This is allied in structure to *H. heros*, Guér.; in both species the sixth sternite of the male has four longitudinal carinæ, excluding the raised lateral margins, the outer pair ending in a small spine and with a large tubercle at the base, but the seventh sternite is broadly rounded at the apex in *titan* and truncate in *heros*. I do not think that *titan* is a mere colour variety, though *heros* varies much in colour, especially on the thorax; but it may be a local race.

XXXIII.—The Homologies of the Anal Plate in Antedon. By F. A. BATHER, D.Sc., F.R.S.

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OF late years, since rigid distinctions were first drawn between the various plates in the posterior interradius of Palaeozoic Crinoids, the plate which appears, migrates, and disappears in the posterior interradius of the larval Antedon, and is called the anal plate, has been regarded as homologous with the plate generally known as anal x (the brachianal of Bather, 1890) in the Crinoidea Inadunata and Flexibilia. Dr. Austin Hobart Clark, however (1912, Journ. Washington Acad. Sci. ii. pp. 309-314, and 1915, Monogr. Existing Crinoids, vol. i. part 1, pp. 331-339 *), attempts to prove that the anal of Antedon is homologous with the radianal (Bather, 1890). A plate presumed to be the same occurs in the young of Promachocrinus. The representative of anal x is found by Dr. Clark in the posterior one of the small interradial plates occasionally observed in Antedon and other normal comatulid genera, while in Promachocrinus he would homologise it with one of the additional arm-bearing plates (pararadials, Bather, 1900).

Considering the extensive use that has been made of the anal plates in the classification of the Palaeozoic Crinoids, it seems advisable to examine Dr. Clark's arguments. But first let us recapitulate the main characters of anal x and the

radianal, as seen in the Inadunata and Flexibilia.

Both of these plates are intimately connected with the

^{*} The references, except when otherwise stated, are to the latter work.

right posterior radius. This is universally admitted with regard to the radianal, which is in its origin the right posterior inferradial, in other words part (if not really the whole) of the radial itself. The same connection does not appear to be so generally recognized in the case of anal x, but this connection is one of the reasons that led me to give that plate the name brachianal. Facts proving the connection were published in the 'Geological Magazine' for January 1899, and summarized in Lankester's 'Treatise on Zoology,' part iii.

Echinoderma, pp. 120-122 (1900).

The geological history of the radianal is briefly as follows:— It begins in Ordovician times as an inferradial *. Then, as the posterior interradius widens, the radianal of the Dicyclic Inadunata moves to the left of the right posterior radial, and, while retaining its contact with the lower margin of that plate and with the two underlying basals, comes also into contact with anal x, if that plate be present (e. g., Palaeocrinus and Botryocrinus). In Silurian and Devonian times the widening of the interradius continues, the radianal continues to move to the left and comes into contact with a plate (rt) which sinks down on the right side of the anal tube between x and r.post.R. (e.g., Euspirocrinus). This arrangement is emphasized in such Carboniferous genera as Poteriocrinus. In some later forms of the same group the radianal may stretch upwards, as the body of the animal with its anal structures comes to lie on rather than in the dorsal cup; but while the other anal plates (x, rt) pass up beyond the limits of the cup, the radianal invariably retains that connection with the lower slope of r.post.R. which bears witness to its inferradial origin. This arrangement is best shown in some North-American and British species of Ulocrinus, and I have recently discussed them in regard to this feature †. A parallel

† 1917, Trans. Geol. Soc. Glasgow, xvi. pp. 210-212. On p. 211, in line 4 of the middle paragraph, "left posterior basal" is a slip for "right posterior basal." Of course, RA never touches l.post.B. in any genus.

^{*} An inferradial is the lower half of a transversely bisected radial, the upper half being distinguished as superradial. These terms were chosen to indicate the truly radial nature of these plates. O. Jaekel and A. H. Clark call the inferradials "subradials." To this term there are two objections. First, it implies that the plates are not radial elements, but independent plates developed below the radials. This, however, does not appear to be the intention of those two authors. Secondly, the term subradial was used for the basals by De Koninck, and Dr. Clark seems to have forgotten (p. 104) that in this use De Koninck was followed by several American writers of repute down to the end of the nineteenth century. As to possible homologies of the inferradials, see Bather, 1900, 'Treatise on Zoology,' iii. p. 112, and 1913, Bull. Mus. Ottawa, i. pp. 9, 14.

course is followed by the Eupachycrinus series. In many allied forms (e. g., Delocrinus) it is plain that the radianal had disappeared before the migration of the other anals from the cup was complete. There is no evidence that the radianal ever followed those plates outside the cup limits. It could only do so by losing its primitive morphological connection with the lower end of r.post.R., a connection which it invariably retains throughout the manifold modifications of the anal area. The fate of the radianal, as indicated by the fossils from Cambrian to Permian, is to disappear by atrophy or resorption while still below the upper margin of the dorsal cup. In the fossils from the Trias to the Pleistocene no trace of it is found.

In the Monocyclic Inadunata the history of the radianal is somewhat different. In the Pisocrinidae and their descendants it is pushed to the right of r.post.R. instead of to the left, and is eventually squeezed out of existence at the lower

end of the cup; it never rises between the radials.

In the Palaeozoic Flexibilia Impinnata the radianal may assume a position abutting on anal x, similar to that in Botryocrinus (vide supra), or it may remain below r.post.R., or even be thrust down into the basal circlet. The essential point in the present connection is that no part of it ever rises between the radials, as in the Dicyclic Inadunata. The facts are given by Springer (1906, Journ. Geol. xiv. pp. 516-519). If any of the later crinoids, including the comatulids, are descended from the older Flexibilia, and correctly classed as Flexibilia Pinnata, then it is important to note that the radianal has not been observed in the adult of any one of them from Triassic to Recent times.

Returning to anal x, and confining our attention to the Dicyclic Inadunata, we find it beginning in Ordovician genera above, or partly above, or between the two posterior radials. In the last two cases it rests on the posterior basal, but if a radianal be present it abuts or in part rests also on that plate. It sinks furthest down into the cup in forms with a wide anal area, such as Carabocrinus and Thenarocrinus, or in the peculiar Gasterocomidae, where the anus opens on the side of the cup itself. Further width is attained, especially in Poteriocrinus and its allies, by the sinking of right and left tube-plates (rt and lt) into the cup, the former even meeting the radianal. The extreme of this development is reached in some Lower Carboniferous genera, such as Woodocrinus. Then begins the consolidation of the cup and the raising of the viscera. As the rectum passes upwards, so

also does its proximal supporting plate x, which thus gradually rises above the radial circlet, until the two posterior radials meet beneath it (e.g., Erisocrinus). Thenceforward, from the Trias onwards, the identity of anal x is lost in the general plating of the adult anal tube when such a structure exists.

Apart from all hypothesis, the historical facts make it clear that anal x and the radianal are structures differing in origin and development and ultimate fate. While anal x has supra-radial relations, those of the radianal are inferradial. While anal x finally passes up out of the cup, the radianal is resorbed when within the cup limits.

If, then, in recent crinoids a plate is observed in young stages between the posterior radials, and then migrating upwards beyond the limits of the cup, it is natural, on the theory of recapitulation, to regard that plate as x rather than

as the radianal.

Let us now consider Clark's arguments.

First, as to the anal of Antedon and similar forms. He says this is more closely connected with r.post.R. than with l.post.R. But this is just what I have always insisted on as the case with anal x in the Ordovician and Silurian Inadunata. If this tendency of the Antedon anal to keep to the right "is a fact of the very highest importance," then I welcome it as confirming the views I have always expressed

concerning the true anal x.

Clark then passes to the anal in the young of Promachocrinus (p. 332). First he describes it as arising "in the rhombic area between the corners of the basals and orals" before any of the radials appear. That is to say, it lies in the right posterior radius. "Soon afterward the [r.post.] radial appears, just to the right of and in line with" the anal plate. This radial grows faster than the anal and gradually "surrounds" it, so that the anal "comes to lie in a deep concavity in the side of the radial." Later the r.post. "radial extends itself beneath the anal and the concavity becomes straightened out and disappears, the anal concurrently being shoved diagonally forward (to the left) and disappearing by resorption." In a subsequent paragraph it is added that the concavity which receives the anal is in "the lower left hand portion of the radial," also that the anal migrates upwards.

These facts, says Dr. Clark, "leave no room for doubt that the so-called anal of the pentacrinoid larvæ is nothing more

nor less than the radianal of the fossil forms."

In the absence of figures for *Promachocrinus* it is impossible to be perfectly clear as to the precise relations of the plate in question to the right posterior radial; but the description is far from convincing me that Dr. Clark's conclusion is justified. In the well-known figures of the *Antedon* larva by W. B. warpenter and others, and in those of *Hathrometra proliva* Chich Clark here reproduces from Mortensen as evidence in his favour, I find nothing to indicate that the anal is anything other than anal x. The upward migration of the plate entirely favours this view. If the anal of *Antedon* be not homologous with the plate in *Promachocrinus*, then the latter might possibly be the radianal, since it does not migrate beyond the limits of the cup. That fact, however, is scarcely conclusive, since there is a special reason for it in this genus, as will shortly appear.

Let us, then, see what further arguments Dr. Clark has to offer. "Since," he writes, "the radianal is represented in the pentacrinoids of the comatulids we should expect also to find in the posterior interradius a second plate which we could with a reasonable degree of probability identify as the representative of the plate known as anal x; and such a plate actually occurs." This, of course, would be almost con-

clusive; but the statement needs careful checking.

First, consider the facts adduced for genera with five radials, as in Antedon. Wyville Thomson (1865, Phil. Trans. p. 540) "in one or two cases observed" in Antedon bifida, "about the time of the first appearance of the anal plate, a series of five minute rounded plates developed interradially between the lower edges of the oral plates and the upper edges of the basals." The fate of these plates is uncertain. Thomson himself identified them with certain perisomic interbrachials of the adult, but P. H. Carpenter (1884, Chall. Rep. p. 40) doubted this, and regarded them as true interradials, ultimately resorbed in Antedon, but homologous with the permanent interradials of Thaumatocrinus. With these plates A. H. Clark (p. 335) homologizes five plates which appear in Comactinia (species not stated) at the time of formation of the first primibrachs (IBr₁) and lie on the shoulders of the radials at such a height that their upper halves are between the IBr₁. In a single specimen of Comactinia meridionalis (p. 317, fig. 412) each such plate was surmounted by two others. In Comatilia iridometriformis (of rather later stage, pl. ii. figs. 528, 529) a "large rounded" plate rests in each interradius above the interbrachial processes of the radials.

If these plates in Comactinia and Comatilia are homologous with those first observed by Thomson in Antedon bifida, then they seem to support Thomson's interpretation of those Further, plates occupying such a position in the adults of Palaeozoic crinoids, or in such Mesozoic genera as Guettardicrinus and Uintacrinus, are no longer called "interradials" but "interbrachials," and are not regarded as homologous with the true interradials of such forms as the Rhodocrinidae. Consequently there does not seem to be good reason for regarding such plates in the ordinary comatulid larva as homologous with true primary interradials. Their late appearance in development also suggests that they do not represent plates of former importance in the cup. Even if these plates were primary interradials, they would not, in my opinion, have any bearing on the anal question. Anal x is a characteristic plate of the Inadunate Crinoids—in other words, of those crinoids which are devoid of true interradials or of any interbrachially situate cup-plates in interradii other than the posterior. Whatever anal x may be, it is a special plate developed or adapted for the widening of the anal area and the support of the rectum. The same is the case with the corresponding plate in the Adunata and the Flexibilia. There is no reason for regarding it as one of five primary interradials, retained while the other four have disappeared. Consequently the existence of plates, whether interbrachials or true interradials, in all five interradii of certain comatulids, does not prevent us from regarding the specially developed anal plate as the homologue of anal x.

Dr. Clark's final argument, on which he lays most stress, is drawn from Promachocrinus and Thaumatocrinus. Ever since P. H. Carpenter described Thaumatocrinus renovatus in 1884 there has been a tendency to regard the plate in the posterior interradius, which supports a short somewhat armlike process, as an anal plate. It is, however, one of five similar plates, each separating the adjacent radials, and therefore, so long as attention was confined to the original specimen, all to be regarded as true interradials. Dr. Clark still so regards them, and at the same time homologizes the posterior one with anal x. That homology is open to the same objections as have just been raised in the case of the

supposed interradials of the ordinary comatulids.

Dr. Clark's own work, however, by putting a new complexion on T. renovatus, has made his homology even more difficult of acceptance. He has shown, in the first place, that T. renovatus is the young of the species later described 20*

as Promachocrinus abyssorum. The process borne by the posterior plate is indeed a developing arm, and Clark suspects "that smaller arms borne on the other interradials have been lost... During growth the posterior interradial arm of Thaumatocrinus becomes reduplicated on all the other interradial plates, and all of the five interradial arms gradually increase to the size of the five primary arms so that the 10-armed Promachocrinus abyssorum results" (p. 338). It follows from this that the supposed interradials of Thaumatocrinus, including the posterior one or supposed anal, are of precisely the same nature as the five arm-bearing plates which in Promachocrinus have been added to the five normal radials of the ordinary comatulid. Dr. Clark calls all these plates "interradials," a term which suits his argument, but

which scarcely seems justified.

In 1900 (Lankester's 'Treatise on Zoology,' iii. p. 150) I suggested that these "interradial radials" were of the same nature as the arm-bearing plates in the cup of the Monocyclic Inadunata Calycanthocrinus and the Catillocrinidae, for which plates Jackel in 1895 had devised the excellent term "pararadials." Dr. Clark now tells us how the pararadials of the Promachocrinidae develop. They "arise very early in life and are from the first equal in height to the radials. They are probably . . . best interpreted as a sort of lateral budding from, or a delayed reduplication of, the radial to the left. As the radials move apart [the pararadials] continue to broaden, and their development in all ways is proportionate to their breadth as compared with the breadth of the normal primary radials" (p. 337). The development of the arms which they support bears a similar relation to the arms borne by the normal radials. The opinion that each pararadial is in a sense derived from the radial to the left of it is confirmed by various facts. Thus the posterior pararadial always maintains "a closer relation with the" left posterior radial than with the right posterior (p. 336). In some thirty 6-rayed specimens of Promachocrinus studied by Dr. Clark the supernumerary ray is in all cases but two inserted to the right of the left posterior radial, and receives its food-groove from the groove-trunk leading to that radial (p. 338).

The posterior pararadial appears to originate slightly before the others; in the original specimen of *Thaumatocrinus* renovatus its arm was more developed, and, as just stated, it is sometimes the only one to be formed. These facts are very simply explained as due to the relatively greater widening of the posterior interradius by the pressure of the rectum. It is not necessary to suppose, as Dr. Clark does, that the posterior pararadial represents a phylogenetically persistent anal x, which subsequently is reduplicated in the other interradii.

The facts given by Dr. Clark seem to me to show that the pararadials of the Promachocrinidae are really of radial origin. There is no more reason to regard them as interradials than there would be in the case of the Catillocrinidae. A similar proliferation of arm-bearing, or, rather, brachiolebearing, elements is seen in many Cystidea Rhombifera, e. g., Cheirocrinus (Bather, 1913, Trans. R. Soc. Edinburgh,

xlix. p. 446, figs. 52-55).

Dr. Clark, it is true, has some ingenious remarks, apparently intended to show that there is no real difference between a radial and an interradial. To quote from his paper of 1912 (p. 312): "while a plate if situated below the ventral edge of the perisomic surface may give rise to a simple series of more or less similar plates running up to the edge of the ventral surface, and possibly continued further along the anal tube, the same plate if situated just at the ventral surface will give rise to an arm or a group of arms exactly like those arising from the radials. The character of the ossicles following a plate is not determined so much by the character of the plate itself as by its position in reference to the boundary between the dorsal and ventral surfaces of the animal." This seems to me hopelessly inconsistent with well-known facts. On the one hand, there are plenty of genera in which the anal is on a line with the radials and yet does not give rise to an arm (e.g., Hexacrinus); on the other, there are genera in which some radials, though on a level with the others, cease to bear arms (e.g., Tribrachiocrinus, Sycocrinus).

We have, then, found no reason for accepting Dr. Clark's statement that a "representative of anal x actually occurs" along with the plate which he calls the radianal. Consequently that argument for the radianal nature of the latter plate falls to the ground. The facts do, however, throw light on the non-migration of the anal in Promachocrinus, the peculiarity which, it was admitted, might conceivably encourage one to regard it as the radianal (antea, p. 298). Dr. Clark says (p. 337): "I have examined pentacrinoids of Promachocrinus kerguelensis in which both the radianal and anal x are present, the former dwindling, the latter increasing in size. They are situated side by side between the two posterior radials." Obviously the lateral growth of the

posterior pararadial (Clark's "anal x") prevents the upward migration of the anal (Clark's "radianal") and inhibits its further growth, partly by drawing on its stereom for its own supply of calcium carbonate.

We may, therefore, continue to regard the anal in the Promachocrinidae as homologous with that of the other comatulid larvae, and, in all, as the representative of anal x.

XXXIV.—On the Arrangement of the small Tenrecidæ hitherto referred to Oryzorictes and Microgale. By Oldfield Thomas.

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There has long been some doubt as to the distinction from each other of the two genera Oryzorictes and Microgale, the latter of which I described in 1882, twelve years after Grandidier had described the former, and in consequence of this doubt the generic allocations used by Forsyth Major in describing the many new forms of Tenrec-shrews which he discovered during his successful expedition of 1894–96 have never been revised or confirmed.

I have now had an opportunity of going over the Museum material of the group with a view to putting its generic arrangement more in order than it was left by Dr. Major, who never completed the admirable work he began on it. No additional specimens have been received since his collection came, but the fine series he obtained, combined with those previously collected by Mr. Deans Cowan and worked out by me, have enabled me to obtain some idea of the natural arrangement of the group.

I find that it may be divided into five genera, whose chief characteristics are set out in the following synopsis:—

A. Claws not markedly fossorial, the anterior not or little longer than the posterior. Canines not dominant, commonly low and bifid, and never surpassing the anterior incisors.

a. Molars with marked internal lobe. Incisors diminishing backwards, the canine considerably longer than i³. Muzzle little elongated, the teeth touching each other. Fore-claws not longer than hind.



Bather, Francis Arthur. 1918. "XXXIII.—The homologies of the anal plate in Antedon." *The Annals and magazine of natural history; zoology, botany, and geology* 1, 294–302. https://doi.org/10.1080/00222931808562316.

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