general setæ of the body as terminating in a bifid extremity like those of the Tubificidæ and some other families of aquatic Oligochæta. On the other hand, the characteristic *f*-shaped setæ of the terrestrial Oligochæta are often found among aquatic genera; it is the converse that is rare.

2. Notes on *Anodon* and *Unio*. By Oswald H. Latter, M.A., formerly Berkeley Fellow of Owens College, Manchester, 1888, late Tutor of Keble College, Assistant Master at Charterhouse. (Communicated by Frank E. Beddard, M.A., Prosector to the Society.)

[Received November 13, 1890.]

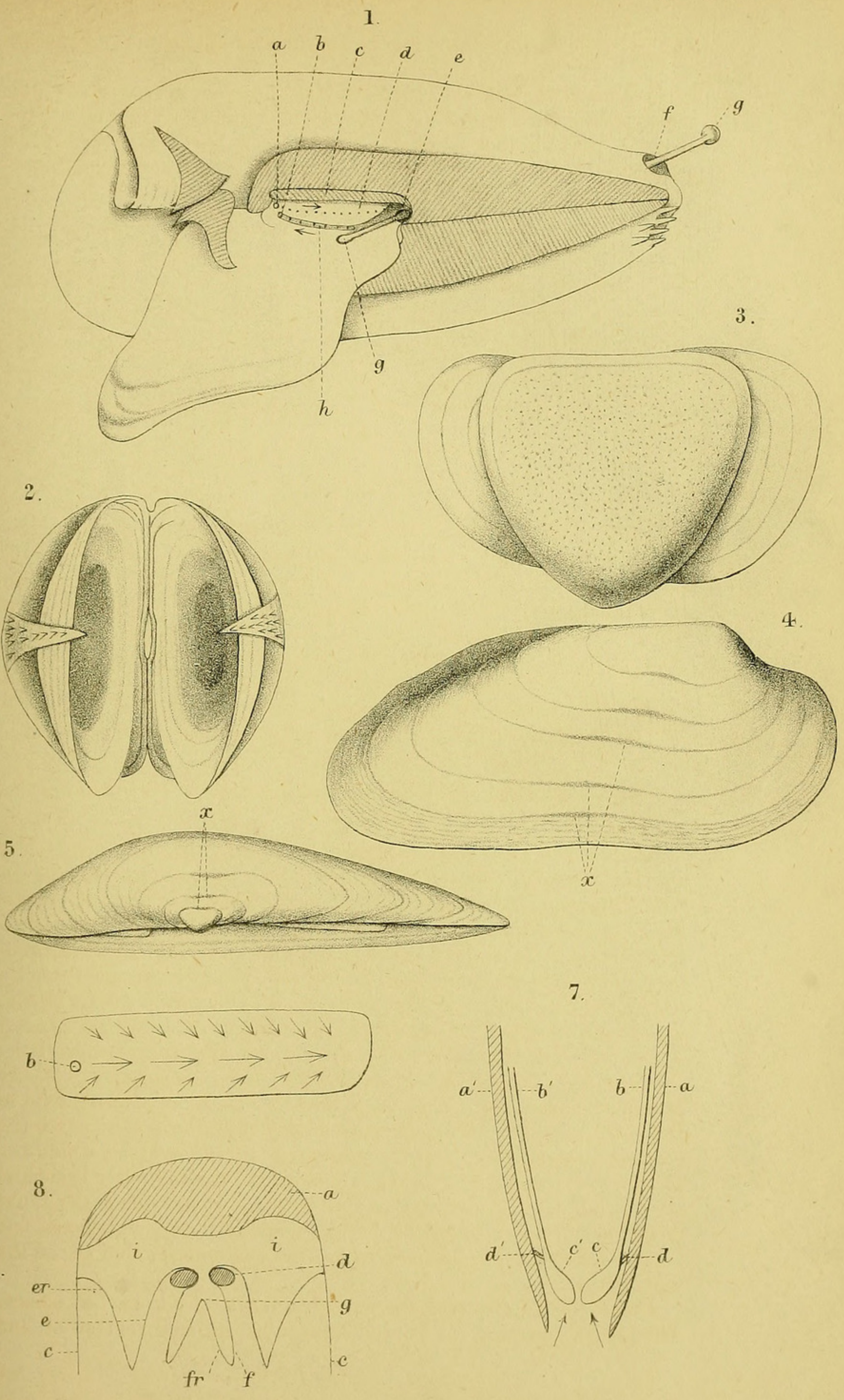
(Plate VII.)

The following observations have been made from time to time during the last two years while working at *Anodon* and *Unio* for other purposes. I have thought it worth while to bring them together and publish them apart from the anatomical and other details which I hope to complete shortly. My investigations were begun in Manchester in 1888, while I held the Bishop Berkeley Fellowship, and I may take this opportunity of thanking the donor of that emolument for the facilities thereby afforded me and also Prof. Milnes Marshall for his kind advice and assistance in many ways.

I. *The Passage of the Ova from the Ovary to the External Gill-plate.*

In 1830 von Baer gave in Meckel's 'Archiv,' 1830, pp. 313–352, an account of this process, which has, so far as I can ascertain, been tacitly accepted by all later writers on the subject. My own observations have led me to somewhat different conclusions. Von Baer's account is briefly as follows:—The ova pass along the inner branchial passage, being prevented from falling into the internal gill-space by the labour contractions of the foot; thence they pass into the cloaca, into which the outer branchial passage also opens. All the muscles of the body are in a state of contraction during the passage of the ova, and furthermore the cloaca is small. In consequence of the muscular contraction the shell is closed and the ova accumulate in the cloaca, a few perhaps being emitted into the water before the closure is complete. The only direction therefore along which the pressure of ova can be relieved is forwards along the outer branchial passage and thus to the external gill-space. It is to be noticed that von Baer does not state that he has *observed* these phenomena, but merely draws his conclusions from the anatomical relations of the various organs.

I have myself observed the passage of ova as far as the cloaca. The genital aperture, as is well known, is situated ventral of and



J. Smit lith.

Mintern Bros. imp.

ANATOMY OF ANODON & UNIO.

somewhat posterior to the external aperture of the nephridium; it is slightly anterior to the commencement of the free detached dorsal border of the inner lamella of the internal gill-plate. The ova may be seen through the thin epithelial covering on the dorsal margin of the foot, passing along the oviduct to the genital aperture. After escaping through this pore they are conveyed backwards along the external surface of the nephridium. This surface is densely covered with cilia borne upon tall columnar cells, with a large oval nucleus lying in their lower portion and resting on a definite basement membrane. In the middle line of the nephridial surface the cilia are longer and drive the ova straight backwards; towards the ventral and dorsal sides of the nephridial surface the cilia are shorter and drive the ova obliquely backwards and towards the line of the longer cilia, so that the latter tend to keep the ova in the middle line where the ciliary currents are strongest. The arrows (Plate VII. fig. 6) show the direction of the currents. The total effect of the cilia is therefore to drive the ova straight backwards along the middle line of the nephridial surface. In the course of about 50 seconds an ovum is thus swept back to the slit between the retractor pedis muscle and the point of fusion of the internal gill-plates. Through this slit the ova pass, meet the stream of ova from the other side of the body, and so reach the exhalant branchial current and the cloaca. The process goes on for several days (10 or 11) in each individual. This being the case, according to von Baer's theory the shell must remain closed during the whole of this period, or, in other words, respiration be suspended for nearly a fortnight. This appears to me incompatible with the continued life of the individual.

In order that the ova may reach their final resting-place there must be some reversal of the respiratory currents. I was unable to detect any reversal of *ciliary* currents by experiments with colouring-matter, and it is improbable that any such reversal occurs. I have, however, observed (*v. infrà*, p. 55) a violent reversion of currents, due, I believe, to suction, during the emission of *Glochidia*. This suction is probably effected by relaxation of the adductors and consequent partial opening of the shell while the right and left mantle-margins are kept in contact so as to block the aperture at all other parts except the two siphonal notches, of which the exhalant in particular remains open. The thickened margins of the mantle thus serve to temporarily close the aperture between the two valves, and, if my explanation be correct, the muscle-fibres of the mantle between the point of attachment of the mantle to the shell and its free border may tend to draw the right and left thickened borders together in the middle line, while also increasing their thickness and offering a more solid resistance to the water. Furthermore, when once the thickened borders of the mantle are in apposition and the shell commences to gape, the pressure on the right and left free borders will tend to drive them even more closely together; for the line of the mantle which is attached to the shell must of necessity follow the outward movement of the valves when gaping commences, and the free borders unite to form a bluntly pointed longitudinal ridge with divergent sides; the pressure of water falls on these divergent sides and drives them together—the whole structure thus acting in the manner of the mitral valve of the human heart. It is probable that the flexible margins of the valves are also driven together by the pressure of water. The diagram exhibited (Plate VII. fig. 7) may make this clearer.

I am inclined to think, then, that a suction of this kind is used to swiftly draw the ova forward into the external gill-plate. Direct observation on this point is well nigh impossible owing to the necessity of disturbing the animal or even partly opening the shell in order to ascertain whether or no ova are in transit. The fact that violent suction does take place in the case of the *Glochidia* is beyond doubt; the exact mode of causing the suction is, for our present purpose, of less importance.

The question naturally occurs, why do not the ova find their way into the internal as well as the external gill? The reason is, I think, twofold. In the first place, the space between the lamellæ of the external gill is considerably greater than that between the lamellæ of the internal gill. In the second place, as I have ascertained by careful dissection of many individuals, the inner lamella of each external gill-plate extends further towards the dorsal surface than the outer lamella of each internal gill-plate, and stretches over towards the middle line so as to greatly diminish or even totally close the aperture leading into the space within the internal gill. In some cases the inner lamellæ of the external gill-plates of the right and left sides actually come in contact with one another in the median line posteriorly [1].

The diagram (Plate VII. fig. 8), which is a modification of Lankester's diagram (Encycl. Brit. 9th ed., Art. "Mollusca," fig. 135 D, p. 690), will make these relations clearer.

II. *The Attachment of the* Glochidia *to the Parent Gill-plate.*

It is well known that the epithelium of the external gill-plate secretes a nutritive mucus in which the young are imbedded and thus retained within the gill. This mode of attachment is, however, not permanent; for if, as is often the case, the *Glochidia* are retained for a long time after they have attained maturity, a large number escape from their egg-capsules, and the so-called "byssus," becoming entangled in the gill-filaments and bars of concrescence, serves to secure them until they are forcibly expelled from the parent. I have found that the number of *Glochidia* in any given parent which have escaped from their egg-capsules varies with the period during which they have been retained since the attainment of pre-parasitic maturity. It thus appears that as the nutritive mucus is used up, and its power of retaining the *Glochidia* within the gill is therefore

[1] This, of course, applies only to the post-pedal portion of the gill-plates. In the region of the foot the "labour contractions" close the space between the lamellæ of the internal gill, as stated by von Baer.

diminished, a secondary mode of attachment becomes of all-importance and is furnished no longer by the parent but by the adult members of the Glochidian family, in whose neighbourhood the mucus has been chiefly absorbed and who alone are provided with fully developed byssus-filaments. This phenomenon is the more interesting as furnishing yet another case of prolonged attachment to the parent of the young of freshwater animals (*vide* Sollas, "On the Origin of Freshwater Faunas," Scientific Transactions of the Royal Dublin Society, vol. iv. ser. ii., 1886).

III. *Emission of* Glochidia.

The female *Anodon* is usually stated to retain the *Glochidia* within the external gill-plates until fish are in the neighbourhood. This is certainly not always the case, for *Glochidia* were frequently emitted in large masses and long cords after I had gently stirred the water in which the Anodons were lying. Schierholz ("Entwick. der Unioniden," Denk. d. kais. Akad. d. Wiss. 1889, lv. pp. 183–214) states that nodular ejection of *Glochidia* is abnormal, due to imperfect aeration of the water and necessity of using the outer gill for respiratory purposes, that normally ejection takes place singly with the egg-capsules (cast off), which float off and leave the larvæ in masses on the bottom. I fear I am unable to endorse this account *in toto*; nodular ejection undoubtedly is abnormal, but ejection in cords I have always found to occur in healthy individuals supplied with well aerated water, and on one occasion have seen it occur in an undisturbed *Anodon* in its native water. It would seem that any disturbance of the water irrespective of fish, if not too violent, provokes emission of the *Glochidia* in a perfectly normal manner.

It is important to notice that the parent is able *to draw back within the shell the long slimy masses of* Glochidia even after they have been ejected a distance of 2 or 3 inches. The importance of this fact I have already mentioned in dealing with the transit of ova. I observed the *Glochidia* on several occasions, in both *Anodon* and *Unio*, thus forcibly made "to enter a second time into their mother's womb."

IV. *Alleged Swimming of* Glochidia.

The belief that *Glochidia* can swim by clapping their valves together "like *Pecten* or *Lima*" appears to be very general in this country, in spite of frequent denials (*e. g.* Schierholz, *loc. cit.*). The extent of the swimming-powers consists solely in "swimming to the bottom"; in other words, *Glochidia cannot swim.* A *Glochidium* normally lies at the bottom of the water on its dorsal surface, the ventral surface being upwards and the "byssus" (so-called) streaming up into the water above. In this position the *Glochidium* lies powerless to move in any direction, and here, too, it dies unless a convenient "host" is in some way brought in contact with its "byssus." If the water is disturbed the *Glochidia* are carried about by currents, but soon fall to the bottom again and are entirely unable to make headway in any direction, even when they are thus temporarily suspended in mid-water.

The *Glochidia* are evidently peculiarly sensitive to the odour (?) of fish. The tail of a recently killed Stickleback thrust into a watch-glass containing *Glochidia* throws them all into the wildest agitation for a few seconds ; the valves are violently closed and again opened with astonishing rapidity for 15–25 seconds, and then the animals appear exhausted and lie placid with widely gaping shells—unless they chance to have closed upon any object in the water (*e. g.* another *Glochidium*), in which case the valves remain firmly closed. I found this excitement very useful in procuring *Glochidia* widely open. Flooding with hot corrosive sublimate kills them instantly and the shells remain apart.

V. *Relation of* Glochidium-*shell to Shell of Adult.*

So long ago as 1825 it was pointed out by Pfeiffer (Naturg. deutscher Land- und Süsswasser-Mollusken, Weimar, 1825), and more recently by Kobelt and Heynemann, that the shell of the *Glochidium* sits like a saddle over the dorsal and lateral surfaces of the shell of the young *Anodon* or may be seen in uninjured specimens close to the hinge-line. It has not, however, been noticed, so far as I can ascertain, that this temporary situation of the *Glochidium*-shell has a permanent effect upon the shape of the adult shell. This effect will be at once apparent on referring to Plate VII. figs. 2–5.

About 101 days after first attachment to the host and 25–30 days after quitting the host, the shell-teeth of the *Glochidium*-shell project ventrally towards the median line, and as a consequence impinge upon the ventral border of the at present soft shell of the adult at a point about halfway along its length, the result being that at this point the permanent shell is prevented from growing so fast as elsewhere. The permanent shell at this stage, therefore, has its otherwise symmetrical curve sharply interrupted by an irregular notch pointing towards the dorsal surface (*vide* figs. 2 & 3). *This notch, in the vast majority of cases, persists through life* and causes a slight dorsal turn of the curves marking the lines of growth at a point roughly halfway along their length, but, as a rule, slightly nearer the posterior border of the shell. In each successive line of the growth the notch becomes of greater antero-posterior and less dorso-ventral extent, thus tending to become less evident and to disappear. The notch can therefore be seen most easily near the hinge-line (*i. e.* on the first lines of growth) in those shells which have escaped corrosion. In 15 species of *Unio* belonging to the Collection of Admiral Sir John Harvey in the University Museum, Oxford, this notch is evident and undoubtedly caused in the way above described ; it is perhaps present in 2 others (*U. cylindricus* and *U. triangularis*), and is quite clear also in 6 species of *Anodon*. The figures given by Chenu in his 'Manuel de Conchyliologie,' and by M. Henri Drouet, "Unionidæ du Bassin du Rhône," Mém. de l'Acad. des Sci. Arts et Belles-Lettres de Dijon, (4) i. 1888–89, pp. 27–113, pls. i.–iii., show the notch almost without exception. I do not rely strongly on these figures for this particular, as many irregularities of curvature occur, owing to individual injury at some period of life, and it is necessary to examine each specimen personally before deciding whether the notch figured can in every case be assigned to the Glochidian shell-teeth.

I may take this opportunity of corroborating Schierholz's statement (*loc. cit.*), concerning the absence of sexual distinction in the shape of the shell. It is commonly believed that the shell of the female is far more convex and of greater transverse diameter than that of the male. This is not the case: there is no point by which the shell of the female can be distinguished. On several occasions I have requested persons professing to be able to distinguish the sexes in this way to select a few males from my stock: out of 19 thus selected on various occasions only one proved on dissection to be of the male sex, whereas on one occasion a small *U. pictorum*, which was selected as "undoubtedly female" turned out to be a male! I have invariably found males very rare and was long unable to procure one; for instance, of 50 Anodons dredged from a small pond in Norfolk, and averaging between 3 and 4 inches in length, only two were males; the same was true for Anodons and Unios collected out of the canal at Oxford, though here the proportion of males was slightly higher. So rare in fact were the males and so small were the majority of them, that I was tempted to believe that *Anodon* is hermaphrodite, functioning in early life as male and later as female; I made several experiments to investigate this point, but obtained no evidence on either side. Stress of work has prevented me from making any further search in this direction.

VI. *The Cilia on the Foot of Young* Anodon.

While observing young Anodons of 3–6 weeks old (dating from the end of parasitic life), I was struck by the peculiar movements of the cilia covering the foot. While the animal is in motion the foot is first protruded somewhat slowly until it stretches a considerable distance in front of the anterior margin of the shell, the cilia all the while moving with great rapidity and appearing to "feel the way." The foot having been protruded to its utmost extent, the shell is drawn forward by a rapid muscular contraction. As soon as this contraction commences, the cilia suddenly cease moving and stand out from the surface like the bristles of a brush absolutely motionless and rigid. This condition is maintained until the foot again commences to glide forward. I can offer no suggestion as to the meaning or cause of this apparent rigidity other than that the appearances are as though the pressure within the epithelial cells becomes so great that the cilia cannot assume any other position than one perpendicular to the surface, and forming a continuation of the long axis of the cells on which they are severally carried.