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Studies on The Carnivorous Slugs of South Africa,

INCLUDING

A Monograph on the Genus Apera, and a Discussion on the Phylogeny of the Aperidæ, Testacellidæ, and other Agnathous Pulmonata.

By

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With Plates VII–XXIV, and 7 text-figures.

CONTENTS.

INTRODUCTION.

MANY snails and slugs of great interest inhabit South Africa, but very little is known about their anatomy. I have therefore been asked to describe some of these animals, beginning with those in which the shell is degenerate or absent. The present article deals with the slugs belonging to the carnivorous group, and principally with those contained in the genus Apera; and as this genus is a very remarkable one and seems to be confined to South Africa, I am endeavouring to describe it in some detail. Unfortunately, however, the material at my disposal has been limited to a small number of preserved specimens, some of which have proved to be immature. More than half of these specimens were collected and sent to me by Mr. H. C. Burnup, of Pietermaritzburg, to whom I am very deeply indebted. I am also glad to have this opportunity of expressing my thanks to the Rev. Prof. H. M. Gwatkin, to Dr. Doncaster of Cambridge, Dr. Péringuey of Cape Town, Dr. Pilsbry of Philadelphia, Dr. Simroth of Leipzig, and Dr. Warren of Pietermaritzburg, to Major M. Connolly, and to Messrs. Keppel H. Barnard, Walter E. Collinge, John Farquhar, John H. Ponsonby, G. C. Robson, Edgar A. Smith, and William Tams.

THE HISTORY OF THE GENUS APERA.

Nearly forty years ago, when Mr. J. S. Gibbons was visiting Natal, he found a strange slug under a stone in a wood. This animal puzzled him greatly; it seemed more like a Testacella than anything else he knew; yet clearly it was not a Testacella, for where the shell should have been there was merely a little hole—the respiratory orifice.[1] Gibbons therefore sent the slug to Mr. W. G. Binney, with a description of its appearance when alive. Binney examined its radula, and found that its teeth were like those of Glandina. He also discovered that it had no jaw, but that it possessed an internal shell, which was broken when he found it, but which he wrongly assumed to be hexagonal when perfect. And Binney[2] established a new genus for this peculiar animal, and published a description of it in 1879, together with Gibbons's account of its appearance when alive, a rough drawing of the animal, and a figure of its radula. And he named the slug Chlamydephorus gibbonsi.

In 1884 Binney[3] repeated his description of the radula of this slug and reproduced his figure. In the same year Tryon[4] reproduced the rough drawing of the animal, and gave a brief description of the genus, which he placed in the Testacellidæ; and he also amended the spelling of the generic name, changing it to Chlamydophorus. In the following year, however, he reverted to the original spelling, when he described the genus and species in the 'Manual of Conchology,'[5] and again reproduced the rough drawing of the animal.

Now Binney named the genus Chlamydephorus because he said that the mantle covered the whole back. But in this Binney was wrong, as Heynemann[6] was the first to point out,

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[1] *Vide* Collinge, W. E., 'Ann. Natal Mus.,' 1910, vol. ii, p. 164.

[2] 'Bull. Mus. Comp. Zool. Harvard,' vol. v, p. 331, pl. ii, figs. a, b.

[3] "Notes on the Jaw and Lingual Dentition of Pulmonate Mollusks." 'Ann. N. Y. Acad. Sci.,' vol. iii, p. 81, pl. xvii, fig. A.

[4] 'Struct. and Syst. Conch.,' vol. iii, p. 13, pl. ci, fig. 47.

[5] Vol. i (2nd ser.), pp. 7, 17, pl. ii, fig. 95.

[6] 'Jahrb. d. Deutsch. Mal. Ges.,' vol. xii, p. 17, pl. ii, figs. 5–7.

when, in 1885, he published a description and three figures of the external characters of a specimen in the British Museum, labelled "Cape Colony." He thought that the animal was nearly related to Testacella; and as he showed that it had no mantle on its back, he suggested that the generic name should be changed to Apera.

In 1890 Prof. T. D. A. Cockerell[1] published a short description with measurements of what appears to be the same specimen, and he said that Heynemann's name would probably have to be used, as Chlamydophorus (differing from Binney's name only by one letter) had been employed by Harlan for a genus of Mammalia in 1825.

In 1892 Mr. E. A. Smith[2] described the external characters of a new species of Apera, very different from A. gibbonsi, which Mr. H. C. Burnup had found in Natal, and he named it Apera burnupi. He also thought that Apera was the best name to use, as Chlamydophorus had been employed in the Mammalia, but he attributed the latter name to Agassiz ('Nomenclator Zoologicus, Mammals,' 1842, p. 8), instead of to Harlan. Prof. Cockerell[3] then discovered that Apera was preoccupied in botany, and therefore thought that it might be better to use Binney's name with the original spelling. He placed the genus in the Testacellidæ. On the other hand, Dr. Simroth,[4] after studying Heynemann's article, suggested that the genus might be allied to the Janellidæ, its carnivorous characters having arisen independently of those of Testacella. He thought that the fragmentary condition of the shell, as found by Binney, might be natural; but had difficulty in explaining how it was that Apera had two pairs of tentacles and Janella only one. In 1895 Apera and Chlamydephorus were treated as though they were separate genera by Dr. A. H. Cooke.[5]

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[1] 'Ann. Mag. Nat. Hist.' (6th ser.), vol. vi. p. 390.

[2] 'Ann. Mag. Nat. Hist.' (6th ser.), vol. x. p. 466.

[3] 'Conchologist,' 1893, vol. ii. p. 206.

[4] 'Nacktschnecken. Deutsch-Ost-Afrika,' 1895. ex. vol. iv, p. 20.

[5] 'The Cambridge Natural History,' vol. iii. 'Molluscs and Brachiopods,' pp. 333, 334, 440.

Two years later Mr. W. E. Collinge[1] described and figured the alimentary canal, pedal gland, and reproductive organs of a specimen of Apera which he had received from Mr. E. A. Smith. Unfortunately this specimen was not in good condition for dissection, and Collinge's description is inaccurate in several respects, and his figures bear but little resemblance to the natural condition of the organs that they are intended to portray. Moreover the specimen was named Apera burnupi, whereas it really belonged to a quite distinct species. Collinge stated that he considered that Apera had affinities with the Testacellidæ, but he thought that there was a wide gap between it and either Testacella or Daudebardia, and a still wider gap between Apera and Schizoglossa. In the following year Dr. Pilsbry published a short review of Collinge's article in the 'Nautilus.'[2]

In 1899 Paul and Fritz Sarasin[3] brought forward the theory that Apera was ancestral to Atopus. Now Atopus has a large mantle covering the whole body, and the brothers Sarasin therefore rejected Heynemann's interpretation of the morphology of Apera, and advocated the use of Binney's name Chlamydephorus.

In 1900 Collinge[4] received through Mr. J. H. Ponsonby an example of Apera burnupi *Smith*, found by the Rev. J. R. Ward at Richmond, Natal, and belonging to the South African Museum, Cape Town. He at once saw that this specimen differed from the species which he regarded as Apera burnupi, and accordingly he named it Apera natalensis *n. sp.* He made a superficial dissection of some of the internal organs, but the specimen does not appear to have been in a much better condition than that of the other species which he had previously dissected, and his figures of its anatomy are in consequence equally faulty. In the same

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[1] 'Ann. Mag. Nat. Hist.' (6th ser.), 1897, vol. xx, pp. 221–225, pl. v, figs. 1–6.

[2] Vol. xii, p. 12.

[3] 'Die Land-Mollusken von Celebes,' p. 112.

[4] 'Ann. S. Afr. Mus.,' vol. ii, pp. 3–5, pl. i, figs. 3, 4, pl. ii, figs. 14, 15.

paper Collinge published two coloured figures of both species by Mr. F. J. Partridge.

In the following year Collinge[1] had an opportunity of examining a better specimen of the species which he supposed to be Apera burnupi, and he discovered how misleading were his former figures of its anatomy. He therefore published a more accurate figure and description of the reproductive organs of that species. At the same time he criticised the theory of P. and F. Sarasin, and said that Apera was probably closely allied to the Testacellidæ, while Atopus on the other hand seemed to be far removed from that family.

In December, 1901, Collinge[2] described the external features of a new species of Apera found by Mr. R. M. Lightfoot on the slopes of Table Mountain, Cape Town, and published coloured figures of it by Partridge. This species he named Apera purcelli.

Dr. Simroth,[3] in the same month, published a copy of Collinge's figure of Apera natalensis (= A. burnupi *Smith*), in his interesting article on carnivorous snails and slugs. In this paper he unfortunately stated that Apera was without a shell, and again suggested that the genus might have been derived from the Janellidæ, or possibly from some other ancient family of herbivorous slugs found in the Southern Hemisphere, although he admitted that too little was known of the genus to give any value to his hypothesis.

In 1902 Collinge[4] reproduced on a larger scale his second figure of the reproductive organs of the species which he erroneously supposed to be Apera burnupi. In the following year Dr. von Moellendorff[5] removed the genus from the Testacellidæ, and placed it in a family by itself, which he

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[1] 'Journ. of Malac.,' vol. viii, pp. 71, 72.

[2] 'Ann. S. Afr. Mus.,' vol. ii, p. 230, pl. xiv, figs. 1, 2.

[3] 'Naturwiss. Wochenschrift,' vol. xvii, p. 111, fig. 7.

[4] 'Journ. of Malac.,' vol. ix, pl. vi, fig. 66.

[5] 'Conch.-Cabinet (Agnatha),' p. 5.

named the Aperidæ. In 1906 Heynemann[1] devoted a paragraph to the genus in his article on the geographical distribution of slugs. In 1907 Dr. Pilsbry[2] followed Moellendorff's example and placed the genus in the family Aperidæ, which he included in his super-family Agnathomorpha; and he suggested that it might prove to be more nearly related to the Rhytididæ than to the other carnivorous families.

In 1909 and 1912 Simroth[3] included in Bronn's 'Tier-Reich' some of the information given in Collinge's articles, and published copies of four of the figures which had illustrated his first paper in the 'Annals of the South African Museum.'

In 1910 Collinge[4] gave a short account of the external features of the three species of Apera then known to inhabit Natal, together with a definition of the genus, and some remarks on its habits, distribution, affinities, and history. This paper contains valuable quotations from letters of Gibbons and Burnup, but the error about Apera burnupi is repeated. In treating of the affinities of the genus, Collinge again stated that he considered that P. and F. Sarasin were wrong in regarding Apera as in any way related to Atopus; but he now expressed the opinion that it was not related to Testacella either, and thought that it should probably stand by itself as a remnant of some very ancient stock of carnivorous Pulmonates. Accordingly he placed it in a separate family, which he termed the Aperaidæ *fam. nov.*, being apparently ignorant of the classification of both Moellendorff and Pilsbry.

Lastly, in 1912, Major Connolly[5] included Apera in his valuable "Reference List of South African Non-marine Mollusca," following Collinge's nomenclature of the species.

Such is the story of the treatment that Apera has received,

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[1] 'Abhandl. Her. v. d. Senkenb. Naturf. Gesell. (Frankfurt),' vol. xxx, p. 23.

[2] 'Manual of Conchology' (2nd ser.), vol. xix. pp. ix. xi.

[3] 'Klassen und Ordnungen des Tier-Reichs III. Gastropoda Pulmonata,' pp. 143, 611, 612, fig. 42c, pl. iv, figs. 9–11.

[4] 'Ann. Natal Mus.,' vol. ii, pp. 163–170.

[5] 'Ann. S. Afr. Mus.,' vol. xi, pp. 62, 63.

and it is largely a story of mistakes. It will have been seen that four species have been described, three from Natal and one from the Cape, but that very little is known about the anatomy of any of these, as only two reliable figures have hitherto been published of their internal features, namely, Binney's figure of the radula of Apera gibbonsi, and Collinge's second figure of the reproductive organs of the species which he supposed to be A. burnupi. Nevertheless this ignorance does not seem to have prevented malacologists from speculating about the affinities of the genus; for, as we have seen, it has been suggested in turn that it may be related to the Testacellidæ, to the Janellidæ, to Atopus, or to the Rhytididæ, forms which differ immensely from one another. It is hoped that the information contained in the present article may give greater value to such speculations in the future.

In the following pages I am attempting to describe this remarkable genus in as great detail as the limited number of specimens at my disposal will permit, giving numerous figures of its anatomy. Secondly, I am giving a concise description of the distinctive characters—both external and internal—of each species; that is to say, of Apera gibbonsi, A. purcelli, A. burnupi, the species that Collinge erroneously supposed to be A. burnupi, which I am naming A. sexangula, and two new species—A. dimidia from Natal, and A. parva from Grahamstown. And at the same time I am pointing out that there are some very distinct races of A. gibbonsi, which may also prove to be separate species, but which I am provisionally regarding as sub-species until more material is obtainable. After dealing with the relation of these forms to one another, I am describing briefly the species of Testacella that occurs at the Cape, and am then discussing at some length the probable relations of Apera and Testacella to each other and to the remaining genera of carnivorous snails and slugs.

A DESCRIPTION OF THE GENUS APERA.

EXTERNAL CHARACTERS.

General Shape.—The slugs contained in the genus Apera are subcylindrical, tapering gradually towards the head and more abruptly at the hind end, the broadest region being usually behind the middle of the animal. The height is equal to the breadth or sometimes slightly less, while the width of the foot varies from three-fifths to scarcely one-half of the greatest breadth of the body. Most of the species are rather slender, especially A. parva and some forms of A. gibbonsi; and it is interesting to notice that the latter do not contract when about to rest, after the usual manner, but merely bend their bodies at various angles, in which state, Mr. Burnup informs me, they much resemble the rhizomes of ferns.

Size.—So few specimens of Apera have been examined that the mean dimensions attained by each species cannot be stated with accuracy. It seems probable, however, that the average length of each of the three larger species—A. gibbonsi, A. burnupi and A. sexangula—lies between 60 and 65 mm., in the case of specimens preserved in alcohol, although occasional examples may reach a length of nearly 80 mm. On the other hand adult specimens of A. dimidia preserved in spirit are only about 33 mm. long, and A. parva and A. purcelli seem to be still smaller species.

Tentacles.—As usual in the Stylommatophora, there are two pairs of tentacles, the upper pair being retractile and bearing the eyes.[1] The lower tentacles are small, and beneath them there is another pair of short processes of a paler colour, which doubtless correspond to the labial feelers found in most of the carnivorous genera.

Genital Opening.—The common opening of the reproductive organs is on the right side of the head, two or three millimetres behind the right lower tentacle, and about half that distance from the margin of the foot.

[1] See pp. 153, 154 for structural details.

Respiratory Opening.—The aperture of the mantle-cavity or "respiratory orifice" is situated towards the hind end of the back, just to the right of the mid-dorsal line. Its posterior position, about four times as far from the head as from the hind end of the slug, is due to the lengthening of the anterior part of the body and the retrogression of the pallial organs, as in Selenochlamys and Testacella. The dorsal position of the opening is explained by the absence of any external mantle or shield in Apera.[1]

The orifice is always a little nearer the right side than the left, a fact which previous writers seem to have overlooked, although it is of considerable morphological importance, as may be seen from Pl. X, fig. 33 (a transverse section through the respiratory opening of Apera gibbonsi rubella). This illustration also shows that the opening is surrounded by two lips, one within the other. In Apera gibbonsi and A. parva the outer lip projects over the inner lip so as almost to conceal it; but in the other four species the outer lip is much narrower, and leaves a wide circular opening, within which the light-coloured inner lip is exposed to view (Pl. VII, fig. 12; Pl. VIII, figs. 24, 25, 26). The right anterior edge of the inner lip is cleft by an oblique slit, running forwards and outwards from the central aperture.

Keels.—In most of the species of Apera the back is rounded, but A. burnupi and A. sexangula both have four longitudinal keels, two on each side of the body, which may possibly serve to increase the rigidity of the skin. The upper keels of A. sexangula are nearly parallel throughout the greater part of their length, the distance between them measuring about three-fifths of the breadth of the body. When followed backwards, however, they diverge very slightly just in front of the respiratory opening, and then gradually approach each other behind it, until they unite to form a single median keel, 3 or 4 mm. in length, at the hind end of the animal. In A. burnupi the upper keels are further apart, and become very prominent towards the hind end, diverging considerably and

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[1] See pp. 130, 131.

then curving round to meet in a very obtuse angle just above the posterior extremity of the foot.

The lower keels of Apera sexangula extend on each side along the whole length of the animal, about half-way between the upper keels and the edges of the foot. The slug is thus roughly hexagonal in transverse section, but when it contracts the surfaces between the keels become concave. In A. burnupi the lower keels are much nearer the foot than in A. sexangula, and become obsolete towards the hind end of the slug.

The other species of Apera are without any traces of either median or lateral keels. They are bluntly pointed at the posterior end.

There is no caudal mucous pore in Apera.

Dermal Grooves.—In all the species of Apera the back and sides of the animal are covered with a network of grooves, dividing the skin into numerous polygonal rugæ. These grooves are specially deep in A. burnupi. The centres of the rugæ are often raised in well-preserved specimens, and the skin has therefore a granular appearance.

Certain of the grooves are larger than the others, and run in more definite directions, forming as it were the main channels from which branch the smaller grooves that form the network. First there are the two dorsal grooves which run along the middle of the back from the respiratory opening to the head. These are most strongly developed in Apera burnupi, and least conspicuous in A. dimidia, in which species the main grooves are scarcely more distinct than the other grooves of the network. The distance separating the dorsal grooves varies from about one-seventh of the breadth of the body in A. dimidia to less than half that proportion in some forms of A. gibbonsi (Pl. VII, fig. 4). In A. burnupi, A. sexangula, and A. purcelli these grooves are separate throughout their entire length, but in A. gibbonsi, A. parva, and A. dimidia they are united posteriorly, and arise from the respiratory opening as a single groove which divides between 3 and

5 mm. in front of the opening (Pl. VII, figs. 1, 4; Pl. VIII, figs. 22, 24).

A single median posterior groove runs backwards from the orifice. It is usually deep and conspicuous in front, but breaks up into finer irregular grooves before reaching the hind end of the slug.

Well-marked radial grooves diverge laterally from the region of the respiratory opening. About four of these on each side arise from the opening itself, and two or three others branch from the median posterior groove behind the opening. In Apera purcelli, the most anterior grooves, instead of arising from the respiratory opening, branch from the dorsal grooves in front of it (Pl. VIII, fig. 25). As a rule the radial grooves extend down the sides of the body, but in A. gibbonsi some of them usually bifurcate before reaching the edge of the foot. The most anterior grooves of A. gibbonsi, A. parva, and A. dimidia always divide within a short distance of the respiratory opening, the lower branch sloping downwards towards the foot, while the other continues forward. The latter branch soon divides again in a similar manner, and this process is repeated several times, so that an irregular lateral groove is formed, which runs forward parallel to the dorsal groove and gives off oblique sub-lateral grooves parallel to one another. The lateral grooves are seldom well developed in A. gibbonsi and A. dimidia, but the oblique sub-lateral grooves are rather conspicuous in the former species (Pl. VII, figs. 2, 3, 5, 6). On the other hand, in A. parva, A. burnupi, and A. sexangula the lateral grooves are more definite and better developed than the sub-lateral grooves, of which there are only a small number (Pl. VIII, fig. 23; Pl. VII, figs. 11, 13). The lateral grooves of the two latter forms are lower down than those of the other species, and branch from the most anterior pair of radial grooves at a greater distance from the respiratory opening. They run along between the upper and lower keels as far as the head, the right lateral groove ending in the genital opening as in Testacella and other forms. It is probable that the greater development and lower position of the lateral grooves in these two species is due to the presence of the keels. There are no definite lateral grooves in A. purcelli.

The foot-fringe is bounded above by a peripodial groove, which is usually rather deep (Pl. XI, fig. 35). In Apera burnupi and A. sexangula there is a second groove, parallel to the peripodial groove, but separated from it by a narrow row of rugæ, and the radial grooves do not extend below this upper groove, but terminate in it. As a rule the other species have only the single peripodial groove with which the radial grooves unite, but in A. dimidia the upper limits of the lowest row of rugæ are sometimes arranged so as to form an irregular groove parallel to the peripodial groove on each side.

The foot-fringe itself is narrow and is crossed by a number of small vertical grooves, which are often continued across the edges of the foot-sole. In contracted specimens many of these transverse grooves extend right across the sole, although they are never so numerous in the middle as at the edges. A conspicuous but irregular longitudinal groove often runs along the centre of the foot-sole, but this also is probably due to the contraction of the specimens. In some examples two grooves diverge from a point at the hind end of the foot-sole and extend forward nearly parallel to the edges of the foot, thus dividing the hinder part of the sole into median and lateral areas. Occasionally these grooves may be traced forward for about two-thirds of the length of the animal, but they are more usually confined to the hind end, as shown in Pl. VII, fig. 9, and in many specimens they are entirely absent. In Natalina I have sometimes found similar grooves towards the hind end of the foot; but none of the grooves on the foot-sole seem to have so much systematic value as those on the back and sides of the slug, for they may be present or absent in different individuals of the same species.

Colour.—The skin of Apera is coloured, and the colour is almost entirely due to pigment. It is true that specimens of the more darkly coloured species when preserved in spirit sometimes have a slightly bluish or bluish-green tinge, and that this is probably due not to pigment, but to minute particles in the outer layer of the skin which intercept the blue rays. It is doubtful, however, whether this interference effect would be as noticeable in living specimens.

Apera possesses two chief kinds of pigment: the first is dark and relatively stable, the second is lighter, very unstable, and superposed upon the first.

The dark pigment is usually brownish-grey, varying from dull brown in typical examples of Apera gibbonsi to dark grey in A. purcelli. It does not spread uniformly over the back and sides of the animal, but is more concentrated in some parts than in others. In the first place the dark pigment tends to be aggregated into small irregular patches, which give the slug a mottled appearance. This tendency is least apparent in Apera purcelli, and most marked in A. dimidia, A. burnupi, and some varieties of A. gibbonsi. In these animals the patches of colour are well defined, so that the skin is conspicuously mottled. When the dark patches are examined through a strong lens they are seen to contain minute lighter specks, which are probably caused by the dermal mucous glands.

Secondly, the dark pigment generally shows a tendency to become concentrated along the sides of the dermal grooves. Thus in A. gibbonsi the oblique sub-lateral grooves are usually rendered more conspicuous by the way in which the patches of pigment tend to coalesce along their courses.

Thirdly, the dark pigment is more abundant on some regions of the body than on others. In Apera gibbonsi it is concentrated dorsally, although a lighter band is generally left along the very centre of the back (Pl. VIII, figs. 14–19). On the sides of the animal the mottling becomes sparser, and it dies out before reaching the foot-fringe. In the keeled species, as well as in A. dimidia and A. purcelli, the dark pigment tends to be concentrated laterally, so as to form an irregular longitudinal band on each side of the body. Between the bands there is a lighter dorsal area, palest at the edges, but a little darker in the middle; below them the colour shades off gradually towards the foot. This arrangement of the pigment is best developed in Apera dimidia (Pl. VIII, figs. 20 and 21), but it is also fairly conspicuous in A. burnupi, where the dark mottling is concentrated to form a band on each side below the upper keels. In A. sexangula and A. purcelli the bands, though present, are less noticeable and the colour is more evenly distributed, although the edges of the keels of A. sexangula are almost free from pigment.

It will be seen that in these four species the pigment tends to form a pattern similar to that found in the genus Arion. On the other hand in Apera gibbonsi the scheme of coloration is different, and the narrow lighter band which this slug usually has along the centre of the back recalls the similar band possessed by many species of Veronicella. It should be noticed that this difference in the position of the greatest concentration of the pigment is not correlated with the difference in the position of the lateral grooves; for in A. dimidia the grooves are situated as in A. gibbonsi, while the dark bands are lower down and occupy a similar position to those of the keeled species.

Apera dimidia is singular in having small patches of the dark pigment on the foot-sole (Pl. VII, fig. 9). But in some specimens of A. sexangula and in at least one example of A. gibbonsi minute reddish-brown specks are scattered over the body, and in the former species these extend on to the foot.

The lighter pigment is usually of some shade of orange, but varies from pale orange-yellow to dull red. It is generally diffused over the whole surface of the body, including the foot-sole, but is often darker above than below, the backs of Apera burnupi and A. gibbonsi rubella being especially deeply coloured. But this pigment is very unstable, and specimens which have been preserved in spirit seldom show more than very slight traces of it. In the case of an example of A. gibbonsi rubella, which was drowned by Mr. Burnup, the red pigment came out of the skin when the animal was dead, and coloured the water in which the slug was immersed. Notwithstanding the dark grey mottling of this form, the living animal is of a reddish colour, changing to orange below, as the unstable colouring matter is sufficiently abundant to mask the darker pigment underneath.

The coloration of a typical specimen of Apera gibbonsi increases its resemblance to the rhizome of a fern, and the chestnut-brown colour of A. burnupi may help to render the slug inconspicuous among dead leaves. Even the reddish colour of A. gibbonsi rubella may serve to conceal the animal, although the bright pigment of the red variety of Arion ater is supposed to act as a warning colour. Mr. Burnup found a specimen of this Apera in the bush at Durban, and he noticed that a few of the dead leaves[1] under which the slug was found were of a dark brownish-red colour, strongly veined, and curled up into rolls, and these were so very like the slug that it might easily have been mistaken for one of them.

On the other hand, it seems possible that the unstable red and orange pigments found in Apera and other slugs which are often carnivorous, as well as the similar bright colours so characteristic of most of the snails belonging to the Streptaxidæ, may be partly due to their animal food. It is known that this is the case with the red pigment found in the flamingos, the scarlet ibis, and the roseate spoonbill; for the colour tends to disappear when the birds are deprived of their natural food, which consists chiefly of mollusks and other invertebrates. M. F. Woodward[2] has described the rich orange colour of the edge of the mantle in specimens of Natalina caffra which were fed on snails and beefsteak, and Miss Davies[3] mentions the brilliant orange-red colour of

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[1] Dr. J. Medley Wood, Director of the Natal Herbarium, has kindly examined one of these leaves, and thinks that it probably belongs to Combretum krausii.

[2] 'Proc. Mal. Soc.,' 1895, vol. i, p. 271.

[3] 'Proc. Roy. Soc. Victoria,' 1913, vol. xxi, p. 222.

the mantle-border and foot in Paryphanta atramentaria (*Shuttl.*), another carnivorous snail.

Again, the climate has a marked influence on the colour of slugs, moisture being favourable to the development of dark colours, while heat increases the production of red pigments. Now in Apera gibbonsi rubella both the dark and the red pigments are specially well developed, and this form is at present only known from the coastal region of Natal, which is both moist and warm; whereas the typical form of A. gibbonsi, as well as the other species inhabiting the Province, extend further inland.

Dr. Simroth[1] has maintained that in Testacella the skin probably plays a more important part in respiration than the lung, and it is suggested that in such slugs as these the chief function of the pigment is to assist in the taking up of oxygen. But it does not seem likely that this is the case in Apera. For in this genus the respiratory tissue of the lung is well developed; while, on the other hand, the structure of the integument and the arrangement of the blood-vessels which it contains do not suggest that the skin plays an important part in respiration.

On the whole it seems probable that the pigments of these slugs, like those of many other animals, may be looked upon as by-products of metabolism, which are deposited in the skin usually in such a way as to help to render the animal inconspicuous or to protect it from harmful rays of light, the development of the pigments depending partly on the food, but being also influenced by the climate and surroundings. Yet it must not be forgotten that the coloration of any slug is due not simply to the climate, the food, and the colour of the surroundings, but to the power of reacting to these influences which the animal possesses through inheritance.

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[1] 'Nova Acta Acad. Cæsar Leop.-Carol. Germ. Nat. Cur.,' 1891, vol. lvi, p. 245.

THE STRUCTURE OF THE SKIN.

Epidermis.—The outermost layer of the skin on the back and sides of the animal consists of a well-marked cubical epithelium, which in Apera dimidia attains a thickness of rather less than ·01 mm. (Pl. XII, fig. 37). The cells composing this epithelium are approximately square in section; they stain rather deeply, and each contains a large rounded nucleus. The outer walls of these cells are thickened to form a cuticle, while the remaining walls are much thinner. In this respect, therefore, the epidermis of Apera seems to resemble that of Testacella rather than that of Daudebardia, in which all the walls of the epidermal cells are thickened,[1] or of Paryphanta, in which a cuticle is said to be absent.[2]

The epidermis does not change its character on the dorsal side of the foot-fringe, as in such forms as Daudebardia[3] and Cystopelta,[4] but on the sole of the foot it becomes quite different. Here the epithelium is columnar rather than cubical, and the inner ends of the cells taper and interdigitate with the underlying connective tissue, so that the limits of the epithelium are very ill-defined (Pl. XII, fig. 38[5]). Excepting towards the edges of the foot-sole, the outer end of each cell is produced into a number of delicate cilia, which in A. dimidia measure about ·0035 mm. in length.

Inner Layers of the Skin.—In the outer part of the connective tissue, which everywhere underlies the epidermis, are embedded the dermal mucous glands and the pigment-granules. The mucous glands (Pl. XII, fig. 37) are oval or pear-shaped, and reach a considerable size, although each is formed from a single cell. The protoplasm of the cell is

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[1] Plate, L. H., 'Zool. Jahrb.,' 1891, vol. iv, p. 529.

[2] Beutler, B., 'Zool. Jahrb.,' 1901, vol. xiv, p. 374.

[3] Plate, op. cit., p. 527.

[4] Davies, Miss O. B., 'Proc. Roy. Soc. Victoria,' 1912, vol. xxiv, p. 332.

[5] I am indebted to Mr. W. Tams for kindly taking this photomicrograph.

chiefly confined to a thin layer lining the base of the gland and containing the rather large nucleus; the rest of the interior is filled with mucous secretion, which can be extruded through a narrow pore between the cells of the epidermis. Dr. Plate has separated the unicellular mucous glands of Testacella[1] and Daudebardia[2] into two classes, according to the nature of this secretion. A similar classification seems applicable to the dermal glands of Apera, for in sections some of the glands are seen to be entirely filled with a vacuolated colourless secretion, while in others the mucus has become concentrated into a compact, deeply stained mass in the centre of the gland. No dermal glands of either kind occur in the foot-sole. In this respect Apera resembles Paryphanta,[3] and contrasts strongly with Testacella[4] and other forms. Possibly the great development of the pedal gland may have rendered the unicellular glands unnecessary, although in Paryphanta the pedal gland is not much more highly developed than it is in Testacella.

The minute granules of dark pigment occur in the connective tissue between the mucous glands, being chiefly aggregated just beneath the epidermis. Some of the granules are contained in pigment-cells, others appear to be irregularly scattered about, but possibly these may occur inside delicate branches of the pigment-cells.

Beneath this glandular zone the connective tissue contains blood-vessels, nerves, and numerous muscle-fibres, longitudinal, radial, oblique, and circular, the last-mentioned being especially abundant near the inner surface of the skin.[5] In Apera dimidia there are more muscle-fibres in the foot than in the connective tissue of the back and sides. This

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[1] Op. cit., p. 530.

[2] Op. cit., pp. 527, 528.

[3] Beutler, op. cit., p. 375.

[4] Lacaze-Duthiers, H. de, 'Arch. Zool. Expér.' (2nd ser.), 1887, vol. v, p. 526.

[5] I use the term "skin" in a wide sense to include the whole body-wall, for no sharp line can be drawn separating the subcutaneous tissue with its muscle-fibres from the dermis or cutis vera.

zone of connective tissue is extremely thick, especially towards the hind end of the animal; indeed, the most remarkable thing about the skin of Apera is its great thickness and strength. Only in the region of the head, where flexibility is essential, is the skin moderately thin. Its thickness further back in A. gibbonsi is well shown in Pl. X, fig. 32. On the other hand, A. dimidia has a somewhat thinner skin than most of the other species, though even in this form its thickness is not inconsiderable, as will be seen from Pl. XI, figs. 34 and 35. This unusual thickness of the skin can easily be explained. In Apera the shell is so degenerate that it can no longer fulfil its proper functions. Yet the slug still needs protection from other animals seeking to prey upon it, and from the pressure of the soil if it burrows in the ground like Testacella, and also from excessive evaporation. And it still needs a firm attachment for its powerful retractor muscles. Therefore the skin has taken over the functions of the shell, and has become adapted to fulfil these functions adequately. The Rev. Dr. Cooke[1] has recently called attention to a case among the Polyplacophora in which the protection once afforded by the shell has been transferred to the integument. But in that case the mantle has taken the place of the shell, while in the present instance it is the skin itself which has been strengthened.

The blood-vessels contained in the skin are irregularly disposed, though most of them run in a longitudinal direction. They communicate with the body-cavity or hæmocœle by minute pores, which can be seen puncturing the inner surface of the skin (Pl. X, fig. 32). In all parts of the skin these vessels are provided at rather frequent intervals with powerful sphincters composed of circular muscles (Pl. XIII, fig. 40). Similar sphincters have been described by Dr. Simroth and P. and F. Sarasin[2] in Veronicella (a genus in no way allied to Apera); and it has been suggested that they serve to prevent the reflux of the blood when the animal moves.

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[1] 'Proc. Mal. Soc.,' 1913, vol. x, pp. 321, 322.

[2] 'Die Land-Mollusken von Celebes,' 1899, p. 90, pl. xiii, figs. 122, 123.

Perhaps in Apera they also assist the circulation of the blood in a similar manner. But it seems possible that their chief function may be to enable the animal to increase the turgidity of some or all of the dermal vessels when it contracts, and thus to give greater rigidity to the skin either as a whole or in part. For if the slug by closing the sphincters could thus increase the pressure in the dermal blood-vessels, the skin would become much more rigid in consequence, just as the strength of the stem of an herbaceous plant is largely due to the turgidity of its cells.

THE SHELL, THE MANTLE-CAVITY, AND THE MANTLE.

The Shell.—The small shell of Apera lies deep in a little pocket in the skin just behind and to the left of the respiratory opening. As a rule its length is only about one-fourteenth of that of the animal (in alcohol). When viewed from above the somewhat oval contour of the shell is seen to be interrupted by a broad sinus which extends backwards from the front end more than half way along the right side. The posterior part of the shell is thus broader than the anterior half, which projects forward on the left side of the respiratory opening. The sinus is deepest in Apera gibbonsi, and shallowest in A. purcelli and A. dimidia. It will be seen from Pl. XIII, figs. 42, 45, 48, and 51, that the shell of Apera is often much less flattened than is usually the case with the internal shells of slugs. In A. burnupi and A. sexangula it is very convex, and culminates in a conical apex, which overhangs the posterior margin of the shell. In A. purcelli the apex projects still further, but it is rounded instead of conical, as is also the case in A. dimidia, in which the apex is less prominent. Lastly, in A. gibbonsi and A. parva the shell is more depressed, and the apex is in front of the posterior margin.

The shell is extremely thin and translucent in Apera purcelli and A. dimidia. In the other species it is thicker and more calcareous, especially in full-grown specimens, though it is usually very brittle. Indeed in some examples of A. gibbonsi its thickness is sufficient to suggest that the chief function of the shell in this species and its allies may be to enable the animal to get rid of any excess of calcium carbonate in its blood. It is difficult to see what other function it could fulfil; and if it were to be regarded as a purely vestigial structure with no function at all, one would have expected it to have become much smaller as well as flatter in this species than in the more primitive forms such as A. purcelli. Yet, while the shape has degenerated, the relative size has remained the same and the thickness has greatly increased.

THE SHELL-SAC.—The pocket in which the shell lies has no communication with the exterior, but is close to the inner surface of the skin (Pl. X, fig. 33). In those species in which the shell has a prominent apex, the floor of the sac is raised towards the hind end to form a papilla fitting into the hollow of the shell. Where the margin of the shell rests upon the floor of the pocket, there is a fold, which separates the central part of the floor underlying the interior of the shell from a narrow rim beyond it.

The shell-sac is lined by a well-defined epithelium. On the roof of the cavity this epithelium is very thin, being formed in Apera dimidia of a compact layer of small cells which are slightly broader than they are high. Underneath the shell the epithelium is thicker in the same species, and composed of larger cells, whose height exceeds their breadth. These larger cells are continued over the edge of the fold mentioned above, the transition from the thicker to the thinner epithelium taking place on the outer side of the fold.

THE MANTLE-CAVITY OR LUNG.—The mantle-cavity occupies the region below the shell and the respiratory opening, and also extends a short distance further forward. It is, nevertheless, mainly behind instead of above the body-cavity or hæmocœle, from which it is separated by a muscular diaphragm sloping obliquely downwards and backwards. There is, however, a funnel-shaped prolongation of the body-cavity which extends backwards for a variable distance beneath the mantle-cavity, and raises its floor along the middle. This feature is well shown in Pl. XI, figs. 34, 35, and Pl. XII, fig. 36, for the prolongation is unusually large in Apera dimidia and A. purcelli.

In horizontal section the mantle-cavity or lung is roughly triangular, with the large pericardium occupying the centre of the broad anterior part, which is thus divided into a right and a left wing (Pl. IX, figs. 27–31). The right division opens widely behind into the posterior part of the mantle-cavity, but the left division is cut off by the kidney, which extends obliquely backwards from the pericardium and fuses with the left wall and the roof of the cavity. Thus the left anterior division only communicates with the rest of the mantle-cavity by a narrow space round the top and front of the pericardium and kidney. It is, therefore, not surprising that the walls of this part of the cavity are without respiratory tissue. But the right anterior division, which communicates more freely with the air, and the greater part of the posterior half of the cavity have their walls richly supplied with pulmonary veins. These vessels branch repeatedly, and in the larger species the fine branches form a complicated network which divides the surface into numerous alveoli. The thinness of the epithelium which separates the blood in these vessels from the air in the mantle-cavity will be seen from Pl. XII, fig. 39. The only portion of the posterior half of the cavity that is devoid of respiratory tissue is a part of the roof[1] and the immediate neighbourhood of the respiratory opening and the anus just below it.

At the hind end the cavity tapers to a point. In Apera gibbonsi this point is below the extreme hind end of the shell-sac; but in species such as A. sexangula and A. dimidia it is within the papilla which is formed by the floor of the shell-sac projecting into the hollow apex of the shell. Hence in these species the hind end of the mantle-cavity is inside the shell itself.

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[1] See p. 187.

I have only been able to examine the minute structure of the epithelium lining the mantle-cavity in one species, namely A. dimidia. In this species (and probably also in the others), that part of the posterior half of the cavity where there is no respiratory tissue is lined by moderately large cells, slightly higher than they are broad, and strongly ciliate near the respiratory opening. These cells are continuous through the aperture with those of the epidermis. The whole of the remainder of the cavity, including both of the anterior divisions, is lined by a pavement-epithelium of cells so thin that the nucleus of each usually forms a knob-like projection in the centre of its surface.

The Mantle.—Apera has no external mantle—a remarkable fact that was first pointed out by Heynemann.[1] Yet it cannot be entirely without a mantle, for, as we have just seen, it possesses both a mantle-cavity and a shell; and all Gastropods that have a shell also possess a mantle, as the shell is always secreted by the mantle. I therefore regard that part of the integument which forms the roof of the mantle-cavity beneath and around the shell as being undoubtedly homologous with the mantle. Moreover I believe that the mantle is not entirely concealed from view in all the species of Apera, for it seems probable that it forms the inner lip of the respiratory opening, and that the upper surface of this lip may be regarded as part of the upper surface of the mantle (Pl. X, fig. 33). This theory is confirmed by the occurrence of an oblique cleft in the inner lip of the opening in a similar position to the cleft which runs from the opening to the edge of the mantle in an ordinary slug.

We may suppose that Apera has been evolved from a snail, having on its back a mantle covered by a shell. It might well be an advantage to such an animal to get rid of this projection, especially if it burrowed in the ground in search of worms. Accordingly both mantle and shell seem to have sunk into the back and to have become covered by folds of the surrounding skin which have grown over it on each side.

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[1] 'Jahrb. d. Deutsch. Mal. Ges.,' 1885, vol. xii, p. 19.

The upward growth of the skin on the right side would tend to cover the respiratory opening, which would be in its usual position in the right margin of the mantle. To obviate this, the mantle edge, with the opening, would have to move up towards the middle line, and the growth of the right side of the shell would be retarded in consequence. And at the same time the fold of the skin would be likely to grow more slowly immediately opposite the opening than before and behind it, thus forming a notch in the edge of the fold. Eventually this fold of the skin would unite with the other in the middle line excepting at the notch, which would be converted into an opening above the original respiratory opening in the mantle-edge.

This hypothesis may not be correct, but it has at least the merit of explaining not only the absence of an external mantle in Apera, but also the dorsal and slightly asymmetrical position of the respiratory opening, the fact that the opening has an inner and an outer lip, the former with an oblique cleft, and the peculiar sinus in the right side of the shell. So far as I am aware the morphology of the mantle and shell of Apera differs from that of all other Pulmonates.

THE PEDAL GLAND.

The pedal or supra-pedal gland attains a greater development in Apera than in any other genus of snails or slugs known to science. It consists essentially of a long duct with glandular walls, which opens in front between the mouth and the anterior end of the foot, and ends behind in a small vesicle.

The Position and Length of the Gland.—In the herbivorous genera of snails and slugs the pedal gland is usually more or less embedded in the muscular tissue of the foot, and this is also the case in Daudebardia,[1] Plutonia,[2] and the Trigonochlaminæ[3]; but in Apera it lies freely in the lower

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[1] Plate, L. H., 'Zool. Jahrb.,' 1891, vol. iv, p. 525.

[2] Simroth, H., 'Nova Acta Acad. Cæsar Leop.-Carol. Germ. Nat. Cur.,' 1891, vol. lvi, p. 229.

[3] Simroth, H., 'Festschrift Leuckarts,' 1892, pp. 53, 55; etc.

part of the body-cavity, as in Natalina, Rhytida, Paryphanta, Schizoglossa, Testacella, Streptaxis, Atopus, and a few other carnivorous genera, and is only held in position by the pedal artery which supplies it with blood. This artery confines the gland to the anterior part of the body-cavity, for it runs back above the gland, giving off branches to it as it goes, and, after becoming attached to the posterior vesicle for a short space, it dips down and unites with the upper surface of the foot about the middle of its length. The pedal gland, however, is many times longer than this free portion of the pedal artery and is consequently thrown into numerous folds and loops. In Apera sexangula the gland pursues a comparatively regular zig-zag course, bending alternately to the right and the left about half a dozen times (Pl. XIII, fig. 57). But in A. burnupi and A. purcelli, and in the posterior part of the gland in the remaining species, the loops are deeper and more complicated, twisting about in all directions (figs. 52–56). The gland attains its greatest length in A. burnupi, in which its folds not only extend up the sides of the body-cavity, but even curve over on to the top of some of the other organs (Pl. IX, fig. 30).

The Glandular Tissue.—The pedal gland of Apera is not only unusually long, it is also often exceptionally broad, as, for example, in A. burnupi and in the anterior half of its length in A. dimidia (Pl. XIII, figs. 56, 54). In A. gibbonsi and A. parva it is more slender (figs. 52, 53), possibly because the great size of the odontophore in these species leaves little room for the growth of any other bulky organ in the anterior half of the body-cavity.

The breadth of the gland is due to an enormous development of glandular tissue on the floor and sides of its duct. In Apera purcelli, A. burnupi, and A. sexangula this glandular tissue extends along the whole length of the duct as far as the terminal vesicle; but it is less abundant towards the posterior end and the gland becomes rather narrower behind in consequence. In A. gibbonsi rubella the glandular tissue becomes still scarcer towards the hind end, and disappears entirely just before the vesicle is reached, while in the other races of A. gibbonsi and in A. parva the last few millimetres of the duct are quite destitute of gland-cells. Finally, in A. dimidia the glandular tissue only extends along half the length of the duct, the posterior half being entirely without it, and therefore much narrower than the anterior half (Pl. XIII, figs. 54, 59, and 60).

Pl. XIV, fig. 63 shows the structure of the glandular tissue near the front end of the pedal gland in A. gibbonsi rubella. It will be seen that among the large oval gland-cells, which taper towards the duct, there are scattered connective-tissue cells with conspicuous rounded nuclei, and there can be little doubt that it is from these cells that the glands are formed. Similar cells occur near the front end of the pedal gland in A. dimidia, but further back, near the hind end of the anterior half of the gland, no such cells occur, and a transverse section has the appearance shown in Pl. XIII, fig. 59. Possibly the absence of connective-tissue cells from this region may be correlated with the absence of gland-cells still further back. The posterior part of the gland will probably be the first to be formed in development, and if all its cells, apart from those which form the duct itself, are converted into glands, there will be nothing left to replace these when they die and are discharged into the duct; for according to André[1] the gland-cells perish after a certain time and need to be replaced.

Mr. Collinge[2] has stated that the pedal gland of Apera sexangula contains "a large series of microscopic chitinous (?) dart-like bodies," but his figures leave little doubt that these are merely the solidified contents of the glands. In specimens preserved in alcohol this congealed secretion appears through a simple lens as numerous white specks, which often give a glistening appearance to the pedal gland.

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[1] 'Revue Suisse de Zoologie,' 1894, vol. ii, pp. 310, 311.

[2] 'Ann. Mag. Nat. Hist.' (6th ser.), 1897, vol. xx, p. 223, pl. v, figs. 4, 5.

THE DUCT.—The duct of the pedal gland is semi-translucent, and can be seen running along the centre of its upper surface. Near the opening of the gland the duct usually lies more deeply (Pl. XIV, fig. 63), but elsewhere the glandular tissue is restricted to its sides and lower surface, as shown in Pl. XIII, fig. 59. Where the glandular tissue is less abundant the exposed surface of the duct often shows a tendency to have alternate swellings and constrictions. In Apera gibbonsi this culminates in a close convolution of the posterior part of the duct (Pl. XIII, fig. 58), which reminds one of the somewhat similar convolution of part of the duct in Testacella.[1] On the upper surface of the anterior half of the gland in A. dimidia, two brownish lines can often be seen running along, one on each side of the duct, at its junction with the glandular tissue.

In section the duct is approximately circular, without any folds on its floor (Pl. XIII, figs. 59, 60, Pl. XIV, fig. 63). In this respect it resembles that of Testacella, and differs from that of Daudebardia, for in the latter genus, as in most herbivorous snails and slugs, the floor of the duct has two longitudinal folds enclosing a median groove, and the gland-cells only open into this groove, instead of all round the duct.[2] In Paryphanta hochstetteri (*Pfr.*) traces of the folds and median groove seem to occur, but only towards the anterior end of the duct.[3] The duct is lined by an epithelium composed of small cubical cells, and this is surrounded by two thin muscular layers, the fibres of the inner layer running round the duct, while those of the outer layer are longitudinal. Both layers of muscles occur inside the glandular tissue.

THE TERMINAL VESICLE.—After becoming gradually narrower the gland widens again at the hind end to form an oval or pod-shaped vesicle (Pl. XIII, figs. 52–57). In length this vesicle

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[1] See de Lacaze-Duthiers, 'Arch. Zool. Expér.' (2nd ser.), 1887, vol. v, pl. xl, fig. 95.

[2] Plate, L. H., 'Zool. Jahrb.,' 1891, vol. iv, p. 525, pl. xxxii, fig. 16.

[3] Beutler, B., 'Zool. Jahrb.,' 1901, vol. xiv, p. 376, pl. xxvi, fig. 9.

varies from about 1 mm. in the smaller species to more than 5 mm. in a large specimen of Apera burnupi, and its breadth is usually about one-third of its length. The walls of the vesicle are thin and semi-translucent like those of the duct, with which they are continuous. A few gland-cells occur along the ventral[1] surface in A. burnupi, A. sexangula, and A. purcelli, but none at all in the other species. The structure of the walls of the vesicle is similar to that of the walls of the duct, excepting that the cells of the epithelium become somewhat higher on the dorsal side, and among the ordinary epithelial cells there are scattered a few rather small vacuolated cells.

From the dorsal wall of the vesicle there projects into its cavity a remarkable fold, resembling a typhlosole, which fills up a large portion of the interior, so that the cavity is crescentic or horse-shoe-shaped in section (Pl. XIII, fig. 62). If the wall of the vesicle in Apera sexangula be cut open, it will be seen that the fold has a spongy and somewhat laminated appearance. Serial sections through the vesicle of A. dimidia show that in this species the fold is rounded excepting at the ends, where it becomes wrinkled and divided by furrows (cf. Pl. XIII, figs. 61, 62, Pl. XIV, fig. 66). Fig. 66 shows the structure of the fold in A. dimidia. It will be seen that it is entirely composed of vacuolated tissue, which is not bounded by a distinct epithelium. The pedal artery, which always becomes intimately connected with the dorsal surface of the vesicle, gives off a branch into the middle of the fold (Pl. XIII, fig. 62). In A. gibbonsi the structure of the fold is different, for in this species it is divided into a complicated series of narrow lamellæ. Fig. 58 shows the appearance of these as dimly seen through the wall of the vesicle, while Pl. XIV, fig. 65, shows them in section. Each

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[1] I use the terms "dorsal" and "ventral" in a morphological sense, the dorsal side being that to which the artery is attached. Generally, however, the vesicle lies on its side, owing to the twisting of the duct, and the attachment of the artery to the floor of the body-cavity beyond the vesicle.

lamella seems to be composed of a double layer of peculiar rounded or polygonal cells with thick walls.

The hind end of the pedal gland is also enlarged to form a vesicle in Rhytida,[1] Paryphanta,[2] and Schizoglossa,[3] and indeed this is probably the case in all the genera of the Rhytididæ, for I have found such a vesicle in Natalina as well. Moreover, Beutler[4] has shown that in Paryphanta it contains a large fold similar to that in Apera, but apparently less highly specialised in structure. In Testacella there is also a dorsal fold[5] projecting into the duct at the hind end of the pedal gland, but the structure of the fold appears to be very different from that of Apera, and there is no terminal enlargement of the gland to form a vesicle.

Various possibilities suggest themselves with regard to the function of the terminal vesicle of the pedal gland, and the fold which it contains; but so little is known about the physiology of the gland in the carnivorous genera that such speculations can have little value. It is better, therefore, simply to state that the function of these structures is at present unknown.

THE NERVOUS SYSTEM.

The central nervous system of Apera consists of three compact ganglionic masses joined by connectives. The first of these is formed of the cerebral ganglia, the second of the buccal ganglia, and the third of the pedal, pleural, and visceral ganglia.

THE CEREBRAL GANGLIA AND COMMISSURES.—As in nearly all carnivorous snails and slugs, excepting Daudebardia[6] and

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[1] Collinge, W. E., 'Ann. Mag. Nat. Hist.' (7th ser.), 1901, vol. vii, pp. 67, 68, pl. i, figs. 12, 13.

[2] Collinge, op. cit., p. 70, pl. ii, figs. 21, 24; Murdoch, 'Trans. N.Z. Inst.,' 1904, vol. xxxvi, p. 158, pl. vi, fig. 7.

[3] Murdoch, R., 'Proc. Mal. Soc.,' 1901, vol. iv, p. 170, pl. xvii, fig. 10.

[4] 'Zool. Jahrb.,' 1901, vol. xiv, p. 376, pl. xxvi, fig. 7.

[5] Plate, L. H., 'Zool. Jahrb.,' 1891, vol. iv, p. 525, pl. xxxii, figs. 17, 18.

[6] Plate, op. cit., pp. 589, 593.

the Trigonochlaminæ,[1] the cerebral ganglia are situated very near together on the dorsal side of the buccal mass. Indeed, in Apera gibbonsi they are so closely bound to each other by connective tissue that they appear as one (Pl. XIII, fig. 52); and it is only in the smaller species, such as A. parva (fig. 53) and A. purcelli (fig. 55), that they can be clearly seen to be separate ganglia without the help of any reagents. When freed from their surrounding tissue, the ganglia are seen to be oval structures, nearly twice as long as they are broad, and rather nearer together behind than in front (Pl. XV, figs. 70–72). Their average length in Apera is about $\frac{3}{4}$ mm. Towards the outer side of the front end of each ganglion there is a slight eminence formed by the accessory lobe. This is best seen in A. dimidia. In this species the apex of each lobe is prolonged into a filament, which is very like a slender nerve (fig. 71), but is probably the remains of the embryonic cerebral tube which originally connected the accessory lobe with the exterior. Similar accessory lobes have been figured by de Lacaze-Duthiers[2] in Testacella, by Wiegmann[3] in Ennea (Edentulina), and by Beutler[4] in Paryphanta, and the last author has described them at some length.

The cerebral ganglia are joined by two commissures, namely, the cerebral commissure above the buccal mass, and the sub-cerebral commissure below it. The cerebral commissure is very short and broad, and is situated somewhat towards the posterior ends of the ganglia (Pl. XV, fig. 71). The sub-cerebral commissure, on the other hand, is very long and extremely slender. It arises from about the middle of the outer sides of the ganglia, and encircles the buccal mass just in front of the cerebro-pedal connectives and the pedal ganglia, being closely bound to these by connective tissue

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[1] Simroth, H., 'Festschrift Leuckarts,' 1892, pp. 53, 55.

[2] 'Arch. Zool. Expér.' (2nd ser.), 1887, vol. v, pl. xxxviii, figs. 70, 71.

[3] 'Mitt. Zool. Samml. Mus. Nat. Berlin,' 1898, vol. i, pl. iii, fig. 7.

[4] 'Zool. Jahrb.,' 1901, vol. xiv, pl. xxix, figs. 58, 61, and pp. 400–402; see also Pelseneer, 'Mém. Acad. Roy. Belg.,' 1901, ex. vol. liv, pp. 31–37.

(figs. 73 and 74). It thus forms the most anterior element of the nerve-collar. Amandrut[1] has described a similar sub-cerebral commissure in Achatina panthera (*Fér.*), Bulimus funki (*Nyst.*), Nanina cambodjiensis (*Reeve*), and Helix aspersa *Müll.*; but hitherto this slender commissure has been noticed in only a very few Pulmonates and in none of the carnivorous forms. I have found it, however, in Natalina quekettiana (*M. & P.*), the only member of the Rhytididæ whose ganglia I have examined microscopically; and I believe that if malacologists would examine the central nervous system of snails with greater care they would find it in many other pulmonate genera. For among the marine Euthyneura a sub-cerebral commissure has been observed not only in the Pleurobranchidæ and in numerous Nudibranchs,[2] but also in so primitive a form as Actæon.[3] Moreover, I am inclined to regard the sub-cerebral commissure as homologous with the important labial commissure found in the Aspidobranchia, and in Vivipara and Ampullaria among the Pectinibranchia, as well as in the Amphineura, Scaphopoda, and Cephalopoda.[4] In most of these forms the cerebro-buccal connectives arise from the labial commissure instead of from the cerebral ganglia themselves, and in Apera the cerebro-buccal connectives arise from the ganglia very close to the ends of the sub-cerebral commissure.

A little further back arise the thick cerebro-pedal connectives; and behind this again, nearly at the posterior end of the ganglia, the almost equally broad cerebro-pleural connectives arise. In the specimen of Apera dimidia that I

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[1] 'Bull. Soc. Philom. Paris' (7th ser.), 1885–86, vol. x, pp. 107–117; 'Ann. Nat. Sci., Zool.,' 1898, vol. vii, p. 127.

[2] Pelseneer, P., 'Mém. Couronné Acad. Roy. Belg.,' 1893, ex. vol. liii, p. 69.

[3] Bouvier, E. L., 'Bull. Soc. Philom. Paris' (8th ser.), 1893, vol. v, p. 67.

[4] Pelseneer has shown that the so-called "labial commissure" which Pleurobranchæa and a few other forms possess in addition to the sub-cerebral commissure, is merely an anastomosis of two of the nerves to the lips (op. cit., p. 33).

examined, these two connectives were joined on the right side by a short transverse filament not far from their origin (Pl. XV, fig. 71).

THE NERVES OF THE CEREBRAL GANGLIA.—From each cerebral ganglion arise two large nerves which are as thick as the cerebro-pedal and cerebro-pleural connectives. These are the olfactory nerve to the upper tentacle, and the nerve to the lower tentacle. The olfactory nerve springs from the upper surface of the anterior end of the ganglion, towards the inner side (Pl. XV, figs. 70–72). Near its origin there also arise three slender nerves, namely, the two peritentacular nerves, and the optic nerve, which is distinct from the olfactory nerve even from the ganglion. The nerve to the lower tentacle arises nearer the outer edge of the ganglion than the four nerves just described, and external to the accessory lobe. Near it arise the two labial nerves, which are very much narrower than the nerve to the lower tentacle, but not quite so slender as the optic and peritentacular nerves. As in most genera the nerve to the penis also springs from this region in the right cerebral ganglion; it is of about the same thickness as the labial nerves. Bentler[1] states that in Paryphanta hochstetteri (*Pfr.*) the penial nerve does not arise separately from the cerebral ganglion, but seems to branch from one of the other nerves. On the other hand, in the Streptaxidæ[2] the nerve to the penis arises directly from the pedal ganglion, instead of its fibres first traversing the right cerebral ganglion, as is usually the case.

Near the origin of the sub-cerebral commissure a very slender nerve arises on each side, and runs down with it in the connective tissue on the anterior side of the cerebro-pedal connective. Above this connective, on the dorsal surface of each ganglion, there arises another very slender nerve, which at first goes obliquely backwards, but quickly curves outwards, and runs down to the ventral group of ganglia between the two connectives. This is almost certainly the nervus

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[1] Op. cit., p. 400.

[2] Wiegmann, F., op. cit., p. 62.

otocysticus, although I was unable to find the otocysts themselves even in sections of the pedal ganglia. Lastly, a slender nerve arises from each ganglion between the two connectives, usually nearer to the cerebro-pleural connective than to the other. In Apera dimidia, A. purcelli, A. burnupi, and A. sexangula these nerves run back to the anterior end of the buccal retractor, which they innervate. Each gives off two branches close to the cerebral ganglia; one of these anastomoses with the cerebro-buccal connective not far from its origin; the other runs down between the cerebro-pedal and cerebro-pleural connectives, and divides into two about half way to the ventral group of ganglia. One of the divisions of this branch leaves the nerve collar and innervates the retractor of the lower tentacle.[1] The other division continues down to the ventral ganglia; but whether it fuses with the pleural ganglion, as one might expect from Amaudrut's observations,[2] or whether it merely crosses the dorsal surface of the ventral group of ganglia and leaves it again in the wall of the buccal artery, I was unable to discover with the limited amount of material at my disposal. The examination of these slender nerves, deeply embedded amongst the connective tissue and blood-vessels which surround the larger nerve-cords and ganglia, is a matter of considerable difficulty; but it does not even require a compound microscope to see that the anterior end of the buccal retractor in A. dimidia, A. sexangula, and their allies is innervated by nerves arising from the sides of the cerebral ganglia. This is one of the very few respects in which Apera resembles Daudebardia more than any other carnivorous genus with which I am acquainted.[3] In A. gibbonsi the buccal mass with the odontophore is much

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[1] In Natalina quekettiana (*M. & P.*) and Rhytida capillacea (*Fér.*) the retractors of the lower tentacles are also innervated by very slender nerves issuing from the nerve-collar about half-way down each side, and this is probably the case in several other forms as well.

[2] 'Ann. Nat. Sci., Zool.,' 1898, vol. vii. pp. 123–126.

[3] See Plate, L. H., 'Zool. Jahrb.,' 1891, vol. iv, p. 591.

larger, and the buccal retractors are more highly developed, and it might therefore have been expected that these nerves would have been larger and more conspicuous than in the other species of Apera. The opposite is the case. In this form the corresponding nerves are extremely slender. They are joined for some distance with the cerebro-buccal connectives (Pl. XIII, fig. 52), and then leave these and unite with the sheath of the odontophore at the anterior end of that organ. A possible explanation of this apparent anomaly will be found in my account of the morphology of the buccal retractors.[1]

The Buccal Ganglia.—The buccal or stomato-gastric ganglia are situated close together on the dorsal surface of the odontophore, just behind and beneath the front end of the œsophagus. In Apera burnupi and A. sexangula they are usually in front of the cerebral ganglia, the cerebro-buccal connectives curving forwards (Pl. XIII, figs. 56 and 57). In A. dimidia and A. purcelli they are normally situated a short distance behind the cerebral ganglia, when the odontophore is not protruded (figs. 54, 55). Lastly, in A. gibbonsi and A. parva the buccal ganglia are generally very far behind the cerebral ganglia, and the cerebro-buccal connectives are unusually long in consequence, often attaining a length of 5 or 6 mm. in the former species (Pl. XIII, figs. 52, 53, and Pl. XV, fig. 70). This posterior position of the buccal ganglia and the consequent lengthening of the cerebro-buccal connectives is not uncommon among carnivorous snails and slugs, and is entirely due to the increase in size of the buccal mass corresponding to the growth of the radula. As the buccal mass becomes larger and longer, the opening of the œsophagus, with the buccal ganglia behind it, is pushed back until it comes to lie posterior to the cerebral ganglia, and should this process be continued still further, the cerebro-buccal connectives must be correspondingly lengthened if the cerebral ganglia are to remain in their original position near the sense-organs. Moreover, the

[1] See pp. 173, 174.

longer the cerebro-buccal connectives, the more freely can the odontophore be protruded ; for it is evident that when the buccal ganglia normally lie behind the cerebral ganglia, the odontophore bearing the buccal ganglia can be brought forward a distance equal to twice the length of the connectives without moving the cerebral ganglia at all.

The buccal ganglia are rounded or oval, and joined to each other by a short buccal commissure. As might have been expected, they are proportionately larger and closer together in those forms in which the odontophore is very large than in such species as A. burnupi, in which the odontophore is much smaller. In A. gibbonsi the ganglia, when freed from the connective tissue which surrounds them, are seen to be almost as near to each other as are the cerebral ganglia (Pl. XV, fig. 70).

THE NERVES OF THE BUCCAL GANGLIA.—Three slender nerves arise from the anterior part of each buccal ganglion (figs. 70–72). One of these becomes attached to the salivary duct of the same side, and passes backwards to the salivary glands. The other two go to the œsophagus, one bifurcating soon after it leaves the ganglion. Two more pairs of nerves arise laterally from the ganglia and innervate the sides of the buccal mass and odontophore, one pair going forwards and the other backwards. These nerves are especially large in Apera gibbonsi, in which the parts they innervate are so greatly developed. The anterior lateral nerve passes forwards to the side of the buccal mass in front of the œsophagus, and in this species it is generally united at its origin for a very short distance with the cerebro-buccal connective on the same side. In A. sexangula, on the other hand, this nerve appears to be united near the ganglion with the posterior lateral nerve, a fact which is probably connected with the anterior position of the buccal ganglia in this species. The posterior lateral nerve on each side passes to the sheath of the odontophore, and bifurcates as it does so. The outer and more slender branch, after passing through the external longitudinal muscles, runs down the sides of the odontophore in the circular muscles of the sheath, which it doubtless innervates. The inner and larger branch goes more deeply. It runs down in the suspensor muscles of the odontophoral support and then divides, one division running forwards and the other backwards in the angle of the groove between the lower ends of the suspensor muscles and the origin of the lateral retractors of the radula.[1]

The nerves which innervate the central part of the odontophore are widely separated from the other buccal nerves in their origin. They arise from the inner sides of the buccal ganglia, or even from the buccal commissure, and consist of two rather large nerves and usually one or two others which are very much smaller. These nerves pass through the sheath of the odontophore, and run back with the median dorsal muscle until it dips down between the lateral retractors of the radula. They then curve forwards again at a lower level, and are distributed where the retractors are inserted on the radula-sac. But the most remarkable feature about these nerves is their asymmetrical origin. The left of the two main nerves always arises nearer the middle line than the right; indeed, it might be said that while the right nerve arises from the inner side of the right ganglion, the left nerve arises from the commissure, though towards its left end (see especially Pl. XV, fig. 71). This asymmetry seems to be a constant feature of the genus Apera, for I have examined microscopically the buccal ganglia of five specimens, belonging to three different species, and they all show it. Yet it is very surprising, for the odontophore is one of the few organs which is generally supposed to have escaped the effects of the torsion which has played such havoc with the symmetry of Gastropods. And, in fact, the odontophoral muscles of Apera do seem to be quite symmetrically arranged, and the odontophore occupies an approximately symmetrical position, and even the extrinsic buccal retractors show no traces of asymmetry excepting towards the hind end of the animal. Since the cause of this asymmetry cannot be

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[1] See pp. 166, 167.

found in Apera itself, we must inquire whether it can be discovered in the snails from which the genus may have sprung.

There are certain muscles in the odontophore of Apera and Natalina—the flexor muscles of the odontophoral support—which, when they are contracted, tend to curve up its front end. When this happens the odontophore is likely to turn on to its right side, for there is not room for it to become curved in a vertical plane above the pedal gland, and the reproductive organs will prevent it turning on to its left side and curving outwards to the right. And in the only specimen of Apera that I have seen in which these muscles were contracted, the odontophore was on its right side, curving outwards to the left. Now in carnivorous snails with a dextral heliciform or depressed shell, an odontophore which curves outwards to the left will fit into the body-whorl of the shell much better than one that is straight, when the animal retires into its shell; and the oblique pull of the retractor muscles arising from the columella of the shell will tend to maintain this curvature. Thus one might expect to find that in such snails the anterior part of the odontophore would be normally lying on its right side, with the opening of the œsophagus lateral instead of dorsal; and this is exactly what has been found to be the case in Paryphanta hochstetteri (*Pfr.*)[1] and Natalina trimeni (*M. & P.*).[2] The nerve-collar would not be rotated to any extent, as both the cerebral and ventral ganglia would be held in position by the nerves which radiate from them to the skin, tentacles, etc., on each side; but owing to the odontophore curving outwards to the left, the cerebro-pedal and cerebro-pleural connectives would become much more lengthened on the left side than on the right (see Beutler's fig. 60). The buccal ganglia, however, would obviously be involved in the rotation. But owing to the fact that the cerebral ganglia are broader than the buccal ganglia,

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[1] Beutler, B., 'Zool. Jahrb.,' 1901, vol. xiv, p. 377, pl. xxix, fig. 60.

[2] Pace, S., 'Proc. Mal. Soc.,' 1895, vol. i, p. 233.

the left cerebro-buccal connective would become stretched, and would consequently retard the rotation of the buccal ganglia to some extent, so that they would come to lie slightly to the left of the opening of the œsophagus and the median line of the odontophore.[1] The result of this would be that the nerves from the buccal ganglia would slope obliquely to the right, as shown in the accompanying diagram, and this would tend to shift their origin to the right. When the shell became degenerate and the animal assumed a symmetrical form, the odontophore would tend to return to its original condition and to lie in a straight line between the mouth and the buccal retractor[2]; but it might be a long time before the buccal nerves moved back again to their symmetrical position. Now, as I shall attempt to prove later, it is not improbable that Apera may have been evolved from a group of

Text-fig. 1.

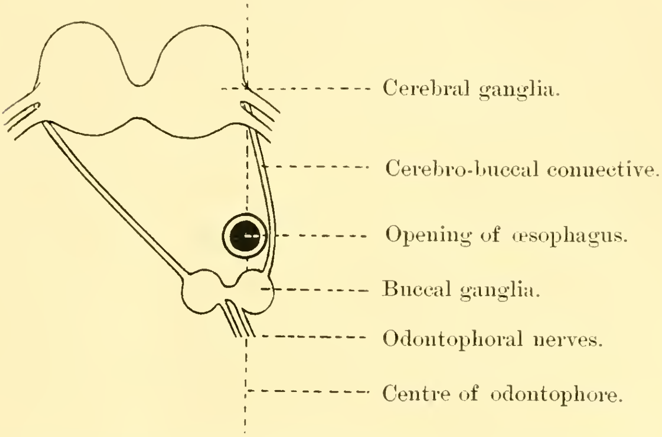

Diagram illustrating the possible origin of the asymmetry of the odontophoral nerves of Apera.

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[1] Cf. Plate, L. H., 'Zool. Jahrb.,' 1891, vol. iv, pl. xxxvii, fig. 102.

[2] The effect of the slightly asymmetrical origin of the buccal retractor would be counteracted by the pressure of the reproductive organs on the right side.

carnivorous snails with dextral heliciform or depressed shells; therefore it seems possible that the above explanation of the asymmetry of the nerves of the odontophore may be not very far from the truth.

The Ventral Group of Ganglia.—Beneath the odontophore or the posterior part of the buccal mass, and a little further back than the cerebral ganglia, there lie six ganglia very close to each other. These are the two pedal, the two pleural, and the two visceral ganglia. In Apera purcelli the limits of each of these ganglia can be clearly seen, although they are very near together; but in some of the larger forms, such as A. gibbonsi, the separate ganglia can only be distinguished with difficulty, so closely are they aggregated (Pl. XIV, fig. 67). These ganglia are joined to the cerebral ganglia by the cerebro-pedal and cerebro-pleural connectives, the length of which varies directly with the size of the buccal mass and odontophore. Thus in A. gibbonsi these connectives are very long, so as to permit of the protrusion of the enormous odontophore (Pl. XIII, fig. 52), while in A. burnupi and A. sexangula they are fairly short. The connectives are sometimes slightly, but rather abruptly, swollen at their junctions with the pedal and pleural ganglia (Pl. XIV, fig. 68).

The most anterior of these ganglia are the pedal ganglia, which are also more ventrally situated than the others. These are the largest ganglia in the nervous system, being even larger in Apera than the cerebral ganglia. They are somewhat oval in shape, and very close together. Two short commissures connect them, one anterior and dorsal, the other further back and more ventrally situated (Pl. XV, fig. 74). The first of these is usually termed the pedal commissure, and is shown in section in Pl. XIV, fig. 68; the second is known as the parapedal commissure, and is seen to be rather thinner than the other in vertical section. Beutler[1] has found both commissures in Paryphanta hochstetteri (*Pfr.*), and it is probable that they occur in all the Euthy-

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[1] Op. cit., p. 402.

neura, both Pulmonates and Opisthobranchs.[1] The anterior commissure appears to be of mixed origin, for an examination of serial sections through the region of this commissure in A. dimidia seems to show that at least in its upper half it is largely composed of nerve-fibres emanating from the pleural ganglia. It is interesting to notice that in the Neritidæ and Helicinidæ the commissure connecting the pleural ganglia, instead of traversing the pedal ganglia, as it seems to do in most forms, remains quite separate from them.[2]

The pleural ganglia are oval structures less than half the size of the pedal ganglia. They are situated more laterally than the other ventral ganglia, but overlap the posterior part of the outer sides of the pedal ganglia, with which they are intimately united by extremely short connectives. Pl. XIV, fig. 68, shows a section of the right pleural ganglion just behind the pleuro-pedal connective.

The two visceral ganglia lie partly between and partly behind the pleural ganglia, to which they are joined by very short connectives. An equally short visceral commissure unites them. They overlap the hind ends of the pedal ganglia, but it need hardly be said that they have no direct nervous connection with these centres. Both visceral ganglia are larger than the pleural ganglia and considerably smaller than the pedal ganglia, but the left is always slightly larger than the right, and gives off a larger number of nerves. For, while the right one is simply the right parietal or supra-intestinal ganglion, the left is to be regarded as formed by the union of the left parietal ganglion with the median abdominal ganglion and is therefore composite. And it is only because the right parietal ganglion is usually much larger than the left that the difference in size between the two visceral ganglia of Apera is not greater. A similar fusion between the left parietal and the abdominal ganglia occurs in the Helicidæ, but so far as I am aware the only

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[1] Pelseneer, P., 'Mém. Acad. Roy. Belg.,' 1901, ex vol. liv, pp. 43–45.

[2] Bourne, G. C., 'Proc. Zool. Soc. Lond.,' 1908, pl. lv, figs. 36, 37, pl. lvi, fig. 38; and 1911, pp. 791, 792, pl. xxxviii, figs. 49, 50.

carnivorous form in which this has hitherto been observed is Rhytida inæqualis (*Pfeiffer*).[1] In Selenochlamys,[2] Testacella, Euglandina, Streptostyla,[3] Salasiella,[4] and Paryphanta[5] the three visceral ganglia remain distinct, and I have found that this is also the case in Natalina and in Rhytida capillacea (*Fér.*). In Daudebardia the abdominal is fused with the right parietal ganglion.[6] Lastly, in the Streptaxidæ, the three visceral ganglia are all more or less fused to form a single mass, which is separated from the pleural ganglia by long connectives.[7]

Some of the nerve-cells in the ventral group of ganglia are remarkably large, especially those in the posterior parts of the visceral ganglia (Pl. XIV, fig. 67). One of the cells in the right parietal ganglion of a specimen of Apera gibbonsi rubella measures ·18 mm. × ·143 mm., and its nucleus is no less than ·16 mm. × ·11 mm. Fig. 69 represents a photomicrograph of a section through one of these large cells in the right parietal ganglion of A. dimidia, and shows the granular appearance of the large nucleus and its prominent nucleolus.

THE NERVES OF THE VENTRAL GANGLIA.—The numerous pedal nerves arise in an irregular longitudinal line along the ventral surface of each pedal ganglion (Pl. XV, figs. 73, 74),

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[1] Fischer, P., 'Journ. de Conchyl.' (3rd ser.), 1873, vol. xiii, p. 8, pl. iii, fig. 6.

[2] Simroth, H., 'Festschrift Leucharts,' 1892, p. 55, pl. vi, fig. 15. According to Simroth, the three visceral ganglia also remain separate in Phrixolestes, but in the other genera of the Trigonochlaminæ they tend to fuse with one another, and even with the pleural ganglia in Trigonochlamys itself (see Bronn's 'Klassen u. Ordn. Tier-Reichs III, Gastr. Pulmonata,' 1910, p. 257, fig. 80).

[3] Crosse and Fischer, 'Mission scientifique au Mexique,' 1878, pl. iv, fig 5.

[4] Strebel, H, 'Beitrag z. Kenntniss d. Fauna Mexik. L.-u. Süsswasser-Conchylien.' 1878, vol. iii, pl. x, fig. 7.

[5] Beutler, op. cit., p. 403, pl. xxix, fig. 59.

[6] Plate, op. cit., p. 590, pl. xxxvi, figs. 94, 97.

[7] Wiegmann, F., 'Mitt. Zool. Samml. Mus. Nat. Berlin,' 1898, vol. i, p. 61.

and are distributed to all parts of the foot. The most posterior nerves, which arise from the extreme hind end of the ganglia, are the largest, and run back for almost the whole length of the animal, as will be seen from fig. 75. This figure also shows that the other pairs of pedal nerves are not arranged quite symmetrically. The pedal gland is innervated by a pair of nerves which branch from the inner sides of the most anterior pair of pedal nerves. The size of these nerves to the pedal gland is in direct proportion to the size of the gland itself; thus in Apera dimidia, with its highly developed pedal gland, the nerve is larger than in A. sexangula, as will be seen by comparing figs. 73 and 74.

From the sides of the ventral group of ganglia a large number of nerves radiate to the skin on each side of the body and head, passing below the tentacular retractors, but above the vagina and the adjacent part of the vas deferens on the right side (Pl. XIII, fig. 57). These are the nerves that de Lacaze-Duthiers termed the "nerves of the neck." The most posterior of these nerves can be seen running back on each side along the inner surface of the body-wall sometimes nearly as far as the diaphragm, thus confirming the hypothesis that all this region of the skin corresponds to that of the neck of ordinary snails and slugs. The posterior ends of the common retractors of the tentacles also receive nerves belonging to this group. All these lateral nerves appear to arise by repeated branching from three main roots on each side of the ventral ganglia. The most anterior root springs from the outer edge of the pedal ganglion a little behind the cerebro-pedal connective. The second arises from the junction of the pedal and pleural ganglia—that is to say, from the very short pleuro-pedal connective. The third and most posterior root arises from the pleural ganglion itself. Fischer's figures of the nervous system in Rhytida inæqualis (*Pfr.*) and the Oleacinidæ also show nerves arising from the pleural ganglia, but according to de Lacaze-Duthiers, Plate, Wiegmann, and Beutler, no nerves arise from the pleural ganglia in Testacella, Daudebardia, Ennea (Edentulina) and Paryphanta.[1] It must be remembered that at least some of these authors believed that the pleural ganglia never did give rise to nerves in the Pulmonata, a belief that Amaudrut[2] has shown to be altogether erroneous. At the same time it is unlikely that all these careful observers would have figured the "nerves of the neck" as arising solely from the pedal ganglia, if in all carnivorous forms they arise partly from the pleural ganglia, as they undoubtedly do in Apera. Moreover the fact that the central roots of these nerves arise in Apera exactly from the junction of the pedal and pleural ganglia also suggests that the more posterior "nerves of the neck" arise indifferently either from the outer side of the pedal ganglia or from the pleural ganglia. This seems to uphold the theory that the outer dorsal portions of the so-called pedal ganglia of most Gastropods are in reality parts of the pleural nerve-centres which have become united with the pedal ganglia, and that all the "nerves of the neck" therefore spring from the pleural division of the central nervous system. The composite nature of the pedal ganglia has been shown to be specially evident in some of the most primitive Gastropods, such as Pleurotomaria;[3] and the fact that the so-called pedal commissure contains, as we have seen, nerve-fibres emanating from the pleural ganglia affords additional evidence in favour of this theory.[4]

The nerves arising from the visceral ganglia are fewer

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[1] For references, see p. 148.

[2] 'Ann. Sci. Nat., Zool.,' 1898, vol. vii, p. 128.

[3] Bouvier and Fischer, 'Journ. de Conchyl.,' 1899, vol. xlvii, pp. 109–143.

[4] It is interesting to note that in Aplysiella and some species of Aplysia, as well as in the Gymnosomata, the cervical nerves also arise partly from the pleural and partly from the pedal ganglia, although they anastomose to form a single plexus (Pelseneer, 'Mém. Couronné Acad. Roy. Belg.,' 1893, ex vol. liii, p. 27, pl. x, fig. 81); while in the Auriculidæ these nerves may arise either from the pleural ganglia or from the pleuro-pedal connectives (Bouvier, 'Comptes Rendus Soc. de Biologie' (9th ser.), 1892, vol. iv, p. 990).

than in most genera, probably because they innervate a region of the body which is greatly reduced in Apera. The origin of these nerves is shown in Pl. XV, figs. 73 and 74, and their distribution in A. dimidia will be seen from fig. 75.

One important nerve arises from the right parietal or supra-intestinal ganglion, not far from its junction with the other visceral ganglion, and innervates the right wall of the mantle-cavity. This may be regarded as the right pallial nerve. The corresponding left pallial nerve is more slender, and arises from the outer or parietal portion of the left visceral ganglion. This nerve innervates the left wall of the mantle-cavity. From the median or abdominal portion of the left visceral ganglion two large nerves arise close together. That to the left becomes closely united for some distance with the buccal retractor in Apera dimidia, and then runs back on the right side of the rectum, and eventually branches around the anus and respiratory orifice. The right abdominal nerve is joined to the aorta for almost the whole of its length, but at its hind end the nerve leaves the blood-vessel and enters the diaphragm, which it probably innervates. Beyond this the nerve becomes attached to the adjacent wall of the pericardium, and can be traced backwards to a point just behind the opening of the reno-pericardial duct. The other nerves from the visceral ganglia are also attached to the aorta for some distance, the left pallial nerve being the first to become free. One or two small additional nerves can be seen with a strong objective to leave the visceral ganglia and run along in the tissue surrounding the aorta, but these are so extremely fine that I was unable to trace them far. Thus only four nerves of any importance arise from the visceral ganglia in Apera—two pallial and two abdominal; and inasmuch as the abdominal portion of the left ganglion is probably itself formed from the union of the sub-intestinal ganglion with the original median abdominal ganglion,[1] it follows that there is but one nerve corresponding to each original ganglion on the visceral loop.

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[1] Pelseneer, P., 'Mém. Acad. Roy. Belg.,' 1901, ex vol. liv, pp. 47, 48.

THE NERVOUS SYSTEM AS A WHOLE.—It will have been seen from the above account that the central nervous system of Apera may be regarded as formed of five sections, each with a single pair of ganglia. These five sections are diagrammatically represented in the accompanying text-figure. There is first the buccal section, which is the most anterior only in A. burnupi and A. sexangula. This innervates the anterior part of the alimentary canal, including the odontophore and salivary glands. Secondly, there is the

TEXT-FIG. 2.

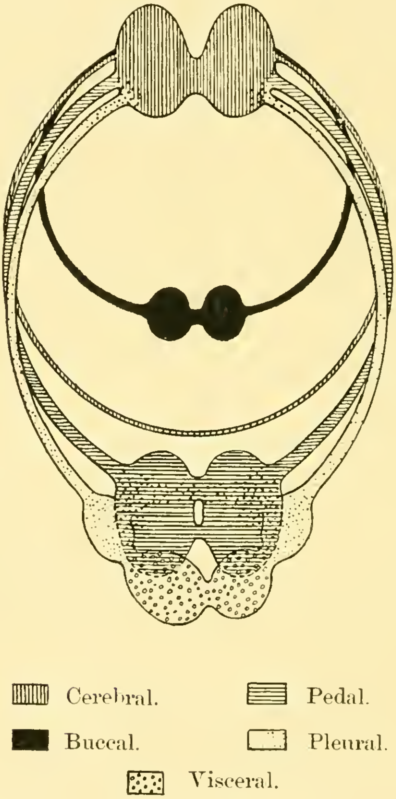

Diagram of the central nervous system of Apera.

cerebral division, which is connected with the sense-organs of the head,[1] and is the only section in which the nerve-cells are aggregated to form ganglia on the dorsal side of the alimentary canal. Thirdly, there is the pedal section, which innervates the foot and pedal gland. Fourthly, there is the pleural section, innervating the sides of the body and head. And fifthly, there is the visceral section, which innervates the neighbourhood of the mantle-cavity.

And just as there are five pairs of ganglia, so also are there five commissures ventral to the alimentary canal, as will be clearly seen from the diagram. Now some authors have thought that there were only three such commissures in the Pulmonata, and very few have found more than four. Must we then regard Apera as exceptional in this respect? I think not. For it seems probable that further researches will show that there are normally five commissures ventral to the alimentary canal in the Euthyneura, although the slender sub-cerebral commissure may have entirely disappeared in some Pulmonates, just as in the Streptoneura the corresponding labial commissure seems to have disappeared in many of the Pectinibranchia.

THE STRUCTURE OF THE UPPER TENTACLES, AND THE TENTACULAR RETRACTORS.

In Pl. XVI, the figs. 80–86 represent photomicrographs of serial sections through the left upper tentacle of Apera dimidia in its retracted condition. It will be seen that the olfactory organ is large and extends forwards in front of the eye, thus reducing the width of the cavity in the retracted tentacle. The eye itself appears to be of the usual structure, the small size of the lens being possibly due to contraction. The retina is very deeply pigmented. The

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[1] It is not improbable that the motor nerve to the buccal retractor should be regarded as belonging to the pleural section, for it arises close to the origin of the cerebro-pleural connective.

nerves from the different parts of the olfactory organ converge and unite behind the level of the eye to form the large olfactory nerve, which runs back for a considerable distance in the centre of the posterior part of the tentacle. The much smaller optic nerve is situated laterally, being embedded in the muscle-fibres on the outer side of the olfactory nerve. These longitudinal muscle-fibres make their appearance just behind the sense-organs, and are chiefly restricted to the peripheral part of the retracted tentacle; but as they are traced backwards they gradually increase in number, and become united into muscular strands, which coalesce with one another to form the retractor of the tentacle. In the spaces between these strands, before they all coalesce, large cells occur, as will be seen from fig. 84. These large cells stain rather deeply, and have rounded nuclei, containing prominent nucleoli. They are evidently homologous with the somewhat similar cells that Beutler[1] found in the tentacles of Paryphanta hochstetteri (*Pfr.*). In this region the tentacle is rather darkly coloured; yet the pigment-granules are not contained in these large cells, but are confined to narrow filaments which surround the cells and the different strands of muscle. Moreover the pigment extends a little further back, even slightly beyond the point shown in fig. 86, where the olfactory and optic nerves emerge from the tentacular retractor and curve over to the cerebral ganglion (Pl. XIII, figs. 52–55).

Not more than 2 or 3 mm. further back the retractor of the upper tentacle is joined by that of the lower tentacle, which is narrower and lies more ventrally. The common retractor thus formed is of no great length. It arises from the side of the body-wall between a quarter and a third of the distance from the head to the hind end of the animal. The common tentacular retractors of each side have no connection with each other or with the buccal retractor; on the contrary, the three retractors have become unusually widely separated in their origin. On the right side the retractors of the upper

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[1] 'Zool. Jahrb.,' 1901, vol. xiv, p. 404, pl. xxix, figs. 63, 64.

and lower tentacles are separated by the penis, which projects between them (Pl. XIII, figs. 52–57; see p. 190).

In one specimen of Apera sexangula I found that the retracted upper tentacles were joined by a transverse connection slightly anterior to their junction with the olfactory and optic nerves (Pl. XV, fig. 76). The transverse connection was pigmented in the same way as the tentacles themselves. This remarkable abnormality reminds one of the more striking monstrosity figured by Forbes and Hanley,[1] in which the upper tentacles of a specimen of Agriolimax agrestis (*Lin.*) were united throughout their entire length.

The posterior ends of the common tentacular retractors receive nerves arising from the pleural ganglia (or possibly from the short pleuro-pedal connectives); and the retractors of the lower tentacles are innervated, as already described, by nerves issuing from the sides of the nerve-collar between the cerebro-pedal and cerebro-pleural connectives, but probably emanating from the cerebral ganglia by the same roots as the nerves to the buccal retractors.

Beneath the tentacular retractors a few smaller muscles arise on each side and run forward to the anterior part of the head. These are best seen in Pl. XIII, fig. 57. The largest of these minor cephalic retractors is inserted in the upper lip of the pedal gland. It is doubtless the contraction of these muscles, together with the combined action of the buccal and tentacular retractors, which causes the front of the head to be invaginated in some specimens.

THE DIGESTIVE SYSTEM.

THE MOUTH AND THE RADULA-SAC.—As in most carnivorous genera, the mouth has three main lips, one dorsal and two lateral, arranged like the sides of an inverted isosceles

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[1] 'Hist. Brit. Mollusca.' 1853, vol. i, pl. JJJ, fig. 4.

triangle. But it will be seen from Pl. XV, fig. 77, and Pl. XVI, fig. 88, that the buccal cavity has four sides, and only appears somewhat triangular owing to the narrowness of the ventral wall. These figures also show the great thickness of the sides of the buccal mass—a feature which is still better seen in Pl. XVI, fig. 87. Externally there is a layer of longitudinal muscles, which is thin in Apera dimidia and A. sexangula, but somewhat thicker in A. gibbonsi. Within this there is a very thick layer consisting chiefly of circular muscles, but also containing some radial and a few longitudinal fibres. The last become more numerous towards the inner surface, so as almost to form a third muscular layer in which the longitudinal predominate over the circular fibres. Lastly, the cavity is lined by a compact cubical epithelium which is continuous over the lips with the epidermis of the skin. The cells composing this epithelium are small, and their nuclei are situated towards their outer ends—that is to say, the ends turned away from the cavity. Towards the opening the epithelial cells become taller, and the translucent cuticle which they secrete is considerably thickened on the lips. There is, however, no jaw in Apera.

At its hind end the buccal cavity extends into a long tubular diverticulum, which opens into the centre of the posterior wall of the cavity. This is the radula-sac, and is shown in longitudinal section in Pl. XVII, fig. 92, and in transverse section in Pl. XVIII, figs. 116–120. It will be seen that a broad fold or cushion projects like a typhlosole from the upper wall into the cavity, and renders the latter crescentic in section. Towards the hind end of the radula-sac the edges of this cushion are spirally rolled (fig. 119). Further forward a narrow longitudinal ridge occurs dorsally at each side of the cushion. The epithelium on the sides and floor of the radula-sac consists of small cubical cells, compactly arranged, and not unlike those lining the buccal cavity itself; but the epithelium on the cushion is of a quite different character, being composed of very tall and remarkably irregular cells

(Pl. XVI, fig. 89). The centre of the cushion is loosely filled with connective tissue. Immediately surrounding the whole radula-sac is a thin layer of circular muscles.

Around the periphery of the hind wall of the buccal cavity there is a circular groove, which is deepened dorsally and ventrally (Pl. XVIII, figs. 115, 116). The dorsal pocket is of no great depth, and is connected with the opening of the radula-sac by a median vertical groove. The ventral pocket, on the other hand, is much deeper, and contains the anterior end of the radula, which is thus folded back below the remaining part in the radula-sac (Pl. XVII, fig. 92). Between the opening of the radula-sac and that of the ventral pocket there is a slight projection formed by the front end of the odontophoral support covered by the radula, and it is this projection that is the first to appear when the odontophore is protruded through the mouth.

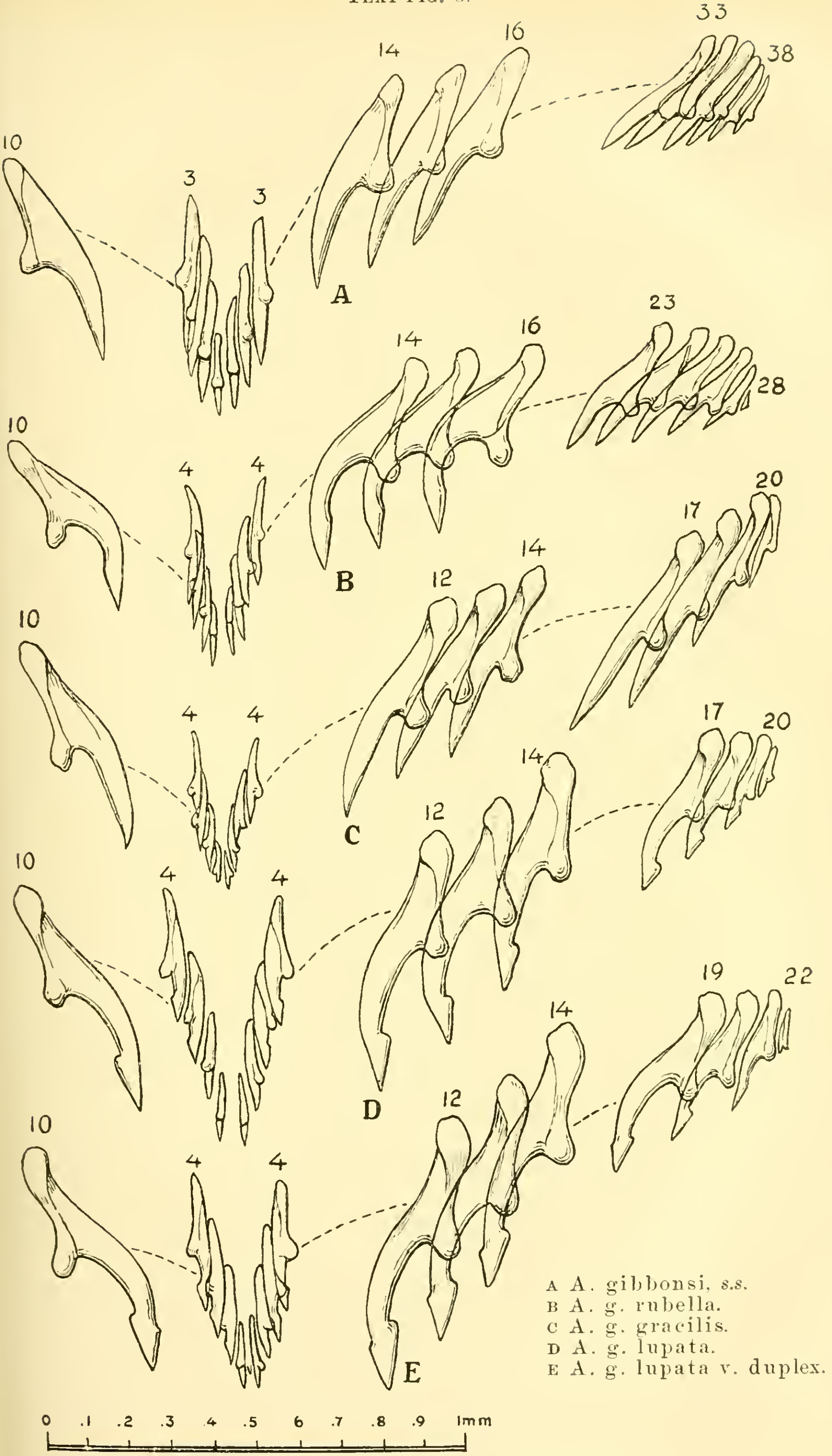
THE RADULA.—The general appearance of the radula, when freed from the surrounding tissue, is shown in Pl. XVII, figs. 97, 98, 99, 102, 107, and 114. It is long and relatively narrow, its breadth being sometimes less than one-sixth of its length. The teeth are thorn-shaped with narrow bases, and they are arranged in rows which diverge obliquely forwards on each side of the middle line. In other words, the radula of Apera is of the same general type as is found in the Rhytididæ, the Oleacinidæ, the Testacellidæ, and, indeed, in all the families of carnivorous snails and slugs excepting the Streptaxidæ, in which the teeth are of a slightly different shape. Nevertheless, the radula of Apera is exceptionally interesting, and shows a diversity which is scarcely surpassed in any genus of the Pulmonata containing so few species.

In the first place, the size of the radula varies enormously. In Apera gibbonsi and A. parva the radula is extremely large; when flattened out it measures about a third of the total length of the animal, and in the former species it is proportionately broader than in the other members of the genus. In A. dimidia the radula is scarcely a sixth of the length of the animal. In A. purcelli it is about a ninth, while in A. burnupi and A. sexangula it is only about a twelfth of the length of the slug.

The diversity in the size of the teeth is even greater. In Apera burnupi and A. sexangula the animal is about 550 times the length of the largest tooth in its radula. In A. dimidia and A. purcelli the proportion is 335 : 1. In a typical example of A. gibbonsi it is about 115 : 1; while in A. parva and A. gibbonsi lupata the animal is only about 66 times as long as its largest tooth, which attains a length of more than 0·6 mm. in the latter form.

But the diversity found in the radula of Apera extends to other features besides its dimensions. Even in the closely related forms which I am provisionally regarding as subspecies of A. gibbonsi, there is a remarkable variation in the form and number of the teeth (Pl. XIX, figs. 123, 124, Pl. XX, 125, 126, and text-fig. 3, A–E). The typical form has the most primitive type of radula, and the others show a progressive adaptation to vermivorous habits. A slug that feeds on worms—and it is known that this species does so—uses its radula, not for rasping off pieces from its victim, but for catching hold of it and drawing it back through the mouth into the crop. For this purpose the teeth must be large, with long sharp points for piercing the worm's skin and firm cuticle; and secondly, the teeth must be shaped so as to retain their position in the skin of the worm when they are pulling it back into the mouth. Accordingly we find, first, a progressive increase in the size of the larger teeth compared with the size of the animal, and especially in the length of their cusps. And in order to make room for these the number of rows is diminished, and the smaller teeth towards the outer edges of the radula, as well as those down the centre, become still less and eventually disappear (cf. Pl. XX, fig. 125, and Pl. XIX, fig. 123, and see also the numbers of the rows, and of the teeth in each row, given on pp. 195–201). Again, we find that the attachment of the teeth to the basal membrane of the radula also increases in length and forms a projecting apophysis, thus

TEXT-FIG. 3.



A A. gibbonsi, *s.s.*
B A. g. rubella.
C A. g. gracilis.
D A. g. lupata.
E A. g. lupata v. duplex.

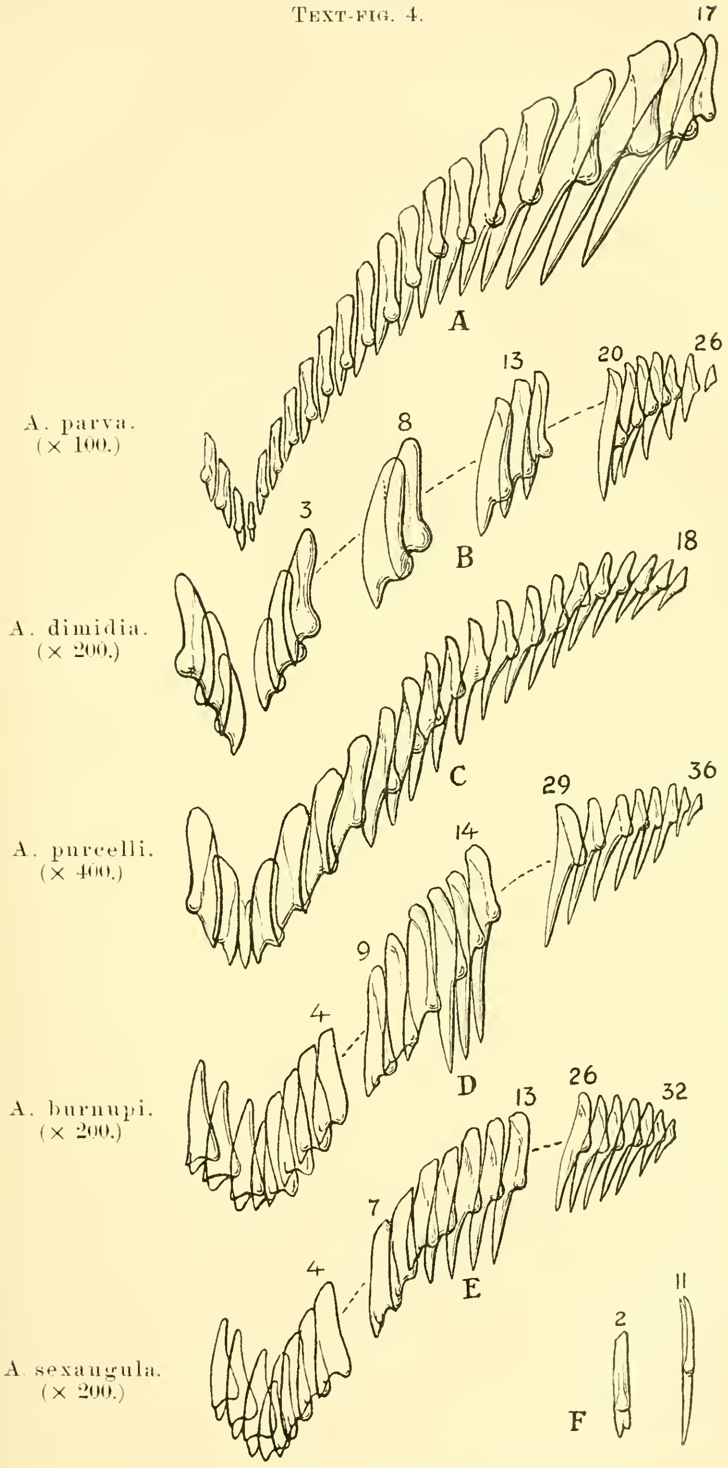
Representative teeth from the radulæ of Apera.

making it more difficult for the teeth to be pulled out of position and keeping them rigidly in place. Lastly, the teeth become modified in one of two ways in order to prevent the worm that they have transfixed from escaping. In A. gibbonsi rubella the cusps are strongly curved so as to form veritable hooks (text-fig. 3, B), and they are also slightly broadened towards the points. On the other hand, in A. gibbonsi lupata the cusps are barbed on the lower side, as in Testacella—a remarkable case of parallel evolution (cf. Pl. XXIV, fig. 157, and text-fig. 3, D). Still more highly specialised is the var. duplex of the same form. In this variety all the larger teeth are doubly barbed, there being a small barb on the upper side of the cusp nearer to the point than that on the lower side (text-fig. 3, E). I do not know of any other Pulmonate in which the radula has become so highly specialised along these lines as it has in this variety. We have to go to the marine carnivorous genera, such as Conus, to find such formidable doubly barbed teeth, and here also we notice that one barb is nearer the point of the tooth than the other. In Conus, however, the barbs are pointed instead of being merely square as in Apera, and the distal barb appears to have been developed first, for the other is often absent or merely represented by a flange. And of course the bases and arrangement of the teeth in Conus are quite different.

The radula of Apera parva bears a general resemblance to that of A. gibbonsi, but the bases of the teeth are not so narrow, the cusps of the inner teeth are slightly shorter, and the teeth become relatively larger towards the edges of the radula (text-fig. 4, A). None of the transverse rows contain more than thirty-five teeth in this species, and some have only thirty-four, as the vestigial central tooth is absent from some of the rows. On the whole the radula of A. parva is less unlike the type found in the genus Rhytida than are the radulæ of the other species of Apera.

In Apera purcelli and A. dimidia the central tooth also degenerates. It is present, though small, in A. purcelli

Text-fig. 4.



Representative teeth from the radulæ of Apera.

(text-fig. 4, c), but no trace of it remains in A. dimidia (Pl. XX, fig. 127, and text-fig. 4, B). The outer teeth of these two species have rather long, slightly curved cusps, and are not very unlike the teeth of the typical form of A. gibbonsi on a smaller scale; but the cusps of the inner teeth are remarkably short and broad, and the teeth have therefore a quite different appearance. In the more primitive species, A. purcelli, only the first three or four teeth on each side are thus modified, but in A. dimidia half the teeth are of this shape. Hence the teeth of these species, unlike those of nearly all other carnivorous forms, are differentiated into laterals and marginals, although there are one or two on each side which might be regarded as transitional. The figures of the radula of A. dimidia (Pl. XX, fig. 127, and text-fig. 4, B) show that in this species the corresponding teeth on each side are not opposite to each other, the right half of the row being in front of the left. A similar displacement occurs in A. parva (text-fig. 4, A), and it is also often observable in A. gibbonsi (Pl. XX, fig. 125); but it occurs occasionally in other carnivorous genera, for I have noticed it in Testacella haliotidea *Drap.*, T. scutulum *Sow.*, Euglandina truncata (*Gmel.*), E. corneola (*Binn.*), and Rhytida franklandiensis (*Forbes*).

In Apera sexangula and A. burnupi the differentiation into lateral and marginal teeth is still more marked (Pl. XX, fig. 128; text-fig. 4, D, E). The marginal teeth are more than twice as numerous as the laterals, and their cusps are long, slender, and nearly straight, those of one row overlapping the bases of the teeth in the row behind. The lateral and central teeth have short broad cusps, and the central tooth—which is only slightly smaller than those on each side of it—is not unlike the lateral teeth of A. purcelli and A. dimidia, though perhaps a little shorter. The cusps of the lateral teeth, however, are not only very short, but they are bifid and end in two points, the inner of which is the longer (text-fig. 4, D–F). Bentler[1] has shown that in Pary-

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[1] 'Zool. Jahrb.,' 1901, vol. xiv, p. 380, pl. xxvii, fig. 23a.

phanta hochstetteri (*Pfr.*) one of the teeth in each row may abnormally develop a double cusp; but I believe that I am right in saying that in no carnivorous genus excepting Apera are some of the teeth normally provided with double cusps, for I regard the bicuspid teeth of Pseudosubulina lirifera (*Morelet*) as something quite different. What is the reason for this remarkable modification of the inner teeth in these two species? Perhaps it may be found that Apera burnupi and A. sexangula live chiefly on some special kind of food, and have their radulæ specially modified in consequence. Or possibly we have here an instance of carnivorous slugs reverting to a partly vegetarian diet, and the lateral teeth are used in eating vegetable and the marginals in eating animal food. The fact that Collinge has found both animal and vegetable remains in the intestine of A. sexangula is in favour of the latter view. In case this hypothesis should prove to be correct, it is interesting to compare the type of radula found in these species with that which is characteristic of the Limacidæ, Zonitidæ, and other omnivorous families. These also have developed thorn-shaped marginal teeth, very similar to those in Apera, and here, too, we find that the lateral and central teeth are shorter and broader with one or two less pointed cusps. Nevertheless, these inner teeth are very different to those of Apera burnupi and A. sexangula, for they are of the ordinary type with broad oblong bases, such as is found in the great majority of herbivorous snails, whereas in the species of Apera the teeth have narrow bases and have obviously been derived from the thorn-shaped type. This difference, however, could be easily explained by supposing that in the Zonitidæ, etc., we have a group of herbivorous snails which have become adapted to a partially carnivorous diet, while in these species of Apera we are dealing with carnivorous slugs which have become partially herbivorous.

Further details about the radula of Apera will be found under the head of the different species. I need only add here that the teeth towards the hind end of the radula are more or less tinged with brown, as is so commonly the case among the carnivorous genera.

The Odontophore.—The hind end of the buccal mass is prolonged beyond the opening of the œsophagus to form the cylindrical muscular odontophore containing the radula-sac. In most carnivorous snails the hind end of the odontophore is curved abruptly downwards, but in Apera, as in Testacella, it has become quite straight, probably owing to the degeneration of the spiral shell. The size of the odontophore—and, to a less extent, the size of the buccal mass in front of it—is proportionate to the size of the radula. In A. burnupi (Pl. XXI, fig. 133) and A. sexangula (fig. 134) it is quite small, being only about 4 mm. long; in A. purcelli (Pl. XIII, fig. 55) and A. dimidia (Pl. XXI, fig. 132) it is much larger; finally, in A. gibbonsi and A. parva (figs. 129–131) the odontophore attains an enormous size, being one of the largest organs in the body. Yet the structure of the odontophore is remarkably constant throughout the genus, the differences between the arrangement of its muscles in the various species being quite insignificant.

The odontophoral support or cartilage is a semi-cylindrical structure which extends along almost the entire length of the odontophore. It is crescentic in section, the convex surface being ventral. In the hollow formed by its upper surface lie the radula-sac and the muscles immediately surrounding it, while the ventral pocket containing the front end of the radula is situated beneath the anterior part of the support, the radula being folded over its anterior end (Pl. XVII, fig. 92, and Pl. XVIII, figs. 115–122). The upper edges of the support are parallel throughout the greater part of its length, but anteriorly they curve inwards towards each other, and then diverge again and slope downwards at the front end, thus leaving an oblique oval aperture where the opening of the radula-sac is situated (Pl. XVII, figs. 95, 100, 105, 112). As might have been expected, this aperture is largest in Apera gibbonsi, and the front end of the support is rounded in this species and in A. parva. On the other hand, in A. burnupi and A. sexangula the aperture is very small, and the front end of the support is pointed (see fig. 112). The hind end of the odontophoral support is rather abruptly truncated. Along the inner surface of the support there runs a median longitudinal furrow, which can be best seen in transverse sections of the odontophore of A. dimidia (Pl. XVIII, figs. 116–121). In the other species it is not usually so well marked.

The odontophoral support is flexible, but much firmer than ordinary muscular tissue, and it is usually semi-translucent; yet it does not contain any cartilage, but is entirely composed of long narrow cells stretching radially from the inner to the outer surface (Pl. XVI, fig. 90). The nuclei of these cells are also lengthened, and are rather more numerous towards the outer than the inner surface of the support, doubtless because the cells are on an average slightly broader towards the outside. Most authors have regarded these long cells which occur in the odontophoral support of carnivorous snails and slugs as being muscle-fibres; but Beutler[1] has disputed this view, and has maintained that in Paryphanta hochstetteri (*Pfr.*) this tissue is not muscular. Now, I should certainly not be inclined to consider these cells as being of the nature of ordinary muscular fibres in Apera, but they might perhaps be regarded as muscle-fibres which have become modified for a supporting or skeletal purpose, and, if this is so, it is possible that they have become more modified in genera such as Paryphanta and Apera than in the types studied by Plate. In Testacella and Daudebardia there are longitudinal muscle-fibres and other cells intercalated among the radial elements of the support,[2] and I have found that this is also the case in Euglandina venezuelensis (*Preston*); but these are entirely absent in Apera, as in Paryphanta[3] and Natalina.[4]

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[1] Op. cit., pp. 380, 381.

[2] Plate, L. H., 'Zool. Jahrb.,' 1891, vol. iv, pl. xxxiii, figs. 30, 31, 39, 41, pl. xxxiv, fig. 51.

[3] Beutler, op. cit., p. 380.

[4] Woodward, M. F., 'Proc. Mal. Soc.,' 1895, vol. i, p. 273.

A longitudinal muscle runs along the upper edge of the support on each side towards its anterior end (Pl. XVI, fig. 90; Pl. XVIII, figs. 116–118), and probably serves to bend up the front of the support, as shown in Pl. XVII, fig. 108, and may therefore be termed the flexor muscle of the odontophoral support. In Apera gibbonsi there is also a very thin layer of longitudinal muscle-fibres covering the ventral surface of the support, and possibly the flexor muscles might be regarded as a special thickening of this layer.

The most important muscles in the odontophore are the powerful retractors, which arise from the odontophoral support and are inserted in the radula-sac. These may be divided into lateral retractors, median retractors, and terminal retractors. The numerous lateral retractors are attached in front to the radula-sac, chiefly around its anterior end, and pass obliquely backwards and outwards on each side, curving over the edges of the support and becoming attached to its outer sides (Pl. XVII, figs. 92, 93, 96, 101, 106, 109, 111, 113, and Pl. XVIII, figs. 116–121). The median retractors are a pair of specially thick muscles, which are attached for some distance to the floor of the radula-sac towards its anterior end, and pass backwards to the extreme hind end of the support (Pl. XVII, figs. 92, 106, and Pl. XVIII, figs. 118–122). They belong to the same series as the lateral retractors, of which they might be regarded as forming the innermost pair. No muscles are attached to the posterior part of the radula-sac, excepting at its hind end, where there is another pair of retractors, which I am calling the terminal retractors. These are not so thick as the median retractors, and pass backwards above them to the hind end of the support (Pl. XVII, fig. 92, and Pl. XVIII, figs. 121, 122). All these retractor muscles have the same function—that of pulling back the radula. In A. gibbonsi some of the more posterior strands of muscle are attached to the inner surface of the support, close to its hind end, while others are not attached to the support at all, but to the hind end of the sheath of the odontophore opposite to the insertion of the extrinsic buccal retractors.

Numerous muscles arise in two rows, one on each side of the mid-dorsal line of the outer sheath of the odontophore, and, passing downwards outside the lateral retractors, are attached to the outer sides of the support just below them (Pl. XVII, figs. 91, 104, and Pl. XVIII, figs. 115–121). These muscles I am terming the suspensor muscles of the support. They are nowhere of any great thickness, but are decidedly thinner behind than in front.

A thin layer of ventral muscles arises from the hind end of the odontophoral support, and is inserted in the anterior part of the radula, or rather in the walls of the ventral pocket which contains it (Pl. XVII, figs. 91, 92, 101, 104, and Pl. XVIII, figs. 117–121). These muscles do not only run longitudinally beneath the centre of the support, but the more lateral strands diverge radially from the ventral pocket of the radula and unite with the suspensor muscles of the support on each side. They serve to pull back the anterior part of the radula over the front edge of the support, and thus to pull forward the radula-sac when its retractors are relaxed, so that the radula assumes the form shown in Pl. XVII, figs. 92, 97, 102, 114. Then, when the teeth have become imbedded in the skin of the prey, these ventral muscles will be relaxed, and the powerful retractors will draw back the radula until it has the form shown in fig. 98.

A slender median dorsal muscle is inserted in the sheath of the odontophore, between the suspensor muscles, a short distance behind the opening of the œsophagus, and is attached posteriorly to the front end of the terminal retractors, its sides also becoming connected with the neighbouring lateral retractors (Pl. XVII, fig. 92, and Pl. XVIII, figs. 116–120). This is evidently homologous with the muscle that Amaudrut terms the "papillaire supérieur." It may assist the ventral muscle in pulling forward the radula-sac, but its chief function is probably to pull back the posterior lip of the opening of the œsophagus when the retractor muscles are brought into play, thus making a wide passage towards the crop.

The sheath of the odontophore is composed of three layers of muscle-fibres. Externally there is a thin layer of longitudinal muscles; within this lies a layer of circular muscles, which is equally thin throughout the greater part of the length of the odontophore, but becomes a little thicker towards the front end; lastly, there is a very thin layer of longitudinal muscles lining the whole of the sheath excepting the dorsal part which lies between the attachment on each side of the suspensor muscles of the support. At its hind end the sheath of the odontophore becomes intimately united with the support and the posterior ends of the retractor muscles, but throughout nearly the whole of its length its only connection with the underlying tissues is by means of the suspensor muscles.

I have examined the arrangement of the muscles of the odontophore in all the species of Apera excepting A. purcelli, and the amount of variation is so small, notwithstanding the diversity of the radulæ, that it must be admitted that these muscles are of considerable systematic importance. It will, therefore, be of special interest to compare the arrangement of the odontophoral muscles of Apera with that which is found in other families of carnivorous snails and slugs.

As an example of the Rhytididæ we may choose Natalina. Nineteen years ago M. F. Woodward[1] published an account of the anatomy of Natalina caffra (*Fér.*), with special reference to the structure of the odontophore; but unfortunately his account shows evidence of inaccuracy. I shall therefore ignore his description and figures, and compare the odontophoral muscles of Apera with those of a species of Natalina, nearly allied to N. caffra, which I have been able to examine myself, namely N. quekettiana (*M. & P.*). On the whole the odontophore of this species resembles that of Apera very closely; it differs, however, in the following features.—(1) Instead of being straight the odontophore is slightly curved towards the left; moreover its hind

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[1] 'Proc. Mal. Soc.,' 1895, vol. i, pp. 270–277, pl. xvii.

end is abruptly bent downwards, and the outer longitudinal muscles of the sheath form a pad extending from the recurved end a short distance forwards along the ventral surface. (2) The lateral retractors towards the posterior end of the odontophore are attached to the odontophoral support just within its edges; further forward they are attached to the outer sides of the support as in Apera. (3) The median dorsal muscle is extremely slender, and the terminal retractor is also very weak, being almost devoid of muscular fibres. (4) The circular muscles of the sheath are much thicker laterally and ventrally, and the suspensor muscles of the support are also much thicker than in Apera. In all other respects the structure of the odontophore is strikingly similar to that found in Apera, and especially to that of A. gibbonsi; for in Natalina quekettiana a thin layer of longitudinal muscles covers the lower surface of the odontophoral support, and some of the posterior retractors are not attached to the support, but arise from the sheath of the odontophore opposite to the insertion of the upper branches of the extrinsic buccal retractors—features which are also found in A. gibbonsi.

The chief differences mentioned above may be easily explained. The curvature of the odontophore is doubtless due to the fact that Natalina possesses a large spiral shell. The greater thickness of the constrictor muscles running in a circular direction, both those in the sheath and those beneath it, is probably connected with the circumstance that Natalina feeds on snails rather than on worms; for, as Woodward has pointed out, the contraction of these muscles will press the radula against the body of its prey, as it tears the teeth through its victim's flesh, a thing that a vermivorous form does not do. The reduction of the median dorsal muscle and the terminal retractor, which might be regarded as its continuation, may be due to the fact that Natalina rasps off portions of its prey, and therefore does not require to enlarge the opening of the œsophagus to such an extent as an animal that swallows worms whole. We see, therefore, that the differences between the structure of the odontophore in Apera and Natalina are of little morphological importance, and are certainly less striking than the differences between the radulæ of the two genera, for the radulæ of Natalina and Apera have become highly specialised in different directions.

Turning now to the Testacellidæ, we find slugs which are vermivorous like Apera gibbonsi and have radulæ remarkably similar to the var. lupata of that species. Yet an examination of the odontophore of Testacella maugei *Fér.* reveals many features in which the arrangement of its muscles is quite different from anything that we have found in Apera or Natalina (Pl. XXIV, figs. 155, 156). The structure of the odontophore of Testacella maugei differs from that which I have described as characteristic of Apera in the following respects.—(1) There is no terminal retractor (unless it is represented by the small connections between the floor of the radula-sac and the median retractor). (2) Perhaps in consequence of this the radula-sac is shorter than the ventral pocket, instead of being much longer. (3) The median dorsal muscle is short, very oblique, and divided into three or four fine strands. (4) The median retractors curve together above the radula-sac to form a tube which is continued to the hind end of the odontophore. (5) The muscles which form the top of this tube are not only firmly attached to the lateral retractors on each side, but also to the sheath of the odontophore; and they are continuous with the extrinsic buccal retractors, which join the posterior half of the odontophore on each side of the mid-dorsal line. (6) The lateral retractors are scarcely divided into separate strands. (7) There seem to be no flexor muscles along the upper edges of the support, but on its inner surface there is a slight median longitudinal ridge which disappears towards the hind end and is connected with the median retractors by a few slender strands. (8) The ventral muscles are rather stouter than in Apera and more definitely split up into separate strands. (9) Anterior to these the suspensor muscles are free, but directed obliquely downwards and backwards from the sides of the roof of the odontophore to the support, parallel to the lateral retractors; further back, however, they are either absent or completely fused with the lateral retractors. Taking into consideration the similarity of the radula of Testacella to that of Apera, it is surprising that there should be so many differences in the muscles which control its movements.

In the Oleacinidæ the odontophore resembles that of Testacella in some of its features, and that of Natalina in others, although it often possesses more primitive characters than can be found in either of these genera. Strebel[1] has given a detailed account of the odontophore of Englandina sowerbyana (*Pfr.*), from which it will be seen that in this species the median retractors enclose the hind end of the radula-sac and become continuous posteriorly with the extrinsic buccal retractor. In this respect, therefore, Englandina sowerbyana resembles Testacella. But this is not the case with many of the other forms, such as E. venezuelensis (*Preston*) or Streptostyla shuttleworthi (*Pfr.*),[2] for in these the radula-sac is long, and its posterior part has not yet become entirely surrounded with muscles, but projects slightly from the hind end of the odontophore. In most genera the posterior end of the odontophore is curved downwards as in Natalina. The median dorsal muscle resembles that of Apera, and the ventral muscles are also like those of Apera and Natalina. On the other hand, the suspensor muscles are like those of Testacella, and I found that Englandina venezuelensis also resembled that genus in having the retractors fused with the sheath of the odontophore towards the hind end. No median ridge or furrow occurs along the inner surface of the support in E. venezuelensis, and I did not find any flexor muscles along its edges. Possibly the longitudinal muscle-fibres within the support take the place in Testacella and

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[1] 'Beitrag z. Kenntniss d. Fauna Mexikanischer L. u. Süsswasser-Conchylien,' 1878, vol. iii, pp. 40–42, pls. xvii, xviii.

[2] Strebel, op. cit., pl. v, fig. 7a.

Englandina of the flexor muscles in Apera and Natalina. It is interesting to notice that while the odontophore in the Oleacinidæ is usually curved as in the Rhytididæ, in several features of its internal structure it appears to resemble the odontophore of Testacella more than does that of Apera.

The Buccal Retractors and Protractors.—In all the species of Apera excepting A. gibbonsi and A. parva, the extrinsic buccal retractor consists of a long, narrow muscle, arising from the right side of the floor of the body-cavity at the entrance to its funnel-shaped prolongation beneath the mantle-cavity or lung. The origin of the buccal retractor is thus nearly as far back as the heart, and is slightly asymmetrical (Pl. XV, fig. 75). In front the muscle bifurcates just before reaching the odontophore, and the two branches are inserted one on each side of its posterior extremity (Pl. XXI, figs. 132–134). As might have been expected, the retractor is narrower in A. burnupi and A. sexangula than in A. dimidia with its larger odontophore.

In Apera gibbonsi and A. parva the retractor is split up into a number of powerful muscles, which radiate from the hind end of the odontophore, and are attached to a considerable area of the floor and the lower part of the sides of the body-cavity (Pl. XXI, figs. 129–131). In A. gibbonsi these muscles originate towards the hind end of the body-cavity, though further forward than the origin of the single buccal retractor in the other species (Pl. IX, fig. 27), but in A. parva the muscles have become shorter and arise from about the middle of the cavity (fig. 28). These muscles are often forked and neighbouring strands occasionally anastomose, but there is frequently a slight gap dividing those on the right side from those on the left. It is easy to see that the same carnivorous habits which have led to the enlargement of the radula and odontophore in A. gibbonsi and A. parva would produce a corresponding development and multiplication of the buccal retractors; and it is also evident that it would be an advantage if the ends of these muscles were distributed over a considerable area, so that the strain produced by the contraction of the muscles was not concentrated on a small patch of the body-wall. But although it is not difficult to derive the many radially disposed retractors of A. gibbonsi and A. parva from the single retractor of the other forms, I would emphasize the fact that the difference is a very great one, and not likely to have been completed within a short space of time. So far as I am aware the only other form which has developed radial buccal retractors at all similar to those of Apera is Selenochlamys.[1]

Since the buccal retractor is inserted in the hind end of the odontophore, it might have been expected that it would receive nerves from the buccal ganglia, which innervate the odontophore and the posterior part of the buccal mass. Yet this is not the case; for while the posterior end of the retractor receives nerves emanating from the right pedal ganglion, the front end is innervated by a pair of nerves from the cerebral ganglia in all the forms with a single retractor. This apparently anomalous innervation may be explained by assuming that the buccal retractor belongs to the same series of muscles as the tentacular retractors, with which it is united posteriorly in the great majority of snails; and that it was originally inserted, like the tentacular muscles, far forward, and in the region innervated by the cerebral ganglia. Later the anterior part, which consists of a right and left division, would become applied to the sides of the odontophore and fused with them, so that the retractor would appear to be inserted in the hind end of the odontophore. This theory is supported by the facts (1) that the nerves to the buccal retractor and to the retractors of the lower tentacles arise from the cerebral ganglia by the same roots, and (2) that the longitudinal muscle-fibres forming the outer layer of the sheath of the odontophore are directly continuous on each side with those of the buccal retractor behind (Pl. XVIII,

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[1] Simroth, H., 'Festschrift Leuckarts,' 1892, p. 55.

fig. 122). This view would also explain how it is that in A. gibbonsi the nerves which innervate the buccal retractor in the other species merely unite with the sheath of the odontophore towards the anterior end of that organ. For we may suppose that in A. gibbonsi and A. parva the odontophore has grown back further than in the other species between the two halves of the buccal retractor, which have thus become applied to its sides, and consequently the free radial retractors of these forms are homologous with only the posterior half of the long retractor found in the remaining species.

We have seen that the origin of the buccal retractor in such forms as Apera dimidia is to the right of the middle line, and that its posterior end is innervated exclusively by branches of the right posterior pedal nerve (Pl. XV, fig. 75). Now the foot is a symmetrical organ, and the anterior part of the retractor is certainly symmetrical, as is proved by its innervation; it might, therefore, have been expected that the posterior part of the buccal retractor would have been symmetrical also, unless it had shifted somewhat to the left because of the pressure of the reproductive organs on the right side, as in the case of Daudebardia saulcyi (*Bgt.*) and Testacella gestroi (*Issel*).[1] Why, then, does the buccal retractor spring from the right side of the floor of the body-cavity in Apera? When an animal possesses a feature which is asymmetrical for no apparent reason, the explanation of that asymmetry is usually to be found by a consideration of the animal's phylogeny. It is highly probable that Apera has been evolved from a snail possessing a depressed or heliciform dextral shell. Now when such a shell is in its natural position upon the back of the animal, its columella is to the right of the aperture. Consequently the columellar muscle, from which the buccal retractor springs, will be towards the right side of the animal. Then, when the shell degenerates, all the upper part of the columellar muscle will disappear, and only the lower part, or

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[1] Plate, L. H., 'Zool. Jahrb.,' 1891, vol. iv, p. 596.

"tail muscle," in connection with the foot, will remain as the direct continuation of the buccal retractor, but it will still be situated towards the right side of the animal. In Schizoglossa we have a slug in which the degeneration of the shell has only partially taken place, and the chief muscle-fibres are still attached to the reduced columella; and it would be difficult to draw a diagram illustrating the theory which I have just set forth more aptly than does Murdoch's figure of the retractor muscles of Schizoglossa novoseelandica (*Pfr.*).[1]

Several pairs of buccal protractors stretch from the outer layer of the walls of the buccal mass to the skin of the anterior part of the head. The longest and most important of these are inserted on each side just in front of the odontophore and below the opening of the œsophagus (Pl. XXI, figs. 129–134). These protractor muscles, together with the intrinsic muscles of the buccal mass, serve to protrude the odontophore, which seems to be protrusible in all the species of Apera. But even in A. gibbonsi the protractors are not very thick; and this is not surprising, for it is evident that less powerful muscles will be required to protrude the odontophore than to retract it after the teeth have become fixed in the skin of a worm.

THE ŒSOPHAGUS AND CROP.—In Apera gibbonsi and A. parva the œsophagus is very short and broad, and merges imperceptibly into the crop (Pl. XXI, figs. 129–131). The latter is fusiform in these species, and after increasing in width it gradually tapers again towards the openings of the hepatic ducts, its broadest part being about twice as far from these ducts as from the opening of the œsophagus into the buccal mass.

In the remaining species the œsophagus is long and narrow, as will be seen from figs. 132 to 134. At its posterior end it enlarges rather abruptly to form the crop, which is usually widest near the front end, but remains fairly broad almost as far back as the ducts of the liver, and then narrows

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[1] 'Proc. Mal. Soc.,' 1900, vol. iv, pl. xvii, fig. 10.

rather suddenly; but, as might have been expected, the crop is much more distended in some specimens than in others.

The walls of the œsophagus and crop are very similar in structure (Pl. XV, figs. 78, 79, and Pl. XXII, fig. 135). The epithelial lining is normally thrown into longitudinal folds, and consists of columnar cells without any cilia. Outside the epithelium of both œsophagus and crop there are three layers of muscle-fibres. The fibres of the inner and outer layers are longitudinal, while those of the intermediate layer run in a circular direction.

THE STOMACH, INTESTINE, AND RECTUM.—Beyond the crop in Apera parva the alimentary canal enlarges to form a small stomach, into which the hepatic ducts open (Pl. XXI, fig. 131). In the other species of Apera (with the possible exception of A. purcelli) there is no true stomach, but the crop passes directly into the intestine at the openings of the hepatic ducts.

At first the intestine bends abruptly upwards and towards the right side of the animal. In A. gibbonsi it then describes a curve on the upper surface of the liver like a reversed S (Pl. IX, fig. 27; Pl. XXI, figs. 129 and 130). The posterior curve towards the left side is somewhat shallower than that towards the right, and beyond it the alimentary canal continues backwards low down on the right side of the posterior end of the liver. In A. parva the intestine, after curving over to the right side of the liver, passes straight backwards, the second curve towards the left side being absent (Pl. IX, fig. 28; Pl. XXI, fig. 131).

In Apera burnupi and A. sexangula the first curve is much deeper, and forms a loop which extends the whole way down the right side of the liver, in which it is partially embedded (Pl. IX, figs. 30, 31, and Pl. XXI, figs. 133, 134). The anterior portion of this loop lies further forward than the openings of the hepatic ducts. The posterior curve is shallow in these species, and the alimentary canal is continued on the right side, as in A. gibbonsi and A. parva. The intestine is considerably narrower in A. burnupi and A. sexangula than in the other species.

In Apera dimidia and A. purcelli the first curve of the intestine lies in a more nearly vertical plane, and does not extend so far towards the right side (Pl. IX, fig. 29, and Pl. XXI, fig. 132). Then, after curving down on the left side, the intestine continues backwards on that side of the liver instead of on the right (cf. Pl. X, fig. 32, and Pl. XI, figs. 34, 35).

Beyond the region of the liver the alimentary canal continues backwards as the rectum beneath the mantle-cavity. It is at first surrounded by the funnel-shaped prolongation of the body-cavity, but further back it curves towards the right side of the animal, and bends up the right wall of the mantle-cavity on reaching the level of the respiratory opening. As will be seen from Pl. X, fig. 33, the anus is immediately below the respiratory opening, and the space between them is partially separated from the rest of the mantle-cavity by an oblique fold of the wall of the cavity, which projects forward on the left side of the space.

The epithelium lining the intestine is composed of very irregular columnar cells, the appearance of which is well shown in Pl. XXII, fig. 137. The inner walls of these cells are produced into a delicate fringe of extremely minute cilia. Outside the epithelium there is a thin layer of circular muscles, and external to this a thin layer of longitudinal muscles. The structure of the rectum is very similar to that of the intestine, excepting that the epithelium is normally thrown into deep folds (Pl. XXII, fig. 136). At the anus, however, the epithelial cells become more regular and oblong in section, and their cilia become far longer and less delicate.

THE SALIVARY GLANDS AND DUCTS.—The salivary glands are fairly compact, and are situated above and on each side of the crop near its junction with the œsophagus. There are always two glands, but in Apera gibbonsi and A. dimidia, and to some extent in A. parva and A. purcelli, they are united above the crop, as in so many of the carnivorous snails

(Pl. IX, figs. 27–29, and Pl. XXI, figs. 129–132). In A. burnupi and A. sexangula the glands are separate, but they are joined to each other by blood-vessels in such a way as to suggest that they may possibly have been more closely united in the ancestors of these species (Pl. IX, figs. 30, 31, and Pl. XXI, figs. 133, 134). The glands are never united underneath the crop, as in many of the Oleacinidæ, but remain widely separate below (Pl. XV, fig. 78).

The salivary ducts are long and very slender, and discharge into the buccal mass on each side of the opening of the œsophagus. The structure of the ducts is shown in Pl. XXII, fig. 138. It will be seen that the epithelial cells are of a peculiar shape and provided with long cilia. The epithelium is immediately surrounded by a layer of circular muscles, and outside these there is a layer of longitudinal muscles in which is embedded the salivary nerve. Within the gland the duct splits up into numerous branches, and in these also the epithelium is surrounded by circular muscles. One of these branches is shown in fig. 139, which also shows the appearance of the glandular cells of which the gland itself is almost entirely composed.

The Liver.—The greater part of the posterior half of the body-cavity is occupied by the liver or digestive gland (Pl. IX, figs. 27–31). In Apera gibbonsi, A. parva, A. burnupi, and A. sexangula the liver consists of two very distinct divisions, one anterior, dorsal, and to the right, the other posterior, ventral, and to the left (Pl. XXI, figs. 129–131, 133 and 134). Not only do these divisions discharge their secretions into the alimentary canal by quite separate ducts, but they are supplied with blood by different arteries, the right division being supplied by one or two branches from the anterior aorta, while the left division is supplied by the so-called posterior aorta. The right division of the liver is divided by the intestine into three main lobes, one lying within the anterior loop of the intestine, another in front of it, and the third behind it, as shown in the figures. Of these the anterior lobe, lying above the hind end of the crop, is the most distinct. Each lobe is again subdivided into a number of lobules, the arrangement of which varies in different individuals. The left division of the liver lies entirely to the left of the intestine, and is about equal in size to the right. It also is divided and subdivided into lobes and lobules, but not so distinctly as is the right division.

In Apera dimidia the liver is also divided into two main divisions, one right and anterior, the other left and posterior; and, as in the other species, these divisions have separate ducts. They are not, however, quite so distinct from each other as in the species mentioned above, and they both receive their blood from a single branch of the anterior aorta, the so-called posterior aorta being absent. Moreover, the disposition of these divisions with regard to the intestine is quite different to that which I have described as characteristic of A. gibbonsi, A. parva, A. burnupi, and A. sexangula. The anterior or right division lies above the crop, entirely in front of the intestine, while the posterior or left division, which is divided into two lobes, occupies a position corresponding to that held in the other species by the two posterior lobes of the right division of the liver (Pl. XXI, fig. 132). This fact suggests that possibly the whole of the liver of A. dimidia corresponds to the right division of the liver in the other species. If this theory be correct, it would explain, not only the anomalous position of the liver with regard to the intestine in A. dimidia, but also its still more surprising blood-supply. We would have to suppose, however, that the origin of the branch of the right hepatic duct coming from the anterior lobe had shifted inwards as far as the intestine itself; but this might have been caused by the greater separation of the lobe due to the lengthening of the right division of the liver as it came to occupy also the position of the left division. And this separation of the two principal branches of the hepatic duct would be merely a case of reversion, for H. Fischer[1] has shown that each division of the liver was probably originally subdivided into two or more lobes,

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[1] 'Bull. Sci. France et Belg.,' 1892, vol. xxiv, p. 331.

which opened separately into the alimentary canal. But it is more difficult to explain why half the liver should disappear in this way. It is known, however, that the reduction of that part of the body-cavity which usually occupies the spire of the shell sometimes produces a corresponding reduction of the left lobe of the liver which it contains.[1] It seems possible, therefore, that in A. dimidia the left division of the liver, instead of merely pushing forward the right, as in the other species of Apera, has disappeared altogether, just as the right division has disappeared in some of the Pectinibranchia.

On the other hand, it is possible that the two divisions of the liver in A. dimidia are actually homologous with the two divisions in the other species. Blood-vessels are always very subject to variation, and if by some mutation the so-called posterior aorta had disappeared, the arteries supplying the right division of the liver would probably extend to the left also. Further, the posterior aorta passes to the left of the intestine, and may to some extent hold it in position (Pl. IX, fig. 27). When, therefore, this vessel is not present, there is nothing to prevent the intestine shifting to the left and coming to occupy the position that it holds in A. dimidia.

Possibly an examination of the liver of Apera purcelli may show which of these views is correct. In this species the intestine seems to occupy a similar position to that of A. dimidia, but unfortunately the liver of the only specimen of A. purcelli which I have been able to examine was in a state of partial disintegration.

Sections through the liver of Apera dimidia show that the food is not confined to the alimentary canal itself, but passes up the hepatic ducts into the lobes of the liver, and probably digestion takes place chiefly inside this organ in Apera as in Atopus.[2] Perhaps the disappearance of a stomach in these genera may be partly explained by this fact.

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[1] Pelseneer, P., 'Mém. Acad. Roy. Belg.,' 1901, ex vol. liv, p. 55.
Simroth, H., 'Naturwiss. Wochenschr.,' 1901, vol. xvii, p. 121.

THE VASCULAR SYSTEM.

The Heart and Pulmonary Veins.—The genus Apera is opisthopneumic, the greater part of the respiratory tissue being behind the heart. Unlike Daudebardia, the auricle has moved round with the pulmonary veins so as to lie obliquely behind and to the right of the ventricle (Pl. IX, figs. 27–31), but it has not rotated so far as in Testacella. The pulmonary veins form a complicated network, variable in its structure; but it is generally possible to distinguish three main vessels converging towards the auricle, namely, the right anterior pulmonary vein, from the corner of the mantle-cavity to the right of the pericardium; the right posterior pulmonary vein, from the region between the pericardium and the anus; and the left posterior pulmonary vein, from the part of the mantle-cavity behind the kidney. Owing to the absence of the respiratory tissue from the left anterior corner of the mantle-cavity there is no left anterior pulmonary vein.

The walls of the auricle are very thin (Pl. XI, fig. 35), but those of the ventricle are extremely thick and muscular (fig. 34). The cardiac muscle-fibres are arranged in bundles passing in various directions, and leaving spaces between them which communicate freely with the central cavity of the ventricle (Pl. XXII, fig. 140). The muscles are thus well supplied with blood without the intervention of any cardiac arteries.

The Arterial System.—The distribution of the principal arteries is shown in Pl. IX, figs. 27–29 and 31. The single aorta leaves the posterior end of the ventricle, passes through the diaphragm, and then bends abruptly to the right and curves downwards, so that it comes to lie on the right side of the liver. In Apera gibbonsi, A. parva, A. burnupi, and A. sexangula the so-called posterior aorta branches off to the left within 3 or 4 mm. of the diaphragm. This vessel passes forwards on the right side of the left division of the liver, keeping to the left side of the intestine. It divides into two or three branches supplying the left division of the liver, but the most anterior branch first passes through the hermaphrodite gland, to which it also supplies blood. In A. burnupi, but not in the other species, this branch also gives off a small artery to the hind end of the right division of the liver. In A. parva the posterior aorta divides immediately into three branches at the point where it separates from the anterior aorta, but in the other species the division of the vessel takes place further forward. No posterior aorta is present in A. dimidia, and there is probably none in A. purcelli either.

I would suggest that perhaps this so-called posterior aorta may be merely the left hepatic artery which has become displaced, and that the Gastropoda (with the possible exceptions of Haliotis and Fissurella[1]) resemble the Amphineura and the more primitive members of the Pelecypoda in having no true posterior aorta. The posterior position of this artery would be accounted for by the posterior position which the left division of the liver has come to occupy owing to the torsion of the visceral hump. Its comparatively large size in most genera might be due to the fact that the left division of the liver is generally much larger than the right, since it extends up the spire of the shell. And as the hermaphrodite gland is usually more or less embedded in the left division of the liver, it would be likely to be supplied with blood by the same artery. This view will be made clear by the accompanying diagrams A to D. Diagram A represents a primitive symmetrical arrangement, and C the condition after the torsion has taken place; B shows a hypothetical stage between A and C, while D represents the most usual arrangement of the arteries and liver in Apera.

The anterior aorta continues forward on the right side of the liver, crossing over the intestine in A. gibbonsi, A. burnupi, and A. sexangula. In A. gibbonsi, A. dimidia, and probably in A. purcelli, it gives off a single artery to the liver on reaching the level of the anterior loop

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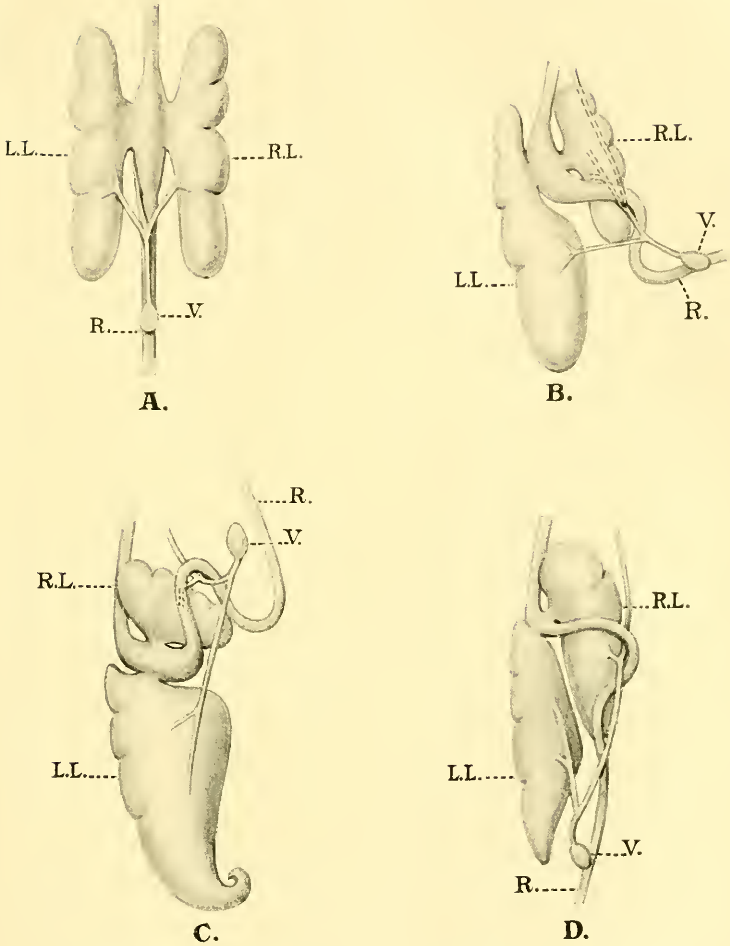
[1] See Wegmann, H., 'Arch. Zool. Expér.' (2nd ser.), 1884, vol. ii. pp. 352, 353, pl. xviii, figs. 1–4; and Boutan, L., ibid., 1885, ex vol. iii bis suppl., pp. 34, 130, pl. xxxiii, figs. 5, 6.

Text-fig. 5.



Diagrams illustrating the hypothetical evolution of the "posterior aorta."
(Diagram D shows the arrangement in *Apera gibbonsi lupata*.)

L.L. = Left division of liver. R. = Rectum.
R.L. = Right division of liver. V. = Ventricle.

of the intestine. This hepatic artery soon divides into two branches. In A. gibbonsi the anterior branch chiefly supplies the anterior lobe of the right division of the liver, while the remainder of the right division is supplied by the posterior branch. In A. dimidia the anterior branch supplies the anterior division of the liver, while the posterior branch supplies not only the posterior division, but also the hermaphrodite gland which it traverses. In Apera burnupi and A. parva the blood-supply of the right division of the liver is similar to that in A. gibbonsi, excepting that the two branches arise separately from the anterior aorta, though very close together. In A. sexangula these arteries also arise separately from the anterior aorta, and their origins are much further apart.

The anterior aorta passes through the loop formed by the intestine in Apera burnupi, A. sexangula, A. parva, and in A. gibbonsi gracilis and A. g. lupata (Pl. IX, figs. 28, 31, and text-fig. 5, D); but in A. dimidia, A. purcelli, A. gibbonsi *s. s.*, and A. g. rubella, the aorta passes straight forward on the right side of the loop (figs. 27, 29). It is very remarkable to find this important difference separating forms which seem to be so closely related that I have not ventured to regard them as distinct species. For the difference amounts to this: that in the first group the aorta, on its way from the dorsally situated heart to the ventral ganglia, passes on the left side of the alimentary canal, while in the second group the aorta passes on the right.[1]

The aorta then runs forward between the digestive and reproductive organs, being often closely applied to the left side of the albumen gland. It gives off to the left three or four arteries to the crop and salivary glands, and to the right at least one artery to the albumen gland and another to the common duct, a branch of the latter going forward to the receptaculum seminis. The aorta then becomes more ventrally situated and

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[1] A similar variation in the course of the aorta has been found by Köhler in the genus Siphonaria ('Zool. Jahrb.,' 1893, vol. vii; compare fig. B, p. 27, with figs. A and C, p. 32).

runs forward towards the ventral group of ganglia. Just before reaching these a pair of arteries is given off to the tentacular retractors (Pl. XIII, figs. 52 and 54–57). In most of the species these arteries unite with the common tentacular retractors just behind the points where the latter divide; but in Apera dimidia they unite with the upper tentacular retractors, and give off small branches to the retractors of the lower tentacles, which join the nerves from the sides of the "nerve-collar" (fig. 54). Finally the aorta fuses with the ventral group of ganglia.

From this point radiate numerous short vessels to the various parts of the central nervous system, etc., as well as two longer arteries, namely, the buccal and pedal arteries.

The buccal artery passes upwards and divides into two branches, one running forwards and the other backwards. In Apera dimidia the posterior branch is about twice as long as the other (Pl. XVII, fig. 103); it runs back to the posterior extremity of the odontophore, which it enters, and then bends round the hind end of the odontophoral support (Pl. XVIII, fig. 122). The anterior branch runs forward and divides into a pair of arteries which apply themselves to the sides of the buccal mass, dividing again as they do so into anterior and posterior vessels. In A. burnupi and A. sexangula the buccal artery branches in a similar manner, but owing to the small size of the odontophore, the posterior branch is no longer than the anterior branch (Pl. XVII, fig. 110). In A. gibbonsi and A. parva, on the other hand, the posterior branch is very long, and in the former species the right and left anterior arteries do not branch from a single median vessel, but arise separately (Pl. XIII, fig. 52).

In Testacella the artery supplying the odontophore with blood behaves differently, for, instead of running straight to the hind end of the organ, it divides into lateral vessels which pass through the sides of the sheath as shown in de Lacaze-Duthier's admirable figures.[1] On the other hand, in Natalina quekettiana (*M. & P.*), this artery behaves in the

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[1] 'Arch. Zool. Expér.' (2nd ser.), 1887, vol. v, pls. xxxv, xxxvi.

same way as it does in Apera. In Euglandina we have an intermediate arrangement, as will be seen from Strebel's figures[1]; for the structure that he described and figured as a median odontophoral nerve from the ventral group of ganglia, is, in reality, the buccal artery, as I have found from an examination of E. venezuelensis (*Preston*).

The pedal artery runs backwards above the pedal gland, to which it gives off branches on each side. In Apera gibbonsi, A. dimidia, and A. sexangula, I have found a very slender vessel uniting the anterior aorta with the pedal artery about half way along the pedal gland (Pl. XIII, figs. 52, 54, and 57). After uniting with the terminal vesicle of the pedal gland, the pedal artery continues backwards and downwards, and becomes more or less embedded in the muscular connective tissue of the foot.

The venous system is largely lacunar, apart from the pulmonary veins already described. Indeed, the only well-defined vessel containing venous blood is the body-cavity itself. I have already dealt with the dermal veins and their curious sphincters, when treating of the structure of the skin.[2]

THE EXCRETORY SYSTEM.

The pericardium communicates with the mantle-cavity by means of a single renal cœlomoduct, divided into an ascending glandular portion, which forms the kidney, and a descending non-glandular portion, which forms the ureter. It will be seen from Pl. IX, figs. 27–31, Pl. XI, figs. 34, 35, and Pl. XII, fig. 36, that the kidney is applied to the left side of the pericardium, and also extends over its posterior part towards the right side, thus broadly connecting the pericardium with the wall of the mantle-cavity, with which the kidney fuses a little further back. Ventrally the kidney is prolonged backwards in the floor of the mantle-cavity on

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[1] 'Beitrag z. Kenntn. d. Fauna Mexikan. L.- u. Süsswasser-Conchylien,' 1878, vol. iii, pl. xvi, fig. 5, pl. xviii, figs. 1, 6, 10; pl. xix, fig. 1, pl. xx, fig. 1.

[2] See pp. 126, 127.

the left side of the rectum and even beyond the anus (Pl. X fig. 33). The walls of the kidney are very much folded internally (see especially Pl. XI, fig. 35), and are lined by an epithelium consisting of glandular excretory cells with conspicuous round nuclei (Pl. XXII, fig. 141).

The reno-pericardial duct is very narrow, but projects some distance into the kidney. Its position is shown in Pl. XI, fig. 35. The epithelial cells lining the duct are provided with very long cilia.

The kidney communicates with the ureter by a minute pore situated in the centre of a slightly raised papilla at the right end of its dorsal extension (Pl. XII, fig. 36). The ureter, as in other sigmurethrous Stylommatophora, is doubled back upon the kidney, and curves round its inner posterior side. Ventrally it is continued backwards beside the ventral prolongation of the kidney, and extends to the extreme end of the mantle-cavity, where it bends abruptly upwards and opens. The ureter is lined by a cubical epithelium, the appearance of which is shown in Pl. XXII, fig. 141. This epithelium becomes thinner over the papilla in which the opening of the kidney is situated; elsewhere it is remarkably like the epithelium which lines the lower surface of the shell-sac.

As in Testacella and the Rhytididæ, there is no secondary ureter; but a rather irregular groove runs forwards from the opening of the ureter along the roof of the mantle-cavity. This groove reaches nearly to the point where the ureter begins, and then bends round and runs obliquely backwards and to the right, to end in the cleft in the inner lip of the respiratory opening. The epithelium lining this groove is similar to that lining the ureter itself, and the groove is probably to be regarded as an incipient secondary ureter, such as is found in many other forms. The somewhat peculiar course of the groove might be explained on the assumption that the respiratory orifice was originally situated further forwards.

THE REPRODUCTIVE ORGANS.

The genital or reproductive organs of Apera are of a simple generalised type, at least so far as their external structure is concerned (Pl. XXIII, figs. 143, 144, 146–149). As up to the present only a very few fully mature specimens have been collected, I have thought it advisable to preserve the reproductive organs of these almost intact, and not to cut them up in order to examine their histology. The following account, therefore, deals chiefly with the external morphology of the genital system. The reproductive organs of Apera purcelli are unknown, the only dissected specimen being immature.

The Hermaphrodite and Female Organs.—The hermaphrodite gland or ovotestis is partially embedded in the right side of the posterior division of the liver (see especially Pl. IX, fig. 31). It is a racemose gland composed of a cluster of oval or pear-shaped follicles. These follicles are smallest in Apera burnupi and A. sexangula (Pl. XXIII, figs. 148, 149). In the other species they are larger and tend to be fewer in number, until in A. parva the entire hermaphrodite gland consists of only about four follicles (fig. 146). The very slender ducts from the different follicles unite to form the hermaphrodite duct, which is long, and usually more or less convoluted and slightly swollen towards the middle of its length, especially in A. dimidia. But the convolution is not so pronounced as in many other genera. In front the hermaphrodite duct becomes embedded in the albumen gland. At the extreme anterior end it is swollen so as to form a minute spherical vesicle, which is doubtless to be regarded as a rudimentary vesicula seminalis.

The albumen gland varies enormously in size according to the exact state of maturity of the individual (cf. Pl. IX, figs. 27, 31). In some specimens it reaches a very large size indeed (Pl. XXIII, fig. 144). The common duct, or ovispermatoduct, is very long and much convoluted and twisted in Apera burnupi and A. sexangula (Pl. XXIII, figs.

148, 149); in A. gibbonsi, A. parva, and A. dimidia it is shorter and generally broader (figs. 143, 144, 146, 147). In some specimens the female or oviducal portion is greatly swollen, as in the example of A. dimidia of which the reproductive organs are shown in fig. 147. The free oviduct is rather long and narrow, and is directly continuous with the vagina, which is also rather narrow but usually somewhat shorter. The vestibule or genital atrium is extremely short.

The Receptaculum Seminis and its Duct.—The spermatheca or receptaculum seminis is an oval vesicle, situated, in A. parva, beside the anterior end of the free oviduct, the receptacular duct in this species being extremely short (fig. 146). In the other forms the receptaculum seminis lies against the anterior end of the common duct, and the length of the receptacular duct is therefore about equal to that of the free oviduct, since the anterior opening of the receptacular duct marks the junction of the free oviduct with the vagina. In Apera gibbonsi the receptacular duct is a simple narrow tube (figs. 144, 145). In A. sexangula it becomes swollen towards its union with the vagina, so that the anterior part of the duct is fusiform (fig. 149). In A. burnupi the anterior part of the duct is still more swollen (fig. 148). Lastly, in A. dimidia the swollen end of the duct has become attached to the adjacent part of the body-wall by a number of muscles on each side (fig. 147). And as we pass up this series the receptaculum itself becomes progressively smaller, and it seems as though the receptacular duct were taking its place. If this tendency were to proceed still further we should have a vesicle which would be indistinguishable from a sessile receptaculum seminis, although in reality it was the swollen anterior end of the receptacular duct, the rest of the organ having disappeared. Possibly this may have happened in some of the genera which are usually described as having a sessile receptaculum.

The Male Organs.—The vas deferens arises from the anterior end of the common duct, and passes forwards close to the free oviduct and vagina as far as the vestibule. It then bends round and runs up the side of the penis. In Apera gibbonsi the vas deferens is rather thick excepting near the vestibule, where it has the more usual form of a very slender duct. In this species, and also in A. dimidia, before the vas deferens unites with the posterior end of the penis, it is slightly swollen for a distance equal to about one-third of the length of that organ, thus forming a rudimentary epiphallus. In A. sexangula this swollen part is very much shorter, and bears at its anterior end a minute flagellum, which, like the vas deferens itself, is closely applied to the side of the penis (Pl. XXIII, fig. 149).

The penis passes between the retractor muscles of the right upper and lower tentacles (Pl. XIII, figs. 52–57). In this respect Apera resembles Testacella, Trigonochlamys, Poiretia, Streptostyla, Strebelia, Rhytida, and Paryphanta, and differs from Daudebardia, Plutonia, Selenochlamys, Natalina, Delos, and the Streptaxidæ, in which the reproductive organs are on the right of both retractors, as was first shown by Pfeffer, Simroth, and Murdoch. In Apera dimidia the penis is fairly short, but a little swollen posteriorly (Pl. XXIII, fig. 147). In A. parva it is about 4 mm. in length, and somewhat fusiform (fig. 146). In typical specimens of A. gibbonsi from Zululand, the penis is also short (fig. 143), but in the other races of that species it is very long and twisted in a peculiar manner (fig. 144). In A. sexangula the penis is long and very narrow, excepting at the posterior end, where it is broad and somewhat flattened (fig. 149). In A. burnupi the anterior part of the penis is also narrow, but it is much shorter than in A. sexangula, and more or less twisted. The posterior broader portion, on the other hand, is longer, and appears to be double, owing to the presence of a deep longitudinal groove on one side; and the vas deferens disappears into this groove about 5 mm. in front of the end of the penis (fig. 148). Possibly this peculiar arrangement may be due to the broad sides of the penis having arched over the end of the vas deferens and joined each other above it; but this hypothesis must remain very doubtful until a sufficient number of specimens of this rare species has been collected in order to justify the dissection of the penis. In a full-grown example of A. gibbonsi rubella from Durban, the penis was found to be quite vestigial.

As so few full-grown specimens of Apera have been collected, I have only felt justified in examining the internal structure of the male organs in two forms, namely, A. dimidia and A. gibbonsi rubella. No penis-papilla is present in either of these species, but in both forms the inner surface of the muscular wall of the penis is completely covered by numerous small papillæ, as shown in Pl. XXIII, fig. 145. These papillæ are diamond-shaped in transverse section, and each ends in a short point. The structure of the papillæ is very similar in the two species, and is shown in Pl. XXII, fig. 142, which represents a photomicrograph of the inner half of a single papilla from the penis of A. gibbonsi rubella. In this form the papillæ become considerably smaller around the opening of the epiphallus, and within the opening they become much narrower in proportion to their length, changing, in fact, from papillæ into filaments. These filaments occur throughout the entire length of the epiphallus. They do not, however, arise from all parts of the inner surface of the wall of the epiphallus, but are arranged in longitudinal rows, of which there are about fourteen in the specimen that I examined. Between the rows the wall of the epiphallus is extremely thin. In Apera dimidia the epiphallus has a different structure, being lined by numerous minute papillæ, closely arranged, and not unlike the papillæ lining the penis, only much smaller. It is somewhat remarkable that while the inside of the penis is so very similar in the two species, the inside of the epiphallus should present such a marked contrast.

The retractor of the penis is attached to its posterior end, and arises from the roof of the body-cavity near the mid-dorsal line. In Apera burnupi, A. sexangula, A. purcelli, and A. parva, it is very long and narrow, arising in A.

sexangula and A. parva less than 4 mm. in front of the diaphragm, and only a very short distance further forwards in the other two species (Pl. IX, figs. 28, 30, 31). On the other hand, in A. gibbonsi and A. dimidia it is broader and very much shorter, the exact position of its origin depending on the length of the penis (figs. 27 and 29). Probably the retractor originally arose in the neighbourhood of the diaphragm; but owing to the posterior position which the diaphragm has come to occupy, the origin of the retractor has moved forward. If this view be correct, the condition found in A. sexangula and A. parva would be the most primitive.

THE SPERMATOZOA.—Pl. XXIII, fig. 151, shows the anterior end of a spermatozoon of Apera dimidia magnified 1200 diameters. It will be seen that the head is curved into the shape of a hook, and is about ·0035 mm. in length. The "middle-piece," or proximal portion of the tail, is surrounded by a spiral filament or flange, very loosely coiled, the whorls being about ·0045 mm. apart. The posterior portion of the tail is extremely long. In Apera sexangula and A. gibbonsi rubella the head of the spermatozoon is straighter and broader, though pointed in front. Fig. 150 shows the anterior end of a spermatozoon of the latter variety. It will be seen that in this form the whorls of the spiral filament are a little nearer together than in A. dimidia, being separated by a distance equal to the length of the head, namely, ·0037 mm.

The spermatozoa of Testacella are very different from those of Apera, as may be seen from Pl. XXIV, fig. 160. In Testacella the head is globular, and there are two spiral filaments surrounding the proximal portion of the tail. Moreover the filaments are much more closely coiled than in Apera, adjacent whorls being only about ·0009 mm. apart in T. maugei. In Rhytida capillacea (*Fér.*) I find that there are also two filaments, but they are not so closely coiled, the whorls being separated by about ·00165 mm.; and in this species, as well as in Natalina quekettiana (*M. & P.*), the head is not unlike that of Apera sexangula and A. gibbonsi rubella. On the other hand, in Streptaxis funki *Pfr.* the head is even more strongly curved than in Apera dimidia; and, as in the Testacellidæ and Rhytididæ, I have found two spiral filaments encircling the proximal portion of the tail, the distance separating adjacent whorls in this species being about ·00115 mm.

The embryology of Apera is unknown.

DISTRIBUTION.

The genus Apera is only known to inhabit the maritime provinces of South Africa. One species—A. purcelli—occurs on the slopes of Table Mountain close to Cape Town; the other forms have only been found in Natal and in the eastern districts of the Cape Province. A. parva is at present only known to occur near Grahamstown; A. sexangula extends from that neighbourhood as far east as Pietermaritzburg; the various races of A. gibbonsi are known to inhabit an area stretching from Pondoland to Zululand; while A. burnupi and A. dimidia have only been found in Natal.

The animals are usually found in the bush, either amongst dead leaves or under stones or logs; but none of the species are at all common. Apera sexangula and A. gibbonsi seem to be the least rare. Of the others only six examples of A. dimidia, four of A. burnupi, two of A. purcelli, and one of A. parva are known to have been collected. It is to be hoped that South African naturalists will gather further specimens of this interesting genus, which not improbably contains more species than are at present known.

THE DIFFERENTIAL CHARACTERS OF THE SPECIES AND SUBSPECIES OF APERA.

Apera gibbonsi (*Binney*).

Chlamydephorus gibbonsi *Binn.*, Bull. Mus. Comp. Zool. Harvard. 1879. vol. v, p. 331, pl. ii, figs. *a*, *b*; Binney. Ann. N. Y. Acad.

Sci., 1884, vol. iii, p. 81, pl. xvii, fig. A; Tryon, Man. of Conch. (2nd ser.), 1885, vol. i, pp. 17, 251. pl. ii, fig. 95; Cockerell, Ann. Mag. Nat. Hist. (6th ser.), 1890, vol. vi, p. 390.

Chlamydophorus gibbonsi *Binn.*; Tryon, Struct. and Syst. Conch., 1884, vol. iii, p. 13, pl. ci, fig. 47.

Apera gibbonsi (*Binn.*); Heynemann, Jahrb. d. Deutsch. Mal. Ges., 1885, vol. xii, p. 17, pl. ii, figs. 5–7; Collinge, Ann. S. Afr. Mus., 1900, vol. ii, p. 4; Collinge, Ann. Natal Mus., 1910, vol. ii, p. 165; Connolly, Ann. S. Afr. Mus., 1912, vol. xi, p. 63.

EXTERNAL CHARACTERS (Pl. VII, figs. 1, 2; Pl. VIII, figs. 14, 15).—Animal slender, tapering to an acute angle at the hind end. Back rounded, without keels. Outer lip of respiratory opening almost concealing the inner lip. Skin coarsely reticulated. Dorsal grooves usually about 1 mm. apart, separated by a single row of rugæ, but united for about 4 or 5 mm. in front of the respiratory opening. Lateral grooves irregular, rather near the dorsal grooves, and seldom extending as far as the head. Radial grooves conspicuous, some being forked. Oblique sub-lateral grooves also conspicuous, and rather numerous; these and the radial grooves terminating in the single peripodial groove.

In the typical form the body is mottled with brown, the small patches of colour being chiefly concentrated dorsally, but leaving a paler band, very sparsely mottled, along the centre of the back from the head to the respiratory opening. Laterally the brown pigment becomes confined to the sides of the grooves in the skin, and dies out completely some distance above the peripodial groove. The ground-colour is pale yellow in specimens preserved in spirit, but living examples are tinged with dull orange, the colour being deepest on the back.

The type was described by Mr. Gibbons as being rather more than 3 in. long when fully extended. The following are the dimensions (in alcohol) of two specimens that I have examined, but the reproductive organs of the smaller one were not quite fully developed.

Length	62 mm.	66·5 mm.
Breadth in middle	9·5 ,,	12·5 ,,
Breadth at respiratory opening	7 ,,	9 ,,
Breadth of foot-sole	5 ,,	5 ,,
Greatest height	9·5 ,,	12·5 ,,
Distance from respiratory opening to hind end	13 ,,	13·5 ,,

INTERNAL CHARACTERS.—Skin very thick. Shell 4 × 2·5 mm., usually thick, depressed, with the apex in front of the posterior margin; sinus deep.

Pedal gland.—Slender; glandular tissue gradually dying out some distance in front of the terminal vesicle; duct closely convoluted posteriorly; fold in terminal vesicle divided into narrow lamellæ.

Nervous system.—Cerebral ganglia closely united; buccal ganglia large, close together, situated posteriorly, and joined to the cerebral ganglia by extremely long connectives; cerebro-pedal and cerebro-pleural connectives also long; nerves corresponding to those of buccal retractors in other species uniting with anterior end of sheath of odontophore, and joined to cerebro-buccal connectives for most of their length; nerves to pedal gland very slender.

Digestive System (Pl. XVII, figs. 91, 92; Pl. XX, fig. 125; text-fig. 3, A, p. 159; Pl. XXI, fig. 129).—Radula exceedingly large, sometimes attaining a length of 21 mm.; central tooth typically present; others not differentiated into laterals and marginals, very large excepting near the edges and the centre; cusps in typical form simple, slightly curved; bases very narrow; apophyses typically not prominent. Formula of type: (27 + 1 + 27) × 52, of a Zululand example: (37 + 1 + 38) × 60. Odontophore also extremely large; posterior end joined to the floor and sides of the body-cavity towards its hind end by numerous radial buccal retractors; odontophoral support rounded in front. Œsophagus short and broad, merging into a broadly fusiform crop. Anterior loop of wide intestine not much deeper than posterior loop; intestine continued posteriorly on right side of liver. Salivary glands united above crop. Liver of two approximately equal divisions, the intestine only traversing the right.

Vascular System.—Pulmonary veins greatly branched. "Posterior aorta" supplying left division of liver and hermaphrodite gland; two arteries of right division of liver arising from anterior aorta as a single vessel; anterior aorta passing to right of intestine in typical form; anterior branches of buccal artery separate throughout.

Reproductive System (Pl. XXIII, fig. 143).—Hermaphrodite gland with rather large follicles; common duct rather short, curving twice to the right and twice to the left; vagina narrow; receptaculum seminis rather large; receptacular duct of moderate length and slender throughout. Vas deferens rather thick excepting near the vestibule, somewhat swollen near the posterior half of the penis to form an epiphallus; penis short and curved posteriorly in specimens from Zululand; penial retractor short.

Habitat.—Typical form: Umgeni valley, Natal (under a stone in a wood; Gibbons); Pietermaritzburg (?, Burnup, Ponsonby); Hlabisa, Zululand (Burnup).

Type.—The type is in the Academy of Natural Sciences, Philadelphia. Other specimens will be found in the Natal Museum, Pietermaritzburg.

Affinities, etc.—This species is the type of the genus. It differs from all the other species in its radula, buccal retractors, receptacular duct, etc. At the same time it shows a remarkable diversity in some of its organs, specimens found in different localities, and even, in one case, in the same locality, constituting races which differ markedly from each other in their radulæ and in a few other important characters. Indeed, it is not at all improbable that these forms will prove to be distinct species. For the present, however, until further specimens have been collected, I have thought it better to treat them provisionally as subspecies of Apera gibbonsi; for although their differences are undoubtedly of considerable importance, in most of their anatomical features they appear to be identical, and it is impossible to distinguish them merely by their external characters, excepting in the case of one form, of which only a single specimen has been collected.

Apera gibbonsi rubella *n. subsp.*

External Characters (Pl. VII, figs. 3, 4, 5; Pl. VIII, figs. 16, 17).—Animal broader than the typical form of Apera gibbonsi, tapering more abruptly at the hind end. Back usually slightly flattened just behind the respiratory opening. Reticulation of skin very similar to that of the typical form of A. gibbonsi, but not so coarse, the grooves being more numerous and less deep. Dorsal grooves usually less than 1 mm. apart, and united for about 4 mm. in front of the respiratory opening.

Body thickly mottled with dark grey (which sometimes has a bluish tinge in specimens preserved in spirit). The small patches of colour are usually ill-defined, and tend to coalesce dorsally, where they are most abundant; but a narrow paler band, more sparsely mottled, is generally left along the centre of the back from the head to the respiratory opening. Laterally the dark pigment is chiefly concentrated on the sides of the grooves in the skin, but it dies out completely a short distance above the peripodial groove. The ground-colour of specimens preserved in spirit is whitish, tinged with dull red dorsally, but living examples are deeply coloured with an unstable orange-red pigment, so that the animal is usually reddish-brown above, merging into deep reddish orange on the sides, while the foot-sole is of a paler orange colour.

The following are the approximate dimensions (in alcohol) of the smallest specimen with fully developed reproductive organs, and of the largest specimen, which I have examined.

Length	49·5 mm.	. 67 mm.
Breadth in middle . . .	10 ,,	. 13·5 ,,
Breadth at respiratory opening	9 ,,	. 11 ,,
Breadth of foot-sole . .	5·5 ,,	. 6 ,,
Greatest height . . .	9·5 ,,	. 13·25 ,,
Distance from respiratory opening to hind end . .	10 ,,	. 13 ,,

Internal Characters.—Glandular tissue of pedal gland reaching nearly as far back as the terminal vesicle. Radula (Pl. XX, fig. 126; text-fig. 3, B, p. 159) without central tooth; cusps of teeth very strongly curved, slightly broadened towards the points; apophyses very prominent; formula of a specimen from Equeefa: (28 + 0 + 28) × 51; of a young example from Equeefa: (24 + 0 + 24) × 44; of a specimen from Durban: (34 + 0 + 35) × 48. Liver sometimes shorter and broader than in typical form (Pl. XXI, fig. 130). Penis long and twisted (Pl. XXIII, fig. 144). The anterior aorta passes on the right of the intestine (Pl. IX, fig. 27), and all the other anatomical characters seem to be identical with those of the typical form (Pl. X, figs. 32, 33; Pl. XIII, figs. 41, 42, 52; Pl. XIV, figs. 63–65, 67; Pl. XV, figs 70, 77–79; Pl. XVII, figs. 93–98; Pl. XXII, figs. 138, 139, 142; Pl. XXIII, figs. 145, 150).

Habitat.—Equeefa, Natal (Burnup); Durban (under dead leaves in the bush which fringes the shore; Burnup).

Type.—The type of subspecies is in the Natal Museum, Pietermaritzburg. Another specimen will be found in the British Museum.

Affinities, etc.—The chief characters which distinguish this form from Apera gibbonsi *s.s.* are its broader shape and darker colour, its radula, and its penis (although it is not known whether the penis of the typical form is always as short as it is in the Zululand specimens). It is possible that this may be a geographical variety of A. gibbonsi, as the two forms are not known to occur in the same district, but the radulæ are so different as to suggest that this may prove to be a distinct species. The single specimen from Durban differs from those found at Equeefa in being without a paler dorsal band, in having more teeth in each row in its radula, and in the penis being abnormally reduced to a minute vestige. The resemblance of this specimen to certain dead leaves amongst those under which it was found has already been referred to (see p. 122). Mr. Burnup informs me that this subspecies contracts after the usual manner when about to rest, instead of merely bending its body at various angles like the typical form of A. gibbonsi.

Apera gibbonsi gracilis *n. subsp.*

External Characters (Pl. VII, fig. 6).—Animal even more slender than the typical form of Apera gibbonsi, tapering to a very acute angle at the hind end. Outer lip of the respiratory opening not concealing so much of the inner lip as in the other forms of A. gibbonsi. Reticulation of skin coarse, as in the typical form; dorsal grooves united for 6 mm. in front of the respiratory opening.

Body rather sparsely mottled with brown, as in A. gibbonsi, *s. s.*; the patches of colour, however, are not concentrated on each side of the mid-dorsal area, but extend across it, so that there is no median paler band.

The following are the measurements of the only specimen that has been found:

Length . .	44 mm.	Greatest height .	6 mm.
Breadth in middle	6 ,,	Distance of resp. opening from hind end . .	11 ,,
Breadth at resp. opening . .	4·5 ,,		
Breadth of foot-sole	3 ,,		

Internal Characters.—Shell (Pl. XIII, fig. 43) rather longer and narrower at the posterior end than in the other forms of A. gibbonsi. Radula (Pl. XIX, fig. 123; text-fig. 3, c, p. 159) with fewer teeth than that of any of the other forms; central tooth absent; first on each side extremely small; outer teeth larger than in the preceding forms; cusps only slightly curved, not broadened or barbed; apophyses very prominent; formula: $(19 + 0 + 20) \times 34$. Anterior aorta passing through loop of intestine; branches of pulmonary veins not very numerous. Penis rather long and twisted. Other characters agreeing with those of A. gibbonsi *s. s.*

Habitat.—Equeefa, Natal (Burnup).

Type.—The type of subspecies is in the Natal Museum, Pietermaritzburg.

Affinities, etc.—The single specimen of this form differs greatly from the last subspecies, although it was found in the same locality. In some respects it is intermediate between Apera gibbonsi *s.s.* and the next subspecies, but it seems impossible to associate it with either of these forms, and it must therefore stand alone until further examples have been collected. It will be noticed that owing to the length of the posterior extremity the respiratory opening is proportionately further forward than in the other forms.

Apera gibbonsi lupata *n. subsp.*

External Characters (Pl. VIII, figs. 18, 19).—Animal intermediate between A. gibbonsi *s.s.* and A. g. rubella both in shape and in the reticulation of the skin, being usually a little broader and less coarsely reticulated than the typical form of A. gibbonsi, and a little narrower and less finely reticulated than A. g. rubella. Colour variable: sometimes dark like A. g. rubella, sometimes light as in A. gibbonsi *s.s.* In the typical form the mottling is inconspicuous and there is only a very slight trace of the paler median dorsal band.

This form (and possibly also the last subspecies) may be slightly smaller than A. gibbonsi *s.s.* The following are the measurements of a specimen which seemed to be practically mature:

Length . .	46 mm.	Greatest height .	7 mm.
Breadth in middle	7·5 ,,	Distance of resp. opening from hind end . . .	8 ,,
Breadth at resp. opening . .	6 ,,		
Breadth of foot-sole	4 ,,		

Internal Characters.—Shell much depressed. Radula (Pl. XVII, fig. 99; Pl. XIX, fig. 124; text-fig. 3, d, p. 159) with a comparatively small number of very large teeth; central tooth typically absent; cusps somewhat curved and conspicuously barbed on the lower side; apophyses prominent; formulæ of two specimens (the second slightly immature): (20 + 0 + 20) × 44, (21 + 0 + 21) × 38. Anterior aorta passing through loop of intestine (text-fig. 5, D, p. 183); pulmonary veins not very numerous. Penis long and twisted. Other characters agreeing with those of A. gibbonsi *s.s.*

HABITAT.—Port Shepstone, Natal (Burnup).

Var. duplex *n. var.*

CHARACTERS.—Back distinctly mottled, with a well-marked paler median band, the coloration being very similar to that of Apera gibbonsi *s.s.* Cusps of teeth rather longer than in the typical form of the subspecies, and having an additional barb on the upper side near the point (excepting in the smaller teeth); apophyses very prominent; a vestigial central tooth is present in most of the rows (text-fig. 3, E, p. 159); formula: (22 + (1) + 22) × 42. Otherwise similar to the Port Shepstone specimens of A. gibbonsi lupata.

HABITAT.—Port St. John's, Pondoland (one specimen; Mrs. E. Warren).

TYPE.—The types of subspecies and variety are in the Natal Museum, Pietermaritzburg. Another specimen of the subspecies will be found in the British Museum.

AFFINITIES, ETC.—This subspecies is especially characterised by its large barbed teeth. The course of the anterior aorta also serves to separate it from the typical form of Apera gibbonsi, as well as from A. g. rubella. But although the average shape of this subspecies is slightly different from either of these forms, the differences are so small that in practice I find that it is quite impossible to distinguish, without dissection, light specimens of the present subspecies from A. gibbonsi *s.s.*, and dark examples from A. g. rubella, unless, perchance, the odontophore is sufficiently protruded to enable one to see the teeth. It follows, therefore, that none of these three forms can be identified with certainty from an examination of their external characters only. It will be noticed that this race of A. gibbonsi seems to have a more westerly distribution than the preceding forms.

Apera parva *n. sp.*

External Characters (Pl. VIII, figs. 22, 23).—Animal very slender, tapering to an acute angle at the hind end. Back rounded, without keels. Outer lip of respiratory opening almost concealing the inner lip. Skin coarsely reticulated. Dorsal grooves about ⅓ mm. apart, separated by a single row of rugæ, but united for 3 mm. in front of the respiratory opening. Lateral grooves near the dorsal grooves and extending forwards to the head, the right one ending in the genital opening. Radial grooves well-marked, but fewer than usual, only three arising from the respiratory opening on each side (in addition to the two median grooves). Oblique sub-lateral grooves less numerous than in A. gibbonsi, being absent from the anterior third of the animal. Both radial and sub-lateral terminate in the single peripodial groove.

Mr. Farquhar informs me that the living animal is fawn-coloured; dark dorsally, but much lighter below. In alcohol the specimen has become yellowish brown, as shown in the figures.

The following are the dimensions of the slug in alcohol; but when alive and moving Mr. Farquhar tells me that it attained a length of about 35 mm.

Length . .	25 mm.	Greatest height .	3 mm.
Breadth in middle	3 ,,	Distance from resp. opening to hind end . . .	5·5 ,,
Breadth at resp. opening . .	2·4 ,,		
Breadth of foot-sole	1·9 ,,		

Internal Characters.—Skin very thick. Shell (Pl. XIII, fig. 44, 45) 1·6 × ·9 mm., thick, depressed, with a flattened apex in front of the posterior margin; sinus of moderate depth; left posterior angle obliquely truncate.

Pedal gland (Pl. XIII, fig. 53).—Slender; glandular tissue gradually dying out a little behind the middle of the gland; duct less convoluted posteriorly than in A. gibbonsi.

Nervous system.—Cerebral ganglia clearly separate; buccal ganglia situated posteriorly and joined to the cerebral ganglia by long connectives; cerebro-pedal and cerebro-pleural connectives rather long.

Digestive System (Pl. XVII, figs. 100–102; text-fig. 4, A, p. 161; Pl. XXI, fig. 131).—Radula very large, 8 mm. long; central tooth very small, absent in some rows; others scarcely differentiated into laterals and marginals, becoming extremely large towards the edges of the radula; cusps simple, very slightly curved, short towards the centre of the radula, longer towards the edges; bases broader than in A. gibbonsi; corresponding teeth not opposite to each other; formula: (17 + 1 + 17) × 48. Odontophore also very large; posterior end joined by numerous short radial buccal retractors to the sides and floor of the body-cavity about the middle of its length; odontophoral support rounded in front. Œsophagus short and broad, merging into a fusiform crop. Between the crop and the wide intestine is an oval stomach, into which the hepatic ducts open. Second loop of intestine absent, the alimentary canal curving over to the right side of the liver and then passing straight backwards. Salivary glands contiguous above the crop, but less closely fused than in A. gibbonsi. Liver in two approximately equal divisions, the intestine only traversing the right.

Vascular System (Pl. IX, fig. 28).—Pulmonary veins not very numerous. "Posterior aorta" dividing at its origin into three branches which supply the left division of the liver and the hermaphrodite gland; right division of liver supplied by two arteries from the anterior aorta, which arise separately but close together; anterior aorta passing through loop of intestine; anterior branches of buccal artery leaving the posterior branch as a single median vessel.

Reproductive System (Pl. XXIII, fig. 146). — Hermaphrodite gland composed of only about four follicles, which are relatively very large; albumen gland in the specimen examined extending to the left side of the body-cavity, passing between some of the posterior buccal retractors; common duct rather short, curving twice to the right and once to the left; vagina rather narrow; receptaculum seminis further forward than in the other species; receptacular duct broad and extremely short. Vas deferens not enlarged to form an epiphallus; penis straight, rather short, and slightly swollen in the middle; penial retractor long and narrow.

Habitat.—Near Fern Kloof, about three miles south of Grahamstown, Cape of Good Hope (in a stony place with very little grass, at least 200 yards away from the bush; Farquhar).

Type.—The type is in the Natal Museum, Pietermaritzburg.

Affinities, etc.—The only example of this species at present known was discovered by Mr. John Farquhar, of Grahamstown, on October 12th, 1913. In many respects the slug bears a close resemblance to Apera gibbonsi, and it might easily be mistaken for a young specimen of that species. Nevertheless, it differs from all the forms which I have included under A. gibbonsi in so many characters that there can be very little doubt that it is specifically distinct. The following are the features in which some of the most important differences occur: the size; the number of the radial and sub-lateral grooves; the distance between the cerebral ganglia; the size of the teeth towards the edges of the radula, and the width of the bases of all the teeth; the position of the origin of the buccal retractors; the stomach; the course of the intestine; the division of the arteries to both portions of the liver; the hermaphrodite gland; and the length of the receptacular duct and of the penial retractor, these last features being perhaps the most striking of all.

Apera dimidia *n. sp.*

External Characters (Pl. VII, figs. 7–9; Pl. VIII, figs. 20, 21, 24).—Animal sometimes slightly swollen towards the middle, tapering to a blunt point at the hind end. Back rounded, without keels. Outer lip of respiratory opening narrow, exposing the inner lip. Skin covered with a network of grooves, among which the main grooves are less conspicuous than in the other species of Apera. Dorsal grooves about 1 mm. apart (notwithstanding the small size of the species), usually separated by a double row of rugæ, but united for about 3 mm. in front of the respiratory opening. Lateral grooves rather near the dorsal grooves, irregular, but sometimes extending as far as the head. Oblique sub-lateral grooves also irregular, seldom reaching the peripodial groove, and less numerous than in A. gibbonsi, being usually absent from the anterior third of the animal. Radial grooves fairly well marked dorsally, but like the sub-lateral grooves they cannot always be traced as far as the peripodial groove. The upper limits of the lowest rugæ on each side often form an irregular longitudinal groove near the peripodial groove and parallel to it.

Body conspicuously mottled with greyish-brown pigment, which is chiefly concentrated to form an irregular and somewhat discontinuous dark band along each side of the animal. Between these bands is a much paler dorsal area only sparsely mottled, darkest around the anterior border of the respiratory opening and lightest at the edges next to the dark bands. Below these the skin is darker than it is dorsally, being more thickly mottled, especially next to the dark band, though the pigmentation extends down to the peripodial groove. Both dorsally and laterally there is a tendency for some of the pigment to be concentrated in the dermal grooves, thus emphasizing the reticulation. Small patches of the same pigment are sparsely scattered over the foot-sole. The ground-colour of specimens preserved in spirit is yellowish white.

The following are the dimensions (in alcohol) of two specimens, in both of which the reproductive organs were fully developed:

Length . . .	32·5 mm.	. 33·5 mm.
Breadth in middle .	6·5 ,,	. 7·5 ,,
Breadth at respiratory opening . . .	4 ,,	. 4·75 ,,
Breadth of foot-sole .	3·75 ,,	. 4·25 ,,
Greatest height .	6 ,,	. 6·5 ,,
Distance from respiratory opening to hind end . .	6 ,,	. 6·25 ,,

INTERNAL CHARACTERS.—Skin not quite so thick as in most of the species (Pl. XI, figs. 34, 35; Pl. XII, figs. 36–39; Pl. XIII, fig. 40). Shell (Pl. XIII, fig. 46) 3 × 1·8 mm., thin and translucent, convex; apex rounded, quite at the posterior end; sinus rather shallow.

Pedal gland (Pl. XIII, figs. 54, 59–62; Pl. XIV, fig. 66).—It has the glandular tissue entirely concentrated in the anterior half, which is very broad in consequence; fold of terminal vesicle not divided into narrow lamellæ.

Nervous System (Pl. XIV, figs. 68, 69; Pl. XV, figs. 71, 73, 75; Pl. XVI, figs. 80–86).—Cerebral ganglia with prominent accessory lobes; buccal ganglia normally situated posteriorly, joined to cerebral ganglia by comparatively short connectives; nerves to pedal ganglia large.

Digestive System (Pl. XVI, figs. 88–90; Pl. XVII, figs. 103–107; Pl. XVIII, figs. 115–122; Pl. XX, fig. 127; text-fig. 4, B, p. 161; Pl. XXI, fig. 132; Pl. XXII, figs. 136, 137).—Radula 4·8 mm. long; central tooth absent; about thirteen laterals with very short curved cusps, and the same number of marginals with longer narrower cusps, on each side: corresponding teeth not opposite to each other; formula: (25 + 0 + 26) × 61. Odontophore rather large, with a single buccal retractor. Œsophagus narrow and as long as the salivary ducts; crop swollen anteriorly; loops of wide intestine nearly vertical, mainly on the left side of the posterior division of the liver. Salivary glands united above anterior end of crop. Anterior division of liver above crop and in front of intestine.

Vascular System (Pl. IX, fig. 29; Pl. XXII, fig. 140).—Pulmonary veins not very numerous; no "posterior aorta"; two main arteries of liver arising from anterior aorta as a single vessel, posterior artery supplying hermaphrodite gland as well as posterior division of liver; anterior aorta passing to right of intestine.

Reproductive System (Pl. XXIII, figs. 147, 151).—Hermaphrodite gland oblong, with moderately large follicles; hermaphrodite duct rather more convoluted and swollen in the middle than in the other species; common duct rather short, curving twice to the right and twice to the left; vagina broader than in A. gibbonsi; receptaculum seminis small; receptacular duct much swollen anteriorly, the swollen part being attached to the adjacent body-wall by short transverse muscles on each side. Vas deferens becoming slightly swollen near the posterior half of the penis to form an epiphallus; penis short, broadened posteriorly; penial retractor also short.

Habitat.—Port Shepstone, Natal (Burnup); Town Bush, Pietermaritzburg (on a mossy stone; Mrs. Warren); Equeefa, Natal (Burnup).

Type.—The type is in the British Museum. Other specimens will be found in the Natal Museum, Pietermaritzburg.

Affinities, etc.—This species may be distinguished at a glance from young specimens of any of the forms of Apera gibbonsi by its dark lateral bands, while the absence of keels separates it from the other species found in Natal. Internally it differs widely from A. gibbonsi and A. parva in its radula, buccal retractor, œsophagus, liver, receptacular duct, etc.; while in no other species is the pedal gland so broad in front and so slender behind.

This species was first discovered by Mr. Burnup in March, 1903.

Apera purcelli *Collinge.*

Apera purcelli *Cllge.*, Ann. S. Afr. Mus., 1901, vol. ii, p. 230, pl. xiv, figs. 1, 2; Connolly, Ann. S. Afr. Mus., 1912, vol. xi, p. 63.

External Characters (Pl. VIII, fig. 25; and 'Ann. S. Afr. Mus.,' vol. ii, pl. xiv, figs. 1, 2).—Animal rather broad anteriorly, tapering to a blunt point at the hind end. Back rounded, without keels. Outer lip of respiratory opening narrow, exposing the inner lip. Skin with well-marked reticulation, the rugæ being rather large for the size of the slug. Dorsal grooves less than ½ mm. apart, separated throughout their length by a single row of rugæ, not united in front of the respiratory opening. Radial grooves well-developed, and extending down to the single peripodial groove, which is not very deep. The most anterior radial grooves branch from the dorsal grooves near the respiratory opening, instead of arising from the opening itself. There is not even a trace of lateral grooves, excepting perhaps for a very short distance; but irregular oblique grooves occur in front of the radial grooves, and these correspond to the sub-lateral grooves of other species.

Body dark grey or bluish black, the pigment being chiefly concentrated in the dermal grooves and thus emphasizing the reticulation. On each side there is a suggestion of a slightly darker lateral band, the intervening dorsal area being a little paler, although it tends to be darker towards the centre than next to the obscure lateral bands. Below these the skin becomes much lighter, the pigment dying out completely before it reaches the peripodial groove. The foot and the ground-colour of the back is whitish yellow in the case of specimens preserved in spirit, but in living examples the foot is said to be ferruginous.

According to Mr. Collinge the type (in alcohol) is 25 mm. long, and its foot-sole is 4 mm. in breadth. I have only seen a young specimen, of which the following are the measurements:

Length . . .	16 mm.	Greatest height .	3·5 mm.
Breadth in middle	3·75 ,,	Distance from resp. opening to hind end . . .	3·75 ,,
Breadth at resp. opening . .	2·25 ,,		
Breadth of foot-sole	2 ,,		

INTERNAL CHARACTERS.—Skin thick. Shell (Pl. XIII, figs. 47, 48) 1·2 × ·6 mm. (in the immature specimen whose measurements are given above), thin and translucent, very convex; apex rounded, overhanging the posterior margin to a considerable extent; sinus shallow.

Pedal gland (Pl. XIII, fig. 55).—Glandular throughout its entire length.

Nervous system.—The various ganglia more distinctly separate than in most species of Apera; buccal ganglia situated posteriorly, joined to cerebral ganglia by comparatively short connectives.

Digestive System (Pl. XIII, fig. 55; text-fig. 4, c, p. 161). —Radula (of immature specimen) 1·8 mm. long; teeth less numerous than in most species; central tooth small; three or four laterals with very short cusps, and about four times as many marginals with longer narrower cusps, on each side; formula (of immature specimen): $(18 + 1 + 18) \times 41$. Odontophore with single buccal retractor. Œsophagus narrow; loops of intestine nearly vertical, mainly on the left side of the liver. Salivary glands more or less united.

Anterior aorta passing to the right of the intestine, "posterior aorta" probably absent. Penial retractor long, as in the next species.

HABITAT.—Table Mountain, Cape Town (scarce; Lightfoot).

TYPE.—The type is in the South African Museum, Cape Town. An immature specimen will be found in the Cambridge University Museum of Zoology.

AFFINITIES, ETC.—This rare species is the only member of the genus that is known to occur in the west of the Cape Province. In some respects it resembles Apera dimidia more than any of the other species, but it differs from both A. dimidia and A. gibbonsi in having the dorsal grooves separate throughout their entire length, in the glandular tissue extending to the terminal vesicle of the pedal gland, and in the long penial retractor. In these features the present form resembles the keeled species of Apera. Unfortunately the reproductive organs of this species are practically unknown, and it is to be hoped that further specimens will be discovered so that these organs may be described.

Apera burnupi *Smith.*

Apera burnupi *Smith*, Ann. Mag. Nat. Hist. (6th ser.), 1892, vol. x, p. 466.

Apera natalensis *Collinge*, Ann. S. Afr. Mus., 1900, vol. ii, p. 3, pl. i, figs. 3, 4, pl. ii, figs. 14, 15; Simroth, Naturwiss. Wochenschr., 1901, vol. xvii, p. 111, fig. 7; Simroth, Bronn's Klass. u. Ordn. d. Tier-Reichs III, Gastr. Pulm., 1909, p. 143, fig. 42 *c*, pl. iv, figs. 9, 10; Collinge, Ann. Natal Mus., 1910, vol. ii, p. 167; Simroth, Bronn's Klass. u. Ordn. d. Tier-Reichs III, Gastr. Pulm., 1912, p. 611; Connolly, Ann. S. Afr. Mus., 1912, vol. xi, p. 63.

EXTERNAL CHARACTERS (Pl. VII, figs. 10, 11; Pl. VIII, fig. 26; and 'Ann. S. Afr. Mus.,' vol. ii, pl. i, figs. 3, 4).—Animal broad and flattened towards the hind end, tapering anteriorly, with four longitudinal keels, two on each side of the body. Notwithstanding the two pairs of keels the animal is squarish in section, excepting posteriorly, as the lower keels are not far from the edges of the foot. Upper keels prominent though blunt, nearly parallel to each other in the middle of the body and separated by about seven-eighths of the breadth of the animal. Anteriorly they converge a little towards the head. In the posterior three-eighths of the slug the upper keels become very prominent, at first diverging and then curving round to meet in a very obtuse angle above the posterior extremity of the foot (but the angle is probably less obtuse in young than in adult specimens). They thus enclose a large flattened oval area, sloping downwards and backwards, and having the respiratory opening slightly in front and to the right of its centre. Lower keels less prominent, twice as far from the upper keels as from the edges of the foot, extending for nearly three quarters of the length of the animal but not reaching the hind end. Foot rather broad, but tapering behind as in the other species, so that the posterior dorsal expansion of the body overhangs the edges of the foot on each side. Outer lip of respiratory opening rather narrow, exposing the inner lip. Skin coarsely reticulated, the rugæ being especially prominent on the anterior part of the back. Dorsal grooves very conspicuous, about 1 mm. apart (or rather more in the centre), separated by a row of rugæ which is usually double in the middle of the body, converging as they approach the respiratory opening, but not uniting with each other. Lateral grooves deep but rather irregular, extending along each side of the body as far as the head, a little nearer the upper than the lower keels, the right one terminating in the genital opening. Below each lateral groove another more irregular groove branches from the most anterior radial groove and runs forward above the lower keel until it unites with the lateral groove on the side of the head. There are two or three irregular sub-lateral grooves on each side, and also three or four equally irregular supra-lateral grooves, parallel to the most anterior radial grooves and connecting the dorsal grooves with the lateral grooves on each side of the back. The upper keels are notched by these supra-lateral grooves as they cross them, but the keels are more deeply notched by the radial grooves, which are rather numerous and very conspicuous. Both radial and sub-lateral grooves terminate below in a longitudinal groove, parallel to the peripodial groove, but separated from it by a narrow row of rugæ. In addition to the usual transverse grooves there is an obscure longitudinal groove on the foot-fringe, also parallel to the peripodial groove.

Body mottled with greyish-brown patches of colour, which sometimes have a greenish-blue tinge. The mottling is chiefly concentrated on the sides of the body between the keels, but patches of colour also occur between the lower keels and the peripodial groove, and more sparsely on the dorsal area. The ground-colour of specimens preserved in spirit is usually pale yellow slightly tinged with reddish-brown dorsally; but in living examples the skin is more deeply coloured, the back being reddish-brown, and the sides and foot-sole tinted with orange-red.

The following are the dimensions (in alcohol) of the type of A. natalensis according to Collinge, and of the still larger specimen belonging to the South African Museum shown in Pl. VII, fig. 10:

Length	65 mm. .	77 mm.
Breadth between upper keels in middle	10 ,, .	12·5 ,,
Breadth between upper keels behind respiratory opening .	13·5 ,, .	17 ,,
Breadth between lower keels in middle	— .	14·5 ,,
Breadth of foot-sole . .	9·5 ,, .	11·5 ,,
Greatest height (15 mm. in front of respiratory opening) .	— .	14 ,,
Distance from respiratory opening to hind end . . .	— .	18·5 ,,

Internal Characters.—Skin extremely thick, especially towards the hind end (Pl. IX, fig. 30). Shell (Pl. XIII, fig. 49) 5·5 × 3·2 mm., of moderate thickness, convex, with a conical apex projecting slightly beyond the posterior margin; sinus rather deep.

Pedal gland (Pl. XIII, fig. 56).—Exceptionally large, its loops wrapping round the other organs; glandular tissue extending throughout its entire length.

Nervous system.—Buccal ganglia situated anteriorly; connectives short.

Digestive System (Pl. XVII, figs. 108, 109; Pl. XX, fig. 128; text-fig. 4, D, p. 161; Pl. XXI, fig. 133).—Radula (of large specimen) 6 mm. long; central tooth present, with a very short single cusp; eleven laterals with short double cusps, and more than twice as many marginals with long, narrow, nearly straight cusps, on each side, the transition between laterals and marginals being abrupt; formula (of large specimen): (25 + 11 + 1 + 11 + 25) × 77. Odontophore small, with a single slender buccal retractor; odontophoral support bluntly pointed in front. Œsophagus narrow and as long as the salivary ducts; crop cylindrical; intestine narrow, first loop deep, posterior continuation on right side of liver. Salivary glands separate. Liver of two approximately equal divisions, the intestine only traversing the right.

Vascular System (Pl. IX, fig. 30).—Pulmonary veins forming a network. "Posterior aorta" supplying left division of liver and hermaphrodite gland, and sending a small branch to posterior end of right division of liver; remainder of right division supplied by two arteries from the anterior aorta, which arise separately, but close together; anterior aorta passing through loop of intestine.

Reproductive system (Pl. XXIII, fig. 148).—Hermaphrodite gland composed of relatively smaller follicles than in A. dimidia; hermaphrodite duct convoluted; common duct very long, rather narrow, and much convoluted and twisted; vagina bent at right angles towards its anterior end; receptaculum seminis small; receptacular duct greatly swollen towards the anterior end. Penis moderately long; anterior part narrow and more or less twisted, posterior part broad and appearing as though it were double owing to the presence of a longitudinal groove along one side; vas deferens disappearing into this groove about 5 mm. from the posterior end of the penis; penial retractor long and narrow.

HABITAT.—Chase Bush, Pietermaritzburg (Burnup); Richmond, Natal (nearly in the centre of a rotten log; Ward).

TYPE.—The type of A. burnupi is in the British Museum, of A. natalensis in the South African Museum, Cape Town. Another specimen will be found in the Natal Museum, Pietermaritzburg.

AFFINITIES, ETC.—This striking form differs widely from all the preceding species not only on account of its conspicuous keels, but also in the double cusps of the lateral teeth of the radula and the separate salivary glands.

Apera sexangula *n. sp.*

Apera burnupi "*Smith*": Collinge. Ann. Mag. Nat. Hist. (6th ser.), 1897, vol. xx, p. 221, pl. v. figs. 1–6; Pilsbry, Nautilus, 1898, vol. xii, p. 12; Collinge, Ann. S. Afr. Mus., 1900. vol. ii, p. 4, pl. i, figs. 5, 6; Collinge, Journ. of Mal., 1901, vol. viii, p. 71, fig. 1; Collinge, Journ.

of Mal., 1902, vol. ix, pl. vi, fig. 66; Simroth, Bronn's Klass. u. Ordn. d. Tier-Reichs III, Gastr. Pulm., 1909, pl. iv, fig. 11; Collinge, Ann. Natal Mus., 1910, vol. ii, p. 166; Simroth, Bronn's Klass. u. Ordn. d. Tier-Reichs III, Gastr. Pulm., 1912, p. 611; Connolly, Ann. S. Afr. Mus., 1912, vol. xi, p. 62.

External Characters (Pl. VII, figs. 12, 13; and 'Ann. S. Afr. Mus.,' vol. ii, pl. i, figs. 5 and 6).—Animal rather slender, approximately hexagonal in section, owing to the presence of four prominent longitudinal keels, two on each side of the body. Upper keels separated by about three-fifths of the breadth of the slug, and nearly parallel to each other, excepting posteriorly, where they diverge very slightly just in front of the respiratory opening, and then gradually converge behind it, until they unite to form a single median keel, 3 or 4 mm. in length, at the hind end of the animal. Lower keels extending along the whole length of the slug, about half way between the upper keels and the edges of the foot, but sloping downwards towards the hind end. The areas between the keels are nearly flat when the animal is in motion, but when it contracts they become deeply concave. Body, as seen from above, tapering to an acute angle posteriorly, but when viewed from the side the hind end appears blunter owing to the short median keel (though not always so rounded as in fig. 13). Outer lip of respiratory opening narrow, exposing the inner lip. Rugæ minutely subdivided. Dorsal grooves well marked, usually about 1 mm. apart, separated by a row of rugæ which is single in front and behind but often becomes irregularly double towards the middle, converging slightly as they approach the respiratory opening, but not uniting with each other. Lateral grooves also conspicuous, extending along each side of the body as far as the head about half way between the upper and lower keels, the right one ending in the genital opening. Sub-lateral grooves few and irregular, only two or three being traceable on each side. Radial grooves well marked, forming slight notches in the keels where they cross them. Both radial and sub-lateral grooves terminate below in a longitudinal groove, parallel to the peripodial groove, but separated from it by a narrow row of rugæ.

Body mottled with greyish-brown pigment, excepting along the edges of the keels. The colour tends to be more concentrated towards the hind end, and along the sides of the animal just below the upper keels, although it extends down to the peripodial groove. As a rule, minute reddish-brown specks are also thickly scattered over the body, and these, unlike the greyer patches of colour, occur also on the foot-sole, though much less abundantly than on the back. The ground-colour of specimens preserved in spirit is yellowish-white, very slightly tinged with dull red dorsally; but in life the skin is more deeply stained with dull red pigment, the general colour of the living animal being usually chestnut or reddish-brown, paler on the keels and foot.[1]

The following are the dimensions (in alcohol) of a small but mature specimen, whose reproductive organs are shown in Pl. XXIII, fig. 149, of a slightly larger example in which the genital system is not quite fully developed, and of an unusually large specimen in the Natal Museum, of which Mr. Burnup has kindly given me the measurements.

	mm.	mm.	mm.
Length	52·5	56	77
Breadth between upper keels in middle	4·5	6	10·5
Breadth between upper keels at respiratory opening	4	4	8·5
Breadth between lower keels in middle	7·5	10	16
Breadth of foot-sole	4	4·5	10·5
Greatest height (in middle)	7	9	15·5
Distance from respiratory opening to hind end	11·5	13	16

INTERNAL CHARACTERS.—Skin thick, especially towards the hind end. Shell (Pl. XIII, figs. 50, 51) 4 × 2 mm., of

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[1] For a description of the living animal, see 'Ann. Natal Mus.,' 1910, vol. ii, pp. 166, 167.

moderate thickness, convex, laterally compressed, with a prominent conical apex projecting beyond the posterior margin; sinus of moderate depth.

Pedal gland (fig. 57).—Much smaller than in the last species, curving alternately to the right and to the left in a comparatively regular manner; glandular tissue extending throughout its entire length.

Nervous system (Pl. XV, figs. 72, 74, 76).—With buccal ganglia situated anteriorly; connectives short; nerves to pedal gland rather slender.

Digestive System (Pl. XVI, fig. 87; Pl. XVII, figs. 110–114; Text-fig. 4, E, F, p. 161; Pl. XXI, fig. 134, Pl. XXII, fig. 135).—Radula 4 or 5 mm. long; central tooth present, with a very short, broad, single cusp; eight or nine laterals with short double cusps, and more than twice as many marginals with longer narrower cusps, on each side, the transition between laterals and marginals being rather abrupt; formula (of a Port Shepstone specimen): (23 + 9 + 1 + 9 + 23) × 63. Odontophore small, with a single slender buccal retractor. Œsophagus narrow, shorter than the salivary ducts; crop swollen between the salivary glands; intestine narrow, first loop deep, posterior continuation on right side of liver. Salivary glands separate. Liver of two approximately equal divisions, the intestine only traversing the right.

Vascular System (Pl. IX, fig. 31).—Pulmonary veins forming a network. "Posterior aorta" supplying left division of liver and hermaphrodite gland; right division supplied by two arteries from the anterior aorta which arise at some distance from each other; anterior aorta passing through loop of intestine.

Reproductive System (Pl. XXIII, fig. 149). — Hermaphrodite gland consisting of a cluster of small follicles; hermaphrodite duct only very slightly convoluted; common duct very long and much convoluted and twisted; vagina rather broad; receptaculum seminis rather small; receptacular duct fusiform, swollen towards the anterior end. Penis long and narrow excepting at the posterior end, where it is broadened; end of vas deferens swollen to form an epiphallus about 2·5 mm. long, which bears anteriorly a minute flagellum; penial retractor long and narrow.

Habitat.—Port Shepstone, Natal (Burnup); Hilton Road, near Pietermaritzburg (Burnup); Grahamstown, Cape of Good Hope (Farquhar, French).

Type.—The type is in the British Museum. Other specimens will be found in the Natal Museum, Pietermaritzburg, in the South African Museum, Cape Town, and in the Academy of Natural Sciences, Philadelphia.

Affinities, etc.—This species resembles Apera burnupi in many respects, and was at one time confused with that species. Nevertheless, the two forms can be very easily distinguished by their external characters alone, for in the present species the upper keels meet at an acute angle behind, where they form a short median keel, and the lower keels are equally prominent and extend the whole way to the hind end of the animal. The colour of the two forms is also different. Internally the most conspicuous features in which the present species differs from the last are to be found in the pedal gland and the reproductive organs.

Hitherto this species has usually been known as "Apera burnupi," but an examination of the type-specimen of A. burnupi leaves no doubt that that name should be applied to the preceding species, which Collinge subsequently named A. natalensis, and it has therefore been necessary to give a new name to the present form.

THE PHYLOGENY OF THE SPECIES OF APERA.

It is evident that Apera burnupi and A. sexangula are closely related to each other. Of these it is probable that the former is the more highly specialised; for in the pedal gland, the reproductive organs, and the keels, A. sexangula seems to be rather more primitive than A. burnupi. A wide gap separates these two species from those without keels; nevertheless, A. purcelli resembles A. burnupi and A.

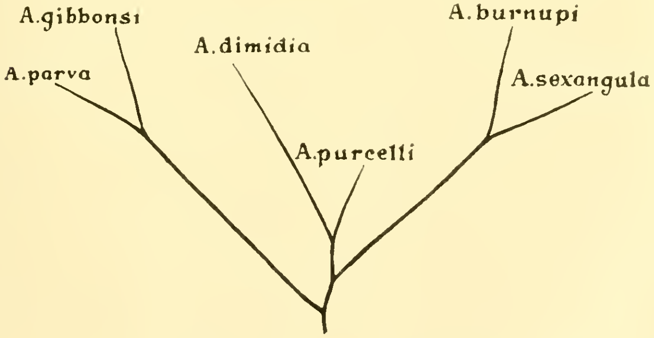
sexangula in not a few characters, notably the pedal gland, the long penial retractor, and the complete separation of the dorsal grooves. Moreover, it is probable that the ancestral form from which A. burnupi and A. sexangula have been evolved resembled A. purcelli still more closely, since the keels and the double cusps of the lateral teeth of these species cannot be regarded as primitive characters. Yet it is not likely that in A. purcelli we have the direct ancestor of these two species, for A. purcelli has in some respects become modified in a different direction, its central tooth having become smaller and the course of the intestine having become quite different from what we must regard as the more primitive arrangement found in A. burnupi, A. sexangula, and A. gibbonsi. It is therefore probable that A. purcelli must be regarded as having diverged somewhat from the branch which gave rise to the keeled species.

Apera dimidia in some respects resembles A. purcelli, but it is much more highly specialised. The glandular tissue of the pedal gland has become entirely concentrated around the anterior half of the duct; the central tooth of the radula has disappeared, and the laterals have become more numerous; the penial retractor has become quite short; the dorsal grooves are united posteriorly: in fact, while A. dimidia has probably been derived from the same branch as A. purcelli, it has diverged very far from both A. purcelli and the keeled species.

Apera gibbonsi and A. parva differ widely from the other species in their enormous radula and numerous radial buccal retractors, as well as in the œsophagus, receptacular duct, shell, coloration, etc., and apparently in the structure of the terminal vesicle of the pedal gland. In some respects they resemble A. dimidia most closely, especially in the absence of glandular tissue from the posterior end of the pedal gland, the short common duct, the union of the dorsal grooves in front of the respiratory opening, and the position of the lateral grooves; and it might be possible to regard A. gibbonsi and A. parva as being derived from the same branch as A. dimidia, but having become still more highly specialised in many ways. On the other hand, we find that these species seem to be more primitive than either A. dimidia or A. purcelli not only in the uniformity of the teeth of the radula and the presence of a well-developed central tooth in typical examples of A. gibbonsi, but also in the arrangement of the intestine and liver. Now the nature of these characters renders it improbable that if they had once become so much modified they would revert to their original condition; and I am therefore inclined to regard the resemblances between A. gibbonsi and A. parva on the one hand, and A. dimidia on the other, as due to parallel evolution.

Apera gibbonsi and A. parva are probably even more closely related to each other than are A. burnupi and A. sexangula. But A. parva is decidedly more primitive than A. gibbonsi in its nervous system and long penial retractor, and in possessing a true stomach. On the other hand, in a few features, such as the buccal retractors and hermaphrodite gland, we must regard A. parva as being more highly specialised than A. gibbonsi or any other member of the genus.

If these views be correct, the phylogeny of the species of Apera might possibly be somewhat as shown in the above genealogical tree.



THE OCCURRENCE AT CAPE TOWN OF TESTACELLA MAUGEI *FÉR.*

This well-known species[1] is the only carnivorous slug, in addition to those belonging to the genus Apera, which is known to occur in South Africa, for it is probable that Ceratoconchites schultzei (*Simroth*) is the larva of a fly.[2]

The genus Testacella can be distinguished at a glance from all the other genera of slugs known to inhabit South Africa, because in this form alone the hind end of the back is covered by an external shell. In some respects the anatomy of Testacella resembles that of Apera, but it is so well known that it is unnecessary for me to describe it here. More than a hundred years ago Cuvier[3] gave an account of the internal organs of one member of the genus; and since then the researches of Gassies and Fischer, de Lacaze-Duthiers, Plate, Simroth, and others, have given us a fuller knowledge of the anatomy of Testacella than of almost any other carnivorous snail or slug.

The following are the principal characters by which Testacella maugei can be distinguished from the other species of the same genus: (1) the comparatively large size of the shell, and its length and convexity; (2) the widely separated origin of the lateral grooves; (3) the presence of a central tooth in the radula; (4) the small number of the buccal retractors; (5) the unusual length of the tentacular retractors, and the fact that they both arise to the left of the middle line; (6) the swollen anterior end of the receptacular

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[1] See Appendix for the more important references to Testacella maugei.

[2] Simroth, H., 'Zool. Anz. Leipzig,' 1907, vol. xxxi, pp. 794, etc.; Simroth, H., 'Deutsche Südpolar Exped.,' 1910, vol. xii, Zool. iv, p. 172; Böttger, O., 'Abhandl. Senckenb. Naturf. Ges. Frankfurt,' 1910, vol. xxxii, p. 433.

[3] 'Ann. Mus. d'Hist. Nat.,' 1804, vol. v, pp. 435–444, pl. xxix, figs. 6–11.

duct, its comparatively great length, and its lateral junction with the receptaculum seminis; (7) the convolution of that part of the vas deferens which lies next to the free oviduct; (8) the length of the narrow anterior part of the penis, and its broader posterior end, without any flagellum.

It will be seen from Pl. XXIV that the specimens of Testacella from Cape Town which I have examined possess all these characters, and I have, therefore, no hesitation in assigning them to T. maugei. Nevertheless the South African examples of this genus have usually been named "T. aurigaster *Layard*."[1] Now, although Major Connolly[2] believes that Layard published a description of this supposed species, I have not been able to find any such description, nor any type-specimens, and I cannot therefore state definitely that T. aurigaster is a synonym of T. maugei, as it is conceivable that more than one species of Testacella may have found its way to Cape Town during the last sixty years. At the same time, all the specimens that I have seen labelled "T. aurigaster" have proved to belong to T. maugei, and I think that T. aurigaster may be safely expunged from the list of South African Mollusca.

The slug occurs in gardens at Cape Town, and I have little doubt that it has been introduced into South Africa by man, notwithstanding Dr. Simroth's arguments in favour of the possibility of Testacella being a native of that country.[3] I believe that the natural distribution of the genus Testacella is limited to the western part of the Palæarctic region, from Great Britain and Hungary to the Canary Islands, and that

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[1] The following is a copy of a manuscript note written by Layard himself, for which I am indebted to Major Connolly: "*Testacella aurigaster Layard. I only found this shelled slug in the Gardens round Cape Town. It was common in the grounds of the South African Museum, which was built at the lower end of the Botanical Garden in Cape Town. The belly of the animal was a rich golden yellow, hence the name selected. It devours large worms, & will afsimilate individuals far larger than itself!*"

[2] 'Ann. S. Afr. Mus.,' 1912, vol. xi, p. 64.

[3] 'Zool. Anz. Leipzig,' 1907, vol. xxxi, p. 796.

its occurrence in Philadelphia, Cape Town, and Auckland is due to the agency of man. Testacella maugei occurs not only in the south-west of England, but also in Portugal, Madeira, and the Canaries; and it seems to me that it might easily have been transported to South Africa from any of these localities, amongst the roots of plants. For the species of Testacella are especially common in the rich soil of gardens where worms are abundant; and it is known that under adverse conditions a specimen can surround itself with a sort of cocoon of hardened slime which protects it from drought, and may remain dormant in this state for several weeks.

It will be seen from Pl. XXIV, fig. 159, that in some of the South African specimens the posterior end of the penis is curved round in a peculiar manner, and the retractor muscle is attached to the vas deferens, a short distance in front of it.[1] Possibly this unusual arrangement may have been partly caused by the way in which the animal contracted when it was killed, for it only occurred in some shrivelled specimens, which, in other respects, seemed to be identical with the rest.

Figs. 157 and 158 represent two of the shells labelled "T. aurigaster" in the MacAndrew collection at Cambridge. The first shows the usual shape of the shell in T. maugei, while the second may be assigned to the variety aperta *Taylor*,[2] a form which was originally described from the Azores.

THE AFFINITIES OF APERA AND TESTACELLA.

The Evolution of Carnivorous Characters.

Both Apera and Testacella undoubtedly belong to the group of the Stylommatophora comprising the carnivorous

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[1] The junction of the retractor muscle with the vas deferens is also shown in Webb's figure of the genital organs of T. maugei ('Journ. of Malac.,' 1897, vol. vi, pl. vi, fig. 3).

[2] 'Monog. L. and F.-W. Mollusca Brit. Isles,' 1902, vol. ii, p. 24, pl. i, fig. 15.

snails and slugs, a group which is usually known as the Agnatha, since very few of these forms possess a jaw. But to state this is to say very little about the affinities of these genera, for it is doubtful whether the various carnivorous snails are at all closely related to one another, some authorities asserting that the tribe Agnatha is polyphyletic.

Certain eminent malacologists have held that the Stylommatophora may be divided into two groups, one mainly herbivorous, the other mainly carnivorous; and they would account for the diversity of the carnivorous forms by supposing that they had evolved in a manner parallel to the gnathophorous families, which show a similar diversity. This view was well expressed by Fischer, who, writing so long ago as 1873, said: "Je suis persuadé qu'on pourra constituer, dans quelques années, une série d'Agnathes ou Testacellidæ ayant une grande extension, et dont les genres seront représentatifs de ceux des Helicidæ, ainsi que, chez les Mammifères, certains groupes des Marsupiaux représentent d'autres groupes des Monodelphes."[1] On the other hand, many modern authorities maintain that the various families of carnivorous snails and slugs have been evolved independently from different families of the Gnathophora, and that they are in reality no more nearly related to one another than are the European and Tasmanian wolves. The characters which the agnathous families undoubtedly possess in common they would explain as being due to convergence, brought about by their common acquisition of carnivorous habits.[2] Now there is no à priori objection to this second view, for we know that many gnathophorous forms occasionally devour animal food, and there seems to be no reason why this should not have become the usual diet in some cases. The question, therefore, can only be settled by a careful examination of the comparative anatomy of the various families included in the

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[1] 'Journ. de Conchyl.,' vol. xxi, p. 12.

[2] See an interesting paper by Dr. Simroth ('Naturwiss. Wochenschr.,' 1901, vol. xvii, pp. 109–114, 121–127, 137–140), in which he has ably advocated the polyphyletic origin of the carnivorous snails and slugs.

Agnatha. If we find that two agnathous families only resemble each other in those features which are likely to have been acquired through carnivorous habits, and are very similar to different gnathophorous families in their other characters, then we may assume that they are probably of different origin ; but if we find that the resemblances between two families of agnathous snails cannot all be explained in this way, and that these families are in their most important features more similar to each other than to any families of the Gnathophora, the probability is that they are closely related. It is evident, however, that before we can discuss the affinities of any particular genus, we must have a clear idea as to how a snail is likely to become modified if it adopts carnivorous habits, and which of the features characteristic of Apera, Testacella, and the other genera included in the Agnatha, are likely to be due to their animal food.

Snails and slugs find their food chiefly by means of their sense of smell, and one might expect this sense to be especially well developed in the carnivorous forms, because animals which move slowly enough for snails to catch them must be very much more difficult to find than plants. Now in many of the Agnatha, and more especially in the Rhytididæ and the Oleacinidæ, the olfactory organs at the tips of the upper tentacles are so large that the eye comes to occupy a position some distance behind the extremity.[1] Moreover Plate has shown that Testacella, unlike most of the Stylommatophora, retains a pallial olfactory organ. The unusual development of these sense-organs might be expected to lead to a corresponding development and concentration of the sensory nerve-centres, and accordingly we find that in nearly all the carnivorous forms the cerebral ganglia are large and close together, Phrixolestes being perhaps the most notable exception.

Carnivorous snails and slugs prey chiefly upon the herbi-

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[1] See Strebel, H., 'Beitrag z. Kenntn. d. Fauna Mexikan. L.- u. Süsswasser-Conchyl.,' 1878, vol. iii, pl. xv, fig. 1 *c*; Suter, H., 'Journ. of Mal.,' 1899, vol. vii, pl. iii, fig. 1 *a*.

vorous forms and on worms, for most arthropods move too quickly and are too well protected by their chitinous exoskeleton to fall a prey to snails. Now worms burrow in the soil, and snails hide themselves in crevices and retire deeply within their shells when attacked; it is therefore evident that a carnivorous snail will find the presence of a bulky unyielding shell on its back a great inconvenience when it is trying to get near its victim. In order to obviate this difficulty the shell has become modified in various ways. In the first place we find that in Paryphanta it has become more or less flexible owing to the degeneration of the inner calcareous layer. Secondly, the shape of the shell has become altered in many of the carnivorous genera. In Diplomphalus, for example, the shell has become greatly flattened. This will enable the animal to penetrate into crevices, but it is obvious that the breadth of the shell will have to be reduced as well as its height, if the snail is to crawl into narrow holes. Now the only way in which both the height and breadth of a depressed or heliciform shell can be reduced is by the curvature of the axis or columella, until its direction corresponds more nearly with that in which the animal moves; and this is what has occurred in that remarkable genus of carnivorous snails, Streptaxis. If, however, the shell has a raised spire, the columella naturally takes up a position parallel to the direction in which the animal moves, and in this case it is only necessary for the height of the spire to be increased in order to reduce the diameter of the shell. This is what has taken place in the large genus Ennea, in which only the young form retains a comparatively low spire. In Diaphora this principle is carried to an extreme, some species having shells with greatly produced spires composed of as many as twenty whorls. Indeed, so long does the spire become that the animal can no longer occupy the whole of it, and secretes a new internal wall cutting off part of the upper whorls, which may become decollated, as in D. telescopium *Mlldff.* A more efficient method of reducing the diameter of the shell (but one which probably necessitates a greater change in the structure of the animal) is for the whorls themselves to become laterally compressed. This has taken place to some extent in Streptostele and Obeliscella among the Streptaxidæ, but it is especially characteristic of the Oleacinidæ. In some members of this family, such as Streptostyla gracilis *Pilsbry*, the whorls have become so narrow that the form of the shell closely resembles that of the marine carnivorous genus Conus—a striking example of convergence due to the acquisition of similar habits. Thirdly, the position of the shell may be altered, so that the part of the animal in front of the shell becomes lengthened. This is admirably shown in Hedley's figure of Rhytida lampra (*Pfr.*),[1] but it occurs to some extent in most of the carnivorous genera. A variety of this modification is found in such forms as Ennea densecostulata *Mlldff.* and Diaphora eutrachela *Mlldff.*, in which the greater part of the shell has moved further back by the elongation of the last whorl towards the mouth. Fourthly, the shell may not only be moved backwards, but it may become reduced and flattened, until it either disappears altogether as in Selenochlamys, or sinks into the skin as in Apera. No projection will then remain to impede the animal's progress when it follows worms into their burrows, and it is more especially in the vermivorous genera that this extreme modification seems to have occurred. We see, then, that the acquisition of carnivorous habits may lead to a great alteration in the structure, form, position, or size of the shell.

The movement of the shell to the hind end of the body, and its gradual degeneration, will greatly modify the animal itself. Many of the organs will be subject to partial detorsion. The lung and respiratory orifice will move back with the shell and mantle, so that the animal will become opisthopneumic; and it is probable that it is a direct advantage to a carnivorous form to have its respiratory opening near the hind end of the back, because this is the part which is least likely to be

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[1] 'Proc. Linn. Soc. N.S.W.' (2nd ser.), 1891, vol. vi, pl. iii, fig. 3.

covered when the greater portion of the body is under the surface of the ground or inside its victim's shell. The anus will move back with the respiratory opening, and the rectum will thus be directed posteriorly (text-fig. 5, cf. C and D, p. 183). With the degeneration of the shell the pallial organs will become modified, and the posterior position of the pulmonary veins may pull round the auricle until it lies posterior to the ventricle, as in Testacella and a few other genera (text-fig. 6, p. 244). The organs which formerly occupied the visceral hump will become reduced in size and pushed forward into the general body-cavity. The pressure of these will retard the backward growth of other organs such as the receptaculum seminis, and it is therefore not surprising to find that the slugs have as a rule shorter receptacular ducts than the snails to which they are probably most nearly allied. The columellar muscle will disappear with the degeneration of the shell, and the various retractors that originally arose from it will become attached to different parts of the skin, which will become thickened to take the place of the shell (see p. 126). And as the anterior part of the body becomes lengthened, the origins of the tentacular and penial retractors will tend to move forwards. Thus the mere fact that animal food is less easily accessible than vegetable food may lead to profound changes in the anatomy of a snail which becomes carnivorous.

When the snail has approached its victim it will require to feel exactly where to attack it with its radula, and will, if possible, try to prevent the animal escaping until the teeth are fixed in its flesh. Accordingly we find that nearly all the carnivorous genera have a pair of special feelers at each side of the mouth beneath the lower tentacles. In Euglandina these feelers are very long and are supposed to be used for prehension, but according to F. M. Woodward[1] their function in Natalina caffra (*Fér.*) is probably purely tactile. Miss Davies[2] has recently discovered that in Paryphanta com-

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[1] 'Proc. Mal. Soc.,' 1895, vol. i, p. 271.

[2] 'Proc. Roy. Soc. Victoria,' 1913, vol. xxv, p. 225.

pacta *Cox & Hedley* and P. atramentaria (*Shuttl.*) these papillæ are glandular in structure. Now in Peripatus, an arthropod genus whose habits are not unlike those of the carnivorous snails and slugs, there are two large slime-glands which open on the oral papillæ, and their secretion is used to entangle the prey. The carnivorous slug Atopus also possesses two large glands opening one at each side of the mouth; and Simroth,[1] who first discovered them, has suggested that their function may be similar to that of the slime-glands of Peripatus. We have already seen that the pedal gland is developed to an unusual extent among the carnivorous genera. Now this gland also opens close to the mouth, and I would suggest that its secretion may play some part in overpowering the prey. The form of the pedal gland in Apera has come to resemble in some respects that of Simroth's glands in Atopus, and nearly twenty years ago André[2] suggested that the secretion of the pedal gland in the Stylommatophora might be used in feeding as well as in locomotion. We may at least say this: that the remarkable development of the pedal gland in the Agnatha, as well as the presence of the labial feelers, may not improbably be due to their predaceous habits.

It is unnecessary to attempt to prove that the acquisition of carnivorous habits might lead to a modification of the radula and the surrounding structures: obviously these would be among the first organs to be affected. It will be sufficient, therefore, if I point out the chief ways in which the radula has become transformed. In the first place, it has increased in size, and especially in length, and become capable of far greater protrusion than in the herbivorous forms. Secondly, the individual teeth have become much larger, especially those occupying an analogous position in the radula to that held by the canine teeth in the jaw of the Mammalia; and to make room for these, the central teeth and those at the extreme edges of the radula have become vestigial or have

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[1] 'Naturwiss. Wochenschr.,' 1901, vol. xvii, p. 122.

[2] 'Revue Suisse de Zoologie,' vol. ii, p. 332.

entirely disappeared. Thirdly, the main cusps of the teeth have become far longer and more sharply pointed, so as to penetrate the victim's skin, and the secondary cusps have completely gone, excepting in some of the more primitive genera of the Oleacinidæ. And as all the teeth have become simplified in this manner, the differentiation between laterals and marginals has been lost, though it has been reacquired in most of the species of Apera and Natalina, and to some extent in Gnestieria. Fourthly, the bases have also become lengthened in order to prevent the teeth from being bent outwards. Fifthly, the rows of teeth have become sharply angled in the centre, owing to the way in which the radula is forcibly drawn back over the anterior edge of the odontophoral support into the narrow radula-sac.

The muscles of the odontophore have become correspondingly enlarged. In the more primitive forms the hind end of the radula-sac still projects from between these muscles; but in those that are more completely adapted to a carnivorous existence the odontophoral muscles have entirely surrounded the radula-sac, and form a very large cylindrical structure.

This growth of the odontophore leaves little room for the development of other bulky organs in the anterior part of the body, especially as it is an advantage to a carnivorous form not to have a very large head and neck. I therefore suggest that this is the reason why the genital ducts of carnivorous snails and slugs are without large accessory organs. There would be no room for the development of a dart-sac, for example, in a snail with a very large odontophore.

The growth of the odontophore would also tend to increase the size of the body-whorl of the shell. If this were laterally flattened as in the Oleacinidæ, it is evident that when the snail withdrew into its shell, the hind end of the odontophore would come to press against the outer side of the shell in the neighbourhood of the posterior end of the mantle-cavity. The result of this would be that the posterior limit of the cavity would be pushed forwards in the middle, and with it the heart and the lower end of the kidney. The upper end of the kidney, being near the suture of the shell, would remain in its original position; and accordingly we find that in the Oleacinidæ the kidney is obliquely lengthened in a very characteristic manner.

The cerebral, buccal, and ventral ganglia would be pushed further apart by the growth of the buccal mass and odontophore, and thus we find that in many of the carnivorous forms the cerebro-buccal, cerebro-pedal, and cerebro-pleural connectives are unusually long (see pp. 141, 146).

The extrinsic buccal retractors would become strongly developed at the same time as the intrinsic muscles of the odontophore. So long as they sprang from the columellar muscle, they would undergo little change beyond an increase in their thickness, although I have found that their anterior ends tend to split up into a number of separate strands in the Rhytididæ. But in those forms in which the shell is degenerate and the skin is taking its place, we frequently find that the retractors of the odontophore arise from a large area of the integument; as, for example, in Apera gibbonsi, Testacella haliotidea *Drap.*, and the Trigonochlaminæ (see pp. 172, 173).

A jaw becomes superfluous in a snail or slug in which the radula is protruded far beyond it, and Simroth[1] has shown that it would be a positive disadvantage in a vermivorous form, because if it bit off pieces from its prey, the latter would escape. Accordingly the jaw is absent or extremely degenerate in nearly all carnivorous genera excepting Plutonia, in which Simroth states that the sharp edge is covered by a softer downward growth.

As in other carnivorous animals, the digestive region of the alimentary canal becomes reduced in size. This is most apparent in the slugs, for in these the pressure of the organs which formerly occupied the visceral hump tends to diminish anything in the body-cavity that is unnecessarily large. In Atopus and Apera the true stomach has almost completely disappeared, the crop passing straight into the intestine; and

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[1] Op. cit., p. 113.

in these forms, and possibly in others also, digestion takes place partially within the lobes of the liver. In nearly all the carnivorous genera the length of the intestine and rectum is more or less reduced.

Finally, Simroth considers certain peculiar connections between the genital ducts of a few of the carnivorous genera to be modifications to facilitate self-fertilisation, and he attributes this to the somewhat isolated life which a vermivorous slug is likely to lead. But I have not found these modifications in the forms which I have examined, and it remains to be proved whether they are at all general among the Agnatha.

Such are the changes which are likely to take place in the organisation of a snail when it acquires carnivorous habits. We are now in a position to discuss whether Apera, Testacella, and other predaceous forms, are really closely related to one another, or whether their resemblance is merely due to the fact that they have all become carnivorous.

The Phylogeny of Apera and other Naked Carnivorous Slugs.

I think that Simroth is the only author who has suggested that the genus Apera has been evolved directly from an herbivorous slug. As already mentioned, he put forward the theory that Apera might have been derived from the Janellidæ. But Plate[1] has shown that the slugs belonging to this family differ from most of the Stylommatophora, not only in being without lower tentacles, but in other important characters, such as the respiratory tissue, which takes the form of numerous fine tubes radiating from the mantle-cavity and recalling the tracheæ of arthropods. Now Apera possesses none of these features. Moreover, it would be difficult to imagine a radula more unlikely to develop carnivorous characters than that of Janella, with its

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[1] 'Zool. Jahrb.,' 1898, vol. xi, pp. 193–280, pls. xii–xvii.

myriads of minute multicuspid teeth. I have therefore no hesitation in saying that Apera is in no way allied to the Janellidæ.

Nor do I know of any other herbivorous family from which Apera is at all likely to have been derived. And the fact that the carnivorous characters are so highly developed in Apera is against the theory that the genus has been directly evolved from any herbivorous form. It seems certain that the ancestors of Apera must have been carnivorous for a very long time; and it is not likely that these ancestors would all die out without leaving any descendants excepting this single genus. The question is whether we can find any carnivorous genus of slugs or snails resembling Apera in characters which are not likely to have been developed independently through the common acquisition of predaceous habits.

Collinge has already pointed out how improbable is the theory of P. and F. Sarasin that Apera is closely allied to Atopus.[1] This genus and the other members of the Rathouisiidæ differ widely from Apera and every other carnivorous form in a number of important characters, such as the wide separation of the male and female openings, the presence of Simroth's glands, the structure of the foot, the very large mantle, and the structure of the liver; while they only resemble them in the radula, the absence of a jaw, and a few other points connected with their carnivorous habits. I agree with Simroth in regarding the Rathouisiidæ as being more nearly related to the Veronicellidæ than to any monotrematous carnivorous family; indeed, I have little doubt that, with the exception of the Veronicellidæ and the Onchidiidæ, no family of the Stylommatophora is less closely related to Apera than the Rathouisiidæ.

Plutonia, a carnivorous slug found in the Azores, is perhaps less unlike Apera than is Atopus; but it differs from it in the mantle, the laterally compressed form of the body, the presence of a jaw, the absence of a penial retractor,

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[1] For references, see pp. 111–113.

the presence of a secondary ureter, and other characters.[1] On the whole it is extremely improbable that Apera is related to Plutonia. It is possible that the latter genus may be allied to the Trigonochlaminæ, but Simroth has given weighty reasons in favour of its having been evolved from the species of the Vitrininæ inhabiting the shores of the Atlantic, and not from any carnivorous group.

The only other carnivorous forms without external shells which are known to science are the genera from Transcaucasia placed in the Trigonochlaminæ. One of these—Selenochlamys—bears a very striking resemblance to Apera, as will be seen from Simroth's figures.[2] Almost the only external differences between Selenochlamys and Apera are that in the former genus the visible mantle is a little larger, the foot is more distinctly tripartite, and there is a median dorsal keel extending from the mantle to the hind end of the animal. This last difference is the most conspicuous, and yet it is not greater than the difference between Apera sexangula and A. gibbonsi, dimidia, or purcelli. And when we turn to Simroth's description and figures of the internal anatomy of Selenochlamys, we at once notice the similarity between the radial buccal retractors in this genus and those of Apera gibbonsi and A. parva. A closer inspection, however, reveals many differences. The nerve ganglia of Selenochlamys are all separate; the pedal gland is narrow, straight, and almost entirely embedded in the foot; the vagina is extremely short; the right tentacular retractor does not cross the penis. Moreover there appears to be no shell, so that the morphology of the mantle must be quite different to that of Apera. Indeed, I think that there can be little doubt that we have in the superficial resemblance between Apera and Selenochlamys a remarkable instance of convergence due to the acquisition of similar carnivorous habits; and that the only affinities of Selenochlamys are with the

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[1] Simroth, H., 'Nova Acta Acad. Caes. Leop.-Carol. Germ. Nat. Cur.,' 1891, vol. lvi, pp. 223–229.

[2] 'Festschrift Leuckarts,' 1892, pl. vi.

other members of the Trigonochlaminæ, which Simroth has shown to have probably been derived from the Parmacellinæ. This view is confirmed by the geographical distribution of the genera.

We may now consider the carnivorous genera which still retain an external shell, for it seems certain that the shell of Apera was originally external.

The New Zealand genus Schizoglossa resembles Apera in many ways, but it differs in its reproductive system, for in Schizoglossa the male organs are much reduced, and there is no receptaculum seminis.[1] These features alone render it improbable that Apera has been derived from Schizoglossa. According to Murdoch[2] the reproductive organs of Paryphanta busbyi (*Gray*) bear a considerable resemblance to those of Schizoglossa, and I think that there can be little doubt that the latter genus has been evolved in New Zealand from that section of the Rhytididæ to which Paryphanta busbyi belongs.

Strebelia possesses a receptaculum seminis, but in this genus the penial retractor is attached to the vas deferens instead of to the penis itself. And, judging from Strebel's figures, the salivary glands are united below the crop, and not above it as in Apera.[3] Moreover, it does not seem likely that a purely South African genus should have been evolved from a slug which is only found in Mexico.

There remain the European carnivorous slugs, Daudebardia and Testacella. Of these Daudebardia differs widely from Apera in its pedal gland, nervous system, reproductive organs, excretory system, etc. There can be no doubt that Apera has not been evolved from Daudebardia. On the other hand, Testacella has many points in common

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[1] Hedley, C., 'Proc. Linn. Soc. N.S.W.' (2nd ser.), 1893, vol. vii, p. 390, pl. ix, fig. 4, pl. x, fig. 9; Collinge, W. E., 'Ann. Mag. Nat. Hist.' (7th ser.), 1901, vol. vii, p. 72, pl. ii, fig. 30.

[2] 'Trans. N. Z. Inst.,' 1903, vol. xxxv, pp. 260, 261, pl. xxvii, figs. 4, 5.

[3] 'Beitrag. z. Kenntn. d. Fauna Mexikan. L.-u. Süsswasser-Conchylien,' 1878, vol. iii, pls. i, ii.

with Apera; indeed, if we take into consideration both the internal and external characters, I do not think that any other genus resembles Apera so closely as does Testacella. The pedal gland of Testacella lies free in the body-cavity as it does in Apera. Both genera are opisthopneumic, and in both the primary ureter opens at the posterior end of the mantle-cavity. The reproductive organs of the two genera are on the whole very similar, and in both the right tentacular retractor crosses the penis. But if we compare the genera more closely we find that there are several small differences which it is not easy to explain away. In the first place, the auricle in Testacella has come to lie directly behind the ventricle, whereas in Apera the heart has not been rotated so far. Yet Testacella cannot be derived from Apera, because it still retains an external shell. Secondly, the foot of Testacella contains numerous dermal mucous glands, while that of Apera has none. Thirdly, the pedal gland of Testacella has no terminal vesicle. Fourthly, the left parietal ganglion has not become fused with the abdominal ganglion in Testacella, but all the visceral ganglia remain separate. Fifthly, the arrangement of the odontophoral muscles, and the structure of the odontophoral support, and even the blood-supply of the odontophore, show surprising differences in the two genera, as we have already seen. And, lastly, there is the difference in the geographical distribution of the two genera. On the other hand, the resemblances are found to be largely of a negative character, if we except those which might be due to the common acquisition of vermivorous habits by both forms. Therefore it will be well to look further before we assume that Apera is related to Testacella. It is true that there are no other carnivorous genera in which the shell has become reduced, but it is possible that the nearest living allies of Apera may have quite large shells, for when once the presence of a shell is found to be a disadvantage, its degeneration probably takes place rather rapidly.

Pilsbry has suggested that Apera may possibly be allied to the Rhytididæ, and I am inclined to believe that Pilsbry is right. Beutler has examined the histology of the skin of Paryphanta, and has found that the foot is without dermal mucous glands, as it is in Apera. The pedal gland in the Rhytididæ not only lies freely in the body-cavity, but it is often somewhat contorted, and, as in Apera, it ends in a vesicle containing a broad fold. In Paryphanta, Natalina, and Rhytida capillacea (*Fér.*), the visceral ganglia are all separate, as in Testacella, but in Rhytida inæqualis (*Pfr.*) Fischer has shown that the left parietal ganglion is united with the abdominal ganglion exactly as in Apera. I have already shown that the arrangement of the odontophoral muscles in at least one member of the Rhytididæ is very similar to that found in Apera, and, judging from Beutler's account, the structure of the odontophoral support is also similar. The reproductive organs of Rhytida and Paryphanta are on the whole very like those of Apera, and in these genera the right tentacular retractor crosses the penis. The members of the Rhytididæ also resemble Apera in having no secondary ureter. Indeed, almost the only differences that I know of between Rhytida and Apera are those which would be likely to be brought about by the degeneration of the shell and its further retrogression to the hind end of the animal, and we have seen that this is a modification which is especially liable to occur in carnivorous forms.

Another fact in favour of the theory that Apera has been evolved from the Rhytididæ is to be found in the geographical distribution of that family, for it occurs not only in the Australian region, but also in South Africa itself. It is true that Apera has almost certainly not been evolved from those members of the Rhytididæ which are now found in South Africa: these have retained their separate visceral ganglia, but have become specialised in another direction, as is shown both by their radula and their reproductive system, in which the penis lies to the right of the tentacular retractors. But the presence of these snails in Africa renders it not at all improbable that forms more like Rhytida inæqualis may also have once extended into that region, and given rise, by the degeneration of the shell, to Apera, just as in New Zealand another branch of the family has probably given rise to Schizoglossa.

It is not unlikely that the Rhytididæ originated in early Mesozoic times, or perhaps even before the end of the Palæozoic era, in Gondwanaland—that great Southern continent which is supposed to have extended from Australia and New Zealand across the Indian Ocean, through Africa, and even as far as South America.[1] A little later the more highly specialised Streptaxidæ may have arisen in the same region. These did not reach Australia, perhaps because it was already cut off by the sea, but in other regions we may suppose that they would enter into competition with the Rhytididæ. In South Africa, where only the small pupiform Streptaxidæ occur, the Rhytididæ were able to withstand their competition by becoming more specialised themselves, either by the degeneration of the shell (Apera), or merely by an increase in the size of their teeth and a slight modification of their reproductive organs (Natalina). But further north, where we find the heliciform Streptaxidæ, with their oblique columella, the Rhytididæ were almost entirely exterminated, only leaving Natalina morrumbalensis (*M & P.*), N. permembranacea *Preston*, and possibly the species of Tayloria,[2] as relics of their former distribution. Whether the Rhytididæ ever reached South America is at present unknown. They may have done so, and have then been exterminated by the heliciform Streptaxidæ, which are not uncommon in South America. I

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[1] Hedley has suggested that the Rhytididæ are of Antarctic origin (' Proc. Linn. Soc. N.S.W.,' 1899, vol. xxiv, p. 398), but, while admitting the possibility of this theory, I agree with Pilsbry in being unable to find any evidence in its favour (' Rep. Princeton Univ. Exped. Patagonia, 1896–1899,' vol. iii, Zoöl., 1911, p. 631).

[2] Thiele, J., 'Deutsch. Zentral-Afrika Exped. 1907–8,' vol. iii, 1912, p. 187.

would suggest, however, that it is quite possible that some of the South American carnivorous genera such as Guestieria, which Kobelt places in the Streptaxidæ, may prove to belong to the Rhytididæ when their anatomy has been examined.

Even if this view of the phylogeny of Apera is accepted, I would not advocate the placing of the genus in the Rhytididæ. The gap which separates Apera from any known member of that family is a very wide one, and the isolation of the genus is by no means over-emphasized by placing it in a family by itself.

The Phylogeny of Testacella and its Possible Allies.

Most modern malacologists are agreed that Testacella is allied to Daudebardia, and that these genera have been derived from Hyalinia or some closely related form. Now it must be admitted that the resemblance between Daudebardia and Hyalinia is very striking. Whether we regard the nervous system or the reproductive system or the excretory system, the similarity is equally remarkable. Even in the digestive system the difference is not very great, for Hyalinia is frequently carnivorous, and most of its teeth have become thorn-shaped, while Daudebardia still retains a small jaw, and the odontophoral muscles in this genus do not completely surround the radula-sac. Moreover, the evolution of Daudebardia from Hyalinia is to a great extent recapitulated in development, young specimens of Daudebardia having a shell very like that of Hyalinia, into which the animal can withdraw itself.[1] In my opinion the evidence of Daudebardia alone is almost sufficient to prove that the carnivorous snails and slugs are not monophyletic; for I think that we must admit that Daudebardia has been evolved from Hyalinia or some closely allied form, and I do not

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[1] See Simroth, H., 'Nova Acta Acad. Cæs. Leop.-Carol. Germ. Nat. Cur.,' 1891, vol. lvi, p. 270.

suppose that anyone would maintain that all the carnivorous snails and slugs, including such genera as Atopus and Varicella, had been derived from this source.

But while I agree that Daudebardia has probably arisen from the Zonitidæ, I cannot admit that Testacella is closely allied to Daudebardia and has had a similar origin.

Testacella differs widely from Daudebardia in many respects. In Testacella the apex of the shell is directed backwards, the columella being parallel to its greatest length (Pl. XXIV, fig. 161); in Daudebardia the columella is nearly at right angles to the length of the animal and the major diameter of the shell, as in Hyalinia. In Testacella the pedal gland lies freely in the body-cavity, and is very different in structure from that of most snails and slugs, a fact that has been specially emphasized by André[1]; in Daudebardia the pedal gland is embedded in the foot, and Plate[2] has shown that it has the usual structure, the duct having two ventral longitudinal folds enclosing a furrow into which the gland-cells open. In Testacella the epidermal cells have their walls thickened on the outer side only; in Daudebardia they are thickened all round.[3] Testacella has no jaw; in Daudebardia a jaw is present. In Testacella the radula-sac does not extend nearly to the hind end of the odontophore (Pl. XXIV, fig. 156); in Daudebardia it projects beyond the odontophoral muscles. In Testacella the visceral ganglia are all separate from one another; in Daudebardia the abdominal ganglion is united with the right parietal ganglion, as is the case to some extent in Hyalinia also. In Testacella the auricle is behind the ventricle; in Daudebardia the auricle is in front of the ventricle, as in Hyalinia. In Testacella the heart is to the right of the kidney; in Daudebardia and Hyalinia it is to the left. Testacella has no secondary ureter; Daudebardia agrees with Hyalinia in possessing one. In Testacella the receptacular duct is moderately long;

[1] 'Revue Suisse de Zoologie,' 1894, vol. ii, pp. 318–321.

[2] 'Zool. Jahrb.,' 1891, vol. iv, p. 524, pl. xxxii, fig. 16.

[3] Ibid., pp. 527, 529.

in Daudebardia it is extremely short. In Testacella the vagina is not surrounded by any glandular tissue; in Daudebardia the anterior end of the vagina is encircled with glandular tissue, as in Hyalinia. In Testacella the penis passes between the right tentacular retractors; in Daudebardia, as in Hyalinia, it lies outside both retractors. In Testacella the genital opening is on the side of the head; in Daudebardia and Hyalinia the opening is further back. In short, the two genera only resemble each other in a few features which would be likely to be developed in any vermivorous form, and they differ in nearly every other respect.

The dissimilarity in the nervous system is alone almost sufficient to prove that the carnivorous characters of Testacella have been acquired independently of those of Daudebardia. It is a general rule in the animal kingdom that nerve-ganglia tend to unite and not to separate; therefore we cannot derive Testacella, with its distinctly separate abdominal and right parietal ganglia, from forms in which these ganglia are more or less united; and this is the case in Hyalinia as well as in Daudebardia, notwithstanding Plate's statement to the contrary.

Now, if Testacella is not allied to Daudebardia, there is no reason for supposing it to have been derived from the Zonitidæ. This has only been thought to be the case because Daudebardia has almost certainly been evolved from that family, and Testacella was supposed to be related to Daudebardia. In Testacella, as in Apera, the carnivorous characters have reached a very high state of specialisation, and it is therefore more probable that Testacella has been evolved from some family of carnivorous snails.

Beutler[1] considers that Paryphanta may be ancestral to Testacella. Now Paryphanta certainly resembles Testacella much more closely than does Daudebardia. Indeed in its visceral ganglia it is more like Testacella than Apera. But Testacella differs from Paryphanta,

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[1] 'Zool. Jahrb.,' 1901, vol. xiv, p. 407.

just as it differs from Apera, in the pedal gland having no terminal enlargement, and in the presence of longitudinal fibres in the odontophoral support and of dermal glands in the foot. And if a shell of the shape of that of Paryphanta degenerated, it would assume a form like that of Schizoglossa, and not like that of Testacella. Moreover, while it is easy to attach too much importance to geographical distribution, it does not seem probable that a western Palæarctic genus of slugs should have been evolved from a snail found in New Zealand.

But is there no family of carnivorous snails inhabiting Europe, in which the columella is parallel to the greatest length of the shell, and the odontophoral support contains longitudinal fibres? The Oleacinidæ possess these characters, and in many other ways bear a close resemblance to Testacella, and it is from the Oleacinidæ that I believe Testacella has been evolved.

Although the majority of the recent species of the Oleacinidæ are found in Central America and the West Indies, in Tertiary times the family was represented by many forms in Western and Central Europe, and one genus—Poiretia—still lingers in the Mediterranean region. We know that the shell is liable to degenerate and recede to the posterior end of the animal in the Oleacinidæ as in other carnivorous families, for it has done so in Strebelia. If the degeneration were to proceed further than it has done in this American genus, the shell would assume the form found in Testacella maugei. This is seen from the parallel case of the degeneration of a shell with a pointed spire found in the Succineidæ, which is well illustrated on plate lxxiii of H. and A. Adams' 'Genera of Recent Mollusca.' Further, we find that the abrupt truncation of the columella which is characteristic of Poiretia, Englandina, Oleacina, etc., occurs also in Testacella scutulum *Sow.* It is significant also that as early as the Eocene period the aperture in some of the European Oleacinidæ had already become as large as that of any of the recent American members of the family excepting Strebelia[1]; for as a general rule, the larger the size of the aperture, the smaller is the size of the shell as a a whole in proportion to that of the animal.

It is not only in the shell, however, that the Oleacinidæ resemble Testacella. In both, a deep cleft in the mantle-edge extends forwards from the respiratory opening beneath the right lip of the shell; and Simroth has found that in Poiretia this cleft contains an olfactory organ, resembling the similarly situated olfactory organ of Testacella. Poiretia also has small labial feelers, very like those of Testacella. So far as I am aware, the histology of the foot and pedal gland in the Oleacinidæ has not been described; but, judging from Strebel's figures,[2] the pedal gland lies freely in the body-cavity in the more highly specialised members of the family, just as it does in Testacella. A jaw is absent in nearly all the Oleacinidæ, as in Testacella. We have already seen that the odontophoral muscles in the Oleacinidæ are more like those of Testacella than are the muscles of any other form which has been examined; and I have found that in Euglandina the structure of the odontophoral support agrees exactly with that of Testacella. In most of the Oleacinidæ the salivary glands are united, but according to Reymond[3] they are separate in the European genus Poiretia, as in Testacella. This, however, is not a very important character, for, as we have seen, the glands may be separate or united in different species of the same genus. The nervous system in the Oleacinidæ is also identical with that of Testacella, all the visceral ganglia remaining separate, although they are sometimes very closely aggregated in Euglandina. The similarity of the reproductive system is equally striking. It is true that the receptacular duct of Testacella is shorter

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[1] See 'Jahresh. Ver. Naturkunde Württemb.,' 1907, vol. lxiii, pl. ix, fig. 8.

[2] 'Beitrag z. Kenntn. d. Fauna Mexikan. L.-u. Süsswasser-Conchylien,' 1878, vol. iii, pl. xix, fig. 1.

[3] 'Journ. de Conchyl.,' 1853, vol. iv, pp. 16–29, pl. i, fig. 1.

than in most genera of the Oleacinidæ excepting Strebelia, but I have already shown that this is what we might expect in a genus with a degenerate shell. The other female organs seem to be identical. The penis often ends in a cæcal diverticulum in the Oleacinidæ, which, however, is quite short in Poiretia, and absent in Englandina, Salasiella, Streptostyla, and Strebelia. In Testacella we frequently find a vestige of this diverticulum, especially in T. haliotidea *Drap.* In the Oleacinidæ an epiphallus is usually, though not invariably, inserted between the penis and the attachment of the penial retractor; this is also the case in Testacella haliotidea, and sometimes in T. maugei (Pl. XXIV, fig. 159). Pfeffer has shown that in Englandina liebmanni (*Pfr.*) the retractor springs from the apex of a flagellum, exactly as it does in Testacella haliotidea, and the same author has demonstrated that the internal structure of the penis of Englandina is not unlike that of Testacella.[1] Indeed, the similarity between Testacella and the Oleacinidæ seems to me to be even closer than the similarity between Apera and the Rhytididæ.

The fact that the heart in Testacella is on the right side of the kidney, with the auricle directly behind the ventricle, affords further evidence in favour of this view, as will be seen from the accompanying diagram. The usual position of the heart in Hyalinia, Rhytida, and similar genera, is shown in text-fig. 6, A—drawn from a specimen of Hyalinia draparnaudi (*Beck*). In Daudebardia, according to Plate, the heart is turned slightly to the right as shown in diagram B; but it will be seen that the auricle is still in front of the ventricle, and the kidney is still mainly on the right side of the heart, though the shell no longer extends far beyond these organs. In Apera the heart has rotated further in the same direction and is not protected by the shell (diagram C); the auricle has now come to lie further back than the ventricle, and the kidney is behind and to the

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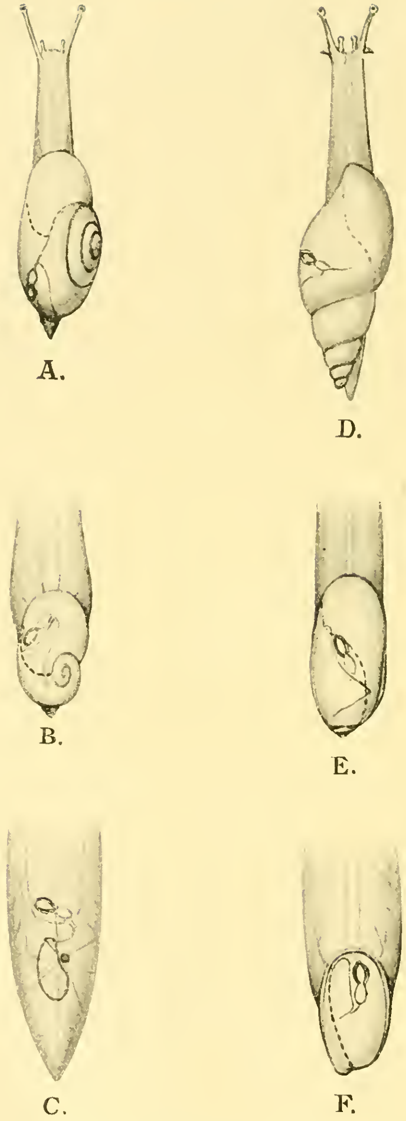
[1] 'Jahrb. d. Deutsch. Mal. Gesell.,' 1878, vol. v, p. 81.

TEXT-FIG. 6.



Diagrams illustrating the rotation of the heart in the evolution of carnivorous slugs from snails.

A. Hyalinia, Rhytida, etc. B. Daudebardia. C. Apera. D. Englandina, etc. E. Strebelia. F. Testacella left of the heart. Turning now to the Oleacinidæ, we find that in Euglandina, Streptostyla, etc., the heart already occupies a position similar to that which it holds in Apera, as is evident from diagram D.[1] This is probably due partly to the pushing forwards of the ventricle owing to the pressure of the hinder portion of the odontophore,[2] and partly to the shape and consequent orientation of the shell.[3] Diagram E shows the position of the heart and kidney in Strebelia, so far as I can judge from Strebel's figures, and it will be seen that with the reduction in the size of the shell and its retrogression to the hind end of the animal, the heart has rotated a little further. It is but a short step from this to the condition shown in diagram F, which illustrates the position of the heart in Testacella, with the auricle directly behind the ventricle. Sixty years ago Reymond expressed the opinion that Testacella was "a Glandina with a rudimentary shell," and if we substitute the word "vestigial" for "rudimentary," I believe that Reymond expressed the truth.

At the same time I am aware that the most eminent modern authorities have expressed a contrary opinion. Dr. Pilsbry[4] states emphatically that the relationships of the European carnivorous slugs (including Testacella) are with the Aulacopoda, and not with the other carnivorous families; and Simroth entertains the same view. The only facts which Pilsbry brings forward in support of this hypothesis are (1) that the European carnivorous slugs have lateral and pedal grooves, which he states that the other families do not possess, and (2) that the cerebral ganglia are generally united by a rather long commissure in the European slugs, while in the other families the cerebral ganglia are in close contact. Let us examine these points.

In the first place, lateral grooves occur not only in Testa-

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[1] See also Strebel, op. cit., vol. iii, pl. v, fig. 5.

See p. 229.

[3] Cf. Naef, A., 'Ergebn. d. Fortschr. d. Zool.,' 1911, vol. iii, p. 131, fig. 19.

[4] 'Manual of Conch.' (2nd ser.), 1908, vol. xix, p. viii.

cella, Daudebardia, and the Trigonochlaminæ, but sometimes also in the Oleacinidæ, Rhytididæ, and Aperidæ. I have already described them in Apera, where they may be very conspicuous (Pl. VII, figs. 11 and 13). Collinge[1] shows them in his figures of Schizoglossa novoseelandica (*Pfr.*), and they are present on both sides in Natalina quekettiana (*M. & P.*), though rather ill-defined. In Euglandina venezuelensis (*Preston*) I have also found both lateral grooves, but the right groove is more conspicuous than the left. In these genera, however, the right lateral groove ends in the genital opening, whereas in Daudebardia it passes below the genital opening and unites with the peripodial groove.[2] Now, Testacella differs from Daudebardia in this respect, and agrees with the other families of carnivorous snails.[3]

In Daudebardia there is a deep peripodial groove, cutting off a broad foot-fringe, which is cleft at the hind end by a short groove probably representing the lost mucous pore.[4] A peripodial groove is also present in the Aperidæ and Streptaxidæ, and although it is often absent or only slightly developed in the Rhytididæ and Oleacinidæ, Reymond states that it is fairly deep in Poiretia. In these forms, however, there is no trace of a caudal mucous pore. This is also the case in Testacella, which possesses a peripodial groove shallower than that of Daudebardia and nearer the edge of the foot.[5]

Lastly, Daudebardia resembles the Trigonochlaminæ, Limacinæ, and related groups, in having two conspicuous longitudinal grooves on the foot-sole, approximately parallel to each other. As a rule no such grooves are found in the other families of agnathous snails and slugs, but we have seen that occasionally similar grooves occur towards the hind end

[1] 'Ann. Mag. Nat. Hist.' (7th ser.), 1901, vol. vii, pl. ii, figs. 26, 27.

[2] Plate, L. H., 'Zool. Jahrb.,' 1891, vol. iv, pl. xxxii, fig. 1.

[3] See de Lacaze-Duthiers, 'Arch. Zool. Expér.,' 1887, vol. v, pl. xxx, fig. 11.

[4] Wiegmann, F., 'Mitt. Zool. Samml. Mus. Berlin,' 1898, vol. i, p. 62.

[5] Compare Plate's figs. 3 and 11 on pl. xxxii, op. cit.

of the foot in Apera and Natalina; they are, however, very inconstant, and instead of being parallel they diverge forwards and seldom extend for more than half the length of the animal. Authorities differ with regard to the foot-sole of Testacella: Plate states that longitudinal grooves are present; Taylor[1] says that they are absent; Pfeffer[2] found them only in the anterior two-thirds of the foot-sole; Simroth[3] saw traces of them towards the hind end of the foot in a few individuals only. I have examined the foot-sole in about a dozen examples of Testacella maugei from various localities, and I found that about half the specimens showed no trace of longitudinal grooves, while in the others the grooves were present, but they were much less conspicuous than in Daudebardia, etc., and diverged forwards from the hind end as in Apera. In other words, the grooves on the foot-sole of Testacella, instead of being constant and approximately parallel, as in the other European carnivorous slugs, are divergent and very inconstant. We see, then, that the evidence of the various dermal grooves of Testacella is against Pilsbry's hypothesis instead of in favour of it.

Turning now to the evidence afforded by the length of the cerebral commissure, we find that while in Daudebardia and the Trigonochlaminæ the commissure is moderately long, in Testacella, as in the Oleacinidæ, Streptaxidæ, Rhytididæ, and Aperidæ, the commissure is quite short, and the cerebral ganglia are in consequence close together. This fact was clearly stated by Strebel[4] thirty-six years ago, and has been abundantly confirmed by subsequent investigations. It is therefore evident that the only features upon which Pilsbry seems to base his theory of the affinities of Testacella are found on examination to support the contrary hypothesis.

[1] 'Monog. L. and F.-W. Mollusca Brit. Isles,' 1902, vol. ii, p. 2.

[2] Op. cit., p. 75.

[3] 'Nova Acta Acad. Cæs. Leop.-Carol. Germ. Nat. Cur.,' 1891, vol. lvi, p. 241.

[4] Op. cit., vol. iii, p. 5.

If the views which I have brought forward are correct, all the carnivorous genera of slugs, with the exception of those belonging to the Trigonochlaminæ and to the Rathouisiidæ, have been derived independently from different snails by the parallel degeneration of the shell. This will be made clear from the following table :

American Oleacinidæ → Strebelia.
European Oleacinidæ → Testacella.
Southern Rhytididæ → Schizoglossa.
Northern Rhytididæ → Apera.
European Zonitinæ → Daudebardia.
Atlantic Vitrininæ → Plutonia.
Transcaucasian Parmacellinæ → Trigonochlaminæ.
Oriental Ditremata → Rathouisiidæ.

But even if we admit that Apera has probably been evolved from the Rhytididæ and Testacella from the Oleacinidæ, the question of the affinities of these genera is not yet settled ; for Pilsbry[1] states that the Oleacinidæ and Rhytididæ are closely related to each other, and if this be the case Apera and Testacella might still have been derived from a common predaceous ancestor, instead of their carnivorous characters having been acquired independently.

Now it is true that the Oleacinidæ and the Rhytididæ have many characters in common, but if we except those which would be likely to be caused by their carnivorous habits the remaining features are chiefly such as are possessed by nearly all the more primitive sigmurethrous Stylommatophora. And there are at least two important differences between the families—their distribution and their shells. The difference in distribution, however, is less important than it appears, for, on the one hand, it is quite conceivable that the Oleacinidæ may have once inhabited tropical Africa, and, on the other hand, we have already seen that the Rhytididæ may occur in tropical America. But the difference in the shells cannot be so easily explained away. In the Oleacinidæ the

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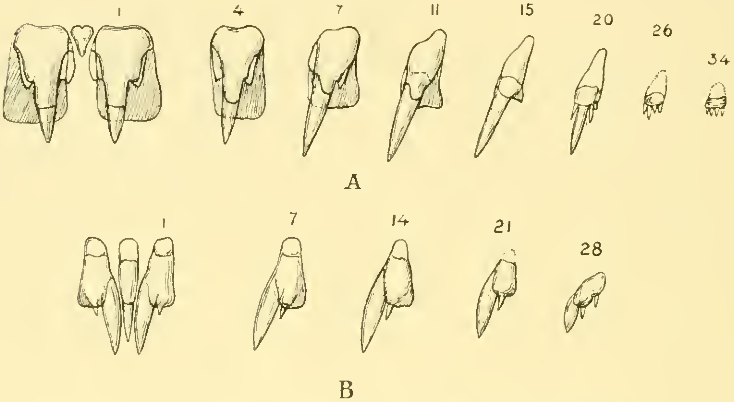
[1] Op. cit., vol. xix, p. xiii.

shell is elongate, with a pointed spire and laterally compressed whorls, and the columella is truncated or folded. In the Rhytididæ, on the other hand, the shell is heliciform or depressed, with a very obtuse spire and laterally expanded whorls, and the columella is neither truncated nor folded. I fail to see how it is possible to derive the shell of the Oleacinidæ directly from that of the Rhytididæ or vice versâ. If these families are really related, it can only be indirectly, and we must postulate a large number of intervening forms, with shells intermediate in shape.

But it might be asked whether we do not find such a series of intermediate forms in the Streptaxidæ; and as a matter of fact in this family we have every gradation from heliciform shells such as Artemon and Imperturbatia to cylindrical shells like Ennea, and from these to pointed shells with laterally compressed whorls such as Streptostele and Obeliscella. May it not be that the Streptaxidæ have been derived from the Rhytididæ and the Oleacinidæ from the Streptaxidæ? In my opinion the Streptaxidæ may possibly have been derived from the Rhytididæ, for I have recently dissected a form which proves to be in some ways intermediate between the two families. The great majority of the Streptaxidæ, however, have come to differ widely from both the Rhytididæ and the Oleacinidæ in their nervous system, their reproductive organs, and even in their radula; and I think that there can be no doubt at all that the Oleacinidæ have not been derived from that family. Therefore, if Pilsbry's view is correct, we must suppose that all the forms intermediate between the Rhytididæ and the Oleacinidæ have died out completely, which does not seem a probable hypothesis.

Dr. Simroth has suggested that the Oleacinidæ may have been derived from the Achatinidæ. Now I regard the striking resemblance between the shell of the American genus Euglandina and the African genus Achatina as almost certainly due to convergence; because Euglandina, with its long labial papillæ and closely aggregated nerve-ganglia, is probably one of the most recently evolved genera of the Oleacinidæ. Indeed, its distribution suggests that it may not have arisen until after the final separation of the West Indian Islands from the mainland. I think that most zoologists who have studied the Oleacinidæ will agree that the most primitive genera in the family are those with long spires, namely Spiraxis, Pseudosubulina, and Varicella. These genera are very unlike Achatina, but they are exceedingly similar to the more primitive members of the Achatinidæ, if we include the Stenogyrinæ and Cœliaxinæ in that family. It is, in fact, almost impossible to say whether some groups of species should be placed in the Stenogyrinæ or Oleacinidæ until their radula has been examined. I believe, therefore, that the Oleacinidæ have been derived from gnathophorous snails closely allied to the Stenogyrinæ or even belonging to that subfamily.

Text-fig. 7.



A. Curvella caloraphe *Preston*, Brit. E. Africa.
B. Varicella nemorensis *Ads.*, Jamaica.

Representative teeth from the radula. × 400.

The chief differences between the internal anatomy of the Stenogyrinæ and that of the Oleacinidæ are to be found in the radula. We know, however, that the Stenogyrinæ are sometimes predaceous,[1] and that their teeth are liable to alter in form and acquire carnivorous characters. This is well shown in text-fig. 7, A, which represents part of the radula of an African member of the Stenogyrinæ; and Crosse and Fischer[2] have figured the radula of an American species—Leptinaria lamellata (*Pot. & Mich.*)—in which the outer lateral teeth have become similarly lengthened. Moreover, we find that the radula of the more primitive genera of the Oleacinidæ is not of the specialised carnivorous type found in the higher members of the family and in the Rhytididæ. Thus in Varicella the radula is usually quite small, the rows of teeth are nearly straight, the bases of the teeth are broader and shorter than in the usual carnivorous type, and there is a small additional cusp outside the main cusp (text-fig. 7, B). This last character is especially significant, as the small cusp is obviously a vestigial ectocone, such as we find in so many herbivorous genera. I am indebted to the Rev. Prof. Gwatkin for kindly allowing me to examine the mounted radulæ of a large number of carnivorous forms, and I find that this additional cusp occurs in all the species of Varicella represented in his collection, namely, V. nemorensis *Ads.*, phillipsi *Ads.*, dissimilis *Pilsbry* (= similis *Ads.*,) and venusta *Ads.*, although it is extremely minute in the last species. It is therefore very surprising that it has been entirely overlooked by previous observers, who have figured the radulæ of V. phillipsi and V. nemorensis. Unfortunately I have not had an opportunity of studying the radula of Spiraxis, a genus which may be even more primitive than Varicella; but I have examined that of Pseudosubulina lirifera (*Morelet*), and find that in this form the second cusp is also present and is larger than in Varicella, although in other ways the radula has become more highly specialised. Strebel has shown, however, that in Pseudosubulina there is a vestigial jaw, the structure of which is not unlike that of the jaw in the Achatinidæ.

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[1] Johnson, C. W., 'Nautilus,' 1900, vol. xiii, p. 117.

[2] 'Mission scientifique au Mexique,' pt. 7, 1877, pl. xxviii, figs. 8–10.

In my opinion these facts are sufficient to prove that the Oleacinidæ have not been evolved from the Rhytididæ, but have arisen directly from a gnathophorous family.

Perhaps it might be said that the Oleacinidæ cannot have been evolved from the Achatinidæ, because in the latter family the central teeth of the radula are almost invariably much smaller than the laterals, whereas in the more primitive members of the Oleacinidæ the central teeth are sometimes nearly as large as those on each side of them, notwithstanding that the teeth in the middle of the radula tend to diminish in size among carnivorous genera (cf. figs. 7, A and B). But I do not maintain that the Oleacinidæ have been evolved from any of the recent genera of the Achatinidæ. It must be remembered that already in Upper Cretaceous and Eocene times the Oleacinidæ were represented by forms which can hardly be regarded as primitive; the family, therefore, cannot have arisen very much later than the Jurassic period. Now the small central teeth are not an absolutely constant feature of the Achatinidæ even at the present day, and it is not improbable that in Mesozoic times the radula was still of the more generalised type found in the closely allied family Megaspiridæ. Indeed, it is possible that in the Jurassic period the Achatinidæ may not yet have definitely separated from the Megaspiridæ. Callionepion may perhaps be regarded as a descendant of a form intermediate between these two families, and in this genus the central teeth are nearly as large as the laterals. Moreover, the penis has a continuation in Callionepion, which reminds us of the similar structure found in Englandina liebmanni (*Pfr.*), and other members of the Oleacinidæ.[1] Lastly, the shells of the typical section of Spiraxis in some respects resemble the Megaspiridæ quite as much as the Stenogyrinæ, which also suggests that the Oleacinidæ may have diverged from the Acha-

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[1] Pilsbry and Vanatta, 'Proc. Acad. Nat. Sci. Phila.,' 1899, pp. 371–373, pl. xv, figs. 3, 8, and Pilsbry, 'Man. of Conch.,' 1904, vol. xvi, p. 178, pl. xxxi, figs. 7, 8.

tinidæ when this family was scarcely distinct from the Megaspiridæ. Nevertheless, until further anatomical investigations have been made, it is impossible to say exactly to which group now living the Oleacinidæ are probably most nearly related.

It is equally difficult to form an opinion as to the place of origin of the family, for both the Achatinidæ and the Megaspiridæ have an extremely wide distribution. Perhaps the Oleacinidæ may have arisen near the southern or south-eastern shores of that continent which geologists believe to have stretched from Western Europe to America during a large part of the Mesozoic era. If this were the case, the south-eastern expansion of the area of distribution would be prevented by the extensive "Mediterranean Sea" which then existed; the gradual growth of the North Atlantic would separate the European from the American forms, and the subsequent incoming of the Glacial Period would restrict the northern distribution of the family. On the other hand, the Oleacinidæ may possibly have arisen further south, and have entered America by way of the old land-connection which probably extended from Africa to Brazil. The absence of the Oleacinidæ from the Ethiopian Region is a possible objection to this theory; but perhaps the family may have once extended into that area, and may have there been exterminated by the elongate Streptaxidæ — Ennea, Streptostele, and their allies—which would probably enter into competition with them, but appear to have arisen just too late to follow the heliciform Streptaxidæ across to the Neotropical Region. The limited distribution of the Oleacinidæ in South America is, however, another objection to the theory of their southern origin, and the first view that I have given seems to me to be the more probable. I am therefore glad to see that Pilsbry now upholds the more northerly origin of the family,[1] although seven years ago he thought that the probabilities favoured the hypothesis that the Olea-

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[1] 'Rep. Princeton Univ. Exped. Patagonia 1896–1899,' vol. iii, Zoöl., 1911, p. 625.

cinidæ arose in the Brazil-African continent.[1] All this is highly problematical; but the uncertainty which surrounds the precise origin of the Oleacinidæ does not affect the general conclusion that the family is probably more nearly related to the Achatinidæ and their allies than to any of the other carnivorous forms excepting Testacella.

It is not necessary for me to discuss at length the phylogeny of the Rhytididæ; this family is evidently of very ancient origin—possibly it is the oldest of all the carnivorous families—and I do not suppose that anyone would maintain that it had arisen from the Oleacinidæ. I hope to deal in greater detail with the affinities of the Rhytididæ and Streptaxidæ when treating of the South African members of these families; and I have already said enough to show that in all probability the carnivorous characters of the Rhytididæ and Oleacinidæ, and therefore of Apera and Testacella, have been acquired independently. The remarkable resemblance between Apera and Testacella seems only to be another example of convergence due to the common acquisition of carnivorous habits.

One thing is quite clear from the preceding argument: the tribe Agnatha is not a natural group, and should therefore find no place in the classification of the Pulmonata. The Rathouisiidæ should be placed with the Veronicellidæ among the Ditremata, as some authors have already done. The Trigonochlaminæ, Plutoniinæ, and Daudebardiinæ should be placed among the Aulacopoda or Oxygnatha, next to the Parmacellinæ, Vitrininæ, and Zonitinæ. The Oleacinidæ and Testacellidæ should form a group by themselves, near the Achatinidæ and Megaspiridæ, if my views are correct; and to this small group Mörch's term Agnatha may well be applied, for his original description is simply: "Agnatha. Ohne Kiefer: Oleacina, Testacella."[2] The Rhytididæ, Aperidæ, and probably the Streptaxidæ, should be placed in another

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[1] 'Man. of Conch.,' vol. xix, p. xiv.

[2] 'Mal. Blätt.,' 1859, vol. iv, p. 109.

group, for which we may adopt Pilsbry's term Agnathomorpha.[1] Whether the purely American family Circinariidæ should also be placed in this group I am unable to say. Pilsbry considers that it is allied to the Streptaxidæ, but Simroth believes it to be related to the Zonitidæ. There are possible objections to both these views, but as I have not had an opportunity of examining any members of the Circinariidæ myself, I will refrain from expressing an opinion upon its affinities.

Thus the carnivorous snails and slugs should probably be classified as follows:

- Sigmurethra
  - Agnatha . . .
    - Testacellidæ.
    - Oleacinidæ.
  - Agnathomorpha
    - Aperidæ.
    - Rhytididæ.
    - Streptaxidæ.
  - Circinariidæ.
  - Aulacopoda or Oxygnatha
    - Daudebardiinæ.
    - (Zonitinæ).
    - Plutoniinæ.
    - (Vitrininæ).
    - Trigonochlaminæ.
    - (Parmacellinæ, etc.).
- Ditremata . . . . . . Rathouisiidæ.

While it is hoped that this classification rests on a firmer basis than previous attempts of a similar nature, it must be remembered that we still know very little of the comparative anatomy of the carnivorous snails and slugs. To give a single example: about a hundred species of the genus Ennea are known to occur in South Africa alone, and I believe that I am right in saying that not a single feature of the anatomy of any of these species has been described. As we are equally ignorant of the anatomy of many other carnivorous genera, it is at present impossible to do more than give a rough outline of their probable affinities. Let us hope that the time will soon come when collectors of shells will cease to throw away

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[1] 'Proc. Acad. Nat. Sci. Phila.,' 1900, p. 564.

the animals when cleaning their specimens, but will study their anatomy instead.

APPENDIX.

REFERENCES TO TESTACELLA MAUGEI *FÉR.*

The literature on Testacella maugei is so extensive that it has been deemed more convenient to give the following list of some of the principal references to this species in the form of an appendix. Those references in brackets relate to fossil shells which have been assigned to T. maugei, although it is possible that some of them, such as T. asinina, may have belonged to species which, while nearly allied to this form, were really distinct from it. Most modern writers place the form found in New Zealand in this species, notwithstanding that Hutton stated that its radula differed slightly from the type usually found in T. maugei; I have therefore included the references to it in the following list, although I have not had an opportunity of examining a New Zealand example myself.

Testacella haliotoides *Lam.*, Sys. An. s. Ver., 1801, p. 96; Woodward, Man. Moll., 1854, p. 169, fig. 94.

Testacella haliotidea (pars) *Drap.*, Hist. Nat. Moll. Fr., 1805, pl. viii, figs. 46–48; Lowe, Rep. Brit. Assoc., 1883, p. 549.

Testacella haliotidea var. scutulum *Moq.-Tand.*, Hist. Moll. Fr., 1855, pl. v, figs. 20, 21.

Testacella maugei *Fér.*, Hist. Moll., 1819, vol. ii, pp. 94, 95, pl. viii, figs. 10–12; Miller, Ann. Philos. (new ser.), 1822, vol. iii, p. 380; Sowerby, Genera Shells, 1822, Testacella, figs. 7–10; Fleming, Hist. Brit. Anim., 1828, p. 257; Desh., Dict. Class. d'Hist. Nat., 1830, vol. xvi, p. 179; J. D., Mag. Nat. Hist., 1833, vol. vi, p. 45, fig. 8, *c*, *d*; Lukis and J. D., Mag. Nat. Hist., 1834, vol. vii, pp. 225, 229, figs. 40, *c*, *d*, 41, *f*, *g*; d'Orbigny, Moll. des Iles Canaries, 1834, p. 48; Gray, Turton's Man. L. and F. W. Shells, 1840, pl. iii, fig. 18; Encycl. Brit. (7th ed.), 1842, vol. xv, pl. ccclxvii, fig. 5; Penny Cyclopædia, 1842, vol. xxiii, p. 246, figs. *a*, *a*, *b*; Reeve, Conch. Syst., 1842, vol. ii, pl. clxi, figs. 7–10; Morelet, Moll. Terr. et Fluv. Portugal, 1845, pp. 48, 49; Forbes and Hanley, Hist. Brit. Moll., 1853, vol. iv, p. 28; Albers, Malacographia Maderensis, 1854, pp. 13, 14, pl. i, figs. 9–11; H. & A. Adams, Gen. Rec. Moll., 1854, vol. iii, pl. lxxii, figs. 7, 7*a*; Grat., Distr. Géogr. des Limaciens, 1855, pp. 15, 16; Tapping, Zoologist, 1856, vol. xiv, p. 5102; Woodward, Man. Moll., 1856, p. 465, fig. 262; Gassies and Fischer, Actes Soc. Linn. Bordeaux, 1856, vol. xxi, pp. 36–39, pl. i, figs. 2, 5; Grat., Distr. Géogr. Moll. Girond., 1858, p. 72; Morelet, L'Hist. Nat. Açores, 1860, p. 143; Norman, Proc. Somerset Arch. and Nat. Hist. Soc., 1861, *ex* vol. x, pp. 11, 12; Bourg., Rev. and Mag. Zool. (2nd ser.), 1861; vol. xiii, p. 514; Jeffries, Brit. Conch., 1862, vol. i, pp. 147, 148; Reeve, Brit. Moll., 1863, pp. 32, 33; Paiva, Mon. Moll. Ins. Mader., 1867, pp. 6, 7; Massot, Ann. de Malac., 1870, vol. i, pp. 145, 146; Mousson, N. Mém. Soc. Helv. Sci. Nat., 1873, *ex* vol. xxv, p. 11; Wollaston, Testacea Atlantica, 1878, pp. 13, 14, 72, 73, 310, 311; Tryon, Man. Conch. (2nd ser.), 1885, vol. i, p. 8, pl. i, figs. 1–3; de Lacaze-Duthiers, Arch. de Zool. Expér. (2nd ser.), 1887, vol. v, pp. 469, etc., pl. xxix, figs. 7, 8; Pollon., Boll. Mus. Zool. Anat. Torino, 1889, vol. iv, No. 57, pl. i, fig. 1; Simroth, Nova Acta Acad. Caes. Leop.-Carol. Germ. Nat. Cur., 1891, vol. lvi, pp. 230–245, 266, etc., pl. x, figs. 1, 2, 5–7; Plate, Zool. Jahrb., 1891, vol. iv, pp. 518, 519, 524, 542–552, 560–562, 566, 588, 594, 595, 614, 618–620, etc., pl. xxxiii, figs. 44, 46, 47, pl. xxxiv, figs. 62–65, pl. xxxvi, fig. 91, pl. xxxvii, figs. 101, 115, 116; Collinge, An. Mag. Nat. Hist., 1893, vol. xii, p. 24, pl. i, fig. 3; Locard, Coquilles Ter. France, 1894, p. 18, figs. 5, 6; Webb, J. of Malac., 1895, vol. iv, p. 74, pl. ii, figs. 1, 4, pl. iii, figs. 7, 8; L. E. Adams, Coll. Man. Brit. L. and F.-W. Shells (2nd ed.), 1896, pp. 41, 42, pl. ii, fig. 3, pl. vii, fig. 12; Webb, J. of Malac., 1897, vol. vi, pp. 49, 52, 56, pl. vi, fig. 3; Taylor, Mon. L. and F.-W. Moll. Brit. Is., 1902, vol. ii, pp. 21–27, figs. 32–42, pl. i, figs. 9–16, pl. iv; L. E. Adams, J. of Conch., 1911, vol. xiii, p. 212.

[Testacella asininum *de Serres*. Ann. Sci. Nat., 1827, vol. xi, p. 409.]

[Testacella asinina *de Serres;* Gassies and Fischer, Actes Soc. Linn. Bordeaux, 1856, vol. xxi, pp. 41, 42, pl. ii, fig. 3.]

[Testacella lartetii *Dupuy*, J. de Conch., 1850, vol. i, pp. 302–304, pl. xv, figs. 2, *a–d*; Gassies and Fischer, Actes Soc. Linn. Bordeaux, 1856, vol. xxi, pp. 40–41, pl. ii, fig. 2.]

[Testacella bruntoniana *de Serres*, Mem. Terr. Transp., 1851, p. 51; Gassies and Fischer, Actes Soc. Linn. Bordeaux, 1856, vol. xxi, p. 42.]

[Testacella deshayesii *Mich.*, Desc. Coq. Foss., 1855, p. 3, pl. ii, figs. 10, 11.]

Testacella burdigalensis *Gassies & Baudin*, Cat. Moll. Ter. and Fluv. Fr., 1855, p. 2.

Testacella oceanica *Grat.*, Distr. Géogr. des Limaciens, 1855, p. 15.

Testacella canariensis *Grat.*, Distr. Géogr. des Limaciens, 1855, p. 16.

[Testacella monspessulana *Grat*, Distr. Géogr. des Limaciens, 1855, p. 16.]

[Testacella browniana *Grat.*, Distr. Géogr. des Limaciens, 1855, p. 16.]

[Testacella occitaniæ *Grat.* Distr. Géogr. des Limaciens, 1855, p. 16.]

[Testacella altæ-ripæ *Grat*, Distr. Géogr. des Limaciens, 1855, p. 16.]

[Testacella aquitanica *Grat*, Distr. Géogr. des Limaciens. 1855, p. 16.]

[Testacella nouleti *Bourg.*, Hist. Mal. Colline de Sansan, 1881, p. 15].

Daudebardia novoseelandica *Hutton*, Trans. N. Z. Inst., 1881. vol. xiv, pp. 152, 153, pl. iii, fig. E; pl. iv, fig. M.

Testacella vagans *Hutton*, Trans. N. Z. Inst., 1882. vol. xv, p. 140; 1883, vol. xvi, p. 209, pl. x, fig. T; Tryon, Man. Conch. (2nd ser.), 1885, vol. i, pp. 11, 12; Musson, Proc. Linn. Soc. N. S. W., 1890, p. 885; Suter, Trans. N. Z. Inst., 1892, vol. xxiv, p. 279.

Testacella aurigaster *Layard*; Connolly, Ann. S. Afr. Mus., 1912, vol. xi, p. 64.

According to Gassies and Fischer, and Simroth, Plectrophorus orbignyi *Fér.*, 1819, is also probably founded on specimens of this species.

EXPLANATION OF PLATES VII–XXIV,

Illustrating Mr. Hugh Watson's paper on "The Carnivorous Slugs of South Africa."

PLATE VII.

Fig. 1.—× 1·1. Apera gibbonsi *s.s.*; dorsal view; probably from Lower Umfolosi Drift, Zululand.

Fig. 2.—× 1·1. A. gibbonsi *s.s.*; side view; Hlabisa, Zululand.

Fig. 3.—× 1·1. A. gibbonsi rubella, young; side view; Equeefa, Natal.

Fig. 4.—× 1·1. A. gibbonsi rubella; dorsal view; Equeefa, Natal.

Fig. 5.—× 1·1. A. gibbonsi rubella; side view; Equeefa, Natal.

Fig. 6.—× 1·1. A. gibbonsi gracilis, type; side view; Equeefa, Natal.

Fig. 7.—× 1·1. A. dimidia, type; dorsal view; Equeefa, Natal.

Fig. 8.—× 1·1. A. dimidia; side view; Port Shepstone, Natal.

Fig. 9.—× 1·1. A. dimidia; ventral view; Equeefa, Natal.

Fig. 10.—× 1·1. A. burnupi; dorsal view; Richmond, Natal.

Fig. 11.—× 1·1. A. burnupi; side view; Chase Bush, Pietermaritzburg.

Fig. 12.—× 1·1. A. sexangula; dorsal view; Port Shepstone, Natal.

Fig. 13.—× 1·1. A. sexangula; side view; Port Shepstone, Natal.

PLATE VIII.

Fig. 14.[1]—× 1. Apera gibbonsi *s.s.*; dorsal view; Zululand.

Fig. 15.—× 1. A. gibbonsi *s.s.*; side view; Zululand.

Fig. 16.—× 1. A. gibbonsi rubella; dorsal view; Equeefa, Natal.

Fig. 17.—× 1. A. gibbonsi rubella; side view; Equeefa, Natal.

Fig. 18.—× 1. A. gibbonsi lupata; dorsal view; Port Shepstone, Natal.

Fig. 19.—× 1. A. gibbonsi lupata; side view; Port Shepstone, Natal.

Fig. 20.—× 1. A. dimidia; dorsal view; Equeefa, Natal.

Fig. 21.—× 1. A. dimidia; side view; Equeefa, Natal.

Fig. 22.—× 1¼. A. parva; dorsal view; near Fern Kloof, Grahamstown.

Fig. 23.—× 1¼. A. parva; side view; near Fern Kloof, Grahamstown.

Fig. 24.—× 3. A. dimidia; dorsal view of hind end; Equeefa, Natal.

Fig. 25.—× 3½. A. purcelli; dorsal view of hind end; Table Mt., Cape Town.

Fig. 26.—× 2. A. burnupi; dorsal view of hind end; Chase Bush, Pietermaritzburg.

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[1] Figs. 14–23 show the colours of specimens preserved in alcohol.

PLATE IX.

Fig. 27.—× 2½. Apera gibbonsi rubella; general dissection from above.[1]

Fig. 28.—× 5. A. parva; general dissection from above.

Fig. 29.—× 4½. A. dimidia; general dissection from above.

Fig. 30.—× 2. A. burnupi; general dissection from above.

Fig. 31.—× 2¾. A. sexangula; general dissection from above.

PLATE X.

Fig. 32.—× 25. Apera gibbonsi rubella, young; transverse section through the region of the buccal retractors.[2]

Fig. 33.—× 25. A. gibbonsi rubella, young; transverse section through the region of the anus.

PLATE XI.

Fig. 34.—× 25. Apera dimidia; transverse section through the region of the heart.

Fig. 35.—× 25. A. dimidia; transverse section through the region of the reno-pericardial duct.

PLATE XII.

Fig. 36.—× 25. Apera dimidia; transverse section through the region of the anterior end of the ureter.

Fig. 37.—× 128. A. dimidia; transverse section through the skin of the back.

Fig. 38.—× 300. A. dimidia; transverse section through the skin of the foot-sole.

Fig. 39.—× 118. A. dimidia; transverse section through the right corner of the lung.

PLATE XIII.

Fig. 40.—× 300. Apera dimidia; transverse section through a sphincter of a dermal blood-vessel.

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[1] The specimens shown in figs. 27–31 have been cut open a little to the left of the mid-dorsal line, and, excepting in A. burnupi, the digestive and reproductive organs have been slightly separated in order to show the course of the anterior aorta.

[2] The sections represented on Plates X to XII are shown as viewed from the front.

FIG. 41.—× 3. A. gibbonsi rubella; dorsal view of shell; Equeefa.

FIG. 42.—× 3. A. gibbonsi rubella; side view of shell; Durban.

FIG. 43.—× 4. A. gibbonsi gracilis; dorsal view of shell.

FIG. 44.—× 6. A. parva; dorsal view of shell.

FIG. 45.—× 6. A. parva; side view of shell.

FIG. 46.—× 4. A. dimidia; dorsal view of shell.

FIG. 47.—× 7. A. purcelli; dorsal view of shell.

FIG. 48.—× 7. A. purcelli; side view of shell.

FIG. 49.—× 2. A. burnupi; dorsal view of shell.

FIG. 50.—× 3. A. sexangula; dorsal view of shell.

FIG. 51.—× 3. A. sexangula; side view of shell.

FIG. 52.—× 3. A. gibbonsi rubella; dorsal view of pedal gland, central nervous system, etc.[1]

FIG. 53.—× 8. A. parva; dorsal view of pedal gland, central nervous system, etc.

FIG. 54.—× 6. A. dimidia; dorsal view of pedal gland, central nervous system, etc.

FIG. 55.—× 8½. A. purcelli; dorsal view of pedal gland, central nervous system, etc.

FIG. 56.—× 3. A. burnupi; dorsal view of pedal gland, central nervous system, etc.

FIG. 57.—× 5. A. sexangula; dorsal view of pedal gland, central nervous system, etc.

FIG. 58.—× 6. A. gibbonsi lupata; posterior end of pedal gland.

FIG. 59.—× 46. A. dimidia; transverse section through glandular part of pedal gland.

FIG. 60.—× 46. A. dimidia; transverse section through duct of pedal gland behind glandular part.

FIG. 61.—× 46. A. dimidia; transverse section through anterior end of terminal vesicle of pedal gland.

FIG. 62.—× 46. A. dimidia; transverse section through terminal vesicle of pedal gland, showing blood-vessel entering the fold.

PLATE XIV.

FIG. 63.—× 114. Apera gibbonsi rubella; transverse section through one side of pedal gland near its anterior end.

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[1] In the specimens shown in figs. 52–57 the œsophagus, penis, etc. have been turned aside in order to display the underlying organs.

Fig. 64.—× 22. A. gibbonsi rubella; side view of part of pedal gland.

Fig. 65.—× 119. A. gibbonsi rubella; transverse section through fold in terminal vesicle of pedal gland.

Fig. 66.—× 114. A. dimidia; transverse section through fold in terminal vesicle of pedal gland.

Fig. 67.—× 25. A. gibbonsi rubella; ventral group of nerve ganglia.

Fig. 68.—× 60. A. dimidia; section through pedal ganglia and pedal commissure, cut slightly obliquely, and showing pleural ganglion on the right and cerebro-pedal connective on the left.

Fig. 69.—× 120. A. dimidia; sections of nerve-cells in right parietal ganglion.

PLATE XV.

Fig. 70.—× 16. Apera gibbonsi rubella; cerebral and buccal ganglia.

Fig. 71.—× 32. A. dimidia; cerebral and buccal ganglia.

Fig. 72.—× 25. A. sexangula; cerebral and buccal ganglia.

Fig. 73.—× 30. A. dimidia; left half of ventral group of ganglia.

Fig. 74.—× 33. A. sexangula: right half of ventral group of ganglia.

Fig. 75.—× 6. A. dimidia; semi-diagrammatic figure showing the distribution of the nerves from the ventral group of ganglia.

Fig. 76.—× 5. A. sexangula; tentacular retractors of an abnormal specimen.

Fig. 77.—× 26. A. gibbonsi rubella; transverse section through mouth.

Fig. 78.—× 15. A. gibbonsi rubella; transverse section through crop and salivary glands.

Fig. 79.—× 100. A. gibbonsi rubella; transverse section through wall of crop.

PLATE XVI.

Fig. 80.—× 50. Apera dimidia; transverse section through retracted upper tentacle in front of eye.

Fig. 81.—× 50. A. dimidia; transverse section through retracted upper tentacle, showing anterior part of eye.

Fig. 82.—× 50. A. dimidia; transverse section through retracted upper tentacle, showing posterior part of eye.

Fig. 83.—× 50. A. dimidia; transverse section through retracted upper tentacle just behind eye.

Fig. 84.—× 50. A. dimidia; transverse section through retracted upper tentacle behind eye.

Fig. 85.—× 50. A. dimidia; transverse section through retracted upper tentacle considerably behind eye.

Fig. 86.—× 50. A. dimidia; transverse section through retracted upper tentacle at entrance of olfactory and optic nerves.

Fig. 87.—× 60. A. sexangula; longitudinal section through mouth.

Fig. 88.—× 60. A. dimidia; transverse section through mouth.

Fig. 89.—× 118. A. dimidia; transverse section through radula sac.

Fig. 90.—× 118. A. dimidia; transverse section through part of odontophoral support.

PLATE XVII.

Fig. 91.—× $2\frac{1}{8}$. Apera gibbonsi *s.s.*; side view of odontophore without its sheath.

Fig. 92.—× $2\frac{1}{8}$. A. gibbonsi *s.s.*; longitudinal section of odontophore.

Fig. 93.—× 2. A. gibbonsi rubella; dorsal view of odontophore without its sheath.

Fig. 94.—× 2. A. gibbonsi rubella; ventral view of odontophore without its sheath.

Fig. 95.—× 2. A. gibbonsi rubella; dorsal view of odontophoral support.

Fig. 96.—× 2. A. gibbonsi rubella; side view of radula with its retractor muscles.

Fig. 97.—× 2. A. gibbonsi rubella; side view of radula without its muscles.

Fig. 98.—× 2. A. gibbonsi rubella; side view of radula without its muscles (retracted).

Fig. 99.—× 3. A. gibbonsi lupata; side view of radula without its muscles.

Fig. 100.—× 5. A. parva; dorsal view of odontophoral support.

Fig. 101.—× 5. A. parva; side view of radula with its retractor muscles.

Fig. 102.—× 5. A. parva; side view of radula without its muscles.

Fig. 103.—× 6. A. dimidia; ventral view of odontophore.

Fig. 104.—× 6. A. dimidia; side view of odontophore without its sheath.

Fig. 105.—× 6. A. dimidia; dorsal view of odontophoral support.

Fig. 106.—× 6. A. dimidia; side view of radula with its retractor muscles.

Fig. 107.—× 6. A. dimidia; side view of radula without its muscles.

Fig. 108.—× 4. A. burnupi; side view of odontophoral support.

Fig. 109.—× 4. A. burnupi; dorsal view of odontophore without its sheath.

Fig. 110.—× 6½. A. sexangula; ventral view of odontophore.

Fig. 111.—× 6½. A. sexangula; dorsal view of odontophore without its sheath.

Fig. 112.—× 6½. A. sexangula; dorsal view of odontophoral support.

Fig. 113.—× 6½. A. sexangula; side view of radula with its retractor muscles.

Fig. 114.—× 6½. A. sexangula; dorsal view of radula without its muscles.

PLATE XVIII.

Figs. 115–122.—× 55. Apera dimidia; serial transverse sections through the odontophore.

PLATE XIX.

Fig. 123.—× 30. Apera gibbonsi gracilis; front end of radula.

Fig. 124.—× 30. A. gibbonsi lupata; front end of radula.

PLATE XX.

Fig. 125.—× 25. Apera gibbonsi *s. s.*; part of radula.

Fig. 126.—× 25. A. gibbonsi rubella; part of radula.

Fig. 127.—× 127. A. dimidia; part of radula.

Fig. 128.—× 127. A. burnupi; part of radula.

PLATE XXI.

FIG. 129.—× 2. Apera gibbonsi *s. s.*; general view of digestive system.[1]

FIG. 130.—× $1\frac{3}{4}$. A. gibbonsi rubella; general view of digestive system.

FIG. 131.—× 5. A. parva; general view of digestive system.

FIG. 132.—× $3\frac{1}{2}$. A. dimidia; general view of digestive system.

FIG. 133.—× $1\frac{2}{3}$. A. burnupi; general view of digestive system.

FIG. 134.—× $2\frac{1}{8}$. A. sexangula; general view of digestive system.

PLATE XXII.

FIG. 135.—× 113. Apera sexangula; transverse section through œsophagus.

FIG. 136.—× 125. A. dimidia; transverse section through rectum.

FIG. 137.—× 135. A. dimidia; transverse section through wall of intestine.

FIG. 138.—× 135. A gibbonsi rubella; transverse section through salivary duct.

FIG. 139.—× 119. A. gibbonsi rubella; transverse section through part of salivary gland.

FIG. 140.—× 119. A. dimidia; section through wall of ventricle.

FIG. 141.—× 135. A. dimidia; section through part of kidney and wall of ureter.

FIG. 142.—× 194. A. gibbonsi rubella; side view of the end of a papilla from inside penis.

PLATE XXIII.

FIG. 143.—× 2. Apera gibbonsi *s. s.*; reproductive organs.

FIG. 144.—× 2. A. gibbonsi rubella; reproductive organs.

FIG. 145.—× 8. A. gibbonsi rubella; interior of penis and epiphallus.

FIG. 146.—× 6. A. parva; reproductive organs.

FIG. 147.—× 4. A. dimidia; reproductive organs.

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[1] In the specimens shown in figs. 129–134 the right division of the liver, with the adjacent parts of the alimentary canal, is lying to some extent on its right side, in order to show the origin of the hepatic ducts, etc. (Compare figs. 27–31, in which the lobes of the liver are shown more nearly in their natural position as seen from above.)

Fig. 148.—× $2\frac{1}{4}$. A. burnupi; reproductive organs.

Fig. 149.—× $2\frac{1}{2}$. A. sexangula; reproductive organs.

Fig. 150.—× 1200. A. gibbonsi rubella; anterior part of a spermatozoon.

Fig. 151.—× 1200. A. dimidia; anterior part of a spermatozoon.

PLATE XXIV.

Fig. 152.—× 1·8. Testacella maugei; dorsal view; Cape Town.

Fig. 153.—× 1·8. T. maugei; side view.

Fig. 154.—× 3·4. T. maugei; general dissection, viewed obliquely from the right side.[1]

Fig. 155.—× 3·3. T. maugei; side view of odontophore without its sheath.

Fig. 156.—× 3·3. T. maugei; longitudinal section of odontophore.

Fig. 157.—× 100. T. maugei; representative teeth from the radula.

Fig. 158.—× 4. T. maugei; side view of junction of penis with vas deferens and penial retractor in specimen shown in fig. 154.

Fig. 159.—× 4. T. maugei; side view of junction of penis with vas deferens and penial retractor in another specimen from Cape Town.

Fig. 160.—× 1100. T. maugei; anterior part of a spermatozoon.

Fig. 161.—× 1·5. T. maugei; ventral view of shell; Cape Town.

Fig. 162.—× 1·5. T. maugei, var. aperta; ventral view of shell; Cape Town.

Explanatory References.

alb. gl. Albumen gland. *ant. aor.* Anterior aorta. *aur.* Auricle.

b. art. Buccal artery. *b. c.* Buccal cavity. *b. gang.* Buccal ganglion. *b. mass.* Buccal mass. *b. mass. n.* Nerve to sides of buccal mass. *b. protr.* Buccal protractors. *b. retr.* Buccal retractors. *b. retr. n.* Nerve to buccal retractor.

c.-b. con. Cerebro-buccal connective. *cer. gang.* Cerebral ganglia. *c. m.* Circular muscles of sheath of odontophore. *com. d.* Common duct. *c.-ped. con.* Cerebro-pedal connective. *c.-pl. con.* Cerebro-pleural connective. *c. r.* Circular muscles of radula-sac.

---

[1] The liver is shown turned over to the left, and the reproductive system (excepting the penis) is displaced to the right; the arteries are omitted.

diaph. Diaphragm. *⚥ d.* Hermaphrodite duct. *d. m.* Dorsal median muscle. *d. ped. gl.* Duct of pedal gland.

epiph. Epiphallus.

f. Flexor muscle of odontophoral support. *f. ov.* Free oviduct.

gen. atr. Genital atrium. *⚥ gl.* Hermaphrodite gland.

hep. d. Hepatic ducts.

i. l. Inner longitudinal muscles of sheath of odontophore. *int.* Intestine. *i. od. n.* Inner odontophoral nerves.

lab. n. Labial nerves. *l. abd. n.* Left abdominal nerve to anus. *l. hep. d.* Left hepatic duct. *l. liv.* Left liver. *l. pal. n.* Left pallial nerve. *l. par. + abd. gang.* United left parietal and abdominal ganglia. *l. ped. gang.* Left pedal ganglion. *l. pl. gang.* Left pleural ganglion. *l. r.* Lateral retractors. *l. sal. d.* Left salivary duct. *l. sal. gl.* Left salivary gland. *l. tent. n.* Lower tentacular nerve. *l. t. retr.* Lower tentacular retractor. *l. t. retr. n.* Nerve to lower tentacular retractor.

m.-cav. Mantle-cavity. *m. r.* Median retractors.

n. n. Nerves of the neck.

od. Odontophore. *od. s.* Odontophoral support. *œs.* Œsophagus. *œs. n.* Nerves to œsophagus. *o. l.* Outer longitudinal muscles of sheath of odontophore. *olf. n.* Olfactory nerve. *o. od. n.* Outer odontophoral nerve. *opt. n.* Optic nerve.

ped. art. Pedal artery. *ped. n.* Pedal nerves. *ped. gl.* Pedal gland. *ped. gl. n.* Nerve to pedal gland. *pen. n.* Penial nerve. *pen. retr.* Penial retractor. *perit. n.* Peritentacular nerves. *post. aor.* Posterior aorta.

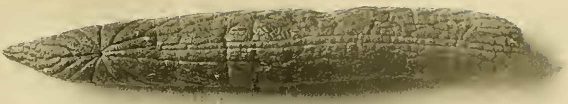
r. abd. n. Right abdominal nerve to pericardium. *rd. s.* Radula-sac. *rec. d.* Receptacular duct. *rec. sem.* Receptaculum seminis. *r. liv.* Right liver. *r. pal. n.* Right pallial nerve. *r. par. gang.* Right parietal ganglion. *r. ped. gang.* Right pedal ganglion. *r. pl. gang.* Right pleural ganglion. *r. sal. d.* Right salivary duct.

sal. d. Salivary duct. *sal. gl.* Salivary gland. *sh. od. n.* Nerve to sheath of odontophore. *sh.-sac.* Shell-sac. *s. m.* Suspensor muscles of support. *st.* Stomach. *subc. com.* Subcerebral commissure.

tent. art. Tentacular artery. *tent. retr.* Tentacular retractor. *t. r.* Terminal retractors.

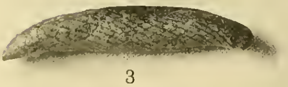
ur. Ureter. *u. t. retr.* Upper tentacular retractor.

vag. Vagina. *vas def.* Vas deferens. *ventr.* Ventricle. *ves. ped. gl.* Vesicle of pedal gland. *v. m.* Ventral muscles. *v. p.* Ventral pocket.



1

2



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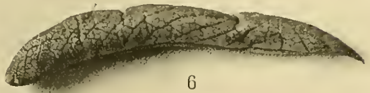

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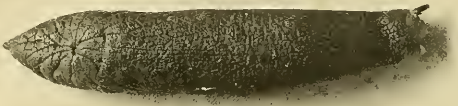

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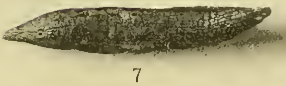

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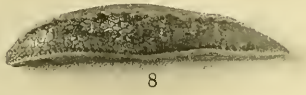

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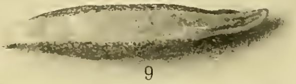

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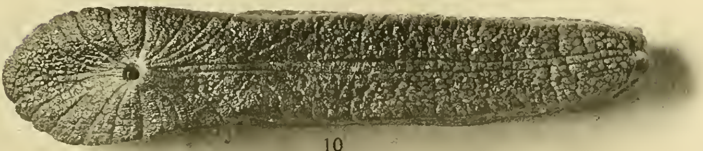

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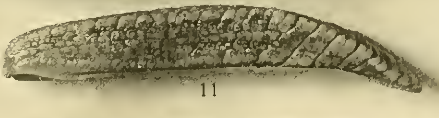

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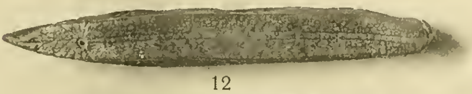

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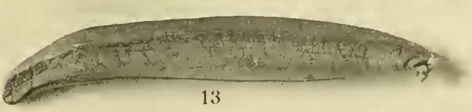
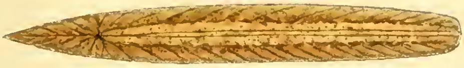


13

Photo. by Watson. Collotype.

Species of *Apera* from Natal. × 1 1.

Figs. 1, 2, *A. gibbonsi s.s.*; 3-5, *A. g. rubella*; 6, *A. g. gracilis*; 7-9, *A. dimidia*; 10, 11, *A. burnupi*; 12, 13, *A. sexangula*.



14.

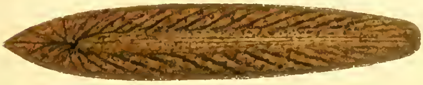
15.

A. gibbonsi.

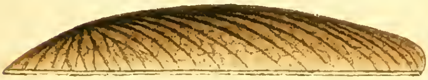
18.

19.

A. g. lupata.



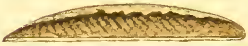
16.



17.

A. g. rubella.

20.



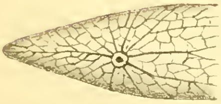
21.

A. dimidia.

22.

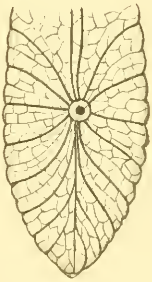
23.

A. parva. × 1¼.



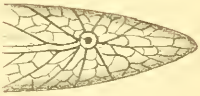
24.

A. dimidia. × 3.



26.

A. burnupi. × 2.

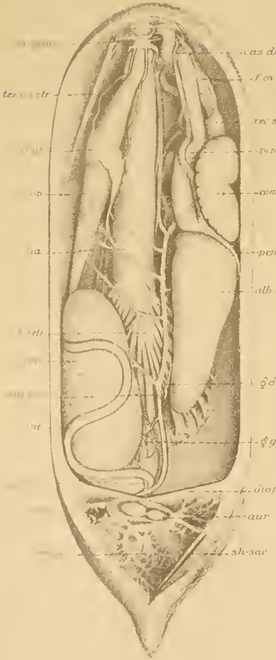


25.

A. purcelli. × 3½.

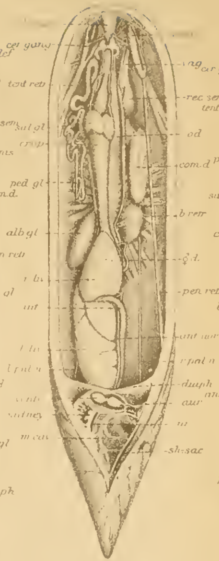
Watson del. J. Green Chromo.

APERA: EXTERNAL FEATURES.



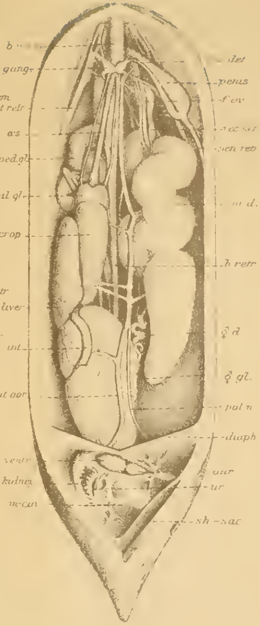
[illegible]

A g rubella



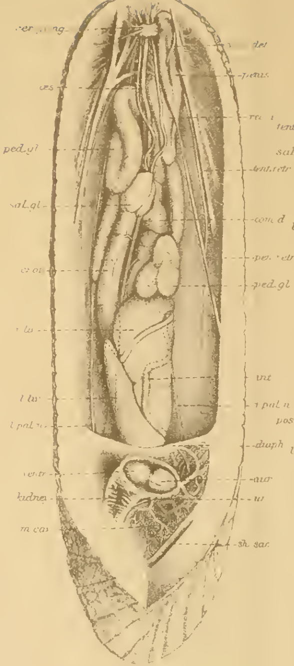
[illegible] × 5

A parva



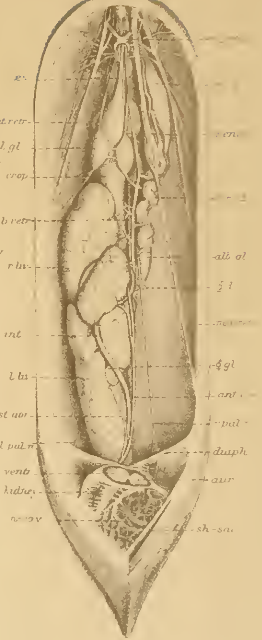
29 × 4½

A umidia



30 × 3

A burnupi.

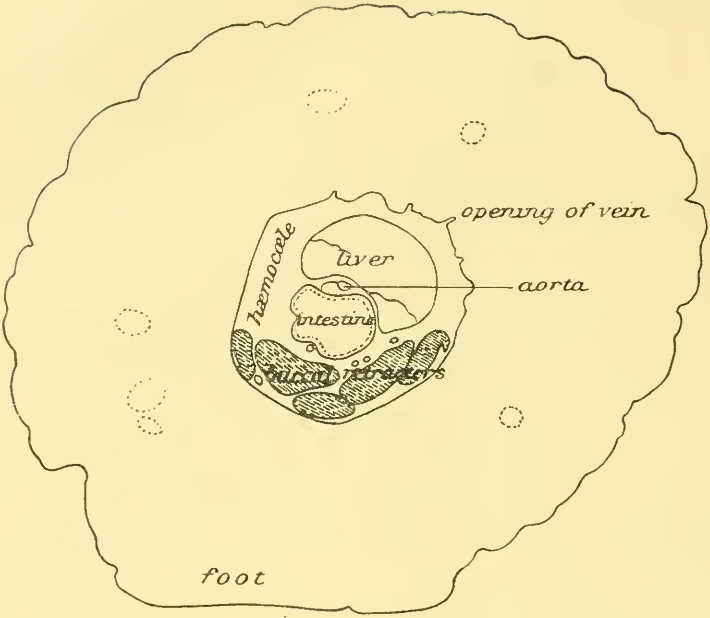


31 × [illegible]

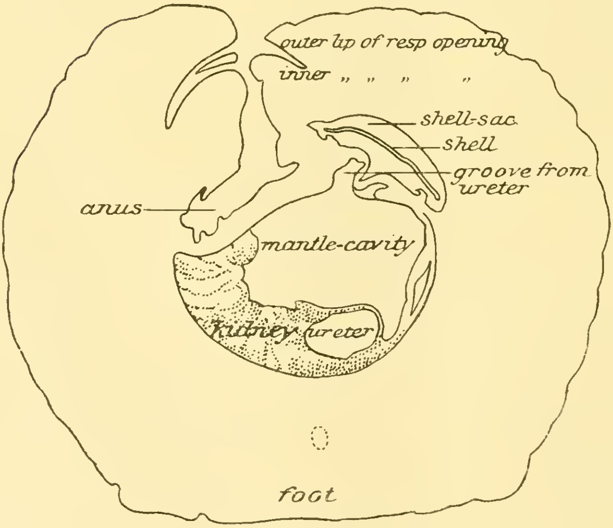
A sexangula

Apera. general dissections

Pl. X.

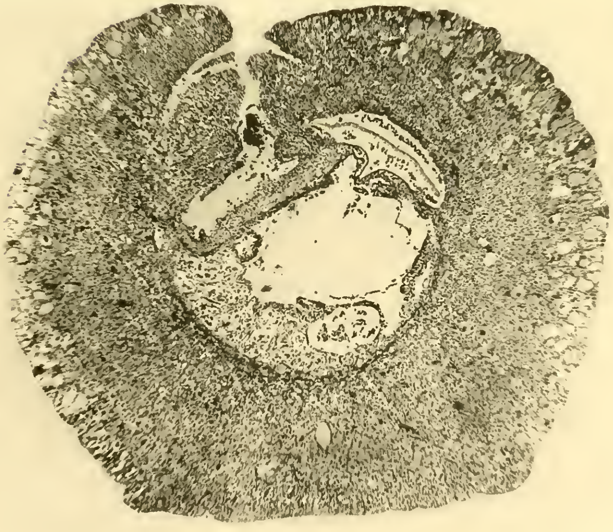

opening of vein
hæmocœle
liver
aorta
intestine
buccal retractors
foot

32.


outer lip of resp opening
inner „ „ „ „
shell-sac
shell
groove from ureter
anus
mantle-cavity
kidney
ureter
foot

33.

32.

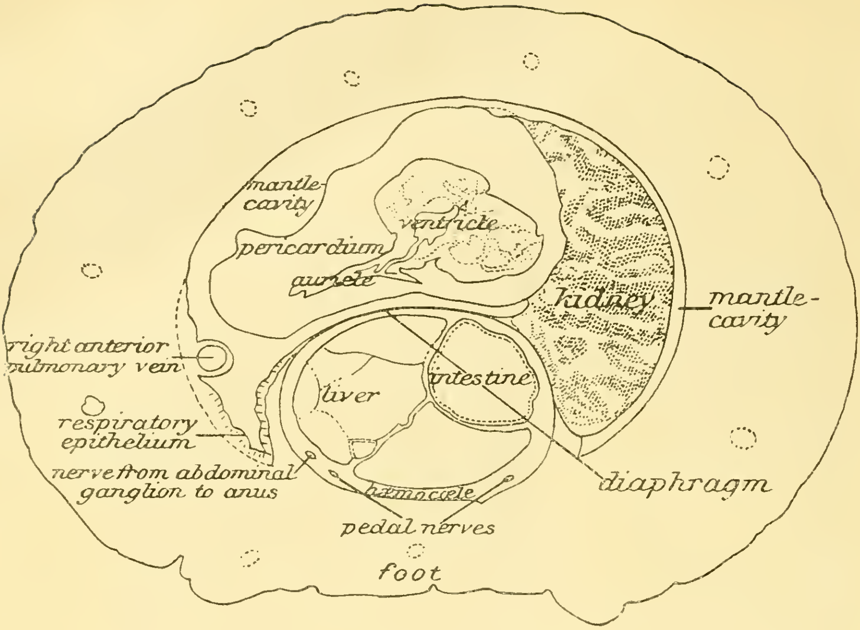


33.

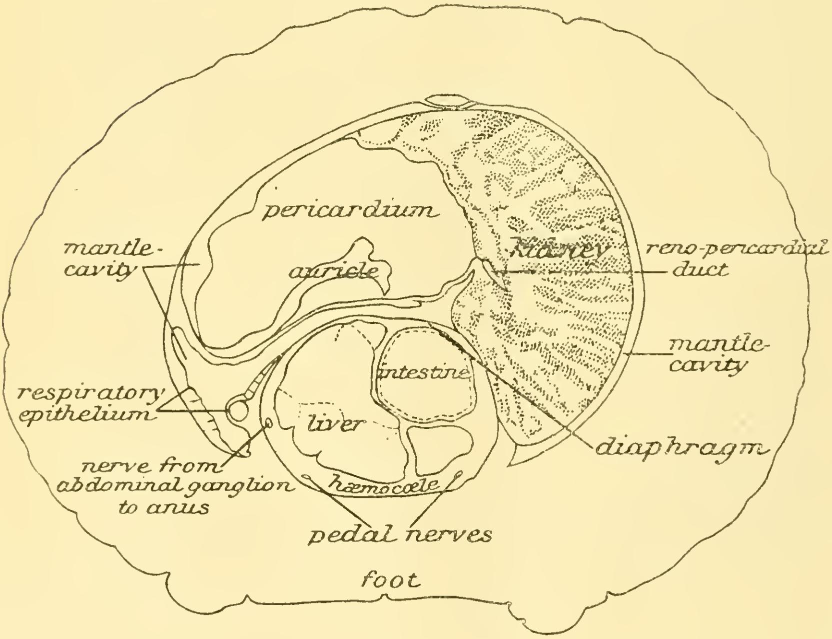
Photo. by Watson

Collotype.

Sections of *Apera gibbonsi rubella*. × 25.

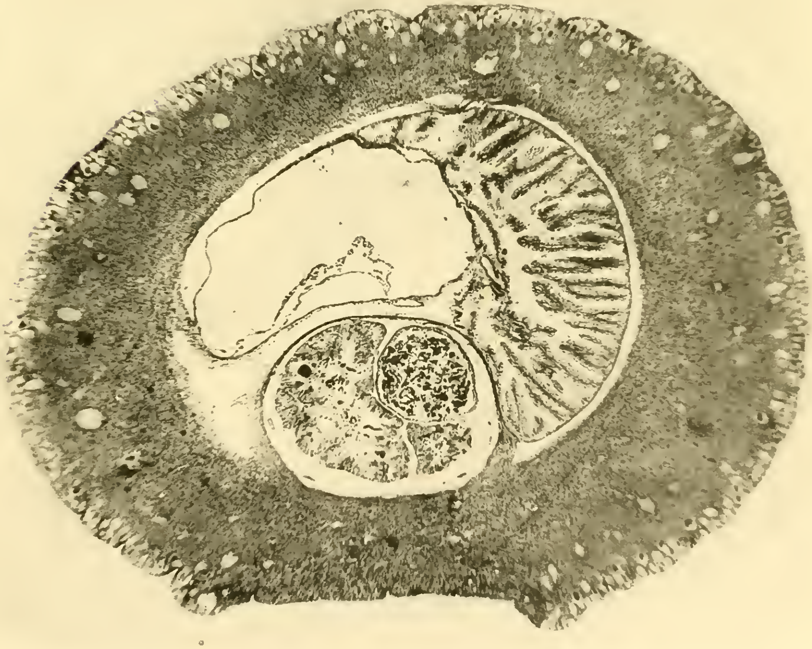

mantle-cavity
ventricle
pericardium
auricle
kidney
mantle-cavity
right anterior pulmonary vein
liver
intestine
respiratory epithelium
nerve from abdominal ganglion to anus
hæmocœle
diaphragm
pedal nerves
foot

34.


pericardium
mantle-cavity
auricle
kidney
reno-pericardial duct
mantle-cavity
intestine
respiratory epithelium
liver
diaphragm
nerve from abdominal ganglion to anus
hæmocœle
pedal nerves
foot

35.

34.

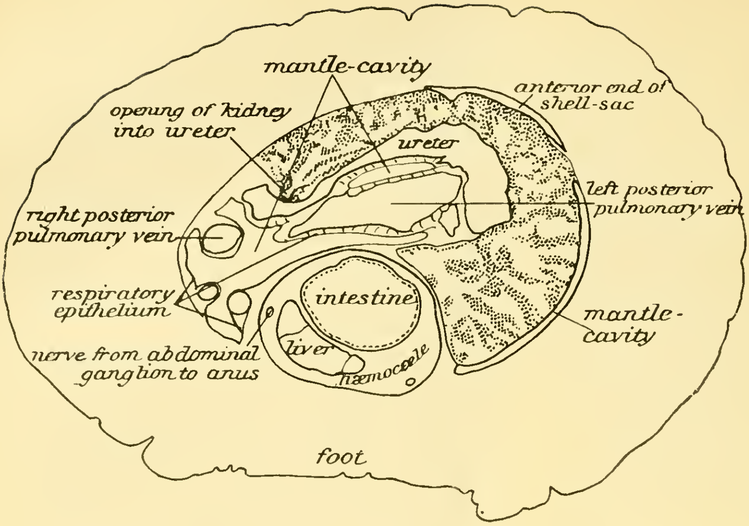


35.

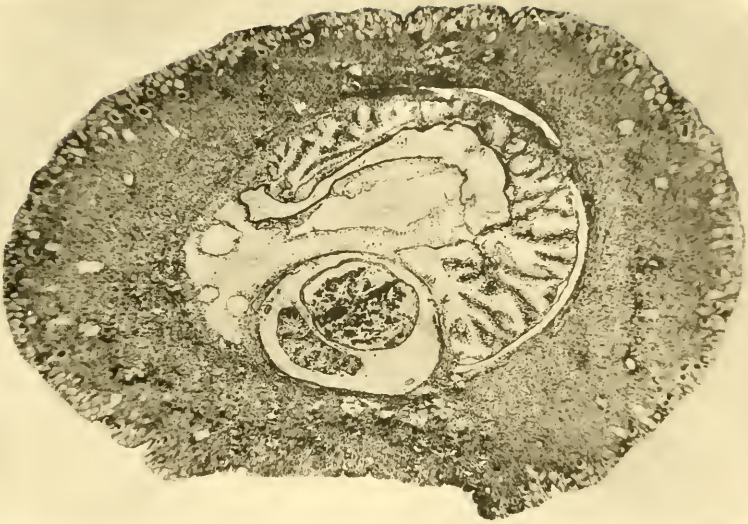
Photo. by Watson.

Collotype.

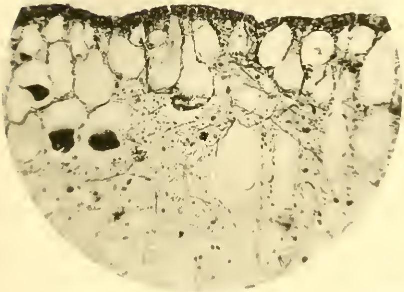
Sections of *Apera dimidia*. × 25.


mantle-cavity
opening of kidney into ureter
anterior end of shell-sac
ureter
left posterior pulmonary vein
right posterior pulmonary vein
respiratory epithelium
intestine
mantle-cavity
nerve from abdominal ganglion to anus
liver
hæmocœle
foot

36.



36, × 25.



37, × 128.
Dorsal Skin.

38, × 300.
Foot-sole.

39, × 118.
Corner of Lung.

Photo. by Watson & Tams.

Collotype.

Sections of *Apera dimidia*.

40 × 300 A. dimidia.

41 × 3 A. g. rubella.

42 × 3

43 × 4. A. g. gracilis.

44 × 6

45 × 6

A. parva

46 × 4

A. dimidia.

47 × 7

48 × 7

A. purcelli.

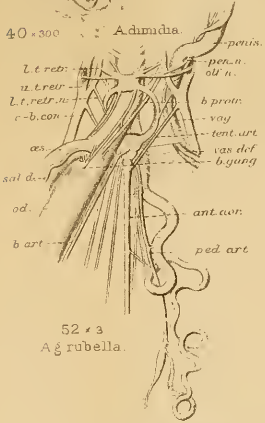
49 × 2

A. burnupi

50 × 3

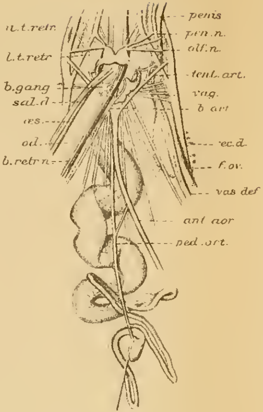
51 × 3

A. sexangula



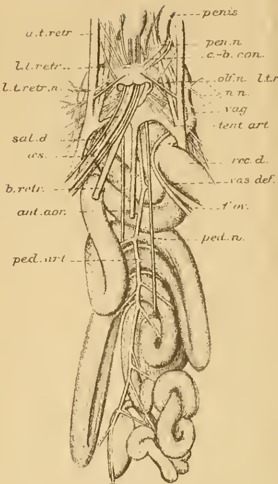
52 × 3

A. g. rubella.



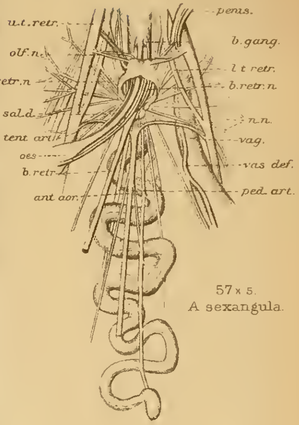
54 × 6

A. dimidia.



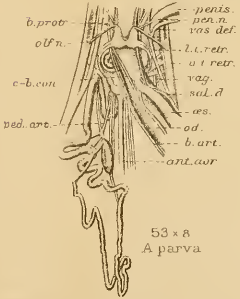
56 × 3

A. burnupi.



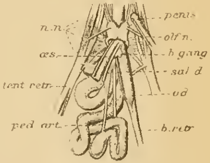
57 × 5.

A. sexangula.



53 × 8

A. parva



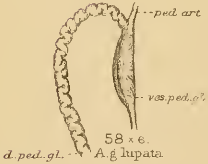
55 × 8½

A. purcelli

60 × 46

61 × 46.

A. dimidia.



58 × 6.

A. g. lupata

59 × 46

62 × 46

Apera shell, pedal gland, etc.

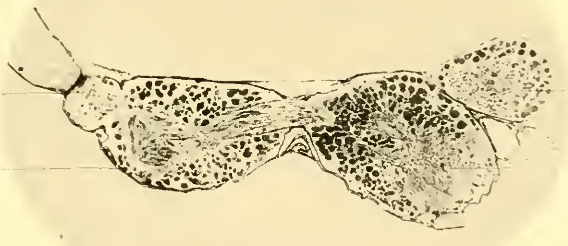
Watson del.

Huth. London

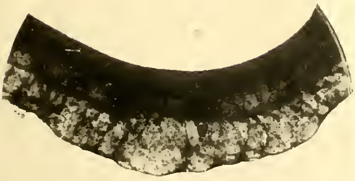
67, × 25,
A. g. rubella.

63, × 114,
A. g. rubella.

65, × 119,
A. g. rubella.

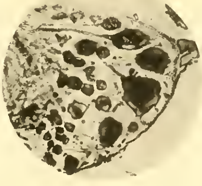


68, × 60. A. dimidia.

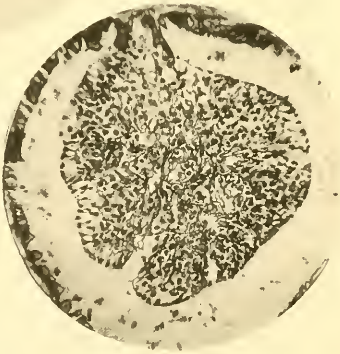


64, × 22, A. g. rubella.

Photo. by Watson.



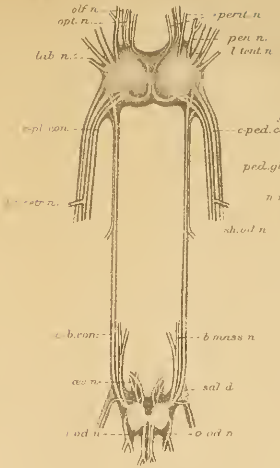
69, × 120, A. dimidia.



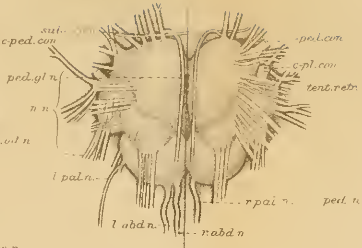
66, × 114, A. dimidia.

Collotype.

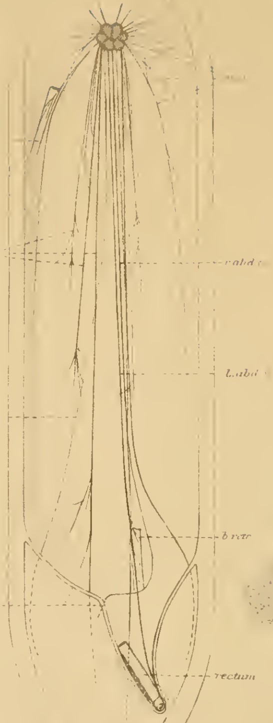
Apera : Pedal Gland (figs. 63-66) and Ventral Nerve-Ganglia (figs. 67-69).



70 × 16 A g rubella



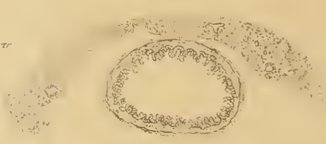
73 × 30 A dimidia. 74 × 33 A sexangula.



A dimidia

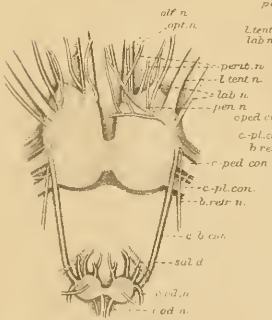
76 × 5 A sexangula

77 × 28 A g rubella

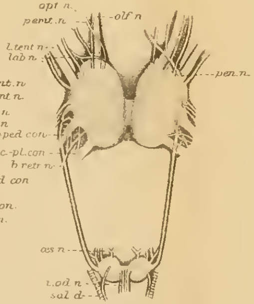


78 × 5 A g rubella

79 × 100 A g. rubella

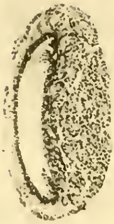


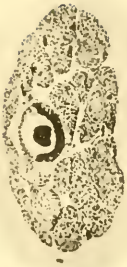
71 A dimidia



72 × 25 A sexangula

Apera nervous system, etc


80


81


82

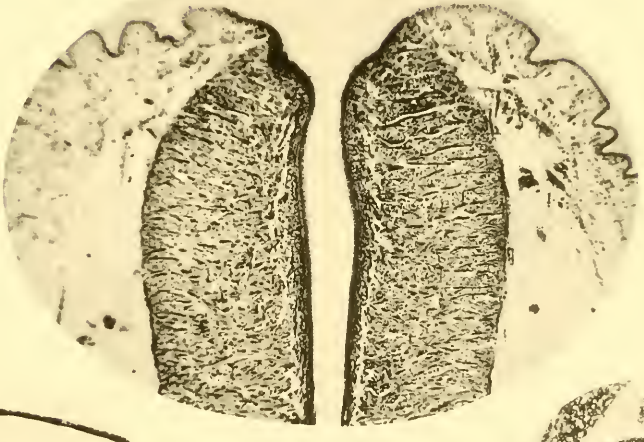

83


84

Upper Tentacle, × 50


85


86


87, Mouth, × 60


89, × 118, Radula-Sac.


90, × 118, Odontophoral Support.


88, Mouth, × 60

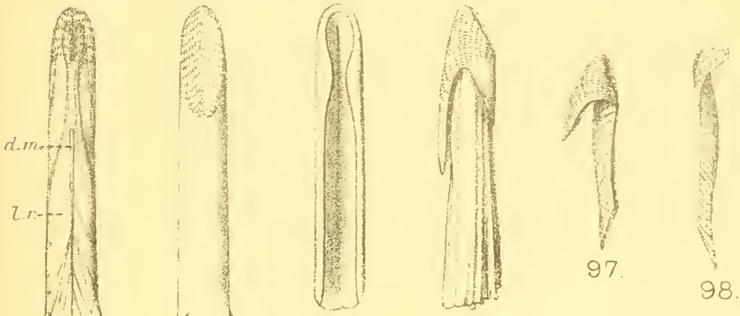
Figs. 80-86, 88-90, *A. dimidia.*

Fig. 87, *A. sexangula.*

Photo. by Watson. Collotype.

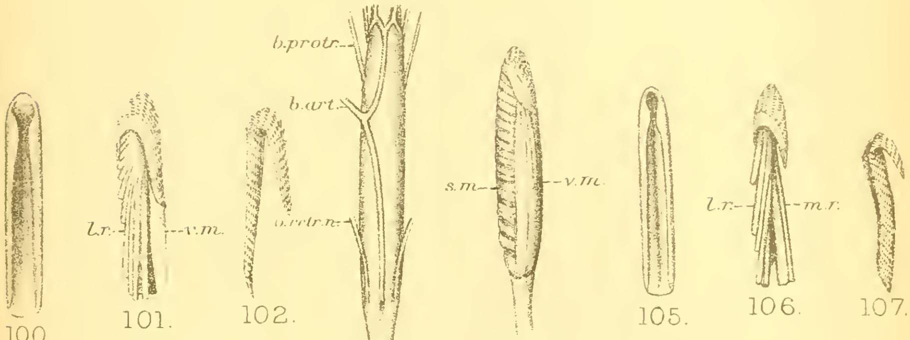
Apera : Sections of Tentacle and Buccal Mass.

91 A. gibbonsi s.s × 2⅛ 92.

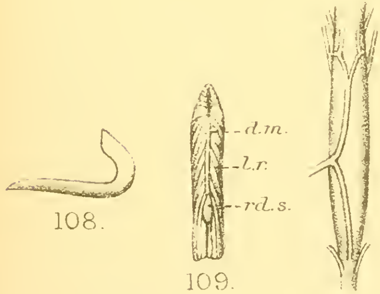


93. 94. A. g. rubella × 2. 95. 96. 97. 98.

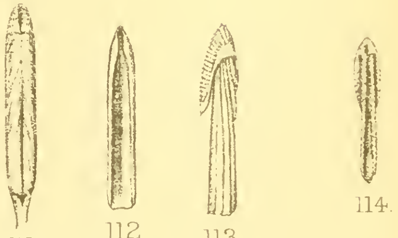
99. A. g. lupata × 3



100. 101. A. parva × 5. 102. 103. 104. A. dimidia × 6. 105. 106. 107.



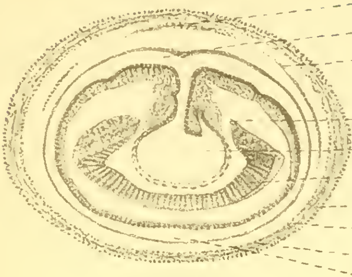
108. 109. A. burnupi × 4. 110.



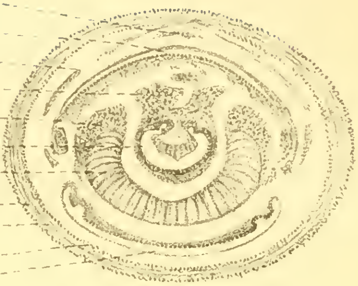
111. 112. 113. A. sexangula × 6½ 114.

Watson, del.
Huth, London.

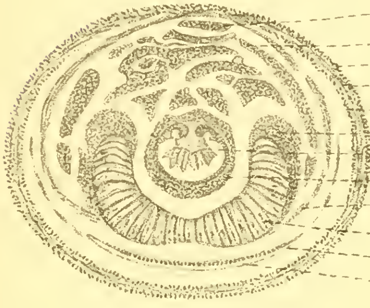
Apera odontophore.



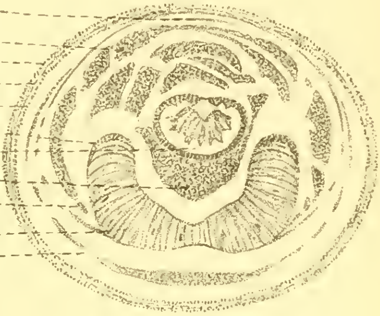
115.



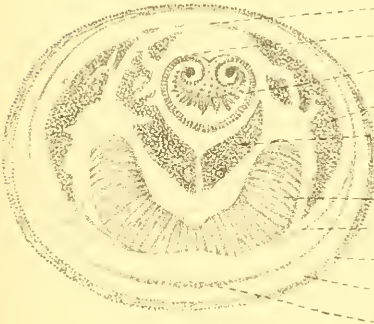
116.



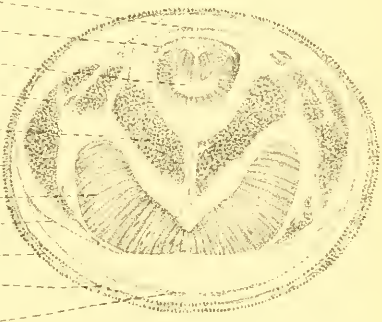
117.



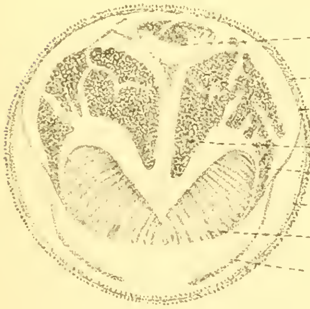
118.



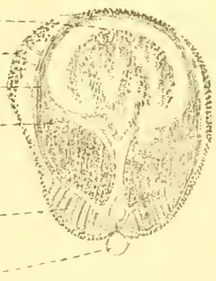
119.



120



121.

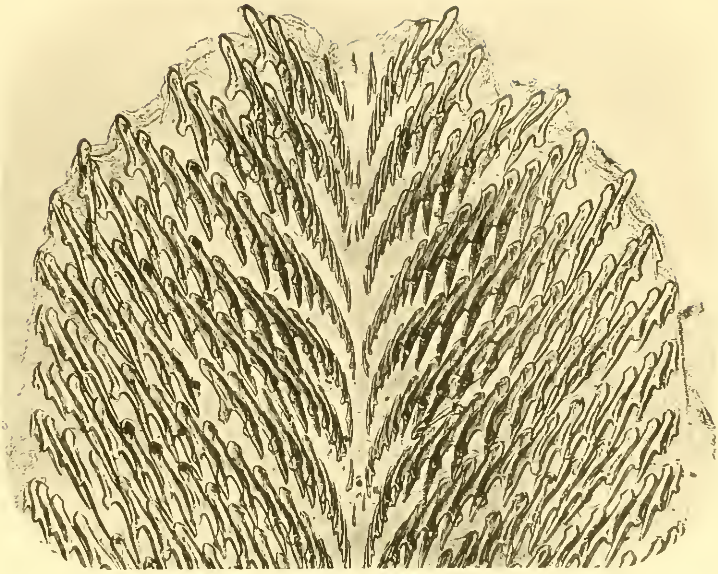


122.

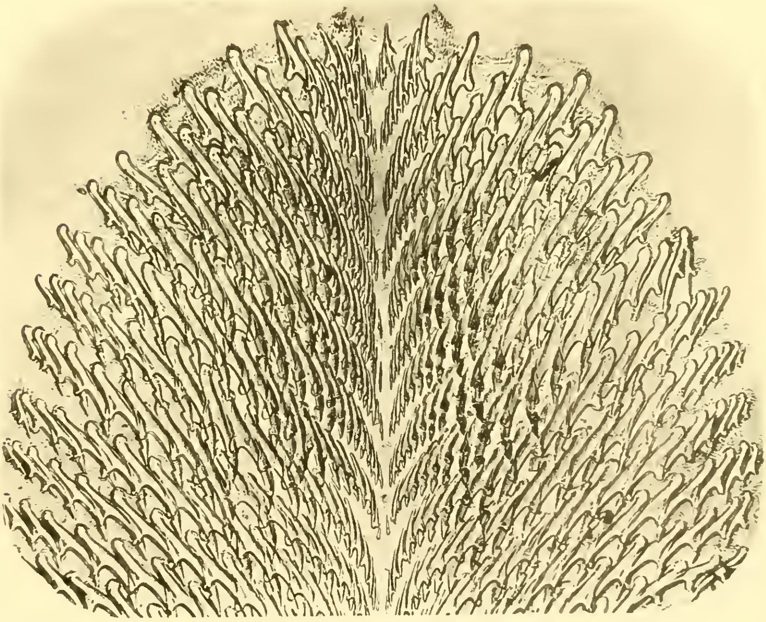
Watson del. Huth, London.

Apera dimidia: *trans. sections through the odontophore.*

× 55



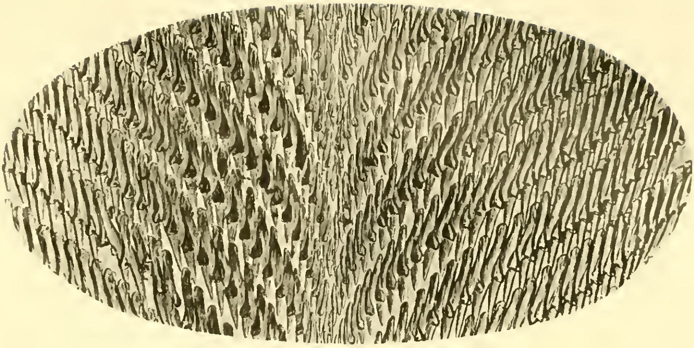
123, A. gibbonsi gracilis, × 30.



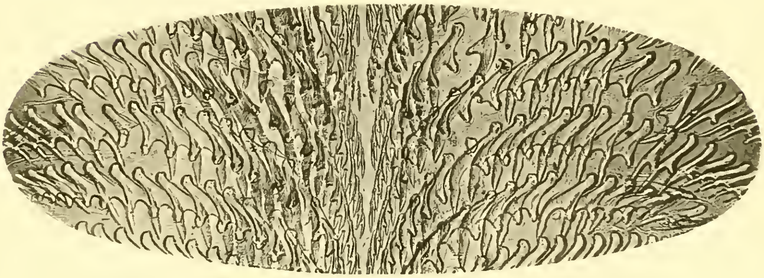
124, A gibbonsi lupata, × 30.

Photo. by Watson
Collotype.

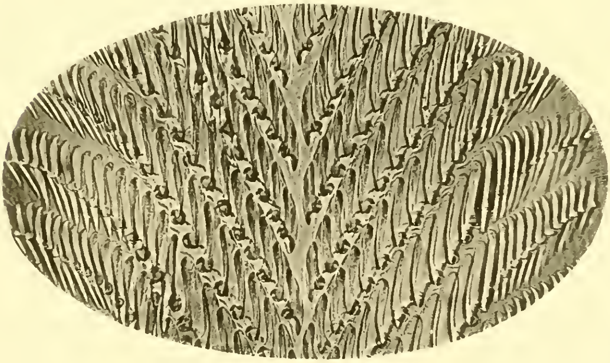
Apera : Radulæ.



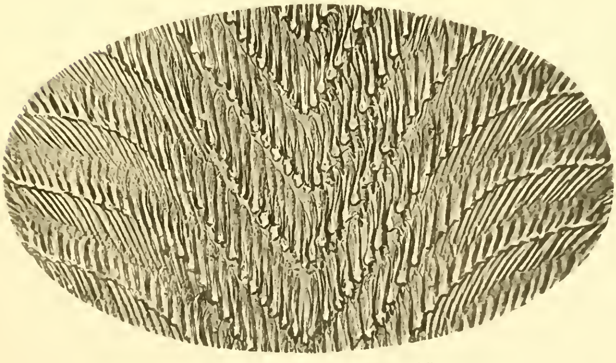
125, A. gibbonsi s.s., × 25.



126, A. g. rubella, × 25.



127, A. dimidia, × 125.

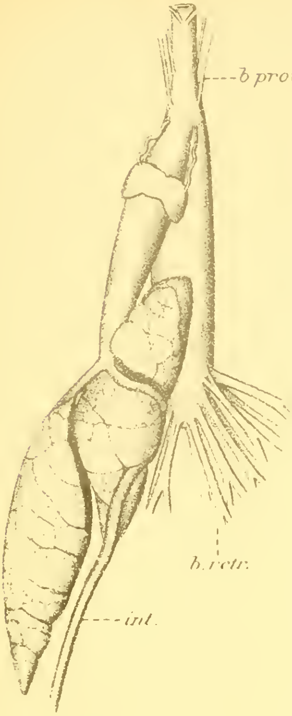


128, A. burnupi, × 125.

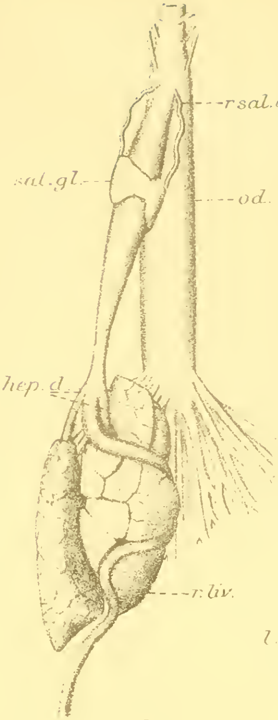
Photo by Watson.

Collotype.

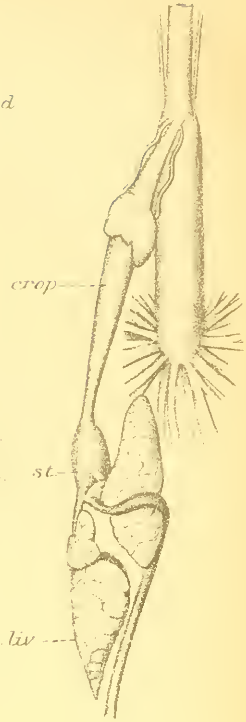
Apera : Radulæ.



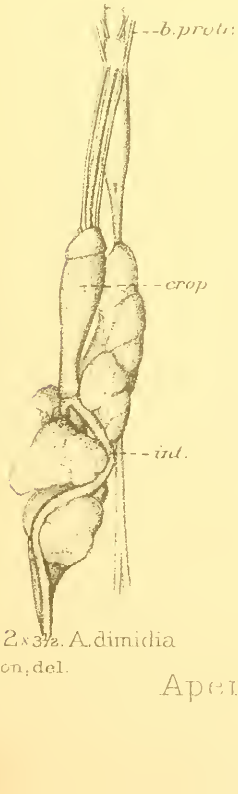
129 × 2 A. gibbonsi s. s.



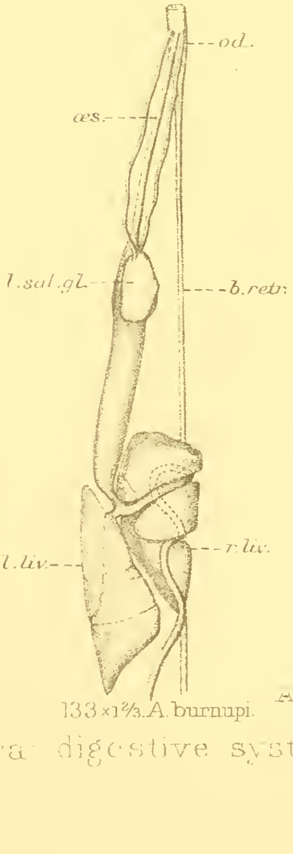
130 × 1¾ A. g. rubella



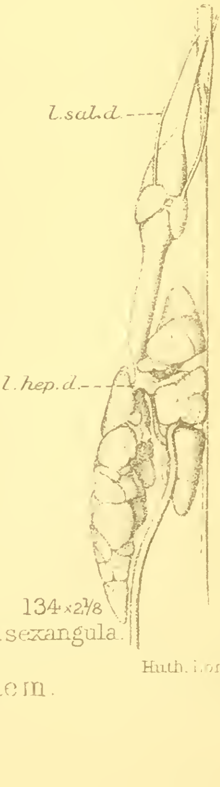
131 × 5 A. parva



132 × 3½. A. dimidia



133 × 1⅔. A. burnupi.



134 × 2⅛
A. sexangula.

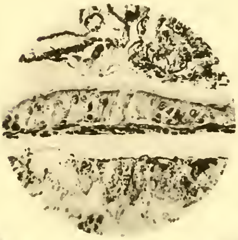
Watson, del.

Huth, Lond.

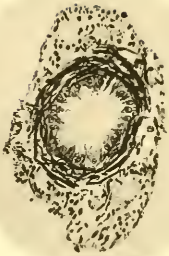
Apera: digestive system.

135, × 113,
Œsophagus.

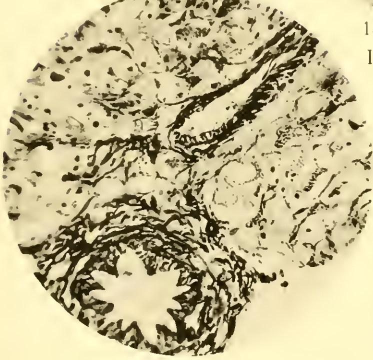
136, × 125,
Rectum.



137, × 135,
Intestine.

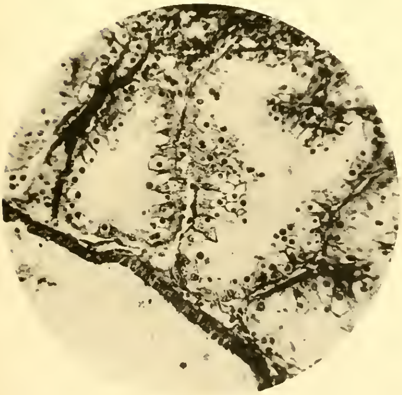


138, × 135,
Salivary Duct.

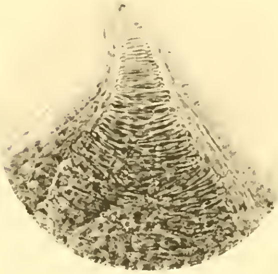


139, × 119,
Salivary Gland.

140, × 119,
Ventricle.



141, × 135,
Kidney.

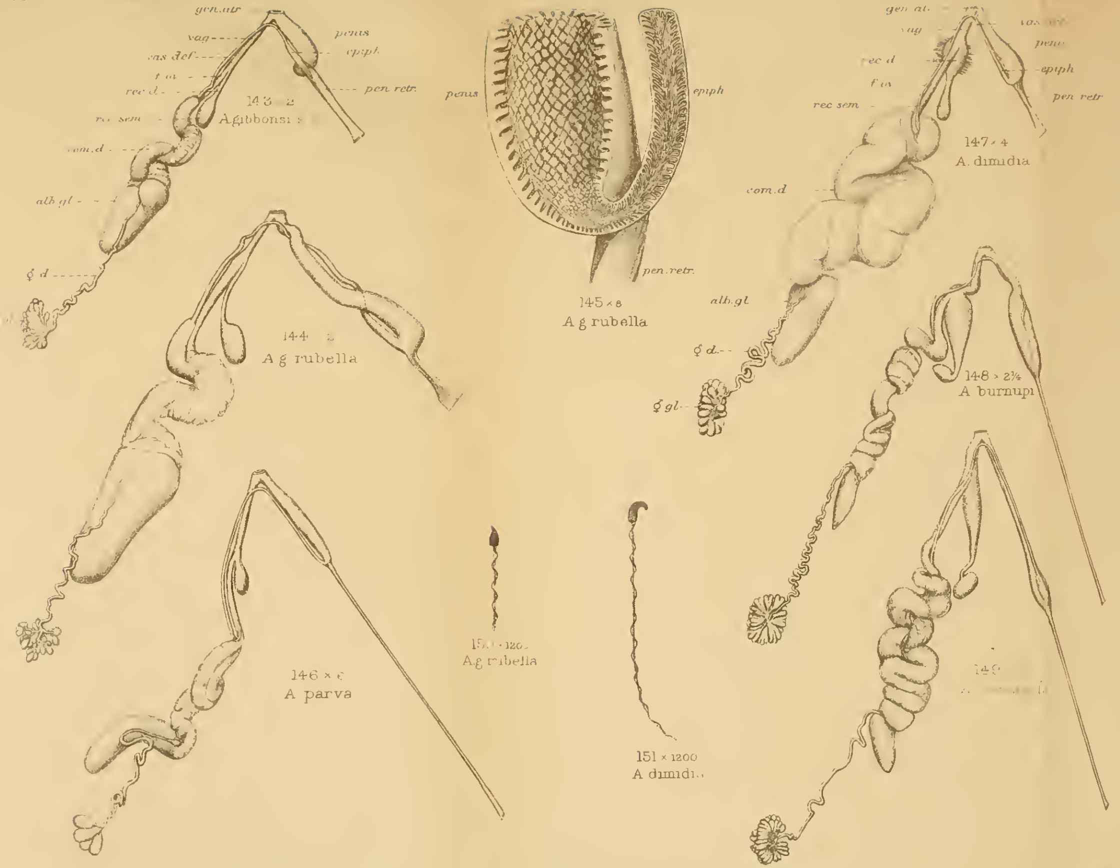


142, × 194,
Papilla
in Penis.

Photo by Watson. Collotype.

Apera : Histology.

Fig. 135, *A. sexangula* ; 136, 137, 140, 141, *A. dimidia* ; 138, 139, 142, *A. g. rubella.*



143 × 2
A. gibbonsi

144 × 2
A g rubella

145 × 8
A g rubella

146 × 6
A parva

147 × 4
A. dimidia

148 × 2¼
A burnupi

149
[illegible]

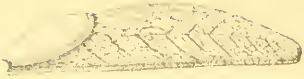
150 × 1200
A.g rubella

151 × 1200
A dimidia

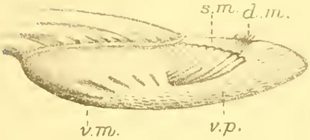
[illegible] [illegible] London

Apera reproductive organs

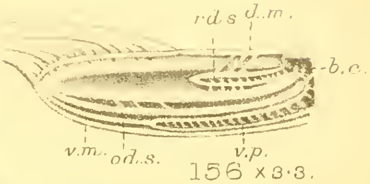
152 ×1·8.



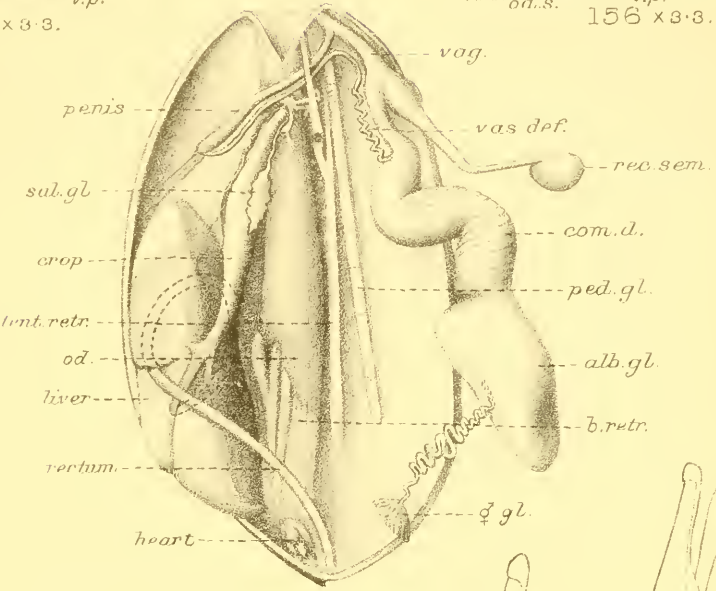
153 ×1·8.



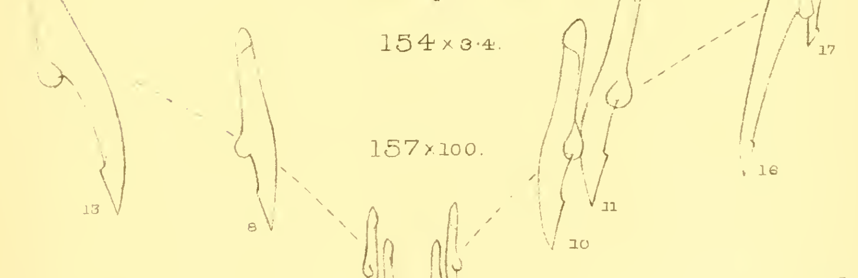
155 ×3·3.



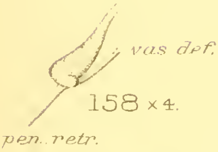
156 ×3·3.



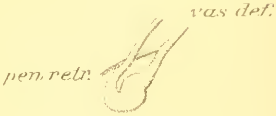
154 ×3·4.



157 ×100.

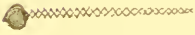


158 ×4.



159 ×4.

161 ×1·5.



160 ×1100.

162 ×1·5.

Watson del.
Huth London.

Testacella maugei; *Cape Town.*