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TRANSACTIONS
OF
THE LINNEAN SOCIETY.

- I. *On the Genus Actinometra, Müll., with a Morphological Account of a new Species (A.) polymorpha from the Philippine Islands.*—Part I. By P. HERBERT CARPENTER, M.A., Assistant Master at Eton College. (Communicated by W. B. CARPENTER, C.B., M.D., LL.D., F.R.S., F.L.S.)

(Plates I.–VIII.)

Read June 21st, 1877.

THE principal part of the investigations, of which the results are set forth in the following pages, were carried on during the year 1876, in the Zool.-Zootomical Institute of the University of Würzburg, under the superintendence of its director, Prof. C. Semper. I would here express my most sincere thanks to Prof. Semper, not only for the generous manner in which he placed at my disposal all his specimens of *Act. polymorpha*, which he had himself collected in the Philippine Islands, but also for the ready and valuable advice which he constantly afforded me during the progress of my work, and for the free use which he permitted me to make of his extensive library. I am also greatly indebted to Dr. Sandberger, Professor of Geology in the University of Würzburg, to the authorities of the University Library, and to Professor Dr. Hahn, of the Royal Library at Munich, for the means of reference to many books which would otherwise have remained inaccessible to me; and I desire to record my best thanks to all these gentlemen for the ready kindness with which they met my frequent and numerous wants.

I. HISTORICAL.

(§ 1) In the remarkable work of Linckius¹ upon the “Sea Stars,” the modern family Comatulidæ (J. Müller) is described under the name of Crinitæ, or Comatæ Stellæ, as a group distinct not only from the Asteridæ, but also from the Ophiuridæ and from *Astrophyton* (*Euryale*, Lamarck), with which they have been united by many later systematists.

¹ JOHANNIS HENRICI LINCKII Lipsiensis • De Stellis Marinis liber singularis, Lipsiæ, 1733, p. 53.

Linck included three genera in this family, or, as he called it, "Classis." The first of these he named *Δεκάκρημος*, to indicate "stellam marinam decem caudis crinitis radiantem;" and he referred to it three species:—(1) The "*Crocea zaffarana Neapolitanorum*," or *δεκαδασυακτινοειδής* of Fabius Columna¹, whose description he quotes; (2) the *Decempeda Cornubiensium* of Llhuyd², which Linck figured and named "*Stella δεκάκρημος rosacea*;" and (3) the "*Δεκάκρημος fimbriata Barrelieri*"³, which was named by Linck *barbata*, as he supposed it to be different from the other two. All three, however, are really identical, being simply local varieties of one and the same species, viz. the British *Antedon rosacea*, or the *Comatula mediterranea* of Lamarek. Thus, Fabius Columna described the Neapolitan variety, and Barrelier another obtained at the mouth of the Tiber, while Llhuyd based his description upon specimens found upon the coast of Cornwall near Penzance.

Linck's second genus, the *Τρισκαιδεκάκρημος*, was based upon a specimen with thirteen arms, previously described by Petiver⁴ as "*Stella chinensis*;" this specimen, however, was suspected by Linck to have been mutilated. His third genus he called "*Caput-Medusæ*," and described it as including those specimens which "ex centro corporis parvi umbonatique per quinque truncos primum bifidi, mox nullo constanti numero multifidi, in 60 et plures sureulos geniculatos rectos simplices abeunt, quos gracilescentes fibrillæ aliæ pilorum instar vestiunt."

Linck referred two species to this genus, viz. *Caput Medusæ cinereum* and *C. brunnum*; and he gave good figures of both (tab. xxi. n. 33, and tab. xxii. n. 34), from which it may be determined with tolerable certainty that they represent species now known to belong to two different types among the Comatulæ—namely, to the genera *Antedon* and *Actinometra* respectively.

(§ 2) Although Llhuyd⁵, and after him Rosinus⁶, had explicitly pointed out the relationship between the recent Comatulæ and the fossil Crinoidea, and although Linck, while supporting and repeating Llhuyd's views, had clearly differentiated the former from the Asteroidea and Ophiuroidea, yet Linnaeus⁷, instead of adopting the more correct views of some of his predecessors as to the true relations of the Crinoidea, was so misled by the jointed structure of their stems as to rank them among zoophytes in his genus *Isis*, whilst he grouped the Comatulidæ, together with all the other Starfish, under one common name *Asterias*. Linck's three species of *Decacnemus* were rightly regarded by him as identical; and he placed them, together with Petiver's *Stella chinensis*, in one species, *Asterias pectinata*, to which he also referred a specimen previously described by Retzius⁸. We now know, however, that this last is an *Actinometra*, dif-

¹ Phytobasanus, sive Plantarum aliquot Historia. Neapoli, 1592.

² EDUARDI LUTRI • Lithophylacii Britannici Ichthyographia • p. 149. Londini, 1699.

³ JACOB BARRELIERI • Plantæ per Galliam, Hispaniam et Italiam observatæ • Paris, 1714, p. 131.

⁴ • Gazophylacium Naturæ et Artis, • Londini, 1711: and also • Aquatiliæ animalium Amboinensium Icones et Nomina, • 1713.

⁵ Prælectio de Stellis marinis Oceani Brit. nec non de Asteriarum, Entrochorum, et Echinorum Origine, pp. 149–155, Oxford, 1733.

⁶ Tentamen de Lithozois ac Lithophytis olim marinis, jam vero subterraneis, prodromus; sive de stellis marinis quondam, nunc fossilibus, disquisitio. Hamburg, 1719.

⁷ • Systema Naturæ, • editio decima tertia (Lipsiæ, 1788), pars vi. p. 3166.

⁸ Nova Acta, Stockholm, 1783, p. 234, n. 12.

fering very considerably from the type represented by *Decacnemus (Antedon) rosacea*, although resembling it in only having ten arms.

In like manner both of Linck's species of his genus *Caput-Medusæ*, the one an *Antedon* and the other an *Actinometra*, were united by Linnæus, together with a many-armed specimen described by Retzius, into one species, *Asterias multiradiata*.

(§ 3) For some years after the commencement of the present century the Linnean nomenclature held its own, and the few species of recent Comatulæ with which the naturalists of that time were acquainted were described as different species of the Linnean genus *Asterias*.

The first among the post-Linnean zoologists who recognized the claims of this form of Sea Star to a distinct generic rank was De Freminville¹, who in 1811 presented to the Société Philomatique de Paris a "Mémoire sur un nouveau genre de Zoophytes de l'Ordre des Radiaires," to which he gave the name of *Antedon*. His definition of the genus was as follows:—"Animal libre, à corps discoïde calcaire en dessus, gélatineux en dessous, environné de deux rangées de rayons articulés, pierreux, percés dans leur largeur d'un trou central; ceux du rang supérieur plus courts, simples, et d'égale grosseur dans toute leur longueur; ceux du rang inférieur plus longs, allant en diminuant de la base à la pointe, et garnis dans toute leur longueur d'appendices alternes également articulés; bouche inférieure et centrale."

It is not very clear which of the two apertures on the ventral (or, as he called it, inferior) side of the disk was regarded by De Freminville as the mouth; it is very probable that, as he was only able to examine a spirit-specimen, he failed to recognize more than one—that namely, which, placed at the extremity of a long tube projecting from a point near the centre of the disk, we now know to be the anus.

Adams², who had studied living specimens of Linck's *Decacnemus rosacea*, had, however, pointed out some years previously the existence of two orifices to the digestive cavity; but his observations seem to have escaped notice; for Lamarek³, Miller⁴, and many other naturalists, all regarded the aperture at the end of the anal tube either as the mouth alone or as a combined mouth and anus; and it was not till 1823 that the existence of distinct oral and anal orifices was fully recognized.

It was announced as a new discovery by Leuckart⁵, in a letter to Von Schlotheim; and he was followed shortly afterwards by Meckel⁶, Gray⁷, and Hensinger⁸.

¹ Nouv. Bull. d. Scien. par la Soc. Philomat. tom. ii. p. 349. Paris, 1811.

² "Description of some Marine Animals found on the Coast of Wales," Trans. Linn. Soc. vol. v. p. 7 (1800).

³ Système d'Animaux sans Vertèbres, 2^{me} éd. (Paris, 1816), tom. ii. p. 532.

⁴ A Natural History of the Crinoidæ (Bristol, 1821), p. 128.

⁵ Von Schlotheim, Nacht. z. Petrefact. Abth. ii. p. 48 (Gotha, 1823); and Leuckart, "Einiges über Astriiden Geschlecht *Comatulæ* Lam. überhaupt, und über *Com. m. liberrima* insbesondere," Zeitsch. für organ. Physik, iii. p. 385 (1823).

⁶ "Ueber die Oeffnungen des Speisekanals bei den Comatulæ," Meckel's Archiv für Physiol. Band iii. p. 470 (1823).

⁷ "Notice on the Digestive Organs of the Genus *Comatulæ* and on the *Crinoidæ* of Miller," Ann. of Philos. n. s. vol. xii. p. 392 (1826).

⁸ "Bemerk. über d. Verdauungskanal der Comatulæ," Meckel's Archiv für Physiol. 1824, p. 317; and "Anl. Untersuch. d. *Comatulæ mediterranea*," Zeitsch. für organ. Physik, iii. p. 366 (1823).

De Fremenville's specimen was found on the keel of a vessel which had come from a warm climate; it had ten arms and twenty cirrhi, and was named by him *Antedon gorgonia*. He gave no further description of it, but simply referred to the figure of *Stella decacnemus rosacea*, Linck, in the 'Encyclopédie Méthodique'¹, which represents the ordinary European *Comatula rosacea*, as it is now called.

This species, however, is not identical with De Fremenville's *Antedon gorgonia*, which was referred by Lamarck² to his *Comatula carinata*, under which name he described some specimens brought by Peron from the Isle de France. Nevertheless the two species resemble one another in some important points, viz. the presence of ten arms, of a central or subcentral mouth, and of an excentric anal tube.

In 1815 Leach³ rescued the three genera contained in Linck's classis *Crinita* from the confusion of the Linnean genus *Asterias*, and united them into one genus, *Alecto*, comprising three species, viz. *Alecto europæa* (= *Decacnemus rosacea*, Linck), *Alecto horrida* (= *Caput-Medusæ*, Linck, or *Asterias multiradiata*, Linn.), and *Alecto carinata* (which seems to have been the same as De Fremenville's *Antedon gorgonia*).

Leach defined *Alecto* as having the "os inferius, irregulare," a description which would suit equally well either for the true mouth or for the anal opening, though perhaps more applicable to the former. He seems, however, like his predecessor De Fremenville, to have regarded the mouth as situated at the extremity of the anal tube; for in the explanation to Schweigger's figure⁴ of Leach's specimen of *Alecto horrida* the latter is described as the "röhrenförmig hervorstehender Mund." It is obvious, therefore, that we cannot make any use for systematic purposes of the definitions of *Antedon* and *Alecto* as given by Leach and De Fremenville respectively, as far as the position of the mouth is concerned.

Schweigger's figure of the disk of *Alecto horrida* shows clearly enough that the five trunks of the ambulacral grooves converge towards the centre of the disk, as in *Antedon rosacea* (*Alecto europæa*, Leach), Plate I. fig. 1. Leach's *Alecto horrida* was therefore a true *Antedon* in the modern sense of the term, although belonging to that division of the genus in which the repetition of the bifurcation of the ten primary arms is carried to a great extent.

(§ 4) Leach was apparently unacquainted with the memoir of Fremenville; but the same was evidently not the case with Lamarck (1816), who, like Leach in the previous year, united Linck's three genera into one, to which he gave the very appropriate name *Comatula*⁵. His definition of the genus differs but little from that given for *Antedon* five years previously by De Fremenville, whose original specimen Lamarck seems to have examined; and it is difficult to see why he did not adopt the name *Antedon* to designate the genus, which, like Leach and De Fremenville, he clearly distinguished as belonging to a different type from the Asteridæ, Ophiuridæ, and Euryalæ.

¹ Partie des Vers, pl. 42. fig. 6.

² *Tom. cit.* p. 534.

³ Zoological Miscellanies, vol. ii. p. 61: London, 1815.

⁴ Beobacht. auf naturhistorischen Reisen, p. 66, and Taf. iv. fig. 42: Berlin, 1819.

⁵ *Tom. cit.* p. 539.

Lamarek included eight species in his new genus *Comatula*. In only three of these is the mouth at or near the centre of the disk, viz. *C. mediterranea* (= *Stella decacnemus rosacea*, Linck), *C. carinata* (= *Antedon gorgonia*, Frem. ?), and *C. adeone*.

In all the other five species described by Lamarek, viz. *C. solaris*, *C. brachiolata*, *C. rotalaria*, *C. fimbriata* (= *Stella chinensis*, Petiver), and *C. multiradiata* (= *Caput-Medusæ brunnum*, Linck), the mouth (as I know from examination of the collection of Comatulæ in the Paris Museum, which still contains many of Lamarek's original specimens) is nowhere near the centre of the disk, which is occupied by the anal tube, but is excentric, or even marginal. At the same time the five primary groove-trunks do not converge towards the centre of the disk, as in *Antedon rosacea* (*Com. mediterranea*, Lam.) (Pl. I. fig. 1), but they unite more or less completely into a horseshoe-shaped furrow, at one point of which is situated the excentric mouth (Pl. I. figs. 2-5).

This type will be described further on, under the name of *Actinometra*. Lamarek, who found it in more than half of the species constituted by him, seems to have regarded it as common to all Comatulæ. His description of it is worth quoting, as it is the first notice of a true *Actinometra* that I have been able to find. He says¹:—"Le disque inférieur ou ventral offre un plateau orbiculaire plus large que le dorsal, entouré de rayons simples, cirreux. Près de la circonférence de ce plateau, on aperçoit un sillon irrégulièrement circulaire qui s'ouvre sur la base des rayons pinnés, et se propage le long de leur face inférieure, aussi que de celle des pinnules. Ce sillon néanmoins, ne s'approche point de la bouche [*i. e.* the anal tube] et ne vient point s'y réunir, comme cela a lieu pour la gouttière des rayons dans les Astéries. Au centre du disque inférieur ou ventral des *Comatules* la bouche, membraneuse, tubuleuse, ou en forme de sac, fait une saillie plus ou moins considérable suivant les espèces."

Although *Antedon* and *Alecto* were both constituted previously to *Comatula*, yet Lamarek's authority was sufficient to establish the latter name, and to bring it into general use, though Cuvier adopted Leach's genus *Alecto*, and used it in preference to *Comatula*. The latter, however, was more generally employed by all subsequent observers (who pointed out Lamarek's error respecting the position of the mouth) thenceforward till the time of Johannes Müller.

(§ 5) During this period the skeleton both of the recent and of the fossil Crinoids was made the subject of careful investigations by Miller² and Goldfuss³. The latter author divided his class Stellerites into two Orders:—(*a*) Stilasterites, or Gestielte Seesterne; and (*b*) Asterites liberi, or Freie Seesterne. The former he again divided into Articulata and Inarticulata, placing in the first group a number of fossil Mesozoic Crinoids, viz. *Eugeniocrinites*, Miller, *Solanocrinites*, Goldf., *Pentacrinites*, *Encrinites*, and *Apiocrinites*.

In his descriptions of these genera he adopted and considerably improved the somewhat inapplicable system of nomenclature, introduced by Miller for the parts of the skeleton of the fossil Crinoids and of *Comatula*.

Portions of his diagnoses of *Eugeniocrinites* and *Solanocrinites* are of considerable interest, both zoologically and morphologically. Of the former, he says⁴:—

¹ *Tom. cit.* p. 532.

² *Loc. cit.*

³ Petrefacta Germaniæ, i. (Dusseldorf, 1826-35).

⁴ *Tom. cit.* p. 162.

“Die kurze runde mit einem runden Kanale durchbohrte Säule besteht aus wenigen walzigen verlängerten Gliedern, und nimmt am obern Ende allmählig zu. Ihre Gliederung wird oft nur durch Ringe angedeutet, unten endet sie in starken Wurzeln. Das letzte verdickte Säulenglied vertritt die Stelle des Beckens und articulirt durch eine Gelenkfläche mit den Rippengliedern.”

The term “Becken” is here meant to signify the circle, of basals which, in *Pentacrinus* and other stalked forms, intervenes between the stem and the circle of first radials, the “Rippenglieder” of Goldfuss.

These basals are also present in *Solanocrinites*, which genus, as Goldfuss well remarks, “hat in verschiedener Hinsicht Aehnlichkeit mit den *Pentacriniten*, und bildet zugleich einen Uebergang zur Gattung *Comatula*.”

Its most important characters are as follows¹:—

“Die Säule ist sehr kurz, beinahe so dick als der Kelch, fünfseitig und an ihrer Basis nicht mit Wurzelsprossen, sondern mit ausstrahlenden Runzeln versehen. Ihre Glieder sind mit einander verwachsen und haben an den Seitenflächen Gelenkhöhlungen für den Ansatz zahlreicher dicker Hülsarme. Die oberste Gelenkfläche der Säule zeigt fünf strahlenförmige Erhabenheiten, auf welchen das Becken articulirt. Das Becken wird nicht durch das oberste Säulenglied vertreten, sondern es besteht aus fünf Gliedern, welche zwischen die Nähte der fünf Rippenglieder eingefügt sind, oder sie bedecken. Die fünf Glieder des Beckens bilden entweder nur schmale Strahlen, die zwischen die Nähte der Rippenglieder einsenken (*S. costatus*, *S. scrobiculatus*), oder sie sind breiter, stoßen seitlich an einander, und stellen eine tiefe mit 5 Strahlenfurchen ausgehöhlte Gelenkfläche dar (*S. jageri*).”

The first genus in Goldfuss’s order “*Asterites liberi*” is the *Comatula* of Lamarek, of which he says, “Diese Gattung bildet den Uebergang von den Stilasteriten zu den freien Seesternen und steht zunächst mit den *Solanocriniten* in nächster Verwandtschaft.”

Besides describing five fossil species, he gives some account of two recent ones, dwelling more especially upon the structure and composition of the skeleton.

Thus “Bei der *C. mediterranea* besteht die Säule aus drei Gliedern: das Becken fehlt, und die Rippenglieder sitzen unmittelbar auf dem letzten Säulengliede.” “Bei der in den Ostindischen Meeren lebenden *C. multiradiata* Lam. hingegen, finden sich Beckenglieder, so dass man berechtigt sein könnte sie als eine eigene Gattung zu betrachten. Ihr Säulenrudiment besteht aus einem einzigen schüsselförmigen Gliede, an dessen Rande fünf schmale dreieckige Beckenglieder ansitzen und mit ihm verwachsen sind. Diese stoßen mit ihren Seitenflächen nicht an einander, sondern stehen so weit entfernt dass die ersten Rippenglieder unmittelbar zwischen ihnen auf dem Säulengliede ansitzen, und sie durch einen Abschnitt der unteren Ecke zwischen sich aufnehmen. In der Mitte des innern unteren Randes jedes Beckengliedes entspringt ein zahnförmiger Fortsatz, der sich als knospeliger schmaler Streifen bis zum Mittelpunkte des Säulengliedes verlängert, in welchem er durch eine Rinne aufgenommen ist. Diese Beckenglieder sind also denen der *Solanocriniten* vollkommen analog.”

(§ 6) Goldfuss, who, though acquainted with the name of *Alecto*, yet used *Comatula*

¹ *Tom. cit.* p. 166.

² *Tom. cit.* p. 202.

in preference to it, paid very little attention to the soft parts of either of the *Comatulæ* which he dissected.

In the following year, however, De Blainville¹ described the visceral mass at some length. Like his predecessors, he adopted Lamarck's genus *Comatula*, making it the only representative of his section, "Les Astérencrinides libres," while at the same time he acknowledged the prior claims of de Freminville's name *Antedon*. He was, of course, acquainted with Lamarck's error respecting the position of the mouth, which he described as "assez antérieure, isolée, membraneuse, au fond d'une étoile formée par cinq sillons bifurqués." The species which he dissected was a foreign one preserved in spirit; it had a large number of arms; and from the not very clear description which he gives of its ventral surface it would seem to have been a true *Actinometra*.

After speaking of the tentacular furrows on the ventral surface of the arms, he says², "En suivant ces espèces de sillons dont le nombre est proportionnel à celui des digitations du rayon, on arrive par un sillon unique pour chacun d'eux et qui en occupe la base, au centre d'une sorte d'étoile à bords épais, frangés, et par suite à la bouche qui est au fond. L'étoile formée par la réunion des sillons des rayons n'est pas symétrique, c'est à dire que ses branches sont très-inégales: les unes que j'appellerai les antérieures, étant bien plus courtes que les autres, ou postérieures. Il en est résulté que la bouche n'est pas au centre de l'étoile, mais bien plus proche d'un côté que de l'autre: elle est assez difficile à voir au contraire d'un autre orifice, dont il va être question, et que M. de Lamarck paroît avoir pris pour elle. Elle est profondément enfoncée dans l'étoile des sillons: elle est ronde, sans aucune armature et conduit immédiatement dans l'estomac."

The above description implies, if I rightly understand it, that the mouth of De Blainville's specimen was nearer to one side of the disk than to the other, so that the primary trunks of the ambulacral grooves were of unequal lengths. This will be subsequently seen (section 14) to be the principal distinctive character of the genus *Actinometra*.

De Blainville evidently attached no importance to the position of the mouth as a character of systematic value in the determination of the species of recent *Comatulæ*; and from his definition of it as "assez antérieure," it would almost appear as if he supposed the other species to agree in this respect with the one dissected by him.

This is, in fact, the case in five out of the eight species described by Lamarck, with which De Blainville was probably acquainted, and to which he added no new ones, except that he gave the name of *Comatula barbata* to Linck's third species of *Decacnemus*, the *fimbriata* of Barrelier, or "*barbata*" of Linck. Lamarck had been uncertain to which of his species he should refer it, although, as we have seen above (section 1), it is really only a local variety of his *C. mediterranea*.

Like the other naturalists of his time (1838), Agassiz³ also adopted *Comatula* in preference to the other generic names of this type, but defined it as having the "bouche centrale enfoncée," and with the five "rayons du disque bifurqués," thus limiting the number of arms in the genus *Comatula* to ten only. At the same time he erected Lamarck's species *C. multiradiata*, with sixty or more arms, into a new genus, *Comaster*, which he defined as

Manuel d'Actinologie, (Paris, 1834) p. 249.

² *Op. cit.*, p. 251.

³ "Prodrome d'une Monographie des Radiaires ou Échinodermes," Ann. des Scien. Nat. 2^e série, Zool. vii. p. 257.

follows:—"Ce genre a la même organisation que le précédent; mais les espèces ont les bras ramifiés au lieu de les avoir simplement fourchus." Agassiz consequently used *Comatula* simply as equivalent to the *Decacnemus* of Linek, while his new genus *Comaster* was Linek's *Caput-Medusæ*, or the *Comatula multiradiata* of Lamarck. Of the seven other species constituted by the last-mentioned naturalist, only two, *C. rotalaria* and *C. fimbriata*, have more than ten arms; in both of these the number of arms is usually twenty, though it may reach twenty-four, or possibly even more. Strictly speaking, therefore, these two species, according to the above definition, should be referred to *Comaster*, and not to *Comatula*.

This character, the number of arms, upon which Agassiz founded a generic distinction, is, in fact, extremely variable, and by no means of generic importance; in fact, as Goldfuss¹ remarked a little later, "Wollte man mit Agassiz die Theilung der Arme als hinreichendes Gattungsmerkmal ansehen, so würde man folgerecht gezwungen sein fast jede Art der Crinoideen als Gattung aufzustellen."

Leach and Lamarck had already recognized this fact in uniting Linek's three genera under a common name; and it is not a little strange that Agassiz should have seen fit to separate them again. His doing so, however, led to somewhat important consequences from a systematic point of view. Turning to the fossil *Comatulæ*, we find that Agassiz erected the *C. pinnata* of Goldfuss into a new genus, *Pterocomma*, and grouped together his other three species, *C. tenella*, *C. pectinata*, and *C. filiformis*, under the generic name *Saccoma*; while he expressed his belief that *Solanoocrinus* was really related to the *Comatulæ*, and more especially to the problematical fossil described by Goldfuss under the name of *Glenotremites*, which he rightly recognized as the centrodorsal piece of a free-living Crinoid.

In the year 1840 a new fossil *Comatula* was described by Hagenow² under the name of *Hertha mystica*. The specimen, consisting of the united first radials and hemispherical centrodorsal piece, was somewhat worn; but Hagenow was able to recognize the resemblance between it and the remains of *Solanoocrinus*, and the corresponding parts of Goldfuss's *Comatula multiradiata*, except that he was unable to find any trace of the external basals which Goldfuss had described in both the above cases; and though he seems, and (as we now know) correctly, to have suspected "das Vorhandensein etwa verdeckt-liegender Beckenglieder," he was, of course, unable to come to any satisfactory conclusion upon the point.

(§ 7) The year 1840 is a noteworthy one in the history of our knowledge of the Crinoidea; for it marked the appearance of the first of a series of classical memoirs by Johannes Müller, who laid the foundation of nearly all our knowledge of the zoology and morphology of the group: the first³ of these was devoted to an anatomical account of the recent and very rare genus *Pentacrinus*, together with many observations upon *Comatula*.

¹ "Beitr. z. Petrefactenkunde," N. Acta Acad. Leop.-Carol. Nat.-Cur. xix. A. p. 348.

² "Monogr. d. Rügen'schen Kreide-Versteinerungen, II. Abtheil. Radiarien und Annulaten," Neues Jahrb. Mineralogie, 1840, p. 664.

³ "Ueber den Bau des *Pentacrinus caput-Medusæ*," Abhandl. d. Berlin. Akad. 1843; Abstract in Monatsb. derselben, 1840; also in Wiegmann's Archiv f. Naturgesch. 1840, i. p. 307.

Müller seems at first, not unnaturally, to have supposed that Goldfuss was right in referring the many-armed specimen dissected by him to the *Comatula multiradiata* of Lamarek, for which species he adopted Agassiz's name *Comaster*¹. But he did not use it precisely in the same sense as Agassiz, who, in his definition of the genus, makes no mention of the external basals, the presence of which was regarded by Goldfuss as the principal character distinguishing *Comaster* from *Comatula*.

Müller adopted *Comaster*² in the sense in which Goldfuss used the name; and when he subsequently discovered³ that the *Comatula multiradiata* or *Comaster* of Goldfuss was not specifically identical with the specimen described as *Comatula multiradiata* by Lamarek, he retained the name *Comaster* for Goldfuss's specimen only, which, like *Solanocrinus*, is remarkable for having "kleine basalia zwischen den Insertionen der Kelehradien, oder sogenannten Beckenstücke welche den eigentlichen Comatulen gänzlich fehlen"⁴.

At the same time he gave a careful description⁵ of Lamarek's original specimen of *Comatula multiradiata*, based upon an examination of it by Troschel; but as he regarded *Comaster* and *Solanocrinus* only as one subgenus of *Comatula*, he gave it a new specific name "*multifida*," on the ground that "die *Comatula multiradiata* Goldfuss, als die zuerst genau beschriebene, den Speciesnamen *multiradiata* behalten muss." Lamarek's specimen was thus restored by Müller to its previous position among the "Comatulen im engern Sinne, nämlich Gattung *Alecto*, Leach (*Comatula*, Lamarek)," which he grouped together with *Comaster* into one family, *Comatulinae*. The fossil *Solanocrinus* was regarded by him as identical with the latter form, while he referred the *Hertha mystica* of Hagenow, and *Pterocoma*, Ag. (*C. pinnata*, Goldf.), to *Comatula* or *Alecto*; for at that time (1841) he used the two names indifferently, considering them (as, indeed, they originally were) equivalent to one another.

Goldfuss put forward about the same time a somewhat similar classification.⁶ In a subsequent abstract (with additions) of his 'Beiträge zur Petrefactenkunde,' [which had been published two years previously (1839)] he speaks of the two species dissected by him as "die Typen der zwei nächst bezeichneten Genera (*Comatula*, *Comaster*), welche daher nebst den zwei zuletzt folgenden (*Solanocrinites*, *Gasterocoma*) als Verzweigungen des Lamarek'schen weiten Geschlechts *Comatula* zu betrachten sind." He did not, however, agree with Müller in regarding *Solanocrinites* and *Comaster* as identical, partly, apparently, because nothing was known of the arms of the former, and partly because of the differences in the form of the "Knopf," or centrodorsal piece, which he called a short stem—although, as Müller showed, this is not a character of any generic value.

Although Goldfuss had at first supposed⁷ that the basals were really absent in *Comatula mediterranea*, and that the first radials therefore rested directly upon the top of the centrodorsal piece, or, as he expressed it, on the last stem-segment, he seems subsequently to have changed his opinion; for in his definition⁸ of the genus *Comatula*, given in 1839,

¹ "Beiträge zur Petrefactenkunde," *loc. cit.* p. 349.

² Wiegmann's Archiv, 1840, i. p. 309.

³ "Ueber die Gattungen und Arten der Comatulen," Wiegmann's Archiv, 1841, i. pp. 140, 147.

⁴ "Bau des *Pentacrinus*," *loc. cit.* p. 27.

⁵ Wiegmann's Archiv, 1841, i. p. 147.

⁶ Neues Jahrbuch für Mineralogie, 1841, p. 818.

⁷ Petrefacta Germaniæ, *tom. cit.* pp. 203, 204.

⁸ Beitrüge, &c. *loc. cit.* p. 349.

he says, "Auf dem letzten Säulengliede ruhen fünf Beckenglieder, und auf jedem derselben ein Rippen- (=second radial) und ein Schulterglied (third or axillary radial), auf welchem zwei einfache Arme eingelenkt sind," from which it is evident that he was wrongly led to regard the first radials as representing the basals of *Comaster* and *Pentacrinus*. This mistake is hardly a surprising one when we consider the remarkable metamorphosis undergone by the embryonic or primitive basals, and their concealed condition in the adult *Comatula mediterranea*.

Müller, who examined a very large number of species of *Comatula*, never found one in which the basals appeared externally, as described and figured by Goldfuss in *Comaster*, and remarked¹:—"Daraus geht hervor, dass die Gegenwart wirklicher Basalia ohne Zerlegung bei einer lebenden Comatule, auch dann, wenn sie wirklich solche besitzt, schwer zu erkennen sein muss. Die Unterscheidung der *Comaster* und *Comatula* wird daher bei der Ordnung der lebenden Comatulen unpractisch." In fact he appears to have given up the genus *Comaster* altogether; for he adds in a note:—"Kürzlich habe ich die einzige im Museum zu Bonn befindliche *Comatula multiradiata* (nicht das von Goldfuss zerlegte Exemplar, wovon ich nichts mehr vorfand) untersucht. Ich habe daran nichts von Beckenstücken erkennen können. Die Gattung *Comaster* ist daher wohl zu unterdrücken." He seems finally² to have thought that it might possibly be identical with the *C. Bennettii* of the Leyden Museum. As, however, *Comaster* has not been seen by any naturalist since the time of Goldfuss, its position must still remain in doubt.

(§ 8) Up to the time of Müller no one paid any attention, from a systematic point of view, to the arrangement of the tentacular furrows on the ventral perisome of the disk of *Comatula*; but Lamarck and De Blainville had, as we have already seen, examined and described, with more or less accuracy, a condition which we now know to differ very considerably from that presented by the *Decacnemus* of Linck, or the *Antedon* of De Freminville. Both these observers seem to have regarded the former condition as the normal one, and as common to all *Comatulæ*. Müller, who does not seem to have been acquainted with their descriptions (for he makes no mention of them), took up the subject systematically, and soon discovered that, using the distribution of the tentacular furrows as a basis of classification, he could distinguish two, as he thought, very distinct types of the genus *Comatula*, which he named *Alecto* and *Actinometra* respectively. In his earlier communications³ on the subject he described the ordinary *Comatula* and *Pentacrinus* as having a central mouth and symmetrically distributed tentacular furrows; *i. e.* the five main trunks formed by the union of the furrows of the five groups of arms converge directly towards the centre of the disk, being separated by five "interpalmar" areas, one of which, slightly larger than the rest, is occupied by the anal tube, which is therefore excentric in its position (Pl. I. fig. 5, *An.*).

During his visit to Vienna in 1840 Müller had an opportunity of examining an un-

¹ 'Ueber die Gattung *Comatula*, Lam., und ihre Arten,' Separatabdruck aus den Abhandl. Berlin. Akad. 1849, p. 8.

² *Ibid.* p. 29.

³ "Bau des *Pentacrinus*," loc. cit. p. 47, and Wiegman Archiv, 1840, i. p. 311.

usually large specimen of the *Comatula solaris* of Lamarek—unfortunately, however, only a dry one, which he found to differ so greatly from the other *Comatulæ* then known to him, that he described it under the name of *Actinometra imperialis*¹, “welche generisch von andern durch die Bildung ihres Scheitels verschieden zu sein schien. Auf dem Scheitel der mit blumenartigen Kalkblättchen bedeckt ist, ist keine Spur von den Furchen zu sehen, die bei den Comatulen von den Armen zum Munde führen. Auch ist dort nichts vom Munde zu sehen. Die Mitte der Bauchseite nimmt eine Röhre ein. Die Arme haben die ventrale Furchen der Comatulen, die Furchen der zehn Arme münden aber in gleichen Abständen in eine die Scheibe am Rande umziehende Cirkelfurche. Diese eigenthümliche Bildung liesse sich durch eine unsymmetrische Vergrösserung desjenigen Intertentacularfeldes, worin die Afterröhre steht, über den ganzen Scheitel und auf Kosten der anderen Intertentacularfelder erklären, so dass der Mund aus der Mitte des Scheitels ganz an die Seite zwischen je zwei Armen geräth; es ist mir aber nicht gelungen den Mund hier zu finden.” (Pl. I. fig. 2.)

In a subsequent visit to Lund, Müller examined two dry specimens of *Comatulæ*, which had been described by Retzius² many years previously under the names of *Asterias pectinata*³ and *Asterias multiradiata*. These he found to belong to the same type as the Vienna specimen, which he had already designated *Actinometra imperialis*, and which he supposed to be distinct from the true *Comatula solaris* of Lamarek. When he visited Paris, however, in 1844, he examined Lamarek's original specimen of this species, and convinced himself of its specific identity with his Vienna *Actinometra*. Consequently he withdrew the specific name “*imperialis*,” and described the type simply as *Actinometra solaris*⁴. Müller was unable to determine the position of the mouth in the dry specimens of the Lund and Vienna Museums on which he founded his new genus *Actinometra*; but subsequently he was able to examine many spirit-specimens both of his typical species, *Act. solaris*, and also of other “Comatulen von jener Anordnung der Furchen, sowohl zehnamige als vielarmige Siehe die beistehende Figur von *Comatula Wahlberghii*”⁵ (Pl. I. fig. 3). This last species he describes a few pages further on as *Comatula (Actinometra) Wahlberghii*.

He did not, however, appear to regard the position of the mouth as of any systematic importance; for he goes on to say:—“Der Mund ist bei der in Frage stehenden Ab-

¹ Wieg. Archiv, 1841, i. p. 141; and “Neue Beitr. z. Kenntniss der Arten der Comutalen,” Wieg. Archiv, 1843, i. p. 132.

² Dissertatio sistens species cognitae Asteriarum. Lundæ, 1805.

³ The specific name “*pectinata*,” Linnaeus, included both Retzius's specimens and the *Dicænaeus* of Linck. These belong, however, to two very different types of the genus *Comatula*, and must be carefully distinguished from one another. The former is, as above mentioned, an *Actinometra*, while the latter was called *Alecto* by Müller, being simply the common *Comatula mediterranea*, Lam. Pennant, Adams, and others naturally employed the Linnean name for this last species; but Dujardin, following Retzius and Müller, applied it also to Retzius's original specimen, which is really an *Actinometra*, and not an *Alecto*, like *C. mediterranea*. This has given rise to much confusion in the synonymy of these two species.

⁴ Wiegmann's Archiv, 1843, i. p. 133.

⁵ ‘Gattung *Comatula*,’ pp. 12, 13.

⁶ *Ibid.* p. 9.

weichung allerdings vorhanden, er liegt ganz zur Seite, doch ist dies nicht die Ursache des Unterschiedes, es gibt vielmehr auch Comatulen von der gewöhnlichen Anordnung der Furchen, bei denen gleichwohl der Mund seitlich, die Afterröhre central steht. Fig. von *C. multiradiata* (Pl. I. fig. 4). Die fragliche Abweichung beruht vielmehr darauf, dass die fünf Furchen nicht symmetrisch für die fünf Gruppen der Arme vertheilt werden, sondern dass von den fünf Furchen einzelne herrschend werden und Aeste an die meisten Arme abgeben. Indem diese Hauptfurchen, nachdem sie die Scheibe umzogen, sich wieder annähern, so entsteht der Schein eines Cirkels. An in Weingeist aufbewahrten Exemplaren sieht man indess, dass es kein geschlossener Cirkel ist;" and further on (p. 10) he says, "Ich werde daher bei den Arten wo fünf centripetale Furchen beobachtet sind, den Namen *Alecto* in Klammer dem Gattungsnamen *Comatula* beifügen, wo aber weniger Furchenstämme den excentrischen Mund erreichen, den Namen *Actinometra* demselben Gattungsnamen *Comatula* folgen lassen. Also z. B. *Comatula (Alecto) europæa*; *Comatula (Actinometra) solaris*."

Müller does not appear to have been acquainted with De Fremenville's name of *Antedon*; but he distinctly states that Leach's genus *Alecto* was constituted a year earlier than Lamarek's *Comatula*. He had in his earlier communications employed the two indifferently and as equivalent to one another; but when he became acquainted with the type represented by *Comatula solaris* and elevated it into a new genus, or rather subgenus, *Actinometra*, in contradistinction to *Alecto*, he retained Lamarek's name *Comatula*, probably on account of its being so well known, and employed it to designate the genus in which he included the subgenera *Alecto*, *Actinometra*, and *Comaster*.

Thus the sole character by which Müller distinguished the first two of these subgenera from one another was the number of groove-trunks reaching the peristome, irrespective of the position of the mouth. It is therefore easy to understand that, as many of the specimens which he examined were dry, and as in others, although preserved in spirits, the arms were contracted over the disk so as completely to conceal it, he was unable satisfactorily to determine more than three species of *Actinometra*. Two of these, *Act. solaris* and *Act. Wahlbergii*, have been already mentioned; the third was the small *Comatula rotularia* of Lamarek.

(§ 9) The *Asterias pectinata* of Retzius, which presented the same "Bildung des Scheitels" as *Act. solaris*, resembled it so greatly in other respects, that Müller regarded the two as almost identical, or, at any rate, as presenting only varietal differences¹.

He seems also to have come to the conclusion that the other species described by Retzius, the *Asterias multiradiata*, Linn., had a prior claim to this specific name over either of the similarly named types described by Goldfuss (*Comaster*) or Lamarek (*Comatula multiradiata*); for he described it as "*Comatula (Alecto) multiradiata* nob."². It is difficult to understand why he called it *Alecto*; for he had already³ described this

¹ 'Gattung *Comatula*,' p. 52.

² *Ibid.* p. 25.

³ Wiegmann's Archiv, 1843, i. p. 133, and 'Gattung *Comatula*,' pp. 9, 10.

Lund specimen as belonging to the type of his new genus *Actinometra*, in which not five, as in *Alecto*, but “weniger Furchenstämmen den excentrischen Mund erreichen.”

Müller further examined a specimen of the “so-called” *C. multiradiata* in the Bonn Museum; and although he did not actually include it in his type under that name, yet he seems to have been inclined to do so; for he says¹ that “es stimmt durch den Besitz der Syzygien an den Axillaria der Arme mit *Comatula multiradiata* Retz.,” but adds, “Mund excentrisch, 5 Furchen der Scheibe sammeln die Furchen der respectiven Arme und kommen am Mund zusammen.” (See Pl. I. fig. 4.) Here, again, it is evident that Müller’s description of *Alecto* will not hold good; for according to his own descriptions, the Lund and Bonn specimens of *Comatula multiradiata*, Müll., however much alike in other respects, differ so greatly in the distribution of the ambulacra on the disk that one is *Actinometra* and the other *Alecto*.

Müller also referred three specimens contained in the Paris collection to this type; and he was perhaps thinking of the condition of the ambulacra presented by them when he added the following sentence to his previous description of the Lund specimen, and named the type *Alecto*². “Mund excentrisch, aber an Weingeistexemplaren ergibt sich dass die fünf zum Munde führenden Furchen sich ganz symmetrisch für die fünf Gruppen der Arme vertheilen.” This arrangement, which he called the “gewöhnliche Anordnung der Furchen,” had been already³ figured by him as occurring in *C. multiradiata*, which, as he says, differs from the ordinary *C. mediterranea* in the excentric position of the mouth (Pl. I. figs. 1, 4).

It is thus evident that, according to Müller’s own nomenclature, two types, differing only in the “Bildung des Scheitels,” but almost precisely similar in every other respect, viz. the Lund specimen, on the one hand, and the Paris specimens, on the other, were referred by him to the same species, *Alecto multiradiata*, Müller. It will, however, be shown further on that the distinction drawn by Müller between *Alecto* and *Actinometra* is not a real one, and that the Lund and one of the Paris specimens, both of which have an excentric mouth and a central or subcentral anal tube, really belong to one and the same species, *Actinometra multiradiata*.

(§ 10) For a short time after the publication of Müller’s *Comatula*-memoirs the genera *Alecto* and *Actinometra* remained as he left them, both being regarded as subordinate types of Lamarck’s genus *Comatula*.

A singularly minute fossil species, discovered by Philippi⁴ between the valves of an *Isocardia cor* from the Sicilian Tertiaries, was named by him *Alecto alticeps* because of the height of its “Kelchstück,” a character found both in *Alecto Eschrichtii* and in *A. phalangium*, as Müller had already pointed out. A few new fossil species of a more or less doubtful nature have been since described, and variously referred either to Müller’s family Comatulinae or to new and distinct types.

The typical genus of this family, *Comatula*, Lam., has undergone numerous changes in its definition. Roemer, who at first revived Linck’s name *Decacnemus*, subsequently

¹ ‘Gattung *Comatula*,’ p. 29.

² *Ibid.* p. 26.

³ *Ibid.* p. 9.

⁴ “*Alecto alticeps*, n. sp., eine tertiäre Comatula-Art von Palermo,” Neues Jahrb. für Mineral. 1844, p. 540.

withdrew it in favour of *Comatula*¹, the “Knopf,” or centrodorsal piece of which was described by him as an “Ueberrest der verkümmerten Säule,” while, like his predecessors, he mentioned the absence of basals. The existence, however, of external basals, both in *Solanocrinus* and in *Comaster*, led him to regard them, like Müller, as generically identical; and he used the name *Comaster* for this type in preference to *Solanocrinus*, as it “bezieht sich nicht nur auf einen lebend und vollständig bekannten Typus, sondern drückt auch die Verwandtschaft richtig, wie *Solanocrinus* unrichtig, aus.” About the same time D’Orbigny², and, a few years later Pietet³, transferred the name *Comatula* to this last-mentioned type, in which the basals appear externally; while they revived Linck’s name *Decacnemus* (or, as they named it, *Decameros*) for the *Antedon* of De Freminville and the *Alecto* of Leach. They characterized the genus as only differing from *Comatula*, in their sense, in the total absence of the five basals, so that the radials rest directly upon the centrodorsal piece. Fortunately, however, this peculiar inversion of the nomenclature employed by Müller was not destined to last; for in Bronn’s ‘Klassen und Ordnungen des Thierreichs’⁴, all the above genera are united into one, *Comatula*, which with *Glenotremites* and another doubtful fossil constitute the family Comatulidæ. *Saccocoma* and *Marsupites* are restored to the places originally assigned to them by Müller, in special groups, Costata and Tessellata respectively, among the unstalked Crinoids; while *Eugeniocrinus*, which Goldfuss regarded as nearly related to *Solanocrinus*, is placed with a few similar forms in a family Eugeniocrinidæ, which, together with the Pentaocrinidæ and Apioocrinidæ, make up the group Articulata of Müller.

(§ 11) The family Comatulidæ was considerably enlarged a few years later by Dujardin and Hupé⁵, who included in it, as D’Orbigny and Pietet had already done, not only the tribes Comatuliens and Saccocomiens, but also the Eugeniocriniens, which both the above authors had ranked among the stalked Crinoids, while *Marsupites*, which they referred to the Comatulidæ on account of its calyx being free, was transferred to the Cyathocrinidæ by Dujardin, who could “ne voir qu’un caractère secondaire dans l’absence d’une tige chez plusieurs de ces Crinoïdes.” He distinguishes the three tribes as follows:—“Nos trois tribus seront suffisamment caractérisées: la première, celle des Eugeniocriniens, par son calice adhérent ou pedonculé, jamais libre; les deux autres, dont le calice est libre à l’état adulte, se distinguent parce que celle des Comatuliens porte cirrhes ou rayons dorsaux, dont la dernière, celle des Saccosomiens, est censée dépourvue.”

The position of *Eugeniocrinus* does not concern us at present. Let us now investigate the species included by Dujardin in the tribe Comatuliens. Under this head he ranks three genera, viz. *Comatula*, Lam., *Actinometra*, Müll., and *Comaster*, Ag., using the latter name in the sense in which it was employed by Müller and Römer, namely as equivalent to *Solanocrinus*. Dujardin’s genus *Comatula*, however, is not precisely equivalent to that of Müller, who included in it the two genera or subgenera *Alecto* and

¹ *Lethæa geognostica*, iii^{te} Auflage, 1851, Theil iv. p. 133, and Theil v. p. 177.

² Cours élément. de Paléontol. et de Géol. stratigraph. 1850–1852, vol. 2, i. pp. 138, 139.

³ Traité de Paléontol. (Paris, 1857) vol. iv. p. 288.

⁴ Band ii. Aktinozoen (1860), p. 233.

⁵ Hist. Nat. des Zoophytes, Échinodermes, (Paris, 1862) p. 186.

Actinometra. The latter was erected into a separate genus by Dujardin, who limited the application of the name *Comatula* to those forms only which had been described as *Alecto* by Müller—those, namely, in which five main groove-trunks reach the mouth, irrespective of its position, to which Müller seems to have attached no importance as a character of any systematic value; so that Dujardin, following him, says of the mouth of *Comatula* (i. e. *Alecto*) that it is only “ordinairement au centre”¹.

Further, Dujardin, though really employing the name *Actinometra* in the same sense as Müller did, does not describe it in the same way; he takes no account of the number of groove-trunks reaching the peristome, to which Müller attached so much importance, but simply says², “Ce genre ne diffère guère des vraies Comatules que par la position de l’anus au centre et de la bouche au bord du disque. Il en résulte que les gouttières ambulacraires, au lieu de se rendre à la bouche en suivant la direction des bras comme chez les Comatules, s’infléchissent et suivent le contour du disque.” Dujardin adds, with perfect truth, that the distinctive characters of *Actinometra* are hardly yet sufficiently established. It will be shown, further on, that his definition of the genus is really the correct one, and that we must refer to it all those forms of *Alecto* (*Comatula*, Dujardin) in which, as described by Müller³, the anal tube occupies the middle of the disk, “so dass der Mund seitlich gegen den Rand der Scheibe rückt, ohne dass die *Ambulacra* ihre symmetrische Vertheilung auf die 5 Armstämme einbüßen” (Pl. I. fig. 4). As Müller had only employed the names *Alecto* and *Actinometra* to designate subordinate types of the *Comatula* of Lamarek, it is rather unfortunate that Dujardin should have erected the latter into a separate genus, in contradistinction to *Comatula*, and restricted this name to the *Alecto* of Müller; for we now know, as mentioned in section 5, that most of the species described as *Comatula* by Lamarek belong really to *Actinometra*, not only in the somewhat limited sense in which this name was used by Müller, but also in its wider application as employed in this memoir.

Thus, for example, Müller stated expressly⁴ that Lamarek’s original specimen of *C. solaris* in the Paris Museum is identical with the large Vienna specimen, also bearing the name of *C. solaris*, Lam., which he made the type of his new genus *Actinometra*.

Dujardin, however, paid no attention to this identification of Müller’s, and described the two specimens as *C. solaris* and *Act. imperialis* respectively, simply on the basis of Müller’s original diagnosis, published before his visit to Paris. Dujardin thus made not only two different species, but also two different genera, out of the same type, while he makes a third species out of the *Asterias pectinata* of the Lund Museum, which Müller regarded as a variety of *Actinometra solaris*.

I have examined a considerable number of specimens of this type, and find it to exhibit an enormous range of variation in minor points, such as the number and relative proportions of the cirrus-segments, the colouring, the presence or absence of a faint keel on the dorsal side of the arms, &c., and am convinced that none of these can be regarded as of specific value. A number of such varieties group themselves around a

¹ *Op. cit.* p. 194.

² *Op. cit.* p. 208.

³ “Nachtrag zu der Abhandl. über die Comatulen,” Monatsb. der Berlin. Akad. 1846, p. 177.

⁴ ‘Gattung *Comatula*,’ p. 13.

type possessing certain definite characters, by which it may be distinguished from other types forming the centres of similar groups of varieties; but the characters above mentioned are usually so excessively variable within each group, that it becomes utterly impossible to make any use of them as specific distinctions, as Dujardin has done.

Dujardin seems to have detected Müller's oversight in classing the *Asterias multiradiata* of Retzius as an *Alecto* after previously describing it as an *Actinometra*; for he transferred it to this genus under the name of *Actinometra multiradiata*, and adopted Müller's specific designation *multifida* for the original specimens described as *Comatula multiradiata* by Lamarek. The third form to which this name has been applied, viz. the *C. multiradiata* of Goldfuss, was regarded by Dujardin as a separate genus on account of its possessing external basals, or, as he called them, "interradials;" and he restored to it the old name of *Comaster*, which had been given up by Müller, including in this genus, as Rømer had previously done, all the species of *Solanocrinus*.

(§ 12) Müller had, as we have seen above, referred both *Alecto* and *Actinometra* to the one genus *Comatula*, while Dujardin limited the application of the latter name to the species of *Alecto* only, and gave up the name of *Alecto* altogether, as had been previously done by D'Orbigny and Pictet. This was a step in the right direction; for, as Müller had already pointed out, this name had been employed since 1821 to designate a section of the Polyzoa established by Lamouroux. It is a pity, however, that Dujardin, instead of limiting the application of Lamarek's name *Comatula* to the species of Müller's subgenus *Alecto*, did not revert to the old name of *Antedon*, which was proposed by his countryman De Freminville in 1811, and had since received but little notice. This step was taken by Mr. Norman¹ a few years later. He did not, however, use *Antedon* as precisely equivalent to *Alecto*, but applied the name to those forms only in which the mouth is central and the anus lateral; and he has been followed by nearly all the subsequent writers upon the Crinoids.

The etymology of *Antedon* is somewhat obscure. De Freminville described his typical species as *Antedon gorgonia*, which gives no information as to the gender of the name. Mr. Norman, however, arrived at the conclusion that it is masculine, and hence described the common British species as *Antedon rosaceus*. In this respect all the later writers have agreed with him with the exception of Pourtales², who employs *Antedon* as a feminine name; and in this step he has since been justified by the result of the recent etymological researches of Mr. Spedding³.

It will be used in the same manner in the following pages, both because this seems to be etymologically correct, and for the sake of convenience; since, as long as Müller's system of trinomial nomenclature is employed for the *Comatulæ*, it is far simpler to write *Comatula (Antedon) rosacea* than *Antedon rosaceus*=*Comatula rosacea*. In any case, we are now acquainted with so many different types, *Antedon*, *Actinometra*, *Comaster*, *Phanogenia*, and *Ophioerinus*, to all of which Lamarek's designation *Comatula*

¹ "On the Genera and Species of the British Echinodermata," Ann. and Mag. Nat. Hist. ser. 3, vol. xv. p. 98.

² Bull. of the Mus. of Comp. Zool. vol. i. No. 6, "Contributions to the Fauna of the Gulf Stream at Great Depths," p. 111; and No. 11, "List of the Crinoids obtained on the Coasts of Florida and Cuba in 1867, 1868, 1869," p. 355.

³ "Nature," vol. xv. p. 366.

is equally applicable, that this last can only be used to designate the family, while one of the two names, *Antedon* and *Alecto*, which have precedence over it in point of time, has gradually become more limited in its meaning, and the other has ceased altogether to be applied to the Crinoids.

II. ON THE CHARACTERS OF THE GENUS ACTINOMETRA.

(§ 13) We have seen that while the distinction drawn by Müller between *Alecto* and *Actinometra* depended upon the number of groove-trunks reaching the peristome, irrespective of the position of the mouth, the genus *Antedon*, as defined by Mr. Norman, and as subsequently used, is distinguished by having the mouth central and the anus lateral.

There are, however, numerous species of *Alecto* in which, according to Müller¹, “die Afterröhre nimmt die Mitte der Scheibe ein, so dass der Mund seitlich gegen den Rand der Scheibe rückt ohne dass die *Ambulacra* ihre symmetrische Vertheilung auf die fünf Armstämme einbüßen.” These forms have obviously no place in the genus *Antedon*, while they were excluded from *Actinometra* by Müller, who goes on to say, “In andern abweichenden Arten geht die gleiche Vertheilung verloren, indem der excentrisch liegende Mund weniger als fünf Furchen der *ambulacra* aufnimmt, dann werden einzelne dieser Furchen herrschend und verästeln sich, indem sie einen grossen oder den grössten Theil der Scheibe umziehen, auf mehreren Armstämmen zugleich, so dass die Scheibe von einem Furchenkreis umgeben ist, der jedoch an einer Stelle nicht geschlossen ist (*Actinometra*) (Pl. I. figs. 2, 3, 5).

In Pl. I. figs. 6–16 is represented the distribution of the groove-trunks or ambulacra on the disks of the eleven specimens of *Act. polymorpha* which I have been able to examine. A glance at these, no two of which are alike, will suffice to show that within the limits of one and the same species there may occur individuals, some of which would have been referred by Müller to *Alecto*, some to *Actinometra*, and some which, strictly speaking, have no place in either of these genera.

Thus, for example, the specimen represented in fig. 16 would probably have been classed as *Alecto* by Müller; but although five groove-trunks leave the peristome, their branches are by no means equally and symmetrically distributed to the different arms. On the contrary, one of them gives off far more branches than any of the others, supplying *all* the arms borne by two radii (D_1-E_2), together with half of those of another radius (A_1); while another trunk running straight out from the peristome bifurcates but once, and only supplies two of the arms of one radius (B_2). Again, in fig. 15, only four groove-trunks leave the peristome, one of which gives off a large number of branches, as in fig. 16, also supplying all the arms of two radii (D_1-E_2). According to Müller's system, therefore, this individual is an *Actinometra*.

In all the other nine specimens of this species which I have examined, however, there are invariably more than five groove-trunks running out from the excentric peristome (Pl. I. figs. 6–14). Even in the small specimen with thirteen arms, represented in fig. 6, there are six groove-trunks, while in fig. 11 there are eight, and in all the other figures

¹ Berlin Monatsberichte, 1846, p. 177.

either six or seven. In no case are there only five with their branches so regularly distributed as Müller figured them in *Alecto multiradiata* (Pl. I. fig. 4); nor in the single individual with only four primary trunks (fig. 15) is the distribution so regular and symmetrical as in Müller's figure of *Actinometra Wahlbergii* (fig. 3). Further, the distribution of the ambulacra on the disk of the specimen of *Act. solaris*, represented in Pl. I. fig. 5, is by no means so symmetrical as Müller found it to be in the large Vienna specimen which he made the type of his new genus *Actinometra* (fig. 2). It can hardly be said of fig. 5 that the "Furchen der zehn Arme münden in gleichen Abständen in eine die Scheibe umziehende Cirkelfurche."

The above instances, which could be multiplied indefinitely, suffice to show the impossibility of classifying the *Comatulæ* according to the distribution of the ambulacra on the disk. We have already seen (sect. 9) that Müller found the Lund and Paris specimens of his species *Com. multiradiata* to agree in every respect but this; so that, had he adhered strictly to his own system of classification, he would have had to refer the former to *Actinometra* and the latter to *Alecto*. In this case, however, as in all the specimens represented (Pl. I. figs. 2-16), there is one point of agreement, viz. the relative positions of the mouth and anal tube. In the Paris, Bonn (fig. 4), and Lund specimens of *C. multiradiata*, Müll., in both the specimens of *Act. solaris*, represented in Pl. I. figs. 2, 5, in *A. Wahlbergii* (fig. 3), and, lastly, in all the eleven specimens of *A. polymorpha* (figs. 6-16), the centre of the disk is occupied by the anal tube, and the mouth is situated excentrically, either close to the margin of the disk (fig. 11), or at some point rather nearer to the centre.

(§ 14) After arriving at the conclusion that in this character, the central or excentric position of the mouth, lies the real distinction between *Antedon* and *Actinometra*, and that the number of groove-trunks reaching the peristome is a character of very minor importance, I wrote to Dr. Lütken, of the University Museum, Copenhagen, upon the subject, and was not surprised to learn that he had held this opinion for some time past. With his usual kindness he has permitted me to make use of the following extract from an unpublished MS. of his, containing descriptions of some new species of recent *Comatulæ*:—

"One of the reasons why it is so difficult to identify Müller's species is, that he does not always mention the positions of the mouth and anal tube, and the direction of the ambulacra on the disk, but has evidently established a somewhat unnatural distinction between the differences which may occur in these characters. Two cases may occur: in the one the mouth is subcentral ('quite central' probably never occurs), and the ambulacral furrows converging from the arms unite into five trunks, which all run directly towards the mouth along the shortest line; they differ, therefore, but slightly in length; and the 'interpalmar' areas defined by them are of almost equal size, that containing the anal tube having sometimes, however, a slight preponderance in size, especially when the anal tube is placed close to the mouth, almost centrally. In the other case the mouth is removed towards the margin of the disk; and of the ambulacra, those only which come from the arms nearest to the mouth run directly towards that orifice, while the others, and especially the two enclosing the anal area, are obliged to make a large

deviation, and reach the mouth, after a circuitous course, parallel to the margin of the disk. It is often difficult to state the number of ambulacral furrows abutting on the mouth, as they frequently unite immediately before reaching it; in different species, and in different specimens of the same species, I have counted 4, 5, 6, 7, 10 stems originating from the mouth; this difference, therefore, is of no importance at all. The anal tube in all these species [*Actinometra*, mihi] has a central or subcentral position, and the anal area occupies the larger portion of the disk. Using this difference as 'fundamentum divisionis,' I have never encountered a doubt whether any type should be referred to *Antedon* or to *Actinometra*, although I have examined a great number of specimens and species. Moreover the lower or oral pinnules of *Actinometra* are always very different from the others, being flagelliform and presenting a more or less distinct serrature or comb (pinnulæ orales prehensiles); while in *Antedon* they are only slightly differentiated from the others, or are transformed into strong rigid spines, forming a protective covering over the disk [*A. protectus*, mihi]. It will, perhaps, be thought improper to elevate these sections into genera, as the fossil *Antedons* would usually not be generically determinable¹; but they are at least very good subgenera for the distribution of the numerous species. The mode of classification here proposed is concerned with the main point of that established by Müller, but is evidently an amelioration of it. In *Actinometra* he describes the five ambulacra as partially uniting before reaching the mouth, so that their number becomes reduced to three or four [*C. solaris*, Pl. I. figs. 2, 5, and *A. Wahlbergii*, Pl. I. fig. 3], while he refers to *Alecto* all those specimens in which five ambulacra separately reach the mouth, even though this orifice be quite excentric and marginal, and the length of the ambulacra therefore exceedingly different, as in *Alecto multiradiata* [Pl. I. fig. 4]. This mode of distinction used by Müller is, however, very unnatural, and often quite arbitrary or illusory. It is the marginal or subcentral position of the mouth that is of importance; and this character is never ambiguous. *C. multiradiata* [Pl. I. fig. 4] is not less a true *Actinometra* than *A. solaris* [Pl. I. figs. 2, 5] and *A. Wahlbergii* [Pl. I. fig. 3]."

It will be seen from the above note that Dr. Lütken considers *Antedon* and *Actinometra* as two subgenera of *Comatula*, *Antedon* having a subcentral mouth and but slightly differentiated oral pinnules, while in *Actinometra* the mouth is excentric and the oral pinnules bear a terminal comb (Pl. III. figs. 1-3). At the time I received Dr. Lütken's note I had had no opportunity of examining any large collection of *Comatulæ*; and his statement that the oral pinnules of all *Actinometræ* were marked by a terminal comb was therefore new to me. I have since been able to examine a considerable number of *Comatulæ*, and, like Dr. Lütken, have never had the least difficulty in determining to which type any given specimen should be referred, while at the same time I have always² found that in *Actinometræ*, or *Comatulæ* with an excentric mouth, the oral pinnules bear

¹ It will be shown further on that there are very decided differences in the shape of the calyx in the two genera *Antedon* and *Actinometra*. These render the determination of fossil *Comatula* (and also of recent specimens from which the disk is lost) less impracticable than Dr. Lütken supposes.

² The above passage was written early in 1877. Since then I have examined the large collection of *Comatulæ* brought home by the 'Challenger.' Out of nearly fifty species with an excentric mouth, all but two have a terminal comb on the oral pinnules.

a terminal comb. These two characters, however, do not always coexist; for Pourtales¹ describes *Antedon meridionalis*, A. Ag., as having an excentric mouth, while he says nothing about the first pinnule, except that it is "rather long, the first five or six joints webbed by the perisome."

Again, in many of the *Comatulæ* with an excentric mouth which I have examined, the terminal comb is not limited to the oral pinnules only, but may occur at intervals on different pinnules till near the end of the arms, although it is never so well developed as it is on their basal or oral pinnules, fewer of the terminal segments bearing the processes which go to make up the comb.

Lovén² has found the same to be the case in the new *Comatula* which he has described under the name of *Phanogenia typica*. Speaking of the pinnules, he says, on p. 232:—"In nonnullis (omnibus?) articuli 8 l. 9 ultimi convoluti, pectinati, margine ejusvis externo in laminam lanceolatam magnam erectam producto;" but he goes on to say (p. 233). "Os centrale. Tubus analis crassus in media area interradii. Sulci tentaculiferi fere quales in *Antedone*."

Here, therefore, a terminal comb on the pinnules coexists with a central mouth; so that all the four possible variations may occur of these two characters, viz. the position of the mouth and the condition of the terminal segments of the pinnules.

Thus *Antedon rosacca* &c. have a central mouth and no comb.

„ *Phanogenia typica* has a central „ and comb.

„ *Actinometrasolaris* &c. have an excentric „ and comb.

„ *Comatula meridionalis* has an excentric „ and no comb.

Leaving *Phanogenia* out of consideration for the present, as it was unknown to Johannes Müller, the following scheme will represent the relations of *Antedon* and *Actinometra* as used by Dr. Lütken and myself, to *Alecto* and *Actinometra* as used by Müller:—

<i>Alecto</i> .	Ambulacra symmetrically distributed on the disk.	} mouth central. } mouth excentric.	} <i>Antedon</i> .	Oral pinnules not specially distinguished.
<i>Actinometra</i> .	Ambulacra unsymmetrically distributed on the disk.			
		} mouth excentric.	} <i>Actinometra</i> .	Oral pinnules nearly always have a terminal comb.

(§ 15) We are now in a position to investigate which species of the numerous *Comatulæ* described by Müller can be referred to *Actinometra* under its new definition, and what further subdivisions of the genus are possible according to the principles of classification introduced by Müller. Before doing so, however, it will be advisable to devote a little time to a consideration of the descriptive terminology which he employed, and of the manner in which it has been modified by later writers.

In *Pentacrinus* and *Comatula* Müller regarded the arms as starting directly from the five radial axillaries. The two primary arms borne by each of these might either remain

¹ *Loc. cit.* No. 11, p. 355. Pourtales here evidently uses *Antedon* as equivalent to *Alecto*, and not in the sense in which it was employed by Mr. Norman, viz. to designate those forms only in which the mouth is central (or nearly so) and the anus lateral. To avoid confusion, I shall speak of this species simply as *Comatula meridionalis*.

² "Phanogenia, ett hittills okänt släkte af fria Crinoideer," Öfver. af Kongl. Vetensk.-Akad. Förhandl. 1866, No. 9, p. 223.

simple, as in *Ant. rosacea*, or divide more or less frequently into secondary, tertiary, &c. arms, as in *Act. multiradiata* and in *Pentacrinus*; and every segment, like the radial axillary, preceding a bifurcation, was called by Müller a "brachial axillary."

In some of the Tessellate Crinoids, however, the arms do not become free at the radial axillary, but "der Keleh setzt sich noch weiter fort; die Radien zerfallen dann in zwei Distichalradien mit *radialia distichalia*, die jedes mit einem *distichale axillare* enden, wie bei *Actinocrinus moniliformis* und *Eucalyptocrinus*"¹. In this case the distichal radii represent the primary arms of *Comatula* and *Pentacrinus*, though Müller never used the name "distichals" in his descriptions of the species of *Comatula*; for, as in the Tessellata the segments composing two adjacent distichal radii are united laterally with one another by intermediate plates, he regarded them as forming a part of the calyx, and considered the arms of this group as starting from the distichal axillary, and not from the radial axillary, as in the Articulate Crinoids.

The two primary arms, or distichal radii, borne upon a single radial axillary, were called by Müller a "*distichium*;" and the interval between two successive distichia dorsally between the calcareous segments, or ventrally between the corresponding grooves on the disk, was spoken of by him as "*interpalmar*," while the interval between the two primary arms or distichal radii borne by the same radial axillary, or, as Müller called it, "*die Kluft eines Distichiums*," was "*interbrachial*" or "*intrapalmar*."

The words "interambulaeral," "interradial," and "intertentacular," have been also used by Müller and others to designate the interpalmar areas on the disk of *Comatula*. Either of these is preferable to "interpalmar," for reasons which will presently appear, though "intertentacular" is not universally applicable, as in certain *Actinometre* the posterior ambulaeral grooves bounding the large area in which the anal tube is situated are not provided with tentacles at their sides.

The term "interbrachial" is decidedly preferable to "intrapalmar," which was used by Müller to designate the small areas on the disk, bounded by the two branches of each of the five primary groove-trunks. "Intrapalmar" does not convey any clear idea of the relation of these areas to the divisions of the skeleton, while "interbrachial" distinctly indicates that they correspond to the intervals between the two primary arms borne by every axillary radial.

Römer² adopted Müller's nomenclature for the fossil Crinoids, and, like him, considered that the distichal radii, when present and united laterally to one another, formed a part of the calyx; so that the arms were regarded by him as commencing from the axillary distichals, while he distinguished their different divisions simply as rami of the first, second, and third order. De Koninck and Le Hon³, however, regarded the arms as commencing from the first bifurcation, *i. e.* from the axillary radial, whether they become free at once or whether they remain united with the calyx for a longer or shorter distance. Nevertheless they distinguished the arm-segments by different names in the two cases, using the expression "*pièces brachiales*" for the distichals of Müller, *i. e.* for those segments which are immovably united with the calyx, while they gave the name "*articles brachiaux*" to the movable segments, the brachials of Müller.

¹ Bau des *Pentacrinus*, p. 31.

² Lethæa geognostica, Band i. Theil 2, pp. 210, 215.

³ Recherches sur les Crinoïdes du Terrain Carbonifère de la Belgique, (Bruxelles, 1854) p. 69.

This view, although unquestionably correct in the case of the Articulate Crinoids (*Comatula*, *Pentacrinus*, &c.), is, as Roemer has pointed out, beset with some difficulties in its application to the fossil Tessellata; and Schultze¹ accordingly reverted to the original view of Müller, saying, "Die Arme (brachia) beginnen unveränderlich da, wo eine deutliche Gelenkfacette eines festen Kelchstückes, ihren Ursprung anzeigt." In describing the divisions of the arms, he speaks of the brachial axillaries of the first, second, and third order, without giving them any special names. These are perhaps scarcely necessary when the number of segments between each division varies so much in different specimens and in different arms of the same specimen as it does in many fossil Crinoids, and in *Pentacrinus*. Among the *Comatulæ*, however, the number and character of the segments between the successive divisions of the arms exhibit variations which are to a certain extent constant in different species, and thus give us the means of classifying them into larger or smaller groups.

Müller has availed himself of this character to a certain extent in the scheme which he gives² of a classification of the *Comatulæ* according to the presence or absence of syzygia in the various brachial axillaries; but though, in his descriptions of the different species, he furnishes the material for carrying this classification much further, and for separating species which, in his scheme, stand very near to one another, he never made any use of it, simply classifying the *Comatulæ* in the groups which he had constituted, according to the number of their arms—10, 20, 40, or more. Under these circumstances he would have been puzzled where to place *Act. polymorpha*, in which I have found the number of arms to vary from 13 to 39.

(§ 16) It has been already stated that the arms proper of *Comatula* begin from the radial axillaries. In many cases they are united by perisome as far as their second or third division; and in *Act. multifida* this perisome contains numerous small calcareous plates, which render the union of the arms with one another and with the calyx somewhat firmer than usual; but they are never so united as to be immovable, as their various segments are connected with one another, except, of course, at the syzygia, by muscles and ligaments. There is one point about the nature of this union which has not, I think, received sufficient attention; and as it shows clearly that the arms of *Comatula* and *Pentacrinus* begin from the radial axillaries, it is worth considering here. It is this: the first and second segments beyond every axillary, whether radial or brachial, are nearly always united together in the same manner as the second and third (axillary) radials.

Thus, for example, in *Act. solaris*, and in the forms allied to it, the second and third radials are united by a syzygy. The same is the case with the first and second brachials. In *Ant. rosacea*, and in the various species which are closely allied to it, there are no muscles between the second and third radials; but their opposed articular faces present a vertical and not a transverse ridge, and are so united by ligament that the two segments are only capable of a lateral movement upon one another, and cannot take part in any movements of flexion or extension, in which they act as a single segment only. The first and second brachials are united in precisely the same manner.

¹ Monographie der Echinodermen des Eiflerkalks, (Wien, 1866) p. 5.

² Gattung *Comatula*, p. 11.

In both these groups the primary arms do not subdivide; so that the total number of arms is limited to ten; and we are as yet unacquainted with any *Comatula* in which the second and third radials are united by a syzygy and there are more than ten arms¹. This is, however, the case in *Pentacrinus Müllerii*, in which, in like manner, the first and second segments beyond every brachial axillary are also united by a syzygy². On the other hand, *Pentacrinus asteria*, L. (= *P. caput-Medusæ*, Müller), is remarkable for having muscles between the second and third radials as well as between the first and second³. In the same manner the first and second segments beyond every axillary are united by muscles, and the syzygium is between the second and third segments⁴.

In nearly all the *Comatulæ* with which we are acquainted, with the exception of *Act. solaris* and the species most nearly allied to it, the second and third radials are united by ligament only, as in *Ant. rosacea*, their opposed faces being marked by a vertical articular ridge (Pl. VII. figs. 2 b, 3 a, 5 b, 6 a, i). In almost all of these species which have more than ten arms, the first and second segments beyond every axillary are united by ligament only, just like the second and third radials⁵. Thus in *Ant. Savignii* every third segment, so long as the division lasts, is an axillary, and the first and second segments beyond each axillary are united by ligament only. But in *Ant. palmata* only two segments follow each bifurcation, the second of which is again axillary; it is nevertheless united to the first one by ligaments only. I have found these same two conditions to occur together in *Act. polymorpha* (Pl. II. fig. 8), in which the normal number of segments between every two points of division is three (Pl. II. figs. 7, 9, 10), of which the third is axillary with a syzygium, as in *Ant. Savignii*, while the second is united to the first by ligament only. In exceptional instances, however (Pl. II. figs. 8, 11), the second segment may be axillary, and united to the first by ligaments only, as in *Ant. palmata*.

In every case, after the division has ceased, the union of the first and second brachials

¹ There are three *Comatulæ* in the 'Challenger' collection which answer to this description. In two of them the first and second distichals and the first and second brachials are united by syzygies, like the second and third radials. But in the third species there is a curious exception to the rule. The rays may divide eight times; and in the primary divisions there are three distichal joints, the first two of which are united by ligaments and not by syzygy. But in all the subsequent divisions the first two joints beyond each axillary form a syzygy, like the second and third radials.

² This agreement between the mode of union of the second and third radials, and of the first and second brachials respectively, is seen also in *Enerinus moniliformis*, in which these segments are united by syzygia as in *P. Müllerii*. See Petref. Germ. Taf. liv. figs. F, G. The same is the case in *Rhizocrinus* (Sars, 'Crinoides vivants,' pp. 15, 22).

³ Bau des *Pentacrinus*, p. 30, and Taf. ii. fig. 8.

⁴ This does not appear, however, to be always the case; for Müller described the syzygium as uniting the first and second arm-segments in the specimen examined by him, while I have found the same to be the case in a specimen of this species contained in the Zoological Museum of the University of Würzburg, in which there is certainly no syzygial union between the second and third radials. In *Pentacrinus* the opposed faces of two elements, which are united by a syzygium, are simple, and not radially striated as in *Antodon*. Sars has found this to be the case in *Rhizocrinus* also; but in its predecessor, *Apioerinus obconicus*, Goldfuss, the radial striation of the syzygial surfaces is very distinct (Petref. Germ. Taf. lvii. fig. 5).

⁵ The 'Challenger' collection includes two very abnormal species which present a singular exception to the rule. The rays divide three times; and the first two segments (distichals) of each of the ten primary arms are united by ligaments only, like the second and third radials. So far the rule holds good; but with the next arm-division there is a new point of departure. The third or axillary distichal bears the secondary arms, which consist of one axillary segment only. But this segment is itself primitively double, i. e. it consists of two parts united by a syzygy; and the first joints of each of the ultimate arms borne by this axillary agree with it in being syzygial segments.

of the free and undivided secondary or tertiary arms is of precisely the same nature as the union of the first and second segments of the primary arms borne by the radial axillary. In fact, it is not at all uncommon for one of the primary arms to remain simple and the other to divide, as in Pl. II. fig. 9, c, d, e, which shows that the arms taken in the strict sense of the word, cannot be regarded as commencing from any point but the axillary radials.

(§ 17) In practice, however, it is more convenient to regard the arms of *Comatula* as beginning from the last bifurcation, *i. e.* from that axillary the two branches borne by which do not further divide, but remain composed of a series of simple brachial segments (b_1 , b_2), &c. In the ten-armed *Comatulæ* the brachials are, of course, borne directly by the radial axillary. But in those forms, such as *Act. multiradiata*, in which the subdivision of the ten primary arms is carried to a very great extent, it is most convenient to regard as brachials only the segments of the ultimate branches borne by the last axillaries, and to give special names to the segments composing the primary and secondary arms; for we have already seen that the number of the segments composing these arms, *i. e.* between every two successive axillaries, varies in different species, and it consequently becomes desirable to have some system of nomenclature by which these differences can be briefly indicated. Under these circumstances, therefore, the term *distichals* may be applied to the segments composing the ramified primary arms of

the Articulate as well as of the Tessellate¹ Crinoids, but only on the distinct understanding that they are really arm-segments and do not enter into the formation of the calyx, as in the Tessellate; so that the name is purely a conventional one, employed for greater convenience in the description of species.

Supposing the secondary arms borne by the distichal axillaries to divide again, we may consider them as composed of two, three, or four palmar² segments, of which the last is a "palmar axillary" (figs. 10, 11, *p. a.*), and bears two tertiary arms. These may either remain simple and composed of brachial segments, or they may continue to divide more or less frequently. The latter case, however, is somewhat rare; for if complete series of distichals and palmars be developed on each radius, the total number of arms rises from 10 to 40; and there are not many *Comatulæ* in which this number is exceeded.

If we apply this nomenclature to the species of which mention has already been made, we should describe *Antedon Savignii* with 20 arms, as characterized by the presence of three distichals composing each primary arm and bearing the brachials directly, while in *Antedon palmata*, with 30 or 40 arms, there are only two distichals, which are followed by two palmars in the secondary arms. *Act. polymorpha*, again, normally has three distichals and three palmars (Pl. II. figs. 7, 10), while *Act. multiradiata*, Müll., has

¹ *I. e.* As understood by MM. de Koninck and Le Hon.

² I have been accustomed for some years past to use the term "palmar" to designate the secondary arms of the Crinoids. Professor Huxley, in whose lectures I first heard it used in this sense, informs me that he believes it to have been so employed by Müller; but I have searched in vain through Müller's works for any definition of the term.

In his description of the Tessellate Crinoids, however, he describes the plates which continue the series of interradials and interaxillaries in a peripheral direction as "interpalmaria;" and as these partially correspond to the intervals between the secondary arms, when such are developed, the latter may perhaps be not incorrectly regarded as composed of "palmar" segments. It will now be apparent why "interpalmar" is not a very suitable designation for the strictly "interradial" areas on the disk of *Comatula*, as was remarked in section 15.

only two palmars in each secondary arm, although the number of distichal segments in the primary arms is usually three. Another proof, if proof were wanted, that the arms proper of the articulate Crinoids begin from the axillary radial is seen in the fact that whenever there are three segments in a distichal or palmar series, the second of these, which is united to the first by ligament only, always bears a pinnule, while the third, or axillary, is a double segment, *i. e.* it consists of two primitive segments united by a syzygium. This is in precise accordance with what we find in all the ten-armed *Comatulæ*, even in those forms in which, as in *Act. solaris*, the first and second brachials are united by a syzygium like the second and third radials. In these the second brachial or the epizygial element of the syzygium bears a pinnule, while the next segment is also a double one, and corresponds with the compound third brachial of *Ant. rosacea* and of the ordinary ten-armed *Comatulæ*. In these last the second brachial is laterally movable upon the first, and bears a pinnule as in *Act. solaris*, while the third has a syzygium (*i. e.* is a double segment). This is exactly what we find to be the case in those primary and secondary arms of the multiradiate *Comatulæ* which consist of more than two segments.

(§ 18) The principal character of the genus *Actinometra* is, as we have seen in sect. 14, that the mouth is situated excentrically, while the centre of the disk is occupied by the anal tube. The position of the mouth relatively to the radii or ambulacra, however, is not the same in all *Actinometræ*; thus in *Act. solaris* (Pl. I. figs. 2, 5) the mouth lies in a radial or ambulacral plane, while in *Act. Wahlbergii* and many other species (Pl. I. figs. 3, 4, 6-16) it is interradiar or interambulacral. If we place the disk of an ordinary *Antedon* in such a position that the interradiar area containing the anal tube is nearest to us (Pl. I. fig. 1), the odd ambulacrum lies in front of the mouth. Let us designate this as ambulacrum or radius A, and the two branches of its groove-trunk corresponding to the two primary arms as A₁ and A₂ respectively, A₁ being that on the left of the mouth. Proceeding round the disk in the direction of the hands of a watch, we may call the other four ambulacra B, C, D, E respectively, and their primary divisions B₁ B₂ E₁ E₂. The anal area is then bounded by the two postero-lateral ambulacra C, D; and a plane passing through the mouth and anus, so as to divide the disk into two symmetrical halves, passes along the odd ambulacrum or radius A, in front of the mouth, which may therefore be regarded as radial in position.

In *Act. solaris* the same is the case, as may be seen in Müller's somewhat diagrammatic figure (Pl. I. fig. 2)¹, and still better in Pl. I. fig. 5, which was drawn from a spirit-specimen, and not from a dry one like Müller's figure. Here, as in *Antedon*, the odd ambulacrum is in front of the mouth, which, although excentric in position, lies in the radial half of a plane which passes through the mouth and anus, so as to divide the disk into two symmetrical halves. The same is the case in a new *Actinometra* from the

¹ It is not usual to meet with specimens of *Actinometra* in which the branches of the ambulacral grooves are distributed with such symmetry as is represented in Müller's diagrams (Pl. I. figs. 2-4) and in Pl. II. fig. 1. Thus, for example, Müller's figure of *Act. solaris* (Pl. I. fig. 2) is remarkably regular, much more so than that represented in fig. 5; and I have examined other specimens with more than 20 arms and a radial mouth, in which the regularity is by no means so distinct as in Pl. II. fig. 1. A great range of variation in this respect is seen in Pl. I. figs. 6-16, which represent the disks of eleven different individuals of *Act. polymorpha*, no two of which are alike; the position of the mouth, however, is constant in all individuals of the same species.

Philippines (Pl. II. fig. 1) with 23 arms. In both these species the dividing plane passes in front of the mouth between the two primary divisions, $A_1 A_2$ of the odd anterior ambulacrum A, while behind the mouth it is interradiar, and separates the two posterolateral ambulacra C, D.

In *Act. Wahlbergii* (Pl. I. fig. 3), *Act. multiradiata* (fig. 4), and *Act. polymorpha* (figs. 6–16) the case is different. If, as in *Antedon*, we designate the two ambulacra bounding the anal area as C and D respectively, we find that the latter is the odd ambulacrum, and that a plane cutting the mouth and anus is radial behind the mouth, in front of which it passes between the two ambulacra A and B; so that if the centre of the disk be regarded as the centre of radiation, the mouth lies in an interradiar or interambulacral plane. This is clearly seen when we turn to the dorsal side of the disk, in which the radii converge to a central point, and not to an excentric one, like the ambulacra of the ventral side. Thus in Pl. II. figs. 9–11, the position of the mouth relatively to the radii is indicated by a \times , which in each case is between the two anterior radii A and B, or interradiar.

So far as my experience goes, this type of *Actinometra*, in which the mouth is interradiar and the odd ambulacrum lies behind it, is slightly more common than the simpler type, in which the mouth is radial and the odd ambulacrum anterior, as in *Antedon*¹.

(§ 19) We are now in a position to investigate which of the numerous species of *Comatulae* described by Müller belong to the type of *Antedon*, and which to *Actinometra*, and into what groups the latter may be divided according to the principles of classification discussed in the last four sections. Müller's specific descriptions afford very little information in this respect; for though he says that the mouth, in some instances, is excentric, and that in others the oral pinnules have a terminal comb, he does not always do so; and he makes no use whatever of these two characters in his distinction between *Alecto* and *Actinometra*. In some cases he simply designates a species as *Comatula*, without attempting to name it more exactly. This is often, no doubt, simply due to the fact that, in the specimens which he examined, the arms were so closed over the disk that he was unable to investigate the distribution of the ambulacra. This, however, is not the case in the *C. trichoptera* of the Paris Museum, the disk of which can be readily examined; and I believe that Müller did not define this species more precisely because he was unable to decide whether it should be referred to *Alecto* or to *Actinometra*; for in one of the two Paris specimens five groove-trunks start from the excentric peristome, while in the other there are only four. This example alone suffices to show the unsatisfactory nature of the only distinctive character established by Müller between his genera *Alecto* and *Actinometra*. The Paris Museum² contains a very large majority of the

¹ Since the above was written, I have examined three large *Comatula*-collections:—(1) that of the 'Challenger'; (2) that made by Prof. Semper in the Philippines; and (3), thanks to the kindness of Dr. Günther, that in the British Museum.

I have been able to determine the position of the mouth in 80 species of *Actinometra*. In 45 of these it is interradiar, as in *Act. polymorpha*; while in the remaining 35 it is radial, as in *Antedon* and in *Act. solaris*.

² I would here express my most hearty thanks to Mons. Edmond Perrier, Assistant-Naturalist at the Museum of Natural History, Jardin des Plantes, who has charge of the Echinoderm collection, and also to his two Assistants, for the kindness which they showed me during my stay in Paris, and for the readiness with which they afforded me every possible facility in the prosecution of my work.

species of *Comatula* described by Müller, who personally examined this collection. Last autumn (1876) I was also able to examine it for myself, and thus to determine which species should be removed from Müller's genus *Alecto* and transferred to *Actinometra*, in the sense in which this name is understood by Dr. Lütken and myself.

In the following scheme all those species to which no note of interrogation and the name of no authority is attached, have been determined by myself as *Actinometrae*, i. e. as having an excentric mouth and a terminal comb on the oral pinnules.

Actinometra.

With 10 arms.	{	Second and third radials united by a syzygy. Mouth radial.	{	<i>Act. solaris</i> , Müll. <i>Act. pectinata</i> , Müll. <i>Act. brachiolata</i> . <i>Com. purpurea</i> ? 1. <i>Com. rosea</i> ? <i>Act. robusta</i> , Lütken.			
		Second and third radials united by ligaments only. Mouth?	{	<i>Com. echinoptera</i> ? 2. <i>Com. meridionalis</i> ? 3.			
With more than 10 arms.	{	2 Distichals. Axillary has no syzygy.	{	3 palmars. Axillary has a syzygy.	<i>Act. rotalaria</i> , Müll. 4.	
				No palmars.	Mouth interradial.	{	<i>Act. polymorpha</i> . <i>Act. trichoptera</i> . <i>Act. Wadlbergii</i> , Müll.
					Mouth radial	<i>Act. fimbriata</i> . 5.	
		3 Distichals. Axillary has a syzygy.	{	2 palmars. Axillary has no syzygy.	{		<i>Act. multifida</i> . 6.
				2 palmars. Axillary has a syzygy.	Mouth interradial.	<i>Act. multiradiata</i> .	
				3 palmars. axillary has a syzygy.	{		<i>Act. parvicirra</i> . 7. <i>Act. polymorpha</i> . 8. <i>Act. Bonattii</i> , Böhlische. 9.

REMARKS.

1. I have not personally examined either *C. purpurea* or *C. rosea*. Müller seemed to think that the former might be a young condition of *Act. solaris*¹; so that it is most probably a true *Actinometra*. *C. rosea*, however, presents a difficulty; for Müller says expressly² that the first pinnules are not specially distinguished; but, except in this point, he regarded it as very closely related to *C. brachiolata*, which is a true *Actinometra*.

¹ Gattung *Comatulæ*, p. 13.

² *Ibid.*, p. 14

2. *C. echinoptera*, on the other hand, has, according to Müller¹, a very marked comb on the oral pinnules. He says nothing, however, about the position of the mouth; and I have unfortunately not been able to examine the species for myself.

3. According to Pourtales² the mouth is excentric in *Com. meridionalis*; but he makes no mention of a comb on the oral pinnules. If it should be absent in this species, and also in *Com. rosea*, while it is present in *Phanogenia*, in which the mouth is central, it becomes obvious that the only external character, besides the shape of the calyx, on which we can rely with any certainty in the determination of the generic position of any *Comatula*, is the nearly central or the excentric position of the mouth.

4. According to Müller³ there are only two radials in *Act. rotalaria* which are united by a syzygium, while they bear the distichal axillaries directly; and these are also syzygial segments. Although, like Müller, I examined Lamarck's original specimen of this species, I cannot confirm the above statement. It is true that only two radials are visible externally; but this is often the case in *Comatulae*, with a wide centrodorsal piece; and I was quite unable to satisfy myself that they are united by a syzygium, as Müller describes, and as is the case with the second and third radials of *Act. solaris*, while I was equally unable to determine a syzygial union between the two segments of which the distichal series is composed. Lamarck's original specimen of this species in the Paris Museum is wrongly labelled *C. brevicirra*, Troschel.

5. The dry specimen of *Act. fimbriata* in the Paris Museum, from the voyage of Peron and Lesueur, is labelled *C. multiradiata*, Lam.; while Reynaud's original specimens from the Strait of Soude are labelled *C. brevicirra*, Trosch., together with *Act. rotalaria* and the Varas variety of Müller's *C. parvicirra*.

6. In *Act. multifida* the tertiary arms borne by the palmar axillaries may divide again several times. In every case there are only two segments between each division, and all the successive axillaries, like the palmar axillaries, have no syzygia. Although Müller mentions this in his description of the species, it is placed in his scheme in a group in which the axillaries of the arms have syzygia. In reality, however, this is the case with the distichal axillaries only.

7. The type specimen of this last species does not exist in the Paris Museum under that name, nor even under *C. brevicirra*, Troschel, which seems to have been used as an equivalent for it; but I believe that three small spirit-specimens from the voyage of Peron and Lesueur in 1803, which are classed, with two specimens of *Act. pectinata*, under the name of *C. simplex*, are really those which were described by Müller as *C. parvicirra*.

8. It will be noticed that *Act. polymorpha* has already appeared higher in the list as a species in which palmars are not developed. In some individuals but few of the 10 primary arms bear axillaries; so that the total number of arms is less than 20 (Pl. II. fig. 9); while in others all the primary arms divide again, and so do the resulting secondary arms, so that the total number is little short of 40 (Pl. II. figs. 10, 11). This is very unusual; for I only know of two other species which present the same kind of

¹ 'Gattung *Comatula*,' p. 14.

² *Loc. cit.* No. 11, p. 355.

³ 'Gattung *Comatula*,' p. 20.

irregularity. As a general rule all the individuals of a species agree in the presence or absence of distichals and palmars.

9. In *Act. Bennettii* there are more than 70 arms; but all the axillaries are like the first one (distichal), and not different from it, as in *Act. multifida*. According to Müller¹, every fourth segment is an axillary without a syzygium; but Böhlische² has found this to be incorrect. There are, indeed, four segments between every two points of division; but the last two are united by a syzygium; so that the formula becomes three distichals, palmars, &c., of which the axillary has a syzygium. Böhlische's figure of the disk of his specimen is noteworthy; for though five groove-trunks leave the excentric peristome, as in *Alecto*, yet their distribution to the arms is not by any means symmetrical, so that he seems to have decided upon calling it *Actinometra*. Müller named it simply *Comatula*.

(§ 20) In the above scheme are included all the species of *Comatula* which have been determined by myself or by others³, as far as I know, to belong to the type *Actinometra*. Fourteen of these were known to Müller; and of the remaining 23 species described by him I have been able to refer 16 to *Antedon*, viz. :—

<i>Ant. adonæ.</i>	<i>Ant. macrocnema.</i>	<i>Ant. phalangium.</i>
<i>Ant. articulata.</i>	<i>Ant. Milberti.</i>	<i>Ant. Philiberti.</i>
<i>Ant. carinata.</i>	<i>Ant. Milleri.</i>	<i>Ant. Reynaudii.</i>
<i>Ant. Eschrichtii.</i>	<i>Ant. palmata.</i>	<i>Ant. rosacea.</i>
<i>Ant. Jacquinioti.</i>	<i>Ant. petasus.</i>	<i>Ant. Sarsii.</i>
	<i>Ant. Sarignii.</i>	

To these must be added

<i>Ant. armata</i> , Pourt.	<i>Ant. cubensis</i> , Pourt.	<i>Ant. Hagenii</i> , Pourt.
<i>Ant. bicolor</i> , Mus. Paris.	<i>Ant. dividua</i> , Mus. Paris.	<i>Ant. polyactinis</i> , Mus. Paris.
<i>Ant. celtica</i> , Barrett.	<i>Ant. Dubenii</i> , Bölsche.	<i>Ant. rubiginosa</i> , Pourt.

The following list contains the seven remaining species of *Comatula* described by Müller which I have not been able to examine, and of which I know no descriptions from which it is possible to obtain any information as to the position of the mouth or the character of the oral pinnules.

<i>C. Cumingii.</i>	<i>C. elongata.</i>	<i>C. flagellata.</i>
<i>C. japonica.</i>	<i>C. novæ Guineæ.</i>	<i>C. tessellata.</i>

and *C. timorensis*. To which must be added *C. brevipinna*, Pourt.

III. EXTERNAL CHARACTERS OF ACT. POLYMORPHA, AND SPECIFIC DIAGNOSIS OF THE TYPE.

(§ 21) In *Act. polymorpha*, as in all *Actinometræ*, the mouth (Pl. I. figs. 6–16, *m*)

¹ 'Gattung *Comatula*,' p. 28.

² "Ueber *Actinometra Bennettii* und eine neue *Comatula*-Art (*Antedon Dubenii*)," Wieg. Archiv, 1866, i. p. 90.

³ Dr. Lütken has named several new species of *Actinometra* besides *Act. robusta*:—for example, *Act. tenuæ* and *Act. trachypaster*. But his descriptions have not, as far as I know, been published; and I have had no opportunity of examining any specimens of his new species except *Act. robusta*; so that I am unable to place them in the classification given in the previous section.

Grube has described a new *Actinometra* from Borneo, and two new species of what he calls *Comatula*. His descriptions (Jahresber. d. Schlesisch. Gesellsch. 1875, Nat.-Hist. Sect. pp. 54, 55) are, unfortunately for me, not to be obtained in this country.

does not occupy a central or subcentral position on the ventral surface of the visceral mass as it does in *Antedon*, but is placed more or less excentrically, and may be sometimes almost marginal (Pl. I. fig. 11). It occupies the centre of the peristome, P, and is bounded by two lips, a large anterior and a smaller posterior one; so that its opening is very inconspicuous, and usually so much extended in a direction transverse to the antero-posterior diameter of the disk, that it presents the appearance of a simple slit, as is well seen in Pl. II. fig. 2.

The circumoral portion of the peristome, or the peristome proper, is a more or less oval depression in the ventral peristome of the disk, which completely surrounds the oral opening, and gives origin to the ambulacral grooves or, more shortly, the ambulacra. Beneath this depression lies the water-vascular ring which gives off a trunk under each of the ambulacra radiating from it. The number and distribution of these are very variable, as is seen in Pl. I. figs. 6-16. This principally depends upon the way in which the ambulacra divide, so as to give rise to the groove-trunks corresponding to the ten primary arms. As a general rule, the two ambulacra corresponding to the radii D and E unite into one large posterior trunk, from which the branches are distributed to the various arms into which these radii divide (Pl. I. figs. 8-10, 12-16). In other cases the left lateral ambulacrum, E, leaves the peristome alone (figs. 6, 11); while in others it is partially united with the posterior ambulacrum, D, its anterior division, E₂, leaving the peristome by a separate trunk, while its posterior division, E₁, unites with the posterior ambulacrum (fig. 7).

As a general rule, the right lateral ambulacrum, C, leaves the peristome alone, and supplies the arms of the corresponding radius; but in figs. 9 & 15 it is seen to unite with the posterior division, B₂, of the right anterior ambulacrum, B.

The mode of division of the two anterior ambulacra is excessively variable. As a general rule there are no principal trunks corresponding to the two radii A and B, and the primary divisions, A₁, A₂, B₁, B₂, start directly from the peristome. In the specimens with but few arms, however, each pair may be united for a longer or shorter distance (Pl. I. figs. 6, 7), as in *Antedon* (fig. 1). Not unfrequently the posterior divisions A₁, B₂, of these two anterior ambulacra unite for a longer or shorter distance with the two large aboral groove-trunks, to form an open horseshoe-shaped curve bounding the anal area (figs. 12, 15, 16). The position of the anal tube in this area, and also with regard to the whole surface of the disk, varies somewhat with the position of the mouth; it is rarely, if ever, absolutely central. Its appearance differs very much according as it is full or empty: sometimes its aperture is so completely closed as to be scarcely discernible, though the tube below is widely distended; and sometimes the aperture is patent with its edges everted and crenate, and the tube leading to it quite shrunk and flaccid (Pl. II. fig. 2).

(§ 22) In *Antedon* the median line of the ventral peristome of all the arms is occupied by an ambulacral groove, with a floor of ciliated epithelium. This groove extends also on to all the pinnales, with the exception of those borne by the second distichals and second palmars, &c. (when present), and by the lowest brachial segments. Beneath it lie the radial water-vascular and blood-vascular trunks, between which last and the

ciliated epithelium of the floor of the groove lies a fibrillar structure, to which I have given the name of the "subepithelial band"¹, and to which a nervous character has been attributed by myself and by all the other observers who have described it. Each side of the ambulacral groove is bounded by an elevated fold of perisome, the edge of which is not straight, but cut out into a series of minute valvules, the crescentic or respiratory leaves (Wyv. Thomson), or "Saumläppchen" of the German authors.

At the base of each leaf, and to some extent protected by it, is a group of three tentacles, one of which, the more distal one, is larger than the other two. This trifid group of tentacles and the cavity of the respiratory leaf adjacent to them receive a common branch from the radial water-vessel. These groups of tentacles alternate on the opposite sides of the ambulacral groove from the base to the tip of each arm, and are distributed in the same manner at the sides of the ambulacra of the disk, though they are not so markedly developed, especially near the peristome, where every lateral branch of the water-vessel supplies only one tentacle. The crescentic leaves at the sides of the groove are also far less distinct than in the arms, the edges of the folds of perisome bounding the groove being only marked by a faint wavy line, and not distinctly cut out into "Saumläppchen."

In many *Actinometrae*, however, the above description only applies to the arms of the two anterior radii, A, B (Pl. II. figs. 2, 4), and to more or fewer of the antero-lateral arms, C₁ and E₂. The arms of the posterior radius, D, and of the posterior divisions of the lateral radii, C₂ and E₁, are often entirely devoid of tentacles; and in many of them the ventral perisome not only exhibits no ambulacral groove, but is, on the contrary, *convex*, as in the oral pinnules of *Antedon* (Pl. II. figs. 5, 6).

We have just seen that in *Act. polymorpha*, as in all *Actinometrae* with an interradii mouth, the anal area is bounded by two large aboral groove-trunks, which start from the posterior angles of the peristome, and form a horseshoe-shaped curve, the limbs of which are unequal in size (Pl. II. fig. 2). The smaller right limb is formed by the right lateral ambulacrum, C; while the larger left limb represents the posterior ambulacrum, D, combined with part or the whole of the left lateral ambulacrum, E. In neither of these limbs are the tentacular groups and crescentic leaves so well developed as they are in the two anterior ambulacra. After the branches to the two antero-lateral primary arms, C₁ and E₂, have been given off, or sometimes even sooner (Pl. I. figs. 13, 15), the tentacles at the sides of the two aboral groove-trunks become more and more insignificant, and finally disappear altogether, while the position of the crescentic leaves is only indicated by a very faint wavy line at the edge of each groove.

In small specimens with but few arms (Pl. I. figs. 6, 9) the grooves of the posterior (D) and postero-lateral arms (C₂, E₁) may remain in this condition; but in larger specimens with many arms all trace of the crescentic leaves disappears, and the two edges of the groove meet and unite so as to produce the condition represented in Pl. II. figs. 5 & 6, where the ventral surface of the arms and pinnules is convex, and does not show the least trace of a groove of any description.

¹ "Remarks on the Anatomy of the Arms of the Crinoids. Part I," Journ. of Anat. and Physiol. vol. x. p. 579.

The position of the point at which the two folds of perisome bounding the sides of the original ambulacral groove meet and unite, varies extremely. The fusion may, though rarely, take place on the disk; sometimes it is at the base of the arms, and sometimes not till near their middle or terminal portions. In any case, however, the fusion, whenever it occurs, is so complete that all trace of the original ambulacral groove is entirely obliterated.

(§ 23) The bearings of this fact upon the different views advanced by Greeff¹ and Ludwig² respecting the homologies of the ambulacral grooves of the Crinoids will be best discussed at a later period, when the changes undergone by the various structures underlying the grooves are described and illustrated. One point, however, must be noticed here on account of its importance with respect to the two views now entertained regarding the nervous system of *Comatula*.

As long ago as 1865 it was stated by Dr. Carpenter³ that the cord which traverses the length of the arms between the subtentacular and cœliac canals, "and which was regarded by Professor Müller as a nerve, really belongs to the reproductive apparatus. But it will also be shown that a regular system of branching fibres proceeding from the solid cord (described by Professor Müller as a vessel) that traverses the axial canal of each calcareous segment of the rays and arms, is traceable on the extremities of the muscular bundles; and reasons will be given for regarding these fibres as probably having the function of nerves, though not exhibiting their characteristic structure." During his residence in the Philippine Islands, Professor Semper had also discovered that the arm-nerve of Müller is really a part of the generative system; and in a short paper⁴ published some time after his return he announced this fact, and suggested at the same time, "dass der bisher immer als Gefäss aufgefasste Strang im innern des Kalkskelettes ein Nervenstrang sei, und dann wäre wohl das im Kelch liegende sogenannte Herz als ein Ganglion anzusehen."

These observations of Dr. Carpenter's and Professor Semper's were unfortunately overlooked for many years, so that even as late as 1874 Müller's erroneous statements with regard to the nervous system of *Comatula* were repeated in the valuable text-book of Gegenbaur⁵ and in many smaller works. At the commencement of 1876, however, two very different views respecting the nervous system were put forward nearly simultaneously by Greeff and by Dr. Carpenter. The former⁶ described the whole floor of the ambulacral grooves on the arms and disk of *Ant. rosacea* as constituting a radial nervous system, starting from an oral nervous ring in the peristome, and corresponding

¹ "Ueber den Bau der Echinodermen. III. Mittheilung," Sitzungsab. der Gesell. z. Beförder. d. gesamm. Naturwiss. zu Marburg, 1872, No. 11, p. 155.

² "Beitr. z. Anat. der Crinoideen," Nachrichten von der Königl. Gesells. der Wissens. u. der G. A. Universität zu Göttingen, 1876, No. 5, pp. 107, 108.

³ "Researches on the Structure, Physiology, and Development of *Antedon rosaceus*. Part I.," Philos. Trans. vol. clvi, p. 705.

⁴ "Kurze anatom. Bemerk. über *Comatula*," Arbeit. aus d. zool.-zootom. Inst. zu Würzburg, Band i. (1874), p. 262.

⁵ Grundriss der vergleich. Anat. p. 222.

⁶ "Ueber den Bau der Crinoideen," Marburg. Sitzungsab. 1876, No. 1, Jan. 13, p. 21.

in position and histological structure with the typical Echinoderm nerves. At the same time he denied the nervous nature of both the structures described as nerves by Müller and Dr. Carpenter respectively, viz. the genital cord, the so-called "rachis," on the one hand, and the axial cords in the centre of the calcareous segments on the other.

A week after the publication of Greeff's views, Dr. Carpenter¹ announced his belief that a complicated apparatus, "consisting of the outer cylinder of the Crinoidal stem, of the five-chambered central organ formed by the dilatation of that axis within the centro-dorsal basin, and of the cords proceeding from it to the arms and cirrhi," should be regarded as the central portion of a nervous system. This view was based both upon anatomical and upon physiological considerations:—

(a) That while a single arm may be made to coil up by irritating one of its pinnules, the whole circle of arms closes together when an irritation is applied to the pinnules, which arch over the mouth—an act which affords a strong indication of the "internuncial" action of a definite nervous system.

(b) That stimulation of the central quinquelocular organ ("heart" of Müller and Greeff) contained in the calyx, with which the axial cords of the arms are in connexion, is followed by sudden and simultaneous flexion of all the arms.

(c) That these axial cords give off successive pairs of branches, which ramify upon the muscles connecting the arm-segments.

Shortly after the announcement of these views on the part of Dr. Carpenter, Ludwig² described a *ventral* nervous system as existing in *Comatula* in common with all the other Echinoderms. He attributed a nervous character, not to the whole epithelial floor of the ambulacral grooves, as was done by Greeff, with whose researches he was unacquainted, but to a fibrillar layer beneath it, and more or less distinctly separated from it. This layer, which was also discovered independently by myself³ and Teuscher⁴, and was regarded by us both as of a nervous nature, is the "subepithelial band" mentioned in sect. 22. Ludwig, like Greeff before him, denied the nervous character of the dorsal axial cords of the arms; Teuscher discussed it as possible, but hesitated to accept it on account of the morphological difficulties involved in such a view.

Baudelot⁵, who seems to have been unacquainted with Dr. Carpenter's earlier statements, was apparently struck with the nature of these cords, though he could not regard them as nervous. After describing their structure and their union in the calyx to form the pentagonal commissure, he adds, "Ainsi donc chez les Comatules il existe des parties qui évidemment n'appartiennent point au système nerveux (!), et qui dans leur disposition aussi bien que dans leur structure offrent une analogie presque complète avec les cordons nerveux des autres Échinodermes." It must be remembered that Baudelot wrote before the discovery of the so-called "ventral nerve" of *Comatula*; but, in any case, I do not quite see the force of his "évidemment."

¹ "On the Structure, Physiology, and Development of *Autelon rosaceus*," Proc. Roy. Soc. no. 166, Jan. 20th, 1876, pp. 219–226.

² Göttingen Nachrichten. no. 5, Feb. 23rd. 1876, p. 106.

³ Journ. Anat. Phys. x. p. 578.

⁴ "Beitr. z. Anat. der Echinodermen, I. *Comatula mediterranea*," Jenais. Zeitsch. B. x. p. 253.

⁵ "Contribution à l'histoire du système nerveux des Échinodermes," Arch. de Zool. Exp. et Gén. i. p. 211.

In the centre of every segment of the skeleton of *Act. polymorpha* and of all the other *Comatulæ* which I have examined, from the first radials to the ends of the arms and pinnules, and also in the cirrhus-segments, these axial cords increase considerably in size, and give off four principal branches. Two of these run towards the ventral side, and in the calyx disappear in the neighbourhood of the muscles connecting the segments, though I must confess that I have never been able to trace them any further (Pl. VIII. fig. 3, *a'*). In the arm-segments, however, they continue their course towards the ventral surface and break up into numerous branches, some of which, as I have already described¹, extend to the tips of the crescentic leaflets at the sides of the tentacular furrow. The two inferior or dorsal trunks run towards the surface of the skeleton; and while some of their branches are lost in the plexus of tissue forming its organic basis, others seem to become connected with epidermic structures in a manner which will be described at length further on.

Not one of the German observers makes any mention of these branches, although two of them at least have examined *Antedon Eschrichtii*, while they have all cut sections of the arms of species of *Actinometra*, in which genus I find them to be particularly distinct. It is obvious that the facts above stated strongly support the view expressed by Dr. Carpenter and by myself, that the axial cords of the arms are of a nervous nature; and the experiments made by Dr. Carpenter² at Naples have shown conclusively:—

1. That the quinquelocular organ is the instrument of the perfect coordination of the swimming movements of the arms, which involve the conjoint contraction of several hundred pairs of muscles.

2. That nothing contained in the visceral mass is essential to the perfect coordination of the swimming-movements, and that therefore the subepithelial band or ambulacral nerve of the German authors has no immediate relation to those movements, even if it be a nerve at all.

3. That section of the subepithelial band in an arm does not prevent its playing its usual part in the regular swimming-movements.

4. That destruction of the axial cord of an arm by the application of acid causes the arm to become rigidly stretched out, while all the others work as usual.

Since the publication of these experiments Greeff seems to admit the nervous nature of the axial cords, and of the yellowish fibrillar envelope (Pl. VII. figs. 1-3, N) of the quinquelocular organ from which they proceed. Ludwig³, however, while allowing their force, cannot admit the existence in the Crinoids of an antiambulacral nervous system, of which we know as yet no homologue in the other Echinoderms, but sees no difficulty in regarding the quinquelocular organ, its fibrillar envelope, and the axial cords proceeding from it, as parts of a blood-vascular system, like that of the other Echinoderms, although he admits (p. 87) that “ihnen vergleichbare Gebilde sind bis jetzt bei anderen Echinodermen nicht bekannt geworden.” The axial cords of the

¹ Journ. Anat. Phys. x, p. 544.

² “Supplemental Note to a Paper on the Structure, Physiol. and Develop. of *Antedon roseus*,” Proc. Roy. Soc. no. 169, 1-76.

³ “Beitr. zur Anat. der Crinoiden,” Sep.-Abdruck aus der Zeitsch. f. wissensch. Zool. B. xxviii. Heft 3, p. 81.

calcareous segments are regarded by him (pp. 80, 86) as "unverkalkt gebliebene Theile der bindegewebigen Grundlage der Kalkglieder, deren Aufgabe es ist, aus dem Blutgefäßsystem, genauer aus den fünf Kammern die kernnährende Flüssigkeit aufzunehmen und den Arm- und Pinnulagliedern zuzuführen."

Without going into the question as to how far the organic basis of the calcareous skeleton can be regarded as of a connective-tissue nature, I would only remark that it is difficult to see why the axial cords, which Ludwig supposes to consist of uncalcified connective-tissue fibres, should give off branches the terminations of which are entirely outside the skeleton, as is the case with those which reach the crescentic leaves at the sides of the tentacular groove, and which therefore cannot take any part in the nutrition of the tissue forming the organic basis of the skeleton.

(§ 24) This is not the place for a full discussion of Ludwig's views on the nervous system of *Comatula*; but one point must be briefly referred to. I have already¹ stated that in some arms, and in most of the pinnules, of many *Actinometra*, the subepithelial band or nerve of Ludwig is entirely absent, and also that "if the axial cords are not nerves, and if the subepithelial bands are to be regarded as the only nervous structures in the whole Crinoid organization, the difficulty presents itself that the oral pinnules of the European Crinoids, and more than half the arms, with the majority of the pinnules of some forms of *Actinometra*, are entirely devoid of a nervous supply.

"The oral pinnules of *Antedon* have been shown by Dr. Carpenter² to be extremely susceptible of irritation; when they are touched in the living animal, the whole circle of arms is suddenly and simultaneously coiled up over the disk, while irritation of one of the ordinary pinnules is simply followed by flexion of the arm which bears it.

"The structure of these oral pinnules, which are borne in *Antedon rosacea* by the second brachials, differs very considerably from that of the pinnules borne by the other brachial segments; for not only are they sterile, but they have neither tentacular apparatus nor ambulacral groove, their ventral surface being slightly convex instead of being concave as in the ordinary arms and pinnules. This has been mentioned by Teuscher³; but he has omitted to state that the ordinary ciliated epithelium of the ambulacral groove, with its subjacent nervous layer and nerve-vessel, are also absent." Ludwig entirely ignores this argument, although he confirms the above statement concerning the oral pinnules of *Antedon*; in the text he is obliged to confess that "Fraglich est mir geblieben ob die oralen Pinnule einen Zweig des radiären Nerven besitzen oder nicht" (p. 75); while his figure of a section of an oral pinnule (pl. xvii. fig. 55) entirely confirms the statement quoted above, to which, however, he makes no reference.

This condition, which is limited in *Ant. rosacea* to the oral pinnules, sometimes exists in whole arms and in all the pinnules borne by them in many species of *Actinometra*. Even in the arms which come off from the anterior or oral side of the disk the ambulacral groove does not give off regular branches to the pinnules borne by the third and successive brachial segments; but a variable number of these first pinnules (sometimes only

¹ "Remarks on the Anatomy of the Arms of the Crinoids, part ii." Journ. of Anat. and Physiol. vol. xi. October, 1876, p. 89.

² Proc. Roy. Soc. no. 166, p. 226.

³ Jenaische Zeitschrift. x. p. 249.

three or four, sometimes as many as forty) resemble in this respect the oral pinnules, their ventral surface being convex, and devoid of any ciliated epithelium or subepithelial band; while their water-vessel is simple, without any lateral extensions to respiratory leaves and tentacles. In these oral arms, however, branches of the ambulacral groove enter the pinnules sooner or later, so that the terminal ones are always provided with a distinct tentacular apparatus, while the floor of their median groove is of the usual character, consisting of a ciliated epithelium and a subepithelial fibrillar band.

We have seen in sect. 22 that in many cases the ambulacral grooves going to the aboral arms become less and less distinct as they get further and further from the peristome, and that their tentacles diminish and finally disappear. At the same time the floor of the groove becomes very much reduced in extent, its epithelial layer thinner and thinner, and the subepithelial band almost invisible, until, in those cases in which the two sides of the groove meet and unite, the ciliated epithelium and subepithelial band disappear altogether. Consequently, when this union takes place on the disk, whole arms are entirely devoid of any nervous supply, if we suppose, with Ludwig, that the anti-ambulacral axial cords are not of a nervous nature, and that the "subepithelial bands" are the only nervous structures in the arms. In such cases it would naturally be expected that these arms would be incapable of performing the regular swimming-movements like those in which there is an open ambulacral groove and a subjacent "ambulacral nerve;" but Professor Semper, who has kept *Actinometra* in his aquaria for weeks together, informs me that he never saw the least trace of any irregularity in the alternating movement of their arms while swimming.

The gradual obliteration of the ambulacral grooves by the approximation and fusion of the elevated folds of peristome at their sides, which may occur to so great an extent in *Actinometra*, is found also at the ends of the arms and pinnules of *Antedon Eschrichtii*. Ludwig states (p. 75) that their terminal segments have no ambulacral groove or tentacles; and he gives a figure of a section through the end of a pinnule (pl. xiii. fig. 12), the ventral surface of which is convex, while there is no ciliated epithelium or subepithelial band (ambulacral nerve), although in the text Ludwig makes no mention of their absence. I have found the gradual obliteration of the groove in these cases to take place in precisely the same manner as in *Actinometra*, the only difference being that the point at which the sides of the groove meet and fuse is much further from the disk in the one case than in the other.

If we suppose, with Ludwig, that the subepithelial band is the sole structure of a nervous nature in the whole Crinoid organization, it is difficult to understand the fact, which Ludwig himself admits (p. 10), that it gives off no branches except those which go to the tentacles. It is true that in the Ophiuridea the ambulacral nerve does give off branches which go to the muscles, besides those proceeding to the tentacles, as described by Lange¹, Teuscher², and Simroth³; but the researches of the first-mentioned observer render it very doubtful whether the representative in the Ophiuridea of the

¹ "Beitr. z. Anat. und Histiol. d. Asterien und Ophiuren," Morphol. Jahrb. ii. Heft 2, p. 241.

² "Beitr. &c., II. Ophiuride," Jenais. Zeitsch. x. p. 274.

³ "Anat. und Schizogonie der *Ophiactis virens*, Sars," Zeitsch. f. wissenschaft. Zool. xxvii. p. 473.

subepithelial band of *Comatula* takes any part in the formation of these branches. Ludwig further admits that he has been quite unable to find any sense-organs at the ends of the arms or pinnules of *Comatula* like those which exist in the Asteridea, and, in discussing the views of Greeff, expresses it as his opinion (p. 78) that "die subepitheliale Faserlage, welche durchsetzt wird von fadenförmigen Verlängerungen des darüber gelegenen Epithels allein den Nerven darstellt." There can, I think, be little doubt that this subepithelial band is of the same nature in the Crinoids and Asterids; and it is therefore very interesting that the nervous nature of this structure in the Asterids has recently been disputed by Lange¹, who regards as nervous only some cellular masses separated from the subepithelial band by a lamella of connective tissue, and projecting into the lumen of the two nerve-canals. He believes these cell masses to swell into a large ganglionic mass beneath the pigment-spot; while, in his opinion, the subepithelial band, together with the ciliated epithelium and the cuticula, constitutes a protecting integumentary layer. Lange finds a corresponding condition in *Ophiura texturata*, in which the radial nervous system is better developed than in the Asterids, and consists of a series of paired ganglionic masses, connected with one another by transverse and longitudinal commissures. On the ventral side of this ganglionated cord is a longitudinal band, which Lange regards as the homologue of the protecting integumentary layer forming the floor of the ambulacral groove of the Asterids, and which, as is universally admitted, corresponds to the subepithelial band, epithelium, and cuticula of the ambulacral grooves of the Crinoids.

Lange's views have been partially accepted by Simroth²; but the correctness of them is altogether denied by Teuscher³, who regards Lange's nervous cell-masses in the Asterids simply as the "geschichtetes Epithel" on the wall of the nerve-canals; while the terminal ganglionic mass under the eye-spot described by Lange is represented by Teuscher (pl. xix. fig. 22) simply as a "bindegewebiges Polster." Ludwig⁴, too, speaks of the nervous cell masses as local thickenings of the epithelium of the nerve-canals, which are not present in every species. This is naturally a very strong argument against Lange's views; but Ludwig omits to apply similar reasoning to his own opinions regarding the Crinoid nerves. The subepithelial bands (*his* nerves) are not constant in every arm of many species of *Actinometra*. Still less do Teuscher and Lange agree about the nervous system of the Ophiurids; Lange's ganglionic masses are described as artificial by Teuscher, who, as in the Asterids, regards as the nerve only the fibrillar structure representing the subepithelial band of *Comatula*.

The question is still an open one; and it is therefore of no slight interest to learn that the supposed ambulacral nerve, or subepithelial fibrillar band, is not always present in the arms of *Comatula*, and that even when it exists it is certainly not motor in function, even if it be a nerve at all⁵.

¹ Morph. Jahrb. ii. 274.

² Zeitsch. f. wiss. Zool. xxvii. pp. 556-560.

³ "Beitr. &c., III. Asteriden," Jen. deutsch. x. p. 513.

⁴ "Beiträge zur Anatomie der Asteriden," Zeitschr. für wiss. Zool. xxx. p. 191.

⁵ It is worth noticing here that the "ambulacral nerve" of *Comatula* must be derived either from the mesoblast or from the hypoblast of the embryo. It is developed immediately beneath the tentacular atrium of the pentacrinoid larva, which Götte has shown to be the most anterior portion of the left peritoneal sac. This is lined by hypoblast,

(§ 25) We have seen in sect. 22 that in certain of the arms of *Actinometra* the water-vessels are simple tubes, like the integumentary water-vessels of the *Molpadidæ*, and are not in connexion with any tentacular apparatus. Whether the mouth be radial or interradial, the non-tentaculiferous arms are invariably the aboral ones; so that in the latter case they belong to the trivium (Pl. I. figs. 6-15), and in the former to the bivium (Pl. I. fig. 5)¹. This last, however, is not always the case; for I have a specimen of *Act. solaris* in which an anterior arm (C_1) of one of the two ambulacra of the bivium is tentaculiferous, while a posterior arm (E_1) in the trivium has no tentacles; it is nevertheless aboral in position, as may be seen from Pl. I. figs. 2, 5.

In only one individual of *Act. polymorpha* (Pl. I. fig. 15) have I found a non-tentaculiferous arm on one of the two anterior radii (A, B.); but this was a very remarkable case. Out of 31 arms, 19 were entirely devoid of a tentacular apparatus; and in 15 of these the fusion of the two sides of the ambulacral grooves had taken place either on the disk or in the basal arm-segments, so that an "ambulacral nerve" was wanting in nearly half the total number of arms. In the other four non-tentaculiferous arms the groove remained open for a short distance, and then closed in the manner above described. Three of these four arms constituted the anterior division (E_2) of the left lateral ambulacrum; but the fourth was the first arm of the left anterior ambulacrum (A_1), and was borne upon the same palmar axillary as a well-developed ordinary tentaculiferous arm. Pieces of the middle portions of these two arms are represented in Pl. II. figs. 3 and 5, and their terminations in figs. 4 and 6. With this exception, I have invariably found the non-tentaculiferous arms on the aboral side of the disk; their number and distribution, however, vary extremely, not only in different species but in different individuals of the same species.

Thus in *Act. polymorpha*, in Plate II. fig. 8, the former is as low as $\frac{6}{20}$ of the total number of arms, while in fig. 15 it reaches $\frac{19}{31}$. Even in two individuals with the same number of arms it may be different; thus in figs. 8 and 9 it is $\frac{6}{20}$ and $\frac{11}{16}$ respectively, and in figs. 12, 13 it is $\frac{10}{28}$ and $\frac{15}{28}$. The individual represented in fig. 12 was also remarkable for the fact that one of its aboral arms belonging to the posterior division of the left lateral ambulacrum (E_1) was tentaculiferous, while those on either side of it were not so.

In all the specimens of the type of *Act. polymorpha* which I have examined, and in three of its varieties, of which I have, unfortunately, only single specimens, more or

and appears to be separated from the hypoblastic epithelium lining the water-vascular ring by a remnant of the mesoblastic tissue which occupied the blastocoel of the Echinopodium. One or other of these two layers, the hypoblast lining the atrium, or the mesoblast between it and the epithelium of the water-vascular ring, must give rise to the "ambulacral nerve," which cannot be in any way derived from the epiblast. I am inclined to believe that the "nerve" is most probably of mesoblastic origin, and that the remainder of the mesoblast (in this position) is converted into the muscular layer of the ventral wall of the water-vascular ring; while the blood-vascular ring is a remnant of the primitive blastocoel. Huxley ('Anatomy of Invertebrata,' p. 55!) has suggested a similar origin for the nerve-canals (perihæmal canals, Ludwig) of the Asterids.

¹ In all these figures (Pl. I. figs. 5-16) the tentaculiferous ambulacra are indicated by dark lines, and the non-tentaculiferous grooves by fainter lines.

fewer of the arms have no tentacular apparatus; but in the fourth variety (Pl. I. fig. 16) all the arms are of the usual character, with open ambulacral grooves fringed with crescentic leaves and groups of tentacles. I have found the same variation to occur also in *Act. solaris*. In this case the number of arms is limited to ten, which may be all tentaculiferous, or from one to four of the aboral arms may have no tentacular apparatus.

[*Note.* February 1879.—No less than 23 out of 48 species of *Actinometra* brought home by the ‘Challenger’ have more or fewer grooveless arms. I have cut sections of these arms in two species, and have obtained the same results as with *Act. polymorpha* and *Act. solaris*. The “ventral nerve” and ambulacral epithelium are conspicuous by their absence, while the axial cords in the skeleton give off branches freely in the centre of each arm-joint, as I have already described for other species, both of *Antedon* and of *Actinometra*. Two points are noteworthy. In one species one of the posterior ambulacra stops quite abruptly on the disk, and the two arms to which it would naturally have gone, with its “nerve,” tentacles, &c., receive no branches from any of the adjacent grooves to supply the deficiency. Again, in one of the largest *Comatulæ* I have ever seen (a ‘Challenger’ specimen from the Philippines) there are more than 100 arms, many of which are both grooveless and nerveless, as I have found from sections. But these abnormal arms are not limited to the hinder part of the disk as is usually the case: for there are several on each radius.]

The distribution of the non-tentaculiferous arms in *Act. polymorpha* varies, like their number, to a very great extent. In any case they always occur on the odd posterior radius, D (Pl. I. fig. 8); when more are developed they may occur on the posterior divisions, C₂ and E₁, of the two lateral radii, C, E; and they may then be called postero-lateral (Pl. I. figs. 6, 12–14); and when the proportion of non-tentaculiferous to tentaculiferous arms becomes very great, more or fewer of the antero-lateral arms, C₁, E₂, belong to the former class (Pl. I. figs. 7, 9–11, 13), while in exceptional cases non-tentaculiferous arms may occur even on the anterior radii (fig. 15, A).

(§ 26) The condition of the ambulacral groove and of the tentacular apparatus is not the only point in which the anterior or oral may differ from the posterior or aboral arms. The former taper very slowly, contain far more segments, and are much longer than the latter, while the form of their terminal portions and of the pinnules which these bear is altogether different (Pl. I. figs. 4, 6). When viewed from the dorsal side (Pl. II. fig. 7) the basal portions of the two kinds of arms are precisely similar; they widen slightly between the first and second syzygia, *i. e.* from the third to the tenth brachial, remaining uniform till the third syzygium on the fourteenth brachial, after which they begin to taper. Up to about the twenty-fifth or thirtieth segment the oral and the aboral arms decrease in width at about the same rate; but from this point onwards there is a great difference between them. The arms borne by the two anterior radii, A and B, taper very slowly, the length of their segments increasing considerably, while the breadth only diminishes very gradually; at the same time the middle and terminal pinnules, in which no genital glands are developed, become very long and filiform, and remain so until the last few segments, when their length suddenly diminishes very considerably (Pl. II. fig. 4).

I have never been able to ascertain what is the precise mode of termination of these anterior arms; even when the arm ends in such a manner that there is no reason to suppose that its terminal segments have been broken off, its few last pinnules appear simply as immature, and the last pair are separated by a delicate prolongation of the arm-stem, on which no pinnules have been as yet developed. Dr. Carpenter¹ has found the same "growing-points" at the ends of the arms of *Ant. rosacea*, all of which are of the same character as the oral tentaculiferous arms of *Actinometra*; and he was never able satisfactorily to determine the normal mode of termination of the arms.

With the posterior arms of *Actinometra*, however, the case is different. From the twenty-fifth segment onwards they taper very rapidly, and instead of reaching a length of 145 millims., as the anterior arms with some 150 segments may do, they have only some 80 segments, and rarely attain a greater length than 60-70 millims.

At the same time their terminal pinnules are little, if at all, longer than those of the middle portion of the arm (Pl. II. figs. 5, 6); and the centre of the dorsal half of each of their segments is occupied by a dark-brown egg-shaped body, of a peculiar cellular nature, which I have reasons for believing to be a sense-organ² (Pl. II. fig. 6, *o.b.*). These bodies commence to appear in the pinnules at about the beginning of the second third of the length of the posterior arms, and are continued to their extremities. The pinnules of the last few segments decrease very slowly in size; and the arm ends in an axillary segment which bears *two* pinnules of the ordinary character, each provided with the brown ovoid bodies or "sense-organs" (Pl. II. fig. 6, *o.b.*).

These bodies, which may occur, though but rarely, on one or more of the anterior tentaculiferous arms, do not exist in all the specimens of *Act. polymorpha* which I have examined. In three out of my eight specimens of the type they are entirely wanting; and they are also absent in all the single specimens of the four varietal forms which I have investigated. I have also failed to find them in the non-tentaculiferous arms of *Act. solaris*³.

Between these two kinds of arms, the long anterior ones on the radii A, B, with a wide ambulacral groove and a well-developed respiratory apparatus, and the short posterior ones of the radius D with a closed groove and no external respiratory apparatus, all possible forms of transition may occur. As a general rule, more or fewer of the antero-lateral arms, C₁ and E₂, are tentaculiferous; but they never reach such a great length as the anterior arms, and their terminal pinnules are by no means so long and slender. At the same time the postero-lateral arms, C₂ and E₁, although generally non-tentaculiferous, have, except in rare cases, a more or less open groove for the greater part of their length, which, while greater than that of the posterior arms of the radius D, is less than that of the antero-lateral arms of C₁ and E₂; and their pinnules increase slightly in length from the middle till near the end of the arm.

¹ Phil. Trans. 1835, p. 723, plate xxxviii. fig. 4.

² Journ. Anat. & Phys. vols. x. xi. *loc. cit.*

³ Sense organs occur in two of the 'Challenger' species—one from Banda (which is probably the young of *Act. polymorpha*), and one (a new species) from the Admiralty Islands. In both cases they are limited to the hinder arms, some of which are grooved and others not.

The arms of *Act. polymorpha* may thus be roughly classified as follows:—

Anterior, on radii A and B, 120–150 segments. Pinnules increasing in length to the terminal ones, which are very long and slender. Tentaculiferous.

Anterolateral, on C₁ and E₂, 100–120 segments. Terminal pinnules long and slender. Tentaculiferous.

Posterolateral, on C₂ and E₁, 80–100 segments. Terminal pinnules stout, and rather longer than the median ones. Usually have “sense-organs” and narrow ambulacral grooves, but are non-tentaculiferous.

Posterior, on radius D, 60–80 segments. Terminal pinnules stout, but shorter than median ones. Sense-organs. Usually no grooves. Non-tentaculiferous.

Another difference between the anterior and posterior arms is that the genital glands in the latter are far more developed than in the former. Not only is their number greater, although the total number of pinnules on a posterior arm may not be much more than half that of an anterior arm, but they also attain a very much greater size; the basal and median pinnules of an anterior arm being very much less swollen than the corresponding pinnules of a posterior arm. A similar inequality in the development of the genital glands has been noticed by Alex. Agassiz¹ as occurring in the Echini. This difference in length in the anterior and posterior arms of *Act. polymorpha*, and in the character of their terminal pinnules, seems to be to a certain extent dependent upon the condition of the respiratory apparatus occupying their ventral surface. When this is well developed the arm seems to have the power of indefinite growth; for in the single specimen (Pl. I. fig. 16) in which all the thirty-three arms were normal and tentaculiferous as in *Antedon*, there was no very appreciable difference in the lengths of the anterior and posterior arms². The shape of the terminal pinnules, however, was of a slightly different character in the two cases, though the development of the genital glands was about the same; and we have just seen that those arms are the shortest in which the ambulacral groove entirely closes, and the water-vessel is reduced to a simple tube without any lateral tentacular branches, while it is in these arms only that any definite mode of termination is known. This may occur before half the number of segments have been developed which are commonly met with in an anterior tentaculiferous arm.

(§ 27) The ventral surface of some of my specimens of *Act. polymorpha* is marked by small calcareous concretions, somewhat resembling the “blumenartige Knötchen mit mehreren blattartigen Fortsätzen” described by Müller³ in the Vienna specimen of *Act. solaris*. When present, they are usually scattered around the peristome, and

¹ ‘Revision of the Echini,’ part iv. pp. 680, 681.

² Not only are the arms of different lengths in the ‘Challenger’ species of *Actinometra*, which have ungrooved hinder arms, but there are three species in which the anterior arms are longest, although all, anterior and posterior alike, are grooved and bear tentacles. In another species the arms are all grooved and all equal in length, but the distribution of the syzygia is quite different in the anterior and posterior arms.

³ ‘Gattung Comatula,’ p. 12.

disposed along the edges of the primary groove-trunks proceeding from it, and there are generally some upon the sides of the anal tube. They are particularly well developed in the dark variety from Ubay, in which all the arms are tentaculiferous.

(§ 28) The "oral pinnules" of *Act. polymorpha*, those, namely, which arch over the disk so as to protect it, are borne by the second distichals and second palmars when these are present, but in any case upon the second brachials, those of the distichals and palmars being the longest. They are all very long and slender, consisting of some 30 or 40 segments; and their terminal portions exhibit the peculiar characteristic comb made up of processes which rise from the outer margin of the ventral surface of each calcareous segment (Pl. III. fig. 2), just as in *Act. solaris* and *Act. pectinata* (Pl. III. fig. 1). The number of segments on which these processes may be developed varies from 10-12 on a distichal pinnule, to 6-8 on a brachial pinnule; but in cases in which no second distichals or palmars are developed, so that the pinnule on the second brachial is the first of the series, it is much longer than usual, and more of its terminal segments bear the comb-like processes.

The oral pinnules of the dark Ubay variety of *Act. polymorpha* differ considerably from those of the type and of other *Actinometra*; not only are they much stouter, but their terminal comb is differently constituted (Pl. III. fig. 3). As is usually the case, the lower processes gradually develop themselves from the outer margin of the ventral surface of each calcareous segment; but towards the end of the pinnule they gradually come to rise less and less from the outer margin, and more and more from the median portion of the ventral surface of each segment, until finally, on the last two or three segments, they are developed from the inner margin. Consequently the comb, when viewed from above, is seen not to lie altogether on the outer side of the pinnule, as is usually the case, but to start from the outer side, cross its ventral surface, and finally come to lie on the inner side of each pinnule, *i. e.* on the one nearest the arm.

Both in the type of *Act. polymorpha* and in all the four varieties, the pinnules diminish in length from that of the second distichal (when present) to those borne by the fourth and fifth brachials; that of the sixth brachial is longer, and usually contains well-developed genital gland, so that it is slightly swollen. From this point onwards the pinnules increase in length till about the thirtieth brachial, after which their length and character vary according as the arm is tentaculiferous or non-tentaculiferous.

(§ 29) The dorsal aspect of *Act. polymorpha* differs from that of most *Antedons*, and especially from that of *Ant. rosacea*, in the fact that the plane of the second and third radials, like that of the first, is parallel to the vertical axis of the calyx, and not inclined to it, as in *Antedon*; so that the dorsal surfaces of the whole of the pieces of the calyx lie in one horizontal plane. The centrodorsal piece is circular (Pl. II. figs. 9, 10, *cd*), or pentagonal (fig. 11), and conceals a large portion of the pentagon formed by the first radials, less in young specimens with but a few arms (fig. 9) than in large and full-grown specimens with many arms (Pl. II. figs. 10, 11 & Pl. VI. fig. 2). It is usually a flattened plate with a slight concavity in the centre of its outer surface; and around its margins

are disposed some 20 or 25 cirrhi in one row, but with occasional traces of a second, in which the cirrhi alternate in position with those of the first row. The number of segments in each cirrhus is normally from 11 to 14, of which the last forms a recurved claw, while a more or less distinct spine is usually visible upon the dorsal edge of each of the three or four penultimate segments (Pl. III. figs. 8-11).

In Pl. II. fig. 8, is seen an abnormal condition of the centrodorsal piece, which is of an irregular oval form, and so extended as to conceal large portions even of the second radials. These last are usually more or less completely united with one another laterally. The amount of their union is to a certain extent dependent upon the number of arms developed. Thus in the small specimen with only 13 arms, represented in Pl. II. fig. 9, the second radials are not united laterally for more than half their length; in fig. 10 (26 arms) the union is somewhat more complete, and even more so in fig. 8 (28 arms), while in the variety with 39 arms, represented in fig. 11, the second radials are completely and closely united with one another all round. This rule, however, appears to be only a specific one, and not generally applicable to all *Comatulæ*; for in the 80-armed *Phanogenia* the second radials, as figured by Lovén¹, do not appear to be united with one another any more closely than they are in the small 13-armed specimen of *Act. polymorpha* (Pl. II. fig. 9).

In *Act. polymorpha* the two segments (first distichals, palmars, or brachials) borne by any axillary are united to one another laterally to about very much the same extent as the second radials are; *i. e.* when the number of arms is small, their first segments, whether primary, secondary, or tertiary, are not laterally united in pairs with such completeness as when the division of the ten primary arms is carried to any considerable extent (Pl. II. figs. 8-11, d_1 , p_1 , b_1).

When the arm-division is unequal it is generally carried further in the trivium or posterior radii, C, D, E, than in the two anterior radii, A, B, which form the bivium. This is well seen in Pl. II. fig. 9, in which no distichals are developed on either of the two anterior radii; and again in fig. 10, in which, while distichals are developed all round, the division is carried no further in one of the anterior radii, while in each of the others from one to three palmar series may be developed. In only four normal cases have I found an anterior radius to bear more arms than a posterior one. In each of these the total number of arms was considerable, and one at least of the two posterior radii bore the same number of arms as the abnormal anterior one. Thus, for example, in Pl. II. fig. 11, each of the radii bears eight arms, with the exception of the posterior one (D), on which only seven are developed. This, however, is an abnormal case of fracture of the whole radius between its second and third segments. The new portion is considerably smaller than the old, the proximal articular face of the new axillary being far less wide than the corresponding distal face of the old second radial; while both the distichal series which it bears are imperfect and abnormal, so that the absence of a further division in one of the secondary arms is not particularly remarkable.

(§ 30) The number of arms that may be developed in *Act. polymorpha* is a character

¹ "*Phanogenia*," loc. cit. p. 239.

of extreme variability. In the specimens I have examined it varies from 13 to 39; so that, with one remarkable exception (Pl. II. fig. 8), the ten primary arms do not, at the most, divide more than twice, while in two specimens with 18 and 13 arms respectively two and seven of the primary arms remain undivided. I believe, however, that, as a general rule, an axillary is developed on each primary arm, and that the amount of further division is variable, but that a tertiary division is probably exceptional, so that the number of arms in this species will be found rarely to exceed 40.

It will have been already apparent from the position assigned to *Act. polymorpha* in the classification given in sect. 20, that I consider the typical number of distichals and palmars in this species to be three, of which the second (*d.*) bears a long pinnule, while the third or axillary segment (*a*) consists of two primitive segments united by a syzygium. A typical specimen of this condition is seen in Pl. II. fig. 10. Out of the twelve specimens of this species which I have examined, but four others resemble this one in having all their distichal and palmar series regularly developed. In each of the other seven specimens one or more of the distichal or palmar series is irregular, consisting only of two segments, the second of which is axillary without a syzygium. In one very remarkable case, represented in Pl. II. fig. 8, one of the palmar series is reduced to a single segment placed on the distichal axillary, being also itself an axillary bearing the brachials directly on one of its articular surfaces, while on the other are two segments which may be called suprapalmar, of which the second (*sp.a*) is an axillary without a syzygium, and bears two arms.

Excluding this remarkable case, the comparative frequency of the usual variations in the distichal and palmar series in the twelve specimens of *Act. polymorpha* examined by me is seen in the accompanying Table. From this it appears that out of 111 distichal

TABLE I.—Showing the Variations in the Distichal and Palmar Series.

Specimen.	Total number of Arms.	Distichal Series.			Palmar Series.				
		Total number.	Of three segments.	Of two segments.	Total number.	On two distichals.		On three distichals.	
						Of two segments.	Of three segments.	Of two segments.	Of three segments.
I.	13	3	3						
II.	18	8	4	4					
III.	20	10	5	5					
IV.	25	10	10	..	5	3	2
V.	26	10	10	..	6	6
VI.	28	10	7	3	5	5
VII.	28	10	10	..	8	1	7
VIII.	31	10	10	..	11	11
Var. 1	20	10	10						
2	29	10	10	..	9	9
3	39	10	8	2	19	2	1	2	14
4	33	10	9	1	13	..	1	1	11
Total....	310	111	96	15	76	2	2	7	65

series 96 were normal, and that out of 76 palmar series 65 were normal, *i. e.* consisted of three segments, of which the second bore a long pinnule, while the third was axillary, with a syzygium. The three forms of variation exhibited by the abnormal palmar series are of considerable interest, because some of them, at least, represent the normal condition of the palmars in other groups of *Actinometra*. Thus the most frequent one, two palmars on three distichals, is typical for *Act. multifida*, while that of three palmars on two distichals is typical for *Act. rotalaria*. The third variation, two palmars on two distichals, occurs in *Act. tenax*, Ltk., and in a few new 'Challenger' species; and it is typical in several species of *Antedon*—for example, in *Ant. palmata* and *Ant. articulata*. Specimens Nos. II. and III. are remarkable for the fact that the numbers of regular and irregular distichal series are in each case equal to one another; so that a specific diagnosis based upon either of these specimens alone, would, as is evident from the above Table, have been entirely incorrect.

The amount of variation in these characters is so enormously great that only after examination of a considerable number of specimens is it possible to draw conclusions of any value respecting the use which may be made of these characters for systematic purposes. The above Table, however, will, I think, show clearly that I am justified in assuming the normal number of both distichal and palmar segments in this species to be three, of which the second bears a long pinnule, and the third is axillary with a syzygium.

(§ 31) The same variability occurs in the position and distribution of the syzygia in the arms, but, as might be expected from the nature of the case, to an infinitely greater extent. In most of his specific diagnoses Müller gives the position of the first syzygium on the arm and the average number of segments which occur between every two successive syzygia throughout the rest of the arm. Only in a very few cases does he make mention of the position of the second syzygium, which I believe to be a character of nearly or quite as great systematic value as the position of the first; and, owing to its greater constancy, of considerably greater value than the number of segments between every two successive syzygia, which I will call the "syzygial interval." It will be seen from Table I. that the total number of arms in the 12 specimens of *Act. polymorpha* at my disposal reached 310: 11 of these were broken below the third segment; but of the remaining 299, the first syzygium was on the third brachial in 283 cases; and in 136 of these the second syzygium was on the tenth brachial. The irregularities in the position of the first syzygium were limited to three specimens, and, as will be seen from Table II., nearly all confined to one variety.

TABLE II.—Showing Irregularities in the Position of the first Syzygium.

No.	Irregular series of Syzygia.	Type.		Variety. 4.
		III.	VI.	
	Brachials.			
1.	On 4, 9, 13.	1
2.	4, 10, 14.	2
3.	5, 13, 16.	1		
4.	6, 10, 14.	1
5.	9, 13, 17.	2
6.	10, 14, 16.	1
7.	10, 14, 18.	1	4	2
8.	10, 14, 19.	1
	Total	2	4	10=16

In nearly every case the irregularity appears to have been the result of regeneration, the arm having been broken, either in the distichal or in the palmar series, or between the third brachial and the preceding axillary, and a new one developed with an irregular syzygial series; although in many cases similarly regenerated arms of other specimens exhibit perfectly normal series of syzygia. One of these unusual cases, in which there is no syzygium on the third brachial (b_3) and the first syzygium occurs on the tenth segment (b_{10}), which is usually the position of the second syzygium, is seen in Pl. II. fig. 8.

We have seen that when the first syzygium is on the third brachial, the position of the second is in the great majority of cases on the tenth brachial; that is to say, the first syzygial interval is six simple segments, while the second and all the subsequent intervals are, as a general rule, only three simple segments, though the range of variation on either side of this number is very great.

Table III. shows the variations in the positions of the second and third syzygia in all those 283 arms in which the first syzygium is on the third brachial. From the last column of this Table it is evident that in *Act. polymorpha* and its varieties the normal position of the second syzygium is on the tenth brachial, and that in those cases in which it does not occupy this position it is much oftener on the eleventh or twelfth segment than on the eighth and ninth; *i.e.* that variation, when it occurs, is in the direction of increase rather than of decrease in the length of the first interval. This is more clearly seen in Table IV., which shows the number of segments intervening between the first and second syzygia in all the above cases.

TABLE III.—Showing the Variations in the Positions of the second and third Syzygia in the Arms of twelve specimens of *Act. polymorpha*.

No.	Positions of the first three Syzygia.	Type.	Var. 1.	Var. 2.	Var. 3.	Var. 4.	Total.	No. of Variations in the first interval.
	Brachials.							
1.	On 3, 4, 5.	1	1	3
2.	3, 4, 9.	1	..	1	
3.	3, 4, 10.	1	..	1	
4.	3, 5, 10.	2	2	2
5.	3, 6, 11.	1	1	1
6.	3, 7, 11.	2	..	2	2
7.	3, 8, 11.	1	1	8
8.	3, 8, 12.	1	2	2	5	
9.	3, 8, 13.	1	1	
10.	3, 8, 14.	1	1	
11.	3, 9, 11.	1	1	23
12.	3, 9, 12.	1	1	
13.	3, 9, 13.	10	7	3	20	
14.	3, 9, 14.	1	1	
15.	3, 10, 12.	1	1	156
16.	3, 10, 13.	3	1	..	4	..	8	
17.	3, 10, 14.	76	10	23	16	13	138	
18.	3, 10, 15.	1	..	1	
19.	3, 10, 16.	1	..	1	..	1	3	
20.	3, 10, 17.	..	3	..	1	..	4	
21.	3, 10, 19.	1	1	
22.	3, 11, 14.	3	1	4	50
23.	3, 11, 15.	33	4	1	3	2	43	
24.	3, 11, 16.	3	3	
25.	3, 12, 14.	1	1	34
26.	3, 12, 16.	30	1	1	32	
27.	3, 12, 18.	1	1	
28.	3, 13, 16.	1	1	2
29.	3, 13, 17.	1	1	
30.	3, 14, 18.	1	1	2	2
Total number of } variations .. }		174	20	28	38	23	283	283

TABLE IV.—Showing the Variation in the number of Segments in the first Interval.

No. of Segments.	0.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	Total.
Type	2	1	..	4	13	81	39	32	1	1	174
Var. 1	14	4	1	..	1	20
2	1	25	1	1	28
3	2	2	2	7	22	3	38
4	2	3	14	3	..	1	..	23
Total	3	2	1	2	8	23	156	50	34	2	2	283

It is also seen in Table III. that even when the second syzygium is abnormally placed, it is usually the case that the interval between it and the third is the normal one of three simple segments, so that series like 3, 9, 13; 3, 11, 15; and 3, 12, 16, are very common. This is well seen in Table V., which shows clearly that the length of the second interval is normally three segments; that, like the first, it tends to vary in the direction of excess rather than of defect, and that the range of variation in both directions is greater in the varieties than in the type of *Act. polymorpha*.

TABLE V.—Showing the Variation in the number of Segments in the second Interval.

No. of Segments.	0.	1.	2.	3.	4.	5.	6.	8.	Total number of Arms.
Type	3	9	151	8	3	174
Var. 1	1	16	3	..	20
2	1	25	..	1	..	1	28
3	4	30	2	1	1	..	38
4	1	21	..	1	23
Total	1	3	15	243	10	6	4	1	283

After the fourteenth brachial a syzygium usually occurs on every fourth segment; so that the number of segments composing the syzygial interval is normally three. It is, however, very unusual to meet with an arm in which this interval is constant throughout its whole length and does not vary to a greater or less extent. In only seven arms out of the whole number which I have examined have I found this to be the case, together with normal first and second intervals, although twenty-three other arms were regular from the second syzygium onwards. These thirty arms were distributed among five out

of the eight specimens of the type, while in none of the other three was the syzygial interval constant throughout the length of any of the arms; the same was the case with the four varietal specimens.

TABLE VI.—Showing the Variations in the Syzygial interval (usually 3 segments) in the Arms of twelve specimens of *Act. polymorpha*.

	Number of Segments in each interval.	Type.	Var. 1.	Var. 2.	Var. 3.	Var. 4.	Total Cases.
1.	0.	7	1	8
2.	0, 0, 0.	3	3
3.	0, 2.	1	1
4.	1.	11	1	12
5.	1, 1.	2	2
6.	1, 1, 2.	1	1
7.	1, 1, 5.	1	1
8.	1, 2.	5	5
9.	1, 2, 2.	2	2
10.	1, 4.	1	1	..	1	..	3
11.	1, 11.	1	..	1
12.	2.	109	3	13	10	11	146
13.	2, 0.	1	1	..	2
14.	2, 1.	3	3
15.	2, 1, 1, 2, 2.	1	1
16.	2, 1, 4, 2.	1	1
17.	2, 2.	31	1	32
18.	2, 2, 0, 2.	1	1
19.	2, 2, 2.	11	11
20.	2, 2, 2, 2.	4	4
21.	2, 2, 2, 2, 2.	4	4
22.	2, 2, 2, 2, 2, 2.	1	1
23.	2, 4.	2	1	..	3
24.	2, 4, 2.	1	1
25.	2, 4, 5, 1.	1	1
26.	2, 5.	..	1	1
27.	2, 6.	1	1
28.	4.	18	18	15	7	24	82
29.	4, 1, 2, 4.	1	1
30.	4, 2.	2	1	..	3
31.	4, 2, 0.	1	1
32.	4, 2, 2, 1, 2.	1	1
33.	4, 4.	..	1	1
34.	4, 4, 1, 2.	1	1
35.	4, 4, 4.	1	1
36.	5.	3	2	1	..	2	8
37.	5, 2.	2	2
38.	5, 2, 1.	1	1
39.	6.	3	1	1	5
40.	6, 4.	..	1	1
41.	7.	1	1	..	2
42.	10.	..	1	1

As might be expected from the nature of the case, the range of variation of the syzygial interval for the whole length of the arms is considerably greater than that of the second interval alone. In the type and in variety 3 it differs also in a tendency to a decrease rather than an increase in the length of the interval, which is more often two segments than four, as is seen from Table VI.; while in the other three varietal specimens the tendency of the variation is to increase in the length of the interval, four segments occurring much more commonly than two. With respect to these varieties, however, it must be remembered that these conclusions are all based upon an examination of single specimens, which, as already mentioned, may in some instances be very misleading.

(§ 32) The colour of *Act. polymorpha* is usually (in spirit-specimens) a yellowish brown, which is much darker in the soft parts of the body than in the elements of the skeleton. In variety 4, from Ubay, the colour is the same as that of the type, but considerably darker, so that the disk appears almost black. In varieties 1 and 2 the colour is rather a greyish brown, which is considerably lighter on the ventral surface of the disk and arms than on the dorsal skeleton; and in variety 3 it is a somewhat reddish brown.

In varieties 2, 3, and 4 the dorsal surface of the skeleton is marked by a median white line, with more or less defined dark borders, which commences on the radials, and extends for some distance onto the arms. Its distinctness varies in different specimens and in different arms of the same specimen; but it is especially well marked in the darkly coloured var. 4, as is seen in Pl. II. fig. 7.

In an adult specimen of *Act. polymorpha* the total diameter, including the arms, is about 200 or 220 millimetres, of which about 20 millims. represents the diameter of the disk alone; but in one young specimen I found these two diameters to measure only 105 and 7 millims. respectively. The three specimens of varieties 2, 3, and 4 were of about the same size as the type, but the single specimen of variety 1 was considerably smaller, its longer diameter being only about 100 millims., and its shorter (that of the disk) about 8 millims. This specimen, however, was, I believe, full-grown; for it had very large and well-developed genital glands; while in the young and small specimen of the type mentioned above, the size of which was about the same as that of variety 1, the genital glands were scarcely developed at all.

(§ 33) The manuscript name of *Act. armata* has been given to the type of *Actinometra* here described, by Professor Semper, on account of the small spines with which the segments of the arms and pinnules are fringed, more especially upon their dorsal and aboral margins. As, however, this character is a very general one among the *Coematulæ*, and as it is by no means so well developed in this type as in many others, I have thought it advisable not to adopt Professor Semper's specific name, "*armata*," more especially as it has been already employed by Pourtales to designate a new American *Antedon*. Under these circumstances, I propose to designate this type as *Act. polymorpha*, having regard to the enormous amount of variation which I have found to exist in nearly all its characters.

I believe it to be very closely allied to, if not actually identical with, the type described

as *Alecto parvicirra* by Müller¹, who gave this name to three small spirit-specimens in the Paris Museum, from the voyage of Péron and Lesueur in 1803, which I recently found there under the name of *Comatula simplex*, Mus. Müller's diagnosis of *Alecto parvicirra* was based upon his examination of the three Paris specimens, which all have an excentric mouth and a terminal comb on the oral pinnules, and is exactly applicable to *Act. polymorpha*, except that he describes the pinnules as "ziemlich gleichförmig." In their yellow colour and smaller size (about 100 millims.) these also differ slightly from the type of *Act. polymorpha*; but without a very much closer examination of them than I was able to make, it would be impossible to arrive at a definite conclusion as to the identity or difference of these two species.

The Vavao variety of *Alecto parvicirra* described by Müller occurs in the Paris Museum under the name of *Comatula brevicirra*, Troschel. This specimen differs from *Act. polymorpha* in many subordinate characters, and is not absolutely identical either with the type or with either of the four varietal specimens which I have examined; and I cannot but regard it as representing another of the slight and probably very numerous modifications of this type, of which I think it most likely that Müller's original species, *Alecto parvicirra*, is also a varietal form.

(§ 34) The following diagnosis will, I believe, be found sufficient for the future identification of *Act. polymorpha* and of the four varieties here referred to.

Actinometra polymorpha, n. sp.

Centrodorsal piece. A circular or irregularly pentagonal disk almost completely concealing the first radials. Surface flattened, and slightly concave in the centre.

Cirri marginal, 15-25, of 11-14 segments, of which the fifth and sixth are the longest; basal ones thick, and wider than long; remainder taper gradually, and terminal ones are laterally compressed; the last 5 or 6 segments have a small dorsal spine, increasing in distinctness up to the penultimate segment, which bears the terminal claw.

Radials 3, of which the first are barely visible; the second are short, and in the middle of the same height as the first, but somewhat lower at the sides, for nearly the whole length of which they are united to one another in pairs.

Axillary radial pentagonal, about twice as wide as the second, to which it is united by ligaments only.

Arms from 13-40; rays may divide three times. First segments borne by each axillary in contact for nearly their whole side.

Distichals and Palmars. When present, 3; second bears a long pinnule, and is united to the first by ligamentous articulation only. Axillary has a syzygium.

Syzygia. First on third brachial, then an interval of 6 segments to the next, and then a general interval of 3 throughout the arm, variable from 0-6, but usually varying to < 3.

Arms. Anterior arms much longer than the posterior, which are usually non-tentaculiferous. Width increases from 3rd to 10th segment, remains uniform till about the 14th, and then decreases, slowly in the long anterior arms, and rapidly in the short posterior ones. Arm-segments wedge-shaped, slightly overlapping one another, and fringed at the borders with short spines.

Pinnules. The second distichal and the second palmar, when present, bear long pinnules, of which the palmar bears the shorter one; the next is on the second brachial, and still shorter, and the length

¹ 'Gattung *Comatula*,' p. 24.

gradually diminishes to the pinnules of the fourth and fifth brachials, which are the shortest on the whole arm. From the sixth brachial onwards the pinnules are long and stout, gradually increasing in length and thickness to near the middle of the arm; the thickness is greatest in the short posterior arms, in which both length and thickness rapidly decrease from the middle to the end of the arm, while in the long anterior arms the thickness slowly diminishes and the length slightly increases, so that the terminal pinnules are long and slender.

Comb. The last six or eight segments of the distichal, palmar, and first eight or ten brachial pinnules have the outer ventral margin of each calcareous segment produced into a small lancet-shaped process which bends over towards the ventral side, so that the end of the pinnule has a comb-like appearance. Many of the other pinnules till near the end of the arm have similar processes upon their four or five terminal segments.

Disk. Mouth excentric and interrarial; posterior ambulacra very indistinct, and often nearly obliterated. Small calcareous concretions occasionally present in the neighbourhood of the peristome and anal tube.

Colour. Yellowish brown to dark brown.

Diameter. About 20 centimetres.

Locality. Bohol.

The following are the points in which the varieties differ from the type as described above:—

Variety 1.

Cirrhi. 25, of 13–15 segments, with terminal claw; spines on dorsal face of terminal segments not very distinct, but the segments are laterally compressed.

Radials. Second radials completely united with one another in pairs.

Arms. 20.

Syzygial interval. Usually 3, but varying from 1–10 segments; generally to >3.

Comb. From 2nd distichal to 6th brachial pinnules, and then, at intervals, to about 20th brachial but no further.

The basal pinnules of the arms have a faint dorsal keel, and the distal ends of their segments are rather wider than the proximal ends.

Diameter. 105 millims.

Colour. Greyish brown.

Locality. Ubay.

Variety 2.

Centrodorsal piece. Small, but rather thick.

Cirrhi. 10, of 11 or 12 segments, with a terminal claw; the fourth and fifth are longest; the spines on the dorsal border begin from the middle segments, and the opposing process on the penultimate segment is well marked.

Radials. Second radials only incompletely united; second and third very convex, and much higher than the first; median dorsal line of skeleton marked by a white line with dark borders, which is lost about the middle of the arms.

Arms. 29.

Syzygial interval. Usually 3, but varying from 1–10 segments; generally to >3.

Comb. Limited to distichal, palmar, and first five brachial pinnules; those of the 6th and next succeeding brachials have a dorsal keel, and the distal ends of their segments are much wider than the proximal ones.

Colour. Greyish brown.

Locality. Cabulan.

Variety 3.

Centrodorsal piece large and thick, with only 3 cirrus-scars.

Radials. Second radials completely united all round. Centre of dorsal surface of the skeleton, from the centrodorsal till near the end of the arms, marked by a faint white line with dark borders.

Arms. 39.

Syzygial interval. Usually 3, but varying from 1-7 segments; generally to <3.

Comb. On second distichal, palmar, and brachial pinnules, and occasionally also on those of the 3rd-5th brachials, but on no others.

Colour. Reddish brown.

Locality. Bohol.

Variety 4.

Centrodorsal piece large and thick, with only 3 cirrus-scars.

Radials. Second radials closely united all round. Median white line on dorsal surface of skeleton very marked.

Arms. 33, all tentaculiferous, and tolerably uniform in length and in the character of their pinnules.

Syzygial interval. Usually 3, but varying from 0-6 segments; generally to >3.

Pinnules. Oral pinnules much stouter than in the type; that of third brachial but little shorter than that of second. Comb limited to these and to the distichal and palmar pinnules, and the processes forming it gradually come to rise from the ventral surfaces of the calcareous segments instead of from their outer margins.

Colour. Blackish brown.

Locality. Ubay.

IV. THE SKELETON.

(i.) *The Skeleton generally with its Ligaments and Muscles.*

(§ 35) The general structure of the skeleton of *Actinometra*, and of the ligaments and muscles which connect its component pieces, is precisely the same as in *Antedon*; and as this has been already described by Dr. Carpenter¹, there is no need to repeat it here: a few points, however, must be treated somewhat more in detail. The component pieces of the skeleton of *Actinometra*, as of all the other Echinoderms, consist of a calcareous reticulation formed by the calcification of an organic basis of a protoplasmic nature, in which numerous nuclei and pigment-granules are imbedded. This "nuclear tissue," as Simroth² has called it, is in the form of a network, around the meshes of which the calcareous material is deposited.

The character of the calcareous reticulation varies greatly in different parts of the skeleton, being much closer at the synostoses and syzygia and at the articular surfaces than in the interior of the segments; and in correspondence with this greater compactness of the calcareous tissue, the organic plexus which forms its basis becomes remarkably modified at these points, as will be seen further on. The various modes of union of the different pieces of the Crinoid skeleton have been closely investigated by Müller and by Dr. Carpenter. The former³ described the stem-segments of *Pentacrinus* as united to one another in two different ways—(1) by the tendons which traverse the whole

¹ Phil. Trans. *loc. cit.* p. 702.

² *Op. cit.* p. 433.

³ Bau des *Pentacrinus*, pp. 17-20.

length of the stem, passing through the substance of its various segments, and (2) by the "elastic interarticular substance" between the individual segments.

The substance of these tendons consists of a white fibrillar tissue very like the tendinous tissue of the higher animals; but Müller supposed the elastic interarticular substance to be of a totally different nature, consisting of "lauter senkrecht stehenden Fasersäulehen, die durch Reihen bogenförmiger Schlingen einfacher Fasern verbunden sind," and "diese Schlingen gehen mit den regelmässigten Arkaden in ganz gleichen Abständen aus einem Fasersäulehen in das andere über." This substance fills up the whole space between the successive stem-segments which is not occupied by the tendons, and is connected in the closest possible manner with the opposed surfaces of every pair of segments, even extending for a short distance into their superficial calcareous tissue. Each of the arcades above mentioned consists of a single primitive fibre, the terminations of which are lost in the "Fasersäulehen;" and the passage of these fibres in loops from one fibrous column to another gives an elasticity to the whole tissue, viz. a power of contraction after lateral displacement, and of extension after vertical compression, although the individual fibres are not elastic in the ordinary sense of the word.

Müller described the basals of *Pentacrinus* as united with the top stem-segments in the same manner as the successive stem-segments with one another, namely, by this elastic interarticular substance, while their sides simply "stossen an einander" (p. 25). This mode of union between the stem-segments was generally called by him a "Nath," or suture; but he sometimes spoke of it as an articulation, though he usually employed this last term only in those cases in which two segments are movable on one another through the intervention of muscles and ligaments which pass between them.

He further described the union between the first radials and the basals of *Pentacrinus* and between the first radials and the centrodorsal piece of *Comatula* as a suture, which name he also gave to the lateral union of the five first radials with one another (pp. 28, 29); but he does not seem to have supposed that in these cases the various elements were connected by the elastic interarticular substance which he found between the likewise suturally united stem-segments. In fact, in speaking of the syzygia, which he called an immovable sutural union of two segments, he said expressly that not only the muscles but also the elastic interarticular substance was absent. On the other hand, the latter is to be found between the segments which are capable of motion upon one another, whether ligaments and muscles be present, as between the first and second radials and between most of the brachials, or ligaments only, as between the first and second brachials and the second and third radials; for Müller described the ligaments connecting two mutually movable segments as having essentially the same structure as the elastic interarticular substance of the stem, except that their surface is plain and not "krausenartig gefaltet" (pp. 30-38).

In those more common cases in which there is a muscular union between two segments, such as the first and second radials, in contact by transverse articular ridges upon their opposed faces (Pl. VII. figs. 1 b, 2 a, 4 b, 5 a; i), Müller drew no distinction between the pair of ligamentous bundles on the ventral side of the articular ridge, and the single

mass which occupies the whole space between the opposed faces on the dorsal side of this ridge, describing them as alike consisting of elastic interarticular substance, the function of which is extensor and antagonistic to the flexor action of the muscles. Dr. Carpenter¹, however, regards the former as interarticular, with the special function of holding the pieces together, but allowing a certain amount of movement between them, while he describes the single dorsal mass as elastic, and as antagonizing by its extensile powers the action of the flexor muscles. Histologically he finds no difference between them, both consisting of minute, straight, and nearly parallel fibres, very much, in fact, like those which Müller described as composing the tendons of the stem of *Pentacrinus*. At their points of attachment to the pieces of the skeleton these fibres pass into their basis substance and become incorporated with it.

The union of the first radials with one another and with the centrodorsal piece, which had been spoken of as sutural by Müller, is described by Dr. Carpenter as "an adhesion of expanded surfaces closely fitted together, and held together by the continuity of their sarcodic basis substance" (p. 704); so that the different elements are cemented together by a "thin layer of sarcodic substance, continuous with that which occupies the meshwork of their own calcareous reticulation." This mode of union may be conveniently described by the word "synostosis," which has been employed by Simroth to designate the mode of union of two faces which "verkitten sich" in the skeleton of the *Ophiuridæ*. It is essentially the same as the syzygial union which occurs between certain pairs of the primitive arm-segments, although differing from it in points of detail.

(§ 36) We have seen that Müller regarded the tendinous tissue of the stem of *Pentacrinus*, and the fibrous ligamentous bundles, or, as he called it, the elastic interarticular substance uniting the movable elements of the skeleton both of *Pentacrinus* and of *Comatula*, as distinct from one another. I believe, however, that they are fundamentally identical, not only with one another, but also with the so-called "cement-substance" between two segments which are united by synostosis. This last consists, in the *Ophiuridæ*, according to Simroth², of connective-tissue fibres which lose themselves in the organic basis of the skeleton, and are of the same nature as the substance of the masses of connective tissue uniting two articulating surfaces, both tissues staining deeply with picro-carmin. I find the same to be the case in *Comatula* and *Pentacrinus*. The tendons of the stem of the latter genus, the ligamentous bundles, composed, according to Müller, of elastic interarticular substance, which connect every pair of movable arm-segments, and, lastly, the "cement-substance," uniting the first radials to one another and to the centrodorsal piece, all stain very deeply with picro-carmin, and are of essentially the same histological structure.

Fig. 4, on Plate III., represents a portion of a horizontal section through the suture, or, as I prefer to call it, the synostosis of two of the first radials of *Pentacrinus*. In the immediate neighbourhood of their apposed lateral faces there are none of the nuclei nor pigment-granules which are imbedded so abundantly in the more internal portions of their protoplasmic ground-substance, and the threads of the plexus of which it is composed

¹ Phil. Trans. *loc. cit.* pp. 703-714.

² *Op. cit.* p. 435.

become excessively attenuated and disposed with great regularity almost parallel to one another. At the same time the meshes of this organic plexus become greatly elongated in the intervals between the parallel threads or fibres, which are connected with one another by very delicate fibrils passing in the form of loops from one fibre to another. These loops, which forcibly recall Müller's description of the arcades connecting the fibrous columns of the elastic interarticular substance in the stem of *Pentacrinus*, are simply the expression of the ends of elongated meshes of the protoplasmic plexus forming the organic basis of the skeleton. In the neighbourhood of each of the two opposed surfaces the fibrous elements of this plexus assume the character of closely placed parallel connective-tissue fibres, with no pigment-granules nor nuclei imbedded in them, but staining deeply with picro-carmin, while the normal protoplasmic basis of the interior part of the calcareous segments is but little affected by this reagent. These fibres pass from the organic basis of the one segment into that of the other so that the two are firmly united, and the superficial denser layer of calcareous tissue is deposited around their ends, which corresponds with Müller's description of the elastic interarticular substance of the stem of *Pentacrinus* as extending for a short distance into the calcareous substance of the opposed faces of the segments. The superficial layer of calcareous reticulation which occupies the small intervals between the ends of the fibres thus becomes extremely close and compact; but the central portion of the fibrous tissue (Pl. III. fig. 4, *L*) does not calcify, remaining as a thin layer of fibrous cement-substance between the two opposed surfaces, precisely like the interarticular substance in the stem of *Pentacrinus*, with which I believe it to be identical. It is, at any rate, of the same nature as the substance of the ligaments connecting the first and second radials, which Müller described as identical with that connecting the stem-segments; for at the angles of the radial pentagon the fibres of the cement-substance connecting the adjacent first radials with one another in pairs pass directly into the fibres of the ligamentous bundles between the first and second radials. These, which are of precisely the same character as the ligamentous bundles between the successive brachial segments, also stain deeply with picro-carmin, and only differ from the cement-substance in the greater length of their fibrous element.

At the points of attachment of the ligaments to the pieces of the skeleton, the meshes of the organic plexus become greatly elongated, and its fibrous bars regularly disposed and connected with one another by loops, as above described. As, however, the distance between the two articulating faces is very much greater than in a synostosis, several of these minute primitive fibrils unite to form one of the larger fibres composing the ligamentous bundle, at the other attachment of which these primitive fibres again separate, become connected with one another by transverse loops, and finally pass into the bars of the protoplasmic plexus forming the ground-substance of the next segment.

(§ 37) I have found the fibres composing the ligamentous bundles between the arm-segments of *Antedon* to terminate in the manner above described for *Pentacrinus*; but in *Act. polymorpha* they do not pass so directly into the organic basis of the segment. At the ends of the ligamentous bundles, where their component fibres begin to break up into primitive fibrils, the latter cross one another in all directions, very much

as described by Simroth¹ in *Ophiactis virens*, so as to form a network of delicate threads without any imbedded nuclei, although it may contain pigment-granules; and this network passes very gradually into the nucleated protoplasmic plexus forming the organic basis of the brachial segments (Pl. III. fig. 7, *L*₁).

The tendons of the stem of *Pentacrinus* are, I believe, of precisely the same character as the ligamentous bundles between the arm-segments, although, of course, enormously longer. They stain deeply with picro-carmin, and are composed of parallel fibres, which may be teased out into very much finer ones, and their upper ends pass into the organic ground-substance of the five basals, precisely in the same manner as the fibres of the arm-ligaments pass into the protoplasmic network composing the organic basis of the successive segments.

In *Pentacrinus Wyville-Thomsoni*, in which the five basals are completely in contact with one another in pairs, the two elements of every pair are united by a synostosis, and the union of the basals with the radial pentagon above them is of the same character. The first radials of *Comatula* are connected with one another and with the centrodorsal piece in the same manner, as is seen in Pl. III. figs. 5, 6, where *L*, *l* represent the tracts of fibrous tissue connecting the first radials with one another and with the centrodorsal piece respectively. The terminal portions of this fibrous tissue become calcified to form the compact superficial layers of calcareous substance on the apposed faces, while the middle portion remains as the fibrous cement-substance uniting the two calcareous segments, which is thus essentially of a connective-tissue nature.

The mode of union of the segments of the calyx of the Tesselate Crinoids, none of which are connected with one another by a muscular articulation like the first and second radials of *Pentacrinus* and *Comatula*, was most probably a synostosis of the same nature as those just described. The immovable sutural unions between certain of the brachial segments to which Müller gave the name of "syzygia," are, in *Pentacrinus*, of precisely the same nature as the synostoses between the segments of the calyx, the organic basis of the one segment being continuous with that of the other through the fibrous cement-substance, which forms a thin layer between the whole of the two simple opposed surfaces. This was described by Müller² as a very delicate membrane, of a different nature from the elastic interarticular substance between the likewise suturally united stem-segments.

In *Comatula*, however, the apposed surfaces of the two elements united by a syzygium are not plain and simple, as in *Pentacrinus* and *Rhizocrinus*³, but marked by a series of radiating ridges, as in *Apiocrinus obconicus*, Goldf.⁴ The ridges of the two surfaces correspond in position, and when the surfaces are in contact are closely applied to one another, and united by fibrous cement-substance as in an ordinary synostosis. The fibrils are very numerous and placed very close to one another, so that the calcareous reticulation forming the ridges is remarkably dense and compact, being formed around the ends of these fibrils where they pass into the organic basis of the segments; and these ridges thus correspond to the whole of the syzygial surfaces in *Pentacrinus* and *Rhizo-*

¹ *Op. cit.* p. 435.² *Bau des Pentacrinus*, p. 29.³ Sars, *loc. cit.* p. 22.⁴ Petref. German. Taf. lvii. fig. 5.

crinus. In the intervals between them the organic basis of the one segment is directly continuous with that of the other, little or no fibrous tissue being interposed.

The muscular fibres of *Actinometra* correspond very closely with those of *Antedon*, as described by Dr. Carpenter¹ and Ludwig²; their expanded terminations are simply applied to the surfaces of the calcareous segments to which they are attached, not passing into their substance as the ligamentous fibres do (Pl. III. fig. 7, *b m*), and there is no trace either of a sarcolemma or of transverse striation.

(ii.) *The Dorsal Cirrhi.*

(§ 38) The Dorsal Cirrhi of *Actinometra* do not appear, so far, at least, as my observations have extended, to be developed over such a large surface of the centrodorsal piece as is the case in *Antedon*. In all the specimens which I have examined the cirrhi are limited to its margin, while its central portion is entirely free from them and usually slightly concave. There is generally only one row of these appendages; but small and rudimentary ones may occasionally be found interposed between the large and full-grown ones at the extreme circumference of the plate, thus forming the commencement of a second row. The number of cirrhi existing at any one time upon the plate-like centrodorsal piece of *Act. polymorpha* varies, I believe, between 15 and 20. Three or, in large specimens (Pl. VI. figs. 1, 2), four are attached on each side of its more or less distinctly pentagonal margin, while in var. 1 (Pl. VI. fig. 14), and in one specimen of the type (fig. 7), the total number reached 25. In var. 2 (fig. 16) there are only 10; while in vars. 3 (fig. 20) and 4 there is no evidence, in the single specimens which I have examined, of the existence of more than three perfect cirrhi in the adult state, as there are no sockets around the margins of the centrodorsal plate for the attachment of a larger number; though there may be minute openings here and there, which appear to have corresponded with the central canals of lost cirrhi, the sockets of which have been obliterated by a later calcareous deposit.

It is not a little singular that the dorsal cirrhi of *Act. polymorpha*, like the centrodorsal piece which bears them, should exhibit such a very slight range of variation, not only in size but also in number (the three varieties just mentioned of course excepted); for in nearly every other part of the skeleton the range of variation is very great. In *Antedon rosacea* the reverse appears to be the case; for the composition of the skeleton is fairly constant in its simplicity, but the cirrhi vary considerably both in number and in size.

In a fully developed cirrhus of *Act. polymorpha* (Pl. III. fig. 8a) the number of segments varies from 11-14, being usually 12 or 13, the last of which is in the form of a strong sharp claw. This is attached by simple suture to the penultimate segment, which is prolonged at the base of the claw into a short opposing process on its concave or aboral margin.

The diameter of the basal segment somewhat exceeds its length; but in the second and third segments this disproportion between the length and breadth is reduced, and in the fourth it becomes reversed, the length of this segment being slightly greater than its

¹ Phil. Trans. *loc. cit.* p. 704.

² Beiträge &c. *loc. cit.* p. 40.

diameter. In the fifth and sixth the proportion between the length and breadth reaches 3:2; and a very slight degree of lateral compression is visible in the latter segment, while the fifth, like the four basal segments, is cylindrical, or nearly so. These are the two longest segments of the cirrus; and from this point onwards the length of the segments gradually decreases, until in the tenth and following segments it becomes again less than the dorso-ventral diameter. At the same time the transverse diameter, which in the first five cylindrical segments is equal to the dorso-ventral diameter, undergoes in the seventh and eighth segments a sudden decrease. A faint indication of this is seen in the sixth segment, and it is continued on to the end of the cirrus, so that its terminal portion exhibits a considerable degree of lateral compression. In correspondence with this, a small spine gradually develops itself on the dorsal margins of the sixth and successive segments, on which it becomes progressively more and more marked, until in the penultimate segment, *i. e.* the last one before the claw, it becomes the short pointed opposing process above mentioned. This series of small spines, like the single penultimate opposing process of the cirri of *Ant. rosacea*, seems to be characteristic of those cirri only which have reached their full development; for scarcely any trace of it is visible in the still immature cirrus represented in Pl. III. fig. 8c. Although its penultimate segment shows a faint indication of an opposing process, the dorsal margins of the segments immediately preceding it are almost, if not quite, even.

The segments of this cirrus, although of the normal proportions, are not so large as those of an adult cirrus, and (counting the terminal claw) are 14 in number, the first seven of which precisely resemble those of the cirrus represented in Pl. III. fig. 8a, with 12 segments and a claw, so that the extra one in the former case would appear to be interpolated between the middle and end of the cirrus. As in *Ant. rosacea*, and for precisely the same reason, greater facility of flexure, the ligamentous substance between the terminal segments is thicker on the aboral side than on the oral (Pl. III. fig. 9b), while in the more cylindrical segments of the basal half of the cirrus the ligamentous substance is tolerably equally developed on both sides (fig. 9a). In correspondence with this, the canal (*c c'*) which occupies the centre, or nearly so, of the circular opposed faces of the basal segments (fig. 9a), lies in the laterally compressed terminal segments much nearer to the oral side of the oval articular faces, more than half of which is occupied by the large fossa for the lodgment of the aboral interarticular ligament (fig. 9b). The opening of the central canal (*c c'*) is surrounded in each case by a more or less prominent articular surface.

(§ 39) Both the single specimens of Varieties 3 and 4 of *Act. polymorpha* which I have been able to examine had unfortunately lost all their few cirri; but in Var. 1 twenty-five still remained attached to the centro-dorsal piece; most of these are fully developed, and present some slight differences from those of the type (Pl. III. fig. 11). Not only is the number of segments greater, varying usually from 13 to 15, besides the terminal claw, but they also differ considerably in their relative proportions; for in the type the fifth and sixth segments are the longest, while in Var. 1 there is less difference between them and the fourth and seventh in this respect. The lateral compression, which is not visible till the eighth segment, becomes somewhat marked towards the end of the cirrus,

which is more distinctly flattened than in the type, although the small opposing spines on the dorsal margins do not appear at all until the three or four penultimate segments; and even on these they are but slightly developed.

In Var. 2 there are only ten cirrus-sockets around the margin of the pentagonal centrodorsal plate, two on each of its sides, and placed close to the angles (Pl. VI. fig. 16). The number of segments in each cirrus is eleven or twelve besides the terminal claw (Pl. III. fig. 10), and the width of the two basal segments somewhat exceeds their length. In the third the length and breadth are nearly equal, but in the fourth and fifth, which are the two longest segments of the cirrus, the proportion between them is as about 4 to 3. The sixth segment is slightly shorter than the fourth, and from this point to the end of the cirrus the length of the segments gradually decreases, while at the same time they exhibit a slight degree of lateral compression. The dorsal spine, the first indication of which is seen in the fifth and sixth segments, becomes very marked indeed towards the end of the cirrus, and develops in the penultimate segment into a stout opposing process.

(§ 40) The development of the cirrhi of *Act. polymorpha* seems to take place somewhat differently from their development in *Ant. rosacea* as described by Dr. Carpenter¹. In the latter species the individual segments usually present all the characters of maturity from a very early date, viz. the relative proportions in the length and breadth of the segments, the bevelling off of the opposed faces on the aboral side, and the development of the opposing process on the penultimate segment. But in some rare cases, even after the cirrus has attained a considerable size and has the normal number of segments, the latter are of a very rudimentary character; their basal segments are the longest, and the following ones rapidly decrease in diameter, so that the whole cirrus tapers considerably from its base to its point. This condition gradually becomes less and less marked as the segments increase in size, and their opposed faces become bevelled off towards the aboral side, so that the cirrus ultimately acquires all the characters of maturity.

This mode of development, which is the exception in *Ant. rosacea*, seems to be the rule in *Act. polymorpha*. All the very young cirrhi, both of the type and of Varieties 1 and 2, which I have met with, taper rapidly from the base to the apex; and while the four or five basal segments exhibit from a very early period the same proportion between length and diameter as is seen in a completely developed cirrus, the following ones are still in a very rudimentary condition. The sixth segment, instead of being as long as the fifth, is much shorter; the seventh is still shorter and more slender, while the terminal segments are little more than a succession of small disks ending in a small and very rudimentary claw (Pl. III. fig. 8 b). They are thus not only of the smallest dimensions, but have a much more immature appearance than the basal segments; and it would therefore seem that the augmentation in the number of segments is effected by the interpolation of new segments, not at the base, as is usually the case in *Ant. rosacea*, but between the middle segments and the terminal claw.

¹ Phil. Trans. *loc. cit.* p. 711.

The fact already mentioned (sect. 38), that in two cirrhi in which the number of segments is different, the character of the first six or seven is the same, would seem to point to the same conclusion.

(iii.) *The Centrodorsal Plate.*

(§ 41) In all the *Actinometra* with which I am acquainted, the external appearance of the "Knopf," or centrodorsal piece, is very characteristic. Like the cirrhi which it bears, it is far more constant throughout a considerable range of species from very various localities, than it appears to be in the individual members of a single species, both of the European and of some of the foreign *Antedons*, even when existing in the same locality.

Thus, for example, the centrodorsal piece of *Ant. celtica* may either be very shallow, flattened, and bluntly rounded off at the base, where it was originally united to the joint of the stem next beneath it, with only two rows of sockets (*U*) for the attachment of the cirrhi (Pl. IV. fig. 1); or it may be deep and nearly hemispherical, with three or four alternating rows of cirrhus-sockets, and terminating inferiorly in a flattened circular or rudely pentagonal base (fig. 6); or, finally, it may have the form of a five-sided pyramid, the apex of which is directed downwards and very slightly truncated, while the sides bear three or four alternating rows of indistinct cirrhus-sockets (Pl. IV. fig. 8). This last character indicates that the animal had attained a considerable age; and as all the specimens of this kind which I have seen have been smaller than normal specimens of *Ant. celtica*, and exhibit slight differences from them in the characters of other parts of the skeleton, I am disposed to regard them as dwarfed varietal forms rather than as young and incompletely developed individuals of the ordinary type.

Again, of the two specimens of *Ant. macrocnema*, Val., in the Paris Museum, both of which were brought from New Holland by Quoy and Gaimard in 1829, one has a large and hemispherical centrodorsal piece, while in the other it is a short pentagonal or nearly circular column, on which the cirrhi are disposed in three or four alternating rows.

These instances, which might be greatly multiplied, suffice to show that the centrodorsal piece of *Antedon* may vary very considerably in its external appearance. In *Actinometra*, so far as my experience goes, it is almost invariably a flattened circular, or rudely pentagonal disk, somewhat hollowed in the centre of its dorsal surface, and with low sloping sides marked out into distinct sockets for the articulation of the cirrhi (Pl. V. figs. 1, 6, 15, and Pl. VI. figs. 1, 2, 7, 14, 16, 20). It generally conceals more or less of the first radials which rest upon it (Pl. II. figs. 9-11, *cd*), but it may sometimes be very irregularly extended so as to conceal a considerable part of one or more of the second radials (Pl. II. fig. 8, *cd*).

As a general rule, only one row of cirrhus-sockets can be traced; but in the large *Act. robusta* (Pl. V. fig. 15) I have found two alternating rows of sockets to be distinctly visible, and even traces of a third row, so that the dorsal surface of the plate becomes slightly convex, though by no means to the same extent as in most *Antedons*. In fact, the flattened plate-like condition of the centrodorsal piece, and the existence upon

it of only one or two whorls of marginal cirrhi, seem to be very characteristic of *Actinometra*; and it would be almost possible to distinguish the *Antedons* from the *Actinometrae* among the *Comatulæ* described in Müller's memoir, by simply referring to his descriptions of the "Knopf."

When the centrodorsal is viewed *in situ*, with all the cirrhi attached around its sides, its central flattened surface appears almost circular; but when the cirrhi are removed, so as to expose the low and more or less sloping sides to which they are attached, the outer margin of the plate is seen to have a distinctly pentagonal form. This is well seen in the large *Act. robusta* (Pl. V. fig. 15), with its three rows of cirrhus-sockets; but in *Act. solaris* (Pl. V. fig. 1) the angles of the pentagon are more rounded off, and there is only one row, a complete one, however, of cirrhus-sockets, while the plate itself is of a considerable diameter, so as entirely to conceal the first radials.

In a variety of this species, which I believe to be identical with the *Act. pectinata* of Retzius and Müller, the diameter of the centrodorsal (Pl. V. fig. 6) is very slight, so that the greater part of the superjacent radial pentagon is visible outside its pentagonal margin; and there are only ten distinct cirrhus-sockets, two at each angle, though one of the angles (the upper one in the figure) is marked by the presence of a third socket, which either indicates the commencement of a second row of cirrhi, or, and more probably, the incomplete obliteration of a pre-existing row.

In *Act. polymorpha* the angles of the pentagonal centrodorsal plate, the diameter of which varies from 3 to 5 millims., are sharp and distinct (Pl. VI. fig. 2); in varieties 3 (fig. 20) and 4, the dorsal and ventral surfaces almost meet at the edge of the plate, which is very slightly truncated, and marked in three places by the large sockets (*U*) for the attachment of the few remaining cirrhi, while other small openings indicate the former existence of others which have been since lost.

In var. 2 (Pl. VI. fig. 16) the diameter of the centrodorsal plate is very small, as in *Act. pectinata* (Pl. V. fig. 6); and, also as in this species, it normally bears ten cirrhi, two at each angle. The sockets for the cirrhi are, however, but slightly marked, so that the edge of the plate is but little truncated, and it can hardly be said to have distinct sides as in *Act. solaris* (Pl. V. fig. 1).

In the type, on the other hand (Pl. VI. figs. 1, 2, 7), and more especially in var. 1 (fig. 14), in which there are 25 cirrhi, the edge of the plate where the dorsal surface passes over into the ventral is obliquely truncated, so that the plate has distinct sides, which are marked by numerous cirrhus-sockets, as in *Act. solaris* (Pl. V. fig. 1). Towards the ventral surface the angles of the pentagonal margin of the plate are prolonged into five short processes (Pl. VI. fig. 14, *t*), each situated between a pair of cirrhus-sockets (*U*). Their distinctness varies in different individuals; they are especially marked in var. 1 (fig. 14), and in that specimen of the type which resembles it in having 25 cirrhi (Pl. VI. fig. 7), and they are best seen after removal of the centrodorsal plate from the radial pentagon which rests upon it. They exist also in the other varieties of *Act. polymorpha* (Pl. VI. figs. 16, 20), though they are not so distinctly visible externally, owing to the greater extension of the dorsal surface of the plate than is found in the type and in

var. 1, since it is not reduced in size by the truncation of its edges, as is the case in these forms.

(§ 42) The meaning of these processes becomes apparent when we examine the ventral or superior surface of the centrodorsal plate which bears the superjacent radial pentagon. Its condition in *Act. polymorpha* is rather complicated, and will be better understood after an examination of the simpler forms of this surface presented by other species of *Comatula*.

In the large variety of *Ant. celtica*, the cavity of the centrodorsal piece (Pl. IV. fig. 2, *cd.c*) is very deep, and its opening on the flattened ventral surface has a circular or somewhat pentagonal form. Between the angles of this internal pentagon and those of the outer more distinctly pentagonal margin of the piece run five slight ridges or elevations (*i.e.*). In the intervening radial areas (*r.ar*), between these ridges the surface is somewhat depressed, so as to receive the convexities of the dorsal surfaces of the first radials that rest upon it, while the five ridges correspond with five slight furrows marking the lines of junction of these surfaces on the dorsal aspect of the radial pentagon (Pl. IV. fig. 3), and are therefore interrarial in position.

In *Ant. celtica* these ridges are tolerably uniform in width throughout their whole course; but in *Ant. rosacea* (Pl. IV. fig. 15) they are considerably wider at their internal or central ends than they are towards the external pentagonal margin of the piece, so that they have an elongated triangular form. From the base of each triangle a shallow depression extends a little way towards its apex, cut out along the median line of the ridge; but it soon becomes obliterated by the gradual approximation of its two sides, which meet and form a simple ridge, like that of *Ant. celtica* (Pl. IV. fig. 2), extending outwards to the margin of the plate.

The central ends of the radial areas into which the ventral surface of the plate is divided are marked in *Ant. rosacea* by five shallow depressions (Pl. IV. fig. 15, *q*), placed close to the margin of the internal cavity, which bends somewhat inwards at these points. These depressions correspond in position with five large radial openings on the dorsal surface of the pentagonal base of the calyx (Pl. IV. fig. 16, *Q*), and receive the blind ends of five diverticula of the body-cavity, which are enclosed between the five radial spout-like processes of the rosette (Pl. IV. figs. 13, 16, *p*) and the internal faces of the first radials. They are, however, occasionally absent in *Ant. rosacea*, while, on the other hand, traces of them may occur in *Ant. celtica*. In fact, the differences which I have described above in the appearance of the ventral surface of the centrodorsal piece of these two species must not be regarded as representing more than two extreme variations of one and the same type.

(§ 43) We shall now be able to understand the meaning of the short processes (*l*) above mentioned, which are seen projecting from the angles of the centrodorsal plate of *Act. polymorpha*, when viewed from below. It will be best to begin with the examination of the ventral surface of the centrodorsal piece of variety 1 (Pl. VI. fig. 15), in which they are more distinctly marked than in the type. This surface rises slightly from the circumference towards the centre, which is occupied by the opening of a shallow cavity, the centrodorsal cœlom (*cd.c*), the diameter of which is rather less than

one third of the total diameter of the plate. The floor of this cavity is marked by minute punctations (*u*), which are the internal orifices of canals proceeding from it towards the dorsal surface of the plate. They originally opened externally on the summits of the small tubercles occupying the centres of the sockets for the articulation of the first developed cirrhi in the young animal; but their openings have gradually become obliterated by the deposit of new material upon the central portion of the external surface of the plate, as described by Dr. Carpenter¹ in *Antedon rosacea*. This is accompanied by the continual removal of old material from the internal surface, so that the minute openings (Pl. IV. fig. 15, *u*) seen on the central part of the floor of the internal cavity of the centrodorsal piece are the original external openings of the first developed canals, which have subsequently become closed externally by the new material deposited upon the central part of the dorsal surface. The internal openings of the canals proceeding to the last developed cirrhi are much larger, and placed more towards the periphery of the floor of the cavity. Similarly in *Actinometra polymorpha*, the internal openings of the canals proceeding to the existing marginal cirrhi on the plate-like centrodorsal piece are placed under its projecting rim, so as not to be visible from above. There are usually one or two large openings under the central margins of each of the radial areas (Pl. VI. figs. 3, 8, 10, 15, 17, 21, *var.*), and the canals which proceed outwards from these internal openings break up into five branches, one of which reaches the summit of each of the small tubercles occupying the centres of the five cirrhus-sockets, which are placed along the outer or peripheral margin of each of the corresponding radial areas (Pl. VI. figs. 1, 2, 7, 14, 16, 20, *U*). These canals enclose the axial cords of the cirrhi (Pl. VIII. figs. 1, 3, 4, 5, 6, 8, *u.c.*), which proceed from the fibrillar envelope of the quinquelocular organ contained in the cavity of the centrodorsal plate (Pl. VIII. figs. 1, 2, 3, 7, *N*), and surround the cirrhus vessels arising from its chambers (figs. 2, 3, 7, *ch*), from each of which there arises a single trunk², dividing, sooner or later, into branches for the individual cirrhi. In the specimen of var. 1 represented in Pl. VI. fig. 15, the division is not completed within the cavity of the centrodorsal plate, as two or, sometimes, even only one aperture can be seen under the inner margin of each of the radial areas, so that the primary trunk enters the substance of the plate, and there divides into the five branches for the cirrhi placed on the outer margin of each radial area.

The rim of the cavity of the centrodorsal plate of *Actinometra polymorpha*, var. 1 (Pl. VI. fig. 15, *cd.c.*), is ten-sided, or nearly circular, and is not marked by shallow radial depressions, like those described above in *Ant. rosacea* (Pl. IV. fig. 15, *q*). The radial areas rise very slightly from their peripheral to their central margins, and are marked by various indistinct ridges and furrows. Their sides rise towards the five inter-radial elevations, which, though not very much raised above the general surface of the plate, are nevertheless very distinct; for they are wide and marked by shallow grooves

¹ Phil. Trans. *loc. cit.* pp. 742. 743.

² This is in precise accordance with the origin of the vessels proceeding to the cirrhi which are borne on the stem of *Pentacrinus*. At every nodal segment the five chambers which are placed radially around the central axis of the stem enlarge slightly, and each gives off a single vessel to one of the five cirrhi.

(Pl. VI. fig. 15, *b.g.*), which occupy the greater part of their width, so that the simple ridge, as seen in *Ant. cellica* (Pl. IV. fig. 2, *i.e.*), is here represented by the two sides of the groove which is cut out along its median line. In *Ant. rosacea* (Pl. IV. fig. 15), as we have already seen, these sides meet at a very short distance from the central end of the groove so as to obliterate it. In this form, however, they approach one another very gradually, and only just meet within the margin of the plate; but the ridge formed by their fusion does not end here as in *Ant. rosacea*, for it is continued a short distance beyond the general surface of the plate, so as to appear as a short process (*t*) extending outwards from the angle between two sides of its external pentagonal margin. Consequently these five short processes appear on the dorsal aspect of the plate, prolonging its angles outwards, as we have seen in sect. 41 (Pl. VI. fig. 14, *t*).

(§ 44) The grooves (*b.g.*) which are thus cut out along the median line of the interradial elevations on the ventral surface of the centrodorsal plate of *Actinometra* are of no little importance; for there lie in them, as will be seen further on, the five rays of the basal star (Pl. VI. fig. 13, *S*), which is in close connexion with the dorsal surface of the radial pentagon; they may therefore be called the "basal grooves" (*b.g.*).

As a general rule, these interradial elevations and the basal grooves are, like the rays of the basal star, entirely devoid of pigment, which is, however, very abundant in the organic basis of the calcareous reticulation composing the rest of the ventral surface of the plate; so that when this is first exposed by the removal of the centrodorsal from the dorsal surface of the radial pentagon which rests upon it, five white rays are visible on a dark background. Unless the plate is immediately removed from the alkaline solution used to effect its separation, this distinction in colour between the radial and the interradial portions of its ventral surface rapidly disappears, owing to the destruction of the pigments contained in the former.

The development of these basal grooves is not only different in the type and in all the varieties of *Act. polymorpha*, but it differs in different individuals of the type, and even to a certain extent in the same individual.

In the specimen of the type represented in Pl. VI. figs. 7, 8, which, like variety 1, had 25 cirrhi, two only of the basal grooves are seen; for the other three are occupied by the rays of the basal star (fig. 8, *S*), which have become detached from the rest of the star and from the first radials with which they were connected. But even these two grooves do not resemble one another; one extends almost to the margin of the plate, beyond which the interradial ridge formed by the union of its sides is continued as a short process (*t*), just as in var. 1 (fig. 15). The other open groove, however, terminates very soon, as its sides, widely separated at its central end, bend sharply towards one another, and meet some distance within the margin of the plate, to which the ridge formed by their union does not extend, for it terminates abruptly in a blind and rounded extremity.

In variety 1 (Pl. VI. fig. 15) the basal grooves (*b.g.*) are narrow, and after increasing a little at first, diminish gradually in width from their central to their peripheral ends; but in the specimen of the type (fig. 8) they are much wider in proportion to their length, and the width increases slightly from their base to about the middle of their

course, so as to give a leaf-like appearance to the rays of the non-pigmented interradiar star on the ventral surface of the centrodorsal plate.

In another specimen of the type, however (Pl. VI. fig. 3), the sides of the narrow basal grooves are almost parallel, and in every case meet at some distance within the margin of the plate, while the interradiar ridges resulting from their union scarcely extend at all beyond the angles of the external pentagon.

Lastly, in the monstrosity represented in Pl. VI. fig. 10, the dorsal aspect of which is seen in Pl. II. fig. 8, both ridges and grooves are extremely indistinct, and in no case reach the outer margin of the plate; while the margin of the internal cavity is markedly pentagonal in form, and not ten-sided nor circular, as is the case where there are five distinct interradiar elevations alternating with the five radial areas (Pl. VI. figs. 3, 8, 15); and it does not project inwards so far as to conceal all the openings (*u*) of the canals leading to the marginal cirrus-sockets, as is the case in the other two specimens of the type (figs. 3, 8, and in var. 1 fig. 15).

In all these three specimens of the type the ventral surface of the centrodorsal plate is not nearly so flattened as in var. 1, but rises very distinctly between its external and its internal margins, while the radial areas are marked in the same way by various indistinctly marked radiating ridges and furrows; though as the floor of the central cavity is also somewhat thicker, its depth is but little if at all greater. The same is the case in the other three varieties, in each of which the basal grooves differ slightly in form from one another and from the type. In every case they are widest about the middle of their length, as in one of the specimens of the type (Pl. VI. fig. 8, *b.g*); this is most marked in var. 3 (fig. 21), and least in var. 2 (fig. 17). They reach almost, if not quite, to the margin of the plate, though the ridges formed by the union of their sides extend but little if at all beyond it, except in var. 3 (figs. 20 & 21), in which two of the angles of the external pentagon are marked by traces of the small processes (*t*) so distinctly seen in var. 1 (figs. 14, 15). In this variety the course of the interradiar ridges is indistinctly visible on the dorsal surface of the plate (fig. 20), which is slightly hollowed in the centre. The floor of the central cavity is, however, very thick and solid, and its middle portion presents no trace whatever of any perforations for the canals of pre-existing cirri, though those proceeding to the three marginal cirrus-sockets are just visible under the projecting lip (fig. 21, *u*), which conceals several others. These indicate that more cirri either have been or would have been developed had the animal lived longer, their external openings having been obliterated in the former case (the more probable one) and not yet formed in the latter.

45 In *Act. solaris* (Pl. V. fig. 2) the ventral surface of the plate-like centrodorsal piece is very nearly flat, as in *Act. rosacea* (Pl. IV. fig. 15) and in *Act. polymorpha*, var. 1 (Pl. VI. fig. 15), rising but slightly from the circumference towards the centre, and marked by five interradiar elevations, along the top of each of which runs a long and narrow basal groove (*b.g*). Its width is tolerably uniform from its base until near its end, where its sides suddenly approach one another, and meet at a little distance within the margin of the plate, where the ridge formed by their union also ceases without extending outwards beyond the general surface of the plate. The same is the case in

the large *Act. robusta* (Pl. V. fig. 14), in which three of the basal furrows are widest at their central ends, and consequently triangular, while the others are somewhat irregular in shape.

In both these specimens numerous small openings are visible on the floor of the central cavity of the centrodorsal piece, but the principal ones leading to the marginal cirrhus-sockets are concealed under its projecting lip. In the small centrodorsal piece of *Act. pectinata*, however, these last are very distinct (Pl. V. fig. 7. *u*) and correspond in number to the eleven external cirrhus-sockets (Pl. V. fig. 6, *U*), so that the five principal cirrhus-vessels leaving the quinquelocular organ would seem to divide at once within the cavity of the centrodorsal piece, and not within the substance of its walls, as is the case in *Act. polymorpha*. The ventral surface of the centrodorsal plate of *Act. pectinata* (Pl. V. fig. 7) is by no means so flattened as in the closely allied *Act. solaris* (fig. 2), but rises considerably from the circumference towards the centre, and the inter-radial ridges are well marked. The basal grooves (*b.g*) are narrow and parallel-sided, and terminate within the margins of the plate, beyond which the interrarial ridges are not continued, so that there are none of the small processes extending outwards from the angles as in some forms of *Act. polymorpha*. The median line of each of the radial areas is occupied by a deep depression, which is particularly distinct at its central end. A similar depression, though developed to a less extent, exists also in *Act. polymorpha*, Var. 2 (Pl. VI. fig. 17, *r.ar*).

(§ 46) Nearly all the observers who have studied *Comatula* have regarded the "Knopf," or centrodorsal piece, as of essentially the same nature as the stem of the stalked Crinoids. The first author who put forward this opinion was Schweigger¹; and Miller's views², published two years later, were fundamentally the same, though somewhat modified in form; for the centrodorsal piece was regarded by Miller as composed of two separate pieces, one forming the floor of the cavity and the other its sides and rim. The former was described by him as a pentagonal unperforated plate, "analogous in situation to the first columnar joint of the Crinoidea; but as it is not required to transmit the passage to the alimentary canal³ (no prolongation of the column existing in this animal), it is without central perforation."

The other or ventral half of the centrodorsal piece was regarded by Miller as an annular or basin-shaped plate, representing the "pelvis" or basal circle of *Pentacrinus*, though he described it as marked externally by numerous sockets for the attachment of the cirrhi, which in *Pentacrinus* are borne by the stem-segments only, and never by the basals.

Goldfuss, who in most points followed Miller's views, differed from him considerably with regard to the nature of the centrodorsal piece of *Comatula mediterranea*, which they had both studied; and his conclusions, though not absolutely correct, are much nearer the truth than those of Miller. Finding most specimens to bear three rows of

¹ *Op. cit.* p. 64.

² *Op. cit.* pp. 129, 130.

³ It must be remembered that the canal which occupies the centre of the Crinoidal stem was originally supposed to be a continuation of the alimentary canal, and not, as we now know it to be, of the general perivisceral cavity or coelom.

dorsal cirrhi, he described this species as having a column of three segments, and gave a sectional figure in support of his statements¹, which shows three segments below the circle of first radials, each bearing a row of cirrhi. It is doubtful how far this figure can be relied on as accurate, though I have occasionally met with somewhat similar appearances myself. Goldfuss, like Miller, was unacquainted with the remarkable condition of the basals in this type; and as the "pelvis" described by Miller in *Comatula* was rightly regarded by him as representing a part of the stem of *Pentacrinus*, he was led to believe in the absence of basals in *Com. mediterranea*, though he found them in the *Com. multiradiata* (*Comaster*), in which he described the rudimentary column as consisting of only a single segment. Müller was led, by his comparison of the component pieces of the calyx of *Comatula* with those of the calyx of *Pentacrinus asteria* (*Cuput-medusa*), to recognize the very close general correspondence between them; and he pointed out² that the presence of cirrhi at the upper end of the stem of the Pentacrinoid larva on the one hand, and on the centrodorsal plate bearing the first radials of the young *Comatula* on the other, indicate that the latter is comparable to the stem of *Pentacrinus*, which bears the cirrhi in verticils separated by longer or shorter intervals. This view of Müller's was pretty generally recognized as the true one, and it was adopted and greatly strengthened by Wyville Thomson and Dr. Carpenter, who came to precisely the same conclusions upon developmental grounds. The former defined it as representing a "coalesced series of the nodal stem-joints in the stalked Crinoids," namely, of those joints which bear whorls of cirrhi, so that "the centrodorsal plate with its dorsal cirrhi in *Antedon* is the homologue of the stem with its cirrhi in the stalked Crinoids." Ludwig³ also, while referring to the development of the centrodorsal as the enlarged uppermost stem-segment, speaks of it as "ein zusammengedrängter, oberer Stengelabschnitt, in welchem das verkalkte Gewebe keine Sonderung in untereinandergelegene Glieder erfahren hat."

(§ 47) The first rudiment of the stem of the Pentacrinoid larva as described by Wyville Thomson⁴ consists of a series of delicate calcareous rings forming a curved line, which passes backwards from beneath the centre of the lower ring of plates, the embryonic basals. Within each of these is formed a hollow sheaf of parallel calcareous rods, united together by short anastomosing lateral branches; the upper one of these, on which the lower edges of the basal plates rest, soon becomes considerably wider and thicker than the rest. "During the earlier stages of the growth of the Pentacrinoid it is simply a circular band of the ordinary calcified areolar tissue, enclosing a sheaf of the peculiar fasciculated tissue of the stem, gradually enlarging, with a central aperture continuous with the bore of the tube-like stem-joints."

This ring is subsequently developed into the permanent centrodorsal piece; but the rudiments of the first dorsal cirrhi do not appear around its lower contour until very much later. New rings are developed immediately beneath it, until there are fifteen or sixteen

¹ Petref. German. p. 202.

² Bau des *Pentacrinus*, p. 10.

³ "Zur Anatomie des *Rhizocrinus lofotensis*," Zeitschr. für wiss. Zool. Bd. xxix. p. 127.

⁴ "On the Embryogeny of *Antedon rosaceus* (Linck) (*Comatula rosacea* of Lamarck)," Phil. Trans. 1865, pp. 536, 537.

in all, the length and diameter of which are gradually increased by the deposition of new calcareous material at their extremities and upon their outer cylindrical surface.

Dr. Carpenter¹ has shown that, at or about the period at which the suppression and metamorphosis of the embryonic oral and basal plates begins, "the production of new calcareous segments in the stem appears to cease, and a remarkable change begins to show itself in the one on which the calyx rests. Instead of increasing in length, its original annular disk augments in diameter, becoming convex on its lower surface and concave on its upper, and it extends itself over the bottom of the calyx in such a manner as to receive in its concavity the apices of the basal plates;" and that portion of its under surface which extends itself beyond the segments whereon it rests begins to be marked by small tubercles, which are the origins of the dorsal cirrhi, while it also "augments not only in absolute but in relative diameter, extending itself over the dorsal or outer surface of the basal plates, which at the time of the detachment of the body from the stem are almost entirely concealed by it. A second whorl of cirrhi is now developed, after the same manner as the first, between the latter (with which it alternates in position) and the base of the calyx (pl. xlii. fig. 3), and a third whorl generally makes its appearance before the detachment of the Pentaerinoïd, so that the young *Antedon* possesses *ten* cirrhi in different stages of advanced development, and from *one* to *five* still rudimentary."

After the detachment of the young *Antedon* from its stem a minute five-rayed perforation is visible for a short time in the somewhat depressed central portion of the inferior surface of the centrodorsal piece. It is the remains of the original "communication between the cavity of the basin-shaped plate and the central canal that is still left in the upper segments (at least) of the stem. This perforation, however, is very soon closed up by an extension of the calcareous network, so that no trace of it remains visible either internally or externally."

We have thus seen that the centrodorsal piece "first presents itself in a form which nowise differentiates it from the other joints of the cylindrical stem, but begins to take on an extraordinary increase in a peripheral direction at the time when the dorsal cirrhi first sprout forth, and thenceforward remains in closer connexion with the calyx than with the rest of the stem, from which it separates itself so soon as the dorsal cirrhi are sufficiently developed to serve for the attachment of the animal." Each of these cirrhi receives a "sarcodic thread, which proceeds from the sarcodic axis contained within the cavity of the basin, and runs along the central canal of the cirrhus to its termination."

New cirrhi gradually appear between those previously formed and the base of the calyx, and each receives a peduncle of sarcodic substance from the central axis; and "since the arrangement of the whole aggregate of such peduncles is distinctly verticillate, the want of a definite plan in the grouping of the cirrhi on the external surface of the centrodorsal plate seems attributable to their very close apposition."

During the whole period of the growth of the centrodorsal basin there is a "progressive exuviation of the first-formed cirrhi from within outwards, concurrently with the development of new ones near the margin, those cirrhi which surrounded the summit of the

¹ Phil. Trans. *loc. cit.* p. 732.

stem being first shed and their sockets filled up by new deposit, and the space thus formed being gradually widened by the progressive exuviation of the cirrhi that bound it, and the filling up of their sockets." Thus the flattened central portion of the dorsal surface of the plate by which it was originally attached to the joint of the stem next beneath it increases very much in extent, and finally comes to bear a considerable proportion to its diameter (Pl. IV. fig. 1). In *Act. polymorpha* (Pl. VI. figs. 2, 7, 14, 16, 20), as we have seen, it extends over the whole of the dorsal surface of the plate, and to a certain extent also in *Act. robusta* (Pl. V. fig. 15). In *Ant. Eschrichtii*, however, it does not reach any great extent, for most of the first-formed cirrhi do not appear to be cast off as in *Ant. rosacea* and *Ant. celtica*, or, if they are lost, their sockets are not obliterated, but they seem to be replaced by others, for I have frequently found young and rudimentary cirrhi among the larger and perfectly developed ones around the central portion of the large hemispherical "Knopf" of this species¹.

(§ 48) In most pedunculate Crinoids, in which the calyx rests upon the uppermost segment of the stem, this segment, instead of being the largest, is the smallest, being the latest formed, while the base of the calyx is formed by the thickened and expanded basals. Hence, as Dr. Carpenter remarks², "it seems clear that the extraordinary development of the highest segment of the stem into the centrodorsal basin, which is characteristic of the mature *Antedon*, is connected with the multiplication of the prehensile cirrhi which extend themselves from its dorsal surface."

At the base of the quinquelocular organ, and lying on the bottom of the centrodorsal basin, but enclosed, together with the five chambers, in the above-mentioned fibrillar envelope (N), which is probably of a nervous nature, there is, both in *Antedon* and in *Actinometra*, a succession of verticils of five triangular leaflets³. As already shown by Dr. Carpenter, there can be little doubt but that the lower ones of these mark the origins of the earlier cirrhal cords from the crinoidal axis. They increase in size from below upwards, and from the extremities of some of the upper leaflets there issue groups of three diverging cords that proceed to the cirrhi which are developed at a later period around the periphery of the centrodorsal piece.

Greeff⁴ has found the older cirrhus-cords still in connexion with these leaflets. Apparently unaware of the original existence and subsequent removal of the cirrhi corresponding to them, he drew a distinction between the vessels which they enclose, and which end close under the dorsal surface of the plate, and the vessels enclosed in the

¹ I cannot altogether confirm Müller's statement ('Gattung *Comatula*, p. 239 (3)) that the central apical portion of the centrodorsal in *Ant. Eschrichtii*, where it was formerly united to the stem, may be covered with cirrhi. In all the individuals of this species which I have examined (and they are many) there is always a small apical space quite free from cirrhi; it may not be wider than the diameter of a large cirrhus-socket, but it is always to be found. I imagine that by the expression "Da es *Antedon*-Arten giebt, bei denen auch der mittlere Theil des Centrodorsale Cirrhen trägt (*Antedon Eschrichtii* z. B.)" (Crinoideen, p. 69, note), Ludwig does not mean any thing more than that the centrodorsal is covered with cirrhi to a much greater extent than is usual in most *Comatula*, where there is generally a central space of considerable extent entirely free from cirrhi. Schlüter has also expressed his doubts respecting the accuracy of Müller's statement.

² Proceedings R. S., No. 166, 1876, p. 218.

³ These are seen in section in Pl. VIII. figs. 3, 7.

⁴ Marburg Sitzungsberichte, No. 5, 1876, p. 91.

more peripherally placed cords proceeding from the upper leaflets, which enter the later-developed cirrhi. Ludwig¹ regarded them as rudimentary structures in *Ant. rosacea*, because he found them in *Ant. Eschrichtii* to enter the more centrally placed cirrhi, which are not removed, but persist throughout life, as already mentioned. It will be evident, however, from the facts stated above, that these cirrus-cords, which end on the dorsal surface of the plate, are not rudimentary structures, but the proximal ends of more complete cords that have undergone a retrogressive metamorphosis, which in *Ant. Eschrichtii* is not carried so far as in *Ant. rosacea*.

These facts all tend to strengthen the view first expressed by Wyville Thomson, that the centrodorsal piece represents a coalesced series of the nodal stem-joints of the stalked Crinoids. In *Ant. Eschrichtii* six or even more rows of cirrus-sockets may be traced on the hemispherical surface of the "Knopf," each row corresponding to a node in the stem of *Pentacrinus*. Even in those *Actinometrae* in which only one row of sockets is visible externally, the composite character of the centrodorsal piece is indicated by the verticils of degenerate cirrus-vessels at the base of the chambered organ (Pl. VIII. figs. 3, 7), and by the partially obliterated openings on the central part of the floor of the centrodorsal cavity (Pl. V. figs. 2, 7, 14; Pl. VI. figs. 3, 8, 10, 15, 17, *u*).

Sometimes, indeed, the "Knopf" may actually assume a more or less columnar form, as in the specimen of *Ant. macrocnema* mentioned in sect. 41, and in the genus *Solanocrinus*; in both of which three or four alternating rows of cirrhi are visible. In these forms we may reasonably suppose that the columnar centrodorsal was developed by the enlargement of the uppermost stem-segment on which alternating whorls of cirrhi successively appeared, just as in *Ant. cellica* (Pl. IV. figs. 1, 6, 8), *Ant. rosacea* (fig. 14), and *Act. robusta* (Pl. V. fig. 15), but not in such numbers as to obscure the alternate arrangement (p. 69).

(§ 49) Götte², to whom we owe a series of most beautiful observations on the development of the water-vascular system and perivisceral cavity of *Comatula*, has recently questioned the accuracy of those observations of Wyville Thomson and Dr. Carpenter, according to which the uppermost of the embryonic stem-segments develops into the centrodorsal piece, and has also attacked the view that it may possibly in some cases arise from the fusion of two or more stem-segments as represented in Goldfuss's figure.

His description of its origin is as follows:—"Die Anlagen der Centrodorsalplatte sind schmale, aber doch netzförmige Skeletstreifen, welche gleichzeitig mit den Basalia an deren unteren Rändern entstehen und die obersten, noch eng zusammengedrängten Stielgliederanlagen umgeben (fig. 13). Es ist daher später, wenn diese Stelle sich verschmächtigt, nicht immer ganz leicht, jene Anlagen der Centrodorsalplatte von den obersten Stielgliedern zu unterscheiden. Beachtet man jedoch, dass sie anfangs das 5.-8. Stielglied, und nachdem diese abwärts gerückt sind, das 9., 10., 11., 12. u. s. w. umschliessen, was Thomson überhaupt nicht erwähnt, so kann man sich der Ueberzeugung

¹ Beiträge, *loc. cit.* p. 69.

² "Vergleich. Entwicklungsgesch. d. *Comatula mediterranea*." Archiv, f. mikrosk. Anat. Bd. xii. 1876, p. 597.

nicht verschliessen, das die Skeletzone, aus welcher die Centrodorsalplatte hervorgeht, unabhängig von den eigentlichen Stielgliedern, mehr in Anschluss an die Basalia und wohl als rudimentäre Wiederholungen derselben sich entwickelt. Besonders lehrreich für diese Auffassung sind die gar nicht seltenen stiellosen Missbildungen der Comatulalaven welche ich beobachtet habe. An solchen finden sich in der hinteren Körperhälfte, welche ihre ursprünglichen Dimensionen behält, statt der Stielglieder grosse netzförmige Platten welche den Raum zwischen den Basalia und dem Endknopf ausfüllen (pl. xxviii. fig. 50). Vergleicht man sie mit den viel schwächeren Anlagen der Centrodorsalplatte, so spricht die Darstellung sehr an, dass sie durch die Stielbildung in ihrer Entwicklung gehemmt und im umgekehrten Falle gefördert werden."

The only normal figure given by Götte in support of his views represents a ciliated larva, very much younger than the pentacrinoid stage, and with only eight stem-segments, over parts of the four uppermost of which are traces of a calcareous network connected with the lower end of one of the embryonic basal plates. This network, which reaches a more extensive development in the malformation represented in Götte's other figure, does not appear in any one of Wyville Thomson's figures of *Comatula* larvæ, either in the free-swimming or in the pentacrinoid condition. As his observations were carried on for four years, in each of which he followed out the development of several broods of embryos, it is impossible to suppose that he can have overlooked it had it been present in the larvæ of the British variety investigated by him. It is possible that the early-formed irregular calcareous ring, "considerably wider and broader than the ordinary rings of the stem, which lies immediately beneath the basal plates, and subsequently develops into the permanent centrodorsal plate," may represent the network figured and described by Götte. But then, as the latter says, Thomson makes no mention of its extending downwards around the other stem-segments; he gives, however, a series of figures which, taken in connexion with those of the later stage given by Dr. Carpenter, demonstrate conclusively that the above-mentioned ring *does* develop into the permanent centrodorsal piece. Götte gives no figures whatever of the pentacrinoid stage. If, as I believe to be the case, the network described by him as the rudiment of the centrodorsal piece really *does* represent the primitive centrodorsal ring of Wyville Thomson, commencing, be it remembered, as a network of small curved hollow spicules, then his observations are in complete accordance with the views of Wyville Thomson and Dr. Carpenter. Götte offers no explanation of its downward extension over the remaining stem-segments as described by him in the Mediterranean variety; and nothing of the kind is described by the two above-mentioned observers as occurring in the British variety, unless, indeed, it be the deposit of calcareous material upon the outer cylindrical surface of each stem-segment by which its diameter is increased.

It is possible that this deposit might commence to be formed at an earlier period in the Mediterranean variety than in the British one; but it is difficult to understand its downward extension from the rudiment of the centrodorsal plate as described by Götte.

(§ 50) The condition of the centrodorsal piece in *Ant. rosacea* and in *Actinometra* gives us, I believe, the means of understanding a problematical Cretaceous fossil, first

described by Goldfuss¹, of which neither he nor any subsequent observer has given a satisfactory explanation².

Glenotremites was at first placed by Goldfuss among the *Echinoidea*, and was supposed by him to have some relationship with the *Cidaridae*. It is a somewhat hemispherical body, in the centre of the flattened upper surface of which is a large round opening, called by Goldfuss the mouth. "Um den Mund liegen fünf grösse ovale Löcher und zwischen diesen fünf flache Rinnen, die sich bis zum Rande erstrecken, wo ihre Vertiefung nicht ausläuft, sondern durch einen erhabenen Saum begränzt wird. . . . Die Löcher gehen trichterförmig in die Tiefe; die Rinnen sind die Felder der Fühlergänge." These grooves were supposed by Goldfuss to be perforated by minute pores for the passage of tentacles.

The convex dorsal side of the body bears numerous sockets for the attachment of cirrhi; but Goldfuss compared these at first to the large tubercles of the *Cidaridae*. At the apex are five smaller apertures; and Goldfuss suggested that these might be respiratory and the others genital, or, more probably, that both, like the cirrus-sockets, marked the points of attachment of various kinds of spines. Subsequently, however, in his description of a second species, *G. conoidens*, he spoke of the larger apertures as ovarian openings, and recognized the resemblance between the sockets on the convex surface and the similar ones on the dorsal surface of the centrodorsal piece of *Comatula* to which the cirrhi are articulated; and he suggested that *Glenotremites* might be more nearly related to the *Comatulidae* than to the *Echinidae*, as he had at first thought. Agassiz³ adopted this view, and placed *Glenotremites* among the Crinoids, and near to *Comatula*. Like Goldfuss, he regarded the central aperture as a mouth; but the five punctated grooves radiating from it, which were supposed by Goldfuss to be provided with tentacles, were regarded by Agassiz as the points of insertion of the radii. He did not attempt to explain the five large openings on the ventral surface and the five smaller apical ones. Roemer⁴, who, like all subsequent writers, accepted the view that *Glenotremites* is the centrodorsal piece of a Crinoid allied to *Comatula*, regarded the former as "trichterförmigen Arm-Anfängen oder Mund-Winkeln," but did not understand those of the dorsal surface.

D'Orbigny⁵, who confused *Glenotremites* with *Comaster* and *Solanocrinus* under one name, *Comatula*, and Pietet⁶, who retained it as a separate genus, did not attempt to offer any further explanation of its peculiarities, and, so far as I know, Agassiz and Roemer's views have been generally accepted.

¹ Petref. German. i. p. 159, Taf. xlix. fig. 9, Taf. li. fig. 1, and ii. p. 186, Taf. clx. fig. 18.

² The following section was written early in 1877, and was in the hands of the Secretary of the Linnean Society in June of that year. The substance of a portion of it was referred to in my paper on *Pentacrinus* and *Rhizocrinus* ('Journal of Anatomy and Physiology,' Oct. 1877, p. 45). I am therefore exceedingly glad to find, from a paper published early in 1878 ("Ueber einige astylide Crinoiden," Zeitschrift der deutschen geologischen Gesellschaft, Jahrgang 1878, p. 33), that Schlüter has independently given the same explanation of *Glenotremites* as had occurred to myself. I learn from his paper that even as late as 1871 Goldfuss's original views were still held by Geinitz (Elbthalgebirge, i. 1871, p. 91).

³ Prodrôme, loc. cit. p. 289.

⁴ Lethæa Geognostica, v. p. 177.

⁵ Cours élémentaire, ii. p. 138.

⁶ Traité de Paléontologie, iv. p. 290.

That *Glenotremites* is the centrodorsal piece of a *Comatula* there can, I think, be little doubt; but I see no reason to regard the central opening as a mouth, any more than in any other of the centrodorsal pieces represented in Plates IV., V., and VI. In all these cases the centrodorsal cavity, as we know from Götte's observations, is derived from the posterior part of the right peritoneal diverticulum of the larval alimentary canal, and is therefore a part of the general body-cavity or enterocoel. It is occupied by the dorsal half of the quinquelocular organ which rises through its central opening, the so-called mouth of *Glenotremites*, and is continued as the "axial prolongation" (Pl. VIII. fig. 3, *a.p*) through the central aperture of the rosette upwards into the middle of the visceral mass.

In *Ant. rosacea* this central opening is surrounded by five depressions (Pl. IV. fig. 15, *q*), which are the dorsal terminations of the five radial diverticula of the body-cavity enclosed between the radial spout-like processes of the rosette and the internal faces of the first radials. These diverticula exist both in *Antedon* and in *Actinometra* (Pl. VIII. fig. 3, *a.r.c*), but do not always reach the ventral surface of the centrodorsal piece as in *Ant. rosacea* (Pl. IV. fig. 15). If we suppose the above-mentioned depressions (*q*) placed radially around the centre of this surface to be deepened sufficiently to become openings leading into the centrodorsal cavity, they would occupy precisely the same position as the so-called genital openings¹ of *Glenotremites*; and simply effect a more open communication between the two parts of the coelom contained in the centrodorsal piece on the one hand, and the general cavity of the calyx on the other, than when the ventral surface of the former presents only a single central opening, as in *Antedon* and *Actinometra*.

If the view advanced above be correct, it follows that the peripheral part of the areas around the "genital openings" of *Glenotremites* are the representatives of the radial

¹ These so-called "genital openings" were described by Goldfuss as "Löcher." Schlüter, however, merely speaks of them as "Gruben" (pp. 33, 42), and uses the same term for the whole cavity of the centrodorsal piece, "welche das Herz (??) oder gekammerte Organ aufnimmt," and is therefore spoken of by him as the "Herzgrube." But from his expressions, "centrale Herzgrube fünfseitig" or "zehnseitig," he obviously intends "Herzgrube" to mean nothing more than the central opening of the ventral surface of the centrodorsal, which he elsewhere calls the "Nahrungs-canal" (!), although he evidently understands its real meaning.

I cannot therefore clearly make out from Schlüter's paper whether the "Radialgruben" are real perforations or mere depressions, as in *Ant. rosacea*, which, by-the-by, is the same species as the *Antedon europæus* of Greeff, and not different from it as Schlüter seems to think. His figures (pl. i. figs. 1, 4, & 10, and pl. ii. figs. 1 & 3) appear to represent ventral openings in the centrodorsal of some fossil *Antedons*, just as described by Goldfuss in *Glenotremites*; but then he refers (p. 33) to Ludwig and Greeff (!) as describing the radial pits of *Ant. rosacea* as "sackförmige, in den Kalkscheitel eindringende blindgeschlossene Erweiterungen der Leibeshöhle."

His use of the word "blindgeschlossene" would seem to indicate that the "Radialgruben" of his specimens are really pits, closed below as in *Ant. rosacea*, and not actual openings; for in the latter case these extensions of the coelom contained within the radial axial canals would have opened into the centrodorsal cavity (also a part of the coelom), *i.e.* into that part of it which was not filled up by the chambered organ, and they could not then be accurately described as "blind." The "Radialgruben" seem, however, to have been actual perforations in *Ant. semiglobosus* (Schl. pl. i. fig. 10); for Schlüter speaks of them (p. 42) as "mit der Centralgrube verschmolzen (reichen aber tiefer hinab)," though he suggests the possibility of this being due to an accidental fracture of their central bony border. The point is one of some interest; for in no recent *Comatula* yet known are the "Radialgruben" more than simple pits, such as are generally found in *Ant. rosacea*.

areas on the ventral surface of the centrodorsal piece of *Ant. rosacea* (Pl. IV. fig. 15, *r.ar*), in each of which lies the convex dorsal surface of a single first radial.

What, then, are the five radiating punctated grooves which Agassiz and Roemer regarded as the articular surfaces for the attachment of the five arms of *Glenotremites*? I believe them to be the representatives of the basal grooves on the ventral surface of the centrodorsal piece of *Actinometra* (Pl. V. figs. 2, 7, 14, Pl. VI. figs. 3, 8, 10, 15, 17, 21, *b.g*). They are sometimes slightly developed in *Ant. rosacea*, one lying between every two of the depressions (*g*) mentioned above (Pl. IV. fig. 15), in precisely the same manner as the grooves and "genital openings" alternate on the ventral surface of *Glenotremites*.

We thus see that the peculiarities of the ventral surface of *Glenotremites* may be readily explained by what we know of the corresponding parts in *Antedon* and *Actinometra*. The apertures in the centre of the dorsal surface admit of an equally simple explanation.

The quinquelocular organ forming the dorsal termination of the axial prolongation of the adult *Comatula* consists of five chambers, arranged around a central axis which contains numerous vessels. In *Pentacrinus* there is no centrodorsal piece, but the quinquelocular organ is contained in a cavity, the sides of which are formed by the first radials above and by the basals below. Its five chambers are not closed below, but narrow considerably, and are continued down the stem as five long vessels arranged symmetrically around a central axis. The same appears to be the case in the stem of the Pentacrinoid larva of *Comatula*; for, as already mentioned, Dr. Carpenter has described a minute five-rayed perforation occupying the central portion of the dorsal surface of the recently detached *Antedon*. I regard this perforation as homologous with the five small apertures arranged around a single central one on the dorsal surface of the centrodorsal piece of *Glenotremites*, and with the similar openings on the underside of the calyx of the other stalked Crinoids—for example, of *Cupressocrinus*. The fact that the young *Antedon rosacea* has only three rows of dorsal cirrhi when liberated from its stem, while there are four or six rows on the dorsal surface of *Glenotremites*, does not at all tell against this view. Indeed Sars¹ has shown that the pentacrinoid stage persists in *Antedon Sarsii* very much longer than in *Ant. rosacea*, and he has found specimens with nearly thirty cirrhi still in a pedunculate condition, the cirrhi being placed in such close proximity to one another that any trace of a distinct order in their arrangement was entirely obliterated. The exterior of the centrodorsal piece of *Ant. Sarsii*, therefore, immediately after its liberation from the stem, would present (its size, of course, excepted) a very similar appearance to the convex dorsal surface of *Glenotremites*, viz. a central five-rayed opening, or possibly even a single opening with five others round it, the rest of the surface being covered with sockets for the articulation of the dorsal cirrhi.

(iv.) *The Pentagonal Base of the Calyx.*

(§ 51) In all the *Actinometrae* with which I am acquainted the Pentagonal Base of the calyx formed by the close mutual adhesion of the five first radials, together with the

¹ 'Crinoides vivants,' p. 57.

rosette or metamorphosed basals, differs in many points from that of *Ant. rosacea* and of all the other species of *Antedon* which I have examined.

In all of these the external or distal faces of the first radials slope at a considerable angle from above and within downwards and outwards, so that a view of the upper or ventral aspect of the radial pentagon formed by their union (Pl. IV. figs. 4, 17) shows, not only their small superior or ventral faces around the central funnel-shaped space (*F*), but also the greater part of their inclined external faces (Pl. IV. figs. 6, 8, 14), viz. the fossæ (*f*) for the attachment of the muscles between the first and second radials (Pl. IV. fig. 5, *r.m*) and the smaller ones (*h*) which lodge the interarticular ligaments, the distal opening of the central canal (*c.e*), and the large transverse articular ridge (*i*), together with more or less of the large fossa (*j*) which lodges the elastic ligament. The amount of this fossa which is visible on the ventral aspect of the radial pentagon varies in different cases.

In correspondence with this inclination of the distal faces of the first radials of *Antedon* to the vertical or dorsoventral axis of the calyx, their ventral faces are much reduced and are very small in comparison with the dorsal ones.

When the ventral surface of an isolated first radial of *Ant. rosacea* is examined (Pl. IV. fig. 12 a), it is seen to be divided into a central and a peripheral portion by two curved ridges, bending towards each other along the median line, and there separated by a furrow (*f*₁). The central portion only is the true ventral face of the radial. It slopes inwards, so as to contribute to the formation of the central funnel-shaped space (Pl. IV. fig. 17, *F*) occupying the centre of the radial pentagon, and partially filled up by a calcareous network formed by the inosculation of processes which proceed from the internal and ventral faces of the surrounding radials (Pl. IV. fig. 12 a, *c.n*). The peripheral portion, on the other hand, slopes outwards, and is, in fact, the upper or ventral half of the inclined external face (fig. 14), namely, the large vertical lamellæ in which the muscular fossæ are excavated. The upper and inner edges of these lamellæ form the curved ridges above mentioned, each of which has two limbs, one superior (fig. 12 a, *g*₁), which is horizontal, or nearly so, and forms the external boundary of the ventral face, and one inferior (*g*₂), which descends along the median line of the inclined external face towards the great transverse articular ridge (*i*); it is separated from the corresponding inner edge of the other muscular fossa by the furrow (*f*₁), which may therefore be called "intermuscular."

These curved ridges thus produce great inequalities in the ventral aspect of the radial pentagon (Pl. IV. fig. 17). The walls of its central funnel present an alternation of radiating ridges and furrows, of each of which there are ten. Five of the furrows (*c.i.f*) correspond with the divisions between the component pieces, and are therefore *interradial*, while the ridges which bound them are the superior limbs (*g*₁) of the curved ridges above mentioned, one belonging to each of the two contiguous radials. Of the other five furrows, one passes along the middle of each of the five radials, and both the ridges which bound it belong to the same piece—being, in fact, the median or descending margins (*g*₂) of the large vertical lamellæ in which the muscular fossæ (*f*) are excavated. These furrows, therefore, are simply the intermuscular furrows of the distal faces (Pl. IV.

figs. 12 a, 14, f_1), and they only appear on the ventral aspect of the radial pentagon because of the inclination of these faces to the vertical axis of the calyx. They do not appear to exist in *Ant. celtica* (Pl. IV. figs. 4, 6, 8), in which the radial muscles are far larger than in *Ant. rosacea*, so that the vertical lamellæ to which they are attached attain a much greater size. These are placed at such an angle to the dorsal portions of the distal faces of the radials that they stand up nearly vertically, and form the outer wall of the central funnel-shaped space (fig. 4, F) which leads downwards into the cavity of the centrodorsal piece. Its pentagonal rim is formed, as in *Ant. rosacea* (fig. 17), by their superior margins, two of which, belonging to contiguous radials, bound each of the five ventral interrarial furrows (*c.i.f*) which mark the angles of the pentagon. In the centre of each of the five sides of this pentagonal rim is a deep notch (fig. 6, f_2); but it does not descend on to the distal face of the corresponding radial so as to form an intermuscular furrow bounded by the median descending margins of the muscular fossæ, as in *Ant. rosacea* (figs. 14, 17, f_1); for these fossæ are so large, and extend so far towards the median line, that their inner margins unite and form a prominent vertical ridge (figs. 4, 6, g_3), which passes below into the elevated rim around the opening of the central canal (*c.c*).

(§ 52) These five notches in the sides of the pentagonal rim of the central funnel of the radial pentagon in *Ant. celtica* (Pl. IV. fig. 6, f_2) represent the points at which in *Ant. rosacea* the superior or central end of each intermuscular furrow (f_2) passes at a slight angle, due to the inclination of the distal face, into a shallow depression (figs. 12 a, 17, *c.r.f*) occupying the centre of the small ventral face of each first radial. This depression, which is much better developed in *Actinometra*, is far more distinct in some specimens of *Ant. rosacea* and *Ant. celtica* than in others, and in the dry state is barely visible. When, however, the interior of the calyx is viewed from above after the visceral mass has been removed, so as to lay open the circumvisceral cœlom, and expose the ventral aspect of the radial pentagon, the position of the ventral radial and interrarial furrows is indicated by dark lines converging towards the centre (fig. 5). These are due to the fact that the parietal layer of the peritoneum which lines the interior of the calyx descends into these depressions, so that its pigment is here more thickly aggregated than on the rest of the ventral surface. A similar slight depression lined by the pigmented peritoneum exists on the median line of the ventral face of the second and third radials and of the basal brachial segments, and it lodges the dorsal portion of the cœliac canal, which, in the intervals between the segments, sends down diverticula between the muscles connecting them, so that its course is readily traceable by the greater intensity of the pigment along the median line of the segments and between the two muscles connecting every pair (fig. 5, *r.r.f*). At the base of the arms the cœliac canal becomes broken up by connective-tissue septa into a number of intercommunicating spaces, which open freely into the general cavity of the calyx or circumvisceral cœlom. The dorsal part of the canal, however, retains its primitive relation to the skeleton and muscles, and is lodged in the furrows on the ventral faces of the radials (fig. 5).

We have already seen that the inner wall of the funnel-shaped space (F) occupying the centre of the radial pentagon is formed by the inclined ventral faces of the five first

radials (figs. 4, 12 a, 17). These are not simply plane, but are usually more or less divided up by delicate calcareous processes which extend to meet the ventral face of the rosette, and collectively form a complicated network (*c.n*), filling up the central funnel, and often partially bridging over the ventral radial furrow, so as to convert it into an incomplete canal.

At the inner margin of the ventral face this furrow turns downwards, and passes directly into a nearly vertical furrow occupying the median line of the proximal or internal face (Pl. IV. fig. 12 c, *a.r.f*), and more or less completely converted into a canal by the union of irregular processes, which extend themselves from its sides to meet the rosette. As it descends towards the dorsal face and passes between the inner raised edges of the two apertures (*a'*, *y*) of the central canal, this axial radial furrow becomes a complete canal, for its edges are closely applied to the inflected margins of one of the five radial spout-like processes of the rosette (Pl. IV. figs. 13, 16, *p*).

The five canals thus formed may hence be regarded as enclosing cavities directly continuous with the coeliac canals of the arms, in the direction of which they lie; and they thus enclose portions of the body-cavity, which I will call the radial coelom¹.

They open on the dorsal surface of the radial pentagon by five large openings (Pl. IV. fig. 16, *Q*), that correspond with five more or less distinctly marked circular depressions, which are placed radially on the ventral surface of the centrodorsal piece around the margins of its central cavity (fig. 15, *q*), and the canals end blindly in these depressions. Where these canals are enclosed by the spout-like processes of the rosette, they are completely shut off both from one another and from the dorsal extension of the coelom which occupies the central funnel-shaped space within the radial pentagon (figs. 4, 17, *F*), and passes down into the cavity of the centrodorsal piece through the central opening of the rosette (fig. 16, *r.o*). On the ventral side of the rosette, however, these radial axial canals are only partially complete, and are in free communication with the numerous plexiform spaces into which the funnel-shaped space is broken up by the above-mentioned calcareous network. The central portion of this system is very irregular; but peripherally the plexus becomes more regular, and five axial interrarial canals are traceable between the five radial ones, with which, as with the centre of the plexus, they are in free communication.

These interrarial canals are continuous with the interrarial furrows which are visible on the ventral aspect of the radial pentagon (Pl. IV. figs. 4, 17, *c.i.f*), and they enclose diverticula of the circumvisceral coelom to which the name interrarial coelom may be given. They do not descend so far towards the dorsal surface as the axial radial canals, and are not, like the latter, enclosed (normally, at any rate) by spout-like processes of the rosette; for their course towards the dorsal surface is terminated by the five short triangular processes of the rosette (figs. 3, 7, 13, 16, *o'*), which are directed towards the sutures between the five radials.

(§ 53) This is well seen in Ludwig's schematic vertical section through the body of *Ant. rosacea*², in which the radial coelom (*Lr*) is rightly represented as both longer and

¹ The general relation of these axial radial canals is precisely the same in *Actinometra* as in *Antedon*. See Pl. VIII. figs. 3, 6, *a.r.c*.

² Beitrage &c. Taf. xix. fig. 74.

larger than the interradianal cœlom (*Li*). It is also seen in Taf. xv. figs. 25, 26, on a larger scale; and in Taf. xiv. figs. 20–24 both the radial and the interradianal diverticula of the body-cavity are seen in transverse section, separate from one another towards the dorsal side, but communicating freely nearer the ventral surface, both with one another and with the centre of the plexus. In figs. 20–24, Ludwig has accidentally lettered them *L'* and *L''* respectively. This is unfortunate, as these letters are employed by him in his other figures to designate the circumvisceral and axial body-cavity; while in fig. 26 he uses the same letter *L* to designate the system of plexiform spaces occupying the central funnel of the pentagonal base, as he employs in his other figures for the intervisceral division of the body-cavity.

This hardly agrees with his text; for on p. 43 he says:—"Ueber den ersten Radialien löst sich die axiale Leibeshöhle in eine Summe von mit einander allseitig communicirenden Maschen räumen auf, welche zwischen die ersten Radialien eindringen, hier das dorsale Organ [*i. e.* axial prolongation] umgeben und endlich mit zehn blindgeschlossenen Fortsetzungen endigen, von denen fünf radiär gerichtet sind (*Li*), fünf interradianal (*Li*). Der Dorsaleanal [=cœliac canal] des Armes giebt seine Lage dicht über den Kalkgliedern und zwischen und über deren Muskelpaaren nicht auf bis er über dem ersten Radiale angekommen ist, wo er sich gleichfalls in die schon erwähnten Maschenräume auflöst. Letztere stehen also in Verbindung mit der axialen Leibeshöhle und mit den Dorsaleanalen der Arme, aber sie dehnen sich auch ferner nach oben und seitlich aus, und erfüllen hier den Raum der rings um die axiale Leibeshöhle zwischen dem Ventralcanal und dem Dorsaleanal in der radiären Hälfte, zwischen Ventralperistom und Dorsalperistom in der interradianalen Hälfte der Scheibe übrig bleibt." This space, the general perivisceral cavity, falls naturally, as Ludwig has pointed out, into two divisions—one external or circumvisceral, between the visceral mass and the body-wall, and corresponding to the "cœlom" of Dr. Carpenter; and one internal or intervisceral, surrounding the axial body-cavity (or axial canal of Dr. Carpenter), and occupying the spaces between the various coils of the alimentary canal within the visceral mass. This last corresponds to the intramural spaces and mesenteric sinuses of Dr. Carpenter¹, and not to the former only, as Ludwig appears to think (p. 55).

Of all the divisions of the body-cavity this intervisceral cœlom is the one which is least directly connected with the plexiform network between the first radials (Ludwig, figs. 26, 74, *L*) and with the cœliac canals of the arms; for it is completely separated from the latter by the visceral layer of the peritoneum, except at the minute aperture in the under surface of the visceral mass, where the axial prolongation, coming up from the quinquelocular organ through the central vacuity of the pentagonal base, enters the intervisceral cœlom contained within the visceral mass. When the latter is turned out of the calyx the intervisceral cœlom contained within it is, of course, removed at the same time, while the plexiform system of spaces between the first radials, and the continuations of the cœliac canals of the arms which terminate in it, are laid open; both of these, therefore, are manifestly portions of the general *circumvisceral* cavity surrounding the visceral mass. Ludwig, however, makes the following statement (p. 90):—"Die Hauptab-

¹ Proc. R. S. no. 166, 1876, pp. 216, 217, 225.

schnitte der Leibeshöhle in Scheibe und Armen stehen miteinander paarweise in engerer Beziehung, indem sich die axiale Leibeshöhle fortsetzt in die Ventralkanäle [subtentacular] der Arme und Pinnulae, die interviscerale in die Dorsalkanäle [coeliac] und die circumviscerale in die Genitalkanäle."

I cannot corroborate this statement except with regard to the axial body-cavity, the connexion of which with the subtentacular canals of the arms was first shown by Dr. Carpenter.

The ventral portion of the circumvisceral body-cavity, viz. the limited and much divided space between the parietal and visceral layers of the ventral peritoneum, certainly does stand in direct connexion with the genital canals of the arms; but its dorsal portion, viz. the space between the visceral mass and the skeleton of the calyx, is, as already mentioned, far more directly a continuation of the coeliac than of the genital canals. The former gradually increase in size as they approach the disk, becoming very large in the second and first arm-segments, and traversed by numerous connective-tissue bands, which are directly continuous with those of the circumvisceral space; while the genital canal remains relatively small, and is nothing more than a space in the horizontal septum separating the subtentacular and coeliac canals.

The beautiful investigations of Götte¹ have shown that the primitive coelom of the pentaeroid larva of *Antedon* consists of two parts: (1) an oral or ventral one, developed from the left peritoneal diverticulum of the primitive alimentary canal; and (2) a dorsal one, which sends a prolongation backwards into the stem, and is developed from the corresponding right peritoneal diverticulum. These divisions of the primitive coelom had been previously described by Dr. Carpenter², Metschnikoff³, and Greeff⁴, to all of whom, however, their origin was unknown. The last observer regarded the ventral division as "den vom Wassergefäßsystem und der hinteren Leibeshöhle geschiedenen ursprünglichen Blutsinus;" for he supposed it to be continuous with the cavity of the axial prolongation, which he called the "dorsoventral Gefäßstrang." Dr. Carpenter has found, however, that this structure breaks up into five branches, one of which goes to each of the primitive rays, and develops into the so-called "genital rachis" of the arms, while the oral coelom of the pentaeroid larva (the "Bloodsinus" of Greeff), sends off an extension into each of the arms as its subtentacular canal. In the direction of the radii it forms, of course, the subtentacular canals of the disk; but elsewhere, or interradially, it becomes gradually limited by the enlargement of the visceral mass, and by the formation of adhesions between its upper surface (visceral layer of the peritoneum) and the parietal layer lining the under surface of the ventral perisome; so that the ventral portion of the circumvisceral coelom enclosed between these layers, to which the primitive oral coelom gives rise, becomes very much reduced in extent. We do not yet know the precise origin of the genital canals of the arms; but it seems most probable that, like the ventral portion of the circumvisceral coelom with which they are connected in the disk, they are developed out of the lower or dorsal half of the extension into the

¹ *Op. cit.* p. 591. Taf. xxvi. fig. 19.

² *Phil. Trans. loc. cit.* p. 728; *Proc. R. S.* no. 166, p. 228.

³ "Beitr. z. Entwicklungsgesch. einiger niederen Thiere," *Bull. de l'Acad. Imp. des Sciences de St. Pétersb.* tom. xv. 1871, pp. 502-509.

⁴ *Marburg Sitzungsberichte*, 1876, No. 5, p. 89.

arms of the primitive oral cœlom—the upper or ventral portion of which gives rise to the subtentacular canals of both arms and disk.

The dorsal or aboral cœlom of the pentaerinoïd larva lies beneath the annular mesentery, and forms the dorsal half of the primitive circumvisceral cœlom, long before the alimentary canal is sufficiently convoluted to give rise to a distinct intervisceral cœlom. Like the oral cœlom it sends off radial extensions into the developing arms, but *beneath* the horizontal partition extended from the mesenteric bands, and these become the cœliac canals. Its dorsal prolongation gives rise to the cavity of the centrodorsal piece, and ultimately to the central canals of the calcareous segments. Both of these, together with the plexiform space between the first radials and the cœliac canals converging to it, are therefore, like the greater part of the circumvisceral cœlom, derived from the right peritoneal diverticulum of the primitive digestive cavity; while the left one gives rise to the subtentacular canals of the disk and arms, and to the ventral portion of the circumvisceral cœlom. The primitive distinction between the oral and the aboral cœlom of the larva, indicated by the mesenteric fold, becomes, however, gradually obliterated by the development of numerous similar septa of connective tissue, and by the growth of the alimentary canal and its consequent winding.

The axial canal, continuous above with the oral, and below with the aboral cœlom, is produced by the limitation of the central space left by the coiling of the intestine around the stomach; while the remainder of the spaces between the coils become the intervisceral cœlom, which is therefore not developed to any extent until after the cœliac canals of the rays have been extended from the primitive aboral cœlom.

(§ 54) All the species of *Antedon* do not agree with *Ant. rosacea* and *Ant. celtica* in the great inclination of the distal faces of the first radials to the vertical axis of the calyx, so that these faces enter into the composition of the ventral aspect of the radial pentagon. In a new and undescribed *Antedon* from the Philippines this inclination is very slight; and in a view of the pentagonal base from above but little more is seen than the proper ventral faces of the component radials. In this respect, therefore, forms such as these present an approximation to *Actinometra* (Pl. V. fig. 4, Pl. VI. figs. 5, 12, 23), in which the distal faces of the first radials are nearly or quite vertical, and do not at all enter into the composition of the ventral aspect of the pentagonal base, which consists simply and entirely of the five adjacent ventral faces of the component radials.

In *Ant. rosacea* (Pl. IV. fig. 17) these form a five-pointed star, the central surface of which slopes rapidly downwards and inwards as the inner wall of the central funnel (*F*); while its five rays correspond with the divisions between the component radials, and are bounded by the large ridges which form the upper and outer margins of the two adjacent muscular fossæ (*f*) of every pair of contiguous radials (Pl. IV. fig. 12 a, *g*₁). The sutures between the radials are marked by slight depressions of their ventral surfaces, and these are completed by the ridges at their sides into the ventral interrarial furrows already described (Pl. IV. figs. 4, 17, *v.i.f*); they occupy the five rays of the star, and alternate with the five shallow depressions (*v.r.f*) lying in the centre of the ventral faces of the first radials. In *Actinometra*, as will be seen further on, these depressions become very marked; but in *Ant. rosacea* they are hardly deep enough to be called furrows, and are

generally more or less concealed by the calcareous network occupying the opening of the central funnel. They are the ventral continuations of the five canals enclosed by the radial spout-like processes of the rosette, and they pass downwards and outwards in the reentering angles of the star into the intermuscular furrows on the distal faces of the component radials (Pl. IV. figs. 12 a, 14, 17, *f*₁). These reentering angles, which are bounded by the superior margins of the two muscular fossæ of each radial, are more open in *Ant. cellica* (fig. 4) than in *Ant. rosacea* (fig. 17), so that the rim of the central funnel becomes more nearly pentagonal, having somewhat the shape of a *Goniaster*. This is still more marked in *Ant. Eschrichtii*, while in *Actinometra* it becomes a regular pentagon (Pl. V. fig. 4, Pl. VI. figs. 5, 12, 23).

In correspondence with the nearly vertical position of the distal faces of the radials in *Actinometra*, their ventral faces, which in *Ant. rosacea* and *Ant. cellica* have a very steep inward slope, occupy a nearly horizontal position, sloping but very gently inwards towards the central space, so that the opening of the funnel becomes widely expanded. Its inner walls, formed by the adjacent ventral faces of the contiguous radials, which are relatively much larger than in *Antedon*, are generally more or less sculptured out into a series of radiating ridges and furrows, the number and distribution of which vary in different species.

(§ 55) In *Act. pectinata* the ventral surface of each first radial (Pl. V. fig. 9 a) is nearly as even and regular as that of *Ant. cellica* (Pl. IV. fig. 4) or *Ant. rosacea* (Pl. IV. figs. 12 a, 17), and in some cases it may be even more so. It is, however, both absolutely and relatively larger, as it is not encroached upon by the distal face, which stands nearly at right angles to it, and the furrow (*v.r.f*) occupying its median line is far more distinct than in either of the two species of *Antedon*. These points are clearly seen in a comparison of figs. 5 on Plates IV. and V., which represent the ventral aspect of the calyx, as seen after removal of the visceral mass, in *Ant. cellica* and *Act. pectinata* respectively. In the former (Pl. IV. fig. 5) the second and third radials and the bases of the arms are at a higher level than the pentagon of the first radials, owing to the inclination of the distal articular faces of the latter; but in *Actinometra* (Pl. V. fig. 5) the whole ventral surface of the calyx is in one horizontal plane, as the opposed articular faces of the first and second radials are parallel to the vertical axis of the calyx, and not more or less inclined to it, as in *Antedon*.

We have seen that in *Ant. rosacea* the lateral margins of the ventral faces of the first radials (Pl. IV. figs. 12 a, 17) are somewhat depressed, so that when two pieces are in contact a shallow interrarial groove marks their line of union on the ventral side. It is deepened into a furrow (*v.i.f*) by the elevation at its sides of the ridges forming the superior margins of the muscular fossæ of the inclined distal face. This interrarial depression also occurs in *Act. pectinata* (Pl. V. figs. 5, 9 a &c.); but as the vertical lamellæ (fig. 9 c, *g*) in which the muscular fossæ are excavated are very small, and do not extend inwards so as to encroach upon the ventral face, there are no ridges at the sides of this interrarial depression (fig. 5, *v.i.f*) converting it into a deep furrow as in *Ant. rosacea* (Pl. IV. fig. 17), so that it is far less conspicuous than the corresponding radial furrow (Pl. V. figs. 5, 9 a, *v.r.f*).

The ventral aspect of the radial pentagon of *Act. solaris* (Pl. V. fig. 4) consists almost entirely of the conjoint ventral faces of its component pieces; the distal faces are very slightly inclined to the vertical axis of the calyx, so that portions of the fossæ lodging the radial muscles and the interarticular ligaments become visible (Pl. V. fig. 4, *f*, *h*). The ridges (*g*₁) which bound the muscular fossæ superiorly form by their apposition the outer margin of the ventral surface of the pentagonal base, which is interrupted at ten points, five being radial and five interrarial. The former, which lie between the two muscular lamellæ of each radial, indicate the union of the intermuscular furrows of the distal face with the ventral radial furrow occupying the median line of the superior face (Pl. V. fig. 4, *c.r.f*); while the latter, which are at the angles of the pentagon, are the outer ends of the ventral interrarial furrows (*c.i.f*) corresponding with the sutures between every two contiguous radials, the superolateral edges of which are slightly cut away, so that by the apposition of every two pieces an interrarial furrow is formed.

These interrarial furrows, like the radial ones, slope gently inwards towards the centre. The two sets, as soon as they pass into the axial furrows on the internal faces, become respectively converted into five radial and five interrarial axial canals by the union with one another in successive pairs of small processes extending from the intervals between them towards the central calcareous network (Pl. V. fig. 4, *c.n*). These processes are the central ends of ridges which are developed on the two halves of the ventral surface of each first radial, between its median furrow (*c.r.f*) and its lateral margins. The small and irregular furrows between them usually converge towards the radial or interrarial furrows, where they begin to descend into the corresponding axial canals; but in two cases (Pl. V. fig. 4, *x*) they are also converted into canals by the small bridge-like processes above mentioned. These intermediate canals, like the normal radial and interrarial ones, are in free communication with the rest of the spaces in the calcareous network, just as in *Ant. rosacea*; but the radial ones do not extend so far towards the dorsal surface of the pentagonal base as in this species, as will be seen when we come to study its dorsal aspect (Pl. V. fig. 3).

(§ 56) In *Act. robusta* (Pl. V. fig. 11) this sculpturing or development of ridges and furrows on the ventral faces of the first radials is carried much further than in *Act. solaris*. The muscular fossæ (*f*) are also somewhat deeper, and the median radial furrows which proceed inwards from the intervals between their superior margins (*g*₁) along the ventral faces of the radials are broken up very soon into a number of small irregular furrows; all converge, however, towards the centre, by the development of numerous ridges of a similar nature to those rising from the lateral halves of the ventral faces in *Act. solaris*.

These ridges completely obliterate all traces of any regularity in the passage of the radial furrows into the central calcareous network (*c.n*), as was so marked in *Act. solaris* (fig. 4). The interrarial furrows, too, are not particularly distinct, as the ventral surfaces of the radials fall away but little towards their lateral margins. Towards the centre, however, they become more distinct, and are bridged over by processes extended from the above-mentioned ridges, so that they pass downwards as canals into the system of plexiform spaces occupying the central funnel of the pentagonal base. The position of

one of these axial interrarial canals is indicated, in Pl. V. fig. 11, by a brown bristle (II) which has been passed along it.

In the type of *Act. polymorpha* the distal faces of the radial pentagon are placed somewhat more vertically than in *Act. solaris*, so that scarcely any trace of the muscular fossæ is to be seen on its ventral aspect (Pl. VI. fig. 5). This is still more the case in var. 4 (fig. 23), in which the ventral aspect of the radial pentagon exhibits nothing but the extremely sculptured and inclined ventral faces of its component pieces; it is divided into a very large number of ridges and furrows, nearly every one of the latter having a canalicular opening into the central network (*c.n.*). The radial furrows are thus entirely obliterated; and as there is no corresponding intermuscular furrow on the distal face (as in *Ant. celtica*, Pl. IV. figs. 4, 6), there is nothing to indicate their position on the outer margin of the radial pentagon. But the interrarial furrows (Pl. VI. fig. 12, *v.i.f.*) are readily distinguishable by their being somewhat deeper and straighter than the secondary radial furrows. This is also the case, but to a less extent, in the type (fig. 5) and in varieties 2 and 3; but var. 1 is somewhat different, and in this respect approaches *Antedon rosacea* more than any other *Actinometra* with which I am acquainted. The distal faces of the radial pentagon (Pl. VI. fig. 12) are perceptibly inclined to the vertical axis of the calyx, so that even the opening of the central canal (*c.c.*) appears on its ventral aspect. The muscular fossæ (*f.*) are deep, so that their superior margins project inwards and encroach somewhat on the ventral faces; and the median furrows of the latter are tolerably deep, their outer extremities passing over into the intermuscular furrows (*f₁*) of the distal faces. The interrarial furrows between the elevated lateral halves of the ventral faces (Pl. VI. fig. 12, *v.i.f.*) are also deep, but the ventral faces are plain and scarcely at all sculptured, so that both radial and interrarial furrows pass down with tolerable regularity into the peripheral axial canals of the central calcareous network (*c.n.*).

(§ 57) In *Antedon rosacea*, as we have already seen, the five radial diverticula of the cœlom terminate blindly on the ventral surface of the centrodorsal piece in five depressions (Pl. IV. fig. 15, *q*), which are disposed around the opening of its central cavity (*cd.c.*). In correspondence with these depressions the dorsal surface of the pentagonal base presents five large openings (Pl. IV. fig. 16, *Q*), disposed in like manner around the margins of its central space. These openings are the dorsal terminations of the five radial axial canals, and are formed by the application of the five radial spout-like processes of the rosette (figs. 13, 16, *p*) to the inflected margins of the two openings (*x'*, *y*) on the internal face of each first radial (fig. 12 *c*), through which the secondary basal cords (Λ_2 , Υ_1) pass on their course from the fibrous mass enveloping the quinquelocular organ to the circular commissure contained within the radial pentagon (compare Pl. VIII. fig. 2).

The existence of these five large openings (Pl. IV. fig. 16, *Q*) is due to the fact that the dorsal face of each first radial presents a deep notch in the centre of its inner margin (fig. 12 *b*, *Q'*); this notch indicates the continuation towards the dorsal surface of the radial axial furrow on the internal face (fig. 12 *c*, *a.r.f.*); and when this furrow becomes converted into a canal by the application to its inflected edges of one of the spout-like processes of the rosette, the notch on the dorsal face also becomes converted into a cir-

cular opening. So far as I know, these openings are tolerably constant on the dorsal surface of the radial pentagon of *Ant. rosacea*; but the five depressions corresponding to them on the ventral surface of the centrodorsal piece are very variable in the distinctness of their development; and Dr. Carpenter has found that in some cases they may be absent altogether¹.

This last condition, in which there are no radial depressions (*q*) on the ventral surface of the centrodorsal piece, appears to be the normal one in *Ant. celtica*, in which I have rarely found any traces of such depressions (Pl. IV. fig. 2). The margin of the central opening is usually almost circular, though sometimes bluntly stellate as in *Ant. rosacea* (fig. 15); at the same time, the five openings (*Q*) upon the dorsal surface of the radial pentagon are but little developed or even entirely absent. In Pl. IV. figs. 3, 7, they are represented as present in the small variety and absent in the large one; but I have sometimes found exactly the reverse to be the case.

We shall find the same variability in the presence or absence of these openings in *Actinometra*, not only in different individuals of the same species, but in the same individual. This fact shows that too much reliance must not be placed on the presence, absence, or difference in size of similar openings in the calyx of the fossil Crinoids (the interrarial "Lücken" in *Cupressocrinus*, for example) as characters of any systematic value. The absence or slight development of these openings in *Ant. celtica* is principally due to the fact that the inner margin of the dorsal surface of the first radials is not notched but straight, the radial axial furrow not being continued so far towards the dorsal surface as in *Ant. rosacea*; and also that processes grow inwards from the two sides of the dorsal end of each of the five spout-like rays of the rosette, so that the lumen of the canal it encloses becomes much diminished; while in some cases similar processes are put forward from the margin of the first radial, which unite with the others so completely as entirely to obliterate the lumen of the radial axial canal, and thus form its dorsal boundary.

(§ 58) The dorsal aspect of the pentagonal base of the calyx of *Actinometra* is by no

¹ Schlüter (*op. cit.* p. 37) has proposed a division of the (fossil) *Comatulæ* into two groups, characterized as follows:—(1) Centrodorsal with no radial pits and a round "Nahrungscanal" (central opening); and (2) Centrodorsal with radial pits and a quinquepartite opening.

These characters, however, are far too uncertain to be of any systematic value. For example, Schlüter himself notes the absence of the "Radialgruben" in his own specimen of *Solanocrinus scrobiculatus*, while they were present in one examined by Quenstedt (*Echinodermen*, p. 179). I have some specimens of *Ant. celtica* answering to the first, and others to the second of the above definitions; and although most specimens of *Ant. rosacea* would be classed in group (2), yet individuals with a pentagonal or even quinquepartite opening, but no radial pits, are not uncommon. This last condition is very common among the 'Challenger' *Antedons*. In fact, the radial pits of *Ant. rosacea* and *Ant. celtica* are peculiar to these species, and not always present even in them. In no other recent *Comatula* have I found any thing exactly like them. They are not parts of the generally concave surface of each radial area, but have distinct peripheral borders marking them off from these surfaces, and corresponding to the openings of the radial axial canals enclosed within the spout-like processes of the rosette. In *Act. pectinata*, *Act. polyacrotus*, var. 2, and in a new 'Challenger' *Antedon* there is a distinct pit at the central end of each radial area, which is merely the deepened termination of a depression occupying its median line. Its nature (secs. 45 & 61) is essentially the same as that of the radial pits of *Ant. rosacea*, but its appearance is very different. Hence I cannot corroborate Schlüter's statement that "Manche Arten" possess "Radialgruben." He only describes them in 5 out of his 11 fossil species, besides the *Solanocrinus scrobiculatus* examined by Quenstedt.

means of such a simple nature as it is in *Ant. cellica* (Pl. IV. figs. 3, 7), where it consists solely of the five adjacent dorsal surfaces of the component radials. These are somewhat elevated in the centre but fall away towards the sides, where they are separated from one another by slight furrows, corresponding in position with the five inter-radial ridges on the ventral surface of the subjacent centrodorsal piece (Pl. IV. fig. 2, *i.e.*). In *Actinometra*, however, these dorsal interrarial furrows are very marked; but they are not usually visible on the dorsal aspect of the radial pentagon, as they are occupied by five long processes which radiate outwards from the angles of the central vacuity in which the rosette lies (Pl. V. fig. 3; Pl. VI. figs. 4, 9, 13, 24, *S*).

The presence of these rays of the basal star introduces an element of considerable complexity into the dorsal aspect of the pentagonal base of *Actinometra*; and its nature will be best understood if we commence with the study of its component pieces in the large *Act. robusta*. The dorsal face of each first radial of this species (Pl. V. fig. 12) is slightly convex, so as to fit into the somewhat depressed radial area corresponding to it on the ventral surface of the centrodorsal piece (Pl. V. fig. 14, *r.ar*). The centre of its inner margin is, as in *Ant. rosacea*, marked by a deep notch, which indicates the position of the axial radial furrow occupying the median line of the internal face (fig. 10, *a.r.f.*). The latter is converted into a canal by the union of its inflected edges with those of one of the radial spout-like processes of the rosette (figs. 12, 13, *p*), in the manner already described by Dr. Carpenter for *Ant. rosacea*.

The central notch on the inner margin of the dorsal face thus becomes a round opening (fig. 12, *Q*), similar to that seen in *Ant. rosacea* (Pl. IV. fig. 16, *Q*). A bristle passed through this opening towards the ventral side, therefore, will follow the course of one of the axial radial canals, in which its lower end is concealed by the spout-like radial process of the rosette (Pl. V. figs. 12, 13, *I*). On the ventral side of the rosette the radial axial canal is incomplete, as the furrow on the internal face is only partially bridged over by the calcareous processes which extend themselves from its sides to meet the rosette; the bristle which lies in the furrow is therefore visible here and there through the openings in the network (*c.n*) formed by the inosculation of these processes (figs. 10, 13, *I*). This is best seen in fig. 13, which is a view of two radials from within, together with that portion of the rosette which corresponds to and is united with them; and also in fig. 10, which represents the internal face of a single radial, from which the portions of the rosette that are normally united with it have been removed, so that the whole of the internal face is exposed. The bristle *I* is seen to lie in the deep furrow between the two raised edges of the apertures (*x'*, *y*) of the central canal, and to pass upwards under the network extending from the ventral half of the internal face, where it follows the course of the axial radial furrow and emerges on the ventral aspect of the radial. The furrow in which it lies is here continued into the numerous irregular furrows of the ventral face which converge towards the centre of its inner margin (Pl. V. fig. 11).

Just above the dorsal surface of the radial, the axial furrow occupying the median line of its internal face gives off a large horizontal diverticulum into the substance of its calcareous tissue, which extends outwards for some distance between the central canal and the dorsal surface of the radial (fig. 10, *r.c'*); and, like the axial furrow or canal as

it is in the natural condition when the rosette is *in situ*, encloses a dorsal extension of the body-cavity or coelom. I have seen no trace of these diverticula in any other species of *Comatula* that I have yet examined; but they are very large and well marked in each of the five first radials in *Act. robusta*.

(§ 59) The furrows which occupy the median line of the ventral and internal faces of the first radials thus terminate in *Act. robusta* (Pl. V. fig. 12) precisely as in *Ant. rosacea* (Pl. IV. fig. 16), by five large openings (*Q*) on the dorsal aspect of the radial pentagon, which are closed in the natural condition by the ventral surface of the centrodorsal plate on which the radial pentagon rests.

In *Ant. rosacea* the course of the slightly marked interrarial furrows which pass down from the ventral aspect of the radial pentagon into the peripheral portion of the central calcareous network is terminated inferiorly by the five triangular interrarial processes of the rosette; for the apices of these processes unite with the two members of every pair of contiguous radials, just between the two adjacent apertures of their central canals (Pl. IV. figs. 3, 7, 16, *o'*).

In *Actinometra*, however, the interrarial furrows both are more marked on the ventral surface of the radial pentagon, and, like the radial ones, become converted into canals, terminating by five openings upon its dorsal aspect.

In *Ant. rosacea* the edge which separates the lateral and dorsal faces of each first radial is tolerably sharp and straight (Pl. IV. fig. 12 b, c); but in *Act. robusta* it is somewhat truncated (Pl. V. figs. 10, 12, 13), so that when the lateral faces of two radials are in apposition a deep interrarial furrow appears along the line of union of their dorsal surfaces (fig. 12, *a, i, f*). In the middle of the inner margin of the floor of this furrow is a notch similar to that marking the centre of the inner margin of the dorsal face of each single radial, both in this species and in *Ant. rosacea* (Pl. IV. fig. 12 b, *Q'*), except that two radials take part in its formation instead of only one. This notch marks the continuation towards the dorsal surface of an interrarial furrow from the ventral aspect of the pentagonal base.

The edges between the internal and lateral faces of each first radial are truncated in the same way as those between the dorsal and lateral faces (Pl. V. figs. 10, 13). In the natural condition, therefore, when the lateral faces of all the radials are in apposition with one another in pairs, there are five axial interrarial furrows alternating with the radial ones, which occupy the median lines of the internal faces. The ventral portions of these, as of the axial radial furrows, are partially bridged over by the inosculating calcareous processes which extend themselves towards the ventral aspect of the rosette from the internal faces of the five first radials, so that a bristle passed along their course is only partially visible (Pl. V. fig. 13, II).

These superior portions of the axial interrarial furrows are in free communication, both laterally, with the radial furrows occupying the intervals between them, and centrally with the remaining spaces of the calcareous network, of which system these two sets of furrows form the peripheral part. Inferiorly, *i. e.* towards the dorsal surface, each of these axial interrarial furrows passes between the two outer lips of the adjacent apertures (*x, x'*) of the central canals of two contiguous radials along the line of union of

which the interrarial furrow is situated. The outer lips of these apertures, like the inner ones (Pl. V. fig. 10), are raised and applied to the similarly inflected edges of the five spout-like *interrarial* processes of the rosette, so that the furrow lying between the apertures becomes converted into a complete canal. A bristle, therefore, which lies in the course of this furrow (Pl. V. figs. 12, 13, II) is concealed by the interrarial process (*o*) of the rosette. The dorsal end of the latter unites with the margins of the notch described above at the central end of the dorsal interrarial furrow, so as to produce a roundish interrarial opening on the dorsal aspect of the pentagonal base, through which the bristle passed along the axial interrarial furrow emerges from its concealment beneath the interrarial process of the rosette (figs. 12, 13, II). The manner in which these openings are closed in the natural condition by the central ends of the rays of the basal star will be best described further on.

(§ 60) In the condition and relative inclination of their dorsal and internal faces, the first radials of *Act. robusta* are more like those of *Ant. rosacea* than those of any other of the various *Actinometrae* which I have examined. In *Ant. rosacea* the ventral surface of the centrodorsal piece (Pl. IV. fig. 15) is almost flat, as the five radial areas into which it is divided lie nearly in a horizontal plane; and the corresponding dorsal surfaces of the five first radials are likewise horizontal, and form an angle of but little more than 90° with the internal faces (Pl. IV. fig. 12 b, c). In *Act. robusta* this angle becomes more obtuse, so that the dorsal surfaces of the radials are somewhat inclined to the horizontal plane (Pl. V. figs. 10, 13); and, in correspondence with this, the radial areas on the ventral surface of the centrodorsal (fig. 11, *var.*) have a slight downward and outward slope between their central and peripheral margins, so that the whole surface rises very gradually from the circumference towards the centre.

This is also the case in *Act. solaris*, in which the dorsal surface of the radial pentagon slopes slightly downwards from its margin towards the opening of the central vacuity in which the rosette is situated (Pl. V. fig. 3), so as to correspond with the gradual elevation between the circumference and centre of the ventral surface of the centrodorsal on which it rests (fig. 2).

Act. solaris also agrees with *Act. robusta* in the fact that the sides of the dorsal interrarial furrow (fig. 3, *a.i.f*) which is produced by the truncation of the adjacent superolateral edges of two contiguous radials are simple and straight, and not raised into leaf-like folds, as in *Act. pectinata* (fig. 9 b) and *Act. polymorpha* (Pl. VI. figs. 9, 13, 24; Pl. VII. figs. 1 d, 4 d, b.g).

In *Act. solaris* there are none of the apertures which occur in *Ant. rosacea* and *Act. robusta*, by which the axial radial canals open upon the dorsal surface of the radial pentagon (Pl. IV. fig. 16, and Pl. V. fig. 12, *Q*). We have already seen (sect. 57) that they may be absent in *Ant. cellica* (Pl. IV. fig. 3); and their absence in *Act. solaris* is due to the same cause as in this case, viz. to the want of a central notch on the inner margin of the dorsal face of each first radial, and to the obliteration of the lumen of each canal by the ingrowth of calcareous tissue from its sides.

In the closely allied *Act. pectinata*, however, these openings may be present (and not improbably also in other specimens of *Act. solaris* than the one which I have examined);

for the inner margin of the dorsal face of each first radial exhibits a slight median notch (Pl. V. fig. 9 b, *Q'*), though it is by no means so distinct as in *Ant. rosacea* (Pl. IV. figs. 12 b, 16) and *Act. robusta* (Pl. V. fig. 12).

In this species too the ventral surface of the centrodorsal plate (Pl. V. fig. 7) rises very perceptibly from its circumference towards its centre; and the dorsal face of each first radial is very considerably inclined to the vertical internal face, the angle between the two almost reaching 135° (Pl. V. fig. 9 b, c). Consequently, when the radial is viewed from its dorsal side, the large projecting lips of the two apertures of its central canal are seen below the central or inner edge of the inclined dorsal face (fig. 9 b, *x'*, *y*). These are not seen in a similar view of a first radial of *Ant. rosacea*, in which the inclination of the dorsal to the internal face is very little over 90° (Pl. IV. fig. 12 b, c).

(§ 61) In *Ant. rosacea* and *Act. robusta* the slight convexities of the dorsal surfaces of the first radials fit into the correspondingly slight concavities in the centre of the radial areas on the ventral surface of the centrodorsal piece (Pl. IV. figs. 2, 3, 15, 16; Pl. V. figs. 12, 14). In *Act. pectinata*, however, these areas are occupied by median depressions, increasing somewhat in depth from their peripheral to their central ends (Pl. V. fig. 7, *r.ar*); but the dorsal faces of the first radials do not exhibit corresponding ridges, for they have similar median depressions, which are also deepest at their central ends (Pl. V. fig. 9 b, c, *d.r.f*).

When, therefore, the dorsal surface of the radial pentagon and the ventral surface of the centrodorsal piece are in their normal state of apposition, they are separated from one another along the median lines of the five radials by five cavities or radial spaces; these are largest at their central ends, and extend in a peripheral direction to open externally by five small openings situated on the margin of the small centrodorsal piece, beneath the radial pentagon which rests upon and extends considerably beyond it.

These "radial spaces" are seen in section in Pl. VIII. figs. 5-8, which represent parts of four sections selected out of a series that was cut through a decalcified calyx of *Act. pectinata*.

The section represented in fig. 5 was cut across the angle of two radials (*A*, *B*) near the edge of the centrodorsal piece, and the open outer ends of the radial spaces are cut somewhat obliquely (*r.s*). Fig. 6 represents a section much nearer the centre, and the closed inner ends of the radial spaces are seen just beneath the lower ends of the axial radial canals (*a.r.c*), but not communicating with them. In fig. 7 two other spaces are seen, cut almost longitudinally, as the section is one from the other side of the centre, through the radii, *C* & *E*, almost in the direction of their axial nervous cords (*n*), beneath which are the radial spaces (*r.s*) between the dorsal surfaces of the first radials and the ventral surface of the centrodorsal piece. Lastly, in fig. 8, which represents a section still farther from the centre, and cut transversely to the direction of radius *D*, the closed central end of the corresponding radial space is seen, as in fig. 7, on the dorsal side of the axial nervous cord (*n*); at either side of it (*s*) is the expanded lower end of one of the axial interradiar canals seen in fig. 7 (*a.i.c*).

The external medium which occupies these radial spaces between the radial pentagon and the centrodorsal piece is only shut off from the dorsal portion of the calom en-

closed within the radial pentagon, and from the centrodorsal cœlom, by the small bony bars at their expanded central ends, which form the thickened inner or central edges of the dorsal faces of the first radials (Pl. V. fig. 9 b, c.) They are slightly developed in one of the varieties of *Act. polymorpha*, in which the radial areas of the small centrodorsal piece (Pl. VI. fig. 17, *r.ar*) and the corresponding dorsal faces of the first radials (Pl. VII. fig. 4 a, d) both exhibit median depressions, which gradually increase in depth from their peripheral to their central ends. In both these cases the centrodorsal piece is relatively very small and by no means conceals the first radials, while its ventral surface rises very considerably from the circumference towards the centre (Pl. V. fig. 7, and Pl. VI. fig. 17). The meaning of these radial spaces is to me quite obscure. In no other *Comatula* have I found any thing at all comparable to them except in *Act. robusta*, where the axial radial canals give off horizontal diverticula (Pl. V. fig. 10, *r.c'*), which extend outwards in a peripheral direction in the substance of each first radial just beneath its dorsal surface. These, enclosing diverticula of the dorsal portion of the cœlom, are, of course, in indirect communication with the external medium, while the radial spaces in *Act. pectinata* are altogether outside the substance of the first radials, communicate directly with the exterior, and are completely shut off from the dorsal cœlom. There is, therefore, scarcely any resemblance between the two sets of cavities, although they occupy very nearly similar positions, *i. e.* between the centrodorsal piece and the whole or the greater part of the mass of the first radials.

In some species of the fossil *Apiocrinus*, however, cavities similar to the radial spaces in *Act. pectinata* appear to exist between every pair of contiguous basals and the first radial, which rests upon them and alternates with them in position. As the basal circlet is generally regarded as comparable to a stem-segment, it is evident that the positions of these cavities in *Act. pectinata* and in *Apiocrinus* respectively are homologous with one another. In *Apiocrinus rotundus* five lateral openings were discovered by Miller¹ on the circumference of the body, "in or between the lateral surfaces of the joints of the pelvis (basals) and the insertion of the first costal (radial) joints," which in one case he thought he was able to trace as a canal or perforation "passing through the joint of the pelvis into the space between it and the costal joints, extending perhaps thence into the perivisceral cavity" (*i. e.* into the dorsal division of the body-cavity).

Miller supposed these to be the openings of oviducts leading to an ovary situated in this dorsal cœlom, just in the same manner as the five openings on the ventral surface of the centrodorsal piece of *Glenotremites* were (till lately) regarded as genital openings, although the genital glands of all the recent Crinoids with which we are acquainted are situated in the arms and pinnules.

Similar openings to those seen by Miller in *Ap. rotundus* have been described in *Ap. obconicus* by Goldfuss², who also supposed them to lead into the body-cavity. This is, however, certainly not the case with the homologous openings in *Act. pectinata*.

The interarticular pores in the upper part of the stem of *Pentacrinus* are also homologous with the external openings of the radial spaces in *Act. pectinata*. They are the

¹ *Op. cit.* p. 31.

² Petref. German. p. 187. Taf. vii. fig. 5, a, b, c.

openings of spaces between the successive segments, which are similarly situated, with regard to the radial symmetry of the animal, to the radial spaces in *Act. pectinata*, viz., in the direction of the radii; and they are produced in the same way, by the apposition of two grooves radiating outwards from the centre of each stem-segment, which are largest at their central ends and shallowest towards the periphery.

(§ 62) In *Ant. rosacea* and *celtica* (Pl. IV. figs. 3, 7, 16), and in *Act. robusta* and *solaris* (Pl. V. figs. 3, 10, 12, 13), the sides of the interrarial furrows (*d.i.f*) on the dorsal surface of the radial pentagon are simple and straight; but in *Act. pectinata* that portion of the dorsal surface of each first radial which is next to its truncated lateral edge is raised into a sort of curved ridge or fold (Pl. V. fig. 12 b, *b.f*), so that in the natural condition of mutual apposition of the five first radials the dorsal interrarial furrows become somewhat lancet-shaped. They correspond in position with the basal grooves on the ventral surface of the subjacent centrodorsal piece (Pl. V. fig. 7, *b.g*), and in the cavity formed by the apposition of the edges of these two grooves lie, as will be subsequently seen, the five rays of the basal star.

The first radials of *Act. polymorpha* are very similar to those of *Act. pectinata*. Those of variety 1 (Pl. VI. fig. 12) are like those of the type (Pl. VII. fig. 1), except in the simpler condition of their ventral surface, which is far less marked by secondary ridges and furrows than is the case in the type (Pl. VI. fig. 5). In the other three varieties, the first radials of which resemble one another very closely, this sculpturing of the ventral surface is even more marked than in the type (Pl. VI. fig. 23; Pl. VII. fig. 4c). The angle between the dorsal and internal faces is considerably less in the type (Pl. VII. fig. 1 a,d) and in var. 1 than in varieties 2, 3, and 4, the first of which resembles *Act. pectinata* in the presence of a median depression of the dorsal face (Pl. VII. fig. 4 a,d, *d.r.f*), which corresponds with a similar depression along the median line of the radial areas of the small centrodorsal piece (Pl. VI. fig. 17, *r.ar*). This dorsal interrarial furrow does not exist in varieties 3 and 4, nor in var. 1 (fig. 13), while there is a trace of it in some specimens of the type, but not in others (figs. 4, 9). In like manner the development of the openings of the radial axial canals on the dorsal surface of the pentagonal base, which are so large in *Ant. rosacea* and in *Act. robusta* (Pl. IV. fig. 16; Pl. V. fig. 12, *Q*), is in *Act. polymorpha* extremely variable. In two specimens of the type (Pl. VI. figs. 4, 11) they are entirely absent, as in *Act. solaris* (Pl. V. fig. 3); in another the inner margin of the dorsal face of each first radial exhibits a slight median notch (Pl. VI. fig. 9; Pl. VII. fig. 1 a, *Q'*), which would be completed into an opening by the apposition to it of the end of one of the radial spout-like processes of the rosette.

In variety 1 this notch is fairly marked, and five small openings are consequently visible around the central vacuity, on the dorsal surface of the pentagonal base (Pl. VI. fig. 10, *Q*). In varieties 2 (Pl. VII. fig. 4a) and 3 it is somewhat more distinct; and in var. 4 it exists in three of the first radials, but not in the other two, so that there are only three openings on the dorsal surface of the pentagonal base (Pl. VI. fig. 24, *Q*).

The extent to which the basal folds are developed at the sides of the dorsal interrarial furrows is also very variable in *Act. polymorpha*. We have seen that, although

absent in *Act. solaris* (Pl. V. fig. 3), they are well marked in the closely allied *Act. pectinata* (Pl. V. fig. 9b, *b.f.*). In two specimens of the type of *Act. polymorpha* (Pl. VI. figs. 4, 11) they are absent altogether, while in a third they are very well marked (fig. 9, *b.f.*), as also in each of the varieties, three of which are represented in Pl. VI. figs. 13, 24, and Pl. VII. fig. 4a. In all these cases the borders of the interrarial furrows on the dorsal surface of the pentagonal base, which are produced by the apposition of the truncated superolateral edges of every pair of contiguous radials, assume a leaf-like appearance, owing to the presence of the folds at their sides. The precise shape of these leaves, which is different in the type and in all the four varieties, corresponds very closely with the shape of the basal grooves on the ventral surface of the centrodorsal piece, with which they also correspond in position. They further resemble them in the fact that they are entirely devoid of the pigment which is so abundant on the other parts of the surfaces of the radial pentagon and centrodorsal piece; so that when these last are separated from one another, the dorsal interrarial furrows on the pentagonal base, like the basal furrows on the centrodorsal piece, stand out sharp and distinct as five white leaflets on a dark-brown background. They are best marked in var. 4 (Pl. VI. fig. 24, *b.f.*), in which the basal folds of every pair of contiguous radials are rather widely separated from each other about the middle of their length. This is also the case, though to a less extent, in var. 1 (fig. 13), where, as in var. 4, the dorsal interrarial furrows correspond very closely in shape with the basal grooves on the centrodorsal piece (fig. 15).

This is particularly distinct in the specimen of the type represented in Pl. VI. figs. 8, 9, in which one of the basal grooves is much shorter than the rest, and does not reach the margin of the centrodorsal piece. The basal folds at the sides of the dorsal interrarial furrow corresponding to this aborted groove are also imperfectly developed, so that the borders of its outer end are simple and straight; as they are throughout the whole course of the furrows in *Act. solaris* (Pl. V. fig. 3) and *Act. robusta* (Pl. V. fig. 12).

This last condition may also occur in the type of *Act. polymorpha* (Pl. VI. figs. 4, 11); and in correspondence with it the basal grooves on the centrodorsal piece are simple and almost parallel-sided (Pl. VI. figs. 3, 10, *b.g.*), just as in *Act. solaris* and *Act. robusta* (Pl. V. figs. 2, 14).

This correspondence in the appearance of the dorsal interrarial furrows and basal grooves which is also seen in *Act. polymorpha*, var. 2 (Pl. VI. fig. 17; Pl. VII. fig. 4a), is not, however, an invariable one; for in *Act. pectinata* the basal folds are very well marked (Pl. V. fig. 9b, *b.f.*), and the dorsal interrarial furrows, therefore, leaf-like in appearance, as in most specimens of *Act. polymorpha* (Pl. VI. figs. 9, 13, 24). The basal grooves, however, on the ventral surface of the centrodorsal piece are narrow and parallel-sided (Pl. V. fig. 7, *b.g.*), just as in the allied species *Act. solaris* and *Act. robusta* (Pl. V. figs. 2, 14).

The external or distal faces of the first radials of *Act. polymorpha* differ not a little from the corresponding faces in *Ant. rosacea* and *Ant. cellica* (Pl. IV. figs. 4, 6, 8, 12a, 14, 17); in which, especially in the latter, the fossæ (*f.*) for the attachment of the muscles

are very large, and considerably more extensive than those which lodge the interarticular ligaments (*h*).

In *Act. polymorpha* (Pl. VI. fig. 1; Pl. VII. figs. 1 b, 4 b), however, the muscular fossæ are very small, being best developed in var. 1 (Pl. VI. fig. 12, *f*); while the fossæ (*h*) lodging the interarticular ligaments are very extensive, and separated by the downward continuation of the intermuscular furrow (*f*), which reaches the dorsal margin of the opening of the central canal (*c.e*). The external faces of the first radials of varieties 2 (Pl. VII. fig. 4 b), 3, and 4 resemble one another, but differ from the corresponding faces in the type (Pl. VII. fig. 1 b) in being somewhat higher in proportion to their width, and in the fact that the fossæ (*j*) lodging the elastic ligaments are relatively smaller, not extending so far into the lower or dorsal angles of the face as is the case in the type.

(v.) *The Basals.*

(§ 63) We have already seen that all the older observers regarded *Comatula* as devoid of those five pieces resting upon the top segment of the stem to which, in the other Crinoids, Müller gave the name of "basals;" and it was not until Dr. Carpenter¹ discovered the extraordinary metamorphosis undergone by the embryonic basals of *Comatula* (*Antedon*) *rosacea* and their transformation into the "rosette," that the existence of basals, although internal and concealed in the adult animal, was recognized.

The rosette of *Ant. rosacea* and *Ant. cellica* (Pl. IV. figs. 3, 7, 16, *R*) is a peculiarly shaped circular plate, occupying the dorsal half of the central cavity in the pentagonal base of the calyx, which lies much nearer to the dorsal surface of the pentagonal base in the latter species than in the former.

A normal rosette consists of a disk perforated in the centre with ten rays proceeding from it. Five of these rays (Pl. IV. fig. 13, *o'*) are short, triangular in form, and nearly flat, and their position is interrarial, as they are directed to the sutures between the five radials, their apices joining the contiguous pairs of these just between the two adjacent apertures (*x*, *x'*) of their central canals.

Alternating with these five interrarial processes of the rosette are five radial ones (fig. 13, *p*), each of which has parallel margins inflected on its ventral aspect in such a manner as to form a groove; while the process itself is so curved towards its dorsal aspect that this groove reaches the periphery of the rosette, and then terminates abruptly as if truncated.

The inflected margins of each of these five radial or, as Dr. Carpenter has called them, "spout-like" processes of the rosette are applied to the similarly inflected margins of the dorsal half of the axial radial furrow, lying between the two apertures of the central canal on the internal face of each first radial (fig. 12 c, *x'*, *y*). In this manner a complete radial axial canal is formed, which, as we have already seen, terminates on the dorsal surface of the radial pentagon by the opening *Q* (fig. 16), or becomes closed before it reaches the dorsal surface by the union of ingrowths developed from its walls.

Besides this very intimate union between the peripheral portion of the rosette and the

¹ Phil. Trans. 1865, pp. 744, 745.

internal faces of the first radials, its central portion is also frequently connected with the radial pentagon by delicate processes, which sometimes sprout forth irregularly from the inner margins of the component pieces of the latter; but sometimes form a more regular ingrowth, which considerably contracts the central space on the ventral aspect of the disk, and becomes continuous with an annular projection from the ventral face of the rosette.

(§ 64) Before attempting to understand the complicated condition of the basals in *Actinometra*, it will be well to study the mode in which the embryonic basals of *Ant. rosacea* become metamorphosed into the rosette, as described by Dr. Carpenter, from whose memoir the following account is principally taken.

In the young animal each basal is a flattened irregularly pentagonal plate, the apex of which lies between a pair of radials that partially rest upon it. On the ventral surfaces of the basal plates lie the five primary basal cords V , W , X , Y , Z , proceeding from the angles of the quincloocular organ. Each of these divides into two branches, V_1 , V_2 , Z_1 , Z_2 , the secondary basal cords, which pass on to the ventral faces of each pair of contiguous radial plates, *e. g.* X_2 and Y_1 to one radial, X_2 and X_1 to the next, and so on.

Both basals and radials gradually become much thickened by an endogenous extension of the calcareous network, which takes place in such a manner that the basal cords come to lie in furrows channelled out on the ventral surfaces of the plates. By a further endogenous growth of the radial plates these furrows are converted into canals (the "central canals" of Johannes Müller), which at first lie close under the ventral surfaces of the plates, but come gradually, by a continuation of the same process, to lie in their central axis.

In the basals, however, this process of endogenous growth is followed by one of absorption; for the cribriform film of which each basal is originally composed, and which still forms its external layer, now undergoes absorption, especially in its central portion, where it covers in the dorsal side of the primary basal cord; so that the central space left by the incomplete union of the proximal ends of the five embryonic basal plates is extended on its dorsal aspect into five broad rays, though on its ventral aspect, where it is bounded by the last-formed portion of the endogenous reticulation, it shows no corresponding increase. It is this last-formed ventral portion which persists in the adult as the five triangular interrarial processes of the rosette (Pl. IV. figs. 3, 7, 13, 16, *d'*).

The formation of the five radial or spout-like processes is somewhat more complicated. The removal of the external layer in the centre of the dorsal aspect is carried so far as to leave nothing but a kind of thickened margin along those sides of the plate which are received between the first radials; and by an extension of the same process along the median dorsal line of each plate as far as its salient angle, so as completely to remove the terminal portion of its inferior or dorsal layer, its two lateral portions become separated from each other at their distal ends, and remain as small curved processes extending outwards. Those of every two contiguous basals now unite to form a sort of ray curving towards the dorsal aspect: and this is the rudiment of one of the five radial or spout-like processes of the rosette, the shape of which becomes much more strongly pro-

nounced with the subsequent increase of its size (Pl. IV. fig. 13, *p*). The rosette is thus essentially formed at the expense of the secondary or ventral layer of the original basals, the ends of the curved spout-like processes being the sole residue of their primary or dorsal layer; and since, by the removal of the median portion of that layer in each plate, the primary basal cords are left bare upon their dorsal aspect, they now pass from the angles of the quinquelocular organ into the central canals of the first radials, on the inferior or dorsal side of the calcareous skeleton which occupies the base of the calyx; instead of reaching them by passing, as they did in the first instance, along its superior or ventral face or, as at a later period, through the middle of its substance.

Each of these primary basal cords, X , Y , &c., which are thus interrarial in position, divides into two branches, X_1 , X_2 , Y_1 , Y_2 , &c., towards the periphery of the rosette, on the dorsal surface of which it rests. These branches lie in the shallow channels which mark the union of the base of each interrarial triangular process (fig. 13 b, *o'*) with the two curved lateral processes above mentioned, each of which unites with a corresponding process from the adjacent basal to form one of the five spout-like rays (*p*) of the rosette. The apex or peripheral end of each triangular process is directed to the suture between two contiguous radials (figs. 3, 7, 16, *o'*), to which it is attached just between the two adjacent apertures (*x*, *x'*) of their central canals. Into these canals pass the secondary basal cords X_1 , X_2 , one into each of the two contiguous radials, so that one lies on each side of the interrarial process of the rosette.

(§ 65) As a general rule, this process, both in *Ant. rosacea* and in *Ant. cellica*, is short, triangular, and slightly curved towards the ventral side. It is not always so, however, for I have frequently met with specimens of *Ant. rosacea* in which one or more of the interrarial processes of the rosette, after bending for a short distance towards the ventral side, turns suddenly downwards, and extends towards the dorsal surface of the radial pentagon. At the same time the parallel margins of each of these abnormally developed processes are so inflected towards the dorsal surface as to form a narrow *interrarial* spout-like process. This is so applied to the projecting and similarly inflected outer edges of the adjacent openings of the central canals (*x*, *x'*) in two contiguous radials as to convert the interrarial furrow lying between them into a complete axial interrarial canal, precisely similar in character to the radial axial canals already described (§§ 52, 57).

In one case which I have met with, four out of the five interrarial processes of the rosette were of this character. In the rosette represented in Pl. IV. fig. 13, only two of the interrarial processes (*o*) are long and spout-like, the other three (*o'*) are short and triangular, like those of a normal rosette.

This abnormal condition of the interrarial process of the rosette of *Ant. rosacea* is of considerable interest, as it is the normal one in *Actinometra* and in many species of *Antedon*.

Not only the interrarial, but also the radial processes of the rosette of *Ant. rosacea* may exhibit departures from their usual shape; for the removal of the primary or dorsal layer at the salient angle of one or more of the five embryonic basals may be incomplete, so that the ends of the curved rays of the rosette exhibit lateral processes,

which are the remains of the upper margins of the primitive basal plates on which the first radials rested. Occasionally the apex of the original basal is left unabsorbed, so that the two lateral curved processes which remain after the removal of the primary external layer along the median line of each plate remain in connexion with one another; as is seen in the bottom part of the rosette represented in Pl. IV. fig. 13. The triangular interrarial process (o'), which is developed from a secondary calcareous deposit on the ventral side of the original basal, has here become more or less completely united with these primary bars connecting the two lateral portions of the basal. The latter retain their primitive relation to the first radials, for they remain united with them along the inner margins of their dorsal faces (fig. 16, *b.b*); and as they partially cover in the secondary basal cords, X_1 , X_2 , &c., on their dorsal aspect before they enter the central canals of the first radials, I will call them the "basal bridge" (Pl. IV. fig. 13, *b.b*).

This basal bridge is well seen *in situ* in the specimen of *Ant. rosacea* represented in Pl. IV. fig. 16. It is remarkably well developed, being nearly as distinct as in *Actinometra* (Pl. V. figs. 3, 12, and Pl. VI. figs. 4, 13, 24, *b.b*), in which its presence is normal, and not abnormal, as in *Ant. rosacea*. It is also slightly developed in the specimen of *Ant. cellica* represented in Pl. IV. fig. 3; but in fig. 7 no trace of it is visible.

(§ 66) This tendency to an incomplete metamorphosis of the embryonic basals of *Ant. rosacea*, and consequently to the abnormal persistence of a more embryonic condition than usual, is of considerable interest, because in *Actinometra* and in many *Antedons* a basal bridge, representing the apex and unabsorbed margins of the embryonic basal plates, is normally present (Pl. V. figs. 3, 8, 12, and Pl. VI. figs. 4, 6, 13, 18, 19, 22, 24, *b.b*). While at the same time, as already mentioned, the interrarial processes of the rosette (o), which are developed from a secondary or ventral layer, are large and spout-like, as is abnormally the case in *Ant. rosacea*, and acquire a connexion with the remains of the primary or dorsal layer which forms the basal bridge. The complicated rosette thus constituted also becomes united with the large, more or less spindle-shaped, rays of the basal star (S), the origin of which, as will be subsequently seen, is totally different from that of the rosette.

A single "compound basal," as it may be called, of *Actinometra*, thus consists of two distinct elements—(i) the incompletely metamorphosed embryonic basal, and (ii) a single ray of the basal star. Its position is interrarial, as it occupies the space enclosed between the apposed edges of the basal furrows on the ventral surface of the centrodorsal piece, and of the interrarial furrows on the corresponding dorsal surface of the radial pentagon (Pl. VI. figs. 4, 13, 24, S).

An isolated compound basal which is thus constituted, when seen from its dorsal side (Pl. V. fig. 8 b, Pl. VI. fig. 22 b), shows :—(i) more or less of the calcareous network ($c.n$) which unites the ventral surface of the rosette to the internal faces of the first radials; (ii) a large interrarial spout-shaped process (o); (iii) two small, radial, curved processes (p'), extending outwards from the base of the interrarial process, and representing the unabsorbed lateral portions of the primary layer forming the embryonic basal plate.

(iv) The basal bridge (*b.b*), consisting of two calcareous bars, that represent the unabsorbed peripheral margins of the embryonic basal on which two first radials rested. They extend towards one another from the outer ends of the small radial processes, until they meet at a point that represents the apex of the embryonic basal, and is situated on the dorsal side of the peripheral end of the interrarial process (*o*), developed from the secondary or ventral layer, which becomes united with the basal bridge.

(v) The ray (*S*) of the basal star, which is joined to the interrarial process and to the basal bridge, along the line of union of the two primary bars constituting the latter with one another and with the secondary interrarial process, *i. e.* at the apex of the embryonic basal. The development of this ray is quite different from that of either the primary or the secondary portions of the compound basal. It is really a tertiary structure, being nothing more than a deposition of calcareous material in the substance of the connective tissue of the synostosis between the centrodorsal piece and the radial pentagon.

(vi) At the sides of the interrarial process (*o*), bounded laterally by the radial processes (*p'*), and externally by the bars of the basal bridge (*b.b*), are two large apertures, *x*₁, *x*₂, *y*₁, *y*₂, &c., in each compound basal. Through these apertures pass the secondary basal cords, *X*₁, *X*₂, *Y*₁, *Y*₂, &c. (Pl. VIII. fig. 3), which result from the bifurcation of the primary cords, *X*, *Y*, *Z*, proceeding from the angles of the quinquelocular organ. The two secondary cords lie in the depressions on the dorsal surface of the compound basal, between the central ends of its radial and interrarial processes. They then pass outwards through the apertures (*x*₁, *x*₂, &c.) beneath the bars of the basal bridge, and enter the adjacent openings (*x*, *x'*, &c.) on the internal faces of the two contiguous first radials¹, which contribute to form the dorsal interrarial furrow occupied by the single fusiform ray (*S*) of the corresponding basal.

The ventral surface of each of these rays of a compound basal (Pl. V. fig. 8a; Pl. VI. figs. 6, 18, 22 a) is not flat, like the dorsal surface, but occupied by a prominent median ridge, so that the ray is triangular in section. This ridge does not extend quite to the central end of the ray, which is occupied by a considerable depression (*s*), forming the peripheral end of the groove contained in the spout-like interrarial process (*o*). In the natural condition, when the basals are *in situ* and in connexion with the radial pentagon, the inflected edges of this process unite with those of the axial interrarial furrow to form an axial interrarial canal. This terminates on the dorsal surface of the radial pentagon by a small opening situated at the central end of the dorsal interrarial furrow (Pl. V. fig. 12, II), in which furrow the tertiary element (*S*) of the corresponding compound basal is received. The depression (*s*) at the central end of the ray (Pl. V. fig. 8a; Pl. VI. figs. 6, 18, 22 a) lies over this opening, and thus forms a blind end to the axial interrarial canal (Pl. VIII. figs. 3, 5, 7, *a.i.e.*; fig. 8, *s*)—precisely in the same manner as the depressions (*q*) on the ventral surface of the centrodorsal piece of *Ant. rosacea* (Pl. IV. fig. 15) receive the blind ends of the axial radial canals which open on the dorsal surface of the radial pentagon by the five large openings, *Q* (Pl. IV. fig. 16).

A view of a single compound basal does not, of course, show one of the large and

¹ In Pl. V. fig. 13, four of these openings are seen on the internal faces of the two contiguous first radials, viz. *x'*, *y'*, *z'*, *z*.

spout-like radial processes of the rosette; for each of these is a composite structure, formed by the apposition of two of the small curved lateral processes of contiguous basals (Pl. VI. fig. 22, p'). This is seen in Pl. VI. figs. 6, 18, 19, particularly in the last two; for the union of the adjacent lateral processes (p') of the two contiguous basals which are there represented, is seen to be incomplete, so that a slight fissure is visible along the median line of the dorsal surface of the composite radial process (fig. 19, p). The peripheral end of this radial process is united to those of the interrarial processes (o) at its sides by the bars of the basal bridge ($b.b$). Their central ends are also united around the opening of the rosette (Pl. VI. figs. 4, 19, 24, R); but their median portions are separated by the two apertures (x_2, y_1) by which the two adjacent secondary basal cords (X_2, Y_1) pass out under the bars of the basal bridge, to enter the two openings of the central canal on either side of the axial radial furrow on the internal face of the first radial (Pl. V. figs. 9 c, 10; Pl. VII. figs. 1 a, 4 a, x', y), with the inflected inner edges of which the radial spout-like process (p) unites.

The openings (x_1, y_2) by which the other branches (X_1, Y_2) of the two primary basal cords pass outwards to reach the central canals of the other two radials corresponding to these two basals are best seen in a dorsal view as shown in Pl. VI. fig. 19. This also shows the two outer lateral processes (p') of these united basals, which would naturally unite with those of the two next contiguous basals, one on each side, to form two more radial spout-like processes.

(§ 67) The tertiary elements which form the rays of the basal star vary very considerably in their shape and in the completeness with which they are developed, just as do the interrarial furrows on the dorsal surface of the radial pentagon in which they lie. In *Act. solaris* (Pl. V. fig. 3, *d.i.f*) these have no curved folds at their sides, and the rays of the basal star (S) are only imperfectly calcified rods, long and narrow, like the basal grooves on the ventral surface of the centrodorsal piece into which they are received (Pl. V. fig. 2, *b.g*). In *Act. pectinata*, however, although the basal grooves are long and narrow as in *Act. solaris* (Pl. V. fig. 7), yet the dorsal interrarial furrows are widened by the presence of large curved basal folds at their sides (fig. 9 b, *b.f*); and in correspondence with these the tertiary basal elements (fig. 8, S) are much wider, and also far more perfectly calcified (being solid throughout), than is the case in *Act. solaris*.

In *Act. robusta* the central ends of these basal rays are wide and stout, and completely calcified as in *Act. pectinata*; but their peripheral ends are much thinner, and consist of a simple curved plate, which forms a sort of bridge over the dorsal interrarial furrow (Pl. V. fig. 12, S), the borders of which are straight, as in *Act. solaris* (fig. 3, *d.i.f*), and not marked by any lateral folds. The basal grooves on the ventral surface of the centrodorsal piece are also simple and nearly parallel-sided (fig. 14, *b.g*).

In *Act. polymorpha* and its varieties the condition of the basal star varies extremely, like that of the basal folds and basal grooves, the development and shape of which exhibit a very close correspondence with the appearance of the rays of the basal star.

Thus, in that specimen of the type of *Act. polymorpha* in which the basal grooves are narrow and parallel-sided, and all terminate well within the margin of the centrodorsal piece (Pl. VI. fig. 3, *b.g*), while no basal folds are present at the sides of the dorsal inter-

radial furrows (fig. 4, *d.i.f*), the rays of the basal star are short and flattened, and do not by any means reach the angles of the radial pentagon (fig. 4, *S*). Their dorsal surface is somewhat depressed along the median line, while the depression (fig. 6, *s*) at the central end of the ventral surface which receives the blind end of the axial interrarial canal is continued outwards in a peripheral direction somewhat further than in *Act. peclinata* (Pl. V. fig. 8a, *s*); and the median ridge which runs from its end to the apex of the ray is less marked than in this species.

In another specimen of the type, however, in which both basal grooves (Pl. VI. fig. 8, *b.g*) and basal folds (fig. 9, *b.f*) are wide and well marked, the basal rays are stout and thick, with a fairly distinct median ridge on their ventral surface. In fig. 8, three of them are seen occupying their normal position in the basal furrows on the ventral surface of the centrodorsal piece, with which they are closely connected, while the other two rays have remained in connexion with the rosette and radial pentagon.

In a third specimen of the type the rays of the basal star are very imperfectly developed; two only extend for any distance towards the angles of the radial pentagon (Pl. VI. fig. 11, *S*), while of the other three little or nothing is to be seen. In this specimen, as in the one first described, there are no basal folds, and the basal grooves are parallel-sided and only imperfectly developed (fig. 10, *b.g*). It is also remarkable for the fact that the absorption of the apex and outer margins of each embryonic basal plate seems to have been very incomplete; for the bars of the basal bridge are so wide, and extend so far towards the centre from the inner margins of the dorsal surfaces of the first radials, with which they are closely united, that they entirely conceal the apertures in the compound basals (Pl. V. figs. 3, 8; Pl. VI. figs. 4, 6, 13, 18, 19, 22, 24, x_1 , x_2 , y_1 , y_2 , &c.) through which the secondary basal cords pass in order to reach the central canals of the first radials. Consequently nothing is seen of the rosette in a dorsal view of the pentagonal base but its central opening surrounded by a raised rim (Pl. VI. fig. 11, *r.o*). In all the other figures, however (Pl. V. fig. 3; Pl. VI. figs. 4, 13, 24), these apertures are large and distinct, every one being situated between a radial (*p*) and an interrarial process (*o*) of the rosette.

In *Act. polymorpha*, var. 1, both basal grooves (Pl. VI. fig. 15, *b.g*) and basal folds (fig. 13, *b.f*) are well marked and somewhat lancet-shaped in form; the rays of the basal star which occupy the former are much flattened dorsally (fig. 22b, *S*), as in one of the specimens of the type (fig. 4, *S*). They are not, however, so short as in this case, but, like the basal folds at their sides, reach the outer angles of the radial pentagon.

This is also the case in the other three varieties. In var. 4 the basal folds diverge considerably at about the middle of their course (fig. 24, *b.f*), so that the dorsal interrarial furrow is here very wide, and then rapidly narrows towards its peripheral end. In correspondence with this, the basal rays also widen somewhat from their narrow central ends, and then begin to decrease in width as they approach the angles of the radial pentagon (fig. 24, *S*); they are also marked by a slight median furrow along their dorsal surface, as is the case in one specimen of the type (fig. 4, *S*). In varieties 2 and 3, as in the type, and in var. 1, the basal rays are widest at their central ends (figs. 13, 19, 22, *S*). In both cases the basal grooves (figs. 17, 21, *b.g*) and basal folds (Pl. VII.

fig. 4d, b.f) are well developed and somewhat lancet-shaped in form, as in var. 1 (Pl. VI. fig. 13, b.f; fig. 15, b.g).

In var. 2, and still more in var. 3, the mode of union of the bars of the basal bridge (figs. 19, 22 b, b.b) with one another and with the basal rays (*S*), is seen very distinctly at the central end of the latter; much more so than in *Act. pectinata* (Pl. V. fig. 8 b), in which, as in the other specimens figured (Pl. V. fig. 3; Pl. VI. figs. 4, 11, 13), the various elements of each compound basal are so completely united, that the lines of union between them become almost indistinguishable.

(§ 68) The complicated condition of the basals described above in *Actinometra* is not altogether peculiar to this genus, as I was first inclined to believe; for in *Ant. Eschrichtii* a basal star may be developed to a greater or less extent. In his paper on *Phanogenia* Lovén gives a diagram¹ of the dorsal aspect of the pentagonal base of the calyx of this species for comparison with that of *Phanogenia*. It shows five large rays extending from the periphery of the rosette to the outer angles of the radial pentagon, with the constituent elements of which they alternate in position; and in the text he speaks of them as belonging to the rosette. Unfortunately, his paper is written in Swedish, so that I have been unable to ascertain precisely what his views were with respect to the homologies of these rays.

His figure also shows five radial openings on the dorsal surface of the pentagonal base, which correspond with the dorsal openings of the radial axial canals in *Ant. rosacea* (Pl. IV. fig. 16, Q).

In neither of the two specimens of *Ant. Eschrichtii* which I have been able to examine do these openings exist, so that they are probably somewhat uncertain in their occurrence, as in *Ant. celtica* (Pl. IV. figs. 3, 7); and in neither of these specimens is the basal star developed to any thing like the extent that it is in the specimen figured by Lovén. In one (Pl. IV. fig. 10, *S*) the rays are excessively small and inconspicuous, only extending for a very short distance along the dorsal interradyal furrows (*d.i.f*), while the corresponding basal grooves on the interradyal elevations of the centrodorsal piece are also very slightly developed (fig. 11, *b.g*). The basal bridge also, connecting two successive rays of the basal star, is barely traceable around the inner margin of the radial pentagon (fig. 10, *b.b*).

In the other specimen which I examined the basal rays were somewhat better developed, occupying a larger portion of the dorsal interradyal furrows, and extending further outwards towards the margin of the radial pentagon; although still remarkably slender and delicate, somewhat as in *Act. solaris* (Pl. V. fig. 3, *S*), and by no means so large as in the specimen figured by Lovén².

The interior of the calyx of *Ant. Eschrichtii* is much simpler than that of *Actinometra*,

¹ *Loc. cit.* p. 230, m.

² Since the above lines were written, I have examined several other specimens of *Ant. Eschrichtii*. None of them have the radial openings above mentioned, nor are the rays of the basal star so large as in the specimen figured by Lovén; but they are always present, though less regularly developed than in *Actinometra*. Further, my work on the 'Challenger' *Comatule* has brought out the fact that a basal star is nearly always present in *Antedon* as well as in *Actinometra*, so that the British species (*Ant. rosacea*, *Ant. celtica*) are remarkable for its absence, rather than *Ant. Eschrichtii* for its presence.

as will be seen by comparing Pl. IV. fig. 9 with Pl. V. fig. 13, both of which represent the internal aspect of two united first radials. In *Actinometra* (Pl. V. fig. 13) there is an abundant calcareous network (*c.n*) in connexion with the internal faces of the radials, which are marked by well-developed radial and interrarial furrows. In *Ant. Eschrichtii*, however (Pl. IV. fig. 9), the processes forming this network are but little developed; there is no axial interrarial furrow, and even the radial one is indistinct, except near the dorsal surface, where it passes between the raised edges of the two apertures (*x'*, *y*, *y'*, *z*) of the central canal which unite with the inflected edges of a radial spout-like process (*p*) of the rosette.

The interrarial process of the rosette (*o'*) is short and broad, but without the spout-like character which it has in *Actinometra*—being simply directed, as in the normal condition of *Ant. rosacea* (Pl. IV. figs. 3, 7, 16), to the line of suture between the two contiguous radials, to which it is attached between the two adjacent apertures (fig. 9, *y*, *y'*) of their central canals.

(§ 69) The remarkable variation in the extent to which the rays of the basal star may be developed, as described above in *Actinometra* and in *Antedon Eschrichtii*, is due to the fact that they are not calcifications in a nucleated protoplasmic network like the ordinary elements of the skeleton. They are the result of a calcareous deposition, of a more or less regular character, around the connective-tissue fibres which effect the synostosis with the centrodorsal piece of every pair of contiguous radials along the line of contact of the latter; so that their position is, as we have already seen, interrarial.

In Pl. III. fig. 5 is seen the lower end of a vertical section cut transversely to the plane of synostosis of two decalcified first radials (*r*₁) of *Act. polymorpha*, close to their peripheral margin where they are not concealed by the centrodorsal piece, so that the fibres of the elastic ligaments connecting them with the second radials are cut somewhat obliquely (*l*₁).

The threads of the protoplasmic network of which the organic basis of the radials is composed pass somewhat rapidly at their surfaces into the connective-tissue fibrils (*L*) which run horizontally between them and effect the synostosis. These fibrils being very closely set, the superficial portions of the calcareous reticulation forming the skeleton of the radials, which are ossified around their ends, are very much more dense than the central portion produced by calcification of the protoplasmic network.

Pl. VIII. fig. 4 represents a section, from the same series as the previous one, across the line of union of the same two radials (*A*, *B*), rather nearer to the centre of the calyx, so that their dorsal surface appears no longer free, but partially covered by the centrodorsal piece (*cd*). The lower portion of this section, more highly magnified, is seen in Pl. III. fig. 6. The synostosis of the radial areas of the centrodorsal piece with the dorsal surfaces of the first radials is effected by simple and not specially numerous connective-tissue fibres (*l*); these pass directly from the protoplasmic basis of the one piece into that of the other, in a direction vertical to the plane of the opposed surfaces, just as in an ordinary synostosis. But in the direction of the interrarii the course of the fibres is different, and they have a deeper origin in the substance of the centrodorsal piece than those which occupy the radial areas (Pl. III. fig. 6).

There are three principal masses of these longer interrarially placed fibres:—two smaller

ateral ones (S_3), in which the fibres have the same direction as those occupying the radial areas; and a large median mass, in which the fibres ascend vertically for some distance (S_2) and then diverge to the two sides (S_1), where they pass into the protoplasmic basis of the radials; and the horizontal fibres (L) which pass between the radials fill up the open angle caused by the divergence of the ascending fibres. There is thus a much greater development of connective-tissue fibres, effecting the synostosis of the centrodorsal piece with the radial pentagon, in the interrarial than in the radial planes. This is well seen in Pl. VIII. fig. 3, which represents a longitudinal section through the calyx of *Act. polymorpha*. On the right side it is interrarial, passing through the synostosis of the first and second radials of the two radii, A , B ; and the connective-tissue fibres (S_2) connecting the centrodorsal piece with the edges of these two radii are longer and more abundant than those on the left side (l), passing between the centrodorsal piece and the first radial of radius D , which is cut longitudinally.

This is also seen in Pl. VIII. figs. 5-8, which represent portions of four out of a series of sections through a decalcified calyx of *Act. pectinata*. These are in the same plane as the section of the calyx of *Act. polymorpha* represented in fig. 4, *i.e.* transverse to the synostosis of the radii A , B on the one side of the centre, and to the radius D on the other.

Fig. 5 represents a section, rather nearer the centre than fig. 4, passing vertically along the axial interrarial canal (*a.i.c.*); beneath the dorsal end are seen the vertical ascending fibres (S_2), which have a much deeper origin in the substance of the centrodorsal piece of this species than in *Act. polymorpha*. The diverging fibres are not seen, as they give rise by their calcification to the long basal ray (Pl. V. fig. 8, S); and this section passes through the depression at the central end of its ventral surface (Pl. V. fig. 8 a, s) in which the axial interrarial canal terminates.

Fig. 6 is somewhat nearer the centre, but still shows the long vertical fibres (S_2) in the interrarial plane, together with a portion of the central calcareous network and the axial radial canals (*a.r.c.*) corresponding to the two radii A , B .

Fig. 7 is just beyond the centre, *i.e.* across the inner end of the first radial of D , so that no vertical fibres are visible, as they are only interrarial in position. Two sets of them, however, are seen in fig. 8, which shows the first radial of D cut transversely rather further from the centre, so that the fibres (l) effecting its synostosis with the adjacent radials of C and E are cut obliquely; beneath these are seen the interrarial ascending fibres (S_2), which diverge slightly at their upper extremities (S_1).

These diverging fibres and the upper ends of the vertical ones are the basis around which the calcareous material forming the rays of the basal star is deposited. As the ventral surface of the centrodorsal piece on which these rays rest is much higher at the centre than at the circumference, it is impossible to obtain horizontal sections in which these five rays are seen at all complete. Oblique sections, however, may be obtained in which one or more of them are cut along the greater part of their length. Two such sections, seen from their dorsal side, are represented in Pl. VIII. figs. 1 & 2; their lower left-hand portions lie nearer the dorsal surface of the calyx than the upper right-hand portions.

The centre of fig. 1 is occupied by the fibrous envelope N of the quinquelocular organ, from the dorsal portion of which cords ($n.c.$) proceed to the cirrhi (cir). At the top and

right of the figure are seen portions of three first radials (r_1), the central parts of which are lighter than the more peripheral parts, as the section here passes through the slightly developed unpigmented fibrous tissue (l) connecting the radials with the centrodorsal piece (cd), the peripheral portion of which consists of the same pigmented protoplasmic network as the substance of the radials.

Two of the synostoses between the latter are seen at the top of the figure; but they do not quite reach to the centre, where their place is occupied by the central ends of two of the rays of the basal star (S_1), the remaining three rays of which are visible in the lower part of the figure for the greater portion of their length. Two of them are also seen in the left or more dorsal portion of the next section (fig. 2), which also shows three synostoses (L) between the radials in the right or more ventral part of the figure.

The sections of these rays of the basal star appear very dark, not from the presence of pigment, which is entirely wanting in their fibrous basis, but because of the abundance and very close approximation of the fibres of this basis; these are the diverging and vertical fibres seen in Pl. VIII. figs. 3, 4, and more highly magnified in Pl. III. fig. 6 (S_1, S_2). Just in the same way, in Pl. VIII. fig. 3, the section appears much darker on the right-hand side, where it cuts the closely approximated connective-tissue fibres effecting the synostosis between two first radials transversely, than on the left-hand side, where it passes through the more open protoplasmic network of the individual segment of a single radial, D .

(§ 70) This great development of fibrous tissue along the interrarial portions of the centrodorsal piece and of the pentagonal base of the calyx accounts for the fact, often mentioned already, that there is no pigment in the substance of the rays of the basal star (which is a more or less complete calcification of the central portions of these interrarial fibrous masses), nor in the walls of the basal grooves on the centrodorsal piece, nor in those of the dorsal interrarial furrows on the inferior surface of the pentagonal base, which are calcifications of the smaller lateral masses of long fibres running directly from the organic basis of the centrodorsal piece into that of the first radials (Pl. III. fig. 6, S_3). These lateral fibres have a common point of origin in the substance of the centrodorsal with the vertical and diverging fibres (S_1, S_2), around which the calcareous tissue of the basal rays is deposited. It is therefore easy to understand that the calcification may in some cases be so complete that the basal rays formed around the median fibres (S_1, S_2) may become completely united with the walls of the basal grooves formed around the lower ends of the two lateral fibrous masses (S_3); as is the case in the specimen of *Act. polymorpha* represented in Pl. VI. fig. 8, where two of the rays of the basal star (S) are so completely united with the floor and sides of the basal grooves in which they lie that the line of junction between them becomes indistinguishable.

The fact that the rays of the basal star are calcifications in connective tissue and not in the ordinary nuclear tissue which forms the organic basis of the other parts of the skeleton, also affords an explanation of the great variations in the extent to which the rays are developed. The general arrangement of the fibres constituting the interrarial portions of the synostosis between the centrodorsal piece and the radial pentagon is essentially the same in *Antedon* as in *Actinometra*. In *Ant. rosacea* and *Ant. cellica* they

never seem to undergo calcification, though this may take place in *Antedon Eschrichtii*, either only very slightly, as in the two specimens examined by myself (Pl. IV. fig. 10, *S*), or to a considerable extent, as in that figured by Lovén. In *Actinometra* also the extent of calcification of the rays of the basal star is very variable. In one specimen of *Act. polymorpha* scarcely any trace of them is visible (Pl. VI. fig. 11, *S*); in another they are short, but otherwise well developed (fig. 4, *S*); while in others they may extend very nearly to the outer angles of the radial pentagon (figs. 13, 18, 19, 22, 24, *S*).

In *Act. pectinata*, again, we have found them to be large and thick (Pl. V. fig. 8, *S*), while in the closely allied *Act. solaris* (Pl. V. fig. 3, *S*) they were slender rods, only imperfectly calcified here and there—the intervening portions of the dorsal interrarial furrow seen in the prepared skeleton (*d.i.f*) being occupied in the fresh state by masses of fibrous tissue, which are removed by the action of the alkali used in preparation.

(§ 71) We have seen that the basal circle of *Actinometra* is somewhat complicated in its nature, and consists of two entirely distinct elements, viz. a central rosette, which we may fairly suppose to be the result of the metamorphosis of the embryonic basal plates, as in *Antedon rosacea*, and five more or less completely ossified rays extending from it in a peripheral direction.

The rosette is situated on the ventral side of the quinquelocular organ, from the fibrous envelope of which proceed the primary basal cords. These are very short, and soon bifurcate, so as to give rise to ten secondary cords, which pass through the ten apertures ($r_1, r_2, \dots, r_{10}, z_2$) in the peripheral portion of the rosette in order to reach the central canals of the first radials.

As already remarked by Ludwig, we may fairly regard those elements of the skeleton in which the bifurcation of the primary basal cords occurs as homologous throughout the different genera of the Crinoids. This leads us to the conclusion that the rosette of *Antedon* and *Actinometra* is homologous with the united central ends (at least) of the basals of *Pentacrinus*, which are perforated by canals that lodge the five bifurcating fibrillar cords proceeding from the dorsal angles of the quinquelocular organ, and not from its ventral angles as in *Comatula*.

The question now arises, Where are we to seek for the homologues of the five rays of the basal star in most *Comatulæ*? Unfortunately the only type in which we find a condition any thing like that described above is a fossil one, the *Solanocrinus* of Goldfuss; so that it is difficult to ascertain the precise relation of its basals to the canals proceeding from the quinquelocular organ that was undoubtedly contained in the cavity of its deep centrodorsal piece.

The upper surface of the latter, according to Goldfuss², presents “five radiating elevations on which the pelvis articulates.” They correspond to the interrarial elevations on the ventral surface of the centrodorsal piece of *Antedon* and *Actinometra*.

The basals themselves vary in appearance in the different species. In *S. costatus* and *S. scrobiculatus* they are only “fünf schmale Strahlen die sich zwischen die Nähte der Rippenglieder einsenken;” but in *S. Jægeri* they are much wider, “so dass sie auf der ganzen Gelenkfläche zusammenstossen und hier fünf ausstrahlende Furchen zur Aufnahme

¹ Beiträge &c. *loc. cit.* p. 67.

² Petref. Germ. *loc. cit.* p. 166.

der Säule bilden" (p. 168). This species, however, is possibly not a *Solanocrinus* at all, but the head of a stalked Crinoid.

In both these cases the peripheral ends of the basals appear on the external surface of the calyx, between the centrodorsal piece and the radial pentagon, although the extent to which they are visible is very different.

The long and narrow prismatic-shaped basals of *S. costatus* evidently represent the five rays of the basal star of *Actinometra*. The interrarial elevations on the ventral surface of the centrodorsal piece are marked by five median grooves for the reception of the basals, just like the basal grooves of *Actinometra*; and these interrarial elevations are continued beyond the margins of the radial areas, just like the small processes (*t*) in some species of *Actinometra* (Pl. VI. figs. 14, 15). They correspond with five longitudinal ridges on the outer surface of the columnar centrodorsal which separate the rows of cirrus-sockets.

We do not, of course, know whether there was a rosette in *S. costatus*. I am inclined to think that this was not the case, as the central ends of the five basals are in contact with one another laterally for a short distance, instead of being united by narrow bars forming a basal bridge, as in *Actinometra*; and their internal or proximal faces were probably perforated by the opening of a short bifurcating canal lodging the fibrous cords on their way to the central canals of the first radials, as in the closely similar basals of *Pentacrinus asteria*. Hence these five basals as a whole would represent the circle of compound basals in *Actinometra*, viz. the rosette together with the rays of the basal star. Whether, however, only the united central ends of the basals of *S. costatus* represent the embryonic basal plates, like the rosette of *Antedon* and *Actinometra*, or whether the whole star results from a metamorphosis of the embryonic basals, is a question which must remain in doubt, though the latter is by far the more probable supposition. Apart from the analogy of *Pentacrinus*, as the peripheral ends of the basal rays extend beyond the margin of the radial pentagon, it is hardly likely that they can be the result of calcification in the interrarial portions of the synostosis between the radial pentagon and centrodorsal piece, as in *Actinometra* and *Antedon Eschrichtii*.

The calyx of the doubtful *S. Jaegeri* presents a great advance upon that of *S. costatus* with respect to the development of the basals, which led Pictet¹ to propose the erection of this species into a separate genus. Instead of being long and narrow, and in contact only by their central ends, as in *S. costatus* and *S. scrobiculatus*, they are broad and wedge-shaped, and in contact along their whole sides, so as to form a complete calcareous disk entirely separating the radial pentagon from the centrodorsal piece.

This is occasionally their position in *Pentacrinus*, though there are but few species of that genus in which the basals are relatively so large and complete as in *Solanocrinus Jaegeri*.

In *P. asteria*, and in the two fossil species *P. briareus* and *P. subangularis*, they are small and cuneiform and only in contact by their central ends, just as in *S. costatus*, so that the greater portion of the radial pentagon is in contact with the top stem-segment. In *P. Mülleri* they are in contact for about half their length, and then diverge, while in *P. Wyville-Thomsoni* they are completely united with one another along the

¹ *Op. cit.* p. 288.

whole length of their sides, so as entirely to cut off the radial pentagon from the top stem-segment, just as in *S. Jægeri*.

There can therefore be little doubt that the basals of *Pentacrinus* are homologous with those of *Solanocrinus*, and therefore analogous to the compound basals of *Actinometra*, which, as we have seen, are not entirely developed out of the embryonic basal plates. It would seem, in fact, as if in *Pentacrinus* and *Solanocrinus* the embryonic basal plates became directly transformed into the basals of the adult; while in *Comatula* they undergo metamorphosis into the central rosette by the absorption of the greater portion of their dorsal or primary tissue, and the development of a secondary ossification on the ventral side of the original plates.

In *Aut. rosacea* the metamorphosis is much more complete than in most *Antedons* and in *Actinometra*, in which new skeletal elements are developed by a more or less complete tertiary ossification in masses of connective tissue, that correspond precisely in position, and to a certain extent also in shape, with the basals of *Solanocrinus* and *Pentacrinus*. The latter being most probably direct products of the growth of the embryonic basals are therefore strictly homologous only with the rosette of *Actinometra*, although analogous in position to the whole circle of compound basals in this genus, viz. to the rosette and basal star taken together.

(§ 72) It is interesting to observe the different position of the basals with regard to the chambered organ in *Comatula* and in the various species of the stalked Crinoids.

In *Comatula* this organ is situated in the cavity of the centrodorsal piece (Pl. VIII. fig. 3) which is on the dorsal side, not only of the radial pentagon, but also of the rosette or metamorphosed basals; and the nervous cords proceeding from its fibrillar envelope to enter the central canals of the first radials come off from its ventral angles.

The large centrodorsal piece of *Comatula* is developed by the growth of the top stem-segment of the Pentacrinoid larva. In *Pentacrinus*, which remains pedunculate throughout life, the top stem-segment is the youngest and smallest. Its central cavity is far too small to contain the quinquelocular organ forming the upper end of the central axis of the stem, which contains five longitudinal chambers expanding slightly at every nodal segment, where each of them gives off a single cirrus-vessel¹.

There is no special increase in the diameter of these chambers in the top stem-segments, and they do not expand into the large chambers of the quinquelocular organ until near the level of the ventral surface of the basal circle which surrounds the dorsal half of the chambered organ. The ventral portion of the latter is contained in the lower part of the central funnel-shaped space enclosed within the radial pentagon, where it is surrounded by a very dense calcareous network, through which the axial prolongation containing the superior continuations of the five chambers of the quinquelocular organ ascends, on its way to enter the visceral mass, just as in *Comatula*. In consequence of this relatively higher position of the chambered organ in *Pentacrinus* than in *Comatula*, the nervous cords which enter the central canals of the first radials come off from its dorsal angles, and not from the ventral ones as in *Comatula*.

In *Comatula*, therefore, the walls and floor of the cavity enclosing the chambered organ

¹ *Pentacrinus* and *Rhizocrinus*, loc. cit. pp. 43-46.

are formed almost entirely by what was once a stem-segment; while in *Pentacrinus* this cavity is a part of the central space enclosed within the radial and basal pentagons, which respectively form the ventral and dorsal portions of its side walls. Among the fossil *Apioocrinidae* we find an intermediate condition between these two extremes. Thus in *Ap. mespiliformis*, as seen in Goldfuss's figure¹, the first radials are small, but the basals are very large and curved outwards, so as to enclose a large central cavity; this we may fairly suppose to have lodged a chambered organ, as Ludwig² has found that in *Rhizocrinus*, the modern representative of this family, the axis of the stem expands into a chambered organ just as described above in *Pentacrinus*. I have found the same to be the case in *Bathycrinus*.

This organ is contained in *R. lofotensis* in a large and apparently simple segment, described by Sars³ as the expanded uppermost stem-segment. Pourtales⁴, however, for reasons which will be discussed further on, regards it as composite and as representing the five basals. In this case the relative position of the chambered organ is precisely identical with that which we may suppose it to have occupied in *Ap. mespiliformis*, namely, on the dorsal side of the radial pentagon, but not within the uppermost stem-segment, as in *Comatula*. In *Ap. rosaceus*⁵ the relative position of the chambered organ must have been very much as in *Pentacrinus*, though slightly higher; for the cavity in which it was contained was almost entirely enclosed between the enlarged first radials, while the basals only form its floor and the very lowest portion of its side walls. Lastly, in *Ap. Milleri*⁶ the chambered organ must have lain altogether on the ventral side of the basals; the superior surfaces of which form by their apposition the floor of a cavity whose side walls are entirely composed of the adjacent inner faces of the contiguous first radials.

This condition is thus precisely the opposite of that which we find in *Comatula*, where the cavity containing the chambered organ is not only altogether outside the radial pentagon, but also on the dorsal side of the rosette or metamorphosed basals.

(§ 73) In the works both of Goldfuss and Miller may be found incidental suggestions that the "basis," or circle of basals, and, indeed, the whole of the lower part of the calyx of the stalked Crinoids, may be regarded as representing expanded stem-segments, each broken up into five parts. Müller, however, was the first to put this idea into a definite form. He described the basals of *Pentacrinus* as a metamorphosed stem-segment⁷, or as "zerfallene Theile eines obersten Stengelgliedes;" for they correspond in position with the five leaf-like figures on the articular surfaces of the stem-segments which mark the positions of the five longitudinal tendons.

The fibrous bundles composing these tendinous cords are separated from one another by a very regular calcareous network, which is deposited around and between them, somewhat as in the rays of the basal star of *Actinometra*. They are attached (by their

¹ Petref. Germ., Taf. lvii. fig. 1, n.

² "Zur Anatomie des *R. lofotensis*," Zeitschr. f. wiss. Zool. Bd. xxix. p. 122.

³ Crinoïdes vivants, loc. cit. pp. 4, 12.

⁴ "On a new Species of *Rhizocrinus* from Barbadoes," Zoological Results of the Hassler Expedition, p. 28. Cambridge, U. S., 1874.

⁵ Petref. Germ., Taf. lvi. fig. 3, a.

⁶ Petref. Germ., Taf. lvii. fig. 2, n.

⁷ "Bau des *Pentacrinus*," loc. cit. pp. 16, 25.

upper ends) to the lower surfaces of the five basals in the same way as the ligaments of the arms are attached to the brachial segments, the fibres of the one passing gradually into the protoplasmic basis of the other. The basals cannot, however, be regarded as simply ossifications in this fibrous tissue of the same nature as the basal rays of *Actinometra*; for, as shown above, there is every reason to believe that they are developed, like the other elements of the skeleton, out of the embryonic basal plates; although, so far as position is concerned, they are precisely homologous with the calcareous deposits within the tendinous cords of the stem.

On the other hand, the basal rays of *Actinometra*, which are similar in position, though not in origin, to the peripheral portions of the basals of *Pentacrinus*, are of the same nature as the calcareous tissue of the leaf-like areas of the stem-segments, being simply the result of the deposition of calcareous material around and between connective-tissue fibres.

In many of the fossil *Articulate* Crinoids the lateral union of the basals with one another is so very complete that the lines of junction between them are not always visible, and the "basis" has therefore been described either as entirely absent or as replaced by the uppermost stem-segment, which, according to Müller's view, it is supposed to represent.

This is particularly the case in the *Apiocrinidæ* and in *Eugeniacerinus*. Miller, who was the first to describe the latter type¹, mistook the first radials of *E. caryophyllatus* for the basals, and described them as firmly anchylosed to what he supposed to be the "superior columnar joint." Goldfuss², however, rightly determined this last to be a part of the first radials, which are very much prolonged downwards, while, at the same time, he described the basals as replaced by the enlarged uppermost stem-segment, which articulates with the inferior surface of the elongated first radials. Römer³ did not accept this view of Goldfuss's, although he recognized that the "superior columnar joint" of Miller was simply a dorsal prolongation of the first radials; but, like Miller, he described these last as the basals.

It is most probable that Goldfuss's view is the truer one, as in Hagenow's figure⁴ of *Eugeniacerinus Hagenowii*, in which the first radials are not prolonged downwards as in *E. caryophyllatus*, the piece on which they rest, representing that which Goldfuss called the enlarged uppermost stem-segment of *E. caryophyllatus*, is seen to be distinctly composite; for its external surface is marked by five sutural lines, alternating in position with those between the first radials, and evidently indicating the lines of union of five basals.

The geological collection of the British Museum, which I have been able to examine, thanks to the kindness of Mr. Henry Woodward, contains a very interesting series of specimens from the Chalk which are labelled *Apiocrinus ellipticus*.

In some of them the basals form a complete ring, separating the radials from the upper stem-joint, which is very much enlarged. But in other specimens the basals appear

¹ *Op. cit.* p. 111.

² *Petref. Germ. tom. cit.* p. 162.

³ *Lethæa Geognostica*, ii. Theil 4, p. 115.

⁴ *Min. Jahrb. loc. cit.* ix. p. 13.

externally merely as small triangular pieces, not meeting laterally; so that they exhibit the same differences as the basals of *Pentacrinus* and of *Solanocrinus*. In many specimens the sutures between the basals, radials, and top stem-joint are clear and distinct; but in others there is no trace of them at all, just as in some examples of *Eugeniocrinus* and *Rhizocrinus*; but this is hardly a satisfactory reason for supposing the basals to be internal and concealed, as has been done in the case of the last-named genus.

Even in some species of *Pentacrinus* the basals appear to be very closely united to one another, and to assume the form of an uppermost stem-segment. Thus in *P. scalaris*, Goldfuss¹, there is no appearance whatever of small wedge-shaped basals, such as are found in *P. briareus* and in *P. asteria*; but, as remarked by the Messrs. Austin², they appear to be united into a single plate, which resembles an "enlarged columnar joint." The same was probably the case in the Jurassic genus *Isocrinus*, described by Von Meyer³, though it is, of course, possible that in both these cases the basals may have been internal and concealed, as in *Comatula*.

I have endeavoured to show elsewhere⁴ that in the recent *Rhizocrinus* we find a strikingly similar case to that presented by *Eugeniocrinus*, viz., the sutures between the basals, visible externally in one species and not in another, or, rather, *not invariably* in another. In *R. lofotensis* the first radials rest upon a large and expanded apparently simple segment, which was described by Sars⁵ as the expanded uppermost stem-segment; and a small circular plate situated in the central vacuity between the first radials, with which, as well as with the enlarged uppermost stem-segment, it is closely connected, was regarded by him as representing the metamorphosed embryonic basals of *Comatula*.

Pourtales's observations⁶, as well as my own subsequent ones, have led me to believe that the piece called the enlarged uppermost stem-joint of *R. lofotensis* by Sars and Ludwig⁷ is composed (if not entirely, at any rate in great part) of five closely anchylosed basals. Schlüter⁸ is evidently not acquainted with the evidence on which this view rests, or he would scarcely suggest that *R. Rawsonii* might not be a *Rhizocrinus* at all, because its basals differ from those described in *R. lofotensis* by Sars and Ludwig; although these two observers are not themselves in accordance as to which parts of the interior of the calyx are to be regarded as concealed basals.

Sir Wyville Thomson⁹ takes the same view as Pourtales and myself; for he describes how "in *Rhizocrinus* the funnel-shaped piece formed by the coalescence of the basals with the fused first radials above and the dilated upper joint of the coalesced upper joints of the stem beneath, makes up a large part of the cup;" and his descriptions of the calices of *Hyocrinus* and *Bathycrinus*, both genera allied to *Rhizocrinus*, together with

¹ Petref. Germ. tom. cit. p. 173, Taf. ix. fig. 10, b.

² 'A Monograph on Recent and Fossil Crinoidea,' p. 121 (Bristol, 1845).

³ "*Isocrinus* und *Chelocrinus*," Museum Senckenbergianum, p. 251 (Frankfurt, 1837).

⁴ "*Pentacrinus* and *Rhizocrinus*," loc. cit. pp. 47-53.

⁵ Crinoïdes vivants, loc. cit. p. 4.

⁶ Hassler Expedition, loc. cit. pp. 28, 29.

⁷ *Rhizocrinus lofotensis*, loc. cit. pp. 121, 122.

⁸ Op. cit. p. 29. Schlüter was unfortunately unable to make himself acquainted with Pourtales's memoir.

⁹ "Notice of new living Crinoids belonging to the Aplocrinidae," Journ. Linn. Soc. Zool. vol. xiii. p. 48.

the analogies of *Apiocrinus* and *Eugeniocrinus*, strengthen Pourtales's view still more completely.

The occasional fusion of the upper stem-joints with the lower part of the calyx, as described above in the *Apiocrinidae*, is an excellent illustration of Müller's idea respecting the correspondence between the basis and the stem-joints.

This correspondence, however, is by no means entitled to rank as a serial homology. The earliest condition of the basals shows them to be five separate plates developed in a spiral around the aboral cœlom of the Crinoid embryo¹. They have distinct homologies in the apical system of the other Echinoderms²; while the stem-segments, surrounding the aboral cœlom much in the same way as the basal circlet, are simple undivided pieces from the first, and seem to be almost or quite unrepresented in the other Echinoderms.

(vi.) *The Second and Third Radials.*

(§ 74) The second radial of *Act. polymorpha* (Pl. VII. fig. 2), like that of *Ant. rosacea*, is an oval, somewhat discoidal plate, having two nearly parallel faces—one internal or proximal, articulating with the first radial, the other external or distal, articulating with the third radial. The internal face (fig. 2 a) closely resembles the external face of the first radial (Pl. VII. fig. 1 b), with which it articulates, being divided transversely by a large articular ridge (*i*) into a dorsal and a ventral portion; the former is entirely occupied by the fossa lodging the elastic ligament (*j*), which is particularly deep just below the opening of the central canal (*c.c.*). From the ventral margin of this opening arise the two ridges which bound the intermuscular furrow (*f*₁), and are joined near their upper extremities by the transverse secondary ridges separating the large fossæ (*h*) that lodge the interarticular ligaments from those (*f*) lodging the flexor muscles of the ray; the latter are excavated in a pair of thin lamellæ, which extend upwards from the proper ventral margin of the plate, as is seen in a view of the distal face (fig. 2 b, *g*). Besides the above-mentioned ridges and fossæ, which correspond to similar ones on the distal face of the first radial, the proximal face of the second radial shows two lateral processes, in which shallow fossæ (*k*) are excavated. These processes represent the outer portions of the distal face, which is somewhat wider than the proximal one, as the lateral faces are not set at right angles to the two terminal ones, but form an oblique angle with the proximal face, so that the outline of the radial, when seen from the dorsal or ventral side, is trapezoidal in form (fig. 2 c, d). The shallow fossæ which are excavated in these lateral faces lodge the ligamentous substance by which the second radials are united with one another in pairs: the extent of this union is, as above remarked, very variable in different specimens, being generally greatest where the number of arms is largest (Pl. II. figs. 9, 11).

The external or distal face (fig. 2 b) is much simpler in character than the proximal one, as no muscles are attached to the vertical lamellæ which rise from its ventral margin above the articular face proper. This last is divided by a vertical ridge (*i*) that

¹ Götte, *loc. cit.* pp. 595, 620.

² P. H. Carpenter, "On the Oral and Apical Systems of the Echinoderms," *Quart. Journ. Micr. Sci.* xviii. (1878) pp. 371, 382.

passes round the opening of the central canal (*c.c*) into a pair of lateral fossæ (*h*), which give attachment to the large interarticular ligament connecting the second with the third radial. The proximal face is not quite vertical, but slightly inclined towards the distal one, so that the ventral face is not much more than an edge. When the piece is viewed from the ventral side, therefore (fig. 2 c), little else is visible but the fossæ for the muscles (*f*) and interarticular ligaments (*h*) of the proximal face and the intermuscular furrow (*f*) descending along its median line.

The second radials of var. 1 are very similar to those of the type, except that, as in the first radials, the muscular fossæ are relatively somewhat larger. In var. 2, however, they are very much smaller (Pl. VII. fig. 5 a, *f*); and there are no vertical lamellæ projecting from the ventral margin of the distal face (fig. 5 b), as is the case in the type. The lateral fossæ (*h*) lodging the ligamentous substance which connects the second radials with one another are somewhat more marked, as the union of the second radials in pairs is more complete than in the type, though not so complete as in varieties 1, 3, and 4.

The two latter also agree with var. 2 in the fact that the proximal and distal faces of the second radials are nearly parallel, and less inclined to one another than in the type and in var. 1; so that the fossæ for the muscles and interarticular ligaments are barely visible when the piece is seen from the ventral side (fig. 5 c), as there is a proper ventral face. Its median line is occupied by a continuation of the furrow on the ventral surface of the first radial (figs. 4 c, 5 c, *r.r.f*), while its lateral portions are divided up, in the same way as those of the first radial, into secondary ridges and furrows.

(§ 75) The third or axillary radial of *Act. polymorpha*, which gives attachment to two primary arms, presents three articular surfaces—an internal one corresponding to the distal face of the second radial, and two external ones, inclined to one another, with which the bases of the arms articulate.

The proximal face (Pl. VII. fig. 3 a) is precisely similar in character to the distal face of the second radial, being divided, like it, by a vertical ridge into two lateral fossæ (*h*) which lodge the interarticular ligaments. Its articular margin, when viewed from the dorsal side (fig. 3 d), is perfectly straight, and does not project in the middle as in *Ant. rosacea*; so that the possible amount of lateral movement between the second and third radials must be extremely slight. Two vertical lamellæ (*g*) project from the uppermost margin of the internal face; but they do not form part of the surface of articulation with the second radial, as they are excavated into fossæ on their outer side for the attachment of the proximal ends of the outer muscular bundles passing between the axillary radial and the lowest segments of the primary arms. The two inner muscular bundles are attached to the two sides of a projecting wedge-shaped process (*cl*) on the external or distal face, the “clavicular” of Schultze¹, which occupies the angle between the two obliquely placed articular faces for the basal arm-segments. These are of precisely the same character as the external faces of the first radials (fig. 3 b), consisting, besides the muscular fossæ (*f*) just mentioned, of two others for the interarticular ligaments (*h*), and of a large dorsal fossa (*j*) lodging the elastic ligament, and separated from the other two by a transverse articular ridge (*i*), in the centre of which is the opening of the central canal (*c.c*).

¹ *Loc. cit.* p. 5.

The median line of the ventral face (fig. 3 c) is occupied by a ventral radial furrow continuous with that on the ventral face of the first radial; it divides into two branches, one of which passes on either side of the clavicular, in order to be continued on to the basal arm-segments. The proximal end of this furrow is indicated by the deep notch separating the two vertical lamellæ which project upwards from the proper internal face (fig. 3 a, *g*), and through which the base of the clavicular is seen.

In the type and in var. 1 the lateral portions of the ventral face of the third radial are plain, and not sculptured; but in varieties 2-4 they are divided up by secondary ridges and furrows (fig. 6 c), just like the ventral faces of the first and second radials (figs. 4 c, 5 c). In these varieties also there are no vertical lamellæ projecting upwards from the ventral margin of the internal face (fig. 6 a), which is also the case in the external face of the second radial (Pl. VII. fig. 5 b), as the muscular bundles passing between the first and second radials, and between the third radials and basal arm-segments, are smaller than in the type. In var. 2 there would appear to be more power of lateral movement between the second and third radials than is the case in the type; for although, as in the type, there is no projection in the middle of the proximal articular margin of the third radial, yet the distal articular margin of the second radial shows a slight indication of such a median prominence (fig. 5 d), which is absent in the type. It would seem though, to be replaced to a certain extent by the greater thickness of the vertical articular ridge (*i*) around the opening of the central canal, which is seen, in Pl. VII. fig. 2 d, to project a little beyond the level of the dorsal surface of the radial; so that when the opposed ridges of the second and third radials are in contact with each other, the third may possibly have a very slight power of lateral movement upon the second, though by no means so great as in *Act. rosacea*, in which the median prominence on the internal articular margin of the third radial is very marked.

The second and third radials of var. 2 differ from those of the type of *Act. polymorpha* and of all the other varieties in the very marked convexity of their dorsal surfaces, which renders them considerably higher than the first radials; so that when the whole calyx is viewed from the exterior, the inner circle of first radials, which are only very little concealed by the small centrodorsal piece, seems somewhat sunk within the outer circle formed by the second and third radials.

This marked convexity is well seen in Pl. VII. fig. 5, a, d, and fig. 6, b, d, especially when these figures are compared with those of the corresponding parts in the type (fig. 2, a, d, fig. 3, b, d).

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* I have, unfortunately, been unable to get a sight of this paper, and only know of it from the reference to it in Leuckart's 'Jahresbericht.'

DESCRIPTION OF THE PLATES.

The following letters denote the same parts throughout all the Plates.

A, B, C, D, E. The five Radii or Ambulacra.

A₁, A₂, B₁, B₂, C₁, C₂, D₁, D₂, E₁, E₂. The ten Primary Arms.

a.c. Axial cœlom.

a.p. Axial prolongation.

a.i.c. Axial interradial canal.

a.r.c. Axial radial canal.

a.i.f. Axial interradial furrow.

a.r.f. Axial radial furrow.

An. Anal tube.

b₁, b₂, b₃, b₆, b₁₀. First, second, third, sixth, and tenth brachials.

b.b. Basal bridge.

b.f. Basal fold.

b.g. Basal groove.

b.m₁. Muscles between the radial axillary and the first brachials.

b.m₂. Muscles between the second and third brachials.

c.c. Central canal of the calcareous segments of the rays and arms.

c.c'. Central canal of the cirrus-segments.

ch. Chambers of the quinquelocular organ.

cd. Centrodorsal piece.

cir. Cirrus.

cd.c. Centrodorsal cœlom.

cl. Clavicular.

c.n. Calcareous network in the central vacuity of the pentagonal base of the calyx.

co.c. Commissural canals in the first radials.

d.i.f. Dorsal interradial furrow.

cr.c. Circumvisceral cœlom.

d.r.f. Dorsal radial furrow.

d₁, d₂, d.a. First, second, and axillary distichals.

ep. Epithelial wall of the alimentary canal.

F. Central funnel-shaped space enclosed within the pentagonal base.

f. Muscular fossæ.

g. Vertical lamellæ of the calcareous segments.

f₁. Intermuscular furrow.

g₁. Their superior margins.

f₂. Notch representing it in *Ant. celtica*.

g₂. Their inner lateral margins.

g₃. Ridge formed by the union of these in the first radials of *Ant. celtica*.

h. Fossæ lodging the interarticular ligaments.

i. Transverse articular ridge.

i.co. Interradial commissure.

i.e. Interradial elevations on the centrodorsal piece.

iv.c. Intervisceral cœlom.

j. Fossæ lodging the elastic ligaments.

k. Fossæ lodging the ligamentous substance between the sides of the second radials.

L. Ligamentous substance between the sides of the first radials.

l. Ligamentous substance between the first radials and the centrodorsal piece.

L'. Incompletely decalcified portions of the skeleton.

L₁. Interarticular and } ligaments between the first and second radials, or second and third
l₁. Elastic } brachials.

L₂. Interarticular ligaments between the second and third radials.

M. Mouth.

N. Fibrillar nervous envelope of the quinquelocular organ.

n. Axial nervous cords of the rays and arms.

o. Interradial spout-like processes of the rosette.

n'. Their branches.

o'. Interradial triangular processes.

n.c. Axial nervous cords of the cirrhi.

o.b. Ovoid bodies.

P. Peristome.

Pe. Uncalcified peristome between the radii.

p. Radial processes of the rosette.

p'. Small curved processes at the sides of a single basal.

p₁, p₂, p.a. First, second, and axillary palmars.

Q. Radial openings on the dorsal surface of the pentagonal base.

- Q' . Notches on the inner margins of the dorsal faces of the first radials.
 q . Radial depressions on the centrodorsal piece. R . Rosette.
 $r_1, r_2, r.a.$ First, second, and axillary radials. $r.ar.$ Radial areas on the centrodorsal piece.
 $r.c'$. Diverticulum from the radial coelom into the substance of the first radial.
 $r.co.$ Intraradial commissure. $r.o.$ Central opening of the rosette.
 $r.m.$ Muscles between the first and second radials. $r.s.$ Radial space. S . Rays of the basal star.
 S_1, S_2, S_3 . Diverging, vertical, and lateral fibres effecting the interradial portions of the synostosis between the centrodorsal piece and the radial pentagon.
 s . Depressions at the central ends of the rays of the basal star.
 $sp_1, sp.a.$ First and axillary suprapalmars. Sy . Syzygium.
 t . Short processes at the angles of the centrodorsal piece.
 U . Sockets for the attachment of the dorsal cirrhi.
 u . Inner openings of the cirrhus-canal in the centrodorsal piece.
 $v.i.f.$ Ventral interradial furrow. $v.r.f.$ Ventral radial furrow.
 V, W, X, Y, Z . The five primary basal cords proceeding from the angles of the quincloocular organ.
 $V_1, V_2, W_1, W_2, X_1, X_2, Y_1, Y_2, Z_1, Z_2$. The ten secondary basal cords produced by the bifurcation of the primary ones.
 $v_1, v_2, w_1, w_2, x_1, x_2, y_1, y_2, z_1, z_2$. The apertures in the basals through which the secondary cords pass.
 $v, v', w, w', x, x', y, y', z, z'$. The corresponding apertures of the central canals on the internal faces of the first radials.

In Pl. II. figs. 9-11 indicate the position of the mouth (ventral) relative to the radial skeleton (dorsal).

* In Pl. V. fig. 4 indicates the passage of the ventral radial canal into the central calcareous network within the radial pentagon by two openings, instead of by only one as usual.

PLATE I.

Diagrams of the distribution of the ambulacra on the disks of different species of *Comatula*. The red lines mark the interradial intervals. Figs. 1-4 copied from Müller.

Fig. 1. *Antedon rosacea*.

Fig. 3. *Act. Wahlbergii*.

2. *Actinometra solaris*.

4. *Act. multiradiata*.

In figs. 5-16 the tentaculiferous grooves are marked by dark lines, and the non-tentaculiferous grooves by fainter lines.

Fig. 5. <i>Act. solaris</i> . Proportion of non-tentaculiferous arms,		$\frac{4}{10}$
6. <i>Act. polymorpha</i> : Type.	„	$\frac{7}{13}$
7. „ „	„	$\frac{10}{18}$
8. „ „	„	$\frac{6}{20}$
9. „ Var. 1.	„	$\frac{11}{20}$
10. „ Type.	„	$\frac{12}{25}$
11. „ „	„	$\frac{13}{26}$
12. „ „	„	$\frac{10}{28}$
13. „ „	„	$\frac{15}{28}$
14. „ Var. 2.	„	$\frac{10}{29}$
15. „ Type.	„	$\frac{19}{31}$
16. „ Var. 4. All the arms tentaculiferous.		

PLATE II.

- Fig. 1. Diagram of the distribution of the ambulaera in a new *Actinometra* from the Philippines.
2. Superior or ventral aspect of the disk of *Act. polymorpha*, var. 2, the oral pinnules having been cut away near their bases. $\times 3$.
 3. Piece of an ordinary tentaculiferous arm of *Act. polymorpha*, from about the middle of its length, seen from above. $\times 4$.
 4. Terminal portion of the same arm. $\times 4$.
 5. Piece of the middle portion of a non-tentaculiferous arm, borne upon the same axillary as that represented in figs. 3 & 4. Ventral view. $\times 4$.
 6. Termination of the same arm. $\times 4$.
 7. Distichal, palmar, and lower brachial segments of one of the radii of *Act. polymorpha*, var. 4, showing the white line which occupies the middle of the dorsal surface of the skeleton. $\times 4$.
 8. Centrodorsal piece and one radius of a monstrous specimen of *Act. polymorpha*, showing the very irregular form of the centrodorsal piece (*cd*) and the imperfect condition of one of the palmar series, which consists simply of one axillary segment bearing brachials upon one of its distal faces, and two suprapalmars (*sp₁*, *sp₂*) upon the other. $\times 4$.
 9. Diagram of the calyx of a small thirteen-armed specimen of *Act. polymorpha*: Type. $\times 4$.
 10. A similar diagram of a larger specimen with 26 arms. $\times 3$.
 11. A similar diagram of a specimen of var. 3, with 39 arms. $\times 2$.
- The * in these three figures (9, 10, 11) indicates the position of the mouth on the ventral side of the disk relatively to the radial skeleton of the dorsal side.

PLATE III.

- Fig. 1. Terminal comb of an oral pinnule of *Act. pectinata*. $\times 20$.
2. Oral pinnule of *Act. polymorpha*, Type. $\times 10$.
 3. Oral pinnule of *Act. polymorpha*, Var. 4. $\times 10$.
 4. Portion of a horizontal section through the synostosis of two first radials of *Pentacrinus Wyville-Thomsoni*. $\times 110$.
 5. Lower portion of a vertical section through the peripheral end of the synostosis of two first radials of *Act. polymorpha*. $\times 110$.
 6. Lower portion of a similar section, taken rather nearer the centre of the radial pentagon, showing the disposition of the fibres which effect the synostosis of the first radials with the centrodorsal piece, both in the radial (*l*) and the interradian planes (*S₁*, *S₂*, *S₃*). $\times 110$.
 7. Longitudinal section through one of the muscles (*b.m.₁*) and interarticular ligaments (*L₁*) connecting the second and third brachials. $\times 110$.
 - 8-10. Cirrhi of *Act. polymorpha*. Type, and vars. 1 & 2.
 8. Type. $\times 6$. *a*, adult; *b*, very young; *c*, nearly mature.
 9. Isolated cirrus-segments of the Type. $\times 10$. *a*, a basal segment; *b*, a terminal segment.
 10. Cirrus of var. 2. $\times 6$.
 11. Cirrus of var. 1. $\times 6$.

PLATE IV.

Figs. 1-8 of *Ant. cellica*. All $\times 7$.

- Figs. 1 & 2. Centrodorsal piece, after removal of the cirrhi, as seen from its dorsal (fig. 1) and ventral (fig. 2) sides.
- 3 & 4. Pentagonal base of the calyx, as seen from its dorsal (fig. 3) and ventral (fig. 4) sides.

- Fig. 5. Interior of the calyx, as seen after removal of the visceral mass.
 6. Lateral view of the base of the calyx with the centrodorsal piece *in situ*.
 7. Pentagonal base of the calyx of a smaller variety, as seen from its dorsal side.
 8. Lateral view of the base of the calyx of the same variety, with the centrodorsal piece *in situ*.

Figs. 9-11 of *Ant. Eschrichtii*.

- Fig. 9. Two united first radials, together with the portion of the rosette which is in connexion with them, as seen from within. $\times 7$.
 10. Pentagonal base of the calyx as seen from its dorsal side after removal of the rosette occupying its central cavity. $\times 3\frac{1}{2}$.
 11. Centrodorsal piece seen from its ventral side. $\times 3\frac{1}{2}$.

Figs. 12-17 of *Ant. rosacea*, all $\times 7$, except fig. 13, which is $\times 15$.

- Fig. 12. Isolated first radial. *a.* ventral, *b.* dorsal, *c.* internal aspect.
 13. Abnormally developed rosette, with two spout-like interrarial processes (*o*) and a basal bridge (*b. b.*) connecting the ends of two of the radial processes (*p*). $\times 15$. *a.* ventral, *b.* dorsal aspect.
 14. Lateral view of the base of the calyx with the centrodorsal piece *in situ*.
 15. Centrodorsal piece seen from its ventral side.
 16 & 17. Pentagonal base of the calyx as seen from its dorsal (fig. 16) and ventral (fig. 17) sides.

PLATE V.

The figures all $\times 7$, except fig. 8, which is $\times 15$.

Figs. 1-4 of *Act. solaris*.

- Figs. 1 & 2. Centrodorsal piece as seen from its dorsal (fig. 1) and ventral (fig. 2) sides.
 3 & 4. Pentagonal base of the calyx as seen from its dorsal (fig. 3) and ventral (fig. 4) sides.

Figs. 5-9 of *Act. pectinata*.

- Fig. 5. Interior of the calyx as seen after removal of the visceral mass.
 6 & 7. Centrodorsal piece as seen from its dorsal (fig. 6) and ventral (fig. 7) sides.
 8. An isolated compound basal. $\times 15$. *a.* ventral, *b.* dorsal aspect.
 9. An isolated first radial. *a.* ventral, *b.* dorsal, *c.* internal aspect.

Figs. 10-15 of *Act. robusta*.

- Fig. 10. Internal aspect of an isolated first radial.
 11-13. Two united first radials, together with those portions of the rosette which are in connexion with them, as seen from above (fig. 11), below (fig. 12), and within (fig. 13).
 In these four figures (10-13) I. indicates a bristle passed along the axial radial canal; II. another passed along the axial interrarial canal; and III. a third, entering the central canal by one of the apertures on the internal face (*a'*), and coming out through the aperture of the commissural canal (*co.c.*) on the lateral face.

- Figs. 14 & 15. Centrodorsal piece as seen from its dorsal (fig. 15) and ventral (fig. 14) sides.

PLATE VI.

All these figures are $\times 7$, except figs. 6, 18, 19, 22, which are all $\times 15$.

Figs. 1-11 of *Act. polymorpha*, Type. Figs. 1-6, from one specimen.

- Fig. 1. Lateral view of the base of the calyx, with the centrodorsal piece *in situ*.
 2. The same parts seen from the dorsal side.

Fig. 3. Ventral aspect of the centrodorsal piece.

4 & 5. Pentagonal base of the calyx as seen from its dorsal (fig. 4) and ventral (fig. 5) sides.

6. Two united compound basals as seen from their ventral side. $\times 15$.

7, 8, & 9, from a second specimen.

7 & 8. Centrodorsal piece as seen from its dorsal (fig. 7) and ventral (fig. 8) sides. In fig. 8 three of the rays of the basal star are seen occupying the basal grooves (*b. g.*), their proper connexion with the rosette having been broken.

9. Pentagonal base of the calyx as seen from its dorsal side after removal of the rosette and basal star.

10 & 11, from a third and abnormally developed specimen.

10. Centrodorsal piece seen from its ventral side.

11. Dorsal aspect of the pentagonal base of the calyx.

Figs. 12-15 of *Act. polymorpha*, var. 1.

Figs. 12 & 13. Pentagonal base of the calyx as seen from its ventral (fig. 12) and dorsal (fig. 13) sides.

14 & 15. Centrodorsal piece as seen from its dorsal (fig. 14) and ventral (fig. 15) sides.

Figs. 16-19 of *Act. polymorpha*, var. 2.

Figs. 16 & 17. Centrodorsal piece as seen from its dorsal (fig. 16) and ventral (fig. 17) sides.

18 & 19. Two united compound basals as seen from their ventral (fig. 18) and dorsal (fig. 19) sides.

Figs. 20-22 of *Act. polymorpha*, var. 3.

Figs. 20 & 21. Centrodorsal piece as seen from its dorsal (fig. 20) and ventral (fig. 21) sides.

22. An isolated compound basal as seen from its ventral (*a*) and dorsal (*b*) sides.

Figs. 23 & 24 of *Act. polymorpha*, var. 4.

Pentagonal base of the calyx as seen from its ventral (fig. 23) and dorsal (fig. 24) sides.

PLATE VII.

In this Plate are shown the first, second, and third radials of the type of *Act. polymorpha* (figs. 1-3) and of var. 2 (figs. 4-6).

The different aspects shown are designated as follows:—*a*. Internal or proximal face; *b*. External or distal face; *c*. Ventral or superior face; *d*. Dorsal or inferior face.

Act. polymorpha, Type.

Fig. 1. First radial.

2. Second radial.

3. Third or axillary radial.

Act. polymorpha, var. 2.

Fig. 4. First radial.

5. Second radial.

6. Third or axillary radial.

PLATE VIII.

All the figures are $\times 18$. Figs. 1 & 2 of *Act. polymorpha*, Type.

Figs. 1 & 2. Two successive oblique sections through the base of a decalcified calyx, viewed from their dorsal side.

Fig. 1 is the more inferior, *i.e.* nearer the dorsal surface. Its left-hand lower portion shows the centrodorsal piece only, with its marginal cirrhi (*cir.*) which receive fibrillar cords (*n.c.*) from the

central mass (*N*) enveloping the quinquelocular organ. Proceeding outwards from the centre are seen five dark rays (*S*₁), which represent the closely fibrillar organic basis of the five rays of the basal star. In the upper part of the figure two of them are very short, only their central ends being visible, as the section has here passed above the level of their outer ends through the substance of three first radials (*r*₁).

Fig. 2. In this section only two of the basal rays (*S*₁) are visible, as the greater part of it has passed above the level of the synostosis (*l*) between the first radials and the centrodorsal piece. In the centre are seen the chambers of the quinquelocular organ (*ch*), with their ventral openings into the vessels contained within the axial prolongation. At the right of the figure are seen the lower ends of the axial canals, both radial (*a.r.c.*) and interrarial (*a.i.c.*); their cavities are generally crossed by transverse septa, which divide them up into two or three intercommunicating smaller ones. The interval between every two of these canals is occupied by one of the secondary basal cords (*Y*₂, *Z*₁, *Z*₂, &c.), produced by the bifurcation of the short primary cords (*I*₁, *Y*, &c.) proceeding from the angles of the quinquelocular organ. They are connected with one another laterally by interrarial and intrararial commissures (*i.co.* & *r.co.*) and enter the central canals of the first radials (*r*₁) in successive pairs, so that the axial nervous cord (*n*) of each radius is composed of fibres derived from two primary basal cords (*Y*₂, *Z*₁, &c.), just as in *Antedon*.

Fig. 3. A vertical longitudinal section through a decalcified calyx, passing on the right through the synostosis of two first radials (*A*, *B*) and the fibrillar basis (*S*₂) of one of the basal rays, and on the left through the segments (*r*₁, *r*₂, *r.a.*) of radius *D*. The first of these is united to the centrodorsal piece by connective-tissue fibrils (*l*) similar to, but less abundant than, those in the interrarial portion of the section, around which, in the natural condition, the calcareous material forming one of the basal rays is deposited. The passage of the ventral furrows (*v.r.f.*, *v.i.f.*) into the axial canals (*a.r.c.*, *a.i.c.*) is also well seen in this section. Its centre is occupied by the quinquelocular organ, from the ventral portion of which the axial prolongation (*a.p.*) rises into the circumvisceral coelom (*c.v.c.*), which, together with the lower end of the wide axial coelom (*a.c.*), occupies the space between the ventral surface of the skeleton and the lower or dorsal wall of the convoluted alimentary canal. It is traversed by numerous connective-tissue septa, which divide it up into a system of spaces, communicating freely with those both of the intervisceral and of the axial coelom (*i.v.c.*, *a.c.*).

Fig. 4. Transverse section through the synostosis of two first radials (*A*, *B*) near the peripheral margin of the centrodorsal piece (*cd.*), showing the radial (*l*) and the interrarial (*S*₂) fibres which effect the synostosis between it and the united first radials. The latter form the organic basis of one of the rays of the basal star.

Figs. 5-8. Four vertical sections, selected from a series, through a decalcified calyx of *Act. pectinata*.

5. Section through the adjacent inner ends of two first radials (*A*, *B*), showing the axial interrarial canal (*a.i.c.*) between them, and the open outer ends of the radial spaces (*r.s.*) between their dorsal surfaces and the ventral surface of the centrodorsal piece. The central ends of their axial nervous cords (*n*) are cut very obliquely.
6. A section rather nearer the centre, showing the closed central ends of the radial spaces (*r.s.*) of the same two radii (*A*, *B*) and their axial canals (*a.r.c.*); also the four secondary basal cords which unite in successive pairs (*Z*₂, *I*₁ and *I*₂, *H*₁) to form their axial cords, cut obliquely.
7. A section from a little the other side of the centre, through the outer end of one of the chambers (*ch*) of the quinquelocular organ, corresponding to radius *D*. The radial spaces (*r.s.*) of *C* and *E* are cut almost longitudinally; and above them, in the interior of the radials, are seen the axial nervous cords, with one of the two secondary basal cords

(X_1 , Y_2) by which each is connected with the central nervous envelope of the quinquelocular organ. The other branches (X_2 , Y_1) of the two primary cords (X & Y) combine to form the axial cord of the radius D . The inner end of its first radial is seen in the centre of the upper part of the figure (r_1), separated from those of C & E by the axial interrarial canals (*a.i.c.*).

Fig. 8. A section rather further from the centre of the calyx, showing the first radial of D cut transversely, with the closed central end of its radial space (*r.s.*). At the sides of the latter are the expanded dorsal ends of the axial interrarial canals seen in fig. 7; they are received in depressions (*s*) at the central ends of the rays of the basal star, which are ossified around the vertical fibres (S_2) only, and not, like the stouter more peripheral portions of the rays, around both vertical and diverging fibres, as is seen in Plate III. fig. 6, S_1 , S_2 .

II. *On some New Species of Nudibranchiate Mollusca from the Eastern Seas.*

By CUTHBERT COLLINGWOOD, M.A., M.B., F.L.S., &c.

(Plates IX. & X.)

Read March 7th, 1878.

THE very considerable numbers of naked-gilled Mollusca which have been found upon our own shores would lead one to suppose that on other coasts, in which climatal conditions were more favourable, they would be very commonly met with. Having collected not fewer than twenty-eight species upon a very small section of our northerly coasts, I hoped that a careful search upon tropical shores would yield an abundant harvest of these highly interesting and beautifully-tinted animals. In any such research, however, seasonal changes must not be overlooked. There can be no doubt in the mind of any one who has ransacked tropical localities that in them the highest development of colour and the most curious vagaries of form are to be found ; but I am persuaded that a zoologist who pays but a brief visit to a number of coasts in succession is far less likely to make a considerable collection of species of Nudibranchiata than is any one who, confined to a single favourable locality for a considerable period, is thus able to pursue his examination of the same spot through all the different seasons of the year. Hence it is that the collections of Sir W. Elliot on the Madras coast (32 species), of Dr. Kelaart on the Ceylon coast (42 species), and of Mr. Angas in New South Wales (21 species) are so large ; while the voyage of the 'Astrolabe' yielded but 18 new species, that of the 'Samarang' half a dozen species, and my own researches (the fruits of every opportunity within my reach during a period of rather more than twelve months) resulted only in the discovery of the 16 new species described in the following paper.

The greater number of species of this group may be found upon stony shores near low-water mark, and especially at low spring-tide. They adhere to the *under* side of stones, and may be detected by turning them over. Although some of them appear to be capable of swimming, and most of them can float, branchiæ downwards, upon the surface of the water, I never saw them in this position in the sea, however calm. In fact they have invariably been found by me in a passive condition, like little shapeless masses of soft, coloured matter, in depressions and crevices of stones, where they have probably retired at that particular juncture, when the wash of low tide has disturbed the water and rendered it both turbulent and turbid ; from both of which disadvantages the same spot would be free at all times, *except* at dead low-water. I have, however, dredged up a very beautifully-coloured and delicate species from a depth of 20 fathoms, which, notwithstanding the rough handling of the dredge and the company of shells, corallines, and sponges, seemed in no way incommoded or less lively. Again, some species of Nudibranchiata, as *Glauca*, appear to be free ocean-swimmers, and such I have taken in the towing-net in the Formosa channel ; while another species (*Scyllæa pelagica*) is

abundant in the open ocean of the Atlantic, but always adherent by its clasping foot to the fronds of the gulf-weed.

Nor do the exquisite colours of this group depend entirely upon geographical position. On our own northerly coasts richly tinted species occur, such as *Doris flammea*, *D. coccinea*, and many brilliant species of *Eolis*, &c.; while *Doris sordida* is a Red-Sea species, *D. tristis* is from the Madras coast, and *D. exanthema* from Ceylon; and the same remark also applies equally to other genera and families. Nevertheless, as a rule, the more brightly coloured species are more commonly met with on tropical shores; and of the genus *Chromodoris*, remarkable for their brilliancy, no species are found upon our own shores, but, although some occur on the Mediterranean coasts, the majority are characteristic of the hotter regions.

A very remarkable circumstance in the history of these delicate animals is their extraordinary geographical distribution. Mr. Abraham remarks (*l. c. postèa*) that the well-known and almost first-described British species, *Doris tuberculata*, has also been found in New Zealand on the one hand, and at Vancouver's Island on the other; and my own experience has remarkably confirmed the widespread habitats of certain species. Interesting in this respect was the fact of my meeting with the same species, within a few days' or weeks' interval, on different sides of the China Sea. Thus a *Chromodoris* which I had already found in the Pescadores was the first thing I picked up, some time later, on the reef of Labuan (Borneo). Very soon after I met with a second species at Labuan, which I at once recognized as one I had already captured and figured in the Haitan Straits, a little south of the river Min, coast of China. A *Doris* which I found on a submerged reef in the centre of the China Sea, I afterwards found again on another island off the coast of Borneo, west of Sarawak river. A minute species also (probably an immature *Terevlyana*) I found on two occasions in localities separated by 150 miles of sea.

A circumstance due, I think, to what I have already mentioned about seasonal changes is worth recording. I had searched in vain upon some rocks in the harbour of Hong Kong, and having mentioned this to a resident gentleman, who occasionally himself made the same researches, he kindly offered to go with me and show me where he found them. But we were equally unsuccessful, and could obtain none. The same thing occurred at Labuan. Having showed my drawings to a gentleman interested in natural history, he at once recognized them as animals of which he assured me there were many beautiful species to be found; and he also kindly conducted me to his hunting-ground, but equally in vain, and to his surprise he could show me none where he had been in the habit of finding them. In fact, although I met at Labuan with species I had already found elsewhere, I only added one new species to my list at that place. In both these instances I imagine I was at the localities mentioned at unfavourable seasons of the year, and not at those seasons when my informants assured me they had met with numerous species.

I should mention, however, one other Labuan species which unfortunately I was unable to record, owing to the following curious circumstance. It was a large tuberculated *Doris*, of a mottled grey colour, 1 inches long, with capacious tentacles and expansive gill-tufts, of which I found two or three specimens upon a reef in one of these

expeditions. I brought them home, and placed them in water till the next day, intending by daylight to draw and describe them. But on visiting them in the morning, I found that they had performed a spontaneous amputation of the mantle close to the body all round. It was done as cleanly as if by a pair of scissors. A large *Pyrrula* in the same vessel was at first credited with this act; but other specimens having been placed separate in clean water, not being able to attend to them immediately, I found on visiting them next day that they also had amputated their mantles and were destroyed. It appeared to be a suicidal act, or "happy despatch," similar to the self-evisceration of *Holothuræ* and breaking up of *Comatulæ* under the influence of the gradual fouling of the water.

These delicate and beautifully tinted animals are so entirely altered as to their form and colour by spirit, that I can scarcely understand how new species can be satisfactorily described from spirit-specimens. Alcohol bleaches their colours, and contracts to shapelessness the most beautiful elements of their form, the mantle, but more especially the tentacles and branchiæ, so that they bear no resemblance whatever to the living animal. It keeps them, however, fit for dissection. The spicula, odontophores, buccal collars, and other important classificatory characters are thus well preserved. Glycerine, while it keeps for a considerable time their colour and form, renders them soft and comparatively useless for dissection. The only way to retain a correct idea of their living character is to make careful drawings of them in their active condition; and whatever value the present illustrations may have is founded upon this circumstance, for they are faithful to the life.

With regard to the two species of the Polybranchiate family of *Phyllidiadæ* (the only ones I met with, and found side by side in a rock-pool on the coast of Borneo), I have consulted Bergh's elaborate paper in the 'Naturhistorisk Tidsskrift' for 1868-69, and also that in Heft 10 of Semper's 'Reisen im Archipel der Philippinen,' in both of which papers species are described and figured; but although there is some resemblance, I cannot assure myself that the *Phyllidiella pustulosa* figured by him is the same as my *Phyllidia spectabilis*.

Nothing more need be added in these introductory remarks concerning the species to be described in this paper. As to the works to which I have been indebted in the investigation, I would chiefly mention two, viz. the well-known and invaluable 'Monograph' of Messrs. Alder and Hancock, published by the Ray Society, which has been to me as a companion ever since its publication; and, secondly, the "Revision of the Anthobranchiate Nudibranchiate Mollusca," by Mr. P. S. Abraham, in the Proc. Zool. Soc. 1877: other memoirs are referred to in the text.

List of the Genera and Species enumerated in the present Paper.

<i>Doris pecten.</i>	<i>Albania formosa.</i>
— <i>cresecentica.</i>	<i>Triopa Principis-Wallæ.</i>
<i>Chromodoris iris.</i>	<i>Trevelyana felis.</i>
— <i>Bullockii.</i>	<i>Doridopsis arborescens.</i>
— <i>aureo-purpurea.</i>	— <i>rubra.</i>
— <i>tumulifera.</i>	<i>Phyllidia spectabilis.</i>
— <i>tenuis.</i>	<i>Fryeria variabilis.</i>
— <i>funerea.</i>	<i>Scyllæa pelagica.</i>
— <i>Alderi.</i>	<i>Bornella marmorata.</i>

Order *NUDIBRANCHIATA*, Cuvier (1817).

Family DORIDIDÆ, Alder and Hancock (1855).

Genus DORIS, Linnæus (1758).

DORIS PECTEN, Coll., n. sp. (Plate IX. figs. 1-5.)

Length nearly $\frac{1}{2}$ inch. *Body* oval, of a deep greenish-blue colour all over, studded with minute papillæ of a darker tint. *Mantle* large, covering the foot entirely. *Dorsal tentacles* short, lamellated, dark-coloured, paler at the bases. *Branchiæ*, consisting of seven or eight simple leaflets, are ranged in a crescentic form, the horns of the crescent pointing forward and embracing a small crescentic area of a paler tint. *Under surface* of the mantle paler than the upper, and spotted; foot brownish below.

Two specimens of this little *Doris* were found in a rock-pool above low-water mark on Bush Island, entrance to the harbour of Ke-lung, North Formosa, May 29. When at rest, the posterior part of the mantle is drawn in, and the branchiæ are seen in profile, looking like a *comb* stuck in behind, whence its specific name.

DORIS CRESCENTICA, Coll., n. sp. (Plate IX. figs. 6-8.)

Length 3 inches; breadth 2 inches. *Body* broad, flat, tuberculated. *Mantle* capacious, covering the whole body, and largely projecting beyond the posterior extremity of the foot; very broad and round anteriorly, but about the middle of the body constricted on either side to about one half its diameter; edge very thin and flat, and puckered all round the margin with numerous large and small folds. Plentifully covered with large warty excrescences arranged crescentically and concentrically around the anterior and posterior margins, where they are but slightly elevated: an elongated irregular excrescence runs along the centre of the dorsum, commencing anterior to and between the tentacles, and terminating at the branchiæ, on either side of which are arranged large irregular bosses a quarter of an inch high. On either side of the branchiæ there is a plain and thinner irregular portion, larger on the left than on the right side. *Dorsal tentacles* large, club-shaped, acuminate, and arising from a projecting eye-like sheath with irregular opening; the club-shaped portions laminated, the peduncles smooth. *Branchiæ*, of six compound leaflets, much branched, and arranged in a wide, round, anal orifice; the plumes nearly equal in size. *Head* with two small oral tentacles, concealed beneath the mantle.

Colour and general appearance.—General colour a brownish olive, the elevations and bosses paler. Upon the large bosses is a tinge of pink, surmounted by a whitish apex; a similar pink tinge upon the thinner part of the mantle round the margin. The thin non-tuberculated parts of the mantle on either side of the branchiæ straw-colour. Tentacle-sheaths same as the body-colour on which they are situated, the tentacles themselves somewhat darker. Branchiæ pale brown, the stems darker, and the edges of the leaflets whitish. Anal orifice white. Under surface—anterior half of the mantle pale brown-pink; posterior half yellowish, a broad irregular reddish band immediately surrounding the whole body.

Of this remarkable species I found one specimen upon a coral block in a shallow patch about 3 feet deep on the Fiery Cross Reef, China Sea, August 4th. The animal crawled freely, but did not float on its back while under observation. When turned over on its back it at once regained its natural position. The posterior portion of the mantle varied in form from various spontaneous degrees of constriction; sometimes it appeared to be nearly of an oval form, at others it resembled a *Tethys* in shape.

Subsequently I obtained a specimen of this species on the island of Barundum, west coast of Borneo, of a gigantic size for Nudibranchiata, October 8th, upon coral blocks, between tide-marks. Of the two specimens found here, one was $6\frac{1}{2}$ inches long and $4\frac{1}{4}$ wide. In all respects they resembled the one figured, even, to a great extent, in the arrangement of the tubercles or bosses.

From a careful comparison of the description given by Kelaart* of his *Doris exanthemata* with my drawings and descriptions of this species, I have come to the conclusion that they are not identical, although evidently nearly allied. The form of the dorsal tentacles, the crescentic arrangement of the anterior tubercles, as well as several points in the colour, to say nothing of the constriction of the mantle posteriorly (which might be accidental), all point to different species; nor is the foot of the present species deeply grooved and notched in front, as is the species described by Kelaart. I have named my species from the crescentic arrangement of the tubercles on the anterior border of the notæum.

I am by no means certain, though, that the animal named *Doris cerebralis*, Gould†, may not be identical. The Nudibranch referred to, 5 inches long by $2\frac{3}{4}$ broad, is stated to have been taken from a reef in Sandalwood Bay, Feejee Islands. Comparing Dr. Couthouy's coloured sketch with my own, the two not being drawn exactly in a similar position, considerable difference is manifest; but if taken along with Dr. Gould's description in the text, it seems quite possible they may be the same species. Should further research prove this to be the case, *D. crescentica* must necessarily be regarded as a synonym.

Genus CHROMODORIS, Alder & Hancock (1855).

CHROMODORIS IRIS, Coll., n. sp. (Plate IX. figs. 9-14.)

Length $2\frac{1}{4}$ inches. *Body* elongated, slightly tuberculated in profile, presenting two rounded elevations, with depression between. *Mantle* scanty, disclosing the foot on either side and posteriorly; much waved at the margin. Anteriorly there is a thin-lobed fimbriated veil, and posteriorly it is also divided into three lobes immediately behind the branchial tufts. *Dorsal tentacles* slender, conical, and finely lamellated, situated upon slight elevations of the mantle. *Branchiæ* composed of eight or ten simple leaflets arranged in a cup-shaped form like the petals of a flower; the leaflets delicately pinnate. *Foot* large, projecting about $\frac{3}{4}$ inch behind the mantle, and tapering to a point posteriorly.

* Ann. & Mag. Nat. Hist. 3rd ser. vol. iii. p. 300 (1859).

† U. S. Exploring Expedition, Mollusca and Shells, Text, 1852. p. 298, and Atlas, 1856, pl. xxiii. figs. 393 a-c, and Abraham, P. Z. S. 1877, p. 212.

Colour and general appearance.—Mantle deep blue, with a narrow edging of bright yellow, and an irregular yellow stripe on either side of the median line, or broken up into yellow spots. Large black roundish spots are scattered irregularly over the surface. The foot is of a lighter blue colour, spotted irregularly with yellow and black spots; the black ones roundish, the yellow ones forming an irregular line. Branchiæ and tentacles rich vermilion, the latter arising from tricoloured bases.

Spawn, a spiral ribbon of a pale straw-colour, deposited under observation.

Two specimens of this splendid species I obtained in a basaltic rock-pool under a large stone, at Makung, Pescadores Islands, May 12th, about midway between high- and low-water marks. In August of the same year I obtained one specimen of the same species from a reef on the shore of Labuan Island. From the beautiful combination of the three primary colours presented in this species, I have given it the name of the rainbow-goddess Iris.

Gould's *Doris smaragdina** bears a distant resemblance, but is a smaller animal, more greenish, with an indigo-blue margin and mantle, tentacles and branchiæ yellow.

Under *Chromodoris runcinata*† and *C. Semperi*‡ Dr. Rudolph Bergh has described two new species from the Philippines; but though in some points as to coloration and markings there is an approach to *C. iris*, the distinction, in absence of dorsal and marginal yellow stripes, with greyish tentacles and branchiæ and other particulars besides geographical distribution, warrants specific separation.

CHROMODORIS BULLOCKII, Coll., n. sp. (Plate IX. figs. 15-17.)

Length $2\frac{3}{4}$ inches. *Body* rather compressed, translucent. *Mantle* broad and square in front, narrowing behind, and having the sides and posterior portion of the foot uncovered. *Dorsal tentacles* $\frac{1}{10}$ inch long, slender, consisting of a cylindrical pedicle, smooth, and supporting a club-shaped, spirally laminated head. *Branchiæ* consisting of seven simple leaflets arranged in three sets, and arising from a thick retractile peduncle situated in a cylindrical sheath of the mantle, a little more than halfway from the anterior edge of the mantle to the posterior point of the foot. This peduncle gives off one leaflet in front, and two lateral branches, each of which gives rise to three leaflets. The leaflets are angular posteriorly, and edged with delicate papillæ upon the anterior aspect. *Head* concealed by the mantle, and bearing two small oral tentacles. *Foot* long and fleshy, extending nearly three fourths of an inch beyond the posterior edge of the mantle.

Colour and general appearance.—Body semitransparent. Head of a deep amethystine tint, shading behind the dorsal tentacles through paler amethyst to reddish upon the back; an opaque white edging all round the mantle. Peduncles of the tentacles and branchiæ deep amethyst; laminated portion of the tentacles and leaflets of the branchiæ deep orange-yellow. Foot pale amethyst, becoming deeper at the posterior portion, where it is as deep as at the anterior part of the mantle.

* U. S. Exploring Expedition, vol. xii. p. 296; Atlas, pl. xxii. figs. 390 a-c.

† Semper's 'Reisen im Archipel der Philippinen,' 1877, Band ii. Heft 11. p. 479, and Heft 10, pl. 53. figs. 5-12.

‡ Bergh, *op. cit. supra*, Heft 11, p. 482, pl. 55. figs. 2-7.

Of this magnificent species I dredged one specimen in 60 fathoms, off Reeruit Island, North Pacific, about 150 miles N.E. of Formosa. It was quite lively, and lived several days, moving freely about, and floating foot uppermost, but never showing any tendency to leave the surface of the water. I have named it after Captain Charles Bullock, R.N., a gentleman greatly interested in these studies, and from whom I met with much assistance and courtesy.

CHROMODORIS AUREO-PURPUREA, Coll., n. sp. (Plate IX. figs. 18-22.)

Length $1\frac{1}{4}$ inch. *Body* entirely covered by the mantle, except a small portion of posterior end of the foot. *Mantle* ample, entire, smooth, broad anteriorly. In a second specimen the edge of the mantle was somewhat indented in one or two places. *Dorsal tentacles* small, club-shaped, upon cylindrical footstalk, curving backwards and outwards; the club-shaped portion finely laminated. *Branchiæ* of ten leaflets, forming a small double ring; the leaflets conical, pinnate, and diminishing in size from before backwards. *Foot* slightly projecting behind mantle. *Head* rounded in front, with two minute oral tentacles at the sides.

Colour and general appearance.—Upper surface with a general yellow tinge, and covered over with small, irregular blotches of bright yellow, of a roundish or elliptical form. Mantle edged with faint violet, and an irregular row of deep violet-shaded spots running all round upon the faint edging, both being equally distinct upon the upper and under side. The laminated portions of the tentacles dark violet, shading off at the footstalk to the colour of the mantle. Branchiæ, leaflets, and midribs deep violet at their distal ends, becoming paler below, where they merge into the colour of the mantle. Underside yellowish white, with a bright yellow spot invisible from above.

Two specimens were obtained under moderate-sized rough stones upon the inner shore of Slut Island, Haitan Straits, on the Chinese coast, near low-water mark, June 30th.

These animals were very active, moving rapidly along with a gliding motion, at which time their mantles were broad and flowing over the sides, the anterior portion somewhat square. The tentacles were in constant and graceful motion, and they also frequently floated, foot uppermost, on the surface. When at rest, however, the animal assumed a nearly round form.

Mr. Andrew Garrett* has described and figured a new species (his *Goniodoris Tryoni*), 71 millims. long, from the Society Islands (Mus. Godeffroy, Hamburg), which suggests likeness to my *Chromodoris aureo-purpurea*. His example is mentioned as creamy white, margined with violet, and umber or tawny flesh-coloured branchial plumes and tentacles tipped with violet. The body-spots, however, are deep black ocelli surrounded with white. The branchial plume has 24 divisions, the posterior shorter than those in front, and each terminally divided. Dr. R. Bergh later† refers to Garrett's species under the designation *Chromodoris Tryoni*, and further describes and gives the anatomy of other specimens collected by Prof. Semper, these differing slightly in tint and markings. The

* Proc. Acad. Nat. Sci. Philad. 1873, p. 232, pl. iv.

† In 'Reisen im Archip. d. Philipp.' 1877, Band ii. Heft 11, p. 130, and in Journ. d. Mus. Godeffroy, 1877, Heft 14, pl. iv. figs. 12-23.

clearly defined black spots of *Chromodoris Tryoni*, as compared with the yellow blotches in *C. aureo-purpurea* and other particulars noted by Bergh, give me reason to regard that now described from the China coast as entitled to specific rank.

CHROMODORIS TUMULIFERA, Coll., n. sp. (Plate IX. figs. 23–26.)

Length $\frac{4}{5}$ inch. *Body* oblong, depressed, obtuse at either end. *Mantle* ample, covering the whole body, except the posterior portion of the foot; entire, tuberculated. *Dorsal tentacles* smooth and delicate, club-shaped, the club-shaped extremities very finely laminated, and twice as long as the cylindrical pedicle. *Branchiæ* small, consisting of nine simple leaflets, the anterior largest, and diminishing in size posteriorly, the two hindmost being rudimentary. *Head* crescentic, with two acute angles forming small tentacles, one on either side.

Colour and general appearance.—Mantle translucent yellowish white, the upper surface irregularly strewn with large, roundish, well-defined tubercles of a rich carmine colour and tumuliform profile. Round the mantle runs a broadish band of chrome-yellow, defined exteriorly, but somewhat fimbriated interiorly, leaving a narrow edging of the mantle tint all round the outside: upon this edging are two carmine spots on the anterior and two on the posterior angles of the mantle. The tentacles and *branchiæ* are of the same tint as the mantle, the latter delicately formed and difficult of observation.

One specimen of this handsome species found under a moderate-sized rough stone on the south side of Shut Island, Haitan Straits, coast of China, in June. It was a somewhat inactive animal, moving but slowly, but swimming occasionally foot uppermost on the surface.

In August of the same year, being on the island of Labuan, on the very opposite side of the China Sea, I met with this species more than once, at Pulo Pappan and Pulo Daat, two islets between Labuan and the mainland of Borneo. These specimens were about the same size as the Chinese one, but differed in that the carmine tubercles were more numerous and encroached upon the chrome border; the *branchiæ* also were more developed, and I was led to imagine that the specimen figured was a young individual.

In colouring, this animal bears some resemblance to the *Doris petechialis*, Gould*; but this latter is $2\frac{1}{2}$ inches long, $1\frac{1}{4}$ inch broad, has vermilion-coloured tentacles, pinkish *branchiæ*, a more lemon-coloured margin and partially slate-coloured dorsum, and its habitat is Honolulu, Sandwich Islands. Dr. Gould admits his drawings are somewhat imperfect, but sufficient for identification of the species.

The deep carmine spots recall the black ones of Garrett's *Chromodoris Tryoni*, l. c., but in other respects the two cannot well be confounded.

CHROMODORIS TENUIS, Coll., n. sp. (Plate IX. figs. 27–29.)

Length $\frac{3}{4}$ inch. *Body* long and slender, very attenuated when in motion. *Mantle* entire, covering the whole body, excepting the posterior portion of the foot; broad and squarish in front, and narrower from behind the tentacles backwards, bluntly pointed posteriorly. *Dorsal tentacles* short and club-shaped, laminated, the suture anterior.

* U. S. Explor. Exped. Moll. vol. xii. p. 296; Atlas, pl. 22. fig. 391.

Branchiæ small, consisting of seven small and simple leaflets arranged in a circle, the anterior leaflet somewhat larger than the others, and the posterior pair smallest. *Foot* long and narrow, slightly tubular, projecting beyond the mantle posteriorly.

Colour and general appearance.—Mantle opaque white with a slight tinge of yellow, especially on the anterior portion, edged with chrome-yellow, slightly shading off interiorly. The whole mantle is covered with minute roundish spots of carmine, irregularly distributed, absent only from the most anterior portion, the spots varying in size from mere specks to roundish definite spots. Tentacles yellowish, but not so bright as the border of the mantle; the bases whitish. Branchiæ pale yellow. Foot edged with chrome posteriorly, like the mantle. *Under surface* yellowish, foot and mantle with a faint edging of chrome-yellow, the carmine spots showing through at the sides of the head.

Two specimens were found on the under surface of a block of coral in a shoal patch of reef in the midst of the China Sea, named Fiery Cross Reef. It is possible the spot might be uncovered occasionally at low spring tides, but was now 3 feet under water. Notwithstanding this, however, these little creatures when captured were continually crawling out of the water and resting upon the dry edge of the vessel in which they were contained, under which circumstances they had a short and stumpy aspect. When placed in the water they were very lively and at once commenced crawling, having first stretched themselves to double their previous length, with a proportionate tenuity. While crawling they had a remarkably slender and linear appearance. They also swam freely on the surface, foot uppermost. (August.)

In most respects the *Chromodoris tenuis* agrees with the *Doris aspersa*, Gould *, save size, his specimen being $1\frac{1}{2}$ inch long by $\frac{1}{2}$ an inch broad, and its habitat Vincennes Island, Paumotu group. It may be questionable in this case whether we have specific distinction, or whether size and other slight variation may not be attributable to difference of age, sex, or geographical range. The *D. aspersa*, *D. cerebralis*, &c., given by Gould, were drawn from nature by Mr. Joseph P. Couthouy, Naturalist to the U. S. Explor. Exped., and therefore may be deemed reliably correct.

CHROMODORIS FUNEREA, Coll., n. sp. (Plate IX. figs. 30–33.)

Length $1\frac{3}{4}$ inch. *Body* simple, stout, except when actively in motion, when it becomes attenuated, obtuse in front. *Mantle* smooth and entire, having the posterior portion of the foot exposed during progression, well rounded anteriorly. *Dorsal tentacles* small, arising from a small simple sheath, laminated, with scarcely any pedicle. *Branchiæ* composed of seventeen or eighteen leaflets arranged in a convoluted form, the larger leaflets in front, the smaller behind, leaflet irregularly branched. *Head* concealed by the mantle and supporting a pair of oral tentacles.

Colour and general appearance.—Border of mantle narrowly edged with orange; general aspect of the upper surface a rich dark brown, with yellowish-white or white lines, following the direction of the border of the mantle, but in some places slightly ramifying and sometimes anastomosing. The posterior and exposed portion of the foot

* U. S. Explor. Exped. Mollusca and Shells, p. 304; and Atlas, pl. 25. figs. 399 a–c.

is bordered and streaked like the mantle. The tentacles have a white ring, sometimes two rings, round the sheaths; they are reddish above, deepening to dark brown below; rows of opaque white spots are arranged nearly regularly, parallel with the laminae; at the apex is a small whitish ring. The branchiae are reddish, the inner side of the stems of the leaflets marbled below with brown and white; the whole branchial tuft studded like the tentacles with minute spots of opaque white, having a very beautiful appearance. The *under surface* of the foot is white, with an orange border, like the mantle; the sides of the foot striped as above, only the white lines are whiter, but less distinct, and the dark body-colour paler.

This is a remarkably handsome species. The longitudinal white striae become widened when the animal is at rest, and very much attenuated when in progression. The branchiae and tentacles look as though studded with little pearls. It is somewhat remarkable that these animals never floated upon the surface of the water while under observation, and if placed upon their backs always immediately turned over.

These specimens were taken upon a reef east of the island of Labuan, Borneo, and one on the adjacent islet, Pulo Pappan, in August.

CHROMODORIS ALDERI, Coll., n. sp. (Plate IX. figs. 31-37.)

Length 2 inches. *Mantle* capacious, covering the head, squarish in front, slightly emarginated. *Dorsal tentacles* very small, and placed upon very short pedicles, finely laminated, having the commissure anterior; they have precisely the appearance of small cochineal insects. *Branchiae* of ten simple four-sided angular leaflets, some of them bifurcating near the apex, arranged in an imperfect circle, curving outwards and surrounding the anal orifice. *Head* with two small white oral tentacles. *Foot* somewhat tubular posteriorly, and extending about $\frac{1}{4}$ inch beyond the mantle.

Colour and general appearance.—General body-colour an opaque yellowish white or cream-colour, a border of bright orange running all round the edge of the mantle and projecting portion of the foot. Back beautifully marbled with reddish brown, an irregular row of carmine spots placed all round the marbled portion, between it and the orange border. Tentacles laminated alternately with crimson and white. Branchiae reddish, the angles crimson. Under surface of a delicate transparent white.

A most beautiful species, slow in its movements, which were confined to crawling and floating upon its back. One specimen only, found between tide-marks in a sandstone rock-basin in Ke-lung Harbour, North Formosa, May 31st. I have named it after the late Mr. Joshua Alder, whose name will always be connected with the history of this elegant order of Mollusca.

Genus ALBANIA, Collingwood, nov. gen. (1878).

Corpus depressum, molle, semipellucidum. Notæum amplissimum, undulatum et inversum. Rhinophoria flexibilia, sine vaginulis. Caput velo bilobato obsitum. Branchiae e circa 7 foliolis, separatim retractilibus, compositae.

Body depressed, soft, semitransparent. Notæum (mantle) ample, undulated, and turned up at the sides. Dorsal tentacles (rhinophoria) flexible, without sheaths.

Branchiæ consisting of about seven compound leaflets, each separately retractile. Head with a bilobated crenated veil.

I have named this genus after the late Mr. Albany Hancock, a gentleman so well known in connexion with the history of these animals. For euphony's sake I have so adapted the name as to make it agree with Formosa, the native island of this elegant species. The genus must be placed near *Hexabranhus*.

ALBANIA FORMOSA, Coll., n. sp. (Plate X. figs. 1-5.)

Length 2 inches. *Body* extremely delicate, almost semitransparent. *Mantle* broad and capacious, forming, as it were, wings or fins on either side; the edges turned over the back when at rest. *Dorsal tentacles* large and rather thick, consisting of a conical, bluntly pointed, finely laminated portion, with the commissure anterior, mounted upon a cylindrical pedicle of equal length, without a sheath, non-retractile. *Branchiæ* consisting of seven compound leaflets, each having three or four or five branches, and arising from a common thick pedicle, but separately retractile, the whole forming a ring near the posterior extremity of the mantle; very delicate and almost transparent. *Head* with a biereescentic veil, and studded round with a fringe of minute papillæ. *Foot* extending $\frac{1}{4}$ inch beyond the mantle posteriorly, somewhat rounded.

Colour and general appearance.—General tint a pale rose, darker and richer on the back, forming a vandyke pattern nearly regular on either side. Edge of the mantle opaque white, with a wide inner border of crimson, the whole studded with minute whitish translucent points, the greater or lesser abundance of which effects the gradation of colour. Laminated portion of the tentacles crimson; pedicles pale rose. Fringe of the veil orange; veil and posterior portion of the foot yellowish; under surface pale rose.

One specimen of this singular and beautiful Nudibranch was taken in a red sandstone rock-pool in Ke-lung Harbour, North Formosa, May 31st. When placed in a vessel of sea-water it commenced swimming freely with a *vertical* vermicular movement and extreme grace. The mantle was spread out wide, the tentacles thrown back, like ears, and the anterior and posterior extremities of the body thrown upward till they met above, then partially thrown back, the mantle waving in a vermicular manner from anterior to posterior edge. It continued swimming like this for a considerable time. It did not crawl about like other Nudibranchs, but when not swimming remained in a more or less contracted form, the mantle constantly changing its aspect. When, however, I turned it over, it floated on its back like its congeners. I have called the species *formosa*, both from its beauty and the island of which it is a native.

Family POLYCERIDÆ, Alder & Hancock (1855).

Genus TRIOPA, Johnston (1838).

TRIOPA PRINCIPIS-WALLIÆ, Coll., n. sp. (Plate X. figs. 6-11.)

Length $\frac{4}{5}$ inch. *Body* slender, narrow, rounded in front, obtusely pointed behind. *Mantle* scanty, just covering the body, smooth, and furnished with papillæ round the anterior portion and along the sides. The anterior papillæ, eight in number, arranged

in a crescentic form as a veil; the lateral papillæ five on either side. These papillæ consist each of a conical stem with pinnæ, the lateral papillæ being about twice the length of those round the head. *Dorsal tentacles* club-shaped, the upper half swollen and finely laminated, upon a cylindrical pedicle. *Branchiæ* of five leaflets arranged round the anal orifice upon an elevated portion of the body; the anterior leaflet much the largest, and the two posterior minute. Each leaflet simply pinnatifid, and feather-like in general aspect.

Colour and general appearance.—Body of a general pale orange-yellow, darker between the tentacles and along the median line, spotted irregularly with minute dots of orange. Upper half of the papillæ with larger spots of orange. Pinnæ translucent yellowish. Branchiæ pale orange-yellow. Tentacles spotted with orange about the central parts of the laminated portion.

One specimen found beneath stones near low-water mark, on Slut Island, Haitan Straits, coast of China, June 30th. It was rather sluggish in its habits, but swam on the surface, foot uppermost. I have named the species from the resemblance of the branchiæ to the well-known crest of the Prince of Wales.

Genus TREVELYANA, Kelaart (1858)*.

TREVELYANA FELIS, Coll., n. sp. (Plate X. figs. 12–14, immature.)

Length $\frac{1}{8}$ inch. *Body* simple, smooth, of a uniform scarlet colour, the intestines showing darker upon the dorsal surface. *Mantle* indistinct, covering the entire body. *Dorsal tentacles* two, perfectly simple, conical, scarlet. *Branchiæ*, none visible.

Several specimens of this little animal occurred upon a stone in a tide-pool on the basaltic shore of Makung, Island of Pong-hou, Pescadores, in May; and in June, six weeks later, I also found it on Slut Island, Haitan Straits. It was very active and flexible, assuming at different times the most singular forms, resembling in turn a fox, a rabbit, a cat, according to its different attitudes. It swims like the other nudibranchs on the surface of the water, foot uppermost. I cannot speak with great certainty of it, but believe it to be an immature species of *Trevelyana*, the trivial name being added to call other observers' attention to it. *Qu.* In what respects does it stand to the *T. (Stenodoris) rubra*, Pease†, from the Pacific?

Family DORIDOPSIDÆ, Alder and Hancock (1864).

Genus DORIDOPSIS ‡, Alder and Hancock (1864).

DORIDOPSIS ARBORESCENS, Coll., n. sp. (Plate X. figs. 15–17.)

Length $1\frac{3}{4}$ inch. *Mantle* capacious, enveloping the body, and overlapping the foot laterally and anteriorly; the edges deeply cut and puckered all round; smooth and

* *Trevelyana*, Kel. Journ. Asiatic Soc., and Ann. & Mag. Nat. Hist. 3rd ser. (1858) vol. i. p. 257. Messrs. Alder and Hancock, Trans. Zool. Soc. vol. v. p. 132 (footnote) suggest that "this genus may possibly be synonymous with the *Gymnodoris* of Stimpson, Proceed. Philad. Acad. Nat. Sc. 1855."

† Amer. Journ. Conch. vol. ii. p. 206, pl. 4. fig. 2.

‡ See "Indian Nudibranchiate Mollusca," Trans. Zool. Soc. vol. v. p. 124.

velvety. *Dorsal tentacles* rather large, consisting of a thickish footstalk pointing forwards and a laminated club-shaped portion curving backwards; the whole seated within the rim of a narrow retractile sheath. *Branchiæ* very large, consisting of about seven compound ramified leaflets, radiating from around the anal aperture, and situated near the posterior edge of the mantle. The anterior leaflets (pointing forward), when fully expanded, reach nearly halfway over the back; the posterior leaflets smaller. Each leaflet finely pinnatifid, and the whole forming a beautiful star nearly an inch in diameter, concealing the posterior portion of the animal. *Foot* large, occasionally visible beyond the posterior edge of the mantle; deeply cleft posteriorly.

Colour and general appearance.—The whole of the mantle a rich deep velvety blackish brown, edged with light chestnut. The peduncles of the tentacles blackish, translucent; the laminated portion like the mantle, and tipped with chestnut; branchial leaflets dark brown, tipped with light greyish at the edges. Underside of the mantle blackish, translucent; and foot light brown, shading to chestnut along the margin.

Two specimens of this handsome Nudibranch were found among rough stones on Slut Island, Haitan Straits, coast of China, near low-water mark, June 30th.

The animals were sluggish, not moving much, nor fast; they floated readily, foot uppermost, on the surface. The mantle was so capacious that in some attitudes they appeared as broad as long; but when ordinarily crawling, the large and beautiful branchiæ were very conspicuous, occupying nearly the posterior half of the body, and concealing the posterior margin of the mantle and end of the foot, which at that time projects beyond the mantle.

Messrs. Alder and Hancock * have shown that in the case of *Doridopsis nigra* there are at least three or more varieties with gradation of tints and markings, and inhabiting the coasts of the Loochoo Islands, Madras, and Ceylon. Our species, *D. arborescens*, appears quite distinct; but nevertheless, with such tendency to variation in a form closely related, careful comparison with a series might cause a different view to be taken as to its separation or identity with species already described by other authors.

DORIDOPSIS RUBRA, Kelaart. (Plate X. fig. 18.)

Length $1\frac{1}{5}$ inch; *breadth* 1 inch. *Body* thick, sluggish, opalescent. *Mantle* capacious, thin, covering the whole body, except the posterior portion of the foot; smooth, semi-transparent, folded posteriorly during progression. *Dorsal tentacles* pyramidal, short and thick, curved laterally, the footstalks smooth, as long as the upper portions, which are swelled, pointed at the extremities, and laminated. *Branchiæ* consisting of six compound leaflets, like feathers, somewhat unequal in size, surrounding the anus, retractile. *Head* small, covered with the mantle. *Foot* left uncovered posteriorly during progression.

Colour and general appearance.—Mantle of a rich rose-colour, darker in the thicker parts of the back, and paler upon the thinner portions of the sides, marbled on the back when contracted, from corrugation of the surface. Branchiæ of the same rose-tint as

* Ind. Nudib. Moll., Trans. Zool. Soc. vol. v. p. 128.

the mantle. Dorsal tentacles of a rich rose-colour, the footstalks paler. Underside of mantle pale rose, and underside of the foot inclining to yellowish.

One specimen, found under a stone between tide-marks in Singapore harbour, immediately west of the town, in December. It was sluggish in habit, and crawled slowly, but floated upon the surface foot uppermost.

This specimen died in the vessel of water, discolouring the fluid of a pink tinge, which, however, did not appear to injure two Planariæ in the same water.

Two figures of this species occur in Sir W. Elliot's 'Madras Nudibranchs'*. One of these, with black markings on the mantle, is supposed to be the typical specimen, and one of a more pure rose-colour the variety. I am disposed to think, however, that the present description will be found typical, and that those diverging into markings are varieties.

Family PHYLLIDIADÆ, Lamarck (1809).

Genus PHYLLIDIA, Cuvier (1798).

PHYLLIDIA SPECTABILIS, Coll., n. sp. (Plate X. figs. 19-23.)

Length 2 inches; greatest breadth $\frac{3}{4}$ inch. *Body* oval, tuberculated, covered with the mantle. *Tentacles* two, short, placed near together, rather more than $\frac{1}{4}$ inch from the anterior extremity of the mantle, tapering, slightly curved, laminated, black, retractile within a simple fixed sheath, which is situated on one of the tubercles of the mantle.

Upper surface covered with numerous irregularly-shaped tubercles, arranged in groups of from one to ten or twelve, these clusters each perfectly distinct and similarly coloured. The ground of the mantle is jet-black and smooth, forming a network which ramifies among the groups of tubercles; the bases of these groups polygonal, of a pale emerald-green colour, the most elevated knobs being whitish. A narrow, black, irregular edging surrounds the dorsal surface, enclosing all the groups of tubercles, outside which is a smoother and paler, irregular, and very slightly tuberculated margin. *Under surface*—Foot greyish, oval; a small bitentaculated head in front, the tentacles immovable. A narrow cleft bisects the posterior half-inch of the foot. Mantle ample, surrounding the head and foot on all sides. At the junction of the mantle with the foot and on the under edge of the mantle is a close row of lamelliform branchiæ, small in size, the series surrounding the whole body, except the head.

This beautiful *Phyllidia*, in captivity, deposited a long, irregular, and narrow ribbon of spawn, of a whitish colour, from an aperture in the side of the body. One specimen, found under a block of coral between tide-marks on Pulo Barundum (or Marundum), west coast of Borneo.

Doubts might be expressed whether this species may not come under that named *Phyllidia pustulosa*, Cuv., *P. verruculosa*, Cuv., and *Phyllidiella pustulosa*, Bergh†. If

* Alder and Hancock, Trans. Zool. Soc. vol. v. p. 126, pl. xxxi. figs. 1 and 2.

† See Cuvier, Ann. du Mus. (1804) vol. v. p. 268, pl. xviii. A. fig. 8; Mem. p. 3, fig. 8; also Bergh, Monog. p. 511, and in Semper's Reisen im Archip. d. Philipp. Band ii. Heft 10, p. 382.

such should be the case, this Nudibranch has a wide distribution. As I cannot, however, myself regard them as identical, I prefer to give that now described a separate specific designation.

Genus *FRYERIA*, Gray (1853).

FRYERIA VARIABILIS, Coll., n. sp. (Plate X. figs. 24–28.)

Length $2\frac{1}{4}$ inches; breadth $1\frac{1}{4}$ inch. *Body* convex, elongated, thickly tuberculated. *Tentacles* two, situated $\frac{2}{3}$ of an inch from the anterior margin of the body, arising from simple sheaths, in which they are retractile; the sheaths and tentacles black, the latter being also finely laminated. *Mantle* covering the head and sides of the foot, but leaving the posterior point of the foot exposed during progression.

Colour.—The smooth ground-portion black, but supporting a number of irregularly-scattered roundish tubercles, mostly single, a few double or treble; the tubercles largest and most loosely scattered over the central dorsal region, smaller and more closely clustered along the sides. The colour of these tubercles was in one specimen pinkish, in others of a pale emerald-green. In all respects, however, they are evidently the same species. *Foot* smooth, black above where visible. *Under surface*.—Foot dark grey beneath, blackish at the sides. Head small, with two small black tentacles concealed by the mantle. Underside of the mantle blackish. A row of lamelliform branchiæ occupying the junction of the foot and mantle beneath all round the body, excepting only the head. Anus situated under the mantle on the right side, about $\frac{3}{4}$ inch from the anterior margin.

Several specimens were found under blocks of coral on the reef of Pulo Barundum, west coast of Borneo. Animal very sluggish in its movements.

Family SCYLLÆIDÆ, Alder & Hancock (1855).

Genus *SCYLLÆA*, Linnaeus (1758).

SCYLLÆA PELAGICA, Linn. (Plate X. figs. 29–33.)

Length $1\frac{1}{2}$ inch (average). *Body* smooth, opalescent, narrow, compressed, with two broad tentacle-sheaths and two pairs of broad branchial lobes; the posterior portion raised to a crest, wedge-shaped, and notched like a cock's comb. *Dorsal tentacles* two, lamellated, in broad and somewhat clavate compressed sheaths, straight in front and finely serrated and crenated behind, with smooth and entire broad footstalks, the apex somewhat flattened and depressed. *Branchial lobes* broad, flat, in two pairs, situated on broad entire peduncles of nearly equal size; externally smooth, internally having a number of very delicate tree-like tufts irregularly scattered, of varying size, the large below and the smaller above. *Head* with a projecting crenated veil. *Foot* narrow, the edges folding over inwardly, but when the animal crawls on glass a small portion of the foot appears flattened out for the purpose.

Colour and general appearance.—General colour yellowish brown, darker along the edges of the papillary prominences and the tentacles and their connecting ridges, inter-

persed here and there with minute white spots. Tufts on papillæ light brown. On either side of the body is a row of opaque white projecting tubercles; and between them and the papillary prolongations are some minute turquoise spots, three or four in number. The body generally is opalescent, with faint brown markings.

Spawn, a loose straw-coloured coil, entwining the leaves and berries of *Sargassum bacciferum*, and imbedded in a mass of transparent jelly.



Portion of a branch of *Sargassum* bearing a floating bladder, and with (*sp*) a coil of spawn of *Scyllia pelagica* attached. Nat. size.

Considerable numbers of this pelagic species were found upon the *Sargassum* floating in lat. 25° N., long. 37° W., most pieces of the weed having one or more specimens. The animals were in a constant movement of contraction and writhing. In the water they swam freely, moving the head and tail from side to side alternately, so as nearly to touch one another; and when thus swimming were always, owing to the weight of the papillary prolongations and tentacles, back downward, and bore a grotesque resemblance to a four-legged animal with long ears (such as a Skye terrier). They would also attach themselves to the surface of the vessel by a sort of sucker formed by a small cylindrical portion of the foot (fig. 33, Pl. X.). There is no figure of this species in Alder and Hancock's work, nor do I know of any good figure. The present ones are from life, and fig. 30, Pl. X. represents its peculiar falling aspect, as mentioned above.

Alder and Hancock (T. Z. S. v. p. 136) have described a *Scyllia marmorata* and *S. viridis* as new species, the former of which, save in size, differs little, if at all, from the Linnean species *S. pelagica*; but they admit that it is difficult to decide as to what constitute specific differences in the genus. In Dr. Bergh's Monograph of *Scyllæa** there is an excellent *résumé* of the subject, and a number of varieties of *S. pelagica* described and referred to, as well as a good account of the anatomy of the genus given.

Family DENDRONOTIDÆ, Alder & Hancock (1855).

Genus BORNELLA, Gray (1847).

BORNELLA MARMORATA, Coll., n. sp. (Plate X. figs. 31-38)

Body long and slender, with seven pairs of papillæ. *Head* small, with a veil of five

* Semper's Reisen, l. c., Band ii. Heft 8, p. 315 et seq.

or six radiating papillæ on either side, deeply cleft in the middle. *Dorsal tentacles* situated upon thickish footstalks, from which spring one large branch (the uppermost) and four shorter branches, forming altogether a radiating sheath, in the midst of which is a slender laminated tentacle. *Marginal processes* in seven pairs, the anterior longest and most compressed, the posterior pair small and rudimentary. Each pair of papillæ varies in size and development: the first pair consists of three elongated bodies of the size of the largest branch in the radiating sheath of the tentacles; the second pair has two such; the third and fourth also, but smaller; the last pair has but one. On the inner side of each of these bundles is a finely ramified dendriform branchia, not so large as the processes, the processes and branchia all arising from a common stem. *Foot* long, and pointed behind. *Anus* situated on the right side, between the dorsal tentacles and first pair of papillæ.

Colour and general appearance.—Body beautifully marbled all over with streaks of vermilion, strongest on the back, and more delicate and faint on the sides of the foot. Papillæ tipped with vermilion, and also the radiating projections of the veil, but neither are marbled like the body. Dorsal tentacle-branches also tipped with vermilion, and the largest branch marbled.

Three specimens of this beautiful species rewarded a brief search among the rocks near the landing-place at Aden in March. They were under stones, not far from high-water mark. The animals were extremely active, often swimming with a lateral vermicular movement, at which time the body was laterally compressed. They were seldom quite at rest.

I here specifically distinguish this form, although previously* I inclined to regard it as the *B. digitata*, Adams†; but a more careful examination since discloses points of difference which had previously escaped my notice. *B. digitata* was first found at Sunda on floating luci, but it has since been got on the Madras coast by Sir Walter Elliot‡, and in the Philippines by Professor Semper§. Bergh§ enumerates six species belonging to the genus, and he adds very considerably to the account of the anatomy furnished by our countrymen Messrs. Alder and Hancock||.

DESCRIPTION OF THE PLATES.

The line beside certain of the figures denotes the natural size of the animal. The separate figures of tentacles, branchial tufts, and other parts are all considerably enlarged.

PLATE IX.

Figs. 1-5. *Doris pecten*, Coll., n. sp.: 1, general view of animal, its dorsum; 2, under surface of same; 3, a dorsal tentacle (rhinophore); 4, a branchial tuft; 5, outline of the animal at rest.

* "Observations on the Distribution of some Species of Nudibranchiate Mollusca in the China Sea," Ann. & Mag. Nat. Hist. 1868, ser. 4, vol. i p. 91; and 'A Naturalist's Rambles in the China Seas' (London, 1868), p. 9.

† Voyage of the 'Samarang,' p. 67, pl. xix, fig. 1.

‡ Trans. Zool. Soc. vol. v. p. 131.

§ Reisen im Archip. d. Philipp. Band ii. Heft 7, p. 301.

|| Loc. cit. T. Z. S. *suprà*.

- Figs. 6-8. *Doris crescentica*, Coll., n. sp. : 6, general view of animal, its dorsum (nat. size) ; 7, a dorsal tentacle and its sheath, anterior view ; 8, a branchial tuft (or branch). Sketch taken from specimen obtained at the island of Barundum, west coast of Borneo.
- Figs. 9-14. *Chromodoris iris*, Coll., n. sp. : 9, lateral view of animal in progression, the branchiæ partly closed ; 10, another view of the same, with the branchiæ fully expanded ; 11, a side view of the animal contracted and at rest ; 12, a lamina of the branchiæ ; 13, a dorsal tentacle ; 14, the spawn.
- Figs. 15-17. *Chromodoris Bullockii*, Coll., n. sp. : 15, the animal in progression ; 16, the underside of the head ; 17, plan in outline of the branchial laminae.
- Figs. 18-22. *Chromodoris aureo-purpurea*, Coll., n. sp. : 18, dorsal surface of the animal in progression ; 19, outline from above of the animal at rest ; 20, diagram of the mode of arrangement of the branchiæ ; 21, a branchial lamina ; 22, a dorsal tentacle.
- Figs. 23-26. *Chromodoris lunulifera*, Coll., n. sp. : 23, dorsal surface of the animal in progression ; 24, a tubercle of the dorsum seen in profile ; 25, a branchial lamina ; 26, a dorsal tentacle.
- Figs. 27-29. *Chromodoris tenuis*, Coll., n. sp. : 27, upper surface of the animal in progression ; 28, the under surface of the animal as seen swimming with foot ; 29, anterior view of a dorsal tentacle.
- Figs. 30-33. *Chromodoris funerea*, Coll., n. sp. : 30, animal in progression as seen from above ; 31, a dorsal tentacle ; 32, a branchial tuft ; 33, an outline plan of the branchiæ.
- Figs. 34-37. *Chromodoris Alderi*, Coll., n. sp. : 34, dorsal surface of the animal in progression ; 35, laminae of the branchiæ ; 36, a dorsal tentacle ; 37, the suctorial mouth.

PLATE X.

- Figs. 1-5. *Albania formosa*, Coll., nov. gen. et sp. : 1, animal in movement as seen swimming, its upper surface ; 2, the veil ; 3, a tuft of the branchiæ ; 4, a dorsal tentacle ; 5, an outline of the under surface.
- Figs. 6-11. *Triopa Principis-Wallia*, Coll., n. sp. : 6, animal in progression, upper surface, the branchiæ expanded ; 7, side view of the animal at rest ; 8, a papilla of the dorsum ; 9, a papilla of the head ; 10, a dorsal tentacle ; 11, outline of a branchial twig.
- Figs. 12-14. *Trevelyana felis*, Coll., n. sp., immature : 12, animal in progression ; 13, animal as contracted at rest ; 14, natural size.
- Figs. 15-17. *Doridopsis arborescens*, Coll., n. sp. : 15, the animal in progression ; 16, outline of the under surface of the body ; 17, a branchial tuft.
- Fig. 18. *Doridopsis rubra*, Kcl. : diagram of the branchiæ.
- Figs. 19-23. *Phyllidia spectabilis*, Coll., n. sp. : 19, upper surface of the animal ; 20, outline of the under surface of the same ; 21, a dorsal tentacle and sheath ; 22, diagram portion of branchiæ ; 23, the spawn.
- Figs. 24-28. *Freyeria variabilis*, Coll., n. sp. : 24, animal, its upper surface ; 25, diagram of the under and lateral surfaces, showing position of branchiæ ; 26, an under view of the head ; 27, a dorsal tentacle ; 28, sketch portion of the branchiæ.
- Figs. 29-33. *Scyllaea pelagica*, Linn. : 29, dorsal surface of the animal ; 30, position which the animal assumes in falling through the water ; 31, a dorsal tentacle sheath ; 32, branchial tuft covering the inner surface of the body ; 33, the foot from below.
- Figs. 34-38. *Bornella marmorata*, Coll., n. sp. : 34, outline sketch of the head ; 35, a dorsal tentacle ; 36, the veil ; 37, a branchial lobe ; 38, markings on the mantle.

III. *On the Anatomy of Ants.* By Sir JOHN LUBBOCK, Bart., M.P., F.R.S., F.L.S., D.C.L., LL.D., Vice-Chancellor of the University of London, President of the Entomological Society.

(Plates XI. & XII.)

Read February 6th, 1879.

Introductory Remarks.

IN conjunction with the observations on the habits of Ants, which the Society has done me the honour of publishing from time to time in the Journal, I have also been studying their anatomy, especially with reference to the muscular system. Of the anatomy of the head I have already given some account in the 'Transactions of the Microscopical Society,' 1877*.

The present paper is devoted to the thorax, with special reference to *Lasius flavus*. Though it is founded on numerous dissections, and on more than 1000 sections beautifully prepared for me by Mr. Newton, of the School of Mines, and Mr. Robertson, of Oxford, it is still very imperfect; and I am only induced to bring it before the Society in its present incomplete state because, while I hope it will be found to add somewhat to our knowledge, I see little prospect of being able to work out the subject as thoroughly as I could wish.

As a general rule, the thorax of insects is considered to consist of three more or less well-marked segments, usually known by the names suggested by Nitzsch—prothorax, mesothorax, and metathorax.

Dr. Ratzburg, however, published in 1832 a memoir ('Ueber Entwicklung der füsslosen Hymenopteren-Larven, mit besonderer Rücksicht auf die Gattung *Formica*'), in which he maintained that the fifth segment of the larva forms, not the so-called "scale," or first abdominal segment, but the hinder part of the thorax. This view has also been maintained by Audouin and Latreille; while, on the contrary, others, as, for instance, Kirby and Spence and MacLeay, consider the thorax of these insects to be composed of three segments, as usual.

Burmeister, indeed, roundly observes ('Manual of Entomology,' Shuckard's transl. p. 85) that Audouin's assertion is unfounded.

Lepelletier de St.-Fargeau, in his 'Histoire Naturelle des Hyménoptères' (1836), expresses the same opinion. "Il me paraît," he says, "plus simple parler comme voient mes yeux." Westwood also, in his excellent 'Introduction to the Modern Classification of Insects' (1840, p. 227), adopts the same view. It may, he admits, "be asserted that, as the body of the imago possesses two or three segments fewer than exist in the body of larva, we may suppose that the loss of one of these segments takes place at least in this manner, and in this part of the body. This, however, can only be done by admitting that the head and three thoracic segments of the imago are composed of five larva-segments instead of four, an admission negatived by all analogy with pedate larvæ."

* See Quekett Lecture, Monthly Microscopical Journal (1877), vol. xviii. p. 121.

Newport, in his article "Insecta," in the 'Cyclopædia of Anatomy and Physiology,' p. 920, says:—"at first we were inclined to Audouin's opinion, more especially on account of what we shall presently find in Lepidoptera, in which the fifth segment, in its atrophied condition, is as much connected with the thorax as with the abdomen. On further examination, however, we are satisfied that that portion of the metathorax which is posterior to the incisure belongs to the third segment of the thorax."

Fenger, in his "Allgemeine Orismologie der Ameisen" (Arch. für Naturg. 1862, p. 315), treats the thorax as consisting of three segments, and does not even hint at any difference of opinion on the subject. Mayr also, in his excellent 'Die europäischen Formiciden,' p. 4, and Schenck, in his "Beschreibung nassauischer Ameisen-Arten" (Jahrb. des Ver. für Naturkunde im Herz. Nassau, 1852), adopt the same view. Lastly, Forel ('Fourmis de la Suisse,' p. 5) says that the thorax "se divise en trois segments, comme chez tous les insectes : prothorax, mésothorax et métathorax."

It would perhaps hardly be appropriate to refer to more general or condensed works in which the thorax is stated to consist of three segments, as, for instance, by Owen ('Lectures on Invertebrate Animals,' p. 193), Claus ('Grundzüge der Anatomie,' p. 557), Rolleston ('Forms of Animal Life,' p. eix), &c.; for these eminent authors, though expressing no qualification, perhaps only meant to describe a general, and not necessarily an invariable, rule.

Huxley, in the 'Introduction to the Classification of Animals,' p. 58, observes, with his usual care and accuracy, that "three, or perhaps, in some cases, more, somites unite, and become specially modified to form the thorax."

Notwithstanding the high authorities who have adopted the opposite opinion, and although the first appearance of the thorax seems to support their view, for my own part I cannot but think that Ratzeburg's opinion was correct. Packard ('Guide to the Study of Insects,' p. 66) has given figures of the metamorphoses of *Bombus*, from which it seems clear that the fifth segment of the larva forms the posterior portion of the thorax of the perfect insect. Lacaze-Duthiers (Ann. des Sc. Nat. 1853, p. 231), Palmén (Zur Morph. des Tracheensystems), and Reinhard (Berl. ent. Zeits. 1865) also advocate the same view.

The position of the spiracles affords also strong evidence in support of the same opinion. It is generally stated in works on the anatomy of insects that there are on the thorax two pairs of spiracles, the first between the pro- and mesothorax, the second between the meso- and metathorax.

According, indeed, to Burmeister ('Handbook of Entomology,' p. 164), this is also the case with the Hymenoptera, which "all possess four (spiracles) in the thorax, two of which are upon the limits of the prothorax, between it and the mesothorax, and the other two lie between the meso- and metathorax. In the Hymenoptera, in which the thorax consists of a hard, horny case, and the segments are closely united together, the posterior pair of spiracles lie upon the metathorax itself, whereby they distinguish themselves from all the other orders." In fact, however, as may be seen from the accompanying figures (Pl. XI. figs. 2, 4, 5), the thorax of Ants possesses, not two, but three, pairs of spiracles.

The two first pairs are situated between the pro- and mesothorax and the meso- and

metathorax, as usual, and evidently correspond with the two pairs of thoracic spiracles of other insects. The third pair is situated at the side of the so-called metathorax; but in no case whatever do we find among insects two pairs of spiracles on one segment. Such an arrangement would be contrary to the whole plan of organization of the Arthropoda. It is obvious, therefore, that the third pair of spiracles corresponds to that which in other insects lies between the thorax and the first abdominal segment. Burmeister, as we have seen, remarks that certain Hymenoptera "distinguish themselves from all other orders" in having a pair of spiracles "on the metathorax itself;" but he supposes that these correspond to the spiracles which are ordinarily situated between the meso- and metathorax, overlooking the fact that these spiracles also exist as usual. It seems clear, therefore, that the portion of the body posterior to the third pair of spiracles really corresponds to the first abdominal segment in ordinary insects.

Nor are the respiratory organs alone in pointing to this conclusion. The internal chitinous appendages clearly divide the thorax into four portions; and I think it may be said that the thorax contains four ganglia, though the last (Pl. XI. fig. 2, *G*⁴, Pl. XII. fig. 2) is certainly not large.

The Prothorax.

The upper part of the prothorax, or pronotum, is formed in *Lasius flavus* by a single arched chitinous plate (Pl. XI. figs. 1, 4, & 6, *B*), which slopes downwards from its posterior border towards the head, where it forms a sort of keel (Pl. XI. figs. 1 & 2). Seen externally and from the side, its lower border appears to join the upper edges of the propectus; but a transverse section (Pl. XII. fig. 4) shows that this is not so, but that the propectus is continued for some distance beyond the lower margin of the pronotum, and is then connected with it by a membrane which passes from the upper margin of the propectus to the lower one of the pronotum: The propectus tapers in front (Pl. XI. fig. 5), terminating on each side in two teeth, which lock into two corresponding teeth (Pl. XI. figs. 6 & 7, and Pl. XII. fig. 1, *A*) or processes at the back of the head. The propectus is divided into two plates (Plate XI. fig. 2, *C* & *T*), one anterior and one posterior, which, moreover, are divided into lateral regions by a central ridge. The anterior plate of the propectus has in front a deep bay or depression, at the two horns of which are the above-mentioned teeth or processes. Each region of the anterior division of the propectus has therefore roughly the form of a triangle with arched sides. The posterior division of the propectus is elliptic in form, and not so large as the anterior division, to which it is firmly attached.

The propectus is therefore attached to all the surrounding chitinous plates by flexible, though tough, membranes. It hangs, indeed, something like the under body of a carriage; and from the fact that the anterior horns of the prothorax interlock with the posterior processes of the head, if the propectus is turned round it carries the head with it. On the other hand, if the head be retracted, the posterior processes of the head, from their position with reference to the anterior horns of the prothorax, prevent the head of the insect from being turned round against its will.

The posterior surface of the propectus is connected with the anterior edge of the mesopectus by a tough, but flexible, membrane.

I have found it difficult to understand the descriptions given of the interior skeleton of the thorax by previous writers, nor do their figures give much assistance. In the normal insect-thorax there appear to be seven principal processes—four springing from the back, and called by Kirby and Spence the phragma, prophragma, mesophragma, and metaphragma; and three from the sternum, named by the same authors profurca, mesofurca, and postfurca. In the worker Ants the four superior processes are not developed, but the furca, mesofurca, and postfurca are very important; they give attachment to various muscles, and serve also to protect the nervous system. Kirby and Spence, however, dismiss them very summarily, and, as regards the processes of the endosternum, state that they “are not sufficiently remarkable to require particular notice”*. Burmeister† says that in the prothorax (of the Hymenoptera) “there are two strong pointed processes, each of which has a double root. The exterior one comes from the margin of the prosternum, and the interior one from the central ridge of the same part. Between these roots the muscles of the coxæ pass, and between the processes themselves run the pharynx and the nervous cord; and it is to these processes that the connecting muscles of the pronotum and prosternum are attached. In the mesothorax we first find the prophragma, a small, not very high, horny partition, which descends from the anterior margin of the mesonotum; and we next find a delicate ridge, which encompasses the whole distinctly separated mesonotum. The mesosternum and scapulae are closely joined in a half-ring, and from the central carina of this ring springs a broad strong ledge, which at its upper margin is furnished on each side with a strong process; they form with the ledge a rectangular cross, and serve as points of insertion for the muscles of the coxæ of the middle legs, lying on each side contiguously to the central ridge.” As regards the metafurca, all he tells us is, “between the metanotum and metaphragma the two large side pieces and their auxiliaries lie, separated from each other by furrows, from which, internally, strong ridges spring, and to which the muscles of the posterior legs are attached.”

Graber, in his admirable ‘Die Insekten,’ truly observes that the endoskeleton has been almost entirely neglected by recent entomological writers. I trust, however, that the following description and the accompanying figures may give some idea of the endoskeleton as it exists in the workers of *Lasius flavus*.

The hinder plate of the propectus turns upwards at approximately a right angle, and is produced into the antefurca (Pl. XI. figs. 1, 2, 5, & 6; Pl. XII. fig. 8), a chitinous process which extends more than halfway up the dorsum, leaving, however, a central orifice (Pl. XII. fig. 4) through which the nervous chords penetrate, while the œsophagus and the heart pass between the upper edge of the antefurca and the dorsum.

As seen from behind (Pl. XII. fig. 4) it has the form of a cross with four arms. In the middle of the centre piece is an oval orifice, the wider end below, through which the nervous system passes. The centre of the upper part sends out a process both anteriorly and posteriorly, as shown in Pl. XI. fig. 2; in fact it forms a sort of case for the protection of the ganglia.

* ‘Introduction to Entomology,’ vol. iii. p. 587.

† *Op. cit.*

The medifurea (Pl. XI. fig. 2; Pl. XII. fig. 5, *Med*) rises from the medipectus. It is much more elongated and slender than the antefurea, and has the form of a Y, the upper arms of which, however, are connected by a cross bar, thus leaving a triangular orifice with rounded angles, through which runs the nervous chord. To a process of the cross bar is attached the muscle which elevates the prothorax.

The postfurea (Pl. XI. fig. 2 and Pl. XII. fig. 6) also has somewhat the form of a Y. The stem, however, is much shorter, the branches are curved, and the cross bar is absent. The postfurea arches forwards, so that the upper part of the arms approach those of the medifurea, with which they are connected by tendinous fibres. Between the medifurea and the postfurea lies the third thoracic ganglia.

Muscles of the Head.

There are two elevators of the head on each side (*a* & *a'*). The first (Pl. XI. figs. 1, 2, & 5, *a*) is a thin muscle, which rises from the back near the middle line, at the junction of the pro- and mesothorax, and, passing forwards, is inserted at the upper margin of the occipital foramen, where the posterior margin of the head joins the intersegmental membrane. The second is more powerful. It (Pl. XI. figs. 1, 2, *a'*) rises from the anterior surface of the upper part of the antefurea, and, passing forwards and slightly upwards, is inserted close to the preceding. The heads of attachment of this muscle reach almost across the segment.

The first depressor of the head (Pl. XI. figs. 1, 2, *b*), like the second elevator, is attached to the anterior face of the antefurea, but at a lower level, and, passing over the prothoracic ganglion, is attached to the inferior margin of the occipital foramen.

The second depressor of the head (Pl. XI. fig. 1, Pl. XII. fig. 1, *b'*) is attached to the central and hinder part of the propectus, and, passing directly forwards, is also attached to the lower edge of the occipital foramen.

The rotators of the head are five in number on each side. The first (Pl. XI. figs. 1, 2, & 4, *c*) rises from the middle of the lateral wall of the pronotum, and, passing downwards and inwards, is attached to the anterior toothed process of the propectus. The second rotator passes from the middle of the lateral wall of the propectus (Pl. XI. figs. 4, 6, & 7, *c'*), and is attached to the outer anterior toothed process of the prosternum. The third rotator (Pl. XI. figs. 4, 6, 7, *c''*) lies rather nearer the middle of the segment. In front it is attached to the inner toothed process, and posteriorly to the lateral and posterior wall of the propectus, a little behind the preceding. The fourth rotator (Pl. XI. figs. 1, 2, 6, *d*) commences at the anterior process of the propectus, close to the preceding, and, passing backwards and slightly inwards, is attached to the anterior central process of the antefurea. The fifth rotator (Pl. XI. figs. 1, 2, & 6, *d'*), rises with the preceding, but passes diagonally across the segment to be attached to the lateral edge of the antefurea.

Although the muscles of the head of Coleoptera, as described by Straus-Durekheim in *Melolontha*, and as given generally by Burmeister in his 'Handbook of Entomology,' are more complex than those which are found in Ants, yet neither of these authors describe any muscle exactly comparable to the following.

This muscle (Pl. XI. figs. 1, 5, *e*) differs from the preceding in that, while they taper

as they pass forward, it, on the contrary, rises from the anterior surface of the pronotum by several, somewhat diverging heads, and, passing backwards and slightly downwards, is attached to the upper part of the antefurea. It would therefore seem to draw the propectus, and consequently to push the head, forwards. It is obvious that if the head is projected forwards, and the propectus then retracted, so that the head could move freely towards each side, it would be easily turned by the rotators above described. On the contrary, if it be retracted, or if the propectus be thrown forward, so that the posterior process of the head interlocks with the anterior processes of the propectus, the head would be so situated as to retain its position even against a considerable force.

The next muscles to be mentioned are the elevators of the antepectus; these are two in number. The first (Pl. XI. figs. 1, 2, 4, 5, and Pl. XII. fig. 4, *f*) rises from near the middle of the pronotum, and, passing downwards, is attached to the anterior process of the antepectus. The second is weaker; it is attached to the side of the pronotum, and, passing downwards (Pl. XI. fig. 5, *f*¹) and slightly inwards, is also attached to the anterior process of the antepectus, close to the preceding. The attachment of the first large rotator of the head (*c*) lies between those of these two muscles, as may be seen in Pl. XI. fig. 5, where *f* and *f*¹ represent the heads of these two muscles, which, when they contract together, would tend to elevate the antepectus.

The depressor of the antepectus is smaller. It commences (Pl. XI. figs. 5, 6, 7, *g*) at the lower edge of the pronotum, and, passing upwards, is attached to the upper edge of the antepectus, which therefore, on contracting, it draws downwards.

Front Legs and their Muscles.

The legs consist of the following segments :—1, coxa; 2, trochanter; 3, femur; 4, tibia; and 5, tarsus, this latter being composed of five segments.

The description given by Straus-Durekheim of the muscles by which the legs are moved has been adopted by most subsequent writers. According to him, the anterior legs have five muscles, four flexors and one extensor. The first flexor rises from the superior lateral and anterior surface of the prothorax, and is attached to the posterior border of the coxa. The second and third flexors rise from the superior and posterior surface of the prothorax, and are attached to the coxa just outside the preceding. The fourth flexor rises from the external portion of the posterior surface of the “rotule,” and is attached to the posterior edge of the coxa. Lastly, the extensor rises from the pronotum, near the first flexor, and acts immediately in opposition to the preceding.

The number of muscles in the Ant appears to be greater than in *Melolontha*, and the disposition is in many respects dissimilar.

The first muscle of the leg (Pl. XI. figs. 4, 7, and Pl. XII. figs. 1, 4, *h*) rises from the anterior lateral wall of the prothorax, and, passing downwards and backwards, is attached to the upper anterior angle of the condyle of the coxa, which, therefore, it would tend to draw forwards and inwards.

The second (*i*, Pl. XI. figs. 1, 2, 4; Pl. XII. figs. 1, 3, & 4) lies transversely in the lower and posterior portion of the antepectus. In Pl. XI. figs. 1 & 2 it is seen in section. In Pl. XI. fig. 4 it is severed close to its attachment. It rises from the central ridge

of the antepectus, and, passing transversely across the segment, is attached to the posterior and outer edge of the leg, at the summit of the projecting head or condyle. It would tend to extend the leg laterally.

The third (*i*¹, Pl. XII. fig. 4) is attached to the antefurca, and, passing downwards and outwards, is attached close to the preceding.

The fourth and fifth muscles of the fore legs are of a different character, penetrating into the coxa. The fourth rises from the upper edge of the antepectus in front of the antefurca (Pl. XI. fig. 4, and Pl. XII. fig. 4, *k*), and passes downwards into the coxa.

The fifth rises partly from the hinder wall of the antefurca, partly from its posterior spur (Pl. XI. figs. 1, 2, 4, & 7, *l*), and, like the preceding, passes down into the coxa. The upper part of the muscle is joined by some fibres, which pass round the posterior process of the antefurca and are attached to the pronotum.

The seventh is attached to the outer and posterior edge of the coxa, and, passing backwards and inwards, is attached to the anterior surface of the medifurca. It is not, however, well shown in any of my sections.

In addition to these muscles, the coxa contains two others, one of which rises from the upper and outer wall and passes downwards and inwards, while the other, rising from the upper and inner wall, passes downwards and outwards.

The small trochanter (Pl. XII. fig. 1, *tr.*), in addition to the above-mentioned fibres of the flexor of the femur, contains only a short single muscle, which at its lower end is attached to the thigh.

The femur (Pl. XII. fig. 1, *fm*) contains two muscles. The extensor is attached to the upper surface of the segment, the fibres being attached to one side of a long tendon, which at its lower end is attached to a chitinous piece at the upperside of the head of the tibia. The flexor is situated rather on the lower side of the segment; but the fibres diverge from both sides of the tendon, and some of them cross those of the extensor muscles. Some of the central fibres pass into the trochanter, and are attached to its inner margin. The lower end of the tendon of the flexor is attached to a chitinous process.

The tibia presents some very remarkable points, with reference to which I may perhaps be permitted to quote a passage from a paper of mine published in the 'Microscopical Journal,' 1877.

Remarks on the Tibial Organ.

In the year 1844 Von Siebold* described a remarkable organ which he had discovered in the tibiæ of the front legs of *Gryllus*, and which he considered to serve for the purpose of hearing. These organs have been also studied by Burmeister, Brunner, Hensen, Leydig, and others, and have recently been the subject of a monograph by Dr. V. Graber†, who commences his memoir by observing that they are organs of an entirely unique character, and that nothing corresponding to them occurs in any other insects or, indeed, in any other Arthropods.

* "Ueber das Stimm- und Gehör-Organ der Orthopteren," Wiegmann's Arch. f. Natur. 1844.

† Die tympanalen Sinnes-Apparate der Orthopteren, von Dr. Vitus Graber, 1875.

I have therefore been very much interested by discovering in Ants a structure which seems in some remarkable points to resemble that of the Orthoptera. As will be seen from a glance at Dr. Graber's memoir, and the plates which accompany it, the large trachea of the leg is considerably swollen in the tibia, and sends off, shortly after entering the tibia, a branch, which, after running for some time parallel to the principal trunk, joins it again. See, for instance, in his Monograph, pl. ii. fig. 43, pl. vi. fig. 69, pl. vii. fig. 77, &c. Now I have observed that in many other insects the tracheæ of the tibia are dilated, sometimes with a recurrent branch. The same is the case even in some mites.

I will, however, reserve what I have to say on this subject, with reference to other insects, for another occasion, and will at present confine myself to the Ants. If we examine the tibia, say of *Lasius flavus*, we shall see that the trachea presents a remarkable arrangement, which at once reminds us of that which occurs in *Gryllus* and other Orthoptera. In the femur it has a diameter of about $\frac{1}{3000}$ of an inch; as soon, however, as it enters the tibia it swells to a diameter of about $\frac{1}{500}$ of an inch, then contracts again to $\frac{1}{800}$, and then again, at the apical extremity of the tibia, once more expands to $\frac{1}{500}$. Moreover, as in *Gryllus*, so also in *Formica*, a small branch rises from the upper sac, runs almost straight down to the tibia, and falls again into the main trachea just above the lower sac. The remarkable sacs at the two extremities of the trachea in the tibia may also be well seen in other transparent species, such, for instance, as *Myrmica ruginodis* and *Pheidole megacephala*.

At the place where the upper tracheal sac contracts there is, moreover, a conical striated organ (*x*), which is situated at the back of the leg, just at the apical end of the upper tracheal sac. The broad base lies against the external wall of the leg, and the fibres converge inwards. In some cases I thought I could perceive indications of bright rods, but I was never able to make them out very clearly. This also reminds us of a curious structure which is found in the tibia of Locustidæ, between the trachea, the nerve, and the outer wall, and which is well shown in some of Dr. Graber's figures.

Other Organs of the Prothorax.

The anterior pair of spiracles, as already mentioned, lie (Pl. XI. figs. 4, 5, *Sp*¹) between the pro- and mesothorax. The tracheal tube immediately behind the spiracle is provided with a short muscle, as already described in other insects by MM. Landois and Thelen*. The ganglion (Pl. XI. figs. 2, 6, & 7, *G*¹) is of considerable size, and is connected anteriorly with that of the head, and posteriorly with that of the mesothorax, by a double commissure. In the latter case the commissures pass through an orifice in the antefurca, which thus not only serves as a support to the muscles, but also as a protection to the nervous system.

The œsophagus passes straight through the prothorax, and, indeed, does not enlarge into the crop until it reaches the enlarged part of the abdomen. In the upper part of the prothorax lie the large thoracic salivary glands (Pl. XI. fig. 2, *gl*).

A considerable part of the upper and anterior portion of the prothorax is occupied by the thoracic salivary glands, which I have already described in the 'Microscopical Journal.'

* Zeitschr. f. wiss. Zool. 1867, p. 187.

They consist of a number of branched and twisted tubules which gradually unite in a single duct. This duct then swells into a capacious receptacle, after which it contracts again, and after joining the corresponding duct from the other side, passes through the neck into the head, and then, after a meandering course, opens at the upperside of the under lip. The duct consists of an epithelial layer of cells, within which is a structureless membrane, strengthened, as is so often the case with the ducts of glands, by chitinous ridges, which give it very much the appearance of a trachea. Fig. 3, Pl. XI., represents a glandular organ situated in the lower part of the thorax of *Myrmica ruginodis* immediately above the base of the anterior leg.

Mesothorax and Middle Legs.

The mesothorax is much more closely connected with the metathorax than with the prothorax (Pl. XI. fig. 2). Like the prothorax it consists of an upper and lower more or less arched plate. The upper plate or mesonotum (Pl. XI. figs. 2, 5, 6, *Mes*) is oblong, somewhat emarginate behind, the spiracles (Pl. XI. figs. 2, 4, *Sp*²) being situated at the posterior angles. In front the mesonotum projects some way over the sides of the prothorax; and as the middle legs are attached quite at the posterior end of the metapectus, they, as well as the posterior legs, lie under the metanotum, and seem at first sight as if they belonged to the hinder division of the thorax.

The depressor of the prothorax (Pl. XI. figs. 2, 4, 5, *m*) arises from the junction of the meso- and metathorax, beneath the spiracle, and passing down and forwards is attached to the lower posterior edge of the prothorax, which therefore it would tend to draw downwards.

On the other hand, the elevator of the prothorax (Pl. XI. figs. 2, 5, *n*) rises from the upper part of the antefurca, and passes backwards and downwards to a spur of the medifurca just above the mesothoracic ganglion.

The second pair of legs has, according to Straus-Durekheim's description of *Melolontha*, three flexors and two extensors. The arrangement, however, is very different from that in the Ant.

Graber, in his excellent work, refers specially to four muscles; the first (*ulm*, in his fig. 61) rises from the central ridge of the sternum, and, passing directly outwards, is attached to the inner edge of the coxa, which therefore it would draw inwards and downwards. The next two (*shm* 1 and 2, in his fig. 61) rise one behind the other from the side of the thorax, and would, on the contrary, draw the leg outwards and upwards. The fourth also lies behind the other two, but would specially draw the leg upwards.

As regards the Ant, the principal muscles which move the middle legs are shown in Pl. XI. fig. 4, Pl. XII. fig. 2.

The first muscle (*o*, Pl. XI. figs. 4, 5, and Pl. XII. figs. 2 & 5) rises partly from the upper lateral wall of the mesonotum immediately under the spiracle, partly from the medifurca, and passing downwards contracts into a tendon which is continued into the leg. It would tend to raise the leg.

The second rises from the anterior edge of the medipectus (Pl. XII. fig. 2, *p*), and passing straight back is attached to the anterior edge of the coxa.

In opposition to this the third muscle rises from the anterior portion of the central ridge of the medipectus (Pl. XII. fig. 2, *q*), and passing outwards and backwards is attached to the inner posterior edge of the coxa.

The fourth rises from the posterior portion of the central ridge of the medipectus, and passing outwards is attached (Pl. XII. fig. 2, *r*) to the inner edge of the coxa.

The fifth rises partly from the anterior wall of the medipectus (Pl. XII. fig. 2, *s*), partly from its median ridge, under *q*, and is attached to the outer anterior edge of the coxa.

The last (Pl. XII. figs. 2, 5, *t*) rises from the medifurca, and passing downwards and forwards is attached to the outer edge of the coxa.

Posterior Portion of Thorax.

The first elevator of the abdomen (*a*, Pl. XI. figs. 2 & 5) rises from the metanotum, on each side of and not far from the central line, and, running parallel to the same muscle on the other side, is attached to the upper anterior edge of the so-called knot.

The second elevator of the abdomen (*v*¹, Pl. XI. fig. 2, Pl. XII. fig. 2) rises from the postpectus, and passing upwards, outwards, and backwards is attached to the upper lateral anterior edge of the abdomen. It would draw the abdomen upwards and at the same time sideways.

The depressor of the abdomen rises partly from the metanotum behind the first elevator, and partly (*c*, Pl. XI. fig. 2, Pl. XII. fig. 2) from the upper part of the postfurca, and passing backwards and downwards is attached to the lower anterior edge of the abdomen.

The rotator of the abdomen rises from the metanotum just behind the first elevator (*w*, Pl. XI. figs. 2, 5, and Pl. XII. fig. 2), and passing backwards, downwards, and outwards is attached to the lateral edge of the first abdominal segment.

I now pass to the muscles of the posterior leg.

The first muscle of the leg rises partly from the lateral wall of the metanotum (*x*, Pl. XI. fig. 5, Pl. XII. fig. 2) and partly from the upper part of the postfurca, and passes downwards and backwards into the coxa.

The second muscle also rises from the postfurca below the preceding (Pl. XII. fig. 2, *x'*), and passing downwards and backwards is attached to the upper posterior margin of the coxa. It terminates above in a strong chitinous tendon, which is connected with the postfurca by a number of tendinous filaments.

The third muscle rises from the lateral wall (Pl. XII. fig. 2, *y*) of the mesothorax, partly from that of the metathorax, and passing backwards is attached to the outer edge of the leg.

The fourth muscle is attached to the anterior edge of the postpectus (Pl. XII. fig. 2, *y'*), and passing backwards and outwards is attached to the external margin of the leg close to the preceding.

The fifth is also attached to the anterior edge of the postpectus, but, passing directly backwards (Pl. XII. fig. 2, *z*) above the preceding is attached to the exterior and anterior margin of the leg.

The sixth muscle is attached to the anterior edge of the metathorax, and passes

directly backwards (Pl. XII. fig. 2, z^1) and over the preceding to the internal and posterior edge of the posterior leg.

Although the workers of Ants do not possess wings, Dewitz has shown * that the larvae possess "imaginal disks," like those from which the wings of the males and females are developed, but smaller. These embryonic wings reach no more advanced stage than that which they have already acquired in the full-grown larva, and in the imago no trace of the front wings appears to be discernible, while it is curious that the hinder wings, though they are smaller in the males and females, are in some cases still indicated by a minute protuberance.

The presence of wings necessarily entails many other differences, and consequently

The thorax of the male and female Ants is very unlike that of the workers—not, indeed, in the arrangement of the muscles already described, but by the changes and additions contingent upon the presence of wings. The females, as is well known in most cases, strip off their wings soon after the marriage-flight. In *Anergates alrotulus* the males are wingless, and, according to Schenck†, the queens in some cases do not acquire wings. The great muscles of flight are, as might be expected, very large in the winged Ants; on the other hand, they are few in number, more simple, as it would appear, than those of most other insects. There are, indeed, several small muscles attached to the wings; but the main muscles are only four in number—two elevators and two depressors, which therefore are the same for both the wings. Among most other insects there are said to be an elevator and a depressor for each wing; in the Lepidoptera, Hemiptera, and certain Hymenoptera (Sawflies) the depressors on each side have coalesced, while in Ants and their allies the same is also the case with the elevators.

The depressors (Pl. XII. fig. 8 & 9, β) are powerful muscles which occupy a considerable part of the upper portion of the thorax. They rise from the mesonotum and pass horizontally backwards, lying close to one another along the median line. At their posterior end they are attached to the two processes of the metaphragma (Pl. XII. fig. 8) (costal of Chabrier), an arched process concave in front and convex behind, which, starting from the true hinder edge of the metathorax, passes downwards, terminating in two processes.

The elevators (Pl. XII. fig. 8 & 9, θ) of the wings lie almost at right angles to the preceding. They rise from the meso- and metasternum, and passing upwards and forwards outside the preceding are attached to the wall of the back.

Immediately under the metanotum in this part of the body lies the so-called "metathoracic gland." It consists of a number of large nucleated cells opening into a vestibule (Pl. XII. fig. 7) by short minute ducts. The inner wall of the vestibule, at least in the workers of *Lasius flavus*, is thrown into several curved ridges, from which proceed a number of strong hairs. The vestibule in this species is elliptic in form and opens to the outside by a wide mouth. In other species the shape is different; in *Myrmica ruginodis* it is somewhat S-shaped and the hairs are smaller; in *Lasius fuliginosus* it falls into two divisions, the outer one funnel-shaped, the inner thrown into a number of spherical chambers. This organ seems to be less highly developed in the males and females than in the workers.

* Zeitschr. f. wiss. Zool. 1878.

† Jahrb. des Ver. für Naturkunde im Herz. Nassau, p. 6.

The abdomen is moved by two muscles (Pl. XI. fig. 2, Pl. XII. fig. 8) situated in the so-called first segment or knot.

The first of these muscles occupies the greater portion of the upper part of the knot, and, passing downwards and backwards, is attached to the lower wall of the abdomen.

The second muscle is attached to the anterior wall of the knot, immediately below the preceding, and, passing straight backwards, is attached to the upper wall of the abdomen.

DESCRIPTION OF THE PLATES.

The lettering used for the different figures is as follows :—

<i>H.</i> Head.	<i>Pr.</i> Prothorax.	<i>Mes.</i> Mesothorax.	<i>Met.</i> Metathorax.
<i>Sp</i> ¹ . 1st pair of spiracles.		<i>Sp</i> ² . 2nd pair.	<i>Sp</i> ³ . 3rd pair.
<i>Z.</i> Membrane connecting the thorax with head.			
<i>Z</i> ¹ . „ „		the propectus with medipectus.	
<i>Z</i> ² . „ „		the pronotum with the propectus.	
<i>An.</i> Antefurca.			
<i>Med.</i> Medifurca.			
<i>Po.</i> Postfurca.			
<i>gl.</i> Site of thoracic salivary gland.			
<i>P.</i> Propectus.	<i>Pr.</i> and in some figures <i>B.</i> Pronotum.		<i>H.</i> Processes of the head.
<i>X.</i> Processes of the propectus.	<i>G</i> ¹ . 1st ganglion.		<i>G</i> ² . 2nd ganglion.
<i>G</i> ³ . 3rd ganglion.	<i>G</i> ⁴ . 4th ganglion.		<i>L</i> ¹ . Base of 1st pair of legs.
<i>L</i> ² . Base of 2nd pair of legs.			<i>L</i> ³ . Base of 3rd pair of legs.
<i>C.</i> Anterior plate of propectus.			<i>T.</i> Posterior plate of propectus.
<i>Ab.</i> Abdomen.	<i>fm.</i> Femur.	<i>tr.</i> Trochanter.	<i>Ce.</i> Coxa.

MUSCLES.

<i>a.</i> 1st elevator of the head.	<i>a</i> ¹ . 2nd elevator of the head.	<i>b.</i> 1st depressor of the head.
<i>b</i> ¹ . 2nd depressor of the head.	<i>c.</i> 1st rotator of the head.	<i>c</i> ¹ . 2nd rotator of the head.
<i>c</i> ² . 3rd rotator of the head.	<i>d</i> & <i>d</i> ¹ . 4th and 5th rotators of the head.	
<i>e.</i> Protractor of the head.	<i>f.</i> Elevator of antepectus.	<i>f</i> ¹ . Elevator of antepectus.
<i>g.</i> Depressor of antepectus.	<i>h.</i> 1st muscle of anterior leg.	<i>i.</i> 2nd muscle of anterior leg.
<i>i</i> ¹ . 3rd muscle of anterior leg.	<i>k.</i> 4th muscle of anterior leg.	<i>l.</i> 5th muscle of anterior leg.
<i>m.</i> Depressor of prothorax.	<i>n.</i> Elevator of prothorax.	<i>o.</i> 1st muscle of middle leg.
<i>p.</i> 2nd muscle of middle leg.	<i>q.</i> 3rd muscle of middle leg.	<i>r.</i> 4th muscle of middle leg.
<i>s.</i> 5th muscle of middle leg.	<i>t.</i> 6th muscle of middle leg.	<i>u.</i> 1st elevator of abdomen.
<i>u</i> ¹ . 2nd elevator of abdomen.	<i>v.</i> 1st depressor of abdomen.	<i>v</i> ¹ . 2nd depressor of abdomen.
<i>w.</i> 1st rotator of abdomen.	<i>x.</i> 1st muscle of posterior leg.	<i>x</i> ¹ . 2nd muscle of posterior leg.
<i>y.</i> 3rd muscle of posterior leg.	<i>y</i> ¹ . 4th muscle of posterior leg.	<i>z.</i> 5th muscle of posterior leg.
	<i>z</i> ¹ . 6th muscle of posterior leg.	
<i>β.</i> Depressor of wings.		<i>θ.</i> Elevator of wings.
<i>π.</i> Elevator of abdomen.		<i>φ.</i> Depressor of abdomen.

PLATE XI.

Fig. 1. Vertical and longitudinal section through the prothorax of *Lasius flavus*. $\times 125$.

H, posterior wall of head; *B*, pronotum; *P*, propectus; *Z*, membrane connecting the head and the pronotum; *Z*¹, membrane connecting the head and the propectus; *L*, base of leg cut short; *An*, antefurea. Muscles:—*a*, first, and *a*¹, second elevator of the head; *b*, first, and *b*¹, second depressor of the head; *c*, first rotator of the head; *d*, fourth, and *d*¹, fifth rotator of the head; *e*, protractor of the head; *f*, elevator of antepectus; *i*, second muscle of anterior leg; *l*, fifth ditto.

Fig. 2. Longitudinal and vertical section through the thorax of *Lasius flavus*. $\times 125$.

H, posterior part of head; *Pr*, prothorax; *Mes*, mesothorax; *Met*, metathorax; *C*, anterior plate of propectus; *T*, posterior plate of propectus; *G*¹, first, *G*², second, *G*³, third, and *G*⁴, fourth thoracic ganglion; *gl*, thoracic salivary gland; *Sp*², second, and *Sp*³, third spiracle; *Z*, membrane connecting the head and the pronotum. Muscles:—*a*, first, *a*¹, second elevator of the head; *b*, first depressor of the head; *c*, first, *d*, fourth, and *d*¹, fifth rotator of the head; *f*, elevator of antepectus; *i*, second muscle of anterior leg; *l*, fifth muscle of anterior leg; *m*, depressor, and *n*, elevator of prothorax; *q*, third, and *r*, fourth muscle of middle leg; *u*, first, and *u*¹, second elevator of abdomen; *v*, first depressor of abdomen; *w*, first rotator of abdomen; *x*, first muscle of posterior leg.

Fig. 3. Glandular organ at base of prothorax in *Myrmica ruginodis*. *L*, upper portion of coxa of anterior leg. $\times 200$.Fig. 4. Vertical and longitudinal section through the thorax of *Lasius flavus*. $\times 125$.

Pr, pronotum; *P*, propectus; *Sp*¹, first, *Sp*², second, and *Sp*³, third spiracle; *L*¹, base of anterior leg; *L*², base of middle leg; *L*³, base of posterior leg; *Cx*, coxa. Muscles:—*c*, first, *c*¹, second, and *c*², third rotator of the head; *f*, elevator of antepectus; *h*, first, *i*, second, *k*, fourth, and *l*, fifth muscle of anterior leg; *m*, depressor of prothorax; *o*, 1st muscle of middle leg.

Fig. 5. Thorax of *Lasius flavus*, seen from above and somewhat flattened out. The external hairs are omitted. $\times 125$.

Pr, prothorax; *Mes*, mesothorax; *Met*, metathorax; *Sp*¹, first, and *Sp*³, third pair of spiracles; *Z*, membrane connecting the thorax with the head; *An*, antefurea; *Sgl*, site of the postthoracic glands. Muscles:—*a*, first, and *a*¹, second elevator of the head; *c*, first rotator of head; *e*, protractor of head; *f* and *f*¹, the two elevators of the antepectus; *g*, depressor of antepectus; *l*, fifth muscle of anterior leg; *m*, depressor, and *n*, elevator of prothorax; *o*, first muscle of the middle leg; *u*, first elevator of abdomen; *w*, first rotator of abdomen; *x*, first, *y*, third muscle of posterior leg.

Fig. 6. Longitudinal and horizontal section through the prothorax of *Lasius flavus*. $\times 125$. Seen from below.

P, wall of the propectus; *B*, wall of the pronotum; *Z*¹, membrane connecting the pro- and medipectus; *X*, processes of the propectus; *H*, processes of the head; *G*¹, first ganglion; *An*, antefurea. Muscles:—*b*, first depressor of the head; *c*¹, *c*², cut ends of the rotators of the head; *d*, *d*¹, rotators of head; *g*, cut ends of depressor of antepectus.

Fig. 7. Section through the prothorax at a rather lower level than the preceding. $\times 125$.

P, wall of the propectus; *B*, wall of the pronotum; *Z*¹, membrane connecting the pro- and medipectus; *X*, processes of the propectus; *H*, processes of the head; *G*¹, first ganglion; *G*², second ganglion; *L*, base of the leg; *An*, antefurea. Muscles:—*c*¹, second, and *c*², third rotator of the head; *g*, depressor of antepectus; *h*, first, *k*, fourth, and *l*, fifth muscle of anterior leg (part of these being cut across).

PLATE XII.

Fig. 1. Propectus of *Lasius flavus*, seen from below. $\times 100$.

H, head; *B*, pronotum; *P*, propectus; *X*, processes of the propectus; *W*, processes of the head; *Z*, membrane connecting thorax with head; *Ce*, coxa; *tr*, trochanter; *fm*, femur. Muscles:—*b*, first, and *b'*, second depressor of head; *c*¹, *c*², second and third rotators of head; *g*, depressor of antepectus; *h*, first, and *i*, third muscles of anterior leg.

Fig. 2. Longitudinal and horizontal section through the posterior portion of the thorax of *Lasius flavus*. $\times 125$.

Pr, posterior margin of prothorax; *Mes*, mesothorax; *L*², base of second, and *L*³, base of third pair of legs; *G*, second, and *G'*, third thoracic ganglion; *Ab*, commencement of abdomen. Muscles:—*o*, first, *p*, second, *q*, third, *r*, fourth, *s*, fifth, and *t*, sixth muscle of middle leg; *u*, first, and *u'*, second elevator of abdomen; *v*, first depressor of abdomen; *x*, first, *x*¹, second, *y*, third, *y*¹, fourth, *z*, fifth, *z*¹, sixth, and *z*², seventh muscle of posterior leg.

Fig. 3. Longitudinal and horizontal section through the thorax of *Lasius flavus*. $\times 125$.

Fig. 4. Transverse and vertical section through the prothorax of *Lasius flavus*. $\times 125$.

B, pronotum; *P*, propectus; *LL*, bases of legs; *Ce*, coxa; *G*, ganglion; *An*, antefurca; *Z*², membrane connecting the pronotum and propectus. Muscles:—*c*, first rotator of head; *f*, elevator of antepectus; *h*, first, *i*, second, *i'*, third, *k*, fourth muscle of anterior leg.

Fig. 5. Transverse and vertical section of thorax of *Lasius flavus* passing through the second pair of spiracles and the base of the middle legs. $\times 125$.

*Sp*² *Sp*², spiracles of second pair; *Med*, medifurca; *LL*, bases of legs; *u*, elevator of thorax; *o*, first, and *t*, sixth muscle of middle leg.

Fig. 6. Transverse and vertical section through the thorax of *Lasius flavus*, showing the postfurca. $\times 125$.

Fig. 7. Metathoracic organ of *Lasius flavus*. $\times 125$.

Fig. 8. Longitudinal and vertical section through the thorax of a queen of *Lasius flavus*. $\times 50$.

H, head; *a'*, elevator of head; *b*, first depressor of head; *G G G G*, ganglia in depressor of prothorax; *β* , depressor of wings; *θ* , elevator of wings; *π* , elevator of abdomen; *ϕ* , depressor of abdomen.

Fig. 9. Longitudinal and vertical section through the thorax of a male of *Lasius flavus*. $\times 50$.

An, antefurca; *β* , depressor of wings; *θ* , elevator of wings.

IV. *On the Extinct Land-Tortoises of Mauritius and Rodriguez.* By ALFRED C. HADDON, B.A., Scholar of Christ's College, and Curator in the Museum of Zoology and Comparative Anatomy of the University of Cambridge. (Communicated by Prof. NEWTON, M.A., F.R.S.)

(Plate XIII.)

Read November 20th, 1879.

HAVING been recently engaged in determining and cataloguing the large series of bones of the extinct Land-Tortoises of the Mascarene Islands contained in the Museum of the University, it has appeared to me that some notes made during that undertaking might, if published, be of interest to zoologists in general and herpetologists in particular; for though a portion of the series was submitted to Dr. Günther when preparing his admirable monograph*, yet a very considerable portion, in some instances containing more perfect specimens, has been received since the publication of that work, and has therefore never been described, while the whole forms the largest assemblage of these rare remains that has yet been collected.

All the specimens in this series were presented to the University by Mr. Edward Newton, M.A., C.M.G., formerly Colonial Secretary of Mauritius, and now Lieutenant-Governor of Jamaica. Those from Mauritius were obtained, with one or two exceptions, from the mud and peat of the Mare aux Songes, where they were found, together with numerous remains of the Dodo and other extinct members of the fauna of that island, under circumstances which have been described by the late Mr. George Clark †. The portion of the series received in 1867 was examined by Dr. Günther, and several of its specimens have been described and figured by him in his work above mentioned; but the larger portion did not reach the Museum till the summer of the present year, 1879. The bones from Rodriguez were received in like manner at two different times; but they were all obtained from the caves of that island, the first portion having been collected by Sergeant Morris, who was working under the direction of Mr. George Jenner, during the excavations and explorations made at the expense of the British Association for the Advancement of Science between 1866 and 1871, inclusive ‡, and the second portion having been obtained similarly by Mr. James Caldwell on his visit to the island in 1875 §. This last collection was received at our Museum during the past summer and, like the Mauritian series, which arrived at the same time, has not had the advantage of Dr. Günther's inspection.

* 'The Gigantic Land-Tortoises (Living and Extinct) in the Collection of the British Museum.' By Albert C. L. G. Günther, M.A., M.D., Ph.D., F.R.S. London, 1877.

† "Account of the late Discovery of Dodos' Remains in the Island of Mauritius." By George Clark. The Ibis, 1866, pp. 141-146.

‡ Report of the British Association, 1865, p. xli; 1866, pp. 401, 402; 1867, pp. 287, 288; 1872, pp. 23, 24.

§ "Notes on the Zoology of Rodriguez." By J. Caldwell, C.M.Z.S. Proc. Zool. Soc. 1875, pp. 644-647.

In writing the following remarks, it is needless for me to mention the inestimable assistance that I have derived from Dr. Günther's elaborate monograph, as well as from a comparison of the specimens in our Museum which have been named by him. Indeed without these latter I could hardly have determined and catalogued our more recent acquisitions; but since they are so extensive, it seems to me desirable that some detailed account of them should be given, not with the view of superseding, but of supplementing, the excellent descriptions which he has already given. I think it cannot but be gratifying to him to find that the larger amount of materials at my disposal enables me to confirm in almost every respect the conclusions at which he had arrived.

In all cases I have closely followed his treatment of the subject, in order to facilitate comparison.

I. TORTOISES OF MAURITIUS. *Testudo triserrata* and *T. inepta*.

The remains of these, the two common Mauritian species, when sufficiently perfect, can, with the exception of the femur and the smaller leg-bones, be easily distinguished, the other forms indicated by Dr. Günther, *Testudo indica* and *T. leptoenemis*, being of doubtful value. *T. indica* is known from the shell only, "the upper profile of which is straight, and not declivous in front;" while *T. leptoenemis* rests alone on the scapula, pelvis, and femur; but its scapula does not differ from that of *T. triserrata*, though its pelvis and femur are "more slender than in either *T. triserrata* or *T. inepta*."

Skull.—The additions are:—(1) a portion of the occipital and tympanic regions of a moderately sized skull; but not having the maxilla it is impossible to refer it to either species.

(2) A slightly imperfect lower jaw of a very large specimen of *T. inepta*, from the deposits of Flacq.

Mandible, extreme length and breadth..... 78 millim.

Carapace.—Only a small fragment of a plastron.

Vertebral column.—A single example of the seventh cervical, centrum only. It is biconcave, the hæmal spine as in *T. Foscæri*. There is a groove between it and the tubercles of the anterior zygapophyses, and a deep fossa on the upper surface behind the anterior zygapophysis on each side, as in the sixth cervical of *T. Foscæri*, and as is also occasionally found (see examples in the Museum) in the seventh vertebra of the same animal.

	millim.		millim.
Extreme length of centrum	38	Length in median line.....	34
„ width	27	„ „	18
„ depth	19	„ „	6

Shoulder-girdle.—Two right and five left can without difficulty be referred to *T. triserrata*. Of these there is nothing worthy of notice.

Of the three right and three left which are supposed to belong to *T. inepta*, two are of unusually large size. One right shoulder-girdle, marked $\frac{21.7.66}{92}$ (Pl. XIII. fig. 7), has the *coracoid ankylosed*: though this character is supposed to be peculiar to *T. triserrata*, yet it is found, probably as an individual variation, in this specimen, the compressed

curved precoracoid (“acromion”) &c. proving it to be *T. inepta*. This peculiarity can be paralleled with the case of the corresponding bone of the Rodriguez tortoise.

There is no fresh example of *T. inepta*, var. *Boutoni*.

T. inepta.

	A. millim.	B. millim.	millim.	millim.
Length of scapula (measured from the suture with coracoid)	177	170
Circumference in its middle	72	72
Longitudinal diameter of glenoid cavity	40 (worn)	40
Length of precoracoid (acromion)	95	92
Length of coracoid	102	91
Greatest width of coracoid	69	broken
Least circumference of shaft of coracoid	49	50

The great amount of variation in the shape of the coracoid in *T. triserrata* is worthy of special attention. Though all the well-marked specimens in our collection have passed through the hands of Dr. Günther, he only remarks (*l. c.* p. 46) that “the coracoid lamina [is] sometimes deeply grooved.” The amount of the variations can be well understood by reference to Plate XIII. figs. 1-5.

The anterior side is sometimes produced into a long spur. The posterior may become straight rather than bowed for the greater portion of its length, as may also the internal edge (‘epicoracoid’ region). The shaft may be narrow, or broad and flattened; but it is in the blade that we see the greatest variations. This may be almost smooth, concave above, and gently convex on its inferior surface, as in the typical example (Günther, pl. xxiv. fig. B), or flat superiorly, with the concave inferior surface traversed by prominent longitudinal ridges, or convex on the upper surface, with the concave lower surface strongly marked by prominent palmated ridges. The interspaces may become so thin as to be more or less perforated.

The relative measurements of these bones also vary very considerably, as the following table shows:—

	A (type). millim.	B. millim.	C. millim.	D. millim.	E. millim.
Length of coracoid	74	75	66	76	76
Greatest width of coracoid	61	71	63	58	67
Least circumference of coracoid ..	54	66	47	62	63

It will thus be seen that while the length averages about the same, the width and circumference of the shaft vary greatly, the normal proportions being, length of coracoid n , breadth $n-9$, circumference $n-15$.

The study of all these variations irresistibly calls to mind the remarks of Messrs. A. and E. Newton*, the truth of which has been subsequently confirmed by the latter gentleman and Mr. J. W. Clark†, in their respective memoirs on the osteology of the extinct Didine bird of Rodriguez, as to the wonderful variability of that species. To quote the former:—“There does not seem to be a single bone in the skeleton of *Pezophaps solitaria* which is not liable to greater or less individual variation of some kind or other, . . . but

* “On the Osteology of the Solitaire or Didine Bird of the Island of Rodriguez, *Pezophaps solitaria* (Gmel.).” By Alfred Newton, M.A., and Edward Newton, M.A. Phil. Trans. 1869, p. 330.

† “On the Osteology of the Solitaire (*Pezophaps solitaria*, Gmel.).” By Edward Newton, C.M.G., and John Willis Clark, M.A., Superintendent of the Museum of Zoology and Comparative Anatomy in the University of Cambridge. Phil. Trans. vol. 168, p. 451.

the individual variation is not at all confined to absolute size; it extends to the relative proportion of divers parts of the bones, to processes or depressions upon them, such as are commonly held to be specifically characteristic, so that it is often utterly impossible to predicate any definite limits of individual modification. . . . Nor is the variability of which we speak wholly dependent on age or sex."

To find that the same results attend the examination of these Tortoise-remains cannot fail to suggest the possibility that when a sufficient series of specimens of *any animal* is compared a similar amount of variability may be observed; and if this consideration should lead to nothing else, it should at least make us, in many cases, hesitate about describing a new species of vertebrate from a single bone, or even from several fragments.

A second variety of coracoid has been added, which, since it is free, may be safely referred to *T. inepta*; of this we have three examples, one, however, being fragmentary. They differ from the former type in both form and size (Pl. XIII. fig. 6). The absolute length is much greater than in *T. triserrata*; the neck is more slender, and the posterior edge straighter, as is also the internal margin. Even in these few examples we see ample evidence of tendency to variation. The great difference of the length of this bone in the two species is well seen by averaging the relative proportions; for taking the length of the coracoid to be n , the average breadth would be about $n-30$, and the least circumference $n-47$.

Humerus.—Six right and eight left belong to Dr. Günther's group *a* (*T. triserrata*).

Two right and four left of *T. inepta* (group *c*); one of the latter is of enormous size. In one or two examples the hollow behind the head is extremely shallow, as in Dr. Günther's group *b*, thus showing that the latter is merely a variation; indeed it is often rather difficult to distinguish between humeri supposed to belong to the two kinds of tortoises.

	<i>T. triserrata</i> , millim.	<i>T. inepta</i> , millim.
Length of humerus from summit of head to middle of trochlea	175	250
Narrowest circumference	70	112
Longest diameter of head	43	50
Shortest diameter of head	34	35
Extreme breadth between condyles	71	83

Ulna.—Three right examples apparently belonging to the same species.

	millim.
Extreme length	114
Narrowest circumference	44

Radius.—Three specimens, only one of which is perfect. Dr. Günther's types *a* and *c* may be easily recognized. The one right, *a*, has a rather slender shaft.

One well-marked right example of *c*; the other, left, is only a distal fragment; it would, however, be somewhat larger.

	<i>c</i> , millim.
Length of radius	175
Circumference in narrowest part	38
Longitudinal diameter of semilunar facet	30
Transverse diameter of semilunar facet	20

Pelvis.—*T. triserrata*. We have two pelves nearly perfect, three fragments, and one right pubis. Two are of great size; although one of these is of such large size, yet the os ilium is very narrow and thin. This is probably due to bone-absorption owing to age. The terminal portion of the pubic process is flattened horizontally, and is surrounded laterally by a deep groove.

The distinctive characters of *T. leptocnemis* appear of too slight a character to be of great certainty, especially as no perfect pelvis is known.

T. inepta. Our previous collection of portions of a male and female pelvis has been greatly enriched by the addition of four perfect pelves and of three halves. There is one immense os ilium, which is very broad but much compressed, and evidently belonged to a very old male. There is a femur probably belonging to this pelvis.

	<i>T. triserrata</i> .		<i>T. inepta</i> .	
	millim.	millim.	millim.	millim.
Longest inner vertical diameter of pelvis from summit of ilium to symphysis	156	..	138	..
Longest inner horizontal diameter of pelvis	120	..
Shortest inner horizontal diameter of pelvis between ilio-pubic prominences	80	..
Longest diameter of foramen obturatorium	36	..
Width of symphyseal bridge	25	..
Breadth of posterior portion of ossa ischii	55	..
Length of os ilii	140	..	108	147
Least width of os ilii	29	..	25	40
Proximal width of os ilii	54	85+

Femur.—The sixteen new examples have so much the same facies that it is impossible to distinguish between the two species. There does not seem to be a specimen of *T. leptocnemis*.

	millim.
Length of femur	194
Least circumference	90
Width of condyle	73

This femur probably belongs to *T. inepta*.

Tibia.—Two right and two left. These show no peculiarity, except that one is stouter than the others.

	millim.
Length of tibia	144
Circumference, least	55
Breadth at upper end	46

II. TESTUDO VOSMERI. Rodriguez.

All the remains from this island are referable to one species only, notwithstanding the large series of bones examined. The experience of Dr. Günther points to the same conclusion.

Skull.—The additions to our previous fragment consist of one imperfect specimen of large size, two occipital crests, and one very perfect example of a young individual, the lower jaw being also present.

The largest probably measured $11\frac{1}{2}$ millim. long.

Carapace.—There are two small carapaces, with their plastra, one being very perfect, and the posterior marginal plates of a third and large example; also two

plastra of small size, and a portion of a much larger one. In all the thinness of the bones is very remarkable.

Length of Carapace.		Width of Carapace.		Sternum.		Caudal plate.	
In straight line.	Over curve.	In straight line.	Over curve.	Length.	Width.	Length.	Width.
millim.	millim.	millim.	millim.	millim.	millim.	millim.	millim.
13 $\frac{3}{4}$	16 $\frac{1}{2}$	9 $\frac{1}{2}$	17 $\frac{3}{4}$	9 $\frac{3}{4}$	7 $\frac{3}{4}$	1 $\frac{1}{4}$	3 $\frac{1}{4}$
..	..	9 $\frac{1}{2}$ +	9	1 $\frac{9}{16}$	3

Vertebral column.—We have 74 specimens of cervical vertebræ, all being well represented except the 1st, of which no example is known. The 6th does not present the foramen noticed by Günther (*loc. cit.* p. 57; also Ann. & Mag. N. H. 1873, xi. p. 397); for out of our 13 specimens of this bone only one has a perforation, which is very small, and might even be accidental. The foramen apparently only occasionally is present, and that only in old animals.

There are several examples of dorsal and caudal vertebræ.

In the majority of cases it has been impossible to distinguish between the slender and the stout varieties. There is a certain amount of variation in the size of the hæmal spine, in the thickness of the centrum, &c.

	2nd.	3rd.	4th.	5th.	6th.		7th.	8th.
	millim.	millim.	millim.	millim.	A. millim.	B. millim.	millim.	millim.
Length of centrum.....	39	51	66	51	60	64	50	41
Depth of centrum in the middle	10	9	9	10	14	13	18	10
Horizontal width of middle of centrum	7	8	10	9	16	18	17	18
Width of anterior condyle.....	12	broken	14	40
Width of anterior glenoid cavity	20	15	..	26	..
Width of posterior condyle	1	..	18	18	13	20
Width of posterior glenoid	12	15	31	..
Distance of outer margins of anterior zygapophyses.....	16	broken	25	20	29	..	25	30
Distance of outer margins of posterior zygapophyses.....	20	23	23	19	broken	..	28	37

Shoulder-girdle.—There is great uniformity about these bones, the chief degrees of variation being in the form of the transverse section of the scapula near the glenoid fossa. The general form of the pectoracoid ("acromion") reminds one of the same bone in *T. triserrata*, in being laterally compressed proximally, and vertically compressed distally. In his monograph, Dr. Günther remarks (p. 59), "It must be mentioned that there are in the collection a right and a left scapula, evidently belonging to the same individual, which differ remarkably from all the others in not having the coracoid ankylosed, although the individual appears to have been fully adult, and in having the body of the scapula proper uniformly compressed. It is difficult to account for this apparently individual aberration." Now, out of the 85 scapulæ in our collection, there are 32 in which the coracoid is ankylosed to the remainder of the shoulder-girdle, leaving 53 in which that bone is distinct; of these, 23 are of larger size than the smallest of the ankylosed bones, several being considerably so. Thus it seems to be a characteristic of this species for the coracoid to be very irregular in its ankylosis with the coraco-scapula.

It is interesting to note that in one example there is a tendency towards the formation

of a coracoid foramen by ossification from the coracoid and precoracoid extending into the epicoracoid region.

	Coracoid ankylosed. millim.	Coracoid free. Total. (Large examples.)		Total. millim.
		millim.	millim.	
Right	9	29	(11)	38
Left	23	24	(12)	47
Total.....	32	53	(23)	85

	Coracoid fused.			Coracoid free.	
	A. millim.	B. millim.	C (smallest). millim.	millim.	millim.
Length of scapula measured from the suture with the coracoid	105	..	75	132+	..
Circumference in its middle	35	40	8	50	..
Longitudinal diameter of glenoid cavity	24	30	19	30+	..
Length of coracoid.....	49	..	35	..	60
Greatest width of coracoid	38	..	27	..	48
Length of precoracoid (acromion).....	48	..	39	50+	..

Humerus.—There is nothing peculiar in our 54 specimens, the largest bone measuring :—

	millims.
Length (measured in a straight line from the summit of the head to the middle of the trochlea) ..	171
Circumference of the narrowest part of the shaft	62
Longest diameter of head	33
Shortest diameter of head	29
Extreme breadth between the condyles.....	50+

Pelvis.—Most of our examples are young, the symphysial bridge still being very narrow.

Femur.—One of the SS femurs is of gigantic size :—

	millim.
The extreme length being	166
The least circumference	68

In conclusion, I would draw the attention of herpetologists to these collections of Mascarene Tortoise-remains, now in the Zoological Museum at Cambridge, since they form by far the most complete series of specimens of these very interesting extinct reptiles. I also add my best thanks to Prof. Newton for his kind help whilst preparing these notes.

For the convenience of those who may wish to prosecute further the study of these animals, as well as to show the amount of materials on which the present remarks are based, I append a list of the specimens in the Museum of the University which I have consulted.

Testudo triserrata. Mauritius.

- 6 skulls and 2 lower jaws. (C.) One figured, Günther, pl. xxiii. fig. A.
- 1 skull. New Coll.
- 4 humeri, right. (C.)
- 6 „ „ New Coll.
- 2 „ left (C.)

- 8 humeri, left. New Coll.
 11 shoulder-girdles, right. (C.)
 2 „ „ New Coll.
 10 „ left. (C.) One figured, Günther, pl. xxiv. fig. B.
 5 „ „ New Coll.
 7 pelves (or portions). (C.) One figured, Günther, pl. xxviii. fig. c; 2 others mentioned.
 6 „ „ New Coll.
 2 portions of carapaces. (C.)
 5 plastrons, adult male. See Günther, p. 45. One figured, pl. xx. fig. E.
 1 carapace. Figured, Günther, pl. xx. fig. D.

Sp. incert. Mauritius.

- 1 femur, left. (C.)
 8 „ „ New Coll.
 6 „ right. (C.)
 8 „ „ New Coll.
 3 tibiae. New Coll. (One C.)
 2 „ „
 2 radii. „
 1 „ „
 3 ulnae. „
 1 portion of plastron.
 1 „ 7th cervical vertebra.

Testudo inepta. Mauritius.

- 5 skulls and 2 lower jaws. (C.) 1 skull and jaw, figured Günther, pl. xxiii. fig. B.
 1 lower jaw. New Coll.
 3 humeri, right. (C.)
 2 „ „ New Coll.
 3 „ left. (C.)
 4 „ „ New Coll.
 1 coraco-scapula, right. (C.)
 2 „ „ New Coll.
 1 „ left. (C.) *T. Boutoni*, var.
 4 „ „ New Coll.
 3 coracoids. New Coll. (2 right and 1 left.)
 2 pelves (or portions). (C.)
 8 „ „ New Coll.
 Portions of one carapace.

	<i>T. triserrata.</i>	<i>T. inepta.</i>	Sp. incert	Total in each collection.
Old collection (C.)	48	15	10	73
New collection	28	24	26	78
	—	—	—	—
Total of each species	76	39	36	151

V. *On the Morphology of the Skull in the Amphibia Urodela.*By Professor W. K. PARKER, *F.R.S., F.L.S.*

(Plates XIV.—XXI.)

Read June 19th, 1879.

Species 1.—Salamandra maculosa.

1st Stage.—Embryos from the Oviduct a week or two before the time of exclusion *,
1 inch long, with three pairs of feathery gills.

THE embryo of the Spotted Salamander has large external gills, like the larvæ of other "Urodela Caducibranchiata," but in this stage they are at their fullest development. They soon shrink when the larva is ripe; in one of these earlier embryos, 1 inch 1 line long, the *left* branchiæ were just disappearing. These are the youngest I have examined of this species; they were not more advanced in development than the larvæ of various congeners only half their size. The chondrocranium gets a considerable start of the bony deposits, and is rather massive; yet, although massive, it is a curious piece of open work (Pl. XIV. figs. 1, 2), both roof and floor being largely deficient of cartilage. The cartilage itself is composed of very large cells, and when treated with an ammoniacal solution of carmine is an exceedingly beautiful substance, as seen through the microscope, even with rather low powers.

The skull at this stage has already undergone a considerable amount of modification by the coalescence of originally unrelated parts, and also by the growth of crests and conjugational bands on parts that are homologous †. The originally distinct front and hinder basal bands of cartilage now form one continuous tract on each side; the foremost pair, the trabeculæ (*tr*), have united with each both before and behind, and also with the hinder pair of cartilages—the parachordals, or investing mass (*iv*). The latter cartilages have united near the end of the skull with each other, laterally with the ear-capsules, and in front, as just stated, with the hind part of the trabeculæ, so that the base of the cranial framework is now well laid down; it is, however, but two thick planks of cartilage fixed together, in front and behind, by cross bars in each region. This is quite in conformity with the Urodelous type of chondrocranium, which is always largely imperfect in the middle both below and above.

The hinder or parachordal conjugation is a narrow and incomplete band (Pl. XIV. fig. 2, *iv, nc*), on which the notochord rests; but the internasal band in front is much larger.

* These and most of my specimens of this Amphibian were the gift of Mr. Tegetmeier.

† For an account of the earlier conditions of the skull in the Urodela I must refer the reader to my recent memoir in the 'Philosophical Transactions,' 1877, plates 21–29, pp. 529–597.

This new growth of cartilage binds together the primary cornua trabeculæ between the nasal sacs (*ol, na*); it is scooped both in front and behind. The scooping in front faces the re-entering angle between the cornua, and the space there is often a real hole in the Urodeles—a mesorhinal, vertical passage. The hinder scooping is a correlate of the swollen fore brain which rests upon it, and from which the olfactory crura are given off, right and left, to the nasal sacs (figs. 1, 2, *c.tr, na*). The internasal region of the cornua is elevated, and on this rest the crescentic olfactory capsules, the simple rudiments of the nasal labyrinth; they are now beginning to coalesce with their trabecular undersetters.

Between the eyes the trabeculæ have sent up a sharp wall to the brain-cavity, right and left; regionally, these walls answer to the orbitosphenoids and alisphenoids of the higher Vertebrata; and the optic and trigeminal nerves (2, 5) in their exit show the true landmarks. But in this very primordial and ancient kind of skull the segmentation into separate *neural* cartilages is quite suppressed; only where the notochord lingers can any trace of somatome division be seen.

This wall is steeper than it appears to be as seen from above and below (figs. 1, 2, *tr*), but a section (Pl. XV. fig. 1, *tr*) shows its depth. Its inwards curve below makes a floor to a slight extent; and near both ends of the wall there is a slight attempt at roofing-in of the skull (Pl. XIV. figs. 1, 2). The floor also is slightly chondrified backwards from the internasal plate. In the young the front margin of this plate (*in.c*) is a crescentic notch, finished by the cornua (*c.tr*).

Behind, also, the floor is more finished; for the investing mass ensheaths the notochord near the foramen magnum, and the apices of the trabeculæ have coalesced in front of its apex. The perfect arch of cartilage in the occipital region is, at the keystone (*s.o*), about one third as broad as the floor; but the floor is mainly finished by the enclosed notochord.

In front of that arch there is no cartilage in the roof, the thickest part of the internasal plate not rising more than halfway to the proper roof.

The occipital condyles (*oc.c*) are well formed; they are oval, looking inwards towards the notochord, and being most seen on the lower side (fig. 2). The huge ear-sacs are quite perfect as to cartilage; the curves of the enclosed canals have thrust them into the sides of the skull, aborting the alisphenoidal crest of the trabeculæ, so that those end in front of the junction of the anterior with the posterior canal (fig. 1, *a.sc, p.sc*) in the ear-sac. In front and behind the ampullæ of the canals make the sac bulbous; and the horizontal canal (*h.sc*) forms the cave of the outer face, the rudiment of the *tegmen tympani*. The glossopharyngeal and vagus nerves (9, 10) emerge between the sac and the occipital ring behind; and the 5th and 7th (5, 7), or trigeminal and facial nerves, escape between the sac and the cranial wall in front.

In the fore part of the head the cornua trabeculæ are squarish; their inner edge is thickened where the simple crescentic nasal cartilage is becoming grafted upon them (figs. 1, *c.tr, na*).

The outer margin of each cornu is cut away in a crescentic manner, and the nasal sacs lie on and outside the bars; the outer nostril is near the front laterally, but the inner (*i.n*) is further back. This inner nostril is bounded on its inner side by the vomerine

tooth-tract (*v*), and by a small semioval cartilage behind. This is the "ethmo-palatine" element, a rudimentary preoral bar (fig. 1, behind *na*). The base of this small, but important rudiment is attached to the most outbent part of the trabecula; its apex looks directly outwards.

Besides this *antorbital* rudiment, there is a large postorbital cartilage in union with this simple chondrocranium. This is the suspensorium, whose free part is the quadrate, with its condyle (*q*). The suspensorium is half the size of the ear-capsule; it is a trifurcate cartilage. The longest and slenderest of the forks is the "ascending process" (*a.p*); its direction is inwards, upwards, and a little backwards; it has coalesced with the trabecular crest near its top, and forms a bridge over the first or orbito-nasal branch of the trigeminal nerve (5¹).

The next fork is the "otic process" (*ot.p*); it grows directly backwards, and clings like a snail's foot to the outside of the ear-sac, embracing, by its pedate end, the ampulla of the horizontal canal. The third fork or, rather, descending crus is the quadrate region of the suspensorium (*q*); it grows forwards, so as to end opposite the middle of the inter-orbital region, and outwards from the skull to a distance equal to the width of the skull. The oblique end is scooped a little on its upper face for the mandible (fig. 1); the articulation is made at right angles with the long axis of the skull. These are all the chondrified parts that form this simple skull; yet, few as they are, the elements are diverse in nature.

The parachordals and the trabeculæ are most probably homologous tracts; but the sense-capsules and the antorbital and postorbital cartilages belong to two other categories; the former are paraneurals, and the latter are visceral or facial arches.

Before passing to the lower parts of the face I must remark upon a change that has begun in the ear-capsule. The walls of this sac had become well chondrified; but a remarkable cleft has appeared on its under surface, nearly in the middle. The cleft is the rudimentary "fenestra ovalis" (*fs.o*), and the thin ragged edge of cartilage that now imperfectly hides the enclosed otolith is the rudiment of the *stapes*, not yet severed from the capsule*.

The manner in which the fast-growing capsule literally *bursts* is very remarkable; the dehiscence gives rise to a triradiate opening, and in the hinder part of the space there is a thick ingrowth of the outer wall, which passes into the vestibule upwards and forwards, and forms a partial irregular septum (fig. 2, *fs.o*) to the capsule.

As the Urodeles are the fathers of all those that prepare a movable *stapes* for the more accurate transmission of the waves of sound, the mode of growth of this part in them is of the greatest interest.

The lower arches (Pl. XIV. fig. 3) are shown in relation; in the first two the upper element, or suspensory part, is not shown; that of the first has coalesced with the skull; that of the second, the hyomandibular, is suppressed in most of the "Caducibranchs" and in some of the "Perennibranchs," *e. g.* in *Menobranchus*. This is a correlate of the early closing-in of the first *cleft*; in no Urodele that I have seen is there the same degree of

* For a full description of the formation of the fenestra ovalis and stapes, see my recent memoir on the skull of the Urodeles in the 'Philosophical Transactions' for the year 1877.

modification of the "epihyal" element as one sees in most Batrachia. The basal element is deficient in the first two arches, but the second arch is attached to the fore end of the first basibranchial piece; there are only a first and a second; and the hyoid and two first branchial arches are attached to the foremost piece (fig. 3, *h.hy*, *e.br¹*, *e.br²*, *b.br¹*, *b.br²*).

The free mandible (*mk*) is a single rod, right and left; it undergoes no subterminal segmentation. This pair of bars is united together by membrane, so as to form a half-bent bow. The distal end of each is slender and terete, but further up it gradually becomes very solid, suddenly narrowing again, to form a rounded angle. Near the angle above there is a transverse condyloid region, not very distinct from the rest of the cartilage. These bars alone have bony films upon them; they will be described with the other bony deposits. The length of the mandible (*mk*) and its place of articulation with the suspensorium correspond with what we find in the Frog when the gills are wasting.

In the hyoid bar the slender part is above, and the thickening, which is sudden, is retained, with but little diminution, to the rounded extremity. This bar is flatter than the mandible, and has its distal *fourth* segmented off to form a hypohyal (fig. 3, *e.hy*, *h.hy*).

Its size, thickness, and position with relation to the suspensorium correspond with the stage of the Frog just mentioned.

Each bar passes within, and is attached by ligament to, the mandible; the distal end of each hypohyal is loosely tied to the fore end of the first basibranchial (*h.hy*, *b.br¹*).

Of the next four arches, the branchials, only the two first have a distal or ceratobranchial element; and the last epibranchial piece (*e.br⁴*) does not carry gills. The first and last have one, and the second and third two rows of denticles forming the *gill-colander*; the four epibranchials lessen from before backwards elegantly. They are all falciform, but rather thick.

The first basibranchial (fig. 3, *b.br¹*) is evidently the keystone of the two foremost arches, their ceratobranchials being articulated with it; it is high, but thickish also, and its greater height is in front of the first branchial. The second basal piece (*b.br²*) is a flattened spatula, whose narrow attached end is articulated to the lower edge of the first basal segment; it ends behind in a broad blade, whose margin is straight.

The osseous centres are already numerous; the largest of these is the parasphenoid, which forms a thin floor of lath-like bone to the base of the chondrocranium from end to end, or nearly. The apex of the notochord is ensheathed by an imperfect "cephalostyle;" but this is now wasting, and is not distinct from the parasphenoid: in some Caducibranchs (e. g. *Seironota*) this centre ensheaths the fore half of the notochord and is autogenous.

Above, the frontals and parietals are forming the roof; these will be described in the next stage; the squamosals (*sq*) are applied as splints to the suspensoria.

Distinct premaxillaries, dentaries, splenials, and articulares (*px*, *d*, *sp*, *ar*) are now well seen; the maxillaries (*mx*) are later in their appearance than these.

The fore part of the palate is beset with teeth, like the pharyngeal teeth of Osseous Fishes; these are arranged in an arc on each side, whose concavity is inwards. The fore part of each tract is broad, and in this part the teeth are cemented to a thin bony

plate, the vomer (*v*); the rest thin out into a small row of denticles, only attached to bone in front. The bone whose fore end carries these hinder teeth is the pterygo-palatine (*p.pg*); it commenced as a palatine, carrying its own share of the teeth, but threw out a pterygoid spur, which the teeth did not follow in its diverging course. The teeth will approach still nearer to the mid line, and the non-dentigerous plate will become segmented from the rest, and bend outwards to the zygoma.

The relation of the cartilaginous to the bony parts will be still better seen by reference to the figures of *sections*, which were made from an embryo somewhat more advanced.

The *first* transversely vertical section (fig. 4) was made just in front of the internasal plate (*in.c*); it shows the thickness of that plate, and the position of the nasal roofs (*ol*) and trabecular cornua (*c.tr*). These latter make a floor quite similar to the roof; the roof itself has already been grafted on to the internasal plate. Where the union is taking place there the nasal processes of the premaxillaries (*n.px*) are seen in section, whilst below, the vomer and its teeth (*v*) are seen beneath the trabecular nasal floor.

The *second* section (fig. 5) shows the same bones and cartilages as the first, but at the hinder margin of the internasal plate (*in.c*). The olfactory nerves (1) find their way to the nasal sacs between the upper and lower cartilages (*ol*, *c.tr*), and the middle space is continuous with the cranial cavity.

The *third* section (Pl. XV. fig. 1) was made directly through the eyeballs (*e*), through the middle of the brain (lettered *c*² by mistake).

The trabeculae (*tr*) have become strongly crested, and the crest at this part is orbito-sphenoidal; the floor is finished by the gently bulging parasphenoid (*pa.s*), and the roof is filling in from the edges by the frontals (*f*).

On the palate, one third the way from the skull to the face, the pterygoid spur (*pg*) has been severed. The rest of the skeleton here to be seen is below the mouth. The outermost of these bars is the mandible (*mk*), and its ovoidal section shows the articulare on the inside and the dentary on the outside (*ar*, *d*).

Next to these come the ceratohyals (*c.hy*); they have an ovoidal outline, but the narrow end is below, whilst in the mandible it is above. The ceratobranchials are severed close behind the first basibranchial, so that the fore end of the second is cut through (*b.br*²); the lesser second ceratobranchials lie in a higher plane than the larger first pair (*c.br*¹, *c.br*²).

The *fourth* section is a little oblique (Pl. XV. fig. 2); it is behind the eye, and catches the mid brain (*c*²) and backwardly turned lower part of the fore brain; the top of the infundibulum (*inf*) is seen in it, but not its connexion with the pituitary body.

On one side the fore face of the ear-sac (*au*) is laid bare, but not on the other; on this latter side the pedicle of the suspensorium (*pd*) is seen to ascend over the orbito-nasal nerve (5¹), and to be coalesced with the alisphenoidal crest of the trabecula (*tr*); there is no union besides this ascending process to the skull wall. The quadrate cartilage is in relation with the articular end of the mandible (*q*, *ar*); from its upper edge the otic process (*ot.p*) is seen to rise.

On the other side the ascending process is cut through, and the Casserian ganglion is exposed; it is seen between the trabecula (*tr*) and auditory sac (*au*). The para-

sphenoid lies between the trabecular sections, and the parietals are finishing the roof over the hind brain. The sections of the arches are made through a more backward part; they differ but little from the last, yet the hyoid (*c.hy*) has been severed where it is smaller, and the second basibranchial lies low in the throat; the pterygoid bone is running towards the quadrate (*q*).

The *fifth* section (Pl. XIV. fig. 6) is through the apex of the notochord (*nc*); the anterior semicircular canal (*a.sc*) is severed near its junction with the posterior and the horizontal canal (*h.sc*) through its middle.

The roof of the ear-capsule is perfect, but the floor is imperfect; for the fissure for the fenestra ovalis is now gaping, and part of the jagged edge of cartilage is becoming rounded into the stapes (see Pl. XIV. fig. 2, *fs.o*).

The superoccipital margin is imperfect here; below, the imperfect *cephalostyle* (*nc*) is seen to be united with the parasphenoid.

The *sixth* section (Plate XV. fig. 3) was made behind the superoccipital roof, through the posterior semicircular canal and the hind part of the horizontal (*p.sc.*, *h.sc*). The cartilage grows inwards round the latter, and mesiad of this inflection we see the cleft which becomes the fenestra ovalis. This section is behind the occipital roof, and through the middle of the cranial notochord and the most solid part of the basal plate.

The *seventh* section (Plate XV. fig. 4) is near the back of the ear-capsule; it is the front face of a solid section that is figured, taken a little in front of the condyles for the *allus*. The ear-walls are seen to be thick, and the sides of the parachordals (*iv*) are solid as compared with the conjugational plate on which the huge notochord lies. The razor has passed through the glossopharyngeal and vagus nerves (9, 10) at their exit, the former of these nerves being close to the membranous labyrinth, and burrowing the periotic cartilage.

2nd Stage.—Ripe embryos of Salamandra maculosa, 1 $\frac{2}{3}$ inch long.
(“*Cryptobranch stage.*”)

Like the young of the Surinam toad (*Pipa*), the young Salamanders at birth are ready for terrestrial life; they, however, have had *branchiæ* before their escape from the oviduct. The young *Pipæ* never develop gills, and are developed in *quasi-uterine* pouches. The changes seen in the skull of this stage as compared with the last are very great; they probably only took ten or twelve days for their development: the chondrocranium, in the earlier stage, was very perfect, ripe for metamorphosis into a true Salamandrian bony skull.

The basal region (Pl. XV. fig. 6) is large and oblong; and if the suspensoria be removed, the sensory organs, in front and behind, form nearly equal expansions. In the earlier stage the hinder, or auditory, were very large compared with the front, or olfactory masses.

From the foramen magnum to near the front of the internasal plate the whole base is floored by one huge lamina of bone, the parasphenoid (*pas*), and through it the nakedness of the proper cranium can be seen.

From the region between the internal nostrils (*in*) to that between the foramina ovalia the whole floor is imperfect, so that there is scarcely a trace of cartilage

beneath the fore and the hind brain. This space is called *pituitary*; but the pituitary body only occupies a foot breadth at the end of this great field. This main basal fontanelle is followed by another, the "posterior basiscranial fontanelle" of Rathke. This is formed by a reopening of the original membranous space on each side of the notochord, between the ends of the trabeculae and the apices or fore ends of the parachordals.

The cranial notochord is still large; it is bounded in front by the trabeculae, and behind it lies on the basal plate; it fills the space between the occipital condyles, as it emerges to become the axis of the spinal column (fig. 2, *nc*, *oc.c*).

The occipital arch has become bony, all but the mid line, above and below (*e.o*, *f.m*). This bony tract stretches over the epiotic and opisthotic region of the auditory capsule.

Scarcely distinct from this tract below is another (*pro*) which runs in a crescentic manner as two wings of bone, one on the antero-inferior, and the other on the antero-superior face of the auditory capsule. Thus the "sacculus" of the fenestrate region is still floored with cartilage: a band of cartilage also intervenes between the epiotic and prootic bony tracts, and along the actual front face of the capsule; this latter tract has a plaster of cartilage upon it, derived from the basal plate, and this generally remains soft in relation to the suspensorial pedicle. The fenestra ovalis is now perfect, and is filled with a thickish cartilaginous stapes (fig. 6, *st*). The skull in front of the ear-sacs is entirely unossified, yet there has appeared a bony plate on each side, which in osseous fishes is an ectostosis. This is the prefrontal or ectethmoid (*e.eth*).

The sphenoidal walls of the trabeculae (*tr*) are more perfect, but scarcely overlap above, so that the fontanelle is complete. In front the nasal roofs (*na*) are of great extent, and they are quite confluent with the very wide trabecular cornua. The ethmo-palatine cartilages (fig. 6, outside *pa*) have also united themselves to the posterior edge of the nasal curtain.

Other most instructive characters have now appeared: the internasal plate (*in.c*) has lost its hinder projection and has gained one in front; this is the prenasal rostrum (*p.n*), a process not common in the Urodeles, and suppressed in many of the Anura. In the latter group the primary cornua trabeculae give off a small process, the "prorhinal;" it is a *secondary* cornu: this is fairly seen in the ripe young of the Salamander (fig. 6, *e.tr*), and will persist in the adult (Pl. XVI.). The rest of each cornu forms the subnasal lamina, or trabecular floor of the nose, as in the Frog.

The large suspensorial cartilage is still only confluent with the skull by its ascending process (*a.p*) over the first branch of the fifth nerve; the "pedicle" proper is never more than a bulging of the lower face of the ascending process in this species. The otic process (*ot.p*) is well developed, and clings by its expanded face to the most projecting part of the ear-sac. A pterygoid process (*e.pg*) has appeared.

The quadrate region of the suspensorium is now largely ossified (*q*), as is the rule in the tailed Amphibia, and the exception in the Anura; the condyle still looks forwards, and reaches to an imaginary line across the middle of the skull.

Thus we see that, including the quadrate bones, there are only *three* pairs of osseous centres found, as yet, in the substance of the chondrocranium.

Many other bony plates, however, have been developed in the overlying fibrous tracts; the chief of these is the parasphenoid (*pa.s*). This bone rounds gently to a blunt point behind, beneath the foramen magnum, and to two blunt points in front, close behind the prenasal rostrum; the basitemporal region is widest and is notched. Running in an arched manner round the front of the parasphenoid is a chain of four dentigerous bones; the foremost of these are the larger, these are the vomers (*v*); they keep their width throughout. Behind the vomers are the palatines (*pa*); these are little wedges, with their point behind. In the last stage they were continuous with a *pterygoid* expansion; this is now a large distinct bone.

This pterygoid bone (*pg*) is a large broad wedge, whose point, severed from the pointed end of the palatine, looks forward, but lies further outwards than the end of the palatine. Its hinder end is roughly semicircular, and forms a clamp to the suspensorium from the exit of the trigeminal nerve inwards to the quadrate condyle outwards. The outer surface of the suspensorium is bound by its own splint, the squamosal (*sq*), which also helps to make the tegmen tympani outside the horizontal canal.

The great upper fontanelle is closed in by two pairs of bones, the frontals and parietals (*f, p*), that are nearly equal; the parietal is a much larger bone in the Urodeles than in the Anura.

The parietals not only run in and form a wall-plate to the trabecular crest, but they also overlies the hind part of the frontals; these, again, are in their turn overlapped by the nasals and nasal processes of the premaxillaries. The nasals (fig. 5, *n*) are small suberescence bones; they cover in but little of the nasal roof. The nasal processes of the premaxillaries (*n, pa*) are as long as, but narrower than, the marginal part of these bones: they are larger in the Urodeles than in the Anura. External to these the maxillaries (*mx*) have enlarged; they have an ascending facial part, and a styloid zygomatic process (fig. 5); but the palatal part, as in the premaxillaries, is very narrow. On their upper edge, below the external nostril (*e.n*), there is a small septo-maxillary (*s.mx*).

Between the hind part of each maxillary and nasal, on the hinder part of the nasal dome, there is a thin bony lamina, answering to the ectosteal plate of the Fishes' prefrontal (ectethmoid); it retains its distinctness here, and thus has to be called the external ectethmoid (*e.eth*). The sphenethmoidal bony centres are all that are yet wanting to make up the sum of the bony centres seen in the skull of the adult.

The metamorphosis of the inferior arches takes place after birth; they have now merely increased in size; the branchials are now at their fullest development, and will soon suffer extensive absorption.

3rd Stage.—Skull of the adult Salamandra maculosa.

The skull of the adult of this species shows at once the likeness and the unlikeness of this type to that of an average Batrachian; yet in reality this skull differs as much from that of *Rana temporaria* or of *Bufo vulgaris* as it did in its early conditions and in the mode of its metamorphosis. But scattered up and down the great Batrachian "Order" there are remarkably generalized types, whose skulls, now in this and now in

that, agree with this of the highest kind of "Caducibranchiate" Urodele. I shall therefore carefully set down the characteristics of this skull, and then it can be used as a measure, being "perfectissimum in suo genere," of the lowness or height, in type, of the skulls of other Urodeles, and also as a test of what is normal or aberrant in the skulls of the Batrachia. This species and *Rana temporaria*, therefore, will be taken as convenient, and yet worthy, representative Salamandrian and Batrachian types. They are culminating forms, being most perfectly specialized according to their kind. The general resemblance of this skull to that of a Grey Frog is seen at once (Pl. XVI. figs. 1-3); but attention to details will give us a large number of important differences.

When this skull is stripped of its investing bones (fig. 4) we see how little change, except that of ossification and increase of size, has taken place. The very strong occipital arch has this normal amphibian weakness, namely, that an oblong tract both of roof and floor remains unossified; in the floor the shrunken notochord still remains.

The condyles (*oc.c*) are best seen from below (fig. 2); they are large, oval, and slightly pedunculated; they are very wide apart. A large rounded fossa divides this arch above, on each side, from the periotic mass, but there is no suture; below, the regions melt insensibly into one another (fig. 2). But both below and on the inside (fig. 5) the double passage for the glosso-pharyngeal and vagus marks the bounds of these two territories. The occipital ring expands greatly on each side to embrace and unite with the large ear-masses; but both above and below the shortness of the cartilaginous tracts causes an emargination of great size, both before and behind, in this annular growth.

The front emargination of the floor is the hinder margin of the posterior basieranian fontanelle; its fore boundary is formed by a bridge (*a.tr.*), which is cartilaginous in the middle and bony at its large piers. Did these osseous tracts meet, we should have the "prootic bridge" of the Bony Fishes; the real morphological nature of this band is of great interest.

The hinder part or threshold of the skull was formed by the *separate* and somewhat late "parachordals," or investing mass; the bridge is formed by the posterior ends of the trabeculae, which had united, in the first stage described, with the parachordals, and ran into each other in front of the notochord (Pl. XIV. fig. 1, *nc, tr, ir*). So that two things have taken place—much of the cartilage has become bone, and old cracks have opened again, by relative shrinking of that which does not ossify.

The occipital arch is not more strongly united to the auditory masses than the trabecular walls; the alisphenoidal region is strongly cemented to these masses by a remarkable trespass of each *prootic* centre.

The early condition of the trabecula alone can explain this curious *endoskeletal* skull. These rods embrace the notochord by their hinder ends, and then turn rather suddenly outwards (Huxley on *Menobranchus*, P. Z. S. 1874, pl. xxxi. figs. 1, 2, *Tr, Ch*).

In this adult skull the confluent ends of the trabeculae form a thin narrow band of cartilage, passing transversely (with a little backward deflection) across the cranial floor. Towards the side each bar suddenly thickens, and is bent on itself so as to form an acute angle; in front of the bend it becomes very solid, and at the bend there is the

alisphenoidal crest. Between this crest and the ear-mass the great trigeminal nerve passes out through the foramen ovale (5).

The synchondrosis seen in front of the bend does separate the orbito-sphenoidal (*sp.e*) from the alisphenoidal regions; but the bony matter behind the cartilage is all an outgrowth from the prootic. This outgrowth is double, growing, as we saw, into both wall and floor. The bony matter is not perfect in the inside (fig. 5); there is a vertical band of cartilage directly in front of the foramen ovale (5), which broadens both above and below.

The optic foramen (2) is formed in the middle of a large membranous fontanelle, as in the Frog; this space is margined with cartilage on the outside (fig. 3. 2). In front of that ring there is solid bone up to the olfactory capsules (*na*); those right and left bony walls correspond to the annular sphenethmoid of the Frog, but they are not conjugated together, either above or below. The coping of this hardened wall is thick (fig. 4, *sp.e*), but below it thins out and turns inwards. There is some floor to the skull in front; for the internasal plate (*i.n.e*) is scooped, and the fore end of each bony wall is cemented to the other by an elegant crescentic growth of cartilage, which has a thickened rim.

The crescentic edge of the internasal plate below is of much smaller extent than the upper, and extends further back; therefore there is some floor; on each side, just in front of the bone, the olfactory crus escapes (figs. 4 & 5. 1). The large internasal plate takes in most of the cornua below; but the internal angle of each is developed into an inturned tongue of cartilage, the "prorhinal" (*c.tr*); and between these two a similar process grows from the mid line: this is the prenasal rostrum (*p.n*). These three outgrowths seem to be the non-segmented rudiments of the paired and unpaired elements of the foremost visceral arch, whose *splints* are the premaxillaries.

The thickened internasal plate above is shaped like the letter X; for its hind margin is crescentic, its fore margin deeply notched in a rounded manner, whilst its solid middle part is bounded by a crescentic ridge behind, and in front grows into diverging ridges, the ridges to which the backs of the olfactory crescents are cemented. This structure is eminently *Selachian*, but also foreshadows the nasal labyrinth of the higher Vertebrata.

The original crescent of cartilage closes round the outer nostril (*e.n*), and this is further occluded by a membranous valve, which is fan-shaped, with the narrow part looking forwards. The nasal sacs are hollow below; but the trabeculae floor them to some extent on the inner side. This part is invested by the huge vomers (*v*); but the ant-orbital part, besides dipping down, has a new selvedge added to it. This is the ethmo-palatine cartilage (*e.pa*), which is very apt to coalesce with the antorbital part of the nasal capsule.

The auditory capsule is nearly all solid bone; but there is a cartilaginous tract outside the ampullæ of the anterior and horizontal canals (*a.se*, *h.se*). This is a character of considerable morphological import; for this unossified tract was originally a growth from the basal plate, and with this the otic process of the suspensorium coalesces.

There is a well-ossified lip, like the mouth of a pitcher, to the fenestra ovalis: it looks

outwards and backwards; the thick, oval, closely-fitting stapes (*st*) remains cartilaginous, and is only attached to the suspensorium by a ligament*.

The suspensorium has changed greatly since the time of birth; in direction it has moved its condyle from being opposite to the middle of the skull to an imaginary line drawn across at the end of the parasphenoid: this is equal to its average position in adult Batrachia. It is foot-shaped below, the base looking outwards and backwards; all but the articular face is ossified (*q*) up to the middle of the otic process; also the part to which it adheres, and with which it becomes confluent, is soft. The ascending process (*pd*) is small and terete; it remains confluent with the alisphenoidal region. This pedicle has a bulbous enlargement, like that which bears the condyle of the pedicle in a Frog.

But little of this expansion, which articulates with the ear-mass, is seen from below (fig. 2), for it is ensheathed by the pterygoid (*pg*). This bone is hammer-shaped, and its long head binds on the pedicle within and on the inside of the quadrate by its outer lobe. The handle has used up the cartilage that grew from the suspensorium (Pl. XV. fig. 5); it is grooved where the cartilage lay (figs. 1, 3, 4), and its bluntly pointed end has turned outwards to be tied by ligament to the zygomatic process of the maxillary (*mx*).

On the other hand, the bone from which it was segmented, the palatine (fig. 2, *pa*), has grown further inwards, and reaches further backwards than the foramen ovale (5). It has coalesced with the dentigerous region of the vomer (*v*), and the two tooth-bearing tracts are rib-like bars of bone, whose arrangement under the parasphenoid is *lyriform*. To one fresh from mere mammalian morphology, these sigmoid rods, and the edentulous plates growing like wings from them in front, would be an inexplicable puzzle.

The anterior expansions are a new development of bone from the simple larval vomers, and are a *caducibranchiate* character. They are very elegant; between these wings there is a large semielliptical notch revealing the internasal cartilage and rostrum; their margin at this point is curled upwards. Their outer margin is lessened by a large rounded notch, which bounds the internal nostril (*i.n*); behind this there is a lobe which does not extend so far outwards as the fore part. They unite by "harmony" for a short distance between the dentigerous bars; the internal nostril has its rim finished, outside by the maxillary (*mx*), and behind by the ethmopalatine cartilage (*e.pa*).

The maxillaries have much, and the premaxillaries some, palatine expansion (fig. 2, *pa*, *mx*); altogether this is a very hard and finished palate for so low a type. The palatine process of the premaxillary is short (fig. 2); its nasal process (*n.pr*) is long and inbent towards its fellow at the middle; the frontals run under these bars, and in front of the frontals the internasal cartilage is seen. The maxillaries (figs. 1 & 3, *mx*) have a large and swollen facial plate; and behind the nasal region these bones run back

* Mr. A. Doran has shown me a stapes, said to belong to this species, which is ossified and has a stalk. I find nothing of the kind in the specimens dissected by me; and I think it probable that that specimen (in the Hunterian Museum) belonged to another kind. Hereafter I shall have to describe this sort of stapes in *Spelerpes* and *Desmognathus*; it exists also in the *Menopoma*.

beyond the apices of the pterygoids as far as in an average Batrachian : there is, however, no quadrato-jugal to bind them to the quadrate ; they are free as in Osseous Fishes. The dentigerous line, continuous in front with that of the premaxillaries (fig. 2), extends nearly to the distal end. Above, at the junction of these bones, and outside the external nostril (*e.n*), there is a small graniform septo-maxillary (figs. 1 & 3, *s.mx*). The squamosals (figs. 1 & 3, *sq*) have a convex, suboval supratemporal region (fig. 1), and a large oblong preopercular part (fig. 3); above, they lie over the two first ampullæ and the tegmen tympani, whilst the descending part strongly binds upon the outer face of the suspensorium. After being broad above, and narrowing somewhat down the shaft, the bone has a broad arcuate base fitting against the expansion of the quadrate, towards the condyle.

Over the nasal region there are two pairs of bones on each side; the nasals (*n*) are the inner, and the ectethmoid plates (*e.eth*) the outer of these. The nasals have an anterior margin, which is concave, to fit against the external nostril (*e.n*); their main part is wedged in between the nasal processes of the premaxillaries, the ascending plate of the maxillaries, and the ectethmoids; their hinder angle rests upon their frontals.

These latter bones (*e.eth*) are oblong; they form, as it were, two horns to the pair of frontals (*f*), stretching outwards and forwards; the orbito-nasal nerve (5') passes into the olfactory sac between their outer end and the high part of the maxillary. These bones remain distinct. Taken together, the frontals and parietals (fig. 1, *f, p*) have an hour-glass-shaped outline; this figure is made up of four nearly equal bones.

In front, the frontals are overlapped by the nasals, nasal processes of the premaxillaries, and ectethmoids; behind, they repeat this imbrication by lying on the parietals, towards which they narrow, whilst towards them the parietals are narrowed. The superorbital margin (figs. 1 & 3) is strong, but not overarched; there the parietal runs forward, coping the cranial wall.

Behind, the parietals are trilobate; the first or outer lobe binds on the front of the ear-mass; the middle lobe covers the junction of the anterior and posterior canals; the third or inner lobe meets its fellow over the supraoccipital region, tiling that roof nearly to the edge of the foramen magnum.

The great parasphenoid (figs. 2, 3, 5, *pa.s*) has its narrow anterior part invested by the vomers, and its middle region by the long palatines; behind, it is wide, and rendered irregularly crenate by four pairs of notches; there are three denticulations on this foliaceous part.

The inferior arches now come under review. The first of these is the free mandible; this is now a flat arcuate bar, well ossified by the long sheathing articulare (figs. 3 & 5, *w*), which has ossified nearly all the cartilage except the oblong cylindroidal condyle. The articulare reaches far forwards, but is encased in two splints; in front of the condyle it sends upwards a coronoid process. The external dentigerous splint, the dentary (*d*), reaches from the chin to the angle of the jaw, and ends only slightly in front of the end of the articulare. On the inside it lies over the edges of the jaw, but is deficient in the middle. This deficiency is made up by a long curved dentigerous lath, the splenial (fig. 5, *sp*); the bone is pointed at both ends, and reaches from the

chin to the coronoid process. The Salamander has no mento-Meckelian bone, and the Frog has no splenial. The angle of the jaw is attached to the outside of the apex of the ceratohyal by the mandibulo-hyoid ligament (*c.hy*, *m.h.l*). The same part of the hyoid is attached to the suspensorium by the hyosuspensorial ligament.

The suspensorium is attached to the oval cartilaginous stapes by the suspensorio-stapedial ligament. The *first cleft* closes early. Thus there is no tympano-eustachian cavity, no "annulus," and therefore no membrana tympani. The columella is represented by the suspensorio-stapedial ligament, over which the facial nerve passes.

Thus the high type of Urodele is much less specialized in these respects than the Frog. It is a much higher creature than the Frog's Tadpole prior to the absorption of the tail, for in its own diverging line it ascends to a considerable vertebrate height; yet in some metamorphic peculiarities it rises no higher than the Batrachian larva.

The hyobranchial series of arches have undergone great change (Pl. XIV. figs. 3 & 7), and have all continued soft except the distal part of the 2nd basibranchial (*b.br²*).

The hyoid bar (*c.hy*) has become much flattened, and its ventral end is the wider; the distal piece is quite detached, and is now directed forwards instead of backwards, parallel with the 1st ceratobranchial (*c.br¹*), which is a longer rod and is more directly attached to the ceratohyal.

The 1st epibranchial (*e.br¹*) has reached the median piece, some distance behind its distal segment. It is still a large cartilage, but is made still larger by the confluence with it of the 2nd epibranchial, which is now fused with its own ceratobranchial piece (fig. 3, *c.br²*). These latter bars, right and left, articulate with the oblique end of the 1st basibranchial (*b.br¹*), which now has *four* cartilages directly articulated to it instead of *two* (figs. 3 & 7). All except the broad end of the 2nd basibranchial (*b.br²*) has been absorbed, and that has become a V-shaped bone, with the tips of its crura soft. It is now a median bilobate "thyrohyal," being applied to the front of the *larynx*—a very simple structure, but cartilaginous.

This is, on the whole, the kind and degree of modification undergone by this series of cartilages in the "Caducibranchs;" but we shall find some curious modifications in other types of the group.

Species 2.—Notophthalmus viridescens.

1st Stage.—Larvæ 1 inch $2\frac{2}{3}$ lines long *.

My large larvæ of this North-American Newt show some very instructive conditions of the urodelous skull; the skull of the adult also is very important. The larvæ at this stage are as much developed, on the whole, as the ripe young of the Spotted Salamander (Pl. XV.); I suspect them to have been nearly ready for metamorphosis into Caducibranchs. They show a remarkable difference as to the *time* at which certain changes take place. In some respects they are far less developed than my first stage of the type just described (Pl. XIV.), and in others are far more advanced than the second. The

* This and the remainder of the types to be described in the present paper are the gift of Prof. St. George Mivart, F.R.S.

adult skulls have much in common ; but this is more massive (Pls. XVI. & XVII.) and longer.

In these full-gilled larvæ the occipital arch (Pl. XVII. figs. 1-3) is well ossified, and the ossification on each side runs continuously over the inner part of each auditory sac, so that the exoccipitals and prootics (*e.o., pro*) are not separate. There is a distinct and widish tract of super- and basioccipital cartilage (figs. 1, 2), and a solid facet of cartilage for each condyle (*oc.c*). These oval elevations look backwards and inwards. The interspace between them is square and large; it is filled by a rudimentary vertebra, whose centrum has coalesced with the centrum of the "atlas," between its large pedunculated "præzygapophyses."

In one specimen (figs. 1 & 2) there was scarcely more conjugating cartilage in the basioccipital region than is seen in the adult *Proteus* and *Menobranchus*; for the parachordals (*iv*) had retreated already from the trabeculæ, whose hind part (its parachordal tract) had been already absorbed (figs. 1, 2, *tr, iv, nc*); but in the other larva (of the same size) there was a U-shaped posterior basiscranial fontanelle, traversed by the thick notochord, and bounded in front by the thick broadish trabecular band (fig. 3, *tr, nc, p.bc.f, iv*). This is the band which is persistent in the Salamander (Pl. XVI. fig. 4), but which so soon vanishes in this type, but not always at the same time in different individuals.

Laterally the trabeculæ were confluent with the parachordal cartilages and also with the cartilaginous regions of the ear-sacs; beyond that point they had grown into side walls to the skull, which were of great height in reality, but bulged considerably.

In the ripe Salamander's larvæ (Pl. XV.) there was no appearance of bony deposit in the side walls; but here, from the optic foramen (2) to a short distance from the nasal region, the whole wall is solid bone (figs. 1 & 2, *sp.c*). Yet in front of these tracts the whole of the structures represent a very early condition in other types (e.g. *Siredon*, *Salamandra*).

Three pairs of splints have not yet appeared, namely the nasals, ectoethmoid, and maxillaries; this stage thus corresponds with the adult *Proteus* and *Menobranchus* *.

Three pairs of cartilaginous growths are seen here, of which only one pair occurs in the first of those "Perennibranchs;" and one tract seen in them is wanting here; for the long internasal part of the trabeculæ has no conjugatory tract, as in *Proteus* and *Menobranchus*; but what they lack these have, namely, a large flat lobe outside the end of each rod (*c.tr*); these give the form of a hatchet to the fore part of the trabeculæ.

These larvæ correspond with those Perennibranchs in having a distinct "antorbital" or ethmopalatine cartilage (*e.pa*) on each side; it is, however, shorter and broader than in them (Huxley, *op. cit.* pl. xxx. fig. 1, *A.o.*, and Pl. XVII. figs. 1 & 2, *e.pa*). But they have acquired a new structure of intense importance; this is a sickle-shaped olfactory cartilage, or nasal roof (*na*) †, which is absent in *Proteus* and imperfect in *Menobranchus*.

* For the figures of these types, see Huxley, P. Z. S. 1874, pls. xxix. xxx., and my recent paper in the Phil. Trans. "On the Skull of the Urodeles."

† After Prof. Huxley's paper was published, he expressed to me his doubt of the distinctness, in any case, of this, the foremost of the "paraneural" cartilages: the figures here given may serve to expel that doubt. The chondrocranium of *Menobranchus*, as figured by him, has much less basal cartilage in it than it had at an earlier period.

In *Salamandra* the lobe sent outwards from each trabecula forms the subnasal lamina, and the end of the trabecula gives off in the adult the "prorhinal" process.

The auditory capsules are still very large, relatively; above, the anterior and posterior canals (*a.sc*, *p.sc*) are surrounded by bone; and below (fig. 2) the vestibule is surrounded on its inner side by a somewhat narrower tract. The huge semicircular canals above (fig. 1), and the swelling vestibule with its enclosed otolith, give form to the auditory sac; the horizontal canal (*h.sc*) affects the form most, bulging over the side and enlarging the fore part so as to make the sac pyriform. The stapes (fig. 2, *st*) lies behind the middle; it is an elegantly oval plate, and lies in a fenestra ovalis much too large for it. Between the ear-sac and the occipital ring the glosso-pharyngeal and vagus nerves are seen emerging (fig. 2); under the ampulla of the horizontal canal the facial nerve (7) is seen to pass across under the otic process of the suspensorium (*ot.p*).

In the angle between the skull-wall and the ear-sac the great Gasserian ganglion (5) can be well seen, its first branch passing beneath the ascending process of the suspensorium (figs. 1, 3, 5, *a.p*); and in a notch on the back of the sphenethmoid the optic nerve (2) runs out. The first nerves pass through the trabeculae much further forwards.

The suspensorium still retains its early position and unossified condition. It is a large multilobate mass. The transverse condyloid scooped distal end looks forwards; from that part the cartilage thickens rapidly, and spreads into three processes, two running inwards, and one outwards and backwards. Of the inner processes, the *upper*, or ascending process (*a.p*), is the smaller; it coalesces with the side of the skull-wall, near the top.

The lower inner process is the pedicle (fig. 2, in front of 5); it is much larger, and its round end pushes inwards, without coalescing, in front of the ear-sac; *all* the branches of the trigeminal nerve pass over this process. The outer or otic process (fig. 1, *ot.p*) is raised into a curved ridge above, and this elevation winds round the front of the auditory sac, halfway to the skull-wall, taking the same curve inward as the ascending process.

The pterygopalatine bone (*p.pg*) is somewhat constricted behind the teeth, and ends behind in a subflabelliform flap, which binds the suspensorium below; but there is no *pterygoid process* of cartilage growing from the suspensorium. Therefore this skull corresponds, here, to the 1st stage of the Salamander's (Pl. XIV.); and it also corresponds with the lower Perennibranchs in form of the vomer in front, which is a long falcate dentigerous plate, converging towards its fellow.

The premaxillary is an elegant azygous bone, with its dentary margin arcuate, and having from its top, at the middle, a thick ascending process, which ends in two long lathy nasal processes (*n.px*), that overlap the frontals (*f*) halfway to the parietals (*p*). As in many Urodeles, the sharp notch between these two processes has in it a rounded tubular cavity, the "median nasal passage," whose counterpart is to be seen in the Lamprey and Hag-fish; it is a non-functional, *historical* space.

The frontals (fig. 1, *f*) overlies the parietals (*p*) as much as they are overlain by the nasal processes of the premaxillaries.

In this embryonic condition the vomers are wide apart behind, and the trabeculae are

half-naked between them and the large basal splint, the parasphenoid (fig. 2, *pa.s*). This bone reaches more than halfway to the fore end of the long vomers, and nearly to the rim of the foramen magnum; it is narrow, and for the foremost two fifths deeply split, a small third lobe lying between the two sharp processes. This is a rare condition of this bone, which is only slightly split or gently emarginate as a rule.

A thin subcutaneous tract of bone binds the suspensorium on the outside. This is the squamosal (*sq*); at present it is very *ichthyic*, and is mainly composed of the preopercular portion. Several other bones appear afterwards; we shall find them in the skull of the adult specimen.

The inferior arches (Pl. XVII. fig. 4) are now in their most perfect condition, the three gill-bearers being in full function; they are in all essentials like those of *Salamandra maculosa* (Pl. XIV. fig. 3).

The mandible is lodged in a trough-like articulare (*ar*); a long splenial (*sp*) runs along the inner side, and the outer face is invested by the dentary (*d*).

The hyoid (*c.hy*) is shaped like a scythe-blade; it is thickish, especially below. At that end a short hypohyal (*h.hy*) is segmented off.

These are the four normal branchial arches, the last of which is functionless. According to rule, the two first only have a ceratobranchial element (*c.br.^{1 & 2}*), the rest are merely epibranchials (*e.br.^{3 & 4}*). The 1st basal piece (*b.br.¹*) receives the 1st and 2nd ceratobranchials by articulation; the hypohyals are attached loosely by ligament; the 2nd basibranchial (*b.br.²*) carries nothing, lies on a lower plane than the 1st, and has its distal end pedate.

The Skull of Notoplithalmus viridescens. Second or adult stage.

The adult of the specimen dissected by me measured $3\frac{1}{4}$ inches from snout to end of tail. I had no other stages to examine but these two, the larva and the adult; but they are possessed of the true characteristics of an old and a young, or of a low and a high, Urodele. This skull is not unlike that of our native large Newt (*Triton cristatus*), and differs considerably from that of the viviparous Salamander (Pl. XVI.), being longer and stronger.

Here, indeed, and in some related types, as in my next instance, *Cynops* (Pl. XVIII.), we have a very fine piece of skull-building, a bony cranium, forming as safe a structure as could well be provided for any creature whose safety is founded on "the brittle strength of bones."

It is an almost perfect *osteocranium*, cartilage persisting merely where cartilage is a necessity to this kind of organization. The halves of the occipital arch meet above (Pl. XVII. fig. 5); but there is a small patch of cartilage on the threshold (fig. 6).

The small crescentic condyles (*oc.c*) are but little seen above, as they look principally downwards and backwards; they are wide apart, having a round notch between them for an intercalary vertebra.

The ear-masses are large and very strongly ossified; the large posterior canal (fig. 5, *p.sc*) runs along nearly parallel with the occipital rim to meet the anterior arch (*a.sc*). The two arches join at a right angle, and the foremost has a crescentic ridge traversing

it, whose convexity is backwards. The ampulla of the horizontal canal (*h.sc*) is hidden by this ridge, for its outer end joins the squamosal (*sq*). That canal lies in strong roof ("tegmen") laterally; this is enlarged by the squamosal; and the soft end of the "otic process" (figs. 6, 7, *ot.p*) lies lodged between the two bones. The elegant bulging of the vestibule in the same figures forms a lozenge-shaped convex tract below, bounded on the inside by a sulcus, and on the outside by the "tegmen." A smaller lozenge exists in the hind part of the larger; this is the cartilaginous stapes (*st*), fastened to the rim of the 4-sided fenestra ovalis. At the antero-internal angle of the vestibular swelling, just outside the basitemporal projection of the parasphenoid, the 7th nerve escapes.

The whole side wall, or sphenethmoid (figs. 6, 7, *sp.e*), is ossified from the prootic (*pro*), with which it is ankylosed, to the nasal sac. At its hinder fourth the optic nerve (2) escapes; then there is a lesser foramen for some of the orbital nerves, and close in the axil, between the wall in front and the ear-sac behind, the 5th nerve escapes. Part of the unossified nasal roof (*na*) can be seen forming a curtain to the external nostrils (*en*), and another part behind and below, attached to this, and most probably confluent with it, is the ethmopalatine (fig. 6, *e.pa*).

The suspensorium is much less retracted than in the Salamander (Pls. XVI. and XVII.); the pear-shaped condyle is in front of the foramen ovale. It is nearly all ossified by the quadrate (*q*); the upper part is completely hidden by the pterygoid (*pg*); but the otic process (*ot.p*) remains as a tongue of cartilage attached to the grooved "tegmen."

The pterygoid (*pg*) has its short part swollen towards the skull; this is seen to cover the pedicle, when the skull is examined from below (fig. 6). The outer margin strongly binds the inner face of the quadrate, and the bone from thence becomes a blunt style, attached by a short ligament to the maxillary (*mx*).

The dentigerous segment of the larval pterygopalatine bone (figs. 1, 2, *p.pg*) is completely confluent with the vomer of the same side (fig. 6, *pa, v*). The space between these palatal bars is narrow, but gradually widens backwards.

About a fourth of the bone (less on the left than on the right side) becomes segmented off as a postpalatine bone. I call this a *postpalatine* because I cannot reconcile it with the mesopterygoid*. It may, however, be the same bone, for it comes off from the same part of the palatine as that which gave off the pterygoid. At any rate the palatine itself, here, only answers to that curved ridge of a bird's palatine that cleaves to the parasphenoidal rostrum.

Where these palatal beams widen there they become vomerine; that widened part, with the ethmopalatine cartilage, bound the internal nostril (*in*) behind. The bone narrows again to form the inner rim of the internal nostril, and then grows into a hatchet-blade, whose back has a round notch. The two notches together form an oval fenestra.

The outer bones of the fore face have an equal development of *hard palate*, as we see

* In a generalized Woodpecker (*Picumnus minutus*, see Trans. Linn. Soc. ser. 2. vol. i. pl. 5) I found a distinct postpalatine bone. In that group the mesopterygoid is not fretted off, as in most "Carinatae."

in the two vomers. The premaxillary (*px*) yields a very large transversely oblong plate to the palate in front; the dentary margin is only gently arcuate, and the ascending nasal process (figs. 5, 7) is a smallish wedge. The maxillary (*mx*) gives off a considerable palatine plate, and is of great height in the cheek (fig. 7); its long jugal process is arched downwards, and only reaches two thirds of the distance from the high part of the bone to the quadrate (*q*). These bones, as also all the subcutaneous scutes for this strong skull, are rough on their outer surface.

The nasals (*n*) are large, thick, scabrous, multilobate plates; their strong median suture is notched before and behind,—before to receive the apex of the nasal process of the premaxillary, and behind to form, with the frontals (*f*), a small fontanelle. This space communicates with the more regular opening between the vomers below; and this merely functionless cavity is the adult remnant of the “middle nasal passage” seen in the larva (figs. 1, 2).

The frontals (*f*) are bevelled at their antero-external angle, to receive the outer nasal roof-bone, or external ethmoid (*e.eth*). This is a roughly pentagonal plate; it corresponds with the bone which ossifies the prefrontal of an Osseous Fish, but is parosteal in these types.

The orbito-nasal nerve runs in between this bone and the maxillary in the *lacrymal region* (fig. 7). The frontals are imbricated on the parietals (*p, f*); they scarcely exceed them in length, but are broader. This breadth is gained by the development of a much better orbital rim than is seen in *Salamandra* (Pl. XVI.).

The free outcurved part of the rim reaches to the squamosal; in front, it is finished by the ectethmoid; and below, the jugal process of the maxillary almost completes the bony circle of the eye. The rugæ and their interspaces, especially between the inner and outer part of the frontals, very much resemble what is found in so many Teleostean Fishes. The parietals (*p*) really form a wall in this species as well as a roof; and a strong ridge, which converges in a subarcuate manner towards its fellow behind, makes a very definite upper boundary to the temporal fossa. The size of the muscles causes the skull to have a *waist* at that part; and the fossa itself is completely surrounded by bone.

The parietals end behind abruptly, the temporal ridges in each angle projecting somewhat; but each bone is lifted and bevelled a little over the junction of the anterior and posterior canals (*a.sc, p.sc*).

The frontal and sagittal sutures run on to the end, and in front is the nasal suture, over the snout; these are roughly denticulate.

The side view (fig. 7) shows how well made are the orbital plates of the frontals and the temporal plates of the parietals.

The hammer-shaped squamosals (*sq*) have their supratemporal equal to their preopercular region; the former is roughly ribbed along its outer edge above, and the latter is carinate, the keel running down into the pointed lower end, and binding on the quadrate (*q*).

The flat top of the squamosal (fig. 5) is scabrous; its supratemporal part is twice as large as its postfrontal projection. A notch behind, under the tegmen, exposes the otic process.

There is another facial bone in this species, the small, graniform, septo-maxillary (fig. 7, *s.mx*).

The forked, narrow, fore end of the parasphenoid (fig. 6, *pa.s*) is largely invested by the palato-vomerine plates; further back it gradually expands to the basitemporal angle, which is short and rounded. Behind this, as the bone narrows backwards, there is another like projection, and at the middle the bone ends in a rounded manner. This bone is subearinate between the palatines; the keel is grooved along its middle; and in the interauditory region the crest swells into a gentle convexity.

Thus we see that even the huge parasphenoid becomes specialized, and even ornate, in the higher Caduceibranchs.

The mandible is arched from chin to angle, both outwards and upwards (figs. 7 & 8); the two bars form a strong and strongly bent bow. The articular part is highest, and this height culminates in a sort of coronoid process, formed on the outside by the dentary (*d*), and on the inside by the articular (*ar*). The splenial (fig. 4, *sp*) is a delicate style, most pointed in front. There is but little cartilage left, and this is mainly articular; the condyle is placed obliquely, it looks upwards and backwards.

The hyobranchial apparatus (fig. 9) has undergone similar changes to that of the Salamander (Plate XIV. fig. 7); but there are some remarkable differences.

The ceratohyal (*c.hy*) has become rounded and ossified in its upper half; its lower half is very flat and is soft. The hypohyal (*h.hy*) has become loosened from the main piece, and now articulates directly with the soft fore end of the first basibranchial.

Like the ceratohyal, the 1st branchial retains its relative size. The two pieces are soldered together, and yet each has its own bony shaft (*e.br*¹, *e.br*¹). There is a little cartilage at the free end of each segment; and that of the ceratobranchial articulates with the soft hind part of the 1st basibranchial. A delicate arcuate rod of cartilage articulates with the same tract, but behind it. This is bowed inwards as much as the ossified bar is bowed outwards; it is the second cerato-branchial (*e.br*²) whose upper piece has been absorbed. This rod is fused with the synchondrosial cartilage of the one in front of it.

The two other arches have been absorbed; and so also has the 2nd basibranchial, all but the lobes at its distal end (figs. 4 & 9, *b.br*²). These are now thick semioval thyrohyals. Behind these nuclei, which bound the glottis (*gl*), there are two more patches of cartilage (*lv*); they are roughly-perforate irregular rudiments of the arytenoid cartilages.

All but the ends of the 1st basibranchial (*b.br*¹) is occupied by a shaft-bone, so that there are *seven* of these rods in these metamorphosed arches.

Both the Anura and the Urodela curiously foreshadow the hyoid and thyrohyals of the higher types; but the Frog casts its shadow towards the Mammal, and the Newt towards the Bird.

Species 3.—The Skull of Cynops pyrogaster (adult).

This Japanese Newt is larger and stouter than the last type; its skull is very massive, and greatly resembles that of *Notophthalmus*, but is still more dense and strong. This

form belongs to the same natural group as the last; and the morphological differences between the two are, indeed, interesting, but somewhat trivial.

The occipito-otic region (Pl. XVIII. figs. 1, 2) is strongly in contrast with the rest of the skull; the whole skull is a sort of short stout mallet, the handle being all the middle and front regions, and the head the ear-masses, formed into one by the occipital arch and its over- and underlying splints.

The arch of the occiput leans forwards, so as to show the floor from above. This floor is widely emarginate, to receive the *odontoid vertebra* (not *process*), which is an exact miniature of the odontoid process of the Ox. The exoccipital bones are very closely applied both above and below; the wavy facets (*oc.c*) are subpedunculate and look downwards and inwards. Above, the huge canals of the ear (*a.sc*, *p.sc*) elbow inwards to the rim of the arch; they leave a hollow outside, which swells again with the horizontal canal (*h.sc*); this is overlapped by the squamosal (*sq*). The anterior region of the auditory sacs and occipital arch is covered by the parietals (*p*); below (fig. 2), the pedicle of the suspensorium, invested by the pterygoid, hides the ear-mass in front.

The vestibule, behind the foramen for the 7th nerve, is well defined, but does not bulge so much as in the last kind (Pl. XVII.). The fenestra ovalis, in its hinder margin, looks outwards and backwards. The oval stapes (*st*), with its nucleus of bone in the centre, resembles, on a large scale, the blood-corpusele of a Newt.

The tegmen is irregularly scooped, and is enlarged by the squamosal (fig. 2, *sq*). The whole mass is very wide, directly transverse behind, with the middle region having the condyles projecting on each side of the median emargination. The pterygoids, suspensoria, and squamosals, together, grow like trifurcate antlers, from the broad, transversely oblong, occipito-otic mass.

From the auditory capsules, onwards, the skull-walls are ossified, as "sphenethmoids," nearly up to the internal nostril (fig. 2, *i*); the rest remains soft (figs. 2 & 3, *sp.e*). The external nostril is well rimmed by the olfactory cartilage (*na*, *e.n*). The internal nostril is margined behind by the ethmo-palatine cartilage (*e.pa*), which coalesces with the nasal wall.

The optic nerve (2) passes out at the hinder third of the sphenethmoid; the 5th (5) between that bone and the prootic (*pro*, *sp.e*), and the orbitonasal pierces the ectethmoidal plate (*e.eth*, 5).

When the skull is seen from its fore end (fig. 6) the large fenestra for the olfactory crura (1) are seen; the 9th and 10th nerves (fig. 2. 9, 10) emerge close on the outside of the occipital condyles (*oc.c*); the first of these burrows in the capsule, but the vagus escapes in the chink between it and the exoccipital, so that a small bar of bone can generally be seen dividing the foramen into two.

As in the last species, the suspensorium looks forwards as well as outwards, not gaining that backward position seen in the Salamander (Pl. XVI.); it is well ossified (*q*), and has a cylindroidal condyle. The otic process (*ot.p*) is triangular, soft, and free.

The pterygoid cartilage (*e.pg*) has been ossified by the pterygoid bone, especially at its origin, and thus a separate epipterygoid has been formed. The strong pterygoid bone

strongly binds the suspensorium and its pedicle, and then runs directly forwards as a round-pointed tongue, which does not nearly meet the maxillary, that bone being short.

The palatines are like those of the last kind; they are long flaps of bone, running back from their union with the vomers, and are serrated with small teeth along their inner edge; the *right* bar has a separate postpalatine detached from, and one third the length of, the main piece*.

The left bar reaches further back than the other, even with its additional piece. The fore palate is not so extensive as in *Notophthalmus*, the palatine plate of the vomers being less; each bone is rimmed round the oval middle nasal space. The premaxillary and maxillaries (*px*, *mx*) are quite similar to the last; but the jugal process of the maxillary is much shorter and the bones are stouter.

The nasal process of the premaxillary is grooved and pitted in front; the building together of the fore face and nasal openings is shown in a front view (fig. 6, *n.px*, *na*, *e.n*). On the right side two small irregular septo-maxillaries (*s.mx*) are seen resting on the maxillary; on the left side there is a small grain resting on the alinasal cartilage.

The ectethmoid (*e.eth*) is a very strong wedge, finishing the antero-superior region of the orbit, and pierced for the orbito-nasal nerve (fig. 3. 5).

Each nasal (*n*) has a crescentic notch in front and an oval lobe behind. Their rough common suture shows two lozenge-shaped gaps that communicate with the internasal recess.

The frontals (*f*) are strong, and give off a thick scabrous postorbital process from their orbital rim and plate; the squamosal (*sq*) forms a squamous suture with this process.

The parietals (*p*) are about equal in size to the frontals, and each bone has a strong transverse ridge behind the temporal fossa, which is triangular; it is scooped behind this ridge. The frontal, coronal, and sagittal sutures are very irregular and coarsely toothed.

As in the last, the squamosal (*sq*) is a large T-shaped bone, carinate, both along its outer edge above, and down its preopercular bar in front and below. The parasphenoid (*pa.s*) gradually widens to the interauditory region, and then suddenly narrows again to its transverse end close in front of the odontoid notch; it gently bulges along the basi-cranial floor.

The mandible (figs. 4 & 5) is a very stout bar, which is arched upwards as well as outwards. The dentary (*d*) nearly reaches the condyle outside, and the deep trough-shaped articulare (*ar*) helps it to form the coronoid process. The splenial (*sp*) is a long f-shaped splint, following the curve of the dentigerous ridge of the dentary; it is pointed at both ends; the condyle is cylindroidal.

The hyobranchial apparatus closely resembles that of *Notophthalmus*, but has some curious differences. Every part is stouter; the hypohyals (*h.hy*) look forwards; the 1st epi- and ceratobranchials (*e.br*¹, *c.br*¹) are not fused, either with each other or with the 2nd cerato-branchial (*c.br*²); and this bar is also ossified. The thyrohyals, formed from the 2nd basibranchial (*b.br*²), are better formed than in the last; the

* The suture is not drawn in fig. 2.

laryngeal patches (*lx*) are quite similar. Altogether the skulls of *Cynops* and of *Notophthalmus* are only unlike in non-essentials.

A considerable number of the Caduceibranchs agree with each other in all that is essential in their skulls; but others show remarkable modifications, as I shall soon show.

Species 4.—Skull of Taricha torosa (adult). North America.

This skull is only two thirds the size of the last; it is flatter and feebler, but agrees in all essentials with the stronger specimen. The cartilaginous basi- and supraoccipital regions (Pl. XIX. figs. 4, 5, *s.o.*, *f.m.*) are wider, in conformity with the less intense ossification of the skull generally.

The occipital condyles (*oc.e*) are distinctly pedunculated, as a correlate of the deep odontoid notch; they look a little inwards and downwards, but most backwards.

The auditory masses are one continuous bone on each side with the occipital moiety; they look forwards and outwards, and the general outline behind is crescentic, not straight, as in *Cynops*. The semicircular canals are strongly marked on the huge ovoidal ear-masses (fig. 4); below, the fenestra ovalis is largely surrounded by unossified cartilage; and the oval stapes (*st*) is also soft. Above, there is a fissure in the prootic filled by cartilage; this is continuous with the facet to which the pedicle is attached, as in the adult Frog. Here, outside the hole for the facial nerve (7), the prootic itself forms a sheath to the raised facet for the pedicle (*pd*), which is hidden by the rim of the pterygoid (*pg*).

From the middle of the optic passage (2) to the foramen ovale (5) there is a cartilaginous (alisphenoidal) tract, and then the sphenethmoid (*sp.e*) runs nearly to the curved ethmopalatine (*e.pa*).

The nasal capsules (*na*) are entirely unossified; the external nares (*e.n*) are small and round, the internal nostrils are large (fig. 5, *i.n*). The internasal lamina can be seen both above and below (figs. 4 & 5), forming the hinder boundary of the internasal recess (*m.n.p*).

There is a strong quadrate bone (*q*) in the suspensorium. The condyle looks forward, as in the last two kinds. The fore part of the suspensorium gives off a long pterygoid process, which is longer than the pterygoid bone; from its base upwards the suspensorium is unossified, its pedicle being closely locked within the pterygoid. This species has the condyle of the pedicle most like that of a Frog. From the rim of this joint the pterygoid bone runs inside the quadrate, wedge-like, and then forwards, supporting the counterpart cartilage; the latter touches the zygomatic process of the maxillary (*mx*), but the apex of the bone does not. The falcate palatines (fig. 5, *pa*) are imbricated beneath the vomers (*v*), and the convex edge is not a sharp blade, but a *saw*, the teeth being uniserial and inturned (on the right side of fig. 5 the palatine is represented as absent). The concave back of this little saw corresponds with the outer edge of the parasphenoid (*pa.s*).

The hard palate is not so well developed as in the last two kinds. The vomers (fig. 5, *v*) are rough miniatures of a pruning-hook, the semicircular notch margining the inner nostril (*i.n*). The convex back of the hook is articulated by suture to the palatine plates

of the premaxillary and of the corresponding maxillary (*px*, *mx*). The "helve" of the blade is the palatine, and each blade is wrought into sutural teeth to unite, by squamous suture, with the underlying fore end of the palatine, which carries, now, all the true teeth; for the vomer has become edentulous.

We have thus, in this species, a most instructive analysis given us of the skull of the two last kinds (compare Pl. XVII. fig. 6, Pl. XVIII. fig. 2, and Pl. XIX. fig. 5). Moreover, this skull, which stands related to the last two, like a young individual, is also intermediate between them on one hand and *Desmognathus* and *Spelerpes* on the other (Pl. XXI.).

In *Amblystoma* (Phil. Trans. 1877, pl. 24. fig. 6) the palatine, as in *Polypterus* and the Batrachia, is a transverse bone, which, with the ethmo-palatine, its cartilaginous consort, represents the ornithic "os uncinatum." In *Spelerpes* and *Desmognathus* (Pl. XXI.) I shall describe a palatine which is both transversely and basally developed, as in those Batrachia which have a broad inner part (e. g. *Bufo aqua*).

In *Taricha* (Pl. XIX. fig. 5) the palatine (*pa*) has no transverse part, but it is longitudinal or basal, altogether; yet it does not run much more than half as far backwards as in the last two kinds.

The median palatine region of the premaxillary (*px*) is a grooved emarginate wedge. The nasal process (fig. 4) is a very curious structure; there are two spatulate free processes, but these are confluent from the middle forwards; and this part is largely sulcate, the valley being surrounded by a ridge, which is round in front, and which at the sides passes into the free lobes.

The uniting portion ends in a rounded notch, which is converted into a large oval hole by the internasal cartilage behind. The same cartilage is seen to bound it below (fig. 5, *m.n.p*), between the hooked vomers.

In this careful finish of a *useless* middle cavity or passage, *Taricha* approaches *Spelerpes* and *Desmognathus* (Pl. XXI.); those surroundings are not less perfect in the last two kinds (Pls. XVII. & XVIII.).

The maxillary (*mx*) in this flatter skull has a lower facial plate; its palatine portion also (fig. 5) is less extensive; but its jugal process is unusually long, passing some distance behind the pterygoid (*pg*). The septo-maxillary is not apparent.

The nasals (*n*) are more rounded and thinner; the orbital process of the ectethmoid (*e.eth*) is a sharper spur, but forms part of a very similar superorbital ridge; that part of the frontal (*f*) articulates over the temporal fossa with the squamosal (*sq*).

The frontals do not quite cover the internasal cartilages, and on each side they are dented by the nasal processes of the premaxillary, and overlapped by the nasals and ectethmoids. In their turn they are imbricated upon the parietals (*p*), which run on between, as well as beneath them.

Together the parietals (*p*) form a roughly pentagonal plate, divided irregularly by the sagittal suture.

Each bone is imbricated upon the prootic over the anterior canal (*a.se*), and the two run straight across the occipital arch, a little in front of the shelving upper edge of the foramen magnum.

The parasphenoid (*pa.s*) is essentially like that of *Cynops*. The postorbital part of the large squamosal is almost as large as the part which lies over the two anterior ampullæ; the fore part curves inwards to join the postorbital process of the frontal. A carinate preopercular process runs down outside the suspensorium, binding the quadrate (Pl. XIX. fig. 5, *sq, q*).

The mandible (figs. 6 & 7) is feebler, lower in the coronoid region, and has a smaller splenial bone (*sp*); the condyle is a large oval tract of cartilage. Each ramus, as usual, is tied to its fellow at the chin by a strong interosseous ligament.

The hyobranchial apparatus (Pl. XIX. fig. 8) might have belonged to a half-grown *Cynops*; the bony centres are shorter, only half as much developed, and there is no bone in either the first basibranchial (*b.br*¹) or on the second cerato-branchial (*c.br*²). Another arrested state is shown in this, that the whole end of the second basibranchial (*b.br*²) remains as a transverse *thyrohyal*, and is not broken up into two segments, as in the last two kinds.

Thus this species, conforming on the whole very accurately to the highest Caduceibranchiate type, is, nevertheless, somewhat arrested in development as compared with some other kinds.

Species 5.—The Skull of Onychodactylus (? species). Japan. Total length of animal
2½ inches.

The study of this type wrought much surprise in me: to all appearance it seems to be a genuine Caduceibranch, yet in development it has not advanced much further than in the ripe young of *Salamandra maculosa* (Pl. XV.); and its position in the "Order" would appear to be among the Cryptobranchs, or those whose branchiæ are almost absorbed. When I come to describe the skulls of the Menopome and Siren, it will be seen that in many respects they are quite as much metamorphosed in their skull as this species.

The sharp toe-ends of this kind suggest the presence of *nails*; but I could find no special development of the epidermis on the upper surface; yet I carefully examined the toes at Prof. Mivart's request, to whom I owe this and many more Amphibian treasures.

The cranial territories are very equally composed of cartilage and bone; and the secondary bony plates correspond to those of the larvæ of Caduceibranchiate skulls—larvæ that have their gills full-sized or in full play.

The existence of so small an Amphibian as this lingering on the headland of the lowest tribes is very interesting, more especially as it coexists in Japan, if not with the lowest, yet with the largest of these waifs of a subextinct group. I refer to *Sieboldia*. In South Europe we have the *lowest*, namely *Proteus anguinus*; but this creature is an "albino" prisoner in the waters under the earth. Yet, with the exception of this kind and of the Gigantic Salamander of Japan, I am not acquainted with any other species of the lowest group outside North America.

There, still flourish the *Menobranchus* (which is next above the *Proteus*), the *Menopome*, the *Siren*, and the *Amphiuma*; the small *true* Caduceibranchs (they are all of small size) have a wide geographical distribution.

In this chondrosteous skull the exoccipital (Pl. XIX. figs. 1 & 2, *e.o.*) runs over the epiotic and opisthotic regions, reaching the fenestra ovalis below (fig. 2, *fs.o.*), and covering the arch of the posterior canal (fig. 1, *p.sc.*) above.

An oblong band of cartilage finishes the roof and the floor of the occiput (*s.o.*, *b.o.*) and these tracts pass further forwards into right and left tracts of cartilage that intervene between the exoccipitals and the prootics (*pro*). These latter bones are less developed above than below; above, they skirt the fore margin of the auditory mass, and then leave the arch of the horizontal, and the ampulla of the posterior, canal unossified (fig. 1, *h.sc.*, *p.sc.*). Below (fig. 2), the bony tract has grown to the outer margin, but the vestibule is soft; thus the fenestra ovalis has half its rim unossified. The 9th and 10th nerves (9, 10) are well enclosed in bone, which, as usual, runs between them.

The position of the fenestra ovalis (the stapes was lost in dissection) is postero-external. The sphenethnoids (*sp.e*) barely harden half the interorbital walls; they reach neither to the nasal region in front nor to the optie foramen behind; thus the whole alisphenoidal region and the hind part of the orbitosphenoidal is unossified (fig. 2); so, also, is all the nasal region, which is floored by very large leafy trabecular cornua (*c.tr.*), and bounded behind by the ethmo-palatine cartilages (*e.pa.*).

The condyles of the suspensorium look forward and reach nearly to a line drawn across the optie nerves (2) at their exit; there is a quadrate bone (*q*), which, however, does not ossify half the cartilage. The otic process (*ot.p*) is not hidden by the pterygoid bone, but the pedicle is. This species agrees with the Menopome in having that bone (fig. 2, *p.pg*) divided from the palatine. It is a curious sort of small hatchet, with a rounded blade that binds upon the inner face of the suspensorium, and a haft which is bent outwards, and ends in a sharp point in front, which has no teeth on it. The large vomers (*v*) are perfectly larval, and are confluent with the small palatines; they meet in front, and then form an elegant arch, whose anterior margin carries teeth. The inner end of each bone is rounded, and the outer sharp, the sharp end overlapping the pterygo-palatine. Just in front of the middle of each plate there is a rounded inner lobe.

This arch is behind the large flabelliform cornua trabeculae. In front of those lobes there is a larger dentigerous arch, very elegant and forming nearly a semicircle. All except the extremities of this bone is formed by very large premaxillaries (*px*), the ends by small maxillaries (*mx*). As in *Proteus*, *Menobranchus*, the Siren, Menopome, Axolotl, and Spotted Salamander (Pls. XIV.–XVI.), there are two premaxillaries; but most of the Caducibranchs have but one, as in the last two instances.

The nasal process of each bone is slender, and the palatal edge of each bone is narrow; the maxillary (*mx*) is a small style attached to each outer end. The nasals (fig. 1, *n*) are oblique lozenge-shaped bones, pointed in front, and to a less degree behind; the nasal processes of the premaxillaries rest on them, they on the frontals (*f*), and the frontals on the parietals (*p*), by a normal regular imbrication.

A conchoidal ectethmoid (*e.eth*) flanks each nasal, and also partly the outer edge of the frontal. The interorbital region of the skull being very long, the frontals and parietals are very long and narrow; the latter run far forwards as a wall-plate to the skull, and are largely overlapped by the frontals.

The supratemporal region of each parietal is bilobate; it lies over the anterior canal (*a.sc*); behind this expanded part each bone slowly lessens towards its fellow at the mid line; they leave much of the supraoccipital region naked.

The squamosals (fig. 2, *sq*) are mere splints binding the suspensorium, and running along the side of, and somewhat above, the ear-mass.

On the floor of the skull we see a very long, delicate, inferiorly bulging parasphenoid (fig. 2, *pas*); in the space between the fore part of the two vomers it is very splintery; it gradually narrows to the foramina ovalia, and then spreads into a large ox-face of bone. This basitemporal part has a pair of large rounded lobes, with a lesser pair both in front and behind these: the end is transverse and somewhat emarginate; it reaches much further back than the parietals.

The mandibular arch (fig. 3) is a delicate and very elegant bow, much unlike the same arch in the stout Newt just described, and very *larval* in character. The Meckelian core of cartilage (*mk*) is unaltered by its investments; it reaches the chin inside the dentary (*d*), and its thick hinder part lies in the articulare (*ar*) as in a trough. That bone is scarcely more than *three fifths* the length of the mandible, and the splenial (*sp*) is very small and lies on the fore end of the articulare. The condyle is oval and large, as in larval Caducibranchs; it rolls loosely on the slightly scooped condyle of the suspensorium.

As in the Menopome and Siren, the hyobranchial apparatus has undergone but little change; there has been no absorption of the hinder arches, and their denticulations remain: these things all show that this type is not a true Caducibranch.

The hyoid and 1st branchial are much alike, but the latter is the longer and slenderer; they both remain soft. Their subdivision differs; for the ceratohyal (*c.hy*) cuts off a hypohyal (*h.hy*), here unusually large; but these two together correspond morphologically with the ceratobranchial; for the epihyal is suppressed. The thick 1st ceratobranchial (*c.br*) is attached to the middle of the 1st basibranchial, a long oval cartilage (*b.br¹*), and the 2nd ceratobranchial (*c.br²*) to its end. This last bar is as long as the one in front of it, but is very much slenderer; it also has acquired an imperfect bony shaft. Its epibranchial piece (*e.br²*) carries the 3rd and 4th arches, which are composed, as usual, of merely the epibranchial segment (*e.br³ & 4*). The 2nd basibranchial (*b.br²*) has begun the usual metamorphosis; its fore half has become membranous, and the hind half is ossified, all but the outer lobes, the only parts that are left in *Notophthalmus* and *Cynops* (Pls. XVII., XVIII.). The presence of *three* bony centres, and the absorption of the hindermost median bar in front, are the most marked evidence of metamorphoses of these bars.

Considering our great poverty as to existing Perennibranchiate and Cryptobranchiate Urodeles, this curious sharp-toed Japanese Salamander turns out to be a form of no little importance. It is a very useful stepping-stone from the lower to the higher kinds of its own "Order."

Species 6 & 7.—The Skulls (larval and adult) of Spelerpes rubra, and larval skulls of Spelerpes salmonea.

These North-American Caduceibranchs measured as follows :—The adult *S. rubra* $4\frac{1}{2}$ inches long, and the young (with gills) 1 inch 10 lines; the larval specimens of *S. salmonea* measured 2 inches 1 line and $3\frac{3}{4}$ inches. The larvæ of this genus reminded Prof. Mivart ('On the Common Frog,' p. 48) of *Menobranchus*; they struck me as being like *Proteus*. We were both right; for they strongly resemble and very accurately represent both those Perennibranchs. The youngest of these larvæ (*S. rubra*) was of considerable length, namely $1\frac{5}{8}$ inch, and yet the structure of its skull is extremely simple, and differs in nothing essential from that of the adult *Menobranchus lateralis* (compare Pl. XX. figs. 1 & 2 with that type: see Huxley, P. Z. S. 1874, pls. xxix. & xxx.).

This larval skull is curiously illustrative of the extreme variability of *the time* in which ossification is set up, and harmonizes with what I find in the Batrachia, namely, that of the most generalized kinds, some skulls are most feebly ossified, and others are a mass of dense bone, with scarcely a suture left.

Here there is no distinction even between the preotic and exoccipital; all the occipitotic region on each side is one undistinguishable tract of bone (Pl. XX. figs. 1 & 2, *pro*, *e.o*); and these bony territories have met in the supraoccipital region, although they have a broad synchondrosis below. There is a character here which strikes the eye at once, namely, that the foramen magnum is nearly as wide as the average width of the cranial cavity. This is surely a *low* character.

The condyles (*oc.c*) look obliquely upwards, like ordinary "pre-zygapophyses," and between them there is a very wide crescentic notch for the "odontoid vertebra." There is a rudiment of a bony roof to the skull running forwards from the supraoccipital region. This bony tract first grows inwards as a lobe, and then stops short over the Gasserian ganglion; thence the skull-wall is unossified, and only behind does it lean over the brain.

The whole configuration of the semicircular canals (fig. 1, *a.sc*, *p.sc*) is stamped upon the bony *periotic*. These structures are very large.

It will be seen that above, in front of the two ampullæ, there is a tract of cartilage; this is an upgrowth from the basal plate (trabeculo-parachordal), and is *normally related* to the pier of the mandibular arch, the "suspensorium." On the lower face of the ear-capsule there is some cartilage left; this is a trilobate tract beneath the "sacculus;" outside this tract is the large fenestra ovalis (*fs.o*), with its correspondingly large stapes (*st*).

A considerable blood-vessel is seen entering into (? emerging from) the membranous labyrinth at the inner edge of the regularly ovoidal stapes, whose narrow end looks forwards and outwards.

There is a short canal for the facial nerve (fig. 2. 7), but it soon escapes from the capsule, and runs outwards and forwards beneath the apex of the otic process (*ot.p*), some distance in front of the stapes.

The 9th and 10th nerves (9, 10) are seen escaping from the skull through their twin-passage, between the condyles and the ampulla of the posterior canal (*p.sc*).

From the front of the ear-capsules to the frontal wall there is nothing but a pair of cartilages, the trabeculæ; these bulge externally, are concave within, are of moderate height, that is, they are as high as this flat skull is *within*, reaching above to the frontals and parietals (*f, p*), and below to the parasphenoid (*pa.s*).

As they approach the nasal sacs they become flat and depressed; having lost their *wall* character, they became part of the *floor* only. Each plate of cartilage is bowed outward twice—first in the alisphenoidal region, and again in the ethmoidal; but on the whole they gently approximate, but are a good distance apart at their end. Then they are first rounded and then each is flattened out into a small flabelliform “cornu” (*c.tr*).

Close behind these cornua the trabeculæ are undergoing *conjugation*, each bar sending inwards a small internasal lamina (*i.n.c*). Between the body of the premaxillary and these processes there is a large internasal cavity (*m.n.p*).

In similar larvæ of *Salamandra maculosa* (Pl. XIV.) the notochordal region was well floored with cartilage, the large expanded ends of the trabeculæ having coalesced with equally large parachordal tracts. Even in the adult of that kind there was still the trabecular bridge, then a fontanelle, and then the true parachordal tract. Here, however, so early in life, the parachordal cartilages only form a conjugating belt over the end of the parasphenoid (*pa.s*). Thus it is evident that all the inturned *parachordal* part of the trabeculæ and of the fore half of the hinder cartilages, or true parachordals, have been entirely absorbed, leaving the vicarious parasphenoid to make the floor.

I have watched this process in larvæ of *Triton cristatus* and in *Notophthalmus* (Pl. XVII.). In this latter kind two larvæ of precisely the same size differed greatly; in one (figs. 1 & 2) the trabecular ends were reduced to a small lobe, and in the other (fig. 3) they were still of good size, but they had become quite free from the hinder cartilage.

In both *Proteus* and *Menobranchus* the adult skull is much simpler than the embryonic. My dissection of the latter kind shows more basal cartilage than the one dissected by Professor Huxley (*loc. cit.*). In small young specimens I am confidently expecting to find a much fuller development of the basal cartilage than is to be seen in the adult*.

At present, as in the adult *Proteus*, there is, as yet, no olfactory cartilage; the sacs lie on and outside the trabeculæ. Behind the internal nostrils (*i.n*) there is on each side a free cartilage having a totally different morphological meaning to the nasal sacs, namely the ethmopalatine (*e.pa*); it is a small semioval free bud, attached to the trabecula at its postnasal bend, and is the orbito-nasal landmark.

The postorbital region is marked off by the large suspensorium, whose condition suggests considerable ripeness in this embryo, much in contrast with the slow metamorphosis of the fore part of the head.

The condyle is opposite the optic foramen; the cartilage next to it is ossified as a quadrate (*q*), but from the middle all is soft. The true swinging-point is bilobate,

* I am not aware that any *brain-bearing* vertebrate shows a more simple cranium in its early condition than the larvæ of the Urodeles; but they possess every thing that is wanted to make up a “chondocranium” in any type. Birds and mammals have nothing but the two “parachordal” cartilages, passing into the two “trabeculæ cranii,” and the two “intertrabecular” tracts; and even these are, I suspect, merely differentiated, the parachordals from the trabeculæ, by the latter getting the start in chondrification.

vertically; the upper lobe is the ascending process (fig. 1, *a.p*); it has coalesced with the alisphenoidal crest near the top.

The lower lobe, or pedicle (fig. 2, *pd*), is much less distinct than the upper, and seems like a swelling on the under face of that cartilage; the orbito-nasal and Vidian nerves pass between this swelling and the skull-wall under the ascending process. The outer or otic process (*ot.p*) applies itself, like a snail's foot, to the antero-external face of the ear-capsule; it is rounded below (fig. 2), but raised into a distinct ridge above (fig. 1), which reaches to the anterior ampulla (*a.sc*). In this stage the otic process is quite like what is seen in newly metamorphosed Batrachia, notably in *Pseudis paradoxa*.

The suspensorium is confluent with the skull only by its ascending process; the other process, right and left, plays freely on the auditory capsule, and is set in a bed of delicate connective tissue. The fore margin of the suspensorium shows no pterygoid process, although the ethmo-palatine cartilage (*e.pa*) is quite apparent.

The lozenge-shaped dentigerous palatine bone has already sent backwards a large, flat, edentulous pterygoid process, so that we have the widely distributed pterygo-palatine bone (*p.pg*)^{*}.

The whole bone reaches from the quadrate to the vomer (fig. 2), and the two bones with the two vomers (*v*) mark out half a long ellipse. The vomers are falcate, and nearly meet in the middle by their broad hooked end; they are dentigerous, and are about half as wide as the pterygo-palatines. In front of the vomers we have the median nasal passage (*m.n.p*) in the middle, and the trabecular cornua (*c.tr*) at the sides.

In front of these there is the dentary margin of the premaxillary (which is not double as in *Proteus* and *Menobranchus*); above (fig. 1) its nasal processes (*n.px*) are large and

* As the parasphenoid is the great primordial basal bony plate, so is this the first of the palatals, as we see in the Dipnoi, which have so few bony laminae applied to the solid chondrocranium, a step beyond the Chimæroids and ordinary Selachians. Higher up it is curious to see the persistency of the pterygo-palatine. In the generalized *Hatteria* (see Günther, Phil. Trans. part ii. 1867, plate i. fig. 2) the huge pterygoid has a large flat anterior part, which reaches and articulates with the corresponding vomer. In *Anguis fragilis* this fore part of the pterygoid bone is separate as a "mesopterygoid." The true longitudinal palatine of the *Hatteria* lies outside the vomer and pterygoid.

In Birds the pterygoid grows forward to the vomer (generally composed of a right and left bony centre); but, as in *Anguis fragilis*, there is afterwards a separate piece cut off as a mesopterygoid. In all the Carinatae, except the Woodpeckers and the Galline and Anserine groups, this takes place; and, oddly, the new bone soon coalesces with the inner edge of the great palatine, which is longitudinally placed, lies outside the pterygo-vomerine series, and reaches from the pterygoid to the front of the nasal labyrinth. I have shown that *Picumnus minutus* has a postpalatine, like *Cynops* and *Notophthalmus*; and the Passerinae have an additional cartilage besides the ethmo-vomerine and pterygoid (the pterygoid of a bird is formed in nascent cartilage and is cartilaginous behind); and this transpalatine occurs in *Siridon*. In the Bird it ossifies separately, and then coalesces with the outer part of the great palatine, as the mesopterygoid does with the inner edge.

Further, the ethmo-palatine of the Frog, when the transverse bony plate has grafted itself on the cartilage, corresponds with the os uncinatum of the Bird (*Corythæa*, *Trogon*, *Psittacus*); and this *anterior transverse bone* is fore-shadowed in those Urodeles that have a transverse bony palatine running under their ethmo-palatine cartilage, as in *Amblystoma*, *Spelerpes*, and *Desmognathus*. Stepping, then, across the wide space between the Dipnoi, the low Urodeles, and the larvæ of the higher kinds to the Bird, we have one safe determination to stand upon, namely, the relation of the primordial pterygo-palatine to the corresponding vomer. The other parts that come in, in the metamorphosis of the Urodeles, or in the ascent up the tribes, are new things—*specializations*.

lanecolate. The posterior nares (*in*) are in their usual relation to the vomers; but there are no maxillaries outside, nor nasals and ectethmoids above.

The two pairs of roof-bones (*f, p*), with the nasal processes of the premaxillaries, are adapted to each other by wedge-shaped imbrications; the frontals reach the internasal cartilage, and the parietals overlap the occipital belt slightly (fig. 1).

The parasphenoid (fig. 2, *pas*) is oblong, with rounded corners, and is further irregular by increasing somewhat from before backwards: the vomers underlie it a little in front; it reaches nearly to the foramen magnum behind.

The squamosals (*sq*) are nearly equal in their supratemporal and preopercular regions. It will be seen that I have figured one and part of another vertebra. The first of these is imperfect, having no arch; in the other the arch has been cut away. This second joint carries the skull on its long pedunculate "pre-zygapophyses," and between these the curious elongated centrum of the intercalary (odontoid) vertebra is fixed. It is ankylosed to the second centrum behind, and in front carries a bilobate mass, having a form somewhat like *dumb-bells*.

As this intercalary vertebra is inconstant, and as it *may represent part of the occiput* in the Sauropsida and Mammalia, for their hypoglossal is a cranial nerve, but is *spinal* in these low types, I shall describe this segment the more carefully.

In these types the notochord shortens rapidly (figs. 4 & 6, *nc*), whilst in *Seironota* the cephalic part is large, and partly segmented into two imperfect transient cranial centra. But if the cephalostyle is absorbed in *Spelerpes*, the notochord makes up for it in the intercalary segment. In the large semicircular notch between (not behind) the occipital condyles a *third* pair of "parachordal" cartilages appear (besides the ordinary pair and the parachordal region of the trabeculae). These nuclei of cartilage become ossified, and then coalesce by a bridge of bone; hence their dumb-bell shape. Meantime the long tract of notochord has become ensheathed with bony substance, and its apex embraces the bony stolon between the lateral lobes, and coalesces with it, its own end being emarginate, and more developed below than above the transverse plate.

Here we have the *three* normal elements of a vertebral centrum; and this curious structure is in front of the atlantean segment, a perfect and large vertebra, made to carry the skull. Thus the human odontoid process, which is merely the ossified notochordal *core* of the "atlas," enucleated from the symmetrical sides, and ankylosed to the "axis," is here represented and foreshadowed by a distinct meta-somatonic joint, with middle and side elements combined.

The inferior arches scarcely yield in interest to the skull itself, and show that these types are certainly related to the lowest sort of Perennibranchs.

The cartilaginous pith of each mandibular ramus is very solid, especially towards the articular end; that part rests in a delicate bony trough, the articulare (Pl. XIX. fig. 9, *ar*), and the outside is invested by the bony element (*d*). Where these bones meet on the inside, just in front of the highest or coronoid part, there is a small dentigerous plate, the splenial (*sp*). Here the splenial is very small; in *Proteus* it also is so, and that type has no hypohyal. Here it is only indicated by a groove crossing the inner face of the bar below (*c.hy, h.hy*). The branchials are normal as to form, but abnormal as to

number. *Proteus* and *Menobranchus* have only three; the 4th epibranchial is also wanting here. Thus in several points these larvæ approach the lowest "Perenibranchs."

Notwithstanding the large size of this larva, the flat 2nd basibranchial (*b.br*²) is very imperfectly differentiated from the 1st (*b.br*¹); as to *form*, these parts are quite normal.

Skull of larva of Spelerpes salmonea, 2 inches 1 line in length.

The metamorphosis of this type of skull has been as profitably followed in the larvæ of *two species* as if I had possessed all of them of the same kind. The head of the one just described is broader, and more like that of *Menobranchus*; in this species (Pl. XX. figs. 3-6) we have a nearer approach to the sharp eel-like head of *Proteus*. Therefore also, as these are more advanced than the last, we have to deal with characters that are due to metamorphism, and also with those that are due to specific difference.

The notch between the occipital condyles (figs. 3, 4, *oc.c*) is shallower; for the 1st or odontoid and 2nd or atlantal vertebrae are much shorter than in the last species.

Although more advanced, the supraoccipital region (*so*) is not yet ossified; the basioccipital is more so, and we see the very small remains of the cephalic notochord (*nc*), so unlike what is to be observed in many Urodelous larvæ at this stage.

The occipital roof is of larger extent, and the auditory capsules are directed more outwards in front, carrying with them the suspensoria, which thus give the larvæ a wider gape.

The amount of cartilage seen on the front face of the capsule from above (fig. 3) is the same as in the last; but the vestibular shell has a more even and a narrower rim of cartilage round the fenestra ovalis, all but its outer side (fig. 4). It will be seen in these two embryos (figs. 3, 4, 5, & 6) that the "tegmen tympani" is more tilted upwards, so that the fenestra and its lid, the stapes (*st*), are brought very close to the outer edge (see also the difference in Pl. XX. figs. 9, 10).

Ossification is spreading from the centre to the circumference of this plate, a neat margin of cartilage still remaining.

This oval bony centre has two curious enlargements on its surface; one is a boss on its hinder half for the insertion of the muscular fibres that roughly represent the *stapedius* muscle, whilst the other, on the fore half, is a neat round handle to this vestibular lid (figs. 4 & 10). As the plate itself has a rim of cartilage, so this rod has a core at its distal end; hence it is evident that a distinct rod of cartilage has been ensheathed by a hollow process from the stapedia bone, just as the prootic ensheaths the trabeculae in these larvæ (see especially fig. 6) and in the adult *Proteus*.

We shall see that this cartilage may have its own osseous centre (see Pl. XVIII. fig. 9, in *Desmognathus*, on the *left side* only); that is, however, when it does not grow so close to the stapes. Now here, it would seem, we have at last found a veritable medio-stapedial. *Proteus* has an unmetamorphosed hyomandibular; and what more natural than that these *proteiform* larvæ should repeat that segment, and use it as a "columella"?

In the adult (Pl. XXI. figs. 2 & 3, *st*) the stapes lies close to the edge of the tegmen and its squamosal tilings, and the facial nerve (7) passes close beneath the otic process of the suspensorium.

The explanation of what is seen in these small kinds comes from the Menopome. In that type, and in the *Siren*, there is an oval hyomandibular, *over* which the facial nerve passes; but in the Menopome the columella also is very large, perfect, and elegant.

In the Menopome, the gigantic *Sieboldia*, my figures (to appear in the Zool. Trans. for 1881) show this cartilage sticking by its broad foot to the top of the suspensorium and squamosal above and behind, and having its narrow end inserted into a bony stapelial sheath. This cartilage is formed beneath that fold of skin which is the operculum of the first cleft. That cleft, in the Selachian, is only left open above; in the Urodeles it is closed; but in the huge types just mentioned a "pharyngo-hyal" and an "epihyal" appear; the *former* becomes the "*columella*;" in the Frog both elements are included in that rod*.

The main difference between the fore part of the skull of the youngest larva of *Spelerpes salmonea* and that of *S. rubra* (figs. 1-4) is the slender face and more advanced condition of the specimen.

We have now the right and left moieties of the sphenethmoid (fig. 3); for close behind the ethmo-palatine buds (*e.pa*) the skull-wall is ossified: these growths are still soft. The internasal laminae (*i.n.c*) are not so much advanced as in the last instance, but the ethmo-palatines are larger.

The suspensorium, besides being more out-turned, has sent forth a small pterygoid tongue of cartilage (*e.pg*); but this shows at present so little affinity for the bony plate beneath it that it crosses it at a right angle. The cartilaginous process has at present the same outward direction as the body of the suspensorium.

The investing bones and the inferior arches had nothing in them differing from the last to make them noteworthy; the more pointed skull of necessity has narrower roof- and floor-bones.

Skull of larva of Spelerpes salmonea, 3 $\frac{3}{4}$ inches long.

These larvæ were much longer than the last, they were just ready for undergoing the Salamandrian metamorphosis, and yielded some very interesting results. One of the most important of these is the slowness of these larvæ in acquiring those characters which would lift them up out of the level of *Proteus* and *Menobrancheus*.

Large as these specimens were, I could detect no additional parts to the fore face; they were as simple there as in the types just mentioned.

There is not much at present to remark upon in the occiput; the cartilage above is less, but it is undiminished below; and this specimen had more notochord (fig. 6, *nc*) than the last.

* The account given of the columella of these Urodeles in my "Abstract" (Linnean Society's Journal, Zoology, vol. xiv. p. 719) is incorrect; it is not a "pseudo-columella;" the facial nerve passes *over* it.

The odontoid vertebra (*od.v*) clearly shows its three elements, and these are all grafted upon the "atlantal" or second joint (*v1*). The skull is here seen to be most carefully articulated to the spine. The auditory capsules are a little more protruded outwards, carrying with them the suspensoria.

The capsules are very large, owing to the great development of the three canals (fig. 5, *a.sc*, *h.sc*, *p.sc*). The hinder ampulla gives a very swollen appearance to the capsules even below (fig. 6). From this convexity we pass forwards to another, the vestibular; its ossification is advancing rapidly, leaving but little cartilage along the fenestra (figs. 6 & 8). But the stapes and the window it fills are tilted now, so that they are only seen obliquely in a basal view; thus the handle, or *stapedial* rod (fig. 6, *sp.e*, fig. 8, *co*), is getting nearer the top of the "tegmen." The relation of that rod to the facial nerve is best made out by paring these parts away, and seeing them from within (fig. 8, 7, *pro*, *st*). The nerve is imbedded in the prootic for some distance; in fig. 8 its course outside the bone is indicated by dotted lines up to the free edge.

The occipito-otic bone is spread into the base of the skull, ossifying the remains of the parachordals behind and the stunted ends of the trabeculæ in front; a notch shows the division of these two regions. In front of the foremost basal lobe the bone ensheaths the alisphenoidal wall for a short extent; thence to the optic nerve (2) the wall is soft; but in front, nearly up to the small distinct semioval ethmo-palatine (*e.pa*), the sphenethmoid (figs. 5-7, *sp.e*) has spread.

Directly in front of those bony tracts the trabeculæ, in their ethmoidal region, have united; there is a broad internasal lamina (*i.n.c*), gently emarginate behind and more so in front.

The suspensorium is altered in some respects; the pedicle (*pd*) is a more distinct swelling; the quadrate ossification (*q*) is larger; and the pterygoid cartilage (*e.pg*)* is not only larger, but has also changed its direction; it now runs parallel with the inner edge of the pterygo-palatine bone. That bone (figs. 5, 6, *p.pg*) has become inordinately large, and the toothed region is now confined to the outer margin of the broad trilobate anterior part. This bone lessens its breadth two thirds in the hinder half; it turns outwards in a pedate manner, and is now applied to the lower face of the suspensorium, almost reaching to the quadrate hinge.

The vomers also (*v*) are altered; from their primary suberescient form (fig. 2) they have now become, like those of the low Perennibranchs, straight, with an inner hook, the hook and the outer margin only being dentigerous. Nearly the width of the ethmo-palatine cartilages intervenes between the vomers and the pterygo-palatines.

The parasphenoid (fig. 6, *pa.s*), by its splintery fore edge, nearly reaches the middle nasal hole (*m.n.p*); it only very gently increases in breadth up to the basitemporal region; it then is twice somewhat produced outwards, most at the first pair of projections, and ends behind, a little in front of the foramen magnum, by a slightly emarginate edge.

* In fig. 6, Pl. XX., this is lettered *e. pa* by mistake.

Although nearly ripe for metamorphosis, there is but little promise in this stage of the strange things that will appear in a few weeks afterwards.

The Skull of an adult Spelerpes rubra, $4\frac{1}{2}$ inches long.

This skull, all things considered, is one of the most remarkable I have seen; in passing from the larval state to the adult, we seem to have climbed halfway up the vertebrate scale. In its completeness, now that all the *new things* have been added, it has become a singular commixture of the lower ichthyic, and the higher reptilian, styles of cranial architecture.

In making this building grow, Nature has brought out of her treasures, and fitly framed together, things new and old; thus, well observed, this skull may teach us much of what is possible in the morphological stages of a vertebrate cranium.

Having gone so far, if the life-power of the individual had sufficed, such a skull, one could imagine, might have gone on changing: a few steps in one direction would have made it like that of the Emu, at the base of the Bird series; or in another, that of a Monotreme, at the base of the Mammalian group.

The large pedunculated occipital condyles (Pl. XXI. figs. 2, 3, *oc.c*) are wide apart, and the posterior basiscranial emargination is perfectly filled by the curious intercalary odontoid vertebra (*od.v*), which, being ankylosed to the next (*v¹*), gives the larger joint an almost exact resemblance to the second ("odontoid" or "axis") vertebra of an Ox. Yet we have just seen that this bigger vertebra is the atlas to this skull, and that the "odontoid process" is in reality a small postcranial vertebra, without an arch, and segmented from the hind margin of the parachordal tract.

There is a considerable tract of cartilage, both above and below, in the occiput (figs. 1, 2); for the rest, the occipito-otic mass, right and left, is continuous solid bone; yet this bony tract stops at the foramen ovale (5); for the ossification of the endocranium is not intense in this type.

The auditory masses are very large and rugged; the huge posterior canals (*p.sc*), as they turn outwards and backwards, have a sulcus separating them from the sharp edge of the exoccipital, where it forms on each side a rim to the foramen magnum.

A very large triangular space exists between the emarginate occipital roof and the front, almost transverse, margin of the "atlantal" vertebra.

Most of the anterior canal (*a.sc*) is tiled over by the parietals (fig. 1, *p*); but the bony matter projects from beneath the notched edge of those plates, forming a crest for the origin of the fibres of the temporal muscle.

As the anterior canal is roughly covered by the parietal bone, so is the horizontal (*h.sc*) by the supratemporal part of the squamosal (*sq*), which ploughs itself into the substance of the prootic, raising it beyond its upper edge into a rough semicircular ridge.

Mesial of this ridge, the prootic is scooped for the temporal muscle; thus there is a crescentic fossa, with its convex margin outside; it reaches to the large oblique bulk formed by the posterior canal.

The under face of this ear-capsule is very different from that of most high "Urodelous" skulls.

In those massive *typical* Caduceibranch skulls just described, *e. g.* *Notophthalmus* (Pl. XVII.) and *Cynops* (Pl. XVIII.), the vestibule is in the form of a smooth *bulla*, with the stapes set on behind; and that plate is either quite soft or very slightly ossified; it is also relatively small.

In *Spelerpes* (Pl. XXI. figs. 2, 3, and Pl. XVIII. fig. 10) the vestibule is but little protuberant; its fenestra is lateral, and, corresponding with the stapes, very large.

At the inner margin of the fenestra the bone is scooped, and partly unossified at the edge. This is seen in the oblique view (Pl. XVIII. fig. 10). The outer margin of the fenestra ovalis is right under the tegmen, made larger and more beetling by the postero-inferior edge of the squamosal (*sq*). This change of position is due to a sort of vegetative affinity or attraction between the stapes and the stapedial rod (*st, eo*), which is found in the inner layer of the temporal plane.

The 7th nerve (7) first burrows in and then grooves the prootic a good distance in front of the stapes; in its escape it curves a little backwards, and then turns obliquely forwards and outwards under the otic process and its ossifying quadrate centre.

It will at once be seen that this is a very different relation of nerve and rod to what is seen in the Batrachia, where the hyomandibular, mostly late in appearance, passes under the facial nerve to apply itself, not to the outer face of the stapes, but along its antero-superior margin, pushing into the scooped fossa that *leads to* the fenestra ovalis. Moreover, in the Batrachia the stapes never yields any bony matter to the columella; in them the stapes is seldom ossified; and the columella generally cuts off the segment that grows into the front of the fenestral fossa.

One more point of interest is to be noted here: the lowest Perennibranchs have their stapes thoroughly ossified; the highest Caduceibranchs, like the Batrachia, have it soft; here, in *Spelerpes*, it ossifies early, and becomes a very perfect and elegant shutter to that small oval window.

In the walls of the skull, from the foramen ovale (Pl. XXI. figs. 3, 5) to a small opening behind the optic passage (2), the alisphenoidal region is soft; then the wall is hard, up to a small distance from the nasal sacs.

The nasal sacs (fig. 1, *na*) can be seen outside their roof-bones and also in front, forming a rim to the external nostrils (*e.n*); but on the whole they are most carefully encased in bone.

Yet in the last stage these olfactory paraneurals were not chondrified, nor even the nasals, ectethmoidals, or maxillaries developed.

The condyle of the suspensorium reaches further forwards than the foramen ovale (5); it is scooped in an angular manner (fig. 2), and above it the quadrate (*q*) grows upwards to the pterygoid cartilage in front, and to the top of the otic process behind. But the pterygoid cartilage and its base, running upwards as the ascending process to the alisphenoidal wall, is all soft.

In this thing *Spelerpes* is contrary to the ordinary Caduceibranchs, namely, that

instead of the pterygoid process of cartilage growing *rapidly* at first, and then, during metamorphosis, becoming less and less, it comes late, grows slowly, and then does not diminish in size.

This is a correlate of the curious abortion of the bony pterygoid which usually seizes upon the cartilage, converting it into its own substance. This outgrowth of cartilage is falcate, with the convex margin inwards, and the point looking towards the point of the short zygomatic process of the maxillary.

The large pterygo-palatine bone is now reduced to two remnants, one in front and one behind; three fourths of it has been absorbed. The pterygoid piece (behind *e.pg*) is an irregularly five-sided plate, applied to the inner face of the suspensorium in front and below; it does not project forwards, but its edge there is concave; above it is only half the width of the quadrate.

The foremost patches of teeth have crept off the vomers (*v*) on to the palatines, just where these bones have coalesced, so that the exposed part of the vomer is edentulous. Each palatine bone (*pa*) is mainly directed transversely; it extends outwards much further than the hinder process of the vomer, to enclose the inner nostril (*i.n*), and somewhat underlies the more extended ethmo-palatine cartilage (*e.pa*). Towards the mid line it is curved backwards, lies beneath the parasphenoid (*pa.s*), has its concave facet scooped, and soon ends in jagged projections.

Below, close behind the vomer, where the bone is the thickest, there is a row of sharp decurved teeth, arranged in sigmoid manner. The greatest arch in this series is between the internal nostril and the mid line of the skull; turning backwards, the right and left rows nearly meet. Although the palatine bones go no further backwards, the tooth-tracts do; they are continued so far back as to end opposite the foramen for the facial nerve (7). At first in a single row, and almost close together, they gradually widen their plot until there are five or six teeth in one transverse line; the interspace along the middle of the parasphenoid also gently widens.

These lanceolate tracts, with their out-turned sigmoid fore end, are very elegant; they are the so-called *sphenoidal* teeth. These rasp-like tracts existed before the palatine bones were formed, and grow far backwards, independently of them, where the bone has been absorbed.

The vomers (fig. 2, *v*) are some distance apart, except behind, where they unite with the palatines. Together they form a deeply notched *fan*, and each leafy plate has a deep rounded notch on each hinder margin for the internal nostril (*i.n*). Their interior margin is ragged, and their very large palatal development causes the palatine plates of the premaxillaries and maxillaries (*px*, *mx*) to be narrow. Reference to the figures of the last stage (Pl. XX. figs. 5, 6, *v*) shows how strangely these bones have altered from their larval form.

The premaxillary (*px*) is scarcely less transformed: looking at the bone in the three larvæ, we see it formed of a gently arcuate dentigerous part in front, and of two long, lanceolate nasal processes that run back and lie over the frontals; the middle nasal passage (*m.n.p*) is seen between the roots of these crura and the internasal cartilage (*i.n.c*).

Below (Pl. XXI. fig. 2, *px*) there is no appreciable palatine belt behind the tooth-bearing edge right and left, and the outer parts of the bone are flat (figs. 1, 3); but in the middle this bone is greatly developed vertically. Below (fig. 2) the two crura appear in front of the vomers; but between those bones they have coalesced; thus an oval space is enclosed (*m.n.p*). The coalesced part runs some distance backwards as a "median palatine process;" behind it is another space, over which lies the internasal plate of cartilage.

Above (fig. 1, *n.px*) the original distinctness of the nasal processes is seen in front by a deep hole, and behind by a sharp notch; the two bars have grown into a very large tract, which reaches back as far as the hind margin of the nasal sacs.

The middle nasal passage (*m.n.p*) is made into a deep well, with an everted funnel-like mouth, which is so greatly lipped behind as to overshadow the solid continuation of the bone, and give it the appearance of being a totally distinct plate. The nasals, also, clinging to the well's mouth, hide the median part; and it, in turn, becoming narrow and splintery, is imbricated on the frontals (*f*), wedging them apart. The large nasals (fig. 1, *n*) are roughly pentagonal; they have a concave edge forwards, towards the nostrils (*e.n*), and a sigmoid edge outside; they project towards one another behind the notched lip of the nasal *well*, getting under it. Behind, they run transversely, with irregular teeth, imbricating the frontals on the outer part, but not reaching nearly so far back as the premaxillary.

The ectethmoids (*e.eth*) are large conchoidal bones, that reach as far as the outer angle of each nasal in front, and clamp the orbital edge of each frontal for some distance.

Each maxillary (fig. 3, *mx*) is like a hatchet, the blade being its facial plate, and the handle its zygomatic process; but the blade is cut away in front; in that notch there is a graniform septo-maxillary (*s.mx*).

To cover much of this long skull the frontals (*f*) are long; they are widest in front, are deflected over the cranial wall (fig. 3), but have little orbital development. Where they begin to overlap the parietals (*p*) the skull is narrowest, and suggests the appearance of the outline of an hour-glass.

The end of the frontals is more than halfway from the foramen opticum (2) to the foramen ovale (5); the frontal suture is most irregular; the edges of the bones being very thin, and, as it were, lacerated.

The parietals (*p*) are much more elegantly finished. Each bone forms a wall-plate in the interorbital region almost to the ectethmoid, and this part really becomes a *paries*, as it descends with considerable steepness. The two bones gradually widen up to the auditory masses, and then they suddenly attain their greatest width, not lessening much behind, but ending transversely. Where they lie over the hind skull the parietals seem to have been fitted on in a plastic condition, so thoroughly do they fit to each rising and falling of the substance beneath. The dovetailing of the *sagittal suture* is perfectly mammalian in its complexity; the squamous sutures also, laterally, are very irregular over the anterior canal (*a.sc*); the posterior canal (*p.sc*), where it joins the anterior, lifts the *lambdoidal* edge of each parietal bone. The squamosals (*sq*) seem to grip the ear-masses; below, indeed, they are merely a thick wedge, binding the quadrate; but above,

the supratemporal tract is oblong, curved, ridgy, and scabrous; curling over the tegmen tympani, it imbeds itself into the very substance of the bony roof of the horizontal canal (*h.sc*).

From above (fig. 1, *sq*) this upper part looks like a distinct plate from the lower. The side view (fig. 3) corrects this false impresssion.

The parasphenoid (fig. 2, *pa.s*) is not less elegant than the other parts; its narrower fore part is concealed by the palato-vomerine ankyloses; thence it slowly widens, is much hidden by the long tooth-beds, and then becomes winged behind.

The larger basitemporal projections are hooked; then come lesser snags; and behind, near the foramen magnum, the bone is transverse and gently emarginate.

This bone is gently convex along its dentigerous part, but more so beneath the medulla oblongata, where the endo-cranium is still deficient.

The mandible (figs. 3 & 4) is quite normal; on the outside (fig. 3) is seen the dentary (*d*), nearly reaching to the angle, and the coronoid region of the articulare (*ar*) is seen above it. The condyle is cylindroidal; in front of it the still thick cartilage lies in the trough of the articulare, which is not so long as in many kinds of Urodeles. The splenial (*sp*) is a long, narrow, pointed splint, with but four teeth in old specimens; the teeth gradually become uniserial and are carried by the dentary.

The hyobranchial series of arches (fig. 5) have undergone their share of metamorphosis (compare Pl. XIX. fig. 9 with Pl. XXI. fig. 5); and although several parts have been absorbed, they are still a large and elegant structure. The hyoid arch is now perfectly divided into a long, flat, curved, ceratohyal (*c.hy*); and a small terete hypohyal (*h.hy*), which is loosely connected with its own main bar, and is turned backward to articulate with the fore end of the first basibranchial (*b.br¹*). The first branchial arch is now composed of two pieces of equal length; the lower piece (*c.br¹*) is dilated and emarginate below, and is attached loosely to its own basal bar (*b.br¹*). The upper piece (*e.br¹*) is only dilated below, where it has received into itself the substance of the second epibranchial; both the ceratobranchials (*c.br¹*, *c.br²*) articulate with it; thus only the lower segment of the second branchial arch is present now. This second ceratobranchial is a slender rod, gently sigmoid, and articulates with the end of the first basibranchial and the end of the first epibranchial.

The 1st basibranchial is broad and spatulate in front, with a straight fore edge; it then narrows, and is elegantly enlarged behind for the facets of the 2nd ceratobranchial. The main bar of the 2nd basibranchial (*b.br¹*) has been quite absorbed, but its dilated hind part exists as a large bony "thyrohyal;" it is in the form of an unbent bow, the two horns of which are united by a thick oval mass, the remnant of the longitudinal bar.

I am able, thanks to Prof. Mivart, to give an illustration of another adult of this group of Caduceibranchs.

Species 8.—The Skull of the adult Desmognathus fuscus.

This is another N.-American Newt of the same group as the last; its skull differs only in unimportant particulars, but some of these are very instructive. This skull is alto-

gether shorter and has a better finish, with denser and more polished bones; it evidently belonged to a more aged individual, as it has lost its *sphenoidal teeth*.

The occipital condyles (Pl. XXI. figs. 6-8, *oc.e*) are very large and pedunculated; the facets look more downwards than upwards; the space between them is a measure of the size of the intercalary (*odontoid*) vertebra. The occipital arch is, on each side, entirely confluent with the auditory mass; above (fig. 6) the arch is finished by suture, below (fig. 7) by a narrow tract of cartilage.

The auditory masses are much less rugged than in *Spelerpes*, the divisional fossa and the swelling arches of the semicircular canals being more hidden by the more perfect bony encasement; and the parietals (*p*) are imbricated on the hind skull more smoothly and with more exquisite finish.

The cartilaginous tract between the prootics and the sphenethmoids (*sp.e*) is very small, just a little rim to the hole for the trigeminal nerve; but on the outer region above there is a tract of cartilage where the otic process has coalesced with the capsule (Pl. XXI. figs. 6, 8 and Pl. XVIII. fig. 9, *ot.p*).

But below (Pl. XXI. fig. 7 and Pl. XVIII. fig. 9) the quadrate has run its bony substance into the apex of the process; and between this part the horizontal canal (*h.se*) is completely encased in bone. The sulcus between the conjoined and the single canals above (fig. 8, *a.se*, *p.se*, *h.se*) is shallow and crescentic; the squamosal (*sq*) does not climb on to this space nearly so much, but is more lateral.

Below (Pl. XXI. fig. 7 and Pl. XVIII. fig. 9) the fenestra ovalis is sublateral, but it is less, as also its enclosed stapes (*fs.o*, *st*); that plate is roughly pyriform in outline, is unossified at its rim, and has on its broad hinder part a boss for the muscular fibres that are inserted in it. Also on the outer margin in front of the boss there is on the *right* side a bony columellar handle, which is attached by ligamentous fibres to the under surface of the "tegmen" (Pl. XXI. fig. 7 and Pl. XVIII. fig. 11, *co*, *st*)*. But on the *left* side (Pl. XXI. fig. 7 and Pl. XVIII. fig. 9) this rod is smaller, and its hinder end is attached by a ligament nearly its own length to the stapes; the fibrous tissue is continued from its fore end to the tegmen and otic process. This is the *upper* end of the "suspensorio-stapedial ligament," such as is found in other Urodeles.

This curious onesidedness and irregularity, and the free development of this element in the *Menopome*, leave no doubt in my mind as to its nature; the facial nerve (7) passes out beneath the otic process, further forwards, in front of this small *columella*.

The sphenethmoids (*sp.e*) reach from the rim of the foramen ovale to a short distance from the nasal region; they are fenestrate for the optic nerve (2), and they form a hard, strong wall to this well-built little skull.

Only the narial rim (*e.n*) and the ethmo-palatine (*e.pa*) can be seen without dislocating the bony plates, which are most artistically fitted and compacted together.

The condyles of the suspensorium are behind the foramina ovalia as much as they are in front of it in *Spelerpes*; the quadrate (*q*) ossifies up to the pointed apex of the otic process (Pl. XVIII. fig. 9, *ot.p*), but the front of the suspensorium above is soft.

From the front a similar, but smaller pterygoid process (*e.pg*) runs forwards and out-

* In Pl. XVIII. both figs. 9 and 11 are reversed.

wards, more outwards than in the last; and although somewhat smaller, it comes near to the larger maxillary spur (*mx*). This pterygoid blade has a base of cartilage, which runs inwards to the alisphenoid region, and outwards into the fore part of the otic process; but behind, the quadrate (Pl. XXI. fig. 7 and Pl. XVIII. 9, *q*, *ot.p*) is seen as a very solid wedge of bone, jammed closely in between the prootic and squamosal (*pro*, *sq*), and flanked on its inner edge with the small pterygoid bone (*pg*). The condyle, carrying a very solid mandibular ramus (figs. 7, 8, 9), is large, and has a deep and elegant trochlear cavity.

The pterygoid bone (*pg*) is still smaller than in the last; it is a small ear-shaped plate lying in the axil of the suspensorium, binding it on its inner face, and the prootic on its antero-inferior aspect, just in front of the escaping facial nerve (7).

The other part of the palato-pterygoid bone (*pa*) is twice as large as the pterygoid; each plate is a small irregular hatchet, with a pointed blade that looks backwards; the back of the two blades are apposed, and each *handle* runs outwards and a little forwards, nearly completing the rim of the inner nostril (*i.n*), and partly underlying the corresponding endoskeletal part, or ethmo-palatine (*e.pa*). The thickest part is where the blade and handle join; and there the bone is overlain by the vomer (*v*). These bones, now, as well as the vomers, have lost their teeth, most probably, in this case, through age. The whole plate is bound to its fellow by suture behind, and by simple harmony in front; and this structure is very remarkable in appearance, both the large vomerine and the lesser palatine wings being separated by the pyriform internal nostrils (*i.n*). The bones at the middle of the vomer, in one part of the suture, are deficient, and leave an oblong membranous space beneath the septum nasi.

The palatine plates of the vomers are less than in the last kind, and those of the jaws are larger (fig. 7, *v*, *px*, *mx*); that of the premaxillary can be well seen in front of the vomers.

That bone is of less extent at its dentary margin than in *Spelerpes*, but its palatine plate is more perfect, and the opening of the middle nasal cavity (*m.n.p*) is longer, both above (fig. 6) and below (fig. 7).

The upper surface of the premaxillary (fig. 6, *px*) is smooth and even; for although the cavity in it is large and well defined, yet it is not wrought into a rimmed funnel, as in *Spelerpes*; yet the bone is sulcate behind the upper opening.

In front, on each side, the branches of the orbito-nasal nerve escape in the sloping fore part of the bone at its solid part; then a bony lamina is continued backwards, enclosing the canal, and then widening, to end in two triangular processes that bind on the fore part of the frontals (fig. 6, *n.px*, *f*). At its narrow part the premaxillary is overlapped by the nasals (*n*). These are very irregular triangles, with a concave base looking forwards, and partly enclosing the cartilaginous narial rim (*e.n*); their outer side lies on the maxillary (*mx*), and their apex on the corresponding frontals.

Contrary to wont, the ectethmoid (*e.eth*) is not seen outside the orbit; whereas in *Spelerpes* it has an unusually large external plate. In *Desmognathus* this is partly due to the lesser size of the bone, partly also to the larger and more perfect facial plate of

the maxillary (*mx*). These latter bones unite freely with both the nasals and frontals; in *Spelerpes* they reach neither of these. The zygomatic process is also much more developed, almost equal to what is seen in the Batrachians.

On the *right* side (Pl. XXI. fig. 6, *s.mx*) there is a very small septomaxillary; it rests upon the junction of the maxillary with the premaxillary. Thus there are two instances of asymmetry in this skull; for on the *left* side the small stapedial rod is, contrary to wont, distinct.

The frontals and parietals (*f, p*) are exquisitely finished and smooth; yet there is but little orbital development of either (fig. 8). Their sutures, the frontal and sagittal, seem to belong to some much larger animal. They are like what we see in Mammals; but the dovetailing projection and notches are out of all proportion to the size of the bones thus interlocked.

The lambdoidal suture is squamous and almost transverse.

The squamosal (*sq*) is more ichthyic than in the last; it appears but little on the upper surface (fig. 6), and rather serves above as a buttress to the ear-mass set under the "tegmen." It is a short wedge, thick above and roughly pointed below.

The parasphenoid (figs. 7, 8, *pa.s*) is more primordial in form than in *Spelerpes*; it is oblong in the long interorbital region, has a short triangular ascending basitemporal process, and under the medulla oblongata it is almost straight-sided again, but wide; it ends subtransversely, with a bevelled crenate margin, a moderate distance in front of the foramen magnum.

The mandible (figs. 8, 9) is very stout and solid, and shows why the suspensorial condyles should have been so well scooped. The dentary (*d*) reaches nearly to the end of the ramus: it has a very high and thick edge at the chin for its fellow; it has coalesced with the splenial (fig. 9, *sp*), and has overlapped and partly absorbed the articulare (*ar*) and the Meckelian rod. The articulare has largely ossified the cartilage, leaving, however, a solid cylindroidal condyle; it sends upwards a strong rounded coronoid process in front of the condyle.

The hyobranchial series is much like that of *Spelerpes*; it is still slenderer, and equally unossified. The ceratohyals (fig 10, *c.hy*) are quite like those of the last; but the hypohyals (*h.hy*) are stouter, and are directed forwards and inwards, instead of the contrary direction seen in *Spelerpes*. The first cerato-branchial (*c.br¹*) is lanceolate, instead of being dilated ventrally. The first epibranchial (*e.br¹*) is still slenderer than in the last; it is not dilated to receive the next rod, which is merely applied to its inner side. The first cerato-branchial lies against the basal piece, as in the last, and the second articulates with its end; but this second bar (*c.br²*) is longer than in *Spelerpes*, and instead of being bent forward is bent backwards.

The bony remnant of the second basibranchial (*b.br²*) is only half as large as in the last. It has two projections at the middle. Unlike the last, it is altogether bony, having no soft cartilage tipping its horns.

Summary and Conclusion.

These instances of the Structure and Development of the Skull in the Caducibranchiate division of the Urodeles are intended to be a continuation of my recently published account of the skull in the Tailed Amphibians in the Philosophical Transactions. But I am only in the midst of things at present; and this paper must be followed by one giving the development of the skull in *Triton*, the structure of the adult skull in the Menopome and Siren and Amphiume and the skull of an old *Sieboldia*.

When time has permitted all these things to appear, and when my fast-growing materials relative to the *Anurous* type of skull have seen the light (Phil. Trans. pt. 1, 1881), then it will not be difficult to dilate upon the growth and architecture of the skull in these most instructive metamorphosing "Ichthyopsida." Meantime a narrower scope will be of some use; for the tail-bearing forms undergo great and important changes during their life-history, and in them we seem to see low and ancient types of "Dipnoi" making trial of land-life, and becoming, in very various degrees, adapted to their new surroundings.

On the other hand, the Batrachia appear to be the terrestrial outcome of low and generalized tribes, which were not Marsipobranchs, nor Chimæroids, nor Selachians proper, but all these in potency if not in specialization. The few bony plates that in the Dipnoi become attracted to the chondrocranium, and wedded to it—these appear early in the life of each individual Urodele.

These, and scarcely any others, are the heritage of the lowest Perennibranchiate forms, as *Proteus* and *Menobranchus*; and every larval Urodele is like the fishes at first, and only after a time gains the additional parts that characterize the most developed types of the group.

Some of these almost rival the more ambitious tailless Amphibia; they form a sort of parallel "leader" in the vertebrate life-tree, but more simple and more stunted.

Metamorphoses so wonderful as these Amphibia are seen to undergo (they transform themselves openly, and not in secret places, as is the wont of most Vertebrates), render them invaluable to the student; for they train the mind, and make it much more easily take the stamp of morphological teachings.

The Urodeles are inferior to the Batrachia in that they do not often metamorphose their hyomandibular into a columella. This cartilage, or "pharyngo-hyal rod," never gains an annulus tympanicus; for their first cleft is not only *closed*, it was never open, and was arrested early.

One type has a simple hyomandibular, viz. *Proteus*; but it remains unchanged, as in *Ceratodus*, *Nolidanus* &c.

This type of skull differs from that of the Batrachia in that it never acquires a cartilaginous floor, and its sides, ossifying, do not unite to form a girdle-bone.

The pterygo-palatine arch, such as we see in the Batrachia, is always formed in the Urodeles of two totally separate elements, which never unite; as in the Skate, there is a distinct "ethmo-palatine" and a *pterygoid process* of the suspensorium. Moreover, the bony plates that are applied to these two elements begin irrelatively to them, as the homologue of the archaic pterygo-palatine submucous plate of the Dipnoi, by subdivision

and curious metamorphosis, both in form and in position, this bone yields the ossifying elements to each of these diverse and never united parts. Instead of repeating the “labials” of the Lamprey and its relations, they have, both in their larval and adult condition, the “median nasal cavity.” Also, having no labials to metamorphose, they have no superadded narial valves, and no ossified mento-Meckelian pieces in their mandibles.

The premaxillary is often azygous. They have no “quadrato-jugal” binding the maxillary to the quadrate; they may have a small jugal, and a small additional temporal; both these exist in *Amblystoma opacum*.

Equally with the Batrachia they have, as a rule, *in the adult*, no supra- nor basi-occipital; but *two* rudiments of occipital centra may exist for a few weeks of larval life, as in *Seironota perspicillata*.

Again, the Urodeles differ from the Batrachia in developing the curious intercalary vertebra, the “odontoid” pre-atlantal rudiment.

Their basal palatine, their palatine and sphenoidal teeth, their dentigerous splenial, their distinct hypohyal, the formation of their thyrohyal from the dilated end of a median branchial piece—all these things distinguish this lower tail-bearing group from the higher tailless section of the Amphibia.

Finally, there are curious dovetailings of the characters of the two groups: for instance, there is usually no ossified quadrate in the Batrachia; it is exceptionally unossified in one of the “Urodeles” (*Siren lacertina*).

The divided state of the girdle-bone is seen in the anurous *Pseudophryne Bibronii* and other Australian types; these also have a rudimentary occipital centrum, or basi-occipital.

Pipa, like the Urodeles, has no quadrato-jugal, and has the quadrate ossification.

The Bombinator (*B. igneus*) and *Pseudophryne Bibronii* have no columella; the former and *Pelobates fuscus* have no “annulus:” all the “Anura” want this for a time; it appears at very variable periods in them. In the Urodeles the trabeculae do not, as a rule, develop a secondary cornu (prorhinal) from the inner angle, such as is seen in Batrachia and embryo Sharks.

APPENDIX.

Since the above descriptions were written (latter part of 1877) my first paper on the Urodelous type of skull has appeared in the Philosophical Transactions (1877, pls. xxi.–xxix. pp. 529–597). Of my own finished work there still remains for publication after this the development of the skull in the Common Newts (*Triton cristatus*, *Lissotriton punctatus*), the skull of the adult Menopome, and of the half-grown and adult *Siren lacertina*. But the MS. for the present communication was no sooner finished than I received from Dr. Robert Wiedersheim, of Freiburg, his two invaluable Memoirs on these types.

I. The first of these is on the anatomy of *Salamandrina* (*Seironota* &c.) *perspicillata*, and *Geotriton* (*Desmognathus*) *fuscus* (Genoa, 1875). This exquisite work contains figures and descriptions of several other kinds besides these two. In my paper just referred to, I give the skull of both the larval and adult *Seironota perspicillata*.

II. The second work is entitled 'Das Kopfskelet der Urodelen, ein Beitrag zur vergleichenden Anatomie des Wirbelthier-Schädels' (Leipzig, 1877).

III. A third Memoir has now appeared (1878) by the same excellent anatomist, viz. "Zur Anatomie des *Amblystoma Weismanni*" (Zeitsch. f. wiss. Zool. Bd. xxxii. taf. xi., xii.).

In the second of these important works there are not only figures and descriptions of the skulls of *adults* of many of the kinds worked out by me, but also several that I have not been able to obtain. These are as follows:—1. *Amphiuma tridactylum*, 2. *Cryptobranchus japonicus**, 3. *Ellipsoglossa naevia*, 4. *Ranodon sibiricus*, 5. *Plethodon glutinosus*, 6. *Batrachoseps attenuatus*, 7. *Gyrinophilus porphyriticus*, 8. *Anaides lugubris*, 9. *Speerperes fuscus*, 10. *Triton subcristatus*, 11. *Triton platycephalus*, 12. *Salamandra atra*, 13. *Amblystoma punctatum*. In this invaluable work figures are given also of the skulls of *Triton* (*Notophthalmus*) *viridescens*, *Desmognathus fuscus*, and *Triton torosus* (*Taricha torosa*), which are also figured and described in the present communication.

IV. It is also proper to mention here a Memoir by Dr. PHILIP STÖHR (Prosektor am vergleichenden anatomischen Institut zu Würzburg), entitled 'Zur Entwicklungsgeschichte des Urodelenschädels' (Leipzig, 1869).

There are very few things in these works that I see occasion to criticise, but very much indeed to praise; but there is one thing that must be noticed as an error in the second work, namely, the cartilage attached to the stapes in the skull of the *Menopome* (pl. ii. figs. 24, 25, *Op*) is much too small; it was evidently drawn after it had become shrunken. In the same plate (fig. 16) an error of my own is corrected ("Skull of Urodeles," pl. xxvii. fig. 6) which failed to give a "splenial" to the mandible of *Proteus anguinus*. At the least these works double our knowledge of the *adult* skulls in these types; and with these works before him, my published paper in the 'Philosophical Transactions,' and the plates and descriptions now given, the reader will be able to form a very good idea of the Urodelous type of skull, its modifications, and its development. I shall, however, to help to this end, make a few comments on what is displayed in the plates of Prof. Wiedersheim's second work.

Plate i. fig. 1. This figure of the skull of *Menobranchus* shows a fenestrated cartilaginous nasal roof (*N.K*, Nasenkapsel). Prof. Huxley (Proc. Zool. Soc. March 17th, 1870, plate xxx. fig. 1, p. 197) does not give this.

Plate i. figs. 11, 12, *H.F.* The hyomandibular is shown in *Siren*; the author calls it "hinterer, mit dem Hyoidbogen durch ein Ligament verbundener Fortsatz des Quadratum." This *epihyal* element is partly confluent with the back of the suspensorium.

Plate ii. figs. 21, 22, and figs. 24, 25, *H.F.* shows the same part in *Cryptobranchus*

* Worked out since.

and *Menopoma*. I have worked it out in *Siren*, *Sieboldia*, and *Menopoma*, and am confident of its real nature; it is twice as large, and not confluent, in *Proteus*.

Plate ii. In fig. 22, *Op*, a stapelial stem is figured in *Cryptobranchus* as well as in *Menopoma* (figs. 24, 25). This is the curiously modified pharyngo-hyal cartilage and stapes, confluent.

Plate v. In *Ellipsoglossa* (fig. 65), in *Ranodon* (figs. 69, 70), and in *Amblystoma punctatum* (figs. 76, 77), the hyomandibular (*H.F.*) is shown; in *Ranodon* there is evidently an additional stem to the stapes (*Op*).

The antorbital ("ethmo-palatine") cartilage is shown (*A.F.*) to be confluent with the pterygoid process of the suspensorium (*Ptc*) in *Ranodon* (pl. v. figs. 69, 70), a most important modification; for in the Batrachia that is a *primary* state of things, which here is manifestly caused by confluence of the parts.

In the Toads (*Bufo vulgaris*, *pantherinus*, &c.) the subdivision of this part is secondary, both of the palatine from the pterygoid and of the former from the trabecula.

In pl. vii. fig. 94 another most important exceptional condition is shown in *Batrachoseps*, which is common enough in the Batrachia, viz., a large fontanelle in the roof of the skull, arising from the deficient growth of the frontals and parietals.

In pl. i. fig. 8 (*Bs.II*, *II.p.II?*) the hyoid of *Amphiuma* is shown to be broken up, distally, into even more pieces than I have found in *Menopoma*, where each *hypohyal* is composed of *three* cartilages. A curious thing also occurs in Osseous Fishes, where the hypohyal segment, quite distinct, is ossified by two centres.

The figures of transversely vertical sections of adult skulls and the various modifications of the hyobranchial arches in the adult are beautifully perfect, copious, and instructive.

The remarkable (*Petromyzine*) "cavum intermaxillare resp. nasale (*Ci*) is shown in most of the types. I know of nothing in the morphology of the skull more tantalizing than these structures. Surely some low ichthyic types will help us to connect this structure with the azygous nose of the Lamprey*.

* Dr. Wiedersheim's description of the skeleton of *Pleurodeles Wallii* (Morphologische Studien, plate ii. figs. 8-16. pp. 27-42, Jena, 1880) may now be added to the above.

DESCRIPTION OF THE PLATES.

The abbreviations used in the different figures are as follows :—

<i>al.s.</i> Alisphenoidal region.	<i>i.n.</i> Internal nostril.	<i>px.</i> Premaxillary bone.
<i>a.p.</i> Ascending process of suspensorium.	<i>i.n.c.</i> Internasal cartilage.	<i>py.</i> Pituitary body-space or region.
<i>ar.</i> Articulare.	<i>iv.</i> Investing mass.	
<i>a.sc.</i> Anterior semicircular canal.	<i>lx.</i> Larynx.	<i>q.</i> Quadratum (bone or region of).
<i>a.tr.</i> Apex of trabecula.	<i>m.h.l.</i> "Mandibulo-hyoid ligament.	<i>s.mx.</i> Septo-maxillary bone.
<i>au.</i> Auditory capsule.	<i>mk.</i> Meckel's cartilage.	<i>s.o.</i> Supraoccipital region.
<i>au.c.</i> Auditory capsule (or cavity).	<i>m.n.p.</i> Middle nasal passage.	<i>sp.</i> Splenial bone.
<i>b.br.</i> Basibranchial.	<i>mx.</i> Maxillary bone.	<i>sp.e.</i> Sphenethmoidal bone.
<i>b.hy.</i> Basihyal.	<i>n.</i> Nasal bone.	<i>sp.t.</i> Sphenoidal teeth.
<i>b.o.</i> Basisoccipital region (or rudiment).	<i>na.</i> Nasal roof-cartilage (nasal "paraneural").	<i>sq.</i> Squamosal bone.
<i>c.br.</i> Cerato-branchial.	<i>nc.</i> Notochord.	<i>st.</i> Stapes.
<i>c.hy.</i> Cerato-hyal.	<i>n.px.</i> Nasal process of premaxillary bone.	<i>t.cr.</i> Tegmen cranii.
<i>co.</i> Columella.	<i>oc.c.</i> Occipital condyle.	<i>tr.</i> Trabecula.
<i>c.tr.</i> Cornu trabecular.	<i>od.v.</i> Odontoid vertebra.	<i>t.ly.</i> Tegmen tympani.
<i>d.</i> Dentary bone.	<i>ol.</i> Olfactory capsule.	<i>v.</i> Vomer.
<i>e.eth.</i> Ectethmoidal bone.	<i>o.s.</i> Orbito-sphenoidal region.	1. Olfactory nerve.
<i>e.n.</i> External nostril.	<i>ol.p.</i> Otic process of suspensorium.	2. Optic nerve.
<i>e.o.</i> Exoccipital.	<i>p.</i> Parietal bone.	5. Trigeminal nerve.
<i>ep.</i> Epiotic.	<i>pa.</i> Palatine bone.	5 ¹ . First or orbito-nasal branch of trigeminal nerve.
<i>e.pa.</i> Ethmo-palatine cartilage.	<i>pa.s.</i> Parasphenoid bone.	5 ² , 5 ³ . Upper and lower maxillary branches of trigeminal nerve.
<i>epy.</i> Epipterygoid cartilage.	<i>pd.</i> Pedicle of suspensorium.	7. Facial nerve.
<i>eth.</i> Ethmoid.	<i>pg.</i> Pterygoid bone.	7 ¹ . Palatine ("Vidian") branch of facial nerve.
<i>f.</i> Frontal bone.	<i>p.pa.</i> Posterior palatine bone.	8. Auditory nerve.
<i>f.m.</i> Foramen magnum.	<i>p.pg.</i> Palato-ptyergoid bone.	9. Glosso-pharyngeal nerve.
<i>fo.</i> Fontanelle.	<i>p.px.</i> Palatine region of premaxillary bone.	10. Vagus nerve.
<i>fs.o.</i> Fenestra ovalis.	<i>pro.</i> Prootic bone (or region).	
<i>h.hy.</i> Hypohyal.	<i>p.sc.</i> Posterior semicircular canal.	
<i>h.sc.</i> Horizontal semicircular canal.		

PLATE XIV.

Fig. 1. Skull of an embryo of *Salamandra maculosa*, three-fourths ripe (1st Stage), upper view. $\times 17$ diameters.

2. The same, lower view. $\times 17$ diam.

3. The visceral arches of the same skull, upper view. $\times 17$ diam.

4. Vertically transverse section through fore part of nasal region of a similar skull. $\times 17$ diam.

Fig. 5. Another section taken further back. $\times 17$ diam.

6. A section of the same skull through the middle of the auditory capsule. $\times 17$ diam.

7. Hyobranchial arches of adult (*3rd Stage*), one side partly removed. $\times 5$ diam.

PLATE XV.

Fig. 1. *Salamandra maculosa*. Another section (*1st Stage*), through the eyeballs. $\times 17$ diam.

2. A similar section made behind the eyeballs. $\times 17$ diam.

3. A section made through hinder part of auditory capsule. $\times 17$ diam.

4. A section made at junction of exoccipital region with ear-capsules. $\times 17$ diam.

5. Skull of a ripe embryo of same species (*2nd Stage*), upper view. $\times 15$ diam.

6. The same, lower view. $\times 15$ diam.

PLATE XVI.

Fig. 1. Skull of the adult *Salamandra maculosa* (*3rd Stage*), upper view. $\times 5$ diam.

2. The same, lower view. $\times 5$ diam.

3. The same, side view. $\times 5$ diam.

4. Chondrosteous endocranium of same, upper view. $\times 5$ diam.

5. Vertical section, with investing bones, showing interior of skull. $\times 5$ diam.

PLATE XVII.

Fig. 1. Skull of *Notophthalmus viridescens* (larva), 1 in. $2\frac{2}{3}$ lines long, upper view. $\times 15$ diam.

2. The same, lower view. $\times 15$ diam.

3. Part of skull of a similar larva, upper view. $\times 15$ diam.

4. Visceral arches of same, upper view. $\times 15$ diam.

5. Skull of adult of same species, upper view. $\times 7\frac{1}{2}$ diam.

6. The same, lower view. $\times 7\frac{1}{2}$ diam.

7. The same, side view. $\times 7\frac{1}{2}$ diam.

8. Mandible of same, inner view. $\times 7\frac{1}{2}$ diam.

9. Hyobranchial arches of same, with larynx, upper view. $\times 7\frac{1}{2}$ diam.

PLATE XVIII.

Fig. 1. Skull of adult *Cynops pyrogaster*, upper view. $\times 6\frac{2}{3}$ diam.

2. The same, lower view. $\times 6\frac{2}{3}$ diam.

3. The same, side view. $\times 6\frac{2}{3}$ diam.

4. Mandible of same, outer view. $\times 6\frac{2}{3}$ diam.

5. The same, inner view. $\times 6\frac{2}{3}$ diam.

6. Front view of skull of same. $\times 13\frac{1}{3}$ diam.

7. Hyobranchial arches of same. $\times 6\frac{2}{3}$ diam.

8. Part of auditory capsule and stapes of second larva of *Spelerpes salmona**. $\times 22\frac{1}{2}$ diam.

9. The same part in the adult skull of *Desmognathus fuscus*, left side. $\times 20$ diam.

10. The same part of the skull in the adult *Spelerpes rubra*. $\times 20$ diam.

11. Stapes of *Desmognathus fuscus*, right side. $\times 25$ diam.

PLATE XIX.

Fig. 1. Skull (part) of *Onychodactylus*, adult, upper view. $\times 10$ diam.

2. The same skull (perfect), lower view. $\times 10$ diam.

* Inadvertently this is given as $\times 30$ in the plate itself; and the figs. 9 and 10 have been wrongly numbered in the plate.

- Fig. 3. Visceral arches of same, part of upper view. $\times 10$ diam.
 4. Skull of adult *Taricha torosa*, upper view. $\times 10$ diam.
 5. The same, lower view. $\times 10$ diam.
 6. Mandible of same, outer view. $\times 10$ diam.
 7. The same, inner view. $\times 10$ diam.
 8. Hyobranchial arches of same species. $\times 4$ diam.
 9. Visceral arches of larva of *Spelerpes rubra*, upper view. $\times 13$ diam.

PLATE XX.

- Fig. 1. Skull of larva of *Spelerpes rubra*, 1 in. 10 lines long, upper view. $\times 15$ diam.
 2. The same, lower view. $\times 15$ diam.
 3. Skull of 1st larva of *Spelerpes salmonea*, 2 in. 1 line long, upper view. $\times 10$ diam.
 4. The same, lower view. $\times 10$ diam.
 5. Skull of 2nd larva of *Spelerpes salmonea*, $3\frac{3}{4}$ in. long, upper view. $\times 7\frac{1}{2}$ diam.
 6. The same, lower view. $\times 7\frac{1}{2}$ diam.
 7. Side view of part of same. $\times 7\frac{1}{2}$ diam.
 8. Part of auditory capsule of same, showing inner face of stapes. $\times 22\frac{1}{2}$ diam.
 9. Part of auditory capsule of *Spelerpes rubra* (larva), lower view. $\times 30$ diam.
 10. The same in 1st larva of *Spelerpes salmonea*. $\times 30$ diam.

PLATE XXI.

- Fig. 1. Skull of adult *Spelerpes rubra*, upper view. $\times 5$ diam.
 2. The same, lower view. $\times 5$ diam.
 3. The same, side view. $\times 5$ diam.
 4. Mandible of same, inner view. $\times 5$ diam.
 5. Hyobranchial arches of the same. $\times 5$ diam.
 6. Skull of adult *Desmognathus fuscus*, upper view. $\times 6$ diam.
 7. The same, lower view. $\times 6$ diam.
 8. The same, side view. $\times 6$ diam.
 9. Mandible of same, inner view. $\times 6$ diam.
 10. Hyobranchial of same. $\times 6$ diam.

VI. *On the Tusks of the Fossil Walrus, found in the Red Crag of Suffolk.* By E. RAY LANKESTER, M.A., F.R.S., F.L.S., Professor of Zoology and Comparative Anatomy in University College, London.

(Plate XXII.)

Read 6th May, 1880.

IN the year 1865 I described, in a memoir published by the Geological Society of London, the tusks of a large mammal closely resembling, if not identical with, those of the living Walrus. Several large fragments of these tusks, obtained from the base of the Suffolk "Crag," had come to my knowledge, when, in the summer of 1864, I was shown a small fragment of a similar tusk by Professor P. J. van Beneden at Louvain. This fragment had been obtained from the Antwerp Crag; and at the time of my visit Professor Van Beneden did not indicate to me what conclusion he had formed as to its nature. Subsequently, in the autumn of 1864, Professor Van Beneden communicated in a letter to me his conclusion that the fragment of a fossil tusk in his possession had belonged to a Walrus-like animal, for which he informed me that he intended to use the generic term *Trichecodon*.

Having myself in the meantime ascertained that the Suffolk specimens presented all the essential structural features of the Walrus-tusk, I proceeded to figure and describe them, adopting, with acknowledgment, the generic name suggested by Prof. Van Beneden, and supplying a specific title: I named the fossil Walrus of the Suffolk Crag *Trichecodon Huxleyi*. At the same time I may point out that I was unable to adduce any character in support of a generic distinction between the Walrus now inhabiting the polar sea and that which lived in the Miocene period. It was therefore only in response to Prof. Van Beneden's suggestion that the genus *Trichecodon* was proposed; and I am anxious now to withdraw my use of that term, and to refer the Suffolk tusks to the genus *Trichecus* simply. The fossil Walrus of the Crag, indicated by the fragments of tusks already made known, and by other more perfect specimens to be described below, will therefore stand simply as *Trichecus Huxleyi* (Lankester, sp., 1865).

I am glad to take the present opportunity, when I am about to submit some excellent drawings of two nearly complete tusks from Suffolk, of clearing up, as far as I am concerned, a certain confusion which has arisen in connexion with the nomenclature of the fossil Walruses of the Pliocene deposits of Suffolk and Belgium. A splendidly illustrated memoir on the fossil remains of marine Carnivora obtained from the environs of Antwerp has recently been published by Professor Van Beneden ('Annales du Musée Royal d'Histoire Naturelle de Belgique,' tome i. 1877). In this work a large number of bones belonging to various Walrus-like individuals are figured, and are referred by Prof. Van Beneden to two genera, *Trichecodon* and *Alachtherium*. I am not anxious on

the present occasion to discuss the value of the characters by which Prof. Van Beneden considers himself justified in founding two genera—the one, *Alachtherium*, having been previously proposed without any definition by the Vicomte du Bus (Bulletin de l'Acad. Roy. Belg. 1867, p. 562), whilst the other had been adopted by me for the Walrus-like tusks in 1865. But I must point out that though Prof. Van Beneden figures a number of bones of his Walruses, he is unable to bring any evidence with regard to the tusks beyond that afforded by the small fragment which I saw in 1864. There is actually *no evidence whatever* that the particular bones referred by Prof. Van Beneden to the genus *Trichecodon* have any thing to do with the fragment of a tusk in his possession; certainly there is nothing to show that these bones have any special relationship to the Suffolk tusks to which in 1865 I applied the generic term *Trichecodon*. As applied to bones, “*Trichecodon*” is an obvious misnomer; and there appears to be no reason whatever for assigning that name to the bones to which it has been assigned by Prof. Van Beneden, rather than to the bones to which he has applied Du Bus's generic term “*Alachtherium*.” The genus *Alachtherium* was indicated by Du Bus in 1867. The first published reference to *Trichecodon* by Prof. Van Beneden is in 1871 (Bulletin de l'Acad. Roy. Belg. 2nd ser. t. xxxii. p. 164), where he cites both bones and the solitary fragment of a tusk (which is all as yet recorded from Belgium), and applies to these remains the title *Trichecodon Koninckii*.

It must be obvious that, in default of specimens showing both bones and tusks in juxtaposition, it is perfectly hopeless to attempt to identify either Prof. Van Beneden's own fragment of a tusk or the Suffolk specimens with those bones which he calls *Alachtherium* on the one hand, or with those which he calls *Trichecodon* on the other. At the same time, should there really be only *one* Walrus-like animal proper to this period, neither *Alachtherium Cretsi* of Du Bus (1867), nor *Trichecodon Koninckii* of Van Beneden (1871), has priority as its title, but *Trichecodon Huxleyi*, mihi (1865). Further, if it should appear (as I am inclined to think it will) that there is insufficient ground for the generic subdivisions indicated by the terms *Alachtherium* and *Trichecodon*, the species *Trichecus Huxleyi* will yet have precedence, and any bones which may be referred to the same species as that which carried the tusks which are so well represented in Suffolk will have to bear the title *T. Huxleyi*.

This being the case, the following passage extracted from Prof. Van Beneden's memoir appears to me to be open to correction on one or two important points. He says, p. 53, under the heading *Alachtherium Cretsi*, “On a trouvé en Angleterre d'énormes dents dans le crag que l'on avait même attribuées au Dinotherium et qui proviennent probablement de l'animal qui nous occupe. Une dent canine est figurée dans les Proceedings de la Société Géologique de Londres de 1865, pl. xi. En 1865, M. Ray Lankester fait mention de ces dents à la Société Géologique de Londres; mais [A] comme on ne connaissait que le genre que j'avais établi sous le nom de *Trichecodon*, il avait cru devoir les attribuer à une espèce nouvelle, qu'il dédia à M. Huxley, *Trichecodon Huxleyi*. Mais comme nous avons deux genres fossiles différents de Trichécidés, l'*Alachtherium* et le *Trichecodon*, [B] auquel des deux ces grandes défenses appartiennent-elles? [C] Nous pensons que c'est à l'*Alachtherium*, qui s'éloigne plus

du morse que l'autre, et avec d'autant plus de raison que [D] nous possédons des défenses de *Trichecodon* qui ont un tout autre caractère."

In the first place, with regard to the passage marked A, it has escaped Prof. Van Beneden's memory that he had not established the genus *Trichecodon* in 1865, but suggested the name in a letter to me as one well fitted to indicate the fossil tusks of a Walrus-like animal. Accordingly there was no thought of any genus or species founded by Prof. Van Beneden when *Trichecodon Huxleyi* was described by me, for the very sufficient reason that no such genus and no species of it had been described at that time by the learned anatomist of Louvain.

With reference to the question marked B, there is no room for doubt, since the genus *Trichecodon* was instituted by me for the very tusks in question.

In the sentence marked C, the Professor expresses an opinion which is entitled to all the weight which his authority can give. He considers that the Suffolk tusks should be connected with the bones to which he applies Du Bus's generic title *Alachtherium*, for the reason that these bones are less like those of the living Walrus than are the second series, to which he assigns the name *Trichecodon*. If his opinion were correct, the genus *Alachtherium* (1867) would have to give way to the earlier published name *Trichecodon* (1865). But I cannot admit that there is the remotest evidence for the connexion of the Suffolk tusks with the bones called *Alachtherium* rather than with any other Walrus-bones, since no Walrus-tusk has been found in connexion with Walrus-bones in either Suffolk or Belgium.

Finally, Prof. Van Beneden states (in D) that he possesses tusks of his *Trichecodon* (1871) which have quite a different character from those of my *Trichecodon* (1865). He does not figure these tusks nor elsewhere describe them. I find no reference to them in his description of *Trichecodon Koninckii*. No tusk was obtained in relation with the bones which he describes under that name. The single fragment of a tusk, which is the only tusk at present recorded (except in the passage just quoted) from the Belgian Crag, presents no character which can separate it from the Suffolk tusks, or lead to its identification with any particular Walrus-bones.

Further, supposing that there were such evidence forthcoming, it would be necessary not to refer my *Trichecodon Huxleyi* to some new genus, but to create a new designation for Prof. Van Beneden's later described form, and thus to avoid applying to it a designation already in use.

My conclusion, therefore, from a careful consideration of Prof. Van Beneden's statements in his large monograph (1877), and from that of his shorter memoir (1871), and of Du Bus's account of *Alachtherium* (1867), is that there is no evidence for the association of the tusks of *Trichecus* (*Trichecodon*) *Huxleyi* of Suffolk with any one set of the bones of Walrus discovered at Antwerp rather than with any other; and inasmuch as the tusks which we now possess furnish as sound a basis for generic and specific characterization as do detached and fragmentary bones of the general skeleton, the title *Trichecus Huxleyi* should hold its place; whilst, further, if the generic term "*Trichecodon*" is to be used at all, it is applicable not to bones which give no specific

information relative to the teeth, but to the teeth themselves, in the sense in which I made use of it fifteen years ago at Prof. Van Beneden's suggestion.

New Specimens of the Tusks of Trichecus (Trichecodon) Huxleyi, and Comparison of these with the Tusks of Trichecus rosmarus.

Two of the finest collections of the fossil bones and teeth derived from the base of the Suffolk "Crag," viz. that of Mr. Whincopp of Woodbridge and that of Mr. Baker of Woodbridge, have been broken up and dispersed during the last few years; on the other hand, the Ipswich Museum, which already possessed some valuable specimens, has been enriched by the acquisition of the collection of the Rev. Henry Canham, purchased and presented by Sir Richard Wallace, Bart., and by specimens presented by Mr. Packard, of Birkfield. The Ipswich Museum now contains the finest series of these remains in any one collection. The two large tusks drawn in Pl. XXII. figs. 1 & 2, formed part of Mr. Canham's collection. They are the finest specimens which have been discovered, being nearly complete tusks, and were kindly lent to me by Dr. Taylor, F.L.S., the Curator of the Ipswich Museum, for study and illustration.

From an examination of the large series of tusks of *Trichecus rosmarus* preserved in the Museum of the Royal College of Surgeons (for the opportunity of studying and measuring which I am indebted to Prof. W. H. Flower, F.R.S.), I have been able to form some conclusions relating to the absolute size, sectional diameter, curvature, fluting, attrition, and similar points exhibited by these great canines at different ages and in the two sexes.

Such a series of Walrus-tusks as that in the Museum of the Royal College of Surgeons exhibits a very great variety of forms and sizes; and the first point to which I have to draw attention is that the variation is precisely parallel to the variation met with in the fossil Walrus-tusks of the Suffolk Crag. The chief differences of form which I have been able to recognize are connected as follows with age and sex:—

1. Small tusks, almost straight, with unworn points and large pulp-cavity. These belong to young individuals, and may differ a little according to sex.

2. Full-sized tusks, more slender and more curved than No. 3. The fluting or ridges on the flattened sides of the tusk much less pronounced than in No. 3. These appear to belong to the females of *Trichecus rosmarus*.

3. Full-sized tusks not longer than No. 2, but less curved and more massive, having a larger transverse diameter and a more decided grooving and ridging of the flattened sides of the tusk. Some of the tusks of this type are nearly straight; others are slightly curved; but they appear never to be so much curved as are No. 2.

4. Short massive tusks, with the pulp-cavity filled by osteodentine. These are the tusks of old individuals worn down, and exhibit a difference in their transverse section and bulk, according as they have been derived from male or female.

The differences presented in this series of recent Walrus-tusks is paralleled by those of *T. Huxleyi* from the base of the Suffolk Crag.

We have not unfrequently small specimens from the Suffolk Crag corresponding to Group 1 of the recent tusks—that is to say, little or not at all worn, but very slightly

curved, and with evidence of a large conical basal pulp-cavity. The specimen drawn in fig. 7 is a somewhat large example referable to this group.

As parallel to the second group of recent Walrus-tusks, I am able to cite the beautiful example drawn in Plate XXII. fig. 2, besides numerous fragments. The relatively large curvature, the relatively slender proportions, the great lateral compression, and the feebly marked surface-fluting, as compared with tusks referable to the next group, are unmistakable characters in which this set of the fossil tusks agree with those known to belong to females of the living *Trichecus*.

The largest, most massive, longest, most strongly ridged specimens which are found in Suffolk, agree with the similarly characterized male tusks of living Walrus in being also less curved than are those of the female. A fine example of the male tusk from Suffolk is drawn in Plate XXII. fig. 1. The base of a still larger specimen, indicating the largest Walrus-tusk, recent or fossil, which I have encountered *, is drawn in fig. 3. In fig. 4 is drawn the point of a tusk, probably that of a male (on account of its strong fluting), although exhibiting much greater *lateral compression* than is usual in the tusks of the living male Walrus. Such flattened tusk-points are not uncommon in Suffolk, and *possibly* indicate a Walrus-like animal distinct from that with less-compressed tusks.

Lastly, we have from Suffolk specimens corresponding exactly to the 4th group of tusks noted above as distinguishable in the collection of the Royal College of Surgeons. One of these is drawn in fig. 5, and another in fig. 6. They are distinguished by the wide base, filled with a solid osteodentinal core and a (comparatively) very rapid tapering of the tooth, which is relatively short and stumplike. These are undoubtedly old worn-down tusks, and may be either those of males or of females.

Observations on the Curvature and Maximum Size of recent and fossil Walrus-tusks, and on the Fluting and Proportions as exhibited by Transverse Sections.

I obtained a number of outlines of the transverse sections of Walrus-tusks preserved in the museum of the Royal College of Surgeons by means of modelling wax applied as a ring to the tusk; the ring was removed after pressure, and a pencil was drawn around the inside of the ring when held on a piece of paper. These transverse sections may be compared with those of the fossil tusks, and give the best means of estimating the differences which the two sets of tusks (the living and the fossil) present in respect of fluting and transverse proportions.

It is to be noted that the fluting of the recent tusks is very varied in the different specimens studied. The tusks are always oval in section, being somewhat compressed laterally. One may find a single groove only on each side of the tusk; or there may be two grooves on the outside of the tusk and none on the inside, or there may be merely the faintest indication of grooving (see figs. 8 to 14).

The same variation obtains in the fossil tusks from Suffolk; some are more, some less deeply fluted. But, as compared with the tusks of living *Trichecus*, the tusks of *Tri-*

* A specimen of the tusk of *T. rosmarus* recently acquired by the Royal College of Surgeons' Museum, to which my attention has been called by Prof. Flower, is fully as large as this.

cheeus Huxleyi show a somewhat deeper and more constant fluting; whilst, further, it is distinctly to be noticed that the transverse section is narrower than that of *T. ros-marus*; that is to say, the fossil tusks are more compressed laterally than are the living ones.

It is not possible to give the curvature of the Walrus-tusks in a numerical form; but, as compared with those of living Walrus, the fossil tusks exhibit a more marked curvature. The tusks of living Walrus vary in this respect very greatly. Whilst the tusks of females are more curved than those of males as a rule, we also find that some male tusks are nearly straight, whilst others are curved. As to absolute size, there can be no doubt, from the measurements which I have taken, that the fossil tusks are larger than the average of recent specimens. The largest tusk in the College-of-Surgeons' Museum is $26\frac{1}{2}$ inches long*, as measured in a straight line, between the extreme points of base and crown. The fossil specimen of the tusk of a male *Tricheeus Huxleyi* drawn in fig. 1 would have measured, when complete, as much; the fragment drawn in fig. 3 indicates a much larger tusk; whilst the tusk of a female drawn in fig. 2 is larger than any recent female tusk which I have examined.

APPENDIX, JULY 17TH.

The varieties of form presented by the tusks of the recent and fossil Walrus are due, as pointed out above, among other things, to two independent conditions, which may affect any two tusks compared in different degrees, viz. attrition and growth. Growth does not necessarily proceed *pari passu* with attrition; and consequently tusks of the same age may be of various lengths, owing to the varying amount of attrition to which they have been subjected.

The growth of the tusk consists in a continual addition to its base, that which was the base or socketed portion of the tusk at one period of life becoming the naked and even the terminal portion at a later period (see woodcut, where 1, 2, 3, 4 represent successive bases with pulp-cavity). At a certain period of life the tusks cease to grow, as is indicated by the reduction and even complete filling of the shallow pulp-cavity. The biggest tusks will necessarily, *ceteris paribus*, be those which, having ceased to grow, have during the period of growth suffered least from attrition.

The mode of wearing-down of the tusk is made obvious from the examination of worn tusks, when the new outline formed by the wearing-down of the tusk is found to have a certain relation to the fluting of the surface, which, in an unworn tusk, is parallel with the unworn outline. It is found that the wearing of the tusk is greater on the convex or anterior border of the tusk than it is on the concave or posterior border, and is so considerable on the convex face as to preserve the tapering form of the tusk although the point is rapidly worn away. This is shown in the woodcut, where the successive outlines, A, B, C, D, indicate a series of stages in the attrition of the tusk. If the full-grown tusk had never suffered in any way from attrition, it would present the complete

* The specimen referred to in a previous note, however, measures 31 inches in length along the chord, and $34\frac{3}{4}$ inches along the greater curvature.

outline shown in the figures. A combination of such base-lines as 2 and 3 with such successive attrition-outlines as B, C, D, gives the possible variations of a tusk traceable to the causes of "growth" and "attrition." The base-line 1, with the unworn point-outline A, gives the form of very young tusks.

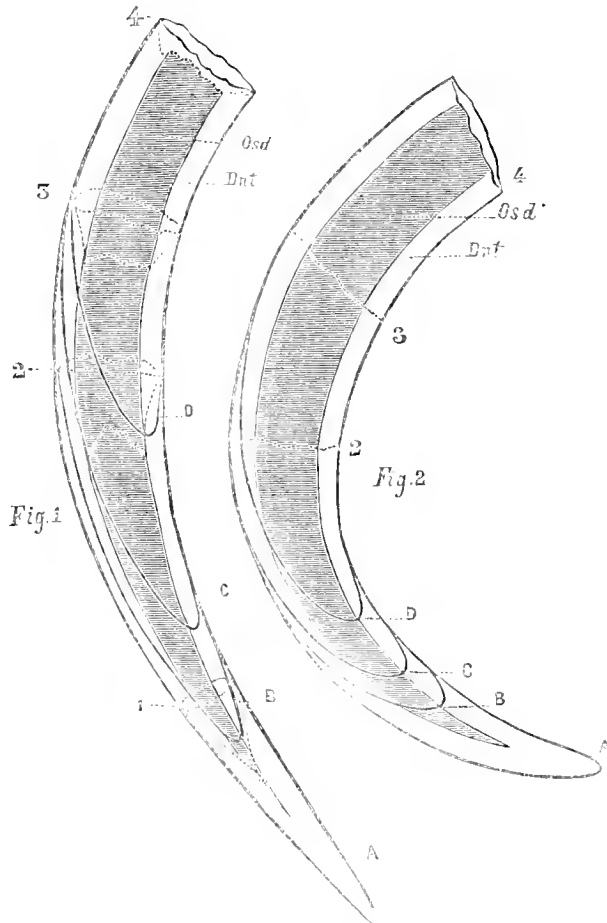


Diagram to illustrate the growth and attrition of the Tusk of Walrus:—
Fig. 1 with less, and fig. 2 with greater primitive curvature. *Osd*, osteodentine; *dnt*, dentine; A, original point of tusk; B, C, D, successive positions of the point, resulting from attrition; 1, Early position of the base of tusk and pulp-cavity; 2, 3, 4, Successive positions of the base-line and pulp-cavity due to new growth.

It will be observed that the successive attrition-outlines cut into the osteodentinal core of the tusk; and this fact enables us, by a careful inspection of the surface of a Walrus-tusk, to determine approximately the amount of wear to which it has been subjected. A *short* tusk is not necessarily an old tusk; but if it have not its osteodentine largely exposed on the convex border, its form is due to such a combination of growth and attrition as we should obtain in the woodcut by taking the base-line 2, together with the attrition-outline B.

When we add to the varied combination of various conditions of growth and attrition the primary individual variations of the tusk, viz. greater or less curvature, greater or

less lateral compression, greater or less amount of fluting, we have set forth the whole series of elements which are factors in the form of any given Walrus-tusk.

The effect of a greater primary curvature on the appearance of the tusk at different stages of growth and attrition will be obvious from the second woodcut, one remarkable fact being that a short tapering tusk may be produced at an early stage of growth and attrition, not unlike that which is the final stage (outline 4 D in fig. 1) in the straighter tusk.

The causes of attrition of the Walrus-tusk are not found in the mere rubbing of the points upon ice studded with sand particles, but in the longitudinal movement of the tusks in digging up the sea-bottom when the Walrus is in search of Mollusca, and very probably also in the longitudinal movement of the tusks against rock-surfaces when they are employed to scrape off attached Mollusca, such as Limpets.

That the tusk-tissues are very easily worn down is proved by the condition of a skull in the collection in my charge at University College, London, where the points of the two tusks in a skull of Walrus have been worn flat by movement on the shelves and tables of the Museum.

An important fact in this connexion is the nature of the sea-bottom and sea-shore which were frequented by the fossil Walrus of the Crag. It is an established conclusion that this late Miocene (Diestien) sea, with its *Pyrgula*, *Folula*, *Cassidaria*, *Pholadomya*, and such forms, and its Teuthophagous Whales (Ziphioids) and its huge Sharks, was *not* an ice-bound sea. The tusks of the Walrus, then, are only secondarily, and not primarily related to its movements upon shore-ice.

At the same time, from what we know of the structure of this part of Europe, it is certain that the Diestien Walrus had no very hard rocks against which to wear down its tusks.

And accordingly we find (as it seems to me) a less extensive attrition of the fossil than of recent Walrus-tusks, and, as I have pointed out above, a greater primitive curvature and a greater lateral compression. The combined effect of these special factors in the case of the fossil tusks accounts for the differences of form which some of them present when compared with tusks of the living Walrus.

DESCRIPTION OF PLATE XXII.

- Fig. 1. Tusk of male *Trichecus Hurleyi* from the Suffolk bone-bed at the base of the Red Crag, nat. size. The specimen is preserved in the Ipswich Museum.
- 1 *a*. Transverse section of same, taken at base.
- 1 *b*. Transverse section taken at the point.
- Fig. 2. Tusk of female *Trichecus Hurleyi* from the Suffolk bone-bed at the base of the Red Crag, nat. size. The specimen is preserved in the Ipswich Museum.
- 2 *a*. Transverse section at the base.
- 2 *b*. „ „ about basal third.
- 2 *c*. „ „ about distal third.
- 2 *d*. „ „ near the point.
- Fig. 3. Tusk of a very large male of *Trichecus Hurleyi* from the Suffolk Crag, nat. size. From a cast in the British Museum: the specimen was formerly in the collection of Mr. Baker of Woodbridge, and is now in the York Museum, Reed collection.
- 3 *a*. A transverse section near the base.
- Fig. 4. Point of probably a male tusk from the Crag, nat. size, remarkable for great lateral compression. Ipswich Museum.
- Fig. 5. Old worn-down tusk from the Crag of Suffolk, nat. size. Ipswich Museum.
- 5 *a* & 5 *b*. Transverse sections of base and apex of the same specimen.
- Fig. 6. Another worn-down tusk from the Suffolk Crag, also in the Ipswich Museum, nat. size.
- 6 *a*. A transverse section near its point.
- Fig. 7. An incompletely grown tusk from the Suffolk Crag, nat. size. Ipswich Museum.
- 7 *a*. Transverse section at its proximal end.
- Fig. 8. Transverse section of a male tusk of *Trichecus rosmarus*, $26\frac{1}{2}$ inches long, taken at 6 inches from the base.
- Fig. 9. Same tusk as fig. 8, transverse section at 4 inches from the point.
- Fig. 10. Transverse section of a young tusk of *Trichecus rosmarus*, 8 inches long, taken at $2\frac{1}{2}$ inches from the base.
- Fig. 11. Transverse section of a male tusk of *T. rosmarus*, 21 inches long, taken at 5 inches from the base.
- Fig. 12. Transverse section of an old worn tusk of *Trichecus rosmarus*, 10 inches long, and of conical form, taken at $1\frac{1}{2}$ inch from the point.
- Fig. 13. Similar section at 4 inches from the point.
- Fig. 14. Similar section at 6 inches from the point.

VII. *The Parasites of Elephants.* By T. SPENCER COBBOLD, *M.D., F.R.S., F.L.S.,*
Foreign Member of the Royal Agricultural Academy of Turin.

(Plates XXIII. & XXIV.)

Read April 7th, 1881.

Preliminary Remarks.

CONSIDERING the importance of Elephants as domesticated animals and the abundant opportunities for post-mortem examinations that occur in India, it is surprising how little has been done towards completing our knowledge of the parasites of these large quadrupeds. As we proceed it will be found that most of the facts of parasitism at present known have been gathered from the examination of animals that have died in captivity either in Europe or in America.

For some years past I have been engaged in collecting materials, which thus far have only served to supply occasional and very incomplete records; moreover the notices in question have chiefly appeared in a periodical inaccessible to most naturalists.

Either from the mistaken notion that the study of parasites is unattractive, or that it is unremunerative, this subject has been strangely neglected; for there is no animal of equal importance with the Elephant about whose parasites so little is known. Naturalists abroad have done almost nothing in this direction; and of those at home one noteworthy exception alone occurs in the person of the late Dr. Baird, who described several species contributed by Dr. Murie and Mr. Gerrard respectively to the British Museum. The entozoa preserved in that institution, however, have been for many years past practically inaccessible to investigators.

It is now desired to supply a summary of all that has hitherto been published, corrected and extended by data that are entirely new. Only such anatomical details as present points of zoological interest can be given; but it is proposed to supplement the natural-history facts with certain particulars which serve to explain the rôle of parasites in the production of fatal epizootics. This method, with the Society's approval, may stimulate further inquiry, and thus ultimately lead to the adoption of measures calculated to lessen the mortality amongst domesticated Elephants.

The materials placed at my disposal for this investigation have been contributed at different times, and severally, by Professor Huxley, by Assistant Commissary-General Colonel H. P. Hawkes, of the Madras Staff Corps—whose earlier contributions reached me through the late Dr. Baird and Dr. Hugh Cleghorn.—by Veterinary Surgeon Thacker, also of the Madras Army, by Mr. John Henry Steel, A.V.D., late Demonstrator of Anatomy the Royal Veterinary College, and by Veterinary Surgeon Frederick Smith, who had professional charge of some Elephants that died at the stables attached to

Sanger's Circus. An independent examination of the viscera of one of the Circus animals likewise supplied me with several new species of internal parasites. I am also indebted to Prof. Flower and Dr. Garson for permitting the examination of two tusks preserved in the Hunterian Museum.

At the time that Dr. Baird wrote his first paper (1859) only two species of Entozoa were supposed to infest the Elephant; and one of these had been imperfectly described. He then added a third. In 1868 Dr. Baird indicated a fourth species; and one year later the hitherto imperfectly but best-known parasite was pretty fully described by myself. Thus up to the year 1869 only four internal parasites were known to infest Elephants; and of these one had been referred to the genus *Ascaris*, two to the genus *Sclerostoma*, whilst the fourth species was supposed to be identical with the common fluke. This was an error. To show how little progress has since been made, I may observe that when, so lately as 1878, Dr. O. von Linstow published his useful 'Compendium der Helminthologie,' the actual number of known and really genuine species had not increased. To be sure, Dr. von Linstow did not hesitate to record the occurrence of six distinct species; but he accomplished this result by placing the fluke parasite under three separate specific names. There is not the smallest ground on which to justify this process of species-splitting. If my determinations are correct, it follows that up to the present time only four Entozoa proper to Elephants are known to science; however, notwithstanding my reduction of Dr. von Linstow's list, and the consequent rejection of several recorded species, I am now enabled to furnish proofs as to the occurrence of at least twelve distinct species of internal parasites in the Indian Elephant. This includes the bots or larvæ of a dipterous insect. Of the external parasites I have made no special study; but if these be added to the parasitic fauna, the total number of Ectozoa and Entozoa comprises not less than fourteen good species. A simple table will best express their zoological position and relations.

PARASITES.	ENTOZOA ...	<i>Ascaris louchoptera</i> , Diesing.	}	NEMATODA ...	}	HELMINTHA.		
		<i>Sclerostoma sipunculiforme</i> , Baird.....						
		<i>Strongylus clathratus</i> , Baird.....						
		<i>Strongylus foliatus</i> , sp. nov.						
		<i>Strongylus falcifer</i> , sp. nov.						
		<i>Dochmius Sangeri</i> , sp. nov.						
		<i>Filaria Smithii</i> , sp. nov.....		}				
		<i>Amphistoma Hawkesii</i> , Cobb.						
		<i>Amphistoma ornatum</i> , sp. nov.						
		<i>Amphistoma papillatum</i> , sp. nov.						
		<i>Fasciola Jacksoni</i> , Cobb.						
	ECTOZOA ...	<i>Gastrophilus elephantis</i> , Cobb.	}	}				
		Ova of a dipterous insect (Selater) ...						
		<i>Hæmatomyzus elephantis</i> , Piaget						
		<i>Homopus elephantis</i> , Mégnin.....						
			ARACHNIDA ...					

For reasons that will be given later on, I have not reckoned Selater's dipterous ovum as representing a separate species.

Description of Species, and Comments.

1. ASCARIS LONCHOPTERA, Diesing.

A. lonchoptera, Diesing, Syst. Helm. Bd. ii. S. 176, Supp. S. 560; idem, Denkschrift. d. math.-nat. Cl. d. k. Akad. d. Wissenschaften, Bd. xiii. S. 13 (with figures).

Ascarides, Jackson, Catalogue of the Anat. Mus. &c., Boston, 1847, p. 317.

Strongylus elephanti (sic), Rudolphi, Synopsis Entozoorum, Berlin, 1819, p. 36.

Body of uniform thickness, but rather narrowed in front and behind, with an acutely pointed conical tail. *Head* with three large almost spherical lips, the margins of the neck having two lateral semilanceolate winged appendages.

Male unknown.

Length of the female 3 inches (or more). Breadth fully $\frac{3}{4}$ of a line.

Hab. Biliary ducts and duodenum of *Elephas indicus*.

The only published description of this worm is that given by Diesing. He states that the parasite was discovered quite accidentally by Herr Mayor in the year 1822. Several parasites (but it is not stated how many) were found in the gall-ducts of an Asiatic Elephant. This animal had been held in captivity at Geneva, where it was destroyed on account of madness (wegen Lobsucht). Not until the year 1847 do we find any second record of the occurrence of this entozoon. In this instance several specimens were obtained from the biliary ducts and from the duodenum of an Indian Elephant which died in captivity at Boston, U. S. A. It is not stated how many of the parasites existed; but Dr. J. B. S. Jackson, to whom both the find and its record are apparently due, states that these *Ascarides* were associated with numerous flukes. As Dr. Fitz has recently pointed out, the flukes themselves were at the time considered to be examples of the common liver-fluke of ruminants (*Distomum hepaticum*).

It would be interesting to have further particulars respecting the American "find." Of the Geneva specimens, only two, both females, were sent to Vienna; and these were originally entered in the Catalogue as *Strongyles*. As at present we possess no published description of the male parasite, it may be that the Boston-Museum specimens would, if carefully examined, supply us with the missing link. Even the few particulars that we have respecting the characters of the female worm require verification. The specimens noticed by the illustrious Rudolphi were the same as those described by Diesing; and supposing that Rudolphi actually examined the worms, it is difficult to understand why he should have called them *Strongyles*, or rather, why he should have placed them amongst his *species dubiæ*, and, as such, in the genus *Strongylus*. The conspicuously three-lipped mouth ought to have afforded sufficient proof of its true generic position. But for Diesing's figures, one might still have remained sceptical as to the ascarid character of the Geneva specimens; and certainly as regards the nature of the Boston find I am still somewhat in doubt, all the more so since the specific characters of the flukes found with the *Ascarides* were from the outset misunderstood. Perhaps Dr. Fitz, who has cleared up certain points respecting the organization of the flukes, will set this matter at rest. At all events, until our own naturalists in India bestir themselves and

make fresh finds, it may be said that the first helminth discovered to infest the Elephant is just that very species about whose structure and economy we are least informed.

2. *SCLEROSTOMA SIPUNCULIFORME*, Baird. (Plate XXIII. figs. 1, 2, & 6, 7, 8.)

S. sipunculiforme, Baird, Proceed. Zool Soc. 1859, p. 427; also P. Z. S. 1868, p. 262 (with figures).

Body smooth, with extremely fine transverse striæ, sipunculiform, thickset. *Head* distinct, separated from the body by a distinct neck or constriction. *Mouth* circular, armed with numerous upright denticles arranged in two rows, with four larger teeth, one on either side, and one in front and behind, springing from between the denticle-rings. *Bursa* longer than broad, apparently supporting twenty rays, the anterior ray being double, the posterior ray quadruple, its innermost division supporting two rudimentary branches of unequal size; posterior lateral ray short. *Spicules* equal, long, straight, and narrow. *Tail* of the female obliquely truncate, the extremity conical and suddenly turned backwards. *Reproductive outlet* immediately above a projecting lobe or tubercle in front of the tail. *Anus* situated in a deep hollow at the base of the cone-shaped end of the tail.

Length of male nearly 1 inch (11 lines).

Length of female above 1 inch (14 lines).

Hab. Intestines of *Elephas indicus*.

If this description be compared with that given by Dr. Baird, it will be seen that our records differ in several important particulars. As regards the position of the reproductive outlet of the female, I have relied upon his authority; but in respect of other characters, especially those of a microscopic kind, my interpretations of the facts observed are wholly different.

As the study of the helminth-fauna of Elephants is in its infancy, it is necessary to be precise in the few details at my command. According to Baird the body is "cylindrical in shape, thicker in the middle, tapering towards each extremity, and finely striated across, though the striæ are rather distant from each other." This is correct, except that Baird's description of the distant striæ must, I think, refer to two or more rings in the neighbourhood of the neck, since the ordinary striæ placed between these rings and all over the body are excessively delicate markings. They cannot be clearly seen under low magnifying powers; and therefore I have not attempted to represent them in my enlarged representation of the neck and head. In respect of the head itself, Baird says it is "rather large, cylindrical, about one line in length, thicker than the neck, and separated from it by a distinct line or groove. This groove I find to be succeeded by other similar rings below it; and as they are tolerably distant from each other, I think Dr. Baird must have referred to them when he spoke of the striæ as being rather widely separated. The remainder of his description of the head stands as follows:—"The mouth is orbicular, placed in the centre of the truncated part of the head, and surrounded with two horny capsules or bullæ, the limbs or margins of which are each armed with a row of numerous teeth. The limb of the external capsule is the larger of the two, and the teeth, though numerous, are less so than in the internal limb, and are stronger and pointed outwards. The limb of the inner capsule is much smaller, the teeth

very minute, and exceedingly numerous. This portion of the body does not differ in the two sexes."

With this part of Dr. Baird's description my observations generally agree; but he appears to have overlooked the four larger equidistant denticles, of which the lateral pair are especially conspicuous. I examined the mouth with some care. By a little pressure the buccal apparatus and narrow muscular œsophagus are well seen under a half-inch objective, several abductor and adductor muscles being plainly visible through the transparent skin. The buccal cavity itself is broadly cup-shaped, being armed, as Baird has said, with two rows of closely set and erect denticles. I did not observe any marked disparity of size, as between the two sets of teeth; and their number is probably the same. I twice counted the denticles of the outer circle, and found their number to be 44; consequently, with the four larger teeth, the mouth cannot be armed with less than 92 of these organs. The length of each tooth was about the $\frac{1}{250}$ of an inch only, the teeth of the inner circle alternating in position with those of the outer.

The bursa, or hood, of the male worm is a very striking object. By reason of the unusual number of rays or, rather, I should say, of ray-divisions, a correct interpretation of these parts is not easy. Dr. Baird's account and that which I am about to offer are scarcely reconcilable. If my account should prove the more correct, it must be remembered that Dr. Baird had not the advantage of knowing Schneider's published views respecting the typical number of parts to be recognized in this organ. It is difficult to interpret the facts given in Dr. Baird's memoir, though they have evidently been recorded with great care.

"The tail of the male," says Dr. Baird, "is in the form of a membranous expansion or pouch surrounding this extremity of the body, and is divided into three lobes. The central lobe is the largest, and is supported by seven ribs or rays, three in the middle and two at each side. The three central ribs are dichotomous, and the middle one of these has its two branches sending off two or three short processes, like buds; the two others are simple. Of the lateral ribs (two on each side) the innermost one is dichotomous, the two branches into which it is divided sending off short processes or buds; the outer rib is simple. The two lateral lobes of this caudal expansion are smaller than the central one, and are each supported by four simple ribs."

In the right and left views (profile and oblique respectively) which I have selected for general illustration of the appearances presented by the tail of the male worm, little more than the points of the rays can be seen (Pl. XXIII. figs. 2 & 8). As there shown, nearly all the rays extend to the border of the hood, whilst some of them point beyond the ordinary level of the margin, which consequently assumes a slightly serrated outline. This appearance is not constant. Having only two specimens of the male to examine, I found some difficulty in arriving at a true interpretation of the parts; but I believe they are correctly rendered in the accompanying scheme. It is, of course, immaterial to which half of the hood-rays the description is taken to refer, since, practically, the arrangement and symmetry are perfect throughout. The anterior ray (*a*, *a'*) is dichotomous and cleft to the base. The antero-lateral ray (*b*) is straight and simple. The middle ray (*c*, *c'*) is dichotomous, cleft to the base, and the branches incline toward

each other at their points. The postero-lateral ray (*d*) is simple, and rather short. The posterior ray is furnished with a remarkably broad base (*e*); it is tetrachotomous (*e'* to *e'''*), its innermost branch being united at the upper part to its fellow of the opposite side. The innermost branch gives off two rudimentary secondary branches, the inner of the two necessarily lying nearly parallel to that of the opposite side, and therefore also parallel to the intervening middle line forming the vertical axis of the hood. As regards the membrane of the bursa itself, the three lobes are fairly distinct, the posterior lobe being large, well marked, and slightly truncated at the apex.

If the above description be compared with that given by Dr. Baird, a correspondence may be traced here and there. Thus his so-called middle ray of the central lobe evidently agrees with the inner division of the posterior ray in Schneider's system (as applied to the present species). Thus, also, the two or three bud-like processes to which Baird refers must clearly be the same as those rudimentary rays observed by myself, and called the outer and inner secondary branches of the innermost division of the great posterior ray. Of course in attempting to reduce and describe this complicated set of rays to the proper number assumed by Schneider to be typical of the strongyles, my interpretation may be open to dispute. I do not think there is any important error in this record, although the occurrence of such a number of separate ray-divisions in any single hood is altogether outside my previous experience.

The spicules of *Sclerostoma sipunculiforme* are long, equal, and remarkably narrow. They measure about $\frac{1}{15}$ of an inch in length, and have their points irregularly twisted, and directed backwards. In their retracted state they are apt to be overlooked, although gentle pressure of the covering glass will readily reveal their presence and position (Pl. XXIII. fig. 2). When partly exerted, their shafts protrude from a cloacal outlet immediately in front of which there is a conspicuous prominence (Pl. XXIII. fig. 8). Neither in Dr. Baird's figures nor in his description of this worm is there any mention made of the existence of the spicules. Doubtless they were retracted within their sheaths, and thus escaped observation. As these organs vary remarkably in the different species of strongyles infesting Elephants and other animals, no diagnosis can be considered complete if all mention of their characters be omitted.

Dr. Baird's description of the tail of the female worm agrees generally with what I have observed. "It terminates," as he says, "in a rather long sharp point, which is oblique in position to the body, owing to a sort of tubercle about half a line from its

Fig. 1.

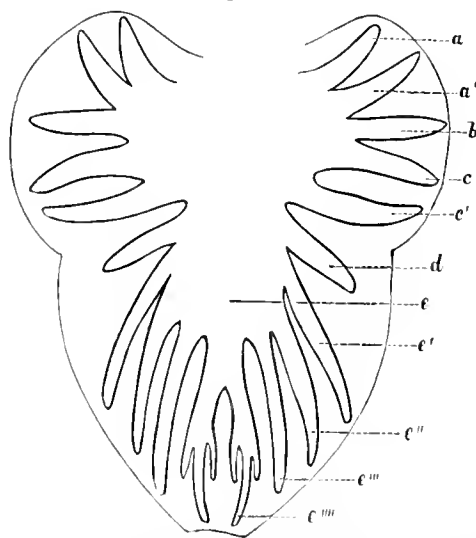


Diagram of the hood and rays of *Sclerostoma sipunculiforme* ($\times 36$ diameters).

extremity, under which is situated the anus. This aperture is very distinctly seen immediately underneath the tubercle; and the vulva, which is not very conspicuous, and is in the form of a narrow slit across the body, is situated immediately above the tubercle."

Seen in profile from the side, the observer cannot fail to remark upon the resemblance which the tail of the female shows to the outline of a Chinese lady's foot; the narrow lower end of the body having the form of the ankle, and the so-called tubercle corresponding with the heel (Pl. XXIII. figs. 6, 7). I made no special examination of the internal anatomy of this species; but so far as the transparency of the body permitted, the arrangements seen by me corresponded with what Baird has stated to occur. "The œsophagus is rather long, and terminates in a lobed stomach which extends for a short distance and then ends in a straight intestinal canal running through the whole length of the animal. The uterus is peculiar in form, and presents a very pretty appearance under the microscope; it is two-branched, and has during its length several expansions or swellings followed by contractions. The ovaries are very long and twisted round the intestine."

In the course of his paper Dr. Baird calls special attention to the relative size of the sexes, more particularly with the view of comparing the characters of this species with those displayed by certain well-known *Sclerostomata* from the horse (*S. armatum* and *S. tetracanthus*) and other animals. In Baird's specimens the males were longer than the females—a circumstance which, as his remarks imply, is of most unusual occurrence. There may have been some mistake here; at all events, in my set of specimens the females are longer than the males. Not improbably Dr. Baird's female worms were immature. Another curious feature connected with the external anatomy of this species related to the presence of certain markings beneath the skin. These appearances were evidently seen by Dr. Baird, who, strange to say, refers them to the species which I shall next describe. More than this, they are actually figured in one of his otherwise generally accurate woodcuts, and are held to be of value in reference to the identity of the species. Thus, as will be seen, Dr. Baird has selected this very striking appearance as affording sufficient grounds for the special nomenclature which he proposed for the following species. Accordingly he has named that worm *Sclerostoma clathratum*, on account of the clathrate or lattice-like markings which may be seen at or near the surface of the body. Now, after a long study of this matter, I am obliged to conclude that the enlarged figure of the head of the female worm given by Baird, in which the appearances in question are represented by no means accurately, is not that of his second new species, but really and truly a representation of the head of the species now under consideration. If this surmise be correct, it might seem necessary to alter Baird's nomenclature; but although, in my view, the specific name applied by him is altogether a misnomer, I propose to retain the nomenclature which, by some oversight, he concluded to adopt.

The appearances in question are very peculiar. They are not due to external sculpturing, as Baird's figure would imply, but to the presence of an internal network, limited, as I think, to the surfaces of the longitudinal muscles. Under low magnifying

lenses the markings pretty closely correspond with the polyhedral networks figured as well as described by Schneider from two species of *Gordius*. In our Elephant's nematode the network seems to lie somewhat deeper (Pl. XXIII. figs. 1, 2). To myself the finer markings present the appearance of vascular ramifications proceeding from common stems, each muscle having a group of its own. There are thus several sets of vessels; and these groups, as such, do not anastomose with each other. Probably there are main trunks connecting all the secondary stems together; and, taken as a whole, they have not the uniformly reticulated characters seen in the network of the *Gordii*. I believe them to form special developments of the water-vascular system. Their structure deserves further study. I should not, indeed, have hazarded thus much concerning them, had not Dr. Baird emphasized their importance as a basis of specific nomenclature. As it appears to me, either Dr. Baird or his artist has made the head and neck of a female *Sclerostoma sipunculiforme* do duty for the next equally well marked species; at least I find the clathrate appearance in this worm, and not in the worm which he has called *Sclerostoma clathratum*. The two worms are undoubtedly good species; and their respective heads bear no sort of resemblance to each other, either as regards form, size, markings, or oral armature. If Dr. Baird's own admirably clear diagnosis be examined, one can hardly fail to see that his description of the head and neck of *Sclerostoma clathratum* only corresponds with some of the particulars given in the illustration to which I have referred. In making this statement I am far from supposing that my own observations are free from error.

3. STRONGYLUS CLATHRATUS, Baird. (Plate XXIII. figs. 3, 4, 5.)

Sclerostoma clathratum, Baird, Proceed. Zool. Soc. 1868, p. 262 (with figs.).

Body linear, subfiliform, cylindrical, but rather suddenly narrowed in front and behind. *Head* small, scarcely half the width of the body, truncated, surrounded by five very small auricular folds. *Mouth* armed with a few teeth. *Bursa* broader than long, obscurely three-lobed; anterior ray short and double; antero-lateral ray simple and straight; middle ray double, of very great size; postero-lateral ray moderately long and slender; posterior ray cleft at the extremity. *Spicules* two, broad, and highly coloured. *Tail* of the female bluntly pointed, with the reproductive outlet slightly removed from the base in front.

Length of the male 2 inches.

Length of the female 2 inches to 3 inches.

Hab. Stomach and intestines of *Elephas indicus* and *Loxodonta africana*.

In my account of the previous species the origin of the nomenclature adopted by Dr. Baird is explained; and, excepting that I prefer to place this worm with the strongyles, properly so called, rather than in the genus *Sclerostoma*, no alteration of the title seems necessary. If our diagnosis be compared, it will be seen that whilst much has here been added, little, save as regards the clathrate character, has been altered in respect of Dr. Baird's description. With the exception of the enlarged head of the female worm, all the figures given by Dr. Baird are thoroughly characteristic, and probably

accurate. That marked by him 2 *a* (woodcut P. Z. S.) is perplexing. The head is not only altogether out of all proportion, but the slight cutaneous folds, which form mere sculpturings or elevated lines, have in his figure all the appearance of large auriculate lappets (see Plate XXIII. fig. 3). As already explained, lattice-like markings have not been seen by me in this worm. Dr. Baird's life-size representations correctly show that the head and neck are finely drawn out to a blunt point; but the enlarged figure of the head above referred to conveys the contrary impression. Although not expressly so stated, his figures imply that the heads of the two sexes closely resemble each other in respect of shape, if not in size. This is usually the case in Nematodes. Unfortunately I do not possess a female *Strongylus clathratus*, and have therefore been guided in my inferences from the characters presented in the head of the male worm. It follows from this that what has here been said respecting the form of the tail of the female rests entirely on Dr. Baird's authority; and here also I may remark that his enlarged view of the tail of the female, which I have no doubt is correct, presents no trace of the remarkable latticed structure that forms so striking a feature in his enlarged representation of the head and neck of the female. In the male *Sclerostoma sipunculiforme* this network occurs both near the head and tail, and throughout the length of the body. It occurs in the female likewise; but I have not shown it in my less highly magnified illustrations of the tail of that species.

In reference to the habitat of this worm, Dr. Baird states that his specimens were obtained by Dr. Murie from the stomach of a young female African Elephant (*Loxodonta africana*). These Dr. Murie sent to the British Museum. The Elephant died in London in October 1867; and Dr. Baird concludes his account of the worm by saying, "I am not aware of any Entozoa having been previously described as inhabiting the body of this species of Elephant." Dr. Baird's conjecture was perfectly correct; and although I have to record the occurrence of a dipterous larva in the African Elephant, yet even up to the present time no other true helminth than that discovered by Dr. Murie has yet been described from this animal. My own specimens of *Strongylus clathratus* were obtained from the Indian Elephant (*Elephas indicus*), and were, I believe, all removed from the small intestines. In Murie's find "the specimens were rather numerous, and, with only one exception, all were females." It is stated that the male worm was white, whilst the others were of a "dark brownish red colour, the contrast between the two sexes being for a long time distinctly visible." As Baird says, on comparing this parasite with the previous species, the head of *Strongylus clathratus* "is much smaller, both in male and female, and the caudal bursa differs in structure from that of *Sclerostoma sipunculiforme*." As supplementing the diagnosis, he adds the following particulars:—"The head is distinctly separated from the rest of the body, and is cylindrical and small; the mouth is dentated inwardly, and on the outer edge is marked with five distinct auricles, which descend upon the upper portion of the body, but do not form a distinct part of it. The body is attenuated at both extremities, and is linear in shape; in the female it is, as it were, minutely clathrate, being situated transversely with fine lines, and having the spaces between the lines minutely longitudinally striated or sulcated, giving, under tolerably high power, the appearance of being latticed or

clathrate. The tail is obtuse, not so sharp-pointed as in *Sclerostoma sipunculiforme*, and has the genital organs situate a short distance from the extremity. It is frequently, but not in all cases, convolute. The body of the male is longitudinally striated; and the bursa at the extremity of the tail is lobed."

Notwithstanding what I have advanced respecting the clathrate appearance, the fact of my not having examined a female worm of this species will probably leave the question still an open one. As regards the male, the characters of the hood are particularly striking, even more so than they are in *Sclerostoma sipunculiforme*.

Whilst Dr. Baird's enlarged view of the bursa makes this sufficiently apparent, he has not supplied any description of details. In the hood before us we find two enormously exaggerated divisions of the middle ray (*c, c'*); but in *Sclerostoma sipunculiforme* we found that most of the rays were of more or less uniform length and thickness. Here also we have the anterior ray double (*a*), with its halves closely applied, as obtains in most Strongyles; we have the antero-lateral ray (*b*) simple and widely separated from those above and below it; we have the ends of the huge finger-like divisions of the middle ray (*c, c'*) extending far beyond the terminal points of the posterior rays; and we have both postero-lateral (*d*) and posterior rays (*e*) reduced to within extremely narrow limits. Any one at all familiar with the typical forms of Strongyle bursæ cannot fail to see at a glance that the morphological departures here displayed are not merely distinctive of the species as such, but altogether unique in themselves. In this connexion another noteworthy feature relates to the form of the spicules. Neither in this nor in the preceding species do these organs appear to have come under Dr. Baird's observation. Whilst retracted they are not readily visible under the microscope; however, a strong light, aided by slight pressure, is sufficient to expose them to view. In this species each spicule consists of a shaft which is truncate above and pointed below. The lateral blade-like expansions are unequally developed, the right side being flabelliform, diaphanous, and marked by branching striae, which proceed from the axis and are radiantly disposed (Pl. XXIII. fig. 5). The spicules are of equal size, each measuring $\frac{1}{20}$ of an inch in its long diameter. Immediately above the hood, and in front of the spicule, there is a slight enlargement, which, even in spirit-specimens, preserves a yellowish colour (Pl. XXIII. fig. 4). This is probably an unusually large seminal reservoir.

Concerning the special part played by this and the preceding species in the production of injury to the host, evidences will be produced at the close of this memoir.

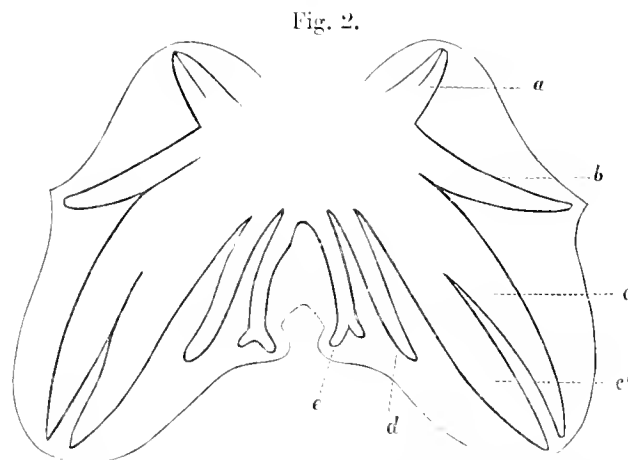


Diagram of the hood and rays of *Strongylus clathratus*
($\times 24$ diam.).

4. *STRONGYLUS FOLIATUS*, sp. nov. (Plate XXIII. figs. 9-13.)

Body smooth, of nearly uniform thickness, finely striated transversely. *Head* indistinct, truncated in front, with five small auriculate folds. *Mouth* slightly oblique, leading to a deep buccal cup, armed with a few coarse teeth, succeeded by a long muscular œsophagus. *Neck* marked by two short conical papillæ at the upper part, one on either side, and by two larger and longer tapering papillæ placed lower down. *Hood* bilobed, foliate. *Rays* few in number, and widely separated. *Spicules* long, flattened, and twisted at the base, tapering and finely pointed below at the apex. *Tail* of the female well marked, long and conical, with a wavy contour, directed backwards, and rapidly narrowing to form a subulate point. *Anus* in front, and immediately above the base of the tail.

Length of the male $\frac{1}{2}$ an inch.

Length of the female $\frac{5}{8}$ of an inch.

Hab. Tumours within the coats of the stomach of *Elephas indicus*.

On the 24th of August 1876, I examined part of the carcass of an Elephant at the Royal Veterinary College. The viscera had been removed from one of several animals that had died at the Circus stables of Mr. Sanger. Mr. Steel, during his previous dissections of this animal, had already encountered some parasites; but in addition to these, I obtained others occupying tumours in the walls of the stomach. The morbid swellings were of two sizes, the larger and more rounded kind containing the species under consideration, the smaller and comparatively flat tumours being occupied by worms of a different generic type.

On the external or mucous surface of one of the larger growths there was an opening of the diameter of a crow-quill. This appeared to be the only communication between the cavity of the stomach and the interior of the tumour. On section the growth displayed a coarsely alveolar structure, its freely intercommunicating loculi being filled with thick mucus, in which a few parasites were found imbedded.

The swellings in question are very similar to the well-known verminous tumours, occupied by maw-worms, of the horse; the parasites, however, are perfectly distinct. Through the help of Mr. Spooner Hart of Calcutta, I have had opportunity to examine specimens of the growths removed from a horse that died at Calcutta stables. In Mr. Hart's experience these formations are rather common in India; but it would probably be incorrect to assume that they are more prevalent in eastern countries than in Europe. Be that as it may, it is scarcely more than forty years since M. Valenciennes found these singular worm-tumours to exist in eleven horses out of the twenty-four animals whose stomachs he specially submitted to examination. Not improbably, therefore, if medical men, army veterinary surgeons, and others practically interested would make use of their opportunities, the statistics of gastric parasitism, both as affecting elephants and horses, would afford much curious instruction. The natural-history value of the facts would be further increased by similar investigations amongst the Rhinoceroses and other large herbivora. Although Schneider and Molin have both described parasites taken from similar tumours in the American Tapir, we as yet know absolutely nothing of the entozoa infesting the Tapir of the Malayan peninsula.

In reference to the reproductive apparatus of *Strongylus foliatus*, I am unable to state the position of the female outlet, whilst the rather small hood of the male presents appearances that are difficult of interpretation. The anterior ray (*a*) is clearly dichotomous and normal in other respects. The next ray, or pair of rays (*b*), forms a puzzle. Either the antero-lateral ray is altogether suppressed, or, if present, it is dichotomous and very similar in appearance to the anterior rays, the two halves being closely applied. According to Schneider's mode of interpretation, the antero-lateral ray is invariably single; and thus, if his view be correct, the lower half of the ray (*c*) must, in the particular case before us, belong to the middle ray. Strange as it may seem, this is probably the correct interpretation of the facts here exhibited. From this it will follow that the next two large and conspicuous rays (*c'*, *d*) are not (as one might have supposed) the divided shafts of a great dichotomous middle ray, but the upper division (*c'*) represents the lower segment of the middle ray (as in Schneider's system), and the lower division will thus represent the usually solitary postero-lateral ray (*d*). The latter ray, according to Schneider, is also always single. In this fashion I am contented to interpret the facts, though, looking to the exaggerated ray-divisions in question, it is difficult to disassociate them so as to conform to Schneider's plan. It seems as if the large pair of half-rays must correspond with the yet more exaggerated half-rays of the great middle ray of *Strongylus clathratus*. When we come to the posterior ray (*e*) all difficulties of homology vanish. In *Strongylus foliatus* it is dichotomous or deeply cleft, the base being united to its fellow of the opposite side.

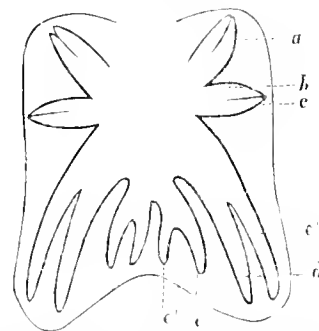
The spicules, though offering nothing remarkable in structure, are characteristic of the species. At the base they are bent in a spiral manner, and slightly flattened. Their shafts lie parallel to one another, and become narrowed very gradually towards the tips, where they are slightly turned forwards and finely pointed. Each measures about $\frac{1}{16}$ of an inch from end to end.

In regard to the membrane of the hood, I should have stated that under moderately high powers one may observe regularly arranged and excessively delicate striæ radiating from the base to its circumferential border.

5. *STRONGYLUS FALCIFER*, sp. nov. (Plate XXIII. fig. 14, and Plate XXIV. figs. 1-3.)

Body of a bright orange-red colour anteriorly, more or less curved, smooth, and rather narrowed in front and behind. *Head* well marked, short, with radiating external lines, and truncated. *Mouth* simple, surrounded by an outer series of four large conical papillæ and by an inner circle of numerous small papillæ or granulations; oral cavity shallow. *Bursa* conspicuously three-lobed, with the posterior rays large and dichotomous. *Spicules* long, strongly bent towards their ends, which are blunt, spatulate, and

Fig. 3.

Diagram of the hood and rays of *Strongylus foliatus* ($\times 60$ diam.).

directed backwards. *Tail* of the female very distinct, scythe-shaped, and finely pointed. *Reproductive outlet* placed at a short distance above the anus, at the base of the tail.

Length of the male 1 inch (or 11 to 13 lines).

Length of the female 1 to $1\frac{3}{5}$ inch (or 12 to 20 lines).

Hab. Intestines of *Elephas indicus*.

With the unassisted eye this species is readily recognized by its bright colour, the orange-red tint about the head gradually becoming feeble towards the anterior third of the body. Out of two dozen examples of this worm I only secured two males; and these were picked out from amongst a quantity of other nematode species. The worms had not been well preserved; and their bodies had become coated with fungi.

Not wishing to mutilate the only two male worms I possessed, my interpretation of the appearances of adhesion and union at the base of the bursa may be partly incorrect. So far as I made out, the rays not only conform to the type-number, but present little that is striking either as regards their shape or their arrangements. Speaking generally, those of the side lobes of the hood are short and stumpy, whilst those of the middle lobe are comparatively large and long. The anterior ray (*a*) is dichotomous, with adherent divisions. The antero-lateral ray (*b*) is simple and normal in position. The middle ray (*c c'*) is bifurcated, and has its branches rather widely apart. The postero-lateral ray (*d*) is comparatively long and well within the middle hood-lobe. The posterior ray (*e e'*) is unusually large, and divided into subequal halves, both of which nearly reach the lower border of the hood. A considerable space separates the inner branch from its fellow of the opposite side.

The spicules form a striking object. Viewed from before or in front, the two shafts present a lyrate figure, owing to their lower ends being bent first outwards laterally, then inwards laterally, and finally, in an oblique direction, backwards divergently (Pl. XXIV. fig. 2). Seen in profile the shafts appear rather narrower; and they appear to lie parallel to each other, except at their somewhat flattened and blunt points. The sheaths in which the spicules usually lie, more or less concealed, can be seen within the half-transparent body, powerful adductor muscles being inserted at the upper or closed ends of these pouches.

The body of the male at the lower part measures about the $\frac{1}{2}\frac{1}{3}$ of an inch in transverse diameter, whilst the spicules, which are of equal size, afforded a length of fully $\frac{1}{3}$ of an inch.

The best-preserved female worms had their oviducts crowded with eggs. Each ordinary ovum gave an average long diameter of $\frac{1}{300}$ by $\frac{1}{350}$ of an inch in breadth. Such eggs contained a dense and finely segmented yolk. On one occasion I observed a solitary empty egg-envelope, which gave a measurement of no less than $\frac{1}{140}$ of an inch from pole to pole, by $\frac{1}{250}$ of an inch in breadth. At the same time, and certainly from the same source, the field of the microscope displayed an embryo that had evidently escaped

Fig. 4.

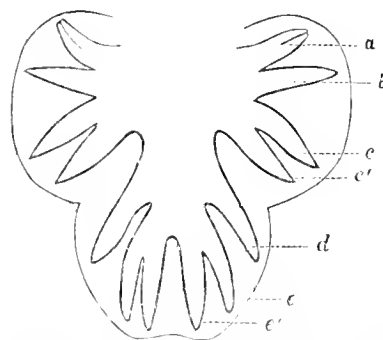


Diagram of the hood and rays of *Strongylus fulcifer* ($\times 43$ diam.).

from this ruptured envelope. The embryo measured $\frac{1}{75}$ of an inch long by something less than $\frac{1}{500}$ of an inch in breadth. Although there were no intermediate stages observed between the two kinds of ovum, I could not regard the presence of the much longer egg and its embryo as merely resulting from accident. Before I examined these worms they had been carefully separated from the other nematodes. As regards the uterus itself, I have only to add that the two horns may be easily traced downwards to their junctions together and with the oviducal or vaginal passage (Pl. XXIV. fig. 3). Distinct openings, with very slightly elevated margins, mark alike the position of the vulva and the anal aperture.

6. *DOCHMIUS SANGERI*, sp. nov. (Plate XXIV. figs. 4-6.)

Body smooth, transversely striated, and narrowed both in front and behind. *Head* very distinct, and bent well forward. *Mouth* simple, oval, and surrounded by regularly disposed elevations; buccal cup capacious, and armed with a few small teeth; pharynx distinct, separated from the œsophagus by a well-defined constriction. *Bursa* obscurely three-lobed, the posterior ray being slender and bifurcated at the extremity, its inner branch extending to the border of the membrane. Spicules short, nearly equal. Tail of the female long and pointed, the tip being subulate, and armed with a short, filiform, transparent, and finely pointed appendage. *Anus* situated at the base of the tail.

Length of the male 8 lines.

Length of the female 10 lines.

Hab. Intestines of *Elephas indicus*.

On the 24th of August 1876, I discovered large numbers of these small worms in the intestinal canal of the Circus Elephant already referred to. To the naked eye they look like ordinary thread-worms; but a hand-lens is sufficient to demonstrate their stronglyloid character. The parts about the mouth were not well made out; but my representation of the head is perhaps sufficiently characteristic (Pl. XXIV. fig. 4).

In its retracted condition the tail of the male worm, when its end is directed towards the spectator, presents a distinctly hexagonal outline, the incurved points of the rays of the hood creating six well-marked angular projections. The appearance in question is at once both striking and delusive. When the hood is flattened or artificially expanded, then an oval or more or less heart-shaped outline results (Pl. XXIV. fig. 5). After repeated examinations I constructed the following diagram. The anterior ray (*a*) is double, and has the divisions closely applied; it is bent forward towards the axis of the body. The antero-lateral is simple, normal, and also bent forward. The middle ray (*c*, *c'*) is dichotomous, and directed at a right angle to the axis of the hood. The postero-lateral ray (*d*) is simple, long and narrow, but does not reach the margin of the membrane. The posterior ray (*e*) is characteristic of the species, being long, narrow, and divided near its end into two unequal portions. The inner branch is nearly twice as long as the outer, and extends to the border of the membrane. When the hood is expanded the end of the posterior ray is widely, because divergently, separated

Fig. 5.

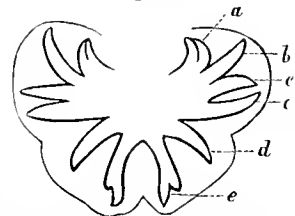


Diagram of the hood and rays of *Dochmius Sangeri* ($\times 30$ diam.).

from its fellow. The third lobe of the bursa is deeply notched in the middle line, thus imparting to the hood a spuriously four-lobed figure. The spicules are short, rather broad at the base, and pointed at the tip or lower end. When the tail of the male is viewed either from the front or from behind, the spicules display the not uncommon **V**-shaped outline.

The tail of the female worm presents well-marked characters (Pl. XXIV. fig. 6). In addition to those mentioned in the diagnosis of the species, the uniform and rather sudden narrowing of the body in this region, together with the presence of a conspicuous and somewhat gaping anal cleft, would render the future recognition of this species a very easy matter, even if no male were procurable. In some specimens the neck in either sex is much more contracted than in the particular example which I have figured.

7. *FILARIA SMITHII*, sp. nov. (Plate XXIV. figs. 7-10.)

Body smooth, with very fine transverse striae, filiform, and of equal thickness throughout. *Head* furnished with two rows of translucent auriculate appendages, supporting a few minute papillæ. *Mouth* simple, surrounded by four small papillæ and numerous slight elevations exterior to the papillæ. *Œsophagus* of great length, without bulb or constrictions. *Tail of the male* short, bluntly pointed, with winged appendages supported by eight stalked papillæ, four on either side. *Spicules* long, slender, unequal. *Tail of the female* short, bluntly pointed, usually directed backwards. *Anus* sub-terminal at the base of the tail.

Length of the male $\frac{1}{6}$ of an inch.

Length of the female $\frac{1}{3}$ of an inch.

Hab. Coats of the stomach of *Elephas indicus*.

The delicate little worms thus named cannot be confounded with the larger species of nematode already stated to occupy tumours in the walls of the stomach of the Elephant. Apart from the relative disparity of the worms themselves, the parasitic growths or abodes containing them are of much smaller size. The tumours enclosing the *Filarie* barely exceed the size of an ordinary filbert nut, presenting also an oval flattened figure. As in the larger formations, however, each tumour displays a single round aperture communicating with the cavity of the stomach. The interior structure of the growths does not depart in any marked degree from the alveolar or multilocular character of the abodes of *Strongylus foliatus*; but a relatively far greater number of worms were found to occupy the "abodes" of this species. I have named the species after the veterinary surgeon through whose instrumentality I had an opportunity of making the "find." Well enlarged, and seen in profile, the head shows sculpturings which together form a double festooned border, whilst within the concavity of each ear-shaped fold of integument there are minute papillæ. In the neighbourhood of the mouth there are also other prominences, as well as special papillary elevations which probably serve as taste-organs (Pl. XXIV. fig. 7).

In consequence of their larger size, the females are easily recognized. The actual position of the reproductive outlet evaded my observation; but the diagonal direction

of an interior tube (which I took to represent the empty vagina) led me to infer that the outlet is placed about $\frac{1}{100}$ of an inch below the point of junction of the œsophagus with the chyle-intestine. The œsophagus itself, in the female, measures $\frac{1}{17}$ of an inch in length, and only $\frac{1}{250}$ in breadth. I subjoin an outline of the female tail. It is here seen strongly bent backwards. Another striking character is that shown by the ova. These minute bodies, linear-oblong in shape, give an average diameter of only $\frac{1}{2000}$ of an inch from pole to pole. Each female worm contains a prodigious number of eggs, probably not less than 100,000, exclusive of the unimpregnated ovarian ova. The perfect ovum always exhibits an embryo folded within its excessively delicate chorional envelope. This embryo itself is thicker in front than behind; but it is bluntly pointed at either extremity. Even at its thickest part the transverse diameter of the body of the embryo scarcely exceeds the $\frac{1}{8000}$ of an inch.

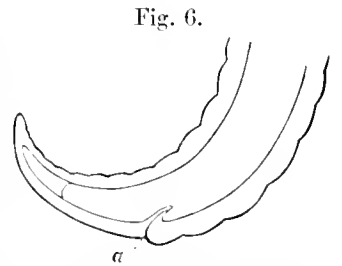
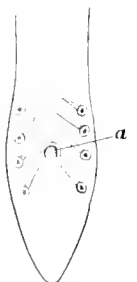


Fig. 6.
Outline of the tail of a female
Filaria Smithii; a, anus
($\times 30$ diam.).

The head of the male forms a miniature representation of that of the female worm. The difference in thickness in the two sexes is considerable, the body of the female measuring $\frac{1}{100}$ and that of the male about $\frac{1}{130}$ of an inch. Seen from the ventral surface, the contour of the tail of the male presents a lanceolate outline and spatulate form. It displays eight papillæ furnished with long stalks (Pl. XXIV. figs. 8-10). On each side three of the papillæ are rooted or arise from above the level of the anal opening, and one originates from below the anus. I did not observe any sessile papillæ beneath the stalked papillæ. The spicules are always visible, whether partially (figs. 8, 9) or wholly retracted (fig. 10). They are strikingly narrow, the anterior spicule being almost twice the length of the posterior. The length of the shorter spicule scarcely exceeds the $\frac{1}{140}$, whilst the anterior one gives a long diameter of fully $\frac{1}{80}$ of an inch.

Fig. 7.



Outline of the tail of a male
Filaria Smithii; a, anus
($\times 30$ diam.).

S. AMPHISTOMA HAWKESII, Cobb.

A. Hawkesii, Cobbold, The Veterinarian, Oct. 1875; ibid. Nov. 1875; also in Treatise on Parasites, 1879, p. 395.

A. Collinsii, var. *Stanleyi*, Cobb., Parasites, 1879, p. 357.

Masuri or *Mussoorie* of the Hindoo Mahouts (Gilchrist, Hawkes, &c.).

Body of a pink colour, smooth, plano-convex, finely wrinkled transversely, bluntly pointed and contracted in front, broadly rounded behind. *Head* surrounded by a few regular but not well pronounced folds, armed with numerous short and extremely minute warty papillæ. *Mouth* terminal, circular. *Ventral surface* often slightly depressed near the centre, forming slight prominences on either side. *Caudal sucker* placed well forward, rather large, circular, with a broad lip and smooth concavity.

Reproductive papilla small, situated nearly midway between the mouth and upper margin of the caudal sucker.

Length, on the average, $\frac{3}{8}$ of an inch; the longest specimen $\frac{7}{16}$ of an inch.

Breadth $\frac{1}{4}$ of an inch.

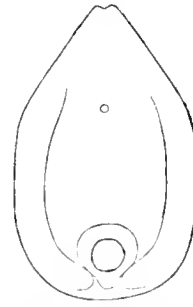
Hab. Large intestines of *Elephas indicus*.

In my general treatise, and likewise in the pages of the 'Veterinarian' antecedently, I have recorded the occurrence of this entozoon; but hitherto it has, zoologically speaking, remained undescribed. My first acquaintance with it dates as far back as June 1875. Towards the close of that month I received from Lieut.-Colonel Hawkes a set of parasites for identification. Attached to the Madras Staff Corps, Colonel Hawkes forwarded the specimens from Secunderabad, at which station there had been a recent and rather serious mortality amongst the Elephants. The cause of that mortality will be subsequently considered when I treat of the injurious effects of the parasites already described. Having explained by a letter to the donor that these parasites were new to science, I provisionally named the species *Amphistoma Hawkesii* in his honor.

In the fresh state the parasites have a bright rosy tint, or, as the finder states, a "delicate flesh-colour." Probably this colour, more or less pronounced, is invariable amongst the Amphistomes; at least such has been the case with all the forms that I have examined in the fresh state. Similarly some Amphistomes received by me from an Indian horse were reported by the finder as having a brick-red colour when removed, post mortem. Here it is desirable that I should speak more fully of these equine Amphistomes. They were found in the year 1875, by Veterinary-Surgeon Collins, of H.M.'s Indian army, stationed at Simla. As equine parasites, however, they do not appear to have been the earliest-seen specimens. None, indeed, had hitherto been scientifically described as coming from the horse; but my attention was subsequently called to a set of specimens preserved in the private collection of Professor Simonds, at the Royal Veterinary College. As since stated in my latest work, the parasites belonging to Simonds were at the time regarded by me as mere varieties of the species found by Vet.-Surgeon Collins. I accordingly spoke of them as *Amphistoma Collinsii*, var. *Stanleyi*. I employed the variation-term in order to give expression to the circumstance that Professor Simonds received his specimens from Vet.-Surgeon Stanley, who also obtained the Amphistomes in India. The date of Mr. Stanley's 'find' has been lost; but from Professor Simonds's recollection it would be about the year 1865.

I have recorded these few facts respecting the equine Amphistomes because, after a recent and more careful study of the worms, I have come to the conclusion that the parasites found by Mr. Stanley, though comparatively large, are really identical with the particular Amphistomes I am now describing from the Elephant. At present, however, I do not pronounce definitely respecting Collins's Amphistome, which will probably be found to remain as a good species. In the horse dissected at Simla,

Fig. S.



Outline of *Amphistoma Hawkesii*
($\times 4$ diam.).

Mr. Collins reckoned that there were about a thousand of these parasites lodged in the colon.

9. AMPHISTOMA ORNATUM, sp. nov.

Body of a pink colour, plano-convex, but slightly concave anteriorly, pointed in front, broadly rounded off behind, and furnished with inconspicuous transversely disposed rugæ. *Head* and *neck* more or less pronounced. *Mouth* surrounded by circular folds, which are armed with prominent, regularly arranged, and bluntly pointed papillæ. *Ventral surface* marked by lateral projections, which fold regularly, sometimes showing a V-shaped groove at the base of the neck. *Caudal sucker* subterminal. *Reproductive papilla* large, and placed well forward.

Length $\frac{1}{3}$ to $\frac{5}{16}$ of an inch.

Breadth $\frac{3}{16}$ of an inch.

Hab. Intestines of *Elephas indicus*.

On the 24th of August, 1876, as already mentioned, I obtained a variety of parasites from one of the herd of performing Elephants that perished at Sanger's Circus. Amongst the parasites were quantities of amphistomes of various shapes and sizes. As all of them were found in the same general situation, I at first concluded that they were of the same species as those sent from India by Colonel Hawkes. However, subsequent investigation led to the conclusion that, although we obtained two distinct forms of Amphistome from the Circus Elephants, neither of them corresponded with the species received from Southern India.

When I removed the parasites from the colon, they had the characteristic bright pink colour, and were so transparent that a pocket lens was sufficient to show the general arrangement of the internal organs. These will be referred to when dealing with the next species.

I separate this form from Hawkes's Amphistome chiefly on account of its smaller size, its more conical figure, its large reproductive papilla, its slightly concave ventral surface, and, more particularly, on account of the presence of papillæ in the neighbourhood of the head. These papillary eminences are so conspicuous that with a magnifying power of three or four diameters their projecting points are rendered visible.

10. AMPHISTOMA PAPILLATUM, sp. nov. (Plate XXIV. fig. 11.)

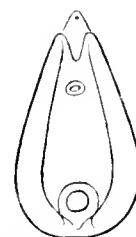
Body of a bright pink colour, smooth, conical, bluntly pointed in front, broadly rounded off behind, with fine and regularly disposed transverse rugæ forming distinct rings in the region of the head. *Caudal sucker* subterminal, very large, its cup being armed with numerous large fungiform papillæ, closely set, and regularly disposed over the entire surface of the concavity. *Reproductive papilla* placed well forward.

Length $\frac{1}{6}$ to $\frac{1}{4}$ of an inch.

Breadth $\frac{1}{8}$ to $\frac{1}{7}$ of an inch.

Hab. Large intestines of *Elephas indicus*.

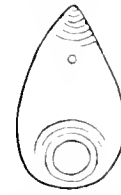
Fig. 9.



Outline of *Amphistoma ornatum*
($\times 5$ diam.).

This species is the smallest of the *Amphistomes* hitherto obtained from Elephants. Regard being had to the occurrence of large papillæ within the cup of the caudal sucker, no one could mistake it for either of the two previously described species. However, it is just possible that the somewhat similar *Amphistome* from the Tapir, described many years back by Diesing, may turn out to be either the same or a mere variety. Dr. C. M. Diesing's *Amphistoma asperum* differs in form, the anterior part of the body being much constricted, whilst the caudal sucker is wider and terminal*.

Fig. 10.

Outline of *Amphistoma papillatum* ($\times 5$ diam.).

The enlarged view that I have given of this worm was taken from a perfectly fresh specimen (Pl. XXIV. fig. 11). In examples preserved in spirit the aperture of the sucker gapes more widely, and consequently looks larger. In the fresh state one not only sees the digestive organs through the transparent envelope, but also the testes, part of the uterus, the branching ducts of the vitellaria, and even also their terminal sacs. The latter are so small that I have not attempted to represent them; moreover, except as regards position, neither these nor the other internal organs offer any striking peculiarities. In this species the vitellary glands are limited to the sides of the body; but in Hawkes's *Amphistome* the sacs and their ducts seem to underlie the whole surface of the body. From hardened specimens I obtained fine transverse sections in which the disposition of the muscle-fibres and general stroma of the body were well displayed.

As a believer in the common origin of all genera and species, of whatever zoological type they may happen to be, I was not unprepared to find representative and parallel forms of parasites in different animals. Thus it seems to me that the two *Amphistomes* known to infest the Tapir represent two of the *Amphistomes* found in Elephants. On the one hand my *Amphistoma papillatum* comes near to *A. asperum*, whilst on the other my *A. Hawkesii* comes near to *A. pyriforme*. The *Amphistomes* of the American Tapir were obtained by Natterer in Brazil in 1829, and were described by Diesing in the *Museum Annals* already quoted. The Vienna helminthologist had not then lost his eyesight; and his elaborate memoir convincingly proves that modern anatomists, notwithstanding our improved methods, have added little to our knowledge of the organization of the trematode worms.

The fungiform papillæ within the sucker of *Amphistoma papillatum* forcibly call to mind the more striking processes lining the ventral disk of the amphistomoid worm which I have called *Gastrodiscus Sounisonis*. In this remarkable genus, established as such by Leuckart, the gastric papillæ display each a central depression at the summit; and I have therefore spoken of them as suckerlets. On this account, also, I pointed to their close affinity with those seen in the equally singular genera *Notocotylus* and *Aspidocotylus*, as established by Diesing. The possession of the small suckers in question, shared as it

* "Neue Gattungen von Binnenwürmern, nebst einem Nachtrage zur Monographie der Amphistomen." *Annalen des Wiener Museums*, 1839, S. 236.

is by all the three aberrant genera, seems to imply that their position amongst the Amphistomes is somewhat doubtful; and I am informed by Professor Leuckart that a recent anatomical investigation of *Gastrodiscus*, made by one of his pupils, tends to confirm this conclusion. Be that as it may, the simple papillæ within the caudal sucking-disk of *Amphistoma papillatum* are evidently of the same character as those found in *A. asperum*. Diesing describes them as little prominences (Erhabenheiten). As contrasted with the integumentary papillæ so frequent on the general surface of the body of Amphistomes the papillæ placed within the disk of *A. papillatum* are remarkably large and altogether distinctive.

11. FASCIOLA JACKSONI, Cobb. (Plate XXIV. fig. 12.)

Fasciola Jacksoni, Cobbold, Quart. Journ. Micr. Science, Jan. 1869; Supplement to Entozoa, 1869, p. 80.

Distoma hepaticum, Jackson (non descriptum), Boston Museum Catalogue, 1847, p. 317.

Distomum elephantis, Diesing, Syst. Helm. Bd. ii. p. 560; Revision der Myzelminthen, 1858, S. 354.

Body flat, orbicular, often folded towards the ventral surface, smooth to the naked eye, but armed throughout with numerous excessively minute dermal spines, which are larger above than below. *Oral sucker* terminal, small. *Ventral sucker* large and well forward. *Reproductive papilla* in the middle line, and placed considerably above the upper lip of the acetabulum; intromittent organ of great length. *Digestive apparatus* branched, its ramifications ending in caecal terminations, which occupy nearly the whole extent of the body internally; œsophageal bulb distinct.

Length $\frac{1}{2}$ to $\frac{5}{8}$ of an inch.

Breadth $\frac{1}{3}$ to $\frac{1}{2}$ of an inch.

Hab. Biliary ducts and duodenum of *Elephas indicus*.

As has been already stated, Dr. von Linstow has fallen into the error of assuming that three species of fluke infest the Elephant. They are, in reality, all one and the same species. Although long previously discovered, this worm was first recognized as a good species by myself in the year 1869. Its discoverer, Dr. Jackson, gave no description of the worm; and it is clear, from what Dr. Fitz has said, as well as from the entry in the Boston Catalogue, that Jackson supposed that he had encountered the common fluke of ruminants in the Elephant. The description originally given by me in the journal above quoted differs in no essential particular from that now offered. I have merely emphasized and extended certain characters.

As causing disease, and zoologically speaking, this entozoon is the most important of the whole group of parasites infesting Elephants. Now that this fact is becoming known to those interested in the preservation of the domestic pachyderms, more attention is likely to be paid to the source and distribution of the parasite. In order, therefore, to clear away certain misconceptions that have already arisen, it is desirable to restate the facts of discovery.

As remarked in my recent work, the first specimens of Elephants' flukes received in this country were transmitted by Vet.-Surgeon Thacker, of the Madras Army. They were, as he expressly remarks, "forwarded for classification." The specimens, indeed,

were brought from India by Dr. Hugh Cleghorn, who conveyed them to the late Dr. Baird, who, again, honourably carried out the wishes of the donor by handing them over to myself. At the Norwich Meeting of the British Association in 1868 two of the flukes were exhibited for the first time in this country; and I then stated that they "were identical with certain flukes long previously obtained from the duodenum and liver-ducts of an Indian Elephant that died in America." I further stated that, although the original 'find' was carefully preserved in the Boston Museum, the worms had never been properly described. In the summer of 1868 fifteen specimens of fluke, removed from one or more Burmese Elephants, had been forwarded to Professor Huxley from Rangoon, and the 'send' was accompanied by a statement to the effect that the parasites were the cause of an extensive and fatal disease in Burmah. Through the kindness of Professor Huxley, I was permitted to make use of his specimens for the purpose of comparison; and thus it became evident that his specimens and mine were of the same species. I then published the original description already referred to; and it was afterwards repeated in the supplement to my elementary treatise on the Entozoa. The second description of the worm was accompanied by an illustration, in which the general plan of the mode of branching of the digestive canals was given on a reduced scale.

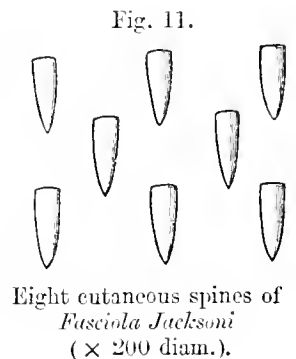
In his well-known systematic work, C. M. Diesing at first recorded the American 'find' in his list of doubtful species; but in his latest revision he formally recognized the fluke as a good species. No description, however, was added. That revision was published in 1858. Three years later, although I had not then seen any specimens, I recorded Jackson's fluke as a *Distoma*, in the Synopsis of the Distomidæ published in the Linnean Society's Journal (1861). These references practically exhausted the literature of the subject up to the year 1873, when I again had occasion to speak of these flukes. ('Manual of the Parasites of our Domesticated Animals,' p. 13). Some of the specimens received from Professor Huxley were afterwards added to the entozoal series of preparations contained in the Hunterian Museum.

I think it necessary to explain the reasons for altering Diesing and Jackson's nomenclature as applied to this species, and all the more so since some helminthologists persist in ignoring the generic term originally employed by Linnæus in connexion with the common fluke of Ruminants. Whilst (excluding the Amphistomes and their allies) I recognize the genus *Distoma* of Retzius as applicable to all the two-suckered flukes that possess a simple unbranched dichotomous gastric organ, I think it unfortunate that my proposal to retain the Linnean generic title, *Fasciola*, for such true flukes as possess a dendriform or branched gastric organ has not been fully accepted. This structural peculiarity is eminently characteristic of a few forms of fluke, and gives us a well-marked type. Besides the species under consideration, only two other flukes are known to possess the dendriform gastric apparatus. We have not yet even encountered any transition types (in this particular), although, on evolutionary principles, one must conclude that, if not now existing, flukes with their digestive tubes much less branched must have existed. The only three fluke parasites yet shown to possess this remarkable dendriform system of gastric canals are the Elephants' fluke (*Fasciola Jacksoni*), the common fluke of Ruminants (*F. hepatica*), and the fluke found by me in the Giraffe (*F. gigantea*).

In 1864 I went fully into this question, and endeavoured to show that, at least as regards the common fluke, the priority of the genus established by Linnæus was indisputable. The genus *Fasciola* was accepted and recognized some twenty years before the genus *Distoma* was proposed by Retzius, and more than thirty years before it was adopted by Zeder and his followers. (For dates, &c., see my 'Entozoa,' 1864, p. 149; also 'Parasites,' 1879, p. 15).

As furnishing interesting evidence of the value of cooperation in zoology, I may mention that in one of my earlier notices I appealed to American naturalists, requesting them to examine the original specimens of *Fasciola Jacksoni* preserved in the Boston Museum. This appeal met with a suitable response at the hands of Dr. R. H. Fitz, who afterwards published the results of his anatomical inquiry. In regard to the original find, we are told that "Dr. Jackson preserved a large number of flukes, and generously placed them at the disposal of Dr. H. P. Quiney, who made and presented to the Warren Museum a series of admirable preparations." These preparations consisted of longitudinal, transverse, and other sections, stained in carmine, and rendered transparent in the oil of colours. Dr. Fitz expressly states that a study of them satisfied him that my "surmise" as to the true character of the species they represented was correct; and I am glad to perceive that so able an observer did not hesitate to accept the generic nomenclature that I had adopted.

The anatomical investigation made by Dr. Fitz resulted in not a few clear additions to our knowledge, especially as regards the sexual organs. There is a very close correspondence between the arrangements of the reproductive parts of this species and those of the common fluke. In some particulars Dr. Fitz's observations and my own are at variance. Thus Dr. Fitz appears to think that I have erred in attributing to *Fasciola Jacksoni* the possession of integumentary spines. In my original diagnosis I affirmed that the body is "armed with minute spines." I still adhere to that matter-of-fact statement; but Dr. Fitz says:—"Instead of finding the body armed throughout with minute spines, the cuticle covering the abdominal surface presents a series of ridges pointing backwards, and extending the entire length of the animal. Traces of a similar formation are present on the dorsal surface or the neck; *elsewhere the back is smooth.*" The italics are mine. I am sorry to correct Dr. Fitz. The little spines not only exist, but when the skin of the parasite is examined by direct light under a 2-inch objective, their equidistant and otherwise regular arrangement becomes obvious. Under higher powers the spines are measurable, giving an average of $\frac{1}{750}$ to $\frac{1}{700}$ of an inch in length, their basal diameter being less than $\frac{1}{2000}$ of an inch. It must be admitted that their size is insignificant when compared with the similar dermal spines of the common fluke. In *Fasciola hepatica* the spines are about twice as long and thrice as broad. The differences therefore are sufficiently striking to be emphasized in any diagnosis of the species; and, further, it may be said that they are perfectly independent of the ridges or folds of the skin described by Dr. Fitz.



On other grounds than those already stated, the peculiarities of the digestive channels call for remark. Although drawn to a large scale (Pl. XXIV. fig. 12), I was not able to represent the entire set of canals. The branches coming off from the main trunks of this dendriform stomach, if such it may be called, are faithfully represented, both as regards number, size, position, and extent of branching. In no two specimens, however, is their form and distribution absolutely identical, though in all these flukes the general arrangement of the canals is the same throughout. The specimen on which I chiefly relied for an interpretation of the facts was injured in the mounting; and in drawing that specimen (without reproducing the injuries), I have derived much help from an outline camera sketch made for me by Dr. John Foulerton. In spirit-specimens the natural green tint or bile-stained appearance of the fresh worms is not entirely destroyed.

In the only hitherto published representation of the worm, I have purposely reduced the digestive apparatus to the lowest possible expression consistent with the general plan ('Entozoa,' Supplement, p. 19). That plan epitomizes, as it were, the larger illustration now given; yet neither the one nor the other fully expresses the degree of complexity which the secondary and tertiary ramifications of the channels exhibit. My drawing represents the tubes and their caecal ends as seen from the back of the worm. Though unaccompanied by any figure, Dr. Fitz's description closely corresponds with what little I had already observed and written on this point; but as he pushes the details much further, and as many of his observations concur with what I have recently ascertained to exist, I prefer to quote his accurate record of the facts, as follows:—"Just beyond the terminal oral sucker is a voluminous bottle-shaped muscular pouch, the pharynx, with which a short tube, the œsophagus, communicates. The latter has a crenated outline, as if capable of a considerable elongation. This tube bifurcates at its lower end; the two short branches thus formed pass respectively to the sides of the animal, and enter the main intestinal canals, which extend, one on either side, almost the entire length of the body. These canals are widely separated from each other until they approach the tail; and between them lie the sexual organs both male and female, towards the front—the remaining space between, behind, and around being filled in by the yolk-glands or tubes and the caecal pouches of the intestine. The latter arise as primary, secondary, and even tertiary divisions, from branches given off more or less alternately from the main canals; and their general direction is backward. Those running towards the median line are short, with comparatively few branches, while the external tubes are considerably longer, often bifurcating before the secondary and tertiary canals arise. The largest number of caecal pouches are thus observed in the outer portions of the parasite. Another peculiarity of the external canals is, that their secondary branches are almost invariably given off from the posterior aspect of the tubes from which they arise."

In describing the other internal organs, Dr. Fitz supplies some interesting particulars; but it is not always clear whether he is dealing with the facts as he actually found them or with appearances which he correctly inferred to exist. Although in my own specimens I obtained clear evidences as to the general distribution of the reproductive organs, and especially of the yolk-glands, yet I could neither trace out the ducts of the vitellaria

nor even the vaginal prolongation of the uterine coils. Their position, however, can be perfectly well understood from the position of the parts actually seen. I have not attempted to figure the yolk-sacs; but the illustration shows a portion of the uterine coils and their contained ova. As in the common fluke, the eggs are oval, and furnished with a lid at one end of the shell. They are comparatively small, affording an average of $\frac{1}{230}$ of an inch in length and $\frac{1}{330}$ in breadth. Dr. Fitz doubts the existence of any true reproductive papilla, but speaks of a pocket or depression midway between the pharynx and the ventral sucker. Certainly the depression referred to is occasionally very marked; but in the centre of this depression, even in the retracted state of the cirrus, there is a papillary eminence, which may be seen with an ordinary hand-lens. The exerted cirrus was not seen by Dr. Fitz; consequently he could not confirm my statement as to its remarkable length. As shown in my figures, this whip-like organ nearly equals in length the transverse semidiameter of the body.

In my previous account of this worm the invariable distention of the digestive tubes by inspissated bile derived from the host has been remarked. Dr. Fitz noticed the same thing in Jackson's specimens. Neither in the common fluke nor in the fluke of the Giraffe has this natural injection been found to be so perfect. For anatomical purposes it renders any artificial distention of the ducts quite superfluous.

NOTE.—The foregoing observations complete my account of the helminths properly so called. Although, without question, as regards their zoological significance and the production of injury to Elephants this class of parasites holds the chief place, yet I cannot omit all notice of the Arthropodous parasites. Doubtless much more remains to be done in reference to the insects and mites that attack Elephants either as parasites or as tormentors. The burden of this research, however, must fall rather on the entomologist than on the helminthologist. Arguing from what is already known respecting the ectozoal Arthropoda of other pachyderms, I should suppose that we have here a wide field for further discovery. When it is considered how large a number of æstridean larvæ take up their abode in herbivorous quadrupeds, to say nothing of the ectozoal Anoplura and Trachearia, it seems strange that not more than three or four arthropodous parasites are at present known to infest Elephants. These I proceed to notice.

12. GASTROPHILUS ELEPHANTIS, Cobb.

Estrus of the Elephant, Cobbold, Catalogue of Entozoa in the Museum of the Royal College of Surgeons, 1866, p. 24.

Estrus elephantis, Steel, Med. Examiner, 1878, p. 886.

Head and neck of the larva turned forwards, prominent, spinous; epicranial lobes armed at the tip. *Maxillæ* large; mandibles concealed. *Somites* of the body all more or less armed, the hook-circles of the middle somites supporting five rows of spines, of which the two upper rows are more conspicuous in consequence of the relatively greater size of the separate spines; penultimate somite with very few spines, and the last somite nearly destitute of them. Caudal lobes furnished with six prominent

papillæ, two in front and four behind, numerous spines occurring in the space between the papillæ and the border of the oval caudal plate.

Length of the larva $\frac{3}{4}$ to 1 inch.

Breadth $\frac{3}{10}$ of an inch.

Hab. Stomach of *Loxodonta africana* and *Elephas indicus*.

When in the year 1865 I rearranged the Entozoa preserved in the Hunterian Museum, I added a few new forms of Cestridean larvæ which had been presented to me by the late Mr. Andrew Murray and by Dr. (now Sir John) Kirk. Amongst the 'bots' obtained during Livingstone's Zambesi expedition were several taken from the stomach of a female Elephant shot by Dr. Kirk himself. Some of these, with others from a Hartbeest, remain in my possession. Those that I placed in the Hunterian Museum were entered in the Catalogue as donations from the eminent naturalists to whom I stood indebted.

Although hitherto undescribed, probably many Indian as well as African sportsmen have encountered these parasites in slaughtered Elephants. Be that as it may, no one appears to have had any opportunity of comparing and identifying the 'bots' derived from the widely dissimilar proboscidean pachyderms of the two countries in question. In the autumn of 1878, one of the victims of the epidemic at Sanger's Circus fortunately supplied me with the means of comparison. The longest of Dr. Kirk's specimens barely measured $\frac{6}{10}$ of an inch, whereas two of the specimens removed from Sanger's Elephant exceeded an inch in length. At first sight probably few would hesitate to separate the bots of the Indian and African Elephants, thus regarding them as the larval representatives of different species of gad-fly. However, a careful examination of the somites, of the arrangements and proportions of the spines, of the papillæ, and of other characters, has convinced me of their identity. Not only so; the African and Indian Elephant bots, though identical in themselves, differ from the bots hitherto found in the stomachs of other animals.

The Indian Elephant, a male, which yielded the specimens obtained in this country, was examined by Veterinary-Surgeon Frederick Smith, R.H.A., and by Mr. Steel, to whose memoir on the circus-epidemic allusion has already been made. Speaking of the post-mortem results, Mr. Steel says:—"The very numerous bots (*Estrus elephantis*) were found in the stomach adhering to the lining membrane. They were, as a rule, larger than the bots of the horse, and exhibited a greater degree of ferocity. As soon as removed from the membrane they struggled violently; and several grasped my finger firmly with their hooklets. The female animal died shortly afterwards; but we had not an opportunity of making a post mortem examination of her. A fourth Elephant died about a week after delivery" [to Mr. Sanger]. Mr. Steel then goes on to speak of the opinion which he gave in a court of law as to the cause of these animals' deaths; but

Fig. 12.



Bot of *Gastraphilus elephantis* ($\times 3$ diam.).

it is evident that the 'bots' were little, if at all, concerned in bringing about the fatal issue.

These bots are perfectly distinct from those obtained from the stomachs of other large animals. Not many years back Mr. Spooner Hart, V.S., of Calcutta, sent me some fine larvæ taken from an Indian Rhinoceros. They are evidently identical with the *Gastrophilus rhinocerotis* obtained by Prof. Owen from the stomachs of African Rhinoceroses (*R. bicornis* and *R. sinus*), and cannot be confounded with the bots of the Elephant. As regards size, the bots of *Rhinoceros indicus* quite equal the measurements recorded by Brauer as characterizing the bots of the African Rhinoceroses.

Parasitic Ova.—In this place it is fitting to notice the curious kind of parasitism believed either to result from or to have some immediate connexion with the deposition of eggs of an insect.

At a meeting of the Zoological Society held on the 21st of February 1871, Mr. Slater showed some tusks of a female Indian Elephant, their surfaces being "corroded or eaten away" near the gums. Egg-like bodies, probably those of a dipterous insect, were found attached below the affected spot. According to Mr. Roden, who shot the Elephant, the eggs were on the tusks at the time he killed the animal; but "there were no maggots in the grooves at the end of the tusks." To whatever circumstances the injuries were due, it is clear that the corrosions were not accidental; for, as Mr. Slater pointed out, a well-known Indian sportsman had already called attention to the matter in the columns of 'The Field.' Under a pseudonym ("Smoothbore") the sportsman solicits information from zoologists, and remarks in particular on the circumstance that the corrosions or injuries "have never been observed in the tusks of the male." In confirmation, Professor Flower also called attention to the fact that the Hunterian Museum contains a pair of tusks similarly marked. Thus, to whatever parasite the appearances in question are due, it is clear that their occurrence is sufficiently common, and that there ought to be no difficulty in procuring materials for further investigation.

Dr. Max Schmidt, the Director of the Zoological Garden at Frankfort, has also referred to the ova of insects on the tusks of Elephants. His well-known memoir is exhaustive and elaborate as regards the general diseases of pachyderms; but little is said about their parasites. Not one of the entozoa of Elephants described by Baird and myself appears to have come under Dr. Schmidt's notice.

Through the help offered by Professor Flower, I have had an opportunity of examining the tusks preserved at the Royal College of Surgeons. In the Catalogue it is stated that one was obtained from a young Ceylonese female Elephant. This tusk was presented to the College by Mr. G. H. K. Thwaites. The other tusk, presented by Mr. Slater, was removed from a wild and full-grown female Elephant killed at Malabar. Both teeth display deep erosions at the surface, near the edge of the gum; and in the smaller specimen from the young Elephant the erosion is about a quarter of an inch in depth. The eggs are deposited on the tusks side by side in single file, but not in perfectly straight lines. They form gracefully curved groups, each group presenting a

festooned appearance. On the small tusk, from which a large number of the eggs had evidently been rubbed off, I counted 150 ova—that is, reckoning the perfect and imperfect shells, as well as the impressions left by such as had been detached. The counting of the eggs and markings on the larger tusk was a more tedious process; but I satisfied myself that at least 2000 ova had been deposited. The Assistant Conservator, Dr. Garson, obligingly removed one or two egg-shells. I found that these ova gave an average length of $\frac{1}{13}$ of an inch. Separately they presented a linear-oblong figure, being rather thicker at one pole than at the other. In a perfect specimen the narrow end measured the $\frac{1}{80}$ of an inch, the broad end being about the $\frac{1}{65}$ of an inch in diameter. From certain appearances I am inclined to think that the intra-ovular maggots make their escape by the opening of the shell in a lid-like manner. Large numbers of the eggs, have their shells open as if three fifths of the exposed surface had fallen away after the manner of a lid. The external configuration shows a rather sudden transition from the thicker to the thinner part of the egg, which circumstance also favours this view. Considering, moreover, the known facts relating to the form and contents of the eggs of gad-flies generally, it appears to me not improbable that the ova in question have been deposited by the mature *Gastrophilus elephantis*. It is a question which the entomologist is alone competent to settle; but I may observe, as favouring this view, that since the tongue of the Elephant could not reach the ova if the gad-flies deposited their eggs on the legs and shoulders (as obtains in the Horse), it becomes a necessity for the gadfly of the Elephant to deposit her eggs either on the coarse hairs in the neighbourhood of the mouth, or in situations similar to those actually occupied by these dipterous ova. It is scarcely likely that the trunk of the Elephant would or could be employed to detach ova measuring only the $\frac{1}{13}$ of an inch in length.

Fig. 13.

Egg of a Dipteran
($\times 20$ diam.).

Ectozaa.—There are two other arthropodous parasites known to infest the Elephant: the one is a huge louse, the other a species of mite. *Hæmatomyzus elephantis* differs from ordinary lice in many particulars, but it has been remarked by Piaget that the reproductive organs resemble those of the genus *Hæmatopinus*. Mr. C. H. Richter described, in the pages of 'Science Gossip' for 1871, what, at the time, was supposed to be "a new form of parasite," which he called *Idolocoris elephantis*. This insect, one line in length, was found upon an Elephant in Ceylon. According to Walker, who defined the genus, it not merely has supplied us with the type of a new genus, but with that of an entirely new family of the *Hemiptera Heteroptera*, coming very near to the bed-bugs (*Acanthidae*). In the same publication (p. 234) Dr. Buchanan White suggested the name *Phantasmocoris* for the genus; but a subsequent writer (*ibid.* p. 278) cleared up the difficulty by referring the parasite to Piaget's *Hæmatomyzus*.

The excellent figures given by Richter and Piaget leave little to be desired; but notwithstanding Piaget's explanation, the specific term *longirostris* would perhaps have

been preferable. This Ectozoon is no longer a rarity, specimens having been exhibited at a recent meeting of the Royal Microscopical Society and elsewhere.

I have nothing new to add respecting the mite of the Elephant. Its position is still doubtful. By Fürstenberg this Acarus was called *Homopus elephantis*, and by Gerlach *Symbiotes elephantis*. According to Mégnin, it is a *nymphe adventive*, or *hypope*, of a variety of *Tyroglyphus siro*, which is very abundant in old forage. Now, if the views of Mégnin be correct, *Homopus elephantis*, considered as a good species, falls to the ground. Not only so; it cannot fairly be called a parasite proper to the Elephant, since its occurrence on the only animal on which it had been found was purely accidental. The original specimens which supplied the means of description were sent by Gurlt to Fürstenberg. They were found in immense numbers on the skin of an Elephant recently packed with straw (*empaillé*). It was referred by Fürstenberg to the parasitic Acaridæ, but not to the true itch-mites, properly so called. As implied by his nomenclature, Gerlach had taken the latter view. After studying Mégnin's criticism of the whole Acarine question, one feels bound to acquiesce in his authority. On the question, however, which he has recently raised respecting the dimorphism of the Cestodes, I think M. Mégnin's views are altogether at variance with any correct interpretation of the facts known to result from experimental research.

So far as I am aware, no other parasites of Elephants have been discovered; but without doubt several more species will in time be brought under observation, especially from amongst the Arthropoda.

Practical Considerations.

Although much has been written on the diseases of Elephants, little has been said of the injuries produced by parasites. Having, by correspondence, supplied Colonel H. P. Hawkes and other residents in India with particulars respecting the various parasites transmitted for identification, these gentlemen have, in their turn, furnished me with the practical results of their observation and inquiry. What I have already published on this head has been either extended or confirmed by subsequent correspondence; but the most considerable additions to our knowledge have been made by the valuable communication of Mr. John H. Steel, in which full details of the *Circus* epizooty are described. If properly looked after, Elephants in captivity ought to suffer less from parasites than their companions in the wild state. We have not, indeed, any reliable facts on which to form an opinion as to the extent to which wild animals are thus victimized. That, like their captive congeners, wild Elephants perish from 'flake-rot,' there cannot, I think, be the slightest doubt; for in the natural state they have the same or even increased facilities for swallowing the parasitic larvæ. Guided by the recent determination of Leuckart respecting the intermediate or Molluscan bearer of the common fluke, there is every likelihood that the mollusk harbouring the Cercarian larva of *Fasciola Jacksoni* is small, and possessed of amphibious habits. Not impossibly more than one species of mollusk is concerned in the intermediate office, although I strongly suspect that in the case of *Fasciola hepatica* the representative Cercarian larvæ limit their temporary residence to the body of a single mollusk. If this be so, *Limnæa truncatula* is the responsible 'host,' and the source of sheep-rot. Be that as it may, we shall never settle this question in connexion with the flukes of the Elephant unless our Indian zoologists take up the study of parasites in the same earnest spirit in which so many of them have advanced other branches of natural history.

Captain Williamson's 'Oriental Field Sports' is one of the earliest works in which any thing is said

respecting the parasitic diseases of Elephants; and what he states about the habits of these pachyderms affords a clue to the source of fluke-infection. Of course, he wrote at a time when it was not known that freshwater mollusks, especially those frequenting marshy grounds, were the responsible media of fluke-infection. Captain Williamson says:—"The Elephant, like the Buffalo, delights in wallowing, and never thrives so well as when he is allowed to visit a rapid stream, there to exercise himself in swimming, as well as to lie immersed and cool himself." Further on he says:—"Elephants are much troubled with worms, for the cure of which complaint the Elephant eats earth; this acts both as an absorbent and operates as a powerful aperient. Those who may have kept Elephants for years, and have not attended to the minutiae, have yet to learn that the Elephant, being sensible of his malady, resorts to this simple remedy voluntarily; all the *mohout* has to do on such an occasion is to keep him from eating other food, but to allow him abundance of drink. If the fæces be inspected there will be seen an amazing number of moving objects, which so much resemble pieces of sugar-cane or of green bough as to require some attention to distinguish. They are ordinarily about the size of a grain of oats, and from their peculiar form no doubt prove particularly distressing and injurious to the stomach and intestines." In making this brief extract I have omitted one or two words and synonymized another. It is clear that Williamson was speaking of the Nematodes, and was probably unacquainted with the fluke-disorder. Referring to the intestinal worms, he remarks the rapid decomposition of Elephants after death, as a ground of apology for not having by dissection ascertained more precisely the true "seat of this disease." He shows that the administration of the "solution of the *Kallah-nimok*, or bit-noben (the quantity, perhaps, of four ounces to as many gallons or more of water)," is amongst the best remedies that could be selected. Williamson says this drug "is well known as the most common purgative in use throughout India." On the authority of Dr. E. J. Waring, I may state that it is merely "an impure chloride of sodium, containing a varying proportion of sulphuret of iron." It is, Waring adds, "a very popular Hindu nostrum."

On the subject of earth-swallowing, the statements of Williamson are quite in harmony with the opinions held in India at the present day. As Mr. George Fleming has remarked, the same opinions are recorded by Captain Forsyth. This sportsman says:—"Elephants are very liable to intestinal worms. They generally cure themselves when they [*i.e.* the worms] get very troublesome, by swallowing from ten to twenty pounds of earth. They always select a red-coloured earth for the purpose. In about twelve hours after, purging commences and all the worms come away. When this occurs the hard food should be stopped for a week, fodder only being allowed, and a ball of spices should be given every day. Some Elephants will not eat earth when they require it, and they are considered a very bad lot in consequence." Probably most of us have witnessed this earth-eating habit of which Indian writers make so much. With others I have watched the same habit on the part of the African Elephants at the Zoological Gardens in the summer time. It is one thing to observe a common-place fact, and quite another to accept popular inferences. The credit for intelligent self-doctoring which the mahouts ascribe to Elephants, is on a par with certain other tales that are told us respecting the wonderful self-culture and instinct of these animals. Assistant Commissary-General Hawkes and other officers, both civil and military, with whom I have conversed, seemed all more or less committed to this view. Speaking of the Amphistomes as *Masuri*, Hawkes says:—"These parasites appear to be very generally present in the Elephant. When their numbers are few, the host is probably not much inconvenienced; but when present in any great quantity they undoubtedly cause much irritation. When this is felt the animal instinctively resorts to a simple and effectual remedy: he eats a quantity of earth, which purges him thoroughly, and expels the Amphistoma. The Mahawats are of opinion that whilst the Elephant is eating earth to relieve himself of the pests, the daily allowance of rice should be scrupulously withheld; and they say that if the rice, which is given uncooked, is eaten by the animal under these circumstances, excessive purgation is induced which frequently results in death." Colonel Hawkes adds that the

Mahawat's name for the disease means 'fasting,' which expression "bears testimony to the generally received notion of the necessity of withholding the rice when the animal is eating earth."

In 1841 Mr. Gilchrist published his often quoted 'Practical Memoir on the History and Treatment of the Diseases of Elephants;' and in this work, without any attempt at scientific definition, he alludes to the parasites termed *Mussoorie*. He also speaks of the Nematodes as *Shotee*, and likewise of the bots or, rather, the disorder they create, under the term 'Lemgun.' The rendering of native names in English varies amongst Hindustani scholars; and thus Hawkes spoke of the Amphistomes and Nematodes as *Masuri* and *Soorti* respectively.

From the evidences I have collected it is clear that epizooties affecting Elephants are more or less frequent in India and the East. The flukes received by Professor Huxley from Rangoon were obtained from an animal which was only one out of many victims that perished from 'rot' in 1867. A resident in Burmah, under the signature of R. B., described this outbreak in a public journal. The Secunderabad epidemic, of which I received full particulars from Commissary-General Colonel Hawkes, was also parasitic, and, in my opinion, partly due to the presence of flukes and partly to the Amphistomes. Speaking of the post-mortem examination, where several kinds of parasites existed, Vet.-Surgeon W. S. Adams says:—"The large number of flukes in the liver and the intestinal parasites account in a great measure for some of the symptoms shown; and these symptoms accord in many respects with those shown in Elephants that died in Burmah during the epizootic in 1867." Mr. Adams adds that the liver-parasite is the same as that which I had described as *Fasciola Jacksoni*; and in regard to the symptoms in the Elephants, he noticed especially the "refusal of food, standing with the mouth open, restlessness, and puffiness about the head and shoulders." Speaking of another of the Secunderabad victims, the same observer remarks:—"There were flukes in the liver, but in no great quantity; and the structure of the liver was sound. Although not assisted by *this* case in attributing the mortality to parasitic origin, I am strengthened in my opinion that the death of the previous Elephant was due to disease caused by the presence of the fluke." Mr. Adams does not himself speak distinctly as to the presence or absence of Amphistomes in the Secunderabad outbreak; but, as we have seen, Colonel Hawkes remarked both upon their prevalence and the power of mischief that they had exerted in this epidemic.

In various published papers I have shown that Amphistomes frequently infest horses in India; and in one case (examined after death, and reported to me by Veterinary-Surgeon F. F. Collins) it was calculated that about a thousand of these parasites were present. "Nearly the whole of them were situated close to the cæcum, and were loose in the gut." Mr. Collins sent me thirty-three of the specimens.

In the Secunderabad epizooty fourteen elephants perished. Writing to me in May 1875, Colonel Hawkes said:—"Out of twenty-eight Elephants under my charge, no less than twelve have died within the last sixteen months, whereas the average annual mortality has been hitherto only two per annum out of thirty-eight on our establishment." My military informant, much to his credit, caused a post mortem to be made in almost every instance; and he supplied me with the results obtained and recorded by the various veterinary surgeons. Two of these records (made by Mr. Adams) I have already quoted. Taking the report as a whole, I am sceptical as to the accuracy of the deductions it embodies. It is clear that the mortality was unusual, not to say unprecedented, and that therefore some special cause must have arisen as a chief, if not as an exclusive, factor in its production. In my opinion, and even supposing the parasites were not the real cause of the mortality, the report is eminently unsatisfactory. Parasites or not, here was a local and fatal epidemic; and yet, as a result of the examination of thirteen carcasses, the deaths are attributed to no less than eight different causes—inflammation of the intestines, inflammation of the lungs and liver, splenic apoplexy, sunstroke, and so forth. Knowing, from long and special professional experience, the scepticism which prevails in the medical world in respect of the injurious effects of parasites, I cannot affect surprise at the conclusions formed by the veterinary surgeons in India. To the mass of practitioners helminthological science and its practical issues remain a *terra incognita*.

Colonel Hawkes himself was evidently perplexed by the record of results. He wrote, saying :—" In every case in which I was present flukes were found in greater or less numbers in the gall-duets of the liver; and the Amphistoma was also as constantly present in the intestines, the Soorti (*Ascaris lonchoptera*), contrary to the general experience of the elephant-attendants, being less frequently met with, though, from its colour and its shape, it is not so easily detected among the huge mass of fieces as the larger Amphistoma." There must, of course, be some misapprehension here, unless the Strongyles are included in the general term of *Soorti*; for the particular nematode above mentioned was not present in any of the bottles of specimens which I received from Secunderabad. " In some cases flukes were in large numbers, apparently collected in bunches in the gall-duets; but disease of the liver did not necessarily appear to follow, nor, where disease was actually present, did it seem to bear a constant ratio to the number of flukes in the gall-duets." Colonel Hawkes subsequently remarked upon the impossibility of concluding to what extent the flukes were responsible for the outbreak, and the difficulty of singling out any symptom as characteristic of their presence. This does not surprise me, considering the number and variety of parasites that were admitted to have been present, not alone in the liver, but also in the intestines. In one instance there was the characteristic swelling beneath the jaw, similar to that found in sheep in the advanced state of 'rot,' when the animals are said to be suffering from "bottle-jaw." This "suggestive" feature, as Hawkes himself called it, seemed in his view somewhat neutralized by the fact that in "only the one other case (in which the parotid glands were swollen) the liver was more healthy and had fewer flukes than any in the whole series" of dead Elephants.

In what has been called the English outbreak, affecting Sanger's performing Elephants, the injuries appear to have been principally due the Amphistomes. In the animal examined by me, these Entozoa were present in prodigious numbers. In all, five animals perished, one during the sea-voyage, and the remaining four some time after their arrival. I feel assured that all the parasites found in these animals were brought by their hosts from India. Mr. Steel records the symptoms separately observed in three of the victims. The record is too long for quotation; and, as one might expect, there is not much that is distinctive about the symptoms. Speaking of the post mortem of a young female Elephant, Mr. Steel states that the large intestine "was studded with very numerous, small, vesicular, blood-coloured parasites, about the size of grains of wheat. In addition, we found specimens of nematode worms intermingled with the bowel-contents, some being found in the dilated portion of the bile-duct, where it terminates at the duodenum. We found a few specimens of a thread-worm on the surface of an incised part." By an anonymous writer in the 'Lancet' it was stated at the time that this female Elephant had suffered from "double pleuritis;" but, as Mr. Steel himself subsequently pointed out, "the absence of a pleural sac has been proved to be a normal condition in this animal." It is worthy of remark that in the case of the remaining patients the treatment adopted sufficed to expel some of the parasites; but from the first it seemed pretty clear that the animals were past all remedial help. One of these young Elephants, a male, died suddenly. "In this case the parasites, both Amphistomata and Ascarides, were much more numerous, the former existing almost in thousands." It was this animal also which supplied the stomach-bots described in this memoir.

Considering the heavy losses thus incurred, it was not surprising that the owner made the matter a subject of litigation on the ground that there had been a breach of warranty. Without giving Mr. Steel's views in full, I may state that he shared with me the opinion that these animals were infested by parasites at the time of their landing in this country; and further, he believed that if it could not be shown that they were the sole cause of the epidemic, the parasites at least very materially contributed to bring about the fatal issue.

One passage in Mr. Steel's communication is perhaps a little too significant. He says:—"The parasites in the bowels gave rise to irritation; and the Amphistomes, like so many small leeches, were withdrawing large quantities of blood from the animal; the bowel-lesions were most marked where these parasites were found." Mr. Steel seems inclined to set little store by the action of the Nematodes;

but as these turn out to be not *Ascarides*, but *Strongyles*, armed with more or less formidable teeth, I am inclined to think that he has underrated their powers of mischief. On the other hand, whilst I quite think with him that the Amphistomes, by their sucking action and consequent irritation, are capable of giving rise to severe inflammatory lesions, yet I doubt their capacity for drawing blood in the way Mr. Steel implies. If the Amphistomes really gorge themselves in this sucking process, they must needs be continually detaching themselves for the purpose of ejecting the contents of the stomach. In true leeches, as also in those *Strongyles* which have bloodsucking propensities, the presence of an anal outlet enables them, whilst still attached, to discharge freely those constituents of the blood that are not necessary for their nourishment.

In reference to the Ectozoa, I possess no sufficient data whereby to estimate their power of producing mischief amongst Elephants. Judging from what happens in the case of other domestic animals, it is certain that strict attention to sanitary matters will diminish the chances of invasion either from external or from internal parasites. Mr. Steel speaks with evident satisfaction of the cleanliness and care taken by the grooms at Sanger's Circus-stables, where the flooring was "subjected to frequent disinfection." At the Zoological Gardens I have frequently made inquiries of the Head Keeper (Seott) whose diligent search for Entozoa has hitherto been attended with negative results. This speaks well for the cleanliness observed there; and at the same time the absence of parasites shows that the habit of earth-eating, which the African Elephants at the Gardens are wont to indulge in, is not consequent upon the presence of Entozoa. This habit is not confined to any one class of animals. My friend Mr. Arthur Folkard, during his residence in Ceylon, noticed that the Elephants of that island were large earth-eaters; and the late Dr. J. P. Rowe assured me that Australian horses and sheep largely indulge in the same propensity. Dr. Rowe thought that the sheep thus sought instinctively to relieve themselves from the irritation produced by parasites in the stomach. My own belief is that when colic-symptoms are associated with a depraved appetite, the animals affected swallow mud, soft earth, or sand indiscriminately. A remarkable instance was brought under my notice by Colonel Hawkes, where the accumulation of "sand or gravel" in the intestines of a military horse amounted to 14½ lb. It was supposed at the time to have resulted from careless feeding with impure grain or rather 'pulse;' but this is impossible, as only two or three ounces of sand could be swallowed as the result of the daily meal. At this rate, as Hawkes observes, "it would take from 77 to 116 days to accumulate 14½ lb. In consequence of this earth-eating habit, he adds (from memory) it was found necessary, some twenty years ago "to remove the mud-walls round the picket enclosing some of the horses of a mounted corps. If the conclusion formed by Commissary Hawkes and others be correct, all foul-feeding horses and elephants must either be suffering from Amphistomes or some other kind of internal parasites. Be this as it may, any sanitary measures which prevent the ingress of parasitic larvæ cannot fail to prove beneficial. In like manner any agencies which prevent a parasite completing its life-cycle must be equally effective. Thus clean water and fodder given to Elephants in captivity prevents the possibility of their contracting either *masuri* or *soorti*. I think it extremely improbable that any Elephant should contract internal parasites in this country. Mr. Steel thinks otherwise, and that, as regards the Trematodes, they, or rather their larvæ, "might make shift with an English mollusk." It is not, however, so much a question of making shift on the part of a Cercarian as it is a question of an allotted or appropriate territory. Some Trematode larvæ are limited to one host, and others to a few hosts. In all cases there is a measure of restriction; and I think we must therefore look to one or more Indian mollusks as the legitimate and and only bearers of the Cercarian larvæ of *Fasciola Jacksoni*. But, as before hinted, the final settlement of this question is not yet awhile. Even with a large accession of labourers in this field of research, the process will be tedious, when it is considered how long a time, aided by frequent observation and experiment, helminthologists have taken to acquire the meagre results already arrived at in connexion with the parasites of cattle; it is evident that as regards the origin of, and transformations undergone by the internal parasites of Elephants, we are only on the threshold of inquiry. It may be said,

indeed, that our efforts have not yet properly commenced. If this be the case, any thing like an exhaustive knowledge of the development of the Elephants' helminthiases is a matter likely to be realized only in the far future. There is not much done to encourage research in this special direction. Those who have charge of Elephants have usually so little knowledge of zoology that their observations are either common-place or altogether unworthy of credence. Even thoroughgoing naturalists shirk the subject. Certainly the 'Challenger' and other expeditions expressly fitted out to collect all kinds of natural-history objects might have accomplished much more in this direction had they been minded to follow the example of previous explorers. The most interesting private contribution of parasites in my possession I owe to the liberality of Mr. Darwin, he having obtained some Eutozoa about forty years ago during his travels in Patagonia. But I must conclude. If the publication of this imperfect memoir should do no more than gain for the helminths greater consideration at the hands of naturalists, I shall feel that my efforts in a really useful though unpopular cause have not been altogether fruitless.

APPENDIX.

Since the reading of this memoir took place, Mr. R. McLachlan, F.R.S., has referred me to a paper written by Dr. F. Brauer in the 16th vol. of the Transactions of the Zoologico-Botanical Society of Vienna. It is entitled "*Pharyngobolus africanus*, ein Oestride aus dem Rachen des afrikanischen Elephanten." Mr. McLachlan also subsequently received a letter from Dr. Brauer, in which the latter *surant* refers to the abstract of my paper already given in the Linnean Society's Proceedings. Not unnaturally Dr. Brauer appears surprised that the parasite described by him has been omitted from my list; and he thinks it probable that his *Pharyngobolus* is either similar to or identical with my *Gastrophilus elephantis*. Dr. Brauer's inference is not correct. The two bots found by Herr E. J. C. Marno in the oesophagus of the African elephant that died at Vienna are quite distinct. Their characters, as given by Brauer with extreme minuteness of detail, neither correspond with those of the bots found by Sir John Kirk in the stomach of the elephant shot by him in Africa, nor do they resemble the characters presented by the bots which were procured from the stomach of one of the Indian elephants which died in this country. The specific differences refer to size, shape, armature, and habitat. In *Pharyngobolus* the larva is, we are told, scarcely more than twice as long as it is broad, and the two anterior rings are only a trifle narrower than the third ring. The number and disposition of the spines are also especially noteworthy. In Brauer's larva each armed segment displays two widely separated circles of spines, the circle occupying the centre of each somite consisting of large spines with their points directed downwards. In our larvæ the armed somites at the middle of the body support several circles of spines, which are closely set together; moreover, whilst the uppermost circle is composed of spines that are paramount in size, the second circle carries rather large spines, the third, fourth, and fifth rows becoming smaller and smaller. Besides these, it will be seen, on comparison, that there are other more or less well-marked differences; and therefore I do not hesitate to say that the throat- and stomach-bots of Elephants represent two totally distinct species of dipterous insects.—T. S. C.

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DESCRIPTION OF THE PLATES.

PLATE XXIII.

- Fig. 1. Head and neck of a male *Sclerostoma sipunculiforme*, showing the double circle of oral denticles, buccal cup, œsophagus, retractor muscles, upper part of the chylous intestine, and the subdermal vascular network. ($\times 33$ diam.)
- Fig. 2. Semiprofile and oblique view of the lower end of the body of a male *Sclerostoma sipunculiforme*, showing the folded hood, the points of the rays, the vascular network, and the position of the spicules in their retracted state. ($\times 27$ diam.)
- Fig. 3. Side view of the head and neck of *Strongylus clathratus*, showing two auriculate folds, the buccal cup, and the œsophagus. ($\times 23$ diam.)
- Fig. 4. Side view of the tail of a male *Strongylus clathratus*, giving a complete representation of the right lobe of the hood and its rays, and also indicating the position of the spicules and caudal swelling in front. ($\times 23$ diam.)
- Fig. 5. One of the spicules of *Strongylus clathratus*. ($\times 40$ diam.)
- Fig. 6. Lower end of the body of a female *Sclerostoma sipunculiforme*. ($\times 13$ diam.)
- Fig. 7. Another view of the lower end of the body of a female *Sclerostoma sipunculiforme*, showing the altered shape of the tail when seen from the front. ($\times 13$ diam.)
- Fig. 8. Additional side view of the tail of the male *Sclerostoma sipunculiforme* (to contrast with fig. 2), showing the altered position and direction of the spicules when exerted. The vascular network omitted. ($\times 27$ diam.)
- Fig. 9. Head and neck of *Strongylus foliatus*, seen from the front, displaying the upper and lower pair of papillæ, mouth, buccal cup, and long œsophagus. ($\times 27$ diam.)
- Fig. 10. Profile view of the left side of the head of *Strongylus foliatus*, showing auriculate folds of the skin. ($\times 33$ diam.)
- Fig. 11. Similar representation of the right side of the head of *Strongylus foliatus*, with the focus altered to show the buccal teeth. ($\times 33$ diam.)
- Fig. 12. Left side of the lower end of the body of a male *Strongylus foliatus*, showing the retracted spicules, bursal lobes, and entire system of rays on one side. ($\times 60$ diam.)
- Fig. 13. Left side of the lower end of the body of a female *Strongylus foliatus*, showing the anal cleft and subulate extremity of the tail. ($\times 40$ diam.)
- Fig. 14. Head, neck, and upper part of the body of a female *Strongylus falcifer*, showing especially the outer and inner series of oral papillæ. ($\times 23$ diam.)

PLATE XXIV.

- Fig. 1. Lower end of the body of a male *Strongylus falcifer*, seen from the front, exposing the interior of the bursa, caudal papilla, lobes of the hood, points of the rays, and more particularly the spicules with their sheaths and retractor muscles attached to the upper end of the blind pouches. ($\times 23$ diam.)

- Fig. 2. Profile view of the lower end of the body of another *Strongylus falcifer*, exposing the bursal lobes of one side and the projecting spicules. ($\times 27$ diam.)
- Fig. 3. Lower end of the body of a female *Strongylus falcifer*, showing the mode of termination of the reproductive and digestive organs, and more especially the characteristic form of the tail. ($\times 23$ diam.)
- Fig. 4. Half-profile view of the head and neck of a female *Dochmius Sangeri*, showing the mouth, buccal cup, œsophagus, and upper end of the chylous intestine. ($\times 33$ diam.)
- Fig. 5. Lower end of the body of a male *Dochmius Sangeri*, seen from behind. It shows the expanded hood and entire system of rays, as well as the spicules in their retracted position. ($\times 33$ diam.)
- Fig. 6. Profile representation of the lower end of the body of a female *Dochmius Sangeri*, showing the anal cleft and finely pointed tail. ($\times 33$ diam.)
- Fig. 7. Upper part of the body of a female *Filaria Smithii*, exposing the head, a double row of auriculate folds, papillæ, œsophagus, and commencement of the chylous intestine. ($\times 30$ diam.)
- Fig. 8. Front view of the lower end of the body of a male *Filaria Smithii*, displaying the spicules, the anal opening, and the relation of the latter to the stalked papillæ. ($\times 30$ diam.)
- Fig. 9. Profile view of the tail of another male *Filaria Smithii*, in which the papillæ are not seen. ($\times 30$ diam.)
- Fig. 10. Another side view of the lower end of the body of a male *Filaria Smithii*. The tail is more curved, the spicules being completely retracted, the papillæ of the left side being also seen throughout their whole extent. (Flattened by pressure, and $\times 50$ diam.)
- Fig. 11. Front aspect of an *Amphistoma papillatum*, giving a general view of the internal organs as seen through the transparent integuments. It also shows the oral sucker, reproductive papilla, circular folds or rugæ of the body, and especially the disposition of the fungiform papillæ within the concavity of the caudal sucker. ($\times 18$ diam.)
- Fig. 12. This illustration represents a *Fasciola Jacksoni*, viewed from behind, and with the aid of transmitted light. It explains the position of the oral and ventral suckers, reproductive papilla, exerted cirrus, two or three of the uterine coils, their contained ova, and also, more particularly, the mode of branching and distribution of the digestive tubes. ($\times 10$ diam.)

VIII. *On the Digastric Muscle, its Modifications and Functions.*By G. E. DOBSON, *M.A., M.B., F.L.S.*

(Plate XXV.)

Read December 15th. 1881.

IN a paper published in the ‘ Proceedings of the Royal Society ’ for March 1881, I have traced the origin of the oblique tendinous intersection of the Digastric Muscle to an originally united condition of the anterior bellies of the muscles of opposite sides in front of the hyoid bone, the superficial tendinous inscription still found traversing the surfaces of the digastrics of many species in which the muscles are not united being shown to be the rudiment of the origin of a tendinous band which once formed the posterior limit and support of the united muscles. I shall now endeavour to trace the leading modifications of this muscle and their relations to its functions.

The representative of the digastric in the lower Vertebrates, as in Reptilia, is a bundle of muscular fibres arising from the occiput and inserted into the posterior extremity of the mandibular ramus, its functions being simply those of drawing the angle of the mandible backwards and upwards, and so separating the jaws in front. Such is its form and such its functions also throughout the class Aves and in most of the species of Mammalia. In many species, however, of the latter class, notably in certain Orders—the Primates and Rodentia—we find it no longer of the simple form above described; its anterior attachment has advanced nearer to the anterior than to the posterior extremity of the mandibular ramus, and the muscle is found to be made up of two bellies, an anterior and a posterior, with an intermediate tendon or tendinous intersection, thus forming a true *musculus digastricus*.

In the Primates, in many species of Rodents, and in a few species of other Orders, the intersecting tendon is connected by ligament or by tendinous fibres with the hyoid bone, the anterior bellies of the muscles of opposite sides uniting in the middle line across the mylo-hyoids, or connected only by the fascial expansion known as the supra-hyoid aponeurosis which extends between their inner margins.

The leading modifications of the muscle may therefore be arranged as follows :—

- I. Single (*M. depressor mandibulæ*), inserted into the posterior extremity of the mandible, as in reptiles, birds, and many mammals.
- II. Double (*M. digastricus*), consisting of an anterior and posterior belly, with an intermediate tendon or tendinous intersection, inserted more or less in front into the side of the mandible, as in the Primates, many Rodents, and some species of other orders.
 - A. Not connected with the hyoid bone; tendinous intersection oblique or transverse.

- a. With the anterior bellies united across the space between the rami of the mandible, the mylo-hyoid muscles feeble or absent.
Ex. *Gymnura rafflesii*, *Epomophorus macrocephalus*.
- b. With the anterior bellies separate, the mylo-hyoid muscles well developed.
Ex. *Erinaceus europæus* and other species, *Cavia aperæa*, *Epomophorus franqueti*, &c.
- B. Connected by ligament or by tendinous fibres with the hyoid bone; tendinous intersection well developed, oblique or longitudinal.
 - a. With the anterior bellies united across the space between the rami of the mandible, the mylo-hyoid muscles feeble.
Ex. *Tupaia ellioti*, *Mus decumanus*, *Myoxus avelanarius*, *Cercopithecus callithricus*, &c.
 - b. With the anterior bellies separate, the mylo-hyoid muscles well developed.
Ex. *Loris gracilis*, *Homo sapiens*.

In the first example cited above, *Gymnura rafflesii*, I found the digastric condition of this muscle well developed. About the middle of the muscle, at its narrowest part, it is traversed by an oblique tendinous intersection more marked internally, arising from the upper margin, which is continued inwards and slightly forwards from its lower and internal margin as a tendinous band across the mylo-hyoid muscle to unite in front of the hyoid bone with the corresponding band from the opposite side. From this tendinous raphé thus formed muscular fibres arise, which, extending forwards and inwards, cover the anterior three fourths of the mylo-hyoid and part of the genio-hyoid muscles, and passing above the margins of the anterior bellies of the digastric muscles of opposite sides, are inserted with them and for some distance in front of them into the rami of the mandible.

This horizontal muscular expansion which takes its origin thus from the tendinous intersection and its median continuation might also be described as a deep division of the anterior belly of the muscle, commencing at the tendinous intersection, and uniting with its fellow of the opposite side along the middle line between the jaws. Its posterior margin, the tendinous raphé above described, is concave, quite free from the hyoid bone, but attached to a fascial aponeurosis, which passes backwards over it and the sterno-hyoid muscles. On removing this muscular expansion the mylo-hyoid muscles are found beneath, very thin, not extending half the distance between the hyoid bone and the symphysis menti.

In *Epomophorus macrocephalus*, *minor*, *labiatus*, and *gambianus* the anterior bellies of the digastric are double, and the deep laminae united not only across the space between the rami of the mandible, as in *Gymnura rafflesii*, but their union extends so far backwards that when the head is bent forwards their posterior free margin passes behind the hyoid bone. The mylo-hyoid muscles are completely absent, their functions being evidently performed altogether by these greatly developed digastrics. It is most remarkable, as showing what extraordinary structural differences may occur in the anatomy of species to judge from external characters very closely allied, that in *Epomophorus franqueti*, *comptus*, and *pusillus* the digastrics are single, and not united

in front, and the mylo-hyoid muscles are well developed; nevertheless, the presence of a nearly vertically transverse tendinous inscription across the digastrics of those last-named species, corresponding precisely in position and direction to the origin of the tendinous raphé bounding the united anterior bellies of the muscles behind in the first named, indicates a united state of the digastrics in a common ancestor. It is especially interesting to note that in these species, where union of the muscles extends so far backwards, the tendinous intersection is vertical or nearly so, and the direction of the fibres of the deep or internal lamina transverse, while those of the superficial external part spring from it at right angles to its direction and pass forwards to their insertion into the mandible. Here, then, we have a vertical tendinous intersection unconnected with the hyoid bone!

In the genus *Erinaceus*, which with *Gymnura* makes up the family Erinaceidæ, although the digastrics are no longer united, a superficial oblique tendinous inscription occupies precisely the same position as in *Gymnura*, though much less developed; it extends from the upper margin of the muscle (which is nearly of the same calibre throughout), and on reaching its lower margin is continued inwards into a fascial expansion extending between the anterior bellies of the muscles of opposite sides, covering the mylo-hyoid muscle, but no muscular fibres arise from it as in *Gymnura*; nevertheless this fascial expansion evidently represents the muscular sheath of the expanded and united digastrics in the ancestral forms.

In *Centetes caudatus* and *semispinosus*, in *Pteropus edulis* and *medius*, and probably in all the species of that genus, in *Epomophorus franqueti*, *comptus*, and *pusillus*, in *Megaderma lyra*, in *Cavia aperæa*, in *Phoca communis*, and in other species, though the fascial expansion be absent or feebly marked, the transverse tendinous inscription is traceable, although its presence in some, as in *Centetes caudatus*, is indicated by a faint superficial oblique line surrounding the muscle.

In *Tupaia ellioti* the anterior bellies of the digastrics also unite in the middle line between the jaws; but there is no separate superficial external lamina in direct continuation with the posterior belly, as in *Gymnura rafflesii*. The intersecting tendon is narrower but more distinct, arises, as in that species, from the upper margin of the muscle, and is continued downwards, forwards, and inwards to unite with the corresponding tendon from the opposite side across the mylo-hyoid, precisely as in *Gymnura rafflesii*; but unlike its free condition in that species it is closely adherent by its deep surface to the mylo-hyoid muscle, and connected with the hyoid bone by a strong fibrous aponeurosis. The united anterior bellies pass forwards, taking their origin from the tendinous raphé, and, separating slightly near the symphysis menti, are inserted into the rami of the mandible, and by a fibrous aponeurosis into the symphyseal angle. The mylo-hyoid muscles, nearly wholly concealed by them, are feebly developed.

In *Mus decumanus* and in other species of the genus the digastrics are united in front, the posterior margin of the united muscles being formed by the united intermediate tendons which are connected with the hyoid bone; in *Myoxus avellanarius* the intermediate tendons are even better developed, and the united anterior bellies are closely connected with the mylo-hyoid muscles. In *Cercopithecus callitrichus*, in *Troglodytes*

niger, and in many other species of Primates, the anterior bellies of the digastrics are united, and the intermediate tendon is well developed and connected with the hyoid bone.

In Man, as an anomaly, the fibres of the two anterior bellies have been found blended together, or the anterior belly has been found double, as in *Gymnura*, the deeper part uniting with its fellow in a median raphé, covering the mylo-hyoid muscle, or the intersecting tendon is not unfrequently continued from one side across to the other, forming a zone immediately above the hyoid bone, to the body of which it is tied down by fibrous tissue; from the upper surface of this the anterior bellies arise.

This united condition of the digastrics in man is very interesting, as it indicates reversion to a condition common in lower species of Primates.

If now we arrange the species of Mammals referred to above according to the relations of the digastric to the hyoid bone, we shall find that they fall into two groups:—in one the muscle is connected with the hyoid, and the species swallow their food while in the erect position, with the head bent forwards upon the chest and the long axis of the cavity of the mouth at right angles with the œsophagus; in the other this muscle is free, and all the species feed while resting on their anterior extremities, having the long axis of the mouth in a line with the œsophagus. In the latter, where a tendinous intersection exists, it is, as I have shown, either the origin of a tendinous band, as in *Gymnura rafflesii*, which, passing obliquely inwards and forwards across the mylo-hyoid, unites with its fellow of the opposite side, or it is very small, forming a mere superficial tendinous inscription, as in *Erinaceus*, indicating a united condition of the muscle in ancestral forms.

Thus among certain Rodents and arboreal Insectivora, as the species of *Tupaia*, which habitually sit erect when feeding, holding their food between their fore feet, the anterior bellies of the digastrics are large and united, and the intermediate tendons well developed and connected by fascial bands with the hyoid bone and by their deep surfaces with the mylo-hyoid muscles, as may be seen in the species of *Muridae* and *Myoxidae*, of which excellent examples are readily available in the rat and common dormouse. In the water-vole (*Arvicola amphibius*), however, the digastrics are connected together in front by fascia alone, and the upper margin only of their intermediate part is tendinous and not connected with the hyoid bone. These animals live on vegetable substances obtained while swimming, and habitually hold the head stretched out in a line with the body. Again, an instructive example is met with in the great Rodent moles (*Blathyrges maritimus*) of South Africa, and in the species of *Spalax* and *Sipheus*, which feed chiefly on the roots of grasses, and while feeding necessarily hold the head in a line with the body, or raised upwards; in them, accordingly, the digastric is quite simple, without tendinous intersection of any kind, and unconnected with the hyoid bone, a true *depressor mandibulæ*.

In those animals, then, which habitually swallow their food while the head is bent forwards at a right angle with the neck, the digastric has functions other than those of a simple *depressor mandibulæ*; it is an important agent in the act of deglutition, such, in fact, as we find it in man. Where, as in reptiles, birds, and most mammals, the position of the mouth with respect to the œsophagus during the act of swallowing the food is

almost in the same right line, deglutition is easily effected by the mylo- and genio-hyoid muscles drawing the hyoid bone and larynx forwards and upwards, so as to allow the masticated mass to get behind them, and so bring it within the grasp of the pharyngeal muscles; but in those animals which feed while in the erect or semi-erect position and the head is bent forwards, so that the cavity of the mouth is at right angles with the œsophagus, it is evident that deglutition must be a much more complex action. In that position the mylo- and genio-hyoid muscles are relaxed, and cannot act efficiently in drawing the hyoid bone upwards and forwards, so as to allow the masticated mass to pass into the œsophagus, into which it has to pass, in fact, round an angle. The difficulty is got over by the connection of the digastric with the hyoid bone. This muscle during the act of deglutition causes the hyoid bone, larynx, and base of the tongue to move through a segment of a circle, the anterior part of the muscle drawing these parts forwards; they are then elevated by the joint action of the anterior and posterior bellies, and finally drawn backwards by the posterior bellies, so as to force the masticated mass into the œsophagus.

This action of the digastric is well known, but its relation to the position of the head while the animal is feeding appears not to have been generally recognized.

With respect to the great development and united condition of the anterior bellies of the digastrics so general in Quadrumana, and not uncommon in Rodentia, it appears to me to be related to the inefficiency of the mylo- and genio-hyoid muscles in the habitually bent forward state of the head. Their separate condition in man is probably due to shortening of the rami of the mandible and greater depth of the symphysis menti, which bring the mylo- and genio-hyoid muscles into a more favourable position for action, as well as affording more extensive attachments. Nevertheless united digastrics have been noted as a muscular abnormality in a few cases, evidently recurrences of a once normal condition of these muscles in ancestors provided with much longer jaws than we have; and I suspect that, when the muscular anatomy of the prognathous inhabitants of Africa has been more fully examined, united digastrics will be regarded as a much less uncommon human muscular anomaly than it now is.

EXPLANATION OF PLATE XXV.

Fig. 1. *Myoxus arellanarius*. United digastric muscles (enlarged).

Fig. 2. *Mus natalensis*. Dissection of inferior gular region, showing the position and form of the united digastrics.

Fig. 3. *Tupaia ellioti*. Dissection similar to the preceding.

Fig. 4. Ditto. Digastric muscle, showing the oblique tendinous intersection passing across from the infero-external margin of the posterior belly of each moiety to support the posterior free margin of their united anterior bellies, uniting with the corresponding tendinous band from the other side (enlarged).

- Fig. 5. *Gymnura rafflesii*. United digastrics, showing conditions similar to those described in fig. 4.
- Fig. 6. *Erinaceus europæus*. Single digastric muscle, showing an oblique tendinous intersection in a position similar to that in *Tupaia* and *Gymnura*, but rudimentary and unconnected with that of the corresponding muscle of the opposite side.
- Fig. 7. *Epomophorus franqueti*. Dissection similar to that shown in fig. 2, showing the position and direction of the muscular fibres (see text).
- Fig. 8. *Cercopithecus callitrichus*. Anterior bellies united, and intermediate tendons well developed.
- Fig. 9. *Troglodytes niger*. Dissection of the infero-lateral side of the neck, showing the positions and attachments of the united digastrics (after Vrolik).
- Fig. 10. *Homo sapiens*. Dissection showing an abnormal united condition of the digastric homologous to that in fig. 8.

IX. *On the Clasping-organs ancillary to Generation in certain Groups of the Lepidoptera* *. By PHILIP HENRY GOSSE, F.R.S. (Communicated by R. McLACHLAN, F.R.S., F.L.S.)

(Plates XXVI.—XXXIII.)

Read May 4th, 1882.

INTRODUCTORY REMARKS: EXISTING AUTHORITIES.

THE lovely insects, of which I am about to treat, have been the objects of so much ardent admiration and intelligent curiosity, so long have they been collected from all regions, so many cabinets are filled with them, so many treatises have been written and compiled about them, that one may well be accused of presumption in daring to suggest the existence of an uncultivated field of observation in their structure. Yet I venture to lay before the Linnean Society a series of facts, yielded to my own examination in the study of these exquisite creatures, which, while they elicit interest and admiration in an unusual degree, seem to me to have been hitherto almost unsuspected. I refer to the complex apparatus with which the male Butterfly has been furnished for the prehension of the female during the copulative function.

In most of the families of the Rhopalocera the organs devoted to this purpose are more or less patent when sufficient magnifying power is used; and these are often exceedingly curious and exceedingly various. If the Papilionidæ have seemed less profusely supplied, it is, doubtless, because in them the prehensile apparatus is concealed beneath special organs (*valves*), which do not to the eye present any feature differing from the scale-clad body. The family, moreover, is almost wholly Trans-European; and thus, though very conspicuous, they lie somewhat beyond the range of ordinary scientific investigation.

I hope I am doing no injustice to my predecessors, in assuming these researches to be new. The older authors have little more than vague allusions to the existence of auxiliary prehensors, and nothing, that I am aware of, concerning those of the *Equites*. Herold (1815) describes and figures† the “spoon-like” valves, and the “triangle-piece” in *Pieris Brassicæ*. Burmeister (1832) describes‡ the outer and inner valves in a Hawk Moth. Kirby and Spence (1828) devote § a paragraph to the prehensors of the class, but dismiss the Butterflies in a few lines. Siebold and Stannius (1848) assign ¶ to the prehensors of the Lepidoptera one fourth of one sentence.

The most important contribution to the subject seems to be a memoir¶¶ read before this Society by Dr. F. Buchanan White, December 21, 1876. This elaborate and very valuable article, illustrated by more than 220 figures, might well seem to leave little room for my researches, but for two reasons:—1, he limits his studies to the Butterflies

* A preliminary sketch of this article will be found in the Royal Society Proceedings, xxxiii. (1871), pp. 23–27.

† Entwickel. p. xiii. pl. iv.

‡ Manual, p. 216 (Eng. ed.).

§ Intro. to Ent. iv. p. 579.

¶ Anat. Inv. p. 462 (Amer. ed.).

¶¶ “On the Male Genital Armature in the European Rhopalocera,” Trans. Linn. Soc. 2nd ser. Zool. i. p. 357.

of Europe, of which only three species come into my subject; 2, he does not look *within* the anal valves, within which my study begins.

Somewhat earlier than this, however, viz. in the 'Proceedings of the Boston (U. S.) Soc. of Nat. Hist.' for April, 1870, Messrs. S. H. Scudder and E. Burgess had published a conjoint memoir, of much interest and value, and illustrated by many highly magnified figures, "On Asymmetry in the Appendages . . . in the Lepidopterous Genus *Nisoniades*." The specific variety and individual uniformity, which I hope to show in the genital armature of *Papilio*, mark the corresponding organs in this genus of Hesperiadæ; nor is the apparatus less elaborate or less curious. The learned authors designate by the terms "clasps" and "upper organ," what Dr. White calls "harpagines" and "tegumen."

Prof. Graber, in his valuable work, 'Die Insekten' (in 'Die Naturkräfte'), 1877, has devoted half a dozen pages to the male genital auxiliaries (äussere Hilfsorgane des Hinterleibes); but has taken no illustration from the Lepidoptera.

I am indebted to my honoured friend Prof. Westwood for bringing to my knowledge some descriptions and figures by Dr. De Haan on the subject, which, so far as they go, do really anticipate my own. The book is rare and difficult to consult; but my son, Edmund William Gosse, has made for me, from the copy in the library of the British Museum, a translation of the Dutch text, and careful tracings of all the figures that relate to the subject.

It is a thin folio, a livraison of a large publication, entitled 'Verhandelingen over de natuurlijke geschiedenis der Nederlandsche overzeesche bezittingen (Transactions regarding the Nat. Hist. of the Dutch Transmarine Possessions), by various authors. The sub-title of the treatise itself is "Bijdragen tot de kennis des Papilionidea: door Willem de Haan." Leiden, 1842.

The observations of this author on the genitalia, since they are brief, and the work is little available to English students, I shall be excused for giving *in extenso*.

"THE SEXUAL ORGANS.

"These parts are, especially in the male, very various in form. The outermost valves [*kleppen*] of *Ornithoptera Amphrisius* shut closely against each other, and conceal two lateral appendages [*zijdelingsche aanhangsels*, = the *harpes* of the following memoir?], which turn over at the end in the form of a hook, and are provided with spines along the upper edge. The truncated, and sometimes even hollow, end of the hinder part of the body, which lies within these valves, bears upon the upper edge a pointed spine bent downwards [=uncus, P. H. G.], with two lateral plates [*zijdelings plaatjes*, = scaphium, P. H. G.?], which lie close to it. From the middle of the hinder part of the body the penis [*roede*] is exposed, which is gristly [*kraakbeenig*], straight, blunt, and shorter than the lateral valves.

"Those of *Papilio Memnon*, *Pammon*, *Heleneus*, *Machaon*, are similar to this, except that the lateral appendages lie along the lower edge, and the hook on the back is usually more elongated; in *Memnon* the penis is thrown over from below. In *P. Coon* the outer valves are wholly opened from above, and, to a great extent, also from below; so that the inner parts are scarcely protected by them: the penis is very pointed, and a little longer than the valves. *P. Liris* and *Polydorus* have the hinder part of the body naked: the valves are very short, armed from within to the top with a hook, and the lateral appendages (of *Amphrisius*) are placed under it; the spine of the back is blunt; besides this there are also two spines present on the upper edge, and these are curved inwards; so that altogether the outer

edge is provided with seven appendages, which all rise free from one another. Between these lies the penis, which, as if pressed together, has a sharp edge above and below.

"In *Thais Hypsipyle* the valves are turned towards one another at the end, open above and below, toothed along the upper edge, and armed along the under edge with a sharp spine; the lateral appendages, and the spine at the back, are very small, and, indeed, scarcely visible. *Parnassius Apollo* has the valves puffed out, and gaping wide open; the lateral appendages are entirely free, of the same length [*cens zoolang*], and in the form of two half-sheaths; the back-spine is broad, and ends in two short points. *Eurytus Cressida* has two flat valves placed on the under side of the body, which are covered from above by the last two abdomen-segments, and show on their inner edge, close to the joint, an indentation. The penis is pointed, and longer than the valves. *Doritis Apollina* has two little pointed valves, also placed under the last two segments."

The work is illustrated by eighteen figures of the sexual parts of eight species, on a scale considerably smaller than mine. They are thus distributed:—

<i>Ornithoptera Amphrisius</i> ...	3 figs.	<i>Thais Hypsipyle</i>	2 figs.
<i>Papilio Coon</i>	3 „	<i>Parnassius Apollo</i>	2 „
— <i>Liris</i>	2 „	<i>Doritis Apollina</i>	2 „
<i>Leptocircus Curius</i>	2 „	<i>Eurytus Cressida</i>	2 „

It so happens that not a single species illustrated by Dr. De Haan is identical with any one of mine; though two approach very nigh, viz. his *O. Amphrisius* to *O. Rhodamanthus**, and *P. Coon* to *P. Doubledayi*.

My own attention was first directed to the subject when, examining the anatomy of the remarkable genus *Euryades*, I referred for comparison to the structure of the genital organs in *Papilio* and *Ornithoptera*. The elaborate apparatus which I found hidden beneath the valves, like delicate surgical instruments in their protecting cases, drew me on into the examination of one species after another, until I had studied and figured nearly a hundred members of these two genera.

Dr. Buchanan White says †:—"I regret very much that, from want of material, I have been unable to examine, amongst the Rhopalocera, any but European species. It is much to be desired that some one, who has at his command a large collection of the butterflies of all regions, should investigate, more extensively than I have been able to do, the structure of the genital armature."

Nothing, unless it be the exquisite beauty of the workmanship, is so astounding as the variety, in form and detail, presented by these hidden instruments. Out of the number that I have examined, I have not found any two species whose apparatus is alike, or even so nearly alike that a moment's observation is not sufficient to show the difference. I do not think this rule of diversity holds in respect of other important organs. I do not know that microscopic examination would show that the antennæ, or the tarsi, or the spiracles, vary markedly in every species ‡.

* Perhaps his *Amphrisius* is the species which in M. Lucas's 'Lepid. Exot.' is so named in the plate, but *Rhodamanthus* in the text. It is certainly not the *Amphrysus* of Cramer's plate 219.

† *Op. cit.* p. 366.

‡ "Aucune autre partie du corps des papillons ne dénote des variations si nombreuses que la terminale avec les organes génitaux des deux sexes; variabilité qui ne nous permet pas de nous occuper de ce sujet d'une façon plus générale, parce que son explication détaillée est l'objet d'une monographie spéciale."—DR. BURMEISTER, *Lepid. d. l. Rep. Arg.* p. 21.

It might seem that, by the aid of organs so uniformly present, so easily examined, and so varied in different species, while constant in the same, great facilities must be afforded for the determination of specific identity and limitation. Yet, in practice, I fear this cannot be carried out, without severing species which otherwise seem most closely allied, and linking others which have little else in common. Look, for instance, at the three African species *Papilio Bromius*, *P. Nireus*, and *P. Phorcus*; how consimilar are these in their forms, colours, and markings! yet how diverse in their whole prehensile apparatus! The shape of the valve, its fringing; the shape of the harpe, its armature; the uncus; the teeth of the scaphium; and, finally, the penis;—all these differ signally in one from their conditions in the others, as may be seen, at a glance, from the following pages. The like terms might be employed concerning *P. Demolens* and *P. Erithonius*.

It needs scarcely to be told that all the following observations were made on *dried* specimens. The desiccation of the soft tissues, causing them to shrink, throws into distinct prominence the hard chitinous organs with which these pages have mainly to do; and *their* form is not affected by drying. Indeed, the density and unyielding hardness of this material are manifest by the depth of colour it can assume, often approaching to black, by its brilliant polish of surface, by its transparency like that of glass, and by the delicacy with which it is fashioned into the thinnest edges and cut into the sharpest teeth, which, strange to say, we never see blunted by use.

Let it be remembered that, while a considerable number of the following descriptions and figures have been confirmed by observations repeated upon two, three, or even more successive examples, many (somewhat more than half) rest upon individuals. These, though made with all care, are like the ἀπαξ λεγόμενα of the critics, and must be accepted with a certain measure of caution.

MANIPULATION.

My methods of manipulation are of the simplest. With a penknife, worn by age to a very fine and keen point, I make incisions, vertically as the insect lies on its side before me, along the hinge-line of one valve (I have usually selected the right): presently, using, with a gentle violence, such a lever as the tip of a toothpick, the valve is *prized* off. By practice, I am able to do this with very little chance of injury to the specimen; and when my examination is completed, I restore the valve to its place, with the minutest touch of gum-tragacanth; so that, when it is dry, and the butterfly returned to the cabinet, I am often quite unable, some time after, even myself to determine, with certainty, of two or three examples in the drawer, which it was that I had used for the operation*.

The detached valve is then submitted to strict search with the various powers of a triple lens, reaching in combination to 24 diam. When the information deducible from this aspect seems exhausted, if the harpe appear to promise any more, I essay to lift it

* The circumstance that the exotic Papilionæ are often of high monetary value has no doubt much impeded our acquaintance with their anatomy. Our museums and private collections are rich in species; but few possessors are willing to submit their treasured beauties to the anatomist's scalpel. Perhaps Prof. Siebold's sarcasm is not yet wholly without force:—"Most collectors seem ambitious only to keep their butterflies neat and untouched, or to gain thereby advantages other than scientific" (On the ♀ of *Pieris Apollo*, Stett. Ent. Zeit., 1851).

from its adhesion to the valve-cavity with the same knife-point. I do not always succeed; but if I do, I have an object, often of brilliant transparency and lustre, and of extreme delicacy, which I can put on a slip of glass, and transfer to the stage of a compound microscope, using any powers that I please.

The organs which project from the abdominal cavity cannot be detached with certainty of success. These, therefore, I usually view with the lens only*. After exhaustive study of these parts, *dry*, since the scaphium and, in part, the penis are composed of soft tissues which change form in drying, I introduce into the cavity, with the tip of a fine hair-pencil, a drop of clear water. This is presently absorbed; the superfluous water is removed with a point of blotting-paper, and the organs are again examined as before. The shrivelled parts have now become much more plump, assuming something approaching the form which they had during life. The study of them in this condition often reveals facts that had been obscure before.

On detaching a valve there are often found many plume-scales and atoms of meconium, scattered over the organs within, as well as all about, the anal cavity. Since these hinder distinct vision, I remove them by touching the parts with the tip of a fine camel's-hair pencil slightly moistened, wiping the tip on a linen cloth after every contact.

Curious records of past history may be read in such impediments. Minute fragments of a pulverulent, drab-coloured, chalky substance are, as I have observed, occasionally found adhering to the harpes. On one occasion I found, on carefully removing one of the valves from a cabinet-specimen of *Ornithoptera Rhodamanthus* ♂, the cavity *quite full* of this substance, partly in coarse powder, and partly in somewhat coherent lumps of the size of mustard-seed downwards. Now, I have no doubt that this male had effected coitus with a female, at so early a period after her evolution from pupa, that she had not discharged the faecal accumulation of the pupa stage, which subsists "*sous la forme d'un fluide jaune ou brun, comparable au méconium des enfants nouveau-nés*" (Burmeister). The excitement of the sexual copula would provoke the instant discharge of the meconium, a large portion of which would fill the valvular cavity of the grasping male; and this, presently coagulating, remained to be at length revealed by my dissecting scalpel.

A phenomenon exactly similar occurred with a specimen of *Papilio Zalmoris*. But in this case the cavity was occupied with a dirty mingled mass of meconium and *body-scales*; and that so fully as completely to conceal all the organs, till it was gradually extracted. These scales were surely those of a female abdomen, removed *in coitu*: the meconium discharged at the same time had agglutinated the scales into a composite mass, which, in drying, had divided into fragments and coarse powder; and these, the male having been presently captured, had remained a record of the history.

See also, for similar conditions, the account of *Papilio Axion*, and of not a few other species.

The illustrative drawings have all been made, not with the aid of the camera, but by the eye and hand alone. They have not been drawn to scale; but those of the *valves*

* I have occasionally viewed these as opaque objects under condensed reflected light, both artificial and solar; but the result has been (in general, though with exceptions) hardly worth the pains.

follow a pretty uniform ratio, which may be set down as about 7 diam., with which ratio the figures of the other organs may be compared.

A GENERAL DESCRIPTION OF THE ORGANS.

The organs with which I propose to deal, as limited to the male sex of Butterflies belonging to the two genera *Ornithoptera* and *Papilio*, are the following:—1. The Valves; 2. the Harpes; 3. the Uncus; 4. the Scaphium; 5. the Penis.

1. *The Valves.*

To the overlapping edges of the eighth abdominal segment, from the indefinite points where the projecting angular portion produced by the rami of the uncus merge into the vertical, to two prominent rounded pieces within the ventral margin, there are united, by free-working joints, two broad plates, well known under the name of valves*. Every collector is familiar with these organs; for he has recourse to them to determine, at a glance, the sex of his specimens, since, in the grand genus *Papilio*, they are peculiar to the male.

Their outline is usually more or less trigonal, often becoming semioval, or even sub-circular. To be more precise, the prevailing shape is that of an oval, or rounded rhomboid, cut off obliquely, so that as we look on the inside of the right valve the tip points to the left—that is, toward the dorsal side.

They are clothed on the exterior with scales like those of the body. Their direction follows the general plane of the sides of the abdomen; they are convex externally, concave internally. Their free edges are commonly furnished with a fringe of modified scales, taking the form of thick hairs, which are parallel, close-set, often dense, and often long; thus these practically enlarge the area of the valves, and help to exclude, more effectually, extraneous matters from the genital cavity when the valves are closed. Sometimes dense brushes of long hair, of quite different structure, arise from within the interior of the valve, which spreading, conceal the margin, and greatly modify the apparent outline; e. g. *Polices*, *Urolegon*.

The fringed edges come into contact when the valves are at rest, inclosing a spacious chamber, the anal, or genital, cavity. The edge is occasionally turned over, narrowly, within; e. g. *Ornithoptera Haliphron*; and still more commonly the interior surface continues flat and level for some distance within the margin, then abruptly drops to the central cavity; e. g. *Agamemnon*, *Hesperus*, *Lycidas*, *Anchisiades*, *Euryleon*. Occasionally a sort of wall, of distinct form and surface, borders the edge, and overhangs the interior; e. g. *Zalmoxis*. The floor of the interior, whether flat or hollow, is often studded with short scattered hairs, each springing from a dimple, or crowning a minute round hillock, where it is not occupied by the harpe: but sometimes this surface is cloth-like; e. g. *Erithonius*, *Lycidas*.

* A better name would be *tegmina*, covers; but this word has been chosen by Dr. B. White for a very different neighbouring organ. *Coli* (κολεός, a sheath or scabbard) might be used; or, to avoid ambiguity with the genus *Colinus* of the botanists, it might be spelled in its Ionic form, κολεός. But I adopt the appellation already in familiar use.

In those abnormal cases in which the valves are partly or wholly aborted, e. g. *Diphilus*, *Polydorus*, *Hector*, the thatch of long hair that occasionally projects from the dorsal arch of the eighth segment, and thus fills up the triangular space left by the receding dorsal edges of the valves, is particularly abundant.

The extremity of the valve shows, in *almost* all cases, some indication of a projection of the outline into a point. Usually this part is as soft and flexible as any other; but in some instances, e. g. *Semperi*, *Uedelegon*, there seems, in its definite form and darker hue, an approach to that condition which occurs in other families of the Rhopalocera, in which the valve and the harpe become one organ*.

Mr. Wallace, in his very valuable Memoir "On Variation, &c., in the Papilionidæ of the Malayan Region" †, is inclined to rest on the peculiarities of the valves of *Ornithoptera* for generic diagnosis. Having rejected certain points that have been relied on, he says, "There remain, therefore, only the characters of the perfect insect, the most important of which are the anal valves in the male. These are very large, ovate or rounded, coriaceous, and not hairy, and are furnished with projecting points or spines (sometimes very conspicuous) which serve to attach the male more firmly to the female in copulâ. In several species, I have observed, these points or hooks were buried in the protruded anal gland of the female, and thus effectually prevented the great weight of the insects causing them to separate upon suddenly taking flight" ‡.

2. The Harpes.

The interior surface of each valve, which, as I have said, is hollow, is the seat of a peculiar organ, which appears to take a very prominent part in the prehensile function. The floor proper of the valve-cavity is a thin membrane of slight tenacity, more or less of a dark brown hue, and of a dull unreflecting surface. Within the hollow lies a plate of what I presume to be pure chitine §, usually as transparent as glass, but tinged with a yellow-brown hue, thickening at various parts, especially at its margins and irregular

* Dr. F. B. White's memoir affords abundant examples of this combined condition. The transition seems to be made in the family (or subfamily) Pieridæ. (See the supplementary note to this Memoir.)

† Trans. Linn. Soc. xxv. p. 35, 1864.

‡ But the valves in *Ornithoptera Armana* and *Amphrysus* are densely fringed with hair-scales: *Papilio Semperi* has as distinct a finger-point to the valve as *O. Amphrysus*; while the broad rounded outline is seen in the valves of *P. Zalmois*, *Acton*, and *Bromius*. This projecting finger-point, moreover, while well marked in *O. Amphrysus* and *Rhodamanthus*, becomes feeble in *Armana* and *Holiphron*, evanescent in *Remus*, and is absolutely wanting in *Brookeana*, where the valve is surrounded by a fringe of unusual density. But generic lines are not mathematical lines: and the features mentioned by Mr. Wallace are certainly characteristic, and, with the prevailing form of the harpe, go far to establish *Ornithoptera* as a good genus.

Mr. Wallace's observation about the function of the points is most interesting: would that we had more of such! but, if I may venture to correct the dictum of so great an authority, I would suggest that, most probably, it was not the flexible finger-point of the valve that had seized the protruded vulva of the female, since it has no resistant power, but the harpe, well toothed, and of almost metallic hardness, that was concealed just beneath the valve-tip. Yet, in some cases, as in *P. Uedelegon*, I am not sure that the valve-point may not have a harpe-power—as I presume that it has in some Pieridæ, as *Callidegetes*.

§ The various degrees of flexibility found in the integuments of insects is believed to depend on the extent to which they are permeated by this substance, "a peculiar azotic matter insoluble in caustic potass" (Siebold, 'Anat. Invertebr.' Lond. 1854, p. 401).

ridges, where the substance deepens in hue, often to an intensity almost black (but still like black *glass*), and where it manifestly acquires great density, elasticity, and hardness, with a reflective power equal to that of polished glass. The gleam and glitter of the surface imparts a wonderful attractiveness to these most diversified organs. The parts thus thickened are also elevated, not merely in the bounding walls and ridges that I have mentioned, but, in general, by the separating of a portion of the organ from the cavity-floor; so that this particular part shall be elevated, and projected freely into the inclosed space between the valves. And these projected portions either take the forms of eurved acute spines, or, more frequently still, are notched into sharp teeth standing in serried rows.

To attempt to indicate the various forms which these curious weapons assume, would be to anticipate the greater part of the descriptive pages which are to follow; for the variety is about commensurate with the number of species examined. I propose presently to attempt a rough casting of them into groups; but it will be little more than an arbitrary classification, useful as an aid to memory, rather than any thing else. Projecting claws, hooks, pikes, swords, knobs, and strange combinations of these, abound, whose prominences are very commonly brought to a keen edge, and then cut into sharp teeth. The species of one group, *Agésilus*, *Parmatus*, have harpes in which many such projections are strangely crowded. In others, *Ulysses*, *Macedon*, the formidable teeth are themselves cut into many minuter toothlets of wonderful delicacy.

Sometimes this polished weapon occupies almost the whole area of the valve-cavity, *Agésilus*, *Podalirius*, *Erithonius*; sometimes it is a slender staff or rod, *Memnon*, *Erechtheus*, *Polymnestor*, with the extremity expanded to form the weapon, whether axe, or sword, or saw, or spear-point. Whatever the form, the base is always expanded, often with ridges (like as where the trunk of a tree dilates into roots), spreading over the basal edge of the valve, and manifestly stretching beyond its area, as is often very clearly seen when the valve is forcibly detached. Examples of what I mean may be seen in my figures of *Papilio*, *Axion*, *Ascalaphus*, *Pammon*, *Macedon*, *Childreus*, *Vertumnus*, *Zalmoxis*, and several others. In all these a kind of disk is observed; which more or less clearly shows that there had been a dilated attachment of the harpe to a surface which had lain in a plane quite different from that of the valve, face to face with it, indeed, close to its hinge. (See, specially, *Euryleon*.)

Hence I very confidently infer the function of two short thick eminences of hard chitine, having convex surfaces, which are generally to be observed occupying the bottom of the abdominal cavity, when the valves are removed; *e. g.* *O. Remus*, *P. Pammon*, *Rhetenor*, *Mayo*. They afford, doubtless, a broad and firm basis for the attachment of muscles which move these important prehensores, so constantly exposed to shocks and violent strains. And the fact of such an attachment explains an otherwise puzzling phenomenon which not very infrequently occurs,—that, when the valve is detached by force, it occasionally comes away empty, the chitinous armature being left behind. (See *infra*, page 293.)

If there existed any reasonable doubt of the work performed by this well-armed organ, it would be removed by a due consideration of that curious accumulation of foreign

matter to which I have already alluded,—the thick mass of dislodged body-scales with which we frequently find the chitinous armature clogged, particularly its serrate parts. How came those scales there? The answer is patent. This apparatus has been provided to enable the male butterfly to grasp and hold the female during the process of impregnation. And these accumulated scales show that this very individual insect had been so engaged only just before its capture and death.

I have hence no hesitation in assigning a distinctive epithet to the organ in question; and it is known, throughout this memoir, by the term Harpe ($\alpha\rho\pi\eta$, a grappling iron)*.

It is the rule, subject to very rare exceptions, that when the two valves are closed, as generally during life, the chief armed parts of the two harpes approach each other at a point in space, within the post-anal cavity, exactly where the tip of the uncus comes down from above. Hence I infer that the function of this latter organ is similar and ancillary to that of the harpes—the three combined constituting a threefold grip, which it would be difficult to break.

It seems scarcely credible that elaborate instruments, such as these, so constantly present in this popular family, and so readily found, should not have already been the subjects of ample examination and familiar knowledge. Yet, with the exception of Dr. De Haan's brief allusion to the "lateral appendages," and one equally brief in Dr. Burmeister's latest work, the 'Lepidoptera of the Argentine Republic' †, I know not any.

I have already spoken with admiration of the surprising variety which the prehensile apparatus displays; it is in the harpes that the extreme diversity mainly resides.

Yet it is by no means a vague, come-by-chance variation; it does not extend to individuals of the *same* species. I have, in many instances, examined several examples of the same species, and have always found that the identity of the harpe is wonderfully close and minute, the diversity very trifling.

3. *The Uncus.*

The eighth segment of the abdomen, in the male of *Ornithoptera* and *Papilio*, in general, has the posterior‡ outline of its dorsal arch produced in the middle line, and terminating in a point, with receding sides; so that, looked at vertically from above, it is

* Dr. White has used the term *harpygo* for the organ which, in the other Rhopalocera, appears to represent the valve and harpe united. But, in the Papilionide, where these are separate, it is desirable that they should receive separate designations. The terms *harpygo* and *harpe* are sufficiently distinct; while they bear a relation to each other not unlike that of the things designated.

† "Entre ces deux valvules, se trouve, dans le fond de la cavité, l'ouverture sexuelle, accompagnée, principalement chez les mâles, par des appendices en forme de tenail, qui renferme l'organe male, le pénis." I conjecture that, by these "appendages in form of pincers," he means the *harpes*. But the term is vague, and I do not feel quite sure.

‡ To avoid ambiguity, I would distinctly notify to the reader that I shall use terms of relative position, as back and front, before and behind, in describing the organs of the genital cavity, as if they were independent organisms, and not parts of the entire animal. Thus, if I speak of the uncus, I might describe it as narrowing *behind* the tip; of the smaller scaphium-tooth as *behind* the larger; of the ariste of the cheeks as directed backwards; of the sheath of the penis as running *back* to its base. Now, in each of these cases, the direction intended is certainly from the tail *towards* the *head* of the insect; yet, limiting our attention to these organs, it would be most unnatural and misleading, to speak, for instance, of the tip of the penis as its hinder portion, of the basal bulb as its front. In speaking of the abdomen generally, or of its segments, I shall use the ordinary terms, as above.

a triangle, of which the base is the edge of the seventh segment, the sides are often incurved, and the point is, in general, prolonged into a strong, horny spine; e. g., *Orn. Amphrysus*, *P. Merope*, *Erechtheus*. This point, however, varies much, in different species, in length, breadth, sharpness, curvature, and direction; and, as it is one of the elements of the prehensile apparatus which I am proposing to describe, I distinguish it by the term *uncus*, a drag-hook. The term "tegumen," adopted by Dr. White, seems hardly appropriate for this spinous, often wiry, point, which is certainly in no sense a *cover*. But it does express the function of the wide annular part of the segment, from which the uncus projects; and in this sense I use it.

Viewed from the side, the tegumen and uncus together often present a very curious resemblance to the skull of a bird without the lower mandible, e. g. *Erechtheus*, *Demoleus*; which latter, however, is simulated occasionally by the *scaphium*, so as to complete the likeness—*Deiphontes*, *Homerus*, *Childrene*, and very curiously in *Parn. Apollo*. I occasionally avail myself of this and like accidental resemblances, for more definite and graphic description.

The extreme point is generally somewhat swollen and flattened, spoon-wise—and this even when the organ is of a wiry slenderness, as in *Rhodifer*. Sometimes it is bilid—*Agamemnon*, *Polydorus*; more rarely even trifid—*Argesilaus*, *Archesilaus*; sometimes it is curved upward—*Agamemnon*; sometimes vertically downward—*Hector*, *Lycidas*, *Agarus*; sometimes it is short, thick, and uncouth—*Antenor*, *Zalmoxis*, *Bromius*; almost straight—*O. Arruana*, *P. Hesperus*, *Rhodifer*; often nearly a half-hoop of very slender wire, displaying a strength, elasticity, and polish, almost of steel—*Vertumnus*, *Macedon*, *Turnus*. The receding margins are often turned up to a height that considerably exceeds the plane of the dorsal surface, which then becomes transversely concave—*Mayo*, *Machaon*, *Zalmoxis*, *Merope*; this surface is sometimes indented with a trilateral (*Antenor*) or quadrilateral (*Argesilaus*) depression. Often it is clothed with a median ridge of long and close-set hairs, which project horizontally, and, so to speak, thatch the cavity and its organs—e. g. *Agamemnon*, *Codrus*, *Homerus*, and, signally, *Diphilus*, and the abnormal *Hector* group, though here there is no *uncus*. More commonly the stiff ridge-hairs are erect—*Erechtheus*, *Rhetenor*, *Merope*; or, at first erect, and then arching forward—*Menestheus*, *Machaon*.

When the valves are perfectly developed, as in *Ornithoptera*, the uncus is projected immediately under the line produced by the meeting of the dorsal edges of the valves; and then the median ridge of long hair helps to fill the blank space between.

The inferior surface of the uncus usually bears two conspicuous laminae descending vertically from it, more or less deep, which take their origin insensibly near the point, and increase in depth gradually—*Erechtheus*, *Rhetenor*, *Helenus*, *Merope*, following the curvature of the margins till they are lost in the descending rami; but in some cases this keel begins at some distance from the point, and with its full depth—*Deiphontes*, *Homerus*.

On each side, near the spot at which the rami of the keel can no longer be distinguished, a conspicuous horny tooth often projects horizontally from the edge of the segment—*Helenus*, *Turnus*.

The uncus is apparently composed of nearly pure chitine, whose varying density is

perhaps indicated by its colour, which may be pale fawn, or rufous, or deep sienna-brown, or even almost black, always with a polished surface.

4. *The Scaphium.*

By this term I indicate a curious organ, which I find almost always present, of complicate structure, apparently having an intimate relation to the uncus, and even, in general, organically united with it, but yet occupying its proper place even in those rare cases in which the uncus itself is obsolete, as in *Orn. Brookeana*, *P. Podalirius*, and *Bathycles*. Indeed in this last-named it is seen to great advantage; and still more so in *Mayo*, the beautiful representative of *Polymnestor* in the Andaman Isles; and most of all in the African *Merope*.

The instant we have removed either of the valves from one of these Butterflies, our attention is arrested by a great mass of shining white tissue, occupying the chief place in the genital cavity, and projecting far into its area. We trace it up to an intimate and apparently organic union with the lower surface of the uncus near its origin, far back in the *palate* of the *bird's skull* (if I may use my own comparison on p. 274, *suprà*), whence it descends and dilates, sending large angular lobes back even into the abdomen (*Bathycles*), but chiefly developed forward, like the contiguous organs. I have likened this prominent part of the organ to a lower jaw (rather *mammalian* than *avian*, however)—*Machaon*, *Turnus*, *Erithonius*, *Demoleus*, *Macedon*; I have likened it also to a boat—*Mayo*, *Pammon*.

Of the function of this conspicuous organ I cannot speak with certainty. I adopt a distinctive appellation for it (presuming it to be important and undescribed), which leaves function untouched, and looks only at the accidental resemblance alluded to—σκάφη, σκαφίον, a boat.

Where it is most perfectly developed, e. g. *Mayo*, the sides swell out like the bows of a ship, while the mesial portion is abruptly thinned away to a deep projection, like a cut-water and a keel. The upper surface forms two dilated margins (the gunwales of the boat), with a deep sulcus between, in which in some cases—*Vertumnus*, *Erechtheus*, *Rhetenor*—the uncus lies. More usually there is considerable vertical space between the uncus and the scaphium-margins. These very generally bear (here the simile shifts back from the gunwales of a boat to a lower jaw) a compound armature, most difficult to explain, but in which surely lies hid the key to the explanation. In some clear examples it mimics the double molar tooth of a mammalian jaw, the outer usually much more distinctly developed than the inner, often rising to a strong, conical, produced spine, which may take the form of a straight blunt pin or peg—*Memnon*, *Nireus*; or that of a canine tooth, erect, acute, recurved—*Mayo*, *Pammon*, *Arcturus*, *Macedon*, *Thoas*; horizontal, recurved—*Machaon*, *Ulysses*; horizontal, decurved—*Rhodifer*. Both may appear as two equal, stout, polished cones—*Homerus*; more commonly the secondary is reduced to a mere conic knob, or is even obsolescent; occasionally a third supernumerary tooth or knob appears—*Mayo*, *Homerus*; and not infrequently *neither* can be detected, e. g. *O. Arriana*.

Besides these teeth, there is another kind of arming: the gunwale-like margin rises

into an elevated ridge, which is thinned off to an edge, and is then cut into a number of parallel erect membranous points or bristles. When the double teeth are wanting this aristate crest appears to supply their place, as in several of the *Ornithoptera*; but yet occasionally *both* are seen, and then the aristæ are more baseward—*Erechtheus*.

But the most remarkable form of the scaphium known to me is that of *Merope*, in which the teeth are stout, broad, and most elaborately notched and bristled on their edges; for the details of which, with other points of interest, I must refer to my account and figures of the species, *ut infra*.

The lower parts of this organ are obscure, descending and receding towards the abdomen. Sometimes it is patent that the descending rami do certainly embrace the basal region of the penis, and appear to unite again below it, but are not, I think, organically united with it—e. g. *O. Amphrysus*, *P. Rhetenor*, *Bathyctes*, *Agamemnon*. But such connexion of the scaphium with the penis cannot by any means *always* be affirmed.

The usual appearance of the organ is opaque white, smooth, shining, like polished ivory, often very pure, particularly the keel. Sometimes, however, it becomes partially or even wholly pale, or even dark, brown—*Podalirius*, *Zalmoxis*, *Lycidas*, *Macedon*—as if the chitinous element pervaded it, which microscopic examination confirms*.

By the same test the substance appears to be mainly muscular—a conclusion to which I had already come from the armature of the double teeth. It was impossible to look upon those formidable weapons, in *Merope*, for example, without inferring that the compact mass upon which they are seated must be muscular, or they would be useless. But I suspect that in this organ reside the muscles which move the uncus—perhaps also, at least in part, the valves and the harpes, for which offices they would need to be vigorous and massive.

Many modifications of the form and conditions of the organ occur in different species, which will be described *seriatim* †.

On the nature, or even the existence, of the scaphium, I have little help from my predecessors. Herold, in *Pieris Brassicæ* ‡, does not distinguish it from the uncus, which I find quite distinct, both being present, but contiguous. He, however, confounds the two organs under the name of the triangle-piece (“Triangelstück”), which he cites from De Geer. The minute projection from beneath the point, which he takes to be the end of the rectum, is surely the keel of a small scaphium. The anus is, as I believe, in the middle of that transverse line at which the muscular base of the scaphium is united to the palate-like under side of the uncus §. (See *P. Arcturus*.)

* The scaphium of *P. Machaon*, macerated and torn from its uncus, showed, at the upper part (the *gummalé*), a clear yellow-brown tissue, with smooth edge, and minute bristles growing from the surface. This ran off into colourless transparent tissue, decidedly fibrous, several of the bundles being formed of longitudinal fibres, which were more or less covered with thin laminae filled with excessively minute but perfectly distinct regular parallel oblique *striae*.

† For some further researches into the structure and relations of the scaphium, made after this memoir was handed in, I beg to refer to the account of *Ornithoptera Rémus*, *infra*.

‡ *Entwicklung der Schmett.* xiii. tab. iv. figs. 3–6.

§ The fact that the uncus is tubular, as may be clearly seen when it is forcibly broken across, suggested the thought that perhaps itself might be the termination of the intestine. But very exact and repeated examinations

Neither Burmeister nor Siebold makes any allusion to the scaphium. De Haan's slight mention of "lateral plates" has been already cited. From his figure, I suppose he alludes to the scaphium, by this phrase. In the numerous figures of Dr. White's Memoir*, minutely beautiful, and carefully executed, as these are, I find no trace of the organ; and I think that probably it is peculiar, *or nearly peculiar*, to the true *Equites*. I say "nearly peculiar," because, though Dr. White finds it not, as a separate organ, in the European Pieridæ, yet I hope presently to show that unequivocal traces of it are to be found in certain members of the family.

5. *The Penis.*

This organ forms, strictly, no part of my subject, which is not the function of generation, nor the organs that perform it, but certain prehensile apparatus that are ancillary to the performance. Yet, as this member is so essentially the centre around which the whole apparatus waits and serves, and as it forms so conspicuous an object in the accompanying designs, I can scarcely avoid giving some account, at least, of its varying form and position.

The penis is usually seen, when the valves are opened, in the lower half of the genital cavity, in the form of a column, more or less cylindrical, varying much in diameter and in length, projecting from the interior of the abdomen. In some instances it is so short as not to appear beyond the walls of the eighth segment, e. g. *Vertumnus*, *Lycidas*; but it is doubtless capable of being protruded, to a certain extent, by its proper muscles†. In others it is so long that it cannot be contained within the cavity, but projects beyond the margins of the valves when these are shut. In *Merope*, *Ucalegon*, *Hesperus*, *Rhetenor*, the tip just reaches the edges of the valves, or exceeds them in a slight degree; in *Podalirius*, *Bromius*, *Macedon*, and still more in *Bothrycles*, the protrusion is remarkable; but, in the *Coon* group, including the beautiful *Rhodifer* lately sent from Andaman, the penis projects from the hinder extremity to an extraordinary degree, like a fine steel wire, that quite arrests the attention as we see the insect in a cabinet. No less notable is the extreme slenderness, and, at the same time, the strength and elasticity, of the organ in the just-mentioned species.

As to position, the penis appears so high as almost to be in contact with the scaphium—*Turnus*; again, almost on the very floor of the cavity—*Deiphontes*; and, in some species or other, in every intermediate stage.

have convinced me that the extremity of this organ is solidly chitinous, and absolutely imperforate, at least in *O. Remus* and *O. Haliphron*. But, when the uncus is removed, there is clearly discerned, under the very middle of the tegumen, a circular orifice leading from the abdomen into a groove, which is hollowed along the median line of the scaphium-sulcus. In dried specimens the intestinal convolutions are reduced to an undistinguishable mass of yellow dust. Yet, on one occasion, I detected (or fancied) a thread connecting the mass with the orifice just described. It had, however, vanished in an instant.

* *Op. cit.*

† In an abdomen of *O. Haliphron* I carefully laid bare the penis till I traced the base of the chitinous cylinder, originating in firm muscular tissue, in the ventral arch of the seventh (that is, the ante-penultimate) segment. But, in *P. Merope*, I laid bare the cylinder to its base in muscular tissue, in the sixth, or even the fifth segment.

A curious variation lies in this circumstance, that, while the proper condition is that the darker, more chitinous side of the cylinder, that which terminates in the finger-point, is uppermost, there are numerous examples in which this order is reversed, and that side is undermost, as in several of the *Ornithoptera*, *P. Agamemnon*, *Agarus*, and others. More rarely this (normally) upper side is only partly turned round; so that the odd notion is suggested, that the penis has the power of turning round on its long axis at the will of the insect.

It is also variously subject to curvature, often simply arched, with the tip downward, by the lengthening of the middle line dorsally—*Mayo*, *Rhodifer*, *Polycaon*; sometimes with the tip upward—*Pammon*, *Hesperas*; sometimes to either side—*Memnon*, *Vertumnus*, *Agesilans*; sometimes it is thrown into a double (sigmoid) curve—*Rhetenor*.

The form is ordinarily cylindrical and tubular—*Pammon*, *Zalmoxis*; sometimes spindle-shaped—*Podalirius*, *Agamemnon*; the upper (denser) line very frequently produced into a finger-like point—*Mayo*, *Nireus*, *Macedon*, of varying length. The extremities of the sides usually expand, so as to make a wide, very oblique trumpet-mouth—*Helenus*, *Erithonius*, *Ulysses*; and sometimes project beyond the general level into distinct lips, or a sort of prepuce, often corrugated—*Erechtheus*, *Mayo*. In *P. Semperi* the expanded orifice is of extraordinary dimensions.

In its structure the penis seems to be formed of two distinct tissues, often well defined. That side of the length which is normally the upper is a cylinder of more or less dense and polished chitine—*Hector*, *Podalirius*, which is lined by another tissue of soft, pulpy, white matter, of shining surface. The former is often (not always—*P. Sesostris*) divided along its underside throughout; and the white tissue then exceeds its bounds—*Hector*, *Macedon*, *Podalirius*; sometimes notably, *Codrus*. This white element has other very singular developments, for particulars of which I must refer to my detailed descriptions and figures, particularly the curious globe protruded from the wiry organ of *P. Doubledayi*, and the still more curious and thought-evoking cases of *Orn. Richmondia*, *Haliphron*, and *Darsius**.

The variety of position and direction assumed by this organ, as has just been described, seems to imply almost unlimited freedom of motion upon its basis. Yet, now and then, we discern surrounding and, as I presume, supporting and restraining ligatures. That the scaphium seems normally to send, inward and downward, fleshy branches, which, in certain cases—*Bathycles*, *Mayo*, *Agamemnon* (all which see for particulars), surround the penis, I have already mentioned. In *P. Erechtheus* a thick white ligament rises from the floor of the genital cavity, or from each of the chitinous knobs which afford interior bases to the harpes, and, thrown over the penis, not far from its tip, appear to bind it downward. But I have seen nothing like this elsewhere.

In *P. Doubledayi* and *Rhodifer* (and also, on De Haan's authority, in *Coon*) the long

* In the great Asiatic Moth, *Attacus Atlas*, where the organ has exactly the same form and position, I find, *during life*, that the terminal tissue, which fills the expansion, is very definitely separated from the brown chitinous wall of the tube; it is pellucid-white, soft, and pulpy.

wiry penis issues from a conical sheath, which closely envelops it, as if an organic part of it. This does not appear to be a process from the scaphium.

Finally there is that remarkable dividing wall, of hard, horny chitine, which I describe and figure in *Erithonius*, perforated in the middle, manifestly for the egress of the penis, yet which, strange to say, I have met with in no other species *.

THE PURPOSE OF THE STRUCTURAL VARIATIONS.

If it be asked, What is the definite purpose, in the economy of the creature, of this extreme variation? I am obliged to answer, I do not know. That, viewed in the large, the object of all these organs that crowd around the termination of the male abdomen is the firm grasp and sustained retention of the female abdomen, in the delicate and most essentially important function of reproduction, is sufficiently evident. But why the diversity of detail? Why would not one good and adequate form suffice, again, and again, and again, subject to no more variation than are the antennæ, for example, or the tarsi?

It naturally occurred to me, very early in these researches, that every peculiarity in the prehensile organs of the male would have a correspondent peculiarity in that part of the female body which they were formed to grasp; and I eagerly turned to the examination of the female abdomen. But the repeated search left, and still leaves, my question—*cui bono?*—without an answer.

The position of these organs, and their relation to the surrounding parts, when *in situ*, show indubitably that it is the *exterior* of the final segments of the female abdomen, that are seized *in coitu*. The harpes and the uncus are certainly not intruded *into* the female abdominal cavity. Thus the field of search is at once limited to the outer surface, from the very nature of things; and this is confirmed by the occasional clogging of the harpes with body-scales, as I have already noticed. It was then sufficient to denude the female abdomen of its clothing-scales, without disturbing the parts.

But though I did this with species after species, selecting those whose males have diversely-armed harpes, no solution of the inquiry was obtained. The females of *Papilio Thoas*, *Polydamas*, *Anchisiades*, *Heltenus*, are, as to the point in question, mutually

* The genital organs and their accessories have been minutely described and exquisitely figured in another Order of Insects. The question may be asked,—What homology (or analogy?) exists between the organs herein described by me and those of Trichoptera described by Mr. McLachlan? I have examined every figure in his great work, and confess that I know not how to institute any satisfactory comparison with those parts in *Papilio*. It is just possible that the “dorsal process,” in such forms as *Rhyacophila*, may be equivalent to my “uncus;” but of “scaphium” I see not a trace. Possibly, too, the “inferior appendages,” so largely developed in the same genus, may represent the “valves;” but the resemblance is most evanescent. The penis seems formed on a plan wholly different.

In one point my own observations agree with those of the learned author—the remarkable fact that no two species seem to have the same forms of armature.

My friend has been so kind as to send me his paper “On the Sexual Apparatus of the Male *Accentropus*” (Trans. Ent. Soc. 1872). Looking at his figures, I should have been inclined to say, if I had not been told, that they represented the parts of some *Papilio* or *Pieris*. We seem to have the valve (*a*), with its dorsal moiety, indeed, absorbed the tegumen projected into an uncus (*b* and *c*): and the scaphium (*d*, *e*) small, but normal in form, connected basally with the uncus, and bearing its usual lateral elevations, duly crowned with teeth or the characteristic aristæ. The parallel is most curious. I should expect some form of harpe lurking within those *appendices inferiores*.

undistinguishable. Under the microscope, the whole surface, after denudation, appears pitted with very minute shallow depressions, each with a knob at the bottom. They are arranged in transverse lines; and those of each line alternate with those of the lines preceding and following it, but this by no means with mathematical precision. These pits are well known as the receptacles of the clothing scales. Possibly, indeed, they may have a second use, even to afford hold for the saw-points of the male harpes; and the clogging scales, carried away by the latter, had been, no doubt, displaced by the saw-teeth in securing their grip-hold.

At the posterior margins of the seventh and eighth segments, these surface-pits appear closer together and larger than in other parts of the female abdomen.

The surface of the ninth segment, which consists of the valvules of the vulva, is peculiar—not clothed with scales, but cloth-like, being composed of hairs nearly erect, placed exceedingly close together, and, though very fine, so short as to be, in places, of a length not more than five or six times their thickness, as may be discerned when under the microscope we view the very edge of the rounded surface against the light.

Now, though it is not improbable that these last-named parts, the exteriors of the valvules of the vulva, may be the spots ordinarily grasped by the approaching harpe-tips, yet I can discern nothing in the nature of their surface, nor in that of the proximate surfaces, to distinguish one species from another—each surface, in one, exactly corresponding to the same surface in each of the other species, whose females I examined. And so there is nothing, so far as I yet know, to account for the astounding variety in the harpes of the males.

Yet, if I see a number of keys, of very minute and elaborate workmanship, all different, I cannot doubt that every one is intended to fit some special lock, though I have not examined the wards; and this conviction is the stronger, the more varied, and the more complex are the keys. We cannot withhold a hearty assent to the conclusion of one of the most eminent of modern physiologists, who, speaking of these organs in the class of insects generally, says, “They prevent allied species from producing bastards by adulterous connexions; for the hard parts of the male correspond so exactly with those of the female, that the organs of one species cannot fit those of another”*. And Léon Dufour speaks of them as “a guarantee of the conservation of types, and a safeguard for the legitimacy of species”†. But I should like to see these axioms demonstrated.

What anomalies remain to be discovered, I cannot guess by the closest scrutiny of the lovely wings spread out in our cabinets. The strangest deviation from normal form that has occurred to my notice, is the unvalved abdominal apparatus in the beautiful *Papilio Hector* of India. It is most aberrant; but what hint of this is conveyed by the gay body and wings? Who could conjecture, by looking over a cabinet, that *Ascalophus* and *Helenus* are so alike in their genital armature, while *Hector* and *Agaricus* are so unlike?

ON THE HARPE-TYPES.

As the harpe appears to be the leading organ in the prehensile apparatus, the most fully elaborated and the most varied, I attempt a grouping of the different forms of this

* Siebold, Comp. Anat. § 354, note 2.

† Ann. des Sci. Nat. i. (1844), p. 636.

organ. The result is an order of succession which, it must be confessed, sets at nought that which is founded on the form, neurulation, and colours of the wings. It is not proposed as, in any sense, a natural arrangement of the species, but as a help to reference and memory, and as a means of comparison of the varying conditions of this special organ. The groups themselves are loosely defined, and run into each other.

It must be recollected that the armature of only sixty-nine species, out of the four hundred and more described *Papilionæ*, is here recorded. A fuller examination will doubtless bridge-over many gaps, and supply other forms.

ORNITHOPTERA.

1. A broad arm ending in a bent spiniferous band.

Armana.
Protonotus.
Richmondia.

Haliphron.
Darsius.
Rhadamanthus.

Heliakon.
Heliakonoides.
Brookeana.

2. A long wire, springing from a square plate.

Amphrysus.

3. A small hollow shell, with toothed edges.

Remus.

PAPILIO.

4. A shaft with securiform head, and generally a tooth beneath.

Memnon.
Mayo.
Erechtheus.
Rhetenor.
Deiphontes.

Schmeltzi.
Polymnestor.
Protenor.
Ascalaphus.
Helenus.

Nephele.
Chaon.
Menestheus.
Pammon.
Agavus.

5. A sword with a saw-edge, or pointed, and set edgewise.

Machaon.
Areturus.

Merope.
Brutus.

6. A long two-pointed blade, not serrate.

Homerus.

7. A long pointed style, not serrate.

Ulysses.

Phorcus.

8. A broad thin plate, with thickened edges, especially the ventral; variously toothed.

Thoas.
Turnus.
Polycon.
Axion.
Hesperus.
Demoleus.

Bathycles.
Agamemnon.
Erithonius.
Anchisiades.
Vertumnus.

Sesostris.
Childreus.
Lysander.
Euryleon.
Ergetes.

9. The plate obliquely truncate, serrate, or running into broad points; with deviations.

Macedon.
Bromius.
Podalirius.

Laticellus.
Semper.
Lycidas.

Doubledayi.
Rhodifer.

10. The points produced into long styles.

Archesilaus.

Zalmoxis.

11. The plate complicate, sending off many laminae and points, often serrate.

Polieenes.

Agesilaus.

Codrus.

Ucalegon.

Parnatus.

12. Rotundo-triangular, with a spoon-like knob, usually studded with points.

Nireus.

Polydorus.

Hector.

Diphilus.

Antenor.

SPECIFIC DESCRIPTIONS.

ORNITHOPTERA ARRUANA, Feld. (Plate XXVI. figs. 1-3.)

In this grand butterfly the *valve* is of unusual size, measuring .3 inch in length, and .33 in breadth. Externally it is uniformly brilliant yellow; internally, rich velvety brown. Its outline is rotundo-triangular, with the dorsal side cut off obliquely at the basal moiety, and the ventral side correspondingly produced. The ventral margin is broad and flat, or rather slightly channelled: there is a projecting blunt tooth, about one third down this margin; and the whole is surrounded by a narrow fringe of hairs, blackish and dull on the dorsal, brassy and glittering on the ventral edge. The ventral margin forms a wide flat shelf throughout, before the level descends to the concavity.

At the very base of the valve begins an ample *harpe*, in the form of a broad plate of glittering chitine, narrowed slightly in the upper part, and then expanding into a spoon-like disk, of which the terminal edge is flat, oblique, and beset with minute black glittering, curved, acute spines, the points directed ventrally, arranged, inexactly, in transverse rows, of which there are about seven on the dorsal edge, diminishing to one before the ventral angle is quite reached*.

The *harpe* consists of two surfaces, as if a tube had been flattened; and, besides this, the upper surface is hollowed both immediately below the spined disk, and in the basal moiety. The terminal portion, about one fourth of the whole, is disconnected with the lining membrane of the valve, to which the remaining portion adheres; but the whole can be lifted, and separated from the valve by delicate manipulation, and placed on a glass slide for higher amplification. The component chitine is now seen to be quite transparent, of a rich yellow-brown colour, deeper at the edges, and specially at the extremity, where the spines are glittering deep black. All over the body of the *harpe* ramify many irregularly sinuous lines, like rivers in a map; and these, I found, by an accidental fracture of the structure, are not on the outside, but on the inside of the walls. When the valves are closed, the pair of spinous disks meet accurately at the very tip of the uncus, as may be seen with the left valve in Pl. XXVI. fig. 3.

The *uncus* is a wire of extreme slenderness, black, polished, very slightly curved, ending in a point, not sensibly dilated, not very acute; the basal portion of the upper surface bears a ridge of close, stiff, black hairs, which stand nearly upright.

* It must be remembered that, as in many other cases, this is the careful description of *an individual*; the minuter features may not be repeated in every example.

The *scaphium* is very difficult to understand without dissection, to which I have been reluctant to resort with so valuable a species, contenting myself with careful study of the parts *in situ*. It seems to me, after much consideration, that the scaphium proper is reduced to a slender "*boat*" running off to a point under the tip of the uncus to which it seems attached, above the triangular basal expansion, by fibrous processes on each side. I can see nothing answering to the ordinary "double teeth." The keel, on the other hand, seems to be unusually developed into the large bagging body which hangs below*.

In the lower part of the cavity is seen the *penis*—here a moderately thick column of polished brown chitine which projects almost horizontally from the abdomen to the edge of the valve, and terminates in a long drawn point, just before which it sends off two expanded foliations on the upper side (the organ being reversed), which are of thinner substance than the tube, and which face each other.

Towards the base of the genital cavity, projecting from one of the lower dilatations of the scaphium, I find, in the forms of this species, particularly distinct in *O. Richmondia*, two short sharp polished spines on each side of the penis, so placed that the four are in a line with it. I cannot suggest the use of them; their position seems to preclude prehension.

ORNITHOPTERA PRONOMUS, G. R. Gray. (Plate XXVI. fig. 1.)

The *harpe* is not distinguishable from that of *O. Arruana*, except that the armed disk is a little wider. In removing the valve, the harpe detached itself, together with a portion of the lining-membrane, so that I could lay it, quite alone, on a glass slide for the stage of the microscope. The black shining teeth are about fifty in number, arranged exactly as in *Arruana*, and interspersed with stout bristles or straight spines, all projecting at nearly a right angle to the plane of the stem. The teeth are some larger than others, irregularly crowded, decidedly curved, stout, pointed, black, glittering in the light; the chitinous substance of the disk and stem translucent, gall-yellow by the transmitted light, varying in depth of tint, according to the thickness, and, as I think, according to the density, of the material.

The *uncus* differs much from that of both the preceding and succeeding forms. It is rather short, not uniformly curved, but bent down near its middle with a kind of knee; it widens rather rapidly to the base; and the vertical rami, which I will call the *keel* of the uncus, increase in depth rapidly. The uncus is not wiry.

I could find not the least trace of a *scaphium*, in the single specimen that I examined.

The *penis*, reversed, was abruptly inclined from near the base downward; so that it lay in the very angle between the valves, and was so long that the tip was fully seen without, pointing obliquely towards the head of the insect. The expanse of the lips was empty to a considerable depth; the median line channelled beneath, as if the integument there were thin, and had contracted in drying.

* Since the above was written I have made examination of the specimen in another mode. Having softened the parts by moisture, I stretched them apart with needles, and thus satisfied myself that my explanation hazarded above is the true one.

The scaphium may have been accidentally lost ; but the peculiarities in the uncus and penis are considerable, and, if these prove to be constant, are good distinctions between this form and its fellows.

ORNITHOPTERA RICHMONDIA, G. R. Gray. (Plate XXVI. fig. 5.)

Here the *harpe* diverges from the preceding forms. The disk is considerably wider and shorter, without any sensible diminution into a neck, and it shows a distinct tendency to that form, which I have compared to an *open hand bent back from the wrist*, conspicuous in the black and yellow species of the genus, but which is scarcely seen in the Priamoid races. The teeth are crowded along the truncate extremity (the "fingers"), and within (on the "palm"), and more on one side than on the other ; but, whereas, in *Pronomus* and *Arruana*, the main crowding is at the left corner (as looked at), here, in *Richmondia*, it is at the right. The teeth, though minute, are seen, when viewed at the proper angle, to be curved, acute, glittering spines ; their number is about fifty.

The *uncus* and *scaphium* are as in *Arruana* ; but the former is somewhat more curved. The *penis* also agrees fairly ; but the expansion (in one examined) was much less corrugated, and had a broader, more truncate point. The organ was manifestly empty, as my lens reached for some distance up the interior. But another example was full, to swelling, throughout its whole length, on the inferior side, with the singular white pulp, which also had filled the expanded lips, and reached to some distance beyond. Moreover, as I had removed the valve from this example, with a slight jerk, there had been projected from it a compact shining white globule of this same matter, as large as a rape-seed, which I have every reason to believe had originally borne the same relation to the penis as the like knob represented in my illustration of *P. Doubledayi* in Pl. XXXII. fig. 18.

ORNITHOPTERA HALIPHON, Boisd. (Plate XXVI. figs. 6 & 7.)

Outline of *valve* rotundo-triangular, the sides much rounded, occasionally so as to approach the circular form. From the tip projects a minute horny point, which bends inward, towards the opposite valve. Interiorly, the margins slightly overlap, and the edges are sparsely set with short hairs. The concavity is smooth, not polished.

The *harpe* occupies the middle of the valve, and is a flattened tube (?) of rufous, transparent, highly polished chitine. It springs from a wide base, like the trunk of a tree, which, on one side, adheres to the base of the valve, and, on the other, to a stout angular projection at the bottom of the abdominal cavity. Thence it pursues the concavity of the valve, narrowing as it proceeds, adhering to the lining-membrane, and scarcely elevated above it, till about two thirds of the length of the valve are reached ; here the chitinous column is detached from the lining, and rises sensibly from it. It is here narrowed to a sort of neck, then abruptly widens to a broad ovate disk, studded all round its margin with stout sharp glittering teeth, fifteen or sixteen in number, all of which point inward when the valve is closed.

The armed disk is abruptly bent backward, and a little to one side. It may not inaptly be compared to an open hand, bent back upon the wrist of a naked arm, as far

as it will go, the upcurved fingers representing the hooked teeth, and supplemented by a ridge of teeth running obliquely across the wrist itself.

The *uncus*.—When the two valves are closed, as in life, the hand-like disks approach each other; and, between the facing rows of teeth, descends the point of the uncus. This organ is not so wiry as in the preceding species, but rather suggests the blade of a clasp-knife, projecting, with a wide triangular base, from the dorsal arch of the eighth abdominal segment, having a moderately curved upper edge, and ending in a sharp hooked point. What looks like the blade is truly the side of each of two vertical rami, which, supporting and strengthening the structure, pass off laterally into the walls of the segment. The whole is formed of hard horny chitine, dense in texture, dark in colour, and glittering in surface, even as are all the prehensile organs which form the subject of the present memoir. Sometimes the edge of the uncus-blade has a conspicuous notch; but the minuter details of all the organs are not absolutely identical in different examples of the same species. One example had a minute supernumerary point just under the proper point; in another, the triangular base, viewed vertically, was distinctly notched on each side, just where it narrowed to form the blade.

The *scaphium* is large and plicated, white, shining, firm, the keel always prominent, but in some more than in others. As in *O. Amphrysus* and *Rhodanocathus*, the rounded lobe on each side rises to a thin crest, divided into notches, each of which is crowned with an erect bristle, rising above the level of the uncus. The horizontal point of this lobe, somewhat condensed in texture, seems to represent the "double tooth" of other species. The median groove receives the blade of the uncus, as into a haft.

The *penis*, as usual in the genus, is large, and funnel-like at its extremity; in position it is reversed, the more chitinous side, which terminates in a finger-like point, being downward. In one specimen, this organ displayed a remarkable phenomenon (which, under modifications, has recurred to me since), which I cannot satisfactorily explain. Even the unaided eye could discern a thick white mass, connecting the trumpet-mouth of the penis with the inferior surface of the scaphium. I immediately introduced a drop of water into the genital cavity, and allowed it to stand awhile. I then removed, with absorbent paper, the superfluous moisture, and applied a considerable magnifying power. The appearance now presented, I have depicted with great care, in Pl. XXVI. fig. 7. A cylindrical column of soft, subgelatinous, milk-white substance, of a diameter slightly less than that of the expanse of the penis, had, apparently, risen vertically from the interior of this organ, till it had come into contact with the scaphium, against which it had flattened by the continued *vis à tergo*. The lower part of this column was tinged with the yellow-brown hue of the organ itself. The chitinous lips of the expansion seemed to have been forced wider apart—split, in short—by the protrusion; and, what seems to me very suggestive, certain lines of very pale chitine-colour, agreeing in form with the outlines of the chitinous lips, looked as if the lining membrane consisted of several coats, and as if these had been protruded, successively, one after another, as the white matter had been pushed out!

But, what is the nature, what the function, of this white jelly-like matter? Is it an integral part of the organ? Is it a secretion from it? Is it the semen, under novel

conditions? Its firm consistency, even when softened by the absorption of water, and its condition, when dry, of a firm, solid, shining white mass, seem inconsistent with such a conclusion. It may, possibly, not be without relevance, that the spinous disks of the harpes were, in this specimen, unusually clogged with meconium and scales, suggestive of a recent coitus at the period of capture.

But I would rather incline to seek analogy with cases, not very infrequent, in which the penis is manifestly separable into two longitudinal portions—a split tube of brown chitine, and a pulpy white mass occupying, and more than filling, it *. (See my figures of *Hector*, *Colrus*, *Agamemnon*, *Erithonius*, *Podalirius*.)

ORNITHOPTERA DARSIVS, Gray. (Plate XXVI. figs. 8–11.)

Valve almost exactly as in *O. Haliphron*, save that the terminal finger-point is a little longer, and spatulate. The interior has a rather wide space within the ventral margin, level with it, before it abruptly drops to the cavity.

The *harpe* also has a general resemblance, but is narrower, the disk more truncate, more excavate, furnished with eight or ten stout and sharp teeth, all marginal. Viewed sidewise (Pl. XXVI. fig. 10) it takes something of the form of the human arm and open hand, but less bent back upon the wrist.

Uncus, much as in *Haliphron*, viewed laterally; vertically, it is more slender, with a slight dilatation just behind the point.

Scaphium, ample, with a deep thin keel, quite white.

The *penis*, in the individual examined, again presented the very remarkable phenomenon which I have described in *Haliphron*. The organ was reversed, slender in the column, with a very ventricose, one-sided trumpet-mouth, that had apparently been split open by the extrusion of a great globose mass of the white substance. Here, as there, several successive laminae had, apparently, been thrust out, in various degrees, just as I have there represented, all showing definite angular points. The white substance, so much resembling the albumen of an egg coagulated, was, when I first looked at it, in contact with the scaphium. It absorbed water: after which I could easily, with a needle, detach minute portions for microscopic examination. These, diffused in a drop of water on a slip of glass, showed no trace of organization, but resolved themselves into irregular atoms of amorphous matter. Fig. 11, Pl. XXVI., represents this penis viewed nearly from the front, when most of the white matter had been removed.

This phenomenon, which has occurred in three distinct species of *Ornithoptera*, viz. *O. Richmondia*, *Haliphron* and *Darsius*, appears to me very curious and puzzling. I have assumed that the strange substance is extruded; but I am not sure. The splitting of the walls of the penis, or, at least, the forcing apart of what, if expansible and separable before, were normally closed, certainly suggests a thrusting-in from without, rather than a thrusting-out from within. Yet this would be, *a priori*, most unlikely. Whence should come the matter? Why should it be pushed into this organ, when it does not pervade and fill the surrounding parts? This thought must be dismissed; and the

* Dr. Burmeister (Man. Ent. 1836, p. 529) speaks of the *turgescence* of the organs of generation, *before and during* copulation.

appearance of the successive coats pushed out, one beyond the other, as well as the flattening and expanding of the white column against the bottom of the scaphium, in the *Haliphron* case, seems to me overwhelming evidence that the movement has been from within.

If we compare the penis as it appears in *Rhodamanthus*, *Amphrysus*, and *Arruana* (see the figures on Plates XXVI. and XXVII.) with the same organ in these three cases, or, better still, the penis in one specimen of *Haliphron* with the same in another, the one filled, and burst, with this white matter, the other normal in form, brown in hue, empty at the lips, without the slightest trace of white matter, the thought occurs that possibly we find here not specific differences, but only two interchangeable conditions. The shining, expansile, open and empty lips may give the ordinary passive condition; the white pulp pervading the tube (see *Hector*, Plate XXXIII. fig. 31), filling the orifice, and expanding it to overflowing, and even to a breaking of bounds, may give the condition when the "*furor igneus*" is raging—may be analogous (I do not say identical, seeing we have to do with bloodless invertebrata) with *erection* and *emission* in the higher vertebrata.

Observations carefully made, *in hac re*, in individuals taken *in coitu*, as well the female as the male, might be of great interest and value.

Supplementary Note to Ornithoptera Darsius.

The globule of white substance from *O. Richmondia*, I submitted to my friend Professor Gladstone, F.R.S., Pres. Chem. Soc., who has favoured me with the following report.

"On examining your little particle, I have obtained a more satisfactory result than I had anticipated. Though the piece of white excretion was no larger than a small pin's head, I have been able pretty well to determine its constitution. It was quite hard, but easily pulverizable, and consists mainly of earthy phosphate and some fatty or oily matter.

"The phosphate melts, when strongly heated, like the 'fusible phosphate' which is common in urinary calculi: but the quantity was so minute that I cannot say, with certainty, whether it contains *magnesia*, as well as *lime*; but my impression, from the chemical tests applied, is, that it does consist of both.

"There is a considerable proportion of *organic* matter mixed with this phosphate. Ether dissolves it out; and, on evaporation, it is obtained again in what, under the microscope, appears as oily drops.

"No trace of uric acid could be detected."

According to Léon Dufour and other anatomists, the urinary organs in insects "always consist of tubes which are inserted in the pylorus and terminate caecally. . . . The granular contents of these vessels . . . flow gradually into the digestive canal. Thus excreted they accumulate in the colon, and are evacuated with the faeces, or separately as a turbid fluid With the holometabolic Insecta, the urine is evacuated isolately when they approach the completion of their pupa state. It is well known that the Lepidoptera, when bursting from their pupæ, emit a considerable quantity of

urine, of a variable colour.” (Siebold’s Comp. Anat.—Burnett’s Transl. 1854, page 441 and note.)

If this statement is correct, the penis is never used for the evacuation of urine: urine being identified with that copious fluid which Dr. Burmeister compares to the *meconium*, and which I have had repeated occasion to mention in these pages. But the frequent recurrence of this white pulpy matter within the penis and manifestly ejected from it appears to show its normal, if occasional, connexion with this organ. I cannot help thinking of the thick white creamy substance, of an overpowering fetor, which I have seen copiously discharged from the cloaca of Serpents, which, however, is said to be the urine, “consisting mainly of uric acid” (Grant, Comp. Anat. p. 631). The oil-globules may possibly look to a changed condition of spermatozoa in residue of semen partly discharged from the organ, or to fatty degeneration of some tissue.

More recently, my kind friend Mr. Robert M. Lachlan, F.R.S., has favoured me with some correspondence on the subject. He mentions to me a fact, of which I was not before aware, that a mass of spermatozoa is sometimes “excluded by other insects in dying;” and this on the authority of the Rev. Alfred E. Eaton, M.A., whose words, in a letter to him, my friend thus quotes:—“*Oligoneuria rhenana* [a May-fly, common on the Rhine] discharges either spermatozoic paste, instead of spermatozoic liquid, or else discharges spermatozoic cysts. I have introduced, into plate iii. of my promised work, a figure of the lobes of the penis with the two threads of paste, or the tubules (as the case may be) like transparent vermicelli, partly extruded. But nothing has been published about this. In other *Ephemeridæ*, the matter ejected is fluid.”

The second of these alternatives is, I think, inadmissible. The matter is not contained in a *cyst*, if this term implies an enclosing wall, but always as a mass of paste, undefined, save by the cessation of its own substance.

Yet later, I had occasion to examine several examples of the noble *Papilio Gigon*, from Celebes. Within the expanded lip of the penis of one of these—protruding, but not extruded—there was a rounded mass of the dried white pulp, which also was seen filling the whole cylinder of the abnormally large organ. I easily detached an atom with a needle, and transferred it, with a drop of water, to the compressorium of a microscope (Powell’s), subjecting it to graduated pressure with a square of thin glass.

The appearance now was as of an infinite multitude of filaments, most unequal and irregular in thickness and direction, anastomosing (or else crossing) at various intervals, and enclosing excessively minute areas, having refractive power. At the edge, where it thinned off to nothing, these areas resolved themselves into minute flattened corpuscles of no definite form, but always with outlines irregularly sinuated, never angled or pointed. These corpuscles, closely appressed in the denser parts, made the bright interspaces, and their edges the darker network. Among them were a few yellowish molecules, larger and more opaque, irregularly roundish, of various sizes, and also a good many clear oil-globules, some few of which last were drawn out into slender tails, of the same substance.

I have taken great pains to be accurate in describing what I saw (under a $\frac{1}{8}$ -in. power); but I fear it is not very intelligible. I had never before examined spermatozoa that

had been dried; but the impression was strong on my mind that this was indeed the nature of what I was looking at. Thus Mr. Eaton's suggestion solves the problem: these discharged masses consist of paste mainly composed of *spermatozoa*.

ORNITHOPTERA RHADAMANTHUS, Boisd. (Plate XXVI. figs. 12-16.)

Valve much as in *Haliphron*. The *harpe* is separable (clean, and with ease) from the parchmenty skin which wholly lines the valve; the latter itself also separable in the dry state. It is a long narrow plate of shining, transparent, yellow chitine, not quite so much dilated at the base, with a cavity sunken in the middle of the basal half, having abrupt irregular edges. The extremity is slightly oblique, pointing dorsally as in *Haliphron*, but not in the least dilated, armed with eighteen stout curved teeth, all placed at the very edge, except two or three which are submarginal. There are also a few long black bristles, or spines, scattered over the surface.

The teeth, as in the allied species, project from the plane; hence, when the harpe is laid on the stage of the microscope (as at Pl. XXVI. fig. 14), an inadequate idea is formed of the power of the armature. When it is tilted, so as to be viewed edgewise, the teeth, which had looked like low cones, are seen to be strong and very acutely pointed semi-crescents, bearing a very close resemblance to the spines on the stem of a rose (see fig. 15, which represents the four teeth on the dorsal margin, viewed sidewise).

A second example had the form of the valve, and of the harpe, almost exactly the same; the teeth seventeen, with almost the very same arrangement, even to the trivial circumstance of two on the ventral curve being double.

In a third example*, the tip or disk of the harpe was a trifle longer, and decidedly bent back (like a hand from the wrist) towards the valve-cavity, the middle part of the arm being bent up to allow this, so that a longitudinal section of the harpe, viewed laterally in the plane of the valve, would assume this form (see woodcut).



Harpe of *O. Rhadamanthus*,
enlarged.

In the intra-abdominal apparatus there is a general agreement with the allied species. But the *uncus* is rather shorter and stouter, with a less graceful curve. The *scaphium* differs much, a difference better expressed by the figures than by words (see Pl. XXVI. figs. 12 and 16). There is a similar aristate crest on each side of the uncus, whose points rise above its level; and from the bottom of the lobe projects a long horizontal black tooth on each side. The scaphium-keel is unusually developed, projecting with a sinuous bend, and having a slightly expanded, corrugated point; its surface bears many irregular, but symmetrical prominences, hollows, and folds of the firm, shining, white tissue, which, here and there, deepens into brown or even black—indicative, I presume, of a more copious supply of the chitinous element to those parts.

* Often my observations have been limited to single examples of each species; wherever, as above, I have had opportunities of comparing other specimens, I gladly record the results. Their cumulative tendency is to show that the features of the prehensile organs, and especially of the harpe, are constant, and characteristic of species, not varying with individuals.

I have noticed that, in this species, when the valves are *in situ*, what I have compared to the wrists of the two harpes meet and close together some considerable distance beyond and above the point of the uncus. This latter, however, is then in actual contact with, or in very close proximity to, the stout spines that beset the ventral edges of the harpe-arms.

N.B.—My examinations and figures are all from specimens which agree minutely with Lucas's description of "*O. rhadamanthus*" (Lepid. Exot.; Paris, 1835, p. 5), called "*O. amphriscus*" in his plate ii. fig. 1, having, on the under side of the fore wing, the nervures and nervules conspicuously bordered with light grey.

ORNITHOPTERA HELIACON, Fabr. (Plate XXVII. figs. 1 & 2.)

Valve more regularly rhomboidal, terminating in a finger-point well formed and symmetrical. Exterior scale-clothing very thin and close, therefore projecting very slightly from the edges, mingled with a few short inconspicuous hairs. The level of the interior forms a narrow shelf as high as the margin on each side, and then descends abruptly to form the concavity. Lining-membrane dull, dark brown.

Harpe attached by a widely dilated base, whence it proceeds in an oblique direction, unusually close to the dorsal margin, and there, bending abruptly at nearly a right angle, projects more than half the length of its disk beyond the dorsal edge of the valve—a circumstance quite abnormal. The stem is nearly parallel-sided, narrower than usual, appearing to the eye as if a cylinder pressed nearly quite flat, with one of the sides wanting in the area of the disk, and at the lower half of the column. But, I think, this appearance is delusive, depending upon the fact that the plate of chitine is thickened irregularly in certain parts, and somewhat bent up at the edges. Disk (Pl. XXVII. fig. 2) wholly hollowed, with a very irregular cavity. The whole organ is glittering; the uneven surface reflecting points of light from every prominence; colour gall-yellow, both by reflected and transmitted light. It is armed with but eight teeth, all standing up around the edge; but the second and fourth, on the ventral side, are either double-pointed, or consist each of two teeth planted close together. All are shaped as in *O. rhadamanthus*. I detected no scattered bristles.

ORNITHOPTERA HELIACONOIDES, Moore.* (Plate XXVII. figs. 3 & 4.)

Valve almost exactly as in *Haliphron*, in outline; finger-point small, but varying in individuals; exterior well clad with white scales, which project as a close, even fringe of hair-scales very narrowly beyond the margins. Interior level, with a narrow shelf on the ventral margin: lining-membrane dull chestnut, or sooty brown.

The *harpe* has a strong general agreement with those of *Darsius* and *Heliacon*; yet two examples agreed *inter se* in points in which they disagreed with *Heliacon*. The terminal moiety is free; and the whole is easily detached with a fine knife-point. The disk is merely a portion bent dorsally, at nearly a right angle, but not reaching the margin of the valve: it does not narrow, is scarcely hollowed, scarcely thickened. It

* I give the name on the authority of Mr. A. Doncaster, of 36 Strand, who supplied me with specimens from Andaman Island. But it cannot be separated, even as a variety, from the preceding.

resembles a very flat spoon or slice, with the edges turned-up like a dish; there is no sensible thickening at the bend (or "wrist"), as is usual; the teeth are about fourteen, sharp and strong, varying in size *inter se*, standing up around the edge, and one or two within the edge. They are not black, as usual, but of a deeper tint of gall-yellow, proper to the chitine. The arrangement was not quite the same in the specimens; but a common pattern was quite discernible. The three behind the bend were much longer and slenderer than the rest, in each example.

Uncus moderately long, little decurved, of a shining red hue, indicating, like the paler colour in the teeth of the harpe, an inferior degree of density in the chitine; rather slender, the base small, the extremity subdigitate.

Scaphium large, long; keel abruptly deflected, much as in *Rhadamanthus*; the aristate lobe set nearer to the base.

Penis dark red, glittering; its extremity widely ventricose, one-sided, exactly as the organ in *Haliphron* and *Darsius* would be if not burst. By looking steadily into the expanded orifice, under a very good light, I could distinctly see that there was nothing in the throat but the wall of the organ, thick, indeed, and apparently composite, but pellucid. Not the slightest trace of the white pulpy matter was visible in any part.

ORNITHOPTERA BROOKEANA, Wallace. (Plate XXVII. figs. 5-8.)

Valve small, of peculiar form, almost circular, with irregular projections, having a marked resemblance to that of *O. Remus*, but still further removed from the normal form. There is no finger-point at the usual place; but a prominent one at a part of the margin diametrically opposite, viz. at the back of the dorsal margin very near the hinge*. The exterior is densely clad with minute scales of dead-black hue, which become a very wide fringe of dense brush-like hair all around the margin. The interior, which is very concave, almost hemispherical, with no submarginal shelves, is lined with a separable membrane, dull black.

Harpe of unwontedly large size, not only relatively, but actually; of peculiar form, broad, fiddle-shaped, concave, the extremity semicircular, expanded, slightly separated from the lining membrane, and bent up; set with about twenty-five very minute, irregular, black teeth, along its upturned edge.

The toothed margins of the opposing harpes converge upon the spot, within the genital cavity, where the hook of the uncus should be. But this ancillary organ is, in *O. Brookeana*, wholly aborted, the posterior edge of the dorsal arch of the eighth segment forming—instead of a projecting triangular point, = the *tegumen* of Dr. Buchanan White,—two rounded lobes, with a deep mesial notch between them (see fig. 10); while the middle of the outline, which ought, normally, to be prolonged into a curved wiry uncus, projects but a very shallow point, barely sufficient to fill the notch.

The *scaphium* is very large; the two lateral hemispherical lobes well developed—with the median furrow, along which the uncus usually passes—but no bounding crests of

* When the valves are shut, these two projecting points, one from each valve, fill up the blank left by the absence of the usual advancing rami of the uncus.

bristles, and no distinct "double teeth." Of the other constituent parts of this organ I must speak with a measure of doubt. In the first specimen of this noble species that I examined, the parts already mentioned were of a dirty drab or "whity-brown" hue; but below them descended what I supposed to be a symmetrical *keel*, of pearly white substance, pellucid, almost semitransparent; very firm, almost cartilaginous, in texture.

But was this, indeed, the *keel*? For, with a very slight touch it came away, and then seemed to be not an animal tissue at all, but amorphous substance.

And, in another specimen of this same species, the scaphium appeared of the form which I have with great care delineated in figs. 7 and 8. Here the keel, or what I identified as such, though of unusual shape and direction, was in the general plane of the organ, with an open expanded extremity, bounded on each side by an ovate knob, and carrying the usual lobes on its upper surface, without elevated crests of aristate points. Immediately beneath, and even in contact with it, but in *direct* position, was seen the trumpet-mouthed penis, with a horny finger-like tip.

The examination of this second specimen augmented my doubts of the nature of what I had seen in the first; and reminded me of what I have recorded in *Haliphron*, *Darsius*, &c. But whether what I saw in *Brookeana* was of the same nature, and, if so, whether it was an excretion from the penis, I have not yet sufficient light to determine.

N.B. In fig. 8, the left valve and its harpe are indicated in faint outline, to show that the point of the scaphium-keel came just within the serrated edges of the two closed and opposed harpes.

ORNITHOPTERA AMPHYRYSUS, Cram. (Plate XXVII. figs. 9-11.)

Valve pure white, on the golden-yellow abdomen; well-developed, large; form that of a semicircle, with the dorsal side cut away obliquely, terminating in a strongly projecting point. Both the margins are fringed with white hair-scales, the ventral narrowly, the dorsal very broadly and densely, its edge forming a right angle with a point in the middle. The finger-point of the valve is unusually large, and slightly incurved, so that, when the valves are *in situ*, the two points cross. I have no reason to believe that these points have prehensile power.

On removing a valve, I could find no trace of a *harpe*; and when—suspecting that this might be accidental, the result of a morbid atrophy—I carefully examined another specimen, in perfect condition, with well-formed abdomen, I still found nothing to break the uniformly concave surface of the valve. Only, at the base, near the dorsal side, there was, in each, a pear-shaped area, occupied by a multitude of very fine and close corrugations in parallel lines. But, afterward, when I was examining the uncus and its accompaniments, the mystery was solved. I observed a long black slender wire, incurved at the tip, projecting from the interior, nearly horizontally, below the scaphium; which I could not at all account for. Tracing this to its origin, I found that it belonged to that one of the valves that yet remained *in situ*; that the place of the corrugated area was normally occupied by a curved plate of polished brown chitine of trapezoidal figure, from the dorso-basal angle of which proceeded the long curved wire, of extreme tenuity throughout.

The two inner angles of the trapezoid were stout short points, rising free from the valve, and all of deep hue and glittering surface, indicative of great density.

This, then, is doubtless the *harpe*; and the reason why I had not found it in either of the separated valves is, that it is very readily detached from the lining-membrane; and so, when the valve is removed from the abdomen, it is apt to leave behind the harpe, which remains *in situ*. It is, indeed, widely different, both in form and position, from the organ, as I have found it in all the other species of *Ornithoptera* that I have examined; but it is probably very effective, as I hope to show.

The *uncus* is long, slender, wiry, horizontal, nearly straight, bent slightly down at the tip, proceeding from a very small triangular base. The *scaphium* is greatly developed, forming various folds, the usual white hue becoming brown, and even black in several places. Its "double tooth" is a long horizontal spine on each side of the uncus, with only a slight projection behind it; and, behind this, the upper edge of the scaphium rises above the level of the uncus, in several minute bristled points.

The *penis* is thick, enlarging to the extremity, which is truncate, with a corrugate expansion, and a terminal finger-point, which, as well as the denser, darker side of the column, is here placed below. It issues from a sheath formed by a descending fold of the scaphial tissues. Between it and the scaphium on each side projects the long wire of the harpe already alluded to. Though its position and direction, when in the valve, look awkward, yet, when viewed *in situ*, we see that, on each side, this acute elastic wire brings its curved point just below the spot where the similar wire of the uncus comes; so that the three points converge, and doubtless secure a very effective grasp of the female abdomen; though I must confess the scaphium appears to be very much in the way.

The *O. amphriscus* mentioned by Dr. De Haan (see p. 267, *suprà*) is certainly not this species; but appears to be the *Amphriscus* figured by Lucas (Lep. Exot.; pl. ii. fig. 1), which is the same as the preceding *O. rhadamanthus* of Boisduval (*ut suprâ*, p. 289).

ORNITHOPTERA REMUS, Fabr. (Plate XXVII. figs. 12-20.)

Valve transversely ovate; a small horny curved finger-point on the dorsal corner of the front edge, not quite constant, being sometimes reduced to a low prominence. There is another similar prominence somewhat more in front, which also varies in height. Little fringe is seen, and that only on the dorsal margin. The cavity is diminished by an obscure, wide, flat shelf, extending along the ventral slope, studded with minute bristles pointing inwards, and also by a curious large knob, at the dorso-anterior corner, very constant, which is followed, in front, very abruptly, by a deep sulcus. This knob is black, hirsute, often hoary, and lies immediately behind the finger. Occasionally, the valve, when detached, brings away a hollow, shell-like, triangular plate of chitine, which had formed part of its hinge.

Harpe an irregular rotundo-triangular shell, or ear-like body, of polished black chitine, broad, but unusually short, often not reaching halfway from the base to the point of the valve. Its edge is seen to be minutely serrate. When removed, and viewed on the stage of the microscope, very obliquely, so as to bring the free edge (the ventro-anterior edge)

into full square view (as in Pl. XXVII. fig. 13), the serration of the edge is seen to be very fine, and slightly irregular. Its base has a remarkable upturned lobe.

The form of this organ may be well imitated, and illustrated, by cutting a paper pattern into the shape of fig. 14, and rolling it into a tube, of which the dotted line is the longitudinal direction. If then it be pulled gently open, it will assume the exact curvature of the harpe. The long oblique point at the lower end of fig. 14 is, *in situ*, upcurved, and appressed to one of the flattened knobs which occupy the floor of the abdominal cavity. The expanse of the harpe resembles clear yellow glass, intensified into nearly black at the edges all round.

The *uncus* is of regular curvature, about one fourth of a circle, moderately slender, black, polished, coming down just between the two shell-like harpes. It is closely embraced by the lateral lobes of the *scaphium*, in which I see no bristle-bearing crest, and no "double teeth." But the upper edges are pilose, with short, stiff, close, shining hair, pointing towards the dorsal surface of the abdomen, as is usually the case with those species of *Ornithoptera* which have not aristate crests.

The *penis* is a moderately thick red-brown column, which protrudes from the midst of the eighth segment into the midst of the genital cavity, curving upward, nearly to the tip of the uncus. It is obliquely truncate at the point, where (in the specimen examined) there was what had the appearance of a *glaus*, surrounded by a preputial thickening. But this is, indeed, so much like the remarkable appearance described and figured in *O. Haliphron* (see p. 285 *supra*) that I am inclined to refer it to the same origin—as if the pulpy substance that (at times) occupies the interior of the penis had been forcibly pushed out from within, against the underside of the scaphium. Here, however, the walls of the penis had not been burst, as there; the orifice was not sensibly trumpet-mouthed; and there was no other trace discernible of the pulpy matter. The mass in question, moreover, instead of being white, was dull brown. Possibly, these features may indicate that the extrusion had not been very recent. The organ is reversed.

The two projecting knobs of hard polished chitine, which serve as ancillary supports for the bases of the valves and harpes, are large and conspicuous. The use of the knobs admitted of no doubt, as I, slowly and gradually, removed one of the valves*.

PAPILIO MEMNON, Linn. (Plate XXVIII. figs. 1–3.) [Cram. i. 91. c.—Borneo.]

Valve-outline ovate, obliquely truncate at base; edge narrowly turned-in, or forming a narrow shelf fringed with short spare hairs; interior floor smooth, but not polished.

Harpe, a narrow blade of dark polished chitine, which, springing from the base of the valve, runs close to the edge of the shelf, all along the ventral margin, to the very point, where it ends abruptly. This long blade may be compared to a knife affixed by its back to the lining membrane of the valve, but sloping inward, its free edge having several excavations in its outline; the organic adhesion of the lower edge is, moreover, lacking for the terminal fourth of its course.

This blade can, without much difficulty, be lifted out of the valve, the basal membrane yielding to force. The outline now can be more correctly perceived. At Pl. XXVIII.

* For further notes on this species see Appendix.

fig. 2, the longitudinal portion is shown, laterally, more magnified, and viewed as a transparent object on the stage of the microscope. It now appears still more like a knife-blade, of thin material, transparent, but of a deep yellow hue, the surface studded with numerous minute round eminences, each of which is surmounted by an erect bristle. The inferior, adhering edge, is thickened into a narrow rim, which is fringed with a row of close-set short hairs which grow in a direction across the blade. The free edge is notched into a number of minute saw-teeth, not quite uniform in size or distance. These serrations are seen only on the blade proper, the free terminal fourth.

The abdominal armature is normal, the *uncus*, the *scaphium*, and the *penis*, being all well developed and of ordinary proportions. When the valves are in place and closed, the tips of the two harpe-blades meet close to the tip of the uncus. The scaphial "double teeth" have this peculiarity: the inner (base-ward) member is obsolescent; the outer stands up quite perpendicular, a straight needle of polished horn. The penis has a broad expanded blunt extremity, which turns towards the right side. Fig. 3 shows these parts *in situ*, the right valve having been detached, the left and its harpe indicated in outline.

The continental form, marked by broad red ocelli with black pupils, more or less conspicuous, at the anal angle of the hind wings beneath, has been lately distinguished, even by such an experienced naturalist as Mr. Wallace, as a true species (Tr. Linn. Soc. xxv. p. 47); and Mr. Kirby gives it a specific place as *P. Agenor* (Syn. Cat. 552). But if any faith is due to the organs of which I am treating, the distinction cannot be maintained.

I examined a ♂, which agreed, in all essentials of form and marking, with Cramer's pl. xci. A, B, whose name of *P. Androgeos* Mr. Wallace would retain. But I can find no feature of valve, harpe, uncus, scaphium or penis, in which it differs to any appreciable degree from examples of *P. Memnon* received from Borneo.

PAPILIO MAYO, Moore. (A. D.) (Plate XXVIII. figs. 4-8.) *

Valve agrees closely with that of *P. Polymnestor*. So also does the *harpe*, as it lies *in situ*; perhaps still more with that of *P. Memnon*. But when lifted from the valve (which is done with readiness) and examined separately, there is considerable difference. The blade is not so regularly securiform, and the end is not so decidedly bent-over; the blade is rudely triangular, serrated with minute teeth all along its dorsal edge, and the greater portion of its broad end.

The *uncus* and its accompaniments are on the type which I have figured in *P. Memnon*. The *scaphium* is very well developed; and I take advantage of this to make a more careful examination of the organ.

If we compare the uncus to the upper mandible of a bird's head, we see a white fleshy body filling the place, and taking much of the form, of the lower mandible. In this

* For a few species examined, I have been dependent on loose abdomens, supplied by Mr. Arthur Doneaster, of 36 Strand, London, who has verified their names. These are indicated by the initials above.

species, as in many others, it takes a boat-shape, swelling into rounded sides, and narrowing abruptly in front.

If now with the point of a needle, we raise the upper mandible till we break it off by force, we see more clearly the upper surface and attachment of the scaphium. At the back of the "palate," there was an organic attachment of the scaphium, all across its width (see figs. 7 and 8), apparently perforate in the middle; and this perforation I take to be the anal orifice, though I have not been able to trace the connexion of it with the intestine. The middle and front are hollow and capacious; the edges (the "gunwales" of the boat) are high, broad, and flat; their summits crowned with what mimic true molar teeth. In the present species, the apparatus (on each side) consists of, first, a small acute, recurved tooth, with a secondary one by its side, nearly transverse to the (supposed) jaw (fig. 7), then a low conical point, and behind this a flat black mass, like a real grinder. The verisimilitude of these points to real teeth, and the organ which carries them to a real jaw, is wonderfully exact, especially as we cannot suppose any chewing-function to exist.

The back (*apparently*, but really fore) portion of the scaphium sends off, below, two rami of the same white flesh, which are soldered to the sides of the eighth segment, near the bottom, leaving a slender aperture through which the *penis* protrudes, whose sheath is, I think, made by, or united with, these rami (fig. 6). This organ comes forth pointing upwards, but then bends to a nearly right angle, and points obliquely downwards. It is flattened, and even guttered along its upper surface, and ends in a bifid point, dilating below into a broad membranous expansion, whose sides fold together, the inferior half of the column apparently the more densely chitinous.

The segment ends below in two large, blunt, extremely polished, hollow tooth-like knobs, placed close together, the inner supports of the harpes.

PAPILIO ERECHTHEUS, DONOV. (Plate XXVIII. figs. 9-13.)

Valve-outline an oblique triangle with swelling sides, or a pointed semi-oval; both margins fringed, the dorsal chiefly, the fringe running to an acute point: interior surface grey, dully shining; a narrow, deep channel runs through the ventral half of the cavity, which else is shallow.

Harpe a knife-like ridge of rich brown chitine, highly polished, affixed by one edge to the bottom of the channel, and running through the length of the valve, parallel to the ventral margin. It has a narrowly dilated base, a wide triangular tooth projecting from near the middle and leaning-over dorsally, and a wide hatchet-like head, which also leans-over. From the adherent edge, on the dorsal side, springs a line of close-set bristles having a golden lustre.

When the harpe is removed from the valve, and examined by transmitted light, both the median tooth and the head appear as thin plates of clear, sienna-brown glass, each brought to a keen edge, and cut into minute saw-teeth, not perfectly uniform. Both plates show dark irregular lines of corrugation meandering like map-rivers on their surfaces.

The *uncus* (figs. 11, 12) is the beak-like produced extremity of the eighth segment, which

takes conspicuously the form of a bird's skull. Ordinarily this part is clothed densely with the common scales and hair-scales; but, when denuded of these, it is seen to be smooth (not polished), thin, pellucid, light brown, composed of a very firm and bony chitine. There is no joint between the ventricose "skull" and the slender "beak," so that the latter can move only as the whole segment moves; but its acute point (as seen in figs. 12 and 13) falls normally just between the two terminal plates of the harpes when the valves are closed. The uncus is slender, wiry, dark brown, glittering, moderately curved, its tip slightly spatulate, its rami coming to a point horizontally and vertically at some distance short of the tip.

Scaphium essentially as in *P. Mayo*; but the sides are much less bulging, the keel not pointed, and the black knobs behind the erect "teeth" are replaced by tufts of crowded brown bristles, which much resemble those usually seen in the *Ornithoptera*, but are not, as there, limited to a linear series on each side. What in *Mayo* I compared to the gun-wales of a boat, are here flat triangular expansions.

The *penis* is short, with a thin expanded orifice, shrivelled, showing no apparent structure.

PAPILIO RHETENOR, Westwood. (Plate XXVIII. figs. 14-16.)

Valve of an outline resembling that of the outer half of a lemon, oblique, the ventral edge by much the longer; exteriorly dull black, thinly clad with scales; hair-scales projecting in a wide and close fringe beyond the dorsal margin, augmented by a forest of slender bristles springing from the interior, so that the actual edge of the valve is here much concealed, except in oblique lights. Along the ventral margin the fringe is thin, and composed almost wholly of bristles from the cavity.

The *harpe*, viewed *in situ*, Pl. XXVIII. fig. 14, is a long tubular rod of glittering chitine, terminating in an oblique hatchet-shaped head, facing the dorsal side, and set with strong bristles below. On carefully removing it from the valve, and changing the angle of vision, we find the head to be much of the form of an American woodman's axe, fig. 15. Its edge is of semioval outline; and, under increased magnifying power, is seen to be notched with teeth of excessive minuteness and of no great regularity, of which the three combined lenses of a specially powerful pocket-glass revealed no trace.

The *uncus* is nearly bill-shaped, with slight curvature, sharp-pointed, deep-bladed, the summit crowned with close, tall, erect hair-scales; the rami stout and broad.

Scaphium large, with a deep vertically truncate *keel*, wide margins, on which stand conspicuous "double teeth," the principal one of each pair being a tall recurved spine. The white fleshy rami of the keel descend to form an investing sheath, whence the *penis* protrudes to a great length, almost horizontally, yet in a sigmoid curve, terminating in a finger-point above, and a triangular expansion with thin edges, below.

PAPILIO DELPHONTES, Wall. (Plate XXVIII. figs. 17-19.)

Valve of the same form as in *P. Rhetenor*, *Protenor*, &c., but peculiar in having the cavity marked on both sides, towards the point, with a number of parallel ridges; both margins are broadly fringed.

The *harpe*, *in situ*, bears a close resemblance to that of *P. Polymnestor*, a slender

tubular rod, with a hatchet-shaped tip bent-over dorsally. But, separating it from the membrane of the valve (to which it adheres somewhat tenaciously), we find that the end, which stands obliquely erect from the plane of the valve, is broadly semicircular in outline, and that this outer edge is serrated with delicately formed but sufficiently strong spine-like, acute teeth (as seen in Pl. XXVIII. fig. 18.).

The *uncus* is long, slender, wiry, curved to one fourth of a circle, clothed along the median line of its summit with a ridge of erect black hairs, tall at the base and diminishing to nothing near the point; the point a small blunt spatula; the under surface a narrow keel of uniform depth.

Scaphium little developed in its white fleshy portion, but well in its horny armature; two black, shining, upcurved, stout teeth projecting from the extremity, each with a low conical knob behind it. Between these, the usual fleshy keel is represented by a narrow plate of shining brown chitine; and true keel there is none*.

The *penis*, of ordinary form and size, projects from the very bottom of the cavity, leaving a great vacant space between it and the scaphium.

PAPILIO SCHMELTZI, Herr.-Schäff. (A. D.) (Plate XXVIII. figs. 20-22.)

Valve rather small, pointed; the narrow hair-like black clothing-scales of the exterior projecting beyond the margins slightly and raggedly. Cavity shallow.

Harpe a chitinous ridge (or thin blade set edgewise) of rufous hue, which runs through the length of the valve (Pl. XXVIII. fig. 20, right valve) in a sigmoid line, not separable from it without tearing. It does not appear to dilate into a lining plate throughout its length. The base spreads like that of a tree-trunk. At the lower curve of the ridge is projected a stout triangular tooth; and the extremity dilates into a broad axe-shaped blade, somewhat thick, as if the axe were unfamiliar with the grindstone. The dorsal side of the ridge is fringed with a line of stiff hairs.

In these observations I have several times fancied a slight difference in the armature of the two valves of the same individual†. In this example it was quite manifest; for in the *left* valve (fig. 21), the sigmoid curve was very much slighter; the lower knob was more produced, and more decidedly a tooth, bent-over dorsally; and the securiform head differently shaped, itself approaching the form of a broad tooth; both projecting towards the dorsal side at an angle of about 45° with the floor of the cavity. There is, too, a secondary ridge, very evanescent, running down from the point toward the dorsal margin of the valve; and a third ridge, which seems not connected with the harpe, running through the length of the valve, centrally.

Up to this point my observation had left the impression that the machinery seemed inefficient in this species; the rounded outline and blunt edge of the "axe-head" seemed incapable of any seizing or holding function, like that of the sharp points with which I had become familiar in these elaborate harpes. But, on submitting it to an increased magnifying power, viz. of 110 diameters, the "axe" assumed a quite different aspect. Now the edge was seen to be studded closely (see fig. 22) with minute, acute,

* But this needs reexamination.

† See the Memoir by Messrs. Scudder and Burgess, on Asymmetry in the Hesperiadæ, in Proc. Boston Soc. Nat. Hist. for April, 1870.

curved teeth, which were also distributed for some distance from the edge, on the surface of the blade. Thus a resemblance is suggested with the harpe in *Ornithoptera* of the *Priamus* group, whose crowded glittering points make, doubtless, a sufficiently effective prehensile apparatus.

The *uncus* does not differ importantly from the same organ in *P. Erechtheus*. It is deeply channelled along its upper surface; and the channel, as well as the summit-ridge of dense black scales, very long and narrow, extends almost to the spatulate point. The white fleshy conical *scaphium* with the "double tooth" on each side, is as in *P. Demoleus*.

PAPILIO POLYMNESTOR, Cram. (Plate XXVII. figs. 23, 24.)

Valve long and narrow, blunt-pointed, semiovate, deeply concave; the margin sharp, not overarching in any part. The dull black scales of the exterior project ruggedly all round to a slight extent, and there is a crowd of slender hairs growing from the floor of the cavity, especially near the tip and the dorsal margin, most of which reach beyond the edge, but do not constitute a fringe.

The *harpe* is of the securiform type, yet with peculiarities of its own. The hollow between the head and the secondary tooth is here filled up, so as to form a long blade with a continuous even outline, which follows the curve of the ventral margin of the valve, and leans considerably inward. The very edge is, so to speak, bevelled off; and, at the lower end, where would be the secondary tooth in the most usual form, project from the very edge six (or seven, one being double) exceedingly minute saw-like teeth. These, as well as the whole plate, are highly polished; indeed, the glittering brightness and deep colour of these prehensile structures, generally, are most attractive features, and convey the idea of their almost metallic hardness. High magnifying power showed minute grey body-scales, still adhering to these teeth, and to the extreme point of the harpe—trophies, doubtless, of battles fought, *prælia Veneris*, in which these are effective weapons*.

PAPILIO PROTENOR, Cram. (Plate XXVIII. figs. 25, 26.)

The *valve* is of the ordinary form, margined by a broad fringe of hair-scales along the dorsal, but nearly bare on the ventral side. The latter has a flat ledge or shelf bordering the margin within, whence the cavity abruptly descends. A broad blade-like *harpe* pursues a corkscrew-like course, affixed by one edge, and running to a free point, the terminal half of the upper edge serrated with numerous, tall, close-set, curved teeth, even to the tip. Pl. XXVIII. fig. 25, shows the interior of the right valve with the harpe *in situ*; fig. 26, the harpe separated, viewed from the ventral side, and further magnified.

The abdominal armature agrees generally with that of *P. Rhetenor* and *Erechtheus*; the *uncus* and penis with the former specially.

* Professor Owen says (Comp. Anat. Invert. 1855, p. 397):—"The structure of the intromittent organ in the Lepidoptera is such as to preclude the repetition of the act; and they consequently live in a state of compulsory monogamy. The bifid hooks on the terminal segment of the dorsal valve of the penis, whilst they seem to retain the female, prevent the entire extraction of the virile organ."

I cannot reconcile this description with any thing I have seen in the Papilionide; and I strongly doubt the inference.

PAPILIO ASCALAPHUS, Boisd. (Plate XXVIII. figs. 27, 28.)

Valve having the outline of the terminal half of a lemon cut obliquely. Interior cavity very slightly fringed on the dorsal side alone, and that chiefly with hairs growing from within; amber brown with a dull satiny gloss. *Harpe* of the pattern of the *Memnon* group, near to that of *P. Deiphontes*; and, like that, serrated along the free erect edge, the form, however, differing in detail, as shown in the figures (27, *in situ* in the valve; 28, removed, viewed from the ventral side, and further magnified).

Uncus with a similar curve to that of *P. Deiphontes*, similarly clothed above, and similarly keeled; but not nearly so wiry, widening rapidly from the point. The *scaphium* is furnished with a thick white keel, whose descending rami behind—that combine to embrace the *penis*, as a sheath for its basal portion—are so short that this latter organ protrudes obliquely upward, its extremity appearing almost close beneath the scaphium-keel*. The “double tooth” is very small, but distinct, erect, and curved back.

I have not yet found any two species so closely assimilated in the details of the prehensile apparatus as *Deiphontes* and *Ascalaphus*; yet the differences here, if mostly minute, are quite distinct. The radiating ridges of the valve, the marginal fringes, the axe-head of the harpe, the scaphial keel, the scaphial double teeth, and the position and direction of the penis, all present marked diversities of form and detail.

I subsequently examined another specimen of *Ascalaphus*. It agreed with this one in the minutest details, except that the tiny half-separated lobe at the point of the harpe I could not find. This was, therefore, in all probability, accidental.

PAPILIO HELENUS, Linn. (Plate XXIX. figs. 1-3.)

We have in the *valve* of this species almost the very counterpart of *Ascalaphus*. The *harpe*, *in situ*, looks different, indeed, because the extremity is not bent-over quite so much, and the line of direction is more incurved in the middle. But, when it is viewed separately, and from the side, it takes almost precisely the same form, broadly crescentic; and its edge is, in like manner, serrated with excessively minute spines.

So the abdominal apparatus is of the same type. The *uncus*, circularly curved, is ridged above with stiff hair. The *scaphium* is almost exactly on the pattern of *P. Demoleus*; but the double tooth more developed, high, slender, acute, incurved. Finally, the *penis* has its more chitinous side uppermost, is dilated at the point, and is of considerable thickness and length.

Papilio Nephelus, Boisd., differs in nothing of importance. The *harpe* runs very close to the ventral margin, but its form is exactly that of *P. Ascalaphus*. *Scaphium* large, and its double teeth almost exactly as in *P. Helenus*.

Papilio Chaon, Westw., scarcely differs, but the *harpe* is not quite so close to the ventral margin.

* Subsequent observations lead me to doubt whether the *direction* of this organ is a character of specific value—whether it is not one of the conditions which vary at different times, even in the same individual.

PAPILIO MENESTHEUS, Drury. (Plate XXIX. figs. 4-6.)

Valve-outline a long, narrow, pointed arch, swelling on the dorsal, excavated on the ventral side; fringed with black bristly hairs around the point, which grow from within the margin, and disguise its form; the ventral margin, from the excavation downward, fringed with close-set long white hair-scales, connected with the clothing of the exterior.

The *harpe*, a slender curved rod of polished black chitine, running up close to the ventral margin, and following its outline; it sends off a strong, acute, conical spine about the middle, which is free, pointing to the dorsal base; in its terminal half, it expands into an ovate blade, convex ventrally, concave dorsally, standing on one edge, and having the free edge, as well as the spine, minutely serrate. Pl. XXIX. fig. 4 represents the right valve, with the *harpe in situ*; fig. 5, the *harpe* dis severed from the valve, viewed on the stage of the microscope as a transparent object. It is now wholly of a rich sienna-brown; the edge cut into curved spinous teeth, far more minute and far more numerous than I have been able to figure. The side, moreover, is marked with a multitude of fine slanting lines crowded together, which, by delicate manipulation of the magnifying power, resolve themselves into so many linear series of very minute pits on the surface, the edge of every one reflecting a semicircle of light.

The abdominal apparatus has much in common with that in *P. Deiphontes*, &c.; and the valvular armature may be resolved into the same type (fig. 6).

PAPILIO PAMMON, Linn. (Plate XXIX. figs. 7-9.)

The *valve* and the *harpe* belong to that general type which we see in the *Memnon* group, the former presenting little notable, the latter coming near to the forms in *Deiphontes* and *Ascalaphus*, especially when it is detached from the valve, as at Pl. XXIX. fig. 8; for, strange as it may seem, the outline of the *harpe*, when detached, is not always the same as when it was *in situ*. In this case, the disk, which takes a hatchet-form, occupies a much greater area of the valve (fig. 7) than in the species named; it is, as in them, of polished, pellucid, brown chitine, the edge serrated, rather unevenly, the whole stem (the haft) and a broad area at the back of the blade (shown at fig. 8) having been in contact with the floor of the valve, while the blade itself stood up free.

The *uncus* is slender, curved almost to a semicircle, with a small spathulate tip, a moderate vertical divaricate beam below, notched on each ramus, and the ridge crowned with erect hairs (fig. 9), which do not diminish in height to the tip, but end abruptly.

The *scaphium* is well developed, nearly free from lateral folds; the "double teeth" prominent, the principal one of the pair projecting obliquely towards the tip of the *uncus*: the fleshy keel thin, short, but very deep, ending in a minute point. The *penis* is long, moderately thick, truncate, scarcely expanded.

At the bottom of the abdominal area (fig. 9) is shown the nearer of the pair of prominent angular knobs, to which had been attached the triangular base of the *harpe*-shaft, and that of the right valve.

PAPILIO AGAVUS, Drury. (Plate XXIX. figs. 10-13.)

From a certain resemblance in the form and colours of this South-American butterfly to the Indian *P. Hector*—near which it is placed, in efforts made by entomologists to

arrange this vast genus in naturally allied groups—I expected to have here another example of abnormality, such as we see in the *Polydorus* group. But, except that the *uncus* is abruptly bent perpendicularly downwards, as it is in *P. Hector*, the organs are of the usual type, though peculiar in detail.

The *valve* is small, semioval, the outline slightly bulging dorsally and fringed only with a few very minute hairs. The interior is almost level for a wide space within the ventral margin, then abruptly descends with a deep cavity, which extends close to the dorsal margin; internal surface cloth-like, nearly black. Within this cavity lies a great semi-crescentic *harpe* of shining chitine, its lower half divided off into a kind of stem, the whole somewhat like a butcher's cleaver with its handle, and all springing from a dilated base by which it is affixed to the proper knob, within the bottom of the 8th segment, apparently distinct from, though in close proximity to, the conjunction of the valve itself with the segment. By removing the *harpe*, which is very readily separated, we see clearly (what is, indeed, discerned by the aid of a pocket-lens, even *in situ*) that the straight side, or what answers to the cutting-edge of the cleaver, is serrated with sharp teeth, somewhat irregular both in size and arrangement*.

The abdominal organs (fig. 13) are remarkable for the abrupt deflection of the *uncus* (perhaps accidental), the extreme minuteness of the *scaphium*, and the great development of the *penis*, which is reversed.

PAPILIO MACHAON, Linn. (Plate XXIX. figs. 11–16.)

In our own familiar Swallow-tail the *valve* is of the ordinary subtrigonal outline, with a rounded point. Externally it is clad with a close dense coat of pale-yellow scales, which do not project beyond either margin; there are, however, black hairs, growing from the interior, more than usually stout, long, and close, along the dorsal side, and forming a produced point. These crowded hairs, the whole cavity being of a sooty brown hue, effectually conceal the marginal line on that side.

A low pale ridge runs through the valve along its central line, which does not seem connected with the *harpe*. Just within the ventral margin, following its line from base to tip, runs a plate of glittering black chitine, fixed to the floor by one edge, while the other is free, and leans over towards the dorsal side. At mid-length its height abruptly increases; and thence to the point it is a keen knife-blade, only cut into minute sharp teeth, about a score in number, exactly like a saw. This *harpe* is of chitine so dense as to appear quite black, but transmitting a rich translucent golden-brown hue when viewed against the light, except a slender line just below the teeth, which is considerably paler, as if there were a band of less density just there, or possibly a groove, though it is not a place at which one would expect the structure to be weakened.

The shining chitinous material is spread widely over the valve-cavity as an exceedingly

* As a rule, I content myself with delineating one of the valves. But of *P. Aquens* I have given the left as well as the right. In the course of examination this left valve came away, leaving the *harpe* still attached to the segment. When I detached this, in turn, I observed what appeared an accessory piece behind the blade, and following a similar curve: this I delineated as I saw it, without understanding it (see fig. 12.) Replacing the *harpe* in the valve, I drew it, as I supposed, *in situ*, as at fig. 11; but, afterwards, having detached the right valve and its *harpe* entire, I saw nothing of this additional piece; I therefore conclude that it is a piece torn off accidentally from the back of the *harpe*.

attenuated plate. It adheres so tenaciously, that I did not succeed in separating it from the lining-membrane without much laceration.

Another example agreed minutely with this description. The only differences that I could detect were, that the valve was slightly narrower, and more acutely pointed, the outline being a nearly perfect isosceles triangle. The harpe extended to the very point of the valve; yet along its edge I could count only fourteen teeth.

The abdominal armature, in general, agrees with such examples as *P. Mayo*. The *uncus* (in the specimen figured) was long, narrow, the margins much elevated, displaying a deep keel, and was so strongly downcurved that the small, polished, spatulate tip was bent considerably within the perpendicular*. Its upper surface is partially concealed under a dense thatch of long arching hair, mingled black and yellow, which, springing from its basal part, projects far beyond its downward curve†.

The *scaphium* is of moderate dimensions, and of normal form, with a rather small keel. The lateral expansions, "gunwales," are wide, and are furnished with "double teeth," the principal of each pair being sufficiently conspicuous, projecting almost horizontally. There is a strong projecting point from each lateral edge of the *tegumen*.

The *penis* is moderately large, trumpet-mouthed, the expanded lips notched (corrugated?) along the edges, and surmounted by a short finger-point. Its protrusion from the abdomen is high, even so as sometimes to press the under side of the scaphium.

Fig. 16, the abdominal organs viewed from the right side with the right valve removed; the left *in situ*, shown in outline.

PAPILIO ARCTURUS, Westw. (A. D.) (Plate XXIX. figs. 17-19).

Valve-outline that of a Gothic arch, with the point rounded and the dorsal side a little hollowed; a wide fringe of coarse brown hair-scales along the dorsal margin. The cavity-floor has an abrupt depression along its middle, broad at the base, and tapering to the point.

Harpe a slender wire bounding this depression ventrally, rising at about two thirds of its length into a rather broad blade, the edge of which leans-over dorsally. More highly magnified, it is seen to be somewhat semioval in outline, curved at the tip into a strong hook, and beset, along its free edge, with a number (about forty-five) of minute close-set, sharp saw-teeth, the intervals between which run down in grooves upon the blade; in other words, the teeth are the extremities of ridges. The whole harpe can be separated from the valve only by tearing the adjacent portions of the lining-membrane, to which it appears to adhere organically, for almost its whole length. Some examples have the blade less irregular in form.

The abdominal organs are almost the counterpart of those in *P. Mayo*. The *uncus* presents nothing worthy of remark. The *scaphium* is scarcely distinguishable from

* But examples differ in this respect, the *uncus* being, in some, nearly horizontal at first, and abruptly and strongly curving toward the tip.

† The organ is perhaps unusually subject to malformation; for, in one example, its form and curve were quite asymmetrical, and it was accompanied by a supernumerary tooth, much like itself, but shorter, on its left side. Yet another example had a shapeless knob projecting from the right side of the *tegumen*.

what I have described and figured under that species, save that:—1. its keel has no minute point, but ends with a deep round thin edge; 2. the double tooth, instead of being followed by a flat black knob, has, in place of it, a second minute conical point, and clusters of bristles.

On my lifting the uncus till I broke it from the tegumen, I could see, by means of a lens, a distinct orifice. I studied it carefully, and am sure it was not a rent, but a true organic orifice, tubular, central in position, under the tegumen, with minute protrusile lips, which merged into the sides of the scaphial groove. This surely was the anus.

The keel, or "cutwater," runs off, as I have just said, to an extremely thin vertical plate. This I suspect to be the seat of some special function; for the terminal portion, for a considerable width from the edge, well-defined, has a peculiar surface, finely granular, almost pilose, whereas the other parts of the surface are shining, white, smooth, though plicate.

I am again struck with the wonderfully close resemblance which the scaphium and the uncus together bear to a bird's skull and beak, with a mammalian lower jaw.

The *penis* is of moderate size, pointing obliquely upward, with expanded lip, thin, transparent, corrugated. It proceeds from the midst of a white fleshy veil*, which occupies the entire back of the genital cavity, formed by the dilated rami of the scaphium†.

PAPILIO MEROPE, Cram. (*A. D. partim.*) (Plate XXIX. figs. 20–23.)

Valve subtrigonal, more or less regular; furnished with a fringe of thick, close, and fine hair-scales, of pale buff hue, which widens uniformly along each margin from base to point. Internal cavity dark brown, smooth but not polished, and beset with a few fine hairs.

Harpe a thin and very narrow lamina running through the whole length, near the ventral margin, and subparallel to it, affixed by its inferior edge, and leaning-over towards the dorsal side. It terminates sometimes in a fine-drawn point, which even extends beyond the limits of the valve, as far as the point of the fringe. At other times the blade is rounded at the end, and of equal width throughout from its abrupt expansion a little way above its base. The terminal third is free, and springs up at an acute angle from the lining-membrane. The whole blade is serrated with minute teeth, more than fifty in all, pointing backward. From the point where the stem dilates to form the blade, a curious finger-like process is given out, which goes nearly across the valve dorsally; it is straight, cylindrical, obtuse, and unarmed.

The *uncus* makes a curve of about a quadrant of a circle, ending in a very sharp spa-

* Equivalent to the "curtain" of the Supplementary Note to *Oenitoptera Remus*, p. 336, *infra*.

† By a subsequent observation of *P. Acteonus*, made under unusual advantages of sun-light, I am able to supplement the above description, but unfortunately not in time to add some figures to Plate XXIX. The scaphium has little resemblance to that of *P. Machaon* or *Zolicon*. It is a perfect boat in form, of what a sailor would call beautiful "lines;" apparently quite empty, save for the two great round-bottomed teeth, one on each side, which take the exact form of the boat-curve. The "cutwater" runs off in front straight and clean, its front edge sloping away downwards; though it is thin, it is immediately behind abruptly hollowed to a yet thinner lamina. The "gunwales" of the boat expand amidship, much like those of a paddle-wheel steamer (when viewed vertically from above), and then descend to unite with the wall of the abdominal cavity. The great scaphial teeth are stout upcurved spines, studded sparsely with minute hairs, while ridges behind and between them bear long, stout, erect bristles.

thulate point, and a deep angular keel. Its summit is crowned with an erect ridge of stiff hair, pointing slightly forward (fig. 23).

The *scaphium* is more than ordinarily developed, and it presents some peculiarities so suggestive that I bestowed upon it more than usual attention. The mass of flesh, of conspicuous whiteness, and glistening at all its prominences, occupies almost one third of the volume of the visible cavity. The keel is deep and ample, though thin; it is much excavated, the surfaces full of irregular hollows, with slender threads, and isthmuses of white connecting flesh stretching across; the hollows are more or less tinged with black, and of a minutely granular surface.

The "double teeth" attain here a development to which I have observed no parallel*. They are seated in the usual place, on the summit of a great rounded mass of polished flesh, which swells out on each side (fig. 22) from beneath the base of the tegumen, gradually becoming of a deeper and deeper hue, apparently more and more chitinous, until the colour merges into the glistening black of the teeth. Of these the principal—which one can scarcely help calling the anterior (though it is strictly the posterior), being next to the point of the uncus—is a broad, curved, acute *spoon*, cut on both its edges, and also *on its bowl*, with stout *serræ*. The other tooth, equally tall, but slenderer, curved in the same direction, viz. toward the base, is similarly serrated on several lines. The whole space between the two teeth is a continuation of the spoon-bowl, and is everywhere studded with sharp points. It is strange that most, if not all, of the serrations are surmounted each by a stiff golden bristle, which seems likely to interfere with their effectiveness†; but the number of pale-yellow body-scales clinging to all parts of these notched teeth show that they have done duty as prehensors. Certainly, viewed in sunlight under the compound microscope, they are formidable weapons to look at.

At its very base, where it springs from under the deep keel of the uncus, the scaphium forms a globose knob, skull-shaped, which is shining brown. But for this, and the tooth-knob, and the cavities of the keel, the whole scaphium is brilliantly white, reflecting the sunlight like the albumen of a boiled egg. The lower portions, both of cheeks and keel, run obliquely downward and abdomenward in strong longitudinal folds.

I know of no species in which the scaphium can be so effectively studied as this. Yet I am compelled to confess an humbling uncertainty of its function. I carefully dissected away the surrounding parts, and found this white organ to be firmly connected with the chitinous base of the uncus (that is, with the eighth segment), and, apparently, with a tube proceeding from the mass of convoluted yellow tubes which lie immediately behind, which I suppose to be the biliary vessels of the colon. The orifice, however, is, so far as I am able to judge, not at the extremity of this organ, as described by Herold (if this indeed is his *Triangelstück*, as I presume), but in the middle of the upper part of its very basis, where it is united with the uncus. Projecting thus between the uncus and the penis, we might call the scaphium a process from the perinæum.

* But see *P. Demoleus*, p. 313, *infra*.

† These great spoon-teeth are thus clearly identified with the aristate cheeks in *O. R. mus.* &c.

Whatever its office, I infer it to be, in part at least, muscular, from its so often carrying those remarkable weapons which I have called "double teeth." For, based on yielding and non-contractile tissue, they would be ineffective and useless; whereas their firm chitinous substance, their depth of colour, and their high polish, indicating hardness, and, as just described, their notched edges and acute points, all indicate vigorous and definite action, dependent on strong muscular contraction.

Nevertheless, I am bound to confess, the position of these weapons and their direction just under the uncus do not seem the most favourable for the only function which we can attribute to them, viz. copulative prehension.

The *penis* is a straight, nearly horizontal column of brown clear chitinous substance, moderately thick, not sensibly expanding, as usual, but rather diminishing to the extremity, and ending in a finger-like point and irregularly lobed lips. I carefully removed the walls of the abdominal segments, till I exposed the root of the cylindrical penis in a mass of muscular tissue, just at the insertion of the sixth segment.

PAPILIO BRUTUS, Fabr. (Plate XXIX. figs. 24, 25.)

The details that I have just been giving were from specimens labelled as having been taken at Calabar, in West Africa; and they agreed in markings, almost exactly, on both surfaces, with the *Merope* of Cramer's plate 378. D, E. But I have examples of a style of colouring that differs much from any that I have seen figured or described by authors. These two males, ticketed *P. Brutus*, I purchased from a small collection made at Ellongo, in Madagascar, are distinguished by having the black spot at the anal angle of the hind wing above *very small*, and the whole of the hind wing below, of a warm yellow-brown hue, with an undefined light dash across the middle, and scarcely any trace of the dark lines so conspicuous in the ordinary forms.

Now, in these Madagascar examples, the *harpe* takes a form very different from that in the continental *P. Merope*. The *valve* has much in common; and so has the harpe, *in its plan*; but the serrated portion, which is marked off by abrupt dilatation, is reduced to a small ovate blade at the very termination; and the projecting arm is placed close beneath it, is swollen in the middle, sinuately curved, and tapered to an acute point. The staff is very long and slender, cylindrical, pale, shining, bending from the base to the dorsal corner, sunken in a deep abrupt depression of the valve-cavity. The head or blade is free, a thin oval plate of polished black chitine, brought to an edge all round, and cut into strong saw-teeth, which are divided by grooves that run up into the area of the blade. Just at the point where it adheres to the lining-membrane, there is an angular expansion of the staff which sends off, nearly at a right angle, the polished taper arm, in quite a different plane from that of the blade; this is not serrated.

This long sharp spine, and its fellow, stretch away on either side of the uncus, when the valves are closed, and are doubtless effective prehensors; whereas the short, blunt arms, in *Merope*, placed so low down in the valves, one cannot well suppose to be of any prehensile power. On the other hand, in *Merope*, the extent of serrated blade is greatly superior.

The abdominal organs are the same, essentially, in both. For though, in one speci-

men, the *uncus* was aborted, leaving only a slight irregularly pointed projection from the *tegumen*, and in each the fleshy portions of the *scaphium* were partly gone, yet in one case the *uncus* was perfect; and in each one pair of the "double teeth" was left, and in one case, one of the other pair; allowing to me to see that their form and armature were exactly as I have described in *Merope*. In one example the entire soft parts of the scaphium were lacking (perhaps eaten by *Psoci*), leaving the central mass that supported the serrate teeth *merely as a thin transparent shell of horny chitine*.

I remarked that the abdominal cavity, in all the specimens that I examined, of both the forms, and all the included organs, even to the fringe of the valves, were much clogged with meconium and adhering body-scales, received, of course, from females.

PAPILIO HOMERUS, Fabr. (Plate XXX. figs. 1-4.)

The grand *P. Homerus* of Jamaica has a prehensile armature of much simplicity, but quite unlike that of any other known to me. The *valve* is somewhat long, with a rounded point bent-over towards the ventral side. It is dull, dark brown, clad with small scales interspersed with hairs, externally; internally it is simply hollowed, the scales scarcely protruding beyond the margin; but a crowd of very fine hairs spring from some distance within the margin, on both sides, and extend considerably beyond it.

The *harpe* consists of a simple rod of brown chitine, hollow throughout, very slender at the base, widening abruptly in the middle into a flattened blade, which terminates in two nearly straight points, of which the dorsal rises above the margin of the valve, and the ventral dives into the hollow. The chitine is darker and, I presume, denser in the vicinity of these points than elsewhere. The whole blade is sparsely beset with long slender bristles. The harpe runs in nearly a straight line along the middle of the valve, through its entire length; but adheres only by the slender portion.

The *uncus* is long and stout, but has only a moderate downward curvature, very regular and graceful, however; the keel, produced by the united *rami* or vertical supports of the sides, is deep. Viewed laterally, the *uncus* ends in a very sharp point; viewed posteriorly, it is a narrow, tapering spathula.

The *scaphium* is broadly boat-shaped, with little depth, and nothing that can distinctly be called a keel; the "double tooth" on each side is remarkably stout and strong, consisting of two conical cusps of shining brown chitine, united on a single basis, seated on an ovate expanse, or dilated lip. These are angular-sided; and the interior edge, especially of the hinder cusp, is beset with numerous short bristles, from which the extreme points are free. A supernumerary spinous tooth, polished, slender, acute, erect, rises from a knob situate centrally in the midst of the scaphial furrow, close to the extremity.

The *penis* is rather small and short, little protruded from the abdomen, chitinous brown, turgid at the extremity, hiant, not expanded, with no finger-point.

PAPILIO ULYSSES, Linn. (A. D.) (Plate XXX. figs. 5-8.)

Valve of more than ordinary dimensions; outline a long semioval, blunt-pointed, with a considerable sinuation on the dorsal side of the point. The black, coarse hair-scales of the exterior project notably along the dorsal margin, and around the tip,

where they are longest; then suddenly cease, giving place to a series of very fine shining hairs, which spring from the cavity, within the ventral margin, and reach beyond it. The whole valve-floor, which is of a bright brown hue and has a velvety texture, is more or less studded with gilded hairs.

The *harpe* is a slender rod, black and polished throughout, affixed to the lining-membrane, parallel with the ventral margin nearly to the valve-tip; then it makes a sudden bend, and projects as a curved acute spine-like point as far as the ends of the dorsal margin-scales. From the bend onward the rod becomes free, springing from the cavity-floor, but proceeding laterally, nearly in its plane, the taper point describing a full semicircle, curving at last quite upward. It is a simple polished wire, densely set along its inner side with long shining hairs, but quite void of serration in every part.

The abdominal organs present some peculiarities of form. The *uncus* is unusually broad and short, taking the shape of a very wide but pointed spoon-bowl, clothed almost to its termination with coarse, brown body-scales, among which individual blue scales gleam like tiny sapphires.

The *scaphium* is of moderate size, its most conspicuous feature being the lateral teeth. The ridge, or cheek, on each side carries a stout and strong spine of polished black chitine, which projects horizontally forward at first, and then bends up at the point, the secondary tooth being represented by a low conical knob at the base. The whole tooth is beset with long bristles, especially about the middle; but immediately in the vicinity of the point these are very few and minute. High magnifying power shows (fig. 8) that, as in *P. Merope*, the scaphial teeth are themselves toothed; but here the notching is shallow, and the minute bristles, instead of being seated on the summits of the toothlets, are sunk in the interstitial angles.

The *penis* is moderately large and protrusile, bending upward and outward its column of brown translucent chitine, and terminating in a dilated, but not expanding, orifice.

PAPILIO PHORCAS, Cram. (Plate XXX. fig. 9.)

Valve small, but comparatively long and narrow, and slightly fringed.

Harpe of the very simplest form, a mere narrow rod-like elevation of the chitine, running, in a slightly bent line, throughout the length of the valve, and terminating in a fine smooth point, which protrudes even a little beyond the fringing hair-scales. The whole rod is of polished dark brown chitine. (Pl. XXX. fig. 9.)

Uncus well developed, long, slender, curved into a nearly complete semicircle. The adjacent parts present nothing calling for special notice.

Here is a very close ally of *P. Nireus*, a West-African species (the specimen labelled as captured at Accra), yet widely differing from both it and its nearer compatriot *P. Brenius*, in the form of the genital armature. It approaches the Oriental *P. Ulysses* and *P. Arcturus* in the form of the harpe, but exceeds both in simplicity.

PAPILIO THOAS, Linn. (Plate XXX. figs. 10, 11.)

In this noble American butterfly, so abundantly found from Virginia to La Plata, we have a new type of valval armature. The outline of the *valve* is rotundo-triangular,

moderately regular, the ventral side the longer, the whole margin broadly and pretty evenly fringed.

The *harpe* consists of a very thin crystalline plate of chitine, which sits close upon the central cavity of the valve. It is thickened on each side into two slender ridges, black, polished, wire-like, which, springing from a wide basis, proceed in curving lines, and meet in an acute point a little on the dorsal side of the extremity of the valve. The extreme point separates from the lining-membrane, and projects at a very acute angle, firm and hard, like the point of a needle. Under a high power the ventral side of the point is seen to be notched into half a dozen minute saw-teeth: the whole triangular hollow plate may be, with care, lifted uninjured from the valve; it is then of a glassy transparency and polish, slightly tinged with brown, like glass very slightly smoked; very slender veins issue from various points of the deep-black thickened marginal walls, and ramify over the clear surface.

The abdominal armature of the first specimen I examined, seemed to be peculiar. A deep, but short, *uncus* was seen descending perpendicularly and abruptly from the tegumen, with almost no curvature at all, the upper surface hollow, from the turning-up of the lateral edges, the tip slightly spatulate.

The *scaphium* was with difficulty recognizable, wide, shallow, and so short as scarcely to reach the vertical uncus.

But a second example proved that this condition of the organs was a case of accidental distortion, not very rare. The uncus now was normal in length and curvature, wide, with a small spatulate point, followed almost immediately, in full depth, by a deep and strong radial keel. (Pl. XXX. fig. 11.)

The scaphium is on the same pattern as in *P. Mayo*, still more closely like that of *P. Helenus*, both the lateral teeth being very stout, long, acute, dark, and polished. The hinder tooth is rather a high conical incurved point on the thin shelly edge of the cheek, whose summit bears a crest of small erect aristæ. The edges are simple, not serrate. Viewed from above, the cheeks take a subglobular, inflated form, and both the teeth of the right side slope-over towards the median line of the uncus. The keel of the scaphium is large but shallow, polished ivory-white, strongly defined in colour from the cheeks. Its form is very boat-like, projecting its point horizontally; the extreme point is minutely complicate in surface, and diverse in colour and appearance from the contiguous parts.

The *penis* presents little noteworthy; it is of moderate dimensions, a tube apparently subcylindrical, but slightly enlarging to the tip, which ends in a lengthened curved acute finger-point.

PAPILIO TURNUS, Linn. (Plate XXX. figs. 12-15.)

Valve very regular in form, of the outline of a Gothic arch, the dorsal margin concealed under long shaggy black hair, springing from within, and projecting far beyond, the edge; the ventral margin is also hairy, but less conspicuously. A flat shelf runs all round, broadest at the extremity, within which the cavity abruptly deepens.

Harpe of the *Thoas* pattern, consisting apparently of a dark shining wire, running up on each side, and meeting in an arch towards the tip. In reality, these are but the thickened edges of a continuous plate of chitine, of extreme delicacy and glassy trans-

parency, which occupies the central area of the valve. Each wiry edge is armed with a prehensor; the ventral edge, a little beyond its middle, bears a long acute spine, which stands up from it, and curves obliquely forwards; the dorsal, a thicker cone, more erect on its base, which first sends off a nearly straight horizontal spine obliquely forwards, and then terminates in a shorter and blunter point.

The *uncus* arches in a regular semicircular curve to a small spatulate point; a deep keel beneath the receding rami: between which issues the moderately large *scaphium*, well keeled, the only peculiarity noticed being that the extremity of the keel, by its deepening hue, appears to become more chitinous, until it ends in a minute horny point. The double teeth are minute, but distinct, conical points.

The *penis* is small and high-situate.

PAPILIO POLYCAON, Cram. (Plate XXX. figs. 16-19.)

Valve-outline subrhomboidal, with rounded angles, thickly fringed on the dorsal (short) side, but thinly on other parts.

Harpe a broad, concave plate of thin, clear, shining chitine, beset with fine, short bristles, pointing outward, as is also the lining-membrane where it is exposed. The ventral edge of this plate is a slender nearly straight rod, polished, black, with a fine-drawn acute point, free for some distance. The upper edge of the thin plate usually springs from the spine a short distance down, and rises into a wide curve; sometimes it follows the spine up to its point, and descends at an acute angle; but presently, on what I may call its dorsal corner, it gives rise to a curious appendage, which usually takes the form of a thick, short, solid column of black chitine, set, all round its summit, with stiff tooth-like spines (fig. 18); but sometimes appears as a smaller knob, with a slender base, whence rise three diverging laminae, united by their inner, and serrate on their outer edges (fig. 17). In either form, the spines are of a clear, glassy, blue-black substance, and most of them are double, *i. e.* each has two points from the same base. The spinous rod of the ventral edge bears a triangular thin elevation (and sometimes a secondary one) near the base.

The *uncus* is long, slender, evenly curved, acute; the keel of its united vertical rami deep, and diminishing in depth gradually to the tip.

The *scaphium* is very ample in all its constituent parts; the cheeks rise into high arching crests, with notched, aristate edges, but destitute of double teeth, so far as I can discern; the sides run down on either hand in great oblique folds; the keel is pointed, large, and deep; all the parts are shining white. The *penis* presented no features worthy of special notice, other than can be observed in the figures.

In my cabinet are examples of six very diverse kinds of butterflies, all large, imposing, and richly coloured, labelled thus:—*Androgeos*, Cram., ♂ and ♀, from Brazil; *Thersites*, Fabr., ♂ and ♀, from Jamaica; *Polycaon*, Cram., ♂, and *Lycophron*, Hübn., ♀, from Corrientes, in the Argentine Republic*.

* These may be readily distinguished thus:—Males: 1, hind wings with no yellow lunules=*Androgeos*; 2, with shallow yellow lunules=*Thersites*; 3, with deep yellow lunules=*Polycaon*. Females: 1, fore wings with a broad straight yellow bar across=*Androgeos*; 2, with a narrow curved yellow band across=*Thersites*; 3, no yellow band across=*Lycophron*, *i. e.* *Polycaon* ♀. I describe from my own specimens, which differ from Cramer's figures. But what I call *Polycaon* may possibly be the *Ochalius* of Boisduval (Sp. Gén. p. 360), with whose description they fairly agree, except that I see no trace of the "red-brown lunules" that he assigns to the hind wings above.

Now the genital armature, in these widely severed forms, is essentially the same. Of that from Jamaica, and that from Corrientes, I have received a considerable number of examples, taken at different times by my own friends; so that I am sure of the habitats. The Jamaican specimens have the isolate knob of the harpe three-sided or concave, the main spine slightly curved, and with but one baseward elevation. The *Androgeos* from Brazil, and several *Polycæons* from Corrientes, show absolutely no difference *inter se*. The characters are constant, so far as my experience goes.

The precision with which this very peculiar harpe is repeated in these widely spread varieties is something noteworthy. It suggests the notion that, in this organ, we have a specific character of much value. *Androgeos*, *Thersites*, *Polycæon*, and *Lycophron*, are assuredly but a single species.

PAPILIO AXION, Boisd. (A. D.) (Plate XXX. fig. 20.)

The armature of this noble butterfly is remarkable. The *valve* is almost as large as that of an *Ornithoptera*, and of similar shape, viz. semioval, or of the outline of a half lemon cut obliquely, the dorsal side by far the shorter, as usual. Exteriously, the valve is clad with dull white scales, which become black at the dorsal edge, and these project pretty evenly beyond the margins. Interiorly, it is umber-brown, with a dull gloss.

From one specimen, on removing a valve for examination, the whole cavity was found quite full of a light brown dust, composed of amorphous fragments (of *meconium*, surely), together with a considerable number of fine hair-like scales, such as are proper to the hinder regions, gathered, I doubt not, from the body of the female during an act of coition.

The *harpe* belongs to the pattern of *Thoas* and *Turnus*. It is an ample plate of thin glassy chitine, which closely lines the greater part of the entire cavity; yet can be easily separated from it, in its integrity, when it is a curious and attractive object. It is a broad hollow plate, of exquisite delicacy and tenuity, translucent, slightly tinged with horn-yellow, the extreme edge, all round, thickened and deepened in colour, polished, and furnished at two points with two long, taper, curved, acute spines, much resembling the prickles of a rose in form, colour, and polish. Both are on the ventral margin, the one just below the apex of the valve being the proper prehensor, laterally opposable, conjoined with its fellow in the other valve, to the uncus. Besides these spines, there are several minuter ones on the dorsal edge, the chitine rising here into a thin wall, which is cut into teeth, three or four, the number and arrangement being not quite the same in two individuals that I examined. The form of the whole harpe varies also; for while, in the specimen figured, which was the first I examined, the apical arch was somewhat flattened (as represented), in a subsequent example the outline was much more graceful, more nearly corresponding to that of the valve, and so more closely resembled the form in *Thoas* and *Turnus*.

The *penis* appears to be small, short, and curved into a semicircle; but it was so closely enveloped in its ligaments, that I could not very satisfactorily examine it.

The *uncus* with its concomitant parts presented nothing specially notable.

PAPILIO HESPERUS, Westw. (Plate XXX. figs. 21-24.)

Valve of the outline of a Gothic arch obliquely cut off at base, wholly surrounded by a dense and wide fringe of grey-brown hair-scales, densest and widest at and around the tip. Interior surrounded by a wide flat shelf, within which the cavity abruptly descends, and is deep.

The *harpe* occupies the whole of this deep area, and fits it accurately with a chitinous hollow plate of extreme delicacy and transparency, thickening and darkening all round into a narrow edge, which stands up free, like a little wall, the summit rising into rounded eminences here and there (Pl. XXX. fig. 21). The structure could not be detached in integrity; the ventral portion of the circuit is represented at fig. 22, viewed from the ventral side. It is now seen that the free edge is cut into saw-teeth, and these by no means simple, but elaborately compound, each tooth, at least for a considerable portion of the edge, being itself cut into three, or even four toothlets, and each of these compound teeth being the termination of a rounded curved ridge on the outer surface of the wall. I have found no structure elsewhere quite analogous to this. Fig. 23 represents some of the teeth on a more enlarged scale.

The abdominal apparatus is of the ordinary type; the *uncus* is moderately long, inclining downwards, nearly straight, crowned with a ridge of stiff erect hairs, deeply keeled. *Scaphium* moderate, double teeth strongly developed, erect, incurved, acute. *Penis* doubly curved, finger-pointed, moderately thick, and so long as to project horizontally between the valves when these are closed.

PAPILIO DEMOLEUS, Linn. (Plate XXX. figs. 25-27.)

Valve-outline an oblique semiovoid; exteriorly clad with a coat of drab-white, short scales, which project in a very slight fringe just around the extremity. Interiorly the surface smooth, but not shining; the cavity rather narrow, running to a point, bounded by a broad flat shelf on each side, of which the dorsal extends only half down, the ventral the whole length.

Harpe a broad thin plate of yellow transparent chitine, not very concave, reaching to within two thirds of the valve's length; its ventral edge an elevated ridge, apparently tubular, with an expanded base; the ridge, like a clear glass tube, is marked, at short intervals, by ten or twelve distinct black transverse lines, suggesting joints, or rings of metal binding a pipe for increased strength. Close to, but not quite at, the extremity of this ridge, which diminishes to a thin scalpel-like edge, there is a single minute black tooth projecting obliquely towards the dorsal side, the upper edge of which, in the specimen examined, showed a few minute notches, possibly accidental. The area of the harpe is corrugated into fine ramifying wrinkles, and studded with very minute circular areolæ (pits?), from each of which springs a hair, varying in fineness. The lining-membrane of the valve is similarly studded, the areolæ and hairs specially crowded toward the point. The fringing hairs (hair-scales) are in the same plane as the valve-surface; these perpendicular to it. Besides these hairs, there lie, about the area of the harpe, many body-scales, of varying forms, which, derived doubtless from the other sex, usefully illustrate the function of this organ.

The abdominal apparatus is normal, and well developed. The *uncus* is moderately long, well curved, slender to the tegumen, terminating in a minute spathula; the keel, reaching to the point, is moderately deep, the edges not upturned.

Scaphium of the pattern seen in *P. Merope*. Its keel is more produced, and of less irregular surface. Its "double teeth" are not quite so much developed, particularly the secondary one of each pair, which is little more than a conic knob, both, however, set with prominences and bristles as in that species, though in a less degree.

Penis of moderate length and thickness, increasing to the extremity, which is truncate, blunt, without lateral expansions.

PAPILIO BATHYCLES, Zink. (Plate XXXI. figs. 1-5.)

Here are very abnormal structures.

The *valve* is small, short, almost semicircular, widely fringed with dense white hair-scales. The *harpe* is a broad segment of a sphere, of glassy chitine, thickened at the two margins, and rising at the summit into two divaricating branches, each of which, the dorsal especially, is studded with short stiff blunt teeth; on the dorsal edge, near the base, there is also a conical process. Parts of the surface are beset with fine scattered bristles.

There is no *uncus* proper. The regions are sheltered by a dense horizontal thatch of long white hair-scales. When these are removed (by the persevering friction of a camel's-hair pencil cut short), we get an instructive sight of the organs. The median line of the eighth segment projects into a very shallow point, from under which a well-formed white *scaphium* is moderately developed. At fig. 3 is shown the transverse terminal line of the eighth segment, and a vertical view of the scaphium; the lip-like lateral edges bear no trace of the ordinary "double teeth." At fig. 4 is given a lateral view of the organs. The vertical dotted line shows where the lateral edge of the dorsal arch of the eighth segment falls normally; but this has been removed, so that we can still follow the outline of the scaphium somewhat further into the abdomen. The median line of the arch is supposed to be retained, forming the roof of the cavity; and to this we perceive the scaphium is organically attached, descending from it in a great angular heel, in the free interior, and projecting, in the familiar form, from beneath and within the spreading rami of the uncus, where this is (as is usually the case) present. From the median part of its inferior surface there descend membranous laminae of irregular shape, perforated to allow the exit of the penis. Here this organ, seen *in situ* at fig. 4, and its tip, more magnified, at fig. 5, is of great length. It appears to be invested with a thin glistening membrane, but only partially throughout its length, expanding and dilating near the tip, which, furnished with a minute finger-like point, is free. In the normal condition it protrudes far beyond the limits of the closed valves.

Thus every one of the organs is remarkable. The valve, the harpe, the uncus (absent), the scaphium, the penis, all present something unusual. The very simplicity of the scaphium, its lack of teeth, spines, or bristles, seems to deny the "reason of its being."

PAPILIO AGAMEMNON, Linn. (Plate XXXI. figs. 6-8.)

Valve small, short, rotundo-triangular, fringed with long hairs, not very dense. There is a broad, flat shelf, going nearly all round, except at the base: this shelf is beset with stout but short hairs, which bend over the inner edge; and the very edge itself is fringed with short stiff bristles, almost like spines.

At the base of the cavity lies the *harpe*, a shallow cup of chitine, thickened around the edge, and slightly free; on its dorsal side it rises into a tooth-like lobe of thin but dark brown chitine, of rotundo-triangular outline, which does not appear to be serrated (Pl. XXXI. fig. 6).

The circumference of the abdominal cavity is densely set with projecting hair-scales, which in particular rise from the summit of the ultimate segment to its very point, and then, arching forward, form a long horizontal thatch. When these hairs are detached (as, in part, at fig. 7), the point, ordinarily the *uncus*, is seen to be short and slightly bent upward, and, viewed vertically (as at fig. 8), to be truncate, and even very slightly bifid at the tip. Below, there is a well-formed but very small *scaphium*, with no armature; and then a *penis* of much slenderness, and so long that its point protrudes from between the valves, when these are closed. The chitinous portion is downward, ends in a point of great tenuity, and forms an imperfect tube with arching edges above, within which, prominent near the tip, is a pulpy white tissue. The sheath of laminae descending from the scaphium is conspicuous and shaped like an elegantly pointed leaf on each side, united below.

PAPILIO ERITHONIUS, Cram. (Plate XXXI. figs. 9-12.)

Valve of an outline somewhat trapezoidal, with the angles rounded, the terminal angle produced, sometimes truncate, and ending in three small obtuse lobes. A fringe of hair-scales beyond the margin on the dorsal side only; the floor of the cavity, where it is not covered by the *harpe*, having a cloth-like surface, unusual.

Nearly allied, as this Indian butterfly seems, in form and colouring of the wings, to the African *P. Demoleus*, there is no resemblance in the appearance of its valve (see Pl. XXX. fig. 25). Nor is there any more in its *harpe*; for this organ is a shallow cup of chitine, quite filling and accurately fitting the basal half (and more) of the valve-cavity, having its ventral edge thickened, and the dorsal rising into a thin chitinous wall, of considerable height, the summit of which is serrated with sharp teeth (Pl. XXXI. fig. 9). When this *harpe* is carefully separated from the lining-membrane of the valve, it is seen to be less simple; for the elevated dorsal lobe is now seen to consist of three parallel laminae, which are of various lengths and heights, of which the inmost (also the tallest) alone is serrated.

In the abdominal apparatus there is a general agreement with the *Merope* and *Demoleus* pattern, with considerable diversity in detail. The *uncus* is short, little curved, ending in a broad and thick spatulate point, the keel deep, the rami rapidly receding, rising above the level of the summit, and forming a wide triangular arched roof to the cavity. The *scaphium* is minute, but possesses the essential features; the "double tooth" on each side is well marked; the frontal keel, however, is replaced by two erect fleshy

points. The *penis* is somewhat thick, moderately long, blunt-pointed, turgid, the white pulpy tissue copious.

At fig. 11 these organs are represented as viewed sidewise, the surfaces having been denuded of the copious scales and hair-scales, and both the valves removed. At fig. 12 is shown the corneous skeleton of these regions. By one of those fortunate accidents of which an observant scientist is always so glad to avail himself (as he can never command them) a specimen of *P. Erithonius*, which had been badly infested with mould, came to pieces in my hand, and the terminal segment dropped away from all the débris, clean, just as I have sketched it at fig. 11. Here I saw not only the uncus terminating the final segment, and the scaphium attached to it beneath, but, lower down, the orifice for the extrusion of the penis, pierced through the middle of a vertical curtain of very thin horny chitine, which is suspended in place, by attachments on each side, to the lower parts of the dorsal arch of the eighth (?) segment, as well as by two perpendicular ligaments below, which tie it fast, the one to the middle of the ventral arch of the ninth, the other (wider and thinner) to that of the eighth segment.

Perhaps—since I have never met with any thing like this structure, before or since—it may not be impertinent to add that I have not exercised my imagination upon a piece of integument irregularly pierced and fractured; the screens, the orifices, and their edges were quite symmetrical and smooth, exactly as I have represented them; and this chitinous curtain is still in my possession, in excellent preservation.

PAPILIO ANCHISIADES, Esp. (Plate XXXI. figs. 13–15.)

Valve nearly parallel-sided, bluntly arched at the tip; margins furnished, more or less completely, with a narrow fringe of hair-scales. The cavity is abruptly depressed a little way within the margin on each side. Just at the very edge of the descent, on the dorsal side, I observed in *one specimen* two minute black teeth curving towards the cavity; but of these I could find no trace in other specimens.

The *harpe* is a thin concave plate, long, narrow, parallel-sided, seated within the depression, but not reaching either of its margins. It can be easily lifted unbroken and laid on a slip of glass; and is then seen to have a continuous floor of yellow chitine, excessively thin, and yet apparently of two surfaces, since the unequal contraction of drying has raised irregularly ramifying, thickened, fine lines, meandering like rivers on a map; while the bounding lines, and the upper part of the arch produced by their meeting, are of a deep, rich, yellow-brown hue, gleaming and glittering in the changing light, like cut glass. The abrupt termination of this darker part of the arch, within, conveys the idea of an overhanging edge: but this is delusive; for, by careful manipulation under the microscope, I proved that this effect is produced merely by increase of density. The point of the arch is a long taper tooth; and three or four teeth on each side descend along the outer edges of the arch. But the minuter details of number and order are not constant in different examples. The dark tooth-like objects which I have represented within the point, directed inward, are not true teeth projecting from the chitinous surface; for, though they appeared exactly as I have drawn, yet when I slowly and carefully *tilted* the object under the microscope, so as to obtain changing angles of

vision, there was no break of the light reflected from the shining surface. And in other examples there was no trace of them. These appearances, therefore, I cannot satisfactorily explain.

The *uncus* is curved in the usual arc; it is thatched, for most of its length, with coarse shaggy black hair; the extremity forms a thick rounded spoon, bent abruptly downward; the keel produced by the vertical rami is unusually deep.

The *scaphium* is boat-shaped, rather shallow, with a cleft tip, and no proper keel, the sides are full and round; their summits, brown with longitudinal chitinous thickenings, have no trace of the normal "double teeth," but are surmounted with ridges of long stiff bristles.

The *penis* is of moderate dimensions and protrusion, without terminal expansion.

PAPILIO CHILDRENÆ, Gray. (Plate XXXI. figs. 16-18.)

Valve subtrigonal, pointed, nearly equal-sided, sparsely fringed with hair-scales, and beset with hairs, pointing inward from the ventral margin, and specially crowded near the tip.

Harpe nearly coextensive with the valve, springing from the entire base, and forming a concave triangular plate, with both lateral edges thickened, and a strong ridge running up near the middle. The ventral edge rises from an expanded hollow base, like the trunk of a tree, sending off near its middle point a stout sharp erect spine; at its end, where the central ridge meets it, both expand into a sort of hollow hand, turned up and curved-over ventrally, having five short fingers of glittering black chitine on half of its semicircular edge, the rest being a smooth wall. The dorsal edge of the harpe stands close to the edge of the valve, from which it rises into a thin wall of considerable height, leaning inwards, fringed along its summit, bearing a row of fine hairs.

The chief feature remarkable in the abdominal organs is the *penis*, which is rather thick, and so long as to protrude beyond the closed valves; its hue is pale chitine-yellow; its expanded orifice is filled with the white pulpy tissue, which swells beyond the margins; and there are, on the column, successive marks, which are repetitions of the terminal outline. (See the same organs in *Orn. Heliphron*, p. 285, *suprà*; Pl. XXVI. fig. 7.)

PAPILIO SESOSTRIS, Cram. (Plate XXXI. fig. 19.)

The general type is that of *P. Childrenæ*; and the similarity is greater (considering the complexity of the armature) than I have observed in any two forms which may be considered species, or even marked varieties. Yet there are numerous diversities between these two.

The *valve* is of a different outline, parallel-sided and rounded, instead of trigonal and pointed; it is more distinctly fringed, along the dorsal margin and around the end, with close-set hair-scales.

The *harpe*, while of the same pattern, is much modified. Its ventral edge is straight, the solitary spine placed nearer the base, and reduced to a wart. The ridge is now the principal feature, which in *P. Childrenæ* is secondary; it is more curved. The hand-like tip is similar in form; but the short blunt fingers, curving over the cavity, are replaced by sharp teeth, curved like the spines of a rose, nearly in the plane of the valve (as

shown in outline in Pl. XXXI. fig. 19). The wall-like dorsal plate does not end abruptly, but is continued all round the extremity of the valve, and even far down the ventral margin, so that the harpe seems to be *quite* coextensive with the valve. Then, between this wall and the main ridge, there is a secondary ridge, of which just a trace appears in *P. Childrenæ*, but which is here conspicuous; membranous for the most of its length, but supported, near the part where it curves up behind the "hand," by a caning "strut," of deep-brown shining chitine.

These are differences which would require representation on a much increased scale, to make them very appreciable by figures, but which are striking enough on careful examination.

When I came to examine the abdominal apparatus in *P. Sesostris*, I at once found a very glaring aberrance from *P. Childrenæ*. For there was not a trace of an *uncus*, the edge of the upper arch of the eighth segment projecting in only a very gentle curve, beneath which the arch of the ninth was wholly out of sight; the mingled long bristles, black and crimson, that generally project as a tuft, horizontally between the valves, were here bent down vertically into the cavity; and, behind them, a very minute hook was projected. There was, moreover, but the slightest doubtful trace of a *scaphium*, and only when I threw the sunlight far into the abdomen. The *penis*, in size, length and direction, agreed fairly with that of *Childrenæ*, but no white pulp was visible; the whole organ was of an uniform deep shining brown; and instead of expanding, its thickness gradually diminished to the tip.

All the diversities which I have enumerated, minute individually but in cumulation great, seem to me to point to original specific distinction, though the evidence is no incontrovertible.

PAPILIO VERTUMNUS, Cram. (Plate XXXI. figs. 20, 21.)

Valve and *harpe* agreeing in plan with those of *P. Euryleon* (infra), and more essentially with those of *P. Sesostris* and *P. Childrenæ*, particularly the latter. The order of resemblance is—*Childrenæ*, *Sesostris*, *Vertumnus*, *Euryleon*. The two ridges, enclosing a triangular area, are gone in the latter two, and the harpe is a chitinous plate of about equal width throughout. In all, there is the high and broad tooth in the middle of the ventral side, followed, in the latter two, by smaller teeth; the terminal hollow "hand" of *P. Childrenæ* is best represented in *P. Vertumnus*, where the form is similar but wider, and the fringing overcurving teeth are eight.

The abdominal organs are normal. A long slender well-curved *uncus*; an ordinary deep-keeled *scaphium*, with horizontal "double teeth;" and a moderately large *penis*, with expanded orifice, seated far back.

PAPILIO LYSANDER, Cram. (Plate XXXI. figs. 22–24.)

Valve semiovoid; very slightly fringed; a flat shelf within the ventral margin.

Harpe a broad triangular plate, that occupies a great part of the breadth of the valve. From an ample expanded base, by which it was attached to the supporting knob, it springs, tree-trunk-fashion, with wide and thick ridges of glittering chitine, to the summit of the

valve, narrowing as it proceeds. Here another wide branch is united to it, or it may be considered as a descending piece, since it has no affixed base; it skirts the dorsal margin. The union of the two pieces seems perfect, though the substance of the secondary piece becomes exceedingly attenuate there. A broad space, well defined, occupying the middle of the valve, is likewise so exceedingly attenuate, that it is only when we lift the harpe out of the valve, that we perceive, by the continuity of the plate, that this median region is chitinous at all. The extremity of this compound harpe runs to a sharp point, and is notched into four teeth, of which the two on the dorsal side are double. But the arrangement and form of the teeth are not quite constant.

The *uncus* is slender, abruptly bent near the base, thence straight but oblique, to the terminal hook. A small *scaphium*, with difficulty recognizable, was (in one example) attached, very closely appressed to its inferior surface, through its length; the proper "double tooth" on each side was represented by a close-lying horizontal spine, dark, polished. But, in two other examples, the scaphium was wholly absent, or apparent only as a minute amorphous rag of white flesh: while, from the middle of the uncus, descended vertically a divaricating fork of two spines, organically (as it seemed) jointed to the two sides of the uncus. In each case these depending spines were the outer margins of veils of pellucid white flesh; and in one case they inclosed white matter, which appeared identical with the pulpy substance of which I have already spoken. For here, again, the *penis*, which was much distended, had its interior filled, to overflowing, with the shining white substance, which not only occupied its whole gaping orifice, but was carried, as a great ball, upon its extremity.

In another example the penis was very large (see fig. 24), diminishing to the extremity, which was furnished with a hooked, slender finger-point; the outer chitinous integument was split through all the length of the organ that was visible; and (what seemed noteworthy) laterally and asymmetrically; so that a wide, gaping slit, obliquely, along the side, looked as if the integument had been violently burst by distension within. As if to confirm this conclusion, the tube appeared perfectly empty; my eye, with the aid of sunlight, could penetrate through the hiant cleft, far up into the interior, and all round; but could not detect a trace of what sometimes is so prominent, the second tissue; nothing at all, but the thin, transparent, gall-yellow, tubular wall of chitine.

We have surely much to learn yet about these obscure organs, and their functions!

PAPILIO EURYLEON, Hewits. (A. D.) (Plate XXXI. figs. 25, 26.)

Valve nearly semioval, narrowly fringed; the cavity bounded by a marginal shelf, which runs up the ventral side, and a little way round the extremity.

The *harpe* has much resemblance to that of *P. Anchisiades*. It is a rather narrow, parallel-sided, thin, concave plate, both sides of which are bent round dorsally; and the sharp tooth-like points, which in my examples were seven in number, are almost all on the ventral edge, extending from the tip about halfway down. All are overcurved, hard, and horny; the lowest by far the largest. In removing the valve from its attachment, the expanded tissue by which the harpe had been affixed to the basal knob, occasionally so conspicuous at the bottom of the abdominal cavity, came away uninjured; and when

I lifted the harpe from its valve with a scalpel, this basal expansion still came away, as represented in my figures. It appeared shrivelled, thin, and membranous; but a short maceration with water caused this tissue to swell and become plump and soft. It is, I presume, a muscular attachment for the special energetic movement of the prehensile harpe. Maceration produced not the slightest sensible change in the polished chitine, either now or any other occasion.

PAPILIO ERGETELES. Gray. (Plate XXXI. figs. 27, 28.)

We have here another modification of the *P. Luchisoides* pattern of harpe. The ventral side runs up through the very central line of the valve, having a strong tooth projecting from its mid-wall, and three teeth at its extremity, whence a slender branch descends ventrally, as in *P. Lysander*. Then, also, on this edge of the valve, as in the same species, accessory pieces stand up as two half-walls, one within the other, of dark chitine.

The *uncus* and *scaphium* are both normal; the latter specially well formed, though small, with "double teeth." The *penis*, large and uncouth, much as in *Lysander*.

PAPILIO MACEBOX, Wall. (Plate XXXII. figs. 1-3.)

Valve of similar outline to those of *P. Ulysses* and *P. Arcturus*, yet sufficiently diverse in other respects. It is scarcely fringed, except very thinly along the ventral edge; but the whole cavity-floor is studded with minute pits, from each of which springs a fine short hair, some of which exceed the margin.

The harpe is quite peculiar; at the first sight it reminds us of the form common in the *Ornithoptera*, the arm and the bent, spine-studded hand; but, when detached, and examined separately, as shown at Pl. XXXII. fig. 2, the armature is seen to be different, and even yet more formidable. If I may repeat the comparison to a hand, the five fingers, of glittering black chitine, are bent over the palm; and each of the five is notched, all down its front, with sharp teeth, of which the uppermost are the longest and stoutest. This and its fellow must make a very effective pair of graspers!

The abdominal organs are all well developed. The *uncus* arches nearly to a semicircle, terminating in a delicate spathula. The *scaphium* is definitely separated into two portions, the upper, altogether of a rich brown hue, apparently chitinous, which bears the teeth, and the lower, uniformly pellucid white. This latter is the keel, though it is not at all produced. The former, in the place of the usual "double tooth" on each side, has but one, erect, acute, recurved, like a viper's fang; but the termination of the scaphium is cut into three abnormal-teeth.

The *penis* is very long, and somewhat slender, ending in a prodneed finger-like point, and not much expanded. It bends obliquely downward, protruding so far as to reach, if it does not exceed, the limits of the valves.

The harpe was, when I opened the valve, much choked with scales, doubtless from some female.

Another example agreed very closely with the above, save that the teeth of the scaphium were nearer the tip; the inner edges were set with low points, each surmounted by a

bristle; and the secondary tooth was represented by a rounded eminence, on which there was a crest of stout glittering arista.

PAPILIO BROMIUS, Doub. (Plate XXXII. figs. 4-6.)

Valve almost circular, margined, at the ventral edge and at the extremity, by dense fringes of coarse hair-scales, and, along the dorsal edge, by sparse fine long hairs.

Harpe, a bold triangular hollow plate of chitine with thick edges, springing from an expanded base, which almost fills the basal portion of the valve-cavity, and then, rising erect, throws forward a broad truncate sharp edge, cut into four great teeth.

Uncus short, triangular, horizontal, strongly and deeply keeled. *Scaphium* large and conspicuous, the keel bent obliquely downward, the "double teeth" replaced by a long and high crest on each side, having several points. *Penis* of excessive length, slender, wire-like, bent downwards, and conspicuously protruding between the bottoms of the valves, *in situ*; extremity shaped like a horse-hoof.

This is one of the most instructive cases that I have met with. Having examined the South-African *P. Nireus* in three examples, and found no difference in the structure, or arrangement, or relative size, of the parts, in the three, I thought of the West-African *P. Bromius*. The two are so much alike, in every apparent feature, as to warrant the conclusion that they are but "local variants" of one and the same species. But lo! here, in these hidden organs of a function of the most vital importance to the creature, I find with amazement a radical and very extensive diversity.

In one* the valve is trigonal, in the other circular; in one the harpe is a long spoon, studded with cone-points; in the other a horse-head with four teeth; in one the uncus is long and of extreme tenuity, in the other short, deep-keeled; in one the scaphium bears a pair of blunt erect pegs, in the other a series of compressed ridges; in one the penis is short, elevated, and terminates in a finger-point, in the other very long, depending, unarmed.

Can these be descended from a common parentage? and are the diversities merely the result of changes in the climate, soil, and food produced on a party of emigrants, in the course of many generations? Or are they not, rather, powerful, if unexpected, witnesses to the primal diversity of *Papilio Nireus* and *Papilio Bromius*, as distinct creations of the Almighty God?

PAPILIO PODALIRIUS, Linn. (Plate XXXII. figs. 7-10.)

The *valve* is thin, narrow, sharp-pointed, more developed on the dorsal than on the ventral side, the latter remarkably excavated toward the base; the fringe of hair-scales, moderate at other parts of the margin, is so enlarged around the excavation that the irregularity of outline is not readily noticed (see Pl. XXXII. fig. 7).

A *harpe*, having a base as broad as the whole base of the valve, narrows at about the middle, where it terminates in a summit of dark chitine, shaped somewhat like an eagle's head and beak, looking towards the ventral side. From the thinness of the valve, and from the readiness with which the harpe comes away, the latter is favourable for

* See p. 328, *infra*.

microscopic examination (see fig. 8). It is now perceived to be a broad concave plate, rising into somewhat thicker walls at the sides, and having an elevated thin ridge running up in the midst. The "eagle's head" is very sensibly thickened, and abruptly, so as to assume the semblance of a twofold wall of the tissue; but very careful manipulation has convinced me that this appearance is illusory. All over the thinner region meander those irregular lines which I have noticed before, so much like rivers on a map, and which I suspect are caused by the shrivelling of the investing tissue in drying. Besides these, there are a few scattered bristles, each rising from a minute elevated knob or bulb. The very edge of the "eagle's head" is a little arched-over; its line is uneven, but I cannot detect any serration in any part.

There is no trace of an *uncus*. The posterior margin of the upper arch of the eighth segment, when viewed vertically (as at fig. 9), is nearly straight, or follows an uniform slight curve, with no attempt at central projection. Immediately beneath its middle is seen a small but distinct *scaphium*, with the "double tooth" strongly developed in its principal member, black, long, nearly straight, horizontal, reaching to the extremity of the scaphium, the secondary visible only as a low shining knob. The sides of the scaphium are rounded, concave exteriorly; and a very distinct thin white keel is below.

Dr. Buchanan White, in his beautifully illustrated memoir, has given a vertical figure of what he considers the tegumen of *P. Podalirius* (pl. lvi. fig. 39 b), which, in his text (p. 361), he says is "almost bilobed." But I venture to think he has fallen into error here, careful lateral examination showing that this structure proceeds from beneath the straight edge of the tegumen, as I indicate at fig. 10. It is certainly, therefore, the scaphium, as the whole details prove.

The *penis* consists of a blade of glittering black chitine, folded longitudinally, and ending in a slender finger-point, with a knob at its origin. Thus folded, the sheath does not half contain the white pulpy portion that runs along apparently within it, and at the tip expanded beyond the finger. Possibly in life the firm chitinous sheath is semi-tubular, and takes this folded form by drying. It sheds some light on the curious appearance of the organ in *P. Codrus* (infra).

I have examined minutely two examples of this species, and find no appreciable difference in any of the organs observed.

PAPILIO LATREILLII, Don. (Plate XXXII. fig. 11.)

Valve regular in outline, ovate, nearly equal-sided, pointed; the exterior clad with a dense coat of close-set scarlet hair-scales, which project, in an even thick fringe, beyond the ventral margin throughout, but not sensibly on the dorsal margin, of which a few black hairs only occupy the terminal moiety. Interiorly it is deeply and evenly hollowed; along the midst of the cavity runs an irregular-shaped *haape*, adherent to the lining-membrane (though readily detached), dilating into a broad blade of brown chitine, serrated with minute teeth along its edge, and projecting a prominent angle at each end. This blade is free, and stands up at an oblique inclination from the cavity.

The intravalvular organs I have examined imperfectly, and only *in situ*. The *uncus*

appears long, slender, and circularly arched, much as in *P. Demoleus*; the *scaphium* large, truncate, unkeeled, somewhat as in *P. Homerus*.

PAPILIO SEMPERI, Feld. (Plate XXXII. figs. 12-14.)

The *calce* is moderately large, of irregular outline, having prominent rounded angles, and a sharp projecting tooth at the summit. Exteriorly it is clothed with a coat of short scales, which are black from the base to the middle, and scarlet thence to the tip. Interiorly, the margins are exceeded by a broad fringe of hair-scales, which help to fill up, and so conceal, the irregularities of the outline.

The *harpe* is a shining chitinous plate, running through the length of the valve mesially, projecting two broad and sharp angular points at the extremity, and one in the middle of the ventral side. Pl. XXXII. fig. 12 shows the valve with the *harpe in situ*; but if the *harpe* be removed, which is done with great ease and perfectness, and viewed almost along the plane in which it lay in the valve, its form is very different; for the terminal portion curves upward, so that the points stand upright, and enclose a great semicircular area, as shown at fig. 13.

The *uncus* presents little that is notable: it is nearly straight, with the point sharp and bent down, bill-hook fashion; and its *scaphium* is rather small, and destitute of "double teeth." The *penis* is of extraordinary dimensions, the triangular dilatation of its extremity being enormously developed. At fig. 14 are presented these organs *in situ*, as they appear viewed from the right side, both the valves having been removed.

PAPILIO LYCIDAS, Cram. (Plate XXXII. figs. 15, 16.)

The *calce* is trigonal, short and wide, the margins fringed with black shining hairs mostly springing from within; the interior surface dark brown, velvety, nearly flat to a considerable distance within the margins, then suddenly sinking to a deep semicircular cavity. Within this hollow is seated a short *harpe*, having a widely expanded base, sloping away to the ventral side, and soon rising to a free flat column of dark-red glittering chitine, which is produced at the two corners into long sharp spines. Besides these, there are two minor spines from the slanting dorsal edge, and one near the base in the ventral. I discern no trace of serration in any part.

The abdominal apparatus seems peculiar. The beautiful clothing-scales, velvet-black alternating with pale-yellow, project densely from the segment around the cavity, when a valve is removed, so as greatly to conceal the interior. My cabinet possesses but a single example of the species, which is both beautiful and rare; and this I was reluctant to destroy, contenting myself with close and long-continued study of such organs *in situ* as a powerful hand-lens could resolve. Conspicuous is a slender well-formed *scaphium*, projecting horizontally, of a shining brown hue, with the "double teeth" small and low, but duly developed. At first there seemed no trace of an *uncus*; but at length I found it very far back, under the thatching roof-scales, small and short, sloping downward from its origin, and presently bent with an abrupt angle to a quite vertical line, or even a trifle within the vertical. Its form and direction, as well as I could see it, are much as in *P. Hector*. The *uncus*, then, it is evident, can here present no

antagonism to the projecting spines of the harpe. These points, in the closed condition of the valves, meet at the very tip of the scaphium ; yet the scaphial teeth, which in some species are long and formidable spines, are here minute and apparently useless.

To complete the series of anomalies, I could find no trace of a *penis*. By so holding the abdomen that the nearly level sun's rays shone into the cavity, I once or twice detected a glittering point very far within ; whether this was a penis, or whether the organ had been accidentally lost in my preparatory manipulation of the specimen, I dare not say.

PAPILIO DOUBLEDAYI, Wall. (Plate XXXII. figs. 17, 18.)

Valve having the outline of a tall cone, edged by a very broad fringe of close-set hair-scales—yellow at their bases, and becoming pale scarlet at their tips—which are continued from the exterior surface.

The *harpe* is commensurate with the valve itself, from which I am not able to separate it. The extremity is double, the dorsal point continuing the general plane ; the ventral really much longer, though not apparently, because it bends upward in the line of vision ; it is fringed with fine short diverging hairs, proper to its point (*i. e.* not continuous with the exterior clothing). The dorsal edge also bends up, and becomes semi-erect ; its outline is so cut that, in the middle, it forms a sharp tooth, pointing backward. Except this, I find no serrations in any part of the structure. The prehensile function seems to be limited to the upcurved dorsal point, and to be feeble.

The *uncus* and its accompaniments are exactly as in *P. Rhodifer* (infra), even to the protrusion of the wiry *penis*, with the single exception that the *scaphium* is here deeply keeled, whereas the keel seems totally absorbed in *P. Rhodifer*.

I subsequently examined another example, in which the penis was exactly as in *P. Rhodifer*, except that the finger-point was not so produced, and the lower lip-like lobe was rounded and of a deep red hue ; but the extruded bladder described there was here a perfect little globe of translucent yellow substance, projecting like a bubble from the expanding lip.

A third example had the tip of the very same form, but without a trace of the vesicle, the hollows of the bifid extremity white and shining.

PAPILIO RHODIFER, Moore. (A. D.) (Plate XXXII. figs. 19-21.)

In the *valve* of this Andaman representative of the *Coon* group there is a marked generic resemblance to that of *P. Doubledayi*, together with ample specific difference. The description of the valve of *Doubledayi* will well suit this of *Rhodifer*, save that the fringe, which is even broader, is of a purer scarlet hue, and the outline is still more disguised by the dorsal projections.

The *harpe* is again commensurate with the valve, and inseparable from it by mechanical lifting ; though, as in *Doubledayi*, the brilliant glittering polish of the entire surface, which distinguishes the harpe proper from the dull lining-membrane of the cavity, shows in each case that it is organically distinct from the valve. Here the extremity is treble ; the dorsal point, much larger, and directed much more laterally, than in *Doubledayi*, stands erect ; while the ventral division sends off from its surface, a little below its tip,

an adventitious lamina, of conical outline, which also stands up in the line of vision, and doubtless constitutes an auxiliary prehensor. All the three points are thickly beset with fine hairs, which make the resolution of their form difficult, and, one would think, must interfere with their prehensile effectiveness. There is no secondary tooth on the dorsal edge, which curves inward in a deep semicircular sweep to the broad expanded base.

The *uncus* is very long, and of excessive slenderness, almost quite straight, its extremity accurately reaching the point where the dorsal elevations of the two harpes meet and touch each other. The *scaphium* is very small and shallow; its "double teeth" conspicuous as a great spine on each side, having a downward curve. The most remarkable feature is the *penis*, which, like the *uncus*, is of extraordinary length and slenderness, resembling an attenuated, highly polished, black wire, nearly straight, proceeding from its conical investment almost directly downwards, and actually protruding between the valves below to the distance of an eighth of an inch; so that the insect could be easily handled and turned about by it, as if it were an inserted pin. The extremity of this organ is produced above (*structurally* above, though *actually* beneath, because its position is reversed) into a finger-point, which is abnormally long and acute; while below it forms a wide, somewhat tumid, trumpet-lip, of exceedingly attenuate transparent yellow chitine (?). So far the appearance has been paralleled in many other examples of the organ; but what follows is more remarkable. From out of the trumpet-like orifice proceeded what seemed a blown bladder, wider than the orifice itself, as if it had expanded as it issued, not quite globular, of a substance resembling that of the lip, but still more delicately thin, which, however, had dried in form and in place. It had all the appearance of an integral organic tissue—not of an excretion.

PAPILIO ARCHESILAUS, Feld. (Plate XXXII. figs. 22–24.)

Valve rotundo-triangular; the extremity very obtuse, but fringed with graduated hair-scales projecting into a long and sharp point; the other margins only minutely fringed. The middle of the cavity is occupied by a large *harpe*, crescentic when viewed vertically to the plane of the valve; the cusps, which point ventrally, are raised considerably from the floor; the one next the base pointed, the other obliquely truncate. Both the points, and the interior curvature, as well as a ridge that takes a parallel curve, are serrated with sharp teeth.

The *uncus* is horizontal in its total direction, but has a double sigmoid curve; and its extremity, which is suddenly bent downward, is trifid, with blunt points. The *scaphium* is small, and so closely adherent to the *uncus* that the boundaries can scarcely be discerned. I detect no trace of the "double teeth." The *penis* presents nothing specially notable: it is small, fingered, and retreating.

PAPILIO ZALMOXIS, Hewits. (Plate XXXII. figs. 25–28.)

Valve large, trigonal, with rounded angles, nearly equal-sided. Exterior densely clothed with shaggy fur of hair-scales, which project from all the free margins, forming an even, wide, buff fringe to the interior side, which is deeply concave, almost hemispheric.

rical. From the dorsal margin rises a wall-like ridge of shaggy surface and summit, which inclines towards the concavity, curves around the point, and then ceases. From a broad conical eminence at the base (the attachment to the basal knob) rises the *harpe*, a plate of chitine nearly filling the concave floor, its ventral edge elevated into a ridge, which curves in a semicircle to the dorsal wall; the middle of this ridge is lengthened into a long polished black curved spine, broad at its foot, becoming slender towards its tip, which projects over the fringe of scales, just reaching its extremity. At first sight the point of this spine appears simple; but higher magnifying power shows that the extreme point is flattened, and cut into four very minute transverse teeth, of which one is longer and larger than the rest.

The *uncus* is reduced to a small horizontal projection of the tegumen, bluntly pointed, of polished brown chitine, the lateral rami rising considerably above the level of its median ridge, the midst of which is studded with hair arching outwards. Depending from it is a sufficiently ample *scaphium*, of which the two sides slope downward and outward, and the keel descends from the angle. No distinct "double teeth" are developed. The colour of this organ, usually white, was, in two examples examined, of a dull blackish brown; and the surface was shrivelled and corrugated, not symmetrically, and not alike in the two examples. The *penis* is long and slender, slightly enlarged at the tip, black, polished; in one example it reached almost the edge of the valve-fringes when closed.

PAPILIO POLICENES, Cram. (Plate XXXIII. fig. 1.)

The *valve* is one of the most aberrant that I have seen. It is parallel-sided, the end a segment of a circle with a projecting point; exteriorly it is very densely clad with long scales and hairs, the dorsal half black, the ventral white, the colours abruptly divided. The interior aspect is affected by this clothing; all up the ventral side the white furry coat forms a projecting back-ground to the valve, increasing around the extremity, till it becomes nearly half as long as the valve itself. But up the dorsal side the outline is quite lost in close black hair, which, at this quarter of the end, becomes suddenly a thick tuft longer than the valve.

The *harpe* is very complex, and hard to define, harder still to describe in words. Near the tip there are three transverse rows of strong teeth:—first, one tooth at the very edge, making the point, and another at its dorsal side; below a ridge runs across, bearing six stout and prominent teeth; and below this, from the dorsal margin, arches out a thick arm bearing a sort of open hand or curved claw, of four fingers. All of these stand up from the cavity, and project inward. Each ridge, moreover, sends down one or more longitudinal ridges, more or less jutting into points. The whole constitutes a very elaborate prehensile instrument, quite unique, so far as I have seen.

The *uncus* is also abnormal. It is very short, broad, rounded at the tip, with slight curvature, of pale yellow chitine. I could not detect any sign of the *scaphium*; but my observation was unsatisfactory.

PAPILIO UCALEGON, Hew. (A. D.) (Plate XXXIII. figs. 2, 3.)

Valve very small, parallel-sided; the extremity round, with a regular wart-like pro-

jection at the tip, which is darker and seems firmer and denser than the substance of the valve, as if it partook of the nature of a prehensor. The dorsal margin is fringed by very long projecting hairs; and the interior cavity is thickly beset with fine shining pale hairs, in irregular groups, which spring from various points, and make it difficult to see the outline of the parts. In the delineation, I have omitted most of these tufts of hair, as otherwise nothing could be represented. The *harpe* is complex. First, from the dorsal margin, a little below the projecting terminal wart, rises, almost erect, a stout black polished spine; then, further down the same margin, but a little within, is a similar smaller spine of clear yellow chitine. From a base occupying the whole width of the valve, proceeds along the middle of the cavity an irregularly curving, stout, thick rod, whence, beyond the middle, springs an erect, black, polished spine; the rod then expands, and terminates in a free claw of two pincers, notched along their opposing edges.

The whole anal region is protected and concealed by a wide canopy of long, projecting, parallel scale-hairs, over all, which reaches far beyond the fringes of the valves. These proceed from the dorsal arch of the eighth segment; and other long scales proceed from the sides of the same. When these are all removed, we see a moderately long *uncus*, very slender, acute, nearly straight, and horizontal. Below it is the *scaphium*, dark but translucent, shining yellow, shallow, and narrow but long, the "double teeth" discernible only as a slight thickening.

The *penis* is very long, narrow, pointed, in contact with the lower surface of the scaphium, beyond whose extremity it protrudes.

This and the preceding, both African species, have, in their irregular and complex armature, much in common, with ample diversity.

PAPILIO AGESILAUS, Boisd. (A. D.) (Plate XXXIII. figs. 4-6.)

Valve externally thickly clothed with scales, half white, half black, the colours abruptly divided. Along the ventral margin, around the extremity, and nearly halfway down the dorsal side, a close fringe of long black hairs extends, springing from the very edge. This considerably augments the apparent area. The cavity is almost wholly occupied by a large and very elaborate *harpe*, whose structure I do not quite understand; for though it can be separated for examination, the process inevitably distorts the parts, and alters their relation to each other. There seems to be a great arching ridge of dark chitine, right across the middle, ending in a great erect double claw, near the ventral margin; more or less structurally connected with this, by the chitinous base, rise two other erect pieces, the three standing triangularly, and bending toward each other. From the arching ridge extends a (comparatively) great spoon-like plate, nearly filling the terminal moiety of the valve, its ventral edge, running about parallel with the ventral edge of the valve, of denser and darker chitine than the rest, cut into close minute saw-teeth. This saw-like edge stands, throughout, free above the level of the valve-floor.

An examination of the left valve in some measure cleared the difficulty—at least so

far as to show that what I have called the spoon-like plate is not, as looked at, concave, but convex, the outside of a hollow cone or helmet.

The tegumen, *in situ*, is concealed under the seventh segment, even when this has been considerably denuded; the *uncus*, however, protrudes, but much disguised. For it is almost straight, projecting horizontally, with a slight sigmoid curve, and having for its termination, instead of the usual spatulate point, three short, slightly divergent fingers. Beneath this representative of the *uncus* there is the long narrow *scaphium*, with shallow keel; but, from the close contiguity of the parts, and their minuteness, I could not be quite certain of the presence of the "double teeth," though once or twice I thought I discerned them.

If we compare this fine American butterfly with the still finer, closely related *P. Arche-silaus* of Felder (p. 324 *suprà*), we find almost identity in the form of the *uncus*, but great divergence in the forms of the valve and the harpe.

PAPILIO PARMATUS, Gray. (A. D.) (Plate XXXIII. fig. 7.)

This Australian cousin of the preceding species has a valve and a harpe equally complex, and equally hard to demonstrate; while the details of the armature seem altogether its own.

The *valve* is unusually small; and the presence of many irregular tufts of close long hairs, in unwonted places, greatly conceals and disguises the structure.

The *harpe* is, as I have said, very complicated, composed of many pieces, whose forms and positions and directions seem to have no intelligible relation to each other, or to the common object. There appears to run around the terminal portion of the valve a slender chitinous framework, which has two, if not three, projections parallel to each other, one much slenderer and longer than the other, forming a free arch. Down the dorsal side is a thin wall, rising in the middle into a tall, thin, erect, curved tooth, directed backwards. On the ventral side a ridge runs, within which, near the middle, is a semiglobular plate of deep-brown chitine, having two tall erect incurved faces, the inner forming a simple broad tooth, the outer and opposite cut into many acute serratures.

The abdominal apparatus, so far as I have been able to resolve it, seems to consist of a very small and compact *scaphium*, with the *uncus* (ill-defined) lying close upon it, and a *penis* moderately produced, reversed, terminating in a swollen extremity and a curved finger-point.

These very elegant butterflies appear emphatically and characteristically *Papilionæ*; yet, in their prehensile armature, they show a manifest approach to those extra-Papilionidan families in which the valve and harpe are united to form a single complex prehensor.

PAPILIO COBRUS, Cram. (Plate XXXIII. figs. 8-12.)

Valve parallel-sided, circular-ended, fringed with very long, badger-grey, shining hairs. A broad shelf runs obliquely across the end, and narrows down the sides. Near

the median line of the cavity, from a base that spreads like the base of a tree-trunk, runs up a narrow *harpe*, nearly to the arch, and then bends over towards the dorsal margin. It consists, on the ventral side, of three parallel laminae, divided by deep *sulci*, but united beneath, where the whole is in union with the lining-membrane. Of these laminae, the one next the ventral margin rises, abruptly, near its middle, to a higher level than the others, which it maintains. All three have the free edges cut into saw-teeth, on the ventral coarsely, on the others finely.

The abdominal apparatus is very abnormal. I cannot find any trace of an *uncus*, nor of a *scaphium*—unless, indeed, a minute rounded projection clothed with white hairs, in the usual place of these organs, represents either or both of them. Then, the *penis* appears to be double or even treble; for after I had removed, for examination, one organ, which corresponded, in position and form, to the penis*, there remained another which had been beside it; and this consisted of two parts—a hard chitinous thin blade which terminated in a slender spine, and a membranous investiture which ran up its side half embracing it, separating near the tip, and forming a thin yellow finger-like lobe.

All these organs, however, need fuller examination. The termination of the abdomen is profusely studded with long crowded grey hairs, under which they are almost hopelessly concealed; they are, moreover, very minute. The specimen examined was the only example of the species in my cabinet. I have represented what I saw; but I am not satisfied. The species is manifestly very anomalous.

PAPILIO NIREUS, Linn. (A. D.) (Plate XXXIII. figs. 13–16.)

Valve approaching a trigonal form; scales of exterior slightly fringing the edge. Cavity moderately deep; a fringe of long hairs springs from the whole length of the dorsal margin, and arches over the interior.

Harpe a flattened rod or narrow plate, perhaps hollow, springing from an expanding base, and following the middle of the floor to the extremity, where it becomes spatulate (Pl. XXXIII. fig. 13). It is with ease removed entirely from the valve, when we see that the spoon-like tip, which is sometimes flat, sometimes hollowed, is studded with short stout spines, closely set over its surface (fig. 15), and that the dilated base rises into two or three conical eminences, one of which is cut into saw-teeth along its dorsal edge (fig. 14).

The *uncus* is an exceedingly slender spine with a fine-drawn point, projecting nearly horizontally, with the slightest possible curve downward. It is keeled to about mid-length. The *scaphium* is much more conspicuous, bent obliquely downward, with two stout, blunt, erect, chitinous processes, which appear to represent the normal “double teeth.” The *penis* has a long finger at its upper extremity. *In situ*, all these parts are concealed by the coarse shaggy coat of scales with which the abdominal segments are clad †.

* I regret that I can say no more than this: but, when I had laid this organ on a glass slide for examination, a draught of air carried it away, and I could not find it again.

† See remarks on *P. Bromius*, at page 320, *suprà*.

PAPILIO DIPHILUS, Esp. (Plate XXXIII. figs. 17-20.)

(1. The larger race, figured by Esper, Aus. Sch. tab. xl.)

The genitalia are developed under peculiar conditions here. Looking at the σ , we see at first no appearance of the usual valves, and the whole aspect is abnormal. The eighth segment does not protrude from under the seventh, but sends out, just at the edge of the latter, a dense arching thatch of long, horizontal, scarlet hair-scales (see Pl. XXXIII. fig. 20), under which the genital organs are widely exposed, much as in *Eurycus* and *Euryades*.

The *valves* must be searched for, and then will not be easily recognized. Each is very small, not more than .05 inch in total length, not clad with scales externally; indeed, I think it would be correct to say, there is no valve at all, but only a naked *harpe* of valve-shape. Its outline is that of a hand-bell; the margins are thickened, and united at the summit into a rounded knob (=the handle of the bell), which is beset with minute curved spines, and bends-over towards the dorsal side*.

The *uncus* is a nearly straight wide process, semitubiform, the extremity truncate, but cut into seven obtuse teeth. The *scaphium* is seen beneath, narrow, short, with only a suggestion of the usual "double teeth." The *penis* is more normal, wiry, polished, acute, projecting beyond the surrounding organs, slightly above the horizontal.

(2. The small race.)

I received a variety from Malacca, much smaller and more elegant than the Java type as figured by Esper, pl. xl., and by Cramer, pl. cxxxviii.; the wings longer and narrower in proportion, the colours much brighter, and the white spot of the macular band in the hind wings longer and narrower, with other slight differences. In this, the bell-shaped valveless *harpe* is exactly as in the larger form, and is of the very same dimensions.

The *uncus* appears in this variety somewhat more truncate, shorter and less cut into points, so far as I have been able to examine it; the *scaphium* more keeled, and the other accessories the same. There is a pair of organs forming the floor of the anal cavity, with prominent points, the edges beset with long hairs, which I at first thought might possibly represent the ordinary valves; but so shallow that the *harpes* are separate from, and project above, them. But these are possibly the pair of strong angular projections to which the expanded bases of the *harpes* are usually attached. Their high position here agrees with the position of the *harpes*, and confirms my conclusion of *their* nature.

PAPILIO POLYDORUS, Linn. (Plate XXXIII. figs. 21-23.)

There is much resemblance between the terminal region of the body in this species and that in *P. Diphilus*, as might be anticipated; but the structure is here even more aberrant. The horizontally projecting thatch of scarlet hairs is still more copious, descending much further on each side, and even continuing, in coarser form and more irregular arrangement to the bottom. Thus, though the shining black *genitalia* can be seen, nothing can be defined till this shaggy thatch is removed; which is accordingly done in my sketch of the parts *in situ* (Pl. XXXIII. fig. 21.) Probably the protecting

* Compare it with fig. 15 of *Nircus*.

office of the ordinary valves is to some extent supplied by this thatching, the valves being almost aborted.

The *uncus* is here a stout, short, bifurcate process, the two points not quite equal *inter se*, acute, notched below. They are followed by a couple of pear-shaped organs, of highly polished, glittering, brown chitine, each terminating in an oblong knob, beset with minute spinous teeth. In fig. 21, they are seen *in situ*; in fig. 22 the right is seen interiorly, showing that it consists of a hollow shelly case, with the edges curved-over. The knob bends upward, toward the bifurcate uncus, but comes considerably short of it (as shown in fig. 21, where both the right and left knobs are seen), whereas in *P. Diphilus* the knobs close on the truncate tip of the uncus.

There can hardly be a doubt that these organs are homologous with what I have called "valveless harpes," in *Diphilus*. But, tracing them to their origin, we find that they spring from a point on each side, within the descending rami of the uncus, *i. e.* within the walls of the ninth segment: whereas the valves are appendages of the eighth, and are always outside the walls of the uncus*. Thus it is perhaps possible to consider these spinous knobbed organs the homologues of the teeth of the scaphium, which (in *P. Merope*) we have seen to be serrated. The scaphium itself I do not find in *P. Polydorus*, unless it is a shining white mass (in texture like the white of an egg boiled hard), into which the pear-shaped organs merge at their bases.

What I suppose are the *valves* proper (or their representatives), are a pair of organs (seen *in situ*, in fig. 21 below the pear-shaped bodies, with the *penis* protruding from between them) which certainly spring from the bottom of the eighth segment. Fig. 23 represents one of them, the left, viewed internally; it bears a semitubular ridge of chitine running through its midst, terminating in a minute point. This (supposed) valve is hollow, and is beset, on both margins, with long straight bristles.

If this analogy is true, it must be true also in *P. Diphilus*: but the application seems more difficult there.

It may be interesting to compare De Haan's description with mine above, every word of which, I may say, was written before I saw his. He says, "*P. Liris* and *P. Polydorus* have the hinder part of the body naked; the valves [kleppen] are very short, armed from within to the top by a hook [?, P. H. G.], and the lateral appendages [zijdelingsche aanhangsels] of *Amphrisius*† are placed under it: the spine on the back is blunt [uncus? P. H. G.]; besides this, there are also two spines present on the upper edge, and these are curved inwards; so that, altogether, the outer edge is provided with seven appendages‡, which all rise free from one another. Between these lies the penis [roede], which, as if pressed together, has a sharp edge above and below"§.

* The harpe however, has a double basis normally first to the valve, secondly to the knob which projects from the floor of the genital cavity. This latter is, I think, situate within the ninth segment.

† These are, I presume, what I have called the harpes in this Memoir.

‡ If I understand him, I can find but six: viz. the two points of the bifid uncus, the valveless harpes (or scaphial teeth): and the two bristled valves? But I am not sure that I follow his identifications. He seems to imply a terminal point to the uncus, besides and between the two points which alone I find in *Polydorus*; and in his figures of *Liris* he represents such a point. *Polydorus* he has not figured. Possibly he did not examine both minutely.

§ Nat. Gesch. Ned. O. B., Papilionidea, p. 17.

PAPILIO ANTENOR, Dru. (Plate XXXIII. figs. 24-26.)

Valve of the rotundo-triangular outline common to the genus *Ornithoptera*, and nearly as large as in some species of that genus. Exteriorly of an uniform drab-white; a fringe, of dense hair-scales, projects beyond the dorsal margin, the continuation of the common clothing; the ventral margin is unfringed. Interiorly, the lining-membrane is of a rich umber-brown hue, dully shining; the contour forming a wide flat edge or shelf all round, whence it falls abruptly in a deep cavity. This is occupied by a wide bell-shaped *harpe* of glossy chitine, hollow, like the cavity which it occupies, and terminating in a rounded knob, slightly bent towards the dorsal side. This is almost exactly the figure and appearance of the (presumed) *harpe* in *Diphilus*, only that I cannot detect the slightest trace of serration on the knob or on any other part. The knob is spoon-shaped, hollow, with an elevated, thickened, overturned edge.

The *uncus* is nearly horizontal, straight, short, bluntly pointed, being thickened at the edges and tip. The surface, though shining, is uneven, and lacks that glittering polish which this organ usually displays. A shallow sulcus runs along the summit to the point. Below, attached to it by short white fibres, is a small *scaphium*, in which I detect no teeth. The *penis* is very minute, and scarcely visible, far within the abdominal recess.

PAPILIO HECTOR, Linn. (Plate XXXIII. figs. 27-31.)

We have here the same type of structure as in *Polydorus*, but with remarkable modifications of the organs in detail. There are, again, no proper *valves*; the posterior extremity appears as an oval opening; the area occupied by a confused set of shining black knobs, surrounded by a dense horizontal thatch of scarlet hair, which, however, is not so long as in *Polydorus*.

The *uncus* is a short spatulate point, abruptly bent perpendicularly from the middle of the transverse edge of the downsloped roof of the ninth segment. Its shape, as seen directly from behind, is shown at fig. 28.

At its point just meet the summits of a pair of organs, answering to the (suggested) scaphial teeth (see *Polydorus*, p. 330), but of very bizarre form. Sidewise they are not unlike the corresponding organs in *Polydorus*, very highly polished, like them; but when looked at directly from below, each is seen to send off a broad process of sub-triangular outline, horizontally, toward the middle of the cavity. The process is a sort of flat cushion, apparently of short close pile, throughout which are set minute slender needle-like spines vertically. The end is a thickened knob, whence descends obliquely a group of very long straight bristles (see fig. 29, the right "scaphial tooth" seen from below).

What I suppose to answer to the valves, are still further disguised here, each being a slender straight rod (fig. 30), with the point bent dorsally, nearly at a right angle, and bearing a short spine; while the dorsal margin is so beset with short straight bristles, as to give to the whole organ the appearance of a comb. The base is broadly dilated; and the pair incline towards each other, so that the summits are almost in contact.

Between them projects the very much developed *penis*, the tip forming a curved acute

spine, reaching beyond the level of all the other organs, and the preputial (?) appanage forming two ample parallel leaf-like expansions, greatly lengthened, situate on the dorsal side (fig. 31).

Professor Westwood, who figures this showy species in 'Arcana Entom.' i. pl. 3, mentions the affinity shown by its larva and pupa with those of *P. Polydorus*, on the authority of Horsfield and De Haan. And, what is much more curious and inexplicable, there is a very close resemblance between all* these organs in *P. Hector* (including, notably, the bent bristled expansions) and the corresponding organs in a great Asiatic Silk-moth (*Anthea Roylei*).

CLASPING-ORGANS IN BUTTERFLIES OF OTHER FAMILIES.

I subjoin a few notes made on species of other Families, chiefly the *Pieridae*, because it is interesting to trace the gradual disappearance of a vanishing organ or set of organs.

Pieris. The valve of *P. Antodire*, of South America, a very charming microscopic object, densely clad in its snow-white hair-scales, is essentially that of a *Papilio*. The harpe is a thin sharp knife-edge, colourless, glassy, running transversely across, not far from the base, and rising into a broad tooth in the middle. The tegumen has the bird's beak-form; but I see no development of a scaphium. The penis is large and prominent.

The valve of *P. Automate* is much the same. A harpe runs obliquely from the base to the upper part of the dorsal edge—a colourless glassy ridge, with a free point. The valve, in both of these two species, is armed with a projecting semicircular hook on its margin, at, or close to, the tip.

In *P. Rape* the uncus is well developed; but I find no trace of a harpe, nor any structure corresponding to it or displacing it.

P. Brassicae possesses a well-formed valve, whose outline may be described as a circle within the angle of two sides of a square, of which one is the base. The other side is the ventral, which runs up with a stiff straight edge, and terminates in a hooked point. As harpe, an acute spine of transparent chitine runs from the base nearly to the middle, and then bends up toward the dorsal side. Herold takes no notice of this little glassy rape.

Callidryas. *C. Eubule* has a very curious valve, armed as elaborately, and as singularly, as that of many a *Papilio*. Its outline is somewhat pear-shaped, having a large hook at the extremity, and a broad shoulder on the dorsal side, each of which rises into an upturned black chitinous tooth. Through the middle of the valve runs a wide and deep depression, in which the floor is so thin as to be translucent. In the very centre there is a curious, oblong, free body, of orange hue, studded with a score of erect, blunt, black spines, equally thick throughout, looking like needles carelessly stuck in a pine-cushion, or, like the shell of a sea-urchin; it is connected, by a projecting arm, with the dorsal margin. There is a beak-like uncus, little hooked, beneath which projects a conical scaphium,

* Except the uncus. The form of the tegumen in *A. Roylei* may be imagined by supposing a normal uncus, only with the terminal half divided into two divergent spines, and the interval between these filled up, to a line stretched from point to point, with a downy chitinous membrane, and then bent down.

In *Polydorus*, these points remain bifurcate, as they are in the American Moon-moth (*Actias Luna*).

transparent, and of extreme tenuity. The penis is of unusual length and slenderness, resembling a very fine copper wire.

In *C. Stalira*, the valve is still more remarkable. Here the pear-shape is lost; for the extremity runs into a long, sharp, curved spine, and the dorsal shoulder has two wide semicircular excavations, on the eminence between which stands, attached by one angle, a triangular plate, the outer edge of which is notched into a dozen saw-teeth. This, I presume, is a harpe, and replaces the pineushion of *C. Eubule*. The tegumen projects in a long shallow *channel*, which can hardly be called an uncus, though it replaces one; beneath this is seen a minute scaphium, which simulates the form of an uncus. The penis is long, arching, and wiry, much as in *Eubule*.

Gonepteryx. The valve of *G. Rhamni* is small, but well made, rotundo-triangular, oblique, terminating in three hornypoints, of which the dorsal one is a rather long, slender, acute spine, which leans across the valve, so as to project beyond the ventral edge. This represents, but is not, a proper harpe. There is a small well-formed uncus, which, strangely, is translucent white, and a large penis, but no trace of a scaphium.

In the fine *G. Leachiana* of Brazil the valve is much like this, with very wide fringes of yellow hair-seales. The terminal point is long, slender, upcurved; and the two dorsal points both belong to that which supplants a harpe. There is a proper uncus, small, hooked, and a scaphium, very minute but apparently normal, beneath it. The penis, in this species, is long and prominent; its terminal expansion takes the singular form of two triangular lobes, looking exactly like the anal and dorsal fins of a mullet.

G. Clorinde, of Paraguay, has a similar valve. The uncus is a large blunt hook, polished white, like ivory, which bears beneath it a perfect little scaphium, in which, I believe, I can trace the "double teeth," though excessively minute.

Hebomoia. *H. Glaucippe* is well armed. The valve is an oblique trapezoid, ending in two stiff slender spines; the ventral margin semioval in outline, furnished with a broad white fringe. Its long very slender harpe runs transversely across the base, which throws up an elevated tooth at the dorsal end, and terminates ventrally in a more or less produced hook. It is quite papilionine in aspect, though no part, I think, is serrated. There is a long black uncus nearly horizontal, but bent down at the point. This is furnished with an ample scaphium of a polished brown hue, quite dark in parts; it has a long keel, projecting beyond the hook of the uncus, with long and deep rami, and a stout, horizontal, decurved black tooth on each side.

Terias. The valve of *T. Heccabe* is semicircular, running off to a tooth-like point at the vertex. The concavity is deep, almost hemispheric; and the margins are very broadly turned over, their inward edges elaborately furnished with spines, long, slender, sharp, arching over the cavity. On the dorsal side of the terminal tooth rise two of these spines, and a third on the ventral side, while the ventral point of the basal side runs off into a stout and sharp hooked point. There seems to be no harpe.

The uncus may easily escape recognition. Not only is it exceedingly minute, but it *seems* to be replaced by a projection with two points, the upper curved downward, the lower, longer, curved upward; but the former is the uncus, the latter its scaphium.

Colias. Here the genital armature is become very aberrant. *C. Edusa* has a short, thick, obtuse uncus, and no valves nor harpes, but fixed side pieces in place of valves, in which I can detect little analogy with *Papilio*.

Morpho. In *M. Menelaus* I find valves much as in *Papilio* but without harpes, an uncus broadly triangular but with a good hooked beak-like point, very deeply keeled, and a projecting penis. The tooth on each ramus of the uncus is more than usually separate and strong. I see no trace of a scaphium.

Nor in *M. Epistrophis*, in which for a while I fancied I did see a rudiment of the organ far up in the cavity; but very precise and repeated observation under a high power, with light thrown well into the spot, convinced me that I was looking into the anal orifice, and that there was not the least trace of a scaphium.

In this species there are well-developed valves, but small, and of delicate texture, of which the tip, preceded by a pointed fringe of very long silver hairs, is of hard, dark chitine, turned up at an angle, *with a serrated edge*, of which the teeth are large, and *cut into minute toothlets* along their sides. Here, then, we have one of the most peculiar characteristics of a harpe transferred to the valve.

Dynastor. But in the fine *D. Darius* the transition is complete. Here is a narrow, parallel-sided but very deep uncus, and a pair of horny stout organs in the place of valves, and having much of their outline, but bearing along the thickened dorsal margin a double row of strong spinous teeth, black and glittering, most formidable to behold. The valve with its harpe has become what Dr. White would call a true *harpago*, distantly like his beautiful figure of the organ in *Argynnis Laodice* (op. cit. pl. lv. fig. 20).

I now close this Memoir; but the work is very far from complete. It is but an instalment of the subject that I here present to the Linnean Society; a great majority of the recognized species of Papilionidæ being still untouched for this purpose. Yet I have not ceased to work at them; and if life and health be still vouchsafed to me, I hope I may, before long, contribute to science more details of these remarkable instruments, as yet unsuspected*.

Conscious I am, too, that a good deal of imperfection attaches to the observations recorded. Of not a few of the species examined and figured herein, I should be very glad to repeat the examination, if I had more specimens; and Entomologists could scarcely render me a kinder or more grateful service than by sending me examples of *male Papiliones*, however torn in the wings, or even the separated abdomens, if *duly authenticated*, of which they may possess worthless duplicates.

* At the time of this sheet going to press (March 6, 1883), I have accumulated, in MS., descriptions, with drawings, of the genitalia of fifty-six species, in addition to those herein contained, belonging to the genera *Ornithoptera*, *Papilio*, *Picropalpus*, *Scricinus*, and *Leptocircus*.

APPENDIX.

SUPPLEMENTARY NOTE TO ORNITHOPTERA REMUS.

Since this Memoir was completed, and presented, many examples of this magnificent butterfly have been sent to me from Celebes, and also of *O. Haliphron*; and I have examined more than a dozen males of each. The following notes embody my latest researches on the abdominal organs. They are illustrated by figs. 15-19 of Plate XXVII. [N.B. The small letters indicate the same organ or part in each figure.]

Uncus (*a*). When the beautiful patch of velvet-black hair-scales that adorns the dorsum of the eighth segment of *O. Remus* is carefully removed by abrasion, so as to expose the chitinous skin, we see that this is dully shining up to the accurately defined transverse line where the velvet ended. Thence it becomes brilliantly polished, and begins to project into a triangular area, of which the lateral edges are thickened, while the median portion, also thickened, forms the out- and downcurved uncus. Its curvature is not quite uniform: sometimes it is the arc of a circle, sometimes the arc of an ovoid; sometimes it is bent abruptly and perpendicularly downward from its middle.

Scaphium (*b-i*). From a level slightly below the expanding rami of the uncus, apparently in fixed immovable connection with it, spring a pair of slender rods, of similar shining chitine, each of which (*b*) is dilated near its base into a wide lamina exteriorly, which laminae become the firm fleshy tissue of the cheeks (*c*). These together assume the form of one fourth of a globe, cleft by a deep vertical sulcus, which has a continuous floor (*d*). Each cheek has its outer ventricose side obliquely cut away behind: its surface is distinctly granulate, the granules elevated, more and more towards the point and back, into the characteristic stiff, glittering bristles (*e*).

A simple device may assist the comprehension of this form. If the thick rind of half an orange be removed bodily and set on its edge, if then about half of this be cut away slantingly behind, and then what remains be excised into a deep narrow groove mesially, we shall get the scaphium-cheeks of *O. Remus*.

From just below the groove descends vertically a long and narrow pentagonal piece (*f*) of what simulates polished ivory. It is not continuous with the part from which it seems to descend; for, by peering with a lens *under the edges* of the cheeks, we see the summit of the pentagon to be abruptly bent backwards, so as to reach connection with the under surface of the sulcus-floor, far back in the mid-roof of the arch.

Behind this narrow shining pentagon is the keel (*g*); a large plate of whitish tissue, very thin in the middle, which seems attached to the concealed side of the pentagon, but on the abdominal side thickening into broad irregular lobes (*h*), apparently of a different character from the thin central parts. The depth of this organ, and even its shape, differs considerably in different individuals. Possibly it is capable of alteration in form, and may be composed of something analogous to erectile tissue. Indeed, I have fancied that the varying direction of this curious member—sometimes more, sometimes less pendent—may itself indicate a sort of erection. May it be that it is a titillant, excitant,

provocant organ, to be applied to the ♀ vagina, before intromission? The extreme tip seems to be of peculiar structure: it may be glandular, and be the seat of sensation, the *τέρψις ἐρωτικῇ*, of which the hard chitine of the penis seems incapable.

In one example the whole keel was movable, as on a hinge in the interior, whose place is indicated by the dotted curve-line in fig. 15.

The thickened edges unite behind into a very thin median ridge, which, like a groin from a roof, descends vertically, and is lost in the curtain to be presently described. A transverse horizontal section would be somewhat like fig. 19.

In *O. Remus*, and, I believe, in *Ornithoptera* generally, the uncus is soldered by its under surface to the upper surface of the scaphium-cheeks behind, the suture showing a thickened bead. So it is with some *Papilionides*, though with others there is a wide hiatus between these organs to the very base. That the fecal outlet perforates the abdomen-wall at their point of union seems certain. In both *Remus* and *Haliphron* I have demonstrated the presence of an orifice, leading from the abdominal cavity between the uncus and the scaphium, and I have passed a fine needle through it—though, from the extreme minuteness of the parts, and their dry condition, the demonstration was not quite so satisfactory as I could wish. Still I can find no anal orifice *possible* anywhere else than here.

The tissues of the scaphium become attenuated and expanded behind, arching around as a great concave membrane (fig. 15), which limits the genital cavity, and shuts it off from the abdomen as by a falling curtain. It is strengthened by slender ribs of chitine, which run down vertically from the cheeks of the scaphium and from the groin of the keel, somewhat like the nervures in the membrane of the wings, and end in insensible points, near the penis.

Penis. All my examinations still leave much obscurity on the form and conditions of the intromittent organ. Its usual appearance is that of a semitube, or gutter, of brown chitine, whose upper (normally and structurally the *lower* or ventral, for the organ is reversed) side is widely open, which projects from the curtain outward to near the tip of the scaphium-keel. But these gaping sides approach each other in various degrees in various individuals, the organ at times being nearly flat, especially towards the extremity. It is then seen to have angular enlargements at intervals, which, when the sides approximate, appear as sharp projecting ribs. The tip is bevelled off to an acute or subacute point, from each side of which a ridge passes down into the hollow (fig. 20). [These characters were precisely repeated in examples of *O. Haliphron*.]

But I have seen specimens in which the trough was more than filled with a substance which, though it was not white, I suspect to have been homologous with that pulpy matter which I have repeatedly described—the more, since in this case too a portion of it was extruded to some distance from the extremity.

It is difficult to imagine how an open trough can be efficient for the conveyance of the semen into the ♀ vagina. But I venture to suggest, though I have no proof, that in life the tube may be completed by an excessively subtle film, which, in drying, falls on the opposite chitine-surface, so as to be no longer distinguishable.

The falling curtain of the scaphium-base forms below its middle an enveloping sheath for the penis, which sheath then runs back around it to the very origin of the organ. This sheath is close, yet wholly free, allowing independent action to the penis, while it is attached on each side, by a slender ligament, to the floor of the cavity.

Tracing back the organ to its origin, we see that it is fastened by muscles to a thin but wide ridge of chitine, that springs from the bottom of the seventh segment, and stands up erect transversely, yet considerably hollow, the concavity backward. This, I presume, gives the point of resistance for the *retraction* of the organ after coition. The penis, behind this attachment (*i. e.* thoraxwards) enlarges into a thick and long fleshy bulb, which seems free in the hollow of the sixth segment, and bends back upon itself.

The eighth segment at its bottom gives rise to a hollow shell-like plate of firm polished chitine, much larger than that of the seventh just mentioned. This and its fellow form the floor of the genital cavity, surrounding and closing the bases of the valves. To the upper edge of this plate the penis is affixed by a muscular or tendinous cord stretched in the contrary direction to that of the seventh segment. I conjecture that this *projects* the organ in coition, as the former *retracts* it, and that both limit its action to the median line of the body.

Hinge-knobs. Within the plate last described, nearly close to it, and nearly parallel with it, but quite free from it, is that curious piece, on each side, which I have called a knob, but which (here, in *Remus*, certainly) is hollow—a very firm and stout chitinous shell, to which the ventro-basal edge of the valve is closely articulated, and from which the root of the harpe springs.

The small italic letters denote:—*a*, the uncus; *b*, the chitinous lamina of the scaphium; *c*, its cheek; *d*, the suleus; *e*, the aristæ; *f*, the pentagon; *g*, the keel; *h*, its lobes; *i*, its groin.

I add some results from late examinations of a few species of *Papilio*, as chiefly shedding light on the structure and relations of the scaphium.

P. Ascalaphus. The uncus, scaphium, curtain, and penis, can all be resolved into the *Remus* type. The cheek, instead of being erect, leans horizontally outward, making the suleus much broader; the front edge of the cheek is diminished to a slender acute tooth of black chitine; and its hinder portion (= the suleus side in *Remus*) is here the semi-globose “boat-gunwale” of brown chitinous membrane, or thin horny plate, so corrugated as to make strong oblique ridges, sloping inward and forward, on each side of the shallow suleus. The keel, though somewhat changed in form, seems homologous; but the pentagon appears quite wanting.

In *P. Mayo*, and in *P. Memnon*, the general structure is the same; the differences of detail are slight and unimportant.

P. Agamemnon. The back of the upper part of the scaphium is elevated, skull-like, and is thickened into a ridge, where the under surface of the uncus-base is attached to it, I think, organically, as may be seen when the uncus is forced off. This ridge descends obliquely on each side, and forms the lateral margin of the curtain, reaching below the

penis. From the lower edge of each cheek descends a prominent high ridge, which (and its fellow), the intervening membrane being arched, embrace without contact the penis, sending forward on each side that singularly elegant heart-shaped bundle of white flossy filaments which I have described above (see p. 314 *suprà*, and Pl. XXXI. fig. 7). These heart-shaped bundles unite into one beneath the penis, and merge into a horizontal floor of the sheath, which runs back into the cavity of the abdomen. Another less delicate bunch of similar floss is given off on each side from the outer part of the curtain.

P. Anchisioides. The scaphium-sides go back into the ridge of the curtain (as in *Agamemnor*), and sheathe the penis. The scaphium-keel is slit vertically at the front, the slit expanding upwards. It is equivalent to the same part in *O. Remus*; but there is no pentagon, it seems quite aborted. The cheeks are rounded, polished, light brown, and thus chitinous, with a tuft of very short and fine aristæ, seated on the inner curve, to be detected only by very careful focusing against the light, but then indubitably.

P. Macedon. Here, again, as I find by several examples, the scaphium is much the same as in *O. Remus*, only that the front portion of the cheek is hardened and pointed, and so excised as to form the principal tooth. Behind this is a ridge, which runs in an inner line; the aristæ are set from the interior side of the tooth, all along the edge of this secondary ridge. Viewed in front, the appearance much resembles that of *O. Remus*; but the pentagon seems reduced to a mere line, not (visibly) split. The three teeth which I had described and figured, at the point of the united cheeks (see p. 319 *suprà*, and Pl. XXXII. fig. 3), now no longer appeared; their semblance was probably illusory. The descent to the curtain is normal.

These repeated observations make it highly probable that throughout the genus *Papilio*, as in *Ornithoptera*, the scaphium has consimular relations with the surrounding organs, that it is constructed on a common plan though subject to many variations in details, and that it is throughout composed of three distinct portions, which probably possess distinct functions.

DESCRIPTION OF THE PLATES.

[The figures of the valves have been drawn to about six diameters each, and the others enlarged proportionally but not to scale.]

PLATE XXVI.

- Fig. 1. *Ornithoptera Aruana*.—The interior of the right valve with its harpe *in situ*, magnified 6 times.
 Fig. 2. *O. Aruana*.—The harpe, separated and viewed as a transparent object, further magnified.
 Fig. 3. *O. Aruana*.—The whole genital apparatus, seen from the right side, the right valve having been removed.
 Fig. 4. *Ornithoptera Prodomus*.—The disk-like extremity of the right harpe, viewed transparently, magnified about 10 diameters.
 Fig. 5. *Ornithoptera Richmondia*.—The disk of the right harpe, magnified about 10 diam.
 Fig. 6. *Ornithoptera Haliphron*.—The interior of the right valve with its harpe.
 Fig. 7. *O. Haliphron*.—The ultimate segments of the abdomen, and the contained organs, viewed from the right side: the right valve removed; the left with its harpe, *in situ*, represented in faint outline. The uncus, scaphium, and penis; the last surmounted by the unknown white substance.
 Fig. 8. *Ornithoptera Darsius*.—The interior of the right valve, with its harpe.
 Fig. 9. *O. Darsius*.—The harpe, viewed in the same aspect, further magnified.
 Fig. 10. *O. Darsius*.—The same, viewed sidewise.
 Fig. 11. *O. Darsius*.—The extremity of the penis viewed nearly in front, and with most of the white matter removed.
 Fig. 12. *Ornithoptera Rhodamanthus*.—The scaphium and uncus seen from above.
 Fig. 13. *O. Rhodamanthus*.—The interior of the right valve with its harpe.
 Fig. 14. *O. Rhodamanthus*.—The right harpe further magnified.
 Fig. 15. *O. Rhodamanthus*.—Teeth of harpe, viewed laterally, and more highly magnified.
 Fig. 16. *O. Rhodamanthus*.—The scaphium and uncus, together with the penis, seen from the right side.

PLATE XXVII.

- Fig. 1. *Ornithoptera Heliaron*.—The interior of the right valve, with its harpe.
 Fig. 2. *O. Heliaron*.—Disk of same harpe, further magnified.
 Fig. 3. *Ornithoptera Heliaronoides*.—The interior of right valve, with its harpe.
 Fig. 4. *O. Heliaronoides*.—The harpe, further magnified. The outlines around the central figure represent the forms of the teeth opposite to them when these are viewed to advantage.
 Fig. 5. *Ornithoptera Brookeana*.—The interior of right valve, with its harpe.
 Fig. 6. *O. Brookeana*.—The marginal teeth of the latter, more highly magnified, and viewed nearly in the plane of the harpe, so as to show them in elevation.
 Fig. 7. *O. Brookeana*.—The scaphium, viewed vertically from above.
 Fig. 8. *O. Brookeana*.—The scaphium, seen from the right side. The left valve and its harpe are indicated in faint outline.
 Fig. 9. *Ornithoptera Amphrysus*.—The interior of the right valve with its harpe, magnified about 7 times.
 Fig. 10. *O. Amphrysus*.—The abdominal organs, seen from above.
 Fig. 11.—*O. Amphrysus*.—The abdominal organs, seen from the sides, both valves having been removed.
 Fig. 12. *Ornithoptera Remus*.—The right valve and harpe.
 Fig. 13. *O. Remus*.—The harpe, more magnified.
 Fig. 14. *O. Remus*.—The same, in outline, flattened.

Fig. 15. *O. Remus*.—The end of the abdomen, both valves removed, and the walls of the segments in part broken away, to show the scaphium-curtain.

Fig. 16. *O. Remus*.—The uncus and scaphium, from above.

In figs. 16, 17, 18, and 19 the small letters have the following signification :—*a*, the uncus ; *b*, the chitinous lamina of the scaphium ; *c*, its cheek ; *d*, the sulcus ; *e*, the aristæ ; *f*, the pentagon ; *g*, the keel ; *h*, its lobes ; *i*, its groin.

Fig. 17. *O. Remus*.—The same, from the right and somewhat from above.

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Fig. 7. *P. Mayo*.—The scaphium, more magnified, seen from the front.

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Fig. 27. *Papilio Ascalaphus*.—The interior of the right valve, with the harpe.

Fig. 28. *P. Ascalaphus*.—The harpe further magnified.

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Fig. 19. *P. Polycaon*.—The abdominal organs *in situ*, the right valve having been removed.

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Fig. 21. *Papilio Hesperus*.—The interior of the right valve, with the harpe.

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X. *On certain Points in the Anatomy of the Polynoia, and on the Polynoë* (Lepidonotus, Leach) *clava* of Montagu. By ALFRED GIBBS BOURNE, B.Sc. Lond., Univ. Scholar in Zoology, and Assist. in the Zoological Laboratory, University College, London. (Communicated by Prof. E. RAY LANKESTER, M.A., F.L.S.)

(Plates XXXIV.-XXXVI.)

Read January 18th, 1883.

THE investigation of the anatomy of the *Polynoë clava* of Montagu was undertaken, at the suggestion of Professor Lankester, by Mr. W. B. Benham, Demonstrator in Zoology, University College, London. Mr. Benham made a large series of drawings, comparing this species with *Polynoë squamata*; but while working at the Zoological Laboratory at Naples, I was enabled to examine a very large number of living specimens of *Polynoë*, more especially of *P. grubiana*, Clap., which I shall show to be only a variety of our *P. clava*; and as I had obtained certain new results with regard to the anatomy of that and other species of *Polynoë*, Mr. Benham kindly placed his notes and drawings in my hands.

I do not propose to deal at any length with questions of synonymy. The enormous mass of literature upon the group, the number of species which are now known to exist, and the minute characters which separate them, combined with the very general character of most of the descriptions of the older writers, render it undesirable to do so on the present occasion. *Polynoë clava* was first described from the coast of Devonshire, by Montagu* as *Aphrodita clava*; and he fully distinguished between this form and *P. squamata*, Linn.; his single figure, however, is insufficient.

Johnston† also distinguishes between this form and *P. squamata*, and gives the following characters:—

“*L. squamatus*.—Scales ovate and reniform, imbricate, granulous, ciliated on the outer margin; tentacula and tentacular cirri incrassated below the point; bristles of the ventral branch with sharp denticles on the thickened portion of the shaft below the smooth talon-like apex. Length 1-2"; breadth 3".”

“*L. clava*.—Scales subcircular, margined, not imbricate nor meeting on the mesial line, maculated, unciliated on the edge; tentacular and dorsal cirri bulbous below the point; bristles as in *L. squamatus*. Length 1½"; breadth 4".”

Claparède seems to have overlooked the species entirely, and describes his *P. grubiana* as differing from *P. squamata*, Linn., in its elytra not covering the back, in the smooth contour to the elytra, and in the papillate character of the palps.

McIntosh‡ points out that Claparède's *P. grubiana* may be a variety of *Lepidonotus*

* Montagu, Linn. Trans. ix. p. 108, t. 7. fig. 3.

† Johnston, ‘A Catalogue of British Non-parasitical Worms,’ 1865.

‡ McIntosh, Trans. Zool. Soc. ix. 1877, p. 371.

clavus, "since he does not distinguish it from the latter while contrasting it with *L. squamatus*." *P. squamata*, as Malmgren has pointed out, is not found in the Mediterranean; while, at any rate at Naples, *P. grubiana* is the commonest of the Polynoina. I have collected there about a hundred specimens; and thus, while I am convinced that it is the same species as our *P. clava*, I have been startled to observe the great individual variation which may occur in a single species.

The Mediterranean forms possess rather darker scales, but possess in other places less pigment than do the specimens we had obtained from Devonshire; they are moreover considerably smaller.

My observations upon the series of *P. clava* have led me to classify their characters thus:—

<i>Constant.</i>	<i>Variable.</i>
Number of segments in the body.	Size and shape of the body.
Number of elytron-bearing segments.	Elytra, in respect of their size, shape, and tint.
Structure of median tentacle.	Amount of medio-dorsal region of back covered by them; extent to which each overlaps the following elytron; firmness of their attachment to the body.
Structure of lateral tentacles.	Thickness of the anterior margin of the prostomium, influencing the apparent place of origin of the lateral tentacles.
Structure of palps.	Amount of pigment on the body-surface.
Shape of equivalent parapodia.	Presence of acicula in the pygidial segment.
Structure of the notopodial and neuropodial cirri.	
Structure of the ventral tubercles (nephridial papillæ).	
Character of <i>equivalent</i> setæ.	
Fringing of the margin of the elytron (not including the tactile papillæ).	
Position and size of the eyes.	
Mode of origin of the median prostomial tentacle.	
Position of the anus.	
Structure of pygidial cirri.	

The following variations are also to be found in one and the same individual:—

- Structure of the notopodial and neuropodial setæ; their length and number.
- The elytra in respect of size, shape, and amount of granulation on their surface.
- The shape of the parapodia.

This individual variation necessitates great care, in making comparisons between these forms, that exactly equivalent structures be compared.

POLYNÖE CLAVA, Montagu.

Shape of the Body.—As I have pointed out, we can attach very little importance to such difference in the shape of the body as Johnston has described as existing between *P. squamata* and *P. clava*; my specimens of *P. clava* show much more variation among themselves (compare figs. 3 & 4, Pl. XXXIV.). Still less can any importance be attached to the position of the elytra with regard to the medio-dorsal region; whether these latter do not meet, simply meet, or overlap, depends entirely upon the amount of food in the alimentary canal and the number of ova contained in the body-cavity. Figs. 3 & 4 show two extremes in this respect.

The body consists of a prostomial lobe with its tentacles and 27 somites; the 1st of these is the peristomial somite (Huxley), the 2nd the first elytron-bearing somite, and the 27th the pygidial somite. All these segments bear more or less modified parapodia.

Parapodia.—The parapodia in the central region are normal, but at either end of the body they become modified. The normal parapodium consists of notopodium and neuropodium, the latter being about four times the size of the former, which, however, in *P. clara* cannot be regarded as a mere tubercle projecting from the upper surface of the neuropodium (Huxley, *P. squamata*), but more nearly retains its normal position as a lobe of the parapodium corresponding to the neuropodial lobe.

The notopodial acicula is well developed. The notopodial setæ are about twelve in number; but this number is by no means constant, as they are continually falling out and being replaced by new ones; consequently setæ of various stages of growth may be found in one parapodium; there appear, moreover, to be permanent varieties in the notopodial series. Figs. 12, 12 *a*, 12 *b*, & 12 *c* represent such varieties of the notopodial setæ of *P. squamata* (only the extremities are drawn). Figs. 12 & 12 *a* come from short setæ, figs. 12 *b* & 12 *c* from very long ones. In the short setæ there are about 25 pectinated frills, which encircle in the central region about two thirds of the circumference of the blade; but the upper frills, which are more pectinated, encircle much less, and the lower ones rather more; there is only one longitudinal series of frills. The long setæ present series of frills which are not so well developed. The notopodial setæ of *P. clara* are all formed upon the type shown in fig. 11, corresponding to the long setæ of *P. squamata*.

The neuropodial setæ are very similar in two species (Pl. XXXV. figs. 13 & 14). There are two longitudinal rows of 7 or 8 pectinated frills placed opposite to one another, although the fact that the ends of the frills running slightly downwards may give in some series the appearance of the frills alternating on the two sides. The distal rows of frills are more strongly developed than the rest, and present five large teeth upon their free edge. In *P. squamata* the central tooth is relatively much larger than in *P. clara*. The proximal frills are always feebly developed.

The neuropodial acicula pierces a small papilla; dorsad of this papilla there are about six neuropodial setæ, and ventrad about twice that number. This, as Grube points out, is the usual arrangement—twice as many setæ ventrad as dorsad of this papilla.

The notopodial cirrus is more bulbous below the point in *P. clara* than in *P. squamata*.

The neuropodial cirrus of *P. clara* differs from that of *P. squamata* in the same way that the notopodial cirrus does, and is besides shorter and rather stouter.

The papilla (pyriform tubercle of Huxley, ventral papilla of Grube and Ehlers, figured occasionally without description by Claparède and Malmgren) which I propose to call the nephridial papilla, springs, as Huxley pointed out, not from the parapodium, but from the neural surface of the somite itself.

Elytra.—The elytra present various shapes, according to their position, in both species. The shape also varies in individuals, as will be seen by comparing figs. 3 & 4, Pl. XXXIV.

The anterior pair vary in shape between an oblong with rounded corners (fig. 7) and a broad ovate (fig. 4).

The three anterior pairs present a slight roughness on the surface; but the posterior pairs are almost smooth.

The margin is entire, and not fringed.

In *P. squamata* (fig. 10) the surface in all the elytra is very rough, presenting large granular conical lumps, especially developed in the outer and posterior regions of the scale. Some of these granulations are red in colour, giving the rich grey colour which the elytra possess in this species. The outer and posterior margins, and in the anterior pairs the anterior margin also, are richly fringed with long processes, in addition to the tactile papillæ which are scattered over the surface.

Prostomium.—The prostomium differs in shape in the two species (Pl. XXXVI. figs. 15 & 16). In *P. clara* it is much more truncated anteriorly than in *P. squamata*. In the latter species the prostomial tentacles are obviously mere prolongations from its anterior edge. In *P. clara* the anterior portion is much smaller, and there is a tendency to form a transverse ridge, giving the impression, from a dorsal view, that the lateral tentacles spring from underneath the anterior edge of the prostomium. This they undoubtedly do in many species of Polynoina; but, from observations which I have made upon undetermined species collected at Naples and from the Norwegian Fjords, I have come to the conclusion that there may be every transitional condition between these two extremes.

Series of transverse sections have shown that these three tentacles are supplied with nerves directly from the supracæso-phageal ganglions, *i. e.* no doubt have an archi-cerebral nerve-supply, and so are not of the nature of appendages, although they simulate them in structure, but are mere prolongations of the prostomium; they thus have fundamentally the same origin in the whole group. The anterior edge of the prostomium may thin out into the bases of the tentacles; it may be thicker, and tend to form a transverse ridge, which may be produced and overhang the bases of the tentacles; small points may be formed here; and, lastly, these may be carried far forward, and so completely hide the origin of the lateral tentacles. If every intermediate condition between the two extremes can be found, these can hardly be used in generic distinctions.

In *P. squamata* the anterior pair of eyes is much larger than the posterior pair, and lie, as shown in Pl. XXXVI. fig. 15, very near them; but in *P. clara*, while the posterior pair have the same position, the anterior pair, which are of the same size, lie further forward.

First Body-Somite, Peristomial Somite (Huxley).—The most anterior somite of the body possesses much-modified parapodia. A notopodial and a neuropodial lobe may, however, be distinguished; and each bears four setæ. Huxley has described the existence of similar structures in *P. squamata* (an acicula and two minute setæ), and points out that this fact, which Max Müller* described in his account of the development of *Polynœ*, proves the peristomial cirri to belong to a modified somite.

Second Body-Somite, or Buccal Somite.—The second somite is also modified. The notopodial and neuropodial lobes are obscurely divided; both aciculæ are present; the notopodial setæ have the same general structure as in other somites, but the neuropodial setæ resemble the notopodial in structure rather than the neuropodial of other somites. This fact, which appears to have been overlooked, is interesting as connecting the normal parapodium with that of the much modified most anterior body-somite.

* Müller's Archiv, 1851.

This second body-somite appears to be the first elytron-bearing somite in all Polynoia.

The neuropodial cirrus is much modified, resembling a notopodial cirrus in size and shape, is bent inwards towards the mouth (fig. 1. buc. cr.), and is the buccal cirrus (Kinberg.). There can be no doubt that this buccal cirrus is a modified neuropodial cirrus; and the possibility of a neuropodial cirrus simulating a notopodial we have seen a similar case in the prostomial tentacles simulating notopodial cirri is of great importance to us in considering the homology of the pygidial cirri.

Palps.—The palps differ from all the other tentacular structures in being muscular along their whole length. They are capable of great elongation and contraction.

In *P. squamata* they are smooth; but in *P. elytr.* they have six longitudinal rows of tactile papillæ, each provided with its sensory hair.

These palps present more difficulty than do any of the other tentacles or cirri. They originate (sections of *P. (Hermatia) areolata*) just where the prostomium joins the peristomial and buccal somites, although they appear to have more connexion with the prostomium than with the other somites. Their nerve-supply appears to come from the supracrophageal ganglion. Their prostomial connexions are borne out when we compare them with similar organs in such simple forms as the Syllike, where they are evidently prostomial, springing (Claparède, loc. cit.) from its ventral surface.

This view is completely borne out by Max Müller's* account of their development.

Pygidial Somite.—The terminal somite is very much reduced, and appears merely as a support for the pygidial cirri. These resemble notopodial cirri in size and structure. They are well developed in both species under consideration; but in many species of Polynoia they are quite small. In such forms the anus is terminal; but where they are so strongly developed the anus is pushed forwards, and comes to lie on the dorsal surface.

I have found in two or three specimens of *P. elytr.* an acicula (fig. 6) running dorsally, and perforating a well-marked papilla, as do the other aciculæ. In other specimens, of which I have examined a large number with this special point in view, there is a trace of such a structure; but in the majority all trace is gone; possibly the acicula drops out while the animal is thus quite young.

In other undetermined species of *Polynoe* which I have examined there is, as a rule, a small acicula in some, a small acicula accompanied by rudimentary setæ in others, in the pygidial segment, most strongly marked where the segment is little modified. The presence of these structures seems to me of great interest, as showing that the pygidial cirri are the neuropodial (as they are ventrad of the acicula, whether that be neuro- or notopodial) cirri of a much-modified somite, a pygidial somite. Further, just as we found the second body-somite presented a connecting link between the first, the peristomial segment, and the other somites, so in the penultimate somite we find that the setæ are few in number, and not strongly marked in character, connecting the pygidial somite with those in front of it.

Nephridial Papillæ and Nephridia.—Minute and detailed as many of the systematic descriptions of various species of Polynoia are, it is not a little curious that the exist-

* Max Müller, Müller's Archiv, 1891.

ence even of these ventral papillæ has been so very generally overlooked. While Claparède, Malmgren, and Ehlers insert it occasionally in their figures, the only references to it are made by Huxley and Grube. Claparède, however, does describe the papillæ in *Hermadion fragile*, and suggests that it may be the orifice of the segmental organ. Huxley *, in his account of the anatomy of *P. squamata*, which was based upon his own observations, says:—"Springing from the neural surface of the somite, close to the parapodium, there is a small pyriform tubercle, divided by longitudinal grooves into about eight segments. This is possibly connected with the reproductive functions."

Grube † recognizes its wide-spread existence:—"At the point where the parapodium springs from the ventral wall of the body, exists in all Polynoina a very small papilla (ventral papilla), which, at any rate in pregnant examples, is perforated, and serves for the passage of the eggs to the exterior. The animals in which they run out to a point are probably males. I have repeatedly found sticking to the spots slimy masses, which, on account of their resemblance to those observed in living *Heteronereis* forms, I take to be spermatozoa. This papilla is generally present, but, as a rule, absent upon the first 3-6 seta-bearing segments."

I have had an opportunity of examining a very large number of living Polynoina, representing some sixteen or seventeen different species, and am in a position to corroborate Grube's statement as to its universal existence. Both Huxley and Grube accurately describe its position; it springs from the ventral wall of the body itself, and not from the parapodium. It varies very much in size in different species: in *P. clara* it is large and thick (Pl. XXXVI. figs. 17 & 18); in *P. squamata* it is much longer and thinner (fig. 19); in *P. spinifera*, Ehl., it is very slightly developed (fig. 20); and in *P. areolata*, Grube (fig. 21), it is merely a slight swelling of the body-wall, which is perforated. In all the other species examined the extent to which it is developed is intermediate to these conditions.

As Huxley points out, it may exhibit eight longitudinal grooves upon its surface. At the breeding-season the body-cavity is filled with the generative products, rendering the body-wall perfectly tense, and they are forced into the space in the wall of the papilla; the grooves then disappear. The constancy of their number points to some structural basis; but their absence in such a large number of species indicates that they have no very great significance.

The papillæ are absent, as a rule, from the eight most anterior somites, and are continued down to the penultimate somite. In *P. clara* there are eighteen pairs.

Careful and continued examination of various species has proved that they are not connected with the reproductive functions, but are the apertures of the nephridia or segmental organs, as Claparède surmised in his *Hermadion fragile*; serial sections combined with examination in the fresh state, both in the compressorium and after teasing, have revealed the whole structure of these organs (Pl. XXXVI. figs. 22-25).

* Huxley, 'The Anatomy of the Invertebrated Animals,' p. 231.

† Grube, "Bemerkungen über die Familie der Aphroditeen, III. Polynoina," Bericht der schlesischen Gesellschaft, 1876, pp. 26-52.

Ehlers* has described a segmental organ in *P. pellucida* as a contractile sac lying in the parapodium and opening externally by several (4-6) ciliated mouths upon both its notopodial and neuropodial faces, the internal opening lying near the dorsal wall of the somite. Ehlers describes these as occurring in every somite from the second onwards.

Claparède† states that he has observed the ciliated rosettes of Ehlers in *P. lunulata*, but, in spite of the transparency of the animal, has been unable to acquire the conviction of their communication with the segmental organs. I have not studied *P. pellucida*, but, from the analogy of other forms, strongly suspect that what Ehlers has seen is not the segmental organ at all‡. The nephridium, in all the forms which I have examined, is a funnel-shaped tube, the walls of which may be much plaited and folded, but it does not appear to be at all convoluted. This tube opens internally in the ventral region of the body, close to the two ventral muscular masses, and then runs posteriorly ventrally outwards. Near the base of the papilla its lumen dilates, forming a small vesicle, whence a straight tube of even diameter traverses the axis of the papilla. There is no muscular development in connexion with it at any part of its course; it never enters the parapodial region at all; and although ciliated along its whole length from the internal funnel to the vesicle, no cilia are developed at its external opening.

Fig. 22 is a diagrammatic drawing compiled from the series of sections &c.

Fig. 23 is a transverse section of the papilla, and shows the longitudinal grooves, the epidermis, which is continuous with the epidermis of the rest of the body, and the ciliated epithelium cells lining the excretory tube; between these is a layer of connective tissue, branched corpuseles in a connective jelly.

Fig. 24 represents a section of the tube near the internal opening, while fig. 25 is an intermediate section in the region of the vesicle. The body-cavity is packed with ova, which press the two walls of the vesicle together, and in many cases almost occlude the lumen. The ova force their way in between the nephridial epithelium and the epidermis, and thus, on an external examination, give the impression of being within the lumen of the papilla; and this appearance it is which has led previous observers to connect these papillæ with the reproductive function.

How do the generative products pass to the exterior? There certainly are no special ducts; and they cannot either find exit through those nephridia or by pores, temporary (*i.e.* ruptures) or permanent, in the body-wall. Ehlers and Sars both mention such pores as existing in the parapodial wall. The generative products are known to escape by rupture in other marine Annelids, *e.g.* *Polygordius*. All my observations upon living animals favoured this view. I never actually saw the ova or spermatozoa spontaneously shed; but the slightest irritation when the body-wall was tense caused a slight rupture here

* Ehlers, 'Die Borstenwürmer,' 1864-1868, p. 116.

† Claparède, 'Annélides Chétopodes du Golfe de Naples,' p. 374.

‡ Since this was written, Mr. W. A. Haswell, M.A., B.Sc., in "A Monograph of the Australian Aphroditea" (Proc. Linn. Soc. New South Wales, vol. vii.), has described the segmental organ in *P. (Antinoë) proclara* and *P. (Antinoë) Wahlili* allied to *P. pellucida*, Ehlers. That author has also arrived at the conclusion that Ehlers has not seen the true segmental organs, but only intestinal caeca: he describes the former as opening at the ventral tubercles, but does not give any figures.

and there, and the products streamed forth. I have kept such animals for a long period after this, and they have been apparently none the worse. I have certainly never seen ova or spermatozoa in the lumen of the nephridium.

Fig. 26, representing a longitudinal section of a neuropodial cirrus of *P. spinifera*, is inserted to show the large round connective-tissue corpuseles which exist there in addition to the branched cells. The nerve-filament passing up the axis is also shown.

Following the example of Sars, Claparède, Grube, and Ehlers, I have rejected Kinberg's and Malmgren's genera, and have used Savigny's original generic name *Polynoë*. I have shown that so many of the characters used by these authors to found generic distinctions are variable in the same species, and that with regard to others it is easy to find all intermediate variations between two extreme conditions.

I quite agree with McIntosh that the utmost importance may be attached to the exact character of the setæ, but think that he hardly sufficiently insists upon the variation which occurs in these in individuals, and the necessity of comparing equivalent setæ. The setæ, for instance, in the neuropodium of the third body-somite are totally unlike the neuropodial setæ of the somites which follow, and much more resemble notopodial setæ. An immense amount of variation may occur, moreover, in the notopodial setæ in any one parapodium.

With regard to the elytra, I have spoken of them as structures which do not belong to the parapodium. Their attachment is always to the dorsal surface of the somite proper; they occur side by side with notopodial cirri in *Sigalion* and its allies; and I have observed in *P. (Harmothoë) areolata* (I have not examined many other species from this point of view) that distinct rudiments of notopodial cirri—the whole of the basal portion, in fact—coexist with an elytron upon the elytron-bearing somite. The elytra have been spoken of as branchial in function; my sections (*P. areolata*) show that no blood can pass into them. Although they appear to be attached to the somite over a considerable area, the real attachment is almost linear; in the central region there is no attachment, and the epidermis is unbroken. Numerous muscles are attached all round this ring, and serve to move the elytron as a whole. Nerves pass into the substance of the elytron (which is quite solid), and, forming a regular network (which I have stained with gold), end in the numerous small papillæ, which are, no doubt, tactile and similar to those Claparède has described upon the cirri.

Characters of Polynoë clava (Montagu).—These may be summarized as follows:—27 somites; 12 pairs of elytra, borne upon somites 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23. Median tentacle twice as long as the lateral tentacles, bulbous below the apex, with a terminal filament. Lateral tentacles with similar structure. Palps tapering to a point, beset with six longitudinal series of small papillæ. Normal neuropodial setæ clavate, with talon-like apex, 7 or 8 pairs of pectinated frills, the most anterior provided with 5 long teeth upon its fine edge. Notopodial cirri about twice the length of the parapodium, with the same structure as the prostomial tentacles. Neuropodial cirri half the length of the parapodium, tapering gradually to a point, smooth. Elytron only slightly rough on the surface, margin entire. Anus on the dorsal surface. Pygidial cirri resemble notopodial cirri in structure.

DESCRIPTION OF THE PLATES.

pro, prostomium.
per, peristomium.
p, parapodium.
nt, notopodium.
nr, neuropodium.
cr, cirrus.

el, elytron.
pyg, pygidium.
buc. cr, buccal cirrus.
neph, nephridial papilla.
oc, eye-spots.

PLATE XXXIV.

- Fig. 1. *Polynoë clava*, ventral view.
 Fig. 2. *Polynoë clava*, dorsal view, elytra removed: *an*, anus.
 Fig. 3. *Polynoë clava*, dorsal view, body distended, elytra not meeting in the medio-dorsal region: *an*, anus.
 Fig. 4. *Polynoë clava*, dorsal view, body not distended, elytra overlapping in the medio-dorsal region: *an*, anus.
 Fig. 5. *Polynoë clava*, peristomial segment: *nt. cr*, notopodial cirrus; *nr. cr*, neuropodial cirrus; *not. set*, group of notopodial bristles; *nt. ac*, notopodial acicula.
 Fig. 6. *Polynoë clava*, pygidial segment: *pyg. cr*, pygidial (neuropodial) cirrus; *nt. ac*, pygidial (notopodial) acicula.
 Fig. 7. *Polynoë squamata*, anterior elytron. Owing to an error on the part of the lithographer this figure has been turned round; the lettering *ant.*, *post.*, *ext.*, and *int.* indicate its proper position.

PLATE XXXV.

- Figs. 8 & 9. *Polynoë clava*, anterior and posterior elytra respectively: *at*, position of attachment.
 Fig. 10. *Polynoë clava*, portion of elytron.
 Fig. 11. *Polynoë clava*, distal portion of notopodial bristle.
 Fig. 12. *Polynoë squamata*, distal portion of notopodial bristle.
 Figs. 12 *a*, 12 *b*, 12 *c*. Variations of same, all occurring in one parapodium.
 Fig. 13. *Polynoë clava*, distal portion of neuropodial bristle.
 Fig. 14. *Polynoë squamata*, distal portion of neuropodial bristle.

PLATE XXXVI.

- Fig. 15. *Polynoë squamata*, prostomium, showing eyes and bases of lateral and median prostomial tentacles.
 Fig. 16. *Polynoë clava*, prostomium, showing the same.
 Fig. 17. *Polynoë clava*, ventral view of two parapodia: *neph*, nephridial papillæ.

N.B. Figs. 18–21 are drawn to the same scale.

- Fig. 18. *Polynoë clava*, nephridial papilla, showing grooves on surface.
 Fig. 19. *Polynoë squamata*, the same.
 Fig. 20. *Polynoë spinifera*, the same.
 Fig. 21. *Polynoë areolata*, the same.

- Fig. 22. Diagram of the nephridium of the Polynoina: *ci*, ciliated internal opening; *l*, lumen of tube; *v*, vesicle; *neph*, nephridial papilla; *cut*, cuticle.
- Fig. 23. *Polynoë spinifera*, transverse section of nephridial papilla: *cut*, cuticle; *ex. ep.* epidermis; *ct*, connective-tissue cells; *int. ep.* epithelium of nephridial tube; *l*, lumen of excretory duct. $\times 550$.
- Fig. 24. *Polynoë spinifera*, transverse section of nephridial tube near the internal opening: *int. ep.* ciliated epithelium of wall of tube; *c*, granular contents. $\times 550$.
- Fig. 25. *Polynoë spinifera*, transverse section of excretory duct of nephridium in the region of the vesicle, showing collapse of the walls owing to the pressure of the ova in the coelom.
- Fig. 26. *Polynoë spinifera*, longitudinal section of a neuropodial cirrus, showing:—*ct*, branched connective-tissue corpuscles; *c*, large connective-tissue cells; *n*, nerve. $\times 600$.

XI. *On Simondsia paradoxa and on its Probable Affinity with Sphaerularia bombi.* By T. SPENCER COBBOLD, M.D., F.R.S., F.L.S., Correspondent of the Academy of Sciences of Philadelphia.

(Plate XXXVII.)

Read March 15th, 1883.

THIRTY years ago (that is, in March 1852) several examples of a remarkable parasite were discovered by Professor James B. Simonds in the coats of the stomach of a German hog. The "host" died at the Zoological Society's Menagerie, Regent's Park.

The only notice, hitherto recorded, of the worm occupies a few lines of my introductory treatise published in the autumn of 1864 ('Entozoa,' p. 79). The notice is fragmentary and unaccompanied by any technical description of the worm, which, however, I provisionally named *Simondsia paradoxa* in honour of the discoverer. It was only at the last moment, when the said treatise was going to press, that the late Principal of the Royal Veterinary College called my attention to his specimens and drawings; hence the paucity of details, and other deficiencies in the record there given. What, at the time, was regarded as the head of the worm turns out to be its tail; and the inference which Professor Simonds had drawn respecting the strongyloid character of the parasite proves to be incorrect. In justice to the discoverer, it must nevertheless be said that similar misinterpretations have repeatedly occurred, as, for example, in the case of Røederer's *Trichuris*, now universally known as *Trichocephalus*.

Shortly after the original notice appeared, the drawings of *Simondsia* were lost. The illustrations had been executed by a skilled artist, the late Mr. Woodman, under Mr. Simonds's superintendence. Only quite recently, on the occasion of Mr. Simonds retiring from London, the illustrations were found; and thus at length both the drawings and specimens have become available for establishing the genus on a securer basis. As the specimens are unique and also few in number, I have been reluctant to mutilate them; but, fortunately, their transparency is such that nearly all the important parts can be seen without dissection.

Although in 1864 I had only opportunity to make a brief outward examination, enough was seen to justify the employment of a new generic name, whilst the specific title bore reference to the presence of a large spherical and somewhat flattened organ whose significance was altogether paradoxical. The singular development in question many times exceeds in size all the rest of the parasite, its diameter being fifteen times that of the body of the worm at its centre (Pl. XXXVII. figs. 1 & 2). In the original notice this organ was described as consisting of "special folds of integument formed for the lodgement of unusually developed uterine organs;" but there is here a false interpretation. At the time this conclusion was formed I had not examined the organ microscopically, neither had helminthologists been made acquainted with Schneider's

interpretation of the somewhat analogous appearances exhibited by *Sphæruletia bombi*. I am not sure, indeed, that, even now, Schneider's view meets with universal acceptance. In Sir John Lubbock's well-known first memoir on *Sphæruletia* (which not only added largely to our knowledge of the distribution of that parasite amongst bees, but also extended the facts of its minute anatomy), it was reckoned that the male *Sphæruletia* was "twenty-eight thousand times smaller than the female." Now, what our President regarded as the female worm, Schneider avers to be the uterus only, and that which our President not unnaturally regarded as the male parasite, Schneider has declared to be the female worm deprived of her uterus or, rather, having her uterus, several thousand times bigger than her body, in a state of prolapsus*. To this point I shall advert again presently. Meanwhile, with a provisional acceptance of Schneider's view, I think that, while on the one hand we must regard the genus *Simondsia* as altogether unique, we must, on the other hand, recognize its approach towards *Sphæruletia* in respect of the enormously developed reproductive organs of the female, which, in both genera, lie, as it were, outside the body proper.

Until the appearance of Sir John Lubbock's first memoir, in the 'Natural History Review,' the so-called male *Sphæruletia* had never been indicated. If Schneider's views be correct, it obviously results that the male worm is still unknown to science, and that its discovery, as announced in the pages of the 'Review' for 1867, really refers to part of the body of the female *Sphæruletia*: in fact, her uterus was the only part hitherto seen by Dufour and other observers. When, in 1867, Professor Huxley lectured at the Royal College of Surgeons, I understood him to accept Schneider's view without hesitation; nevertheless, in his more recently published 'Manual,' where he deals with the genus *Sphæruletia*, no reference is made to the Berlin helminthologist's opinion. I was especially interested in this question, inasmuch as I had, during the previous year, prepared and mounted several examples of *Sphæruletia bombi* for the College Museum†. From the abdomen of a bee, which was one of the old Hunterian specimens, I removed three *Sphæruletiae*, and, in accordance with Sir John Lubbock's views, described them as "three females, two of them having extremely minute males sexually attached." The catalogue was prepared in 1865, nearly a year prior to the publication of Schneider's well-known monograph.

During the month of May, 1865, the late Dr. Ormerod, of Brighton, sent me some parasites from *Vespa rufa* and *Vespa vulgaris*. These I at once recognized as examples of *Sphæruletia*: and I noted the fact that all the insect hosts were females. This peculiarity of habit agrees with what Sir John Lubbock has observed in the various species of infested *Bombi* and in *Apithous*. Now, whatever be the significance of this singular habit, it is one which is by no means confined to the aberrant genus of parasites in question. The same peculiarity affects *Filaria terebra* which infests the abdomen of the female black-tailed deer (*Cervus columbianus*).

The circumstance that the male *Simondsia paradoxa* (Pl. XXXVII. fig. 3) exhibits

* Monographie der Nematoden, 1866, S. 322.

† Catalogue of Entozoa in the Museum of the Royal College of Surgeons (London, 1866), Nos. 37, 38, p. 6.

no departure from the ordinary nematode type of structure prepares us, in some degree, for a similar outcome in respect of the hitherto undiscovered male *Sphæruletia*. Be that as it may, the mere fact that Sir John Lubbock did not notice any spicule in the body of the alleged male *Sphæruletia* is pretty strong proof that the minute creature was not of that sex. Professor Schneider at once saw the significance of this negative character*.

The chief point of interest in *Simondsia* lies in a correct interpretation of the morphology of the organ which I call the "rosette." I do not pretend to have settled the question of its homology: but, guided by the facts observed, I think that the rosette is a prolapsed uterus. It is thus the equivalent of the so-called "generative animal" of *Sphæruletia*, whilst the body proper represents the "nutritive animal," as interpreted by Schneider. It is furnished internally with two egg-containing horns. The rosette shows evidence of spiral twisting: and this may sufficiently account not only for its flattened spherical figure, but also for its unlikeness, in this respect, to the equivalent organ in *Sphæruletia*. I presume that the branched external processes are homologous with the spherules of *Sphæruletia*, whilst the ultimate cecal capsules have, as far as I know, nothing comparable to them in nature. Their outer surfaces are finely tuberculated. Internally, the ceca and branches of the uterine wall are lined with granular debris, which I believe to be the remains of cells, comparable to the polygonal cells figured both by Schneider and Sir John Lubbock in *Sphæruletia*, such cells being held by the former observer to be characteristic of uterine structure in this class of animals.

No diagnosis, either of the genus or species, having been given, I submit the following:—

SIMONDSIA. Cobb.

A genus of endoparasitic nematodes, in which the female is furnished with an external and much enlarged uterus, whose walls expand into branches terminating in ceca. Females encysted. Males free.

SIMONDSIA PARADOXA. Cobb.

Head bluntly pointed: neck with narrow lateral wings: mouth simple, with two prominent side papillæ: body of uniform thickness generally, but externally supporting, in the female, a large rosette-shaped organ formed by the uterus; tail of the male spirally twisted, suddenly narrowed to a blunt point: spicules two, long and slender: tail of the female twice as thick as the body, conical, bluntly pointed, with three broad-based spines immediately above the anus.

Length of the male half an inch. Length of female six tenths of an inch.

Hab. Stomach of the domestic hog (*S. s. serotia*, var. *domestica*): males free: females encysted within the walls, their heads projecting into the cavity of the organ through a narrow passage of intercommunication.

* Since this paper was read, Prof. Anton Schneider has announced the actual discovery of the male *Sphæruletia* and has cleared up the mystery attaching to its development. See 'Zoologische Beiträge,' Bd. i. S. 1, Taf. 1. Breslau, 1883.

The host was a "boar" suffering from an affection of the skin, a circumstance which led to its being killed and employed for dissection-purposes. Though well fed, it was a poor, lean animal, and, during life, afforded neither sign nor symptom of gastric disorder. Before Professor Simonds detected the parasites, some portions of the stomach had already been removed; and thus it is concluded that many specimens of the parasite escaped observation.

The cavities, or cysts, formed in the walls of the stomach by the female parasite are remarkable structures. Each gastric cyst contained a single female worm. The cysts projected both externally, at the peritoneal surface, and internally, causing a bulging of the mucous membrane.

Professor J. B. Simonds states that there was no evidence of the existence either of congestion or of inflammation in the surrounding tissues. When a cyst was opened, some clear fluid escaped; nevertheless a small aperture at the mucous surface permitted the head and neck of the female parasite to project into the cavity of the stomach. The cavity of each gastric cyst not merely enclosed the body of the worm, but formed, as it were, a perfect cast of the rosette-like organ. On transverse section, each gastric cyst displays six or seven distinct circular rows of depressions internally (Pl. XXXVII. fig. 4). These depressions are regularly arranged, and are themselves made up of smaller cavities, generally from four to six in each of the larger depressions. The ultimate caecal ends of the rosette are received into still smaller cup-shaped cavities proceeding from the secondary depressions. The number of these caeca varies considerably, some of the main branches of the rosette supporting upwards of forty of them.

The formation of these peculiar gastric cysts can only have been brought about by the gradual development of the enclosed parasite, the gentle and equable pressure of the slowly expanding body of the worm causing so perfect an adaptation of the environment that every part of the thin-walled rosette became protected from injury. It is hardly likely that the ultimate purpose of this cyst is concerned with the mere steadying, or fixing of the body of the worm during sexual congress.

The symmetry of form and sculpturing of the cysts thus produced by *Simondsia* is almost as perfect as the somewhat similar appearances seen in fossil casts; and, although their mode of formation must have been essentially different, it is impossible that the analogy should escape notice. From the helminthic standpoint, these gastric cysts must be pronounced unique; nevertheless, in respect of their mode of formation, something of the same kind may be observed in the cast-like depressions formed by the anchored heads of various species of *Teniae* and *Echinorhynchi*. Pentastomes and *Gastrophilus* larvæ also produce depressions of a simple character.

As regards the anatomy of *Simondsia*, I have only further to state that the integument is everywhere striated, except at the surface of the rosette. Only on the tail of the female worm were there any spines observed. They occur on the ventral surface, at a distance of about $\frac{1}{40}$ of an inch from the tip. The spines, three in number, are placed in a transverse row. They are nearly as broad at the base as they are long, separately measuring about $\frac{1}{350}$ of an inch from base to apex. The body of the male worm affords an average diameter of $\frac{1}{80}$ of an inch, the female being one sixth broader; the tail of the

female, however, at a line corresponding with the spines, gives a breadth of fully $\frac{1}{36}$ of an inch. The intestinal tract is simple in both sexes, and terminates close to the end of the tail; but in the female the gut is much widened within the caudal enlargement of the body. In either sex, the œsophagus is of great length, measuring fully $\frac{1}{16}$ of an inch from the mouth to commencement of the chylous intestine. The lateral oral papillæ give a length of about $\frac{1}{360}$ of an inch from base to apex. As regards the reproductive organs of the male worm, we find two long, elastic, and very delicate spicules, each measuring about the $\frac{1}{36}$ of an inch in length, and only little more than the $\frac{1}{1000}$ of an inch in breadth. In the male, both the intestine and the sexual organs terminate in the usual manner. In the female the whole mass of the ovarian filaments, together with the tubæ and uterine branches, are lodged within the rosette; but where the vulva is situated could not be ascertained with certainty. The junction between the tubæ and horns of the uterus is particularly well marked (Pl. XXXVII. fig. 2, *a*); but the mode of union of the uterine horns with the rosette was not observed. Although no vulva was actually seen, it may be surmised to terminate somewhere at the base of the rosette in the ventral line.

The eggs of *Simondsia* are small in size and extremely numerous (Pl. XXXVII. fig. 5). Always more or less elongated, their figure varies considerably, some being oval, others elliptical, with a tendency to become constricted at one or both sides. Some of them finally assume either a reniform or even a more or less hourglass-shaped figure (Pl. XXXVII. fig. 6). Their average length is from $\frac{1}{600}$ to $\frac{1}{850}$ of an inch, their breadth at the centre in constricted specimens being sometimes less than the $\frac{1}{2000}$ of an inch. Their walls display a double contour; and the more advanced of them contain imperfectly developed embryos.

DESCRIPTION OF PLATE XXXVII.

- Fig. 1. Female *Simondsia paradoxa* removed from its cyst: *a*, head; *b, b*, lateral ake; *c*, lower end of œsophagus; *d d*, chylous intestine; *e, e, e*, ceca of the rosette; *f*, tail. $\times 12$ diameters.
- Fig. 2. Detached rosette, with horns of the uterus partly drawn out from the interior: *a, a*, junction of the tubæ with the upper ends of the horns; *b, b, b*, uterine branches. $\times 12$ diam.
- Fig. 3. Small male *Simondsia paradoxa*: *a*, head; *b*, tail. $\times 12$ diam.
- Fig. 4. Section of the wall of the stomach of *Sus scrofa*, showing the interior of a parasite-bearing cyst exposed by transverse section: *a*, lower half of the cyst; *b, b, b*, secondary and ultimate depressions. $\times 6$ diam.
- Fig. 5. Fragment of one of the uterine horns, showing numerous ova in the interior. $\times 150$ diam.
- Fig. 6. Group of eggs, removed from the above. $\times 250$ diam.
- Fig. 7. Outline of the tail of the male worm: *a*, anus; *b*, spicules. $\times 32$ diam. Outlined with the aid of a camera. Original.

XII. *On the Testis of Limulus.* By W. B. S. BENHAM, Esq. (*Communicated by*
Prof. E. RAY LANKESTER, M.A., F.L.S.)

(Plate XXXVIII.)

Read June 21st, 1883.

WHILE working in the laboratory at University College, last October, as one of Prof. E. Ray Lankester's assistants, he suggested that I should examine the testis of the King-Crab. By his kindness (here I will take the opportunity of thanking him for his kind help and suggestions) I was fortunately able to work on the fresh animal. Owing to the difficulty, and the time taken, in removing the carapace, not much could be done in a day; and though it kept fresh till the next day, after that it had to be placed in spirit; in this state the finer networks are easily broken, and the finer blood-vessels may be mistaken for the ducts, though the mistake is soon discovered, owing to the absence of networks in the former. The testis is packed by the ramifications of the gastric gland (the so-called liver), and lies almost superficially.

The only description of the generative organs of the King-Crab appears to be that by Prof. Owen, which was published in the Linnean Transactions for 1873. He there describes and figures a portion of an ovary; his description opens thus:—"The ovarium is a system of ramified tubes and cavities, occupying chiefly the dorsal region of the body; it extends along the median part of the thoracetron" (=abdomen), "and expands laterally in the cephalotron" (cephalothorax). His figure shows rather thick ducts; and the network represented is not extensive, but, so far as it goes, corresponds roughly with the distribution of the testis. It may be said that the testis forms a reticulated tube all over the dorsal portion of the thorax and abdomen, mixed up with the liver. Owen divides the ovary into anterior and posterior median lobes, with anterior, lateral, and postero-lateral branches and networks proceeding from the former lobe.

We can scarcely, as will be seen, divide the network of the testis into such lobes, though roughly there are anterior (thoracic), posterior (abdominal), and lateral (thoracic) networks. As in the ovary, the main duct of the testis, from the external aperture, divides, on reaching the surface of the liver, into three main branches, having about the same course as in the female organ.

Professor Owen's figure represents the branches as symmetrical on each side; such is not the case with the network of the testis, as will be seen. He suggests as a cause for the posterior median lobe of the ovary dividing into two branches, at the junction of abdomen and thorax, which run forward to the anterior median lobe, that the pressure on it, between heart and intestine, which would take place on flexion of the abdomen on the thorax would be too great if median, and hence there is a branch on each side, outside the pericardium. In the case of the testis, the ducts are much smaller than those

represented in his figure of the ovary, so that they occupy but little space between the pericardium and intestine, and the pressure on it would be very slight. The *external aperture*, both of oviduct and sperm-duct, is similarly situated on the posterior face of the VII. appendage, about one third of the distance from its attachment, near the middle line on each side (as shown in fig. 2).

The course of the spermatie network.—The sperm-duct rises from the external aperture on the VII. appendage, upwards and outwards, parallel to the “anterior lamellar” muscle of this appendage. It reaches the surface of the liver, through which it runs, just within the muscle attached to the sixth thoracic limb (fig. 1, D^l D^r).

Lateral network.—Here it breaks up into three branches; one runs backwards and outwards, behind this large coxo-tergal muscle, giving off branches, which anastomose with one another, forming a network, which includes in its meshes some of the smaller muscles of the sixth coxa; the ducts get finer as they recede from the main duct (they are drawn too thick in the figure), and they run to the side and to the posterior corner of the thorax.

Just after passing the large muscle, an anterior duct is given off, passing along the outer edge of the coxo-tergal muscles, forming a network, which probably runs right away to the front; but I was unable to follow it further than is represented in the figure, as here the ducts get very fine and easily break. The second main branch from the duct runs inside the coxo-tergal muscles, forwards, giving off networks between the various muscles, some of the smaller ones being included in the meshes; these networks pass outwards, and probably anastomose with that on the outer side of the coxo-tergals. However that may be, inside it runs right away in front of the muscles, and on its inner side gives off branches to a median network.

The median network.—The third principal branch is represented on the right side, and does not appear on the left, so that there is a certain amount of asymmetry. This runs inwards at first, behind the branchio-thoracic muscle, then forwards along its inner border, where it gives off a network across the middle line, lying between the pericardium above and the alimentary tract below. This network (A , fig. 1) was removed, and cleaned, as far as it could be, from liver and connective tissue, and mounted; it is represented in fig. 3, where A A represent the lateral boundaries; on the ducts are seen the sperm-sacs, which are usually in groups, one of which opens into the duct, and the others into one another.

In front of this network is another continuous with it, but separated from it in the figure, owing to the rupture of some of the finer ducts. The anterior lateral boundary of the left side is formed by a duct running from the front of the left branchio-thoracic obliquely forwards to the right side. The network alongside the second coxo-tergal muscle, the most anterior of the large muscles, sends small branches forwards, but not very far, and backwards a larger duct, whence branches and networks pass between the muscles, probably to join a similar lateral network on the right, as was described for the left side.

The left border of the median network is formed by two very fine ducts parallel with one another, on the inner side of the branchio-thoracic muscle. These two ducts anastomose here and there, and join a network in the abdomen, across the middle line, beneath

the pericardium; the ducts then become excessively fine, and the network, at any rate the sides of it, ends at about the XI. appendage. The network was here incomplete, as I had removed the portion *A* previously to noticing these fine posterior ducts.

The lateral network of the right side is doubtless similar to that on the left; but I did not follow it throughout its extent.

Thus there is a continuous network of ducts more or less all over the body, lying, in the median line, below the pericardium and above the intestine; this median network runs throughout the abdomen and thorax, though the ducts are larger more anteriorly. This corresponds to Prof. Owen's "anterior and posterior median lobe" of the ovary; the lateral lobes or branches of this are represented by the lateral networks outside the coxo-tergal muscles of the thorax.

That the testicular network does thus extend everywhere is shown by the fact that, when the carapace is cut off, a white viscous fluid flows out, which consists of blood mixed with spermatozoa; this soon coagulates.

The *spermatozoa* consist of a small rounded head about $\frac{1}{1000}$ inch in diameter, with a flattened wide "neck" and a long mobile tail (fig. 4). The mobility of the spermatozoa of *Limulus* was discovered and recorded by Prof. Lankester in 1881 (Quart. Journ. Micr. Science, vol. xxi.).

The *sperm-sacs* are seated in groups upon the sides of the ducts; two or three, sometimes more, are in connexion with one another, one of which opens into the duct (figs. 3 & 5). These sacs are subglobular in shape, and are surrounded by a delicate membrane. These are filled with groups of spermatozoa without tails, their further development apparently taking place in the ducts as they approach the aperture. Sometimes sperm-sacs are seen at some distance from a duct, and I could, in many cases, trace no ductule from them (as at *B*, fig. 5). Perhaps it is here that the sperm-cells are produced, and by continual enlargement of the sperm-sacs, by subdivision of the sperm-cells, and stretching of membrane round them they reach the ducts.

All these structures, as well as the caeca of the great gastric gland, are packed by a fibrous connective tissue, which is very loose (fig. 5, *C*).

The *wall of the duct* (fig. 6) is made up of interlaced tendinous-looking fibres; by tendinous I mean that they are more or less highly refractive and parallel to one another. These are arranged longitudinally, circularly, and obliquely, while the inner surface is lined by columnar cells. The duct is often filled with the unripe spermatozoa, which, here and there, have aggregated into rounded masses near the walls (fig. 5, *S*).

Significance of the above observations.—The importance of the observations thus recorded depends upon the fact that in no crustacean do the ducts of the generative glands form a network, whereas in the Scorpion (and other Arachnids), as in *Limulus*, they do. Hitherto the fact that the ovarian ducts of *Limulus* form a reticulum was the only information which we possessed as to the form of the generative organs in *Limulus*. The observations recorded in the present paper show that the duct of the male organ in *Limulus* also has the form of a reticulum. Thus a new and important confirmation is afforded to the proposition maintained by Prof. Lankester in his essay

"*Limulus* an Arachnid," viz., that the organization of *Limulus* is closely similar to that of the Scorpions, and has no special agreement with that of any Crustacea.

A second point of considerable interest is the apparent isolation of many of the spermatie sacs, and the probability that they are *not* diverticula of the spermatie duct but, secondarily, in the course of their ripening acquire a connexion with it, the two structures having developed independently. This is in accordance with what is known as to the essential nature of the genital ducts of Arthropoda, although it cannot be said that we have, at present, a sufficient series of observations upon their development to warrant a generalization.

DESCRIPTION OF PLATE XXXVIII.

- Fig. 1. The carapace has been removed from the cephalothorax (*Ceph*), and the tergum from the abdomen (*Abd*), to show the course of spermatie network amongst the liver (*li*), which is not indicated: *A*, median network; *L*, lateral network; *Cx¹-Cx²*, coxo-tergal muscles, the rounded knobs (*k*) to which these are inserted are parts of the entocoxites of the appendages; *Br.th*, branchio-thoracic muscle; *D^l, D^r*, the left and right main sperm-ducts, dipping down to the external aperture in appendage VII.
- Fig. 2. *Genital operculum*, half nat. size. Posterior face, to show the papillæ in which the external apertures of the genital duct are situated; *gen. d*, sperm-duct dividing into three main branches; *g.p*, its external aperture; *St.g*, stigma; *ts*, tendinous stigmata; *ant.*, anterior lamellar muscle; *ext.*, external branchial muscle.
- Fig. 3. Portion of the median network *A* (fig. 1), magnified about $9\frac{1}{2}$ times; *AA*, lateral boundaries of this portion; *d*, duct; *sp*, sperm-sacs.
- Fig. 4. Mature spermatozoa.
- Fig. 5. Portion of a section showing sperm-sacs, $\times 22$: *d*, sperm-duct; *W*, wall of duct; *L*, epithelium of duct; *S*, aggregations of spermatozoa; *c*, surrounding connective tissue; *M*, membrane of sperm-sac; *B*, sperm-sac with no apparent connexion with duct.
- Fig. 6. Portion of wall of sperm-duct, seen from without; enlarged about 39 times.
- Fig. 7. Transverse section of duct, $\times 39$: *d*, lumen of duct; *L*, epithelium; *n*, nuclei; *W*, wall; *S*, spermatozoa within the duct.

XIII. *The Metamorphosis of Filaria sanguinis hominis in the Mosquito.* By PATRICK MANSON, M.D., Hong Kong. Communicated by DR. COBBOLD, F.R.S., F.L.S.

(Plate XXXIX.)

Read March 6th, 1884.

SIX years ago I described the metamorphosis undergone by the embryo *Filaria sanguinis hominis* in the body of the mosquito*. I hoped that (considering the practical importance of a correct knowledge of the life-history of this parasite) the statements I then made would, long ere this time, have been thoroughly confuted or confirmed. If we judge from the wideness of its distribution and the grave character of the diseases it gives rise to, the *Filaria sanguinis hominis* is infinitely the most important of the animal parasites attacking man, much more important than *Trichina* or *Echinococcus*. Biologically the story of its life-history is interesting, and even more wonderful than is that of either of these parasites. Nevertheless, although from both a practical and a scientific point of view it is important to have this assertion of mine about the rôle of the mosquito cleared up, it still remains but half confirmed, half believed.

With the exception of Lewis in India†, Myers in Formosa‡, and Sonsino in Egypt§, I do not know that any one has worked seriously at the subject. And although both Lewis and Sonsino have confirmed my statements as to the entrance of the *Filaria* into the mosquito, and followed up part of the metamorphosis, neither of them has advanced his observations so far as to be able to confirm my statements as to the later stages of this, or positively to prove that the mosquito is, or is not, the intermediary host.

Some eminent helminthologists in England accept my statements and endorse the inferences I have drawn—Cobbold for example. But in other quarters, so far from securing acceptance of my theory, the work of Lewis, on account of the hesitation and scientific caution with which he expresses himself, has had the effect of inducing a certain amount of scepticism. Leuckart is sceptical; and of course the scepticism of so eminent an authority is of great weight in influencing opinion, especially in Germany. Some of our own zoologists, also, I understand, share the views of Leuckart.

Recently I received a copy of a lecture by Mr. B. Scheube of Leipzig entitled ‘Die Filaria Krankheit.’ In this very excellent lecture occurs the following passage:—“Der englische Parasitolog Cobbold hat Manson’s Ansicht von der Entwicklung der *Filaria sanguinis hominis* adoptirt und auf die Analogie mit der *Filaria medinensis* hingewiesen, welche ihre Metamorphose im Süsswassercyclopen durchmacht. Von Leuckart || dagegen werden gegen die Manson’schen Beobachtungen aus mehreren Gründen starke

* Proc. Linn. Soc. March 7th, 1878. China Customs Medical Reports, Sept. 1877.

† 14th Ann. Rep. of the Sanitary Commissioner with the Government in India.

‡ China Customs Medical Reports, March 1881. 21st issue.

§ Medical Times and Gazette, May 13th, 1883, p. 494; Sept. 22nd, 1883, p. 340.

|| ‘Die Parasiten des Menschen,’ 1. 2. Aufl. p. 85. Leuckart’s Jahresbericht für 1875–79, p. 163.

Zweifel erhoben, welche auch die späteren Mittheilungen von Lewis nicht beseitigen konnten. Letzterer constatirte zwar ebenfalls, dass die *Filaria sanguinis hominis* in den Magen der Moskito übergeht und hier gewisse Veränderungen erleidet; er fand auch bei denselben jugendliche Nematoden, die möglicher Weise einen weiteren Entwicklungszustand der aufgenommenen darstellen, aber es ist durchaus nicht sicher, dass dem in Wirklichkeit so sei. Von einer anderen Seite konnten die Manson'schen Beobachtungen nicht bestätigt werden. Myers wollte dessen Versuche auf Formosa, wo die *Filaria*-Krankheit selbst nicht autochthon vorkommt, nachmachen, kam aber zu dem Resultate, dass die *Filaria*-Embryonen von den Moskito vollständig verdaut wurden Nach alledem müssen wir die Frage über die Entwicklung der Filarie noch als eine schwebende betrachten." These words, I presume, represent the attitude of the scientific and professional mind, on the continent at all events, on the subject of *Filaria*-metamorphosis. My assertions may be true, but in all particulars they have not been confirmed, and the evidence I formerly adduced cannot be considered sufficient.

Impressed by the practical importance and scientific interest of this matter, and being naturally anxious that what I had stated and knew to be true should be accepted, and failing decided confirmation from other observers, I thought I could do some service to my profession and this branch of helminthology if I again went over the ground I had twice before trodden. With these and other criticisms before me I have done so, and now endeavour by a short statement of what I found, once for all to settle the matter. This statement I supplemented with a series of illustrative drawings carefully made from fresh preparations and drawn to scale. And, in order that I may quote the testimony of others, I have shown the whole series of my experiments and preparations to Drs. Macleish and McDougall, medical men residing in Amoy, and perfectly competent judges on such points. I have their permission to say that they believe my descriptions and drawings to be in the main correct. Further, I have forwarded to friends in England and elsewhere microscopic preparations which, should the frail structures they contain retain the appearances they had when they left my hands, cannot fail to satisfy the most cautious and scientific mind.

There are three ways by which we may settle the relationship of the mosquito to the *Filaria* :—

1st. By tracing the *Filaria* into this insect, witnessing its metamorphosis therein, and finally its escape at an advanced stage of development.

2nd. By showing that it is only in those mosquitoes that have fed on filariated blood that the metamorphosis of a nematode occurs—that no such phenomenon can be witnessed in mosquitoes fed on non-filariated blood.

3rd. By filariating a man, or a lower animal, by means of *Filaria* metamorphosed in passing through the mosquito.

The first two of these methods I have employed; the sequel contains a description of my results. The third test of my theory remains to be applied. For myself I have not sufficient hardihood or scientific fervour to attempt it in my own person, but I am convinced that a properly planned and conducted experiment would lead to positive results. Both Lewis and Sonsino, besides other observers, confirm me in the statement that the

mosquito, when feeding on the blood of a filarious subject, imbibes the *Filaria*. Lewis confirms me in the statement that nematodes at a stage of development slightly more advanced than those found in the newly ingested blood are also to be found in the mosquito. But Lewis says he could not satisfy himself that these two forms belong to one and the same species of nematode. Neither he nor Soudano has found advanced forms, so advanced that from their appearance they would be justified in concluding they were fit for independent life. Possibly, suggests Lewis, the more advanced forms are embryos of some other species of nematode, and not the *Filaria sanguinis hominis* at all. In my observations I paid particular attention to this point. If I succeed in connecting the more advanced forms of nematode embryo, as seen by Lewis, with the unquestioned embryo *Filaria sanguinis hominis* found in newly ingested blood, and with the later forms which I had already described as being equipped for independent life, then there is no longer any room for doubt about the rôle of the mosquito, and I can claim that Lewis's observations confirm my own.

I would remind the reader that the parasite called *Filaria sanguinis hominis* is a minute nematode embryo which in certain warm countries is found in the blood of Man. It is the offspring of a mature *Filaria* living in the lymphatic vessels. The young find their way into the blood-circulation along with the lymph.

No form intermediate between the mature *Filaria* and its embryo has hitherto been found in Man. There is no evidence of growth about the embryo, neither has any provision in its structure by which one might suppose it could pass from one man to another been discovered. It seems most probable, therefore, that like many other parasites it requires the services of an intermediary host—1st, to remove it from the body of the host; 2nd, to nurse it till it becomes equipped for independent life; 3rd, to place it in a position for obtaining access to its final host.

In our search for this intermediary host we must be sure the animal we encounter can fulfil these conditions. In addition to this there are two other circumstances in connexion with the *Filaria* which must also be recognized in fitting it with an intermediary host. Such an animal must have a geographical distribution corresponding to that of the *Filaria*; and it must also be nocturnal in its habits. The reason for the first of these conditions is self-evident; the latter is indicated by the curious fact in the history of the *Filaria*, that the embryo appears in the blood only at night. This peculiarity in the habits of the *Filaria* has now been so frequently demonstrated and confirmed that I need concern myself here only with the mention of it.

There are many reasons why one should regard the mosquito as the animal most likely to fulfil all the conditions required. These reasons I will not enlarge on. I will confine myself to the description of what actually occurs in the relationship of the mosquito to the *Filaria*, feeling satisfied that in this is the best proof that the mosquito is the true intermediary host of the *Filaria sanguinis hominis*.

In experimenting with the mosquito there are two points I was careful in attending to; I employed the proper species of insect, and I took care that its only food was the blood of a filariated man. Those who would repeat my experiments must bear these two points in mind. The plan of procedure I found most convenient was as follows:—I

engaged a man in whose blood the *Filaria* abounded. A large square wooden frame (10 ft. \times 10 ft. \times 6½ ft.) covered with mosquito-netting and provided with a door was erected in a room where mosquitoes abounded. Under this mosquito-house the man slept, the door of the house being closed some hours after he had gone to bed. Next morning the mosquitoes that had entered by the door, and preyed on the man's blood, were found clinging to the inside of the netting, their abdomens distended with blood. These my servant captured under a wine-glass, and after paralyzing them with a whiff of tobacco smoke transferred them each to a dry phial covered with gauze. When the insects had recovered from the effect of the tobacco and ascended the side of the bottle for a little distance, a small quantity of water was introduced through a pipette. Latterly I employed large-mouthed stoppered bottles, holding about two ounces, instead of the phials. Tobacco could in this way be dispensed with, and a considerable mortality avoided. The bottles were dated and put under a dark shade. When the weather became cool I got better results by placing the bottles in an incubator, where the insects were kept in a damp atmosphere at a temperature ranging from 80° to 85° Fahr. In this way I endeavoured to imitate nature. Every morning during many weeks a fresh crop of *Filaria*-charged mosquitoes was gathered. For the purposes of this investigation quite a thousand insects had to be provided. From time to time, as required, they were removed from the bottles after being killed by chloroform. The legs and wings and head were torn off. The thorax was then separated from the abdomen, each being placed on a separate slide. In the case of the abdomen the contents were expressed by rolling a penholder from the free to the severed thoracic end; a cover-glass was then placed on the expressed blood. If necessary, a little water or sulphate of soda solution (sp. gr. 1.050) was used to soften the blood and allow of the easy removal of the two large ovaries, which, when crushed, obscure the slide very much. The thorax is best treated by being broken up, and teased out with a couple of sharp needles in a droplet of water, before the cover-glass is applied. Thus prepared, an inch objective readily detects the parasites among the tissues of the insect. To preserve the *Filariae* thus displayed the cover-glass must be carefully lifted up, and what remains on the slide allowed to dry, the large pieces of mosquito debris being first picked off with a fine forceps. After drying for a day or, better, two, it may be stained with an aniline dye (gentian violet answers very well), and after washing and redrying mounted in Canada balsam. In the case of *Filaria* in the blood from the abdomen of the mosquito it is only necessary to dry the preparation before mounting in balsam. The red colour of the blood gives sufficient contrast to display, at all events, the outline of the parasites. Whenever practicable, fresh and unstained preparations should be examined; for while stained specimens show the outline well enough, they are useless in studying the details of internal structure.

My mosquito-house and filarious patient were visited by three species of mosquito, perhaps four. All of these were capable of imbibing the *Filaria*, but only one of them is, I believe, capable of conducting the metamorphosis to a successful conclusion. Both of the impotent species are of the kind known as tiger mosquitoes, *i. e.* their bodies and legs are banded, or flecked with white. One is quite a large insect, half an inch in length, with numerous sooty, easily detached scales; the eggs of this species when

deposited on the surface of water, do not keep together in a boat-shaped cluster, as do those of the true *Filaria* mosquito, but float about separately, tending to adhere to the sides of the bottle. There is no danger of confounding this species with the true *Filaria* mosquito. The other species of tiger mosquito is smaller, and in this way is liable to be mistaken for the *Filaria* mosquito; but a close inspection shows it to be smaller in size and darker in colour than the true species; and, in addition to these points of distinction, the little flecks of white and white bands on legs and body serve, with a little care, to prevent mistake. I have often found the *Filaria* in the blood in the abdomen of both of these mosquitoes, but never in such numbers as one finds them in the true *Filaria* mosquito. In the thorax I have found them slightly advanced in development in the larger tiger mosquito; but although I have examined a considerable number of this species on the third day after they had fed, I have not found the *Filaria* at this later period, when in the true *Filaria* mosquito they abound, and cannot readily be overlooked. I would not be positive on this point, as my observations on the tiger mosquito are not sufficiently numerous; but my impression is that both species are incapable of acting as efficient intermediary hosts.

The true, or what I believe to be the true, *Filaria* mosquito is a brown insect, about $\frac{3}{16}$ of an inch in length, snuff-brown in colour, without any particular markings whatever. In some specimens, and especially some days after feeding, and when her eggs have been deposited, there is an appearance of banding about the abdomen; but there are no distinct markings, as in the case of the tiger mosquitoes. It appears to thrive best when the thermometer ranges from about 75–84° Fahr. In the very hot weather it disappears, or is languid, and the rate of maturation of the ova (in those specimens one can procure) is too quick apparently for the metamorphosis of the *Filaria*. Consequently, experiments in June, July, and August may not be uniformly successful. In Amoy, September and October are the best months for observations on this species. The female alone is the blood-sucker. She feeds but once if not disturbed, and lays her egg about the fourth or fifth day afterwards. Some lay on the third day, and some do not part with their ova till the seventh. As a rule, they die soon after laying, but a few survive till the sixth or seventh day, and in these alone is the metamorphosis of the *Filaria* completed. Perhaps one mosquito in ten attains this age, at all events in confinement. Possibly in normal surroundings a larger proportion survive.

On commencing the study of the metamorphosis of the *Filaria* in the mosquito the first circumstance that strikes one is the largeness of the number of *Filariae* ingested by the insect. In a corresponding quantity of blood, drawn in the usual way from the finger, not one fourth part of the number contained in the blood of the insect's abdomen would be found. It is quite a common thing to find 30 or 40 *Filariae* in the minute speck of blood we express from the abdomen. Often this number is exceeded, and more than once I have found them literally in hundreds. This indicates that the mosquito in some way or another is adapted for fishing the *Filaria* out of the blood stream. The proboscis of the insect, as it lies in the lumen of the vessel from which blood is being imbibed, must tend to arrest the parasites as they are swept against it by the stream, just as a stake in a stream of water accumulates straws and sticks; and the lashing

movements of the little animals tend to entangle them still further, and bring them under the influence of the suction-force exercised by the insect.

Arrived in the abdomen of the mosquito the *Filaria* for a short time retains the appearances and movements that it exhibited while in its human host, and which have frequently been described (fig. 1). Presently a delicate, closely set, transverse striation, as if from general longitudinal shrinking, gradually becomes very evident. The sheath also in many cases can be more readily seen, and oral pouting is very distinct. Within an hour of the time of ingestion, the *Filaria* usually casts its sheath, which, by careful searching, may be seen either trailing after it, or lying across it, or somewhere near. After the casting of the sheath transverse striation and oral pouting become still more distinct, and one can almost fancy the parasite has a true mouth surrounded by lips. It is impossible to determine this, however.

Until the casting of the sheath, the peculiar lashing movements of the animal continue; but when this has been effected a change in the character of these movements is in many instances observable. Hitherto they have been free, lashing, purposeless apparently; and although the little animal has kept in perpetual and vigorous motion, it has never changed, materially, the spot it moved in. There has been no locomotion. But when the sheath has been got rid of, the nature of the motion changes to a snake-like wriggle of regular undulations, which cause a definite forward movement (fig. 2). In many specimens this is very striking. If motion is prevented by some insuperable obstacle in one direction, the *Filaria* retreats and tries in another. It is evidently endeavouring to change its locality.

The object of this singular change in the character of the movements exhibited by the *Filaria* is explained if we examine the thorax in a batch of insects at short intervals after they have fed. We tease it up with needles in a little water, or sulphate-of-soda solution, tearing up the muscles of the wings thoroughly, before applying the cover glass. Examined, thus prepared, within a short time, say half an hour, of feeding, all the *Filariæ* are to be found in the abdomen, none in the thorax; after an hour, two or three may be found moving among the muscles of the thorax; after another hour, many more may be detected here, till at the end of 12 or 18 hours, the thorax is found to be full of parasites. Therefore, the movement of progression we see in the *Filaria* that has cast its sheath in the blood in the abdomen, has for its object the migration of the parasite.

Not all, but a very large proportion of the injected *Filariæ* do thus migrate. My former observations were made entirely on *Filariæ* found in the abdomen, or believed to be in the abdomen. Not suspecting this migration, and finding metamorphosis going on in the abdomen, I may have, unwittingly, included some of the viscera of the former in my examinations of the latter. On that occasion I traced out the metamorphosis to its conclusion, and entirely in what I thought, at the time, were abdominal tissues. It is likely, therefore, that migration to the thorax is not a necessary step indispensable for the welfare of the parasite. But it is certainly the usual first step for the animal to take, and it is a fortunate one in the interests of the observer, as in tracing the subsequent steps of the metamorphosis, the ova, which in the abdomen are so annoying from their obscuring the field when ruptured, are not encountered. Lewis was

the first to mention this migration; until I had read his description of his experiments on *Filaria* metamorphosis, I entirely overlooked this significant point.

Most of those *Filaria* that do not migrate, gradually become granular, their outlines become dim and undefined, and their movements cease. I suppose they are finally digested.

If we examine carefully a *Filaria* that has just reached the thorax, we find that the striation observed in specimens from the abdomen has disappeared; the body is beautifully transparent; there is no sheath or sign of double outline; oral movement still persists, but the general body-movement has slowed down till, in some instances, the animal is almost passive. The body is somewhat thicker and, it may be, shorter, and an obscure undefined cloudiness can be seen in the interior (figs. 3 & 40). How far this dissipation of the transverse striation, slowing of movement, and swelling may be owing to endosmosis of the water that we necessarily employ in mounting the specimen, it is difficult to say. I know that if the young *Filaria* is soured in a large quantity of water, it becomes so transparent that, under a low power, it is readily overlooked or even cannot be seen. Sudden endosmosis, I believe, often ruptures and dissipates it. I therefore, in examining the thorax of the mosquito for the *Filaria* at any time during the first two or three days of the metamorphosis, employed a solution of sulphate of soda (sp. gr. 1050) to tease up the tissues in. After application of the cover glass, the soda solution was gradually diluted by placing a drop of pure water at one edge of the slide, while the solution was withdrawn by a piece of filter paper placed at the opposite edge. The soda solution shrivels, and renders irregular the outline of the *Filaria*, but by gradual dilution, as described, the little animal is rendered plump and natural-looking again. I believe it is the sudden immersion in water that is dangerous to the integrity of the *Filaria*. For convenience in description, I divide the metamorphosis into six stages*. What I have now related constitutes the first stage, viz.—ingestion by the mosquito, transverse striation, casting of the sheath, and subsequent migration. At the conclusion of this stage it is quite a common thing to find, with very little searching, 30 or 40 *Filaria* in the thorax, and very many more can usually be detected half concealed by careful focussing among the viscera and fragments of muscle.

The first noticeable change in the *Filaria* after migration is a shortening and general thickening of the entire body, the extreme tip of the tail being alone exempted from this process. This part retains its original dimensions for a time, while the remainder of the animal continues to swell. Thus the caudal appendage, characteristic of the *Filaria* during the greater part of its stay in the mosquito, is formed. In some specimens a thick hyaline-looking substance seems to cover as an integument the body of the animal from the mouth downwards, stopping short, however, almost abruptly at the root of the tail. The tail in all cases is evidently of the same structure as the interior and mass of the body. In others, the integument I mention is not observable, the tail seemingly

* The reader must bear in mind that this division of the metamorphosis is entirely artificial. No such thing exists in nature. What I describe as stages, in reality overlap each other; the graduations of development insensibly merge one into another.

being differentiated from the rest of the animal simply by its not having partaken in the general swelling (figs. 4-10-38, 41, and 42).

At this stage movement still persists; but as the body swells, motion becomes fainter and more intermitting, till, in many examples, it finally ceases soon after migration has been effected. There is a tendency now for the oral end to become tapered, and more conical, one or more black points being visible at the very end.

The body continues to swell till it has more than trebled its original diameter, and become shorter by one third. Thus the tail comes to look a mere appendage stuck on one end of a sausage-shaped mass.

At first, and often all through the subsequent steps of the metamorphosis, the tail does not correspond with the axial line of the body, but is quite to one side. In others, especially at a later stage, the position of the tail appears to be, and possibly is, axial, although this effect is produced in many instances by the position the animal is viewed in, according as the tail is to right or left, above or below; in both the latter positions it must appear axial, although it may really be quite to one side.

When the body has attained a thickness of about the fifteen hundredth or the two thousandth of an inch it lies sometimes outstretched, sometimes gently bent, occasionally curved on itself, so that mouth and tail are almost touching (fig. 42). The oral end gives the impression that there is an orifice there, but that it is firmly pursed up. Movement of the body is now rarely seen. Occasionally in some there is a slow general bending and extension, and in others a peculiar shivering movement. The tail still at times is vigorously flexed and extended. No organ or structure of any definite kind can be made out even with a high power; only a little in advance of the tail, where the anus is afterwards formed, sometimes an aggregation of minute cells with relatively large nuclei can be seen (fig. 4). The rest of the body is made up of a cloudy granular material enclosed in a very delicate integument. The latter can be made out only after crushing of the body and partial escape of contents, or when the slide has partially dried. In such circumstances we may sometimes see a funnel-shaped mouth into which the delicate integument is reflected (fig. 10).

The thickening of the body, differentiation of the tail, and first indications of a distinct mouth constitute the second stage of the metamorphosis, and usually require two or three days for their completion.

About the third or fourth day we often find the body of the sausage-shaped *Filaria*, which hitherto has shown little or no structure, filled with a crowd of minute shining granules (fig. 11). These, I believe, are nuclei which from extreme transparency and refracting properties, similar to that of the stroma of the animal's body, could not at an earlier stage of development be recognized. In others again, apparently somewhat more advanced, cells to which these nuclei belong become obscurely visible (figs. 12 to 20). These cells are exceedingly minute. Each possesses a distinct nucleus, and together they make up the entire mass of the body and tail inside the delicate cuticle.

About the time the cells become visible the rudiment of the future anus shows itself as a sort of pit or vacuole a short distance in front of the tail (figs. 12, 13, 15, 39, etc.). When viewed in profile this pit or vacuole seems infundibuliform, and the outline of

the margin of the body of the animal is broken at this point. Thus it would seem that here there is a hole in the cuticle. When looked at directly from behind, or in front, it appears round. From its first appearance, and until the last step of the metamorphosis is entered on, granular matter and minute nucleated cells are seen to escape from this point. Very little pressure and sometimes even the mere immersion in water is sufficient to bring about this granulo-cellular discharge from the anus. I do not consider that this discharge comes from inside an alimentary canal, but look upon it as perianal tissue which the exterior tenuity of the walls of the rectum, and the absence at this point of integument, permit to escape, rupture being favoured or brought about by endosmosis of water used in mounting.

Coincident with the appearance of anus and cells the mouth advances in development. From being pursed up it seems to open, and gradually four large fleshy lips are fashioned (figs. 16 to 30).

Then a line, at first very faint and broken, shows itself. Running in the axis of the body for the most part, its destiny appears to be to connect mouth and anus. Around this line as it becomes thicker and longer, cells are seen to be arranged (figs. 14 to 25). The line does not seem to extend in all cases quite to the anus, but terminates, as far as one can make out, in advance of this some little distance among certain comparatively large and prominent cells. By degrees this line, the rudiment of the alimentary canal, becomes thicker, and the arrangement of nucleated cells around it forming the walls of the alimentary tube becomes very distinct. In some instances the line itself is manifestly double-tubular. Probably a fine membrane lines it, continuous at the mouth with the skin, and is the lining-membrane of the future alimentary canal.

How this alimentary line is produced it is difficult to say. It is certainly not a process derived from the integument dipping in at mouth or anus; for, in many instances in which it is visible, it is only so about the centre of the animal, and is not traceable into either mouth or anus. My impression is, that this line is produced something after this fashion :—After the cells I have described as filling the body at the beginning of the third stage have been formed, they arrange themselves into two sets. One set goes to the periphery of the body to form future muscular and fibrous walls: the other set accumulates in single file in the centre of the body in a line extending from mouth to tail. The cells thus arranged in single file divide and subdivide longitudinally as regards the axis of the *Filaria*, the lines of division radiating from the centre of the original file of cells, like the segments of an orange. This would have the effect of making the point of convergence of the lines of cleavage very distinct—the alimentary line. After a time the cells swell out or increase laterally, thus opening out their line of convergence, which thus is converted into a tube, the alimentary canal. This process extends no further back than the anus: but the central line of cells can sometimes be traced as far back as the tail, and it is principally from having seen this post-anal line of axial cells that I infer this method of explaining the formation of the alimentary line and canal.

While the alimentary line and canal are being formed, cells range themselves, as I have just said, around the periphery of the *Filaria*, lining the skin. But between this

tegumentary set of cells and those forming the alimentary canal there is a distinct interval, a sort of peritoneal cavity, in which at a later stage the alimentary tube moves freely, not being attached at any point save at the anus and mouth (fig. 25).

At the conclusion of this, the third stage of the metamorphosis, the *Filaria* measures from $\frac{1}{100}$ " to $\frac{1}{80}$ " in length, by $\frac{1}{850}$ " to $\frac{1}{500}$ " in breadth, or thereabouts. There is considerable diversity both in size and shape. The mouth is wide open; the tail is large and sickle-shaped, and the cells of the body usually dip into it. The alimentary line runs from mouth to anus; and the cellular nature of the entire animal, with the exception of the integument, is easily demonstrated. Motion is entirely suspended.

Growth hitherto has been very slow, but now, when the fourth stage commences, it becomes rapid, the animal quickly attaining a length of from a seventieth to a fiftieth of an inch. The walls of the alimentary canal can be distinctly traced as the walls of a tube from the open mouth to near the anus, but not quite into structural continuity with the latter. The cellular structure of the mass of the body is often beautifully distinct (figs. 23, 24, 25, 26). The body retreats from the tail, which becomes a mere empty integumental appendage, so transparent that it can with difficulty, in many cases, be made out (fig. 34, 35). The addition of water to the preparation causes the little animal often to rupture after a few minutes at one or two points, a cloud of cells and granules escaping.

In not a few instances a vacuole, similar to that which preceded the formation of the anus, is seen at this stage at a point some little distance behind the mouth. This may be the result of endosmosis, but possibly it is the forerunner of vulva and organs of generation. In one instance (fig. 23) I detected a line among the cells which, from its position, forcibly suggested that it was the rudiment of organs of generation; but as this was a solitary observation, I attach no great weight to it. The vacuole, in the position I mention, is quite a common occurrence.

When the body has attained its maximum thickness the fifth stage commences. The cells, especially in the anterior part, gradually lose their distinctness, and the mouth inclines to purse up, while the animal, as a whole, elongates and attenuates. In some the lengthening and thinning begin at the head and extend backwards, so that if we find such a *Filaria* in the middle of this extension-process, it has a narrow anterior half rather abruptly swelling out into a thick posterior half with the dimensions of the previous stage (fig. 27). Such a specimen resembles in shape a hock-bottle. A very few elongate anteriorly and posteriorly simultaneously; and we may find in one undergoing this process a small segment of the middle of the body still thick and unextended (fig. 28). More generally, however, the extension-process occurs simultaneously throughout the body, the fore part being always rather in advance of the rest (figs. 29, 30).

Sometimes at this stage, just before the mouth closes up, the alimentary tube is seen very distinctly. It moves freely in the body-cavity, accommodating itself to the gentle movements which the anterior half of the *Filaria* now exhibits. The pharynx in such a specimen is distinctly indicated by two short parallel or curved dark lines, terminating at one end in the mouth, at the other leading into the oesophagus (fig. 44). At its other extremity the oesophagus ends in a thick bulbous valvular-like arrangement opening into the intestine, which in its turn may be traced as a distinct tube almost to the anus

(figs. 26, 29, 30). When the mouth closes, as it does presently, all or nearly all trace of viscera and all trace of cells vanish. The body assumes a fibrous and very transparent look, and little structure can be made out.

The movements just alluded to begin in the neck of the *Filaria*. At first they are of a gentle to-and-fro swaying character; but gradually, as the whole body becomes attenuated, they extend backwards *pari passu* with the attenuation, and until the entire length of the animal becomes more or less animated. These movements do not last longer than a few minutes, at this stage, after immersion in water, differing in this respect very much from what happens at the next stage.

The fate of the sickle-shaped caudal appendage, which up to this time has been so characteristic of the growing *Filaria*, is a little doubtful. It may be that the extreme end of the now truncated body gradually forces its way into the remains of the tail, from which it had before retreated, stretching it so as to have it as a closely fitting integument. More probably the sickle is cast off in a general ecdysis, which about this stage, I believe, occurs. Fig. 46 tends to show that this is probably what really happens; a new skin is shown covering the papillated tail, inside of and quite distinct from that constituting the "sickle." In the example from which this sketch was made, on tracing the skin, continuous with the "sickle," forwards, a point, about abreast of the anus, was reached where it seemed to be peeling off or breaking down.

About this time at the very extremity of the truncated tail, two or three cells become prominent, their nuclei enlarge, and the surrounding protoplasm is increased in bulk. These cells after a time protrude from the general surface, and gradually become converted into the circle of three or four papillæ which characterizes the *Filaria* at the end of this, and during the last stage of metamorphosis (figs. 30, 31, 43, 46, 32, 33). I am not sure if one or two of these papillæ be not the remains of the stump of the original tail; nor am I quite sure of their number, as it is usually impossible to obtain a view in which all can be seen at once. After a time the papillæ spread out like the petals of a flower, extending considerably beyond the margin of the circumference of the body, so that in time they become the broadest part of the animal.

The purpose of these caudal papillæ is difficult to divine. Possibly they are of use in aiding the animal in its future journey through a human host. One can understand how by opening out on any retrograde movement they will prevent this, give a firm foothold, so to speak, to the boring *Filaria*, and favour forward movement. They are not oral, as I at one time supposed.

Together, the papillæ, the anus, and alimentary line are very deceptive, and give the idea that this part is really the head of the animal, the papillæ apparently surrounding a mouth with organs of generation opening in close proximity, as is so commonly the case in the *Filarie*. But I have satisfied myself that in these features we have really to do with the tail of the animal, not the head.

During the progress of these changes the *Filaria* has gradually stretched from perhaps the fortieth to the sixteenth of an inch in length; at the same time its breadth has decreased one half. The anterior end tapers gradually and is then abruptly rounded off, hardly any structure being visible about it. The posterior end also tapers slightly from

the anus backwards, and its very extremity is covered with the three or four papilla just described. Faint indications of an alimentary canal are at times discernible, but further than this no trace of internal structure can be clearly made out. The parasite has now arrived at the sixth and last stage of its metamorphosis, and its stay in the mosquito is about concluded.

Such specimens as I have been describing as belonging to the fifth stage are to be found only about the end of the sixth, and beginning and middle of the seventh day, from 130 to 156 hours after ingestion. The *Filaria* of the sixth stage I have only seen in mosquitoes from 156 to 160 hours after capture, probably about seven days after feeding. Most mosquitoes lay their eggs and die during the fifth or sixth day after feeding, consequently it is a rare thing to find an insect of the age requisite for the maturation of the *Filaria*. Probably of twenty mosquitoes one or two may attain this. I have seen many *Filariae* in the fourth and fifth stages, but very few in the sixth and last.

During this stage the swaying movements that had commenced during the fifth gradually become more active. The animal is now no longer burst or killed by immersion in water. On the contrary, even as we look at it, the water we have just immersed it in seems to have a vivifying effect on the parasite; its tissues appear to become more consolidated, its motions more active, it seems to feel that it has got into its proper element. It rapidly acquires great muscular power, it wriggles, twists, bends, extends, and lashes about in all directions (figs. 23, 33). As seen with an inch objective it resembles nothing so much as the embryo *Filaria* in the blood looked at through a quarter-inch; the tail, of course, is different, but the character of the movements is exactly the same. One peculiar motion is strikingly like one that is often seen in the blood-*Filaria*. Often it pauses in the midst of its contortions, and suddenly extends itself, remaining outstretched for a moment, its body quivering in a sort of tetanic spasm. Those who have watched the movements of the *Filaria* in the blood will recognize what I mean. In other examples the wriggling movement is not seen, the activity of the animal being expended in frantic rushes forwards and backwards, and in every direction. I presume this description of movement belongs to a slightly later stage than does the wriggling motion; probably it is the motion suited to the time when the mosquito has died and fallen into water, and the parasite has obtained its liberty.

Frequently, during the contortions of the animal, it turns its mouth towards the observer, and seems to be endeavouring to uplift the cover-glass. During this movement we can see that the mouth is pursed up into a cone, the lips being firmly approximated; and, around the spot where the mouth must be, a number of exceedingly minute horny-like papillae are arranged. This may be the boring-apparatus. But the motions of any animal I have examined at this stage have been too incessant to permit a satisfactory view, and these boring-papillae may be, to some extent, matters of imagination. So incessant are the movements that it is quite impossible to obtain satisfactory measurements. After watching one for over an hour, and despairing at length of getting it to slow down, I killed it by instilling a little osmic-acid solution below the cover-glass. It then gradually slowed down, stretched out, and died. I found it to measure $\frac{1}{16}$ " \times $\frac{1}{850}$ ". In a good light this particular parasite was perfectly visible to the naked eye.

I believe the *Filaria*, after it has attained this final stage, has but a very short time longer to pass in the mosquito. I am inclined to think it preys on the tissues of the insect, and thereby contributes to its death. For, in examining mosquitoes found dead on the surface of the water, and which I know could have died only a very short time before, I have been struck with a singular absence of viscera and muscular tissue—the thorax seemed but a hollow shell. Again, some mosquitoes, even after death, cling or stick to the sides of the vessel containing them; in such specimens, also, I have remarked an absence of viscera and muscular tissue. My impression is, that these have been consumed by the *Filaria*, that the death of the insect had been thereby hurried, and that when this occurred the parasite bored its way out of the body, and thence sped to the water. I have never found a *Filaria* in the last stage of the metamorphosis in a dead mosquito; often, however, I have found them at all stages but this, even up to the time when they measure the fortieth or the thirtieth of an inch in length. The final stretching process must be rapidly effected, lasting probably an hour or two; and, as during it the *Filaria* becomes more than double in size, there must be expenditure of the tissues of the intermediary host to provide pabulum for this rapid growth. Hence, in some measure, it comes about that one rarely catches the *Filaria* in the last stage of growth, and that the dead mosquito has an empty thorax.

Such, I believe, is a true description of the life of *Filaria sanguinis hominis* in the mosquito. Some of my interpretations may be wrong, but all the principal facts I have stated are true. I have verified them over and over again.

I can understand how, if fig. 1 and fig. 34 are compared, some doubts may arise as to their connexion. The contrast between fig. 1 and fig. 23, or between fig. 23 and fig. 33, is great—so great that unless one had carefully traced the connecting links step by step, one would positively declare them organisms of entirely different species. Over and over again, when working at the *Filaria* of the fourth or fifth day, I have hesitated to believe it was really the outcome of the *Filaria* I had seen in the abdomen of the mosquito an hour or two after feeding; and I have turned to mosquitoes of the first, second, and third days to reassure myself of the migration to the thorax, the differentiation of the tail, the swelling of the body, the formation of the mouth, anus, and alimentary lines before I was at my ease as to the genesis of the particular organism that I was specially engaged in studying. But now, to my mind, there does not exist the slightest doubt in the matter.

Besides being able to trace the gradation in mosquitoes of different ages, we often encounter specimens of the *Filaria*, at all stages of development from fig. 3 to fig. 14, in one and the same mosquito. Sometimes in an insect in which a *Filaria* like fig. 14 is found, many others, at all stages of development, from fig. 14 to fig. 24, may be encountered. And so with the latest stages: fig. 23 may be found in a slide in which fig. 33 is moving. This gradation is very striking, and clearly indicates the connection between the *Filaria* ingested by the mosquito and the *Filaria* about to leave it.

The most difficult step to follow, and the one over which Lewis apparently hesitated, is that represented from figs. 4–12. If, however, insects of from twenty-four to forty-eight hours after feeding are studied, transition-forms are found in abundance. Figs. 40,

41, 42 are from the same insect. I have seen and sketched specimens resembling figs. 3, 8, and 12 in the same field of the microscope, and lying across each other.

In the little caudal appendage that characterizes the *Filaria* from the second to the fifth stage we have a strong argument for believing we are concerned with the same species during all these stages. It ceases, however, to be distinctive towards the end of the fifth and during the sixth stage; but here a curious circumstance comes to our assistance in establishing identity. The thick cellular body of the fourth and commencing fifth stages is motionless; but as the anterior part fines down and stretches out, it at the same time acquires movement. A difference also obtains between these two parts as regards their capacity for being stained with gentian violet. The posterior and cellular part takes the stain with difficulty, or not at all; whereas the anterior fibrous and active part takes the stain rapidly and deeply. Now we sometimes find a *Filaria* with a long stretch of the fore part of the body in thickness and general appearance like that of fig. 31, and in very active movement, dragging after it a limp and seemingly paralysed posterior and cellular part, rupturing readily on immersion in water, and showing all the characteristics of the cellular stage. Further, on applying the stain to such a specimen, the active fore part is deeply affected, whereas the limp hind part is but slightly tinged*. Such a specimen bridges over the step from figs. 23 to 33. Catching specimens such as fig. 27 and fig. 28 in the act, so to speak, of stretching, distinctly establishes that the *Filaria* of the sixth stage is but an advanced form of the *Filaria* of the fourth, and, by a similar process of reasoning, of the first, and of the *Filaria* in the human blood.

I can imagine that some may found an objection to the theory of the action of the mosquito on the fact that, of the hundreds of *Filariae* entering a certain mosquito, only a dozen or so will attain the more advanced stages of development; and that, of those that do thus advance in development, most perish in consequence of the death of the insect before the *Filaria* is equipped for independent life. It is true that the great majority cease to develop at a very early stage; others, after advancing a little, seem to die and wither. Fig. 36 is from such a specimen. Perhaps only certain tissues or organs of the mosquito favour complete development, and in their blind wandering few of the *Filariae* reach these. But these facts are no argument against the theory that the mosquito is the intermediary host of the *Filaria*: indeed, on the contrary, they are in entire consonance with what we know of the life-histories of other parasites. Of the millions that leave the parent, but one or two ever reach maturity. The journey from the uterus to the spot where maturity is attained is beset with dangers, the measure of these dangers being the prodigious numbers that start on the journey.

* Strange to say, the fully developed *Filaria*, as that represented in figs. 32, 33, does not take the stain well. It seems to me that the age of the integument has something to do with the facility with which the stain is absorbed. Specimens, as at figs. 22, 23, 25, do not stain well, I believe the reason being that the integument in these is old and, presumably, dense. But the anterior half of fig. 27 would stain well: it is the growing half, and, I think, has just undergone ecdysis, and the new skin is easily permeated by the dye. Its posterior half, however, will not stain at all, or but very slightly and unevenly: the old skin is not yet cast, and is dense and impervious. The new skin, after a time, as it ages, also becomes dense, so that by the time the animal has grown to the size of the original of fig. 33, it is impervious, and will hardly allow the passage of the gentian violet.

Frequently during my study of the metamorphosis in the mosquito, it has occurred to me that the later stages of what I describe as the *Filaria* of man in the mosquito, may really be stages in the development of a purely insect parasite like *Gordius* or *Hermis*, and not the *Filaria sanguinis hominis* at all. Perhaps, I conjectured, this animal may escape from the body of the mosquito into water, where it may acquire organs of generation and breed, and its young may afterwards enter the body of the mosquito larvæ, and so complete the cycle. But if this is the case, there must be a time in the histories of the human *Filaria* and this hypothetical animal when it is impossible to discriminate between them. I have never been able to find a break in the chain of development.

Moreover, if the mosquito is liable to be infested by a nematode parasite peculiarly its own, and if the developmental forms I have been describing belong to such a parasite, then we ought to find them in mosquitoes that had fed on non-filariated, as frequently as we find them in mosquitoes fed on filariated blood. If one filarial form could be found in a mosquito fed only on non-filariated blood then my theory about the rôle of this insect is in danger of falling to the ground.

This is a point I gave some attention to. Simultaneously with observations on mosquitoes fed on the blood of my filarious subject, I carried on others on mosquitoes caught in the mosquito-nets of coolies and servants living in my house. The result was very striking. I carelessly assumed that my servants were free from *Filaria*, and did not examine their blood, but trusted to the mosquito to pick out for me those who might be filarious.

Two mosquitoes were brought to me by coolie No. 1. One of these I examined at once—no *Filaria*; the second I kept till the fourth day before examining it—no *Filaria*.

Coolie No. 2 brought two mosquitoes. I examined one on the first day but found no *Filaria* in the blood in the abdomen. The second I kept till the third day. I examined its thorax very carefully, and then had the mortification of finding a sausage-shaped body exactly like that represented at fig. 12. There could be no doubt about its nature. I thought my theory was upset, and all my work useless. At 9 P.M., however, I examined blood drawn from this man's finger, and had the satisfaction of finding in it plenty of *Filaria*; subsequently he contributed *Filaria*-charged mosquitoes for my investigation of the metamorphosis. The mosquitoes he brought me were often devoid of *Filaria*; he was a lazy man, slept much during the day, and in a very dark room such as mosquitoes affect even during the day, hence many of the insects he found in his net were charged with blood drawn at a time when the *Filaria* is not in the general circulation.

Coolie No. 3 brought on one occasion two, and on another occasion five mosquitoes. Their examination gave this result:—

Mosquito examined	on 2nd day.	No <i>Filaria</i> .
"	"	on 3rd day. "
"	"	at 74 hours. "
"	"	at 96 hours. One sausage-shaped <i>Filaria</i> .
"	"	" Two <i>Filaria</i> .
"	"	" Many <i>Filaria</i> .
"	"	" Several <i>Filaria</i> .

Again my theory seemed doomed to collapse. But I examined the man's finger-

blood in the evening with the same results as in coolie No. 2; it contained plenty of *Filaria*.

Coolie No. 4 brought six mosquitoes with this result, that three of them when examined ninety-six hours after capture were found to contain *Filaria*, and three of them yielded no parasitic form whatever. This man's blood was examined at 9 P.M., and, like that of coolies No. 2 and 3, was found to contain many *Filaria*. These coolies all came from Hooreoah, a district to the north of Amoy, in which a very large proportion of the inhabitants are filariated.

It was now evident I must examine mosquitoes from some less questionable feeding-ground before I ventured to draw any conclusion from this endeavour to prove a negative. I had a boy of about 15 years of age for a servant; he was healthy and his blood did not contain *Filaria*. I got this lad to bring me his mosquitoes, with this result:—Eight mosquitoes examined sixty-four hours after capture—no *Filaria* found; one mosquito examined eighty hours after capture—no *Filaria*; one mosquito examined eighty-eight hours after capture—no *Filaria*; five mosquitoes examined one hundred and four hours after capture—no *Filaria*. I examined a few mosquitoes fed on other non-filariated individuals, and with the same negative results.

Many years ago, in searching for the intermediary host of the *Filaria immitis*, I examined many tens, if not hundreds, of mosquitoes that had fed on dogs' blood; but in no instance did I remark, although I was on the outlook for such, an advanced form of filarial development.

Lewis also did not find sausage-shaped nematodes in any mosquitoes but in those that came from a certain room where it was afterwards discovered that a filariated man slept. He examined with a negative result many mosquitoes that had preyed on the blood of dogs or birds.

Similarly Sonsino found *Filaria* in about half his mosquitoes; they were captured in a bed where two men slept, one of whom had *Filaria* in his blood, whereas the other was not thus infested.

The inference from these facts is obvious. It is only mosquitoes that have fed on the blood of filariated men that contain the developmental forms I have described.

In the foregoing I think I have conclusively shown that the mosquito fed on filariated human blood ingests the embryo *Filaria sanguinis hominis*, that while in the mosquito the *Filaria* undergoes great developmental changes, and that it finally quits this insect as a large and powerful animal equipped for an independent life. I have also shown that the mosquito fed on non-filariated blood exhibits, when dissected, no such parasitic forms. I therefore infer that the parasitic forms I meet with in the mosquito fed on filariated blood are really advanced forms of the embryo *Filaria* ingested with the blood, and that the mosquito is the proper intermediary host of the *Filaria*. I do not see how this inference can be avoided. It would be much more satisfactory, and an easier method of demonstration, could we watch an individual *Filaria* in its progress from the circulation down the proboscis of the mosquito into its stomach, watch it wriggling there, cast its skin, and, changing its method of movement, worm its way through the tissues into the thorax, become passive there among the muscles while it acquired size, an alimentary

canal and other organs, and enhanced muscular power; then eat or bore its way through the integuments of the dying mosquito, and finally obtain liberty in the water into which the insect has fallen. It is impossible to do this; but, by comparison of a large number of dissections, we can follow the history of the animal in the mosquito almost as perfectly as if we had watched in transparent tissues the progress of a single individual from the human body to the water.

The experimentum crucis of this theory, as I have already said, I have not had the hardihood to attempt. But from what I have written, any one anxious to make it will have no difficulty in gathering what is likely to be the most successful method. Were I to attempt it I would proceed in this fashion:—I would feed my mosquitoes on a filarious subject, I would collect them every morning, giving each a bottle to itself. Those that survived to the afternoon of the seventh day I would transfer to test-tubes; these I would invert over a watch-glass, containing a little water. When the insect died I would allow it to remain on the water a few hours and then remove it. The water it had fallen into, and which probably now contains the *Filaria*, I would transfer to a stock-bottle containing water. This process I would repeat for several days. I would then administer portions of the contents of the stock-bottle to the subject of the experiment. I would continue this for a month, every day adding fresh mosquito-water to the stock-bottle, and every day administering a draught of its contents. After a time I would commence the examination at night of the finger-blood. I am quite satisfied as to what would be the result.

EXPLANATION OF PLATE XXXIX.

[All the figures with the exception of figs. 10, 31, 35, 37, 43, 44, 45, and 46, are magnified about 188 diameters.]

Fig. 1. The embryo *Filaria sanguinis hominis* as it appears in the blood, or lymph, or in the abdomen of the mosquito immediately after ingestion, $\frac{1}{90}'' \times \frac{1}{3000}''$.

Fig. 2. A *Filaria* about an hour after ingestion by the mosquito. The sheath has been cast, transverse striation and oval pouting are very distinct, and the animal is indulging in the snake-like wriggling by which it moves from the abdomen to the thoracic viscera. In the mosquito from which this specimen was obtained many *Filarie* were found in the newly ingested blood in the insect's abdomen. All were active and transversely striated. Most had cast the sheath. In one the sheath was lying at some distance, in another it trailed after the animal, while in a third it lay across it. Oral pouting was distinct in all; but no double outline, or further structure, could be detected in any of them. In the same insect two *Filarie* were found in the thorax; they were structureless, without sheath, somewhat swollen from endosmosis, an obscure convoluted granular-looking condensation occupying most of the body.

Fig. 3. From the thorax twelve hours after ingestion, $\frac{1}{90}'' \times \frac{1}{3000}''$.

The abdomen of the insect was half filled with blood, in which moved many active, transversely striated, pouting *Filarie*. They had no sheath. In the thorax many were found.

They showed no double outline, transverse striation, or sheath; but oval pouting and some general body-movement still persisted. As yet tail-differentiation was not discernible. Beyond a few undefined specks the body was homogeneous. Perhaps the mouth possessed four lips. Slide prepared with sulphate-of-soda solution gradually washed away with pure water.

Fig. 4. From the thorax 25 hours after feeding. The abdomen of the mosquito still contained fluid, or semifluid blood, about two thirds full. In this eight passive *Filariae* were found; they were granular and evidently dead or dying. Over two dozen *Filariae* were found in the thorax, most of them active, with differentiation of the tail commencing. That represented measured $1\frac{1}{10}'' \times 2\frac{1}{20}''$.

Figs. 5, 6. From the thorax 35 hours after ingestion. The abdomen of the insect was about two thirds filled with blood, in which 12 or 13 undefined, granular, dead, and fading *Filariae* were found. One of them, however, which evidently had been about the periphery of the clot, was well defined, faintly striated, plump, moving freely, and had a tail slightly differentiated. Many were found in the thorax; all of these were passive and had distinctly differentiated caudal appendages. No organs seen; body-contents granular. The body appears to be expanding, the enlargements being most apparent towards the tail end. One measured $1\frac{1}{10}'' \times 3\frac{1}{100}''$, another $1\frac{1}{40}'' \times 2\frac{1}{50}''$. One or two exhibited slight movement, either slow bending and extension, or, at long intervals, sudden jerking extension.

Fig. 7. From the thorax, 39 hours. Large number of *Filariae* in the thorax. For the most the tail was well differentiated. The body of the parasite had become thicker and shorter. In some, on washing away the sulphate of soda solution, a double outline could be made out. Contents cloudy and granular. Jerking movements frequent. A very few of the *Filariae* were shaped and moved as in mosquitoes examined a short time after feeding; that is, they were long, slender, active, with a tapered tail. Between these and the distinctly tailed animal transition-forms were abundant, so that there could be no doubt about the connexion. Specimen represented measured $1\frac{1}{25}'' \times 2\frac{1}{50}''$.

Figs. 8-10. From the thorax of mosquito 46 hours after capture. Many *Filariae* were found in this insect at different stages of development, from the long, slender, rather active *Filaria* with but slightly differentiated tail, to the fat tailed sausage-form with granular contents and intermittently wagging tail. Fig. 10 shows the chitinous integument, dipping into the rudimentary mouth; it is drawn to a larger scale. In one field of the microscope three *Filariae* lay across each other; one had hardly made any progress in development, another was still slender, but the tail was differentiated, while the third was thick, plump, and sausage-shaped.

Figs. 11, 12. From the thorax 56 hours after feeding.

The insect was found dead at 2 P.M., but was seen alive the same morning. Many live *Filariae* found in this insect, exhibiting the extension of the body and flick of tail movement. Fig. 11 showed some body-extension and a remarkable vibration of the whole of the posterior part of the body. The contents were in marked contrast to those of No. 12, being a structureless homogeneous matrix interspersed with innumerable, well-defined, shining granules; it measured $1\frac{1}{25}'' \times 1\frac{1}{70}''$. Fig. 12 measured $1\frac{1}{45}'' \times 1\frac{1}{250}''$; it possessed no body-movement, but only the tail-flick. Its body was made up of distinct cells; one minute, glistening, nucleated, cell-like body was a prominent feature at a point where the anus might be. Many more *Filariae* like these two types in the slide.

Figs. 13, 14. From the thorax 72 hours after capture. Many *Filariae* much broader, and somewhat longer, than those from the mosquito of figs. 11, 12, which belonged to the same batch of insects, and examined the day before. The tail was not seen to move, and no movement of body could be detected. Obscure cellular arrangement of the body. In all specimens a crowd of granular matter escaped from the anus. Fig. 14 measured $1\frac{1}{10}'' \times 7\frac{1}{10}''$ anteriorly, and $\frac{1}{625}''$

posteriorly; it was slightly constricted in the middle. After the slide had been mounted some time, a shrinking of the contents showed the integument of the parasites very distinctly, all exhibiting a marked double outline.

- Fig. 15. From the thorax of a mosquito the date of whose feeding could not be fixed, probably about 80 hours before examination. In its thorax two *Filarie* were found, one partly crushed, the other perfect—as represented. Measurements $\frac{1}{110}'' \times \frac{1}{1000}''$ anteriorly, and $\frac{1}{800}''$ posteriorly. It exhibited occasionally spasmodic jerks. At the head a distinct double outline. An alimentary line ran backwards some distance, becoming convoluted posteriorly, and gradually becoming less distinct till it was lost at the middle third. Anus distinct, open, and emitting a few granules. Tail distinct. Contents of the body obscurely cellular, lobulated, granular.
- Fig. 16. From thorax 97½ hours after capture. A considerable number of *Filarie* found resembling sketch. Body smooth in outline, plump, and healthy-looking. The mouth was four-lipped, and a pharynx could be made out; but no other trace of an alimentary canal unless in one specimen in which a funnel-shaped anus was apparent in the usual situation. The tail was delicate, but moved distinctly. There seemed to be a condensation of tissue near the surface of the body, especially about the waist. There was a shoulder and an anal bulging. Movement of the lips was observed. Measurements $\frac{1}{120}'' \times \frac{1}{1200}''$.
- Fig. 17. From thorax 97 hours after capture; about a dozen sausage-shaped *Filarie* found. Four lips readily made out; alimentary line running from mouth to anus. Cellular matter escaping from anus. Contents of body cellulo-granular, and very obscure. Tail small. Specimen measured $\frac{1}{110}'' \times \frac{1}{750}''$.
- Figs. 18, 19. From the thorax of a *Filaria* found dead (but recently living) 96 hours after capture. Alimentary line very distinct. Body cellulo-granular. Four lips rather pursed up. One measured $\frac{1}{110}'' \times \frac{1}{715}''$. Many similar in this insect.
- Fig. 20. From thorax 144 hours after capture. In this particular insect eight such *Filarie* were found. Mouth, alimentary canal, and anus, well marked in all. Tail was very faint, and it could easily be ascertained that at this stage it was nearly entirely integumented. The longest measured $\frac{1}{80}'' \times \frac{1}{650}''$. In it the cellular structure of the body was very apparent posteriorly; towards the head the cell-outlines could not be made out, the tissues looking granular or homogeneous. The mouth was pursed up. No movement remarked; granular escape from anus considerable. Alimentary line very thick, giving the impression that it was filled with some dark substance.
- Figs. 21–23. From the thorax of a mosquito 128 hours after capture. In this insect about a dozen advanced *Filarie* were found. They were nearly all straight, extended, with truncated posterior ends tipped with a minute, delicate, tegumental tail. Mouth distinctly four-lipped. Shoulder and anal bulging, and waist, inmost. Alimentary canal traceable from the mouth to anus in some, in others gradually losing itself about the middle of the body. Round this line nucleated cells have ranged themselves. In fig. 21 a prolapsus of part of the intestine has occurred. The body is filled with minute, clear, nucleated cells, in all the specimens. In 23, in addition to the alimentary line, traces of what may be commencing organs of generation were seen; a line could be followed from a point a little posterior to the head meandering backwards for some little distance among the cells. Where this line opened on the surface a dimly indicated infundibulum, which may be vulva and vagina, was indicated. Outline of all distinctly double. Fig. 23 measured $\frac{1}{85}'' \times \frac{1}{500}''$; the others about $\frac{1}{90}'' \times \frac{1}{850}''$ and $\frac{1}{85}'' \times \frac{1}{650}''$.
- Fig. 24. From thorax 145 hours after capture. Eight *Filarie* in thorax far advanced in development. The mouth and tail very evident. In some the tail was entirely integumental; in others a papilla from the body projected slightly into it—fig. 34; whilst in others the integument was quite filled up with the same material that made up the bulk of the body—fig. 35. When first

seen, *i.e.* soon after the body of the insect was immersed and broken up in water, part of the alimentary canal was visible as a distinct tube, and the body was for the most part very clear. After a time the alimentary canal became obscured by the cellules becoming granular and confused. Granular matter escaped from the anus. The cellules were smaller than those in figs. 21, 22, & 23. Several parasites were crushed under the cover-glass; in these chitinous integument was readily seen. Measurement $\frac{1}{7.5}'' \times \frac{1}{6.25}''$.

Fig. 25. From the thorax of a mosquito found dead on the morning of the seventh day after capture. The arrangement of cells round the alimentary canal, and on the inside of integument, very easily made out. The cells were plump and nucleated. In addition to the peripheral layer of cells the walls of the body appeared to be strengthened by a sort of thick corium, to the inside of which the cells were attached. There was a distinct space, a sort of peritoneal cavity, between the cortical and intestinal cells. In one specimen the head moved slowly at intervals. Mouth in all pursed up.

Fig. 26. From thorax. Mosquito found dead 144 hours after capture, seen alive 8 hours before. Eight such *Filariae* found. Two of them had slight movement; the largest measured $\frac{1}{6.0}'' \times \frac{1}{7.15}''$; another $\frac{1}{6.5}'' \times \frac{1}{7.15}''$. The sickle-shaped tail was purely integumental, very faint and fine. The body in some projected into this as a papilla; in others it was abruptly truncated. In most the anus was a large bag with well-defined wall, and from it granules escaped. Alimentary canal traced as a tube two thirds down the body, but union with rectum not distinctly discerned. Mouth widely open. Cellular structure of body obscure. Many shining granules in the wall of the alimentary canal.

Fig. 27. From thorax of mosquito found dead and adhering to damp side of bottle, 132 hours after capture. Altogether there were about six *Filariae* in the insect's thorax, and all in an advanced state of development; mouth, anus, alimentary canal, distinct; body cellulo-granular. Mouth in every case pursed up so that the lips were with difficulty defined. The specimen represented was more advanced than the others. The anterior part of body had thinned down and lengthened, while the posterior part remained full size, giving the animal the hock-bottle appearance. The cephalic end very transparent, alimentary tube in it barely visible. Mouth pursed up, and no lips discernible. Cephalic end exhibited slow swaying movement when fresh. Measurements $\frac{1}{8.5}'' \times \frac{1}{12.50}''$ anteriorly, and $\frac{1}{6.25}''$ posteriorly.

Fig. 28. From mosquito 135 hours after capture. Many advanced *Filariae* found in this insect. Some of them showed thinning and commencing extension of cephalic end. The specimen represented had grown at both extremities, particularly at the cephalic; but a portion of the middle of the animal had not yet become extended, hence its peculiar appearance. The entire animal measured $\frac{1}{5.5}''$ in length; the neck was $\frac{1}{10.00}''$, the posterior part $\frac{1}{6.50}''$, and the bulging centre $\frac{1}{5.00}''$ in diameter. Lips distinct; body cellulo-granular; tail, a long delicate sickle. Some motion exhibited.

Fig. 29. From a mosquito 144 hours after capture. Many advanced *Filariae* in thorax, some of them undergoing stretching. One measured $\frac{1}{5.0}'' \times \frac{1}{6.25}''$; another $\frac{1}{6.0}'' \times \frac{1}{7.10}''$. Oesophagus could be made out as a thick-walled tube in most; in some it terminated in a bulbous valvular-looking arrangement, from which sprang the intestine. Mouth distinctly lipped; a pharynx seen in some. In some no tail could be detected, in others a very transparent sickle was seen. Body cellulo-granular; no movements.

Fig. 30. From mosquito 152 hours after capture. About 15 large *Filariae* were found in the thorax. The largest is represented, it measured $\frac{1}{4.0}''$ by $\frac{1}{6.15}''$ posteriorly, $\frac{1}{7.00}''$ anteriorly. A number were found crowded together in one corner of the slide at various stages of extension from the $\frac{1}{10.0}''$ up to the $\frac{1}{5.0}''$ in length. Cellular structure of the body in some most apparent. Oesophagus in some particularly distinct, the single layer of nucleated cells constituting the wall

showing out well. Mouth open, four-lipped, with signs of papillæ on skin (fig. 37). In some no trace of tail, in others a large beautifully transparent sickle into which the body dipped a stumpy papilla. Rectum very evident. Granules in some escaping. A little, but very little, movement in some heads. No trace discoverable of organs of generation.

Fig. 31. From the thorax of a mosquito 156½ hours after capture. The ova had been deposited. In this insect *Filarie* were found at almost all stages of development, from large "sausages" to almost the *Filaria* of the sixth stage. One of the latter measured $\frac{1}{20}'' \times \frac{1}{1000}''$, and had three distinct papillæ on the tail. In this instance motion was most active in the tail, but the head also was animated; a prolapsus of intestine took place about the middle of the body. In another, about $\frac{1}{25}''$ long, the alimentary canal was very distinct, but rapidly became granular; hernia occurred in two places, and the tail and head retreated from their integuments; in the case of the head it left unoccupied about $\frac{1}{1000}''$ of the integument, and in this the involution to line the pharynx was very distinct. In some specimens the transparent sickle-shaped tail still remained.

Figs. 32, 33. The former is somewhat diagrammatic; the latter was constructed from observation of two full-grown *Filarie* at the sixth stage. The following are my notes of examination of the particular insects in which the originals were found:—

(a) A large brown mosquito, 158½ hours after capture, with ova still undeposited. Many *Filarie* were found in the thorax, in the fifth stage, measuring from $\frac{1}{30}''$ to $\frac{1}{40}''$, or thereabouts. One *Filaria* had attained a more advanced stage; it measured $\frac{1}{16}'' \times \frac{1}{25}''$. It possessed great activity, for it was in incessant motion, wriggling, coiling, and uncoiling. One movement was peculiar; it slowly, slightly approximated one end of the body to the other, and then suddenly extended itself. The motion was too quick for the eye to follow. The viscera were very difficult to make out. There were papillæ at one end of the body, the other end was tapered, and then abruptly rounded off. No trace of organs of generation visible. No trace of alimentary canal, or anus, could be made out, all details being obscured either by extreme opacity or extreme transparency of the body. Unlike *Filarie* at an earlier stage, this individual seemed quite at home in the water; the longer it remained in it the more active it became, and there was no bulging of the body or escape of contents. The other *Filarie* found in this mosquito, after moving languidly for a time, gradually became less active, and finally passive. Their bodies at one or two places would bulge and then rupture, intestine protruding. In these *Filarie* details of structure were easily made out. The large *Filaria* was visible to the naked eye.

(b) A large brown mosquito, 159½ hours after capture, eggs still undeposited. The thorax contained about 8 *Filarie*, "sausages" for the most part at an advanced stage. One measured $\frac{1}{50}''$; another measured $\frac{1}{16}'' \times \frac{1}{25}''$. The fore part of the body of this specimen was in constant, active, swaying motion; and the posterior half of the body apparently in the advanced fifth stage, *i. e.* it looked more cellular, was affected by endosmosis, and possessed little motion. The fore part had a firm, fibrous look, and the alimentary canal could sometimes be seen moving inside the muscular and fibrous walls, accommodating itself to every movement. The mouth was firmly pursed up, and the outline of the lips was quite indistinguishable. As it turned at times towards the eye, the very centre seemed as if pointed to a spine, a ring of four or more little spines, or papillæ, surrounding it; this is to some extent imagination, the perpetual movement preventing reliable observation. On the extremity of the tail were two, perhaps three, large, rounded papillæ; close to these, about two diameters of the body in advance, the anus and rectum could be distinctly made out. A hernia of the intestine occurred after this animal had been under observation about an hour. The hernia consisted entirely of intestine, no trace of uterine tubes or testicle. The movement of the head end continued for an hour and a half,

apparently brisker at the end of this time than at the beginning; it was only suspended when the cover-glass was removed, and the slide dried.

Figs. 34, 35. Show with fig. 24 the process of withdrawal of the body from the tail.

Fig. 36. Probably a dead *Filaria* with irregular bulgings, vacuoles, and signs of degeneration.

Fig. 37. Head of fig. 29 more highly magnified, and drawn at a slightly later hour, when the body on dying had somewhat retreated from the integument.

Figs. 38 & 39. From the same mosquito, showing differences in the rate of progression of metamorphosis.

Figs. 40, 41 & 42. Also all from the same insect.

Fig. 43. Caudal papillæ developing.

Fig. 44. Pharyngeal lines very distinct, from a *Filaria* in the fifth stage.

Fig. 45. Showing a sort of horny thickening of the tips of the lips at the fourth and early fifth stages.

Fig. 46. The sickle-shaped integumental caudal appendage not yet shed; caudal papillæ developing, and possessing a delicate skin separating them from the original integument of the earlier stages.

XIV. *On the Compound Vision and the Morphology of the Eye in Insects.* By
B. THOMPSON LOWNE, F.R.C.S., F.L.S., *Lecturer on Physiology, Middlesex Hospital,*
formerly Arris and Gale Lecturer, Royal College of Surgeons.

(Plates XL.-XLIII.)

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THE manner in which the compound eye of arthropods subserves the function of vision has been an undetermined problem since Johannes Müller enunciated his well-known theory of mosaic vision in 1826*.

The views of naturalists on this subject, if we except the extremely improbable and purely hypothetical view recently propounded by Exner†, may be grouped under two heads:—some have supported Müller's hypothesis, or a modification of it‡; whilst others have followed R. Wagner, and held the view more commonly attributed to Gottsche§.

It is well known that Müller supposed that each facet produces a single visual impression and that the whole visual field consists of a mosaic of such impressions; many of his followers have modified this view, by supposing that a small number of visual impressions are originated by each facet, the order of which is neither reversed nor inverted by the dioptric apparatus.

Müller's hypothesis was suggested to its learned author by the radial arrangement of the parts of the compound eye about a hemispherical or nearly hemispherical retina, and by the difficulty of conceiving a retina capable of correcting a mosaic of reversed and inverted images, the order of which is neither reversed nor inverted.

R. Wagner|| was the first to throw doubt upon Müller's view: he mistook the capsule of the crystalline cone for a retina, an error which was also committed by Ruete¶ and Dor**.

R. Wagner and his followers regard the compound eye as an aggregation of simple eyes, the dioptric structures of each producing an image on a distinct retina, in the same manner as the dioptric structures of the vertebrate eye, so that the whole visual field is a *mosaic of reversed and inverted images, the order of which is neither reversed nor inverted*.

The most important paper on this subject, after Müller's work, was undoubtedly a short but well-known contribution to Müller's Archives by Gottsche in 1852. Leeuwen-

* J. Müller, 'Zur vergleichenden Physiol. des Gesichtssinnes des Menschen und der Thiere' &c.

† Sigm. Exner, Biologisches Centralblatt, Jahrg. i. p. 272, and Pop. Science Review 1881, p. 337.

‡ Helmholtz, Du Bois Reymond, J. Notthafft, &c.

§ Will. Zenker, &c.

|| Wiegmann's Archiv, 1835. Bd. i. p. 372.

¶ Gratulationsschrift der med. Fac. zu Leipzig zu C. G. Carus 50-jähr. 1861.

** Archiv d. Sciences Phys. et Natur. 1861.

hoek had long before observed the images produced by the individual facets. Gottsche observed and drew attention to these: he, I believe, was the first who investigated the structure of the great rods (*Sehstäbchen*), and suggested that the highly refractive axial threads, which he discovered in their interior, in some way transmit the images formed by the lenses to recipient nervous structures beneath.

I can hardly imagine that the earlier writers intended to convey the idea that an image could be transmitted, as Dr. Grenacher facetiously suggests*, "as a message is transmitted by a telegraph wire," but suspect that they meant that rays of light from certain definite points in the image are so transmitted. There is, however, considerable ambiguity about Gottsche's paper on this and other points, although he apparently correctly indicated the position of the true recipient layer, beneath the great rods, without actually observing it.

Gottsche's paper appears to have been completely misunderstood by all his critics, who seem to have imported into it a false analogy between the image in the compound eye, and that in the vertebrate eye: the image is thus supposed to fall upon the retina. If Gottsche had intended to convey such an idea his view would have been, as it is generally supposed to be, in direct antagonism to Müller's hypothesis; yet Müller gave a kind of adherence to Gottsche's view, holding it to be consistent with and supplemental to his own.

It appears to me that the whole tenor of Gottsche's paper is an attempt to modify, not to destroy, Müller's theory, although both he and Müller, in the note which accompanies this paper, seem to have forgotten the difficulty which arises from the inversion of the subcorneal image. And further, Gottsche's retina is not the retina of Wagner, Ruete, and Dor. Soon after the publication of this paper Leydig† drew attention to the continuity of the axial structures of the great rods and the crystalline cones; and supposed the cones to be the terminal organs of the optic nerves. His views on the connexion of the cones and the nerve-centre are not easy to comprehend, as he appears to deny the truth of Müller's hypothesis, at the same time that his observations apparently support it.

Claparède‡ then pointed out the apparent continuity of the cone and the corneal facet, in *Typhis*, and found that the cornea, cone, and axis of the great rod, in some insects, consist of the same material; he asks, if it is not possible that these are all concerned in transmitting the image to nervous structures beneath them.

In criticizing the views of Gottsche, Claparède, and Leydig, it appears to me that it should constantly be borne in mind, that they worked at a time when the close relation between physical and vital phenomena was less completely understood than at present, and that they consequently, perhaps unconsciously, ascribed hypothetical vital properties to structures, which will not bear rigorous investigation.

Max Schultze§ first investigated the optical relations of the great rods, and concluded that they are not the terminal organs of the optic nerve, after a most laborious examination of their structure. He also rejected Müller's hypothesis as optically untenable.

* Untersuchungen über das Sehorgan der Arthropoden, p. 10. Göttingen, 1879.

† Müller's Archiv, 1855, p. 406.

‡ Zeitschrift für wissensch. Zool. Bd. x.

§ Schultze, Archiv, Band ii. p. 404.

Boll and Grenacher have, however, more recently adopted a modification of Müller's hypothesis, based upon a view held by Max Schultze. Gottsche described the very remarkable structures, at the inner extremity of the great rods of the lobster, under the term "*doppel-Pyramiden*"*, better known as the spindles. Max Schultze regarded the spindle as the true nerve terminal; it is the "*Retinula*" of Dr. Grenacher †.

On the other hand Wagner's theory has had numerous supporters, for the weak point in Müller's hypothesis is met by it, as many insects with very few corneal facets have evidently extremely acute vision. The absence of any retina in the position of the image below the cornea is, however, fatal to it.

Another difficulty militates strongly against this theory, which has been already dwelt upon by Dr. Grenacher: the extreme minuteness of the subcorneal image would necessitate recipient retinal elements far smaller than any known to exist in the animal kingdom. Moreover, as each corneal image corresponds, as a rule, to an angle of about fifteen degrees, and as the mean difference in the axes of adjacent facets is not usually half a degree, the images of adjacent facets are nearly identical‡, a fact in itself almost fatal to Wagner's hypothesis.

Formerly I accepted a modification of Müller's hypothesis §; but a further investigation has led me to discard both the theories of arthropod vision, and to substitute one which is, I believe, in complete accord with all the facts, and which, so far as I know, has not been even suggested by any previous observer.

The compound eye is divided into two parts by a membrane which I shall speak of as the *membrana basilaris*. The structures between this membrane and the cornea are the crystalline cones and the great rods ||; I regard all these as dioptric structures, and shall speak of the cornea, and all the parts which intervene between it and the *membrana basilaris*, as the *Dioptron*. I shall use the term *great rod* provisionally to designate the complex structure between each cone and the *membrana basilaris*, and *segment of the dioptron* for the parts, collectively, beneath each corneal lens.

Beneath the *membrana basilaris* I have discovered a layer of bacilla, comparable in most respects with the rod and cone layer of the vertebrate, in the place where Gottsche suggested such a structure might exist. This layer is succeeded by others, similar to the nuclear and molecular layers of the vertebrate eye. I shall speak of all these structures as the *Neuron*.

The existence of a continuous basilar membrane, in some arthropods at least, excludes the great rods from any share in the nervous mechanism, a conclusion which also follows from a more complete knowledge of their structure.

Nearly two years ago I made an examination of the eye of a Phume Moth (*Pterophorus pentadactylus*), in normal saline solution, immediately after the death of the insect. I was surprised to find a very considerable deviation from any structure previously described by others or observed by myself. Fig. 3 is a representation of the optical section of a portion of the eye: in this condition the great rods presented the

* Müll. Arch. 1852, p. 484.

§ Phil. Trans. *ibid.* p. 577.

† *L.c.*

‡ Phil. Trans. 1878, pt. ii. pp. 596, 597.

|| "*Rhabdia*" *mili*, Phil. Trans. *l.c.*

appearance of ovoid spindles, each enclosed in a cylindrical sheath. The spindle-shaped bodies underwent rapid change of form from the escape of their contents, so that in a short time they were reduced to the condition of empty shrivelled tubes.

Further observations on various insects have convinced me that such changes usually occur shortly after death, either from osmosis or from alterations of tension.

These observations suggested to me the possibility that the spindles of the great rods should be regarded as lenses of very short focal length, but of great thickness, and that they form a second refractive system, the anterior foci of which correspond with the subcorneal images, and the posterior foci with the bacillar layer of the retina.

According to this view the dioptron is composed of an anterior and a posterior refractive system.

The anterior refractive system of each segment of the dioptron consists of a corneal facet, a lenticulus, to be hereafter described, and the anterior face of the crystalline cone.

These parts form a *subcorneal image*, which lies in the anterior focus of the posterior refractive system.

The posterior refractive system magnifies the subcorneal image, and erects it, at its posterior focal plane, upon the bacilla of the neuron.

It is well known that if an objective is placed in the reversed position beneath the stage of a microscope, and the instrument is focussed for its posterior focal plane, it can be used as a telescope. A segment of the dioptron of an arthropod's eye, according to my view, is comparable to such an instrument, and the whole dioptron to as many instruments as there are segments, each giving a perfect picture of the objects which subtend a small angle with its axis; and thus a mosaic of images, which are erect and not reversed, falls upon the retina.

Although the ordinary simple eyes of insects do not exhibit any structure comparable to the second refractive system of the dioptron, the simple eyes of many larval insects have a posterior refractive system, and afford a complete transition from a simple to a compound eye.

I shall now proceed to the consideration of the details of structure and measurement on which my theory is based, in the following order:—

- I. THE ANATOMY AND FUNCTIONS OF THE DIOPTRON.
- II. THE ANATOMY AND FUNCTIONS OF THE NEURON.
- III. THE DEVELOPMENT OF THE COMPOUND EYE.
- IV. THE MORPHOLOGY OF THE EYES OF ARTHROPODS.

I. THE ANATOMY AND FUNCTIONS OF THE DIOPTRON.

The dioptron in the most highly specialized forms of compound eye, such as are found in the majority of perfect insects, is entirely enclosed in a chitinous case, formed by the compound cornea and the basilar membrane, united to each other by an inflection of the integument, which forms a short hollow cone between them.

The cornea and the basilar membrane are nearly parallel surfaces, so that the whole

lioptron has the form of a round or oval truncated cone, of which the base and apex are subspheroidal or, more generally, cycloidal surfaces*. The older writers named the reflected ring which unites the cornea and the basilar membrane “*the sclerotic*”; I shall designate it the *scleral ring*.

The inner margin of the scleral ring is often thickened, and receives the insertion of one or more muscles (figs. 1 & 1*a. mc.*), which are probably concerned in the adjustment (accommodation?) of the optical apparatus.

The whole interior of the dioptron is divided more or less perfectly into hexagonal or square tubes by fine sheaths† which extend from the margins of the corneal facets to the basilar membrane; each encloses a cone and a great rod, and forms a segment of the dioptron.

The great eyes of the dragon flies (*Æshnia* and *Agria*) have enabled me to detect large lymph-sinuses (*a.b.* figs. 5 & 9) which pass through the scleral ring and connect the lymph-spaces of the dioptron with those of the head.

In *Æshnia* the afferent vessel (*a*) enters the superior internal border of the dioptron: it has distinct walls, and is the anterior extremity of the bifurcated aorta‡. I am unable to say that this is general in insects, but from what I have seen I suspect that it is.

The efferent openings (*b.b.* figs. 5 & 6) are situated in the lower portion of the scleral ring, nearly opposite to the afferent vessel: they are generally, even in very different insects, long slits, across which a number of radiating nucleated fibres *rf* are stretched, between the basilar membrane and the scleral ring. These in sections, vertical to the basilar membrane, present a fan-like arrangement similar to that of the ciliary muscle of the vertebrate.

I have been unable to make out any striæ in these fibres; and as non-striated muscles are not known to occur in insects, I hesitate to regard them as contractile, although one is almost tempted to such a belief from their arrangement and position; perhaps they are simply elastic bands which maintain the tension of basilar membrane, where its attachment to the scleral ring is defective, to permit the circulating fluid to pass out of the dioptron. Their occurrence, however, in the simple eye (fig. 33, *ls.*) around the edge of the corresponding membrane is indicative of an active function.

The tracheal vessels (*t.v.*) of the dioptron consist of a main trunk, which almost surrounds the edge of the basilar membrane, from which numerous branches ramify and anastomose on the neural surface of the membrane (fig. 68).

Vessels from this network perforate the basilar membrane and run outwards, almost to the cornea, between the cuticular sheaths of the segments of the dioptron; they terminate in blind extremities.

In the *Syrphidæ* the tracheæ of the dioptron assume the form of fusiform sacs between its segments; these have very narrow necks where they pass through the basilar membrane.

The basilar membrane is a cuticular structure, which was described by Leydig as a

* Phil. Trans. *loc. cit.* p. 595.

† “Umhüllungsschläuche” of Leydig & authors.

‡ ‘Anatomy of the Blowfly,’ by the author, plate ix. fig. 1.

fenestrated membrane *, and it is usually believed to be perforated for the passage of nerve-fibres to the great rods. In many sections it is easy to see that the membrane is continuous, except where it is perforated by the tracheal vessels. In the great Dragon-flies it is also undoubtedly pierced by the fringes from the pigment-cells of the dioptron, which intercommunicate with the fringes of the pigment-cells, situated on the neural surface of the membrane (fig. 69). In some insects the membrane is actually thickened at the inner terminations of the great rods, so as to form small lenticular swellings (fig. 71); and in a specimen of the eye of a lobster, in which the neural elements beneath the great rods are not in the same line with them, the swellings are prismatic (fig. 70).

In some insects, especially in *Notonecta*, the basilar membrane is strongly ridged, the ridges corresponding with the attachment of the cuticular sheaths of the segments of the dioptron. It is apparently defective in parts, the openings being closed by the cellular layers which cover the two surfaces of the cuticular membrane.

In the crane flies † (*Tipula*), in some Coleoptera (*Telephorus*), and in other insects in which the component segments of the dioptron resemble distinct ocelli rather than parts of a compound eye, the cuticular sheaths of the great rods extend inwards, and also include the nervous structures. The basilar membrane then appears to be actually perforated, so that the inner extremities of the great rods come into contact with the nerve-terminals. This condition, however, is very exceptional, and is capable of explanation from the manner in which the parts are developed.

I shall recur to the consideration of the question of the passage of nerve-fibres through the membrane when I discuss the function of the great rods and the bacilla of the neuron ‡.

The various modifications of the cornea will be more conveniently considered hereafter; I shall only mention in this place the fact that in all those cases in which there are no lenticular facets, and where the cornea is simple and continuous, the outer face of the crystalline cone is strongly curved, being a portion of a prolate spheroid, and therefore probably capable of producing an image of great sharpness. Such a surface has, as is well known, the property of forming a perfect image, when the eccentricity of the generating ellipse is the reciprocal of the refractive index, a condition which appears to me to be very nearly attained in the curvature of these cones.

Prolonged investigation has gradually convinced me that the very considerable differences which the plan of the arthropod eye exhibits in different species and families are due to differences in the consistency and chemical nature of the parts. The highly refractive structures may consist of some modification of chitin, or some allied albuminoid, or of an oil-like fluid contained in the meshes of a fine stroma and enclosed in elastic capsules.

In the former case, where the refractive medium is chitinous, it undergoes but little change of form in the preparation of microscopic sections: in the latter case the fluid escapes from its capsule, and the whole appearance of the parts is modified, even when such solvents as clove oil and absolute alcohol have not been used; and the appearances are still further altered by the use of such fluids in the preparation of sections.

* Müller's Arch. *Lc.*

† Phil. Trans. 1878, *Lc.* p. 579.

‡ See page 409.

In most insects a lens lies under each corneal facet; I shall show hereafter that this lens is sometimes formed from the outer portion of the crystalline cone, and in other cases from the cornea itself, which then assumes the appearance of a honeycomb, the cells containing the lenses.

The consistence of the lens seems to vary very much; in some cases it is apparently fluid, enclosed in an elastic capsule; in the Earwig and the Cockroach I have even been able to separate such lenses from the cornea by pencilling its inner surface; the capsules can then be ruptured, and the fluid seen to escape by pressing on the cover glass; the ruptured capsules exhibit a single tear and fine wrinkles (fig. 21)*.

The refractive index of the fluid with which the lenses are filled is very nearly 2.0; this fluid appears like an oil, but it undergoes slow solution and decomposition by the action of water and weak saline fluids; a comparatively lowly refracting fluid and a fine reddish molecular substance result from their action.

The oil-like fluid is rapidly dissolved by ether and is blackened by osmic acid. Only the red molecular precipitate remains in specimens prepared in the usual way with clove oil. I believe the great brilliancy of the cornea of many insects during life is due to this fluid lens immediately beneath its surface, and that the loss of brilliancy which occurs soon after death, is due to the decomposition of the fluid, or its escape from the lens-capsule.

I am inclined to regard this fluid as an oil of complex constitution, which is possibly rich in sulphur or phosphorus, to which it owes its high refractive index and ready decomposition. Observations with a micro-spectroscope have given negative results.

In other cases the lens, when separated, breaks up like a viscid body; the lens-capsule always appears to contain a stroma, the meshes of which the fluid permeates; and the consistence of the lens depends on the relative amount of the stroma.

Every one who has examined the compound eye since improved methods have been adopted, must have been puzzled by the "*nuclei of Semper*" which figure so prominently in the descriptions of Claparède†. I formerly supposed with Dr. Grenacher that Claparède so designated the nuclei which are frequently seen in the immature eye between the crystalline cone and the facet of the cornea (*en. fig. 3*). But such a view is by no means satisfactory.

I was very much surprised on one occasion, to see the "*nuclei of Semper*," which are really nothing but the shrivelled segments of the lens-stroma, appear suddenly in a compound cornea treated with ether on the stage of the microscope; as the oil dissolved out of the lenses the contents of the capsules split into four parts. I regard this as the result of the shrinking of the stroma. A similar appearance is seen when the cornea of an insect is examined after having been allowed to become partially dried. I have never observed this in specimens prepared in the usual manner with alcohol and clove oil.

In the simple eyes of caterpillars, "*ocelli compositi*" (figs. 36-40), which are un-

* This lens was described by Müller; but its existence has been completely overlooked by recent authors.

† Zeitschr. f. w. Zool. Bd. x.

doubtedly nearly related to the compound eye, a subcorneal lens exists. In these it consists of three segments. A similar lens is seen in the semicompound eyes of isopods, and is regarded by Dr. Grenacher as a cone in a highly modified condition. It consists of only two segments instead of three or four.

The cornea and oil-lens together have a very short focus. The picture formed by these structures is usually from five to ten micromillimetres behind the posterior surface of the lens.

Very great differences of opinion have obtained credence concerning this image since the publication of Gottsche's paper. Many authors, and quite recently Exner*, have denied that any images are formed by the eye when the crystalline cones are *in situ*. I have a specimen of the cornea and cones of a moth (*Smerinthus populi*), mounted in balsam, in which distinct images are formed in the interior of the crystalline cones. In Exner's experiment the crystalline cones were surrounded by a lowly refracting fluid. As the images, according to my calculations, are formed near the focal plane of the inner ends of the crystalline cones, rays emerge from the inner extremities of the cones as parallel rays, or at least approximately parallel. The image cannot therefore be observed by the high powers of a microscope. Exner is undoubtedly quite right when he says that no image can be observed when the cones are *in situ* and surrounded by a lowly refractive fluid; but it by no means follows that none is formed. Indeed the structure of the eye is such that an image must be formed, and it cannot be neglected in working out the manner in which the eye acts as an organ of vision.

The focal length of the corneal lenses of the Fly (*Musca vomitoria*) has been given by me from actual measurement as $\frac{1}{400}$ of an inch†. I have since found that the results obtained by measurement are always greater than those arrived at by calculation; this is partly due to the rapid loss of refractive power immediately after death, but also to the fact that any moisture adhering to the inner aspect of the lenses forms a concave surface as it is attracted by the inflected margins of the corneal facets. I believe that the only satisfactory results are those arrived at by calculation. The greatest difficulty is the estimation of the refractive index. This is often considerably greater than that of Canada balsam, which is sufficiently proved by the formation of a subcorneal image when the cornea and cones of a moth are entirely immersed in it.

Small fragments of glass in water have nearly the same brightness as the cones and lenses of a moth in balsam. By reducing the illumination of the field of the microscope both were just visible with the same illumination, which indicates a refractive index, for the cones and lenses, of 1·8 nearly. Assuming the refractive index to be between 1·5 and 2·0, the focus by the formula $\left(\frac{1}{\mu-1}\right)\frac{rr'}{r+r'}=f'$ will lie between r and $\frac{r}{2}$, when $r=r'$. the value of the fraction $\frac{r}{r+r'}$ varies between 10^a and 20^a in different insects which I have examined. Therefore the focal length of the corneal lens is from five to twenty micromillimetres, and falls well within the crystalline cone, and the rays frequently emerge

* Biol. Centralblatt, i. p. 280.

† Phil. Trans. *l.c.* p. 585.

from the posterior end of the cone as approximately parallel, a conclusion which I arrived at formerly*.

In a specimen of the cornea and cones of the moth (*Smerinthus populi*) mounted in balsam, the micrometer screw shows the distance of the image behind the posterior surface of the corneal lens to be about forty micromillimetres, estimating the refractive index of the lens at 1.68 and that of the balsam at 1.5 $\therefore \frac{1.68}{1.5} = 1.12$, and $40 : \frac{1}{1.12} :: f : \frac{1}{1.68} \therefore f = 26$ micromillimetres approximately. The radius of curvature of the anterior surface of the corneal lens is about forty micromillimetres, and the distance between its anterior and posterior surfaces is 10 micromillimetres, which would give a focal distance of 26 micromillimetres measured from the posterior surface as before, with the same refractive index.

The diameter of the image is approximately 20 micromillimetres, in the same balsam-mounted specimen; it corresponds to an angular aperture of 24 degrees. The distance is $10 \times \cot 12^\circ = 47$ in micromillimetres behind the optic centre; which does not differ widely from the above. The angle was determined by using two lighted tapers as the object. The error arises from the difficulty of determining the exact size of the image that is the distance between the focal points. Of course the plane mirror of the microscope was used in making these measurements.

I formerly† gave the approximate length of the focus of the corneal facets of the hornet as $\frac{1}{200}$ of an inch; it is easy to see that it should have been $\frac{1}{2000}$, with a refractive index which I estimated at 1.53, which is too low, as the refractive index is nearly 2.0 during life—a result which is sufficiently near those given above.

If we assume the outer ends of the great rods to have a spheroid curvature convex towards the cone, the posterior focus of which corresponds to the bacillar layer, all the mechanism is present for the formation of an erect magnified image of the central portion of the subcorneal inverted image upon the sentient structures.

In many insects I have observed such a conformation of the outer ends of the great rods as this theory requires, and I believe that when observation fails to show such an arrangement, this is due to the very profound modifications which these structures undergo when removed from the eye, or during the preparation of the eye for investigation.

J. Müller regarded the great rods as nerve-terminals, a conclusion which was justified by his want of knowledge of their structure, but which is no longer tenable. Gottsche first discovered the compound nature of the great rods, and described, as I have already mentioned, the inner extremities of those of the lobster, as “*double pyramids*.” The structure to which he gave this name is now better known as the spindle; Dr. Grenacher speaks of it as a “*Retinula*.”

Max Schultze examined the structure of the great rods and their spindles in the lobster; he came to the conclusion that the rods are not the receptive elements, but ascribed this function to the spindles. Max Schultze founded this opinion chiefly on

* Phil. Trans. *L. c.* p. 581.

† Phil. Trans. *L. c.* p. 581.

two characters which he had observed in these structures—their tendency to split into transverse disks and their pink colour in the lobster.

The structure and development of the spindles varies considerably in different Arthropods. Sometimes they occupy the whole interior of the great rods, extending from the basilar membrane to the apex of the cone, as in the flies, and more obviously in the eye of the Water Boatman (*Notonecta*); in a greater number of insects, however, they are separated from the cones by a considerable space, the interval being occupied by an albuminous fluid or semifluid substance enclosed in a cuticular sheath, which is surrounded by pigment-cells (fig. 22. *ch.*).

The albuminous contents of this cuticular sheath have a low refractive index, and partially enclose both the cone and the spindle. The diameter of the tube which intervenes between the cone and spindle is subject to considerable variation in the same species of insect. In moths it is usually a very fine thread in specimens prepared by section; but in the recent eye of the very species in which it appears in this form in sections, I have frequently found the tube as wide as the base of the cone (figs. 3 & 27). I believe that the contracted condition is produced by the escape of its contents and the great elasticity of the cuticular sheath itself.

In the perfectly fresh eye of an insect the spindles are very transparent ovoid bodies, attached by their bases, which are truncated, to the membrana basilaris, and surrounded by pigmented fringes from cells, which cover the outer surface of the basilar membrane between the spindles (figs. 2, 3, & 10. *sp.*).

The appearances which the spindles assume after death and in sections prepared for microscopic examination are very various. In the noctuid moths they then appear as chitinous rods; sometimes they even present a stellate transverse section. In a specimen of the eye of a moth (*Hemerophila perfumaria*), prepared with osmic acid and afterwards mounted in balsam, they have assumed the form of absolutely empty shells, which are blackened intensely by the acid.

The spindles of a yellow Underwing (*Triphæna pronuba*, fig. 22 *sp.*) from a specimen preserved in a solution of chloral hydrate which was not replaced by any other fluid, resemble tubes filled with minute spherical granules, which give them a transversely striated appearance. These spindles are white and opaque when seen with reflected light.

In all these cases the form and appearance of the spindle are very different from that which it presents in its normal unaltered condition. The outer end always contracts much more than the inner, so that it has a strong tendency to assume the form of a wine-bottle with a long neck. In the Crane-flies (*Tipula*) I have found that the length of the narrow part of the spindle varies greatly in different specimens (figs. 10–13), so that there is no difficulty in connecting the normal ovoid spindle with the bottle-shaped organ which is usually seen in microscopic preparations.

The spindles of the Crane-flies (*Tipula*) are seen, in transverse sections, to be composed of seven tubes (fig. 14).

In some recent preparations I have succeeded in isolating these (fig. 13); they then curl and twist in a very remarkable manner, in water and glycerine, and they are easily

ruptured by pressure on the cover-glass, when a highly refractive oil-like fluid escapes from them. The axial structure of the great rods in other insects (*Notonecta*) exhibits the same appearances, some of which are figured by Dr. Grenacher*, and I have no doubt that the very fine axial threads seen in the great rods of flies are the shrivelled remains of the spindle.

In the true flies (Muscidæ) the great rods are very highly modified; each consists of six cells (sheathing-cells); these enclose the axial spindle. This can only be satisfactorily examined, in the recent eye, by very careful teasing. The great rods may be thus separated either in normal saline solution, or in very dilute osmic-acid solution, .05 per cent.; in the former fluid the sheathing-cells undergo very rapid disintegration by vacuolation, but this occurs less rapidly in the osmic solution.

The sheathing-cells surround a structure which is fluted like a column, the "Rhabdom" of Dr. Grenacher. This is the spindle; it consists of an elastic sheath, apparently composed of from four to seven component tubes filled with a highly refractive fluid. The fluid rapidly escapes from the injured tubes in minute glistening drops, whilst the tubes themselves become converted into fine threads. In the recent condition the slightest pressure suffices to empty the spindles. The various appearances of the component tubes are represented in the figures (figs. 16-18).

The tubes of which the spindle is formed apparently intercommunicate at the inner portion of the spindle. They twist and curl in glycerine and water as well as in normal saline solution. They are very elastic, and are easily drawn out to several times their proper length, which they regain when the tension is relaxed.

The fluid contents of the spindle are soluble in ether and clove-oil. The fluid is perfectly colourless in the Blow-fly; but the same fluid in the cabbage butterfly has a bright ruby tint when seen through the length of the spindle.

In ordinary transverse sections (fig. 20) the spindle is seen to contain a cavity surrounded by a plicated wall. The boundary of the irregular lumen exhibits six or seven, more rarely four, bright spots: these are the sections of the threads. All these details are correctly figured by Dr. Grenacher†. The outer extremity of the spindle in the flies is nearly hemispherical, and is imbedded in a structure which I formerly described as a tetrasome. This structure, in preparations hardened in chromic acid and its salts, has the appearance of four small spheroid bodies; but in some remarkably distinct sections which were fixed with osmic acid these are seen to be the four segments of a minute lens. The form and relation of this structure to the spindle will be best understood by a reference to fig. 19.

In the Lepidoptera the distance of the external end of the spindle from the cone appears to depend on the habit of the insect. It is furthest removed in the Noctuids, and closest in the Diurna: that is, in the Noctuids it is a larger lens of longer focal length, and therefore it receives a much larger cone of light-rays; in the Diurna the body which I formerly named the "*tetraphore*"‡ appears to be the external portion of the posterior refractive system.

In the Hymenoptera and Neuroptera, it is very difficult to see the parts in their normal

* *L. c.* figs. 51-53.

† *L. c.* fig. 62.

‡ *Phil. Trans.* *l. c.*

condition, as the walls of the refractive structures are very thin, so that in all the specimens which I have examined, the tubes of the spindle, which is very similar to that in the flies, had collapsed.

There are usually two principal layers of pigment in the dioptron—an outer layer, which is thickest at the apices of the cones (fig. 1. pg^1), and an inner layer (pg^3) at the inner extremities of the spindles.

The pigment of the outer layer is generally contained in cells which form a kind of iris around the inner extremity of each cone. It will be convenient to designate these rings of pigment-cells "*irides*," in conformity with the nomenclature of the older writers. There are, as a rule, five or six iris-cells around each cone. These send pigmented fringes outward over the cone and inward over the great rods. In many insects (Hymenoptera and Nematoceros Diptera) the outer set of fringes are replaced by rod-like prolongations of the iris-cells. Each cell has a single pigmented rod, which has a bright, highly refractive spherule at its outer end, immediately beneath the cornea. These may be called ciliary rods (figs. 31 & 32. *cb*).

I have found ciliary rods in all the Hymenoptera and Nematoceros Diptera which I have examined.

In the Dragon-flies the soft cone is surrounded by pigmented fringes. Amongst these there are from twelve to sixteen thread-like processes which are not pigmented; each terminates in a bright, highly refractive spherule, like that of a ciliary rod. These spherules form a ring around the cone immediately beneath the corneal facet. They are figured by Claparède *. I shall speak of these threads as "*ciliary threads*."

The form and connexion of the ciliary rods and threads suggest the idea that they may be concerned in regulating the amount of light which passes through the apex of the cone by means of a local mechanism. The action of light on the highly refractive particles possibly gives rise to a contraction of the iris. Whatever the mechanism by which the size of the aperture in the iris is regulated, it is certain that it is contracted in a bright light and dilated in the dusk, in nocturnal insects at least.

In Moths the well-known luminous reflex of the eye after the insect has been kept for a time in darkness is undoubtedly due to reflection from the spindles, as these are surrounded, in them, by numerous very close parallel tracheal vessels, which form a very perfect reflector. The disappearance of the reflex in the light is certainly due to the contraction of the irides. The gradual contraction of the bright field in each lenticulus of the cornea can be observed by means of a modification of the ophthalmoscope which I devised and shall hereafter describe.

It is a remarkable fact that the irides of the peripheral segments of the dioptron close before those of the central portion when the light falls directly in the axis of the latter, so that when the luminous eye of a moth is observed, it appears as if the bright part gradually became smaller until at last it entirely disappears.

Kühne is certainly mistaken when he says that the luminous reflex is of periodic recurrence †, and cannot be produced in the day. After exposure to a bright light the

* *L. c.*

† W. Kühne, "Observations on *Na'odon* and *Acherontia*," *Untersuch. Phys. Heidelberg*, Bd. i. p. 242.

irides are often a very long time before they dilate, but I have never failed to see the reflex after the animal has been kept in the dark for half an hour, although it disappears almost instantly even in diffused daylight.

In the flies (*Muscidæ*) the cone is surrounded by four large flat cells, which extend from the margin of the cornea to the iris. All trace of ciliary rods and threads is wanting, although the irides are well developed.

The inner layer of pigment-cells is in immediate contact with the basilar membrane; the cells form rosettes around the inner extremities of the spindles, and send pigmented thread-like processes over their surface. In the Dragon-flies these cells give off a number of pigmented fringes which perforate the basilar membrane, and communicate with similar fringes from the pigment-cells of the neuron.

In the flies and in some Hymenoptera an intermediate set of stellate pigment-cells exists (pg^2) between the inner and outer pigment-cells of the dioptron. These cells inter-communicate with each other, and in some preparations this gives the great rods the appearance of branching and uniting with each other. I think that this appearance is usually deceptive: the spindles are certainly always distinct, but appearances in sections of the eye of the Lobster, and in some osmic-acid preparations of the eye of a Moth (*Hemerophila perfumaria*), certainly indicate that the sheaths of the spindles do inter-communicate in some parts of the eye.

I shall conclude my description of the dioptron with an account of some of the modifications in its several parts which I have observed in different insects, and I shall add what I am able concerning their development.

I feel that in many particulars this account will be somewhat incomplete, especially with reference to the development of the several structures; but I am unwilling to delay this communication for a fuller investigation, which will certainly occupy several summers at least.

A. *Modifications of the Cornea and Lens.*

The compound cornea exhibits four distinct types in insects, three of which are seen in the various stages of development in the eye of the Common Cockroach. All these are also found in the perfect condition in other Arthropods. In the earliest stage of development in the larval Cockroach the cornea is simple and continuous, without a trace of faceted structure. In this condition it consists of several transparent cuticular layers (figs. 75 and 76. *c*). The entire cuticular cornea is shed with each ecdysis, and is renewed from a layer of cells which, prior to the ecdysis, is situated between the old cornea and the cone. I believe that the new cuticular cornea is formed beneath, and not on, the surface of this cellular layer. In a larva of a Dragon-fly (*Agrion*), half an inch long, I found a layer of large flat hexagonal cells covering the whole surface of the cuticular cornea, one cell corresponding to each segment of the eye. These cells were firmly united to each other by their edges, and each contained a large lenticular nucleus.

In a section of this cornea the cuticular layers are seen to be very numerous, and they lie beneath the cellular layer. The nuclei of the cells stain very readily with eosin, whilst the remainder of the cornea remains unstained. The outer cellular layer is usually

absent when the cornea is continuous and without facets. I suspect it is shed after the development of the cuticular layers beneath.

I have named this type of cornea the *simple non-faceted cornea*. It is apparently the permanent condition in *Gammarus* and *Branchippus* amongst the Crustacea.

The second type of cornea (fig. 30) is seen in the functionally active eye of the larval Cockroach. It is divided into lenticular facets. I shall speak of this type as the *faceted cornea*.

The faceted cornea exhibits two distinct layers—an outer nuclear layer and an inner laminated layer.

This form differs from the continuous cornea in the persistence and further development of the cellular layer. The large flat nuclei of the cells enlarge at the expense of the cell-substance until they form the whole surface of the cornea, one nucleus forming each facet. This layer, when fully developed, is very hard and brittle. It is no longer stained by eosin, as in its semideveloped condition, but assumes a yellow colour in specimens which have been treated with chromic acid or its salts.

The structure of the faceted cornea is worthy of study in dried insects. I have a beautiful section from the eye of an African Carpenter Bee (fig. 30). The lenticular nuclei are firmly cemented together, and exhibit no trace of minute structure. The laminated portion beneath these consists of from fifty to sixty layers. These follow the contour of the inner surface of the lenticular facets.

Fine lines are also seen running perpendicularly to the laminae. These correspond to the divisions between the facets. There are also distinct lacunae between the laminae, with minute teeth on each side of the lacuna; indicating that the laminated structure is probably due to the existence of finely serrated fibres interwoven with each other.

The third modification of the cornea in the Cockroach is only seen in the final stage of development: I shall speak of it as the *kistoid cornea** (figs. 3 & 10).

I have not met with any description of the kistoid cornea, although it is preeminently characteristic of the most highly differentiated forms of compound eye. It consists of a chitinous (?) cuticular membrane folded on itself so as to resemble a piece of honeycomb, the openings of the hexagonal cells being turned inwards. The closed ends of the cells are segments of spheres: these form the surface of the cornea.

The hexagonal walls of the cells are often highly chitinized and deeply pigmented; the curved ends which form the corneal facets are thin, membranous, and very transparent. The material of which they are formed is usually soft, flexible, and elastic, and the two surfaces of the membrane are parallel to each other.

The cavity of the corneal cell is occupied by the oil-like lens which I have already described.

This lens is certainly developed from the substance of the cornea. I was fortunate enough to obtain sections of the eye of a Blow-fly which throw light upon this point. Fig. 15 shows three segments of the dioptron of an immature imago, which had not long before escaped from the pupa.

* *Κίστη*, a capsule or small case.

Each corneal facet consists of a chitinous membrane overlying a soft substance which is easily stained with logwood or carmine solution.

As development progresses the deeper portion of the cornea becomes more highly refractive, and loses its property of taking up stains. It appears as if the albuminous substance of the young cornea becomes gradually converted into a stroma infiltrated with oil. I have never seen the oil in drops, like those in a young fat-cell. In the rudimentary lens it appears rather as if the oil were evenly distributed throughout the whole substance of the lens.

In the condition which I have just described I have seen no traces either of division of the albuminous portion of the cornea into four, or of four nuclei; but in a still earlier stage there are distinct indications of four nuclei in each corneal facet, and in a later stage the appearance of the "nuclei of Semper" on the addition of ether, or by drying, points to the origin of the corneal lens from four original cells.

In the immature insect, during the development of the eye, a number of capsules, filled with cells containing an abundance of oil in large drops, are seen under the membrana basilaris. Similar cells are shown in some of Claparède's figures, and are named by him basal cells*. These are entirely absorbed during the development of the eye, and it appears probable that they afford the oil required for the formation of the refractive media. I have no doubt they belong to the system of fat bodies in which the larvæ and pupæ of insects are so rich.

The fourth form of cornea is apparently confined, amongst insects, to the imago form of some Gnats, but is also probably the condition in *Mysis*, in its perfect state, and in some other Crustacea. I propose to distinguish this type of cornea as the *lenticular cornea*.

The lenticular cornea consists of a number of well-developed, almost hemispherical lenses, which are nothing more than the united crystalline cones of the larva and nymph.

Dr. Grenacher has correctly figured and described the eye of the larva and pupa of a Gnat; but he adds: "I have only studied the eye of this insect (*Corethra plumicorais*) in the larva and pupa, not in the imago;" and says, "This is a matter of no importance, as the eye undergoes no change in passing from the pupa to the imago"†. I was at once struck by this remarkable statement, as the eye is covered by a smooth non-faceted cornea in the nymph, whilst the corneal facets in the imago are remarkable for their size and very great convexity (fig. 74)—a fact well known to all who have made the most cursory examination of the compound eyes in this family of insects.

A comparison of a section of the eye of the adult larva (fig. 76) or nymph (fig. 75) with that of the imago (fig. 74) shows that the great convex facets of the cornea of the perfect insect are really the ovoid crystalline cones ("spherocoines") of the larva, covered by a thin cuticular membrane, which dips down between them, as the membrane of the kistoid cornea dips between its lenses.

In some of the Gnats the outer nearly hemispherical segment of the cone becomes converted into a nearly globular oil-lens, exactly like the oil-lens of a Crane-fly. The

* *L. c.*

† *L. c.*, p. 94.

inner segment of the cone then bears the same relation to the other refractive structures that the cone bears in the ordinary Diptera and Hymenoptera, or in insects and Crustaceans generally.

The formation of a fluid lenticulus from the substance of the cornea is not confined to the compound eye, but is also seen in the very different simple ocelli of some Arachnids. In a section of the simple ocellus of a Spider (*Salticus scenicus*) (fig. 34), which I prepared in the usual way and mounted in Canada balsam, the corneal lens is absolutely hollow. It evidently contained a fluid during life.

The sudden scintillations, which the bright reflex of the fundus of the eye of this insect exhibits in the living state, seem to indicate a power of accommodation, possibly from the action of muscle fibres which are inserted around the edge of the cornea.

Dr. Landois* traced the development of the subcorneal lens in the compound ocellus of a Caterpillar to a very different source. Soon after an ecdysis he found three spheroidal bodies very similar to those which I have described as a tetrasome in the eye of a larva of *Aceridium*†. These unite to form the lens.

From the manner in which the cornea is formed in Gnats, I think it probable that this subcorneal lens becomes the cornea at the next ecdysis, and that a new lens is then formed from subcorneal cells or nuclei. Although I have not observed either subcorneal nuclei or cells in the eyes of caterpillars, both are very frequently seen in the eyes of larval insects.

I suspect that the compound cornea is developed in a similar manner in some Orthoptera, from the indications I observed in *Aceridium*, but I am uncertain on this point; neither can I do more in the case of the Isopods than point out the very strong resemblance of the subcorneal lenses to those of the compound ocelli of caterpillars.

B. Modifications of the Crystalline Cone.

The outer portion of each segment of the dioptron, between the cornea and the external layer of pigment, may be conveniently termed "*the chamber*" (fig. 10 *ch.*). It is formed by the cuticular sheath of the segment, often thickened by a deposition of chitin; and is lined by fringes, pigment-cells, or ciliary rods.

The chamber contains the crystalline cone (*cc.*), which in many insects is replaced by a coagulable fluid, contained in four vesicles, and in others by four nucleated cells. Dr. Grenacher‡ classifies the eyes of insects in three groups: those with a cone he calls *eueconic*, those with the albuminous fluid *pseudoconic*§, and those with four nucleated cells *aconic*.

Up to a certain point my observations correspond with those of this distinguished author. In all insects the contents of the chamber are developed from four primitive cells||. This condition persists in the Crane-flies (*Tipula*), even in the recently formed imago (figs. 10 & 77); but I have failed to find these cells in the perfectly developed insect, in which the chamber is filled with an albuminous fluid, and I believe that the presence of the four nucleated cells is always evidence of immaturity. Dr. Grenacher's

* Zeitschr. für w. Zool. Bd. xvi.

† *L. c.* Phil. Trans.

‡ *L. c.*

§ Hydroconic, mihi, *L. c.* Phil. Trans.

|| This was observed by both Claparède and Weismann.

pseudoconic type is, according to him, confined to the Diptera with short antennæ. In this, again, I cannot agree with him, as the Dragon-flies exhibit precisely the same conditions, and in the imago of the Cockroach I find a similar semi-fluid cone. In all these osmic acid coagulates the fluid, and even the eyes of flies exhibit a well-marked cone when the preparation has been so preserved (fig. 28).

The elongated cones which have been observed in the eyes of many Arthropods, extending from the cornea to the membrana basilaris (as, for example, in *Hyperia**, *Typhis*†, and some other genera‡), appeared to me for a long time to present great difficulties with regard to the views which I now hold. Further investigation has convinced me that these cones are artificially produced by the coagulation and drying of the albuminous tissues of the cone and spindle, with their cellular sheaths. The evidence of this is seen in numerous specimens of the eye of the Cockroach. In some of these there are distinct elongated cones, whilst in others more successfully prepared the spindle is well seen, and has the same form and structure as it exhibits in *Notonecta* and *Tipula*.

The crystalline cones of the Nocturnal Lepidoptera and of the higher Crustacea are probably morphologically distinct from the structures already described. The highly refractive cone in Nocturnal Lepidoptera is surrounded by a softer, or even fluid, sheathing cone, which extends from the apex of the crystalline cone to the spindle (figs. 3, 26, & 27, *sh*). I regard it (the sheathing cone) as the representative of the cone in the Diptera and Dragonflies.

Both the hard cone and its soft investing substance are divided into four longitudinal segments, indicating their origin from the four cells of the primitive cone; but I cannot at present decide whether the hard cone is formed from the inner portions of these cells or between them, as Claparède § thought not improbable.

In both Noctuid and Crepuscularian Moths, the optical transverse section of the cone often appears to contain four groups of deep purple granules; these, in optical longitudinal sections, are seen to lie on the surface of the cone, and are probably deposited by the decomposition of the fluid which surrounds the cone. In dried as well as in balsam-mounted specimens the sheath is so closely applied to the cone that it appears to form its outer portion, and the coloured granules therefore look as if they were imbedded in the substance of the cone itself||. Unicellular organisms are not infrequently found in the fluid contents of the sheath of the cone: these are undoubtedly parasitic (fig. 27, *z*).

It is by no means easy to understand the contents of the chamber in the Diurnal Lepidoptera in such genera as *Colias* and *Tanessa*, although in *Pieris brassicæ* no difficulty exists, the cone being similar to that of a Noctuid Moth. I have already figured the remarkable modifications seen in the two former genera¶. I suspect that the cells (*c. c.*) in my figure are the representatives of the cone; and that the tetraphore is the outer extremity of the spindle, which retains its ovoid form after the escape of the fluid contents of the tube, and that the tube forms a narrow stalk supporting the chitinized

* Claparède, *l. c.*

† *id.*

‡ Leydig.

§ *L. c.*

|| Perhaps the coloured beads which cover the cone in *Notonecta* have a similar origin.

¶ Phil. Trans. *l. c.* fig. 35.

outer portion of the organ, which does not collapse like the rest of the spindle. This view is supported by a comparison of the outer end of the spindle in the Fly (fig. 19) with the structure in question.

C. *The Great Rods.*

The great rods consist essentially of the spindles and their cellular sheaths. The more important modifications of these structures have already been described, in their relation to the alterations which they undergo after death, and I have nothing to add further with regard to the very remarkable modifications which have been described by myself and others, except that they result from *post-mortem* changes.

The most important point in relation to the theory of Arthropod vision is, however, the direction of the axes of the great rods. It is well known that these are often seen to be strongly curved, even in the most carefully prepared sections, and this fact has been brought into prominence by the opponents of Müller's hypothesis *. Such a curved condition of the rods and spindles would be still more fatal to my own view. I have therefore carefully investigated this point, and conclude that this curvature is the result of changes of tension in the parts of the dioptron, and of the elasticity of the spindles. Sections made through the entire eye, immediately after the death of an insect, show no such curvature of the axes of the great rods when examined as opaque objects with low powers; yet the eyes of the same species exhibit very strongly curved rods when sections of the eye are examined in balsam. The manner in which the isolated rods twist and curl in all fluids shows that they must be powerfully affected by the action of the fluids usually required for the preparation of sections, and their action could scarcely fail to produce contortion of the great rods, even in the closely packed condition in which they exist in the cavity of the dioptron. The curvature would chiefly affect those rods which are nearest the periphery of the eye—a condition seen in all the sections which I have examined. The slightest pressure on the cornea in the recent eye permanently distorts the great rods. Hence it can hardly be expected that the axes of these structures would be undisturbed, at least around the periphery of the eye, in specimens preserved in any fluid which affects the normal tension of the parts.

I have made numerous attempts to determine the optical relations of the dioptric structures of the compound eye by means of a modification of the ophthalmoscope, but at present I have not been able to throw any further light upon the functions of the great rods by this means; except that the colour of the reflex obtained appears to depend on the colour of the fluid contents of the spindle.

I have found the best method of examining the reflex to be the substitution of a reflecting ophthalmoscope for the eyepiece of a microscope. By this means a bright luminous spot may be observed as a real image in the tube of the instrument. A quarter objective must be used, and the mirror of the ophthalmoscope must be strongly illuminated. The microscope is then focussed so that a real image of the corneal facets is seen between the objective and the eye of the observer. By bringing the object-glass gradually nearer to the insect's eye the reflex will come into view.

* Exner. *Biolog. Centralblatt*, i. p. 273.

The reflex appears as a disk having a fiery glow in Moths, and as a bright ruby spot in the Cabbage Butterfly. Sometimes six spots, surrounding a central spot, are seen in the eye of this insect: perhaps these are diffraction-images. A similar appearance is seen when the eye of this insect is observed by the naked eye, except that the spots are black. The central spot is always opposite the eye of the observer, whatever the position of the eye of the insect.

The reflex seen with the micro-ophthalmoscope is green in *Tipula* and bright yellow in the Diurnal Flies. Coloured diffraction-fringes are usually present around the central bright spot in both these insects; but the central image is sometimes surrounded by a perfectly black ring.

The manner in which the luminous reflex scintillates is very suggestive of an alteration in the focal plane of the dioptric structures under the control of the insect.

II. THE ANATOMY AND FUNCTIONS OF THE NEURON.

The neuron consists of a large nerve-papilla, or of a series of papillæ, which arise from the side of the procephalic ganglion, and form a retinal expansion on the inner or neural surface of the membrana basilaris (figs. 41 to 67).

The neuron may be conveniently divided, for purposes of description, into three parts—the retina (*rt.*), the optic nerve (*no.*), and the optic ganglion (*g.*) (fig. 41).

The retina consists of a layer of bacilla, supported by a complex neuroglia (fig. 56).

The bacilla present an inner (*i.*) and an outer segment (*o.*, fig. 53), like those of the rods and cones of the vertebrate retina. Both the inner and outer segments are very easily destroyed, and these structures are best examined by teasing out the recent retina in a very dilute solution of osmic acid, .05 per cent.

The outer segments are cylindrical or conical, highly refractive, easily stained by chromic acid and its salts, but unaffected by logwood. In the Dragon-flies the outer segments often split into transverse disks.

The inner segments are protoplasmic, and are easily stained with logwood and carmine. They are richly supplied with very fine tracheal vessels (fig. 53). The inner and outer segments are of nearly equal length, and measure from 25 to 50 micromillimetres each. The outer segments are usually about 2 μ in diameter, and the inner are somewhat thicker.

The bacilla are usually arranged in bundles, which are bound together by the neuroglia, each bundle corresponding to a segment of the dioptron. In the Cockroach and the Blow-fly I have occasionally found some of the bacilla with the outer segment double, like the twin cones of fishes (figs. 65 & 66); and in some of the bacilla from the latter insect I have occasionally observed a lenticulus (fig. 64) between the inner and the outer segments. This is not stained by osmic acid, and closely resembles the lenticulus described in some vertebrate rods. I have never observed anything like the coloured globules of the cones of birds and reptiles.

The inner segment is usually finely granular, and is continued inwards as the axis-cylinder of a nerve-fibre.

The most remarkable modification of the bacilla is the separation of the inner and

outer segments in many larval forms, in the imago of *Tipula* and in most Noctuid Moths. In these cases a long fine axis-cylinder passes from the outer to the inner segment (figs. 46, 55, 57, & 67).

In the Noctuids a tracheal network is interposed between the inner and outer segments of the bacilla, permeated by the fibres which connect them with each other. The tracheæ form a kind of tapetum behind the outer segments.

A similar separation of the inner and outer segments of the bacilla occurs in the simple eyes of an Arachnid (*Phalangium*), which has been figured by Dr. Grenacher*.

It will be observed that the outer segments of the bacilla, which correspond in character with the outer segments of the vertebrate rods, are turned towards and not away from the refractive media. In this they conform to the usual condition in the invertebrate eye. I regard this as of developmental rather than of functional importance.

The outer ends of the bacilla are separated from the basilar membrane by a layer of fine branching endothelial cells. These are frequently pigmented, and send pigmented fringes inwards, which closely embrace the outer segments of the bacilla. The pigment is not deposited between the bacilla and the membrane, but only around the bacilla. I regard this layer as the analogue of the retinal pigment. It is always black. The pigment is entirely wanting in the Diurnal Flies, but is very abundant in the Lepidoptera, Hymenoptera, and Neuroptera.

The neuroglia of the retina consists of fine fibres (fig. 56), connected with the basilar membrane and with two distinct layers of small stellate cells—an outer layer between the outer and inner segments of the bacilla (*a*), and an inner layer at the inner extremities of the inner segments (*m*²). In many specimens a number of small granules are seen crowded together between the outer segments of the bacilla (fig. 59). I am not certain of their nature, but it has occurred to me that they are possibly the broken outer ends of the bacilla themselves.

Sometimes large soft granular cells are seen in the same position (fig. 58). I think these are an indication of immaturity.

None of my predecessors in this investigation have described the bacilla. It may, therefore, be fairly asked, If these structures exist, how is it that they have been so frequently overlooked?

I think the answer to this question is found in the fact that it is only in very thin sections, such as they had not the means of preparing, that the bacilla can be recognized. In all ordinary sections a thick band of pigment between the membrana basilaris and the optic nerve is all that can be made out. When I wrote my former paper I had only seen the inner segments of the bacilla in the Flies, and I described them as a fascicloid layer†. I did not then understand their significance, and I had been working at the compound eye for over three years before I prepared a section which enabled me to recognize these structures as the terminal organs of the optic nerve.

Again, although the structure of the great rods has been very carefully investigated, that of the neuron has had very little attention paid to it. Even Dr. Grenacher, in his

* *L. c.* fig. 15.

† *L. c.* Phil. Trans.

elaborate work, only represents portions of it in six figures; and these are all diagrammatic outlines, with but little detail.

M. Berger*, who has given the best figures and descriptions, has only worked with comparatively thick sections with low powers, and has not only overlooked the bacilla, but many other very obvious details.

On the other hand, it must be confessed that many observers have believed that they have traced nerve-fibres from the optic nerve into the great rods or their spindles. Dr. Grenacher has given one figure, and only one figure, in which he shows this relation. It represents three of the segments of the dioptron of a Crane-fly†; and in one of the three he has shown a nerve passing through the cuticular membrana basilaris, and ending in one of the cells of the spindle. I have occasionally observed an appearance similar to that represented in this figure, and my observations have led me to the conclusion that the fibres represented are not nervous, but form a portion of the connective framework. In *Tipula* the bacilla beneath each segment of the dioptron are enclosed in a distinct sheath (fig. 57), which often appears to be continuous with the sheath of the great rod. This gives rise to an apparent continuity between the neural and dioptric structures in many sections, and may have led Dr. Grenacher to believe that he had actually traced the nerve into the spindle.

There is no other figure in Dr. Grenacher's work which shows any actual passage of a nerve-fibre into the great rods; but two figures represent nerve-fibres passing up to, but not through, the basilar membrane‡. These are both from the eyes of Crustaceans, in many of which the bacilla are very short. Several figures, of the eyes of Crustacea, actually show the bacilla, although the author has not referred to these in the text. In all the other figures, either the neuron is unrepresented, or it is only shown in outline without sufficient detail.

The retinal layer in Arthropods exhibits two very distinct modifications, which I propose to term the *segregate* and the *continuous retina*.

The segregate retina is characterized by having the bacilla arranged in distinct retinulæ, one for each segment of the dioptron. Each retinula is connected with the ganglion by a distinct fasciculus of nerve-fibres enclosed in a separate pigmented sheath (fig. 57). This form of retina is very frequent in larval insects; it is less often seen in the perfect state. The Crane-flies and some beetles have a segregate retina in the perfect condition: *Telephorus* affords a good example.

The continuous retina consists of a bacillary layer extending over the inner surface of the basilar membrane, connected with the ganglion by a single large nerve-trunk, the fibres of which exhibit a complete decussation (figs. 41, 51, *vt*). The bacilla always, however, show a tendency to be collected in small bundles, one corresponding to each segment of the dioptron, except in some of the Dragon-flies, wherein the central portion of the bacillary layer, at least, does not exhibit any division into separate fasciculi.

The continuous retina is characteristic of the true Flies (Brachycerous Diptera), of some Hymenoptera, Lepidoptera, and Neuroptera.

* E. Berger, "Untersuch. u. den Bau des Gehirns und der Retina des Arthropoden," Arb. Zool. Inst. Wien, tom. i. (1878).

† *L. c.* fig. 44.

‡ *L. c.* figs. 109, 114.

In many perfect insects, and in some stages of development in others which in the perfect form have a continuous retina, conditions exist which are intermediate. For instance, the bacillary layer may be continuous, but the optic nerve split into numerous separate bundles; or the segregate retina may consist of fasciculi so closely united that it is difficult to decide to which form the modification should be assigned. These variations are of developmental significance, as will be shown hereafter.

The fibres of the optic nerve are medullated, although in most preparations all traces of the medullary sheath are lost. It is not, however, difficult to make out the sheath in recent specimens fixed with osmic acid. I now consider the varicose appearance of the axis cylinders which I formerly described to be due to *post-mortem* changes*.

The arrangement of the fibres in separate fasciculi in some insects has already been alluded to. When they form a single nerve-trunk most sections exhibit the complete decussation of the nerve-fibres. In some planes, however, the only indication of such an arrangement is the cut ends of many of the nerve-fibres. Such variations are undoubtedly due to the plane of the section.

When the retina is segregate, the nervous bundles, which unite the retina with the ganglion, do not decussate; but in this case a deeper layer of decussating fibres can usually be seen in the substance of the ganglion itself (fig. 44).

Supporting fibres connect the inner surface of the retina with the outer surface of the ganglion, when the nerve consists of a single trunk (fig. 56, *d*).

The retinal ganglion is spread over the surface of the optic lobe (*op.*) of the cephalic ganglion (figs. 48 & 49).

It usually exhibits at least four layers, although the number is sometimes greater.

In the Fly (fig. 56) the outer layer (*f*) consists of small round nuclei imbedded in a finely granular matrix. The matrix is permeated by fibres connected with a layer of stellate cells (*g*), which lie in the central zone of the next layer.

The second layer, beside containing the stellate corpuseles just alluded to, is chiefly made up of large fusiform cells (*cl*¹), which are connected at both their extremities with fine fibres. The third layer of the ganglion consists of a number of very fine fibres (*h*), which run parallel to the surface of the ganglion. The supporting fibres of the first and second layers spread out into foot-like disks on the surface of the fibrous layer (*i*). The fourth layer (*cl*²) resembles the second, except that I have not detected any stellate corpuseles in connexion with its supporting fibres.

The retinal ganglion is connected with the deeper portions of the optic lobes by fibres (*no*²), between which a large number of tracheal tubes lie. These supply the fine tracheal vessels of the ganglion itself.

In the ganglion of the retina in *Agrion* (fig. 42) there are two extra layers within the inner cellular layer—a second layer of fibres parallel with the surface of the ganglion (*f*²), and a second nuclear layer (*n*²); and the ganglion is connected with the deeper structures of the nervous system by a second layer of decussating fibres (*x*).

In *Tipula* and the Gnats the structure of the ganglion is not so complex. In these

* Phil. Trans. *l. c.* p. 585.

insects (fig. 57) I have been able to make out only two layers—a nuclear layer (*nuc*) and a layer of large fusiform cells (*cl*). The latter are connected by a number of nearly parallel nerve-fibres (*no*²) with a deep ganglionic layer, which consists of small stellate cells (*g*).

III. ON THE DEVELOPMENT OF THE COMPOUND EYE.

The dioptron and neuron are developed from two distinct sources: the former originates from the hypodermis, the latter from a solid outgrowth of the cephalic ganglia; so far, therefore, there is ground for a morphological comparison between the nervous and dioptric structures of the vertebrate and compound eye. The dioptron is comparable with the crystalline lens, whilst the neuron, so far at least, is homologous to the retina.

The researches of Dr. Weismann * have shown that the dioptron in the Fly is formed from a single layer of cells, and my own observations verify this in the case of the Lepidoptera and the Dragon-flies.

It is well known that the outer facets of the eye in the Crustacea are developed later than the more central facets, the eye increasing in magnitude with each successive ecdysis. But I do not know that it has been remarked that the peripheral portion of the eye in insects is less developed than the more central part. I have found this to be the case even in the fully formed imago, whilst a section taken through the eye of an immature imago often throws much light on the manner in which the eye is developed.

In larvæ in which the compound eye is functionally active such sections are still more instructive.

Perhaps it is by the gradual addition of fresh facets that the segregate retina takes its origin. In the Dragon-flies, at least, the continuous retina of the imago is not fully formed until after the final ecdysis, when it gradually replaces the segregate retina of the larva.

The dioptron in its earliest stage of development consists of a single layer of columnar cells, which cannot be distinguished from the ordinary hypodermis of the insect. I have observed this condition in various Lepidopterous larvæ. The columnar cells lie immediately beneath a continuous non-faceted cornea.

At this stage numerous tracheal vessels and stellate cells lie beneath the columnar layer, and processes from the columnar cells pass into the deeper layer, where they communicate with the stellate cells, which belong to the ordinary connective tissue of the insect.

In this respect the columnar cells closely resemble the cells of the sensory epithelium in the Medusæ and Mollusca. The researches of the brothers Hertwig † show that in the Medusæ the cells of the sensory epithelium, in the region of the rudimentary eyespot, become the terminal organs of the nerve. This may possibly be regarded as an indication in favour of the hitherto accepted view that the sensory terminations of the nerve in the Arthropod are developed from the hypoderm. Such a conclusion is, however, in my estimation, no more justified than if it were extended to the case of the crystalline lens of a vertebrate. In the Medusa the epithelial cells, from which the

* Zeitschr. f. w. Zool. Bd. xiv.

† O. und R. Hertwig, Das Nervensystem und Sinnesorgane des Medusen.

nerve-terminals are believed to be developed, are those of an undifferentiated epiblast; whilst in the Arthropod, as in the vertebrate, the great neural tract has already been differentiated before the groundwork of the compound eye is laid in the cells of the hypoderm Metschnikoff*. The hypodermic cells in the region of the dioptron become greatly elongated, and undergo both longitudinal and transverse subdivision; but as the tracheal vessels and stellate connective-tissue cells permeate the hypoderm at a very early stage in the development of the dioptron, it is extremely difficult to determine how much of this structure is derived from the hypoderm and how much originates in mesoblastic elements. The earliest stages of development are far more difficult to follow in the Diptera. This arises from two principal causes: first, the "imaginal disks" from which the integumental structures of the imago are developed are closely united to the nervous system; and secondly, the whole development is very rapid, and the parts are exceedingly soft and easily destroyed.

The compound eye of the larva of *Corethra*, in the earliest stage in which I have yet observed it, closely resembles the same structure (as figured by Metschnikoff†) from *Aphis rosæ*. It consists of a discoid group of pyriform cells, with their long axes at right angles to the surface of the disk. The rounded outer ends of these cells lie immediately under the transparent non-faceted cuticle, which represents the cornea. Their inner extremities are prolonged, and are intimately connected with the deeply pigmented sheath of the optic nerve.

Dr. Weismann‡ has figured the disk from a still younger larva, and shows the nerve ending in a layer of cuboid cells, which, from observations I have made on the very rudimentary eye of a Lepidopterous larva, form, I believe, a distinct layer beneath the disk from which the refractive structures are developed. My own observations have led me to conclude that at this stage the nerve-fibres end in a bed of granular nucleated protoplasm, not unlike a large motorial end-plate (fig. 73). Each of the pyriform cells of the disk has a bundle of rod-like bodies of an orange-brown colour near its outer end. These eventually develop the cone and spindle.

The rods are larger in the cells of the centre of the disk than in those of its periphery; and the whole cell shows symptoms of division into four longitudinal parts.

The close relationship of this disk to the cephalic ganglion, both in *Aphis* and *Corethra*, throws light upon the still more remarkable developmental history of the eye in the true flies, so well described by Weismann.

In these the disk is attached to the optic ganglion by a narrow pedicle, and has no connexion with the other integumentary structures in the pupa. It is one of the remarkable cellular expansions which are known as "imaginal disks." The head and thorax of the imago are formed from a series of these disks, which are really involutions of the epiblast. These are drawn into the interior of the embryo whilst it is yet inclosed in the egg.

The procephalic lobes and all the appendages of the head are distinctly seen as rudi-

* Zeitschr. f. w. Zool. 1871; Monthly Mic. Journ. 1872.

† Zeitschr. f. w. Zool. Bd. xvi.

‡ Zeitschr. f. w. Zool. Bd. xiv.

ments in the embryo some time before the hatching of the egg; but before that event they are withdrawn into the interior of the embryo by a process of invagination during the formation of the fore gut, which lies entirely in front of these structures.

The fore gut forms no part of the alimentary canal of the imago, but is shed with the larval integument in the first stage of the formation of the pupa. This then puts on the same appearance as the embryo had whilst it still lay inclosed in the egg, by the unfolding of the imaginal disks; and these, again, form the anterior part of the body.

After the unfolding of the imaginal disks, the development of the compound eye proceeds in the same manner as in those insects in which it is developed from the cells of the hypoderm.

I believe that the pedicle, which supports the disk from which the dioptron is developed, is merely a portion of the connective-tissue capsule that incloses the ganglion before the evolution of the disks in the formation of the pupa. The optic nerve and retina are formed at a later period.

These facts throw light on the relationship between the ordinary compound eye and the remarkable encapsulated eye of the entomostracous Crustacean, *Leptodora hyalina*, described by Dr. Weismann †. This is deeply seated in the median line of the transparent head, in immediate relation with the cephalic ganglion, and it has no apparent connexion with the skin or surface of the animal.

In describing the variations of the retina I have already adverted to their developmental significance. I have especially studied the developmental relation of the segregate and continuous forms of retina in the Dragon-flies, and there are numerous indications that what I have actually observed in these insects is a common phenomenon amongst the Arthropods. In the earlier stages of the Dragon-fly larva the compound eye is already functional, at least as far as its central facets are concerned. In this condition there are very few facets. Those of the more central portion of the eye have a distinct retinula to each, and each retinula has a distinct nerve-bundle (figs. 43 & 45). As development progresses, new segments are added to the periphery of the dioptron, and the number of retinule increases.

In some sections the continuous retina of the perfect insect (*rt*) is already seen upon the surface of the optic lobe (fig. 44), and the fibres of the nerves from the partial retinæ (*rt**) can be seen passing between its rudimentary elements. The existence of a decussating nerve beneath the continuous retina is very apparent. The retinal ganglion (fig. 44, *g'*) is now deeply seated in the interior of the optic lobe.

Beneath the ganglion, both in this and in later stages, there is a remarkable ganglionic centre (marked *k* in my figures). It is in relation with the retinal ganglion by a second bundle of decussating fibres. It is, I believe, the representative of those remarkable kidney-shaped bodies described by Mr. Newton in his admirable description of the eye of the Lobster ‡.

As development progresses, the continuous retina gradually enlarges, and approaches

† Zeitschr. f. w. Zool. Bd. xxiv.

‡ E. F. Newton "On the Eye of the Lobster," Quarterly Journal of Mic. Science, 1873.

the inner surface of the membrana basilaris of the dioptron (figs. 41 & 45); so that at the final ecdysis it entirely replaces the partial retinae of the larval eye.

This complete change of the larval retina at the final ecdysis is undoubtedly a very remarkable phenomenon. When, however, the epiblastic nature of the nervous system is borne in mind, it is not, perhaps, more remarkable that an ecdysis should occur in relation to the nervous than that it should occur in relation to the cutaneous epithelia. It has occurred to me that the kidney-shaped ganglia already alluded to, which apparently vary much in number in different stages of development, may be really successive rudimentary ganglia and retinae destined in turn to become functional.

The extent of the final continuous retina varies much in different species of insects. In *Agrion* the whole inner surface of the basilar membrane is in contact with the continuous retina in the fully formed imago; but in the great eyes of *Æshnia* it only replaces the central retinulae. The same partial replacement of the retinulae is the condition in many insects in which the eye is only functional in the imago. In these it is probable that the central portion of the retina is continuous from its first formation, and that it is, as it were, supplemented by peripheral partial retinae.

Most of the Lepidoptera apparently exhibit this condition, the continuous retina being most developed in the Diurna. As has been already stated, the larval condition is permanent in the Crane-flies and Gnats; whilst in the Diptera with short antennae, Muscidae and Tabanidae at least, where the formation of the pupa almost partakes of metagenesis, no partial retinae are ever formed. It appears as if the developmental processes had been much abbreviated in these insects, and that the final stage is reached by a single and complete metamorphosis.

IV. ON THE MORPHOLOGY OF THE EYES OF ARTHROPODS.

Although of late the views of Müller with regard to the relations of the simple and compound eyes of Arthropods have fallen into discredit, I must return to these views.

The eyes of the Isopod Crustaceans, which he spoke of as aggregate, are undoubtedly really intermediate between a simple and compound eye. The transition from a few widely separated simple eyes, which form the aggregate eye, is so natural that it has only obtained discredit because there is a wide difference in the structure of the stemmata of insects or Arachnids, and of the compound eye.

The case is, however, otherwise with the simple eyes of larval insects, which are almost identical with a segment of the dioptron of the compound eye. Landois*, describing the eyes of several caterpillars in 1866, remarked that they present a condition intermediate between that of the compound eye and the ordinary simple eye, and proposed the term "*ocelli compositi*" for them. I have figured sections of the eyes of three noctuid caterpillars (figs. 36-40); these exhibit a lens consisting of three segments placed immediately beneath the very convex corneal facet.

* Zeitschr. f. w. Zool. Bd. xvi.

The lens is not unlike the crystalline lens of a vertebrate. It is albuminous, or at least gives a characteristic yellow with nitric acid.

Beneath the lens a fusiform spindle is seen, very similar to the spindle of the compound eye. This has a retinula beneath it consisting of a small fasciculus of bacilla. Several of these eyes are united by a common optic nerve, like the stemmata of insects, and three usually form a group.

I believe that the spindle in this form of eye has the same function as that which I have assigned to it in the compound eye.

A comparison of the figures given by Dr. Grenacher * of the eyes of *Porcellio* and of *Sialis* larva with those of the ocelli of caterpillars which accompany this paper, will show how close the relation of these structures is to each other. On the other hand the absence of a subcorneal lens and spindle, as well as the arrangement of the retinal elements, in the simple ocelli of insects and arachnids, show that these organs are formed on a type which differs essentially from that exhibited by the compound eye.

I believe, however, that the columnar cells immediately beneath the cornea, the vitreous of Dr. Grenacher, represent the dioptron; they are undoubtedly of hypodermic origin, and are separated from the retina by a fibrous membrane which apparently corresponds to the membrana basilaris of the compound eye. Dr. Grenacher figures and describes this membrane † in a species of *Sallicus*, and traces the fibres of which it is composed, from the outer ends of the bacilla of the retina to a number of nuclei situated in a sinus which surrounds its margin. I have made some remarkably good sections of the eyes of *Sallicus scenicus*, in which it is quite easy to see that no such connexion exists between these structures.

In some of these sections the fibrous membrane has completely separated from the bacilla, just as the membrana basilaris separates from the retina in the compound eye.

The sinus (ls, fig. 33) which surrounds the membrane in *Sallicus* contains radiating fibres very similar to those which I have described in the sinus around the margin of the membrana basilaris of the compound eye; and it is these fibres which contain the nuclei to which Dr. Grenacher believes he has traced retinal fibres.

At present the origin of the retina of the simple eye cannot be said to have been determined; I have sought in vain for any reliable indications as to its origin. Dr. Grenacher believes it to arise by a modification of the cells of the hypoderm‡. His arguments in favour of this origin are very unsatisfactory, and apparently indicate that the vitreous and not the retinal elements arise from this layer.

A cellular vitreous is always present in the simple eyes of insects: I formerly failed to demonstrate it in the stemmata in Flies, but I have since found that this layer exists, although from its extreme thinness it is not easily seen except in specimens preserved with osmic acid §.

On this point, at least, I must endorse the views of Von Graber ||, rather than those of Dr. Grenacher. In a very able paper by Prof. E. Ray Lankester and Mr. A. G. Bourne¶,

* L. c. figs. 12, 95, 96, & 97.

† L. c.

‡ L. c.

§ Phil. Trans. L. c.

|| Archiv f. mikrosk. Anat. vol. xvii. 1880, p. 58.

¶ Quarterly Journal of Microscopic Science, Jan. 1883.

the vitreous is said to be absent in the lateral eyes of Scorpions, although it is present in the more highly developed central eye. This is a remarkable exception to the conditions which I have observed; but as I formerly overlooked the vitreous in cases in which I now know it exists, I cannot help suspecting that the cells have been destroyed in some way in the preparation of the sections.

I propose the following classification of the visual organs of the Arthropoda.

- | | |
|----------------------|----------------------|
| I. SIMPLE OCELLI. | III. AGGREGATE EYES. |
| II. COMPOUND OCELLI. | IV. COMPOUND EYES. |

I. SIMPLE OCELLI.—I include under this term the ocelli of Arachnida and the stemmata of perfect insects, and I think it probable that the eyes of the Myriapoda consist of clusters of such stemmata; but at present I am not sufficiently acquainted with the modifications of the eyes of this family to speak with any degree of certainty, as the investigation of the eyes of Myriapods is exceedingly difficult.

II. COMPOUND OCELLI.—I use this term to indicate the ocelli of larval insects in which there is apparently a second refractive system—the spindle, which magnifies and erects the subcorneal image.

I have little doubt that the eyes of the *Coryceidæ*, at least those of *Copilla*, belong to this class; but I have not had any opportunity of examining them, and only judge from Dr. Grenacher's description and figures.

III. AGGREGATE EYES.—I include in this division the semi-compound eyes of Isopods, which appear to be nothing more than aggregations of compound ocelli.

Dr. Grenacher regards the subcorneal lens of the Isopod as a highly modified crystalline cone. I regard it as the representative of the oil-lens of the compound eye, and of the lens of the compound ocellus; perhaps the cone of the compound eye should also be regarded as a highly modified form of lens; at least it departs more from the primitive type than the spheroid lens of the Isopod.

IV. COMPOUND EYES.—These are the ordinary eyes of the Crustacea and Insecta. They exhibit very various forms, and many efforts have been made to classify them, chiefly founded on the variation of the dioptron, and especially those of the cornea and crystalline cone.

All these classifications appear to me unsatisfactory from a morphological point of view, as they do not harmonize with the affinities of the forms of the Arthropods in which the variations occur, neither do they throw any light on the genetic relations of the compound eye.

Perhaps the following classification will be useful in making the relations of the various forms more easily comprehended.

I am so little acquainted with the structure of the eye in the Crustacea from personal observation that I shall confine my remarks chiefly to the conditions which I have observed in the Insecta.

(1.) Eyes in which the dioptron is *incompletely* separated from the neuron, each segment of the former having a distinct retinula. I have observed this condition in the larva of the gnats, in *Tipula* and in the genus *Telephorus* amongst the Coleoptera.

(II.) Eyes in which the dioptron is *completely* separated from the neuron by the membrana basilaris, but in which the retina *is divided into distinct retinulae*. This is the condition of the compound eye of the Dragon-fly larva, in the imago of the Gnats, and in the Orthoptera.

(III.) Eyes in which the dioptron is *completely* separated from the neuron, and the retina *is continuous*, but in which the nerve-fibres of the optic nerve are arranged in *distinct fasciculi*: this condition holds in many Hymenoptera, Hemiptera, and Lepidoptera.

(IV.) Eyes in which the dioptron is *completely separated* from the neuron, in which the retina *is continuous*, and the fibres of the optic nerve *form a single bundle and decussate completely*. This condition is found in the Muscidae, the Diurnal Lepidoptera, and in the perfect form of some Dragon-flies (*Agrion*).

It would appear therefore that the compound eye is to be regarded as a collection of *compound ocelli*, in which the tendency to close union is greater nearer to the surface than in its deeper portion, the optic nerves being the last parts to become fused into a single compound structure.

DESCRIPTION OF THE PLATES.

The small letters indicate the following parts in all the figures.

<i>c.</i> The cornea.	<i>i.</i> Iris cells.	<i>op.</i> Optic ganglion.
<i>cc.</i> The crystalline cone.	<i>k.</i> Deep or kidney-shaped ganglion.	<i>pg.</i> Pigment.
<i>cn.</i> Subcorneal nuclei.	<i>l.</i> Lens.	<i>rf.</i> Radiating fibres.
<i>ch.</i> The chamber.	<i>ls.</i> Lymph-sinus.	<i>rt.</i> Retina.
<i>cb.</i> Ciliary bodies.	<i>m.</i> Basilar membrane.	<i>rt*</i> . Partial Retinae.
<i>cl¹.cl².</i> Outer and inner cellular layers.	<i>mc.</i> Ciliary muscle.	<i>sh.</i> Sheath of the great rods.
<i>g¹.g².</i> Sections of the optic ganglion.	<i>n¹.n².</i> Nuclear layers.	<i>sp.</i> Spindles.
<i>h.</i> Hypodermis.	<i>nuc.</i> Nuclear bodies.	<i>sr.</i> Scleral ring.
	<i>no.</i> Optic nerve.	<i>tr.</i> Tracheal vessels.
		<i>v.</i> Vitreous humour.

PLATE XL.

Fig. 1. A semidiagrammatic section of the eye and optic ganglion of a Blow-fly.

- 1 *a.* The membrana basilaris of the same insect seen from its neural surface. *ped*, pedicle of the scleral ring. Both figures show the large muscle *m.c.* attached to the inner edge of the scleral ring, *sr*.
2. A diagram showing the manner in which the image is formed on the Arthropod retina.
3. An optical section of two of the segments of the dioptron of the Plume Moth (*Pterophorus pentadactylus*).
4. A diagram showing the optical relations of the same.
5. A semidiagrammatic representation of a vertical section through the great eyes of a Dragon-fly (*Aeshnia*), showing the lymph-channels; *a.a.* afferent vessels; *b.b.* efferent openings.
6. A section through the scleral ring and membrana basilaris in the region of the efferent lymph-path, showing the radiating fibres *rf*, from the eye of *Aeshnia*.
7. A similar section from the eye of *Agrion*.
8. A section through the scleral ring, *s.r.*, of *Agrion*, showing a marginal lymph-opening.
9. The afferent vessels of the dioptron of *Aeshnia*.

Fig. 10. An optical section of a segment of the dioptron of *Tipula* in the recent condition.

11. The spindle of the eye of the same, slightly altered by the process of preparation.
12. A similar spindle.
13. A segment or tube of a spindle from the same insect, showing the contracted tube with soft vacuolated material adhering to it, possibly a portion of its contents.
14. *a.* A transverse section through the spindle of the same insect.
14. *b.* A similar section, in which the peripheral tubes have partially collapsed.
15. Three of the peripheral segments of the dioptron of a Blow-fly in the immature condition.
- 16 to 18. Portions of the great rods of a Blow-fly, showing the different appearances which they present, owing to partial or total collapse of the spindle.
16. A portion of the spindle partially emptied by pressure.
17. A specimen showing still further collapse of the tubes.
18. A portion of a spindle showing vacuolation of the sheathing-cells and collapse of the tubes in normal saline solution.
19. The lens at the outer end of the spindle from the same insect, from an osmic-acid preparation; *nuc.* spheroids in the interior of the lens, *sp.* spindle.
20. A transverse section of the great rods, spindles, *sp.*, sheathing-cells *sh.*, and tracheal vessels, *tv.*, from the same.
21. The lens-capsule, ruptured by pressure, from the Earwig.
22. A single segment of the dioptron, and a few bacilla from the Yellow Underwing Moth (*Triphaena pronuba*), from a specimen prepared in chloral hydrate solution.

PLATE XLII.

Fig. 23. A section through the entire eye of a Noctuid (*Xylophasia potyodon*).

24. Transverse sections through the cone of the same insect: *a*, near the base; *b*, near the apex, showing the coloured granules.
25. Transverse sections through the rods and spindles of the same insect: *a*, *b*, *c*, three successive sections through the spindle-sheath; *d*, section through the spindle showing the cells of the sheath; *e*, section through a stellate spindle.
26. The chamber and cone of the same insect. The tube has collapsed.
27. The tube between the cone and spindle, from the eye of a species of Noctuid Moth; the tube contains unicellular parasitic organisms, *z*.
28. The chambers and a portion of the spindles of two segments of the dioptron, an osmic-acid preparation from the eye of a Blow-fly: *oc*, outer portion of the cone; *cc'*, crystalline cone.
29. The spindle from the same, mounted in a dilute solution of osmic acid.
30. A section of the cornea of an African Carpenter Bee (*Xylocopa*), from a dried insect, showing its laminated structure: *c*¹, lenticular layer; *c*², laminated layer; *c*³, inner surface.
31. A single segment of the dioptron of an Ant (*Formica rufa*), showing the ciliary rods *cb*.; 31 *a*, one of the ciliary rods detached and more highly magnified.
32. A similar preparation from the eye of a Wasp (*Vespa germanica*): 32 *a*, one of the same detached and more highly magnified; *cb*¹, refractive granule; *cb*², iris cell; *cb*³, fringe-like process.
33. A portion of the eye of a Spider (*Sallicus scenicus*), showing the fibrous membrane *m*, which separates the dioptric from the nervous structures; *ls*, lymph-sinus, containing radiating nucleated fibres.
34. Two of the eyes of *Sallicus scenicus*.
35. The simple ocellus of a Blow-fly: 35 *a*, one of the retinal elements more highly magnified; *r*¹, outer refractive segment; *r*², intermediate pigmented portion; *r*³, nucleated protoplasmic portion.

- Fig. 36. One of the compound ocelli of a Noctuid caterpillar: *h*, hypoderm; *pg*, pigment covering the spindle.
37. One of the compound ocelli from another Noctuid caterpillar.
38. A similar preparation from a third species of Noctuid caterpillar: *no*, union of three nerve-trunks from three compound ocelli.
39. An oblique section through a similar eye in an embryonic condition.
40. A transverse section of a compound ocellus from a Noctuid caterpillar, showing the iris and lens *in situ*.

PLATE XLII.

- Fig. 41. A transverse section through the entire eye of a Dragon-fly (*Agrion virgo*), from the perfect insect.
42. A highly magnified representation of a portion of the retinal ganglion, from the same preparation: *n*¹, nuclear layer; *cl*¹, cellular layer; *f*¹, fibrous layer; *cl*², second cellular layer; *f*², second fibrous layer; *n*², second nuclear layer; *x*, second decussating layer of fibres.
43. A section through the entire eye of a larval *Agrion*, from a specimen 6 lines long: *rt*^{*}, segregate retina; *g*¹, ganglion.
44. A similar section from a more advanced larva.
45. A similar section from an adult larva.
46. The bacilla from the neuron of the same larva.
47. The bacilla from the neuron of a Dragon-fly larva (*Libellula depressa*).
48. The cephalic ganglia of a Cockroach, from a large larva, seen from behind: *op*, optic lobe; *n*, nerves to partial retinae.
49. The same, seen from before.
50. A transverse section through one of the partial retinae in a rudimentary stage: *no*, one of the optic nerves.
51. A section through the neuron of a Fly (*Syrphus ribesii*).
52. A portion of the retinal ganglion of the same, seen with an immersion lens $\frac{1}{2}$. (The references as in fig. 42.)
53. Two bundles of bacilla from the retina of the Blow-fly, from an osmic-acid preparation, showing the tracheal vessels and cells of the neuroglia: *o* outer and *i* inner segments.
54. A transverse section through the entire eye of a Gnat.
55. Bacilla from the eye of *Tipula*, showing the axis-cylinder between the inner and the outer segments.

PLATE XLIII.

- Fig. 56. A semidiagrammatic representation of the retina of the Blow-fly, drawn from preparations prepared in different fluids, and showing the connexions of the various elements: *a*, neuroglia of the retina, from a chloral hydrate preparation; *b*, the same, from an osmic-acid preparation; *c*, the bacilla, from osmic-acid preparations; *B*¹, outer segments; *B*², inner segments; *d*, the neuroglia of the optic nerve; *e*, the fibres of the optic nerve, from osmic-acid preparation; *f*, outer layer of ganglion, osmic acid; *g*, cells with the supporting neuroglia, chloral hydrate; *h*, transverse fibres, Müller's fluid; *m*², inner limiting membrane of retina; *m*³, endothelium covering the ganglion; *no*², inner nerve-fibres connecting the optic and deep ganglion. The other references are the same as those in the rest of the figures.
57. A portion of the neuron of a Crane-fly (*Tipula oleracea*). The references as in fig. 56.

- Fig. 58. A portion of the retina of a Blow-fly, from a specimen prepared with chloral hydrate, and stained with cosin.
59. A portion of the retina of the Blow-fly, osmic acid.
 60. A portion of the retina of a Blow-fly, Müller's fluid.
 61. A transverse section of a portion of the retina of a Blow-fly, from a specimen prepared with Müller's fluid and mounted in balsam.
 62. A transverse section of a portion of the retina of a Blow-fly, through the inner segments of the bacilla, from a specimen preserved in chloral hydrate and subsequently mounted in balsam.
 63. Two fasciculi of bacilla, from a Hawk-Moth pupa.
 64. Bacilla of a Blow-fly, showing the lenticulus, from an osmic-acid preparation.
 65. Bacilla from the eye of a Cockroach, with double outer segments.
 66. Similar bacilla, from the eye of a Blow-fly.
 67. Bacilla from the eye of a Noctuid Moth.
 68. Tracheal vessels on the inner surface of the membrana basilaris of the Blow-fly.
 69. Retinal pigment-cells and a portion of the basilar membrane of a Dragon-fly (*Eshnia grandis*).
 70. A portion of the basilar membrane from the eye of a Lobster, showing prismatic thickenings at the inner extremities of the great rods.
 71. A portion of the retina and basilar membrane of the Cabbage Butterfly, showing lenticular thickenings.
 72. A vertical section through the basilar membrane of *Syrphus*, showing the cellular sheaths of the fasciculi of bacilla, and the cells around the necks of the expanded tracheal sacs of the dioptron.
 73. The disk from which the retina originates, from a Lepidopterous larva (Noctuid).
 74. Two segments of the dioptron, with their retinuke, from the eye of a perfect Gnat (*Corethra plumicornis*): 74 *a*. A transverse section through the inner extremity of the cone of the same; 74 *b*. A transverse section through the spindle of the same.
 75. A portion of the dioptron of the larva of the same insect.
 76. A section of a portion of the eye of a young Gnat larva.
 77. A portion of the dioptron of an immature Crane-fly (*Tipula oleracea*), which had just escaped from the pupa.

NOTE.—Since the above was sent to press, my attention has been drawn to a short paper by Justus Carrière of Strassburg (Quart. Journ. of Micros. Sci. Oct. 1884, p. 673), "On the Eyes of some Invertebrata," in which my retinal layer is figured. He speaks of it as the "palisade layer." He remains, however, a disciple of established views, and has not given the retinal layer nearly so much attention as it deserves. So far as his observations go, they appear to me to confirm my own, as I firmly believe that M. Carrière, on further investigation, will be led to admit the validity of my views.

XV. *Contributions to the Knowledge of the Genus Anaphe, Walker.* By LORD
WALSINGHAM, M.A., F.L.S.

(Plates XLIV., XLV.)

Read March 20, 1884.

FOR the specimens described in the present communication, I am indebted to the kindness of Colonel J. H. Bowker, of Durban, Natal. In a letter dated July 4th, 1883, he wrote to me as follows:—"I am sending by the 'Moor,' Union steamship, a little box with a nest of the congregating moth. The larvæ are most interesting, often denuding a tree of its foliage; they move in a body, sometimes ten or even twenty yards long, in search of 'pastures new,' and when the time comes, form into a cluster, and form the nest covered with a brown silk. Unless the change of climate has an effect, they will come out about September next. I should suggest the nest being set up in a green-house, not too hot, with a view towards the *morning sun*. A small nest which I sent to the Cape Town Museum produced about 80; judging from the size of the two, the one I send ought to produce about 300. The natives use the silk for medical purposes, somewhat as we use oiled silk." The box reached me at the beginning of August 1883, and I was much surprised to find that the larvæ were alive and apparently healthy. Many of them remained in the so-called nest, but bodies of from twenty to forty constantly came out and moved about, always keeping close to it. They moved in a closely packed mass, following a slightly curved line, much in the same position as that in which the small cocoons may now be seen arranged in the interior of the large one.

On the 9th of August I sent them to the Insectarium in the Zoological Society's Gardens, in Regent's Park, where they have been under the attentive care of Mr. Arthur Thomson until about the middle of March. Mr. Thomson informs me that about 250 moths emerged from the large cocoon. The first on December 3rd, the last on February 14th. One pair copulated and produced eggs. The eggs hatched, but although the name of the food plant had been ascertained from Mr. G. Baker, at Kew, to be *Bridelia mierantha*, Baillon, the dead leaves attached to the nest having enabled him to identify it, it was found impossible to obtain, there or elsewhere, any thing sufficiently nearly allied to it to induce the young larvæ to feed, and they soon all died. Mr. Thomson was successful, at my request, in finding in the glass case a few of their bodies, much shrivelled, but, nevertheless, most interesting, as indicating the probable affinities of the genus to which they belong. The appearance of the moths was followed by the emergence of a number of dipterous parasites. The larvæ did not finally enclose themselves in the large cocoon until about a fortnight after they reached the Insectarium; they must therefore have been about 50 days without food. Some of them died, probably from this cause, without entering the cocoon at all; and I find that one or more have spun themselves up in the outer covering of the main cocoon, without coming to maturity. It will be seen that Colonel Bowker's estimate of the number sent was remarkably correct.

In the British Museum are at least four described species of the genus ANAPHE, viz.—*Anaphe venata*, Butler, from Old Calabar; *Anaphe ambrozia*, Butler, a small species from Angola; *Anaphe reticulata*, Walker, from Natal; and *Anaphe panda*, Boisduval.

The single typical specimen of *Anaphe panda*, from Natal, is precisely similar to those from Colonel Bowker; but placed under the same name is a considerable series of specimens which differ from these in the absence of any transverse dark bar crossing the pale triangular or wedge-shaped space beyond the middle of the anterior wings. In those specimens that space is clear and unclouded, the longitudinal brown lines being confined to the outer side of the oblique fascia, and connecting it, as in the Natal form, with the dark fringes of the apical margin. The brown markings are also somewhat darker than those of *A. panda*. These specimens are from Monga-ma-Lobah, in the Cameroons, and although probably only a local race, are at least as much entitled to specific distinction as is the species named by Walker, *Anaphe reticulata*. The entire absence of variation throughout the large colony sent by Colonel Bowker seems to indicate that the slight differences observable in these local races are constant and reliable, and that there is little or no individual variation.

ANAPHE INFRACTA, sp. n. (Pl. XLV. fig. 8).

Head and palpi ferruginous; antennæ black. Thorax creamy white anteriorly, ferruginous posteriorly, the white divided by a ferruginous streak along the middle, reaching to the head. Fore wings creamy white, with narrow brown margins, the fringes also brown, two narrow brown transverse bands; the first, arising before the middle of the costal margin, tends obliquely outwards to a point slightly beyond the middle of the dorsal margin, where it joins the lower extremity of another narrow brown band, which runs to the costa parallel with the apical margin, the two enclosing a plain wedge-like space of the pale ground-colour of the wing. The outer of these bands is connected with the apical margin by two shorter brown streaks from above and below its middle, the upper one slightly depressed outwardly, the lower one more depressed, reaching the margin slightly above the anal angle. Hind wings creamy white, tinged with ferruginous at the base, and about the abdominal margin, with a very faint indication of a transverse median shade of the same colour, more visible on the under side. Abdomen pale ferruginous, with darker lines at the junction of the segments.

Expanse of male 47 mm.; of female 58 mm.

Monga-ma-Lobah, Cameroons (*G. Thomson*).

Anaphe reticulata, Walker, figured by Herrich-Schäffer (Sammlung ausser-europäischer Schmetterlinge, f. 431), under the name *Arctiomorpha euprepiaeformis*, has two distinct transverse bars across the wedge-shaped pale space, the lower one of the two being continued to the base of the dorsal margin. Two cocoons, said to belong to this species, are in the British Museum, and differ from the one now under notice, so far as I can ascertain, only in their rather smaller size and more irregular shape, and in the colour of the silk of which the small cocoons in their interior are composed. These (which in my specimen are white, with scarcely any brownish tinge) are, in those cases,

f a rich brown, almost exactly the same colour as the external covering of the aggregate mass.

A sixth species was kindly given to me about three years ago by Mr. G. T. Carter, collected by him at Aburi, on the Gold Coast. The single specimen (a male) is now in the British Museum.

The colouring is precisely similar to that of *A. panda*. It differs from all the described species of this genus in having a single band only, crossing the anterior wings; moreover, this band, instead of being somewhat curved outwards, as is the first bar in all other known species, is curved slightly inwards towards the base. The costal margin is brown throughout; the dorsal margin also brown, except a very short space near the base. The fringes of the anterior and posterior wings are also brown. On the underside the upper portion of the central band of the fore wings is visible, and there is a distinct costal spot on the hind wing, which is not visible above.

ANAPHE CARTERI, sp. n. (Pl. XLV. fig. 9.)

Face and palpi ferruginous; head creamy white above; antennæ black. Thorax creamy white in front and at the sides, with a ferruginous blotch behind projecting forward in the middle, in an obtuse wedge-shaped form, but not reaching to the head. Fore wings creamy white, the margins narrowly ferruginous, with a narrow transverse median band of the same colour, which is slightly bent inwards; the fringes also ferruginous. Hind wings creamy white, with ferruginous fringes, except on the abdominal margin.

Expanse 36 mm.

Aburi, Gold Coast (*Carter*).

I find in the Proceedings of the Entomological Society, June 5th, 1878:—

“Mr. D. Greig Rutherford exhibited a series of large cocoons sent by Mr. George Thomson from Mount Camaroons, West Africa, formed by the caterpillars of a species of *Bombyx* allied to *Anaphe panda*, Bdv. They were taken at an elevation of 5000 feet above the level of the sea, and, judging from the nature of certain twigs and pieces of native cord fastened to their exterior covering, appeared to have been found attached to fences or to the caves of houses. The cocoons are light brown in colour, and very irregular in shape, rather flattish, and vary in diameter from four to seven inches.

“Each cocoon contains from 130 to 150 separate cocoons, each enclosing a larva or a chrysalis in various stages of development, the least mature being near the centre of the aggregate mass. To some of the cocoons were attached a case containing what appeared to be the larvæ of some species of *Ichneumon* or dipterous parasite.* All the smaller cocoons are firmly bound together by layers of a coarse silken material, this aggregation being enveloped by a thin brown lining almost of the consistency of parchment, the whole forming a compact mass, which again is surrounded by a loose silken tissue, while a strong covering of the same material envelops the whole. From this it would appear that *A. panda*, like some other species of *Bombycidae*, is social, and that the caterpillars unite in considerable numbers in order to form an aggregate cocoon of sufficient strength

* These were subsequently proved to be Hymenoptera, sp. *Cryptus formosus*, Brullé.

to preserve the chrysalis from the attacks of enemies, and probably also against extreme changes of temperature."

It may be noticed that this description applies in almost every detail to the specimens under consideration, but I would point out one exception.

The plan adopted by the numerous members of this South-African insect republic appears to have been based upon a more perfect recognition of the equal rights of individuals. There is no necessity under their system to trust to the retarded development of those situated towards the interior of their habitation. There are two outlets, and the inhabitants have ranged themselves in two almost equal bodies in such a manner as to secure to each moth a ready means of egress from one or other of these openings. The points of the numerous cocoons are all directed as nearly as possible towards the nearest available outlet, and a separate silken passage seems to have been prepared for the accommodation of each occupant, so that the foremost ones in no way block the way of those situated behind them. Some few of the moths which appear to have been unable to get out, are probably those of which the larvæ were somewhat starved, and therefore imperfectly developed, and which were thus not upon equal terms with their more advanced companions. There are probably some Fellows of the Society who are better capable of judging of the quality of the silk than myself. It seems to me to be extremely strong and tough, although, except on the external covering of the colony, it is not particularly coarse. On winding a small quantity, it appeared to be perfectly continuous, but not easily run off. Although there is far less in quantity on each separate cocoon than on those of *Bombyx mori* and other silk-producing Bombyces, the immense number of cocoons in each colony might not impossibly render it of some economic and commercial value. A silk-plantation on the high lands of Natal would certainly be a pleasant and healthful field of enterprise, and might perhaps turn out to be a profitable one.

The only description I have been able to find of a larva of the genus *Anaphe* is given by Carl Fromholz in a paper in the 'Berliner entomologische Zeitschrift,' Bd. xvii., 1883, Heft i. pp. 9-13, which is illustrated by an octavo plate. This larva was supposed to be that of *Anaphe panda*, and the large cocoon figured on the plate was evidently made by this or some allied species, but the specimens came from the interior of Africa, 250 miles from Dara Salam, and the moth does not appear to have been actually identified. This larva was described from the dead and somewhat shrivelled specimens which reached the author, as "yellowish white," which by no means agrees with the colour of those now exhibited.

The examples now figured were preserved by a process which I have successfully applied to those of the majority of the British Macro-Lepidoptera, as well as to numerous exotic species. They have the head black, divided by a narrow pale line along the middle; the second segment, with two narrow transverse horny plates, separated from each other in the middle, and a narrow black horny plate on the anal segment. The body is of a purplish vinous colour, slightly paler between the segments, with a faintly indicated pale line above the black spiracles, and some pale yellowish white spots at the junction of the segments below them.

The whole body is covered with short black hairs. On the upper portion of each segment are two pale wart-like spots, situated to the right and left of the dorsal vessel. Behind these, and more widely separated from each other, are two smaller, but otherwise similar, spots, whitish hairs springing from all four. Other wart-like spots less distinctly paler than the surrounding skin are arranged on the sides of the segments in the following order; one above and one below, and a third behind and slightly below each spiracle. There is also one above each of the abdominal claspers, which are dull yellowish white, with black hooklets, as are also the anal claspers. The prolegs are black, with a whitish ring around the base of each. All the hairs have small, but sharp spines around them, arranged somewhat in a spiral form from base to tip, the points directed outwards. This formation, as in the case of those of many larvæ of the Lasiocampidæ and Liparidæ, notably in that of *Cnethocampa pityocampa*, W.V., renders them very irritating and difficult to eradicate if, by any means after detachment, they become lodged, with the base downwards, in the human skin.

This genus has been placed among the Liparidæ. In the *Annals and Magazine of Natural History* (4), xix. p. 462, Mr. Butler assigns to it a position between *Marana* and *Numenes*, and suggests that *A. reticulata* and *A. panda* are probably varieties of one species.

The young larvæ above described have so much the character of Arctiidæ, with their clothing of long brown erect hairs, as to suggest the idea that the genus should more properly be included in this family. The most immature forms of larvæ may usually be relied upon to indicate their affinities and probable derivation. In this case it is a fair inference from the evidence they afford that *Arctia* is an older form than *Liparis*, and that the genus *Anaphe* occupies the position of a connecting link between the two families.

Herrich-Schäffer, in creating for this form the generic name *Arctiomorpha*, showed that he had observed its peculiar resemblance to *Arctia*; but he placed it in the family Notodontidæ.

Boisduval, in describing this same species in the 'Voyage de Delegorgue en Afrique Australe,' tom. ii. p. 600, 1847, mentions its resemblance to *Arctia villica*, which I confess I am unable to recognize. The large anal tuft of easily detached hairs on the body of the female is the point in which it most strongly resembles the typical forms of the genus *Liparis*, as well as in its neuration, the median vein of the hind wings having but three branches instead of four as in the Arctiidæ.

I am informed by Mr. Kirby that the dipterous parasites present in the cocoon from Colonel Bowker appear to be closely allied to *Tachina onchestus*, Walker (*List Dip. B.* M. iv. p. 773, 1849). [Two of these emerged on the day the paper was read, and one was shown alive at the Meeting of the Society, along with the series of specimens described in this communication.]

Fromholz, in the paper already referred to, describes under a new genus of Lepidoptera belonging to the Phycidæ, *Zophodiopsis hyænella*, as infesting nests of the species mentioned by him and believed to be *Anaphe panda*. We have therefore the Lepidoptera, Hymenoptera, and Diptera, each represented as parasitically attached to the larvæ or to the habitations of larvæ of this interesting genus.

EXPLANATION OF PLATES.

PLATE XLIV.

Fig. 1. Enveloping cocoon of *Anaphe panda*, Boisd., two-thirds natural size—outside view.

Fig. 2. The same cut open, showing internal texture and arrangement of small separate cocoons. o^1 , o^2 , twigs inserted into the openings.

PLATE XLV.

Fig. 1. Portion of inner surface of enveloping cocoon, showing lining between inner wall and exterior, with modification of smooth surface by introduction of foreign body. 1 *a*. Fibre of envelope, highly magnified.

Fig. 2. Diagram of cross section through the middle. 2 *a*. Outlet at back of same.

Fig. 3. Full-grown larva. 3 *a*. Spines of larva, highly magnified.

Fig. 4. Young larvæ.

Fig. 5. Separate cocoons from interior. 5 *a*. Empty pupa-shell.

Fig. 6. Single brown cocoon, from interior of similar colony in the British Museum.

Fig. 7. *Anaphe panda*, Boisd. ♂.

Fig. 8. ——— *infracta*, Wlsm. ♂.

Fig. 9. ——— *Carteri*, Wlsm. ♂.

Fig. 10. Dipterous parasite, *Tachina onchestus*, Walk. 10 *a*. Empty cocoon of same.

XVI. *On a new Species of Cœlacanthus (C. Tingleyensis) from the Yorkshire Cannel Coal.* By JAMES W. DAVIS, *F.L.S., F.G.S.*

(Plates XLVI.-XLIX.)

Read June 19th, 1884.

SPECIMENS vary very much in size, and occur in all stages of growth between 3 inches and six times that length; their form is somewhat long and slender, with a series of powerful fins well adapted for rapid progression through the water. Examples which appear to have attained the maximum size of about 18 inches in length are taken for the following descriptions. In such a one the head occupies one fourth the entire length, the body, from the pectoral arch to the base of the tail, two fourths, and the tail the remaining fourth. The greatest depth of the body is immediately behind the pectoral fins, where it is 3·5 inches; posteriorly the depth diminishes gradually to the base of the tail, which is 2 inches. The body was probably more or less cylindrical in form, and the lateral diameter little less than that between the dorsal and ventral surfaces. The anterior portion of the caudal fin expands to a diameter of 4 inches, and the rays radiate from the base 3 inches: beyond this the second portion of the tail extends about 1·3 inch, its termination supporting a second series of rays, forming the peculiar prolongation of the caudal appendage characteristic of the genus. In addition to the caudal fin there are seven others—two dorsal and one anal fin, a pair of pectorals, and a pair of ventrals. The posterior dorsal fin (Pl. XLVI. d^2) is located 2·5 inches in front of the caudal (c^1), and is supported by a scale-invested lobe from the body. The anterior dorsal fin (d^1) is about 3 inches in front of the posterior one: in several specimens where this fin is present there does not appear to be any lobe supporting it. The pectoral fins (p) are situated immediately behind the thoracic arch, and, like the ventrals (v) and anal (a), they are lobate. The ventrals are powerful and large fins, placed opposite the space intermediate between the two dorsal fins. The anal fin, 3 inches behind the ventrals, is situated at a considerably shorter distance from the caudal than is the posterior dorsal fin. The whole of the body is invested in a covering of comparatively thin, enamelled, and beautifully ornamented scales; those on the dorsal and lateral regions are broader and have a more obtuse termination than those on the ventral surface. The scales covering the lobes of the fins are smaller than those of the body, and are proportionately thinner. The head is protected by dermal ossifications, the surface of which is covered with enamel raised into, and arranged in, an exquisite series of parallel but sinuous ridges. The external covering of the head is preserved in many specimens, but in all cases more or less crushed and disturbed. The cranial bones include frontals (f), parietals (p), and occipitals (o): a restored outline of their forms, one half the natural size, is attempted on Pl. XLIX. fig. 2, from which it may be inferred that the several bones

constituting the upper surface of the cranium form a compact and closely attached group. Anterior to the frontal bones there is one forming the snout, probably the ethmoid (*eth*), which reaches over and more or less envelops the anterior extremities of the rami of the upper jaw. The orbit (*orb*) is moderately large; its upper boundary is formed by the frontal and parietal bones: between these and the maxilla the structure of the lateral surface of the head is somewhat obscure. There was an important osseous plate extending from the orbit to the opercula, apparently the temporal bone (*t*); and one or more smaller ossicles filled up the interval between the maxilla, the anterior portion of the orbit, and the bones of the cranium. The opercular bones are three in number; the operculum (*op*) was a large bony plate, subtriangular in outline, extending to and overlapping the scapular bones of the pectoral arch. In addition to the operculum there are two other plates, similar in form, but only about one fourth its size: they were probably the suboperculum (*i.op*) and interoperculum (*s.op*), and are represented on Pl. XLVII. fig. 1, and also in the restoration represented on Pl. XLIX.

The upper jaws (*mx*) are frequently observed in specimens, but in no instance with sufficient certainty and clearness to enable an exact description to be given of their form. They were considerably shorter than the mandibles (*M*) of the lower jaw, thickest and strongest beneath the orbit; and, tapering towards the symphysis, the most anterior portion was probably divided by the insertion of the premaxillaries (Pl. XLVII. fig. 11). The mandibles are strong, about 3 inches in length; the lower margin is straight, and was grooved and smooth where attached to the jugular bones; the upper margin is anteriorly depressed, but expands towards the median portion to a height of .35 of an inch above the inferior margin; towards the posterior extremity the surface is again depressed. The presence of teeth in either the maxilla or mandible is somewhat problematical. An examination of many specimens has failed to show an example with teeth *in situ*. At the same time, a number of teeth are occasionally seen mixed with the bones of the head, and it is possible may have been so loosely attached to the jaws that they have invariably become separated after the death of the fish. The teeth are about .1 of an inch in length, smooth, slightly curved, and acutely pointed. The whole of the under surface of the head between the two rami of the lower jaws is occupied by the jugular plates (*ju*): they are large, elliptical in form, internally strengthened by a median process traversing the longitudinal axis of the plate, and externally ornamented by an extremely beautiful arrangement of ridges on the surface of the ganoine, varying much in detail, but running for the most part parallel with its longer axis.

The scales are moderate in size and rather thin. About one third of the surface of each scale is exposed, the remaining portion being covered by the succeeding scales. The outline of the exposed part forms a parallelogram, the exposed margin forming a more or less acutely pointed angle, whilst the margin hidden by overlapping scales is circular. The scales covering the ventral surface are the largest and broadest; they measure .3 of an inch across; the length of the scale is .35 of an inch, of which the exposed surface occupies .2 of an inch. The scales on the sides average the same length as the ventral ones, but are only about .2 of an inch across. The scales decrease in size towards the tail: they do not appear to exhibit any well-defined lateral line; they run

in parallel rows from the dorsal to the ventral surface, diagonally, with a slight sigmoidal curvature. The scales enveloping the lobes of the several fins differ from those of the body only in size; they are much smaller, decreasing as they approach the distal extremity of the lobe.

The external surface is covered with glistening enamel, which is minutely furrowed. The intervening ridges vary considerably in detail, both as to arrangement and form: in some instances the ridges extend parallel with each side of the scale and meet at the point, the successive ridges forming a series of triangles whose apices extend in a line down the middle of the scale; this is especially the case along the lateral surfaces of the body. On other scales, especially along the ventral surface, the ridges extend more or less along the axis of the scale, the longest being in the middle, and becoming gradually shorter on each side, and running out on the margins of the scale, giving it a somewhat jagged and rough outline. The ridges are not unfrequently broken by furrows extending across them, and where this happens the surface has the appearance of being covered with elongated tubercles. Various modifications of the several forms described occur on the scales of a single specimen, and sometimes in close proximity one to another (Pl. XLIX. fig. 3).

The *fins* are supported in each instance, with the exception of the anterior dorsal fin, by a pedunculate, lobate expansion of the teguments of the body. The lobes of the posterior dorsal and the pair of ventral fins are large: in the specimen depicted on Pl. XLVI. they are quite half an inch in diameter; those of the anal fin and the pectorals are not so large. The anterior dorsal fin exhibits the ordinary arrangements of the fin-rays, though they appear to be attached, in the specimen already referred to, without the intervention of a lobe, apparently in close connexion with the neural spines. It is impossible to distinguish the exact number of rays which compose each fin; but twenty rays may be counted fringing the extremity of the lobe of either the dorsal or the ventral fins, and it is probable that this number is fewer than actually exist, because the rays are more or less folded and bent under each other. The pectoral and anal fins were composed of a smaller number. The rays vary considerably in length: those springing from the extremity of the lobe are an inch and a quarter to an inch and a half in length, whilst those above and below gradually diminish, the shortest being less than half an inch in length. The basal portion of each fin-ray, for about two thirds the entire length, is formed of a single bone pierced by a hollow tube, like the spinous bones of the body; the remaining third is divided by numerous transverse jointings into small ossicles.

The caudal fin is very large and powerfully built. The vertebral column extends in a straight line from the body of the fish through, and some distance beyond, the caudal fin. Its length beyond the extremity of the fin-rays shows a considerable amount of variation in different specimens. In the one figured on Pl. XLVIII. fig. 2 the vertebral prolongation barely extends beyond the fin; but in others, and in many instances smaller specimens, there is fully an inch between the termination of the caudal-fin rays and the beginning or basal portion of the smaller rays which form the second caudal appendage. Throughout the whole length of the vertebral support for the second caudal fin there are small rays on both the upper and lower surfaces, which appear to have served as a fin-like

connexion between the first and second caudals. The rays of the larger caudal fin are similar to those already described in connexion with the fins of the body; they are formed of a single pierced ray, connected with the interspinous bones to be mentioned further on, the distal extremity of which is divided by a number of joints with articulating surfaces. The rays are thirty-eight or more in number, half of which are above and half below the median extension of the vertebral column. The second caudal also consists of a number of short rays, which form a duplicate in miniature of the larger caudal fin, without the continuation of the vertebral axis beyond its extremity.

The specimen of which a figure is given on Pl. XLVII. fig. 1 affords an almost perfect representation of the structure of the under surface of the head. The anterior external boundary of the specimen is formed by the right and left ramus of the lower jaw (*m*), each 3·3 inches in length. The space between the rami of the jaw was wholly occupied, when the fish was living, by a pair of jugular plates (*ju*); these extended from a position immediately under the point of contact between the mandibles backwards a distance of nearly 3 inches. The external lateral margins of the jugulars fit to and occupy a groove along the under surface of the mandibles, whilst mesially one appears to have slightly overlapped the other: this is indicated by there being no ornamentation on the inner surface of the left jugular, whilst that of the right one extends to the margin of the plate. On either side may be seen the operculum (*op*), a large subtriangular bone 1·3 inch in diameter. The under surface is represented in this figure; the upper or external surface is covered with a beautiful arrangement of striæ, very minute but distinct, feebly represented by a separate operculum on Pl. XLVII. fig. 7. In addition to the opercula there are two similar but smaller bones on each side, which were probably connected with the operculum, and may have been suboperculum and interoperculum (*s.op* and *i.op*). Fortunately the external bones have been pressed aside and separated, so that the internal arrangement of the branchial arches (*br*) is exhibited. There are five branchial ossifications, extending diagonally from each side of a median support: they are strong, with a more or less sigmoidal curvature, and vary in length between 1·7 and 1·2 inch, the anterior arch being longest, and those placed posteriorly gradually decreasing in length; they have a diameter of about ·2 of an inch. The median support is a strong bone 2 inches in length, ·2 of an inch in breadth near the middle, widening out anteriorly to ·3 of an inch, and terminating in an acute point: posteriorly the surface expands to ·5 of an inch, and bifurcates at the posterior extremity. A detached specimen is represented by fig. 10 on Pl. XLVII. Between the two jugular plates and in front of the median branchial support there is an ossified mass, which may represent the cruciform bone which Prof. Huxley describes as forming the anterior extremity of the strong median ossification in *Cælacanthus lepturus* (Memoirs of Geol. Survey, decade xii. p. 19). In this instance, if the mass represents the cruciform extremity, it is a separate bone. The opposite extremity also differs from the enlarged figure in the Decades, which is described as a "posterior elongated spatulate portion."

The specimen drawn on Pl. XLVIII. exhibits a further extension of that portion of the body forming the junction of the head with the trunk of the fish. The jaws and jugular plates (*ju*) are exposed, and extending from beneath these are a pair of bones (*x*), one on

each side, which constitute a part of the pectoral arch and support the pectoral fins (*p*). The bones are nearly 2 inches in length: their anterior extremities extend towards the median portion of the branchiostegal apparatus, and are separated about an inch from each other; extending in a semicircle, the posterior extremities, somewhat flattened, are attached to the pectoral fins. A process on the outer margin of the bones gave attachment to other members of the pectoral arch, some elements of which are probably represented by the specimens on Pl. XLVII. figs. 4, 5, and 8. A separate example of the bone described above is represented by fig. 12 on the same Plate.

The vertebral column is in no instance preserved, but a decided impression remains in specimens showing its course through the body. The absence of bony vertebrae indicates that they were entirely cartilaginous, and in consequence have not been preserved. Neural spines extended from the vertebral column towards the dorsal aspect of the fish. They are strong and closely set; there are twelve in the space of one inch in that portion of the body surmounted by the anterior dorsal fin; they are 1 inch to $1\frac{1}{2}$ inch in length, being longest and most obliquely placed near the caudal extremity of the fish. The base of the spine attached to the vertebral column was divided, so as to afford a passage through which the spinal cord passed; the bifurcation extends $\cdot 3$ of an inch. The rays are hollow, the enclosed tube occupies about two fifths of the diameter of the spine, and the encircling bone is of a very fine close texture.

Prof. Huxley, in the Memoirs of the Geological Survey, decade xii. pp. 16 and 18, considers that the dorsal fins of *C. lepturus* are supported by large interspinous bones. Numerous specimens of the species now described have afforded no definite indication of such an interspinous bone; but rather seem to show a more close connexion between the spinous processes and the rays of the fin by smaller interspinous bones.

The whole of the ventral portion of the fish, from the insertion of the pectoral fins to midway between the ventral and anal fins, is occupied by an ossified air-bladder, and it is worthy of remark that the whole of this region appears devoid of ribs or hæmal spines: bones are occasionally found lying across this region, but they appear to have been displaced and fallen there accidentally. Posteriorly, hæmal processes, corresponding to those on the neural aspect of the vertebrae, extend to and support the anal fin and the inferior lobes of the caudal fins. The spinous processes are longer in this region than elsewhere, and appear to be directly connected with the rays of the tail without the intervention of interspinous bones (Pl. XLVIII. fig. 2). The connexion between the neural or hæmal spines and the fin-rays is not very clearly defined; but, so far as can be ascertained, there is no special arrangement such as was pointed out by the late Prof. Agassiz ('Poissons Foss.' vol. ii. p. 168). He describes the interspinous bones as ossicles which, instead of being attached by ligaments to the spinous bones on each side, are attached to the end of one of them, so as to form its direct continuation; and the ray, properly so called, is stated to be forked at its base, and embraces the interspinous ossicle in a manner similar to that of the spinous processes embracing the vertebrae. The specimen referred to above exhibits very clearly the attachment of the caudal rays to the spinous (?) bones. The basal extremities of the rays in this species are bent a little to one side, and thin out to a point. The distal extremity of each spinous bone, which is

also pointed, is in juxtaposition with the ray; but there is no appearance of bifurcation on the part of the latter. The terminal extremity of each ray of the caudal fin is divided into numerous little ossicles by transverse joints, as in the case of those of the other fins. The vertebral prolongation extends to a varied extent in different specimens beyond the first caudal fin: in the specimen now figured it terminates with a slightly rounded extremity, coequal with the length of the fin-rays; it is enclosed in enamelled scales quite to the end, from which a number of small rays expand to form the second caudal appendage. The number of rays is not easy to determine, but there are at least twelve of them. In a second specimen, not so large, and apparently pertaining to a younger fish, the vertebral continuation extends an inch beyond the termination of the major fin; its upper and lower surfaces are provided with short fin-rays, and the second caudal fin extends from its extremity, as in the previously described example.

A portion of the suspensory apparatus is represented by the hyomandibular bone on Pl. XLVII. fig. 3. There are also other bones whose position and function cannot be satisfactorily ascertained.

The *air-bladder* was large, and extended from a position immediately behind the pectoral arch a distance of 7 inches, to a point immediately under the second dorsal fin. Its depth is about 1 inch. It presents the appearance of a dull, semi-lustrous body, breaking with an irregular fracture, and capable of division into a large number of very thin layers. The latter are semi-transparent, something like thin layers of shellae. Under the microscope, no very decided characters can be detected; the layers do not present the appearance of osseous structure, but perhaps resemble as much as any thing the chitinous layers of the dermal covering of some insects. The outward appearance is well represented by the artist on Pl. XLVI., extending along the ventral portion of the specimen over two thirds its length, and on Pl. XLVIII. fig. 1 by an oval mass between the pectoral fins, where the scaly covering of the fish has been removed. The structural divisibility into a number of layers appears to indicate that the air-bladder consisted of an outer chamber or sac, divided into a considerable number of compartments by longitudinal septa, these also being, in all probability, subdivided by transverse partitions, which, however, have not been distinguished in the fossil state.

The species of *Cœlacanthus* now described is from the Cannel Coal in the Middle Coal Measures at Tingley, in the West Riding of Yorkshire, and with it have been found a number of other fish-remains. In a paper read before the Geological Society, and published in the Quarterly Journal of the Society for February 1880 *, a detailed description of the stratigraphical position of the Cannel Coal, as well as the manner of its occurrence, is given. In several respects this species possesses distinctive features, which exclude it from either of those described by Agassiz ('Poissons Fossiles,' vol. ii. p. 170), or from those which are described, or whose descriptions have been amplified, in the comprehensive treatise by Prof. Huxley in the Memoirs of the Geological Survey (decade xii.). The most important characters exhibited by the species now described, which I propose

* Quart. Journ. Geol. Soc. vol. xxxvi. p. 56.

shall be designated *Cælacanthus Tingleyensis*, consist in the method of attachment of the rays of the dorsal and caudal fins to the spinous processes of the vertebræ, in the larger number of the fin-rays, and in their extremities being articulated; the ornamentation of the scales and exposed bones of the head consists partly of ridges and also of minute tubercles; and they also differ in the form of the scales.

DESCRIPTION OF THE PLATES.

PLATE XLVI.

Cælacanthus Tingleyensis, Davis (nat. size).

PLATE XLVII.

Fig. 1. *Cælacanthus Tingleyensis*, anterior portion of the body, exhibiting the under surface of the head (nat. size).

Figs. 2-13. Detached bones of the head.

PLATE XLVIII.

Fig. 1. *Cælacanthus Tingleyensis*. Thoracic arch with attachment of the pectoral fins (nat. size).

Fig. 2. Caudal fin of same (nat. size).

PLATE XLIX.

Fig. 1. Restoration of *C. Tingleyensis* (half nat. size).

Fig. 2. Upper surface of head, restored.

Fig. 3. Scales, magnified.

XVII. *On three new Species of Metacrinus.* By P. HERBERT CARPENTER, D.Sc., Assistant-Master at Eton College. *With a Note on a new Myzostoma, by Prof. L. VON GRAFF, Ph.D.* (Communicated by Dr. W. B. CARPENTER, F.R.S., F.L.S.)

(Plates L.-LII.)

Read 5th June, 1884.

THE dredgings of the 'Challenger' at four stations in the Western Pacific and the Malay Archipelago yielded ten species of a remarkable new Crinoid allied to *Pentacrinus*. Most of these were drawn for the Report on the Stalked Crinoids, under the superintendence of the late Sir Wyville Thomson; and when the collection came into my hands after his death, I found the name *Metacrinus* in his handwriting upon a proof copy of one of the plates. This name is consequently employed throughout the 'Challenger' Reports, in which the peculiarities of the genus are fully described. I have elsewhere noticed the one which is most obvious at first sight as specially distinguishing it from *Pentacrinus**, viz. the presence of four, or even of six radials, instead of three only.

The other special marks of the genus are:—1. The large size and somewhat cuboidal form of the basal joints of the lower pinnules; 2. The derivation of the ambulacra of the lowest pinnules, borne on the outer radials, either directly from the peristome or from the five primary ambulacra proceeding from it; 3. The modification of the supranodal stem-joints, as well as in most cases of the infranodal joints. All these characters are well shown in the three species described in the following pages.

The fine species for which the name *Metacrinus rotundus* is proposed (Pl. L. fig. 1) was dredged at a depth of 70 fathoms in Sagami Bay, Japan, by Dr. L. Döderlein, the Conservator of the Natural History Museum at Strassburg, in the year 1881†. He has been kind enough to intrust it to me for description, together with a considerable variety of *Comatulæ* (both *Antedon* and *Actinometra*), which he found to be extremely plentiful in the same locality. These will be considered later; but I would here record my indebtedness to Dr. Döderlein, and beg him to accept my cordial thanks for his kindness.

A fine *Myzostoma*, which I found attached to the *Metacrinus*, is figured and described by my friend Prof. L. von Graff, of Graz. I could find none of these parasites upon the *Comatulæ*, nor were there any loose in the spirit in which they were preserved.

The two other species of *Metacrinus* have been for some years in the collection of my friend Mr. Charles Stewart, F.L.S. He obtained them from the officers of the Eastern Telegraph Company at Singapore, where they were brought up in the process of picking up a cable for repair. They were sent home in spirit; but, by some unfortunate blunder on the part of an ignorant clerk, were taken out and dried upon their arrival in this country. The natural result was, in the case of *Metacrinus superbus*, that a considerable

* Bull. Mus. Comp. Zool. vol. x. 1882, p. 167.

† "Faunistische Studien in Japan, Enoshima und die Sagami-Bai," Archiv für Naturgesch. 49 Jahrg. p. 119.

number of the arms broke at one of the lower syzygies, and the great beauty of a large and perfect Crinoid was irretrievably ruined.

The third species herein described, *Metacrinus Stewarti*, is unfortunately only represented by a stem fragment; but its characters are so different from those of the stem in any species of *Metacrinus* yet known to me, that I have no hesitation in regarding it as belonging to a new specific type.

Although Mr. Stewart had long since commenced to write an account of the fine specimen in his hands, and had also made a few drawings of it, his usual unselfish kindness has led him more than once to offer it to me for description; and when I received Dr. Döderlein's specimen, it seemed to me to be a good opportunity to avail myself of Mr. Stewart's generous offer, and to describe the two species together.

1. *Metacrinus rotundus*, sp. nov. (Pl. L.; Pl. LII. figs. 1-7.)

Dimensions.

Length of stem to twenty-ninth node	44 centimetres.
Diameter „	5 millimetres.
Longest cirrus, 15 joints	17 „
Diameter of disk	18 „
Length of arm after palmar axillary, 130 joints	125 „
„ radial pinnule, 20 joints	20 „
„ distichal pinnule, 20 joints	20 „
„ first pinnule after palmar axillary, 14 joints	9 „

Stem robust, with a rounded pentagonal outline. Usually eleven or twelve, but sometimes as many as eighteen internodal joints. They have fairly well crenulated edges, and their sides bear faint, more or less interrupted ridges, which sometimes become slightly tubercular at the angles. These interrarial tubercles are more marked on the nodal joints, but vary considerably in size. The nodal joints increase in size from above downwards as far as the lower edges of the wide cirrus-sockets, and then diminish again. The sockets extend upwards above the articular surface on to the supranodal joints, which are thus somewhat incised; but each socket terminates below by a well defined lip, which is distinctly above the lower edge of the nodal joint. The infranodals are not incised to receive the cirrus-bases, so that the apposed syzygial surfaces are almost perfectly circular. The cirri consist of 10-15 very uniform squarish joints, the lowest of which are but little wider than their successors. The cirri at the twelfth and next following nodes are larger than those lower down. The interarticular pores disappear between the eleventh and twelfth nodes.

Basals pentagonal, rounded, and prominent. Radials usually five, with a syzygy in the second, and occasionally another in the fourth or axillary.

The rays divide three, or sometimes four times, giving 40-50 arms, which consist of about 130 joints beyond the palmar axillary. They are tolerably smooth and but little serrate in the mediodorsal line, except near the ends.

Primary arms of 7-10, usually eight, distichal joints; secondary arms of 10-18, usually twelve or fourteen, palmar joints. There is occasionally another axillary after twenty or

twenty-two joints more. There is usually a syzygy in the third joint after each axillary. The next is somewhere between the twelfth and thirtieth brachial, and others follow at very irregular intervals.

The three radial pinnules, on the second, third, and fourth radials, are large and prominent, reaching 20 millims. in length, and consisting of 18–20 joints. The three lower ones are massive and cuboidal; the next few flattened laterally, but still stout, and projecting beyond the bases of their successors. This is most marked in the smaller terminal joints, so that the end of the pinnule has a very serrate appearance. The first distichal pinnule is much like those on the radials; but the following ones are smaller and less serrate. The two lower joints are flattened, and much wider than their successors; but this inequality is much less marked after the palmar axillary, and disappears altogether in the later pinnules, which are comparatively small.

The disk is covered by an irregular pavement of small plates, set moderately close, and the ambulaera are well protected by plates; but the perisome at the sides of the disk, between the rays, is almost bare.

Neither are the muscular bundles between the arm-joints covered by plates, which are limited to the ambulaera. They form a fairly regular row on each side, and become differentiated at the bases of the pinnules into more or less pointed side-plates and rounded covering-plates. Colour, a very light yellowish brown, which has scarcely altered in spirit.

Hab. Sagami Bay, Japan; 70 fathoms.

Remarks.—Several well defined characters distinguish this fine species from the various types of *Metacrinus* which were dredged by the ‘Challenger.’

In the first place, like *M. Moseleyi*, it occupies an intermediate position between the two groups into which most species of the genus very naturally fall:—1. Those with four radials, of which the second is a syzygy; and 2. Those with six radials, of which both the second and fourth are syzygies. Variations from these numbers occasionally present themselves in single rays of individual specimens; but, as a general rule, the presence of four or six joints in a ray is a very constant character.

This is not the case, however, in *M. Moseleyi*, two individuals of which were dredged by the ‘Challenger.’ The following variations occur among their ten rays:—

1 ray of three joints, with the second and the axillary a syzygy.						
1	„	four	„	„	„	„
3	rays of	five	„	„	„	a syzygy.
2	„	„	„	„	„	and the fourth a syzygy.
1	ray of	six	„	„	„	a syzygy.
2	rays	„	„	„	„	and the fourth a syzygy.

In the single specimen of *M. rotundus* the construction of the five rays is as follows:—

- 1 ray of six joints, without a syzygy.
- 2 rays of five joints, with the second a syzygy.
- 1 ray of five joints, with syzygies in the second and fourth.
- 1 ray of five joints, with syzygies in the second and axillary.

In three of the rays, therefore, there were six primitive joints, of which the second and third became ultimately united by syzygy in two cases, but remained separate in a third; while in the other two rays there were primitively seven joints.

The type, therefore, is intermediate between those more regular species, such as *M. angulatus* from the Arafura Sea, with five primitive radials, two of which eventually unite by syzygy, and the other group typified by *M. interruptus* from among the Philippine Islands, which have eight primitive radials that form two syzygial pairs.

It is to the species last mentioned that *M. rotundus* presents, on the whole, the most resemblance. There is about the same number of joints in the primary and secondary arms, and the external characters of the stem are very similar in the two types. The number of internodal joints is almost the same; but the horizontal ridges on their surface are much less marked in *M. rotundus* than in *M. interruptus*, while their outline is more rounded and less sharply pentagonal (Pl. LII. figs. 7, 5).

But it is in the characters of the nodal and infranodal joints that *M. rotundus* differs from *M. interruptus*, and still more so from all other species of the genus.

In most Pentacrinidæ the cirrus-facet is limited to the nodal joint, but lies at the broad end of a pear-shaped socket, the narrower part of which is continued downwards on to the infranodal joint, and receives the base of the cirrus. The upper part of this socket in *Pentacrinus* is confined to the nodal joint, not extending above the edge of the cirrus-facet, which is often considerably lower than the vertical height of the nodal joint; while the cirri are mostly directed downwards, and the infranodals are more or less grooved to receive their bases, as described above. In *Metacrinus*, however, the normal direction of the cirri seems to be upward rather than downward (Pls. L., LI., LII. fig. 13); and the cirrus-sockets, therefore, encroach somewhat upon the supranodal, which is thus slightly incised, as may be seen by comparing figs. 1 and 4 on Pl. LII. The former represents a normal internodal joint, and the latter that immediately above the node. The share of the supranodal joint in forming the cirrus-socket is likewise seen in the side-view of the stem (Pl. LII. figs. 5, 12, 18). In most species of *Metacrinus* the infranodal is also slightly grooved to receive the cirrus-bases, and its upper (syzygial) surface is, therefore, more or less stellate, in correspondence with that of the nodal joint above it. This is least marked in *M. interruptus*, the nodal joints of which differ but little in outline from those in other parts of the stem. The cirrus-facet ends below in a well defined rim, which is distinctly above the lower edge of the joint. The syzygial surface, therefore, has almost exactly the same pentagonal form as the ordinary sculptured face of an internodal joint. That of the infranodal is similar to it, and has no reentering angles as is usually the case.

Now in *M. rotundus* there is the same well-marked termination of the cirrus-facet above the lower edge of the nodal joint (Pl. LII. fig. 5), and neither it nor the infranodal is in any way grooved to receive the cirrus-bases (Pl. LII. fig. 3). Their apposed surfaces, however, are not pentagonal, as in *M. interruptus*, but they are almost circular (Pl. LII. fig. 3); and this character distinguishes the stem of *M. rotundus* from that of all the other species of the genus.

The type which approaches it most nearly in this respect is also a Japanese form, viz.

that dredged by the 'Vega' in 1879, at a depth of 65 fathoms, in the Bay of Yeddo. Prof. Lovén has been kind enough to send me some fragments of the stem, and also to permit my friend Mr. W. Percy Sladen, F.L.S., to make an investigation of the type during his recent visit to Stockholm for the purpose of examining the collection of Starfishes in the Museum. I am greatly indebted to Mr. Sladen for the trouble which he took, and for the careful and detailed description of the 'Vega' specimen with which he has furnished me. It has nearly the same number of internodal stem-joints as *M. interruptus* and *M. rotundus*, and the length of the primary and secondary arms is very much the same as in these types. In the number of radials (six, with syzygies in the second and fourth) it agrees with *M. interruptus* and differs from *M. rotundus*; but it approaches the latter form more nearly in the characters of the stem.

Although the diameter of the stem-joints is less than in *M. interruptus*, and still more so than in *M. rotundus*, they are not only relatively but absolutely higher than in these species. They resemble the latter rather than the former in the slight amount of sculpture on their sides, and in their more rounded pentagonal form. As in both these types, the cirrus-sockets end well above the lower edge of the nodal joint; but the syzygial surface, though much less sharply pentagonal than in *M. interruptus*, is far from being as regularly circular as in *M. rotundus* (Pl. LII. fig. 3).

In the robustness and other characters of its stem, therefore, *M. rotundus* is distinguished from the two species which seem to resemble it most, just as it is by the irregularity in the number of radials. The plates of the cup and arms are altogether larger than in most species of the genus, the only ones which approach it in size being *M. angulatus*, *M. cingulatus*, and *M. nobilis*, all from near the Ke Islands (Station 192).

The pinnules borne by the radials and lowest distichals have especially stout joints; and the serrate appearance of their outer extremities, produced by the elevation of the distal edge of each joint, is extremely well marked, so as to recall the distinctive features of *Pentacrinus asterius*.

The disk of *M. rotundus* is excellently preserved, and shows very well one of the special characters of the genus, viz. the origin of the ambulacra of the large lower pinnules either directly from the peristome, or from the five primary groove-trunks before they bifurcate (Pl. L. fig. 2). The interpalmar areas of the disk are paved with small plates, which are pierced by the water-pores, but are not quite so closely set as they are in some of the Pentaerinidae and Comatulæ; while there are few or no plates in the peristome at the sides of the disk between the rays. The disk-ambulacra, however, are protected by several irregular rows of plates, which in some places meet so closely over the middle line of the groove that it is converted into a tunnel. This was the case, not only on the arms, but also in the calyx-ambulacra of the Palæocrinoids, whether the latter were external, as in *Cyathocrinus*, or still further covered by a solid vault, as in *Actinocrinus*.

The arms have no anambulacral plates overlying the muscular bundles, as is so often the case; but the ambulacra are well protected by a double row of somewhat irregular plates, in which there is more or less distinct evidence of bifurcation. This becomes specially marked at the bases of the pinnules, where the proximal limb of the fork

remains as the side-plate, with a squarish base and pointed top; while the distal limb of the fork becomes the rounded covering-plate (Pl. LII. figs. 6, 7). As in all the *Pentacrinidae*, the two series end some little way before the extremity of the pinnule, the ventral groove of which is thus left entirely unprotected. It is rare to find any individuals of *Metacrinus* some part of which does not exhibit irregularities of growth; and *M. rotundus* is no exception to the rule, the seat of the irregularity in this case being the basal ring. One of the basals is much wider than its fellows, and looks as if it were divided into two unequal parts, one of which slightly overlaps the other. This may be due either to an anomalous mode of growth from the beginning, or else to fracture and subsequent reparation. The point is not one of very great importance, but is only of interest from the frequent occurrence of similar irregularities in *Metacrinus* and their comparative absence in *Pentacrinus*, which seems, as it were, to be somewhat more crystallized in the regularity of its characters.

The fine specimen of *Myzostoma cirripedium* (Pl. LII. fig. 19), which is described further on by Prof. von Graff, was attached to this individual; while its cirri afforded anchorage to those of a small *Antedon*.

Dr. Döderlein informs me that it was attached to the tangles, and had the arms closed in over the disk when it was first removed from the water, but that they opened out after a time. Most of them eventually broke off at the syzygy in the third distichal after the specimen had been put into spirit. Its colour, however, has altered but little in consequence.

2. *Metacrinus superbus*, sp. nov. (Pl. LI.; Pl. LII. figs. 8-12.)

Dimensions.

Length of stem to twenty-sixth node	30 centimetres.
Diameter	7.75 millimetres.
Longest cirrus, 68 joints	80.00 „
Diameter of disk	30.00 „
Length of broken arm after suprapalmar axillary, 100 joints	105.00 „
Length of first palmar pinnule, 27 joints	36.00 „
„ „ pinnule after suprapalmar axillary, 22 joints	18.00 „

Stem very robust, with a rounded pentangular outline and smooth flat sides. 9-11 internodal joints, with moderately crenulated edges. The angles of the nodal joints scarcely project at all, and the wide cirrus-sockets between them extend well up on to the supranodals, though but very slightly on to the infranodals. The cirri increase in size down to the seventeenth node, and then remain tolerably uniform. They consist of about 65 stout, but short and wide joints. The interarticular pores disappear at the eighteenth node.

Basals prominent, and widely pentagonal, with downward extensions over the upper stem-joints. Radials wide, usually four in number, with a syzygy in the second.

The rays divide four times, and the outermost of each pair of the arms which are borne by the suprapalmar axillary divides again, so that the number of arms must exceed

100. There are over 100 joints above the suprapalmar axillary, all of them with raised distal edges. This character is not specially prominent on the later joints, but is very well marked on the outermost radials and on the lowest arm divisions.

Primary arms usually of 4-6, but in one case of 10 distichal joints. 7-10 palmars in the secondary arms. Tertiary arms usually of 14-16 (rarely 12 or 18) joints, with another axillary after 16 or 18 (rarely 12, 20, or 22) joints on the outermost of each pair of quaternary arms. The third joint after each axillary is a syzygy; and the second syzygy in the free arms may be anywhere between the thirtieth and sixtieth brachial. Others follow at intervals of 8-20 joints.

The radial, distichal, and palmar pinnules are all large and styliform, especially the two latter. That on the second radial has two large and cuboidal basal joints; but the following ones become rapidly smaller and much flatter.

The first distichal pinnules are much longer again, and consist of nearly 30 joints, of which the basal ones, including even the first two, are much flattened laterally, though of considerable depth. The following ones are of about the same length, but have wider and more massive basal joints. After the first palmar pinnule the size gradually diminishes, rapidly at first, and then more slowly, while the pinnules become more flattened, though the enlargement of the basal joints is visible for some distance out into the arms.

The disk is paved by small irregular plates, which are not very closely set; but the ambulacra are well protected by plates. The brachial ambulacra are limited to the centre of the arm-furrow, and more or less differentiated on the pinnules into side- and covering-plates. Colour in the dry state, a light purplish grey, with a greenish tinge on the tips of the pinnules.

Hab. Singapore.

This magnificent specimen is the largest *Metacrinus*, and, in fact, the largest recent Pentaerinite that I have yet seen. Few species have a stem exceeding 5 millims. in diameter. It reaches 7 millims. in *Pentacrinus asterius* and *Metacrinus nobilis*; but the stem of *M. superbus* is considerably wider than that of either of these two types. The former is the only one which at all approaches it in the number and stoutness of the cirrus-joints, as also in the frequency of the ray-divisions.

The number and very regular grouping of the free arms in *Metacrinus superbus* is a somewhat striking character. Palmars appear to be universally present, so that there are 40 tertiary arms; and, with one exception, all of them which are preserved, either wholly or partially, divide in the same way. Each of them has a suprapalmar axillary; and of the two arms which this bears, the outer, except in one case, divides again; so that each palmar axillary bears 6 arms: 2, 1, 1, 2. If this arrangement extended all round the disk, there would have been 4×6 or 24 arms on each ray, making a total of 120.

It is exactly the same arrangement as often occurs on the distichal axillary of *Pentacrinus asterius*, which has 12 arms to the ray; and also on the radial axillary of *P. Mülleri*, *P. Macleanus*, and *P. Wyville-Thomsoni*. It is of some interest, as affording a clue to the mode of development of the armlets of the Jurassic *Extracrinus*, as I have explained in the 'Challenger' Report.

Metacrinus superbus is somewhat closely allied both to *M. Murrayi* and to *M. nobilis*, having, like them, a smooth flat stem and normally only four radials, and also about the same number of joints in the primary and secondary arms. It has slightly shorter internodes than both these types; and the joints composing them are less sharply pentagonal than in *M. nobilis*, though the sides are not quite so much incurved as in *M. Murrayi*. Both the supra- and the infranodal stem-joints are about as much incised as in the latter species, and somewhat less so than in *M. nobilis*. In neither of these species are there more than about 50 cirrus-joints, and the interarticular pores end at about the tenth or twelfth node; whereas in *M. superbus* there are some 65 cirrus-joints, and the interarticular pores extend down to the eighteenth node—a most unusual distance from the calyx.

Both these types, again, differ altogether from the larger *M. superbus* in the smoothness of the dorsal surface of the skeleton as far as the middle of the free arms; while the terminal portions of their arms are distinctly more serrate than in the corresponding parts of *M. superbus*.

Two of the radial series are slightly irregular in the specimen now under consideration.

The type consists of five primitive joints, the second and third of which have united to form a syzygy; so that the ultimate number of radials is four, with the second a syzygy. On two rays, however, there were six primitive joints. In the one case the second and third united as in the type, while the rest remained free; so that there are two joints between the syzygy and the axillary, as shown in Pl. LI. fig. 1. In the next ray, however, the axillary became united by syzygy to the joint beneath it, and the proximal and distal edges of the hypozygal are raised and thickened, as in the other parts of the ray, but only for rather more than half their width. This is also the case with the proximal edge of the axillary or epizygal, the smaller half of which appears as a simple syzygial line, while the remainder is raised and thickened.

The disk, though mutilated in parts, is very well preserved for a dry specimen, and presents one or two points worth notice. The peristome is large, but has no visible oral opening, and a large number of food-grooves converge upon it, some of which proceed direct from the large lower pinnules, as is always the case in this genus. There is, therefore, a great number of small interambulaeral areas, which are paved by small plates that are pierced by numerous water-pores, but not so closely set as to form a continuous pavement. These perforated plates extend over on to the dorsal side between the ray-divisions, just as they do in *Pentacrinus asterius*; though Müller denied their existence in this position*. The skeleton of the pinnule-ambulaera varies somewhat in appearance, according to the size of the pinnule which bears it (Pl. LII. figs. 10, 11). The side-plates are usually low and rounded, and very different in appearance from the sharply pointed plates which correspond to them in *M. rotundus*. The gradual development of the pinnule-ambulaera from that of the arm is well shown in Pl. LI. fig. 2. In this, as in all species of the genus, the ambulaera do not reach the distal ends of the pinnules, but terminate some little way short of them; and in like manner the terminal portions

* "Ueber den Bau des *Pentacrinus Caput-Medusæ*," Abhandl. d. Berlin. Akad. 1843, p. 49.

of the arms are not only entirely devoid of any ambulacral skeleton, but they bear quite small and rudimentary pinnules, which consist of only two or three minute joints, and appear to remain permanently in this aborted condition (Pl. LI. fig. 4).

Some of the arms, however, have been broken at a syzygy and subsequently repaired, so as to be still in a state of growth, as is shown in Pl. LI. fig. 5. The manner in which their terminal portions, and those of the growing pinnules, are coiled up, as it were, is very singular, and forcibly recalls the characters of the arms and pinnules in *Holopus*.

3. *Metacrinus Stewarti*, sp. nov. (Pl. LII. figs. 13-18.)

Stem robust and pentagonal, the internodes consisting of 11 joints, with moderately crenulated edges. The joints are 6 millims. in diameter, and have slight horizontal ridges on their sides, which are continuous round the angles, so that these are slightly produced. The nodal joints increase in size from above downwards as far as the lower edges of the wide cirrus-sockets, and then diminish again. The infranodal joints are not grooved at all to receive the cirrus-bases; while the supranodals are markedly incised, and contribute to form the upper portions of the cirrus-sockets proper. The cirri are 50 millims. long, and consist of 50 stout joints, the basal ones being much wider than their successors, which are all uniformly cuboidal.

Remarks.—The characters of this stem-fragment are so well defined that I have no hesitation in regarding it as belonging to a species of *Metacrinus* distinct from any yet known; and I am glad to have the opportunity of associating it with the name of my friend Mr. Charles Stewart, F.L.S., to whom I am indebted for the opportunity of describing it.

In the length of the internodes and in the peculiarities of the nodal joints it resembles the stems of *Metacrinus rotundus*, *M. interruptus*, and the 'Vega' specimen. It is larger, however, than all of these, especially the two last, and the joints have much more distinct horizontal ridges. These give it a certain amount of resemblance to the stems of *M. Wyvillei* and *M. cingulatus*, though it differs altogether from these two in the characters of the nodes.

Owing to the headless condition of the fragment. I was at first sight somewhat doubtful as to which way up it should be placed. The line of union of the supranodal and the nodal joints is rather less crenulated than usual, and looks almost like a syzygial line between nodal and infranodal joints (Pl. LII. figs. 13, 18).

The nodal joints (Pl. LII. figs. 14, 18) are enlarged, and increase in size from both ends towards the cirrus-socket, which extends on to what I now know to be the supranodal; but it seemed possible at first sight that this might really be the infranodal, and the stem belong to a *Pentacrinus* with the cirri directed downwards, instead of a *Metacrinus* with upward turned cirri, as is really the case. In fact, the nodal joints have no little resemblance to those of *Pentacrinus Wyville-Thomsoni*, widening downwards to the lower edge of the cirrus-sockets, and then falling away again (Pl. LII. fig. 18). This is also the case in *Metacrinus rotundus*, though to a somewhat less extent (Pl. LII. fig. 5), and the upward extension of the sockets on to the supranodal is somewhat more marked than

in the Japanese species. The supranodal is not merely grooved to receive the cirrus-bases, as in many species of the genus; but it actually contributes to form the curved upper edge of the socket itself, which is thus not entirely limited to the nodal joint.

Traces of this arrangement appear in *Metacrinus rotundus* (Pl. LII. figs. 4, 5), though they are far less marked than in *M. Stewarti*.

In consequence of the upward direction of the cirri, and the termination of the cirrus-sockets well above the lower edges of the nodal joints, the infranodals are not grooved at all to receive the cirrus-bases (Pl. LII. fig. 16); so that there are no re-entering angles in their regular pentagonal outline, which is quite different from the circular syzygial surface in *Metacrinus rotundus* (Pl. LII. fig. 3), and resembles that of *M. interruptus*. The syzygial surface of the nodal joint, however, is somewhat lobate, as in the 'Vega' specimen. This lobate shape is partly the result of the increase in the width of the nodal joint from above downwards, and its diminution again below the level of the cirrus-socket by the downward slope of its outer surface, which thus becomes visible in a view of the joint from beneath, as shown in Pl. LII. fig. 15. This is especially marked in the lower side of the figure, and produces a corresponding incision of the infranodal joint, which must not be mistaken for that produced by the downward extension of the socket to receive the base of a cirrus. This, in fact, really does occur in some abnormal sockets, as shown in the lower part of Pl. LII. fig. 16.

When all these peculiarities are considered together, it will be seen that the stem of *Metacrinus Stewarti* has a distinct character of its own. What its calyx may have been is as yet unknown. That of *M. interruptus*, and also that of the 'Vega' specimen, has six radials, while *M. rotundus* has five (Pl. LII. fig. 1); and it is therefore uncertain in which group *M. Stewarti* should be placed, while it might possibly even belong to the group which includes *M. superbus* (Pl. LI. fig. 1), with only four radials.

A large part of one side of the specimen, including many of the cirri, is wrapped up in a dense mass of what appears to be the remains of a horny sponge, in which are imbedded Foraminifera, broken fragments of shells, and a quantity of earthy and mineral matter. Some of the cirri afford an attachment to sessile Cirripedes (*Terruca*?), as shown on the left-hand side of Pl. LII. fig. 13.

Description of a new Species of Myzostoma. By Prof. L. VON GRAFF, Ph.D.

MYZOSTOMA CIRRIPIEDIUM, sp. nov. (Pl. LII. fig. 19.)

A single well-preserved individual was found by Dr. P. H. Carpenter attached to the specimen of *Metacrinus rotundus* which is described by him in the preceding pages.

Its external form resembles that of *Myzostoma Wyville-Thomsoni*, mihi *, which infests *Metacrinus costatus*, P. H. C., and *M. angulatus*, P. H. C., and has been described by myself in the 'Challenger' Report.

* Zoology of the 'Challenger' Expedition, part xxvii. pp. 45-46, pl. vi. figs. 1, 2.

The very delicate body is in the form of an oval plate, 4.6 millims. long and 3 millims. wide. Its thickness is very slight, hardly as much as in the European *Myzostoma cirri-ferum*; and it is therefore fairly transparent, not only in the clear yellow marginal portion, but also in the somewhat thicker and darker central part within the ring of parapodia. The edge of the body is so much folded over towards the ventral side that the animal appears convex when viewed from above, and concave as seen from beneath.

The unusually extensive ramifications of the digestive canal* almost reach the edge (Pl. LII. fig. 19); and the marginal portion, which is free from them, is not sharply marked off from the rest of the disk.

There are 20 cirri (*c.*), disposed at tolerably regular intervals from one another, except that the ninth and tenth cirri on each side, and also the two of the tenth pair, are somewhat more widely separated. As regards the length of the cirri, the last pair, with a length of 0.77 millim., and the first pair, 0.6 millim., are the best developed. The lateral cirri vary in length from 0.14 millim. to 0.46 millim. The ventral longitudinal furrow is well defined in most of them.

The body-wall bends slightly outwards between every two cirri, as is especially evident in those parts which are not folded over; and the cirri, which are really marginal, thus come to lie in little bays within the edge.

The circle of relatively weak parapodia (*p.*) is situated about halfway between the centre and the edge of the disk, though the fifth pair is much farther from the hinder end than the first pair from the front end. The parapodia reach 0.77 millim. in length, when extended; but there is nothing special either about their form or about the hooklets which they enclose. On the other hand, there is a peculiarity of structure, hitherto observed in no other *Myzostoma*, in the finger-shaped process (*p.c.*) which each parapodium bears at its base on the side turned towards the middle line of the body. This process is markedly distinguished from the marginal cirri by the want of a glutinous cell-groove ("Klebzelle"). It is therefore best designated as a parapodial cirrus; and its function is probably that of a tactile organ, as with the similarly shaped structure in the Chaetopods. The 8 suckers (*s.*) occupy a line situated about halfway between the bases of the parapodia and the edge of the disk. They are very flat, and but slightly prominent, having a somewhat elongated shape, and reaching 0.23 millim. in length and 0.1 millim. in width.

Almost at the same level with the suckers is the ventral mouth-opening (*m.*), situated 0.35 millim. from the anterior end of the body. It leads into a considerably retracted pharynx, the bulbus musculosus of which (*ph.*) reaches the unusual length of 1.23 millims. I could not make out the origin of the individual intestinal diverticula from the central stomach (*st.*); but the rectum (*r.*) is easily distinguished, together with the oviduct (*od.*), which lies above it, and is filled with ova. The cloacal opening (*cl.*) is placed terminally in a slight incision at the hinder end of the body. The two openings of the male genital organs (σ) are simple insignificant clefts close to the outer side of the bases of the third pair of parapodia.

* These are indicated in a semidiagrammatic manner on the left side of the figure only.

DESCRIPTION OF THE PLATES.

PLATE L.

Metacrinus rotundus, sp. n.

Fig. 1. The head and upper part of the stem. Natural size.

Fig. 2. The disk, from above. $\times 3$.

PLATE LI.

Metacrinus superbus, sp. n.

Fig. 1. The head and upper part of the stem. Natural size.

Fig. 2. Portion of an arm, rather below its middle, from the right side. $\times 2$.

Fig. 3. Terminal portion of an arm undergoing regeneration, showing the growing points of its two divisions. $\times 2$.

Fig. 4. Terminal portion of a full-grown arm, with imperfectly developed pinnules. $\times 2$.

Fig. 5. The ambulacral groove, with its branches on to the pinnules, viewed from above. $\times 5$.

PLATE LII.

Figs. 1-7. *Metacrinus rotundus*, sp. n.

Figs. 1-4. Stem-joints. $\times 6$. Fig. 1. Ordinary internodal joint. Fig. 2. Nodal joint; lower or syzygial face. Fig. 3. Nodal joint; upper face. Fig. 4. Supranodal joint; lower face.

Fig. 5. Fragment of stem, showing the cirrus-sockets on the nodal joint. $\times 2$.

Figs. 6 & 7. Side views of pinnule-ambulacra. $\times 25$.

Figs. 8-12. *Metacrinus superbus*, sp. n.

Fig. 8. Nodal stem-joint; upper face. $\times 4$.

Fig. 9. Ordinary internodal joint. $\times 4$.

Figs. 10 & 11. Side views of pinnule-ambulacra. $\times 25$.

Fig. 12. Fragment of stem, showing the cirrus-sockets on the nodal joint. $\times 2$.

Figs. 13-18. *Metacrinus Stewurti*, sp. n.

Fig. 13. The stem-fragment. Natural size.

Figs. 14-17. Stem-joints. $\times 6$. Fig. 14. Nodal joint; upper face. Fig. 15. Nodal joint; lower or syzygial face. Fig. 16. Infranodal joint; upper or syzygial face. Fig. 17. Ordinary internodal joint.

Fig. 18. Fragment of stem, showing the cirrus-sockets on the nodal joint.

Fig. 19. *Myzostoma cirripedium*, sp. n., seen from the ventral side. $\times 28$. *l.* Marginal cirri; *cl.* Cloacal opening; *i.* Intestinal ramifications (indicated only on the left side of the figure); *m.* Mouth; *od.* Oviduct; *p.* Parapodia; *pc.* Parapodial cirri; *ph.* Bulbus musculosus of the Pharynx; *s.* Suckers; *st.* Stomach; *♂.* Male genital openings.

XVIII. *On the Breeding of Salmon from Parents which have never descended to the Sea.*

By FRANCIS DAY, F.L.S.

(Plates LIIL. & LIV.)

Read March 5th, 1885.

CONSIDERABLE attention has been paid in this country to the life-history of the Salmon, but many so-called "facts" heretofore accepted and that still pass current have no better foundation on which to rest than the dogmatic assertion of a self-termed "practical" individual, the theory of an ichthyologist, or the unsupported statement of a museum naturalist; or, as Russel* observed, "the nonsense about the Salmon that has been published under the name of natural history, and thrust down the throats of Parliamentary Committees, is, when looked back upon, appalling in amount, variety, and worthlessness."

It is consequently a subject of great moment that the various asserted facts upon which any doubt still lingers should be accurately sifted, not by a partisan of one party or another, but an independent individual who would, regardless of expense, time, and trouble, undertake such a task in the sole interest of scientific truth and for the good of the fisheries. Such tests have been for the last few years and are still being steadily and unremittingly carried on at Howietoun, and in due time the results, whether in accordance with or opposed to existing theories, will, it is to be hoped, be given to the world.

Pre-eminent among the questions of practical moment, as bearing upon the race of so-called "land-locked Salmon," is whether the *Salmo salar* can be permanently retained and finally breed in fresh water without descending to the sea.

I propose examining this principally from a fish-culturist's point of view, as, owing to the kindness of the owner of Howietoun, I have had the opportunity of witnessing most of the interesting and instructive experiments which are being carried on in that large and well-conducted establishment, and consequently am in a position to give a reply to this question so far as it has there been solved. I have also thought that it would be interesting were I to collect the chief opinions which have been published in the British Isles on this subject, as well as a synopsis of a few of the various experiments which have been undertaken but have failed.

In 1653 Izaak Walton published the first edition of his 'Compleat Angler,' wherein the opinions of the most reliable authors of previous or contemporary times on Salmon-breeding are condensed. He remarks that the Salmon "is said to breed or cast its spawn in most rivers in the month of August: some say they dig a hole or grave in a safe place

* 'The Salmon,' by A. Russel, 1864, p. 32.

in the gravel and there place their eggs or spawn, after the milter has done his natural office, and then hide it most cunningly and cover it over with gravel and stones. 'Kippers' have bony gristle growing out of their lower jaws, and may live one year from the sea, but pine and die the second year. Little Salmon called 'Skeggers,' which abound in many rivers, are bred by such sick Salmon that might not go to the sea, and though they abound they never thrive to any considerable bigness."

Willughby*, quoting a communication to Gesner, tells us that generally about the end of November Salmon ascend for breeding purposes up rivers to their affluents, where the eggs are deposited and the young born: these latter are termed "samlets," while the old fish descend to the sea.

Ray† observed that Salmon are born in the rivers, whence they descend to the sea.

Pontoppidan ('Natural History of Norway,' 1755, Chapter vi. p. 131) remarks that Willughby "also confutes Gesner's opinion, concerning the Salmon's breeding in the sea: he thinks that is done in fresh water, from whence they afterwards go to the sea; but in this he is certainly mistaken. The Salmon unquestionably breeds in the sea, though it is not entirely to be denied that they may sometimes breed in rivers also, for they are found in the midst of Germany, and upper parts of the Rhine, about Basel; but we are very well assured that the Salmon chiefly ejects its roe at the mouth of rivers, where they empty themselves into the sea, or a little way beyond, in the salt water, in this manner: they bend themselves crooked, in order to eject the roe at an aperture under the belly, and in the mean time they stick their heads down in the sand, that they may have the more strength. The male comes presently after, to keep off other fish from devouring the roe, and he then bends his head towards the tail, and ejects his sperm upon the roe."

Passing over the numerous authors who have merely reproduced the remarks of those who have preceded them, we are told by Yarrell‡ that about the end of 1830 water was first turned into a certain pond 3 or 4 acres in extent, situated in Scotland, and in April 1831 one or two dozens of small Salmon fry, 3 or 4 inches long, were taken out of the river and turned in. In 1833 the first fishing was allowed and several Salmon were taken with the fly from 2 lbs. to 3 lbs. in weight; all were perfectly well shaped and filled up, of the best salmon-colour outside, the flesh well flavoured and well coloured, though a little paler than that of new run fish. The same author § remarked that "a knowledge of the growth of young Salmon in a freshwater lake . . . may be useful to those gentlemen who possess lakes near Salmon rivers, from which they can supply them with Pinks: whether the Salmon thus prevented going to salt water will still retain sufficient constitutional powers to mature their roe, and by depositing it in the usual manner, as far as circumstances permit, produce their species, would be a subject worthy of further investigation."

Knox observes (Proc. Linn. Soc. ii. p. 358, Dec. 19, 1854) that "From the time the Salmon enters the fresh water it ceases to feed, properly speaking, although it may occasionally rise to a fly or be tempted to attack a worm or a minnow, in accordance seemingly with

* 'De Historia Piscium,' 1686.

‡ 'British Fishes' (Edition 2), ii. p. 17.

† 'Synopsis Methodica Piscium,' 1713, p. 63.

§ *L. c.* (Ed. 2), ii. p. 16.

ts original habits as a smolt. But after first descending to the ocean and tasting its marine food, it never again resorts to its infantile food as a constant mode of nourishment." He further says, "The absence of this [marine] kind of food forms an insurmountable obstacle to the preservation of Salmon and of some kinds of Sea-Trout in freshwater lakes."

It has been suggested that a sojourn in fresh water, even should such be only temporary, may give the first impetus towards the seasonal development of the sexual organs.

Shaw remarked that solitary instances have occurred of large female parrs having been found in Salmon rivers with the roe considerably developed, and he ascertained that by detaining the female smolt in fresh water until the end of the third winter, individuals are found in this comparatively mature condition. Davy* says:—"I have examined hundreds of parrs. . . . Male parrs I have frequently found with mature milt, but never a female with roe correspondingly developed; on the contrary, in the female fish, without exception, the ovaries have been so small, that had they not been sought after carefully they would have escaped notice." Russel† asks of Mr. Young, "Did he ever see a female parr with a developed roe? He never did and never will"‡.

In this search for roe developed in young Salmon that have not descended to the sea, experiments would appear to have ceased in this country; but after an interval of about 45 years it was intended to carry them on at Howietoun. Still as it would not be improbable that some objection would be raised to young fish for this purpose being removed from rivers to ponds, it was determined to rear the parr from the eggs and see if smolts or grilse when thus raised in suitable ponds and properly cared for would or would not breed in fresh waters.

Brown§ observed that "no female parr has yet been discovered with roe developed." This, I think, must be taken to read that no young female Salmon in the parr livery that has not been to the sea had been discovered with ova fully developed. For, as I sha'l presently endeavour to show, parr or rather smolt with well-marked parr-bands have given fully developed ova at Howietoun. Brown|| determined to endeavour to rear the ova up to the smolt stage, and obtained certain ponds, into one of which the sea ebbed and flowed, at Stonehaven in Kincardineshire. They consisted of two ponds, a freshwater one 40×20 yards, and a saltwater one 60×30 yards. The distance between the ponds was about 30 yards with a fall of eight feet. An iron pipe 18 inches in diameter communicated with the sea. Spawning fish were put into the freshwater pond and afterwards made their way to the sea-pond, but unfortunately poachers destroyed the experiment, which was not renewed.

Clean Salmon having only a thread of milt or roe in them are found in Salmon rivers during December, January, and February. These would seem to be temporarily sterile¶, because ova and milt may be detected by means of the microscope. Mr. F. Fennell gave evidence that these fish do not spawn until the November or December following,

* 'Transactions of the Royal Society of Edinburgh' (Dec. 1854), vol. xxi. p. 253. † 'The Salmon,' 1864, p. 39.

‡ Yarrell is said to have adduced two instances of parr containing ova in the month of March.

§ 'Stormontfield Experiments,' 1862, p. 89.

Op. cit. p. 116.

¶ Siebold has found that certain individuals are not sexually developed; and he supposed that this sterility extended throughout their existence. Widegren and others have opposed this view, contending that such sterility is temporary, merely affecting a few individuals.

remaining for 12 months in the fresh water, their ova developing until they are ready to breed; and although the fish are discoloured, due to their residence, are very good eating. Brown caught one of these fish in a Sutherlandshire river and gave the same report*.

Many have held the opinions which Rasch so fully detailed in 1866 when he commenced by the inquiry why it is that all the male fish, including those that have gone to the sea and those that remain behind in fresh water, have their reproductive organs fully developed, while the female is under the necessity of making the journey to the sea before being able to spawn. He considered that the female in order to reach maturity requires far more nourishment than the male, the formation of eggs necessitating more materials than that of the milt; that in the ovary of the female the eggs are formed nearly simultaneously, and their development is uniform, one being enveloped by as large an amount of albumen as the other. But in order to produce this albumen a far greater amount of nourishment is needed than the little female fish can possibly procure in fresh water—enough for the formation of the embryo, but not sufficient to provide the nourishment necessary to its proper development. He considered that if smolts were prevented going to the sea they would readily accustom themselves to a freshwater home, if the piece of water were sufficiently extensive; and should the water be a very large lake, such as Ladoga, Wenern, or Peipus, and as rich in nourishing food, the freshwater Salmon will then attain about the same size as the Salmon of the sea. He also observed that Hettling hatched out numbers of Salmon ova, which he subsequently turned loose in the Tyri-fiord: and during the two years after, fish had been caught in that lake resembling in every respect Salmon proper.

“The question whether any of the migratory species [of the genus *Salmo*] can be retained in fresh water, and finally accommodate themselves to a permanent sojourn therein, must be negatived for the present. Several instances of successful experiments made for this purpose have been brought forward; but all these accounts are open to serious doubts‡, inasmuch as they do not afford us sufficient proof that the young fish introduced into ponds were really young migratory Salmonoids, or that the full-grown specimens were identical with those introduced, and not hybrids or non-migratory Trout of a somewhat altered appearance in consequence of the change of their locality. We have seen the experiment tried at two places in South Wales, by the Rev. Augustus Morgan and W. Pell, Esq., of Taliaris, and in both cases the Salmon and the pure Sewin§ died when not allowed to return to the sea. However, the latter gentleman pointed out to me that the hybrid fishes from the Sewin and the Trout§ survived the experiment, and continue to grow in a pond perfectly shut up from communication with the sea. In that locality neither these hybrids nor the trout spawn.” (Günther, Catal. of Fishes, vi. 1866, p. 9.) Without alteration, the above passage has been introduced by the same author into his ‘Introduction to the Study of Fishes’ (1880, p. 639).

* ‘Stormontfield Experiments,’ 1854, pp. 94, 95.

† Lloyd (‘Field-Sports North of Europe,’ i. p. 301) remarks that near Katrineberg there is a valuable fishery for Salmon, 11,000 or 12,000 of these fish being taken annually. They are bred in the lake; and, in consequence of cataracts, cannot have access to the sea. They are small in size and inferior in flavour. The year 1820 furnished 21,817. The question is open to discussion whether these fish are true *Salmo salar*.

‡ *Salmo trutta*.

§ *Salmo fario*.

Much of the foregoing seems to me simply hearsay evidence, and several points require elucidation. First, did any stream flow into these ponds? and, if so, of what size? or were they more or less stagnant pieces of water? Secondly, did suitable food exist in these ponds, or were the fishes fed? Thirdly, how was it ascertained that no spawn was deposited?

Respecting this last question, a very interesting observation was made by Mr. C. L. Jackson, Honorary Naturalist to the Southport Aquarium ('Land and Water,' June 10th. 1876), that the "Salmon-trout cast their ova in the salt water in the Southport Aquarium without assuming the appearance of kelts or even leaving off feeding greedily on shrimps. They did not attempt to make a bed, and the spawn was immediately eaten by their fellows."

It will now be necessary to follow out briefly the different stages of growth of these fish, which occurred during the several changes from parr to smolts or grilse. Dr. J. Davy says* "that parr put into a pond from which they could not escape, have grown in two or three years to be about half a pound in weight, and when caught were found to be in excellent condition, and still retaining their original transverse markings." He also (*l. c.* footnote p. 220) remarks:—"The milt of the young fish, so far as I have observed, is always shed before the parr becomes a smolt." It seems evident from the foregoing that by parr he did not intend to include silvery smolts with parr-bands; and if such was his meaning, it is not in accordance with the changes shown by the parrs and smolts at Howietoun, where fish in the smolt† livery gave milt; and the same series of experiments have shown that individual variations in size among those artificially reared, and under identical conditions, can neither be due to the age of the parents nor the character of the stock from which the ova or milt has been procured.

A Committee of the Tay Proprietors, on May 2nd, 1855, was held at the Stormontfield ponds, "to consider the expediency of detaining the fry [which had been hatched March 31st, 1854, and were 3 or 4 inches in length] for another year or allowing them to depart. A comparison with the undoubted smolts of the river then descending seawards, with the fry in the ponds, led to the conclusion that the latter were not yet smolts, and ought to be detained. Seventeen days afterwards, viz. on the 19th May, a second meeting was held, in consequence of the great numbers of the fry having in the interim assumed the migratory dress. On inspection, it was found that a considerable portion were actual smolts, and the Committee came to the determination to allow them to depart. Accordingly, the sluice communicating with the Tay was opened, and every facility for egress afforded. Contrary to expectation, none of the fry manifested any inclination to leave the pond until the 24th of May, when the larger and more mature of the smolts, after having held themselves detached from the others for several days, went off in a body. A series of similar emigrations took place, until fully one half of the fry had left the pond and descended the sluice to the Tay. . . . as the shoals successively left the pond, about one in every hundred was marked by the abscission of the second dorsal fin. A greater number were marked on the 29th of May than on any other day, in all about

* Davy, 'Physiological Researches,' p. 221.

† It is difficult in the following description of the Howietoun experiments to separate the term smolts from grilse, as these fish do not descend to the sea, on the first return from which, in a normal condition, they would be grilse. Anyhow, after the deposition of ova they may be termed grilse.

1200 or 1300 . . . Within two months of the date of their liberation, viz. between the 29th of May and 31st of July, twenty-two of the young fish so marked when in the state of smolts, on their way to the sea, have been, in their returning migration up the river, recaptured, and carefully examined. This fact may be considered as still further established, by observing the increased weight, according to date, of the grilse caught and examined: those taken first weighing 5 to $9\frac{1}{2}$ lbs., then increasing progressively to 7 and 8 lbs., whilst the one captured 31st July weighed no less than $9\frac{1}{2}$ pounds. In all these fish the wound caused by marking was covered with skin, and in some a coating of scales had formed over the part^{*}. This question of smolts returning or not the same year as they migrated to the sea, I do not propose entering on here.

Respecting one half of the parrs migrating seaward one season, and the remainder not doing so until the next year, Russel observes, "A new hypothesis was brought out, to the effect that the females descend the first year and the males the second" (*op. cit.* p. 47). But on investigation it appeared "that the fish remaining during the second year consisted of both males and females, the milt of the males being fully developed, while the roe of the females was discernible only by a microscope" (*l. c.* p. 18).

Mr. Dunbar, who annually hatches about 500,000 Salmon ova in the Thurso river in the county of Caithness, informed Mr. Young that about 8 per cent. became smolts at the end of the first year[†], and about 60 per cent. at the end of the second year, and the remainder, or 32 per cent., at the end of the third year. The fish which were hatched in the spring of 1837 at Drumlanrig did not assume the migratory livery and seek to depart in May 1838 as Mr. Shaw expected, but did so in May 1839[‡]. It has been argued that young Salmon may have their growth stunted and their instinct overruled by being kept in a state of comparative confinement.

"Until the parr takes on the smolt scales it shows no inclination to leave the fresh water. They cannot live in salt water. This fact was put to the test at the ponds, by placing some parrs into salt water—the water being brought fresh from the sea at Carnoustie—and immediately on being immersed in it, the fish appeared distressed, the fins standing stiff out, the parr marks becoming a brilliant ultramarine colour and the belly and sides of a bright orange. The water was often renewed, but they all died—the last that died lived nearly five hours. After being an hour in the salt water, they appeared very weak and unable to rise from the bottom of the vessel which contained them, the body of the fish swelling to a considerable extent. This change of colour in

* Report of Committee on Stormontfield Ponds to British Association, 1856, p. 453.

† I conclude he meant to say at the termination of the first year after being hatched, for they do not descend seawards in their first year.

‡ "It was said of Mr. Shaw's experiments that the two-years' freshwater residence of the fry was ascribable to the difference of temperature between the waters of the Nith from which the ova were taken, and the waters of the ponds in which they were hatched and reared." But where is the evidence as to what was the difference in temperature, or whether there was any at all? On inspecting Mr. Shaw's *Observations*, for information on this point, we can only find that the temperature of the ponds, as compared with that of the river, was on one occasion three degrees below and on another six degrees above. So whatever difference there was, seems to have been in favour of the ponds stimulating, not retarding, as compared with the river or natural habitat. Put suppose it were otherwise, what then? We know that a lower temperature might retard the hatching of the fry by a week or two, or their growth by half an inch or half an ounce; but we have no ground for supposing that it would retard for a whole year such a change as that of assuming the migratory dress." (Russel, *l. c.* p. 48.)

the fish could not be attributed to the colour of the vessel which held them, for on being taken out they still retained the same brilliant colours" *.

In the Brighton Aquarium about 20 small Salmon parr were received from Mr. Berrington, the Chairman of the Usk Board, and these were placed in fresh water, where they soon began to feed and took to their tank. In the succeeding May, about eight months after they had been received, most of them commenced to assume the smolt livery, but four remained as parrs. Salt water was gradually introduced; but this did not prove fatal to the parrs, as it was feared it might, while the smolts became quite rampant with pleasure as the water grew more and more salt, until at last no fresh water was left and it became purely salt. Then the parrs, which had remained parrs up to this time, began to assume the smolt livery, and the change is described as truly marvellous. They ate five times as much as previously, were in incessant and rapid motion all day, and their growth became perfectly astonishing †.

Bertram remarked of the Stormontfield smolts, in 1861, "One fish which had been detained for three years for the purpose of discovering whether the species will grow in fresh water without being permitted to visit the sea, was found to be fully twice the size of the largest smolt" ‡.

The Duke of Buccleuch's gamekeeper at Bowhill was for some years in the practice of putting a few smolts into a freshwater pond, and feeding them regularly with bullock's liver. He reported that the smolts which grew into Salmon thrived for about three years and then died, but that Bull-trout smolts kept in good condition for a longer period.

"Into a deserted stone-quarry near Coldstream, filled with rain-water, two smolts, about 3 inches long, were put by boys out of mere amusement. One of these grew into a Salmon, which when 5 years old, weighing $1\frac{1}{2}$ lb., was caught and sent to Mr. Stoddart of Kelso, who had it boiled for dinner. He reported that it was not unpalatable. The other smolt grew into a Bull-trout and lived for seven years. It died during a very severe winter when, on account of the water being frozen, it could not be fed" §.

"Shaw has demonstrated, in the most conclusive manner, that those small Salmonoids which are generally called Parr, are the offspring of the Salmon, and that many males from 7 to 8 inches long have their sexual organs fully developed, and that their milt has all the impregnating properties of the seminal fluid of a much older and larger fish. . . . No Parr has ever been found with mature ova" ||.

"In the Exe, parr-marked fish (graveling or smolt so-called) have been taken with ova actually exuding from the fish, on and previously to its being handled to remove the hook. Some were sent to me by Mr. England, fishing in the Exe, some four years since, and preserved in glycerine, most certainly as a novelty, since which many such cases have come before me" (Frank Gosden, 'Land and Water').

I think I can adduce conclusive evidence so as to remove any doubt respecting smolts or grilse giving ova without descending to the sea, as they have done so in the

* Brown, 'Stormontfield Experiments,' pp. 61, 62.

† Francis Francis, 'Field,' 1879.

‡ 'Harvest of the Sea,' p. 110.

§ Extract from 'Report of Experimental Committee to Tweed Commissioners.'

|| Günther, 'Introduction to the Study of Fish,' 1880, p. 639.

Howietoun establishment. But the assertion that the milt of parrs has *all* the impregnating properties of the seminal fluid of a much older and larger fish must be received with a qualification, at least if the foregoing is intended to signify that it *always* has such.

It is frequently stated to be the rule that Salmon deteriorate on entering rivers; but this view must be modified by observing that such is also, partially at least, due to their being mostly in a breeding condition, at which period they would naturally fall off in condition, even were they to remain in the sea. At other times some ascend without deterioration, demonstrating such to be possible, owing to the state of health or condition which they were then in.

Shaw mentions * that in January 1837, he took a female Salmon, weighing 14 lbs., from the spawning-bed, from whence he also took a male parr weighing one and a half ounce, with the milt of which he impregnated a quantity of her ova and placed it in a stream connected with a pond, where, to his great astonishment, the process succeeded in every respect as it had done with that which had been impregnated by the adult male Salmon, and exhibited, from the first visible appearance of the embryo fish, up to their assuming their migratory dress, the utmost health and vigour. In January 1838, he took another female Salmon weighing 14 lbs. and two male parrs from the same spawning-bed and impregnated two lots of parr-ova with the milt from the two parrs, and afterwards placed them in two different streams enclosed in boxes, open at the top, temperature 45°. In December 1838 he took a female Salmon from the river weighing 11 lbs., and four male parrs from the same spawning-bed. After impregnating four different lots of ova, one lot to each individual parr, he placed the four parrs in a pond, where they remained until the following May, at which period they assumed the migratory dress. The ova were placed in streams to which no other fish had access, and where they became mature in a similarly progressive manner to those already detailed, thus clearly demonstrating that the young Salmon of 18 months old †, while yet in the parr or early state, actually performs the duties of a male parent before quitting the river. While the males of the three several broods which occupied ponds No. 1, 2, 3 continued in a breeding state, which lasted throughout the whole of the winter of 1838–39, he impregnated the ova of three adult female Salmon from the river with the milt of a male taken from each of the three ponds, and the whole of these ova matured. This, he deemed at once, removed any doubt which may have been entertained regarding the constitutional strength of individuals reared under such circumstances.

At Stormontfield, in the season of 1857 (November or December), milt from a parr was used to fertilize the ova of a 16-lbs. Salmon, and in 1858 they had fry of Salmon, fry of grilse and Salmon, fry of grilse, and the fry of the Salmon and parr. “On the closest inspection, no difference was perceptible either in the form, colour, size, or markings of any of these fish. There were larger and smaller fry to be seen amongst all these hatchings” (Brown, ‘Stormontfield Experiments,’ p. 71).

* ‘Transactions of Royal Society of Edinburgh,’ xiv. p. 561.

† As young Salmon hatch at the latest in March, these young fish must have been at least 21 months of age, if in their second season.

At the same establishment a suggestion which had been advanced—that the anomaly of some parrs migrating at the end of one year after hatching, and the remainder after two seasons, must have been caused by the first being the produce of Salmon, and the second of grilse—was clearly refuted. The fry, which numbered about 200,000, were solely the produce of 19 male and 31 female Salmon, spawned in 1859; and of these some remained in the ponds as parr, while others migrated seawards as silvery smolts. These same experiments showed that marked grilse of one year return as Salmon the next; that all the smolts of one year do not return the same year as grilse, the one half returning next spring and summer as small Salmon (*l. c.* pp. 92, 93); also that marked smolts were caught as grilse the first season and Salmon the second (*l. c.* p. 94).

Again, some authors have held that were Salmon able to migrate into large freshwater lakes, where a sufficiency of suitable food existed, they would be able to return to the streams where they had been reared as well-developed Salmon, a theory denied by others, who assert that Salmon never increase in weight in fresh water; but if this were so, how do they grow at Howietoun?

Dr. Murie (*Proc. Zool. Soc.* 1868, p. 249) gave an account of some Rhine Salmon (*Salmo salar*), hatched in the Gardens of the Zoological Society, in February 1863, and which lived in fresh water up to 1868. In May 1865, at the usual period of migration, those which were smolts tried to leap out of the tank; similar phenomena occurred in 1866, and “it was further observed that those which had assumed the silvery dress in the beginning of the year, again lost it in the autumn and became distinctly parr-marked.” In this autumn a good many died, some in the smolt, others in the parr-livery; and 1867 was a repetition of 1866. During the first and second years the young fish seemed to grow, and attained a length of from 3 to 6 inches. During the third and fourth year they grew much slower, and attained to from 5 to 7 inches in length; only two lived to the fifth year. These fish were kept in a small tank with a running stream of fresh water, a fact which is very necessary to bear in mind, because, although the conclusion drawn that the fishes retained in fresh water were subject to an arrest of growth, such may have been due to the small space in which they were confined, or the limited amount of water which they obtained, irrespective of which, the changes of temperature may have been great.

Yarrell (*Growth of Salmon in Fresh Water*) remarks that the view that “the rate of growth in young Salmon has some reference to the size of the place to which they are restricted, receives further confirmation in these river, lake, and well specimens. The smolt taken from the well in July 1838, where it had been confined for eight months, was rather smaller in size at that time than the smolts in the preceding April, though both were Pinks of the same year, namely 1837. The smolt taken from the lake in August 1838, which then measured $7\frac{1}{2}$ inches, had also grown more rapidly than that in the well, but had not acquired the size it would have gained had it been allowed to go to sea. Further it may be observed, that the Salmon parr from the lake in August 1837, then 18 months old, though perfect in colour, is small for its age; while that of July 1838, or 29 months old, is comparatively still more deficient in growth, supposing both fish to have resulted from Pinks of the year 1836, and been put into the lake at the same time; of which there

was no doubt, since the lake, the formation of which, though commenced in the autumn of 1835, was not finished till February 1836, soon after which the first Pinks were put in."

Before detailing the experiments I would wish to draw especial attention to the necessity of complete segregation of the fishes experimented upon, and the produce reared. Crowding many forms into one tank, and from this crowd selecting various varieties or so-called species simply from their appearance, and hybridizing from them, is likely to occasion irreparable errors and do more injury to investigation than if the subject were left quite alone.

I do not propose giving a detailed account of the Howietoun ponds, how care is taken that no one can have unauthorized access there, nor how the segregation carried on is most complete, as I have reason to believe that a distinct paper on this interesting subject may be expected, the contents of which I should not wish to anticipate.

In December 1880, Sir J. R. Gibson-Maitland, F.L.S., obtained some Salmon in the Teith, from which he procured eggs and milt, and they hatched at Howietoun in March 1881. In due course these young fish were transferred to pond no. 7 at Howietoun, which has its sides and bottom lined with wood, is 100×15 feet in surface extent, 8 feet deep in the centre and $6\frac{1}{2}$ at either side, while the average supply passing through it is a million and a half gallons of water a day.

In July 1883, in the presence of the foreign and other Commissioners to the Great International Fisheries Exhibition, this pond was netted, when it was seen that some of the Salmon-fry, then 2 years and 4 months old, were of a general golden colour, spotted, and in the banded parr-stage livery, while others were beautiful silvery smolts, similar to such as we generally find descending to the salt water, and in which, in certain lights, parr-bands were visible. Although, as a rule, the smolts were the largest, still some few of the parrs exceeded smolts in size. All present were convinced that these fish were the young of the Salmon, and in excellent condition.

October 10, 1883. One of these fish under a pound in weight, in the smolt livery and showing parr-bands in certain lights, jumped out of the pond and was found dead on the path. On being opened it proved to be a female with comparatively large ova, which were of a deep reddish colour, thus almost disposing of the statement already alluded to that "no parr has ever been found with mature ova." I say "almost," because as yet the ova were not quite mature, although they would have become so had not the fish met with an untimely fate; also the objection might be raised that it was a smolt, not a parr. Now although the parr-bands were present certainly the golden tinge seen in the young of the Salmon was absent. Up to the end of November 1883 several of these fish, during the night or early morning, had jumped out of the pond, and it was surmised that some might have been carried off by vermin, as birds or rats, in the early hours. On the 29th two more, one being $11\frac{1}{2}$ inches in length, were found dead, and some vermin had devoured the lower part of its head. It was of a silvery smolt colour with parr-bands. On being opened it proved to be a male full of ripe milt*. A net having been put into the pond three fish were examined. The first was a silvery smolt,

* For descriptions of the specimens see Proc. Zool. Soc. 1884, p. 21.

0.8 inches in length, which in certain lights distinctly showed ten parr-bands, one black spot on the preopercle, three on the opercle, while the upper two thirds or half of the body was spotted with black, as was likewise the lower half of the dorsal fin, which had a white anterior and outer edge. There were some red spots on the body. In this fish the generative organs were not developed. The second was more distinctly parr-marked, but otherwise very similar; it was 9 inches in length. The third was in the parr-livery with 10 well-marked parr-bands on either side and three black spots on the opercle; it was 6.3 inches in length and a male full of milt. As a rule the females in this pond were silvery, with ova which were not quite ripe, while the males on the contrary, being pressed, gave ripe milt. As to colours the fish seemed to be more spotted than is seen in specimens from rivers*, while their bodies were well formed although not of a large size, the largest being $13\frac{1}{2}$ inches long. Those in the golden parr livery appeared to be males, while the silvery smolts were generally females; in all the finger-marks were visible. These fish rendered it very evident that the relative growth of the fry does not depend on the size of pond, quality, quantity, or variety of food, or amount of water, as all had been treated alike, yet they varied in length from four inches to thirteen and a half.

During the month of May 1884 sixteen of these fishes jumped out of the pond and were found dead, and the breeding-organs in all were found to be developing in a satisfactory manner.

August 28, 1884. An examination was made of pond no. 7 and a smolt $1\frac{1}{4}$ lb. in weight was removed†. On being opened it proved to be a female with its ova well forward, the largest being 0.1 of an inch in diameter; the total length of the fish was 14.1 inches.

October 3rd. A smolt 13 inches in length, which had jumped out of pond no. 7, or had been dragged out by vermin, also proved to be a female, and the eggs were 0.2 of an inch in diameter.

Now some of these fishes tried repeatedly to jump out of the pond‡ and these generally met with fatal injuries; they sprung out towards the upper end near where the water entered, as if wishing to *ascend* the stream. Wire netting one foot in height was now fixed around the upper half of the pond, which prevented the fish springing over the bank. About the middle of October, fungus (*Saprolegnia ferax*) broke out among these fish, possibly due to injuries occasioned by striking themselves against the wire netting. It was also observed that they showed signs of ceasing from feeding, so a number of small Lochleven Trout were added to vary the diet, but they did not appear to consume many of them.

* The beautiful illustrations of grilse in Sir W. Jardine's magnificent 'Salmonidæ' do not resemble in colour the Howietoun fish, which latter are more spotted than his 2 lbs. 13 oz. specimen from the Solway Firth, taken in July, and even more so than his $3\frac{1}{2}$ lbs. captured in August.

† Described in Proc. Zool. Soc. 1884, p. 581.

‡ Brown ('Stormontfield Experiments') observes that he "in the month of February 1836, caught a dozen and a half parrs in the Tay, and kept them confined in a stream of running water, and by the month of May the whole of them had become smolts; but some had leaped out of their confinement in their struggle to find their way to the sea, and were found dead on the side of the pond" (pp. 7 and 8).

November 7, 1884. A smolt, or more properly a grilse, $1\frac{1}{4}$ lb. weight, was found lying almost dead by the side of pond no. 7, and from it about one hundred apparently ripe eggs were taken, and milted from a Lochleven Trout. On January 23, 1885, eighteen hatched, and when I saw them on February 10 they looked remarkably well and vigorous, while there did not appear to be any deformities among them. So far as I am aware, this is the first successful attempt in Great Britain at breeding from Salmon which have undoubtedly passed their entire existence in fresh water, while it is likewise interesting as a case of hybridization, and in a form which, so far, at Howietoun had been productive of sterile offspring.

November 11, 1884. About 12,000 eggs of the Lochleven Trout were fecundated from the milt of a grilse, and were placed in hatching-tray no. 1. They did very well, only 87 dead ova being picked out, and hatched on January 28, 1885.

November 14, 1884. The water was let off from pond no. 7, in which the young Salmon had been kept, as it required being re-charred this year, while the contained fish were taken to pond no. 5, just re-done up, and previously inhabited by Brook-Trout, but which were now turned into the burn, as they were too old to be worth further preserving. Sixty-eight young Salmon were transferred, the majority being males, while these fishes showed all the gradations in colouring from the golden and banded parr to the silvery smolts, these latter, however, not having lost their parr-bands, while some of the large smolts or grilse were distended with ova. All the fish in the full parr-livery were males, but smolts and grilse in some instances also had milt. About two dozen eggs were obtained from one of the females, but they did not germinate, probably not being quite ripe. Three smolts which were too much injured to live, due to their persistent attempts to escape, were opened, and the ovisacs were found distended with eggs, almost but not quite ripe, being still slightly adherent to the ovisac.

As these young Salmon became ready for continuing their species, in December the following were obtained and laid down in the hatching-house:—

December 1, 1884. 1500 eggs from two smolts or grilse which were treated with the milt of one of the males. These eggs averaged each 0·22 of an inch in diameter, and were placed in hatching-tray no. 104 *a*: about 400 of these eggs hatched on Feb. 21, 1885.

December 9, 1884. About 4000 ova of these grilse were impregnated with the milt of one of the males. These eggs were each 0·20 of an inch in diameter and were placed in hatching-tray no. 108 *a*: about 2200 of these eggs hatched on Feb. 27, 1885.

On the same day 400 ova of these grilse were treated with the milt of a Lochleven Trout. These eggs were each 0·22 of an inch in diameter, and were placed in hatching-tray 108 *b*. The milt appeared to be strong enough where it acted, but only appeared to do so in half the eggs.

December 13, 1884. About 2500 eggs of the grilse were milted from the same lot in the pond, and placed in hatching-tray 84 *c*. The diameter of each egg was 0·22 of an inch, and about 200 of these eggs hatched on March 5.

At nearly the end of December the remainder or 48 young Salmon which had been bred from, were removed from the wooden-lined pond no. 5 into the earthen pond no. 10, it being of larger size, and none jumped out.

I have already shown that the fact of parr having milt prior to descending seawards has been generally recognized, but that smolts or grilse kept under similar conditions have been almost always on the contrary declared not to give ova. But now we have the experiments made at Howietoun to consider, and these have undoubtedly proved that young male and female Salmon kept in suitable freshwater ponds may develop milt or ova. These fish were hatched in March 1881, and most of the male parr had milt in November 1883, or when 2 years and 8 months old; also two or three smolts of the same age had ova which probably would have matured, but they jumped out of the pond and so met with their deaths. In November or December 1884, or at 3 years and 8 or 9 months' age, all these fishes seemed to be ready to breed, and it appears probable then that Salmon-parr do not possess milt for the purpose of impregnating the ova of the old Salmon, or "to mingle with the River-Trout," as Dr. Günther suggests, but to be ready to fertilize the eggs of any ascending grilse; for in some localities these latter deposit their ova prior to the usual period when adult male Salmon are present for breeding purposes.

Some authors hold that Salmon are freshwater forms that proceed to the sea, and that there is a physiological necessity for their doing so in order to be able to produce ova. Others, who I believe are more correct, consider these fish marine forms that ascend into fresh water to deposit their eggs and rear their young. As it is evident from the Howietoun experiments that these fish can give eggs without descending to salt water, such disposes of the "physiological necessity" theory. Possibly this migration may be classed among the instances of "inherited instinct" and may be lost in such a race of Salmon as have been reared for a few generations in fresh water. It may be that in some such manner the "land-locked Salmon" of various countries have been originally differentiated from their fellows, an interesting instance of which I propose to adduce in this place.

Mr. Douglas Ogilvie in 1881 took about 100 Sea-Trout and Salmon smolts, which he turned into Lough Ash, Co. Tyrone, which has no access to the sea. April 30, 1883, he captured a grilse $14\frac{1}{2}$ inches long in this lake, where Salmon had not previously been seen. Its abdomen was so distended that he considered it would have spawned very shortly, more especially as it was taken at the mouth of the only stream that enters this lough. The specimen is in the Natural History Museum at South Kensington, and there I examined it. I do not hesitate considering it a true *Salmo salar**, while the eggs in spirit as measured by me were each 0·25 of an inch in diameter. Provided there had been a ripe male in the vicinity, there seems no reason why this fish should not have deposited her eggs, and such would thus have given rise to a land-locked race.

"On the approach of autumn," observes Shaw (Trans. Roy. Soc. Edinb. xiv. p. 559, footnote), "the whole of the Salmonidæ, resident as well as migratory, while in fresh water acquire a dusky exterior, accompanied by a considerable increase of mucus or

* Described Proc. Zool. Soc. 1884, p. 584.

slime. The fins also become more muscular. However, on the return of spring, they resume their wonted beautiful silvery colouring, and the fins, the cartilaginous portions of which are frequently damaged during the winter floods, grow up and acquire their former outline."

Different authors have assigned various reasons why a parr on becoming a smolt (which it does, as a rule, when commencing its seaward journey) assumes a silvery livery. Davy* suggested "that the young remain in fresh water until they have acquired not only a certain size and strength, but also additional scales, fitting them, in their smolt stage, to endure without injury the contact of the saline medium." Couch demurred to such an opinion in 1866, observing that the silvery colour of smolts is not due to their acquiring additional scales, but owing to a deposit of bright soft matter which shines through the transparent scales. Dr. Günther† remarks, respecting the River-Trout, that they "frequently retain the parr-marks all their lifetime; at certain seasons a new coat of scales overlays the parr-marks, rendering them invisible for a time, but they reappear in time, or are distinct as soon as the scales are removed. When the Salmones have passed this parr-stage . . . a new coat of scales overlays the parr-marks." But as these fish do not shed their scales, Dr. Günther appears to hold to the untenable proposition that an additional coat of scales is developed on these fishes at certain periods‡. It was likewise stated in one of the conference papers read at the "Great International Fisheries Exhibition" in 1883§, that the young of the true Salmon "do not venture into the sea till another skin of glistening scales has been formed over their first skin. They then receive the name of *smolts*. If put into salt water before getting this silvery dress they die." I do not propose here entering upon the discussion of these opinions, so wide spread, but nevertheless entirely erroneous. Any one who will examine a series of specimens can readily verify for himself that there never is an extra coat of scales as above stated.

Before concluding this portion of my paper, I may observe that the teeth in the vomer of a parr generally are as follows:—three on the head of that bone, below or behind that a pair, next two placed one at an angle to the other, and subsequently eight in a single row, but with their points somewhat divergent. There is very little change seen in those of the smolt, while in a grilse 13 inches long, that spawned this year, the same dentition prevails. This raises the question whether the loss of teeth, as generally seen, is not partly due to the hardness of the food they consume; this, however, is not the case in the Howietoun pond, as what they are fed upon is soft.

I omit any detailed description of the grilse, and decline entering upon a lengthened discussion of the decision of a Committee of the Commissioners of the river Tweed,

* 'Physiological Researches,' 1863, p. 250.

† 'Introduction to the Study of Fishes,' 1880, p. 632.

‡ See Proceedings of Zoological Society, 1884, p. 22, showing the impossibility of an extra coat of scales being developed.

§ "Salmon and Salmon Fisheries," by D. Milne Holme. (Conference Papers, p. 4.)

who stated, in their report for 1863, as follows:—"Our opinion, from the experience of the last twenty years, is, that grilse never become Salmon of any stage whatever." As grilse were reared from Salmon-ova at Howietoun, it may well be asked in reply, if such were a fact, how it is that grilse may be raised from Salmon-eggs. Russel, when refuting this argument of the Tweed Commissioners, and also of Mr. Mackenzie, remarked upon the difficulty of obtaining conclusive evidence after the fish has assumed its migratory habits and can no longer be kept under inspection to see if the grilse becomes a Salmon. But, as I have now shown, the reverse experiment has been successfully carried out at Howietoun, and eggs of Salmon have been proved to give birth to fishes which in time become smolts and then grilse.

A difference of opinion respecting the persistent or variable size of the eggs of Salmonidæ appears to prevail, a difference which could not exist if the authors would take the trouble to measure them when freshly removed from the parent fish, or as lying in the hatching-troughs. For these eggs do not increase in size during the process of incubation, although such as die become sodden, white, and somewhat distended. Unimpregnated eggs do not, as a rule, take on this opaque white aspect, but remain clear throughout the nesting-season, neither do they augment in size.

I propose offering a few remarks upon whether the eggs of the Salmonidæ, of the same species, are invariably of the same size, and especially if the age of the parent has any connection with such differences as may be perceived; also, if any variations in the size of the eggs from a single fish are to be seen.

Harmer in 1767* gave a table showing the number of eggs which he had observed in certain forms of fishes, among which the Salmonidæ were not included. He remarked, "From this table it appears that the size of the eggs is nearly the same in great and small fishes of the same species, at the same time of the year." And these observations may be found, with but little variation, in the writings of authors from that period up to recent years, as perhaps in no branch of biology are assertions once made more adhered to without re-investigation than in Ichthyology. Passing on to the 'Zoological Record' of 1864, p. 179, we find that Professor Malmgren, having observed that certain Salmonoids in a lake in Finland were descendants of the common Salmon, whose access to the sea had been cut off owing to an elevation of the land, mentioned as one of the present differences that this freshwater and dwarfed breed gave smaller ova than *Salmo salar*. In this conclusion Dr. Günther did not coincide, remarking that "the last character [or size of the ova] will be considered very significant by all who may have a more extended knowledge of fishes, as the size of the ova is not only invariably the same in individuals of whatever size, but, as far as our experience reaches, is even often characteristic of the species of a genus." This opinion, slightly modified, Dr. Günther still apparently held in 1880, for he asserted† that "the ova of Teleostean fishes are extremely variable in size, quite independently of the size of the parent species. The ova of large and small individuals of the same species, of course, do not differ in size."

* Transactions of the Royal Society, "On the Fecundity of Fishes."

† 'Introduction to the Study of Fishes,' p. 159.

On the other hand, Mr. E. Blanchard in 1866* observed that the ova “of the grilse are always sensibly smaller than those of the adult Salmon.” Livingston-Stone, 1877 †, remarked that in American Trout (*Salmo fontinalis*) that reside in spring-water, which is equivalent to a diminished supply of food, smaller eggs are developed than in such as reside in brooks. On the McCloud river ‡ “it was noted, in 1878, that the parent Salmon were unusually small, their average weight being under 8 lbs.” This small size was stated to be undoubtedly caused, in whole or in part, by the fishery at the canneries of the Sacramento, where the 8-inch meshes of the innumerable drift-nets stopped all the large Salmon, but let all the small ones through. The eggs when taken proved to be at least one third smaller than those of most previous years, and the average number of eggs to the fish was about 3500 against 1200 in the previous year. Livingston-Stone in 1882 §, writing respecting the eggs of *Salmo fontinalis*, observes that those from the small fish of the elevated rivulets are not so large as those of the finer breeds from warmer streams, concluding that the ova of these last are fully twice as large as those found in the race residing in mountain rivulets. From this period, observations have been frequently recorded to show that the eggs of the Salmonoids undoubtedly differ in size consequent upon certain physical causes; hence the assertion that in this family “the small size of the ova [in *Brachymystax coregonoides*, Günth.] is of sufficient importance to separate these fishes generically from *Salmo*” || may be questionable, especially as the typical specimens examined in London were only 18 and 21 inches respectively in length.

The following figures are all taken from examples in the Howietoun fisheries, unless otherwise noted; and in order to make the statement plainer, the eggs of the various species or crosses of these fish are given :—

<i>Salmo salar</i> , 16 lbs. weight.	General size of eggs	0.24 of an inch.
" "	" "	from 0.25 to 0.30 "
" " small	" "	0.20 "
" " grilse reared in ponds	" "	from 0.20 to 0.22 "
" <i>trutta</i> , small	" "	0.175 to 0.18 "
" <i>leucensis</i> (var.) 8 years old, from one pond, the general size		0.24 "
	but some are 0.22, and a few 0.21, and in three or four	0.20 "
" " 7 years old. General size		0.19 "
" " 6	" "	0.18 to 0.19 "
" " 2 and 3	" "	0.17 "
" <i>fontinalis</i> 4	" "	0.18 "
" " 3	" "	0.17 "
" " 2	" "	0.14 "
Hybrid <i>S. fontinalis</i> , <i>S. alpinus</i> 2	" "	0.13 to 0.15 "

[†] 'Domesticated Trout,' 3rd edition.

‡ Report of United States Fish Commission.

^s Bulletin of the United States Fish Commission, ii, 1882, p. 11.

|| Catal. Fishes Brit. Museum, vi, 1866, p. 163.

The foregoing are only some out of the many measurements which I have made, but they tend to show very conclusively that the size of the eggs in Salmonoids increases with the age and probably the condition of the parents; thus the ova of grilse are inferior in size to those of the Salmon. And in large Trout as in the older Lochlevens there is an augmentation in the thickness of the shell*, a rather important question to the fish-culturist, because such shells require a strong embryo to readily hatch, which is obtained by giving an increased supply of water during their "eyed" period. Whether it was accidental or otherwise, still the Trout eggs obtained latest in the season were of rather larger size than such as had been taken in the earlier months.

Next we come to the consideration of whether any difference is perceptible in the eggs of two parents of the same age that have been kept under identical conditions. Among the young Salmon reared at Howietoun from eggs obtained from the same parents, and reared in the same pond, some taken on December 1st, and again on the 13th, 1884, averaged 0·22 of an inch; some from similar fish on December 9th averaged 0·20 of an inch, while others taken the same day were 0·22 of an inch. The same phenomenon has been observed among the Lochleven Trout, wherein, although the diameter of the eggs of fish at 8 years of age was generally 0·24 of an inch, in some it was 0·22, in a few 0·21, and in three or four 0·20; whilst in six-year-olds it has been observed to vary from 0·18 to 0·19 of an inch. That such variations might theoretically be anticipated most of us must admit, for whatever causes deficiency of nutrition might occasion diminution in the size of the ova. Also the size of the parent ought possibly to be taken into account, for disease, crowding them when young, and other causes may dwarf these fishes, and such would probably give comparatively small eggs.

Can we detect any variation in the size of the eggs given by a single fish? I have already adduced an instance of this among the Lochleven Trout. In November 1884, I placed 80 unimpregnated eggs of one of these fish in a tube of water, wherein they were kept for a week, the water being changed daily. At the end of this period I measured each ovum, and found 75 were 0·25 of an inch in diameter, three were 0·20 of an inch, one was 0·175 of an inch, and one 0·15 of an inch. Looking through the hatching-troughs at Howietoun it appeared that from 4 to 5 per cent. of the eggs are less than the normal size of the remaining 95 or 96 per cent.

I must here refer to the grounds on which I believe that offspring raised from the large eggs are superior to such as are reared from the smaller ones. Two batches of Lochleven Trout were spawned on November 2nd, 1882, the parents of one lot having been hatched in 1875, and of the other in 1876; these ova were similarly treated and the young came out during January and February 1883. At Craigend are two ponds which have been constructed for the reception of young Salmonidæ, each being 100 feet long and about 25 wide: one is nearly on a level with the other, and the same stream passes through both. Into these two ponds the two lots of fry were turned, those from the older (1875) or

* The micropyle in the Salmon's eggs has nine pits or depressions around the opening, whereas there are none in the ova of Trout, including Sea-Trout.

seven-year-old parents having the lower pond, those from the younger or six-year-old fish having the upper pond, while both lots were similarly treated. At the end of November 1883, those in the lower pond were about one fourth larger than those in the upper pond, and as they received the stream after it had passed through the upper pond, this gave reason to suppose that the large eggs produced superior fish to those from the smaller eggs. In 1884 a second experiment was tried in the same two ponds, which were stocked with young Lochleven Trout, bred from parents of the same age, spawned the same day, and hatched in the same room. By the end of the year no difference in size or appearance was perceptible between the two lots. It would thus seem that the larger eggs given from older parents produce fry which grow faster than do those from the smaller eggs furnished by younger parents.

Mr. Francis Francis (Fish Culture, 1865, Appendix, p. 309), when alluding to the Salmon fishery at Doolulla in Ireland, has stated, "A curious fact occurred also, which is worth noting, showing that big smolts make big fish. Among the smolts marked were thirteen which had far outstripped the rest in size; and among the grilse were some which had also considerably outstripped the rest. Most of these smolts were marked. Among the rest was one very fine fellow, which Mr. Ramsbottom had to hold in both hands while he was marked. They were cutting off the adipose or soft fin, and the operator, who held the seissors, remarked as they came to this fish, 'What a pity to mutilate such a fine fellow! We will only cut off a piece of his fin.' And the fin was cut in halves, leaving a small triangular piece. This very fish was caught, and as he was the largest smolt, so it was the largest grilse and weighed $7\frac{1}{2}$ lbs."

The immediate and possibly remote result of having eggs from young fish for stocking purposes is one which requires the earnest consideration of the fish-culturist. For I have already shown that by selection a more rapidly growing race may be reared, and I now propose examining whether small eggs from young parents may not give bad results as to the number hatched or the quality of the young.

For several seasons it had been remarked that eggs from young mothers are subject to a greater percentage of deaths than those taken from older fish. On November 13th, 1884, about 500 eggs having a diameter of 0.17 of an inch were taken from a rising two-year-old Lochleven Trout and they were impregnated from another of the same race of the usual size. Out of these eggs only about a dozen hatched on January 28th, and seven lived to be turned into the rearing-pond. In this instance the immaturity was on the mother's side.

On November 29th, 1883, 4500 eggs of the Lochleven Trout (of the season of 1875) were milted from the parr of a Salmon raised at Howietoun and which had been hatched in March 1881, and consequently were a little over $2\frac{1}{2}$ years of age. The mortality of these ova was only about 2 per cent.; but such by no means gave a true index of the experiment, for when the young hatched January 15th, 1884, nearly all were seen to be suffering from what has been termed dropsy or blue swelling of the yolk-sac*. As the same cross had been made December 24th, 1881, but with older parents, and that without

* Proc. Zool. Soc. 1884, p. 376.

occasioning dropsy, one is irresistibly led to the conclusion that hybridization had nothing to do with these results, which may reasonably be attributed to the immaturity of the male parrs*. As a further confirmation of this view, parrs in 1884 taken from the same lot were found prolific, but with comparatively few cases of dropsy occurring. Among these 4000 dropsical fish, only about 100 lived out the year.

Thus the great mortality from eggs of young mothers was during the incubating stage, but from young males one season older it seems to have shown itself among the fry; passing over another year, we do not find so great a mortality among the eggs nor disease of the young. Bearing on this I may allude to the ova of American charrs having been milted from a Scotch charr in November 1882; one of the progeny gave 146 eggs on November 12th, 1884, or a little under 2 years of age. Only six feeble little ones hatched on February 3rd, 1885. At the same time milt was obtained from some of these hybrids and used to impregnate 4500 eggs of Lochleven Trout; these hatched on February 2nd, but the mortality was large, being upwards of half the eggs, while there were many deformities and some dropsies among the offspring. Males are evidently more matured for breeding-purposes than are females of the same age. I would here advert to a remark I published in 1883†, that in the fresh waters of India due to indiscriminate net-fishing the young (of many forms of fish) have to be raised from ova of such as are merely one or two seasons old, while the younger the parent the smaller the eggs, and this is probably one mode in which races of fish deteriorate.

We now arrive at the question, Why is it that Salmon reared in ponds of fresh water or where they are unable to descend to the sea are variously spoken of? Yarrell tells us of Salmon fry being turned into a pond in 1830, and in 1833 several were taken 2 lbs. to 3 lbs. in weight and perfectly shaped, but he seemed to be in doubt whether they could mature their roe in such localities. Rasch thought that fish thus imprisoned, if the lake were very large, would attain about the same size as the Salmon in the sea. Dr. Murie has shown that an arrest of growth occurred in an aquarium at the Zoological Gardens among young Salmon kept in restricted areas.

I have had the opportunity of examining Salmonoids kept in artificial pieces of water of different extents for various periods of time, the results of some of which I propose alluding to as bearing on this subject.

In October 1879 I received from Mr. J. Carrington, F.L.S., of the Westminster Aquarium, an American charr (*Salmo fontinalis*) 9 inches long, which had been hatched from eggs sent from Lake Huron, and which had been reared by the late Mr. Frank Buckland in his tanks at the Horticultural Gardens, South Kensington. This fish of

* As corroborative of the above view that the milt of these young Salmon-parrs was deficient in marital powers. I may mention that on the same date 1900 eggs of the common Brook-Trout were milted from one of these Salmon parrs which had been dead a few hours. But not a single egg fructified; only 3 turned white in December, 3 in January, and 15 in February, or a total of 21. On March 12th the remainder were still quite clear, but destitute of any sign of a contained embryo.

† 'Indian Fish and Fishing.' Great International Fisheries Exhibition 1883 series, p. 27.

several (? 6) years of age had a head of a longer proportion* than is seen in these fishes kept under normal conditions. In short the fish was not well grown—there had been an arrest of growth due to its various surroundings. At the same time I received from Mr. F. Buckland four examples of undoubted *Salmo salar*, reared by him from eggs received from Huningen, and which were collected from Salmon captured for this purpose from below the falls of Schaffhausen†. As year after year passed by and these fish were still retained in the comparatively small amount of fresh water which sufficed to fill the tanks in the Horticultural Gardens, they became lanky and apparently half-starved fishes, similar to those which have been described by Dr. Murie (*l.c.*, and in his 2nd paper P. Z. S. 1870, pp. 30–50, “Irregularity in the Growth of Salmon”).

Can Salmon be reared in small pieces of water or ponds through which a good current of water is kept flowing and wherein there is a sufficiency and variety of suitable food? To this we have a reply from Howietoun, to which I shall presently allude, that Salmon can be so kept and reared, but the size to which they will yet attain time only can demonstrate.

Certain hybrid Salmon have been reared and kept for some years in the Howietoun ponds: so far most have proved to be sterile, and the size to which they have attained has been unsatisfactory; but the fish have all been well formed and not shown that kelt-like appearance usually deemed so characteristic of Salmon retained in fresh water. The experiments have been as follows:—

On November 25th, 1879, some eggs from the Lochleven Trout were fertilized from the milt of the Salmon. Although many hatched, up to this period none have been found fertile; the largest I have seen was on November 14th, 1884, and it was $16\frac{1}{2}$ inches in length. They were kept in the island pond (which is 210×90 feet and from 10 to 11 feet deep in the centre). On November 28th, 1883, these fish were removed to pond No. 11, where they now remain. On December 24th, 1881, some Lochleven-Trout eggs were similarly fertilized with Salmon milt, and they hatched March 9th, 1882. The young fish were kept in a planked pond, 20 feet long by 5 feet wide, until March 13th, 1884, when they were removed to the octagon pond at Craigend‡, and the largest taken has been 10 inches long.

It seems to me that at Howietoun those hybrid Salmon raised under the same conditions as some *Salmo salar* do not augment in size so rapidly as these latter fish; thus among the hybrids between the Lochleven Trout and Salmon hatched in March 1882, in November 1883 the largest was a little over 7 inches long, while the young *Salmo salar* in the next pond, a year older, were from 4 to $13\frac{1}{2}$ inches long. If future observations shall give the same results it will be necessary to ascertain whether this arrest of growth is due to hybridization (which is unlikely), paucity of space or of water supply, character of the ponds, or has any connection with the food.

* Day, British and Irish Fish. ii. p. 119, pl. exx. fig. 2.

† Journ. Linn. Soc., Zoology, xvi. 1882, p. 397.

‡ These fish began to show symptoms of commencing fertility in May 1885; and on July 4th, owing to the stream giving out due to the hot weather, all but one died.

I may now finally remark upon the facts that pure Salmon have been raised from eggs in the Howietoun fishery, that the young have grown to be parr, smolts, and grilse, and that these have given eggs and the eggs so obtained have been successfully hatched. Many sportsmen and fishermen are now reopening the old question that grilse are not young Salmon*.

The general bearing of the preceding authorities quoted has been in favour of the evidence that Salmon confined in fresh water, and especially within that of limited areas, were incapable of reproducing their kind. On the other hand, the fact obtains that land-locked Salmon, both in Europe and America, certainly reproduce their species in fresh water.

As touching the question at issue, the Howietoun experiments, then, have shown the possibility of not only rearing parr and smolts, but also obtaining ripe ova and milt from them, without their ever having gone to the sea. Thus it is demonstrated that descent to the sea is not, as has been asserted, a dire physiological necessity.

I would here further observe that although time will be necessary before a definite reply can be given as to how these young Salmon raised from the eggs of parents which have not gone to the sea will thrive and how large such fish will become in freshwater ponds, still any unbiassed investigator must admit that, so far as they have gone, the experiments made at Howietoun among the Salmonidæ are pretty conclusive on the following points:—

- (1) That male parrs and smolts may afford milt competent to fertilize ova, but when from fish of the second season, or up to 32 months old, it is (? always) of insufficient strength for strong and vigorous fry to be raised.
- (2) That female smolts or grilse may give eggs at 32 months of age, but those which are a season older are better capable of producing vigorous fry; while for the purpose of developing ova a visit to the sea is not a physiological necessity.
- (3) That young male Salmonidæ are more matured for breeding-purposes than are young females of the same age.
- (4) That although females under 24 months of age may give ova, such are of little use for breeding-purposes, the embryos not becoming well developed or vigorous, while the young when hatched are frequently malformed.
- (5) That the size of the eggs of Salmonidæ varies with the age and condition of the parent; but, as a rule, older fish give larger ova than do younger and smaller ones.
- (6) That among the produce of every female fish there may be found variations in the size of the eggs.
- (7) That from larger ova finer and more rapidly growing fry are produced: consequently that, by selection of breeders, races may be improved; while it is only where segregation is well carried out that such selection is possible.

* On the table, exhibited at the meeting when this paper was read, was a specimen reared at Howietoun from a Salmon egg, the identity of which with grilse I think was beyond dispute. There were also a parr and a smolt shown from the same hatching, evincing the untenableness of the assumption that the latter have an additional coat of scales to what obtains in the parr.

DESCRIPTION OF THE PLATES.

PLATE LIII.

- Fig. 1. *Salmo salar* in the parr livery, a male with ripe milt, hatched March 1881, killed November 27th, 1883. Drawn of natural size.
- Fig. 2. Caudal fin shown in two conditions of expansion ; natural size.
- Fig. 3. *Salmo salar* in the smolt livery, a female with eggs only just visible, hatched March 1881, killed November 1883 ; natural size.
- Fig. 4. Caudal fin ; natural size.

PLATE LIV.

- Fig. 1. *Salmo salar*, a grilse that had been just spawned, hatched March 1881, killed December 9th, 1884. Sketched from the specimen, and of natural size.
- Fig. 2. Caudal fin ; natural size.
- Fig. 3. Scale from above lateral line and below adipose dorsal fin, magnified 20 diameters. From a photograph of the specimen on a glass slide.

XIX. *GOLFINGIA* MACINTOSHII, a new Sipunculid from the Coast of Scotland. By E. RAY LANKESTER, M.A., LL.D., F.R.S., Jodrell Professor of Zoology in University College, London, Fellow of Exeter College, Oxford.

(Plates LV. & LVI.)

Read 18th June, 1885.

WHEN I was staying at St. Andrews last summer (1884) my friend Professor MacIntosh, knowing my interest in the class to which it belonged, very kindly presented me with an exceedingly remarkable Gephyraean which he had obtained ten years previously from a friend who had dredged it in St. Andrews Bay, south of Montrose, at a depth of ten fathoms.

The specimen was obviously something new, and was noteworthy, not only on account of its external structural features, but on account of its large size.

The anticipations, based on its external appearance, were justified by a dissection of the specimen, which I carried out in the intervals of exercise with the club and ball sacred to the classic "green" of St. Andrews; and I have accordingly ventured to dedicate the new genus of Sipunculid worms indicated by this specimen to the local goddess whose cult is historically associated with the most ancient of Scottish seats of learning. "*Golfingia*" forms an appropriate parallel to the Scandinavian genus of Echiurid Gephyraeans called "*Hamingia*" by Koren and Danielssen.

External Features.—*Golfingia*, as exhibited in the spirit-preserved specimen before dissection, presented the appearance drawn in Pl. LV. fig. 1. It measured five inches in length, and consisted of a soft-walled cylinder of white silky surface, marked with dark dots, as in *Sipunculus punctatus*. At either end of this soft-walled cylinder a hard dark brown-coloured spout or smaller cylinder is observed. One of these is the "posterior sclerite" or "scleropyge," the other is the "anterior sclerite" or "sclerorhynchus." In the living state the proboscis or "introvert" which *Golfingia* possesses, like all other Sipunculids, would issue from the sclerorhynchus in the way shown in fig. 2. Both scleropyge and sclerorhynchus are modifications of peculiar structures occurring in *Aspidosiphon*, and are found in the cylindrical form only in *Golfingia*. The scleropyge is the same organ as the posterior "shield" of *Aspidosiphon*, whilst the sclerorhynchus is represented by the anterior shield of *Aspidosiphon* and by the calcareous ring of *Cléosiphon*.

The scleropyge is shown in figs. 3, 4, 5, so as to exhibit its surface-markings. Its walls are very thick and quite inflexible. It probably was moved as though hinged to the soft body, and was used in burrowing in sand. The body-cavity is continued into it, and the nerve-cord extends more than halfway along it, giving off numerous nerve-filaments (Pl. LVI. fig. 11). It is imperforate. The sclerorhynchus is similarly shown in figs. 6, 7, 8.

In the median dorsal line, at the base of the sclerorhynchus, is placed the triangular anal aperture (*a*). Symmetrically on each side are the external apertures of the paired nephridia (brown-tubes), fig. 6, *dl*, *dr*. The sclerorhynchus is as solid and thick-walled as the scleropyge. Its surface is marked by elongated quadrangular areae differing from the rougher transverse rugae of the scleropyge. The anterior extremity of the sclerorhynchus presents an opening (fig. 7). This is the orifice of invagination of the proboscis or introvert, which, when withdrawn, carries with it the tentacular crown and mouth. The form of these parts was made out by dissecting them in their introverted condition (see figs. 9, 10, 12).

The introvert is soft-walled, its outer surface being beset with numerous papillae, and near the mouth with chitinated hooklets (as in many Sipunculids). These are shown from different regions of the introvert in figs. 17, 18, 19, 20, and 21. The introvert measured, when extended, two inches and a half in length (fig. 2 *d*). At its free extremity is placed the mouth *e*, surrounded by a circle of six symmetrical tentacles. Each tentacle is pinnate, carrying two rows of small processes (about twenty-four in all). A single tentacle is shown in fig. 13 and part of one in fig. 14.

Internal Features.—The body-cavity (coelom) is spacious, as in *Sipunculus*. The characters of the coagulated coelomic fluid could not be ascertained.

The long-muscles of the body-wall form a smooth continuous coat, *i. e.* they are not divided into groups, as in *Sipunculus*, *Phymosoma*, and some species of *Aspidosiphon*.

The intestinal coils did not extend further than two thirds of the length of the body. This may have been due to the action of the spirit; but I am inclined to think not. Thus, the posterior third of the body and the scleropyge were simply filled with coelomic fluid, and contained no "floating" viscera. The intestinal coils were held together and to the body-wall by a delicate mesentery, as in *Sipunculus*. The position of the retractor muscles of the introvert, and the relations of the brown tubes (nephridia), rectum, œsophagus, and nerve-cord to these and to one another are shown by the drawings of the dissections made (figs. 9, 10).

There are four retractor-muscles of the introvert, as in *Sipunculus* (not two only, as in *Aspidosiphon*). Two of these are attached anteriorly and dorsally (*h*), and two posteriorly and latero-ventrally (*i*).

The anterior pair arise on each side of the rectum, but not quite symmetrically. The posterior pair arise over (and are perforated at their bases by) the nerve-cord, which lies here on the animal's left side near the middle ventral line.

The anus of *Golfingia* lies at the base of the sclerorhynchus in the middle dorsal line, and the ventral line corresponding to this is the ventral median line. The nerve-cord does not occupy this middle ventral line, and the only internal structures which exhibit a strict bilateral symmetry in their position are the nephridia (see diagrams, figs. 15, 16, *g*). The nephridia lie right and left of the symmetrical sclerorhynchus, equally distant on either side from the anus. In the dissection they are seen as shrivelled brown sacs (figs. 9 & 11). I could not discover their internal openings. In the dissection (fig. 9) the four retractor-muscles are seen attached to the introvert at the point *t*, and the nerve-cord (*ff*)

is seen attached loosely to the whole length of introverted proboscis (*y*). From the middle point between the retractors passes backwards the œsophagus (*l*) lying in close proximity to the rectum; a little way back they are twisted round one another. A curious muscular band (the spindle-muscle of Selenka) accompanies the rectum (figs. 9, 10, *m*), and is attached, after running a length of two inches, to the wall of the intestine. A similar muscular band exists in *Sipunculus nudus* (and most Sipunculids), arising in that animal from the curious little caecal pouch which exists on the rectum at the distance of an inch or so from the anus.

I could not find any trace in *Golfingia* of this cæcum, nor of the "bush-like organs" near the anus, which appear in *Sipunculus nudus*, possibly to represent in a rudimentary form the posterior nephridia (cloacal trees) of the Echiuridean Gephyræa.

Owing to the imperfect state of preservation of the specimen, I am unable to state whether any vascular system of one kind or another exists in *Golfingia*, nor am I able to give any indication as to the position of the gonads.

The distinctness of *Golfingia* from all other genera of Sipunculid Gephyræans will be obvious at once to those who have studied this group of animals. The species I dedicate to my friend Prof. MacIntosh, not only in recognition of his vast services to marine zoology, but in memory of a long-standing friendship marked by many acts of kindness on his part.

The relation of *Golfingia* to other genera of Sipunculidean Gephyræans will be best appreciated by the reader if I make use of the synoptic table recently published by Selenka, and assign *Golfingia* its place in a modification of that table. It is not far removed from *Aspidosiphon*, but differs from that genus both in the form of its sclerites and in the disposition of the retractor-muscles and the character of the oral tentacles.

SIPUNCULOIDEA.

(Slightly modified from "Die Sipunculiden" of Dr. E. Selenka, Wiesbaden, 1883.)

Marine worms with cylindrical elongate bodies, with obliterated segmentation; only in the larval stage sometimes lateral, serial pairs of bristle bundles are present. Larva with a well-marked prostomial area, and a ciliate band, *which is post-oral*. The mouth, lying at the fore-end of the body, is provided with tentacles into which the body-cavity never penetrates, but only the vascular system; in rare cases there are no tentacles. Skin with numerous glands; overlying the cerebral ganglion is often a pair of ciliated tubercles. The long, tubular, alimentary canal is almost in all cases spirally rolled; very seldom is it simply thrown into loops; the anus is dorsal in position and far forward. The front part of the body (introvert) is introversible by the action of retractor-muscles; anteriorly on the introvert are very generally present chitinous hooks. The coelomic fluid contains corpuscles. The closed vascular system encloses a corpusculated fluid, and consists of one or two contractile sacs (hearts)—which accompany the œsophagus and end blindly after a short course—and of the vascular ring and tentacular vessels. The circulation of the blood is effected both by the contraction of the heart's walls and by the action of ciliated cells; in very exceptional cases there is no vascular

system. There are no special respiratory organs. A pair of nephridial sacs (rarely only one) are always present and always (?) have an internal aperture. The reproductive organs lie in the form of transverse ridges at the base of the ventrally attached pair of retractor-muscles (of the introvert); the eggs have numerous pore-canals in their chorion; sexes distinct. Free or living in shells or tubes. In all seas.

KEY TO THE GENERA OF SIPUNCULOIDEA.

I. *The longitudinal musculature of the body-wall is continuous and not divided into separate bands. The retractors of the introvert vary in number from one to four.*

1. PHASCOLOSOMA.—Two nephridia. Numerous tentacles surrounding the mouth in a circle. A complete intestinal coil, unattached posteriorly (only in *M. Hanseni* attached); a spindle muscle is usually present; only on the anterior intestinal convolutions are there one or more ligaments. Adhesive papillae are always absent. Hooklets are generally not present on the introvert. The retractors are four, two or only one. Eggs spherical. In all seas.
2. DENDROSTOMA.—Two freely suspended nephridia. Only four to six pinnate tentacles. A complete, posteriorly unattached, intestinal coil; spindle-muscle always present; ligaments present only on the anterior intestinal coils. Hooklets are present, but may be shed early in life. Four or two retractors. The contractile sac (of the vascular system) generally has caeca upon it. Tropical forms.
3. PHASCOLION.—A single nephridium, only that of the right side, which is attached to the body-wall throughout its length. The intestine forms no spiral or only an incomplete one; there is no spindle-muscle, whilst the loose intestinal loops are attached throughout their length to the body-wall by numerous ligaments. Adhesive papillae are often present. The retractors are not more than two. Eggs spherical. Living in Gastropod shells or in tubes. In all seas.

II. *The longitudinal musculature of the body-wall is divided into 17–41 separate bands. Four retractores introversi.*

4. PHRYMOSOMA.—Body covered with papillae. Numerous filamentous tentacles, which seldom (or never?) surround the oral aperture, but are arranged away from the latter, dorsally in a three-quarter-circle which is open dorsal-wards. No caecum on the rectum. Hooklets nearly always present on the introvert. Four retractors (in *P. Ruppelli* two?). Contractile sacs almost always devoid of villi. Eye-spots are always present. Eggs elliptic, flattened, reddish. Small tropical species.
5. SIPUNCULUS.—Body without papillae. Tentacles surrounding the mouth in a circle. Always one or several caeca on the rectum (except in *S. edulis*?). Hooklets absent, only present in *S. australis*. Eggs spherical. The individual tentacles thick, with an internal vascular network (not three longitudinal vessels merely); generally two contractile sacs. Mostly large forms. In all seas.

III. *In front of the anus and also at the hinder end of the body a distinct shield (corneous thickening of the integument), or in front of the anus a calcareous ring or a tube-like cornification, forming the base of the introvert, and another at the tail-end. Hooklets sometimes present. Longitudinal muscles continuous or divided into bands.*

6. ASPIDOSIPHON.*—An anal and a caudal shield. Introvert eccentric arising from beneath the anal shield ventrally. Tentacles small and not numerous, placed in a semicircle above the mouth.

* See Dr. C. Ph. Sluiter, "Beiträge zu der Kenntniss der Gephyreën aus dem Malayischen Archipel," Naturk. Tidsch. v. Nederlandsch-Indie, Deel xliii. (1884), pp. 26–88, with 4 plates.

Intestinal spire traversed by a spindle-muscle, which is fastened at the hinder end of the body. Only two retractors, ventral in position and often fused with one another.

7. CLÖEOSIPHON.—Directly in front of the anus a calcareous ring, from the centre of which the introvert is extruded. Longitudinal musculature continuous. Hooklets bifid. Tropical.
8. GOLFGINGIA.—A præanal corneous tube (sclerorhynchus) and a caudal corneous tube (scleropyge). The introvert issues centrally from the præanal tube, which is, in fact, its basal portion indurated. Tentacles six, pinnate, surrounding the mouth in a circle. Retractors four, two ventral longer, and two dorsal shorter, the two pairs arising at some distance from one another on the body-wall. Chitinized hooklets are present at the oral extremity of the introvert; further back on the same are found cylindrical and subspherical chitinized papillæ. Longitudinal musculature continuous. Intestine not coiled throughout in a spire, not fastened posteriorly; a spindle-muscle present. Two freely suspended nephridia. Vascular system uncertain. Known species large (eight inches long when expanded).

IV. *Only two lamelliform tentacles. Four retractors. Few intestinal loops, quite free. No vascular system.*

9. PETALOSTOMA.

V. *No tentacles. No vascular system. A single retractor. A single nephridium.*

10. ONCHINESOMA.—Introvert long. Body small, pear-shaped.

11. TYLOSOMA.—No introvert (?). Body cylindrical, thickly beset with papillæ, which are more closely set and larger at the front and hind ends of the body.

DESCRIPTION OF THE PLATES.

Letters apply to all figures.

- | | |
|---|--|
| <i>a.</i> Anus, in the median dorsal line. | <i>n.</i> Musculature of the body-wall (smooth). |
| <i>b.</i> The sclerorhynchus (anterior sclerite). | <i>o.</i> Epidermis and cutis. |
| <i>c.</i> The scleropyge (posterior sclerite). | <i>p.</i> Muscular attachment of the nerve-cord within the scleropyge. |
| <i>dl.</i> } Right and left nephridial aperture. | <i>q.</i> Six terminal filaments of the nerve-cord (cauda equina). |
| <i>dr.</i> } | <i>r.</i> The peri-oral tentacles. |
| <i>e.</i> Mouth. | <i>s.</i> Papillary surface of the introvert. |
| <i>f.</i> Nerve-cord. | <i>t.</i> Point of attachment of the retractor-muscles to the introvert. |
| <i>ff.</i> Nerve-cord attached to the introvert. | <i>u.</i> Chitinized ridges on the cuticle of the introvert. |
| <i>g.</i> Nephridia (brown tubes, oviducts or sperm-duets.) | <i>v.</i> Hooks on the same. |
| <i>h.</i> Anterior retractors of the introvert. | <i>w.</i> Soft papillæ. |
| <i>i.</i> Posterior retractors of the introvert. | <i>x.</i> Chitinized papillæ. |
| <i>k.</i> Rectum. | <i>y.</i> The introvert. |
| <i>l.</i> Oesophagus. | |
| <i>m.</i> Muscular band accompanying the rectum. | |

PLATE LV.

Fig. 1. The specimen of *Golfgingia MacIntoshii* of natural size and appearance, after ten years' preservation in spirit.

2. Diagram of *Golfgingia MacIntoshii*, with expanded introvert and tentacular crown: natural size.

3. Ventral view of the scleropyge.

4. Dorsal view of the scleropyge.

Fig. 5. Lateral view of the scleropyge.

6. Dorsal view of the sclerorhynchus and anterior part of the soft body. Showing anus *a* and position of nephridial aperture *dl*, *dr*.
7. View of the anterior aperture of the sclerorhynchus.
8. Ventral view of the sclerorhynchus.
9. Dissection of the specimen of *Golfigia MacIntoshii*, showing the position of the introvert *y* and its retractor-muscles *hh*, the nephridia *gg*, the nerve-cord *f*, and the rectum *k*, and œsophagus *l*. The body-wall has simply been cut along a line nearly corresponding to the median ventral, and reflected on either side.
10. The introvert and œsophagus have now been thrown forward, after cutting the latter and the retractor-muscles so as to show the position of the anus, and the attachment of the nephridia to the base of the sclerorhynchus internally.

PLATE LVI.

Fig. 11. The scleropyge opened by a dorsal, median, longitudinal slit, so as to show the nerve-cord lying within its cavity.

12. The introvert opened by a longitudinal incision, so as to expose its papillary surface *s* (the true outer surface here seen as introverted); the tentacles *r* and the mouth *e*.
13. A single tentacle enlarged to show the pinnæ.
14. Apex of a tentacle.
- 15, 16. Diagrams of transverse sections taken near the base of the sclerorhynchus, to show the asymmetry of the arrangement of organs; fig. 15 includes the introvert; fig. 16 is just behind it.
17. A portion of the integument from near the oral extremity of the introvert, viewed from the outer surface and showing the mesh-like arrangement of chitinized ridges *u*, and numerous hooklets *v*, also the soft papillæ *w* placed in the spaces of the mesh-work. It is a question as to whether the soft papillæ are an early condition of the chitinized hooklets, or are entirely distinct structures. The position of the hooklets *on* the ridges, and of the papillæ *in the space* enclosed by the ridges, favours the latter supposition.
18. A small piece of the same, showing clearly the relation of the hooklets to the ridges.
19. A similar portion of integument taken a little further back (the hooklets do not extend for more than a quarter of an inch behind the oral aperture), showing the ridges *u*, more powerfully developed, and no hooklets.
20. A similar portion of integument a little further back than fig. 19 (about three quarters of an inch from the mouth), showing the chitinization of the papillæ *x*, and the reduction of the ridges, to pigmented tracts. The chitinized papillæ are apparently the same structures as the soft papillæ *w*, of figs. 17, 18, 19.
21. Lateral views of three chitinized papillæ from the same region.

XX. *On the Variations in the Form of the Cirri in certain Comatulæ.* By P. HERBERT CARPENTER, D.Sc., F.R.S., Assistant Master at Eton College. (Communicated by W. PERCY SLADEN, Sec. Linn. Soc.)

(Plate LVII.)

Read December 3rd, 1885.

IN a paper¹ which appeared in the Journal of the Linnean Society some three years ago, I drew attention to the dimorphic character of the cirri in *Eudiocrinus varians*; and I have since been led to notice the same peculiarity both in *Antedon hystrix*² and in *A. proluxa*. This has induced me to look for it in other types, and I have found that both in *A. Eschrichti* and in *A. quadrata* two forms of young cirrus present themselves in the same individual.

Dr. Carpenter³ has shown how the typical form of cirrus in *A. rosacea* with about sixteen joints may be developed in two different ways. The one process results in what he called the "small mature" cirrus, and the other in the "large rudimental" form. In the first series the mature proportions between the length and breadth of the cirrus-joints are shown at a very early period, and the opposing process to the terminal claw is developed in cirri which do not reach one eighth of their full size. Other cirri, however, of considerably greater length, consist of altogether immature joints with quite different proportions from those of the mature cirrus and no trace of an opposing spine on the penultimate. Both these types are usually to be found on the centro-dorsal of any tolerably mature *Antedon rosacea*; while they may also occur in the first whorl of cirri which are borne by the Pentaerinoïd larva, though both in *A. rosacea* and in the Pentaerinoïds of other species the small mature form is the most common. On the other hand, when studying *Actinometra parvicirra* I could find no young cirri of the small mature type at all, though the rudimental form was fairly abundant.⁴

Now in *Antedon phalangium* not only is this difference between the rudimental and the small mature cirri carried to a very much greater extent than in *A. rosacea*, but the shape and number of the cirrus-joints vary very greatly, both in the same individual and in those from different localities. The two extreme forms are so different in appearance (Pl. LVII. figs. 7 & 33) that if one met with them in an isolated condition, they would most assuredly be referred to different species of *Antedon*; whereas in reality they are connected by the most remarkable series of intermediate gradations. As I have a large

¹ "Descriptions of new or little-known Comatulæ. I. On the Species of *Atlecrinus* and *Eudiocrinus*," Journ. Linn. Soc. Zool. vol. xvi. 1882, p. 497.

² "On the Crinoidea of the North Atlantic, between Gibraltar and the Faeroe Islands," Proc. Roy. Soc. Ed. vol. xii. Session 1883-84, p. 366.

³ "Researches on the Structure, Physiology, and Development of *Antedon* (*Comatula*) *rosacea*," Phil. Trans. 1865, pp. 711, 712.

⁴ "On the genus *Actinometra*, Müll., with a Morphological Account of a new Species from the Philippine Islands," Trans. Linn. Soc. 2nd ser. Zool. vol. ii. 1879, p. 60.

series of examples of this species, formerly so little known, from ten different localities, I have devoted a considerable amount of time and trouble to working out in detail the variations of its cirri, both local and individual, and the results of this investigation are explained in the following pages.

Antedon phalangium was described by Müller¹ as long ago as 1841, though for a long time but little was known about it. The original specimens which Müller described had been obtained at Nice and at Naples; but for many years afterwards no further mention was made of its having been met with, either at these localities or anywhere else. It was obtained off the Tunis coast by the 'Porcupine' Expedition of 1870, though the fact was not recorded at the time; and it was not till 1875 that much attention was directed to it. Professor Marion dredged it in the harbour of Marseilles, and gave a careful analysis of its peculiarities, accompanied by some excellent figures.²

These have enabled me to identify it with the type from the Ross-shire coast which has been so long known to British naturalists by the name of *Antedon cellica*³; and it is of the differences which are presented by the cirri of the Scotch and of the Mediterranean types respectively that I am about to speak.

Besides obtaining *Antedon phalangium* in great quantities at two localities on the Tunis coast, the 'Porcupine' also dredged it at Carthage, off Cape Sagres on the Atlantic coast of Spain, and also off Mondego on the coast of Portugal. Several specimens were likewise obtained by the S. S. 'Dacia' on the Seine bank at a depth of 88 fathoms, and have been put into my hands by Mr. John Murray; while, thanks to the kindness of Professor Marion and of Mr. W. Percy Sladen, I have further been able to examine specimens from Marseilles and from Naples respectively.

Müller's description¹ of the cirri in the Mediterranean variety of this type ran as follows:—"Die Ranken sind zur Grösse des Thiers ganz ausserordentlich lang mit 45 langen dünnen Gliedern. Endglied gestreckt ohne Dörnchen der Innenseite; die Glieder, mit Ausnahme der ersten (an der Basis), sind 2-2½ mal so lang als breit." This is very well shown in the excellent figure given by Marion² of some specimens from Marseilles; and he mentions that the cirri vary in length from 25 to 58 mm. while the number of joints varies from 37 to 51. In Mr. Sladen's Naples specimen the longest cirrus reaches 61 mm. and consists of 48 joints, the three longest of which measure 5 mm.; and it may be noted in passing that only one young cirrus remains attached to the centro-dorsal of this individual. It is a trifle over 5 mm. long and belongs to the rudimental type, consisting of a large number of small annular joints without any trace of a terminal claw. The longest cirrus which I have found in specimens from the Tunis coast measures 52 mm. and contains 47 joints (Pl. LVII. fig. 7); while in one from the Minch there are 51

¹ "Ueber die Gattung *Comatula*, Lam., und ihre Arten." Abhandl. d. k. Akad. d. Wiss. Berlin, a. d. J. 1847 (1849), p. 253.

² "Draguages au Large de Marseille." Ann. des Sc. nat., 6^e série, Zool. t. 8, 1879, pp. 40-45 (of separate copy), pl. 18.

"Note on the European Comatulæ," Zool. Anzeiger, 1881, Jahrg. iv, p. 520, and Proc. Roy. Soc. Edin. vol. xii, pp. 361, 362.

³ *Loc. cit.*, p. 253.

⁴ *Loc. cit.*, pl. 18, figs. 11, 11c, 11d.

joints, though the length is only 47 mm. (Pl. LVII. fig. 29), and in the most extreme form from this locality there are 18 joints in a length of but 35 mm. (Pl. LVII. fig. 33). In the Scotch variety therefore, while the number of joints is but little altered, they are relatively very much shorter than in the Mediterranean examples.

Let us now study the mode of development of these joints and the transitional forms between one kind of cirrus and the other. For the typical form of cirrus in the species we must of course take the long-jointed ones which were described by Müller in the Mediterranean variety (Pl. LVII. fig. 7).

Type A. *Long-jointed*.—The three basal joints are wider than long, but the length gradually increases from the first to the seventh and then remains tolerably constant for some distance, decreasing slowly towards the end of the cirrus. But the terminal joints are not laterally compressed and wider than long, or even square, as is the case in the cirri of most Comatule; for they remain much longer than wide. In fact the width diminishes slightly in the last few joints so that the end of the cirrus has a somewhat tapering appearance, and there is a long terminal claw, without, however, any trace of an opposing spine on the penultimate joint. Most of the cirri are of this type in all the Mediterranean specimens of *Antedon phalangium* that I have seen; and it is also the prevailing one in those from off Cape Sagres and off Mondego. But in those dredged by the 'Dacia' on the Seine bank it is very largely intermixed with another type of cirrus (Pl. LVII. fig. 23), the terminal joints of which are rather short and broad, somewhat as in those from the Ross-shire variety (Pl. LVII. fig. 33).

The 'Dacia' dredgings, and in a less degree also those of the 'Porcupine,' yielded several individuals in various stages of maturity; and I have therefore been able to study the development of the cirri both in quite young individuals and also in those older ones in which new cirri are continually being produced round the margin of the centro-dorsal. So far as I have been able to make out, these typical long-jointed cirri are developed on the rudimental plan. An early stage of their formation is shown in Pl. LVII. fig. 1. The fifth and sixth joints are already distinctly longer than wide; but their successors become rapidly shorter, and the rounded end of the cirrus is made up of a series of annular joints without any trace of a terminal claw. If we make allowance for the great difference between the cirri of the two species, we may place this form between stages C and D of the developmental series described by Dr. Carpenter in *Antedon rosacea*. Its further development is shown in Pl. LVII. figs. 3 and 6. In those two cirri which measure 14 and 22 mm. respectively, and especially in the latter, which has some fifty joints, the lower joints present all the characters of maturity; but the later ones are mere discs, and it is only in the larger one (fig. 6) that there is any indication of a terminal claw and that but a very slight one. The claw becomes more marked in the older cirri shown in figs. 4 and 5, and the later joints lengthen out till their shape more nearly resembles that seen in the mature cirrus (Pl. LVII. fig. 7). As in the case of the rudimental cirri of *Actinometra parvicirra*¹ the addition of new joints seems to take place in the outer half of the cirrus, those at its base presenting most of the characters of maturity at quite an early date.

¹ Trans. Linn. Soc. 2nd ser. Zool. vol. ii, p. 60.

It sometimes happens that the terminal claw makes its appearance when the cirri are much shorter than that represented in Pl. LVII. fig. 5. An instance of this is shown in fig. 2, and the later stages are seen in figs. 8 and 9. The claw is at first almost central in position (figs. 6, 9), but it gradually moves over towards the dorsal side, though no opposing spine is developed, as seen in Pl. LVII. figs. 5 and 8.

I have not found any cirri of this long, smooth, and very long-jointed Mediterranean type among the Scotch individuals of *Antedon phalangium*; the nearest approach to it being the cirrus, of which the end is shown in Pl. LVII. fig. 16. But this rather belongs to the intermediate type (B) next to be described, more southern examples of which are shown in figs. 15 and 17.

Type B. *Intermediate*.—Besides these greatly elongated cirri with numerous joints, the terminal ones of which are very long and slender, most of the specimens from the Mediterranean and from the Seine bank have somewhat shorter and smaller cirri with fewer joints, the terminal ones of which are relatively broader than in the typical form. Of this kind there are many varieties; while there is often a more or less distinct opposing spine on the penultimate, and sometimes also on the previous joint as well. Fig. 17 represents a moderately young one without an opposing spine, and fig. 19 another still younger in which it is tolerably distinct. In both of these cirri the joints exhibit all the characters of maturity, although they are less numerous than in the longer but very undeveloped rudimental form seen in fig. 6. Older cirri of this pattern may either have no opposing spine (fig. 15), though the dorsal edge is very slightly serrate, which is not the case in the type (fig. 7); or it may be present, sometimes with another behind it (fig. 11). In this specimen the joints forming the outer third of the cirrus are distinctly longer than wide; but in those shown in figs. 10 and 14 this is less evident, and in the former the opposing spine is double. This form with broader terminal joints sometimes occurs in the Scotch variety of the species (Pl. LVII. fig. 16); and it thus presents an approach to the cirri with still shorter joints which are so characteristic of this local variety (Pl. LVII. fig. 33). I have not found sufficient material for working out the development of this shorter but still long-jointed form of cirrus; but I think that figs. 12, 13, and 18 represent some of its earlier stages. The second of these, which is not half the length of the very immature form shown in fig. 3, came off the smallest individual of this species which I have seen.

Type C. *Square-jointed*.—Besides the more or less long-jointed cirri typical of the Mediterranean variety, the specimens dredged by the 'Dacia' on the Seine bank bore a number of cirri much more like those characteristic of the Ross-shire form. The end of one of these is shown in Pl. LVII. fig. 23. It has 57 joints which gradually decrease in length from the middle of the cirrus onwards, and the short later ones are somewhat compressed laterally, but about as wide as long. In this cirrus there are spines on both the joints before the claw, while there is a third spine on the rather smaller cirrus shown in fig. 24. On the other hand there may be only one spine (fig. 25), or none at all, as in that shown in fig. 27, which also has a very greatly reduced terminal claw. But the relative shortness of the joints in the outer third of the cirrus is very marked in all these examples.

This, which may be called the square-jointed type, furnishes the greater number of the cirri in the Scotch specimens. A very characteristic example consisting of 51 joints, but only 47 mm. long, is shown in fig. 29, and another variety with the terminal joints longer in proportion to the width than those just below them in fig. 28; while fig. 21 shows another form with shorter joints and two opposing spines. The three youngest cirri of this type that I have been able to find are shown in figs. 20, 22, and 26. The first two of these are from quite young individuals; but the third is from a much older one. The opposing spine and the carination of the later joints which is prominent in the two former is less evident in the larger cirrus, which has rather the appearance of having been developed on the rudimental plan (compare fig. 31); while the two small cirri of the young individuals clearly belong to the small mature type of Dr. Carpenter. The smaller of the two is distinctly shorter, though with wider terminal joints than a rudimental cirrus of type B, from another young individual at the same locality.

Type D. *Short-jointed*.—Besides the square-jointed form of cirrus just described, which is the prevailing one in the Scotch variety of *Antedon phalangium*, several others may be found with the later joints distinctly wider than long. The most extreme form of this short-jointed type which I have seen is shown in fig. 33. Figs. 30-32 seem to represent earlier stages of its development, though I am by no means clear that the last one, if not the other two as well, may not belong to the square-jointed type shown in fig. 29. They are interesting, however, as furnishing an example of the rudimental process of development which we have also studied in the long-jointed Mediterranean variety (figs. 1-6); and a comparison of the two brings out very clearly the difference between the latter and the short-jointed northern form in their immature condition.

Thus in a young cirrus from the Minch shown in fig. 31 there is a distinct terminal claw, and the later joints have almost assumed their final shape; whereas in the much longer but very undeveloped cirrus of the southern type (fig. 6) there is only the merest trace of a terminal claw, and the later joints are still in a discoidal condition. In a later stage, however (fig. 4), they have lengthened out and begun to look more like those of the full-grown cirrus (fig. 7); while in the corresponding stages of the short-jointed variety this great change of form has not taken place, though the size of the joints has considerably increased.

It is difficult to account for these striking variations in the form of the cirri of *Antedon phalangium*. We have here to deal with something more than a mere dimorphism of the cirri in any given individual, such as I have noted in the boreal Comatulæ *Antedon hystrix*, *A. proluxa*, and *A. quadrata*. &c.; for the geographical distribution has to be considered as well. While the two intermediate types of cirrus occur in individuals from every locality, northern and southern alike, the long-jointed form characteristic of the Mediterranean is not to be found in any of the Scotch specimens; while those from the Mediterranean, the Seine bank, and even from 220 fathoms in the Atlantic off the Portuguese coast, have none of the quite short-jointed cirri, such as that shown in fig. 33. Neither is it in any way a bathymetrical variation. The Scotch specimens were obtained in the Minch at a depth of 60-80 fathoms. The 'Dacia' dredged on the

Seine bank at 88 fathoms; while the depth on the Tunis coast where the 'Porcupine' dredged varied from 50 to 120 fathoms, and Marion found the species to be most abundant at Marseilles in 100-200 metres. Temperature variations again seem to have nothing to do in causing this difference, for there are plenty of long-jointed cirri in the individuals brought up from 220 fathoms at a temperature of 52° Fahr., which is very near that observed in the Minch, while the Mediterranean water on the Tunis coast was much warmer.

These variations in the form of the cirri are the more remarkable because in most Crinoids these organs are very constant in their characters. In fact, among the Pentaeriniæ there are several species of which the cirri are so similar that they can hardly be differentiated when removed from the stem. In the genus *Actinometra* the cirri are, as a rule, few in number and poorly developed; but the lower pinnules of the arms often reach a considerable size and are provided with keels and processes of different kinds; and in some species, such as *Actinometra solaris* and its allies, individuals from different localities present much the same sort of variation in the pinnule-characters as we have seen to occur in the cirri of *Antedon phalangium*.

DESCRIPTION OF PLATE LVII.

[All the figures are $\times 5$, except figs. 13, 20, 22, which are $\times 10$.]

Type A. *Long-jointed*.

Figs. 1-6. Young cirri of the large rudimental type; from the Seine bank.

Figs. 8, 9. Similar forms from the Tunis coast.

Fig. 7. Adult cirrus from the same locality.

Type B. *Intermediate*.

Figs. 10, 11, 13, 18. From the Seine bank. Fig. 13 represents a very young cirrus, probably of the small mature type.

Figs. 12, 17, 19. From the Tunis coast.

Figs. 14, 15. From off Cape Sagres.

Fig. 16. From the Minch.

Type C. *Square-jointed*.

Figs. 20, 22. Young cirri of the small mature type; from the Seine bank.

Figs. 23-27. Older cirri from the same locality.

Figs. 21, 28, 29. Older cirri from the Minch.

Type D. *Short-jointed*.

Figs. 30-32. Immature cirri of the large rudimental type; from the Minch.

Fig. 33. Adult cirrus from the same locality.

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