

DISTINCTION BETWEEN SYMPATRIC SPECIES OF *MICRASTER* (ECHINOIDEA) FROM THE ENGLISH CHALK

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ABSTRACT. Sympatric species of *Micraster* recorded from the upper Cretaceous Chalk of England are most easily distinguished from one another by the relative height of their periprocts measured from the base of the test. The observation of Gauthier (1887) and Melville (1954) that *Micraster* species with a high conical aboral surface (so-called 'gibbous' forms) have a lower periproct than the associated non-gibbous forms is confirmed by numerical analysis of samples from the Santonian of Kent (*M. gibbus* and *M. coranguinum*) and the upper Campanian of Norfolk (*M. stolleyi* and the *M. schroederi-glyphus* lineage). The nomenclature of the gibbous species *M. gibbus* and *M. stolleyi* is discussed.

THE genus *Micraster*, which ranges from middle Turonian to lower Maastrichtian, is often represented by a pair of sympatric species consisting of a gibbous species (i.e. one with a high conical aboral surface), and a non-gibbous species.

Throughout most of the nineteenth century all gibbous species were referred to *M. gibbus* (Lamarck, 1816). Whilst usually placed in the genus *Micraster*, Lamarck's species was sometimes regarded as an *Epiaster* (e.g. by Schlüter 1869 and Wright 1878), because of the absence of fascioles on many specimens.

Gauthier (1887) insisted that these gibbous forms be replaced in the genus *Micraster* and emphasized that their most obvious characteristics are the conical shape, the length of the petals, and the low periproct. He also noted that the pores of the unpaired petal are conjugate like those of the paired petals (in contrast with non-gibbous forms in which they are round and in which pores of one pair are separated by granules) and that the subanal fasciole may be present, reduced, or absent (in contrast with non-gibbous forms in which it is always present). In his discussion of *M. gibbus*, Gauthier suggested that the name *Gibbaster* might be used for the gibbous species but he did not designate a type-species for this new genus.

Lambert (1895, 1901, 1911) consistently omitted shape as a characteristic of *Gibbaster* and restricted this name to forms which have a subanal fasciole and conjugate pores in the unpaired petal, *M. fastigatus* Gauthier being designated as type species by Lambert and Thiéry (1924). The latter authors diagnosed *Isomicraster* Lambert, 1901 as having conjugate pores in the unpaired petal and lacking a subanal fasciole and designated *I. stolleyi* Lambert as the type species. Whilst these two taxa (regarded by Lambert and Thiéry as subgenera of *Micraster*) include all the gibbous species, since the shape of the test is no longer a diagnostic feature, non-gibbous *Micraster* with conjugate pores in the unpaired petal could be placed in *Gibbaster*. This has happened in the case of *G. belgicus* Lambert, 1911, the broad flat holotype of which I regard as a typical *M. rogalae*. I therefore reject the use of the nature of the pores in the unpaired petal as a criterion for subdividing the genus *Micraster*.

Most modern workers (e.g. Mortensen 1950; Fischer 1966) have followed Lambert in attaching great importance to the presence or absence of fascioles and have, as Kermack (1954) pointed out, been forced to remove *Isomicraster* from the family Micrasteridae and place it in the Toxasteridae. Having followed Mortensen in such a classification, Fischer (1966) concluded that the micrasterids were derived from the toxasterids via *Isomicraster* even though stratigraphical occurrence does not allow such a phylogeny and Kermack (1954) had shown that *Isomicraster* were evolved from *Micraster* by the disappearance of the fasciole due to natural selection. I wholeheartedly agree with Kermack's statement (1954, p. 421) that 'The presence or absence of a fasciole is therefore a most unsuitable character upon which to build the major subdivisions of the amphisternous spatangoids'. Within the genus *Micraster* a subanal fasciole is often present on specimens of species which have usually been placed in *Isomicraster*: e.g. *M. gibbus* (= *M. (Isomicraster) senonensis* in Kermack 1954) and *M. stolleyi* (R. V. Melville quoted in Mortensen 1951, Nichols 1959). The presence or absence of a subanal fasciole is therefore rejected as a means of distinguishing between sympatric species of *Micraster*.

This paper advocates a return to the views of Gauthier (1887) according to which gibbous *Micraster* are most easily distinguished from non-gibbous species not only by their conical shape but also by the low position of the periproct. Numerical data, derived from samples of gibbous and non-gibbous species collected from the same stratigraphical horizons, are recorded below in support of this assertion.

Method. The height of the highest part of the test (= total height) and the height of the top of the periproct were measured from the base of the test using a microball height gauge calibrated to an accuracy of 0.005 inches (0.002 mm). The instrument and the specimen being measured were placed on a sheet of ground glass so that the base of the height gauge corresponded to the base of the test. As both measurements were taken along the same axis, slight distortion of the specimens does not substantially affect the periproct height ratio (height of the top of the periproct: total height).

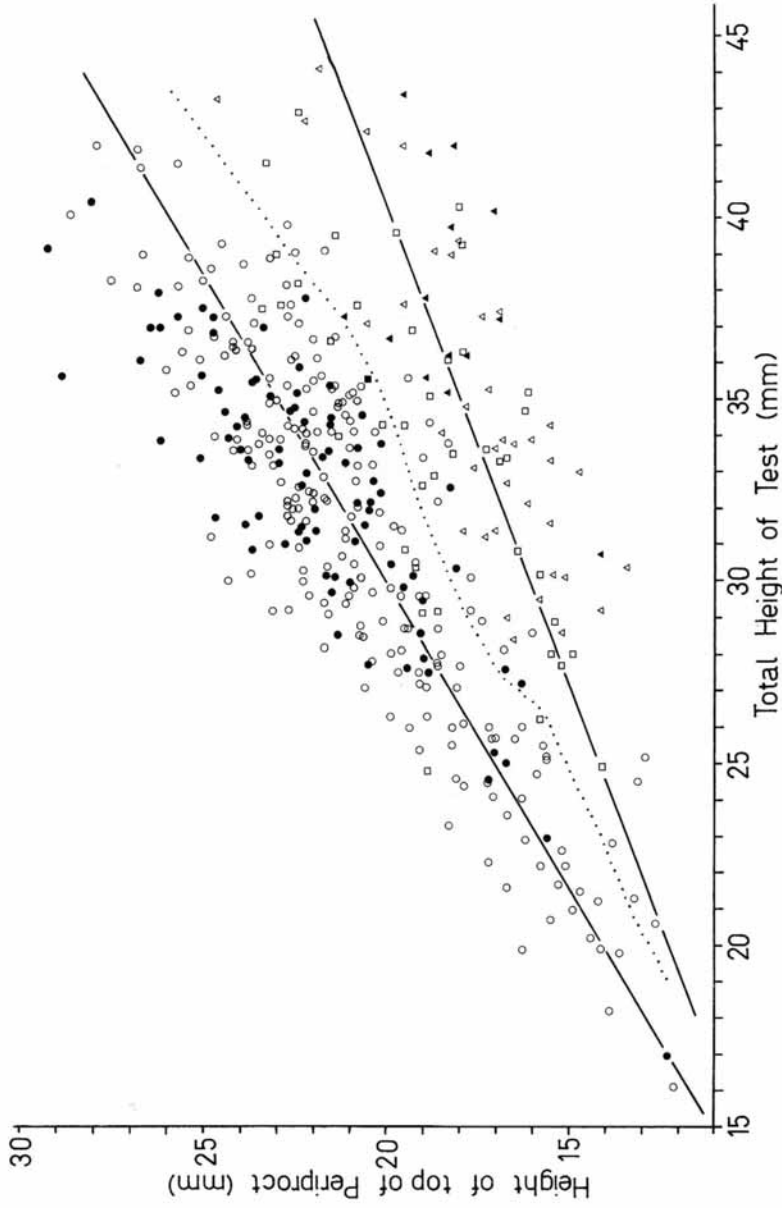
The original data is deposited in the Echinoderm Section, Department of Palaeontology, British Museum (Natural History).

M. GIBBUS AND *M. CORANGUINUM* FROM THE SANTONIAN OF KENT

Material. Rowe's collection of *Micraster* from the *coranguinum* Zone of Northfleet, Kent, now in the British Museum (Natural History). The 516 specimens which form this collection were purchased by Rowe from workers in the local quarry (? quarries) at Northfleet and thus it is impossible to give a more precise definition of the horizon(s) from which they came. The use of such a sample is justified because *M. gibbus* is such a rare species that no collection from accurately known horizons contains it in statistically acceptable numbers and, since this is the same sample which Kermack (1954) studied so thoroughly, the data presented below can be compared with, and supplement, Kermack's results and conclusions. The validity of the Northfleet sample in relation to 'populations' of fossils embedded in the chalk and the succession of living populations of which it represents the remains has been fully discussed by Kermack (1954).

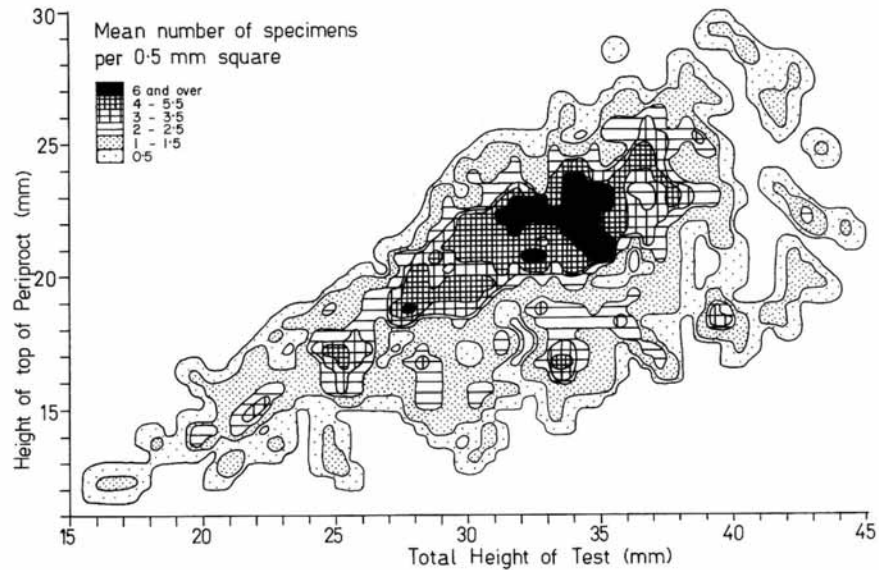
The two measurements could be taken on only 392 of the specimens but I measured only the height of the top of the periproct and used Kermack's (1950) measurements of the total height. Any error introduced by the acceptance of Kermack's measurements will be systematic and will have no significant effect on the graphs or the periproct height ratio.

Results and conclusions. Text-fig. 1 shows a simple plot of the measurements, the different symbols indicating Rowe's manuscript divisions of the sample. The presence



TEXT-FIG. 1. Rowe's collection of *Micraster* from the *coranguinum* Zone of Northfleet, Kent. The following manuscript divisions of Rowe are represented: open circles = '*M. coranguinum* (Leske)'; black circles = '*M. coranguinum* (Leske) var. *laticor*'; black squares = '*M. coranguinum* in all respects, save that there is no fasciole'; open squares = '*M. coranguinum* nearing *Epiaster* shape, but in no other way resembling it' plus '*M. coranguinum* still nearer to *Epiaster* shape, but in no other way resembling it'; open triangles = '*M. coranguinum* nearing or actually reaching *Epiaster* shape, and having a feebly developed fasciole' plus '*M. coranguinum* with anterior ambulacrum in process of modification, and the shape of *Epiaster* but with a slight but definite fasciole' plus '*Epiaster gibbus* save for the anterior ambulacrum'; black triangles = '*Epiaster gibbus*'. See text for further explanation.

of two species becomes evident only in text-fig. 2, which shows the density of the distribution of the specimens in text-fig. 1. Text-fig. 2 was constructed by counting the number of specimens in two overlapping 1-mm grid systems and taking the means of the overlapping quarters, thus tending to diminish the difference between the groups. The trend of *M. coranguinum*, with its periproct situated at about two-thirds of the total height, is clearly seen. *M. gibbus* has a less well-defined trend showing a much lower periproct. The fact that regions of low concentration of specimens occur between the two groups is significant in view of the fact that Kermack (1954) showed Rowe's collection to be biased in favour of intermediary forms.

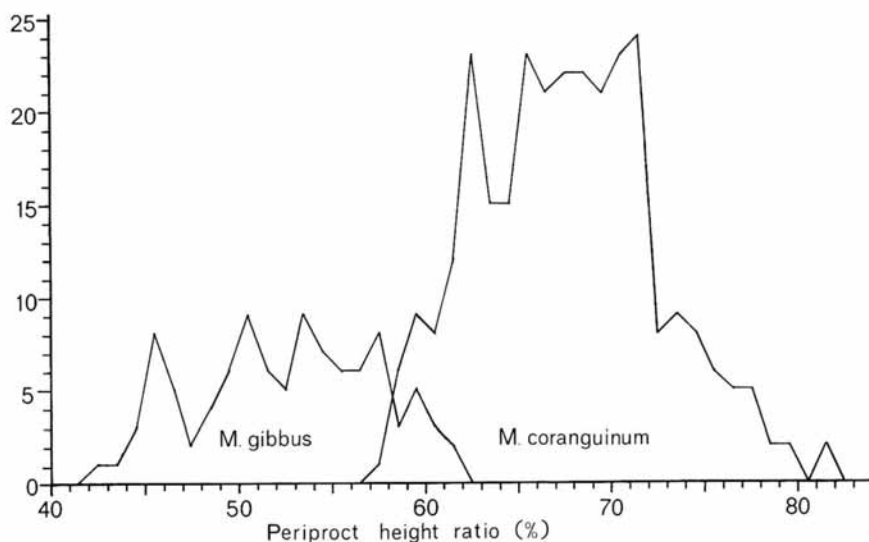


TEXT-FIG. 2. Rowe's collection of *Micraster* from the *coranguinum* Zone of Northfleet, Kent. Density contour graph of specimens in text-fig. 1 indicating the mean number of specimens of two overlapping 1-mm grid systems plotted per 0.5 mm square. *M. gibbus* lies in the discontinuous dense areas of low periproct height. *M. coranguinum* occupies the dense area indicating a periproct height ratio of about two-thirds.

A frequency distribution of the periproct height ratios does not reveal any bimodality unless, as in the hypothetical example given by George (1971, fig. 17), the sample is first subjectively or arbitrarily divided and the two species plotted independently, thus avoiding the frequencies of a particular ratio common to both species being compounded. Text-fig. 3 shows such a frequency distribution in which the sample was arbitrarily divided along the dotted line in text-fig. 1. The latter passes through the areas of low concentration in text-fig. 2. The calculated regression lines of the two species drawn on text-fig. 1 result from this division.

The lack of bimodality in text-fig. 3 is most probably due to a combination of several factors, two of which were discussed by Kermack (1954). Firstly, Rowe's sample of his '*Epiaster gibbus*' is too small for any bimodality to make itself apparent, and, secondly, the ratio of two variates is not a constant but is almost always allometric. The fact that the sample is biased in favour of intermediate forms, as well as *M. gibbus*, increases the difficulty in obtaining bimodality.

Like Kermack, I regard *M. gibbus* and *M. coranguinum* as distinct species between which intermediates occur presumably as a result of interbreeding.



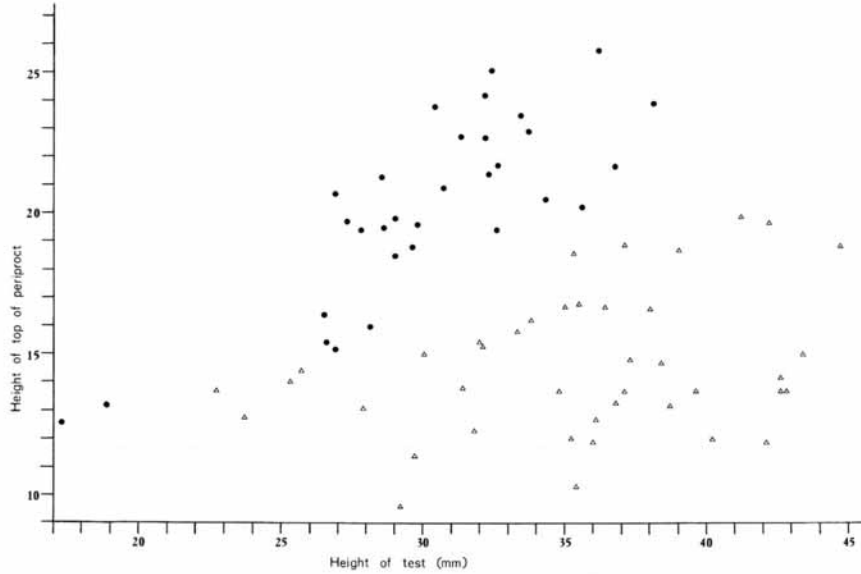
TEXT-FIG. 3. Rowe's collection of *Micraster* from the *coranguinum* Zone of Northfleet, Kent. Frequency distribution of the periproct height ratio. The sample was divided along the dotted line shown in text-fig. 1 which passes through the low density areas of text-fig. 2. Vertical axis indicates number of individuals.

M. STOLLEYI AND THE *M. SCHROEDERI*-*GLYPHUS* LINEAGE FROM THE UPPER CAMPANIAN OF NORFOLK

Material. Seventy-two specimens from the *mucronata* Zone of Norfolk in the collections of the British Museum (Natural History) (Rowe Collection), Institute of Geological Sciences (H. B. Woodward Collection), and the Norwich Castle Museum (Rose and Brydone Collections). Where information on museum specimens allowed, they were assigned to more narrowly defined horizons within the *mucronata* Zone from information given in Peake and Hancock (1961, 1970). The *mucronata* Zone succession is: Basal, Eaton, Weybourne, Beeston, and Paramoudra Chalks, the Weybourne and Beeston Chalks being separated by the Catton Sponge Bed. *M. stolleyi* is represented by 1 specimen from Tharston (Basal Chalk), 6 from Weybourne and Weybourne-Old Hythe, and 4 from Harford (Weybourne Chalk), 5 from Catton (Catton Sponge Bed), 1 from Whitlingham, 1 from Overstrand, 6 from Thorpe (Paramoudra Chalk), and 17 others for which the locality is unknown or vague (e.g. 'Norwich'). The *M. schroederi-glyphus* lineage

is represented by 1 specimen from Stonehills (Eaton Chalk), 3 from Weybourne and Weybourne-Old Hythe, and 9 from Harford and Harford Bridges (Weybourne Chalk), 2 from Catton (Catton Sponge Bed), 4 from Whitlingham (Paramoudra Chalk), and 12 others with unknown or vague localities.

Results and conclusions. In order to obtain samples of statistically valid size, both Kermack (1954) and Nichols (1959) were forced to treat all the *mucronata* Zone *Micraster* as though they came from one horizon. Text-figs. 4 and 5a show that in so doing no distinct break appears between the two lineages in this zone. Text-fig. 5b-d is based on specimens which were assigned to more limited horizons, but statistical validity is here sacrificed.



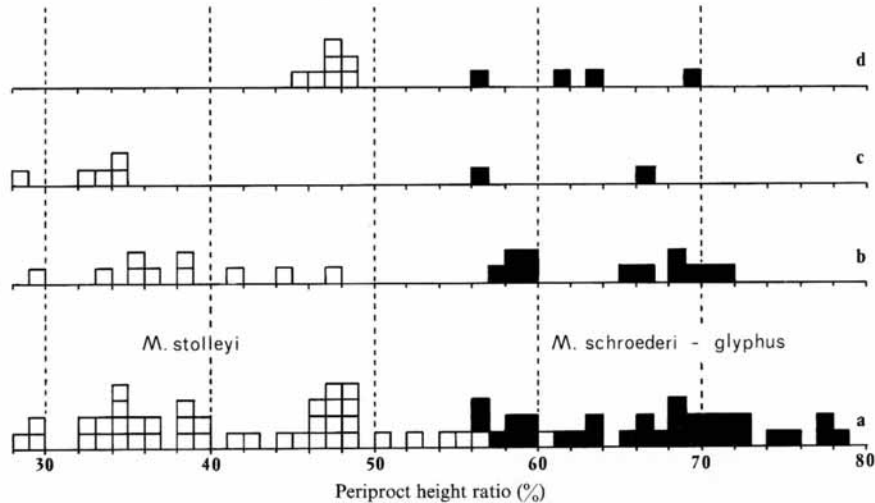
TEXT-FIG. 4. *Micraster* from the *mucronata* Zone of Norfolk. All specimens measured. Black circles = the *M. schroederi-glyphus* lineage; open triangles = *M. stolleyi*. The height of the top of the periproct is in millimetres.

The overlap of *M. stolleyi* and the *M. schroederi-glyphus* lineage in text-fig. 5a is almost certainly due to the effects of allometric growth on the periproct height ratio. The four specimens of *M. stolleyi* with periproct height ratios between 54% and 61% are all small (presumably juvenile specimens) ranging from 32 to 39 mm in length and from 22 to 26 mm in total height (i.e. the four specimens of *M. stolleyi* the furthest to the left in text-fig. 4). Their high periproct height ratios are a reflection of the more tumid shape typical of juvenile specimens of *Micraster*.

The periproct height ratio of the gibbous species is very variable in the *mucronata* Zone as a whole and in the Weybourne Chalk (text-fig. 5a and b), but of very limited variability at certain horizons such that it could be used to define the horizons at

Catton (Catton Sponge Bed, text-fig. 5c) and Thorpe (Paramoudra Chalk, text-fig. 5d). These changes in periproct height ratio may be a reflection of ecological conditions.

Kermack (1954) stated that there are no transitional forms between *M. stolleyi* and *M. glyphus* in the *mucronata* Zone of Norfolk where some aberrant forms, resembling in some ways *M. coranguinum*, are also found. These latter forms are most probably *M. schroederi* Stolley which is the narrow form of *M. glyphus* or, possibly, true aberrant *M. coranguinum*, which occurs in the Santonian of Norfolk, of which the horizon has been mistaken due to insufficient information on the



TEXT-FIG. 5. Frequency distributions of the periproct height ratio of *Micraster* from the *mucronata* Zone of Norfolk. *a* = all specimens measured; *b* = specimens from the Weybourne Chalk (Weybourne, Weybourne-Old Hythe, Harford, and Harford Bridges); *c* = specimens from the Catton Sponge Bed (Catton); *d* = specimens from the Paramoudra Chalk (Thorpe and Whitlingham). Each square represents one specimen. Horizons represented in *b*, *c*, and *d* are included in *a*, but some other horizons are not shown separately.

museum specimens. Nichols (1959) concluded that intermediates exist and that they had a shorter life-span than the extreme forms (i.e. *M. stolleyi* and *M. glyphus*) which he did not regard as good species. I agree with Kermack that *M. stolleyi* and the *M. schroederi-glyphus* lineage are good species. Even if the four small specimens of *M. stolleyi* with relatively high periproct height ratios (discussed above) are regarded as intermediate in morphology to the *M. schroederi-glyphus* lineage, they are not necessarily the product of interbreeding and the two stocks can be interpreted as being genetically distinct.

NOMENCLATURE

Species of *Micraster* have long been renowned for their burdensome synonymies, but it is amongst the gibbous species in particular that nomenclature is most disputed. A lengthy discussion on the status of the subgenera of *Micraster* is avoided by suppressing them on the grounds that they have polyphyletic origins (Stokes 1975), but the nomenclature of the English gibbous species demands a brief explication in view of the names adopted here.

The type specimen of *M. gibbus* (Lamarck, 1816) was figured by Bruguières (1791, pl. 156, figs. 4-6) but the locality and horizon of this specimen, as well as its present whereabouts, remain unknown. However, as Valette (1907) remarked, it is more rational to think that it came from the Chalk of the Anglo-Paris basin rather than elsewhere. I have therefore proposed (Stokes 1975) that the name *M. gibbus* be restricted to gibbous forms from the Coniacian and Santonian of the Anglo-Paris basin, specimens of which agree reasonably with Bruguière's figures. Other authors have used *M. gibbus* in a different sense. Lambert (1895) restricted the name to a form from Nice which Sismonda (1843) called *M. cordatus* despite the fact that Sismonda regarded it as distinct from Bruguière's figures, that it was not figured and that the description could apply to a variety of gibbous forms. *Micraster* were unknown from Nice until the work of Sismonda and thus it is unlikely that Bruguière's specimen came from the Alpes Maritimes. More recently, Ernst (1970) used the name for lower Campanian forms of northern Germany which ought to be called *M. fastigatus* Gauthier, 1887.

Having restricted the name *M. gibbus* to a form from Nice, Lambert (1895) intended that the name *M. senonensis* be given to the Coniacian and Santonian species of the Anglo-Paris basin. 'Le type de moyenne taille', represented by the *Epiaster gibbus* of Wright (1878), being the first of Lambert's four varieties, should be taken as the true *M. senonensis*, and the figures of Wright (1878, pl. 63) will then represent the type specimen. The label accompanying this specimen (British Museum (Natural History) E 1510) suggests, as does the text of Wright's monograph, that it comes from the upper Campanian of Harford Bridges, Norfolk, in which case *M. senonensis* Lambert, 1895 is a senior synonym of *M. stolleyi* Lambert, 1901. To avoid further confusion, I have suppressed the name *M. senonensis* and conserved *M. stolleyi* in its current usage (Stokes 1975).

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