy	GARDET		24	24	24
25	M. numismalis	2024 0 26	1	22.7	21.4	5.5	circa 73	5	5	4	4	?		22.05	69.263	115.438	4	4	Upper Bathonian	Hannonville	LEBRUN [very likely Albert LEBRUN, President of the French republic' from 1932 to 1940]			25	25
26	M. numismalis	2024 0 26	2	25.3	23.8	7.9	92	4 - 5	4.5	5	5	3.6	3.6	24.55	77.115		4	4	Upper Bathonian	Hannonville	LEBRUN	26	26	26	26
27	M. mulleri	2024 0 22	1	34.8	28.8	46.9	circa 114	4	4	Montlivaltia ?				31.8	99.889	133.185	circa 23	23	Bathonian	Gruyères, vallée de Bordeaux (08)	GAIFFE			27	27
28	M. mulleri	2024 0 22	2	23.1	16.5	44.0	88	4	4	Montlivaltia ?				19.8	62.195	82.927	10 - 13	11.5	Bathonian	Gruyères, vallée de Bordeaux (08)	GAIFFE		28	28	28
29	M. mulleri	2024 0 22	3	19.8	19.0	32.5	?	4	4	Montlivaltia ?				19.4	60.939	81.251	?		Bathonian	Gruyères, vallée de Bordeaux (08)	GAIFFE				29
30	M. trochoides	2024 0 23		24.7	23.5	23.1	90	4	4	?		3.6	3.6	24.1	75.702	100.936	5	5	Upper Bathonian	Villey Saint Étienne	THIÉ RY		30	30	30
31	M. decipiens	2024 0 25	1	24.8	24.7	10.0	circa 89	4 - 5	4.5	?		?		24.75	77.744		4	4	Upper Bathonian	Conflans	NICKLÈS [founder of the institute of Geology (now the ENSG) he is at the origin of the collections used here.]			31	31
32	M. decipiens	2024 0 25	2	24.0	22.0	9.5	circa 78	4 - 5	4.5	3 - 4	3.5	circa 2.7	2.7	23	72.247		3	3	Upper Bathonian	Conflans	NICKLÈS			32	32
33	M. decipiens	2024 0 25	3	28.0	26.2	11.0	?	4	4	4	4	?		27.1	85.125	113.501	3	3	Upper Bathonian	Conflans	NICKLÈS			33	33
34	M. decipiens	2024 0 25	4	25.2	24.9	11.6	91	4	4	3 - 4	3.5	3.6	3.6	25.05	78.686	104.915	6	6	Upper Bathonian	Conflans	NICKLÈS	34	34	34	34
35	M. decipiens	2024 0 25	5	18.2	16.6	7.8	?	5	5	?		circa 1.9	1.9	17.4	54.656	91.094	2	2	Upper Bathonian	Conflans	NICKLÈS			35	35
36	M. decipiens	2024 0 29	1	30.2	30.2	15.3	99	3	3	6	6	3.2	3.2	30.2	94.863	94.863	6 - 7	6.5	Upper Bathonian	Villey Saint Étienne	GARDET	36	36	36	36
37	M. decipiens	2024 0 29	2	26	24.6	10.5	circa 97	4	4	4	4	?		25.3	79.471	105.962	?		Upper Bathonian	Villey Saint Étienne	GARDET				37
38	M. labechei	2024 0 33	1	22.2	20.8	7.8	92	4	4	3	3	2.8	2.8	21.5	67.535	90.047	11	11	Upper Bathonian	Conflans	GROTH	38	38	38	38
39	M. labechei	2024 0 33	2	21.8	20.0	7.6	90	4 - 5	4.5	3	3	3.1	3.1	20.9	65.650		8	8	Upper Bathonian	Conflans	GROTH	39	39	39	39



40	<i>M. labechei</i>	2024 0 33	3	19.1	17.8	4.9	circa 84	5	5	3 - 4	3.5	3.3	3.3	18.45	57.954	96.591	10	10	Upper Bathonian	Conflans	GROTH			40	40
41	<i>M. labechei</i>	2024 0 33	4	15.0	14.9	4.1	83	5 - 6	5.5	4	4	1.4	1.4	14.95	46.960		4	4	Upper Bathonian	Conflans	GROTH	41	41	41	41
42	<i>M. mulleri</i>	2024 0 36		22.6	20.3	49.3	95	5	5	4	4	?		21.45	67.378	112.296	22	22	Bathonian	Beney	GARDET		42	42	42
43	<i>M. trochoides</i>	2024 0 40	1	36.2	31.1	27.7	?	3	3	?		?		33.65	105.700	105.700	16	16	Upper Bathonian	Conflans	Cou�� [the famous Dr ��mile Cou��, famous for his self-improvement method based on autosuggestion.]			43	43
44	<i>M. trochoides</i>	2024 0 40	2	34.5	25.2	46.7	?	4 - 5	4.5	?		?		29.85	93.764		?		Upper Bathonian	Conflans	Cou��				44
45	<i>M. trochoides</i>	2024 0 37	3	28.4	24.7	42.8	101	3	3	3 - 4	3.5	2.7	2.7	26.55	83.398	83.398	17	17	Upper Bathonian	Conflans	NICKL��S		45	45	45
46	<i>M. trochoides</i>	2024 0 37	4	27.5	23.4	38.2	?	3	3	3 - 4	3.5	?		25.45	79.943	79.943	8	8	Upper Bathonian	Conflans	NICKL��S			46	46
47	<i>M. trochoides</i>	2024 0 37	5	30.3	24.2	39.3	circa 87	4	4	?		?		27.25	85.597	114.129	9	9	Upper Bathonian	Conflans	NICKL��S			47	47
48	<i>M. trochoides</i>	2024 0 37	6	28.7	24.0	31	circa 79	3	3	4	4	4.5	4.5	26.35	82.770	82.770	10	10	Upper Bathonian	Conflans	NICKL��S			48	48
49	<i>M. labechei</i>	2024 0 34	1	22.9	20.9	5.2	?	4	4	4 - 5	4.5	?		21.9	68.791	91.722	7	7	Upper Bathonian	Gimeys Farm (Sexey-aux-Forges)	GARDET			49	49
50	<i>M. labechei</i>	2024 0 34	2	25.2	23.2	7.3	circa 88	4	4	4 - 6	5	2	2.0	24.2	76.016	101.355	5	5	Upper Bathonian	Gimeys Farm (Sexey-aux-Forges)	GARDET			50	50
51	<i>M. labechei</i>	2024 0 34	3	24	22.7	6.8	?	3	3	6	6	?		23.35	73.346	73.346	5	5	Upper Bathonian	Gimeys Farm (Sexey-aux-Forges)	GARDET			51	51
52	<i>M. labechei</i>	2024 0 34	4	21.6	20.9	6.7	91	4	4	4	4	1.9	1.9	21.25	66.750	89.000	9	9	Upper Bathonian	Gimeys Farm (Sexey-aux-Forges)	GARDET	52	52	52	52
53	<i>M. labechei</i>	2024 0 34	5	16.8	16.3	4.2	circa 96	5 - 6	5.5	5	5	1.4	1.4	16.55	51.986		3	3	Upper Bathonian	Gimeys Farm (Sexey-aux-Forges)	GARDET			53	53
54	<i>M. labechei</i>	2024 0 34	6	22.6	20.0	4.9	89	5	5	?		?		21.3	66.907	111.511	4	4	Upper Bathonian	Gimeys Farm (Sexey-aux-Forges)	GARDET		54	54	54
55	<i>M. labechei</i>	2024 0 34	7	24.7	21.4	6.7	97	4	4	4	4	?		23.05	72.404	96.538	5	5	Upper Bathonian	Gimeys Farm (Sexey-aux-Forges)	GARDET		55	55	55
56	<i>M. labechei</i>	2024 0 34	8	19.2	18.7	4.1	74 likely underestimated	4 - 5	4.5	4	4	2.8	2.8	18.95	59.525		3 ?	3	Upper Bathonian	Gimeys Farm (Sexey-aux-Forges)	GARDET			56	56
57	<i>M. labechei</i>	2024 0 34	9	17.2	16.6	6.8	77	3 - 4	3.5	4	4	1.5	1.5	16.9	53.086		3	3	Upper Bathonian	Gimeys Farm (Sexey-aux-Forges)	GARDET	57	57	57	57
58	<i>M. labechei</i>	2024 0 34	10	21.7	20.9	5.2	?	4 - 5	4.5	3 - 5	4	2.3	2.3	21.3	66.907		5	5	Upper Bathonian	Gimeys Farm (Sexey-aux-Forges)	GARDET			58	58
59	<i>M. labechei</i>	2024 0 34	11	22.4	21.7	5.6	circa 72	3	3	3 - 4	3.5	3.4	3.4	22.05	69.263	69.263	5	5	Upper Bathonian	Gimeys Farm (Sexey-aux-Forges)	GARDET			59	59
60	<i>M. labechei</i>	2024 0 34	12	18.4	17.9	4.0	87	4	4	4 - 6	5	1.1	1.1	18.15	57.013	76.016	2 - 3	2.5	Upper Bathonian	Gimeys Farm (Sexey-aux-Forges)	GARDET	60	60	60	60
61	<i>M. labechei</i>	2024 0 34	13	17.5	17.0	5.7	66	4	4	4	4	2.1	2.1	17.25	54.1853	72.247	3	3	Upper Bathonian	Gimeys Farm (Sexey-aux-Forges)	GARDET	61	61	61	61
62	<i>M. labechei</i> var. <i>cyclolitoides</i>	2024 0 30	1	27.6	27.6	8.2	?	4	4	?		?		27.6	86.6963	115.595	5	5	Upper Bathonian	Conflans	SIMON			62	62
63	<i>M. labechei</i> var. <i>cyclolitoides</i>	2024 0 30	2	20.7	19.8	6.7	95	4	4	4 - 5	4.5	2.0	2.0	20.25	63.6083	84.811	5	5	Upper Bathonian	Conflans	SIMON	63	63	63	63
64	<i>M. labechei</i> var. <i>cyclolitoides</i>	2024 0 30	3	26.3	23.6	10.2	?	4 - 5	4.5	3 - 4	3.5	?		24.95	78.372		7	7	Upper Bathonian	Conflans	SIMON			64	64
65	<i>M. labechei</i> var. <i>cyclolitoides</i>	2024 0 30	4	18.9	17.5	4.7	93	5	5	4	4	1.7	1.7	18.2	57.169	95.282	3 - 4	3.5	Upper Bathonian	Conflans	SIMON	65	65	65	65
66	<i>M. labechei</i> var. <i>cyclolitoides</i>	2024 0 30	5	24.7	23.9	7.0	99	5	5	5	5	2.6	2.6	24.3	76.330	127.217	6	6	Upper Bathonian	Conflans	SIMON	66	66	66	66
67	<i>M. labechei</i> var. <i>cyclolitoides</i>	2024 0 30	6	21.2	19.5	4.7	102	5	5	4	4	2.7	2.7	20.35	63.923	106.538	5	5	Upper Bathonian	Conflans	SIMON	67	67	67	67
68	<i>M. labechei</i> var. <i>cyclolitoides</i>	2024 0 30	7	21.2	19.2	6.2	circa 83	4 - 5	4.5	3 - 4	3.5	1.7	1.7	20.2	63.451		5	5	Upper Bathonian	Conflans	SIMON			68	68
69	<i>M. labechei</i> var. <i>cyclolitoides</i>	2024 0 30	8	21.3	18.8	7.1	82	4	4	2 - 3	2.5	1.8	1.8	20.05	62.980	83.974	7	7	Upper Bathonian	Conflans	SIMON	69	69	69	69
70	<i>M. labechei</i> var. <i>cyclolitoides</i>	2024 0 30	9	23.7	23.5	4.3	circa 86	4	4	?		1.8	1.8	23.6	74.131	98.842	6	6	Upper Bathonian	Conflans	SIMON			70	70
71	<i>M. decipiens</i>	2024 0 38	1	32.2	30.7	19.3	circa 88	4	4	3 - 4	3.5	3.7	3.7	31.45	98.789	131.719	8	8	Upper Bathonian	Fontoy	GARDET			71	71
72	<i>M. decipiens</i>	2024 0 38	2	30.2	28.3	18.1	73	4	4	5	5	2.2	2.2	29.25	91.879	122.505	6	6	Upper Bathonian	Fontoy	GARDET	72	72	72	72
73	<i>M. decipiens</i>	2024 0 38	3	27.5	26.1	15.8	76	3	3	4	4	2.0	2.0	26.8	84.183	84.183	10	10	Upper Bathonian	Fontoy	GARDET	73	73	73	73
74	<i>M. decipiens</i>	2024 0 38	4	24.1	23.7	13.8	circa 92	5	5	4	4	3.3	3.3	23.9	75.074	125.123	4	4	Upper Bathonian	Fontoy	GARDET			74	74
75	<i>M. decipiens</i>	2024 0 38	5	23.2	22.3	10.8	91	4	4	5	5	2.7	2.7	22.75	71.461	95.282	4 - 5	4.5	Upper Bathonian	Fontoy	GARDET	75	75	75	75
76	<i>M. decipiens</i>	2024 0 38	6	21.5	19.1	15.8	91	4	4	4 - 6	5	2.7	2.7	20.3	63.7668	85.021	?		Upper Bathonian	Fontoy	GARDET				76
77	<i>M. labechei</i>	2024 0 41	1	22.9	21.6	8.8	91	4	4	3	3	3.2	3.2	22.25	69.891	93.188	10	10	Upper Bathonian	Conflans	SIMON	77	77	77	77
78	<i>M. labechei</i>	2024 0 41	2	20.3	19.1	10.0	54	3 - 4	3.5	?		2.2	2.2	19.7	61.881		6	6	Upper Bathonian	Conflans	SIMON		78	78	78
79	<i>M. labechei</i>	2024 0 41	3	19.0	17.7	9.9	66	4	4	3	3	3.2	3.2	18.35	57.640	76.854	4	4	Upper Bathonian	Conflans	SIMON	79	79	79	79
80	<i>M. numismalis</i>	2024.0.35	1	20.8	19.4	5.5	circa 70	3 - 4	3.5	3 - 4	3.5	?		20.1	63.137		5 - 6	5.5	Upper Bathonian	Francheville	DELCAMBRE			80	80
81	<i>M. numismalis</i>	2024.0.35	2	20.4	18.6	4.0	98	5 - 6	5.5	4	4	1.7	1.7	19.5	61.252		5	5	Upper Bathonian	Francheville	DELCAMBRE	81	81	81	81
82	<i>M. numismalis</i>	2024.0.35	3	24.5	20.3	5.6	?	3	3	4	4	2.3	2.3	22.4	70.362	70.362	6	6	Upper Bathonian	Francheville	DELCAMBRE			82	82
83	<i>M. numismalis</i>	2024.0.35	4	19.2	17.6	3.1	95	5 - 6	5.5	5	5	?		18.4	57.7973		4	4	Upper Bathonian	Francheville	DELCAMBRE		83	83	83



84	<i>M. numismalis</i>	2024.0.35	5	21.2	16.1	8.3	circa 92	5	5	4	4	?		18.65	58.583	97.638	6	6	Upper Bathonian	Francheville	DELCAMBRE		84	84
85	<i>M. numismalis</i>	2024.0.35	6	16.8	15.5	6.0	circa 74	5	5	?		?		16.15	50.730	84.550	4	4	Upper Bathonian	Francheville	DELCAMBRE		85	85
86	<i>M. numismalis</i>	2024.0.35	7	16.0	15.5	4.4	84	5	5	circa 4	4	2.3	2.3	15.75	49.473	82.455	3	3	Upper Bathonian	Francheville	DELCAMBRE	86	86	86
87	<i>M. numismalis</i>	2024.0.35	8	15.0	12.7	6.4	75	6	6	4	4	2.3	2.3	13.85	43.505	87.010	3	3	Upper Bathonian	Francheville	DELCAMBRE	87	87	87
88	<i>M. numismalis</i>	2024.0.35	9	12.6	12	3.7	47	4	4	4 - 5	4.5	2.1	2.1	12.3	38.636	51.515	3 - 4	3.5	Upper Bathonian	Francheville	DELCAMBRE	88	88	88
89	<i>M. labechei</i> var. <i>numismalis</i>	2024.0.39		20.6	19.9	4.0	71	4 - 5	4.5	?		3.0	3.0	20.25	63.608		6	6	Upper Bathonian	Conflans	NICKLÈS	89	89	89
90	<i>M. labechei</i>	2024 0 44	1	specimen developed from two adjacent planulae (excluded)															Upper Bathonian	Fontoy	GARDET			
91	<i>M. labechei</i>	2024 0 44	2	29.3	27.4	7.9	94	4	4	4	4	2.6	2.6	28.35	89.052	118.736	6 ?	6	Upper Bathonian	Fontoy	GARDET	91	91	91
92	<i>M. labechei</i>	2024 0 44	3	excluded specimen (rejuvenation)															Upper Bathonian	Fontoy	GARDET			
93	<i>M. labechei</i>	2024 0 44	4	25.6	24.8	8.0	82	4	4	6	6	3.4	3.4	25.2	79.157	105.543	5	5	Upper Bathonian	Fontoy	GARDET	93	93	93
94	<i>M. labechei</i>	2025 0 44	5	27.4	25.5	9.5	103	4	4	5	5	3.7	3.7	26.45	83.084	110.778	8	8	Upper Bathonian	Fontoy	GARDET	94	94	94
95	<i>M. labechei</i>	2026 0 44	6	27.8	25.2	8.0	109	4	4	5	5	3.5	3.5	26.5	83.241	110.988	5	5	Upper Bathonian	Fontoy	GARDET	95	95	95
96	<i>M. labechei</i>	2027 0 44	7	29.7	27.2	9.6	95	4	4	?		3.2	3.2	28.45	89.366	119.155	7	7	Upper Bathonian	Fontoy	GARDET	96	96	96
97	<i>M. labechei</i>	2028 0 44	8	28.6	27.4	10.9	95	4	4	5	5	3.7	3.7	28	87.952	117.270	4	4	Upper Bathonian	Fontoy	GARDET	97	97	97
98	<i>M. labechei</i>	2029 0 44	9	27.6	25.3	8.9	96	4	4	4	4	?		26.45	83.084	110.778	5	5	Upper Bathonian	Fontoy	GARDET	98	98	98
99	<i>M. labechei</i>	2030 0 44	10	26.8	26.1	8.2	95	4	4	5	5	?		26.45	83.084	110.778	5	5	Upper Bathonian	Fontoy	GARDET	99	99	99
100	<i>M. labechei</i>	2031 0 44	11	27.6	24.4	10.9	?	?		?		?		26	81.670		?		Upper Bathonian	Fontoy	GARDET			100
101	<i>M. labechei</i>	2032 0 44	12	26.6	25.7	9.2	circa 56	2 - 3	2.5	3	3	?		26.15	82.141		6	6	Upper Bathonian	Fontoy	GARDET			101
102	<i>M. labechei</i>	2033 0 44	13	23.6	22.5	7.1	circa 71	4	4	4 - 7	5.5	3.1	3.1	23.05	72.404	96.538	5	5	Upper Bathonian	Fontoy	GARDET			102
103	<i>M. labechei</i>	2034 0 44	14	28.9	28.2	10.6	circa 62	3	3	4	4	3.9	3.9	28.55	89.680	89.680118	4 - 5	4.5	Upper Bathonian	Fontoy	GARDET			103
104	<i>M. labechei</i>	2035 0 44	15	24.2	22.8	5.5	76	4	4	4	4	2.6	2.6	23.5	73.817	98.423	4 - 5	4.5	Upper Bathonian	Fontoy	GARDET	104	104	104
105	<i>M. labechei</i>	2036 0 44	16	20.3	19.7	6.8	71	4	4	4	4	2.4	2.4	20	62.823	83.764	3	3	Upper Bathonian	Fontoy	GARDET	105	105	105
106	<i>M. labechei</i>	2037 0 44	17	23.1	21.9	8.6	117 int	9 int 4 ext	4	6	6	2.7	2.7	22.5	70.676		4	4	Upper Bathonian	Fontoy	GARDET			106
107	<i>M. labechei</i>	2038 0 44	18	24.7	21.7	8.9	circa 86	4	4	4	4	circa 3.5	3.5	23.2	72.875	97.167	4	4	Upper Bathonian	Fontoy	GARDET			107
108	<i>M. labechei</i>	2039 0 44	19	20.3	20.2	8.4	76	4	4	5 - 7	6	1.7	1.7	20.25	63.608	84.811	4 - 5	4.5	Upper Bathonian	Fontoy	GARDET	108	108	108
109	<i>M. labechei</i>	2040 0 44	20	20.9	18.2	6.8	66 ?	5	5	4	4	2.2	2.2	19.55	61.410	102.349	5	5	Upper Bathonian	Fontoy	GARDET			109
110	<i>M. labechei</i>	2041 0 44	21	26.0	25.9	6.9	97	4	4	5	5	2.5	2.5	25.95	81.513	108.684	?		Upper Bathonian	Fontoy	GARDET			110
111	<i>M. labechei</i>	2042 0 44	22	25.1	22.6	8.0	71	4	4	4	4	2.3	2.3	23.85	74.917	99.889	5 - 6	5.5	Upper Bathonian	Fontoy	GARDET	111	111	111
112	<i>M. labechei</i>	2043 0 44	23	27.5	26.2	9.4	79 ? likely more	4	4	4	4	1.9	1.9	26.85	84.340	112.453	7	7	Upper Bathonian	Fontoy	GARDET			112
113	<i>M. labechei</i> [now attributed to <i>Kobyphyllia</i>]	2044 0 44	24	25.8	24.4	7.6	circa 94	4	4	5	5	2.0	2.0	25.1	78.843	105.124	7	7	Upper Bathonian	Fontoy	GARDET			113
114	<i>M. labechei</i>	2045 0 44	25	22.5	21.8	6.2	?	4	4	?		2.0	2.0				3	3	Upper Bathonian	Fontoy	GARDET			114
115	<i>M. labechei</i>	2046 0 44	26	21.7	19.4	7.7	79	5	5	4	4	2.6	2.6	20.55	64.551	107.585	5	5	Upper Bathonian	Fontoy	GARDET	115	115	115
116	<i>M. labechei</i>	2024 0 45	1	26.8	24.9	9.1	95	3	3	4	4	3.1	3.1	25.85	81.199	81.199	6	6	Upper Bathonian	Conflans	NICKLÈS	116	116	116
117	<i>M. labechei</i>	2024 0 45	2	25.7	24.1	8.4	101	4	4	4	4	2.9	2.9	24.9	78.215	104.287	6	6	Upper Bathonian	Conflans	NICKLÈS	117	117	117
118	<i>M. labechei</i>	2024 0 45	3	22.5	22.4	7.8	circa 88	4	4	?		2.5	2.5	22.45	70.519	94.025	7	7	Upper Bathonian	Conflans	NICKLÈS			118
119	<i>M. labechei</i>	2024 0 45	4	24.9	23.4	8.4	circa 88	4	4	4	4	?		24.15	75.859	101.145	5	5	Upper Bathonian	Conflans	NICKLÈS			119
120	<i>M. labechei</i>	2024 0 45	5	25.9	25.1	8.8	circa 92 but 109 after reparation	4	4	4	4	2.3	2.3	25.5	80.100	106.799	4	4	Upper Bathonian	Conflans	NICKLÈS	120	120	120
121	<i>M. labechei</i>	2024 0 45	6	23.6	21.6	8.7	circa 83	4	4	4	4	2.4	2.4	22.6	70.990	94.654	6	6	Upper Bathonian	Conflans	NICKLÈS			121
122	<i>M. labechei</i>	2024 0 45	7	24.3	22.1	8.1	circa 66	4	4	3	3	2.4	2.4	23.2	72.875	97.167	5	5	Upper Bathonian	Conflans	NICKLÈS			122
123	<i>M. labechei</i>	2024 0 45	8	19.9	19.7	6.8	circa 64	4	4	3	3	2.6	2.6	19.8	62.195	82.927	6	6	Upper Bathonian	Conflans	NICKLÈS			123
124	<i>M. labechei</i>	2024 0 45	9	23.1	22.0	8.3	circa 73	4	4	3	3	4.1	4.1	22.55	70.833	94.444	3?	3	Upper Bathonian	Conflans	NICKLÈS			124
125	<i>M. labechei</i>	2024 0 45	10	22.2	21.6	8.7	90	4	4	3	3	3.8	3.8	21.9	68.7914	91.722	4	4	Upper Bathonian	Conflans	NICKLÈS	125	125	125
126	<i>M. labechei</i>	2024 0 45	11	20.4	20.5	10.4	91	4	4	4	4	3.0	3.0	20.45	64.237	85.649	8	8	Upper Bathonian	Conflans	NICKLÈS	126	126	126
127	<i>M. labechei</i>	2024 0 45	12	21.1	20.2	7.5	92	4	4	4	4	3.3	3.3	20.65	64.865	86.487	5	5	Upper Bathonian	Conflans	NICKLÈS	127	127	127
128	<i>M. labechei</i>	2024 0 45	13	19.6	18.6	6.8	93	4	4	6	6	2.9 ?	2.9	19.1	59.996	79.995	3	3	Upper Bathonian	Conflans	NICKLÈS			128
129	<i>M. labechei</i>	2024 0 45	14	19.3	18.0	6.0	circa 74	5	5	3	3	1.4	1.4	18.65	58.5826	97.638	4 - 5	4.5	Upper Bathonian	Conflans	NICKLÈS			129
130	<i>M. labechei</i>	2024 0 45	15	19.5	16.6	7.7	78	4	4	4	4	2.2	2.2	18.05	56.698	75.597	6	6	Upper Bathonian	Conflans	NICKLÈS	130	130	130



131	<i>M. labechei</i>	2024 0 45	16	18.9	18.0	8.3	78	4	4	5	5	2.1	2.1	18.45	57.954	77.273	2	2	Upper Bathonian	Conflans	NICKLÉS	131	131	131	131
132	<i>M. labechei</i>	2024 0 46	1	29.5	27.9	14.0 ?	?	4	4	?		?		28.7	90.151	120.202	?		Upper Bathonian	Conflans	?			133	132
133	<i>M. labechei</i>	2024 0 46	2	28.8	24.4	11.4	98	4	4	4	4	?		26.6	83.555	111.406	7	7	Upper Bathonian	Conflans	?		133		133
134	<i>M. labechei</i>	2024 0 46	3	27.0	26.4	7.8	80 or 104 according to approximations	3	3	4	4	4.0	4.0	26.7	83.869	83.869	?		Upper Bathonian	Conflans	?				134
135	<i>M. labechei</i>	2024 0 46	4	27.9	23.5	7.4	81	3	3	4	4	4.0	4.0	25.7	80.7278	80.728	6	6	Upper Bathonian	Conflans	?	135	135	135	135
136	<i>M. labechei</i>	2024 0 46	5	27.4	22.6	10.6	96	4	4	5	5	3.2	3.2	25.0	78.529	104.705	5	5	Upper Bathonian	Conflans	?	136	136	136	136
137	<i>M. labechei</i>	2024 0 46	6	24.5	21.0	7.8	86	4	4	6	6	4.3	4.3	22.75	71.461	95.282	5	5	Upper Bathonian	Conflans	?	137	137	137	137
138	<i>M. labechei</i>	2024 0 46	7	22.6	20.7	8.3	95	4	4	4	4	3.2	3.2	21.65	68.006	90.675	4	4	Upper Bathonian	Conflans	?	138	138	138	138
139	<i>M. labechei</i>	2024 0 46	8	23.5	22.2	8.4	89	4	4	4	4	2.2 ?	2.2	22.85	71.776	95.701	4	4	Upper Bathonian	Conflans	?		139	139	139
140	<i>M. labechei</i>	2024 0 46	9	19.5	17.3	6.3	circa 77	4	4	5	5	2.2	2.2	18.4	57.797	77.063	3	3	Upper Bathonian	Conflans	?			140	140
141	<i>M. labechei</i>	2024 0 46	10	19.9	18.5	5.1	circa 88	5	5	4	4	2.9	2.9	19.2	60.310	100.517	3 - 4	3.5	Upper Bathonian	Conflans	?			141	141
142	<i>M. labechei</i>	2024 0 46	11	16.9	16.4	4.3	60	4	4	5	5	?		16.65	52.300	69.734			Upper Bathonian	Conflans	?				142
143	<i>M. labechei</i>	2024 0 47	1	27.2	24.4	8.2	124	4	4	3 - 4	3.5	3.0	3.0	25.8	81.042	108.056	6	6	Upper Bathonian	Seicheprey	GARDET	143	143	143	143
144	<i>M. labechei</i>	2024 0 47	2	21.8	19.2	7.1	?	2	2	4	4	1.8	1.8	20.5	64.394	42.929	5	5	Upper Bathonian	Seicheprey	GARDET			144	144
145	<i>M. labechei</i>	2024 0 47	3	22.1	20.1	5.7	?	4	4	4	4	1.2	1.2	21.1	66.278	88.371	6	6	Upper Bathonian	Seicheprey	GARDET			145	145
146	<i>M. labechei</i>	2024 0 47	4	16.3	15.4	4.3	91	4 - 5	4.5	6	6	1.3	1.3	15.85	49.787		3	3	Upper Bathonian	Seicheprey	GARDET	146	146	146	146
147	<i>M. labechei</i>	2024 0 48		24.4	23.9	11.3	103	4	4	5	5	2.5	2.5	24.15	75.859	101.145	7	7	Upper Bathonian	Conflans	COUÉ	147	147	147	147
148	<i>M. trochoides</i>	2024 0 49		specimen excluded (too poorly preserved)																					
149	<i>M. labechei</i>	2024 0 50	1	24.3	22.9	6.8	98	4	4	4	4	1.9	1.9	23.6	74.131	98.842	4	4	Upper Bathonian	Villey Saint Étienne	?	149	149	149	149
150	<i>M. labechei</i>	2024 0 50	2	24.7	24.3	7.4	95	4	4	5	5	2.8	2.8	24.5	76.958	102.6117	4	4	Upper Bathonian	Villey Saint Étienne	?	150	150	150	150

colored cells were used in the presented univariate analyses