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THE REPRODUCTIVE SYSTEMS AND CLASSIFICATION OF THE STILIGERIDAE (OPISTHOBRANCHIA : SACOGLOSSA)

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SUMMARY

The genus *Limapontia* is included in the family Stiligeridae since species of both taxa display in their reproductive systems a common pattern which is described in detail for *Ercolania margaritae* and its main features are noted in *Calliopaea oophaga*, *Placida dendritica*, and three limapontiid species. The reproductive system of *Hermaea bifida* shows that the genus is related to the Caliphyllidae; that of *Alderia modesta* confirms the status of the family Alderiidae. Pseudo-diauly is defined and a provisional classification of the Stiligeridae is presented to give due prominence to the internal anatomy of the species.

INTRODUCTION

The family Limapontiidae has one genus *Limapontia* containing three species: *Limapontia capitata* (Müller, 1774), *L.cocksi* (Alder and Hancock, 1847) and *L.depressa* Alder and Hancock, 1862. There are about fifty species in the family Stiligeridae making it easily the largest in the order Sacoglossa. In the opinion of Baba and Hamatani (1970a) it has eight genera: *Stiliger, Ercolania, Calliopaea, Placida, Hermaea, Hermaeopsis, Hermaeina, Costasiella.*

Pruvot-Fol (1954) and Baba and Hamatani (1970a) described the classification of the Stiligeridae as chaotic. The situation is no longer so desperate, for recent improvements have resulted in a more orderly arrangement. Before further improvements can be made more needs to be known about the internal anatomy of the animals, and the descriptions given in the first part of this paper are a contribution to that end. They show that stiligerid and limapontiid species have a common reproductive system remarkable, among sacoglossans, for its simplicity and ease of interpretation. The other systems of the genus *Limapontia* are like those of the Stiligeridae and so the family Limapontiidae can be discarded and the genus *Limapontia* added to the Stiligeridae.

For many years the genus *Hermaea* contained the species *H.bifida* and *H.dendritica.* Externally the two species resemble one another but it has long been known that they differ in their internal anatomy. Since *H.dendritica* differs only in one anatomical detail from *Placida viridis* Trinchese, 1873, taxonomists have separated the two Hermaeas by placing *H.dendritica* in a subgenus so that its name is now *Hermaea (Placida) dendritica.* An examination of *H.bifida*, however, showed that its reproductive system is quite unlike

that of *H.dendritica*. The two species, therefore, are not closely related and their differences cannot be adequately expressed in terms of a subgenus. *H.dendritica* should be placed in the genus *Placida* and the genus *Hermaea* transferred to the Caliphyllidae.

MATERIALS AND METHODS

Sacoglossans are difficult to obtain and I thank those who gave me preserved specimens.

K. Baba	*Ercolania boodleae* (Baba, 1937) from Seto, Kii, Middle Japan.
J. S. Bleakney	*Stiliger fuscata* Gould, 1870 from Canning Marsh, Kings Co., Nova Scotia.
R. Burn	*Ercolania margaritae* Burn, 1974 and *Placida dendritica* (Alder and Hancock, 1843); both from Point Lonsdale, Victoria, Australia.
Elaine Cracknell	*Hermaea bifida* (Montagu, 1815); Randall, Orkney, Scotland.
J. Dunne	*Limapontia capitata* and *Hermaea bifida;* Carna, Co. Galway, Ireland.
H. Lemche	*Calliopaea oophaga* Lemche, 1974; North of Armhoved, Samsø, Kattegat, Denmark.
Elizabeth Platts	*Alderia modesta* (Lovén, 1844); Strangford Lough, N. Ireland.
Shelagh Smith	*Limapontia capitata;* Tyningham Bay, Lothian, Scotland, and *Limapontia depressa;* Aberlady Bay, Lothian, Scotland.
I. F. Smith	*Limapontia cocksi;* Broch of Gurness, Orkney, and *Hermaea bifida;* Ophir, Orkney.

I thank Professor Dr. J. Joosse and the histologists of the Vrije University, Amsterdam, for serial sections of *Ercolania margaritae* and *Hermaea bifida,* and P.Marriott who also provided two series of *E.margaritae.*

The specimens were dissected with the aid of a stereoscopic microscope at a magnification of x50. Safranin 0 in 50% Ethanol was used as a dissection stain; the exit region of the central canal stained red and the fertilization region pink. Penial styles were mounted in Berlese's fluid. Serial sections were used to confirm and extend the details observed by dissection. At the end of a dissection the central canal region was mounted in 50% glycerol and examined with a microscope at a magnification of x120; the coverglass was gently manipulated to obtain different views.

KEY TO LETTERING

AC, albumen capsule
AD, duct of albumen gland
AG, albumen gland
AN, anus
B, base of style
BC, bursa copulatrix
BW, body wall
CA, anchoring collar
CN, melanin-coated cushion
CU, cupola
D, follicle ductule
E, exit region of central canal
F, fertilization region of c.canal
FA, famale ampulla
MO, male opening
MV, melanin-black vesicle
O, egg
OL, oviducal loop
OO, oviducal opening
OV, oviduct
P, penis
PP, peridardial prominence
PR, prostate
PT, tip of penis
R, renal pore
RR, renal ridge
S, sperm
SH, penial sheath

FE, fertilization chamber
FD, female duct
FO, female opening
FT, follicle of ovotestis
GD, duct of genital receptacle
GR, genital receptacle
HA, hermaphrodite ampulla
HD, hermaphrodite duct
L, projecting lip of style
LO, large oviduct
M, elastic fibrous tissue
MD, male duct
SO, small oviduct
SP, spines
ST, penial style
T, tail
TE, penial tentacle
V, vagina
VI, normal position of vagina
VA, vaginal ampulla
VD, vas deferens
VE, vestibule
VO, vaginal opening
W, whorls of large oviduct

DESCRIPTIONS

Ercolania margaritae (Fig. 1) is present in top-shore rock pools at Point Lonsdale, Victoria, where it is seasonally abundant (Burn, 1974). Externally it is distinguished by a pair of long rhinophores and a pericardial prominence (PP) that is continuous with a long renal ridge (RR). Its reproductive system is like that of *Olea hansineensis* Agersborg, 1923, described by Gascoigne (1975). The main differences are that in *O.hansineensis* the vagina does not open to the exterior but ends in a bursa copulatrix attached to the body wall and the style is of the penetrant kind, whereas the vagina of *E.margaritae* opens to the exterior and the penis has a coupling style.

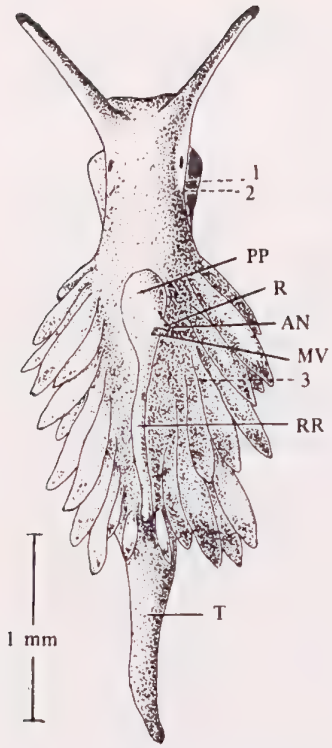
The reproductive system of *Ercolania margaritae* is tightly packed. Fig. 2A is a display diagram drawn to show the various structures; the vagina and central canal are turned over to the left and the large oviduct is displaced to the right. The functional interpretation is based on what is known about *Limapontia cocksi* and *L.capitata;* no direct evidence is at present available for *E.margaritae.*

The ovotestis of *E.margaritae* consists of about 150 follicles that occupy all available spaces from the head to the foot. The albumen gland (AG) is closely applied to the branches of the gut and some lobules extend about half-way into the cerata. The genital receptacle (GR) is a large spherical pouch connected by a short duct (GD) to the anterior end of the central canal on the right side. In serial sections the receptacle contained a mass of amorphous material, probably yolk and albumen. The receptacle duct is not joined to the small or large oviduct. It is easy to be certain of this by dissection, for the genital receptacle floats and can be pulled or pushed aside to reveal the duct.

The vaginal opening (VO) is surrounded by a raised ring of columnar cells and leads into a vestibule (VE). In serial sections sperm and prostatic coagulate were seen along the length of vagina. The vas deferens (VD) is continued beyond the tip of the penis by a squat coupling style (Fig. 2B). The large oviduct (LO) has its origin on the ventral surface of the exit region; it proceeds posteriorly then rises dorsally by two or three whorls (W) and turns anteriorly to the oviducal opening (OO). The hermaphrodite duct enlarges to form an ampulla (HA) that consists of three whorls which expand and uncoil as they increase in volume. The duct then narrows, but enlarges slightly near the origin of the small oviduct which runs posteriorly and enters the fertilization region. The hermaphrodite duct is continued by the vas deferens; the prostate is bilobed.

E.margaritae has a stiligerid reproductive system the main features of which are as follows: A central canal with a fertilization region and an exit region; three ducts enter the fertilization region – the small oviduct, the vagina and the duct of the albumen gland; two ducts leave the exit region – a short receptacle duct and the large oviduct. The vagina either opens to the exterior and a coupling style is present, or it ends in a bursa copulatrix and the style is of the penetrant type. The prostate is bilobed, the albumen gland ends in numerous lobules.

Marcus (1959, fig. 33) published a drawing of the reproductive system of *Stiliger evelinae* Marcus, 1959 which shows that the system is stiligerid. Rao (1937) gave a full description of *Stiliger gopali*



TEXT FIGURE 1. *Ercolania margaritae* — after Burn, 1974. 1, 2 and 3 indicate the position of penial, oviducal, vaginal openings respectively in the groove between the body and foot.

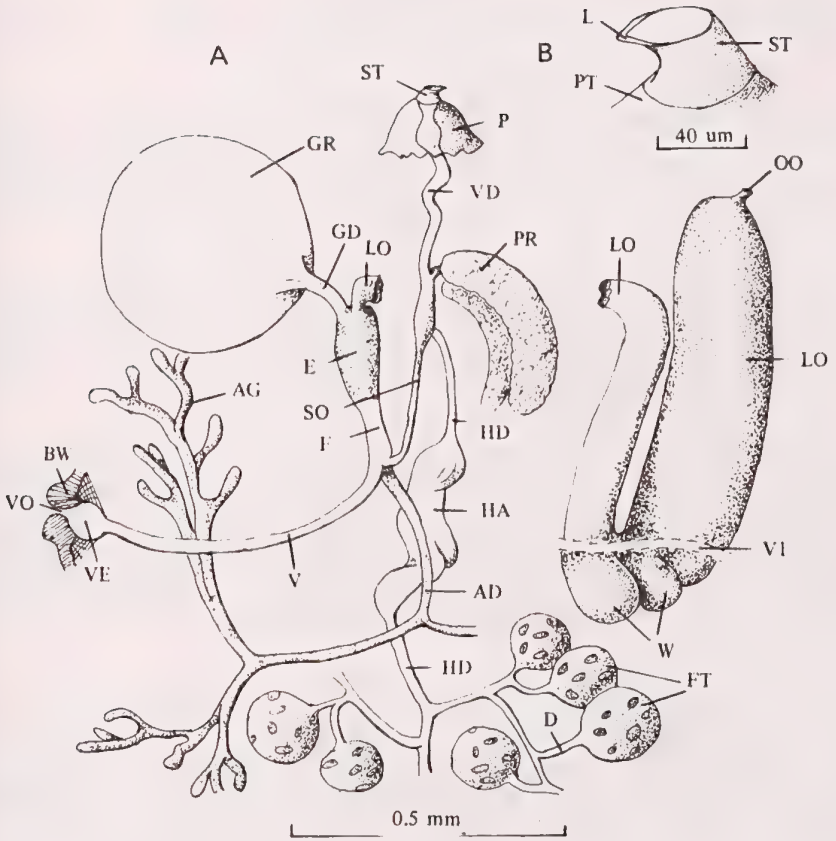
Rao, 1937. A vaginal opening is present and the penial style is of the coupling type. Although some details of the central canal region are not clearly depicted, *S.gopali* probably has a stiligerid reproductive system.

Baba and Hamatani (1970a) gave an account of a species which, in their opinion, is identical with *Stiliger ornatus* Ehrenberg, 1831. They were not able to give a complete description of the reproductive system but their figure (Plate IV, 7) shows that it is stiligerid. They also published (1970b) a description of the reproductive system of *Ercolania boodleae*. The vagina ends in a bursa copulatrix affixed to the body wall; the style is of the penetrant type. The receptacle duct, however, is shown connected to the large and small oviduct. Baba courteously sent the writer specimens of *E.boodleae* and dissections showed that the large and small oviduct are not connected to the receptacle duct; the system therefore is stiligerid.

Seven European sacoglossans were examined; five had stiligerid reproductive systems, the exceptions were *Alderia modesta* and *Hermaea bifida*.

The penial style of *Calliopaea oophaga* (Fig. 3B,ST) is 350 um long, the first part has a diameter of 10 um, it then tapers to a whip-like extension of diameter 2 um. To accommodate this remarkable style during copulation the vagina is lengthened by a loop which widens to form an ampulla (VA). The prostate is bilobed, the albumen gland lobulated. The arrangement of ducts around the central canal conforms to the stiligerid pattern.

Placida dendritica has a penetrant style of length 50 um (Fig. 4B), the vaginal entrance is closed by a large ovoid bursa attached to the body wall. The prostate is bilobed and lobules of the albumen gland enter the cerata. Fig. 4A was drawn from a preparation; the central canal is somewhat out of



TEXT FIGURE 2. A, Reproductive system of *Ercolania margaritae*. B, Penial style.

A FUNCTIONAL INTERPRETATION

Sperm route

Sperm pass from the follicles of the ovotestis (FT) into the hermaphrodite duct (HD). When they reach the ampulla (HA) they are stored temporarily. During copulation sperm are driven forwards along the vas deferens (VD) and on the way secretion from the prostate (PR) is added. The penis (P) is thrust into the vestibule (VE) and sperm are delivered through the style (ST). The sperm are stored along the length of the vagina until required.

Egg route

Eggs move from the follicles into the ampulla (HA) and pass down the small oviduct (SO) to the fertilization region (F) of the central canal. Here the eggs are fertilized and each is coated with albumen. They pass out of the exit region (E) into the large oviduct (LO) where they are wrapped in a coat of mucus. The egg-string passes out of the body through the oviducal opening (OO).

position, nevertheless, it shows a stiligerid disposition of ducts. During one dissection eggs were seen in the dilated small oviduct (SO) and the vas deferens was tough and narrow – perhaps eggs are prevented from entering the vas deferens by its occlusion during egg-laying.

In 1848 Hancock described the anatomy of *Limapontia nigra* (= *L.capitata*) and his drawing, reproduced in Fig. 5, shows the reproductive system to be stiligerid. For the present paper eight specimens of *Limapontia cocksi* and *L.depressa* and eight of *L.capitata* were examined. Each species has a stiligerid reproductive system with the hermaphrodite duct attached to the left lateral corner of the exit region. Special attention was paid to the attachment area. In all dissections and preparations no duct was seen to enter the exit region in this area.

Specimens of *L.capitata* collected near Carna, Ireland, possessed an interesting variation of the stiligerid pattern (Fig. 6). The hermaphrodite duct led directly to the fertilization region and gave off a minute small oviduct, it then proceeded along the left side of the central canal and joined the vas deferens. The penetrant styles of *L.capitata* and *L.cocksi* are alike and in each species the vaginal entrance is closed by a bursa copulatrix. *L.depressa* has a coupling style distinctive of the species; the vagina swells near its opening to form a large ampulla.

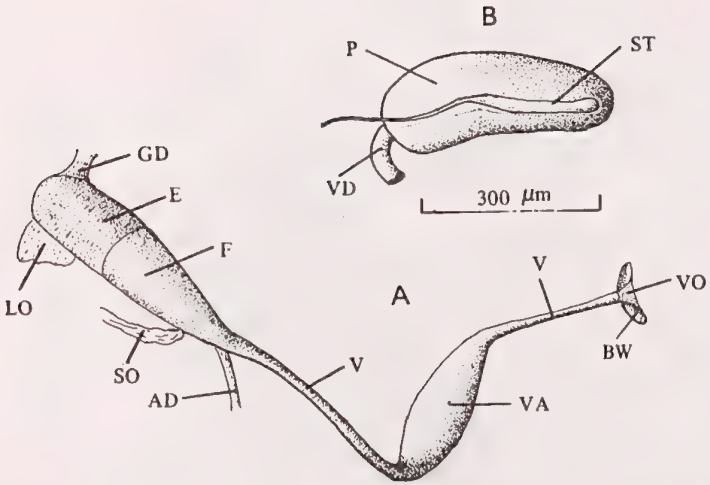
Alderia modesta was examined because it was regarded as belonging to the Stiligeridae by Thiele (1931) and Franc (1968). It was difficult to dissect and the writer was grateful for the assistance provided by the previous work of Marcus and Marcus (1956, Figs. 17 and 19). The follicles of the ovotestis have no ductules, they lie in the pockets of two large sacs which are continued dorsally into an ill-defined ampulla (HA) – this is a unique and possibly archaic arrangement. The prostate (PR) is large but not bilobed. The penetrant style (Fig. 7B) is of length 110 um and diameter 10 um, it bears a single row of spines (in number about 35 and of length 4 um) along its inner curve. The style is distinctive of the species. During copulation it pierces the dorsal surface of the body at random (Hand and Steinberg, 1955).

The small oviduct (SO) originates near the junction of the ampulla and vas deferens. It is soon joined by the vagina (V) which is terminated by a small bursa (BC) situated some distance from the body wall. The albumen gland consists of two lateral branches with numerous lobules; the two branches unite posteriorly. The albumen duct (AD) arises from the posterior part of the gland and runs forward alongside the large oviduct to join the small oviduct a short distance before the latter enters the large oviduct. The entrance to this junction is dome-shaped and is termed a cupola (CU); it stained dark-red with Safranin O. There is no genital receptacle. The large oviduct reaches almost to the end of the body before it loops and runs forward to the oviducal opening.

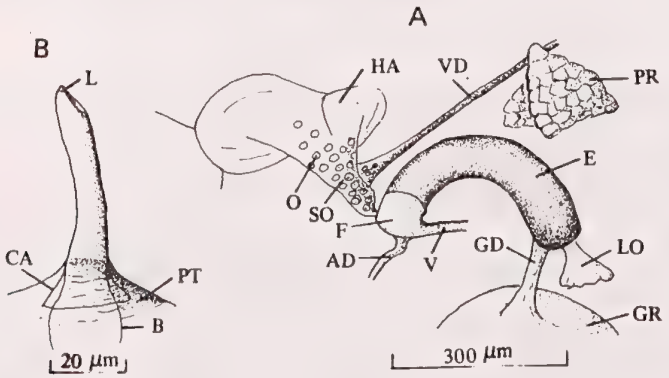
Hermaea bifida and *Placida dendritica* each have two genital openings. In both species the male opening is situated near the base of the right rhinophore. The penis of *H.bifida* ends in a tentaculiform extension (Fig. 8B,TE). *Caliphylla mediterranea* A.Costa, 1867 has a similar penial tentacle which is cuticularised near the end; and so has *Hermaeina smithi* Marcus, 1961, the end bearing a backward projection. The penis of *P.dendritica* differs in that it has no tentacle and is armed with a short penetrant style (Fig. 4B). The prostate of *H.bifida* is small and not bilobed; it is like that of *Hermaeina smithi*, whereas *P.dendritica* has a large, bilobed prostate that is characteristic of the Stiligeridae.

H.bifida has about 50 follicles in the ovotestis, *P.dendritica* has over 200. The albumen gland of *P.dendritica* ends in numerous lobules, some of which extend into the cerata. *H.bifida* has an unusual albumen gland that consists of many thick-walled capsules (AC) of length 0.5mm and width 0.2mm; the capsules are arranged in longitudinal rows along the sides of the body and do not appear in the cerata.

The female duct of *P.dendritica* bifurcates forming a vagina and an oviduct; *H.bifida* has no separate vagina, the female duct functioning as a vagina during copulation and, later, as an oviduct for the passage of eggs. Thus the second genital opening in *H.bifida* is both a vaginal and an oviducal opening, whereas in *H.dendritica* it is only an oviducal opening, foreign sperm entering the



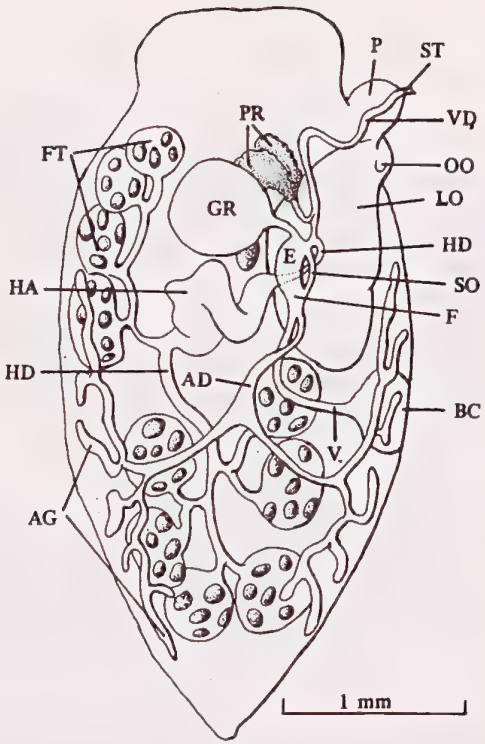
TEXT FIGURE 3. *Calliopaea oophaga*, essential features of reproductive system. A, Central canal and vagina drawn approximately to the same scale as the penis. B, Penis and penial style.



TEXT FIGURE 4. *Placida dendritica*. A, Central canal region. B, Penial style.

vagina after they have been injected hypodermically into the bursa copulatrix. Near its origin the female duct of *H.bifida* swells to form a fertilization chamber (FE) which receives the long ducts of the bursa copulatrix (BC) and the genital receptacle (GR). The bursa lies ventrally between the folds of the oviducal loop and the receptacle is situated on the anterior dorsal surface of the genital mass. In serial sections the receptacle and bursa contained sperm. After the entry of the albumen duct (AD) the female duct enlarges to form an ampulla (FA) which is strengthened at each end by a cupola (CU). The duct then assumes its former diameter and proceeds ventrally to the female opening.

The oviducal loop (Fig. 8A) is bulky and occupies most of the anterior half of the body. It folds on the right side towards the median line and forms a dorsal, secondary loop. When the partner's penis



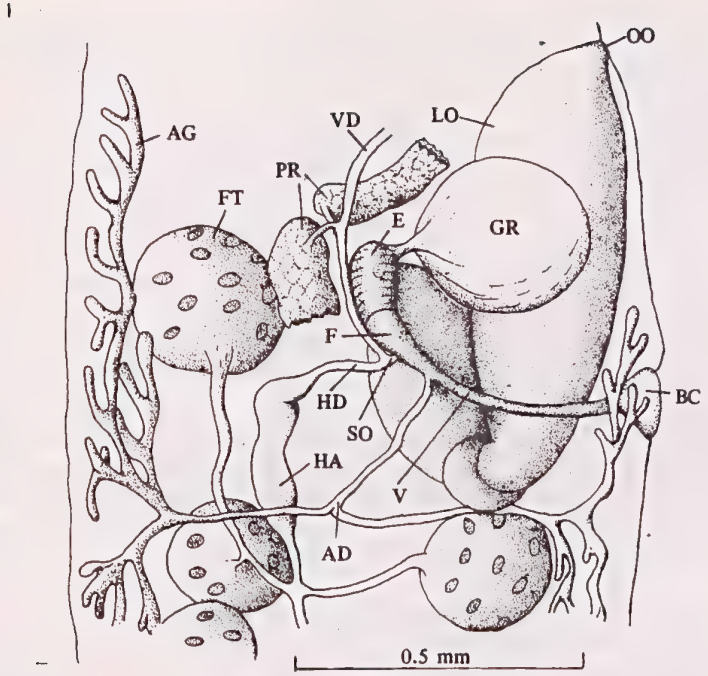
TEXT FIGURE 5. Reproductive system of *Limapontia capitata* — after Alder and Hancock, 1848. In 1847 Hancock dissected *L.capitata* using a lens (x20), some needles, and a compressor. Considering the animals were about 4mm long this was indeed a remarkable achievement.

The details around the central canal were most likely obtained from a ventral view and in making the final drawing from his sketches Hancock omitted to readjust the ducts entering the central canal to suit a dorsal view — hence the small oviduct appears on the right instead of on the left.

is inserted during copulation the combined length of the penis and tentacle ensures that foreign sperm do not enter the oviducal loop. The female duct and the beginning of the loop are both ciliated near their junction and this assists in directing the eggs on to their proper course around the oviducal loop.

Examination of serial sections showed that *H.bifida* is strikingly protandrous. In a young animal in male phase each follicle was full of sperm in all stages, the eggs were small and formed a discontinuous layer below the germinal epithelium, a few occupied small protusions on the surface of the follicle. In the female phase the follicles have prominent lobes containing eggs; sperm are seen only near the ductules. (Fig. 8C).

The reproductive system of *H.bifida* may function in the following way. In the male phase the penis is thrust into the partner's female duct and sperm are delivered into the female ampulla and travel to the bursa. During the female phase the eggs are fertilized and then coated with albumen. They may be retained for a short while in the female ampulla from which they move in single file into the oviducal loop where they are coated with various mucoids and finally are extruded through the female opening as an egg-mass.



TEXT FIGURE 6. ***Limapontia capitata*** **(Carna specimen), dissection sketch of the genital region (drawn with the aid of a stereoscopic microscope at a magnification of x50).**

DISCUSSION

There are several reasons why the classification of the Stiligeridae remained unsatisfactory for so long. Some species are rare, many are cryptically coloured, and few experts collect them. Despite this, great progress has been made. The family Stiligeridae is a tropical-subtropical group and almost half the known species have been discovered within the last fifty years, in Japanese, Australian and American waters. *Ercolania* spp. are rare in the Mediterranean, probably because it is now polluted, but Burn's discovery of *E.margaritae* in Port Philip Bay, Victoria, shows that the genus is still extant and at least one species can be described as locally common and seasonally abundant.

Most stiligerid species are small and their nervous and reproductive systems are complicated. They are difficult to dissect or to reconstruct from serial sections, consequently in descriptions of species external features were over-stressed and internal anatomy neglected. Confusion has arisen from this, for, as will be shown later, species can look alike yet differ considerably in their anatomy.

Authors of standard reference works were obliged to rely mainly on external features when writing their synopses of the Stiligeridae, but some ignored the anatomical details that were available. Franc (1968) dispensed with the family Alderiidae and gave the

characters of *Alderia* as: anus posterior, mid-dorsal; body flattened; foot longer than the body; cerata claviform. The characters selected give no indication that *Alderia modesta* is in many respects an aberrant animal. Its circulation is remarkable, for it has no heart (Engel, Gaerts and Altena, 1940; Evans, 1953). It has a complex, two-layered gut that has been well described by Evans (1953) and Marcus and Marcus (1956). The reproductive system has several unusual features and copulation is by random hypodermic injection. Since the circulatory, alimentary, and reproductive systems are unlike those found in the Stiligeridae this justifies placing *Alderia modesta* in a separate family.

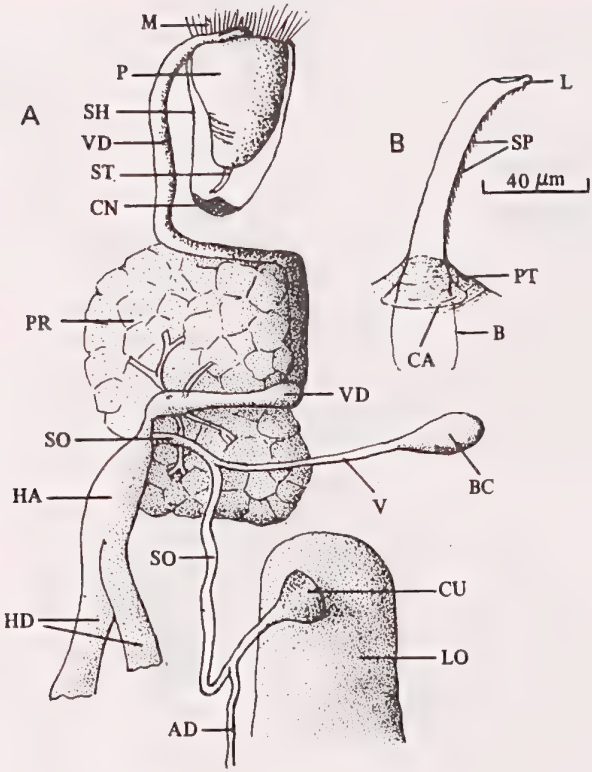
Some stiligerid species are difficult to classify for they resemble in appearance those in other genera, as the names *Hermaea, Hermaeina, Hermaeopsis* imply. A knowledge of the internal anatomy of these species is of great importance and should be given due weight. *Alderia nigra* (Baba, 1937) in a general way looks like *Alderia modesta.* In 1968 Baba published an anatomical description of *A.nigra* which showed that it has none of the aberrant features of *A.modesta.* From his account it is clear that the nervous, reproductive, and alimentary systems of *A.nigra* are those of a stiligerid species. *A.nigra* should have been transferred to the Stiligeridae; however, the evidence provided by internal anatomy was not properly evaluated. The species was retained in the Alderiidae and placed in a new genus *Alderiopsis* (Genus 1).

Baba and Hamatani (1970a) gave a workable key of the Stiligeridae based on the shape of the rhinophores, teeth, penial style, and whether the genital system is triaulic or diaulic. If triauly is defined by the condition that the male duct, oviduct, and vagina each open separately to the exterior, then, to avoid confusion, the key should include another category, 'pseudo-diaulic'. A schema of diauly, triauly, and pseudo-diauly is given in Fig. 9.

Whilst dissecting the reproductive system of each species the rest of the anatomy was examined and external features noted. With this information a classification of the Stiligeridae was drawn up in order to give due prominence to the anatomy of the species and in particular to show how the reproductive system might be deployed. The problem of *Stiliger-Ercolania* complex has been avoided and type-species are not given (the species cited are those which the writer has dissected) for these and other taxonomic matters, it was considered, would obscure the point of the exercise. Key characters are printed in italics.

Family STILIGERIDAE Iredale and O'Donoghue, 1923. Central nervous system with a *short visceral loop bearing only two ganglia.*

A stiligerid reproductive system consisting of a central canal, into which the small oviduct, vagina, and albumen duct enter at one end, and at the other end the short receptacle duct and large oviduct originate; albumen gland extensive, closely applied to the gut; prostate compact, bilobed; penis with a coupling or penetrant style; vagina open or closed; hermaphrodite duct free from, or attached to, the exit region of the central canal.



TEXT FIGURE 7. *Alderia modesta.* **A, Genital region. B, Penial style.**

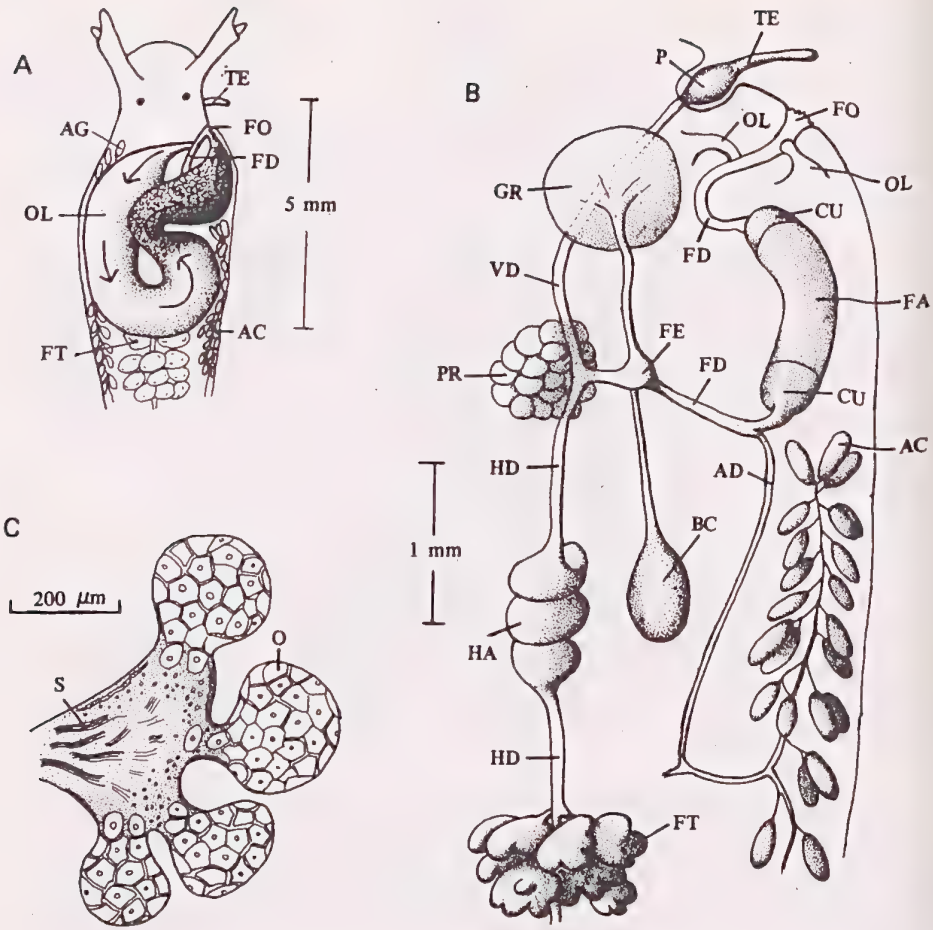
Subfamily STILIGERINAE

External features. Eolid-like animals of size 4-10mm; colour variable; foot rounded anteriorly, ending in a tail; head with a *pair of simple or auriculate rhinophores;* labial lobes indistinct; no tentacles; eyes set at the base of the rhinophores; anus and renal pore anteriorly placed on the dorsal surface near the median line; black melanin vesicle close to anus; *a variable number of cerata;* penis near the base of the right rhinophore; penial opening, oviducal opening, vaginal opening (or bursal swelling) on the right side in the order given.

Internal anatomy. Radula with sabot- or awl-shaped teeth, gut simple, two main lateral branches, lobules extending into the cerata. Heart with a ventricle and auricle in a pericardial cavity; kidney a simple sac attached to the pericardial wall, renal pore minute; reproductive system as for the family, hermaphrodite duct free from exit region of central canal, lobules of the albumen gland enter the cerata; the vaginal entrance may be closed by a bursa copulatrix attached to the body wall; if the vagina opens to the exterior it may have an ampulla along its length.

Genus 1. *Stiliger* Ehrenberg, 1831. Species with no marked variations from the characters of the family.

Stiliger fuscatus Gould.



TEXT FIGURE 8. Reproductive system of *Hermaea bifida*. A, Oviducal loop. B, Display diagram of genital complex. C, Transverse section of a follicle in female phase.

Genus 2. *Ercolania* Trinchese, 1872. Rhinophores long, cylindrical; anus, renal pore, black melanin vesicle on the anterior rectal spout; *pericardial prominence continuous with a long renal ridge* underneath which the kidney extends as a blind tube; lower limb of radula long and straight; teeth retained on ribbon, 4-5 tooth-rudiments.

Ercolania margaritae Burn

Genus 3. *Placida* Trinchese, 1876. *Rhinophores auriculate;* cerata numerous; anus and renal pore on anterior rectal spout; teeth awl-shaped, lower limb of radula long and curved; discarded teeth retained on ribbon, 5-6 tooth-rudiments.

Placida dendritica (Alder and Hancock)

Genus 4. *Calliopaea* Orbigny, 1837. Small, (1-3mm); rhinophores short, few cerata, teeth awl-shaped,

some broader than others, discarded teeth retained on radula ribbon, three tooth-rudiments; *penial style very long* (350 um), *open vagina lengthened by a loop* which bears an ampulla; 1 species feeds on the eggs of tectibranchs.

Calliopaea oophaga Lemche

Genus 5. *Olea* Agersborg, 1923. Small (1-6mm); rhinophores short; few cerata; barrel-shaped buccal mass; *radula vestigial;* penial style minute; vagina ends in a bursa copulatrix; 1 species feeds opisthobranch eggs.

Olea hansineensis Agersborg

Subfamily LIMAPONTINAE

External features. Slug-like snimals of size 4-8mm. *No cerata; no rhinophores* (except *L.cocksi*); colour light fawn to black, sometimes with lighter areas or spots over the body and tail; *eyes set in pale patches on the side of the head;* anus and renal pore on dorsal surface near median line but more posteriorly placed than in Stiligerinae; genital openings as for Stiligerinae.
Internal anatomy. Gut of two main lateral branches with lobules; melanin-black vesicle close to anus; lower limb of radula short and straight; teeth sabot-shaped, discarded teeth not retained on ribbon, three tooth-rudiments (except *L.cocksi*) *hermaphrodite duct attached to the exit region of central canal.*

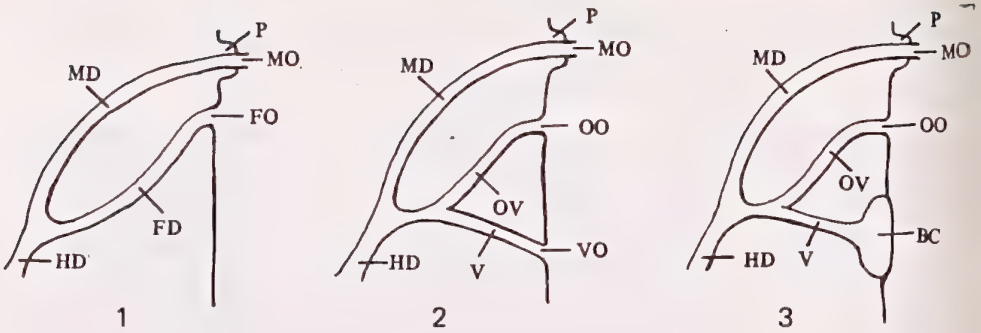
Genus 1. *Limapontia* Johnston, 1836. Characters those of the subfamily.

Limapontia capitata (Müller)
L.depressa Alder and Hancock
L.cocksi (Alder and Hancock)

Boettger (1959) showed that the central nervous system forms the basis of classification in the Sacoglossa. He grouped families with only two ganglia on the visceral loop into the superfamily Stiligeroidea; the genera concerned are *Stiliger, Ercolania, Placida, Calliopaea, Olea, Limapontia, Hermaea, Alderia.* The Stiligeridae forms the greater part of Boettger's group so that in the preceding classification the family has two main characters.

Thiele (1931) restored the order Sacoglossa after Pelseneer had separated it into shelled and unshelled groups; he divided *Hermaea* into three genera. He classified the Stiligeridae into the genera *Hermaeina, Physopneumon, Hermaea, Stiliger, Alderia,* and the family Limapontiidae into *Acteonia* and *Limapontia.* Pruvot-Fol (1954) rightly stressed the importance of the species, and followed, perhaps too closely, the classification of Trinchese. According to Pruvot-Fol the genera of Stiligeridae are *Stiliger, Hermaea, Aplysiopsis, Placida, Hermaeina, Ercolania. Alderia* is placed in the family Alderiidae. The Limapontiidae is grouped with the Elysiidae in the section Pellibranchiata. Baba and Hamatani (1970a) listed the genera of Hermaeidae (=Stiligeridae) as *Calliopaea, Ercolania, Stiliger, Placida, Hermaea, Hermaeopsis, Hermaeina, Costasiella.*

The name Stiligeridae is apt and was used by Thiele and Pruvot-Fol; it is now well established in the literature and there is no zoological advantage to be gained by replacing it by Hermaeidae. The following changes are welcome for they remove much of the dead wood. *Physopneumon* is not considered to be a good genus; it included as subgenera *Placida, Hermaeopsis, Physopneumon* (s.s.), and the generic description would fit *Hermaea bifida.* Lemche and Thompson (1974) gave valid reasons for regarding *Hermaeopsis* as a junior subjective synonym of *Hermaea. Hermaeina* and *Aplysiopsis* are generally accepted as synonyms with *Aplysiopsis* having priority.



TEXT FIGURE 9. Schema of genital openings and main ducts.
1. DIAULY (MO;FO) — as in *Hermaea bifida* and *Hermaeina smithi*.
2. TRIAULY (MO;OO;VO) — *Ercolania margaritae*, *Limapontia depressa*, *Calliopaea oophaga*.
3. PSEUDO-DIAULY (MO;OO) — *Ercolania boodleae*, *Limapontia capitata*, *Placida dendritica*, *Olea hansineensis*.

The Limapontiidae should not have been grouped with the Elysiidae. *Elysia viridis* has three ganglia on the visceral loop (Russell, 1929) and its reproductive system is unlike that present in the Limapontiidae. Reasons have been given for discarding the genus *Acteonia* (Gascoigne, 1973). Sufficient is now known about *Olea* to include it in the family Stiligeridae.

Gonor (1961) described the internal anatomy of *Hermaeina smithi*. Its reproductive system is diaulic, its visceral loop bears three ganglia, and in some features it resembles *Caliphylla mediterranea*. The genus *Aplysiopsis* (=*Hermaeina*) would be better placed in the family Caliphyllidae than in the Stiligeridae. The writer has recently dissected a *Costasiella sp.* Its gut is primitive, there are three ganglia on the visceral loop, its reproductive system is not stiligerid. The genus *Costasiella* could be placed in the family Caliphyllidae as a temporary measure.

Placida dendritica is pseudo-diaulic and *Hermaea bifida* is diaulic – from this stems many of the differences previously noted in their reproductive systems. *H.bifida* and *Caliphylla mediterranea* are both diaulic, their penes are of the same type, both species are markedly protandrous. Each has a large anterior diverticulum of the gut, their radulae and teeth are similar. *H.bifida* is more closely related to the family Caliphyllidae than it is to the Stiligeridae. In the genus *Limapontia* the absence of cerata and rhinophores is of little consequence when compared with the internal anatomy. *Limapontia capitata* has a gut of two main branches with minor lobes; the central nervous system has two ganglia on the visceral loop; the heart and circulation, the renal organ call for no special comment; the reproductive system is stiligerid – therefore *Limapontia* can be included in the Stiligeridae.

A comparative study of the reproductive system shows that the genera may be arranged as follows:

(Diaulic group)
Family: CALIPHYLLIDAE
Hermaea
Aplysiopsis (?)
Costasiella (?)
Family: ALDERIIDAE
Alderia

(Triaulic and pseudo-diaulic group)
Family: STILIGERIDAE
Subfamily: STILIGERINAE
Stiliger
Ercolania
Olea
Calliopaea
Placida
Subfamily: LIMAPONTINAE
Limapontia

This arrangement provides a sound anatomical basis for the Stiligeridae and simplifies matters by removing the diaulic genera.

The taxonomic conclusions resulting from this study are:

1. The family Alderiidae should be retained and *Alderia nigra* transferred to the Stiligeridae.
2. The family Limapontiidae can be dispensed with and the genus *Limapontia* transferred to Stiligeridae.
3. *Hermaea dendritica* be placed in the genus *Placida.*
4. *Hermaea bifida* be transferred to Caliphyllidae.
5. *Olea* can be regarded as a genus of Stiligeridae.

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