On the Dimorphism of the English Species of Nummulites, *and the Size of the Megalosphere in relation to that of the Microspheric and Megalospheric Tests in this Genus.*

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[Plates 3—5.]

(1) *The Dimorphism of the English Species of Nummulites.*

Before the dimorphic character of many of the species belonging to the higher groups of the Foraminifera was established, some of the phenomena dependent on it had been recognised among the fossil nummulites, and attention was called to the peculiar mode of occurrence in pairs of what were then regarded as the different species of *Nummulites* and *Assilina*, in the beds in which they abound.

It was especially by the careful labours of de Hantken and de la Harpe that this phenomenon was brought to light, and the "Law of the Association of Species in Pairs" was formulated by the latter in his 'Étude des Nummulites de la Suisse' (5, p. 63), as follows:—"Les nummulites apparaissent par couples; chaque couple est formé de deux espèces du même groupe zoologique et de grandeur inégale, la grande est sans chambre centrale, la petite en a toujours une."

De la Harpe proceeds to point out that the small species is usually much more abundant than the large, often furnishing 90 per cent. or more of the whole number of specimens present in the deposit.

In gathering materials for his 'Étude,' in which he proposed to deal not with the Swiss nummulites alone, but with the group as a whole, hoping to be able to introduce order into the "Babylonian confusion" in which he found it, de la Harpe received specimens of the English nummulites from Professor Rupert Jones, and in acknowledging them, wrote (October 10, 1879):—

". . . . . (II) *N. variolaria* from Stubbington, and (III) *N. variolaria* from White-Cliff Bay, are exactly the same as the Belgian form. They belong to the type of the species.

"It is remarkable that among your specimens there is not a single *N. Heberti*, which species is nearly always the companion of *N. variolaria*. In Belgium and France, in the upper part of the *variolaria*-beds, there is usually 1 per cent. of *N. Heberti*. In the lower beds (base of the

'Laekenian') these are more numerous (up to 50 per cent.). Is it that *Heberti* is totally absent, or that the number of the specimens you kindly sent me is still too few for strict comparison? This is an interesting question to solve.

"(IV) My best thanks for *N. Prestwichiana*, R. Jones . . . . . I am now working out the Belgian Nummulites. I find in that country eight species, very distinct and easy to separate."

Here follows the list:—

I.	*N. planulata*, Lamk.,	"without central chamber.'
	N. elegans, Sow.,	"with central chamber."
II.	*N. laevigata*, Lamk.,	"without central chamber."
	N. Lamarcki, d'Arch.,	"with central chamber."
III.	*N. Heberti*, d'Arch.,	"without central chamber."
	N. variolaria, Sow.,	"with central chamber."
IV.	*N. d'Orbignyi*, Gal.,	"without central chamber."
	N. Wemmelensis (or *Prestwichii*).	"with central chamber."

De la Harpe continues: "They make four pairs, of two species each, one species being without, the second with the central chamber . . . . . .

"As far as I know, *N. Heberti* and *Orbignyi* have not yet been observed in England. I should be very much surprised if they do not exist in the same beds with *N. variolaria* and *Wemmelensis* (*Prestwichii*). Their absence would be a remarkable exception to the general law of the distribution of Nummulites." The law is then stated nearly in the form given above [10, Supl. Note viii, 2].

Although de la Harpe had done so much to bring to light the essential facts of the case, he had suggested no explanation of this remarkable law. The question of its significance remained for him "sans solution."

In the following year (1880) Munier-Chalmas brought before the Geological Society of France his conclusion, based on the study of four fossil species of *Nummulites* and two of *Assilina*, that the species of these genera are dimorphic, and that the phenomenon of dimorphism would be found to be general (15). The explanation thus offered of the phenomenon of the distribution of the "species" in couples, was that the members of the couple were not, in fact, of distinct species, but that they represented two forms of a single species.

So far, Munier-Chalmas' conclusion was, as subsequent investigations have abundantly proved, entirely right. It has been shown by observations on living foraminifera (13, 14, and 16) that the form with the large central

chamber (megalospheric) may arise as the offspring of the form with a small central chamber (microspheric) (not "without central chamber," as stated by de la Harpe), and there are good grounds for concluding (14, pp. 74 to 77) that the two supposed "species" represent alternating or recurring generations in the life history of a single species. This, however, is to anticipate the history of the subject.

To the entirely right conclusion above stated, Munier-Chalmas unfortunately added an extension of his view which was wrong. It so happened that among the microspheric specimens of the species which he investigated he failed to find any of so small a size as that commonly attained by the megalospheric form; and he concluded that though the two sets of individuals constituting a species were in some unexplained way of different natures, yet that both began life in the guise of the megalospheric form. At a certain stage of growth, it was supposed, the individuals of one, and the more abundant set ceased to grow, while the growth of the members of the other set proceeded. On the one hand, chambers were added in forward continuation of the series already formed, building up the large test of the microspheric form; and on the other, at the centre of the test, the large central chamber was absorbed, and chambers of smaller and smaller size were laid down, continuing the spiral series in a backward direction to the centre.

In January, 1881, the first part of de la Harpe's 'Étude' appeared, and under the head of "Association of Species" (p. 65) he criticised Munier-Chalmas' conclusions. In the same month, writing in association with de Hantken, he addressed a letter to M. Tournouer, of the Geological Society of France (6) in which the same criticisms are set forth.

He had no difficulty in disposing of the second part of Munier-Chalmas' proposition. With regard to the dimorphism of the species of nummulites, he says:—"Une idée qui, sans avoir été formulée, a cependant traversé l'esprit de plusieurs, c'est que ces deux formes sœurs, toujours associées, représenteraient peut-être les deux sexes de la même espèce. Rien dans leur mode de distribution ni dans leur fréquence relative ne s'opposerait à cette hypothèse. En l'admettant tous les faits deviendraient faciles à comprendre. D'autre part, dans les Rhizopodes, non seulement les sexes ne paraissent pas être séparés, mais leurs diverses fonctions ne semblent pas même localisées. Comment donc admettre que deux Rhizopodes bâtis sur des plans différents représentent les deux sexes d'une même espêce? La question reste donc sans solution."*

Driven now, as it would appear, by the error of the second part of Munier-Chalmas' proposition, to adopt an attitude very similar to that which,

* 'Étude,' p. 65.

as we find by his letter to Professor Jones, he would have been "very much surprised" a year and a half before to have found correct, de la Harpe proceeded to state that the law of the association of species in pairs has exceptions. He mentions *N. gizehensis*, *Vicaryi*, *obtusa*, and says that among species with small central chambers (*i.e.*, as we now say, small megalospheres), "il est plusieurs dont les homologues n'existent pas ou n'ont pas encore été découvertes. Citons *anomala*, de la Harpe, *dubia*, de la Harpe, et *subplanulata*, Hantk." Perhaps other species, he adds elsewhere, will be found "privées d'une sœur."

It is true that in the case of *N. Vicaryi* and *obtusa* de la Harpe did not speak from his own observation. They are only cited from Medlicott and Blanford's 'Manual of the Geology of India' (published in 1879), and there is no evidence that either the collectors or describers of these species were looking out for associated forms. So that these cases go for very little.

Moreover, in the second part of the work, being an "Étude détaillée des Nummulites du groupe de la *N. gizehensis* Ehrenb.," de la Harpe points out that this species forms no exception, *N. curvispirus* (a form which he had previously regarded as identical with *N. Lucasanus*) being its habitual companion, associated with it as he elsewhere (7) says, by thousands and millions.

But before leaving de la Harpe, let us hasten to call to mind that in the fourth part of the 'Étude' (consisting of a systematic account of the group of *N. Murchisoni*, a division of the "Nummulites à filets non reticulés") and published after the untimely death (in February, 1882) of this talented palæontologist he departs from the classification proposed in the first part and deals with the species in pairs, describing in each case a megalospheric form immediately after its microspheric "homologue." There is thus some ground for thinking that in the last year of his life de la Harpe returned to the sounder view of the general prevalence of the law of association in pairs which he had himself done so much to substantiate.*

Although fully convinced of the truth of the doctrine of the dimorphism of the species not only of *Nummulites*, but of most† of the higher groups of the foraminifera, I have often felt, and especially before looking into de la

* Since writing this I have found the following passage in a paper read by de la Harpe before the Société Vaudoise des Sciences Naturelles on September 9, 1881 :—(8, p. 437) "Est ce" (*i.e.*, the law of association by pairs) "une règle sans exception ? Oui, nous le croyons. Hâtons-nous d'ajouter que ce n'est que tout dernièrement que nous avons acquis cette conviction." He proceeds to withdraw the case of *Nummulites gizehensis*, as in the second part of the 'Étude.' No mention is made in this communication of the other exceptions insisted on in the 'Étude.'

† I say *most* in view of the peculiar character of the pelagic foraminifera, a group on which I hope shortly to have something to say.

Harpe's position afresh, that his insistence on the exceptions to the law of distribution in pairs was a difficulty which it would be desirable, if possible, to clear up. No one knew better than de la Harpe how widely the law holds good, and yet he insisted on exceptions. If there are strata in which only one form is present, how can this be reconciled with the view that both forms recur at short periods in the life-history of the species?

The difficulty appeared to be emphasised by Professor Rupert Jones' paper (11) on "*Nummulites elegans* and other English Nummulites," in which he for the first time gave an account of the characters and distribution of the English species, and cleared up the confusion which had arisen over the identity of the type specimens of "*N. elegans*," illustrated in Sowerby's 'Mineral Conchology' (20).

The matter of dimorphism is dealt with very sparingly in this paper. It was written seven or eight years after de la Harpe had expressed his surprise at the apparent absence from the English beds of the forms named *N. Heberti* and *N. Orbignyi*, the [microspheric] homologues of *N. variolarius* and *N. wemmelensis* var. *elegans* (to use the name which Professor Jones now applied to the species which he had previously (9) named *N. planulata* var. *Prestwichiana*).

Of the latter it is stated (on page 140) that it is one of the nummulites which have a large primordial or central chamber, and the megalospheric character is shown in figs. 4 and 8 of his Plate 9.

The figure of the section of *variolarius* also shows a small megalosphere at the centre, and the description of this species ends with the words "according to Dr. de la Harpe the *N. variolarius* of the Barton Beds of Stubbington and White Cliff Bay is the same as that of Belgium and typical. He did not find *N. Heberti* (having a small central chamber) with it, though accompanying it in Belgium and France."

Of *N. laevigatus* it is said, "according to Dr. Ph. de la Harpe, the Bracklesham Nummulites comprise both *N. laevigatus* and *N. Lamarcki*, the latter having a large central chamber . . . . ."

It thus appeared to be possible that "*N. wemmelensis* var. *elegans*" and *N. variolarius*, at least as they occur in our English beds, might afford some evidence of a similar nature to that of the supposed exceptions insisted on by de la Harpe; and, at any rate, so far as published descriptions went, they were, in the English beds, forms, to use his expression, "privées d'une sœur."

I therefore spent some days last September in the Isle of Wight and on the adjoining coasts of Sussex and Hampshire in search of the species of nummulites in the Middle and Upper Eocene Beds, with the purpose of examining them from the point of view of dimorphism. I will now give the results.

Nummulites laevigatus (Brug.) (*Lamarcki* d'Arch.).*

This species abounds in some of the upper Bracklesham Beds, near Selsey. It is an admirably clear example of the law of association of species in pairs or as we now say of a dimorphic species, the difference between the two associated forms being obvious to superficial inspection in the sizes they attain (Plate 3, *a* and *b*). As the specimens lie in the beds, and still more clearly on separating them, by a sieve, from the scarcely hardened glauconitic sand in which they are contained, the full grown microspheric forms (*N. laevigatus* (Brug.) proper) are at once distinguished by their large size.

The average diameter of 12 such specimens is 15·8 mm., that of 19 approximately full-grown specimens of the megalospheric form (the *N. Lamarcki* of d'Archiac and Haime) being 4·5 mm.

The relative proportion of large to small forms in four samples (containing in all some 8000 specimens) is 1 : 8·2, 1 : 16·7, 1 : 5·8, and 1 : 10, giving an average of 1 : 10. It must, however, be borne in mind that a certain proportion of the small specimens are young microspheric individuals.

On grinding down examples of the *microspheric* form to obtain sections showing the initial chamber, the diameter of this is found to be in two cases 16 and 19 μ (Plate 3, *b''*).

The megalosphere is very large in this as compared with that found in the other English species. Among 20 specimens the mean between the long and short diameters varies from 355 to 595 μ, and the average is 443 μ, nearly $\frac{1}{2}$ mm. (Plate 3, *a''*).

After this experience at Selsey, it was striking to find the specimens of the little *N. variolarius*, which are thickly scattered through a sandy band in the Bracklesham Beds at White Cliff Bay, and of *N. Orbignyi* (*wemmelensis*) var. *elegans* from the base of the Barton Beds at Alum Bay in the Isle of Wight and at other localities, all attaining an approximately uniform size. In external appearance, therefore, these species showed no indication that they conform to the law of dimorphism.

* In view of the fact that each of the two forms of the species of nummulites has been separately named the question arises (*cf.* M. E. van den Broeck [2]) which of the two names so applied shall stand as that of the species. There seems no reason for departing from the ordinary rules of nomenclature in this instance. I have, therefore, in each case selected for that of the species the name first given, whether to the megalospheric or the microspheric form of it. M. van den Broeck would prefer to select for the specific name that of the megalospheric form (which he, rather oddly, regards as the more "normal" form of the species); concluding that, this form being the more abundant, it will usually turn out to be that first given. As a fact, however, among the 9 species dealt with in this paper the megalospheric form was, I believe, named before the microspheric in only one, viz., *N. variolarius*.

Examination of them by section, however, yielded the following results:—

Nummulites variolarius (Lamk.) (*N. Heberti*, d'Arch.).

Among 168 specimens examined in section 163 are megalospheric, and 5 microspheric, a proportion of 33 to 1.

In the *megalospheric* specimens (Plate 4, *a*, *a'*, *a''*) the mean between the longest and shortest diameters of the initial chamber, as it appears in the section* varies, as shown in fig. 1, from 38 to 102 μ, the average size being about 68 μ. The largest specimen of this form is 2 mm. in the longer diameter of the test, the average diameter in 13 large specimens is 1·8 mm.

In the *microspheric* form (the *N. Heberti* of d'Archiac)† the mean diameter of the initial chamber (= *m*) in the five cases is 15, 16, 16, 16, and 17 μ (Plate 4, *b b'*). Specimens of this form also attain a diameter of 2 mm., and the average in five large specimens is 1·92. There is thus a slight tendency in this species for the microspheric form to exceed the megalospheric in size. (See also the table on p. 311.)

Nummulites Orbignyi (Galeotti), (*wemmelensis*, de la Harpe and van den Broeck), var. *elegans*, Sow.‡

Operculina Orbignyi, Galeotti, 'Mém. couronné. Acad. de Belgique,' T. 13, p. 54.

* I use *M* to indicate this mean value in the megalospheric form, and *m* in the microspheric form.

† In the 'Bull. Soc. Géol. de France,' 1881, p. 172, de la Harpe says "Enfin pour le *N. variolaria*, Sow. : le fait est plus frappant encore ; on est presque toujours obligé de briser ces petites nummulites de Paris, Bruxelles, Gand, Stubbington et Isle de Wight pour savoir si, oui ou non, elles ont une chambre centrale, et si l'on doit les ranger parmi les *N. Heberti* ou *variolaria*."

‡ Perhaps it is due to my readers to set before them as briefly as possible some of the changes of nomenclature of which this pretty little nummulite has been the victim.

In the 'Mineral Conchology,' vol. 6 (1829), p. 76, Sowerby set about describing three species of nummulites, figuring them on Plate 538. The groups of figures in illustration of each species are numbered 1, 2 and 3, though the group numbered 3 comes in the middle and that numbered 2 below. The several figures in each group are not numbered, but by counting the figures and following the order of the numbers of the groups, a number may be given to each figure. In this way the numbers 6 to 11 may be assigned to the figures in group 2, the lowest on the Plate.

The first and third species enumerated are *N. laevigata* and *N. variolaria*, and about their identity there is no question; but unfortunately Sowerby confused two distinct species under the name *N. elegans*, constituting his second species. The two species thus confused appear to have been, as shown by comparing the figures with the specimens in the Sowerby Collection now in the British Museum :—

N. wemmelensis var. *elegans* (called *N. Orbignyi* var. *elegans* in this paper), mounted on tablets 44,007 (1 and 2), and *N. planulata* (Lamk.), said to come from Emsworth, and mounted on tablets 44,007 (3 to 5).

Nummulina planulata, Lamk., var. *Prestwichiana*, T. R. Jones. ('Q. J. G. S.,' vol. 18, 1861, p. 93.)

Nummulites wemmelensis, de la Harpe and van den Broeck, var. *Prestwichiana*, T. R. Jones. De la Harpe's "Étude des Nummulites de la Suisse," 'Mém. Soc. Palæont. Suisse,' vol. 10, 1883, p. 169.

Nummulites wemmelensis, de la Harpe and van den Broeck, var. *elegans*, Sow. T. R. Jones. 'Q. J. G. S.,' vol. 43 (1887), p. 132.

Of the latter no specimens have, in recent years, been known to occur near Emsworth, or indeed anywhere else in England, and it appears probable, as Professor Jones has pointed out (11), that in addition to confusing two species under one specific name, Sowerby assigned a wrong locality to one of them by referring to Emsworth, a village near Chichester, a specimen from a Belgian or some other Continental locality.

In 1861 Professor Jones having specimens from Bed No. 29 of Alum Bay and from High Cliff referred to him for naming, and supposing that all the specimens named by Sowerby *N. elegans* should be referred to *N. planulata*, gave the name *N. planulata* var. *Prestwichiana* to the apparently new variety from Bed 29. (9.)

In 1879 de la Harpe was, as we have seen, reviewing the species of nummulites, and received from Professor Jones specimens from Bed 29. He considered them to represent a local variety of a species widely distributed in Belgium and France, on which in association with van den Broeck, he bestowed the name of *N. wemmelensis* ("Étude," p. 169), distinguishing the Alum Bay specimens under the name var. *Prestwichiana* (or, in the description of Plate 6, as *Prestwichi*).

In the same (posthumously published) work de la Harpe gave the name *N. elegans*, Sow., to a "species" (the megalospheric form of *N. planulata*), which, as he stated, is distinct from *wemmelensis* and its varieties, giving in the list of synonyms :—

1829, *N. elegans*, Sow. (pars) 'Mineral Conchology,' vol. 6, p. 76, Plate 538, figs. 9, 10, 11 (non figs. 6, 7, 8). Thus referring to fig. 10 among others in Sowerby's plate for an illustration of this species.

In 1886, Professor Jones having recognised that some of the specimens named *elegans* in the Sowerby Collection were identical with his *N. planulata* var. *Prestwichiana*, and de la Harpe's and van den Broeck's *wemmelensis* var. *Prestwichiana*, from Bed 29, in Alum Bay, wrote his paper on *N. elegans* and the other English Nummulites (11), in which he withdrew the name *Prestwichiana* and pointed out that the proper name of the species is *N. wemmelensis*, de la Harpe and van den Broeck, var. *elegans*, Sow. (In many parts of the paper the name *N. elegans* is, however, employed.) He also expressed the opinion that one of the sections on Sowerby's tablets was the identical specimen from which fig. 10 in Plate 538 of the 'Mineral Conchology' is taken.

It thus comes about that the same figure (Plate 538, fig. 10) in the 'Mineral Conchology' is claimed by de la Harpe as an illustration of his *N. elegans*, and by Professor Jones as an illustration of his *wemmelensis* var. *elegans* from Bed 29 of Alum Bay.

In this paper I have used the name *N. Orbignyi* (Gal.), which was given in 1837, for the species as a whole, as being that which was first applied to a member (a microspheric specimen) of the main body of it.

N. elegans, Sow. (1829) has, of course, priority over *Orbignyi* (Gal.), but this was applied to a member of the Alum Bay variety, which, according to de la Harpe, is so distinct from the Continental forms that it is impossible to take it as the type of the species (10, p. 92). These Continental forms were named *N. wemmelensis*, de la Harpe and van den Broeck in 1883.

Nummulites elegans, Sow., T. R. Jones. *Ibid.*

I have examined specimens from two localities, my own from Alum Bay and a sample from Huntingbridge. The two sets are somewhat different, and it will be convenient to deal with them separately.

Those from Alum Bay (Plate 5, *m*) are from the bed which is regarded by geologists as the bottom layer of the Barton Clay, passing conformably into the underlying Bracklesham Beds (and often referred to as Bed 29 of Prestwich's section). They are apparently identical with the specimens on the tablets 44,007 (1) and (2) of the Sowerby Collection now in the British Museum.

On grinding down 95 specimens to display the initial chambers, I find 93 to be megalospheric, and 2 to be microspheric, a proportion of 46·5 to 1.

In the *megalospheric* specimens (the *N. wemmelensis* de la Harpe and van den Broeck, var. *elegans*, Sow.) *M* varies (fig. 1) from 66 to 148 μ, the average being about 96 μ (Plate 5, *a*–*a''*).

The largest specimens of this form are about 3 mm. in the longer diameter of the test.

In the two *microspheric* specimens the value of *m* is 17 and 19 μ. The diameter of the test in these specimens does not exceed that of the larger megalospheric forms.*

The Huntingbridge specimens which I have examined were contained in the collection of the Sedgwick Museum at Cambridge and were kindly placed at my disposal by Professor Hughes. They were obtained by Mr. H. Keeping from this locality, which is near Fritham in the New Forest.†

On comparing these specimens with those of Alum Bay certain differences

* On looking closely at tablet 44,007 (1) in the Sowerby Collection in the British Museum, in which three specimens are represented in section, it will be found that one of them (that immediately above the yellow label) is different from the others, and with the assistance of a low power of the microscope it becomes clear that this is a section of a specimen of the microspheric form. It is in fact an example of the *N. Orbignyi* (Galeotti), the apparent absence of which from the English Beds occasioned de la Harpe's surprise.

† In his paper (4) on the Bracklesham Beds of the Isle of Wight Basin, Mr. Fisher says, p. 80, of the beds a few feet lower in the series, "the character of the matrix at Huntingbridge approaches more nearly to some of the Barton deposits than to any of the Bracklesham strata." This was written before Mr. Keeping found the nummulite bed in question, and it would appear that the presence of this characteristic fossil of the lowest Barton bed confirms the suspicion which seems to have been in Mr. Fisher's mind that he was here approaching the upper limit of the Bracklesham series.

The position of the locality is clearly indicated by the reference in Mr. Fisher's paper to the Ordnance Map. On a recent visit to the Forest, I failed to find any one who recognised it by the name of Huntingbridge, and an old keeper told me that it is now known as Three Bridges.

are apparent, as may be gathered from Plate 5, *a* and *a*. In the Huntingbridge specimens the height of the chambers as seen in section (measured along the radius of the test) is less in proportion to their breadth than in those from Alum Bay. Moreover the backward slope of the septa is less marked in the Huntingbridge specimens. In both these respects it happens that these latter vary in the direction of *N. variolarius*. However, in the flatness of the test (*cf. a'* and *a'*) and in the large size of the megalospheres (fig. 1) there is no approach whatever to *variolarius*. In his "Étude" (p. 170) de la Harpe says of the species under consideration:—

"Les cloisons et les chambres sont irregulières dans leur forme, leur nombre, leur épaisseur et leur inclinaison."

I have no reason to doubt, therefore, that Professor Jones was justified (11) in referring the Huntingbridge specimens to *N. wemmelensis* var. *elegans*, *i.e.*, to *N. Orbignyi* var. *elegans*.

Among 44 specimens examined in section (fig. 1) 40 are megalospheric and 4 microspheric, but this proportion is not a true indication of their relative

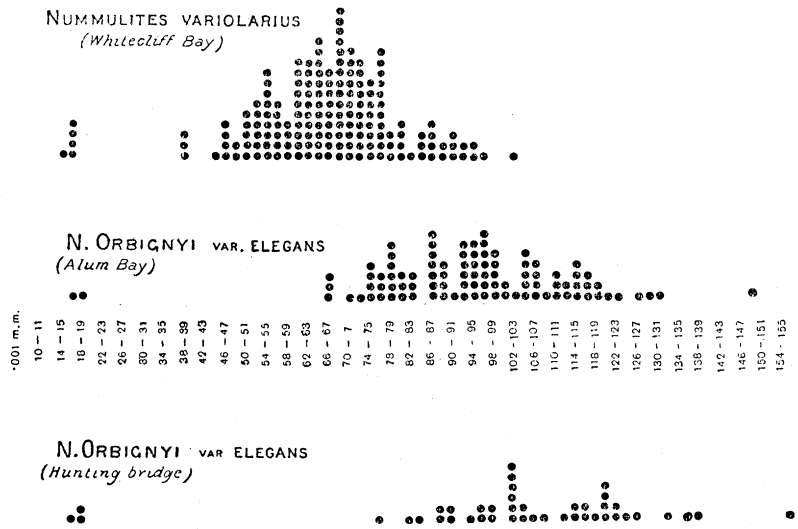


FIG. 1. Diagram showing the diameters of the Initial Chambers of the specimens measured, belonging to the species *Nummulites variolarius* and *N. Orbignyi* var. *elegans*.

Each specimen is represented by a dot. The size of each chamber (*i.e.*, the mean between its long and short diameters, as seen in the section) is indicated by the horizontal distance of the dot from zero, on the left, and may be measured by reference to the scale, indicating 1/1000th of a millimetre (μ's). The dots for chambers of the same size are piled one above another.

It will be seen that in respect of size the initial chambers of the species (or local form) fall, in each case, into two groups, the microspheric and megalospheric.

frequency in the beds because, in this case, the largest specimens are microspheric, and some of these were selected for preparing sections.

In the megalospheric examples (Plate 5, a and a') the value of M varies from 77 to 157 μ, the average being about 106 or 10 μ greater than in the Alum Bay specimens.

The long diameter of the largest megalospheric specimen I have ground down is 2·1 mm.

In the three *microspheric* specimens in which the central chamber showed clearly enough to be measured, the value of m is 16, 19 and 19 μ (Plate 5, β'). The largest microspheric test measures 3 by 2·4 mm. There is thus in this species, though it does not happen to be shown in my Alum Bay specimens, the same tendency as was seen in *N. variolarius* for the microspheric form slightly to exceed the megalospheric in size.

It is thus evident that the English species of nummulites far from presenting exceptions to the law of distribution in pairs, are in exact agreement with that law, although the difference in the sizes of the tests between the two forms present in a stratum is, in the cases of *N. variolarius* and *Orbignyi*, little marked.

We have seen that de la Harpe himself withdrew one of his exceptions, and that two others appear to have been quoted on quite insufficient grounds; and on looking closely into his attitude towards the theory of dimorphism, it appears that his failure to admit it, and insistence on cases to which, as he supposed, it would not apply, may be attributed to the hostility which he rightly felt to an adventitious hypothesis with which that theory in its inception was for a time laden. M. Munier-Chalmas and M. Schlumberger, his colleague, recognised, at a later date, that this hypothesis was untenable, and withdrew it (17). Had he lived to reconsider the position calmly, we can hardly doubt that de la Harpe would have frankly recognised the light which the theory of dimorphism had shed on the matter.

(2) *On the Size of the Megalosphere in Relation to that of the Microspheric and Megalospheric tests.*

From the measurements given above, and also from inspection of Plates 3–5, it is clear that there is a great difference between the size of the megalosphere in *N. laevigatus* and its size in the two other species, and that these also differ in this respect from one another. From a consideration of this contrast the question arose: Is there a definite relation in size between the megalosphere, the initial chamber of the megalospheric form, and the complete test of the microspheric form?

In the life-history of *Polystomella crispa* we know that the megalospheric form arises by an asexual process; the protoplasmic contents of the microspheric form emerging from the test, and dividing up into a large number of megalospheres. These shortly separate and proceed to develop into full grown individuals of the megalospheric form (14, pp. 67 and 68).

In the light of this ascertained fact in the life-history of *Polystomella*, a simple member of the Nummulitidæ, the question under consideration may be put in a different manner: Is there a definite relation between the volume of the protoplasm of the microspheric form and the size of the megalospheres into which it divides?

For a satisfactory answer it was evidently desirable to extend the observations to a wider series of species, and, thanks to the stores of material in the collection presented to this University by the late Dr. H. B. Brady, I have been able to examine six other species (or "pairs of species" on the old view) ranging up to *N. complanata*, the microspheric form of which attains the gigantic proportions of 3 inches in diameter.

As an index of the volume of the megalosphere the cube of its mean diameter has been taken. Similarly for an index of the volume of the protoplasmic contents of the complete test the square of the diameter (d) multiplied by its greatest thickness, *i.e.*, the length of the spiral axis (a) has been taken. Thus ad^2 is the index of the volume of the complete tests, megalospheric and microspheric.

If the tests were all of the same shape and the chambers and septa between them were of the same proportional dimensions and thickness in all the species, the values of ad^2 would give accurately comparable indices of the protoplasmic contents of the tests throughout the series. This is, however, far from being the case. In some species the tests are highly biconvex, in others they are nearly flat; some have large chambers and thin walls, others small chambers and thick walls; and the species differ also in the degree of development and the disposition of the alar prolongations of the chambers. In those sometimes separated under the distinct generic name *Assilina*, the latter are altogether absent. When comparing the results the characters of each species in these respects must be taken into account.

It should be stated further that the measurements which follow can only be regarded as approximately correct. In some cases the only specimens available were glued on museum tablets, and many are more or less worn at the edges. Whenever possible the two forms of a species selected for measurement are from the same locality.

The list of species with the localities of the specimens examined is as follows:—

Nummulites complanatus, Lamk., from Hungary and Bavaria, and its megalospheric form, *N. Tchihatcheffi*, d'Arch.; from Ajka, Vesprimer Comitat, Hungary.

N. perforatus (de Montft.), Vesprimer Comitat, Hungary, and its megalospheric form, *N. Lucasanus*, Defr.; from Zircz, Vesprimer Comitat.

N. gizehensis (Forsk.) and its megalospheric form, *N. curvispirus* (Menegh); bottom of Mokattam Hill, Cairo.

N. laevigatus (Brug.) and its megalospheric form, *N. Lamarcki*, d'Arch. and Haime; from the Bracklesham Beds, Selsey.

N. biarritzensis, d'Arch., and its megalospheric form, *N. Guettardi*, d'Arch. and Haime; from Dahr el Nakhl, Egypt.

N. discorbinus (Schlot.) and its megalospheric form, *N. sub-discorbinus*, de la Harpe; from the top of the Mokattam Hill, Cairo.

N. Orbignyi (Gal.), var. *elegans*, Sow., and its megalospheric form, *N. wemmelensis*, de la Harpe and Van den Broeck, var. *elegans*, Sow.; from Barton Beds, Huntingbridge, near Fritham, Hants.

N. variolarius (Lamk.) and its microspheric form, *N. Heberti*, d'Arch. and Haime; from the Bracklesham Beds, White Cliff Bay, Isle of Wight.

Assilina (*Nummulites*) *exponens* (Sow.) and its megalospheric form *A. mamillata* (d'Arch.); from Traunstein, Bavaria.

The results of the measurements are embodied in the following table. The species are arranged in the order of the volumes of their megalospheres. In each case, after the index of the volume of the test, the ratio which this bears to the index of the volume of the megalosphere is given.

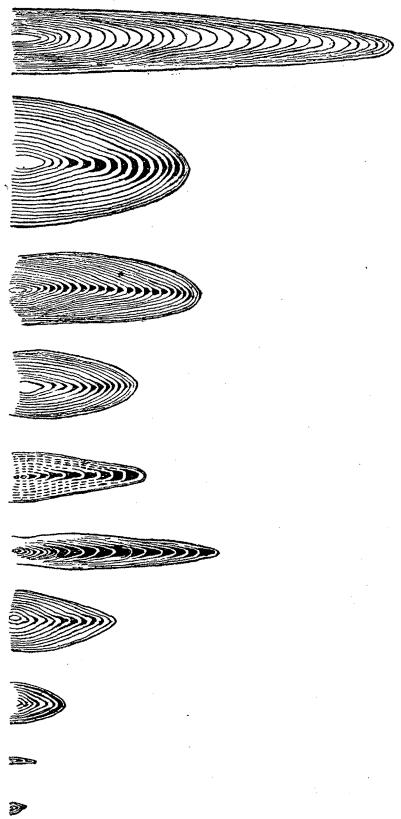
It will be seen from the last column but one that the order of the volume of the megalospheres is, with one exception, the order of the volume of the corresponding microspheric forms.

Turning to the results entered in the last column, the ratios of the volumes of the microspheric tests to those of the corresponding megalospheres, it will be seen that although the latter range from 0·0003 to 1·161 cub. mm., the ratio is fairly constant in six cases, lying between 9000 and 12,500 to 1. Bearing in mind that it is the ratio of the volume of the protoplasmic contents of the tests to that of the megalosphere which we are endeavouring to estimate, the low figure representing *N. Orbignyi*, var. *elegans*, may not be out of harmony with these results when the characters of the species are taken into account. (Compare the large chambers and thin walls of this species as represented in Plate 5 with those of the species shown in Plates 3 and 4.)

Similarly the high figures for *N. biarritzensis* and *N. discorbinus* are swollen owing to the thickness of the shell substance which builds up their

	M. μ.	No. measured.	M^3. μ^3.	Megalospheric form. Diameter (d).	Spiral axis. (a).	No. measured	ad^2.	R ad^2 : M^3.	Microspheric form. Diameter (d).	Spiral axis (a).	No. measured.	ad^2.	R ad^2 : M^3.
N. complanatus ...	1051	(12)	1·161	5·9	2·2	(19)	76·6	66 : 1	51·0	4·3	(13)	11206·2	9652 : 1
N. perforatus	683	(7)	0·3185	5·7	2·83	(8)	91·9	288 : 1	22·1	8·0	(9)	3507·28	11011 : 1
N. gizehensis	540	(13)	0·157	6·2	1·9	(16)	73·0	465 : 1	23·7	3·9	(12)	2190·6	13953 : 1
N. perforatus var. *obesus*	445	(11)	0·088	3·2	1·45	(12)	14·8	169 : 1	12·1	4·1	(11)	600·3	6821 : 1
N. laevigatus	443	(20)	0·087	4·6	1·17	(12)	24·8	285 : 1	17·2	3·45	(12)	1020·6	11731 : 1
Assilina exponens ..	434	(6)	0·0817	8·24	1·34	(12)	90·9	1112 : 1	21·0	2·3	(6)	1014·3	12415 : 1
N. biarritzensis ...	270	(10)	0·019	3·6	1·6	(4)	20·7	1091 : 1	11·49	4·14	(14)	547·5	27375 : 1
N. discorbinus	174	(15)	0·005	3·04	1·65	(15)	15·2	3049 : 1	7·01	2·9	(13)	143·7	28745 : 1
N. Orbignyi, var. *elegans* (Huntingbridge)	106	(40)	0·0012	2·1	0·47	(12)	2·07	1725 : 1	2·7	0·56	(5)	4·08	3400 : 1
N. variolarius	68	(163)	0·0003	1·8	0·77	(13)	2·5	8333 : 1	1·92	0·82	(5)	3·02	10066 : 1

Figures representing half transverse sections of the microspheric tests, × 2.



biconvex tests without any corresponding increase in the volume of their contents.

N. perforatus, however, does appear to have a disproportionately large megalosphere, for the test of the microspheric form is nearly as biconvex as that of *biarritzensis* and *discorbinus*, yet the ratio of its volume to M^3 is not above that of the majority. The disproportion is especially marked in the case of the variety *obesus* of this species, from Beni Hassan, in which the corresponding megalosphere approaches the dimensions characteristic of the typical members of the species, although the microspheric form is much reduced.

On the whole, the results of measurement appear to indicate, for the majority of the species examined, an approximately definite numerical proportion between the volume of the contents of the microspheric test and the volume of the megalosphere. *N. perforatus* departs most widely from that proportion, and the existence of this outstanding case would render it probable that in the others the proportion, if it could be measured exactly, would be found to be only approximately uniform.

In the account given above of the mode of origin of the megalospheric form of *Polystomella crispa*, the parent organism is described as microspheric. This is in accordance with a large series of observations on this species (13, p. 446), and I am not aware of any direct evidence showing a departure from the rule in *Polystomella*.

In other orders of foraminifera, however, viz., in *Cornuspira*, *Miliolina*, *Peneroplis* and *Orbitolites* among the *Miliolidæ*, and in *Cristellaria* (1, Plate 68, fig. 1, and 14, p. 116) among the *Lagenidæ*, it is the fact that the megalospheric form is capable of repeating itself, by giving rise to a brood of megalospheric young.

It appears to me that the approximately close relation which has now been shown to exist between the size of the megalosphere and that of the microspheric form is an indication (though it cannot be considered a proof) that this latter mode of reproduction did not occur among the nummulites of the Eocene Period, as it does not occur (so far as the evidence goes) in their ally, *Polystomella*, at the present day. For if the small megalospheric forms of the species in which microspheric forms attain so large a size were thus to reproduce their like, there seems no reason why the megalospheres thus produced should be of a size proportional to the volume of the microspheric forms.

In the account given in the first part of this paper of the three English species, it will be noticed that though the megalospheres attain very different

diameters the microspheres are remarkably uniform in size, all falling between 15 and 19 μ in diameter. In most of the other species which I have examined in section, the calcite filling of the tests obscures the central chambers so much that it is rarely possible to obtain an accurate measurement of a body so minute as the microsphere. However, in one specimen of *N. gizehensis* this can be done, and the value of m corresponds closely with that found in the three English species, being 20 μ. From these few cases (and I am not aware of any other records of the actual size of the microsphere in this genus) it would appear that the size of the microsphere is independent alike of the size of the megalospheric form and of the ultimate size of the microspheric test into which it grows.

In view of the facts (*a*) that there is good ground for concluding that the microsphere arises by the conjugation of zoospores produced by individuals of the megalospheric form, and (*b*) that the megalosphere arises by an asexual process, the results so far obtained may be stated for the genus *Nummulites* as follows :—

The size of the asexually produced megalosphere is approximately proportional to the volume of the protoplasmic contents of the microspheric parent.

The size of the (probably) sexually produced microsphere is uniform, or nearly so, throughout.

Turning now to the eighth column in the table, showing the ratios of the volume of the megalospheric tests to that of the megalospheres, it will be noticed that as the series of species is followed down, the ratios increase, though with some irregularity, from the top to the bottom. In the little *N. variolarius*, this ratio is almost the same as that for the microspheric form—the tests of the two forms being, as we have seen, almost of the same size. In the other species as the volume of the microspheric form increases so does the proportion which the volume of the megalospheric form bears to the megalosphere decrease.

In the case of *variolarius*, as the tests of the two forms attain about equal sizes, we may suppose that each took about the same time to grow, or, in other words, that the complete cycle of the life-history was divided in two nearly equal parts between the alternating generations. But in the other species it would appear that in proportion as the period of growth of the microspheric form preponderated in the life history, so did that of the megalospheric form diminish—not only in proportion to the microspheric form of the same species, but in proportion also (allowing for the difference in volume) to the period of growth of the megalospheric form in a species such as *variolarius*. Thus, to compare this species with *N. complanatus*, its

megalospheric form, when full grown, attains a size (test included) over 8000 times as large as that of the initial chamber in which it began. In *complanatus* the proportion of these volumes is only 66 to 1.

In the approach to equality in the sizes of the tests of the two forms the species *N. Orbignyi* and *variolarius*, though exceptional among nummulites, agree with the majority of the foraminifera in which dimorphism has been recognised. The genus *Polystomella* is an example among the *Nummulitidæ*, in which the two forms are also of equal size. On the other hand, in *Heterostegina*, probably in *Cycloclypeus* and in at any rate several of the species of *Orbitoides*,* the microspheric form preponderates over the megalospheric, as it does in most of the nummulites. Outside the *Nummulitidæ* we meet with the preponderance of the microspheric form in certain genera of the *Miliolidæ* (*Biloculina*, *Miliolina*, and in *Orbitolites complanata*), and it would be interesting to learn how far a similar correspondence in size between the microspheric form and the megalosphere obtains in these cases, and whether the repetition of the megalospheric generation produces any modification of the results.

These stages in the reduction of the megalospheric or gamete-producing generation are interesting from a wider biological standpoint as affording a parallel with what has occurred in other groups of animals and plants. Thus, to take a particular instance, we may compare the small and short-lived *Nummulites Tchihatcheffi*, a dwarf beside the great disc of *N. complanatus*, with the prothallus of a fern, arising asexually from a spore, and ultimately producing a zygote (by the union of gametes) which grows into the long-lived and comparatively gigantic sporophyte.

When the nuclear history of the foraminifera comes to be more perfectly known, it will be interesting to learn how far it runs parallel in two so widely separated forms. At present our knowledge of it is too incomplete to allow a comparison to be profitably instituted.

While writing the first part of this paper, I was beset by a suspicion that I was perhaps making too much of the difficulties raised by de la Harpe, that everyone who is interested in the life-history of the foraminifera was convinced long ago of the general prevalence of dimorphism, and that I might therefore have set out to fight the already slain.

That this is not the case is shown by a memoir which has just reached me

* See the series of papers published by M. Schlumberger on the subgeneric groups *Orbitoides*, *Orthophragmina*, and *Miogypsina* (19) and the memoir by MM. Lemoine and R. Douvillé on *Lepidocyclina* (12).

by MM. Lemoine and R. Douvillé, *Sur le genre Lepidocyclina* (12), a copy of which I owe to the courtesy of the authors. Written as this memoir has been in close association with M. Schlumberger, who in the fine series of papers on the structure of the tests of the *Miliolidæ* and other forms has done so much, either alone or in conjunction with M. Munier-Chalmas, to establish the dimorphic character of the tests of the species of foraminifera, the views herein expressed carry the greater weight. On p. 7 we read, under the heading Dimorphisme:—

"Chez les Orbitoïdes, comme chez la plupart des Foraminifères on trouve deux séries, une forme A à mégasphère, une forme B à microsphère. On sait maintenant par les observations de Schaudinn et par celles de Lister que ce dimorphisme est dû *dans certains cas** à un phénomène de génération alternante. La forme mégasphérique donne, par sporulation, des zoospores; ces zoospores se conjuguent, et le produit de leur conjugaison, en se développant, donne naissance à la forme microsphérique. Celle-ci par bourgeonnement redonne des formes mégasphériques.

"Le cycle n'a d'ailleurs jamais été suivi complètement. Il est très probable que les formes mégasphériques ou microsphériques peuvent se reproduire directement l'une ou l'autre, sans passer par la forme alternée. Nous ne savons rien des conditions de milieu que déterminent la prédominance partielle ou totale de l'une ou l'autre de ces formes; mais, ce qui est certain, c'est que ces deux formes couplées n'ont qu'exceptionnellement la même extension verticale."

This last passage not only emphasises the view temporarily held, and, as we have seen, abandoned by de la Harpe, of the occurrence of solitary forms in certain beds, but goes far to undermine his law of the association of species, for which there is such abundant evidence.

From the facts of the life-history now known to us, such a phenomenon as the authors describe would mean, if we are to take the vertical distribution of the species in every case as the unaltered record of the phenomena exhibited by it during the period in which it inhabited a given locality, that either at the beginning or the end of that period, or at both, only one phase was present in the life-history, while at another part of that period the species became or had been dimorphic.

But the phenomenon was, I believe, well known to Munier-Chalmas and attributed by him to a redistribution of the materials of a bed under the action of currents—the coarser fragments being deposited here and the finer elsewhere. And until such an explanation has been excluded it is surely

* The italics are the authors'.

unnecessary to introduce so complex and incomprehensible a conclusion into our ideas on the life-history.

That the megalospheric form in some families may reproduce its like for one, and very possibly for a series of generations, is well known, but where is the evidence that the microspheric form ever reproduces the microspheric directly? I have never seen or read of one particle of evidence to this effect. If dimorphism is due "*in certain cases*" to alternation of generations, to what other mode of life-history or cause of any kind is it to be attributed in closely allied forms?

A little further on the authors cite a paper (8A) by M. E. Haug, in which he simply records the fact that, among a number of examples of *N. variolarius* in a certain bed, he did not find the microspheric form (*N. Heberti*); though he is far from drawing the conclusion, which the authors are inclined to draw, that it was, in fact, absent. De la Harpe found, as we have seen, that it is impossible to distinguish this form from the megalospheric, by examination of whole specimens, and in my own experience it was not till I had ground down 45 specimens of this species, all of which proved to be megalospheric, that I happened on an example of the microspheric form. I cannot admit, therefore, that such negative evidence, unless supported by observations on the size of the initial chambers of a large number of specimens, has any force to shake a conclusion so firmly established.

If I put these objections abruptly, I beg the authors to believe that I do so in no hostile spirit, but for the furtherance of the subject in which we are alike interested. It seems to me that we are in danger of letting drop the clue which is within our grasp.

Summary.

The results obtained in this investigation may be summarised as follows:—

1. Both microspheric and megalospheric forms of *N. variolarius* and *N. Orbignyi* var. *elegans* are present in the Eocene Beds of the Isle of Wight and Hampshire, as I believe they will be found to be present elsewhere, except when the materials of a bed have been rearranged under the influence of currents.

2. In these species and in *N. laevigatus* and *N. gizehensis* the size of the microsphere is nearly constant—the diameters in the specimens measured being between 15 and 20 μ.

3. In the nine species and one variety of *Nummulites* and *Assilina* which I have examined, the size of the megalosphere is approximately proportional to the volume of the contents of the microspheric form.

By this result additional proof is given of de la Harpe's conclusion, founded on the mode of occurrence in the beds, and on structural features of the tests of the two forms, that these are in each case truly members of "a pair," or, as we now say, are related as alternating or recurring forms in the life-history of a species.

By (2) and (3) the two modes of reproduction come into marked contrast: the asexually produced megalospheres being approximately proportional in size to the protoplasmic volume of the parent, while the microsphere, probably arising as a zygote, is uniformly small throughout.

4. In several of the species examined, as the microspheric member of the cycle preponderates in the life-history, the megalospheric member decreases, not only in proportion to the size of the microspheric form, but in proportion to the megalospheric members of other species in which the two forms attain approximately equal sizes.

In conclusion, I wish to express my thanks to Dr. Harmer, the Superintendent of the Museum of Zoology in this University, for the free use he has allowed me to make of the ample stores of material in the Brady Collection; and to Professor Hughes for kindly placing at my disposal the specimens of *N. Orbignyi* var. *elegans* from Huntingbridge, contained in the Sedgwick Museum; also to Mr. H. Keeping of that Museum, whose knowledge of the beds of the Hampshire Basin has considerably assisted me.

I have to acknowledge the helpful advice I have received from my friend Mr. A. Harker in preparing the table on p. 311. To Mr. R. B. Newton, of the British Museum, I am also indebted for his assistance when examining the specimens in the Sowerby Collection there contained.

The photographs with which this paper is illustrated were made with the kind help of my brother, Mr. W. T. Lister. They were done with the excellent Zeiss instrument in his possession.

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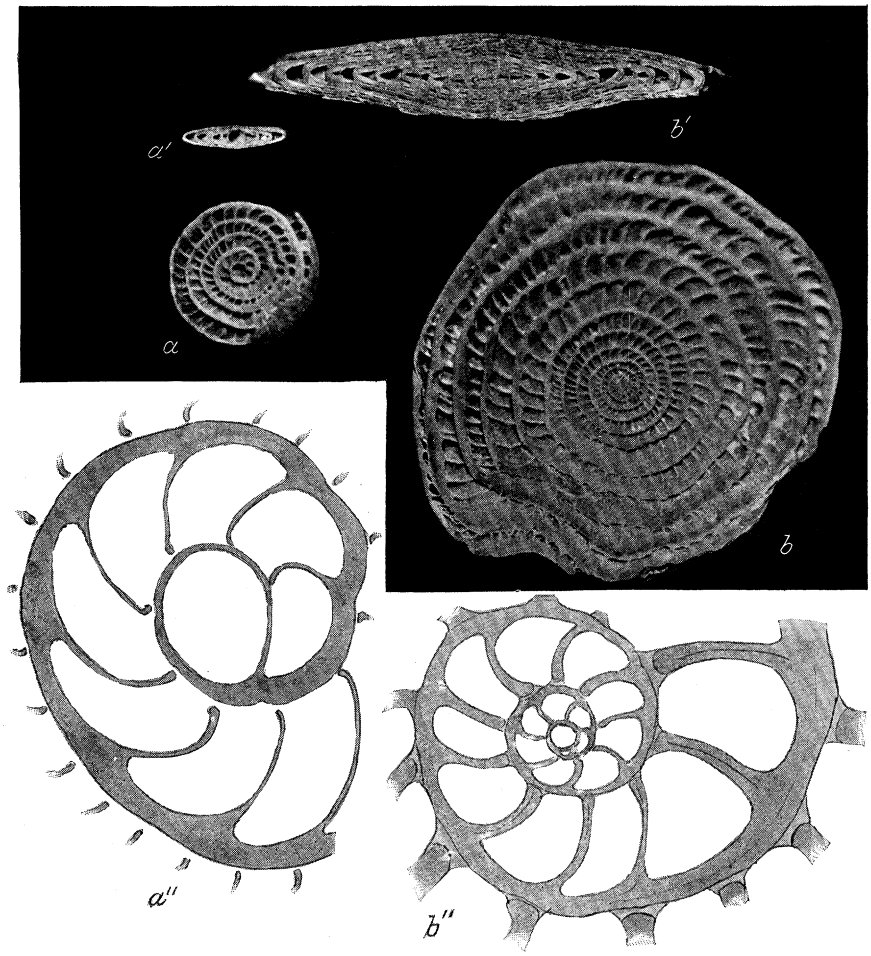
DESCRIPTION OF PLATES.

Plate 3. *Nummulites laevigatus* (Brug.).

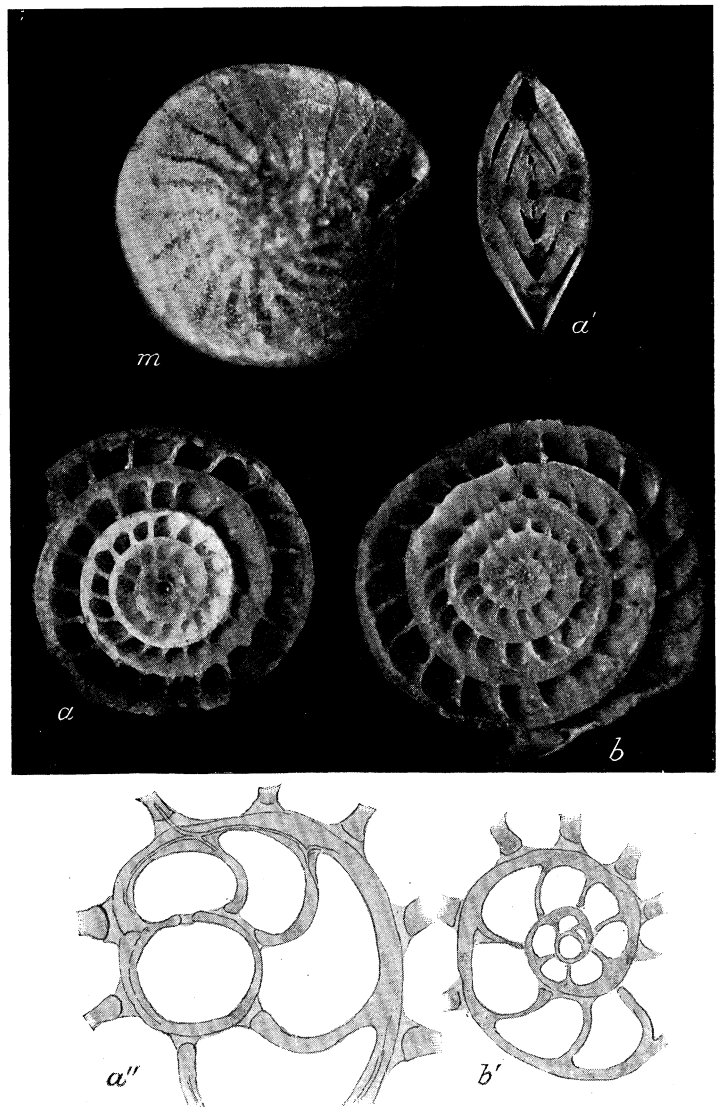
a and *a'*, median and transverse sections of the megalospheric form (= *N. Lamarcki*, d'Arch. and Haime).
b and *b'*, median and transverse sections of the microspheric form. All × 4.
a'', central region of a median section of the megalospheric form. × 38.
b'', central region of a median section of the microspheric form. × 200.

Plate 4. *Nummulites variolarius* (Lamk.).

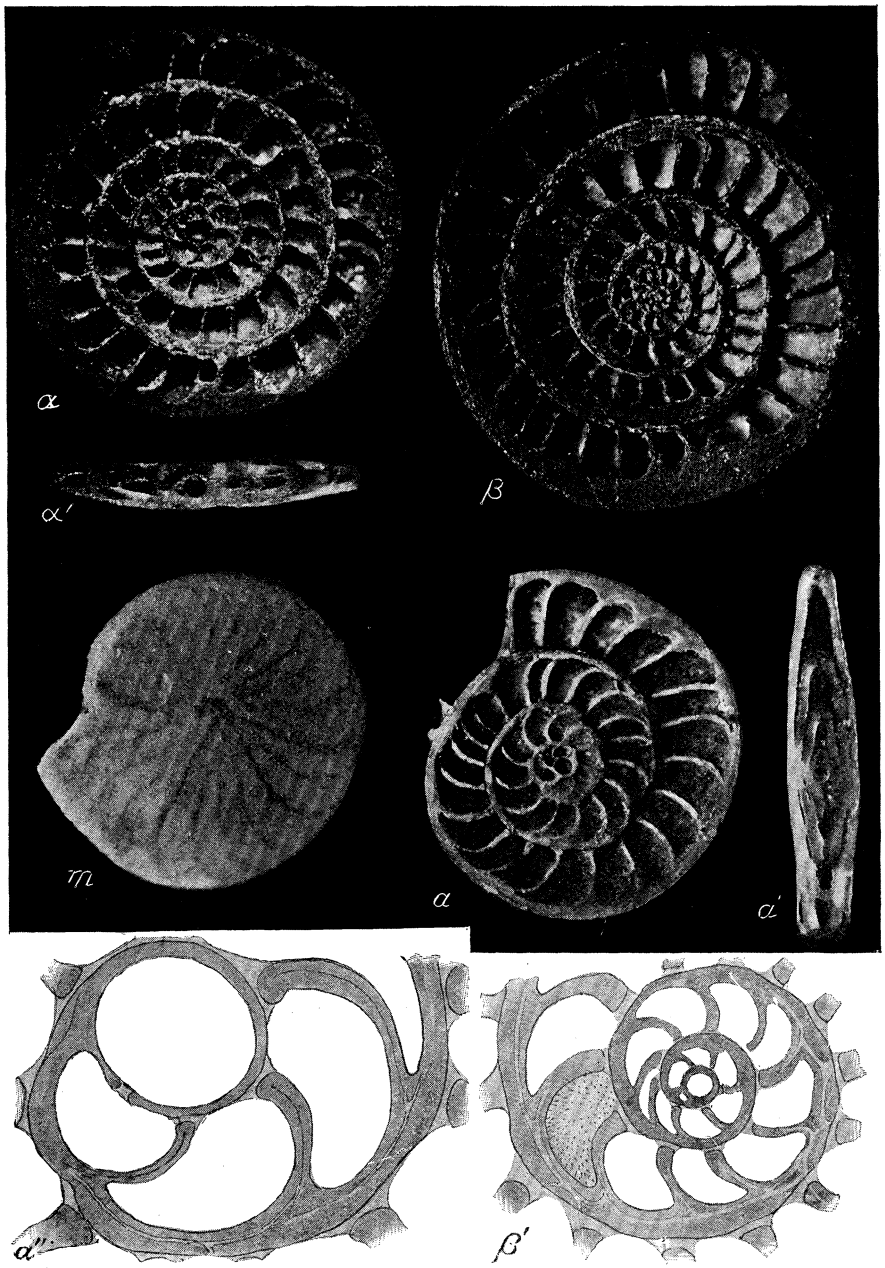
m, side view of the test; *a* and *a'*, median and transverse sections of specimens of the megalospheric form; *b*, median section of a specimen of the microspheric form (= *N. Heberti*, d'Arch.). All × 24.
a'' and *b'*, central regions of sections of the megalospheric and microspheric forms. × 200.



Nummulites laevigatus (Brug.).
(*N. Lamarcki*, D'A. and H.).



Nummulites variolarius (Lamk.).
(*N. Heberti*, D'A. and H.).



Nummulites Orbignyi (Gal.).
(*N. wemmelensis*, D.L.H. and V.D.B., var. *elegans*, Sow.).

PLATE 5. *Nummulites Orbignyi*, Gal. (*wemmelensis*, de la Harpe and van den Broeck), var. *elegans*, Sow.

m, side view of a specimen from Alum Bay ; *a* and *a'*, median and transverse sections of specimens of the megalospheric form, from Alum Bay ; *a* and *a'*, median and transverse sections of specimens of this form from Huntingbridge ; *β*, median section of a specimen of the microspheric form (= the *N. Orbignyi* of Galeotti), from Huntingbridge. All × 24.

a'' and *β'*, central regions of sections of the megalospheric and microspheric forms (*a''* from Alum Bay, *β'* from Huntingbridge). × 200.

In Plates 3 *b''*, 4 *a''*, and 5 *a''* and *β'*, some indication of the presence of the canal system is given, and in 5 *β'*, the further side of one chamber is drawn to show the perforations in the wall. The perforations are not present in the median planes of the tests.

On the Occurrence of Anopheles (Myzomyia) Listoni *in Calcutta.*

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(Received April 15,—Read May 18, 1905.)

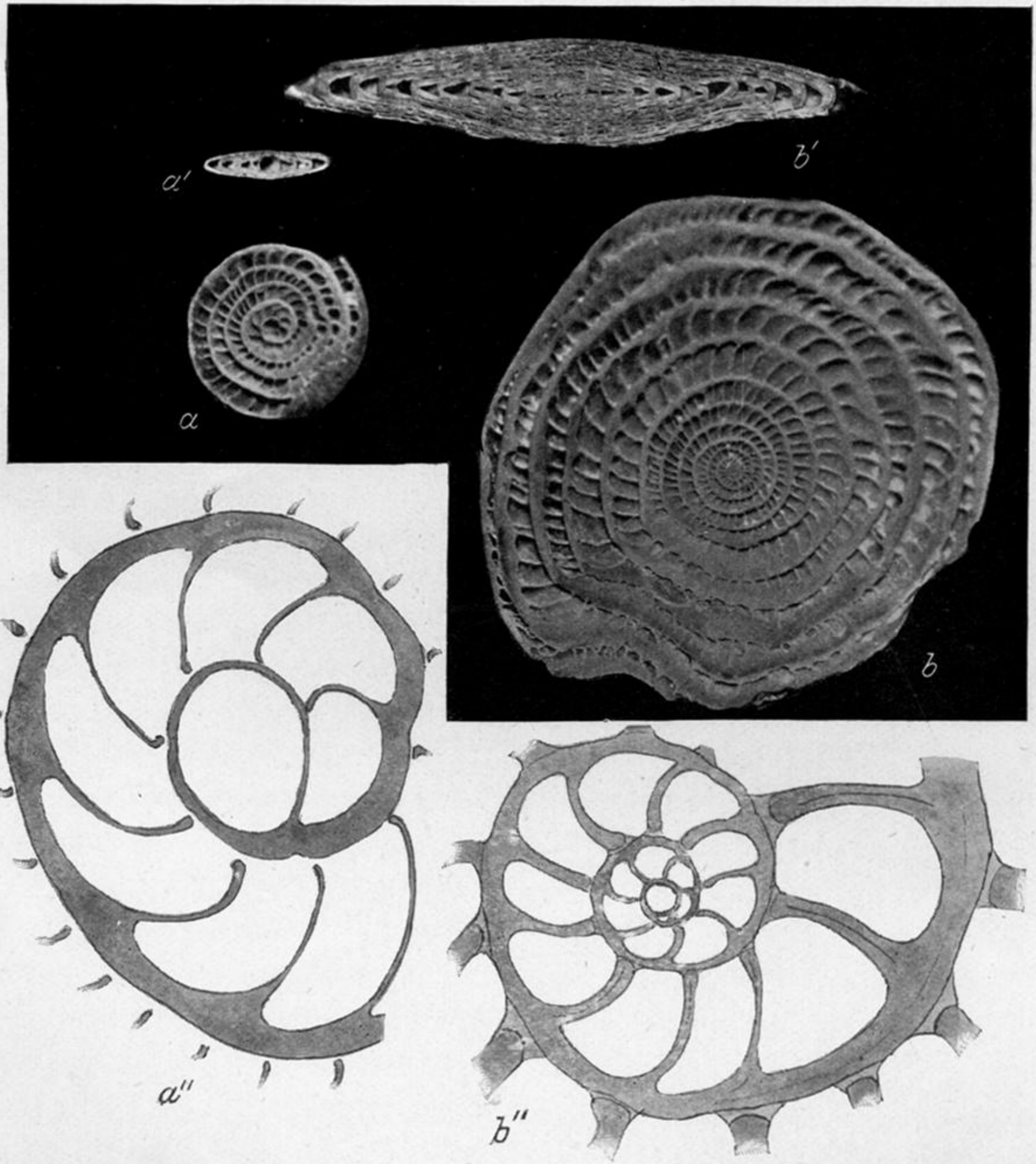
Stephens and Christophers, in their original report* to the Royal Society, on the Relation of Malarial Endemicity to Species of *Anopheles*, state, as their second conclusion, "that the distribution of *A. Christophersi* [= *Myzomyia Listoni*] corresponds closely with an area of extremely high endemicity."

It will be remembered that they were discussing the relation of malarial endemia to species of *Anopheles* in Bengal; that they found this endemia to vary from 0 in Calcutta to 7 in Barrackpore, 12 in Jalpaigori, and 72 in the Duars (increasing as they proceeded north); and that they concluded "that the distribution of certain species coincided with areas of high endemicity, while other species occurred, and even existed in profusion, where very little infection was present."

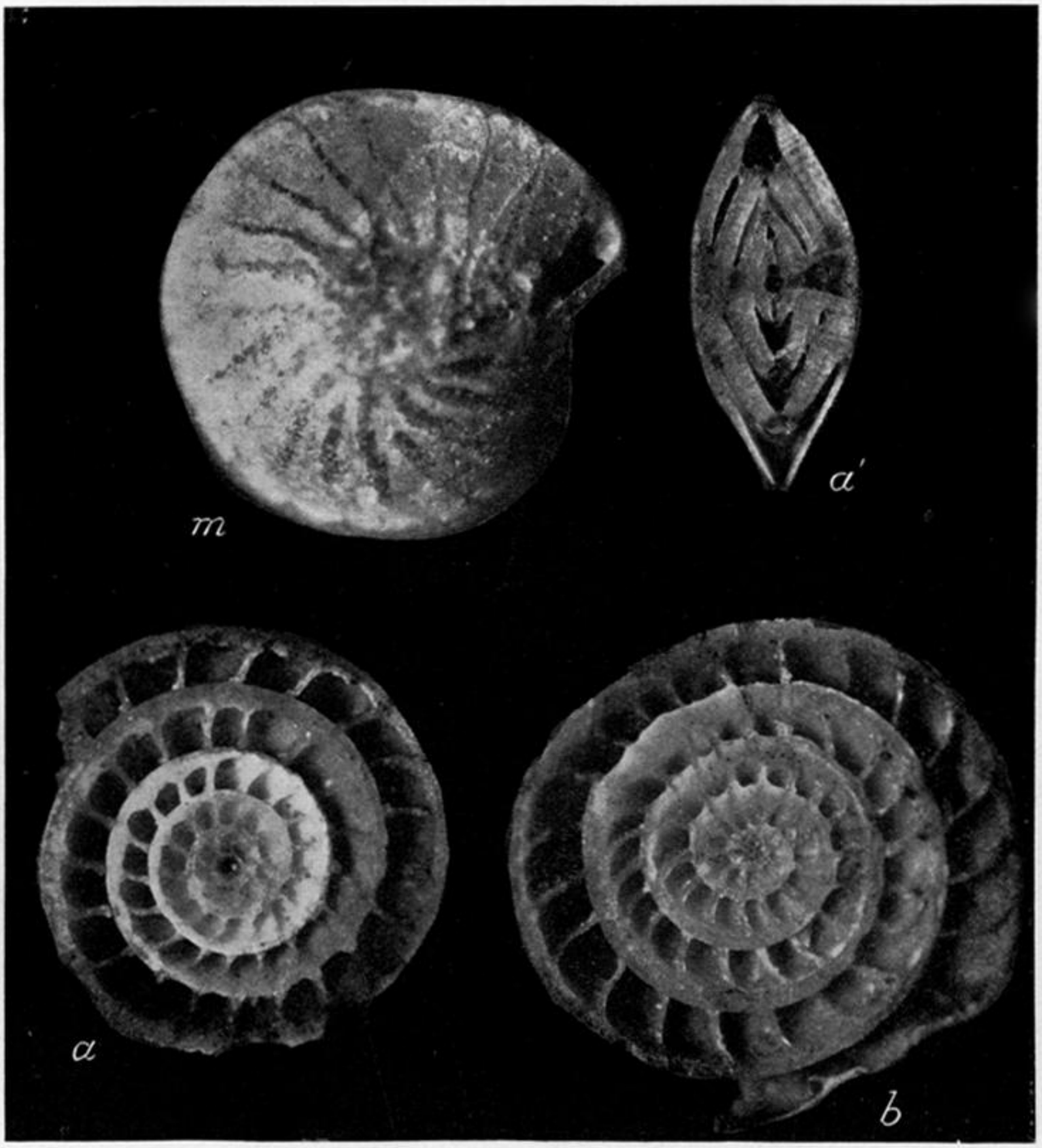
All this is graphically illustrated in their well-known "Sketch Map" (reproduced in their new book) which shows the Calcutta region marked *Rossii*, a non-malarial carrier, and the Duars marked *A. Christophersi* [= *M. Listoni*] an undoubtedly good carrier.

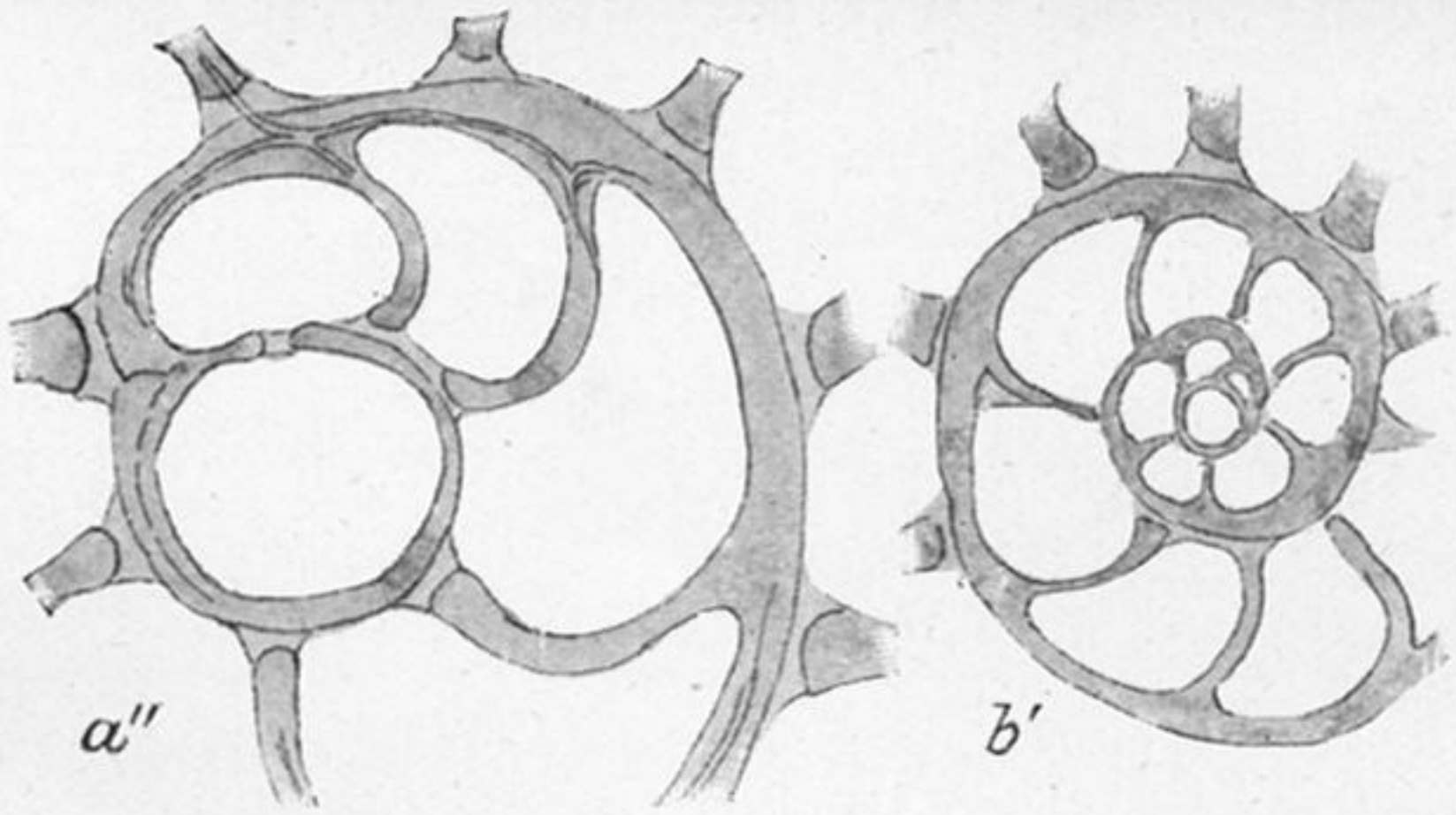
Stephens and Christophers were careful to say that their observations relating to distribution and endemia in Bengal were conducted in June, July,

* Malaria Reports, Sixth Series, March 6, 1902.

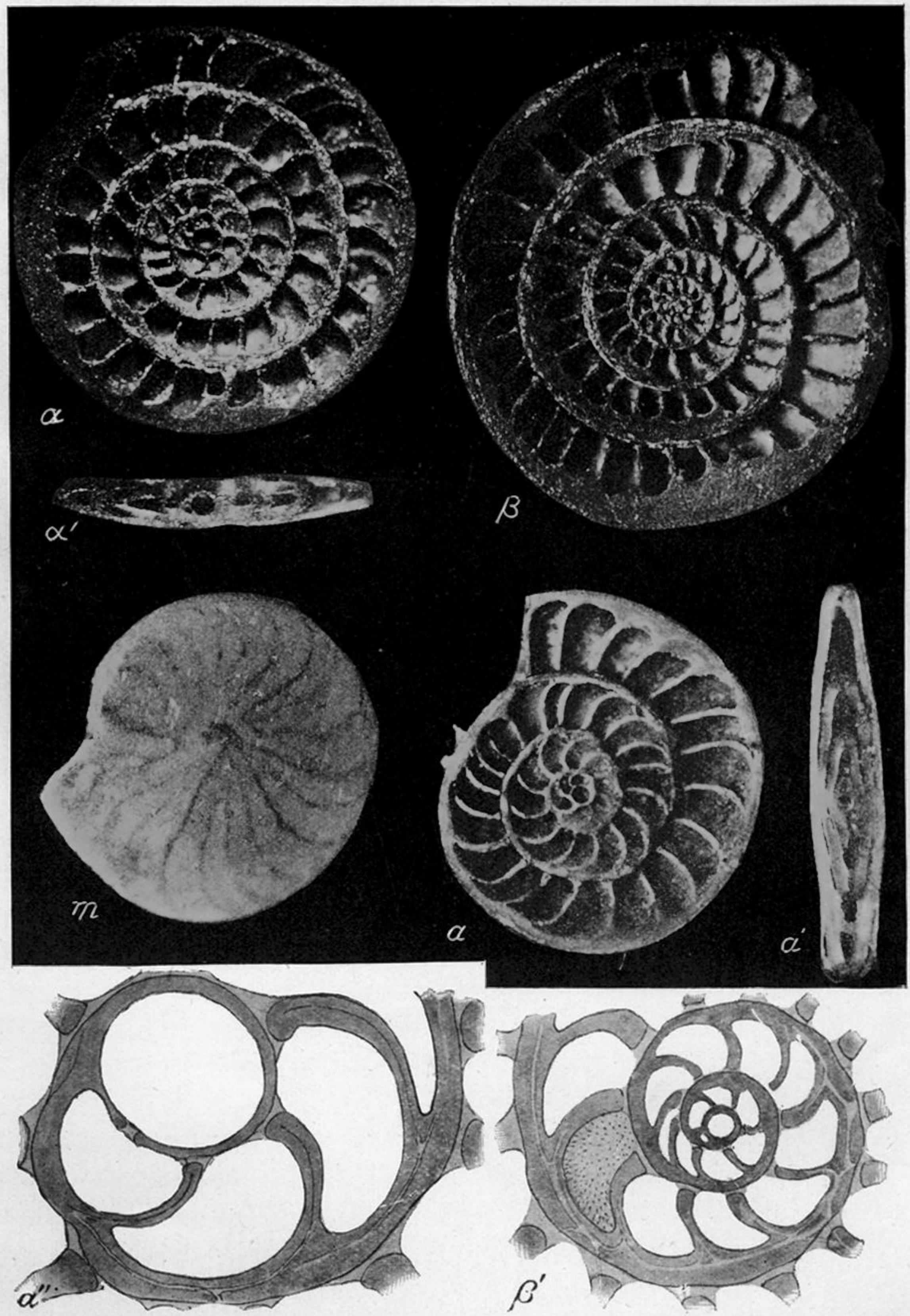


Nummulites laevigatus (Brug.).
(*N. Lamarcki*, D'A. and H.).





Nummulites variolarius (Lamk.).
(*N. Heberti*, D'A. and H.).



Nummulites Orbignyi (Gal.).
(*N. wemmelensis*, D.L.H. and V.D.B., var. *elegans*, Sow.).