

XXXII.—A Specimen of *Helix pomatia* with Paired Male Organs.

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THE specimen of *Helix pomatia* which forms the subject of this communication was found among the class material * in the Zoological Department of the University of Edinburgh. It presents so unique and interesting an abnormality that it is worthy of description in some detail.

The animal was approximately full-grown and possessed a normal dextral shell. On dissection it was observed that, in addition to the usual set of reproductive organs present on the right side, there were, on the left side, certain other structures undoubtedly homologous with the normal accessory male organs. The roof of the mantle chamber was removed,† the body wall cut through by means of an incision in the mid-dorsal line, the flaps pinned out, the alimentary canal and the reproductive organs carefully uncoiled, and the latter laid out to the right side of the animal. The alimentary canal presented no unusual features, and it has been entirely removed. The remaining structures are shown in fig. 2.

The normal reproductive apparatus may be first briefly described. The ovotestis (O.T.) or hermaphrodite gland,‡ which was embedded in the liver, has been dissected out so as to show its ducts which lead into the sinuous hermaphrodite duct (H.D.). This opens into the common duct, but just before doing so it bears two small closely apposed blind diverticula, about 3 mm. long—the vesiculæ seminales—only one of which (V.S.) is shown in the figure; the other, which is slightly smaller, lies hidden beneath. At the point of junction of the hermaphrodite and common ducts there is a large, somewhat tongue-shaped, albumen gland (ALB.G.).§

The common duct is imperfectly divided by two internal longitudinal

* Collected in the neighbourhood of Würzburg.

† The heart, the pulmonary vessels, and the nephridium were quite normal.

‡ The ovotestis was removed and sectioned, and though the histological details were defective it was obviously quite normal in structure. Various stages in development of spermatozoa and ova were seen, including ripe spermatozoa and a considerable number of large oocytes 11 mm. in diameter.

§ This is shown in the figure, as it was pinned out, in an extended form; in its natural condition, as it lies in position in the animal, it is much more curved.

folds into a larger female portion (C.D.F.), the walls of which are strongly plicated, and a smaller male portion (C.D.M.) which is covered by glandular prostatic tissue slightly folded or lobulated. After a course of about 50 mm. the two portions of the common duct become completely separated as the oviduct and the vas deferens.

The oviduct (OVD.) runs forward for about 10 or 12 mm. and then merges into the wider vagina (V.), which leads into the common genital atrium (ATR.). The vagina bears a large clavate dart sac (D.S.) and two tufts of digitiform mucous glands (MUC.G.). In the figure these glands are to a large extent hidden by the dart sac; they are not quite as large as in many other snails of the same collection examined, but, with this exception, the reproductive organs are fully grown. Opening into the female genital canal near the point of junction of oviduct and vagina is the spermatheca or receptaculum seminis (R.S.), which bears a bulbous dilatation (R.S.B.) at its inner end. In the natural position of the parts the tubular portion of the spermatheca lies alongside the common duct and is bound to it by connective tissue.

The vas deferens (V.D.) has at first a somewhat sinuous course; it then loops round the retracted posterior tentacle (TENT.P.R.), runs parallel to and practically along the whole length of the penis (P.), and bends round so as to enter the base of the latter, opening into it upon a knob-like muscular papilla which acts as a protrusible copulatory organ. This organ is enclosed in a thick muscular sheath, the inner surface of which, in the proximal part of the penis, has a rugose appearance. About the middle of the length of the penis, the sheath bears a muscular introversible tube. The part of the sheath distal to this is slightly thinner than the proximal part, but is also traversed by longitudinal folds. This inner sheath is surrounded by a much thinner outer one. The fibres of the thin, but strong, retractor penis muscle (M.RETR.P.) are chiefly inserted into the outer sheath close to the point of entry of the vas deferens into the penis. This muscle serves to retract the copulatory organ and also the penis as a whole. It arises from the posterior region of the mantle slightly to the left of the middle line. In the figure the greater part of the muscle is seen attached to the penis; the remaining short portion is shown at M.RETR.P'. Just before entering the penis the vas deferens bears a long slender diverticulum, the flagellum (FL.), which secretes the elongate spermatophore.

The genital atrium (ATR.) is a short wide tube opening to the exterior by an aperture which, in non-excited specimens, is slit-like and about 2.5 mm. long. This common genital pore is situated just behind and ventral to the posterior or ocular tentacle.

Commencing at a point slightly median or dorsal to the pulmonary aperture, there is a distinct but shallow groove in the skin which leads obliquely forwards and downwards, ending just below the ventral lip of the genital pore.

On looking at the left side of the specimen just behind the posterior tentacle it is at once obvious that certain parts of the genital apparatus are repeated; indeed, there is no difficulty in recognising a penis and its retractor muscle, a vas deferens and a flagellum. These may be first described as they are seen in the general dissection, shown in fig. 2.

The additional penis (P.S.) is as well developed as the normal one, and opens to the exterior by means of a slit-like aperture as large as the normal genital pore on the right side. The retractor muscle (M.RETR.P.S.) is inserted in the usual position at the inner end of the penis; only a short portion is shown at that point in the figure, the remainder (M.RETR.P.S'.) is seen attached to the body wall, its origin being close to that of the retractor of the right penis. Enclosing the bases of these retractors there is a thin connective tissue sheath (SH.), folded at the middle so as to divide the enclosed area into two compartments, one for each retractor. When the flaps of the body wall are replaced in their normal position the origins of the retractor muscles are seen to be a little to the left of the mid-dorsal line, and so placed that the muscles would gradually diverge from one another to their respective penes. The two penes are symmetrically placed with regard to the median plane of the head, and, as already stated, are equally developed.

The extra vas deferens (V.D.S.) is seen in connection with the inner end of the penis, and may be followed along the whole length of that organ until it disappears beneath one of the large retractor muscles of the anterior end; this muscle (M.RETR.) is inserted into the body wall by means of two diverging portions which enclose the distal part of the penis and the proximal part of the vas deferens.

Arising from the vas deferens near the middle of its length is a well-developed flagellum (F.L.S.), the terminal portion of which was accidentally severed and lost during the initial stages of the dissection in class, before the abnormality had been observed. At the point of origin of the flagellum, which is situated somewhat further from the penis than in the case of the normal flagellum, there is a sudden increase in the diameter of the vas deferens, its distal part being about twice as wide as the proximal part. The ocular tentacle (TENT.P.L.) and its retractor muscle pass to the outer side of the penis and neighbouring portion of the vas deferens, as is the case on the right side.

The penial nerve on both sides leaves the cerebral ganglion (C.G.) laterally, anterior to the root of the ocular nerve, and passes into the interval between the penis and vas deferens, being supported by a connective tissue sheet which partially binds these two structures together. The nerve divides into three or four branches, which pass into the penis near the middle of its length. The nerve to the right penis really originates in the pedal ganglion, and traverses the cerebro-pedal connective and a portion of the cerebral ganglion before becoming free as the penial nerve (N.P.), seen in the figure. The actual origin of the left penial nerve (N.P.S.) could not be determined by dissection, so the nerve, the cerebral ganglion, and the cerebro-pedal and cerebro-pleural connectives were excised and sectioned. The preservation of the tissues enclosed within the sheath of the ganglion was, however, so defective that the complete course of the penial nerve fibres could not be followed. The left penial and ocular nerves, on being traced back into the cerebral ganglion, are seen to penetrate the sheath of the ganglion close together and then unite, but soon after this the tissue is so badly preserved that the two bundles of fibres are no longer distinguishable. Whether the penial nerve fibres arise from the ocular nerve, as is *apparently* the case, or whether they actually arise from the pedal ganglion, is unfortunately impossible to decide. In the majority of normal specimens there is, on the left side, a nerve given off from the cerebral ganglion just anterior to the ocular nerve, and reaching the body wall immediately behind the ocular tentacle—that is, in the region of the supplementary penis in the abnormal specimen. It is possible that in the abnormal specimen this nerve has been elevated along with the up-growth of the supernumerary organs.

Dissection of the tissues around the base of the extra penis and vas deferens permits their further course to be traced (see fig. 3). The penis passes through the body wall and opens to the exterior by a slit-like pore (G.O.S.), but probably the portion of the tube immediately internal to the aperture is to be regarded as atrium (see below, pp. 316, 317). The vas deferens (V.D.S.), followed from the inner end of the penis, courses alongside the penis until it reaches the body wall, along which it runs obliquely dorsally for a short distance; it then comes into close association with the skin, so close, indeed, that it was at first believed that the tube actually perforated the skin and opened externally by a minute pore. Further examination, checked by sections of this region, proves that there is no actual opening to the exterior; the vas deferens ends blindly in the sub-epidermal tissue and is bound to the epidermis by a short cord of connective tissue (CON.T.).

On reference to fig. 1 it is seen that the left genital aperture (G.O.S.) is

in the same relative position as the normal one—that is, ventral and slightly posterior to the ocular tentacle (TENT.P.L.). The blind end of the vas deferens is situated immediately below the papilliform area of the skin indicated by the + in fig. 1—that is, about 2.5 mm. posterior and slightly dorsal to the external aperture of the penis. There is also on the left side a groove (EP.GR.)* in the skin, the course of which corresponds to that of the groove of the right side, already described (p. 314). The blind end of the vas deferens lies very close to the dorsal margin of this groove, just before the latter bends ventrally on approaching the genital orifice.

Examination of the internal structure of these extra organs shows that they are quite normally and perfectly developed. The flagellum shows, in section, the usual longitudinal curved or scroll-like internal fold, exactly as in the normal organ, where its function is presumably to aid in moulding the spermatophore. The wall of the flagellum consists of an internal granular epithelium surrounded by a thick layer of longitudinal and circular muscle fibres. The vas deferens is lined by a folded epithelium, outside which is a thin sheath of muscular and connective tissue.

The penis has the usual structure (see p. 313); it possesses a thin outer sheath (fig. 3, P.SH.O.), which surrounds the much stouter inner sheath (P.SH.I.), the latter having about the middle of its length a muscular tubular introvert (INTR.). Enclosed by the proximal part of this inner sheath, the inner surface of which presents the usual rugose appearance, is a muscular copulatory organ (C.O.), on which the vas deferens opens. This organ is fully as large (3 mm. long) as that of the right side of the same specimen and of other specimens examined. In the distal part of the inner sheath there are also longitudinal folds exactly as in the normal organ (see fig. 4). One of these folds ends in a somewhat tongue-like depressed papilla (PA.), about a millimetre wide, the distal margin of which is raised well above the general surface of the sheath. In all the normal specimens which I have examined, a papilla similar in form and size is also present, and lies close to the point at which the penis enters the atrium. Its position and structure suggest that it forms a rudimentary valvular arrangement serving to partially or completely close the penial aperture, especially when the lips of the latter are in the contracted condition. But whatever its function may be, this papilla apparently marks the distal end of the penis; beyond lies the atrium. In the supernumerary penis this papilla† is about 2.5 mm.

* This groove is present in normal specimens on both right and left sides.

† It is interesting to note that the papilla is situated upon the internal wall, i.e. the wall adjacent to the middle line, in both the normal and supernumerary penes, another instance of their symmetrical relations.

from the external aperture, and probably this last portion of the tube ought therefore to be regarded as atrium. This view is supported by the character of the external opening, which agrees in every respect with that of the pore of the normal genital atrium. This left atrium, the inner surface of which is traversed by shallow transverse folds, is rather shorter than the right (normal) atrium, and its walls are slightly thinner.

There is no trace of connection between these supernumerary organs and the ovotestis or the genital ducts of the right side.

The duplication of genital organs in this specimen of *Helix* presents features of interest from three aspects, (1) on account of its rarity, (2) because the form of the supernumerary organs has a significance in relation to the phylogeny of the genital ducts in *Helix*, and (3) in regard to certain points in the ontogeny of the male organs of *Helix*.

This abnormality is not in the same category as those moderately numerous instances in which organs, normally situated in the middle line, have been found in a state of more or less complete division—for example, the penis of mammals. The penis of *Helix* is never median, and there is no trace of any connection between the two penes of this abnormal specimen to suggest that they have been produced by division of a single penis rudiment. In the duplication of the penis and its associated structures this snail presents an example of lateral homœosis which is extremely rare in the Mollusca; in fact the only case,* known to me, at all comparable to this one is Appellöf's (1893, p. 14) record of a specimen of *Eledone cirrhosa* (= *Moschites cirrosa*), in which not only was the third right arm hectocotylised, as usual, but the third left one also. There were on the right arm 57 suckers and on the left 66; both arms presented the normal plan of hectocotylisation and were practically equally developed. There was no corresponding duplication of the internal sexual organs. This specimen therefore presents interesting parallels to the abnormal *Helix* in that (1) the duplicated sperm-transferring organ and the normal one are symmetrically placed with regard to the median plane and are practically equally developed, and (2) there is no modification of the normal sexual organs.

Repetition of the penis on the right side has been twice recorded in *Helix pomatia*, but reference to these cases shows that they are essentially different to the one under consideration. Pegot (1900) described a specimen with three penes, one in its usual position and communicating with the genital atrium by a large canal, the two others, similar in structure but

* A Pteropod with paired penes has recently been described by Meisenheimer; see Addendum, p. 327.

smaller, situated in the vagina. The vas deferens was single in its proximal part but bifurcated distally, each of the two portions passing to one of the supernumerary penes. The vas deferens of the normal penis was represented by a small bud. Each of the penes had a flagellum and a retractor muscle. Paravicini (1898) had previously described a somewhat similar case in which three penes were present and the vas deferens was branched, but only one of the penes was functional. Both these are examples of meristic variation, possibly produced by division of the penis rudiment at an early period of its development, and they differ essentially from the case of the *Helix* with paired penes.

Before passing to the consideration of the significance of the abnormality in regard to the origin and relations of the genital ducts in Pulmonata, it will be of advantage to briefly review the comparative anatomy of the genital ducts of a few Gastropods.

In the Pectinibranchiata (Monotocardia) the genital duct of the female opens into the pallial chamber near the anus. In many of the Taenioglossa and some of the Rachiglossa and Heteropoda the aperture of the genital duct in the male is also situated in the pallial chamber, and in many of the less specialised forms of these groups there is, in those males which possess a penis, a ciliated seminal groove which extends from the genital pore forwards along the right side of the body to the base of the penis, which organ is usually non-introversible and is situated on the head or "neck." The spermatozoa are conducted by this groove from the genital pore to the base of the penis, where they are led into a deep groove or tube which traverses the penis to its tip.

A comparable condition is found in many Tectibranchs, in which the aperture of the hermaphrodite duct is on the right side, within but near the opening of the mantle cavity. From this aperture the fertilised ova escape directly to the exterior, but the spermatozoa pass into a ciliated groove which runs along the right side of the body and head to the penis, which is introversible (except in *Actaeon*).

Within the Pulmonata there are forms which exhibit stages of specialisation of the genital ducts connecting the condition just described with that seen in *Helix*. The most interesting of these stages in relation to the subject of the present paper is that presented by the primitive Auriculid, *Pythia scarabeus*, L., described by Plate (1897) (see text-figure A). In this animal the hermaphrodite- or common-duct opens at the genital pore (G.O.) situated just outside the mantle chamber but near the pulmonary aperture; and from this point a ciliated groove (CIL.GR.) runs forwards on the right side of the body to the aperture of the vas deferens. Here the

spermatozoa are received and conducted by means of the vas deferens (V.D.) to the inner end of the muscular eversible tubular penis (P.), whose external aperture is only a short distance anterior to that of the vas deferens, and just behind the right lip. In the retracted condition the penis, which is

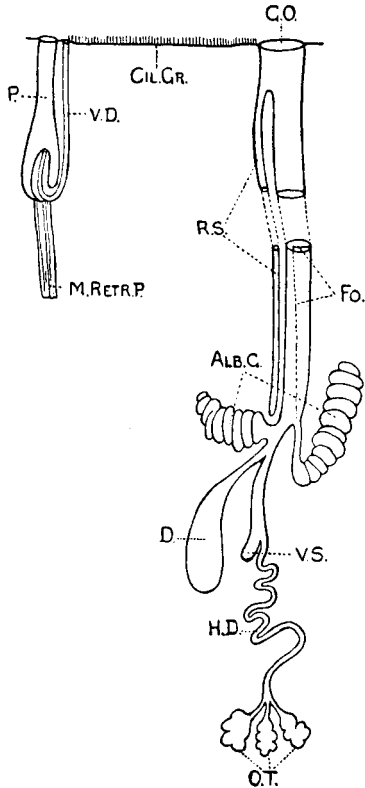


FIG. A.

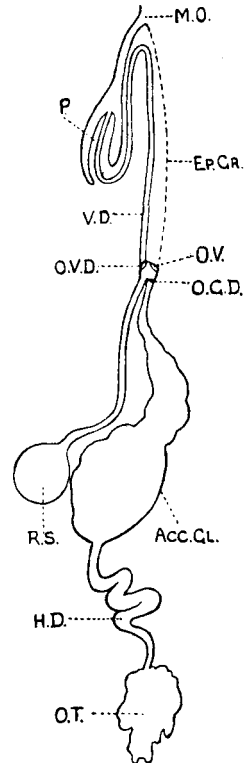


FIG. B.

FIG. A.—Genital organs of *Pythia scarabeus*, L. $\times 5$. After Plate (1897, p. 134, fig. 1).

FIG. B.—Genital organs of *Auricula myosotis*, Draparnaud. $\times 16$. After Pelseneer (1893. Plate xxii fig. 199).

Acc.GL., accessory glands on common duct; ALB.G., albumen glands; CIL.GR., ciliated groove on the surface of the right side of the body; D., diverticulum, probably a mucous gland; EP.GR., edge of lateral groove in the skin; Fo., fold partially dividing common duct into male and female portions; G.O., opening of genital (common) duct to the exterior; H.D., hermaphrodite duct; M.O., male orifice; M.RETR.P., retractor muscle of penis; O.T., ovotestis; O.V., opening of vagina to exterior; O.V.D., point of origin of vas deferens; P., penis; R.S., receptaculum seminis; V.D., vas deferens; V.S., vesicula seminalis.

provided with a retractor muscle, and vas deferens together form a U-shaped loop open at both ends to the exterior.

A further stage is represented by another member of the family

Auriculidae, namely, *Auricula myosotis*, Draparnaud (see text-figure B). The primitive (hermaphrodite) genital opening (O.V.) is just outside the mantle chamber and serves only for the exit of the ova. From this pore there is a lateral groove (Ep.Gr.) running forward to the penis; but lying in the sub-epidermal tissues, just below the groove, there is a ciliated tubular vas deferens (V.D.) which receives the spermatozoa (at O.V.D.) as they issue from the hermaphrodite duct, and conducts them to the large muscular eversible tubular penis (P.). Thus, by conversion of the ciliated seminal groove into a closed tube, the hermaphrodite aperture has been converted into a functionally female aperture, and the male opening (M.O.) has been secondarily moved forwards from its primitive position so that male and female pores are some distance apart.

In the rest of the Pulmonata the hermaphrodite duct divides into male and female ducts. In the Basommatophora the female aperture retains a position similar to that of the primitive genital opening of *Auricula*, so that the male and female pores are separate.* In the Stylommatophora the female pore has undergone secondary forward movement and is closely associated with the male pore, the two openings being situated in a common genital atrium.†

The penis and vas deferens of the abnormal specimen of *Helix* are interesting as showing, as it were, two different phylogenetic stages—namely, the *Pythia*-stage on the left and the normal condition for *Helix* on the right. The supplementary vas deferens and the retracted penis form a U-shaped loop, both ends of which are in contact with the epidermis, as in *Pythia*; in fact, they so closely resemble the corresponding structures figured by Plate in *Pythia* that these organs may be described as having identical relations in the two forms, except that in the supplementary organs of *Helix* the vas deferens has no pore at its epidermal end, and that it bears a blind outgrowth—the flagellum—which is not present in *Pythia*. While it is impossible to explain the cause of the development of the extra organs in this specimen of *Helix*, it would seem that, assuming that like causes produce like effects, whatever cause (in the ontogeny) has brought about their formation must have been closely similar to, if not identical with, that which has been responsible for the development of the corre-

* Except in the genus *Amphibola* and the family Siphonariidae where the male and female ducts open into a common genital atrium.

† Except in the families Oncidiidae and Vaginulidae and the genus *Atopos*, where a separation of the genital pores has been brought about by detorsion, which has caused the anus and the female opening to move backwards, so that the latter now lies, in *Vaginula* about the middle of the right side and in *Oncidiella* and *Atopos* posteriorly near the anus. These are to be regarded as specialised rather than as primitive forms (Pelseneer, 1901, p. 27).

sponding normal organs, since the results are so similar in the two cases. But on the left side the penis and its annexes have been free to develop without the disturbing influences of the vagina, oviduct, and their accessory structures, which, on the right side, have been secondarily moved forwards, in phylogeny, into the sphere of the male copulatory organ. Under these circumstances the supernumerary organs would be more likely to assume a condition more closely resembling that which they would present in the ancestral form in which the male and female genital apertures were some distance apart, and in which, consequently, the male organs developed free from the disturbing elements introduced in later forms by the shifting forwards of the female aperture and its associated structures.

The form of these extra organs (the vas deferens having a close association at one end with the epidermis) which it is suggested, by the above argument, might also be assumed by the corresponding normal organs if they were likewise free to develop independently of the female structures, supports the already well-established view that the present condition of the genital ducts in *Helix* and other Stylommatophora has been derived from a condition existing in the ancestral form in which the vas deferens and penis were connected with the primitive genital aperture by means of a lateral groove, such as is still found in *Pythia*.

The supernumerary genital organs have also a significance in relation to the ontogeny of the male genital apparatus. It is very difficult to reach a definite conclusion concerning the mode of development of the male organs of the Pulmonata from a study of the published accounts; evidently the conditions are complicated and vary considerably in different genera or even species.

Eisig (1869), working on *Limnaea auricularis*, concluded that the genital apparatus is formed in three separate sections which afterwards become connected together: (1) the ovotestis and the hermaphrodite duct; (2) the oviduct, its glands and the prostatic part of the vas deferens; and (3) the penis and the lower (or distal) part of the vas deferens. The penis arises as a solid ingrowth from the epidermis, and the vas deferens is formed as a diverticulum from the free inner pole of the penis. According to Rouzaud (1885) the whole genital apparatus of Pulmonates is the product of a single cellular bud on the inner side of the wall of the neck region at a point which later becomes the site of the common genital orifice in the Helicidae and of the female pore in the Limnaeidae. The penis arises as a secondary bud, which in *Helix* is situated upon the primitive bud, but in *Limnaea* upon the wall of the neck region a short distance from the primitive bud. Rouzaud attributes the separation of the penis rudiment in

Limnaea to its passive migration, but Klotz (1889) denies that any such migration takes place.

Von Jhering and Brock assign to the penis a quite different mode of origin. The former (1875) states that the parts of the genital apparatus in *Helix pomatia* and *H. nemoralis* are not separately developed (differing from Eisig's results on *Limnaea*), but arise as differentiations of a mesodermal rudiment. Brock (1886) describes the first appearance of the penis in *Agriolimax agrestis* (L.), not as a separate structure but as a swelling, afterwards a blind sac, on the purely mesodermal primitive genital duct, which latter is not at first in connection either with the ovotestis or the exterior. He also found that the vas deferens develops as an outgrowth from the inner end of the penis, and its free end unites with and opens into the common duct. The genital duct establishes communication with the exterior by means of the genital atrium opening outwards; there is, according to Brock, no trace of invagination of the skin to form either the penis or the atrium. For several reasons it is unfortunate that Brock's careful work was carried out on *Agriolimax*, which, however convenient it may be from the point of view of microtome technique, is so modified in various directions that it could scarcely be expected that the ontogeny of the genital organs would remain unaffected.* Especially from the point of view of the development of the penis, the particular species (*agrestis*) investigated was very ill adapted for the purpose, as Simroth (1887, pp. 646-647) remarked, because of the indefinite form and structure of that organ in the adult.

Subsequent to the publication of Brock's results Klotz (1889) investigated the development of the sexual organs in *Limnaea ovata* and affirms that the penis arises independently at the hinder margin of the right tentacle, as an ectodermic invagination, thus closely agreeing with Eisig (who, however, described the ingrowth as solid).

A consideration of the above accounts seems to indicate that in *Limnaea* the penis is formed directly from the epidermis either as a solid or a hollow ingrowth, but in *Helix* and *Agriolimax* its development is bound up with that of the genital atrium and the neighbouring parts of the female duct, so that the penis appears to arise from the atrium or from the oviduct, more probably from the former which is relatively long in the earlier stages. The vas deferens, according to Eisig and Brock, arises as an outgrowth from the inner end of the penis, but according to Rouzaud, Simroth and

* See also the observations of Simroth and Babor below (p. 324), which show that the penis in some Limacidae, e.g. *Agriolimax laevis* and *Limax maximus*, is frequently delayed in development.

Klotz, it seems to be produced by a process of splitting from the penis rudiment.

The condition of the supernumerary penis and vas deferens in the abnormal *Helix* indicates that the penis arises from the epidermis as a solid or hollow ingrowth which has been secondarily carried inwards by the invaginating atrium. Its development would be difficult to explain if the penis were differentiated from, and dependent for its origin upon, a primitive mesodermal sexual duct, as held by Brock, for there is no trace whatever of any such duct on the left side of this *Helix*. The supernumerary vas deferens probably arose in the normal way as a diverticulum from the inner end of the penis.

The origin of the penis from the epidermis is in agreement with its phylogenetic history, which points to its appearance as an elevated epidermal organ, at first non-introversible and grooved, but later introversible and tubular, and also better accords with other observations upon abnormalities in the Pulmonata than would the origin of the penis from any part of the female or common sexual ducts. Biatrix (1886) records a specimen of *Helix pomatia* in which the genital apparatus is divided into three quite separate portions: (1) the ovotestis and albumen gland, (2) the dart sac and mucous glands, and (3) the penis and its annexes. The penis and flagellum are quite normal,* but the vas deferens is represented by a short cæcum 4 mm. in length. The atrium appears to be a single swollen prolongation of the penis sheath. Mangelot (1883) describes a specimen of *Helix pomatia* in which the external genital aperture is closed, in consequence of which the atrium and vagina are much dilated by imprisoned fluid contents. The atrium is somewhat oval in shape, and the vagina and penis open into it at opposite ends of its longer axis. The penis has the usual form and size, but the vas deferens is a slender cæcal appendage 6 mm. long, arising from the inner end of the penis. The vas deferens, which bears a flagellum of approximately normal size, has no connection whatever with the common duct, and the only connection between the penis and the vagina is the purely secondary one afforded by the atrium. Both these cases indicate that the penis arises quite independently of the common duct or the vagina, and that its development is, in *Helix*, closely associated with that of the atrium.

That the penis "Anlage" in some cases fails to develop seems to be indicated by the recorded examples of absence of the male sexual organs in the Pulmonata. Such a defect is more readily understood if these organs arise from a separate "Anlage" than if they form an integral part of the

* Except that the retractor muscle is represented by two strands with separate origins, but these unite so that the muscle is single at its point of insertion on the penis.

genital duct from its earliest appearance, for in many cases the rest of the genital apparatus is quite normal. Von Jhering (1885, p. 207) remarks upon the frequent absence of the male apparatus in specimens of *Limax*, and Simroth (1883–1885, p. 223) describes three specimens of *Agriolimax laevis* as being purely female,* though the one figured (Taf. 9, fig. 22H) shows a small papilliform rudiment of the penis but no trace of vas deferens.† Simroth (1890, pp. 21, 22) also figures two examples of *Vitrina lamarchi* which show different phases of reduction of the male apparatus. In one case (Taf. 2, fig. 11) the penis is quite rudimentary in the form of a small nodule on the wall of the atrium; it has no retractor muscle and no connection with the sperm-duct. The figure (Taf. 2, fig. 10) of another example shows a penis only slightly larger, without a retractor muscle, but the vas deferens opens into it. A similar condition to this last is also figured by Simroth (1891, p. 228, and Taf. 9, fig. 13) in a specimen of *Plutonia atlantica*. Collinge records specimens of *Helix aspersa* (1893, p. 237), *Arion intermedius* (1893, p. 238), and *A. hortensis* (1904, p. 15), in which the male organs are wanting; in the two latter the common duct consisted of oviduct only. It is possible that in some of the cases above mentioned the animals concerned were young and proterogynously hermaphrodite, and that although the male organs had not yet made their appearance, they would have done so later. Babor's observations (1894) show that this is probably the case in *Agriolimax laevis*. All the young examples (not more than 2 cm. long) of this slug which he examined (1894, p. 56) possessed only female genitalia, and the gonad contained only ova or ova along with a few spermatogonia. After further growth the penis and its annexes were formed upon the atrium, and so the hermaphrodite organs became complete. In two large specimens, 4 cm. long, the penis was hypertrophied and the gonad was purely male. *Limax maximus* is also proterogynous, but even young animals have a rudimentary penis although the gonad at this time contains ova only (*loc. cit.*, p. 57). When they have reached their definitive size, the animals are hermaphrodite or male, the gonad swarms with spermatozoa, and the penis is large. Babor (p. 58) concludes that in most Limacidae there is a cycle of development, the animal being at first unisexual (in the cases above cited—female), then hermaphrodite, and finally again unisexual (male, in the cases cited).

The examples described by von Jhering, Simroth, and Babor are there-

* The gonad contained ova only.

† Simroth (1892–1893) recorded a specimen of *Limax primitivus* in which a retractor muscle was attached to the wall of the atrium, but there was no penis. Babor (1894, p. 57), however, having examined this example, concludes that a penis is present.

fore probable cases of proterogynous hermaphroditism. The gonad first assumes the female condition, in many Limacidae and possibly in some other Stylommatophora,* in correlation with which the common duct consists of oviduct only, and the penis "Anlage" is, for a time at least, suppressed or remains rudimentary.

It is interesting to note that all the cases (with one exception—Collinge's *Helix aspersa*) of absence or great reduction of male organs† in the Pulmonata have been recorded in genera in which the shell is depressed, reduced, or absent—that is, in the most specialised forms. But in the figures of these specimens of *Limax*, *Agriolimax*, and *Vitrina* given by Babor and Simroth the penis rudiment is invariably found on the wall of the atrium, and there is nothing in the figures to show that the penis is formed upon the primitive genital (which becomes later—the common) duct.

Consideration of the abnormalities described in the preceding pages leads to the conclusion that the penis develops as an epidermal structure which, in the Stylommatophora, is closely associated with, and is secondarily carried inwards by, the invaginating atrium. The intimate connection of the atrium and penis is especially well seen in the supernumerary organs of the specimen of *Helix* described in the earlier part of this paper (pp. 314 to 317) and in the example recorded by Bietrix (see above, p. 323). The origin of the vas deferens as a diverticulum from the inner end of the penis, which only later fuses with and opens into the male part of the common duct, is strongly supported by the conditions seen in the specimens described by Bietrix and Mangenot (p. 323). In proterogynously hermaphrodite forms,

* The absence of penis in other Opisthobranchs seems to be attributable to a similar cause. For instance, Peck (1887-1890, p. 349) describes specimens of *Cymbulioopsis calceola* in which the gonad is in a state of female activity and there is no penis, and Pelseneer (1893, p. 24, footnote 2) gives a similar record in the case of *Clio striata*.

Giard (1888) refers to a specimen of *Paludina* infected with *Distomum militare*, probably a case of parasitic castration, in association with which the penis is reduced; he attributes to a similar cause the occasional absence of penis in specimens of *Pterotrachea*, otherwise showing male characters.

† Reduction of the female ducts has been rarely observed in the Pulmonata or in any other hermaphrodite mollusc (Pelseneer, 1895, pp. 37-38). Schuberth (1892, p. 50) has described an example of *Helix pomatia* in which the oviduct is almost completely atrophied for a distance of 36 mm. from the albumen gland, so that it is present above the prostate as a mere streak. The anterior portion of the oviduct is, however, fully developed. In one or two of the large male examples recorded by Babor the female ducts have undergone partial reduction, but were probably formerly present in a fully-developed condition.

The list of recorded abnormalities in the genital apparatus of Pulmonates, as far as they have come under my notice, may be completed by reference (1) to an anomalous specimen of *Clausilia martensi* mentioned by Babor (1900), in which the penis and vas deferens are fused so as to form a hoop, and (2) to a specimen of *Urocyclus ehlersi*, described by Simroth (1905), in which occlusion of the opening of the penis into the atrium has taken place, and the distal end of the penis has dilated to form a thin-walled spermatophore-sac.

especially in those in which the shell is depressed, reduced, or absent, the development of the penis rudiment may be postponed until the male elements in the gonad are further developed.

SUMMARY.

1. An account is given of a fully grown specimen of *Helix pomatia*, which, in addition to the normal set of reproductive organs present on the right side, possesses also on the left side a set of accessory male organs—namely, a penis and its retractor muscle, vas deferens, and flagellum. There is no trace of connection between these supernumerary organs and the ovotestis or the genital ducts of the right side.

2. The normal and supernumerary penes are equally developed and are symmetrically placed with regard to the median plane of the head.

3. The extra penis has the usual structure; it possesses a fully-developed copulatory organ and a muscular tubular introvert upon the inner sheath.

4. The extra vas deferens opens at one end into the penis and at the other terminates blindly in the sub-epidermal tissue; the blind end is bound to the epidermis by a short cord of connective tissue.

5. The extra flagellum is normal in size and in its internal structure.

6. The penial nerves on both sides have a corresponding course from the cerebral ganglion to their distribution on the penes. Owing to defective preservation it was impossible to determine whether the fibres of the extra penial nerve arise from the ocular nerve, as is apparently the case, or whether they really arise from the pedal ganglion, as do those of the normal penial nerve.

7. The penis opens into a short atrium which communicates with the exterior by a genital aperture of normal size and shape. This supernumerary genital aperture occupies a position on the left side exactly corresponding to that of the normal one on the right side. About 2·5 mm. posterior and slightly dorsal to it is the blind end of the vas deferens, which is situated close to the dorsal margin of the epidermal groove, which traverses the anterior portion of the animal.

8. In the duplication of the penis and its associated structures this snail presents an example of lateral homœosis. The only comparable cases recorded in the Mollusca are a Pteropod with paired penes (see Addendum, p. 327) and a specimen of *Moschites cirrosa*, in which not only was the third right arm hectocotylied as usual, but the third left one also.

9. The supplementary vas deferens and the retracted penis form a U-shaped loop, both ends of which are in contact with the epidermis, and

so closely resemble the corresponding structures figured by Plate in the primitive Pulmonate, *Pythia scarabeus*, that these organs may be described as having identical relations in the two forms, except that in the supplementary organs of *Helix* the vas deferens has no actual opening at its epidermal end and that it bears a flagellum which is not present in *Pythia*. It is suggested that the supplementary organs of *Helix*, having been able to develop free from the disturbing influence of the vagina, oviduct, and their accessory structures (which on the right side have been secondarily moved forwards in phylogeny), have assumed a condition closely resembling that which they would present in the ancestral form in which male and female apertures were some distance apart. The form of the extra organs (the vas deferens having a close connection at one end with the epidermis), which, it is suggested, might also be assumed by the corresponding normal organs if they were also free to develop independently of the female structures, supports the view that the present condition of the genital ducts in *Helix* and in other Stylommatophora, has been derived from a condition existing in the ancestral form in which the vas deferens and penis were connected with the primitive genital opening by means of a lateral groove, such as is still found in *Pythia*.

10. Consideration of this and of other abnormalities which have been described in the Pulmonata leads to the conclusion that the penis develops as an epidermal structure which in *Helix* and other Stylommatophora is closely associated with, and is secondarily carried inwards by, the invaginating atrium. In proterogynously hermaphrodite forms, especially in those in which the shell is depressed, reduced, or absent, the development of the penis rudiment may be postponed until the male elements in the gonad are further developed.

ADDENDUM. (August 3, 1907.)

After this paper was in type a record of another abnormality, presenting a close parallel to the one described on pp. 312 to 317, was brought to my notice by Professor Simroth. Meisenheimer (Pteropoda, in *Wiss. Ergebn. Deutsch Tiefsee-Exped. auf dem Dampfer "Valdivia," 1898-1899*, Bd. ix. pp. 290-291, text-fig. 32: Jena, 1905) describes a single example of the gymnosomatous Pteropod *Halopsyche gaudichaudi*, Souleyet, in which there are two penes symmetrically placed on the right and left sides of the buccal mass. The internal genital organs are quite normal, and the genital duct opens to the exterior on the right side of the body. From this aperture a seminal groove leads forwards to the vas deferens and penis

(cf. text-fig. A, p. 319). On the left side of the animal, in a position corresponding to that of the right penis, there is an equally well-developed penis, with a vas deferens, from which a seminal groove extends backwards some distance, and finally disappears on reaching the dorsal surface of the body. There is no connection between the supplementary penis and the normal genital organs.

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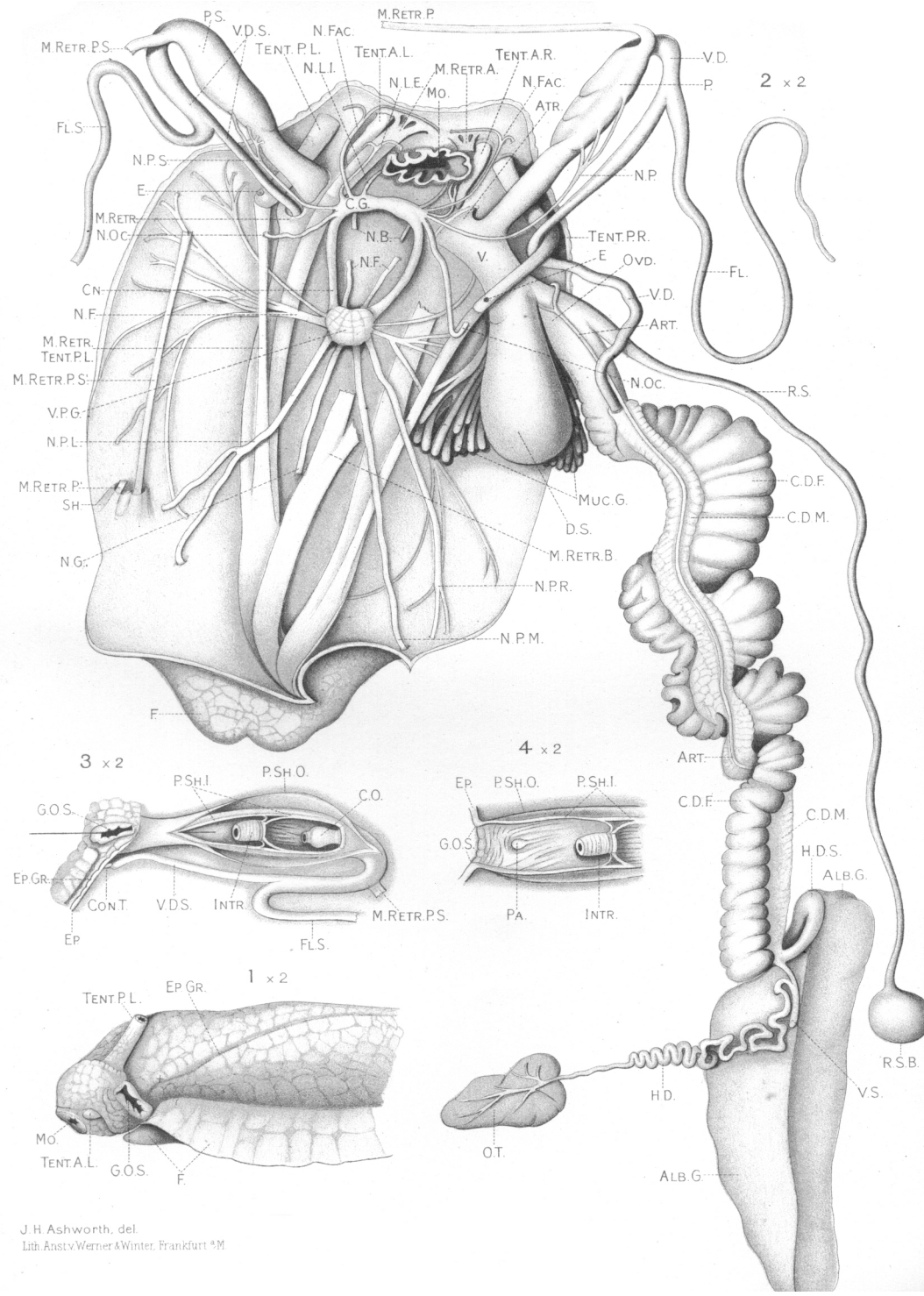
DESCRIPTION OF THE PLATE.

KEY TO THE REFERENCE LETTERS.

ALB.G.	Albumen gland.
ART.	Artery.
ATR.	Genital atrium.
C.D.F.	Common duct, female portion.
C.D.M.	Common duct, male portion, covered with prostatic tissue.
C.G.	Cerebral ganglion in its sheath.
CN.	Connectives (cerebro-pleural and cerebro-pedal) in their sheath.
C.O.	Copulatory organ.
CON.T.	Connective tissue cord connecting the blind end of the supernumerary vas deferens to the epidermis.
D.S.	Dart sac.
E.	Eye.

EP.	Epidermis.
EP.GR.	Groove in epidermis.
F.	Foot.
FL.	Flagellum.
FL.S.	Supernumerary flagellum.
G.O.S.	Supernumerary external genital opening.
H.D.	Hermaphrodite duct.
H.D.S.	Hermaphrodite duct, saccular portion.
INTR.	Muscular introvert on inner sheath of penis.
Mo.	Mouth.
M.RETR.	Retractor muscle of foot, its two portions embracing the epidermal ends of the supernumerary penis and vas deferens.
M.RETR.A.	Retractor muscles of the anterior end.
M.RETR.B.	Retractor muscle of buccal mass.
M.RETR.P. }	The two portions of the retractor muscle of the penis.
M.RETR.P' }	
M.RETR.P.S. }	The two portions of the retractor muscle of the supernumerary penis.
M.RETR.P.S.' }	
M.RETR.TENT.P.L.	Retractor muscle of left posterior tentacle.
MUC.G.	Mucous glands.
N.B.	Buccal nerves (cut short).
N.F.	Pedal nerves.
N.FAC.	Facial nerve.
N.G.	Genital nerve.
N.L.E.	External labial nerve (also supplies anterior tentacle).
N.L.I.	Internal labial nerve.
N.Oc.	Ocular nerve.
N.P.	Nerve to penis (penial nerve).
N.P.L.	Left pallial nerve.
N.P.M.	Median pallial nerve.
N.P.R.	Right pallial nerve.
N.P.S.	Nerve to supernumerary penis.
O.T.	Ovotestis.
OVD.	Oviduct.
P.	Penis.
PA.	Papilla.
P.S.	Supernumerary penis.
P.SH.I.	Inner sheath of penis.
P.SH.O.	Outer sheath of penis.
R.S.	Receptaculum seminis (or spermatheca).
R.S.B.	Bulb of receptaculum seminis.
SH.	Connective tissue sheath enclosing the origins of the retractor muscles of the penes.
TENT.A.L.	Left anterior tentacle.
TENT.A.R.	Right anterior tentacle.
TENT.P.L.	Left posterior (or ocular) tentacle.
TENT.P.R.	Right posterior (or ocular) tentacle.
V.	Vagina.

Ashworth : HELIX POMATIA



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V.D.	Vas deferens.
V.D.S.	Supernumerary vas deferens.
V.P.G.	Viscero-pleural ganglion.
V.S.	Vesicula seminalis.

+ In fig. 1 indicates the position of the epidermal blind end of the supernumerary vas deferens.

FIGURES* OF THE ABNORMAL SPECIMEN OF *HELIX POMATIA*, L.,
ALL TWICE NATURAL SIZE.

Fig. 1. The anterior end seen from the left side, to show the supernumerary genital orifice (G.O.S.). The + marks the position of the epidermal blind end of the vas deferens. For further description, see pp. 315, 316.

Fig. 2. The dissection seen from the dorsal aspect. The alimentary canal, heart, nephridium, and roof of mantle chamber have been removed and the reproductive organs spread out so as to display the various parts. The supernumerary flagellum (FL.S.) is incomplete, its terminal portion having been accidentally severed and lost. The cerebral ganglia (C.G.) are shown still enclosed in their sheath (as the latter could not be safely removed), as are also the connectives (CN.). The sheath has, however, been removed from the viscero-pleural ganglion (V.P.G.), which is seen to be divisible into five portions—a median abdominal ganglion, right and left of which is a visceral ganglion, to the outer side of each of which is a pleural ganglion. The pedal ganglia are more ventrally situated and are not shown in the figure; only a few of the pedal nerves are shown; no attempt has been made to represent those which run posteriorly. On the right side the muscle (M.RETR.) which retracts the anterior end and the foot has been severed; the retractor of the buccal mass (M.RETR.B.) has also been cut through.

For descriptions of the normal and supernumerary reproductive organs, see pp. 312, 313, and 314, 315.

Fig. 3. A dissection of the supernumerary organs from the left or outer aspect. The outer and inner sheaths of the penis have been cut open to show the copulatory organ (C.O.), the introvert (INTR.), and also the rugose folds on the inner surface of the inner sheath. The blind end of the vas deferens (V.D.) is seen close beneath the epidermis, to which it is attached by a short cord of connective tissue (CON.T.). Only a small portion of the flagellum (FL.S.) is shown. A bristle has been passed through the external genital opening into the lumen of the penis. For further description, see p. 316.

Fig. 4. A further dissection of the distal portion of the penis, from the left or outer aspect. The incision in the sheaths of the penis shown in fig. 3 has been continued to the left (that is, distally), so as to extend to the genital opening. The flaps have been turned back so as to afford a clear view of the inner surface of the inner sheath in its distal portion. Note the longitudinal folds and the papilla (PA.). Probably the region from this papilla to the external opening (G.O.S.) ought to be regarded as atrium. For further description, see pp. 316, 317.

* The cost of drawing the figures on stone has been defrayed by a grant from the Carnegie Trust for the Universities of Scotland.

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