supposed aquatic habits of *Prisopus* see Ann. & Mag. Nat. Hist. 1866, xviii. p. 265.

3. In the 'Zoologist' for 1860, p. 7141, MacGillivray described an insect from Aneiteum, New Hebrides, under the name of *Prisopus Carlottæ*. There is an insect in the Museum bearing this name from Aneiteum, which appears to be correctly named, but it has five lamelliform plates at the sides of the metathorax, as in *Cotylosoma*; the posterior one, however, is not visible from above, so that MacGillivray may have overlooked this when he gave the number as four. *Cotylosoma* is evidently very closely allied to MacGillivray's insect, which ought not to be placed in the American genus *Prisopus*.

4. *Cotylosoma* is from Taviuni, Fiji Islands; not Borneo, as stated in Wood-Mason's remarks.

It is not my purpose to characterize *Cotylosoma dipneusticum*; in fact it scarcely needs more than the figure.

LX.—*Notes, Morphological and Systematic, on the Madreporarian Genus* Turbinaria. By H. M. Bernard, M.A. Cantab., F.L.S., F.Z.S.

[Plates XIX. & XX.]

Having been engaged for the last eight months in studying and arranging the Turbinarians in the Natural History Museum, I propose to give a short abstract of some of the more interesting results obtained.

The task has been one of very great difficulty, and I am deeply indebted to the constant consideration and sympathetic advice accorded to me during my work by Dr. Günther, F.R.S., to whose kindness I owe my access to the specimens in the collection; without such encouragement I should hardly have had the fortitude to proceed, in face of the apparent impossibility of ever being able to arrive at a satisfactory system of classification. The nature of some of these difficulties I propose now to describe. I take this opportunity also of thanking Prof. Jeffrey Bell, who has the more immediate charge of the corals in the National Collection, for much assistance, advice, and friendly criticism, which has often been of great value to me.

Without going into the history of the genus, I may briefly say that the Turbinarians, according to the classification of Milne-Edwards in 'Les Coralliaires' (which classification has not been revised in this respect), are the principal genus of the Madreporarian subfamily Turbinariinæ. This subfamily is distinguished by the following characters:—Growth always by gemmation; cœnenchyma abundant, always distinct from the mural tissue, spongy and reticulated; at least six principal septa, equally developed. Of the five genera of the Turbinariinæ three are fossil, leaving two—*Turbinaria* and *Astræopora*—the chief distinction between which is the absence of a columella in the latter.

As compared with the subfamily Madreporinæ, containing the single genus *Madrepora*, the fundamental distinctions given are: in *Madrepora* the cœnenchyma is only slightly, or not at all, distinct from the mural tissue, which is very porous, and the chambers are divided by the directive septa.

My work on the Turbinarians has convinced me that this arrangement is entirely artificial and that it does not accord with the facts. One of these assumed distinctions does not exist, while the most fundamental difference, viz. the methods of budding, is entirely ignored.

It is true that in the introduction to the 'Coralliaires' (p. 35) the method of budding of Turbinarians is referred to; but it is nowhere used in the purely systematic part as a character even of the slightest value.

This abandonment of what appears to me to be the most fundamental taxonomic character of the genus was a retrograde step much to be deplored. The value of the different methods of budding in the classification of the corals had been distinctly laid down by Ehrenberg in 1834 *, while Dana, in 1848, endeavoured to carry it out in detail in his magnificent attempt to classify the zoophytes of the United States Exploring Expedition. The practical rejection of this character by Milne-Edwards in favour of other and more artificial distinctions, whatever other consequences it may have had, has certainly delayed the establishment of a natural system of classification of the corals. It stands to reason that the different methods of budding, with their far-reaching consequences in bringing about the ultimate forms of the coralla, cannot be ignored. Its value is, as I shall show, abundantly exemplified in the case of the genus *Turbinaria*, and it must take its place side by side with other characters if the corals are to be arranged according to the demands of the modern theory of descent †.

* 'Korallenthiere des rothen Meeres,' Berlin.

† That there is a very general revival of the recognition of the value of the method of budding for the classification of the corals may be gathered from the following papers:—S. O. Ridley, "On the Classifi-

Earliest Cup-Stage of Turbinaria.—The corallum of the genus *Turbinaria* is somewhat peculiar in the fact that it typically appears in its earliest stage as a small cup. This cup-stage is, however, generally transitory. As the edge of the cup grows, its shape gradually changes in various ways presently to be described. This important fact has, I believe, never been thoroughly, if at all, recognized. The cup-shape of the corallum was thought to be a specific * distinction, and not what it really is, viz. merely a phase in the ordinary development of the specimens of this genus. The confusion this has caused in the arrangement of the Turbinarians may be more easily imagined than described.

Before, however, discussing the systematic arrangement of the genus, which must for the future be based upon this fact —that every corallum begins typically as a cup—it will be well to describe the method of budding to which this peculiar method of growth is to be attributed.

The earliest development of *Turbinaria* I have not had any opportunity of working out, and all my conclusions have been drawn from an examination of the specimens in the National Collection. Among these are a great number of very minute cups, ranging from 1 inch across, and standing on stalks from 1 inch high. The stalk is always slightly expanded where it adheres to the substratum.

The Stalk and the Axial Polyp.—A cross section through a stalk of a minute cup reveals a single rather large polyp-cavity, surrounded by a thick spongy wall which shows an irregular series of radiating plates (costæ) bound together by irregular concentric synapticulæ ; near the surface the radiating plates project as the ridges which run longitudinally down the surface of the stalk (Pl. XIX. fig. 1).

This central polyp-cavity in the stalk is the parent polyp of the young corallum, and the spongy cœnenchyma is a simple thickening of its walls by the outward radial growth of costæ, which at more or less regular intervals are bound together by concentrically arranged synapticular plates. Surrounding the central cavity, then, there is a series of longitudinal canals running parallel with the polyp-cavity. All these are

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catory Value of Growth and Budding in the Madreporidæ, and on a new Genus illustrating this Point," Ann. & Mag. Nat. Hist. vol. xiii. (1884); and A. Ortmann, "Die Morphologie des Skelettes der Steinkorallen in Beziehung zur Koloniebildung," Z. wiss. Z. Bd. l. (1890).

* Ehrenberg appears to have made it a generic distinction. He revived Oken's genus *Turbinaria* for the stalked forms, and retained Lamarck's genus *Explanaria* for explanate specimens in which, if Turbinarians, the stalk had been obscured.

in open communication with one another and with the polyp-cavity through pores.

This description disposes of Milne-Edwards's distinction between the genera *Turbinaria* and *Madrepora*, that in the former the cœnenchyma is distinct from the mural tissue of the polyp. The description above given would, if we allow for the different density of the structures, apply equally well to a section through an axial polyp of a typical Madrepore. "Concentric circles of thin calcareous structure are seen separated by radiating linear pillars, the circles having been in turn outside walls and the radii either spinules or costæ" *.

An interesting question arises as to whether these radiating plates are true morphological costæ, *i. e.* outward prolongations of the septa. Mr. Brook † found no connexion between the so-called costæ in *Madrepora* and the septa; and the same is true of the few sections of stalks which I have been able to examine in *Turbinaria.* In spite of this fact, however, I am persuaded that primitively such a connexion existed, and that it has been secondarily obliterated. My chief reason for believing that it was the primitive arrangement is to be found in the fact that in many Turbinarians the septa are directly continued into the ridges of the cœnenchyma, and that the direct connexion between the septa and these costæ can very often be traced in the young calicles forming along the margin of a corallum (Pl. XIX. fig. 2). On the other hand, secondary obliteration of the connexion when it ceased to have any special use might easily take place. The process can, indeed, perhaps be traced as follows:—Between each pair of septa the rudiments of new cycles of septa are in many cases visible. In those cases in which the septa are continuous with the ridges of the cœnenchyma other ridges frequently run up to the edge of the polyp-cavity, terminating between the two septa, and are unmistakably suggestive of a fresh cycle of septa. We thus have a great many more radiating costæ than septa abutting on the immediate wall of the cavity, the crowded costæ representing not only the actually developed septa, but rudimentary cycles of septa. If, together with this crowding of costæ round the polyp, we take into consideration the more or less accidental variations in their thickness in the gradual process of strengthening the corallum, there is no difficulty in understanding how the primitive connexion between the costæ and the septa

* Martin Duncan, "On the Hard Structure of some Species of *Madrepora,*" Ann. & Mag. Nat. Hist. 1884, vol. xiv. p. 191.

† "The Genus *Madrepora,*" vol. i. of the British Museum Catalogue of the Madreporaria, 1893, Introd. p. 9.

might be obliterated. It seems to me easier to believe that the costæ have secondarily lost their connexions with the septa than that in those Turbinarians in which they are regularly continuous the arrangement has been secondarily acquired. It is difficult to believe that it is not the primitive arrangement.

The Budding of the Axial Polyp.—The axial polyp in the stalk of a minute Turbinarian colony buds *laterally*, the buds forming a simple ring round the axial polyp. The new polyps radiate upwards and outwards around the axial polyp, which either does not grow any more or else grows very slowly. It is obvious that this single ring of daughter-polyps, cemented together by cœnenchyma, which appears to stream down round the axial polyp, forms, together with the axial polyp, a stalked cup. This cup, according to the angle the ring of buds makes with the axial polyp, and also with the regularity of the ring, may vary considerably in shape.

It is to be noted that the budding from the axial polyp is *lateral*, as in *Madrepora*, and not basal, as Dana, following Ehrenberg's "Stolonformation," described. The error of these distinguished naturalists in this respect was most natural, and arose from the fact that they examined only sections of fronds, not of young cups. A section of a frond alone certainly seems to show at first sight that the budding is basal. This mistake led Dana to place the genus *Turbinaria* (*Gemmipora*) in a different tribe from that of the genus *Madrepora*. In the former the budding was thought to be basal, while in the latter it was lateral, whereas in both cases the budding is lateral.

Comparison between Turbinaria *and* Madrepora.—This central parent polyp of the Turbinarians appears to me, then, in every way comparable with an axial polyp of a typical Madrepore, and *the fundamental difference between the Turbinarians and the Madrepores is due to their different methods of budding* (*cf.* Pl. XIX. figs. 3, 3 *a*).

In the Madrepores the buds appear laterally on the wall of the axial polyp, and the higher this grows the more buds are produced, till each axial polyp is thickly crowded with daughter-polyps, radiating out from it in all directions. Nutrient fluids stream down the channels between the costæ, forming new layers of cœnenchyma round the lower portions of the stock, which may increase in thickness so greatly as to submerge the lower and first-formed buds. If the stem branches, one of the buds becomes in its turn an axial polyp and gives off buds; otherwise the buds do not, as a rule, themselves again bud. In the Turbinarians, on the other hand, only one ring of lateral buds is typically produced by the axial polyp, which then appears to cease to grow any further, the work of building up the corallum being carried on by the ring of buds.

If the facts justify this comparison, and I have little doubt but that they do, it follows that the cœnenchyma which streams down round the axial polyp, thickening its walls and submerging its lowest and oldest buds, is strictly homologous with the cœnenchyma which in the *Turbinaria* streams down to thicken the wall of the axial polyp to form the stalk of the cup and to widen its base of attachment. The structural similarity of the two has been already noted. In *Turbinaria* the cœnenchyma connects further the ring of buds, forming with them the wall of the cup, and ultimately the fronds (Pl. XIX. fig. 3). Mr. Brook *, led astray by the common belief that the budding in *Turbinaria* is quite distinct from that in *Madrepora*, drew a distinction between the cœnenchyma in the two genera, which no longer holds good when the respective methods of budding are correctly understood and compared.

Initial Variations in the Form of the Young Cup.—If the ring of buds rising round the axial polyp is perfectly horizontal, the youngest cup is symmetrical; but if the ring is not horizontal, but forms a wavy line round the axial polyp, then the cup is not symmetrical, but has a wavy edge. Again, if the polyps grow upwards at a sharp angle, the cup is conical or vasiform; if they grow out at a wide angle the cup flattens and may be quite disk-shaped or peltate; and, finally, if in growing outwards they bend downwards, the everted cup may easily form a hemispherical mass, the edges of which creep along the substratum. All these methods of growth take place.

Second and following Generations of Buds.—We may now temporarily dismiss the axial polyp, whose further fate we shall return to presently; the question which concerns us is how and when do the radiating daughter-polyps bud, in order to extend the edge of the cup.

For clearness of description we may assume that, whereas the axial polyp forms a complete ring of buds, each radial polyp produces only a portion of a ring, and that on the side turned away from the axial polyp.

The process appears, judging from a comparison of many specimens, to be as follows:—As soon as the polyps at any time forming the actual edge of the cup have, by outward

* "Affinities of the Genus *Madrepora*," Journ. Linn. Soc., Zool. vol. xxiv. p. 353.

radial growth, diverged sufficiently from their next neighbours to admit of buds appearing between them, these appear, while the parent polyps bend sharply upward towards the axis of the cup. As soon as this bending is effected, a fresh bud or fresh buds grow out close to the bend (*cf.* Pl. XIX. figs. 3, 3 *b*). This new generation (or incomplete ring) of buds may remain for a time hidden in a ridge of the cœnenchyma, which then forms the edge of the cup.

Without the bending up of the polyps as each series ceases to form the growing edge, it is clear that the cup-shape could not be maintained, the corallum would droop and curl under on all sides. It was this more or less sudden bending up of each polyp-cavity, with the bud starting from the bend, which led Ehrenberg to describe it as stolonformation, and not gemmation, and Dana to assert that the gemmation was basal. The more or less sudden bendings upward of the polyps were very naturally mistaken for the bases of the corallites. This, however, is obviously not the case, if the process be followed up from its starting point, viz. the budding of the axial polyp of the stalk of the young cup.

In this way, then, by the continual addition of a fresh series of polyps outside the one last formed, the edge of the corallum grows outwards into an ever-expanding cup or disk.

The Flowing of the Cœnenchyma and the Thickening of the Stalk.—It is obvious that increase of size of the cup or disk requires a stouter stalk and walls—that is, the basal region of the cup has to be thickened. In *Madrepora*, as already described, the basal thickening of each upright branch (consisting of an axial polyp surrounded by irregular tiers of daughter-polyps) can often be seen to submerge the lower earlier-formed buds (fig. 3 *a*). The downward streaming of the fluids can be gathered from the longitudinal channels between the costæ and from the gradually increasing density of the cœnenchyma. The same is the case with *Turbinaria*; while the cœnenchyma of the growing edge of the corallum is spongy both inside and outside of the cup, a short distance from the edge it is furrowed by a system of channels running downwards. The channels are separated by ridges which are, as we have seen, the most distal edges of the costæ. In nearly all cases the gradual thickening of these costæ can be followed from thin echinulate ridges, not thicker than septa near the growing margin, into dense masses in the stalk. This downward flow of matter, however it is to be explained physiologically, is a very striking feature in the Turbinarians. Within the cup it frequently fills up the bottom, often completely submerging all the polyps which formed the cup at its younger stages. Outside it streams down over the stalk, not only thickening it, but expanding its base of attachment. If the slope of the outer surface of the cup does not permit it to run down the stalk, it may either merely thicken the corallum under the layer of intercommunication of the polyp-cavities, or it may even hang down like aerial rootlets seeking to attach themselves to the substratum independently of the original stalk.

Besides giving the corallum the necessary strength to stand erect, this flow of matter is protective. It threatens every parasite which endeavours to gain a foothold. The Balanids have found it necessary to develop elaborate fringes of bayonets to keep off the advancing tide. These are often successful on the upper surfaces, where the flow of the cœnenchyma is not so strong; but such defences are usually of no avail on an under surface. A *Balanus* attached to the under surface is soon engulfed by the coral-substance. In some cases, *e.g.* on perpendicular surfaces where the flow is also great, the *Balanus* manages somehow to keep itself from being submerged; but the efforts of the coral to get rid of the plague are evidenced by the length of the finger-like processes, in the ends of which the *Balani* rest secure. They appear to have risen on the cœnenchyma as it strove to surmount the edges of their bayonetted plates *.

Factors in the Growth of the Corallum.—We have, then, a stalked corallum, with edges *standing up* to form a cup, or *standing out* to form a disk, or *hanging down* to form a hemispherical mass, and we have two factors to account for the further growth of the corallum:—(1) The typical method of budding; (2) the flow of the material building up the cœnenchyma, this flowing being especially marked in *Turbinaria* owing to the great abundance of this tissue. Before showing how these primitive forms of the coralla become variously modified by these two typical elements of increase, it is necessary to describe a third, somewhat irregular, factor, viz. an adventitious bud-formation.

Adventitious Budding.—In nearly all Turbinarian coralla with uneven surfaces the cœnenchyma seems to accumulate in the valleys as it does in the bottom of the early cups, sub-

* A very beautiful correlation exists between the size of the teeth on the plates of the *Balanus* and the echinulations of the cœnenchyma. The fine echinulations in the Turbinarians are met by fine teeth on the *Balanus*; the long echinulations of the *Astræopora* are encountered by correspondingly long bayonets on the plates of the *Balanus*.

While on the subject of parasitic or attached organisms, I may mention that many infesting sponges " imitate " exactly the colour of the corallum, and sometimes also the polyp-cavities in the size of their oscula.

merging the polyps. In these cases it is not infrequent to find such places very thickly studded with minute polyps. So numerous are they that active budding can alone account for them. Without having much actual information to give as to the real origin of these adventitious buds, there seems to be little doubt that while normally the polyps of the Turbinarian colony merely produce their single ring (axial polyp) or portions of a ring (radial polyps), when submerged by cœnenchyma they may continue to put out buds. It is true that there is evidence to show that submerged polyps, if not too deeply covered, may break through again. But when, for instance, the axial and earliest-formed radial polyps are completely submerged in the bottom of the cup by an enormous thickness of cœnenchyma, which is nevertheless thickly studded with minute buds, we can hardly escape from the conclusion that these are due to secondary buddings of the submerged polyps. Further, some glomerate forms, which are characterized by an enormous thickness of the cœnenchyma, show a tendency to secondary budding of the polyps, which can be easily seen. In this connexion it is worth remarking that the limitation of the buds to one ring or to a portion of a ring is probably a derived condition, while the power of producing an indefinite number of buds one above the other, shown in *Madrepora*, is the more primitive. That this limitation actually exists there is abundant evidence, as may be gathered, for instance, from the very uniformity of the earliest cup- or disk-shape of the corallum, and again from sections of glomerate Turbinarians (fig. 7), which show enormous thickening of the cœnenchyma, with corresponding lengthening of the polyp-cavities, often without any traces of secondary budding. But that this adventitious budding undoubtedly exists and plays a part in the ultimate forms of the coralla, perhaps as a return to more primitive conditions, there can be no doubt. It seems, however, to play but a subordinate part, and in discussing the morphological basis of the classification of the genus it may be temporarily ignored. The two prime factors above mentioned are sufficient.

Variations in the Form of the Cup due to subsequent Growth.—Of the three initial forms, dependent in the first place on the angle at which the first buds leave the parent polyp (or, perhaps, on the curving of the daughter-polyp outwards), the cup-shape, the disk-shape, and the hemispherical, the first is that most liable to great modification during the subsequent growth, while the last is naturally that in which form-changes are least to be expected.

The second or disk-shape, inasmuch as it hovers on the borderland between convex and concave, may, according as it is the one or the other, develop either hemispherical masses or the typical cup modifications. In the former case the disk expands on all sides till it covers an enormous area, the centre constantly thickening till it approaches the true glomerate forms, without, however, being really the same; while in the latter its form-changes may follow, somewhat stiffly, the more numerous and luxuriant growths of the true cups.

The instability of the cup-shape is hardly to be wondered at. Even though the first ring of buds is horizontal and uniform, it must obviously become increasingly improbable, as the edge of the cup expands, that the radial polyps round the edge should bud regularly enough and uniformly enough to keep the cup symmetrical. Large regular cups a foot in diameter must thus excite our admiration. There is only one really large cup in the National Collection; it is 16 inches across.

A point which remains to be established by further research is whether this persistence of the cup-shape is accidental or a normal specific character. It is at present impossible finally to decide this question. For the practical purposes of classification we are, however, provisionally compelled to assume that it is a reliable character.

In view, then, of the great improbability that the budding round the edge should be so regular as to keep the cup symmetrical, it is not to be wondered at that in the vast majority of cases the young cup is sooner or later completely obscured by the subsequent growth. The edge begins to fold or frill in various ways; the folding or frilling becomes more and more complicated as it continues; the coral-substance continually streams downwards until the early cup is buried up in the ever-thickening base of the enlarging corallum.

Apparent Periodicity in the Growth.—Before describing the subsequent forms assumed by the cup which it is so far possible to distinguish, an apparent periodicity in the growth requires to be mentioned. In many corals, as is well known, the living colony, secreting the coral-substance, is progressively withdrawn from the older parts of the corallum. The process seems to be uniform and continues as long as the stock lives. The Turbinarians *appear* to differ from this. An old Turbinarian stock is found to consist of many apparently distinct growths. The whole corallum appears to die down periodically, starting into life again along its edges, where growth had temporarily ceased. These new points of growth are not fresh Turbinarians; they form no stalked cups, but they continue the growth of the old and dead stock. This apparent periodical growth is specially marked in erect fronds, because at the boundary line between the new and the old a projecting ridge, studded along its edge with young calicles, often forms a sharp contrast between the two.

This appearance, however, is, in this case at least, entirely delusive, and is due to the occasional streaming back of coral-substance from the living on to the dead portion of the corallum. Fig. 4 (Pl. XIX.) shows a portion of an erect frond which has fortunately fractured through one of these apparent border lines between new and old corallum. The growth is seen to be perfectly continuous, the lower part progressively dying, on the left face (height *c*) faster than on the right (*d*). Two floods of coral-substance have streamed down (to *a* and *b*), but in neither case do they overflow the *dead* corallum, but they submerge the living. Fig. 5 shows a calicle being overwhelmed by finely reticulated cœnenchyma. A study of a fracture passing through the edge of such an advancing flood of cœnenchyma shows that the calicles thus overrun are able to work their way again to the surface. The earlier flood marked *b* was so abundant that it formed the shelf shown in the figure, along the edge of which a number of minute calicles appear. The origin of these calicles I have not made out. I suspect they are due to the secondary budding of the submerged calicles which failed to break through the layer of cœnenchyma which overwhelmed them.

The Turbinarians, then, are no exception to the rule of progressive dying down. The gradual character of this is, however, obscured by occasional downflowings of cœnenchyma forming projecting ridges, which *appear* to indicate distinct periods of growth.

The continued downstreamings of the cœnenchyma, destructive as they are to the lower polyps, clearly add to the thickness of the basal portions of the corallum as the growing edges of the fronds rise higher and higher.

On the other hand, there are cases which can, I think, only be explained on some theory of periodicity of growth. There are specimens in the National Collection in which small points of fresh growth are to be found on the edges of otherwise dead coralla. Certain growth-forms, presently to be described, seem to require such regular periods; but in these cases the new growth, without passing exactly through the early cup-stage, repeats more or less independently the growth of the old stock.

There is one very remarkable specimen in the National Collection in which a new cup develops from the margin of an old one. The old cup has, however, been turned completely over, with the result that its margin has curved upwards all round, and at one point shot up to form a new cup. In this case there was evidently no periodical dying down of the first cup; its normal course was interrupted by an accident.

I have distinguished eight principal growth-forms among the Turbinarians in the National Collection. In addition to these eight there are a few specimens whose method of growth comes under no heading; and, whether they be normal or accidental, we are not in a position to decide until the collection of the Turbinarians is more complete. Each of these eight forms requires description.

First Type of Growth: Crateriform.—This, as the name implies, is a simple persistence of the early cup-form, not at all or but slightly modified. As above stated, the existence of large cups, in face of the great improbability of the budding being sufficiently regular, compels us to attribute a classificatory value to this method of growth. We cannot assume that it is the result of mere favourable chance until by experiment we have proved it. It seems further only natural that of all the various normal growths of the Turbinarians some species should depart less from the initial form of the corallum than others. Be this as it may, until our knowledge of the genus is much more extensive we have no other course open to us than to assume the persistence of the cup-shape throughout life to be a normal character distinguishing certain species from the remaining members of the genus.

The group is also practically of great use, inasmuch as all cup-shaped coralla whose subsequent method of growth is unknown may be provisionally placed in it.

On the outside of the large cup (referred to on p. 508) at various heights there occur several attempts to form small cups, which are generally much distorted owing to the angles at which they project from the parent-stock. These are, I think, to be associated with the streaming of the coral-substance. They appear, at least in many cases, to arise where the downward flow has been hindered by some obstacle.

Second Type of Growth: Peltate.—As above stated, the peltate growth may continue along two distinct lines of development, according as the early disk has the edges tending to fold upwards or downwards. We have here then, from the nature of the case, possibilities for great variation in growth in one and the same species, the peltate young form standing on the border-line between the cup and the glomerate or rather the flat encrusting type of growth. It is significant that it is exactly in this case that the specific value of methods of growth appears to break down, for we find specimens which all appear to belong to one species, viz. *Turbinaria peltata*, forming on the one hand enormous hemispherical masses * and on the other hand systems of erect fronds.

Whether this particular "species" ought to be further broken up according to the different methods of growth it presents I find it very difficult to decide. There are thirty specimens apparently belonging to it in the National Collection, showing every stage of growth between the two extremes mentioned. Taking the coralla alone into account, it does not seem practicable to divide them. Perhaps when the living corals are studied, important differences which would justify their separation may be found.

The large specimens show that as the old stocks die down they are overrun by fresh layers of living coral. The dying down spreads gradually over the surface, and then the dead surface is grown over again by a fresh layer starting from some still living portion. In this way great hemispherical masses are produced by layer overgrowing layer. The layers themselves, however, are not thickened. This fact distinguishes these often glomerate masses from the true glomerate type of growth, in which each layer is itself enormously thickened in the centre and forms a hemispherical mass (Pl. XIX. fig. 7).

Third Type of Growth: Frondens.—This method of growth seems to originate from a deep bowl-shaped cup, the margin of which grows vertically. The constant lengthening of the circumference by the formation of new buds, while the form of the cup does not admit of any great enlargement of the circumference, leads to the breaking-up of the margin into lobes which roll inwards and curl round. Complicated masses of erect fronds, some spirally coiled, may thus arise. I understand this to be what Dana meant by "cucullately" folded. This group is established to take Dana's species *T. frondens* and a few specimens in the National Collection which approach this method of growth.

In these forms accessory lobes seem often to spring out from the faces of the fronds. These were either once marginal, the edge having again united, or are true accessory outgrowths, which are perhaps to be associated with the hindering of the downward flow of the coral-substance. In

* Two magnificent specimens illustrating this method of growth, sent by Mr. Saville Kent from the Great Barrier Reef, are mounted in the public galleries of the Natural History Museum.

the single specimen of a new species, which I propose to call *T. auricularis*, some of the accessory lobes certainly spring from the border-line between the living and the dead coral. Even in some other cases, where the hindrance cannot be so easily concluded, it is probable that it occurs.

Fourth Type of Growth: Foliate.—I propose to group under this heading all those cases in which the edge of the cup grows up into wavy fronds more or less erect, which may fuse irregularly together in every imaginable way. The fronds may be very deep and wide apart, or else very narrow, in which case they are generally very closely packed. Some very remarkable variations in their method of growth are found. In some the under surfaces of the fronds (*i. e.* the surfaces without polyps) are close together, while the spaces between the polyp-bearing faces of the fronds are wide apart; this is the arrangement one would naturally expect to be most suitable for the life of the polyps. There occur forms, however, in which the polyp-bearing surfaces almost touch, and even fuse, while the spaces between the under surfaces where there are no polyps are wide apart. In all cases the early cup is soon completely overgrown and obliterated.

Fifth Type of Growth: Mesenteriform.—This name is borrowed from Lamarck's species, *T. mesenterina*. The growing margin creeps outwards more or less horizontally, or even downwards. It is divided into lobes, which are separated by folds bent vertically upwards (*cf.* diagrammatic drawing, Pl. XIX. fig. 6). These folds are grown round, and then form open cylinders or closed knobs or finger-shaped processes. As the corallum expands the stalk is completely obscured, and its origin from an early cup could never have been guessed. The method of growth is, however, fairly uniform, and is pronounced enough to be recognized without difficulty. There is, further, fortunately a specimen in the National Collection at about the stage figured in the diagram (fig. 6). It forms a connecting-link between the early cup and the flat, nodulated, encrusting masses which show the "mesenteriform" method of growth only along their expanding margins.

Sixth Type of Growth: Tabulate.—I have adopted this name to designate a curious method of growth by no means infrequent. The cup evidently grows out rather flat, with slightly curled-up edges. As it dies down a fresh layer, appearing to start from the edge of the old, not only expands further, but spreads back over the old, and not always in contact with it, but arching over. An old stock thus shows several tiers of more or less horizontal coralla, which may be separated by chambers or fissures. These flat coralla, seldom nodulated, are often of great thickness and strength, as indeed their form requires. They appear very often to be semicircular, as if their shape were adapted to horizontal growth from a more or less vertical substratum. Such a horizontal growth requires far greater strength than does an erect frond. Consequently a section through such a tabulate form shows great thickness of the cœnenchyma both above and below the line of intercommunication between the polyp-cavities. The texture of the cœnenchyma is also very massive and dense.

In this case and in the next it seems to me as if we have periodical growths, or, at any rate, such a modification of the usual progressive dying down that it practically amounts to periodicity.

Seventh Type of Growth: Glomerate.—I was for a long time inclined to consider all glomerate forms as mere varieties of other species, varieties which had become glomerate owing to some accidental influence, perhaps of the form of the substratum; and it is undeniable that the likeness between certain glomerate forms and other Turbinarians found growing near them is very great. But this resemblance admits of another explanation, and will be referred to again. On the other hand, if any classificatory value is to be placed upon methods of growth, and I do not see how this can be disputed, we are bound to look upon the glomerate type of growth as one of the most marked and peculiar.

The corallum expands very little superficially. The cœnenchyma is built up, as it were, *in situ*. It is therefore always irregularly reticulate—that is, it shows none of the regular channels which indicate streamings. The consequence is that the corallites have to lengthen enormously to keep their apertures at the surface of the ever-thickening cœnenchyma. The budding of the polyps is, however, of the usual Turbinarian type, as is well shown in a section revealed by a broken specimen in the National Collection (Pl. XIX. fig. 7).

Here again it appears as if we have periodical growth. A fine specimen in the collection (fig. 8) shows three successive growths in vertical series. It appears as if each new growth must have started from the highest point of the old (perhaps from adventitious budding in the thickest part) and crept slowly out in all directions, covering it up.

We here have an excellent illustration of the great importance of recognizing clearly the essential morphology of the Turbinarians as shown in their method of budding. The method of budding and of growth of these glomerate Turbinarians is quite definite and distinct, and, in spite of the occasional adventitious budding, conforms to the type. And yet these forms have been thought to represent a transition between *Turbinaria* and *Astræopora*, with their very different method of budding and of growth.

Relation of Turbinaria *to* Astræopora.—If there is any connexion between *Turbinaria* and *Astræopora*, it is not by way of their glomerate forms, for both genera have thin creeping as well as solid hemispherical methods of growth. Their affinity cannot be based upon the mere superficial resemblance of certain specialized growths. As far as I am at present in a position to compare them, it appears to me that they have no immediate connexion. The budding of the Turbinarians is probably one of the most specialized to be found amongst Corals, and that of *Astræopora* shows no resemblance to it. The polyp-cavities and the cœnenchyma are far simpler and more primitive in *Astræopora* than they are in *Turbinaria*. The costæ, of which it is built up as one of its chief elements, are in many cases simple echinulations, and still show the primitive connexions with the septa, a connexion which has apparently been secondarily lost in both *Madrepora* and *Turbinaria*. Further, the pronounced columella of *Turbinaria* is not developed in *Astræopora*, although the elements out of which it might be formed are clearly traceable.

In view, then, of these much simpler conditions found in *Astræopora* than occur in either *Madrepora* or *Turbinaria*, it seems to me to run counter to the most elementary canons of morphology to deduce the *Astræopora* from a specialized form of the specialized Turbinarians. Only the most rigid demonstration of ontogenetic simplification in the case of the former could justify such an order of descent. Failing such a demonstration we have to place *Astræopora* as the most primitive of the Madreporidæ, from which, first *Madrepora*, and then *Turbinaria*, as I think, through *Madrepora*, *may* have been deduced. In *Madrepora* the first stage is an encrusting one, as, with some modifications, it always remains in *Astræopora*. The typical method of growth by means of special axial polyps appears later. From such a specialized method of growth the still more specialized type of the Turbinarians can be deduced in the manner above described.

However intelligible and satisfactory such an order of descent may at first sight appear, it can only be accepted provisionally, inasmuch as it is based upon the skeletal structures alone. It can hardly be considered to be established until the soft parts have been studied especially from this point of view. Fowler has shown that differences occur between the polyps of *Madrepora* and of *Turbinaria*; but the morphological value of these differences has to be estimated by extended comparative studies. We have yet to find out how far the living polyps are affected by the different conditions of life, due to the different forms of their coralla.

Eighth Type of Growth: Bifrontal.—Typically the Turbinarians carry polyps on only one side of the corallum. Forms occur, however, with polyps on both faces, this being brought about by the fusion of two fronds back to back. Such fronds, as might be expected, are always more or less erect. Among the specimens contained in Mr. Saville Kent's collection there exist complete series, showing the early cup-form and its subsequent folding. The folds do not form open cylinders, as in the mesenteriform method of growth, but thin vertical plates by the opposing under surfaces fusing together.

Similar fusions occur in all Turbinarians which form upright fronds, but irregularly, whereas in the type of growth under discussion they are the rule, and no free single fronds occur except here and there as horizontal expansions round the base of the corallum. These are to be considered as the continuations of the original edge of the cup, *i. e.* of those portions of the edge between the vertical folds.

These bifrontal growths show the phenomena which I at first took to be indications of regular periods of growth, but which, as above stated, I now think are due to occasional downward streamings of the cœnenchyma.

These definite types cannot be supposed to exhaust the possible transformations of the early cup. When our collections are more complete other normal methods of growth will no doubt have to be added.

Among the methods of growth shown by the specimens in the National Collection which do not as yet admit of being ranked as types there is one which I should like to describe here, as it appears to be too definite to be accidental. Inasmuch, however, as beyond being slightly indicated in one specimen, it actually occurs in only one other, it is not safe to claim it as a type.

One side of a conical cup is pulled down, as shown in Pl. XX. fig. 1, which represents a specimen in the National Collection. Two flaps, starting apparently in this way, grow round the cup closely fused with its outside. On meeting behind the cup they bend round again, and then again, the foldings on each side being almost symmetrical. Fig. 2 *a* is a diagram of the singular method of folding. Fig. 2 gives a sketch of the specimen which has been built up in this way. The original cup is naturally obscured by the continual upward growth of the edges and by the development of tall conical folds (*c*) and of wings (*d*) on the faces and sides of the original flaps, which have grown upwards with the growth of the cup, and also by the downward streaming of the cœnenchyma from within the cup carrying down the lower edge of the flap, so that the stalk is completely obliterated. The lower portion of the stock, especially certain masses of dead corallum, are not easy to understand; it is possible that the cup shown in the diagram and figure as the foundation of the corallum was not the original cup, but a secondary cup-like growth of parts of an old stock. The question is, Is this strangely symmetrical method of modifying a cup typical or accidental? I would like to invite the attention of those who have access to any collections of *Turbinaria* to this point.

Grouping according to Growth probably a natural one.—Accepting these eight types of growth as of practical value in classification, we find that they enable us to divide the specimens into more or less well-defined groups. It must, however, remain undecided whether these are natural groups, although this would certainly appear to be the case, in spite of certain somewhat serious objections. I would instance as the greatest difficulty the fact that certain forms of coralla seem to belong to definite localities. There are specimens from the Torres Straits, belonging to at least two species, which show the same form of corallum. This seems to imply that, at least in these cases, the form is due to the environment. But while this fact cautions us against attributing too high a taxonomic value to the forms of the coralla, it would be rash to deny them all value. In view of the definiteness of some of these types of growth, more than one coming from the same locality, in view also of the possibility at any time of the living colonies being powerfully modified by exceptional conditions of the environment, we are, it seems to me, justified in assuming that these growth-forms are typical developments.

The Taxonomic Characters supplied by the Calicles.—These are far more difficult to define than are the methods of growth. The calicles vary in size, shape, depth, and degree of protuberance according to the part of the corallum they occupy *; even the number of the septa and the size of the columella vary greatly on one and the same specimen. The only practical course is to select those corallites which appear to be typical, *i.e.* which appear to be growing normally on the normal fronds or lobes of the special type of growth of the specimens

* *Cf.* Bell, "Variations in *Turbinaria*," J. R. M. S. 1895, p. 148.

under comparison. The average sizes of the calicles may be taken and the average number of septa. But certain other characters appear to me to be of even greater importance.

1. *Characters of the Protuberant Calicles.*—I do not here refer to the fact that the calicles may or may not protrude, but, *when* they do protrude, to the way in which this takes place. Pl. XX. fig. 3 shows three different ways in which the calicles may raise up the cœnenchyma—the conical, globose, and cylindrical protuberances. Great as is the variation in the *degree* of protuberance found in one and the same specimen, the *character* of the protuberance, when it does occur, is apparently constant. Of course these three types are subject to an enormous number of variations; but every form approaches one or other of these three.

2. *The Character of the Septa.*—I have not found dentition or granulation of the septa of much value, although perhaps they should be taken into account (see below on the cœnenchyma). Of greater value is the relation between the cycles of septa and the polyp-cavity. I have found it useful to draw an imaginary half-radius circle within the aperture of the calicle (Pl. XX. fig. 4, *b*). The septa may (*a*) fall short of this, leaving a large central fossa (fig. 4, *1*); (*b*) they may reach it, leaving a medium-sized central fossa (fig. 4, *2*); (*c*) they may cross it, in which case the central fossa is very minute (fig. 4, *3*); or (*d*) they may be quite irregular, some crossing, others not even reaching it.

Again, the septa in thus projecting into the cavity may run in on a level with the margin and then dip suddenly down towards the columella, or they may curve regularly round, or they may slope down gradually so that the central fossa is funnel-shaped.

We have accordingly many different sizes and forms of fossæ.

3. *The Interseptal Loculi.*—These are also of importance (Pl. XX. fig. 4); they may be large and open or narrow and slit-like. They may be almost square or petaloid, *i. e.* with neatly rounded peripheral margins; they may, indeed, have no distinct peripheral margins, *i. e.* the interseptal space runs on continuously with the surface-furrows of the cœnenchyma. When this is frequent it is an index of the large size of the pores connecting the polyp-cavities between the septa with the canal-system of the cœnenchyma.

4. The columella offers characters of value.

Important as these characters undoubtedly are, it has again to be pointed out that they are only strictly applicable to calicles which appear to be the typical normal calicles of the specimen. Great variations may occur even in these points, according to the position of the calicle and according to its degree of protuberance; but, if due caution is used, a number of good taxonomic characters are thus at hand for use.

On the Influence of Position on the Character of the Calicles.—A great field of investigation is here opened up. I am not referring primarily to the effects of variations in the direction and in the force of the currents and in the quantity of nutrition received, all of which, no doubt, play an important part, but to modifications of form due to internal causes, notably to the streaming of the nutrient fluids in the canal-system. I have already pointed out that the streaming of the cœnenchyma is a factor of prime importance in the building-up of the corallum. This streaming is sufficient in many cases actually to submerge living calicles, which, in some cases, may again break through or else apparently put out a number of secondary buds. In other cases the polyps have continually and progressively to lengthen, in order to keep at the surface of the cœnenchyma; and while calicles situated on rounded knobs are often abnormally large and protuberant, those on erect fronds project but slightly. These facts, taken together with the fact that the canals of the cœnenchyma are in open communication with the polyp-cavities, appear to me to make it highly probable that, just as this flow builds up the cœnenchyma and gives it its appearance of streaming, so it must also affect the skeleton of the calicle itself, through which it doubtless runs. Indeed, in some cases it appears as if the calicles have to be protected against this. In coralla where the downward streaming is very marked by the deep regularly parallel furrows, these, in descending, are turned to right and left whenever they reach a calicle, converging again below it.

This is no fanciful question, but one which may prove of profound significance; for if, in any single coral, the downward flowings of the cœnenchyma can in any way affect the morphology of the polyp, this would have to be taken into account in any attempt to classify the corals according to the type of the polyp. The differences found in the soft parts of the polyp may be secondary and adaptive to the physiological conditions resulting from the forms of the coralla and to the streamings of the contents of the canal-system.

The Cœnenchyma.—This intercalicular tissue is very prominent in *Turbinaria*. It is, as we have seen, comparable in every essential with the cœnenchyma of *Madrepora* and of *Astræopora*; it differs chiefly in its greater abundance and in its distribution, both of these depending upon the method of budding.

Rapidly growing cœnenchyma is always finely reticulate or spongy; where streaming takes place it is often furrowed in the direction of the streaming. The relative breadths of the furrows and of the separating ridges are indicative of the density of the cœnenchyma. When the furrows are narrow and the ridges thick and solid the cœnenchyma is very dense. The lower portions of a corallum are, as a rule, the densest, and this can be traced by the ever-increasing thickness of the ridges and corresponding diminution in width of the furrows.

It is apparent, then, that before any systematic characters can be based upon the cœnenchyma its physiology requires to be understood; for instance, the spongy texture of that of the margin of the cup is often given as a character, whereas it is an invariable rule that in all such rapidly growing portions the cœnenchyma is spongy.

There are, however, peculiarities which are to be noted, viz. the characters of the trabeculæ building up the cœnenchyma. They may be filamentous or lamellate, giving in the former case a spongy, in the latter a flaky appearance to the cœnenchyma, or they may be close and granulated, making the surface look like sandpaper. In others, again, the ridges are continuous, *i. e.* only broken by pores between the neighbouring canals at long intervals; in others the ridges are highly echinulate, even broken up into rows of points representing so many open communications between the furrows, which, when covered over, will become canals.

Further, a certain value may be put upon the fineness or coarseness of the texture. In some it requires a glass to see it at all, in others it is visible to the naked eye.

In connexion with this subject of the general aspect of the cœnenchyma, it is worth noting that this seems to vary with geographical position. There are groups of specimens from various parts of the world evidently in each case collected at the same time and from nearly the same spot. In each case all the specimens of these groups look at first sight strangely alike. This is notably the case with a group from Formosa, with another from Tongatabu collected by J. J. Lister, and with another from Shark's Bay collected by Saville Kent. So strong is the likeness between the specimens in each case, that without some definite principles of classification one could hardly avoid lumping them all together, as, indeed, I found had been done with the Formosa specimens. It was only when, little by little, the different methods of growth and certain characters of the calicles were recognized as of more value than mere superficial resemblance, that I found myself compelled to separate the groups into different species. The remarkable resemblances are due entirely to similarity in the general aspect of the cœnenchyma. The Tongatabu specimens, for instance, have a velvety appearance. The Formosan specimens have a rough look, like a gritty sponge. The Shark's Bay specimens have a solid stony look, the gyrating furrows being separated by broad granulated ridges. Other examples of the same phenomenon might be mentioned. Its cause is no doubt to be sought in the varying physical conditions of their several environments. All corals must in some way be influenced by the varying climatic and other conditions under which they develop. The effects of these are perhaps specially visible in *Turbinaria*, owing to the great abundance of the cœnenchyma in this genus.

EXPLANATION OF THE PLATES.

Plate XIX.

Fig. 1. Section through the stalk of a very young cup-shaped corallum, showing the cavity of the parent polyp, the walls greatly thickened by cœnenchyma.

Fig. 2. A young calicle at the edge of a corallum, growing in the direction of the arrow. The cœnenchyma is built up by true costæ connected by concentric trabeculæ; distally the primitive costæ are distinct, proximally they are already secondarily obscured.

Fig. 3. Diagram to explain the method of budding peculiar to the genus *Turbinaria*. It is seen to be lateral throughout. The downward "flow" of the cœnenchyma has both thickened the stalk and submerged the axial polyp.

Fig. 3 *a*. Diagram to illustrate the relation of the buds and cœnenchyma to the axial polyp in *Madrepora*.

Fig. 3 *b*. Diagram to show the budding of a radial polyp from below. *1*, the axial parent polyp; *2*, a radial polyp; *3*, three polyps budding from *2*, one on each side and the middle one from below, after *2* has bent upwards as shown in fig. 3.

Fig. 4. Fragment of an erect frond (of the *bifrons* type), showing the appearance of periodicity in growth, due to the downward streamings of the cœnenchyma. *a*, the most recent downward flow, submerging the polyps below it (see fig. 5); *b*, a previous very abundant flow, which threw out a ridge along which young calicles appear; *c*, the line of progressive decay, which is advancing more rapidly on the left than on the right, where it stands at *d*.

Fig. 5. A calicle on the line *a* in the preceding figure, being submerged by the downward flow of the cœnenchyma.

Fig. 6. The initial modification of the young cup which gives rise to the mesenteriform type of growth (diagrammatic).

Fig. 7. A portion of a section through a glomerate Turbinarian, showing that the method of budding peculiar to the genus need not be affected by the enormous thickness of the cœnenchyma.

Fig. 8. A specimen of a glomerate Turbinarian, showing three periods of growth.

PLATE XX.

Fig. 1. A peculiar modification of a young cup exhibited by a specimen in the National Collection, which appears to be the first stage in the method of growth shown in the next figure.

Fig. 2. A specimen remarkable for the regularity and symmetry of its method of folding. For the letters see next figure.

Fig. 2 *a.* Diagrammatic horizontal section, to explain the method of folding. The letters mark the edges seen in the actual specimen. *c* and *d* are secondary outgrowths somewhat obscuring the original folding.

Fig. 3. Three types of protuberant calicles, showing the principal methods in which the cœnenchyma is raised by them.

Fig. 4. Diagram to illustrate the principles of classification proposed as regards the form of the calicle. *a,* the margin of the calicle; *b,* an imaginary half-radius circle; *1,* four septa which do not reach the half-radius circle; *2,* a single septum reaching the half-radius circle; *3,* septa crossing the half-radius circle. Between the septa at *1* the interseptal loculi run over into the furrows of the cœnenchyma; at *2* and *3* they are sharply bounded peripherally, and show different shapes of interseptal loculi.

LXI.—*Description of a new Batrachian* (Oreophryne Quelchii) *discovered by Messrs. J. J. Quelch and F. McConnell on the Summit of Mount Roraima.* By G. A. BOULENGER, F.R.S.

OREOPHRYNE, gen. nov. (*Engystomatid.*)

Pupil horizontal. Tongue elliptical, entire, and free behind. Palate smooth. No tympanum; eustachian tubes extremely minute. Fingers and toes short, blunt, without distinct web; foot for grasping, the inner toe opposable and longer than the second. Coracoids and præcoracoids very strong, the former forming an extensive suture with the latter in the middle and enclosing on each side a rather small circular foramen; no omosternum; sternum cartilaginous. Diapophyses of sacral vertebra strongly dilated.

The genus *Oreophryne* is nearest allied to *Atelopus*, D. & B., from which it is, however, well distinguished by the stronger præcoracoids and the curious conformation of the foot, which recalls that of the Hyloid genus *Phyllomedusa.*

Oreophryne Quelchii.

Physiognomy of *Bufo* (*Phryniscus*) *nigricans*, Wgm., or *Atelopus Stelzneri*, Wey. Snout short, rounded, not promi-