ON THE REPRODUCTIVE ORGANS OF PISIONE REMOTA (SOUTHERN), TOGETHER WITH A REVIEW OF THE FAMILY PISIONIDÆ (POLYCHÆTA)*

By K. H. Alikunhi

Received April 1, 1950
(Communicated by Prof. R. Gopala Aiyar, F.A.Sc.)

CONTENTS

1. INTRODUCTORY .......... 14
2. Pisione remota (SOUTHERN) .... 14
3. REPRODUCTIVE ORGANS .... 16
4. GENUS Pisione—REVISION OF CHARACTERS .... 23
5. AFFINITIES ............... 27
6. FAMILY PISIONIDÆ—REVISION OF CHARACTERS .... 29
7. SUMMARY ................. 30
8. ACKNOWLEDGEMENTS ....... 31
9. REFERENCES ............. 31

INTRODUCTORY

An aberrant family of small-sized polychætes with uncertain affinities, the Pisionidæ comprises species which reveal a degree of specialisation that is generally rare in the group. The occurrence of these interesting polychætes in the inter-tidal zone of the Madras beach has been reported in a series of contributions (Aiyar and Alikunhi, 1940; Alikunhi, 1941, 1947), and the anatomical studies of the three new species, Pisionidens indica, Pisione gopalai and P. complexa have now rendered it possible to re-examine the affinities of the family and revise the family and generic characters.

The occurrence of the Irish species Pisione remota (Southern) also in the Madras beach has enabled a detailed study of its reproductive structures, which has hitherto been lacking. An account of the same is set forth in the succeeding pages to facilitate consideration of the affinities of the family.

Pisione remota (SOUTHERN)

Originally described by Southern (1914) from the Irish waters as the type of a new genus Prægeria, it sufficiently resembles the type of Pisione—

* Published with the kind permission of the Chief Research Officer, Central Inland Fisheries Research Station, Barrackpore.
Reproductive Organs of Pisonia remotae (Southern)

P. arstedii Grube—that Hartman (1939) considered its retention as a separate genus unnecessary. A comparative study of the Madras species, Pisonia gopalai which was first assigned to Southern’s genus Prageria (Alikunhi, 1941) and of P. complexa, with the type P. arstedii led the present writer also to agree with Hartman’s views (Alikunhi, 1947). According to the latter Pisonia germanica (Augener, 1924) from the North Sea agrees with the description of Prageria remotae Southern from Ireland. Smith (1932) has found P. remotae occurring in large numbers in the in-fauna of the shell gravel deposits of the Eddystone grounds, Plymouth. Thus, while the species does not appear to have been recorded from outside Europe, its occurrence in the purely tropical environment at Madras is of great interest as it demonstrates the successful adaptation of a species to extremes of environments.

Three species, Pisonia gopalai, P. complexa and P. remotae occur in the inter-tidal zone of the Madras beach. As is common in the sandy beach, they exhibit a degree of zonation in their occurrence, though some overlapping of the different zones does take place. P. gopalai is found in the fine sand at about half tide level, together with Pisonidens indica; while in the coarser sand, nearer to the low tide level, P. complexa abounds. P. remotae confines itself to the rather coarse sand near low water level and is never found in the higher zone in which P. gopalai occurs in large numbers. Rarely, however, all the three species may be found in the same sample of sand taken from the low water level.

Two mature female specimens of P. remotae were obtained (on 17-9-1940) from Sandy Point’, Krusadai Island, in the Gulf of Mannar, in similar substratum and zone as found at Madras.

As in the allied species, a rich development of hypodermal adhesive glands is characteristic of the Madras specimens. This is, perhaps, of extreme importance since the particular environment at low tide level, being subject to the churning and shifting action of the incessant waves, ever holds out the threat of dislocating them from their natural niches. Southern’s descriptions of the external characters is found to be generally accurate when compared to the Madras specimens. In the latter, however, the tip of the parapodial lobe in the anterior segments is distinctly pointed, carrying a minute fillet which terminates in a fine point (Fig. 1 a). This fillet is absent in the posterior parapodia (Fig. 1 b). The setigerous support consists of two acicula and five setae. In the Irish specimens a second simple seta appears in every foot, beginning from the tenth. Such a seta is absent in the Madras specimens, which, however, have in every foot, an additional compound seta with a long terminal blade, as in P. gopalai and P. complexa.
Male: Testis.—The gonads are generally restricted to the middle segments of the body. The male usually has only a single pair of testes. In a specimen with 27 setigerous segments, a pair of testes were present in the 17th segment. A thin covering membrane appears to envelope the testis (Fig. 1 c). When ripe, the two testes coalesce into a single mass, as is found in the other species of the genus. In the testes-bearing segment the gut is generally pushed dorsad and the longitudinal muscles are thin and reduced.

Sperm-sacs.—The testes are followed by a single pair of sperm-sacs which in the majority of specimens are situated in the 19th segment, though they may occur in any one of the segments from the 16th to the 20th. Occasionally two pairs of sperm-sacs and copulatory organs have been found developed in two consecutive segments. For example, in a specimen with 32 setigerous segments, sperm-sacs were developed in the 16th and 17th segments, while, the testes were present in the 15th and 16th.

Genital funnels which develop in association with the nephridia in the testes-bearing segments, resemble those of *P. gopalai* and *P. complexa* in their size, shape and disposition. The nephridial swelling appears small and inconspicuous, compared to the large ciliated organ that is grafted on to it (Fig. 3 a). The nephridial duct behind the septum is enlarged into the sperm-sac. Proximally it is thin-walled and spacious, while, distally it is muscular and thick-walled, with narrow lumen (Fig. 3 a). The inner lining...
epithelium at the distal portion is thin anteriorly, while posteriorly the cells become columnar, highly protoplasmic and provided with refringent granules. Sperms are generally stored in the proximal dilatation. The terminal portion of the nephridial duct—the efferent duct of the sperm-sac—now enters the copulatory organ. The entire modified nephridial duct, except the last ⅓ which is cutinised, is richly ciliated internally.

Copulatory Organs.—In the segment containing the sperm-sacs, the parapodial lobe, unlike the condition in P. gopalai and P. complexa, remains

**Text-Fig. 2. Pisione remota (Southern).—Genital segments of a ripe male showing the general arrangement of the reproductive structures. Drawn from life; specimen pressed under the cover glass, × 100.**

*co.p.* Copulatory process; *m.vc.* Modified ventral cirrus; *ns.gf.* Nephridial swelling and associated genital funnel. *r.pl.* Reduced parapodial lobe; *sp.s².* First dilatation of sperm-sac; *sp.s³.* Second dilatation of sperm-sac. (Other letters as in previous figures.)
distinct though rudimentary and in the form of a conically pointed structure, broad at base and indented behind the tip (Fig. 3a). It carries two acicula and one compound seta which is identical with the one having the longer terminal blade in the unmodified parapodium. The dorsal cirrus remains unchanged. The ventral cirrus is highly modified and is in the form of a stout finger-like process, broad at the base and curved and tapering at the tip which is provided with stiff sensory hairs. The copulatory apparatus consists of this modified ventral cirrus and an elongated process—the copulatory organ proper—developed ventrally to it. The latter is a long, curved, partially retractile structure, tapering to the tip and carries the efferent duct of the sperm-sac. At about its middle is a hood-like process with the tip beset with a number of minute cuticular projections (Fig. 3a), corresponding to the spinous papilla in the copulatory organ in the other two species. Beyond this, is a knife blade-like appendage in the form of a recurved hook with the inner edge cutinised and raised into minute projections. The distal extremity of the copulatory process is curved inwards and at the beginning of the curve there is a slender elongated process with a minute finger-like papilla on one side. The duct of the sperm-sac opens at the tip of the copulatory organ which is blunt and cutinised on the outside (Fig. 3a).

A comparison of the copulatory apparatus in the three species of the genus, viz., P. gopalai, P. complexa and P. remota, shows that even though the structure conforms to a common plan, there are important specific differences. The copulatory organ proper has been shown to be a structure formed de novo from the body wall near the base of the ventral cirrus (Alikunhi, 1947). The position of the copulatory organ in P. remota clearly supports this view; and further evidence that this mode of formation of the copulatory organ is, probably, the general rule in the Pisonidae, is forthcoming from a detailed study of the development and differentiation of similar but more complicated structures in Pisionidens indica (Alikunhi, 1948). In P. gopalai, however, there is an extreme reduction of the parapodia and the ventral cirri of the segment in which the sperm sacs are situated, so that the adult structure is simple and entire. It is interesting that unlike the condition in the other two species, the copulatory structure is curved away from the body in P. remota (Figs. 2, 3a). The shape of the modified ventral cirrus, the undivided nature of the tip of the copulatory hook, and the position and structure of the accessory processes on the copulatory organ are all features in which P. remota markedly differs from P. complexa.

Sperms.—The sperms are non-motile. When mature they are liberated into the coelom, but do not pass into the neighbouring segments (Fig. 2). Each sperm measures about 11 to 14 microns in length. The tail or flagellum
Reproductive Organs of Pisione remota (Southern)

Text-Fig. 3. *Pisione remota* (Southern).—*(a)* Magnified view of the sperm-sac and copulatory organ. Drawn from life; specimen pressed under cover glass, × 135. *(b)* Sperms from the male. From a fresh preparation, × 600.

*ac.* Acrosome; *act.* Aciculum; *bp.* Blade-like papilla; *cs.* Compound seta; *fl.* Flagellum; *h.* Head; *ms.* Muscular sheath; *ns.* Nephridial swelling; *spp.* Spinous papilla. (Other letters as in previous figures.)

is short and slender and is often curved forwards along the side of the head (Fig. 3 *b*). The head portion is thick and spindle-shaped, with a minute pointed acrosome in front and an inconspicuous neck behind. From the acrosome to the neck it measures about 7.5 to 9 microns. In sections of the worm the nuclear portion of the sperm takes deep stain, while the acrosome and neck cannot be made out.

Female.—Ova are developed in the middle and posterior segments. In a specimen with 35 setigerous segments ova were present in the 18th to the 32nd segment, while in another with 52 segments (Krusadai specimen) they were found in the 20th to the 46th. Ova in one segment do not freely pass into the neighbouring ones. They are large and greenish in colour.

Paired genital funnels are developed in all the ova-bearing segments, in association with the nephridia which open to the exterior in the succeeding segment. Following each pair of ovary a pair of receptacula seminis
are developed in association with the nephridial duct (Fig. 4); e.g., in a specimen with 52 setigerous segments and 27 pairs of ovaries, situated in segments 20 to 46, genital funnels were present in all the ova-bearing segments, while receptacula seminis were developed in segments 21 to 47. As in the male, in the ova-bearing segments a large genital funnel gets grafted on to the dorso-lateral aspect of the nephridial swelling. In sections the two structures could be distinguished by the nature of their cells and their different staining reaction (Fig. 5a). Behind the septum the nephridial duct gets enlarged, has thick walls (Fig. 5b), and running external to the oblique muscles assumes a position on the ventral aspect of the receptaculum seminis from which, though in intimate contact, it remains distinct (Fig. 5c-d). Towards the external end of the duct of the receptaculum seminis it is joined by the nephridial duct and the short common duct so formed opens to the exterior ventrally at the parapodial base (Figs. 5e and 6b).

Text-Fig. 4. Pisione remotata (Southern). Three consecutive genital segments of a ripe female, showing the characteristic distribution of the reproductive organs. Drawn from life, × 100.

**ne.d.** Nephridial duct; **o.** Ovum; **rs.** Receptaculum seminis. (Other letters as in previous figures.)
Reproductive Organs of Pisione remota (Southern)

Text-Fig. 5 (a) Pisione remota (Southern).—(a) Transverse section of the nephridial swelling and the associated genital funnel of a female segment. The nephridial portion on the ventral aspect, is relatively inconspicuous, × 600. (b) Transverse section of the nephridial duct, in a female genital segment, immediately behind the anterior septum, × 600. (c) Transverse section through the closed end of the receptaculum seminis of a female (not fully mature). Nephridial duct is distinct, on the ventral aspect, × 600. (d) Transverse section through the middle of the receptaculum seminis of a female (not fully ripe). The nephridial duct is intimately apposed to the ventral wall of the receptaculum seminis, × 600. (e) Portion of a transverse section showing the external aperture of the receptaculum seminis ventrally, at the base of parapodial lobe, × 450.

C. Cilium; gf. Genital funnel; n.ro. Nephridio-receptacular opening; ns. Reduced nephridial swelling. nu. Nucleus; pa. Parapodium. (Other letters as in previous figures.)

Parapodia of the female segments are unmodified (Fig. 4). The receptacula seminis are thin-walled sacs occupying the lateral portions of the segmental compartment near the parapodial base (Fig. 6 a). In the ripe females they are invariably filled with sperms. The cells forming their walls are large and protoplasmic, with big deeply staining nuclei. A few circular muscle fibres are noticed near the external aperture of the receptacular duct (Fig. 5 e).

It is thus seen that a female genital segment in P. remota has a pair of ovaries, a pair of genital funnels in association with the nephridia and
a pair of receptacula seminis (Fig. 6 b), while, in P. gopali and P. complexa the structures are not so crowded and one or more of these may be wanting in any particular genital segment. In the unmodified condition of the paraphodidia of the segments carrying the receptacula seminis and in the absence of any special structures at the nephridio-receptacular aperture, also, P. remota differs from the other species of the genus.

**Text-Fig. 6. Pisione remota** (Southern).—(a) Transverse section of a female 'genital segment showing the receptaculum seminis in the segmental chamber, × 180. (b) Diagram showing the relation between the nephridial duct and the duct of the receptaculum seminis. (c) Sperms from the receptaculum seminis; (1) From a fresh preparation, × 600. (2) From section of the receptaculum seminis, × 600. (3) Diagram of a metamorphosed sperm.

*st.p.* Stiff processes. (Other letters as in previous figures.)

**Sperms from the Receptaculum Seminis.**—The invariable presence of sperms in the receptaculum seminis of the ripe female indicates copulation between the sexes, though the actual process has not been observed. Further, the sperms inside the receptaculum seminis are non-motile and different in structure from those present in the males. After transference to the receptaculum seminis they have lost their characteristic spindle-shaped structure and are found to have acquired a spherical shape with a circket of stiff, tapering, fine processes, probably anteriorly (Fig. 6 c¹). Each sperm is provided with 5 to 8 such processes, the entire structure reminding one, of the characteristic zoospores of plants. After fixation in Bouin's fluid only a portion of its nucleus takes stain and this part is roughly in the form of a V.
Reproductive Organs of Pisione remota (Southern)

Hæmatoxylin, following fixation in Flemming's fluid without acetic, gives a better picture of these sperms, the stiff processes taking moderate stain, when they appear as arising from the circumference of a disc (Fig. 6 c°). There is no formation of spermatophores. The sperms have also undergone considerable reduction in size (Figs. 3 b and 6).

The spherical or disc-like portion of the metamorphosed sperm seems to represent the nucleus or the head, but it does not take uniform stain like the sperm nucleus in the male. The crown of processes, therefore, might have arisen either from the acrosome or from the neck region. Since in P. gopalai and P. complexa the sperms in the receptaculum seminis undergo modifications mainly at the anterior end, it is probable that in P. remota also it is the anterior acrosomal region that has been modified into the stiff processes, the reduced neck and flagellum probably being completely suppressed. These stiff, probably adhesive, processes are reminiscent of the structure of the decapod sperm. It is interesting to note in this connection that according to Riley (quoted by David Sharp, 1918) the spermatheca (receptaculum seminis) in Pronuba (Lepidoptera—Heterocera) contains some curious radiate bodies; while Godman and Salvin also describe similar bodies as existing in butterflies.

The characteristic reproductive structures and the remarkable metamorphosis of sperms in the pisionids studied, probably indicate certain ecological adjustments for ensuring propagation of the species. In polychætes in general, the gonads are very much diffused and in the majority of cases the genital elements are shed into the surrounding medium where fertilization takes place. In the inter-tidal zone, the prevailing extremes of conditions may not ensure the requisite meeting of the opposing elements, with the result that the minute cryptic forms like Pisionidens, Pisione, Microphthalmus, Saccocirrus, etc., have developed specialised accessory structures like sperm-sacs, copulatory organs and receptacula seminis which ensure the successful fertilization of the limited number of ova produced. In these forms ova get fertilized just before or at the point of extrusion. As a further step, the pisionid sperm undergoes metamorphosis and becomes adhesive in nature so that the slightest contact with the ovum will be sufficient to effect fertilization. The rigours of this remarkable inter-tidal zone have thus necessitated elaboration of wonderful structural adaptations that render life and propagation of these little denizens possible in the environment.

Genus Pisione—Revision of Characters

Existing accounts of the generic characters of Pisione have been based on descriptions of external features of P. ørstedi and P. remota, while, nothing
### Table I

**Statement of Distinguishing Characters of the Known Species of** *Pisione Oersted*

<table>
<thead>
<tr>
<th>Specific Features</th>
<th><em>P. oerstedii</em></th>
<th><em>P. remota</em></th>
<th><em>P. gopalai</em></th>
<th><em>P. complexa</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Length</strong></td>
<td>20 mm. to 40 mm.</td>
<td>4 mm. to 10 mm.</td>
<td>4 mm. to 10 mm.</td>
<td>10 mm. to 25 mm.</td>
</tr>
<tr>
<td><strong>Number of body segments</strong></td>
<td>125 to 160</td>
<td>25 to 52</td>
<td>20 to 50</td>
<td>70 to 100 or more</td>
</tr>
<tr>
<td><strong>Buccal spines</strong></td>
<td>Present</td>
<td>Long; 92–95 μ</td>
<td>65 μ long</td>
<td>74 μ long</td>
</tr>
<tr>
<td><strong>Ventral cirrus of buccal parapodium</strong></td>
<td>Globular</td>
<td>Flask-shaped</td>
<td>Globular</td>
<td>Globular</td>
</tr>
<tr>
<td><strong>Ventral cirrus of first parapodium</strong></td>
<td>Long</td>
<td>Long; about 90 μ</td>
<td>Short; about 40 μ</td>
<td>Short; about 56 μ</td>
</tr>
<tr>
<td><strong>Anal segment</strong></td>
<td>Semi-circular</td>
<td>Semi-circular</td>
<td>With conspicuous caudal glands</td>
<td>Semi-circular</td>
</tr>
<tr>
<td><strong>Anal cirri</strong></td>
<td>Two; long</td>
<td>Two; long, swollen at base</td>
<td>Two; long, not swollen at base</td>
<td>Two; long, swollen at base</td>
</tr>
<tr>
<td><strong>Parapodia</strong></td>
<td>Sub-biramous</td>
<td>Sub-biramous</td>
<td>Sub-biramous</td>
<td>Sub-biramous</td>
</tr>
<tr>
<td><strong>Setigerous support</strong></td>
<td>Two acicula and six setae</td>
<td>Two acicula and five setae</td>
<td>Two acicula and five setae</td>
<td>Two acicula and five setae</td>
</tr>
<tr>
<td><strong>Hind lobes of brain extend to</strong></td>
<td>4th setigerous segment</td>
<td>Posterior half of 3rd setigerous segment</td>
<td>Anterior half of 3rd setigerous segment</td>
<td></td>
</tr>
<tr>
<td><strong>Jaws</strong></td>
<td>Two pairs</td>
<td>Two pairs</td>
<td>Two pairs</td>
<td>Two pairs</td>
</tr>
<tr>
<td><strong>Proboscis</strong></td>
<td>Protrusible; with papillae</td>
<td>Protrusible; with papillae</td>
<td>Protrusible; with papillae</td>
<td>Protrusible; with papillae</td>
</tr>
<tr>
<td>Reproductive Organs of Pisonia remora (Southern)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-----------------------------------------------</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Number of pairs of testes</strong></td>
<td>..</td>
<td><em>Always one</em>; confined to one segment</td>
<td><em>Always one</em>; often extending to the adjoining segment</td>
<td><em>One to six or more</em>; each confined to one segment</td>
</tr>
<tr>
<td><strong>Number of pairs of sperm-sacs</strong></td>
<td>..</td>
<td>1 or 2; 2nd saccular dilatation inconspicuous</td>
<td><em>Always one</em>; 2nd dilatation conspicuous</td>
<td>1 to 6 or more; 2nd dilatation absent</td>
</tr>
<tr>
<td><strong>Number of pairs of genital funnels</strong></td>
<td>..</td>
<td>1 or 2</td>
<td><em>Always one</em></td>
<td>1 to 6 or more</td>
</tr>
<tr>
<td>(♂)</td>
<td>..</td>
<td>10 to 30 or more</td>
<td>1 or 2</td>
<td>6 to 20 or more</td>
</tr>
<tr>
<td><strong>Number of pairs of copulatory organs</strong></td>
<td>..</td>
<td>1 or 2; modified ventral cirrus present</td>
<td>Only 1; ventral cirrus absent</td>
<td>1 to 6 or more; modified ventral cirrus present</td>
</tr>
<tr>
<td><strong>Setigerous support of copulatory apparatus</strong></td>
<td>..</td>
<td>2 acicula and 1 compound seta</td>
<td>2 acicula only; compound seta not present at any stage</td>
<td>2 acicula only; one compound seta present in the early stage</td>
</tr>
<tr>
<td><strong>Sperms—From Male</strong></td>
<td>..</td>
<td>Short, thick, non-motile</td>
<td>Slender, non-motile</td>
<td>Slender, long, non-motile</td>
</tr>
<tr>
<td>From Female</td>
<td>..</td>
<td>Non-motile, spherical, with stiff processes</td>
<td>Non-motile, with anterior hood</td>
<td>Non-motile, with broad anterior end</td>
</tr>
<tr>
<td><strong>Number of ovarian groups</strong></td>
<td>..</td>
<td>10 to 30 or more, in consecutive segments</td>
<td>1 or 2; each extending to 6 to 15 segments</td>
<td>6 to 20 or more; in alternate segments</td>
</tr>
<tr>
<td><strong>Number of pairs of receptacula seminis</strong></td>
<td>..</td>
<td>10 to 30 or more</td>
<td>1 or 2</td>
<td>6 to 20 or more</td>
</tr>
<tr>
<td><strong>Parapodia of segment carrying receptacula seminis</strong></td>
<td>..</td>
<td>Unmodified</td>
<td>Completely atrophied; dorsal cirrus and a stump supported by 2 acicula remain</td>
<td>Unmodified; a cirriform process developed at base</td>
</tr>
</tbody>
</table>
was known about their reproductive structures. Hartman (1939) clarified the systematics of the different species assigned to this genus, but his revision of the generic characters was, again, based on some of the external characters only. The detailed investigations of the morphology and anatomy of the three species, *P. gopalai*, *P. complexa* and *P. remota*, have revealed several interesting features particularly in their reproductive system; and have made possible a more specific definition of the genus. The following tabular statement gives the important characters of the four species included in the genus and indicates the salient generic features.

Undoubted morphological similarity between the species, particularly in the nature of the head, the structure of the parapodium and its setigerous support is obvious, and living as they are under more or less identical conditions, almost equally exposed to the influence of the physical factors operating on the sandy beach, this similarity is perhaps only natural. However, beneath these fundamental generic characters, important specific features are outstanding. The conspicuous caudal glands and the slightly elongated ventral cirrus of the first parapodium in *P. gopalai*; the simple semi-circular anal segment and the short ventral cirrus of the first parapodium in *P. complexa*; and, the highly elongated ventral cirrus of the first parapodium, the flask-shaped ventral cirrus of the buccal parapodium, together with the semi-circular anal segment in *P. remota*, are remarkably constant external features that easily distinguish the different species.

In the reproductive system, the formation of specialised copulatory structures for sperm transference, modification of the nephridial duct into a simple sperm-sac for the temporary storing of sperms; elaboration of wide-mouthed ciliated funnels for conducting the genital elements; the development of seminal vesicles for receiving sperms during copulation and the peculiar metamorphosis of the sperms before fertilization, are important features that are common in the three Madras species; while, a series of constant structural differences in the morphology of the different organs, distinguish the species from one another.

In the light of our present knowledge of the morphology and anatomy of the four species included in the genus, the generic characters of *Pisione* may be summarised as follows:

Pisionidae with greatly reduced head; a pair of buccal spines; ventral cirrus of buccal parapodium rounded or flask-shaped; dorsal cirrus elongate; ventral cirrus of the first setigerous segment also elongate, and functioning as tentacular cirrus; dorsal cirrus globular as in the succeeding segments; genital papillae in the form of suckers absent; parapodium simple
Reproductive Organs of Pisione remota (Southern)

sub-biramous, with one or two simple setæ and three or four compound setæ, usually of two kinds; gonads localised to the middle and posterior segments; nephridia with solenocytes; the nephridial ducts in the male genital segments modified into sperm-sacs; one or more pairs of parapodia in the male transformed into copulatory structures which are non-retractile; paired receptacula seminis following the ovaries in the female, and sperms non-motile and undergoing metamorphosis after transference to the receptaculum seminis of the female.

Affinities of the Family Pisionidae Levinsen

The Pisionidae is an aberrant family of small-sized polychætes, generally of cryptic habits. Only two genera, Pisione Oersted and Prageria Southern, were included in this family. Hartman (1939) created a new genus, Pisionella, and showed that Southern’s genus, Prageria is synonymous with Pisione Oersted and recognized only three species, Pisione ærstedii Grube, P. remota (Southern) and Pisionella hancocki Hartman, as valid. The investigations on the fauna of the sandy beach, Madras, initiated by the writer in 1938, have resulted in the addition of a remarkable new genus and species, Pisionidens indica Aiyar and Alikunhi, and two new species of Pisione, viz., P. gopalai and P. complexa; besides the record of P. remota from the same locality.

The existing accounts of P. ærstedii, P. remota and Pisionella hancocki are based on the external characters of a limited number of specimens of each and as such, practically nothing is known about their internal morphology and reproductive behaviour. The affinities of the Pisionidae were, therefore, so far considered only in the light of their known external features. Grube (1857) expressed the opinion that the Pisionidae is related to the Phyllodocidae and the Glyceridae. Ehlers (1901) believed that Pisione is related to the Aphroditidae, Nephthyidae, Hesionidae, Syllidae and Glyceridae. Southern (loc. cit.) considers the family to be closely related to the Aphroditidae, particularly to the sub-family Sigalioninae. According to Hartman (loc. cit.) their affinities are possibly with the Hesionidae on the one hand and with the scale-bearing chaetopods or more nearly, the Sigalioninae on the other. Hartman’s revised statement of the characters of Pisionidae is also based entirely on the external features of the three species P. ærstedii, P. remota and P. hancocki.

Detailed accounts of the internal morphology and reproductive behaviour of Pisionidens indica (Aiyar and Alikunhi, loc. cit.), Pisione gopalai and P. complexa (Alikunhi, loc. cit.) are now available; and with the description of the reproductive structures of P. remota furnished in the present
communication, it is considered desirable to examine the affinities of the family in the light of the important internal features of the different species.

Agreeing with Grube, Aiyar and Alikunhi (loc. cit.) found Pisionidens indica more closely related to the Phyllodocidae and the Glyceridae than to any other family of polychaetes. Subsequent studies by the writer on Pisione gopalan and P. complexa also lend further support to this view. Southern (loc. cit.) concluded that the palps of the Pisionidae are homologous to the palps of the Sigalioninæ, and that the buccal segment is homologous to the segment bearing tentacular cirri in Phola. The cephalic region of Pisionidens indica, with the characteristic palps and tentacular cirri and the absence of buccal spines, however, shows a close similarity to the corresponding region in certain Phyllodocids like Eteone. The undoubted relationship between Pisionidens and Pisione has already been fully demonstrated by the structural similarities in their excretory and reproductive systems. While in P. indica the parapodia are uniramous, with a slender acicular bristle as the only setigerous support of the foot, in the earlier stage, at least in the first six segments, the parapodia are temporarily provided with two acicula and four setae which are almost identical with those in the foot of Pisione. As in the Phyllodocidae, the foot in the Pisionidae is greatly reduced and is almost uniramous (uniramous in Pisionidens) with the notopodium represented by a single aciculum. The resemblance of the compound seta of P. remota, with that of Phola which Southern points out, is rather vague; while the composite bristles from the foot of Pisonella hancocki figured by Hartman (loc. cit.) show a closer resemblance to corresponding bristles of scale-bearing chaetopods. In the nature of the articulation of the terminal blade, the long-bladed compound seta in the foot of Pisione shows a greater resemblance to the median and inferior setae in the foot of Glycera. In the possession of a protrusible pharynx, with a crown of papillæ and four jaws, the Pisionids resemble the Aphroditidæ, certain Hesionids and the Glyceridae. In the Phyllodocidae, however, even though the pharynx is not usually armed (except in Phalacrobothrus (Fauvel, 1923), it is easily protrusible and muscular.

The ecological adaptations of the different forms to particular habitats of each will be largely reflected as modifications in external features; and similarities or differences in these characters should not therefore be taken to represent in full the true affinities of the concerned species. The influence of environment on features of internal morphology will be relatively limited and these characters may be reasonably considered as giving a true indication of the affinities; evidence from external characters supplementing the former. The structure and arrangement of the nephridia and genital funnels in the four species of Pisionids studied, have an important bearing
Reproductive Organs of Pisione remota (Southern) 29

in this connection. The nephridia in all the four species are of the closed variety—the protonephridia type of Goodrich, and are provided with solenocytes. The nearest approach to the Pisionid nephridium is met with in the Phyllodocidae, Glyceridae and the Nephthyidae, and such a resemblance in an important anatomical feature cannot be without significance. In the Pisionidae the nephridia are very much simpler in structure than in the Phyllodocidae but their general resemblance to those of Eteone, etc.; have already been pointed out. In P. indica the nephridia are so well developed in the middle segments that they are very similar to those of Phyllo pdoce paretti, eventhough there is no conspicuous branching of the nephridial swelling. The peculiar structure of the solenocytes of the Pisionid nephridium has already been described (Alikunhi, 1947). In the Aphroditidae, on the contrary, the nephridia are of an entirely different kind, the open funnel type.

The development of conspicuous ciliated organs (Cælomoducts) and their intimate association with the nephridia are features which the Pisionids share in common with the Phyllodocidae, Glyceridae and Nephthyidae. The modus of union between the genital funnel and the nephridium is the same as in the Phyllodocidae and Glyceridae (Goodrich, 1900); and as in the former species the genital funnel attains communication with the nephridium only at the time of sexual maturity. In the Nephthyidae the ciliated organs have not been known to attain communication with the nephridium; while in the glyceridae the former are developed even in the young individuals, though, in some like Goniada only they attain communication with the nephridial duct.

Among other reproductive structures, the occurrence of receptacula seminis appears to be a special environmental adaptation in the Pisionidae, even though structures of similar function have been found in the Alciopinae (Phyllodocidae). Spermathecae are also developed in such different families like the Syllidae, Hesionidae, Spionidae, Saccocirrus, etc., and should be considered as derived independently. It must, however, be mentioned that the Pisionids present a distinct advance over most families of polychaetes, in the localisation of gonads, in the very restricted distribution and constancy in position of the genital funnels, receptacula seminis, sperm-sacs and copulatory organs with regard to the position of gonads, in the development of complicated copulatory organs, in the non-motile condition of the flagellate sperms and in their final peculiar transformations.

RevisIOn of Characters of Pisionidae Levisen

In the light of our present knowledge of the different species included in the family Pisionidae, the following revised statement of the family features is furnished:
Head reduced; prostomium without antennae, and fused with the buccal segment; a pair of well developed palps; dorsal cirri of the buccal parapodia elongate and directed forwards; ventral cirri of the buccal parapodia present or absent; one or two pairs of tentacular cirri carried on distinct segments; one or two pairs of eyes; brain with elongated posterior lobes; pharynx protrusible and provided with four jaws and a crown of papillæ; parapodia uniramous or sub-biramous, with globular dorsal and ventral cirri; simple as well as compound setæ; a pair of anal cirri; body rich in epidermal glands; nerve cords situated in a groove formed by the inner edges of the ventral longitudinal muscles; deccusation of the oblique muscles beneath the nerve cord; nephridia of the closed or protonephridia type, provided with solenocytes; ciliated organs associated with them in the genital segments during the breeding season; sexes separate; gonads highly localised; genital papillæ in the form of well developed suckers present or absent; nephridial duct in the male genital segments modified into sperm-sacs; copulatory organs formed in one or more segments in the male; sperms flagellate—with one or two flagella; but non-motile; and undergoing modifications after copulation; paired receptacula seminis in the female; and fertilisation probably internal.

**Summary**

1. The occurrence of *Pisione remota* (Southern) in the tropical environment at Madras is recorded and the external characters of specimens from Madras compared with those from Irish waters.

2. The reproductive structures in the two sexes have been described in detail.

3. While distinct specific features are found in the detailed structure of the accessory reproductive processes, a strong resemblance to the condition in *P. gopalai* and *P. complexa* is observed.

4. The salient features of the four valid species of the genus *Pisione* have been tabulated and based on this the generic characters have been revised.

5. The affinities of the family Pisionidae have been considered in the light of our knowledge of the anatomy of *Pisionidens indica, Pisione gopalai, P. complexa* and *P. remota*, and probable relationship to the Phyllodocidae, the Glyceridae and the Nephthydidæ has been indicated.

6. A revised statement of the characters of the family Pisionidae has been given, incorporating in it our knowledge of the internal morphology of the species included in the same.
Reproductive Organs of Pisione remota (Southern) 31

ACKNOWLEDGEMENTS

The observations contained in this paper were made during 1940-41, when the writer was working at the University Zoological Research Laboratory, Madras, under the guidance of Prof. R. Gopala Aiyar, then Director of that Institution. The writer is indebted to Prof. Gopala Aiyar for his valuable help and encouragement during the course of the work and also for kindly going through the manuscript and offering valuable suggestions. To the University of Madras, the writer is indebted for the award of a research studentship, during the tenure of which this work was completed. The paper, however, was revised to the present form after the writer took up duties at the Central Inland Fisheries Research Station, Barrackpore.

REFERENCES