The Anatomy of Scalibregma inflatum, Rathke.

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With Plates 13—15.

Contents.

1. Introduction.

My attention was drawn to our scanty knowledge of
Scalibregma when discussing the affinities of Arenicola
with other Polychaetes (1900,[1] p. 544). It was found impos-
sible to make any definite statement regarding the affinities
of these two genera, owing to the small amount of informa-
tion available regarding the structure of Scalibregma.
This Polychaete has received little attention from zoologists,
perhaps on account of its comparative rarity and the some-
what small size of the majority of specimens in museum
collections. Most of the references to this animal in zoolo-
gical literature are mere records of its capture. There are
only three or four memoirs which refer, quite briefly, to some
details of its structure, and only one, by Danielssen (1859,
p. 69), which contains a connected account of its internal
anatomy. This memoir contains no mention of the nephridia,
although the accompanying figures show structures which
are obviously nephridia, but which Danielssen considered to
be ovaries. He also stated that Scalibregma is hermaph-
rodite, and that its nerve-cord is provided with typical
ganglionic swellings. Subsequent authors do not throw light
on any of these matters. In these points there was such
marked difference between Scalibregma and Arenicola,
which in other respects seemed to have much in common,
that I was anxious to reinvestigate the anatomy of the
former as soon as specimens were available, chiefly with the
intention of comparing the nephridia, gonads, and nerve-cord
of these two genera. The material placed at my disposal has
enabled me to study the anatomy and histology of this
northern Annelid, and to determine some interesting points
connected with most of the systems of organs.

I am grateful to the authorities of the United States
National Museum in Washington for the loan of a number
of specimens collected on the east coast of America, and to

[1] The dates in parentheses form references to the literature quoted at the
end of this paper.

Dr. Théel, of Stockholm, and Dr. Appellöf, of Bergen, for the gift of several excellent specimens from the coast of Norway.

This work has been done in the Beyer Zoological Laboratories of the Owens College, Manchester, and in the Zoological Laboratory of the University of Edinburgh.

2. Historical Account.

Rathke (1843, p. 182) founded the genus and species Scalibregma inflatum upon specimens obtained at Molde, in Norway. He described the external characters in considerable detail, directing attention to the form of the parapodia in different regions of the body, and to the brown or black structures upon them.

Three years later M. Sars (1846, p. 91) was fortunate in securing a very large specimen (58·5 mm. long), which he described under the name Oligobranchus roseus. He has given a good account of most of the external characters of the animal, but overlooked the black structures on the parapodia. He considered this animal was allied to the newly described genus Eumenia, Oersted, and he also mentioned its general affinity with the Ariciidæ and the Arenicolidæ.

Danielssen (1859, p. 69) has given the only account of the internal anatomy of Scalibregma. The form of the alimentary canal, the circulatory system, the nervous system, the paired segmentally arranged organs—interpreted by him as ovaries,—and the structures he mistook for testes are described in considerable detail and illustrated by clear figures.

In 1873 Verrill (1873, p. 605) described the external features of a new species, S. brevicauda, which had been obtained off Newhaven, Connecticut, U.S.A., and Hansen (1882, p. 34) found among the material of the North Atlantic Expedition specimens which he referred to new species, S. (?) abyssorum and S. (?) parvum. Wirén (1887) made scattered references to some points in the structure of the alimentary canal, and the arrangement of the muscles and

the four anterior diaphragms. The other references to Scalibregma in zoological literature are mostly mere records of its capture, chiefly in Norwegian waters.

3. Distribution and Habits.

Scalibregma inflatum is recorded chiefly from the North Atlantic and Arctic Oceans; but it is not restricted to these northern seas. The " Challenger " (see McIntosh, 1885, p. 359) captured this species at two stations in southern seas, viz. at station 141, between the Cape of Good Hope and Marion Island, where numerous specimens were dredged from a depth of 98 fathoms, and at station 169, off the east coast of North Island of New Zealand, where a single specimen was obtained from a depth of 700 fathoms.

It is interesting to find that these southern specimens correspond very closely with those obtained from European seas. McIntosh states that the southern specimens are somewhat smaller than European examples, the largest one taken by the " Challenger " being 18 mm. long. This is not a character of any importance, as the size of Scalibregma varies between wide limits. Most of the northern specimens are little, if any, larger than those taken by the " Challenger." Of eleven specimens sent to me from Bergen, six are between 12 and 15 mm. long, two are incomplete but would probably be about 13 and 20 mm. long ; the other three are 26, 35, and 56 mm. long respectively, while eight of the ten complete specimens from the east coast of the United States are between 5 and 9 mm. long. McIntosh remarks that the gills of southern forms are smaller than those of Norwegian examples; but this, again, is a very variable character, depending on the age and size of the specimen. We may conclude, therefore, that the specimens of Scalibregma obtained by the " Challenger " are not distinguishable by any essential and constant character from those taken in the North Atlantic.

S. inflatum occurs in the Arctic Ocean as far eastward as

Cape Grebeni (the southern point of Waigatsch Island) and the Sea of Kara (Théel, 1879, p. 51). It is found off the western shores of Spitzbergen (Malmgren, 1867, p. 77; von Marenzeller[1]), Nova Zembla (von Marenzeller,[2] Théel, 1879, p. 51), and along the western coast of Norway as far southwards as the island of Floroë (Rathke, Sars, Danielssen, Malmgren, Appellöf[3]). Scalibregma is also recorded from the south-western coast of Sweden. Sars[4] found several small examples in Christiania Fjord, and Malm[5] soon afterwards obtained specimens near Göteborg.

Scalibregma occurs on the north, east, and west coasts of Scotland, being recorded from the Shetlands,[6] from St. Andrews,[7] and from Loch Maddy in the Hebrides by McIntosh, and from near Millport in the Firth of Clyde by Kölliker.[8] The last named is the most southerly European station from which Scalibregma has been obtained.

On the western side of the Atlantic this Polychæte has been taken off the western shores of Greenland (McIntosh[9]), and at several stations off the eastern coast of North America, between George's Bank, off Nova Scotia, and Newhaven,

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[1] "Spitzbergische Anneliden," 'Archiv für Naturgeschichte,' 55 Jahrg., p. 129, 1889.

[2] "Die Coelenteraten, Echinodermen, und Würmer der K. K., Österreichisch-Ungarischen Nordpol Expedition," 'Denkschriften der Matem. Naturw. Classe der Kaiserl. Akad. der Wissenschaften,' xxxv, 1877.

[3] "Faunistiske Undersogelser i Herlofjorden," 'Bergens Museums Aaresberetning,' p. 10, No. 11, 1894–5.

[4] 'Bidrag til Kundskaben om Christianiafjordens Fauna,' III, p. 46. Christiania, 1873.

[5] 'Zoologiska Observationer,' p. 88, Kongl. Vet. o Vitt. Samhällets i Göteborg Handlingar. Göteborg, 1874.

[6] "Report on Annelida dredged off Shetland Islands by Mr. Gwynn Jeffreys," 'British Assoc. Report for 1868,' p. 336. London, 1869.

[7] "On the Annelids of St. Andrews," 'British Assoc. Report for 1867,' p. 92. London, 1868.

[8] 'Wurzbürger Naturwiss. Zeitschr.,' p. 243. 1864.

[9] "Annelida obtained during Cruise of H.M.S. 'Valorous' to Davis Straits," 'Trans. Linnean Soc., Zoology,' second series, vol. i, p. 506. London, 1879.

Conn. (Verrill [1]). The specimens sent to me by the Smith-
sonian Institution were taken at four stations off this coast,
the most northerly one being off Nova Scotia, and the most
southerly in latitude 40° N.

Although Scalibregma is found in some places in con-
siderable numbers in shallow water (as in some of the fjords
of Nordland (see Danielssen, 1859, p. 25), it is more usually
obtained by dredging, and sometimes from considerable
depths. Those from the Smithsonian Institution were all
obtained at depths varying from 43 to 99·5 fathoms, and
the " Challenger " specimens were dredged from 98 and 700
fathoms respectively.

Scalibregma burrows in sand, which is often more or less
intermixed with mud or clay, to a depth of one or two feet,
forming long passages which in some places, as in the fjords
of Nordland, are accessible at low water (Danielssen, p. 25).
In its mode of life it evidently strongly resembles the common
lugworm (Arenicola marina) of our coasts.

4. External Characters (13 Pl.).

The general aspect of Scalibregma inflatum may be
described as arenicoliform, but its shape varies considerably
in different individuals. The anterior end of the animal is
short, and resembles a truncated cone (fig. 1). The following
region of the body is inflated to a greater or less degree, the
inflation extending sometimes over only four or five seg-
ments, but more generally comprising about ten segments.
The swollen portion is either globular or more or less cylin-
drical. In many cases, especially in the smaller specimens,
the body swells out abruptly about the fifth or sixth segment,
decreasing in diameter almost as suddenly at the end of the
inflated portion; but in most of the larger specimens there
is a much more gradual transition from the inflated portion
to the regions in front of and behind it, as shown in fig. 1.

[1] " New England Annelida," ' Trans. Acad. of Arts and Sciences,' vol. iv,
Part 2. Newhaven, 1882.

Behind the swollen portion the body tapers gradually to the posterior end.

The animal is strongly convex above but flattened below. There is a depressed area along almost the whole length of the mid-ventral line (marking the position of the nerve-cord), which is divided by transverse grooves into a series of squarish or hexagonal areas (fig. 2). In some specimens the position of the œsophageal connectives is also marked externally by two shallow depressions, the metastomial grooves, which pass round the mouth and unite at the anterior end of the mid-ventral groove.

The head or prostomium is distinct and well developed, forming a somewhat quadrangular mass overhanging the mouth, and bearing at each side anteriorly a short rounded tentacular process (fig. 3).

Immediately behind the head there is an achætous peristomial segment, composed of two annuli. The rest of the body of the animal is divided into segments bearing parapodia. Each of the first three chætigerous segments is composed of three annuli, the middle annulus bearing a prominent pad on each side, from which the neuropodium and the notopodium arise. All the following fully-formed segments of the body are divided into four annuli, on the third of which the parapodia are borne (figs. 1, 2). In the large specimen, 56 mm. long (fig. 1), sixty-one segments (in addition to the peristomium and pygidium) may be distinguished. The parapodia are clearly visible on all the segments up to and including the fifty-third; those of the next four segments are very small, the dorsal cirrus being the only easily visible appendage. The last four segments of the animal are divided from one another only by faint grooves, and do not bear parapodia. Following these there is a very short terminal portion or pygidium, which even in large specimens is only about ·3 mm. long. There are four pairs of branched shrubby gills, situated immediately behind the notopodia of the second, third, fourth, and fifth chætigerous segments (for further description of the gills see p. 262).

Apertures.

The mouth is a wide transverse ventral slit between the
peristomium and the first chætigerous segment. It is overhung
by the prostomium, and is bordered anteriorly and poste-
riorly by papillæ (fig. 2). The pharynx, when fully pro-
truded, is smooth and globular.

The anus is terminal, and surrounded by four slender
anal cirri, two on each side, situated somewhat ventro-
laterally (fig. 6). In one specimen there are five cirri, there
being three on one side and two on the other, but this is
evidently abnormal. In full-grown specimens the cirri are
are about ·8 to 1·0 mm. long, and ·05 to ·06 mm. thick.
There is a small protuberance on each side of the mid-ventral
line of the pygidium, from which the two cirri arise.

The nephridiopores are exceedingly minute and diffi-
cult to see. The first nephridium opens on the fourth
chætigerous annulus, but as this nephridium is very small its
opening can usually be found only in sections. The second
nephridium is a little larger, but its opening is almost equally
difficult to find. The apertures of the succeeding nephridia,
while being small, are however visible in cleared preparations,
and occasionally in surface view of favourable spirit prepara-
tions. Each nephridiopore is a minute oval aperture, situated
ventral and anterior to the neuropodium of the segment on
which it opens (fig. 5). The aperture is close to the anterior
border of the chætigerous annulus, and it is often obscured
by lying in the groove which separates this annulus from
the preceding one. In the most favourable specimens in my
possession the largest nephridiopores are only about ·06 mm.
in diameter. Towards the posterior end of the animal,
where the nephridia become smaller, the nephridiopores
become correspondingly more difficult to see in surface view,
although they may be distinguished in sections in each seg-
ment almost to the posterior end of the worm. In a specimen
13·6 mm. long the last visible nephridiopore is only 1 mm.
from the posterior end of the animal.

At each side of the prostomium there is a narrow longitudinal slit (fig. 3), which leads downwards, backwards, and inwards into the nuchal organ (for description see p. 269).

There are small structures on the body-wall situated in each segment about midway between the notopodium and neuropodium. At first sight they are liable to be mistaken for apertures, and Levinsen (1883, p. 133) suggested that they were sexual openings. On further examination each of these proves to be a depression, from the floor of which a small elevation arises, the apex of which may be seen a little below the level of the mouth of the pit (figs. 1, 4, 5, *S. O.*). These structures are best seen in the segments just behind the branchial region, but on careful examination they may be seen in all the chætigerous segments of the animal. Sections prove that these are lateral sense organs, similar to the " Seitenorgane " described by Eisig (1887) in the Capitellidæ. A detailed description may be found on p. 270.

Size.

Scalibregma inflatum varies in size between wide limits. Of the twenty-two complete specimens in my possession the smallest is 5 mm. long, and the largest 56 mm. long and 10 mm. broad at its widest part. The latter is one of the largest specimens yet recorded (fig. 1). Sars's specimen was 58·5 mm. long and 5 mm. broad at its widest part ; and Rathke's example was one inch and seven lines (about 40 mm.) long and 5 mm. broad. In the specimen 56 mm. long there are sixty-one segments, and a very short pygidium (about ·3 mm. long). Parapodia are clearly visible on the first fifty-three segments, but those of the succeeding segments are very small, or absent altogether. It is interesting to note that in Sars's specimen there are also sixty to sixty-one segments. One of my specimens 35 mm. long contains ova which appear to be almost ripe, so that the animal reaches maturity when little more than half its maximum size.

Colour.

Sars has recorded the colour of his living specimen. The

general colour of the body was vermilion red, the parapodia being light yellow, and the gills blood-red. Rathke's specimens were greenish grey or dirty greenish yellow in colour. My spirit specimens are a pale yellowish brown, due to the large number of yellowish granules in the epidermal cells.

5. Parapodia (Pl. 13).

Each of the parapodia throughout the body is clearly divided into a notopodium and a neuropodium, which closely resemble each other in shape and size. In the anterior fourteen or fifteen segments the parapodia consist simply of two blunt conical mammillæ, each bearing a bundle of setæ. Those of the first five chætigerous segments are situated upon large elevations, each of which is borne chiefly by the chætigerous annulus, but also partly by the annulus before and the one behind it. There are also elevations supporting the parapodia of the next nine or ten segments, but they are smaller than those just described (fig. 1). The parapodia of the anterior portion of the body (as far back as the fourteenth or fifteenth segment) are comparatively small, and the setal prominences, which are bluntly conical, project only a little way from the body-wall. In the succeeding segments the parapodia gradually increase in size, and each is supported upon a flattened base, the two rami of the parapodium and the basal outgrowth forming a large lamella, projecting at right angles to the body (fig. 8).

The notopodium of the sixteenth segment of most specimens bears a small cirrus (*Cirr. D*, fig. 1), and in one or two examples a small dorsal cirrus is also present above the notopodium of the fifteenth segment. The parapodia of the fully developed segments behind this bear both dorsal and ventral cirri. The cirri of the middle part of the body are short, blunt conical outgrowths, but further back they become lamelliform or digitiform structures.

Near the posterior end of the animal the parapodia and cirri are small, and on the last three or four segments, which

are divided from each other only by shallow grooves, parapodia have not yet been formed (fig. 6). Just in front of these there are a few segments (about four) in which the parapodia have only been recently formed, and in these the dorsal cirri are considerably larger than the ventral ones,—in fact, the latter have not yet appeared in some segments which possess dorsal cirri of moderate size. The dorsal cirri are thus formed before the ventral ones. The notopodium and a few of its setæ are formed before the neuropodium appears.

The cirri are sensory structures, and from their earliest appearance are supplied with stout branches from the lateral nerves given off in each segment from the ventral nerve-cord (Pl. 14, fig. 16).

On each cirrus, a little behind its tip, there is a distinct darker area, which is somewhat oval, reniform, or pyriform in shape (fig. 8). In most specimens this area is very obvious, on account of its brown or black colour, but in some its colour is much lighter. This is not a structure separate from and standing out from the cirrus, as the description by Rathke (pp. 185, 186) would lead one to believe. The darker appearance of this portion of the cirrus is due to the presence within it of a collection of special gland-cells, the dark-coloured glandular mass being visible through the semi-transparent walls of the cirrus. Rathke examined and reported on these dark masses in considerable detail, and rightly inferred that they are similar in structure to the black or brown spots on the notopodia of Nereis dumerilii, which he had described on a previous page as glandulai (Hautdrüsen). Sars does not mention them, but Danielssen (p. 75) re-examined them, and came to the conclusion that they are testes, as they are composed of a large number of somewhat coiled tubes, filled with minute elongate bodies, which he took to be " zoosperms." Rathke's interpretation is the correct one; these dark bodies are parapodial glands, the secretion of the cells of which is in the form of minute slender rods (see p. 248). McIntosh (1885, p. 360) remarks that these curved bodies in the parapodia of Scalibregma

are probably homologous with those described by Kölliker and Greef in Ephesia (Sphærodorum).

The cirri arise as solid outgrowths of the epidermis. From their earliest appearance they contain gland-cells, which at first are similar to the ordinary flask-shaped or club-shaped glandular cells found in the epidermis of the squarish elevations of the skin seen in the anterior third of the animal (see p. 252 and fig. 12). The gland-cells of the cirri are at first pear-shaped or club-shaped, and only about 10—12 μ long. They stain deeply with hæmatoxylin, and each has a well-marked nucleus. The secretion is at this time of a finely granular nature. As the cirri increase in size the gland-cells elongate, and when the latter become 30—40 μ in length, their secretion is then clearly seen to be in the form of exceedingly thin rod-like bodies. The cells continue to elongate, and in worms only about 15 mm. long the gland-cells are rather more than ·1 mm. long (fig. 10). The greater part of each cell is occupied by a bundle of fine rods, but in favourable specimens the nucleus may be seen towards the rounded inner end of the cell. There is a small amount of connective tissue around the bases of these rod-secreting cells. In the largest specimens at my disposal, 35 mm. and 56 mm. long respectively, the gland-cells are twisted, and so closely packed together that it is almost impossible to determine the limits of the individual cells. They form a compact, deeply staining mass, situated a little behind the tip of the cirrus (fig. 8).

The very fine-pointed ends of the gland-cells open on the free surface of the epidermis. On examination of medium-sized specimens it is seen that most of the glands of the notopodial cirrus open on its dorsal side, while those of the ventral cirrus open chiefly on the ventral wall (fig. 9).

The rods are at first short, and there are comparatively few in each cell, but later they are much more elongate, and present in large numbers in each cell. In the largest specimen (56 mm. long) the fully formed rods are 40—50 μ in length, and about 3 μ in width at their widest point. They

are spindle-shaped, and taper gradually from about the
middle, where they are thickest, to their very fine-pointed
ends. They are sometimes straight, but more usually are
somewhat curved, sinuous, or twisted (fig. 11). These pecu-
liar glands are not strictly confined to the cirri. In four of
the specimens which have been cut into sections there is,
just below each of the neuropodia of two or three of the
anterior segments (ranging from the third to the sixth), a
collection (or sometimes two) of deeply staining cells in the
epidermis. Each of these cells contains a bundle of rods
exactly like those above described from the parapodial
glands. In two or three cases there is a small bundle of
these rod-forming cells, either in or immediately below the
epidermis, near the terminal portion of the first or second
nephridium. Claparède (1868, p. 15) has noticed the con-
nection of similar rod-containing cells with the excretory
pores in certain Hesionids.

Rod-secreting glands similar to those of Scalibregma
are known to occur in the skin and subepidermal tissues of
a large number of Polychætse. Claparède has described
almost indentical structures (" bacilliparous follicles ") in the
cirri of Phyllodoce, sp. (1863, pl. xi, figs. 19, 20), in
papillæ on the neuropodia of Aricia fœtida (1868, pl. xx,
figs. 2 B, 2 C), in Nereis cirratulus, especially in the
parapodia and their appendices (1868, pl. xxiv, fig. 1 L).
A very useful series of figures of these glands, some original
and others collected from various authors, is given by Eisig
(1887, pl. xxxvii).

6. SETÆ (Pl. 13, fig. 9, and Pl. 15, figs. 25, 26).

Both Rathke and Sars described the setæ of Scalibregma
as simple, fine, capillary bristles, and they quite overlooked
the peculiar furcate setæ which are present in both divisions
of the parapodia throughout the body. Hansen (1882, p. 34)
first observed these curious setæ in the ventral fascicles of
S. (?) abyssorum, S. (?) parvum, and in S. inflatum.

The setæ of S. inflatum are lodged in sacs in the para-
podia, and the tips of the bristles project beyond the promi-
nent lips of these setal sacs. On first examining a para-
podium only the simple capillary setæ are seen, but after
rendering the tissues more transparent by treatment with
warm potash solution the furcate setæ become visible. The
simple setæ project a long way beyond the mouths of the
setal sacs, being exposed for quite half their length, while
the furcate setæ are almost entirely enclosed, only their fine
tips protruding from the mouths of the sacs (fig. 9).

The setæ of a parapodium may be divided into four groups,
there being one group or row of simple setæ and one of
forked setæ in each notopodium and neuropodium. The
simple setæ of the notopodium and neuropodium form two
straight fascicles, projecting from the parapodium in almost
parallel or in very slightly diverging lines; but the furcate
setæ lie in two bundles, which are usually placed so that while
their proximal ends are adjacent their tips are widely diver-
gent, those of the notopodium being directed dorso-laterally,
and those of the neuropodium ventro-laterally. The bundles
of furcate and simple setæ form two almost vertical and
parallel rows in each ramus of the parapodium. The row of
forked setæ is usually the more anterior.

The simple setæ are fine capillary structures, attaining a
length of about 1·7 mm. in the largest specimen (56 mm.
long). They are about 8 μ in diameter at their inner ends,
where they are thickest, and taper gradually to a very fine
point. They are marked in their proximal portion by very
minute longitudinal ridges and furrows. Those setæ which
have not been worn by use bear exceedingly minute hair-like
processes on their distal third (fig. 26).

The length of the furcate setæ is generally about three
fourths that of the simple setæ of the same parapodium. In
the specimen, 56 mm. long, they reach a length of 1·2—1·3
mm. They are considerably stouter than the simple setæ,
being 15—18 μ in thickness at their inner ends. They taper
gradually to the base of the fork, their diameter at this point

being only 6—8 μ (fig. 25). The prongs of the fork are sometimes straight, but more usually curved, their very fine tips pointing away from each other. The two rami are not quite equal; in the largest specimens they are 50—65 μ and 65—75 μ in length respectively. The proximal portion of the edge of each prong bears a number of minute curved pointed processes.

In the large worm (56 mm. long) there are fifty to sixty simple setæ, and about twenty to twenty-four furcate setæ in each ramus of the parapodium of the anterior half of the animal.

On clearing the posterior end of another specimen by treatment with warm potash solution the very small setæ present in the newly formed parapodia are seen. Each of the notopodia and neuropodia in this region bears only one or two simple setæ, accompanied by one furcate seta. Both kinds of setæ are therefore present in the parapodia through-out life.

Furcate setæ were first discovered by Malmgren (1867, p. 187) in Eumenia crassa, and were shortly afterwards observed by McIntosh (1868, p. 419, and pl. xvi, fig. 5) in Eumenia (Lipobranchius) jeffreysii. Théel (1879, p. 49, and pl. iii, fig. 47a) figures them in Eumenia longisetosa, and Hansen (1882, p. 34, and pl. v, figs. 16—19) in Scali-bregma inflatum, S. (?) parvum, and S. (?) abyssorum; but the figures of these authors do not show the minute barbules on the inner side of each prong. McIntosh (1885, pl. xxii A, fig. 21) saw the barbules on both prongs of the forked setæ of his southern specimens of S. inflatum, and figured similar setæ from Eumenia reticulata (1885, p. 360, and pl. xxii A, fig. 20), and S. Joseph (1894, p. 106, and pl. v, fig. 133) has observed them in Sclerocheilus minutus.

The furcate bristles of Eumenia glabra described by Ehlers (1887, p. 170, and pl. xlv, fig. 4) are remarkable for the great inequality in length of the prongs, one being nearly three times the length of the other. Ehlers (1887, p.

127, and pl. xxxviii, fig. 6) has also figured from Nephthys inermis a forked seta, which is similar to those of Scalibregma, except that the two prongs of the fork are equal in length in the former.

Furcate setæ are also known to occur in the Ariciidæ, having been described by McIntosh (1879, p. 504, and pl. lxv, fig. 7) in Aricia greenlandica, by S. Joseph (1894, pl. v, fig. 116, and 1897, pl. xxi, fig. 172) in A. latreillii and A. lævigata, and by Cunningham and Ramage (1888, pl. xxxviii, fig. 7 E; pl. xl, fig. 8 D) in Scoloplos armiger and Theodisca mammillata. The setæ of these worms are, however, evidently quite different to those of Scalibregma, the fork of the former not being fixed quite so symmetrically upon the shaft, and the tips of the prongs are not fine and pointed, but slightly thickened.

Furcate setæ, agreeing in essential characters with those of Scalibregma—that is, possessing unequal barbuled and finely pointed prongs, are practically confined to the genera Eumenia, Lipobranchius, and Sclerocheilus, which on other grounds have been placed with the genus Scalibregma in the family Scalibregmidæ.

7. SKIN.

In the anterior and inflated portions of the animal the annuli bear longitudinal grooves on their dorsal and lateral regions, which subdivide the skin into a series of squarish or oval elevations (fig. 5). These are due chiefly to the fact that the epithelial cells which form them are elongated, columnar cells, while those of the grooves are much shorter, almost flattened cells. Many of the cells of the papillæ are club-shaped, mucus-forming cells, which stain deeply with hæmatoxylin (for other glands of the skin and cirri see pp. 247—249). These cells do not occur in the intervals between the elevations (fig. 12). In some specimens in which there is an excessive amount of inflation of the body, the skin of the inflated region is almost transparent. Behind this region

the elevations become less marked, and in the posterior half
of the animal the skin is subdivided only by the circular
grooves which separate the annuli.

Around the bases of the notopodia and neuropodia of the
segments immediately behind the branchial region there are
sometimes epidermal elevations of considerable size. These
are best developed in old specimens (see figs. 1, 5).

Sections of old specimens show that the yellow-brown
colour of the skin is due to the presence of numerous insoluble
yellow granules in the epidermal cells. These granules are
light yellow when viewed singly, but appear brown in the
aggregate.

There is only a small amount of connective tissue between
the epidermis and the underlying musculature.

8. MUSCULATURE.

Immediately beneath the epidermis there is a layer of cir-
cular muscles, beneath which are the longitudinal muscle
bands which project into the cœlom (fig. 16). The circular
muscles in old specimens usually form a continuous sheet
beneath the epidermis, but in younger ones are sometimes
subdivided into hollow hoops, of which there are two (oc-
casionally only one) in each annulus (fig. 12).

The longitudinal muscles are interrupted along three lines,
viz. on each side at the level of the insertions of the oblique
muscles, and mid-ventrally by the nerve-cord (fig. 16). They
are thus divisible into three groups, of which the two ventral
lie between the nerve-cord and the insertions of the oblique
muscles, the other forming an uninterrupted series extending
over the dorsal and lateral regions of the body-wall. The
ventral bands are rather more strongly developed, especially
in young specimens. The longitudinal muscles are covered by
a very thin cœlomic epithelium.

The oblique muscles are present throughout the chæti-
gerous segments of the body. They are short, thin, narrow
bands arising at the sides of the nerve-cord and inserted into

the body-wall immediately dorsal to the level of the notopodial setal sacs (figs. 14, 16). The nephridia are usually almost hidden from sight beneath these oblique muscles.

The parapodial muscles are moderately well developed (fig. 9). Each bundle of setæ is moved by (1) a number (about five to eight) of slender protractor muscle strands attached to the base of the setigerous sac and to the body-wall near the level of the mouth of the sac, and (2) a few short strands which pass from the base of the notopodial setal sac, and are inserted into the base of the neuropodial sac. By contraction of the latter muscles the bases of the setal sacs approximate, and at the same time the distal ends of the two groups of the setæ are caused to diverge.

Into the inner end of each lateral sense organ a special retractor muscle is inserted. The other end of this muscle is attached to the base of the notopodial setal sac (fig. 9).

The position and arrangement of the four anterior diaphragms and the occurrence of small strands of connective tissue, representing septa, accompanying the segmental vessels in the post-branchial region of the body are described below (p. 255).

There is on each side a short muscle band arising from the lateral body-wall and inserted into the inner and lower end of the corresponding nuchal organ. On contraction this muscle serves to retract the nuchal organ, and also, to a small extent, the prostomium. The latter is well supplied with muscles (fig. 15).

There are several strong muscle strands passing from the buccal mass to the neighbouring body-wall. These are the retractors of the proboscis (fig. 14).

Along almost the whole length of the stomach and intestine there is an incomplete ventral mesentery, consisting of numerous separate muscle strands passing from the ventral wall of the stomach to the body-wall close to the nerve-cord.

9. General Anatomy of the Internal Organs.

Fig. 14 shows the appearance of the animal when opened

by a dorsal incision. The cœlom is spacious, especially in the inflated portion of the animal. It is subdivided anteriorly by four diaphragms or septa placed transversely at the level of the posterior end of each of the four branchiferous segments. Each diaphragm is inserted at the level of the hinder border of the annulus which immediately follows the chætigerous annulus. The second, third, and fourth diaphragms are perforated by the minute funnels of the first three nephridia.

Behind the branchial region the cœlom is not subdivided by transverse partitions, but is continuous to the posterior end of the animal. In the post-branchial portion of the body each of the segmentally arranged blood-vessels is accompanied by a small strand of connective tissue, which near the nephrostome spreads out slightly and is attached to the body-wall a little above the level of the neuropodium. The gonads are developed near the nephrostome on the surface of the expanded portion of this strand (fig. 21). These narrow bands are the equivalents of the septa of the branchial region and of other Annelids, such as Arenicola grubii and A. ecaudata, in which the transition from the narrow bands to complete septa is well seen (Gamble and Ashworth, 1900, pl. 25, figs. 44, 45).

The stomach and intestine are loosely bound to the mid-ventral body-wall by numerous thin strands of muscular tissue, which form an imperfect ventral mesentery. Just as in Arenicola (Gamble and Ashworth, 1898, p. 14) the stomach is probably swung backwards and forwards by the movement of the body, thus bringing about a thorough mixing of the sand, etc., with the secretion of the œsophageal pouches and of the stomach; the muscle strands forming the incomplete ventral mesentery allow a certain amplitude of swing, as the drawing of the dissection shows. In the specimen, the proboscis of which is strongly retracted, the stomach is probably drawn backwards to its most posterior position, as is shown by the backward trend of the blood-vessels.

The intestine is probably moveable in a similar manner, but

to a less extent, as the blood-vessels which pass between the subintestinal vessels and the nephridia and body-wall are capable of considerable extension without injury (see fig. 14).

From the level of the fourth diaphragm to that of the fourteenth seta there are six rather long median blood-vessels running from the ventral vessel to the mid-ventral wall of the stomach, and paired segmental vessels pass right and left from the ventral vessel to each parapodium (and corresponding nephridium) up to the fourteenth. From the fifteenth seta to the end of the animal there are two segmental vessels, an afferent and an efferent, on each side.

The nephridia are to a large extent hidden beneath the numerous oblique muscle bands, and even when exposed by dissection are difficult to see, on account of their small size; they are usually only about ·25 mm. in diameter.

10. Cœlom.

The cœlom is spacious, especially in the inflated region of the animal. It is subdivided by septa only in the branchial region. In the rest of the body the septa are very small, being represented by a thin strand of tissue running alongside the afferent nephridial vessel.

The cœlomic fluid is, as far as can be judged from spirit specimens, very similar to that of Arenicola (Gamble and Ashworth, 1898, p. 29, and pl. 5, fig. 24). It contains the reproductive cells in various stages of growth, and cœlomic cells, some fusiform about 30 μ long, and others spherical or amœboid.

The reproductive cells collect principally in the space between the oblique muscles and the ventral body-wall, especially in ripe females, in which this space is crowded with ova.

11. Alimentary Canal.

Danielssen (1859, p. 69) described the general form of the alimentary canal, pointing out its various divisions, and draw-

ing attention to the nature and probable functions of the
œsophageal pouches, and to some details of the structure of
other parts of the digestive tract, e. g. he observed the
ciliated epithelium lining the œsophagus. Wirén (1887, pp.
30, 37) referred to some points in the histology of the œso-
phagus and stomach.

The mouth (fig. 2) is a transverse slit, situated ventrally
between the peristomial and the first chætigerous segments,
through which the smooth, spherical, eversible pharynx or
" proboscis " may be extruded. The mouth is bordered in
front and behind by papilliform elevations of the skin. The
pharynx, when fully protruded, is a smooth, globular structure,
not provided with spines or any other armature. When it is
withdrawn the anterior part of the alimentary canal—the
part lying in front of the first diaphragm—forms a spherical
mass, from which muscle strands pass to the neighbouring
body-wall (fig. 14).

The œsophagus is a narrow cylindrical tube about 8—9
mm. long (in the specimen 56 mm. long), bearing just in
front of the fourth diaphragm a pair of hollow glandular
pouches, which in this specimen are about 2 mm. long and
1·8 mm. wide. Each is a somewhat heart-shaped sac, at-
tached to the wall of the œsophagus by its apex, its free
wider end being bi- or tri-lobed. The two pouches are
united in the middle line, either directly or by a small median
sac, into which both lateral pouches open. They discharge
their secretion into the œsophagus through a small duct
leading from the median sac.

About the level of the sixth to eighth setæ the œsophagus
passes somewhat suddenly into the much wider stomach,
which even in spirit specimens still bears traces of the
bright orange-yellow colour which Danielssen noticed in
fresh specimens. In all the specimens examined the walls of
the stomach are folded, but whether these folds are natural
it is impossible to state with certainty. The walls of the
stomach and intestine are marked by a number of parallel
lines which pass round the tube from the ventral side to the

dorsal vessel; these are the blood-vessels or sinuses (see below) similar to those described in Arenicola.

About the level of the fourteenth to sixteenth setæ the stomach passes gradually into the intestine, which is a cylindrical tube narrowing slightly towards the anus.

The ventral wall of the anus is slightly notched in the middle line, and on each side of the notch is a protuberance from which the two anal cirri arise (fig. 6).

As pointed out above (p. 255), it is moderately certain that the stomach, and to a less extent the anterior part of the intestine, are swung backwards and forwards during digestion. In addition to this the passage of the contained sand, etc., is aided by the strong peristaltic movements of the anterior part of the intestine which have been observed by Danielssen (1859, p. 70).

The alimentary canal of most of the specimens was distended with fine sand and débris in which quartz grains, spicules, frustules of diatoms, and Foraminifera were clearly recognisable.

Histology.—The œsophagus is lined throughout by ciliated columnar cells. There are no gland-cells in this part of the alimentary canal. The ciliated cells are supported by a thin layer of muscle-fibres. The walls of the œsophageal pouches are raised internally into a number of folds, which are at first mere ridges, but increase in size with the growth of the animal. Each fold consists of two layers of epithelial cells, between which is a blood-sinus, slightly enlarged, near the inner edge of each fold (fig. 23).

On the external surface of the pouches there is a network, apparently a blood-sinus, with which the sinuses of the folds are continuous. The cells lining the cavity of the œsophageal pouches are cubical or flattened, and are not ciliated. The protoplasm of these cells usually contains an enormous number of minute spherical granules (or cavities from which the granules have been dissolved), which give rise to the glandular secretion (fig. 24). The latter may often be seen in masses of considerable size in sections of the hinder

portion of the œsophagus and the anterior portion of the stomach.

The stomach is lined by columnar cells which are strongly ciliated. Among these there are numerous glandular cells which are swollen with granules of secretion and stain deeply with hæmatoxylin. There is an exceedingly small amount of muscular tissue in the walls of the stomach.

The columnar or cubical cells which line the intestine are supported by a thin muscular layer. In the cells of the dorsal and lateral walls of the intestine of large specimens there are very numerous yellow granules, probably chlorogogenous. There is a well-marked ventral groove, the cells of which are columnar and bear long cilia, running along the whole length of the intestine to the anus (fig. 16). I have traced this groove forwards as far as the level of the fifteenth or sixteenth setæ. The function of this groove is probably the same as in Arenicola, viz. to carry backwards along the intestine the digested substances which have been extracted from the sand. In some specimens food particles may be seen in the groove surrounded by a thin covering of mucus. Towards the posterior end of the intestine the whole of its inner wall appears to be ciliated, and the cilia seem to be especially strongly developed in the last few segments. There are two cords situated in the ventral wall of the intestine below the ciliated groove. These, which are best developed in old specimens, are apparently nervous (see p. 268).

12. Vascular System (fig. 14).

Danielssen (1859, p. 70) has described and figured some of the principal parts of the vascular system, but as his account is not complete, and is incorrect in some respects, I propose to describe the vascular system as seen in the dissection of my largest specimen (56 mm. long).

The dorsal vessel arises near the anus, and runs along the whole length of the alimentary canal, breaking up into capillaries on the pharynx. It is closely adherent to the gut, and

receives a large number of fine vessels (or lacunæ; see below, p. 261) from the walls of the stomach and intestine. Near the anterior end of the stomach the dorsal vessel presents a well-marked enlargement, which is apparently constant, as it is present in the other specimens examined. In my largest example this swelling, which, following Danielssen, we may call the blood-reservoir, is 7 mm. long and 1·2 mm. thick in its widest part. Anterior to this the dorsal vessel resumes its normal diameter for a length of about 4—5 mm. and then abruptly dilates into a conical bulb, which Danielssen named the heart, about 1·5 mm. in diameter. The vessel then narrows to its previous size, and gives off four pairs of stout afferent vessels which run along the corresponding diaphragms to the gills. On reaching the pharynx the dorsal vessel divides into two branches, which soon break up into smaller vessels supplying the pharynx, buccal mass, brain, etc.

The ventral vessel arises near the mouth, by the union of small vessels from the prostomium and peristomium. It runs along the whole length of the animal just above the nerve-cord. Soon after its origin it receives four pairs of efferent branchial vessels, and thus becomes almost at once a thick trunk. In each of the post-branchial segments the ventral vessel gives off a pair of slender vessels supplying the nephridia, setal sacs, and neighbouring tissues. Besides these paired branches the ventral vessel gives off to the stomach six median vessels, the first of which is situated just behind the fourth diaphragm, and the last at the level of the thirteenth setæ. In the posterior portion of the animal, behind the twentieth segment, the ventral vessel bears a large number of short, blind, usually curved outgrowths, which are covered with a layer of cells, probably chlorogogenous, and corresponding to the similar tissue clothing the blind outgrowths of the ventral vessel of Arenicola marina (Gamble and Ashworth, 1898, pl. 2, fig. 5).

Along the whole length of the intestine there is a pair of

subintestinal sinuses situated one on each side of the ventral
groove of the intestine (figs. 14—16). These may be traced
from behind forwards as far as the level of the fifteenth setæ,
then they taper rapidly and disappear. Anterior to this
point the stomach receives blood only from the six median
vessels above referred to. In each segment, from the fifteenth
to the end of the body, a pair of vessels collecting blood from
the nephridia and setal sacs opens into the subintestinal
sinuses.

On the walls of the stomach and first part of the intestine
there are numerous fine blood-streams, which carry blood
from the ventral portion of the gut into the dorsal vessel.
These are not distinguishable on the posterior part of the
intestine, as this portion of the gut is surrounded by a sinus,
by means of which blood is conveyed from the subintestinal
sinuses to the dorsal vessel. The whole of the blood in the
walls of the stomach and intestine is contained in sinuses;
the intestine, as seen in section, appears to be quite enclosed
in a blood-sinus. The subintestinal sinuses are somewhat
specialised parts of the general sinus. The dorsal vessel is
not distinct from the sinus in the posterior part of the animal,
but from the level of the twelfth setæ (i. e. a point a little
behind the blood-reservoir) it is distinct, and has a wall of
its own.

In Arenicola the blood in the walls of the stomach and
intestine is apparently contained in vessels in young speci-
mens, but in sinuses in old specimens (Gamble and Ash-
worth, 1900, p. 460) ; but even in the latter it is sometimes
difficult to determine whether the gastric plexus is formed of
vessels or sinuses. In Scalibregma the blood in the walls of
the stomach and intestine is certainly contained in sinuses,
which in the posterior part of the intestine are large.

The body-wall and nerve-cord are very sparingly supplied
with blood. No vessels are distinguishable in the body-wall,
except in immediate proximity to the setal sacs, and these
vessels are few and small.

The walls of the heart and blood-reservoir are very thin,

and their structure is difficult to determine. The walls are composed of a layer of peritoneal epithelium within which a very thin sheet of muscle-fibres may be distinguished. In some sections an exceedingly delicate endothelium appears to be present, but this is difficult to distinguish with certainty. There is no trace of heart body such as is present in the dorsal vessel of some other Polychætes.

Danielssen states that the blood-reservoir and the heart are contractile, alternately expanding and contracting with considerable force, driving the blood forward to the gills. The blood-plasma is red and the corpuscles are few in numbers. They are spherical or ellipsoidal cells, 6—9 μ in diameter, and have prominent nuclei. It is very difficult to ascertain where they are formed, but apparently some arise from the cells lining the wall of the dorsal vessel, especially in the region of the heart and blood-reservoir. In one specimen there is a mass of corpuscles in the ventral vessel immediately behind the fourth diaphragm. These corpuscles resemble in appearance and in reaction to stains the cells lining the wall of the vessel in their immediate neighbourhood. Possibly corpuscles are formed at various points in the vessels.

13. Gills.

The four pairs of gills are shrubby, much-branched outgrowths of the body-wall situated immediately above and behind the notopodia of the second, third, fourth, and fifth chætigerous segments (fig. 1).

Rathke describes the gills as being present on the fourth to seventh segments, and figures three chætigerous segments anterior to the first pair of gills; but other authors describe the gills as being situated on the second to fifth segments. It seems unlikely that Rathke's specimen, while agreeing very closely with other specimens obtained from the same locality, should differ from these only in the position of the gills. It seems probable that in this respect Rathke's account is incorrect.

The first gill is considerably smaller than the other three,

which are nearly equal in size. The branches of each gill
spring from a single stem, which is short and stout, and
soon divides into two main branches, one of which is directed
dorsally and the other ventrally (fig. 4). Each of these
usually divides again into two, and these branch freely,
sometimes dichotomously, or often dividing into three.

In the living animal the gills are red and the fine branches
reddish yellow, due to the contained blood (Sars). The
gills are hollow, each containing a prolongation of the
cœlom. Their walls are composed of single layers of epi-
thelial cells, within which is a delicate cœlomic epithelium
surrounding the axial cavity. Between these two layers is a
thin sheet of muscle-fibres, upon the presence of which the
contractility of the gill depends.

The gills are supplied with blood by four pairs of afferent
vessels given off from the dorsal vessel, and they return
blood by a corresponding number of efferent trunks to the
ventral vessel (fig. 14). The position of the vessels and the
circulation of the blood in the gills is difficult to make out
from my material, as the gills are almost bloodless in all the
specimens.

14. Central Nervous System.

Danielssen (p. 72) has given a brief account of the nervous
system. He figures (pl. i, fig. 3) the nerve-cord as a double
chain, upon which there are ganglia in the middle of each
segment, each giving off a pair of nerves to the body-wall.
From the œsophageal connectives three fine nerves are given
off on each side. The brain, which consists of two masses
connected by a transverse commissure, also gives off three
nerves on each side, which run forwards.

I cannot agree with Danielssen on several of these points,
and especially on the ganglionation of the nerve-cord. I find
that the cord is of almost uniform thickness, there being no
ganglia visible either in dissections or in horizontal sections.

The central nervous system closely resembles that of

Arenicola, especially that of A. claparedii (Gamble and Ashworth, 1900, p. 469), with which it agrees even in many of its details.

The Brain.

The brain is lodged in the middle portion of the pro-stomium (fig. 15). It is somewhat **A**-shaped, the single anterior lobe being in contact with the anterior face and dorsal wall of the prostomium, and the two posterior lobes lying in contact with the inner sides of the two nuchal grooves. In some specimens the anterior brain-lobe is not in close contact with the dorsal prostomial epithelium along its whole length, but in the posterior half is separated from the epithelium by a thin sheet of muscle-fibres. The brain is placed in a slightly slanting position, its anterior lobe being situated more dorsally than the posterior lobes.

The anterior lobe is almost entire, the only trace of division being a very slight groove along its ventral surface ; but the two posterior lobes of the brain are separated from each other by a considerable space lined by cœlomic epithelium, and containing muscle-fibres and blood-vessels.

The dorsal and lateral portions of the anterior brain-lobe consist chiefly of small oval or pyriform cells, some with small deeply-staining nuclei, others with vesicular nuclei, with one or two small dark nucleoli. A few larger cells are found here and there. The ventral part of this lobe of the brain consists chiefly of a delicate neuropile.

The anterior brain-lobe gives off a pair of moderately stout nerves to the hollow tentacles (*N. Tent.*, fig. 15). The nerve spreads out just beneath the epidermis of the base of the tentacle, gradually thinning out towards the tip. The stout œsophageal connectives arise from the brain a little further back, i. e. about the middle of its length. The tentacular nerves receive fibres from the dorsal and ventral part of the anterior brain-lobe, and there is a considerable mass of cells immediately below and to the outer side of the origin of each of these nerves. The connectives also receive fibres from

the dorsal and ventral portions of the brain, and there is a
group of larger nerve-cells just below their point of origin.
The posterior brain-lobes consist of nearly equal parts of
cellular and fibrous elements. The fibrous matter is covered
internally by a thin layer of cells, but externally has a thick
coating of ganglion cells, which are closely applied to the
nuchal epithelium. This mass of cells forms a large gan-
glionic centre. The posterior brain-lobes are broad in front
where they are fused with the anterior part of the brain, and
in this region there are numerous comparatively large nerve-
cells, especially on the inner faces of these posterior lobes
abutting on the cœlomic cavity. On tracing these lobes
backwards along the inner side of the nuchal organ, it is seen
that the cells decrease rapidly in quantity, and each lobe is
continued as a fibrous tract or nerve, which is accompanied
by only a very thin covering of cellular elements (*N. Nuc.*,
fig. 15). This divides into two or three nerves near the
posterior end of the nuchal organ. The nerves lie between
the epithelium and the sheath of the organ.

There is a little neurilemma on the dorsal and ventral faces
of the brain, from which strands pass inwards, supporting the
nervous elements.

The above is a description of the brain of moderately
young specimens 13 to 14·3 mm. long. The average measure-
ments of the brain of five such specimens are ·23 mm. long,
·22 mm. broad, and ·16 mm. deep. As the animal increases
in size the brain not only grows in bulk but undergoes con-
siderable changes in appearance. In a specimen of 56 mm.
long the brain is ·35 mm. long, ·5 mm. wide, and ·35 mm.
deep. The fibrous portion of the brain in this specimen is
proportionately larger and much more complex, and the
neuroglia is better developed than in smaller specimens.
The nerve-cells, some of which are 30 μ in diameter, are
aggregated into definite groups, separated by masses of
fibrous tissue. As in younger specimens the fibrous elements
are chiefly internal, and are covered by the cells. At the
point of origin of the connectives the fibrous matter is ex-

ceedingly abundant, and here, too, on each side are a few large unipolar cells with prominent nuclei. There seems to be a definite nerve-tract arising from this mass of cells and passing into the connective. The fibres of the connective appear to be derived almost entirely from the anterior and middle portions of the brain, only a very small proportion being derived from the posterior lobe. In the posterior lobe there is also a number of larger cells, but the fibrous and cellular elements are in almost the same proportion as in younger specimens.

The Œsophageal Connectives.

The connectives arise from the brain, slightly anterior to the middle of its length. They run just beneath the epidermis, and at first fall nearly vertically downwards near the middle line, then diverge sharply, pass round the mouth, and unite just anterior to the level of the second chætigerous annulus to form the nerve-cord. The course of the connectives is marked externally by the metastomial grooves, which are well seen only in comparatively few specimens.

The connective of each side gives off nerves to at least two, and sometimes three, annuli, through which it passes, and also a nerve through which it runs along the sides of the mouth to the eversible part of the pharynx. The former nerves are situated just beneath the epidermis; the latter nerve, which also supplies the upper lip, may be traced by the aid of its distinct sheath for some distance along the dorso-lateral region of the pharynx between the epithelial and muscular layers, and is probably in connection with the stomatogastric system.

The connectives are composed chiefly of fibrous matter, but there is a thin coating of cells on the external face, and at the point of union of the two connectives there are several larger nerve-cells. The connective is enclosed in a sheath of neurilemma, which is better developed in old specimens, and in the latter sends ingrowths which partially subdivide the connective into two or three.

The Nerve-cord.

The most striking point in Danielssen's description of the nerve-cord of Scalibregma is the ganglionation. I am unable to find any trace of the segmentation or ganglionation of the nerve-cord either in dissections or in sections taken in various planes. Ganglion cells occur, apparently evenly distributed along the whole length of the cord on its lateral and ventral faces, as in Arenicola (Gamble and Ashworth, 1900, p. 480). In most species of Arenicola, however, an indication of the segmentation of the cord is afforded by the presence of giant-cells placed at regular intervals along the cord near the posterior boundary of each segment. In Scalibregma there are no such landmarks, giant-cells and giant-fibres are entirely absent.

The nerve-cord of Scalibregma is not cœlomic in position in any part of its course. It is situated in the body-wall outside the layer of circular muscles, and in close contact with the epidermis (fig. 16).

The cord gives off a pair of nerves situated in each inter-annular groove in the basal portion of the epidermis (fig. 12). The nerves which lie in the groove immediately behind each chætigerous annulus are larger than the rest. Besides these there is a pair of moderately large nerves given off opposite the middle of each chætigerous annulus, which also run between the epidermis and the circular muscles. Each of these nerves (fig. 16) gives off (1) a branch passing into the base of the ventral cirrus, and spreading out beneath the epidermis; (2) a branch to the lateral sense organ; (3) a branch to the dorsal cirrus. The nerve then continues dorsally along the annulus, gradually tapering, and becoming very difficult to trace. The nerve to each cirrus comes into close contact at one point with, and sends fibres to, the corresponding setal sac near its mouth.

In the posterior portion of the animal the nerve-cord lies in very close relation to the epidermis, which is here very thin.

Near its termination in the tail segment the cord gives off a pair of comparatively large nerves supplying the anal cirri.

In transverse section the nerve-cord is oval in shape, being flattened from above downwards (fig. 17). In some specimens it is very much flattened in the posterior region of the animal, whereas in others it is not so compressed.

Ganglion cells occur along the whole length of the cord, being placed on the ventral face and at the ventro-lateral angles. These cells are small and subequal, although here and there a few larger cells may be seen generally situated near the median line in the fissure between the two fibrous tracts. The fibrous matter of the cord is partially subdivided into two by a median vertical sheet of neuroglial tissue, the fibrillæ of which form, in transverse section, a network, more obvious in the ventral portion of the cord. In horizontal sections the neuroglial fibrillæ form wavy strands resembling the neuro-fibrillæ, but the former are generally more deeply staining than the latter.

In older specimens there is a proportionately greater amount of fibrous matter in the cord, and the cells are restricted almost entirely to the ventral face, and most of them are situated in the small fissure between the fibrous tracts, there being very few at the ventro-lateral angles of the cord. In such specimens (30—56 mm. long) the neurilemma sheath and neuroglial network are more highly developed than in younger specimens.

The brain and nerve-cord, and especially the latter, are poorly supplied with blood.

There are two cords (fig. 16, *Int. N.*), best developed in old specimens, running along almost the whole length of the intestine. They are situated in the ventral wall just below the ciliated groove. They are composed chiefly of fibrous elements, but cells are present at frequent intervals. From their appearance and structure they seem to be nervous, but I have been unable to find any connection between them and any other part of the nervous system. The cords become gradually smaller as they approach the posterior end, and finally coalesce. They may be traced as far as the anus.

15. Sense Organs.

The sense organs are (1) the epithelium of the prostomium and tentacles, (2) the nuchal organ, (3) the lateral sense organs, (4) the dorsal, ventral, and anal cirri. Probably also the long capillary setæ should be added to this list. There are no eyes or otocysts.

Prostomial Epithelium.

The epithelium of the anterior and dorsal faces of the prostomium and its tentacles consists of columnar cells, among which slender fusiform sense organs may be distinguished. The latter are generally seen in small groups, and their slender tips are level with or project slightly beyond the outer surface of the cuticle. The bases of these cells are in intimate relation to either the cells of the brain itself or the fibres of the nerves which supply the two tentacles.

The Nuchal Organ (figs. 3, 15).

On each side of the prostomium there is a narrow longitudinal slit which leads inwards and downwards into the blindly-ending nuchal organ. In sections the inner ends of the two nuchal organs are seen lying close together near the middle line, below and behind the brain. The character of the epithelium lining the organ varies considerably. Near the mouth of the depression the epithelial cells are short, columnar, or cubical, and stain lightly, but towards the inner end they rapidly increase in length, and here they are long, narrow, columnar, and deeply-staining, and many of them in the terminal portion are ciliated. In some specimens there is quite a sharp line of demarcation between the cubical and elongate cells. In favourable sections sense-cells may be seen among the columnar cells in the middle and inner portions of the organ. From the inner ends of these fusiform sense-cells slender fibrils may be traced to the adjacent nerve, which is in continuity with the posterior lobe of the

brain. The epithelium lining the inner or terminal portion of the organ is strongly folded, and suggests that this section of the organ is to a certain extent eversible. Possibly the small papilla noticed by Sars in S. inflatum (1846, fig. 21), and by Hansen in S. (?) parvum (1882, p. 34, and pl. v, fig. 8), may be the nuchal organ only partially withdrawn. The retraction of the nuchal organ is effected by a small muscle arising from the body-wall at a point about midway between the notopodial and neuropodial sacs of the first chætigerous segment, and inserted into the inner end of the organ (*Nuc. Retr.*, fig. 15).

Dorsal, Ventral, and Anal Cirri; Setæ.

As pointed out in the section dealing with the ventral nerve-cord, there is a pair of nerves given off in each segment, supplying among other structures the parapodial cirri and the setal sacs. The nerves to the cirri spread out beneath the external epithelium. The nerves which supply the cirri send fibres to the setal sacs near their mouths; these may be traced for a short distance along the sacs towards their inner ends, but owing to their small size they are soon lost from view. They probably end among the bases of the setæ, as Retzius[1] has shown for Arenicola.

The anal cirri are abundantly supplied with nerves by a pair of trunks given off near the termination of the cord. Each cirrus is an epidermal outgrowth, along the whole length of which there is an axial nervous strand. The nerve is surrounded only by a single layer of epidermal cells.

16. The Lateral Sense Organs.

These are the most interesting sense organs of Scalibregma. Levinsen (1883, p. 133) noticed the prominent lips guarding the depression into which the sense organ is withdrawn, but he mistook the structure for an aperture "probably sexual." Théel (1879, p. 49) observed a papilla

[1] 'Biolog. Foren. Forhandl.,' Band iii, Hefte 4—6, p. 85, 1891.

between the two rami of each of the parapodia of Eumenia longisetosa, but he did not recognise the nature of these papillæ.

Our knowledge of lateral sense organs of this kind is due almost entirely to Eisig, who has described their relations and structure in his monograph of the Capitellidæ (1887).

The lateral sense organs of Scalibregma occur in each chætigerous segment throughout the whole length of the body, midway between the notopodium and neuropodium (fig. 1, *S. O.*). The sense organs on the first and second chætigerous segments are small rounded eminences, very difficult to distinguish in surface view, even with a moderate magnification. Those of the succeeding segments are, in preserved specimens, generally sunk and hidden in a depression bordered by prominent lips of epidermis (figs. 4, 5). The essential portion of the organ is liable to be overlooked, and the depression, by reason of its prominent lips, may then be readily mistaken for an aperture. The sense organ itself is a papilla arising from the bottom of the above-named depression, its free, oval, curved surface bearing a very narrow, dark, almost flat area, running dorso-ventrally. The sense hairs arise from this darker area or "hair field" (Eisig), which, in the largest organs of a specimen 56 mm. long, is only about 50 μ long and 10—15 μ broad. In this specimen the surface of the free pole of the largest papillæ is about 250 μ long and 90 μ broad.

The sense organs are best developed in the region of the body just behind the gills. In the posterior third of the animal they gradually decrease in size, and in the last five or six segments they are difficult to find even in sections. About the sixth or eighth segment from the posterior end the organ is recognisable as a minute oval elevation, measuring about 15 μ along its longer diameter (fig. 7).

The structure of these organs can be best studied in thin transverse sections of specimens about 15 mm. long (figs. 28, 29). The organs have attained almost the same stage of growth even in specimens only 5—7 mm. long.

The sense hairs form a dense tuft, covering the flattened area in the middle of the free surface of the papilla. They are moderately stiff hairs, attaining a length of about 40—50 μ, but they are exceedingly delicate, being less than 1 μ thick at their bases. There are a hundred or more hairs in each of the sense organs in the anterior and middle regions of the body. The whole papilla is covered by the thin cuticle continuous with that covering the general epidermis, but over the hair field the cuticle is exceedingly thin, and is pierced by the sense hairs. Beneath the cuticle, over the greater part of the surface of the sensory papilla, there is a layer of columnar or cubical epidermal cells, but in the hair field there is a striking departure from this arrangement. Here, below the cuticle, are long, exceedingly thin columnar cells, closely and regularly arranged. These rods are in most specimens 12—15 μ long (but in the largest specimen, 56 mm. long, they attain a length of 20—25 μ) and about 1 μ wide. They stain darkly, but not quite homogeneously, there being a more deeply-staining, elongated, flattened nucleus near the distal end of each rod. Each rod bears only one or two hairs. The rods are continued inwards as delicate fibrils, many of which may be traced into continuity with the delicate drawn-out ends of pyriform or fusiform ganglion cells, which occupy the axis of the sensory papilla. Many of these ganglion cells are clearly bipolar, the outwardly directed process being, as described above, in connection with the base of a rod, the inward process passing into the nervous mass formed by the spreading out of the spinal nerve in the basal portion of the sensory outgrowth. In older specimens especially, the ganglion cells are nearly all obviously bipolar. These ganglion cells are few in number, there being only about eight or ten in each sense organ. They are usually about 15—20 μ long, and about 8—10 μ wide, and their large nuclei are 6—8 μ in diameter. Occasionally, especially in large specimens, cells 30 μ long with nuclei 8—12 μ in diameter may be seen.

There are other ganglion cells generally aggregated into

a small mass near the base of the papilla, but these cells are rather smaller and more spherical than those described above.

At the base of the papilla, around the nervous axis, there are numerous very deeply staining nuclei-like bodies, about 4—5 μ in diameter. According to Eisig (1887, p. 505) these are to be regarded as nuclei of multipolar ganglion cells which have been deprived of their cellular substance. These nuclei are situated upon a network of fine fibres, probably nervous, since they are in close relation to the fibrils of the branch of the spinal nerve supplying the sense organ. These fibres probably represent the protoplasmic part of the cells of which the deeply staining bodies are the nuclei. These and the basal ganglion cells are more numerous on the ventral side of the axis of the organ than on the dorsal side. This is probably accounted for by the fact that the branch of the spinal nerve enters the papilla on the ventral side. The nerve, soon after entering the sensory elevation, turns nearly through a right angle, and then runs along the axis of the papilla, its ultimate branches terminating among the ganglion cells and bases of the rods (fig. 30).

Inserted into the base of the sensory papilla there is a retractor muscle, the fibres of which spread out fanwise on the basal part of the nervous substance of the sense organ (figs. 16, 29). In some cases the muscle-fibrils extend inwards into the papilla as far as the ganglion cells. In favourable specimens the intimate relation of these muscle-fibrils and the nerve-fibrils may be clearly seen, and it appears probable that there is an arrangement similar to that shown by Eisig for the Capitellidæ (1887, p. 505), viz. that fine processes of the ganglion cells end in the fibrils of the retractor muscle. The muscle is attached to the inner end of the notopodial setal sac.

The position of the sense organ between the two projecting setal sacs affords it considerable protection, and additional protection is given to the sensory area by its withdrawal into a depression of the epidermis by means of the special

retractor muscle. Some such arrangement is necessary to prevent injury to the delicate sense hairs when the animal is burrowing in the sand.

The sense organs differ widely in structure according to their age and the size of the specimen from which they were taken. Very young organs may be seen in sections of the last few segments of an animal.

Sense organs are clearly distinguishable in about the third segment in front of the tail segment (fig. 27). The rods are exceedingly small and difficult to see; they occupy an area equivalent to that of one or two epidermal cells. The sensory area is only 10 μ long. Below the rods are two or three small ganglion cells about 8—10 μ long, and below these are about twenty deeply staining nuclei. In the next anterior segment the rods are rather more obvious, being 5—6 μ long, and in the segment further forward the sense hairs are clearly visible, and have attained a length of about 5—6 μ. In these posterior segments the rods, ganglion cells, and nuclei are closely compressed, and their relations are difficult to determine; but further forwards, as the sense organs increase in size and the various structures become better differentiated, their connections with each other may be more readily seen. The foregoing description on pp. 272, 273, is taken from fully developed sense organs of specimens 13—15 mm. long. In older specimens there are still further changes (fig. 30). The axial portion of the organ becomes more fibrous, the ganglion cells undergo little change, but there are very many more of the deeply staining nuclei at the base of the organ than in younger specimens. The rods also stain more homogeneously, their nuclei being almost invisible, their position being indicated by a slightly darker area in each rod.

Occurrence of Lateral Sense Organs in other Polychæta.

Lateral sense organs are proved to occur in only a very few Polychæta. They are found in the Capitellidæ (with

the exception of Capitella), and their relations and structure have been exhaustively investigated by Eisig (1887, p. 494). E. Meyer[1] has described the small and simple "Seitenorgane" of Polyophthalmus pictus. These are, I believe, the only hitherto published accounts of the lateral sense organs of Polychætes.

These sense organs of Scalibregma closely resemble those of Capitellidæ, except that in the latter there are no large ganglion cells beneath the rods. I have also found similar sense organs in specimens of Eumenia crassa and Lipobranchius jeffreysii, which reached me when this paper was almost completed. In the two latter genera, the depression in which the sense organ is lodged is easily visible on each side midway between the notopodium and neuropodium of each chætigerous segment. In several cases the sensory papilla and the "hair field" can be clearly seen within the depression.

From an examination of published figures of Polychæta it appears probable that "Seitenorgane" are rather more widely distributed than is generally supposed, for there are certain structures shown in these figures which strongly remind one of lateral sense organs, both by their position and appearance. It was stated above (p. 270) that the apertures of the depressions containing the sense organs of Scalibregma have been mistaken by earlier observers for sexual openings. It is probable that certain apertures described as occurring in a corresponding position in other genera may eventually be shown to be depressions lodging sense organs. S. Joseph (1898, p. 371, and pl. xxi, figs. 187, 188) noticed in Ophelia neglecta an oval pore opening into a goblet-shaped depression situated between the two rami of nearly all the parapodia. Kükenthal[2] has also figured a structure in a corresponding position in the

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[1] "Zur Anatomie und Histologie von Polyophthalmus pictus," 'Archiv für mikros. Anat.,' Band xxi, p. 791. Bonn, 1882.

[2] "Über das Nervensystem der Opheliaceen," 'Jenaische Zeitschr. f. Naturw.,' Band xx, p. 510, and Taf. xxiii, fig. 24. Jena, 1887.

parapodia of Ophelia limacina, and Rathke (1843, p. 202, and Tab. x, fig. 15; p. 203, and Tab. xi, fig. 14) has described small apertures similarly situated in Ammotrypane œstroides and in A. (= Ophelia) limacina. He believes these to be ovipores.

The papilla figured by Théel (1879, pl. iii, fig. 46[20]) between the notopodium and neuropodium of Eumenia longisetosa is almost certainly a sense organ. There are, in some specimens of Arenicola cristata (Gamble and Ashworth, 1900, p. 443, and pl. 24, fig. 33), small papillæ, or sometimes depressions, corresponding in position to that of the above-described sense organs, but whether these structures in Arenicola are sensory could not be determined, owing to the defective preservation of the specimens examined.

The Morphology of the Lateral Sense Organs of Polychæta.

The morphology of the lateral sense organs of Capitellidæ has been exhaustively treated by Professor Eisig (1887) in his classical monograph of this family of Polychætes. In the spring of last year, while working in the Zoological Station in Naples, I had the privilege of discussing this question with Professor Eisig, and I am grateful to him for so carefully explaining to me his views upon this subject. He believes that these sense organs are modified cirri, and bases his conclusions on the following arguments. (1) The known sensory nature of cirri, as indicated by the presence on the cirri of some Polychætes of fine stiff hairs. (2) If a gradual shortening of a cirrus took place, the free nerve endings would become more and more aggregated at the free pole of the papilla, thus producing an organ of the same shape and general structure as a "Seitenorgan." (3) Each of the lateral sense organs of Capitellidæ, being situated immediately dorsal to the neuropodium, is considered by Eisig as equivalent to the dorsal cirrus of the neuropodium. He turns for confirmation and support to the parapodia of the

Glyceridæ. In this family the parapodium is not so obviously biramous as in many others, and he considers the whole parapodium of the Glycerids is really a neuropodium (the notopodium being absent) equivalent to that of Capitellids. In this case the dorsal cirrus present on the parapodium of Glycerids would occupy a position corresponding to that of the sense organ on the neuropodium of Capitellids. But, in my opinion, the evidence afforded by the study of the comparative morphology of the parapodia of Glycera and other Polychætes is against this argument and the conclusions drawn from it by Eisig.

The parapodia of several of the Glyceridæ are, at first sight, single outgrowths, in some species the division into two being only feebly marked. Each parapodium is, however, essentially biramous, as is shown by (1) the bifid tip of the parapodium ; (2) the setæ are implanted in it in two more or less distinct divergent bundles. These points may be at once verified by reference to the figures of parapodia of several species of Glycera which Eisig has collected and placed on the last plate of his monograph (see Taf. xxxvii, and note especially G. capitata, fig. 31). The chief differences between the parapodia of the various species of Glycera are traceable to the varying amount of compression and approximation of the parts of the parapodium. In some cases the two rami are so closely approximated that the mouths of the two setal sacs are almost confluent, but even in these cases, on tracing the setæ to their inner ends, it is usually seen that they fall into two distinct and separate groups—a notopodial and a neuropodial. There are usually two acicula in each parapodium, one in the dorsal and the other in the ventral ramus. These acicula are points of insertion of the muscles which move the parapodium and setæ, and the presence of two indicates the essentially bifid character of the parapodium by pointing to the fact that there are two sets of muscles for moving the setæ, one for each bundle (see McIntosh, 1885, pl. xlii, figs. 5, 6, 8, 10).

It is, therefore, most probable that the parapodium of the

Glyceridæ is truly biramous, each ramus bearing a group of setæ. Moreover, the notopodium and neuropodium of Glycerids are equivalent to the correspondingly named structures in other Polychætes, the sole difference being that in the former the typical parts of the parapodium have become more closely approximated and merged into one another than is usual.

This may be further emphasised by a comparison of the parapodia of Glycera and Scalibregma. There is no difficulty in homologising the parts common to both. The parapodium of each of these genera bears two bristle bundles —a notopodial and a neuropodial—and also a dorsal and ventral cirrus. In addition there is in each parapodium of Scalibregma a structure not represented in Glycerids,—the lateral sense organ, which is situated between the two rami in a position corresponding to that of the " Seitenorgane " of the Capitellid parapodium.

Eisig's assumption that the whole parapodium of Glycerids is equivalent to the neuropodium of Capitellids does not appear therefore to hold good. The facts cited above go far towards proving that the Glycerid parapodium contains a notopodium and a neuropodium morphologically equivalent to, but less distinct than, those of Capitellids. If this be admitted, then the assumed homology of the " Seitenorgane " of Capitellids with the dorsal cirrus of Glycerids falls, as the two structures are not in the same morphological position, and have not the same relationship to the respective rami of the parapodia, for the dorsal cirrus is an appendage on the dorsal side of the notopodium, whereas Eisig contends that the " Seitenorgan " represents the cirrus on the dorsal side of the neuropodium.

After a careful examination of the lateral sense organs of Scalibregma, I have come to the conclusion that they are not very intimately related to either ramus of the parapodium, they occupy a position between the two rami. Moreover, a study of the excellent figures which Eisig has given of these organs in the Capitellidæ shows that they are

not related to the neuropodium, and, indeed, if they are connected with one or other division of the parapodium, their relation is rather with the dorsal ramus than with the ventral. The sense organs in several of the Capitellidæ are considerably nearer the notopodium than the neuropodium, especially in the thoracic region (see, for example, Eisig, 1887, Taf. ii, fig. 8 ; Taf. xxiv, fig. 3 ; and Taf. xxvii, fig. 16). The sense organ may be separated from the neuropodium by a considerable interval, containing some other structure, e. g. see Eisig's Taf. xvi, fig. 3, which gives a lateral view of the abdomen of Dasybranchus, each of the sense organs of which is situated some distance from the corresponding neuropodium, and a gill is interposed between the neuropodium and the sense organ. The retractor muscle of the sense organ is, in some genera, derived from the same group of muscles as the protractors of the notopodial setæ, as in Scalibregma (see p. 273, and Pl. 13, fig. 9). In these cases the retractor of the " Seitenorgane " is attached to the inner end of the notopodial setal sac (see Eisig's figure of Notomastus lineatus, Taf. x, fig. 10). The muscles of the neuropodial setæ are never in any way connected with the lateral sense organs.

There is evidently, therefore, little reason for regarding the lateral sense organs of Capitellids even as closely related to the neuropodium, as in those cases in which the sense organs are to some extent associated with one of the rami of the parapodium, the association is invariably with the notopodium and not with the neuropodium. I conclude, however, that the sense organ is not to be regarded as an appendage of, or as intimately associated with, either ramus of the parapodium; it is on neutral ground between the two rami.

I am unable to suggest any alternative to Eisig's hypothesis to explain the origin of lateral sense organs in Polychætes. It may be pointed out that these organs have arisen in a well-protected position near the path of a large nerve—the annular nerve. In course of time the epidermis of this protected area has become much more sensitive than the less

favourably situated cells around, and the former has gradually received a larger nerve supply. The definite sense organ has resulted from a gradual conversion of a number of these protected epidermal cells, perhaps at first into fusiform sense cells, similar to those met with on the cirri or on the general body surface of some Polychætes. These became further differentiated forming rod-like sense elements, and the nervous apparatus connected with their bases became increasingly complex. As shown above (p. 274), when the sense organ appears in the newly-formed segments near the posterior end of Scalibregma, it is distinguishable only by reason of the differentiation of very few epidermal cells into rod-like sense cells, and the presence beneath them of certain nerve-cells; it is never cirriform at any period of its growth.

17. Nephridia.

The character of the nephridia of Scalibregma is practically unknown. All our information regarding these organs is contained in Danielssen's account (1859), in which they are described as the female reproductive organs. In his specimen, which was a large one, he found forty to forty-two pairs of tubular yellowish bodies, one pair in each segment of the animal " from the sixth to the anal segment." Those lying in the sixth to the thirteenth were larger than the others, being about four lines (8 mm.) long. These sac-like bodies were ciliated internally and filled with an enormous number of roundish cells, many of which contained yellowish-green granules. Danielssen believed these organs to be ovaries from which all the ova had been discharged into the cœlom, as at that time of the year (June) the cœlomic fluid contained an enormous number of ova.

The nephridia are almost hidden from view by the oblique muscles which are present in each chætigerous segment throughout the body (fig. 14). The nephridia of Scalibregma are not large sac-like organs as in Arenicola, but slender loops, each formed by a tube bent once upon itself,

The nephridium may, for purposes of description, be divided
into four regions : (1) the funnel, (2) the fine straight tube
which leads directly backwards from the funnel into (3) the
loop formed by a U-shaped tube, the two limbs of which are
parallel and close together, the second limb leading into (4)
the short terminal tube of the nephridium (fig. 18). The only
part of the nephridium visible without dissection is the loop,
which is generally seen through the intervals between the
oblique muscle bands.

The funnel is very small; even in large worms it is seldom
more than ·4 mm. in diameter. The opening is generally
directed ventrally. Both lips are simple, and bear no pro-
cesses. The dorsal lip is larger than the ventral one, and
overhangs the aperture like a hood. Occasionally in large
nephridia the dorsal lip is slightly folded. The funnel is
difficult to see because it is partially hidden by several
blindly ending processes of the afferent nephridial vessel,
which are bound to the funnel by a strand of connective
tissue which represents the septum in the post-diaphragmatic
segments (see p. 255). The funnels of the first three
nephridia are situated on the anterior faces of the second,
third, and fourth diaphragms respectively.

The funnel leads into a short ciliated tube, which generally
runs directly backwards. This portion, even in the largest
nephridia, is only about 1 mm. long, and its lumen is small
(about ·04 mm. in diameter).

The two limbs of the loop of the nephridium, which form
the excretory part of the organ, are closely applied together.
Each is ciliated. The lumen of the straight tube of the
nephridium undergoes a gradual enlargement as this tube
merges into the first limb of the loop, the lumen of the latter
portion being about ·08 mm. wide in large specimens. A
little more than halfway along the first limb of the loop
there is a distinct narrowing of the lumen, which throughout
the second limb is only about ·04 mm. in diameter, so that
the two limbs of the loop may be easily distinguished in
section by the relative sizes of their cavities (see fig. 16).

The loop is nearly 4 mm. long in the largest nephridia. In young nephridia the lumina of the two limbs of the loop are about equal in size.

The terminal portion of the nephridium is generally bent almost at right angles to the loop. It is seldom longer than ·5 mm. It is not distinguished from the adjacent portion of the loop by any external structural character, except in a few cases in which there is a slight dilation of the terminal tube just before reaching the nephridiopore (fig. 18).

The first nephridium is very small, being only 1·5 mm. long in a large worm. The sixth is usually the largest, being 4 to 5 mm. long. In most of the nephridia of large specimens and in the first ten or fifteen nephridia of specimens about 15 mm. long the loop is the most obvious part of the nephridium, the straight tube being only one half to one fourth its length ; but the young nephridia found in the posterior segments have very short loops, considerably shorter than the straight tube of the same nephridium (fig. 21).

The nephridiopores are small oval apertures. The first is situated just below and slightly anterior to the fourth neuropodium, but this is so minute that it can usually be seen only in sections. The others may usually be found either in surface view of favourable spirit specimens, or in specimens cleared in oil (fig. 5). The pores are about ·04—·06 mm. along their longer diameter (see also p. 244).

Histology.—The lips of the nephrostome are lined by a single layer of elongate columnar cells with well-marked nuclei. The cilia are better developed on the dorsal lip (fig. 19). The straight tube behind the nephrostome is lined by almost cubical ciliated cells, the nuclei of which are small and spherical, and lie close to the lumen of the tube. The cells of the loop are larger than those of the preceding portions of the nephridium. In surface view they appear pentagonal or hexagonal, and are closely fitted together at their borders. Their protoplasm contains (in preserved specimens) numerous cavities which in life were probably filled with excretory substances (fig. 20). In some speci-

mens there are numerous small masses of excretory granules
distributed throughout the cells of the loop. These granules
appear dark brown or black when seen in masses, but yellow
or light brown when examined singly. In some specimens
the deposits are in the form of yellowish needle-shaped
crystals. The nuclei of these cells are very small, and
situated very close to the lumen. The terminal tube closely
resembles the adjacent part of the loop, except that there are
fewer concretions in the former. On approaching the
nephridiopore the wall of the tube becomes thinner (fig. 20),
and in some specimens the cells of this part are not ciliated.
There is no muscular tissue in the walls of any part of the
nephridium.

In some specimens Coccidian parasites, which in section
strongly resemble ova, are embedded in the cells of the loop.

The nephridium is covered by a very thin layer of peri-
toneal epithelium, and the blood-vessels seen on the funnel
only lie between the peritoneum and the bases of the excre-
tory cells.

Blood Supply.—The nephridia are supplied with blood
by branches of the afferent branchial vessels which are given
off from the dorsal vessel (as in the case of the first three
nephridia) or by the segmentally arranged branches of the
ventral vessel (fig. 14). The latter vessels usually bifurcate
near the setal sacs, one branch passing to the nephrostome
and the other to the body-wall; the latter vessel usually bears
blind outgrowths which partially obscure the nephrostome.

The nephridia receive only a small amount of blood, the
whole of which apparently goes to the funnel (and to the
rudimentary septum on which the gonads are formed). I
have not found vessels on any other part of the nephridium.

The first three nephridia return blood to the second, third,
and fourth efferent branchial vessels. The nephridia of the
fifteenth and following segments return blood to the sub-
intestinal vessels.

It is interesting to compare Danielssen's observations with
the foregoing. He evidently saw only the loops of the

nephridia, the two limbs of which are indicated in some of the anterior nephridia of his figure (pl. i, fig. 1); in these nephridia the anterior limit is drawn broader than the posterior, as is usually the case in large specimens. He apparently overlooked the first two nephridia, which are small and difficult to see, as they are partially hidden by the diaphragms. He describes the first nephridium as situated in the sixth segment and immediately behind the last diaphragm. This is really the third nephridium, as may be seen from a glance at fig. 14. The yellow granules observed by Danielssen in the cells of the nephridia were probably excretory.

18. Reproductive Organs.

Danielssen (1859, pp. 73—76) described Scalibregma as hermaphrodite. He examined the tubular nephridia, and concluded they were ovaries from which all the ova had been discharged into the cœlom. The parapodial glands present on the dorsal and ventral cirri from the sixteenth to within a few segments of the posterior end of the animal were mistaken by him for testes, and the minute rods which they contain were supposed to be spermatozoa. Scalibregma is not hermaphrodite, it is diœcious. As pointed out above (p. 280), the paired segmental tubular organs are nephridia, and the structures in the cirri are (p. 247) modified epidermal glands which, instead of producing a liquid mucous secretion, give rise to rod-like bodies which may be discharged on the surface of the cirri.

For a considerable time I was unable to locate the gonads, as they are extremely small. The nephrostome is connected to the body-wall by a thin sheet of tissue, which probably represents the septum of the segment. On the surface of this strand, and especially in the region of the smaller lip of the funnel, there is a collection of loosely arranged cells produced by proliferation of the peritoneal cells covering the base of the funnel and the neighbouring portion of the

septum. These cells are the very young reproductive cells. They are found only in the region of the smaller lip of the nephrostome, and for a little distance along the outer side of the straight tube of the nephridium where this organ is in contact with the rudimentary septum. Gonads are present on all the fully grown nephridia, but those on the first and second nephridia are very small. The gonads connected with the first three nephridia are situated on the smaller lips of the funnels and on the neighbouring portions of the anterior faces of the last three diaphragms.

The nuclei of the reproductive cells are large and deeply staining.

It is not possible, I think, to distinguish the sex of a specimen by examination of the cells of the gonad, because they are shed into the cœlom when so small that they have not become sufficiently differentiated to be recognisable as either young ova or young spermagonia. It is only after an examination of the more mature sexual products usually found in the cœlom that the sex of the specimen can be determined.

The reproductive cells leave the gonad when about 10—12 μ in diameter. They increase in size in the cœlom, and by the time they have reached 15 μ in diameter their nature may be determined, as in males division of the cells now takes place, and in females the cells are recognisable as young ova. The ovum continues to grow in size, and its protoplasm—which up to this point has been clear and homogeneous — gradually becomes loaded with spherical yolk granules about 1 μ in diameter, which stain deeply with hæmatoxylin. The largest ova in my specimens are ·12 mm. in diameter; these are probably almost ripe. The nucleus is excentric and vesicular, about 30 μ in diameter, and has a prominent deeply staining nucleolus. The peripheral layer of protoplasm is almost free from yolk granules, but these granules are moderately uniformly distributed throughout the other parts of the protoplasm. The vitelline membrane of these ova is thin.

The spermatozoa develop exactly as in Arenicola (Gamble and Ashworth, 1898, p. 32, and pl. 5, figs. 29—34). The spermagonia fall into the cœlom, and after several divisions give rise to spherical or disc-shaped hollow masses of spermatids. The central cavity of each mass contains a small coagulum, the remains of the blastophore.

By what means the genital products escape is difficult to say. The nephridia are much too small to serve as oviducts, as the width of the lumen of the narrow tube immediately following the nephrostome is only about one third the diameter of a ripe ovum. It is possible that the spermatozoa escape by means of the nephridia. The escape of genital products has been seen by Danielssen, who observed that one of his specimens extruded eggs through a small rupture in the body-wall which appeared when the animal was strongly contracted.

19. The Family Scalibregmidæ.

The family of the Scalibregmidæ was established by Malmgren (1867, p. 186) to contain Scalibregma inflatum, Rathke, and Eumenia crassa, Oersted, there being only one species of each genus known at that time. Since then other species and genera have been described as allied to the foregoing, and have been included in the family, although in some cases their characters do not agree with those of the original genera in one or more important respects. The classification of this family is therefore at present in considerable confusion, and this is further increased by the almost inextricable entanglement of the three principal genera—Scalibregma, Eumenia, and Lipobranchius. The position is rendered more difficult by the fact that some of the species of these genera have been only briefly described, and are known only from the external characters of a single specimen, and this sometimes a mutilated one.

The original description of Scalibregma by Rathke (1843, p. 182), and of Eumenia by Oersted (1844, p. 99),

mentions the presence of gills as one of the diagnostic cha-
racters; and Levinsen (1883, p. 133) includes this among the
characters of the family Scalibregmidæ, but qualifies the
statement by adding that gills are present only in older
worms, or may also be present in younger individuals.

Hansen (1882, pp. 34, 35) described a gill-less worm
obtained by the Norwegian North Atlantic Expedition as
Scalibregma (?) parvum, and McIntosh (Eumenia
jeffreysii, 1868, p. 419; and E. reticulata, 1885, p. 360),
Théel (E. longisetosa, 1879, p. 49), and Ehlers (E. glabra,
1887, p. 169) have referred other gill-less specimens to the
genus Eumenia. Levinsen (1883) renamed Théel's speci-
men Scalibregma longisetosum; but this is not satis-
factory, as an abranchiate species is thus placed in a genus
one of the distinctive characters of which is the presence of
gills. Cunningham and Ramage (1888, p. 655) recognised
that specimens similar to those named by McIntosh Eu-
menia jeffreysii did not belong to the genus Eumenia;
they considered them to constitute a new genus—Lipo-
branchius. The absence of gills in his specimens (which
were 35—37 mm. long) was carefully considered by Théel
(1879) before naming them Eumenia longisetosa. Pos-
sibly with a view of accounting for the absence of gills in
these specimens, or at any rate of minimising the value of
these organs as diagnostic, he states that the gills of Eu-
menia crassa do not begin to grow until the animal has
attained a length of 40—50 mm. The absence of gills in E.
longisetosa might, therefore, be due to the fact that the
specimens were young ones in which gills would have ap-
peared later. But this seems scarcely probable, and Théel's
statement regarding the formation of the gills of E. crassa
at a comparatively late stage of the animal's growth also
seems extraordinary, as in many branchiate Polychætes the
gills are formed in early life when the animal is quite small,
e. g. a specimen of Arenicola marina 4 mm. long already
bears the full number (thirteen pairs) of gills. Théel's state-
ment, moreover, does not agree with that of at least one

author, viz. Johnston (1865, p. 221), who describes a specimen of E. crassa which bears gills and is only one inch and a quarter (about 31 mm.) long. I am indebted to Dr. Théel for two specimens of E. crassa, 29 and 35 mm. long respectively, each of which bears four pairs of gills. Another specimen in my possession, obtained off the south coast of Nova Scotia, is 31 mm. long, and also bears the same number of gills. It would, I think, be better to consider the gills as one of the diagnostic characters of the genus Eumenia, and to consider that Théel's specimens, named by him E. longisetosa, do not really belong to this genus, from which it differs in other respects (see p. 292).

S. Joseph (1894, p. 103) has evidently resolved to maintain the branchiate character of the genera Scalibregma and Eumenia, for he divides the family of the Scalibregmidæ into two sections :

(1) Those with gills—Scalibregma, Eumenia.

(2) Those without gills — Sclerocheilus, Lipobranchius.

In the last-named genus he would place L. jeffreysii, Cunn. and Ram. (= Eumenia jeffreysii, McIntosh), and two other abranchiate species of Eumenia, viz. E. reticulata, McIntosh, and E. glabra, Ehlers. The genus Lipobranchius in his hands thus becomes a somewhat heterogeneous assembly, the members of which agree in general shape and absence of gills, but differ in other characters quite as important, e. g. the prostomium and parapodia. S. Joseph's classification is therefore not entirely satisfactory, and requires some modification.

Before proceeding further it will be advisable to review the chief characters of each of the genera already known, beginning with the best known genera and species.

The genera Scalibregma and Eumenia are very similar, and it is not easy to find many characters by which they may be distinguished.

Taking the species S. inflatum and E. crassa as typical of the respective genera, we may say that the former is more

or less arenicoliform, while the latter is maggot-like and
tapers only slightly at each end. The most obvious external
difference is found on examining the parapodia. In S. in-
flatum the parapodia from the fifteenth segment to the
posterior end project outwards some distance from the body,
forming vertical laminæ bearing dorsal and ventral cirri.
Each of the parapodia of E. crassa is formed by two mam-
millæ which arise separately from the body-wall and bear
the setæ; cirri are absent. There are also anal cirri in S.
inflatum, but none in E. crassa.

The gills of these two Annelids are closely similar. In
Oersted's description of E. crassa it is stated that gills are
found in the six anterior segments, and Johnston states that
they are " confined to the first six segments."

Théel (1879) finds only four pairs of gills. In each of the
three specimens in my possession (two from the coast of
Sweden and one obtained off Nova Scotia) I find only four
pairs of gills situated in the second to fifth chætigerous seg-
ments, thus exactly agreeing in number and position with
those of Scalibregma. The first gill of my specimens of
E. crassa is small, and the fourth is the largest. It is
scarcely probable that any other gills would have been
formed in these specimens, which are about 30 mm. long and
practically mature, as determined by an examination of the
sexual products in the cœlomic fluid. There is, therefore,
some difference of opinion with regard to the number of gills
present in Eumenia crassa. It will be noted that John-
ston does not definitely state that there are six pairs. I
have been unable to procure a specimen bearing more than
four pairs of gills, and though inclining to the opinion that
this is the normal number of branchiæ, I cannot settle this
question definitely until a much larger number of specimens
is available for examination.[1]

[1] Cunningham and Ramage (1888, p. 655, and pl. 42, fig. 18) describe and
figure a specimen named E. crassa, dredged in the Firth of Forth, which
differs in several respects from specimens described by other authors. The
parapodia of their specimen are lamelliform, project prominently from the

The prostomium of Scalibregma inflatum may be described as almost T-shaped, the two horizontal limbs of the letter representing the tentacular processes. The head of Eumenia crassa is more deeply divided in the middle line, and its lateral angles are rounded, and not prolonged into tentacular processes (fig. 13).

These two Polychætes agree in the position and relations of the nuchal grooves and peristomium ; in the appearance and structure of the skin ; in possessing two kinds of setæ, capillary and furcate, in each of the rami of the parapodia; in the presence of a sense organ between the rami of each parapodium.

Internally there is also a strong resemblance between these two worms. (My specimens of Eumenia crassa were unfortunately not in good condition internally, and I was unable to determine some of the finer structural details.) They agree in the following respects :—the general form and relations of the alimentary canal, the situation of the four anterior diaphragms, the musculature, the non-ganglionated nerve-cord, the nephridia, each with simple funnel leading into a slender tube bent once upon itself, a considerable part of the proximal limb of the loop being wider than the distal limb.

Scalibregma inflatum and Eumenia crassa differ only (so far as their anatomy is at present known) in the

body-wall (see fig. 18 B), and bear large flattened leaf-like dorsal and ventral cirri. All other authors agree that the parapodia of E. crassa are without cirri. In the Firth of Forth specimen there are six pairs of gills stated to occur in front of the notopodium of the first six chætigerous somites. In other recorded specimens of this Polychæte the gills are situated behind the corresponding notopodia. The prostomium of the Forth specimen terminates in two diverging tentacles, thus differing from others (see above, p. 290). These points taken in conjunction with the fact that the specimen described by Cunningham and Ramage is an elongate worm gradually tapering from about the eighth or tenth segment to the posterior end, whereas all other recorded specimens are maggot-like, shows that this specimen, if it be E. crassa, is quite different from any other example of this animal recorded from the time of Oersted (1844) up to the present.

shape of the prostomium, the character of the parapodia, and the presence in the former genus of parapodial and anal cirri.

Lipobranchius jeffreysii agrees closely with Eumenia crassa, except that in the former there are no gills. The absence of gills cannot be ascribed to the youth of the specimens, for three of those in my possession are 32, 38, and 40 mm. long respectively, and are almost mature, having ova ·09 mm. in diameter in the cœlomic fluid. These cannot, therefore, be regarded as immature specimens of E. crassa upon which gills would afterwards have been formed, and moreover gills are present in specimens of E. crassa before they reach this size; there are four pairs of gills in a specimen 29 mm. long. Lipobranchius jeffreysii agrees with E. crassa in the shape of its prostomium, and the character of its parapodia, which are without cirri; in fact, given a specimen from which the first six segments have been removed, it would be a matter of some difficulty to determine to which genus the specimen in question belonged.

Among the specimens of Scalibregma sent to me from the United States National Museum there are five small worms 4·6 to 8 mm. long, which have no gills, but otherwise are indistinguishable from Scalibregma. I find that these are not, as I at first supposed, young specimens; some at least are almost sexually mature, e. g. the specimen 8 mm. long contains large ova (·1—·11 mm. in diameter). These, therefore, cannot well be regarded as young specimens of Scalibregma; had they been such their gills would already have been quite obvious structures, for Scalibregma acquires its gills at an early age; a specimen 5 mm. long already bears the full number (four pairs) of well-developed gills. If, therefore, the branchiæ are to be regarded as one of the diagnostic characters of the genus Scalibregma, these abranchiate specimens do not belong to the genus. I propose to call them Pseudoscalibregma.

Several Polychætes have been described which agree with Scalibregma in general characters, but are without gills;

these might also be placed in the genus Pseudoscali-
bregma. S. parvum, Hansen, S. (Eumenia) longise-
tosum, Théel, and Eumenia reticulata, McIntosh, prob-
ably belong here.

S. parvum agrees very closely with the abranchiate spe-
cimens of Scalibregma in my possession in the shape of
the prostomium and in the parapodia, which from the twelfth
segment to the posterior end of the animal form projecting
laminæ, each bearing a dorsal and a ventral cirrus.

Théel's Eumenia longisetosa differs markedly from E.
crassa in several respects, e. g. in the former the prosto-
mium is prolonged at each side into a well-marked tentacular
process; and though the first eleven pairs of parapodia are
small, those of the twelfth and following segments bear leaf-
like cirri. Levinsen (1883, p. 133) and von Marenzeller
(1892, pp. 401, 426) have realised that Théel's specimens
are more closely allied to Scalibregma than to Eumenia,
and have accordingly renamed them Scalibregma lon-
gisetosum. The latter author suggests that the specimens
(which are about 12 mm. long) described by Hansen as S.
parvum are merely young forms of Théel's species, and
from a comparison of the descriptions and figures of the pro-
stomia and parapodia I consider the evidence supports this
view very strongly. S. parvum and S. longisetosum
are, however, abranchiate, and should be separated on that
account from the genus Scalibregma.

Eumenia reticulata, McIntosh, is evidently nearly re-
lated to the foregoing, for its prostomium is prolonged into
tentacles, and its parapodia from the fifteenth segment
onwards to the posterior end of the body form projecting
lamellæ, which McIntosh compared to those of Théel's speci-
mens. McIntosh (1885, p. 361) remarks that " one of the
specimens presented the aspect, dorsally, of Scalibregma
without the branchiæ."

Eumenia glabra, Ehlers, differs so considerably from
any of the species mentioned above, that it is doubtful
whether it should be included in any of the hitherto de-

scribed genera.[1] Its prostomium is drawn out into two well-marked tentacular processes, but its skin appears to be smooth, and (in the figures) bears no signs of secondary annulation, and the parapodia do not project prominently from the body. The posterior end of the animal forms a thin tail, upon the end of which the anus opens. It is distinguished from Eumenia and Lipobranchius by its prostomium and skin, and from Scalibregma by its parapodia and skin.

There still remain for consideration two members of the family, viz. Sclerocheilus minutus, Grube, and Lipobranchius intermedius, S. Joseph. The former was discovered and briefly and somewhat incorrectly described by Grube[2] in 1863, but this description has been revised and extended by S. Joseph (1894, p. 103). The animal is small, only about 5—20 mm. long, and is found living in oyster-shells. The head is of moderate size, and bears two blunt tentacular processes. There are eversible nuchal organs at the sides of the prostomium. The parapodia contain capillary and furcate setæ, and those of the second segment (the peristomium being achætous) also contain stout acicular setæ which are curved near the tip. Behind the twenty-second segment each parapodium bears a small digitiform cirrus below the neuropodium. This is not a gill, as it contains no vessels; it is evidently sensory, as indicated by the presence of · fine stiff hairs upon it. The skin is sculptured as in Scalibregma. There are no gills. There are five[3] (or rarely six) cirri around the anal aperture. The alimentary canal resembles that of the other members of the family except that there are no œsophageal pouches. The brain and nerve-cord agree with those of the other members of the family,

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[1] Ehlers (1887, p. 170) evidently doubted whether this animal should be included in the genus Eumenia, for he says, "Ich stelle diese Art vorläufig in die Gattung Eumenia."

[2] " Beschreibung neuer oder weng bekannter Anneliden, Sechster Beitrag," 'Archiv für Naturgeschichte,' Jahrg. xxix, Band i, p. 50. Berlin, 1863.

[3] Grube describes and figures four anal cirri.

and the nephridia are formed on exactly the same plan as those of Scalibregma, each nephridium being a delicate tube, the excretory portion of which is once bent upon itself. S. Joseph believes that the nephridia act as genital ducts, but this seems improbable, if not impossible, as the lumen of the nephridium is too small to permit the passage of a ripe ovum (judging from S. Joseph's figures, pl. v, figs. 137, 142). The animal derives its name from two plate-like pigmented structures on the head, which Grube believed to be " horny" and protective, but S. Joseph describes them as eyes.[1]

This animal is most closely allied to the gill-less forms of Scalibregma (Pseudoscalibregma), with which it agrees in general shape, in the characters of the prostomium, furcate setæ, nephridia, and nervous system, but differs from them in possessing strong setæ in the second segment, the presence of eyes (?), and the absence of dorsal cirri.

According to S. Joseph (1894, p. 113), his new species Lipobranchius intermedius is very similar in almost all respects to Sclerocheilus minutus, with the exception that the former bears no eyes upon the head and no cirri upon the parapodia. It seems to me that this animal is not a Lipobranchius; it differs from that genus in at least two important respects, viz. the shape of the prostomium and the possession of strong acicular setæ in the first parapodium. This animal is more nearly allied to Sclerocheilus than to any other member of the family of Scalibregmidæ. It may for the present be named Asclerocheilus intermedius, a name which indicates its relationship to Sclerocheilus, and at the same time reminds us that the pigmented plates, the distinctive character of the latter genus, are absent from the former.

It would have been better had the preparation of the following table of characters and classification been post-

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[1] S. Joseph (p. 105) states that these pigmented areas occur on the dorsal surface of the head; while Grube describes and figures them (p. 50, and Taf. v, fig. 3 b) on the ventral face of the prostomium near the mouth.

poned until I had been able to examine many more speci-
mens of some of the species therein mentioned. There
seems little prospect of obtaining further material for some
considerable time, and I have therefore appended the table,
although it cannot be regarded as a final one, as it is defi-
cient in several respects. It is based largely on the results
recorded in the former part of this paper, supplemented by
the diagnosis of the authors responsible for the various
species.

The Scalibregmidæ form a moderately compact family, the
characters of which may be thus stated.

SCALIBREGMIDÆ.

Limnivorous Polychæta, arenicoliform or maggot-like in
shape. Gills, if present, confined to the first five (or six,
according to Johnston) segments. Prostomium small, in
some drawn out at its antero-lateral angles into short pro-
cesses; in others its two lobes are blunt and rounded;
bordered laterally by the two nuchal grooves through which
the eversible nuchal organs may be protruded.

Parapodia consist of almost identical notopodia and neuro-
podia, each bearing setæ of two kinds, viz. simple capillary
setæ, and furcate setæ with unequal, barbuled, pointed limbs.
Between the two rami of each parapodium there is in most
species a small sense organ, which may be withdrawn into a
shallow depression of the epidermis. The segments are sub-
divided into annuli, and the skin, especially in the anterior
part of the body, is usually raised into squarish or oval eleva-
tions. Internally there are four transverse diaphragms
situated at the posterior end of the first, second, third, and
fourth chætigerous segments. The eversible pharynx is
smooth, there being no armature whatever. The heart is
median and is an enlargement of the dorsal vessel. There is
a pair of nephridia in each segment except in a few of the
anterior ones. Each nephridium is a narrow ciliated tube,

the excretory part of which is bent once upon itself; the funnel is small.   Dioecious, gonads microscopic.

Found in the temperate seas of the Northern and Southern Hemispheres, and in the colder seas of Northern Europe.

I. Body arenicoliform, prostomium more or less **T**-shaped, the antero-lateral angles being drawn out to form short tentacular processes.

A. The parapodia of the segments behind the twelfth or fifteenth project prominently at right angles to the body, each forming a laminate appendage bearing a dorsal and a ventral cirrus.   Body often swollen anteriorly.

1. Scalibregma.—Gills present on the anterior segments.

> S. inflatum, Rathke (Oligobranchus roseus, Sars).   Four pairs of gills in chætigerous segments 2—5.   Four anal cirri.

> S. brevicauda, Verrill.   Four pairs of gills on segments 2—5.   No anal cirri described.

> S. (?) abyssorum, Hansen.   Anterior part only known, from one specimen.   Three pairs of gills on segments 2—4.   The prostomium bears very short tentacles.

2. Pseudoscalibregma.—No gills.   No anal cirri described.

> P. longisetosum.   (Eumenia longisetosa, Théel.)   The eleventh or twelfth and following parapodia bear cirri.

> P. parvum.   (Scalibregma [?] parvum, Hansen.)   Cirri present on the parapodia of the twelfth and following segments.   This may be a young form of the preceding species.

> P. reticulatum.   (Eumenia reticulata, McIntosh.)   Cirri on the fifteenth and following segments.

B. The parapodia do not form laminate appendages, and are without dorsal cirri.   Ventral cirri, if present at all, are digitiform and confined to the posterior region.   Each para-

podium is composed of two simple rounded elevations, in which the setæ are lodged.

3. Sclerocheilus.—Two triangular masses of pigment on the prostomium. Strong, curved, acicular setæ are found in the first chætigerous segment. The parapodia in the posterior segments of the animal bear ventral cirri. Four anal cirri present.

   S. minutus, Grube.

4. Asclerocheilus.—Pigment masses absent. Curved acicular setæ finer than those of Sclerocheilus are present in the first three chætigerous segments. No ventral cirri.

   A. intermedius. (Lipobranchius interme-
      dius, S. Joseph.)

II. Body of animal maggot-shaped. Prostomium distinctly divided anteriorly into two by a median groove; each half of the head is blunt and rounded; there are no tentacular processes. The parapodia do not form projecting lamellæ, and do not bear cirri. Each parapodium is composed of two simple rounded elevations which arise separately from the body-wall. Anal cirri absent.

5. Eumenia.—Four (or six) pairs of gills present on chætigerous segments 2—5 (or on the first six according to Johnston).

   E. crassa, Oersted.

6. Lipobranchius.—Gills absent.

   L. jeffreysii, Cunningham and Ramage. (Eu-
      menia jeffreysii, McIntosh.)

20. Affinities of the Scalibregmidæ.

The Scalibregmidæ, as references in the previous portion of this paper have shown, resemble the Arenicolidæ in many of their structural features, and they also agree in some points with the Opheliidæ. These three families have several points in common, as they are limnivorous, and present certain of the peculiarities characteristic of such Polychætes.

They have a spacious cœlom, subdivided anteriorly by dia-
phragms, and non-septate in the middle part of the animal;
the alimentary canal consists of an eversible pharynx, fol-
lowed by an œsophagus bearing a pair of lateral glandular
outgrowths, a dilated stomach with glandular walls, and a
straight intestine, usually with a ventral groove; the blood-
vessels of the middle region of these animals are so arranged
as to leave the stomach considerable freedom of movement,
all the blood-vessels to the stomach passing to its ventral
wall, and being arranged so that they can accommodate them-
selves to the backward and forward motion of this part of the
gut.

The Scalibregmidæ agree with the Arenicolidæ in the
above-named characters, and in the general shape of the
body, the subdivision of the segments into annuli, the sculp-
turing of the skin, the small-lobed prostomium (which, in
some specimens of Scalibregma, is quite comparable to
that of Arenicola claparedii), and the presence (in Scali-
bregma and Eumenia) of gills of a similar type. The
brain and non-ganglionated nerve-chain of Scalibregma
resemble those of the marina section of the genus Areni-
cola. There are also points of difference between these two
families which are of considerable importance. In the
Scalibregmidæ the two rami of the parapodia are practically
identical, but in the Arenicolidæ the notopodium is a
conical elevation, and the neuropodium a cushion-like out-
growth. In members of the latter family the neuropodium
bears crotchets only, and the notopodium bears capillary
setæ; in the Scalibregmidæ both rami of the parapodia bear
two kinds of setæ, capillary and furcate, the latter being
characteristic of the family. In some of the Scalibregmidæ
the parapodia form laminate appendages bearing dorsal and
ventral cirri, which are absent in Arenicola (cirri are very
rarely seen in the posterior region of American specimens of
A. cristata). The gills of Scalibregma and Eumenia
are confined to the first five (or six) segments; they are
never present in the first seven segments of Arenicola.

The dorsal vessel of Scalibregma is dilated just behind the fourth diaphragm to form the heart, which is therefore a median structure, thus differing entirely from the hearts of Arenicola, which are paired, and not directly connected with the dorsal vessel. The nephridia of Scalibregmidæ are minute but numerous, and the simple microscopic funnel leads into a slender U-shaped excretory tube. The nephridia of Arenicola are fewer in number, and are wide sacs, each with a large funnel fringed with ciliated vascular processes. Several of the Scalibregmidæ bear complex, segmental, lateral sense organs, which are not found in Arenicola.

The Scalibregmidæ have only a few features in common with the Opheliidæ. Besides the points mentioned above as common to the three limnivorous families, they agree in the great development of the muscles of the ventral body-wall (especially in Eumenia and Lipobranchius), the nerve-cord without ganglia, the dorsal heart, and the principal features of the circulatory system. The resemblances may be best seen on comparing the Opheliid Ammotrypane œstroides with Eumenia and Scalibregma. The Opheliidæ and Scalibregmidæ differ in their nephridia, those of Opheliids being comparatively few and sac-like; in their prostomia, that of Opheliids is a single conical outgrowth; in their parapodia and setæ. The Scalibregmidæ have little in common with any other family of Polychætes.

We may therefore say that the Scalibregmidæ agree in several respects with the Arenicolidæ and Opheliidæ, and it is difficult to say that they are more related to one of these than to the other, though, on the whole, there are rather more features in which the Scalibregmidæ agree with the Arenicolidæ (e. g. shape, secondary annulation, sculpturing of skin, character of the gills when present, prostomium, brain, and nerve-cord) than with the Opheliidæ. The Scalibregmidæ, however, are clearly distinguished from these families by the presence of the peculiar furcate setæ in the parapodia, and by their numerous delicate nephridia, among other characters.

21. SUMMARY OF RESULTS.

1. Specimens of Scalibregma inflatum from the northern seas of Europe and America are not distinguishable by any essential and constant character from those obtained by the " Challenger " in southern seas.

2. The parapodia of the segments posterior to the fifteenth or sixteenth bear dorsal and ventral cirri which contain large unicellular glands, the secretion of which is in the form of elongate fusiform rods. The fine-pointed tips of the glands pass between the epidermal cells and open on the free surface. The notopodium, its cirrus, and some of its setæ are formed in advance of the neuropodium and its corresponding parts.

3. The setæ of each ramus of the parapodium are of two kinds : (1) simple capillary bristles, the distal third of which bears (in unworn examples) a large number of minute hair-like processes; (2) rather stouter, shorter setæ, furcate distally, the two unequal pointed limbs bearing on their inner faces a number of curved barbules. Both these kinds of setæ are found in the earliest recognisable parapodia. Furcate setæ of this type are practically restricted to the family Scalibregmidæ.

4. The dorsal vessel is dilated at two points to form the blood-reservoir and the heart. There is no cardiac body in the heart.

5. The brain consists of an anterior lobe in relation to the prostomial epithelium, and two posterior lobes, each applied to the inner side of the corresponding nuchal organ. The ganglion cells are found chiefly on the dorsal and ventro-lateral faces of the brain. The anterior lobe gives off a pair of nerves to the tentacles ; the œsophageal connectives arise from the middle region of the brain; the posterior lobes give off nerves which run along the sensory epithelium of the nuchal organs. In old specimens the fibrous part of the brain becomes proportionately larger and more complex, and the ganglion cells become aggregated into groups.

6. The nerve-cord is situated close to the epidermis, and is non-ganglionated. The ganglion cells are distributed along the whole length of the cord on its lateral and ventral faces. The cord gives off in each segment a pair of nerves lying in each interannular groove, and a pair lying in the chætigerous segment. The latter supplies the cirri, sense organs, and setal sacs.

7. A pair of lateral sense organs is present in each chætigerous segment. Each sense organ is a small eminence rising from the base of a shallow depression bordered by prominent lips of epidermis. From a darker area in the centre of the papilla the delicate sense hairs arise. They are implanted in exceedingly slender columnar cells, closely and regularly arranged. These cells are in connection at their inner ends with pyriform or fusiform ganglion cells, which occupy the axis of the sensory papilla. Around and below these are numerous deeply-staining nuclei, which are probably, as Eisig showed, the nuclei of multipolar ganglion cells, the protoplasm of which forms the fine network upon which the nuclei are situated. The sense organ receives a moderately stout branch from the spinal nerve, which runs along the middle of the chætigerous annulus. The sense organ may be withdrawn into the depression in the epidermis by the contraction of a retractor muscle attached to its base. In very young sense organs, such as are found in the last two or three segments of a specimen about 15 mm. long, the rods which occupy the space of only one or two epidermal cells are exceedingly small, and do not bear sense hairs. There are only two or three small ganglion cells at their bases, accompanied by about twenty of the deeply staining nuclei mentioned above. In the next segment anterior to this the rods are more obvious, and one segment further forward the sense hairs may be seen on their distal ends. In old sense organs the axial part of the organ is more fibrous, and the deeply staining nuclei are very numerous.

8. Similar sense organs are present in Eumenia crassa and Lipobranchius jeffreysii.

9. These organs are similar to those described by Eisig in the Capitellidæ, except that in the latter there are no large ganglion cells beneath the rods. The sense organ is not, as Eisig supposed, morphologically equivalent to a neuropodial dorsal cirrus. It does not form part of the neuropodium ; it occupies a position between the two parapodial rami, but it may be connected by means of its retractor muscle to the base of the notopodial setal sac. Eisig believes that the sense organ is homologous with the dorsal cirrus of the Glyceridæ, and that the parapodium of Gycerids is a neuropodium only (the notopodium being absent) equivalent to the neuropodium of Capitellidæ. This view cannot be supported ; the parapodium of the Glyceridæ is essentially biramous, its division into notopodium and neuropodium being less obvious than in many Polychætes, owing to the close approximation of the two rami. (For further details of the discussion see p. 276.)

10. Each nephridium is a delicate ciliated tube opening into the cœlom by a minute simple nephrostome. The excretory part of the tube is bent once upon itself. There is a pair of nephridia in each chætigerous segment except the first three.

11. Scalibregma inflatum is diœcious, and not hermaphrodite, as described by Danielssen. The gonads are formed by proliferation of the cells covering the septum by which the nephrostome is attached to the body-wall. The genital cells fall from the gonad at a very early stage, and complete their growth in the cœlomic fluid. In their structure and stages of growth the ova and spermatozoa closely resemble those of Arenicola. Eumenia crassa and Lipobranchius jeffreysii are also diœcious, and their genital products are similar to those of Scalibregma.

12. The prostomium is an important character in the classification of the Scalibregmidæ. It affords, along with the nature of the parapodia, the most reliable means of determining whether a given specimen belongs to the Scal bregma—or to the Eumenia—section of the family.

13. The Scalibregmidæ resemble the Arenicolidæ and Opheliidæ in several respects, but several of these characters may be largely due to the limnivorous mode of life of the members of these three families. The following characters are common to them :—the spacious cœlom non-septate in the middle region of the body; the eversible pharynx followed by an œsophagus bearing a pair of glandular outgrowths; a dilated stomach with glandular walls and a straight intestine with a ciliated ventral groove; the blood-vessels of the middle region of the gut are arranged so as to allow the swinging movement of the stomach.

The Scalibregmidæ agree with the Arenicolidæ also in the annulation and sculpturing of the body-wall, the prostomium, the brain, and non-ganglionated nerve-cord. They differ in their parapodia, setæ, the position of the gills, the heart, and the nephridia.

The Scalibregmidæ resemble the Opheliidæ in their musculature, the non-ganglionated nerve-cord, and the circulatory system ; but they differ in their prostomia, nephridia, parapodia, and setæ.

The Scalibregmidæ, although allied to some extent to the Arenicolidæ, and to a less degree to the Opheliidæ, form a separate and compact family, one of the most characteristic features of which is the presence of the peculiar furcate setæ in the parapodia.

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EXPLANATION OF PLATES 13—15,

Illustrating Dr. J. H. Ashworth's memoir on "The Ana-
tomy of Scalibregma inflatum, Rathke.

List of Reference Letters.

An. Anus. *Ant. Cr.* Anterior cornu of brain. *Bl. R.* Blood reservoir.
Br. Gill. *Br. Aff.* Branchial afferent vessel. *Br. Eff.* Branchial efferent
vessel. *Cirr. An.* Anal cirri. *Cirr. D.* Dorsal cirrus of parapodium. *Cirr.
Gl.* Gland situated in the cirrus. *Cirr. V.* Ventral cirrus of parapodium.
Cœl. Cœlom. *Cœl. Epith.* Cœlomic epithelium. *Cut.* Cuticle. *Dphm.*[1-4].
Diaphragms. *D. V.* Dorsal blood-vessel. *Ep.* Epidermis. *Ep. Gl.* Gland-
cells of epidermis. *Ep. Pap.* Epidermal papillæ. *F.* Fibrous part of nerve-
cord. *Gang. C.* Ganglion cells. *Gen. C.* Genital cells. *Gr. V.* Ventral
groove of intestine. *Ht.* Heart. *Int.* Intestine. *Int. N.* Nerves (? see
p. 268) of intestine. *Int. S.* Intestinal sinus. *Mo.* Mouth. *M. Long.*
Longitudinal muscles of body-wall. *M. Obl.* Oblique muscles. *M. Ph.*
Retractor muscles of pharynx. *M. Protr.* Protractor muscles of the setal
sacs. *N.* Nucleus. *N. Annul.* Annular nerve situated in the interannular
groove. *N. C.* Nerve-cord. *N. Chæt. Annul.* Annular nerve of chætigerous
annulus. *Neur. S.* Neuropodial seta. *Ngl.* Neuroglia. *Ngl. Sh.* Neuro-
glial sheath. *Nllm.* Neurilemma. *Nm.* Neuropodium. *N. M. C.* Nucleus
of multipolar ganglion cell. *N. Nuc.* Nerve to nuchal organ. *N. O.* Ex-

ternal opening of nephridium. *Notm.* Notopodium. *Not. S.* Notopodial setæ. *Nph.* Nephridium. *Nphs.* Nephrostome. *N. Tent.* Nerve to pro-stomial tentacle. *Nuc. Gr.* Nuchal groove. *Nuc. Retr.* Retractor muscle of nuchal organ. *Œ.* Œsophagus. *Œ. Gl.* Œsophageal glands or pouches. *Per.* Peristomium. *Ph.* Pharynx. *Post. Cr.* Posterior cornu of brain. *Prost.* Prostomium. *Prost. Tent.* Prostomial tentacle. *R.* Rods of lateral sense organ. *S. Aff. V.* Segmental afferent vessel (from ventral vessel). *S. Cap.* Capillary seta. *S. Eff. V.* Segmental efferent vessel (to subintestinal vessel). *Sept.* Septum. *S. Furc.* Furcate seta. *S. H.* Sense hairs. *S. O.* Lateral sense organ. *S. O. Retr.* Retractor muscle of sense organ. *Sp. N.* Spinal nerve. *Stom.* Stomach. *Subint. V.* Subintestinal vessel (sinus). *T.* Tail segment. *V. Mes.* Ventral mesentery (imperfect). *V. V.* Ventral blood-vessel. *I, II, III, IV . . . LX.* Somites beginning with the first chætigerous.

PLATE 13.

All figures, except Fig. 13, are drawn from specimens of Scalibregma inflatum.

Fig. 1.—The large Norwegian specimen, 56 mm. long, seen from the left side to show the external features, prostomium, parapodia, cirri, setæ, gills, segmentation and annulation, the sense organs, etc. The nephridiopores (*N. O.*), the first of which opens on the fourth chætigerous annulus, are very small, and are not well seen in this drawing (see Fig. 5). There are sixty-one segments in the specimen. × 4½.

Fig. 2.—Ventral view of a very regular American specimen which, if com-plete, would have been about 20 mm. long. The prostomium, peristomium and first seven chætigerous segments are seen. The mouth (*Mo.*), bordered by epidermal papillæ, and the secondary annulation of the skin are seen. The nerve-cord runs along the middle line of the median depressed area. × 22.

Fig. 3.—Dorsal view of the anterior end of the same specimen to show the prostomium, nuchal grooves, peristomium, and the first and second chæti-gerous segments, the latter bearing the first pair of gills. × 22.

Fig. 4.—The first gill of the specimen drawn in Fig. 1, along with a por-tion of the second chætigerous and succeeding annuli. Only the dorsal half of the gill is fully drawn; the ventral half is cut down to the bases of the two main branches. × 16.

Fig. 5.—A portion of the tenth chætigerous segment of the left side of the same specimen. Note the four annuli, the skin of which is subdivided into squarish elevations, the epidermal papillæ, the prominent lips of the setal sacs, the sense organ, and the nephridiopore (*N. O.*). × 16.

Fig. 6.—Ventral view of the posterior end of a specimen 13 mm. long, showing the pygidium or tail segment (*T.*), the newly formed body segments

anterior to this, and the cirri and secondary annulation of the older segments. The dorsal cirri are formed earlier than, and are larger than, the ventral cirri. The slightly raised area in the median line marks the position of the nerve-cord (which is non-ganglionated; the appearance of ganglionation presented by the specimen is due to the contraction of the body-wall). The anal cirri on one side have been cut off close to their bases. × 80.

Fig. 7.—Posterior aspect of a parapodium from the specimen drawn on the preceding figure. The parapodium was situated three segments in front of the oldest segment shown in Fig. 6. × 80.

Fig. 8.—The thirty-fifth parapodium of the specimen drawn in Fig. 1. The dark area (*Cirr. Gl.*) in each cirrus marks the position of the gland, which is seen by transparency through the epidermis of the cirrus. The sense organ is situated in and hidden by the small papilla seen between the bases of the notopodium and neuropodium. × 20.

Fig. 9.—The thirtieth parapodium of a specimen 14 mm. long, which was stained, cleared, and compressed in order to bring the muscles into the same plane as the other structures. The typical parts of a parapodium are shown—the dorsal and ventral cirri with their large gland-cells, the notopodium and neuropodium each with simple and furcate setæ, the sense organ and its retractor muscle, and the protractor muscles of the setal sacs. × 80.

Fig. 10.—Five gland-cells from one of the glands shown in the preceding figure. The pointed ends of these unicellular glands pierce the epidermis and open on the free surface. Each gland contains a large number of rod-like bodies. The nucleus of one of the cells is seen near its inner end. × 500.

Fig. 11.—Rods from the parapodial glands of the specimen shown in Fig. 1. Compare their size with that of the rods from a much younger specimen shown in the preceding figure. × 500.

Fig. 12.—A thick longitudinal section (25 μ thick) through an annulus of a specimen 14 mm. long, to show the unicellular glands of the skin, the circular and longitudinal muscles, and the annular nerves. *N. Chæt. Annul.* is a section of the nerve of the chætigerous annulus, which is larger than the nerve (*N. Annul.*) supplying the following annulus. × 270.

Fig. 13.—Dorsal view of the anterior end of a specimen of Eumenia crassa 29 mm. long, to show the prostomium, nuchal grooves, peristomium, and the first and second chætigerous segments, the latter bearing two small gills. × 9.

PLATE 14.

All the figures relate to Scalibregma inflatum.

Fig. 14.—Dissection of the anterior portion of the specimen drawn in Fig. 1, to show the general arrangement of the internal organs. The principal features shown are the four anterior diaphragms, the alimentary canal, and

œsophageal pouches, the vascular system and the nephridia (see also p. 254).
The neuropodia and the afferent nephridial vessels are drawn only in the five
segments immediately behind the last diaphragm, and the oblique muscles,
which are present in all the chætigerous segments, are shown only in the last
three segments drawn on the right side. The incomplete ventral mesentery,
which binds the ventral wall of the stomach to the body-wall near the nerve-
cord, is omitted. In order to prevent confusion, the course of the blood-
vessels running on the left side of the body-wall is not fully shown behind
segment 15. Some of the folds in the wall of the stomach are probably arti-
ficial. × 3.

Fig. 15.—A section passing almost horizontally through the head, pro-
stomium, and first and second chætigerous somites, to show the brain with its
anterior and posterior cornua lying in the prostomium, the nuchal organ, and
its retractor muscle, etc. The ganglion cells which cover the brain are in
close relation to the epithelium of the prostomium and of the nuchal organ.
The section has not passed through the whole length of the anterior lobe of
the brain, only its posterior portion is seen here. × 80.

Fig. 16.—Transverse section of the specimen shown in Fig. 1 passing
through the twenty-fifth chætigerous annulus. The various parts of the
parapodium and the sense organ are seen on the right (cf. Fig. 9). In the
ventral divisions of the cœlom sections of the small tubular nephridia are
seen ; on the left a nephrostome has been cut through. At the base of the
ventral groove in the intestine are two cords (*Int. N.*) seen in section. From
their structure and general appearance they appear to be nervous. × 24.

Fig. 17.—Transverse section of the nerve-cord and surrounding structures
from a specimen 14 mm. long. The fibrous part of the cord is partially sub-
divided by a neuroglial ingrowth. The ganglion cells are situated chiefly on
the ventral side of the cord. The origin of a spinal nerve is seen on the
right. Note also the nuclei of the longitudinal muscle-fibres. × 200.

Fig. 18.—A nephridium from the twentieth segment of the specimen seen
in Fig. 1. The lumen of the nephridium is shown, as seen in optical section
Attached to the nephrostome is the rudimentary septum bearing the genital
cells. × 40.

Fig. 19.—Section of a nephrostome from the thirtieth segment of the same
specimen. The dorsal lip is seen on the right, it is more strongly ciliated
than the ventral lip. On the left is the septum bearing the genital cells.
The blood-vessel lies between the cœlomic and the ciliated epithelium.
× 250.

Fig. 20.—Section of a small nephridium at the junction of the excretory
and terminal portions. The latter is on the right; its cells are cubical or
even slightly flattened, while those of the excretory portion are columnar,
and have vacuoles which in life probably contained excretory products,
× 250.

Fig. 21.—A very small nephridium drawn in situ on the body-wall after the preparation had been stained and cleared. Note the septum accompanying the blood-vessel to the nephrostome. On the right of the nephrostome the nuclei of genital cells are seen. The excretory part of the nephridium— the loop—is at this stage very short. The nephridium is closely invested by a delicate cœlomic epithelium, the nuclei of which are seen at intervals. × 300.

Fig. 22.—Section of an ovum from a specimen 35 mm. long. The peripheral layer of protoplasm is almost free from yolk granules. × 150.

Fig. 23.—Section of a portion of the wall of the œsophageal pouches, to show the blood-sinus enclosed between two epithelial lamellæ. × 50.

Fig. 24.—Some of the cells of the wall, showing the cavities in which the granules of secretion are usually found. They have been dissolved from these cells leaving the cavities empty. × 300.

PLATE 15.

Fig. 25.—Two furcate setæ. A in full view ; B in profile. The portion shown in the figure represents only the distal twelfth of each seta. × 800.

Fig. 26.—The tip of a capillary seta, to show the hair-like processes. The portion figured is only $\frac{1}{25}$ of the seta. × 800.

Fig. 27.—Section of a very young sense organ. The organ was situated ·25 mm. from the posterior end of a specimen 13 mm. long. There was only one chætigerous segment behind this one, and in both these segments the notopodial setæ only were formed, as shown. This is the earliest recognisable sense organ in the specimen. Note the minute rods (R.), the three ganglion cells, and the nuclei of the multipolar ganglion cells (N. M. C.). For further explanation see p. 274. × 600.

Fig. 28.—A rather thick longitudinal section of a sense organ about 3 mm. from the posterior end of the specimen 13 mm. long. The sense-hairs are now seen. This sense organ contains an exceptional number of large ganglion cells. × 500.

Fig. 29.—Transverse section of a parapodium of the same specimen situated 2 mm. from the posterior end. The retractor muscle of the sense organ is seen. See also p. 272. × 500.

Fig. 30.—Transverse section of an old sense organ from the twenty-fifth segment of a specimen 35 mm. long. The fibrous part of the organ is proportionately larger. The ganglion cells are situated nearer to the rods in this organ than in most others. Note the stout nerve supplying the organ entering on the ventral side, and turning almost through a right angle into the axis of the organ. See p. 274. × 200.