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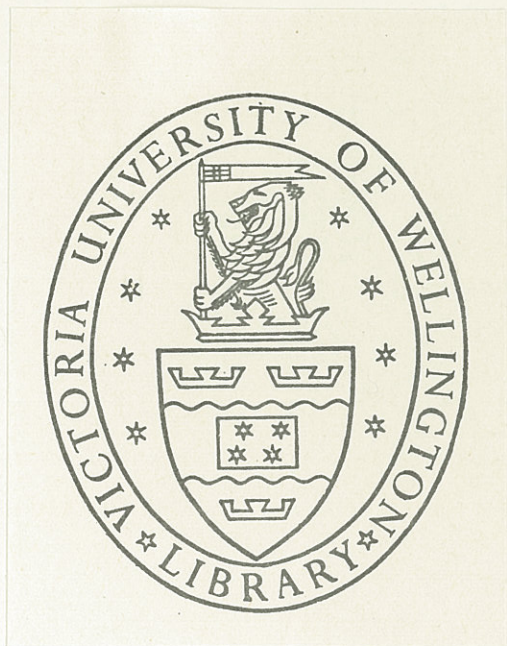
ANATOMY, HISTOLOGY AND FUNCTION OF THE REPRODUCTIVE SYSTEM OF THE TRACHEOPULMONATE SLUG *ATHORACOPHORUS BITENTACULATUS* (Quoy and Gaimard).

D. W. Burton.

ABSTRACT

The reproductive system of *Athoracophorus* is described in detail from serial sections and found to be basically similar in structure and histology to those found in species from other families of terrestrial slugs. The term "oviducal gland" is substituted for the terms "glomerate gland" and "uterus" previously used, and the reasons for this are discussed. Functional aspects of the system are examined.

INTRODUCTION

Until recently, the New Zealand and Subantarctic Athoracophoridae have been a somewhat neglected group. Most workers on the Athoracophoridae have confined their attention to taxonomy and anatomy, and little has been paid to the finer details of their organisation, or to their ecology, development, feeding habits, breeding behaviour, and genetics. There are, of course exceptions, one of the more notable being a contribution by Plate (1898), who investigated the structure of the dorsal tracheate lung and of the renal system in some detail. However examination of reproductive systems has always been limited to dissection alone.

Reproductive systems of a number of species of New Zealand Athoracophoridae have been described by Hutton (1881), Plate (1898), Suter (1913), Burton (1962, 1977), and Climo (1973). The most obvious differences in anatomy between the various species lie in the relative arrangement of the prostate gland (referred to as the bulbose gland by Suter), the uterus, the spermatheca, and the oviducal gland. The naming of the oviducal gland has caused considerable confusion in the past; it has been variously referred to as the glomerate gland by Suter (1913) and Burton (1962, 1977), as the shell gland ("schalenblaschen"—literally shell bubble) by Plate (1898), and as the uterus by Climo (1973). Names put forward for a similar structure in other families of terrestrial slugs include "female gland" in *Arion ater* (Smith, 1966), "nidamental gland" in *Philomycus carolinianus* (Kugler, 1965) and "oviducal gland" in *Agriolimax reticulatus* (Boyne, 1966). Out of this nomenclatural plethora the term "oviducal gland" was finally selected for two reasons. First, the reproductive system of *Athoracophorus bitentaculatus* appears very similar in structure and function to that of *Agriolimax reticulatus*. Second, the lumen of the gland does form the oviduct; the uterus is a much more muscular structure, and quite different in function.

The present study describes the form of the reproductive system and some of its histological features, and the object of the paper is to provide a foundation on which to base further studies on the histochemistry and function of the reproductive systems of the Athoracophoridae, and on their breeding cycles.

MATERIAL AND METHODS

Adult specimens of the slug *Athoracophorus bitentaculatus* were collected from the leaf bases of a flax plant *(Phormium tenax)* in Ngaio, Wellington, from March to September. The animals were narcotised in a relaxed state in mentholised water according to the method of Abdel-Malek (1951). The entire reproductive system was dissected free with the aid of a binocular microscope, fixed in Bouin's solution for three hours, placed in a saturated solution of lithium carbonate in 70% isopropanol for 1 hour, and stored in 70% isopropanol until required. After dehydration, the material was placed in chloroform overnight rather than in xylol, as it was found that clearing in xylol, even for periods as short as 30 minutes, rendered the tissues of the albumen gland very hard and brittle. The entire reproductive system was then embedded in 56°C —melting point paraffin wax and serially sectioned at 7 μm. Sections were stained in either Ehrlich's haematoxylin and alcoholic eosin, or in Masson's trichrome stain, or with PAS, using Delafield's haematoxylin as a nuclear stain.

To facilitate the construction of a sectional diagram of the reproductive system, every 6th section was photographed, and relevant portions of the photographs were traced to build up a composite picture.

GROSS ANATOMY

The reproductive system of the slug *Athoracophorus bitentaculatus* consists essentially of a gonad capable of producing eggs and sperm simultaneously, and a compound tubular passageway through which the sperm and eggs are conveyed externally. Three different major glands feed into this passageway; these are the albumen gland, which secretes a nutrient solution around each egg, the oviducal gland, which secretes a number of encapsulating mucus coats around each egg, and the prostate gland, which produces a secretion of unknown function in which the sperm are immersed. Portions of the passageway are lined with cilia, and the terminal portions are modified into copulatory apparatus. A cutaway diagram to show the relationship of the various structures is given in Figure 1.

The gonad consists of several lobes, closely fitted together. Each lobe consists of a number of tubular acini, each acinus being broadest at the surface of the gonad, and narrowing down to a small efferent ductule which communicates with the lumen of the hermaphrodite duct. The hermaphrodite duct is quite long, highly convoluted and of constant diameter along most of its length but narrow close to the albumen gland; it passes from the ovotestis downward and anteriorly to the medial surface of the albumen gland, which is compact, elongate, medially flattened and yellow in colour. The secretion of this gland passes into an albumen canal, embedded in gland tissue and lying close to the medial surface of the gland. The canal communicates directly with the hermaphrodite duct to form an irregularly shaped chamber, the fertilisation sac.

Two canals lead out of the fertilisation chamber. The first leads straight into the lumen of the most posterior portion of the oviducal gland. This extensive gland is folded into a number of broad convolutions with a continuous lumen. The second canal leading out of the fertilisation pocket is ciliated, and leads straight to the posterior portion of the prostate gland, where it opens into a narrow cleft which passes ventrally
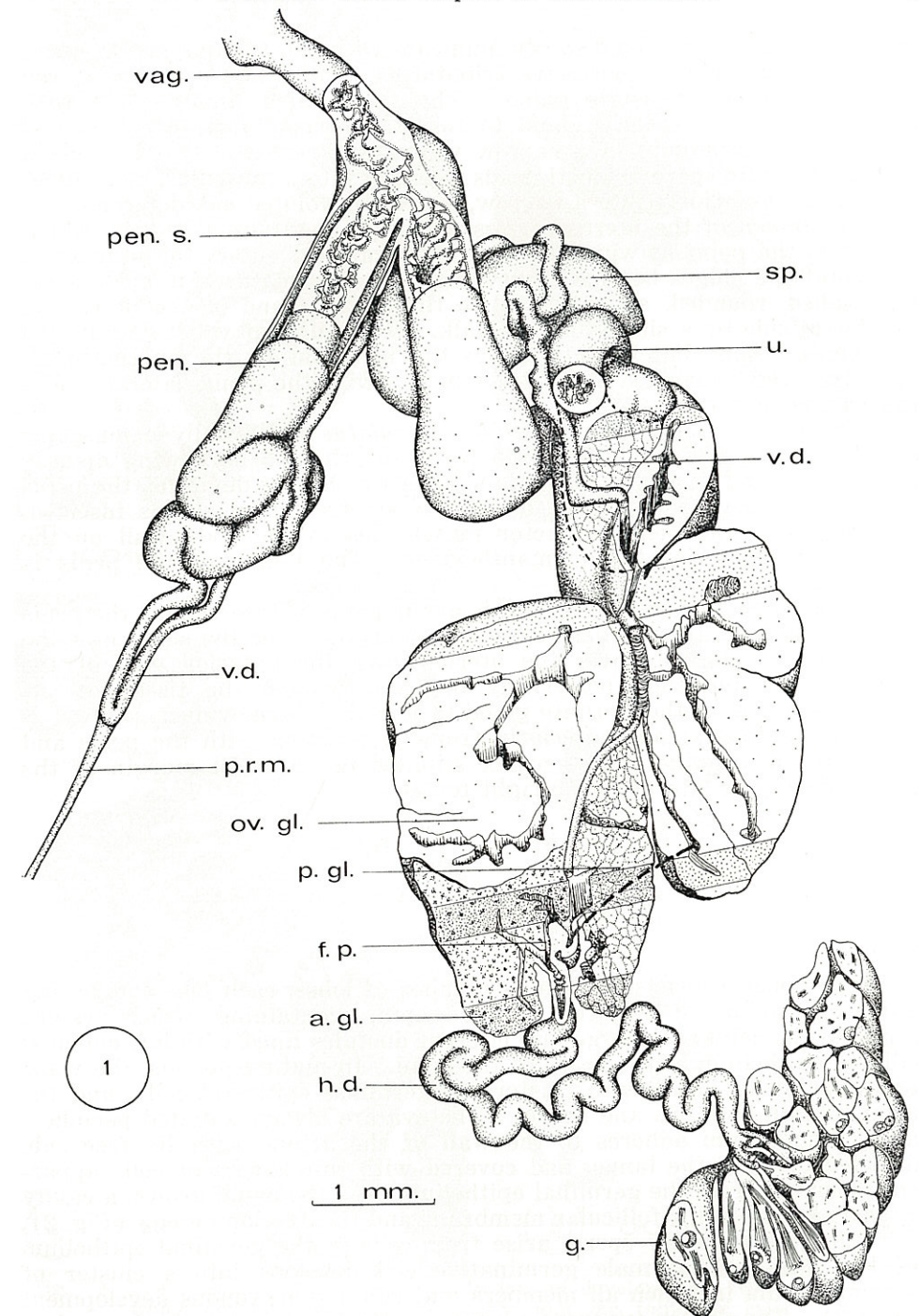
Fig. 1: Cutaway diagram of reproductive system, ventral view. Vertical component not to scale. The connection between the fertilisation pocket and the female duct is out of the plane of section, and is shown dotted.
Abbreviations: a. gl., albumen gland; f.p., fertilisation pocket; g., gonad; h. d., hermaphrodite duct; ov. gl., oviducal gland; p. gl. prostate gland; p.r.m., penis retractor muscle; pen., penis; pen. s., penis sheath; sp., spermatheca; u., uterus; vag., vagina; v. d., vas deferens.

through the prostate gland to communicate with the tubular sperm duct; this passes anteriorly to receive tributaries from other portions of the irregularly-shaped prostate gland. The sperm duct finally joins with the lumen of the oviducal gland to form a spermoviduct, which passes anteriorly to terminate in a narrow ventrally directed cleft. This cleft, at the bifurcatio spermoviducti, leads laterally into a muscular, convoluted uterus, and anteriorly into a narrow, highly convoluted vas deferens.

The lumen of the uterus carries extensive longitudinal ridges, which persist to the point at which the spermathecal duct enters the uterus; at this point the ridges become transverse. The spermatheca is moderately thin-walled, rounded, and attached to the anterior end of the uterus on the dorsal side by a short tubular stalk, the opening of which is guarded by valves. Immediately anterior to the insertion of the spermathecal duct, the uterus makes a Y-shaped junction with the penis, laterally, and the vagina, anteriorly.

The penis of *Athoracophorus bitentaculatus* is basically a muscular convoluted cylinder, contained in a penis sheath, and narrowing distally to join the vas deferens. At the junction with the vas deferens, the penis sheath merges with the penis, and a penis retractor muscle is inserted. The origin of the penis retractor muscle lies in the body wall on the dorsal side posterior to the mantle area. The lumen of the penis is heavily ridged and papillated.

From its junction with the penis at the point of insertion of the penis retractor muscle, the vas deferens runs anteriorly over the surface of the penis to pass dorsally over the uterus down the anterior wall of the spermatheca, and then posteriorly to pass through the tissue of the anterior portion of the prostate gland to join the spermoviduct.

The vagina extends anteriorly from its junction with the penis and uterus to open at the genital orifice situated in the right margin of the head shield, just lateral to the right tentacle.

HISTOLOGY

Gonad.

The gonad consists of a small number of lobes, each lobe comprising numerous acini. Connective tissue septa, containing blood vessels, separate the acini and merge into efferent ductules lined with low cuboidal ciliated epithelium at the bases of the acini. In mature gonads, the walls of the acini are lined with clusters of germinal epithelial cells, and the acini contain both ova and sperm. The ova are always situated peripherally. Each ovum adheres to the wall of the acinus with its free side directed towards the lumen and covered with thin layers of cells apparently derived from the germinal epithelium. As the ovum grows, a cavity appears between this follicular membrane and the developing egg (Fig. 2).

Like the eggs, the sperm arise from cells of the germinal epithelium of the acini. Each male germinative cell develops into a cluster of spermatogonia in which all members undergo a synchronous development (Fig. 3). The cluster apparently becomes attached to a group of germinal epithelial cells, and is arranged with the sperm heads directed towards the periphery of the acinus, and the sperm tails trailing into the lumen (Fig. 4).

In immature specimens, no ova can be seen, although numerous developing sperm may be present (Fig. 5).
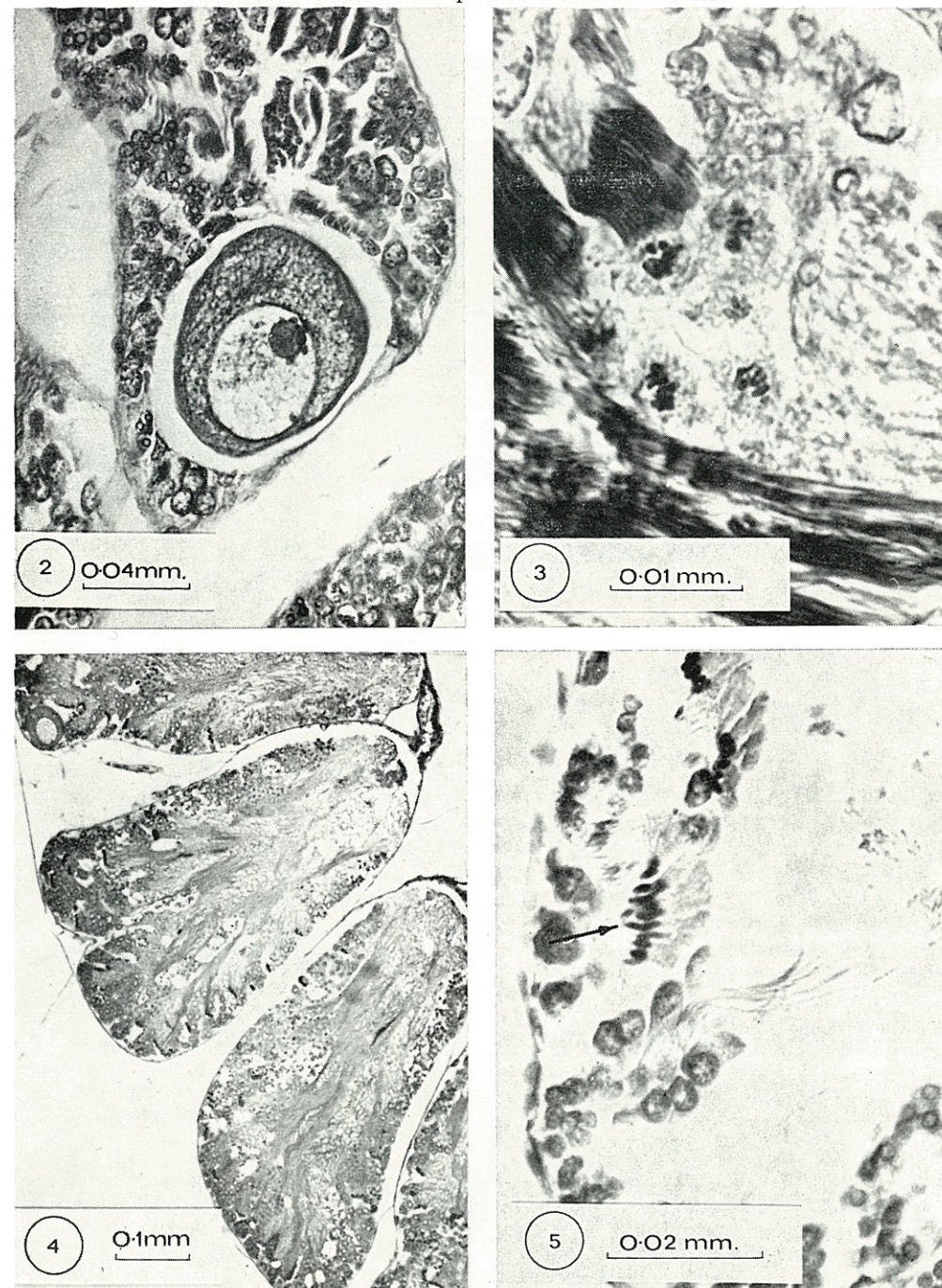
Fig. 2: Cross section of an oocyte fairly late in development, showing the cavity which develops between the oocyte and the follicular cells. Masson's trichrome stain.
Fig. 3: Synchronous divisions in a cluster of spermatogonia. Haematoxylin/eosin.
Fig. 4: Cross section of gonad. Sperm are arranged in clumps with heads close to the acinar wall, and tails trailing into the lumen of the acinus. Haematoxylin/eosin.
Fig. 5: Section through immature gonad, with developing spermatozoa (arrowed). No nurse cells are present. PAS stain.

Hermaphrodite duct.

The tubular, convoluted hermaphrodite duct has a two-layered wall, composed of a thin outer connective tissue sheath closely applied to an inner layer of simple, low columnar ciliated epithelium (Fig. 6). The epithelial cells become taller as the duct nears the albumen gland, and the duct narrows appreciably. In mature animals taken during autumn, the duct is packed with sperm for most of its length, only the end near the albumen gland being clear (Fig. 7). A few scattered flask-shaped mucus cells are present in the epithelial wall.
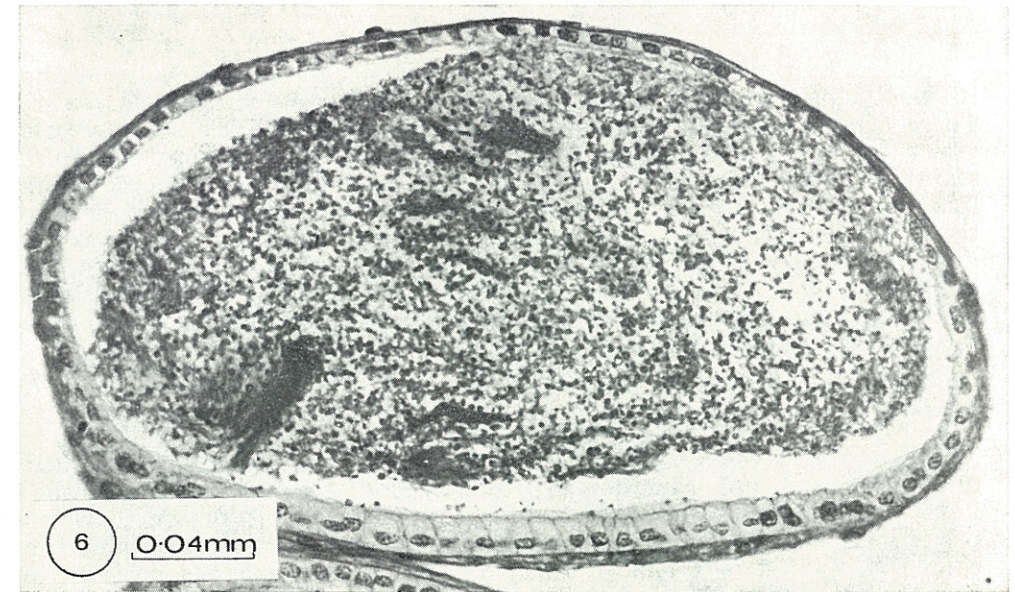

Fig. 6: Cross section of hermaphrodite duct, with ciliated cuboidal epithelium, and a packed mass of sperm in the lumen. PAS stain.

Fig. 7: Cross section of hermaphrodite duct close to albumen gland. No sperm are present, the duct is narrowed and the epithelium is columnar rather than cuboidal. Masson's trichrome stain.

Albumen gland.

The albumen gland is a compound tubular gland, the walls of the tubules being composed of large apocrine gland cells with basal nuclei. These cells contain numerous large ovoid granules, which stain a pale violet colour in haematoxylin/eosin preparations. Scattered granules stain positively with PAS (Fig. 8). A thin layer of squamous epithelium lines the tubules, which are bound together by thin sheets of connective tissue. The tubules of the albumen gland empty their transparent, nutritive secretion into the albumen canal which runs the length of the gland, and is also thinly lined with squamous epithelium. The albumen canal joins the hermaphrodite duct to form a thick-walled chamber, the fertilisation pocket (Fig. 9).

Fertilisation pocket.

The simple columnar ciliated epithelium of the hermaphrodite duct undergoes an abrupt transition to a thick, pseudostratified, ciliated epithelium with a minutely lobulated surface upon reaching the fertilisation pocket. At the level of entry of the hermaphrodite duct and albumen canal, the pocket is U-shaped in cross section, but expands dorsally to form an irregular chamber with thick walls composed of irregularly-shaped cells with basal nuclei and minutely granulate cytoplasm. A thick connective tissue sheath supports the fertilisation pocket, and strands of connective tissue pass through its walls. Close to the origin of the sperm duct the pocket is lined by ciliated cuboidal epithelium containing a few scattered large goblet cells.

Male duct.

The walls of the male duct as it emerges from the fertilisation pocket are composed of ciliated low simple columnar epithelium, supported by a thick outer layer of connective tissue. As the male duct passes anteriorly over the folds of the prostate gland, receiving ciliated ductules from the prostate gland at several points (Fig. 12), the epithelium of the wall gradually changes to simple ciliated cuboidal epithelium. Subepithelial mucus-secreting cells are present in the wall. The duct varies in section from a deep cleft to a round tube, and in the anterior section it is in open communication with the lumen of the oviducal gland to form a spermoviduct (see Fig. 11).

Female duct and oviducal gland.   (Fig. 10)

The female duct forms the lumen of the extensive, broadly convoluted oviducal gland, and is irregular and capacious. It communicates directly with the sperm duct near its anterior end. The oviducal gland is mainly composed of long, relatively narrow cells, with a central irregular nucleus and very pale cytoplasm; a few interspersed smooth muscle cells can also be seen. Connective tissue sheaths the gland, and the lumen is lined with a thin layer of simple squamous epithelium. No cilia are present. Near the bifurcatio spermoviducti the gland cells are somewhat smaller, the epithelial lining of the lumen considerably thicker, and more connective tissue is present. The mucus-secreting cells which make up the oviducal gland do not cease at the bifurcation, but continue for a short distance into the uterus as a subepithelial layer.
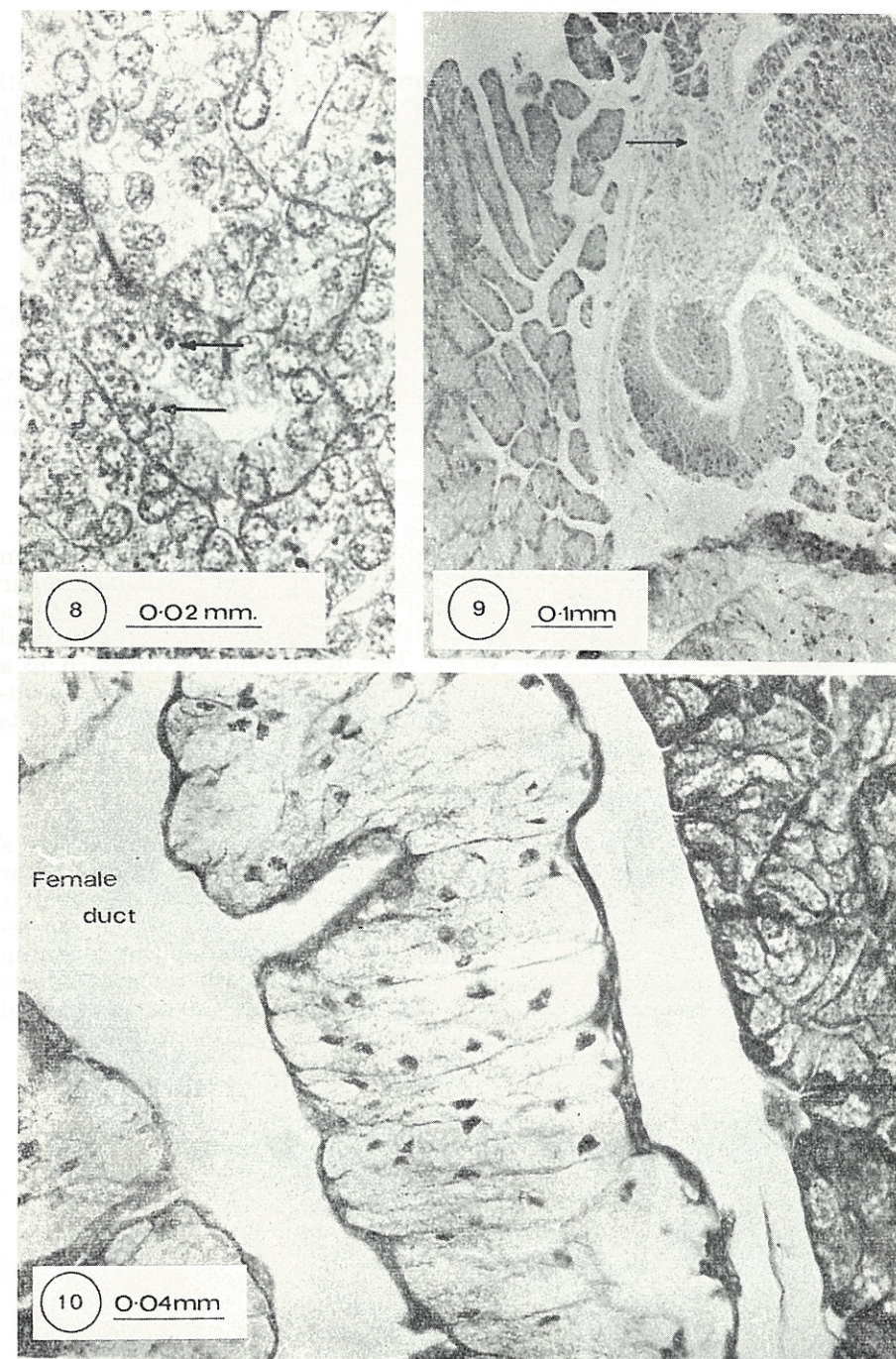
Fig. 8: Section of albumen gland of mature specimen, showing strongly PAS-positive granules (arrowed).

Fig. 9: Section through fertilisation pocket. The hermaphrodite duct (arrowed) joins the fertilisation pocket close to its junction with the albumen canal. Haematoxylin/eosin.

Fig. 10: Section through oviducal gland. Masson's trichrome stain.

Prostate gland.

The compound tubular prostate gland is largely composed of tall pyramidal cells with rounded basal nuclei and densely, minutely granular cytoplasm. A few very narrow interstitial cells with elongate nuclei can be seen between the secretory cells. The tubules of the gland are held together by thin sheets of connective tissue, and have a narrow, ciliated lumen communicating directly with the male duct (Figs. 11 and 12).

Vas deferens.

As the vas deferens diverges from the spermoviduct its epithelial lining is composed of tall, ciliated columnar cells with prominent elongate vacuoles. The cilia disappear a short distance down the vas deferens, but otherwise the appearance of the cells remains the same along the length of the tube. A thin layer of connective tissue sheaths the vas deferens (Fig. 12).

Uterus.

As the uterus passes from the spermoviduct, the epithelium is thrown up into extensive longitudinal folds. The simple, ciliated, columnar epithelium rests on a layer of connective tissue, which is enclosed by a heavy investment of circular muscle, with a thin layer of longitudinal muscle forming the outside of the tube. The uterus spirals forward to a Y-shaped junction with the penis and vagina, and receives the spermathecal duct just posterior to this junction. A heavy layer of mucus coats the uterine wall.

Spermatheca and spermathecal duct.

The spermatheca is simply a large two layered sac, sheathed by a thin layer of connective tissue and lined by simple non-ciliated, low columnar epithelium. The epithelial cells contain large vacuoles similar to those in the epithelium of the vas deferens. As the wall of the spermatheca merges into the spermathecal duct, the cells of the epithelial lining become taller and the connective tissue thicker. Smooth muscle invests the walls of the duct, and the duct's entrance into the uterus is guarded by valves.

Fig. 11: Section through prostate gland and developing oviducal gland of immature specimen, showing the relationship between the male and female grooves. Masson's trichrome stain.

Fig. 12: Section along male groove, with tributaries from prostate gland. Masson's trichrome stain.

Penis.

As the vas deferens nears the distal end of the penis, its wall becomes thickened by a dense layer of circular muscle. This layer merges into the penis sheath, and becomes separated from the penis proper by a fluid-filled space. No longitudinal muscle fibres are present in the sheath. Inside the sheath, the heavily convoluted and folded penis is lined by ridged columnar epithelium resting on connective tissue and surrounded by an inner circular and an outer longitudinal muscle layer. Thick mucus lines the lumen of the penis. As the penis nears its junction with the uterus and vagina, the folding and ridging of the epithelium becomes more prominent, and the muscle layers thicker. The penis sheath merges with the penis at the junction with the uterus and vagina (Fig. 14).

Vagina

The vagina is similar in structure to the uterus but the muscle layers of its walls are thinner.
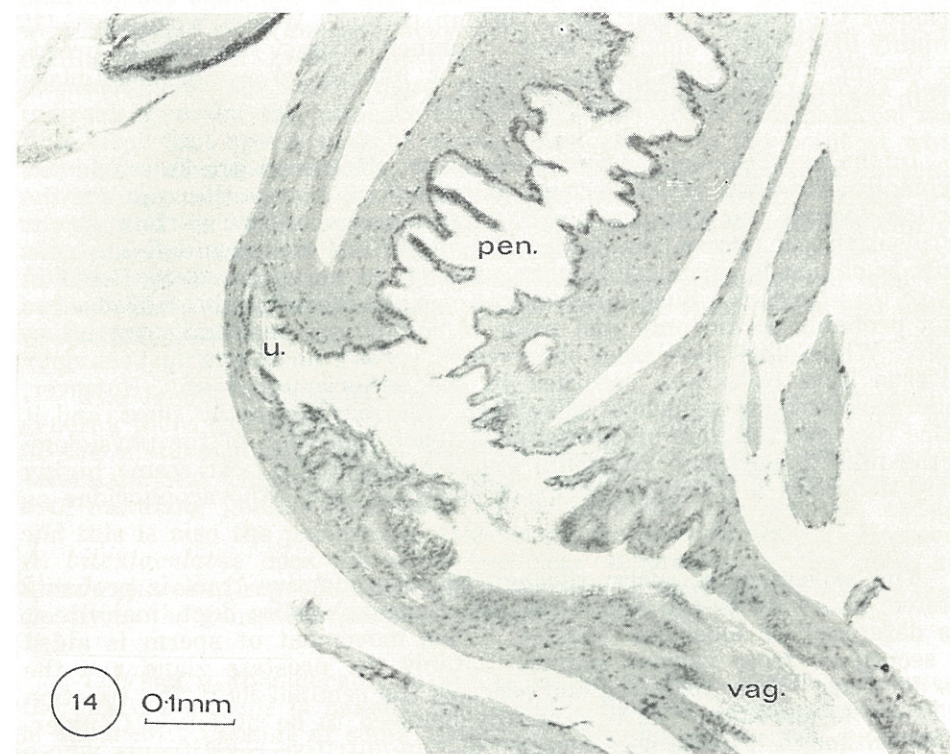
Fig. 13: Section across vas deferens, Masson's trichrome stain.

Fig.   14: Section through junction of penis with uterus and vagina. The bulk of the uterus lies out of the plane of section. Haematoxylin/eosin.

DISCUSSION

Published accounts of the reproductive systems of various species of New Zealand Athoracophoridae generally agree fairly closely. Most accounts show the prostate and oviducal glands as discrete structures, with only minor differences in morphology between the species. An exception is *Pseudaneitea ramsayi* (Climo, 1973) in which the prostate gland and the oviducal gland (called the uterus in Climo's description) form an elongate, intertwined, irregular complex up the central axis of the reproductive system. A similar pattern can be seen in the reproductive system of *Athoracophorus bitentaculatus* and this arrangement is quite different from that seen in *Pseudaneitea papillata*, for example (Burton, 1962). It is still not clear whether a basic difference in the form of the reproductive system does exist, or whether it is due to seasonal or growth factors.

Functional aspects.

Athoracophorus bitentaculatus, like other pulmonate Gastropods, is hermaphroditic, and has a complex reproductive system. This system appears to be capable of producing both eggs and sperm for a considerable period of the year, at least from Autumn through Winter to Spring. It is highly likely that a slug will mate a number of times through the breeding season. When this mating occurs, a number of events take place within the reproductive system to facilitate it.

In the male system, sperm produced by the gonad are stored in the hermaphrodite duct, which becomes distended with sperm, except for the portion nearest the albumen gland. The passage of sperm through the fertilisation sac, down the male duct, and into the vas deferens and penis is obviously not a continuous process, as no sperm were found in any of these organs. Such a movement of sperm through the reproductive tract probably occurs only just prior to copulation, or during copulation itself. While slugs have been observed *in copulo*, no courtship behaviour patterns have ever been recorded in the Athoracophoridae. However, elaborate courtship sequences have been described for many slugs, and it seems that one function of courtship is synchronisation of the physiology of the mating partners (Runham and Hunter, 1970). It seems highly likely that such a courtship sequence occurs in the Athoracophoridae as well.

The movement of sperm through the reproductive tract is probably passive, as all ducts are either ciliated (hermaphrodite duct, male duct, vas deferens) or muscular (penis). This movement of sperm is aided by secretions from various sources, notably the prostate gland and the vas deferens. The prostate gland secretes the seminal fluid, the function of which is uncertain. It is generally believed to be nutritive (Kugler, 1965), although it contains a number of non-nutritive constituents whose function is unclear (J. M. Cummins, pers. comm.). In *Philomycus carolinianus*, subepithelial glands of the spermatic groove produce mucus which binds the sperm together into a sperm thread. Similar subepithelial mucus glands are present in *Athoracophorus bitentaculatus*.

In summary, the sperm is produced by the gonad, stored in the hermaphrodite duct, probably until the onset of courtship, passed by ciliary action through the fertilisation sac and along the spermatic groove to be bound by mucus secretions into a sperm thread, then reaches the vas deferens at the bifurcatio spermoviducti, and passes down into the eversible penis for insertion into the vagina of the mating partner. Once inserted into the vagina, the sperm mass enters the spermatheca, and is apparently stored there until required. The exact mode of sperm transfer into and up the duct of the spermatheca is not known, but the penis would certainly extend as far as the opening of the duct when fully inserted into the vagina, and it is conceivable that the penis could inject the sperm mass directly into the spermatheca. Holm (1946) in studies on *Lymnaea stagnalis appressa* Say, observed that in comparatively young snails, nearly all the sperm transferred at the time of copulation passed into the receptacle, and few sperm were seen in the upper vagina. Furthermore, the sperm in the spermatheca of *Athoracophorus bitentaculatus* is, for the most part, still in a compact, mucus-bound mass, and it seems unlikely that they could swim unaided into the receptacle.

Ikeda (1937) determined that in the slug *Meghimatium bilineatus* the spermatophores received during copulation were retained for a period in the genital atrium, where the sperms were loosened from the sperm mass, and lost their tails. The tailless sperms were then passively conveyed to the spermatheca and stored until oviposition. No tailless sperm were observed in *Athoracophorus bitentaculatus* and this agrees with the finding of Kugler (1965) for the slug *Philomycus carolinianus*. In *A. bitentaculatus*, the sperm mass retained within the spermatheca tends to break up under the influence of the secretions of the spermathecal wall. It is clear that sperm may be moved passively up to the point at which they enter the spermatheca, through either ciliary action or muscular movement. However, the lumen of the uterus is thickly coated with mucus, and its walls are non-ciliated. Presumably, the sperm swim unaided up the uterus to the fertilisation pocket, and if this is the case it follows that the function of the secretions of the spermathecal wall may be twofold, in that they loosen the sperm from the sperm mass and induce sperm capacitation.

The female system is functionally less complex. In pulmonates in general, there is a continuous production of ova, sperm and nutritive cells in the mature gonad, except towards the end of the breeding season (Runham and Hunter, 1970). Smith (1966) observed that in *Arion ater* maturing gonads commence sperm production before ova appear, and this is also the pattern in *Athoracophorus bitentaculatus*. However, *A. bitentaculatus* does not show the clear separation of the male and female phases of reproduction seen in *Arion ater*, and thus conforms more closely to the generally accepted pulmonate pattern.

The egg is considerably larger than the efferent ductule. However, the efferent ductule is heavily ciliated and, like the hermaphrodite duct, is apparently capable of some distention. As the egg is oval, passage of the egg through the narrow efferent ductule probably presents little difficulty. The hermaphrodite duct is normally packed with sperm, but as copulation takes place some time before egg laying, sperm would be cleared from the hermaphrodite duct in time to allow the passage of the ova for fertilisation in the fertilisation pocket. The fertilised ova then

receive the nutritive secretion from the albumen gland, and pass to the oviducal gland to receive a layered, gelatinous shell. The eggs then pass down the uterus to be laid in clusters of 15 to 20; they are round, papillate, gelatinous, light yellow, and up to 3 mm. in diameter.

Overall the organisation of the reproductive system of *Athoracophorus bitentaculatus* shows a striking similarity to that of other slugs, such as *Agriolimax reticulatus* and *Arion ater*. Some differences do occur, such as the enclosure of the penis in a penis sheath and the partial separation of the male and female ducts, but the organisation and histology of the reproductive tract of these species is similar enough to underline once again the conservativeness characteristic of the Mollusca.

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CHROMOSOME NUMBERS IN TWO SPECIES OF *PSEUDANEITEA*
(Athoracophoridae: Gastropoda)

ABSTRACT

A Chromosome count of n=44 has been recorded for both *Pseudaneitea papillata* and *P. aspera*.

INTRODUCTION

Chromosome numbers in molluscs are generally very conservative, and the haploid number seldom varies by more than one or two between the species of a particular family (Burch, 1965; Patterson, 1969). This is not always the case, however; the family Succineidae of the stylommatophoran suborder Heterurethra has species with chromosome numbers varying from n=5 to n=25 (Patterson 1969, 1970). The only other heterurethran family for which chromosome numbers have been recorded is the family Athoracophoridae, which is found on the New Hebrides, New Britain, the Admiralty Islands, the east coast of Australia, New Zealand, and the subantarctic islands. *Aneitea* sp. from the New Hebrides has 44 pairs of chromosomes (Patterson, 1969), and *Triboniophorus graeffei* from New South Wales also has 44 pairs of chromosomes (Burch and Patterson, 1971). These are by far the highest chromosome numbers known for any stylommatophoran land snail, the next highest number reported being n=34 for two slugs of the genus *Milax* (Beeson, 1960).

It has been suggested that the high chromosome numbers found in the Athoracophoridae could be the result of polyploidy (Burch and Patterson, 1971). Clearly cytological studies on the New Zealand species of the family are necessary.

MATERIALS AND METHODS

A large specimen of *Pseudaneitea papillata*, collected from Karori, Wellington, was narcotised in an infusion of tobacco in water. The gonad was removed after four hours, and fixed in two changes of Newcomer's fluid (Newcomer, 1953). Chromosome squashes were stained with aceto-orcein.

The same technique was used for a specimen of *P. aspera*, collected from the Orongorongo Valley.

RESULTS

Cells undergoing male diakinesis in the ovotestis of *P. papillata* had 44 bivalents (Fig. 1). Therefore, this species has the same chromosome number as *Aneitea* sp. of the New Hebrides and *Triboniophorus Graeffei* of Australia. A similar chromosome number was recorded from *P. aspera* (Fig. 2).

DISCUSSION

It is clear that the New Zealand Athoracophoridae have been separated from their relatives in Australia and the New Hebrides for a very long time, and the sharing of a common chromosome number shows that the group displays the same cytological conservativeness seen in most other snail groups. It is still not possible to determine whether the high chromosome number found in the Athoracophoridae has resulted from polyploidy.

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(1) P. papillata
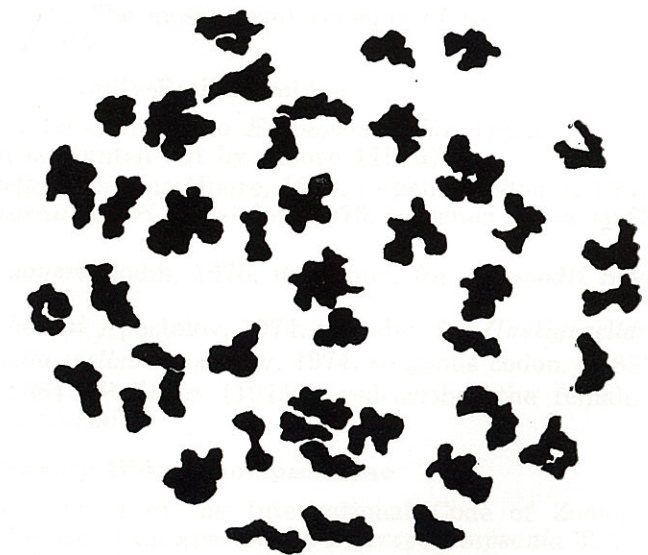
(2) P. aspera   0·01 mm

Figs. 1 and 2: Diakinesis chromosomes (male) from **P. papillata** and **P. aspera.**

KEYS TO AID IN THE IDENTIFICATION OF MARINE HARPACTICOID COPEPODS

Amendment Bulletin No. 1.

by

J. B. J. Wells,

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INTRODUCTION

The purpose of this bulletin is to illustrate one way in which information that has appeared in the literature since publication of my Keys (Wells, 1976) can be incorporated in them. Also, since the Keys were designed to be useful to non-specialists in harpacticoid taxonomy such bulletins (I hope to publish them at regular intervals) may serve to bring to the user's attention all the recent taxonomic literature. In this first bulletin I take the opportunity of correcting errors in the Keys. Some I have noticed myself but my attention has been drawn to others by several colleagues; to them I extend my grateful thanks. Hopefully few now remain but I would welcome notice of any that have as yet gone undetected.

In this bulletin the word *codon* is introduced as the term for the set of character states that characterize a taxon or group of taxa.

Family Canuellidae

1. There are two errors in the Key, correct as follows (p.19):
   Brianola elegans   6:4:4:4 / 6:5:4:4 / a / 3 / 6
   B. sydneyensis   5:4:4:4 / 6:5:4:4 / a / 3 / 6
2. General Notes (p.20): The most recent revision of this family is by Por, 1967, not Por, 1969.

Family Ectinosomidae

1. Family name must be changed to *Ectinosomatidae* (pp.27-36); the faulty latinization is pointed out by Moore (1976).
2. KGG 1: *Arenosetella monensis* Moore, 1976, to genus codon (p.28).
3. KGG 100: *Ectinosoma soyeri* Apostolov, 1975, to genus codon (p.29).
4. KGG 300 (p.33):
   (a) *Hastigerella soyeri* Bodin, 1976, nom. nov. for *H. noodti* Soyer, 1974.
   (b) *Hastigerella bodini* Apostolov, 1974, to codon for *Hastigerella*[a].
5. KGG 500: *Noodtiella wellsi* Apostolov, 1974, to genus codon (p.35).
6. General Notes (p.36): Pallares (1975b) redescribes the female of *Halophytophilus fusiformis*.

Family D'Arcythompsoniidae

As Articles 27 and 32(c) of the International Code of Zoological Nomenclature forbid the use of an apostrophe *D'Arcythompsonia* T. Scott must be corrected to *Darcythompsonia* and the family name changed accordingly. Corrections are required on pp.6, 8, 37, 38 and 39.

Family Harpacticidae

1. KGG 1 (p.43) : *Perissocope exiguus* Pallares, 1975d, new codon—
   2 / 3 :3 :3 / p / 7 :8 :7 / 5 :6 :5.
2. KGG 100 (p.45) :
   (a) *Harpacticus nipponicus* Ito, 1976, to codon for *Harpacticus*[c].
   (b) *Harpacticus septentrionalis yamadai* Ito, 1976 ; add superscript[a] to the species in footnote b) on p.46 and add the subspecies to item 2 in General Notes (p.47).
   (c) *Harpacticella paradoxa* is redescribed by Ito & Kikuchi (1977) ; delete from footnote d) (p.46) and add new codon—
   nor / 7 / 1 ♀ / 5 :5 / 0-1 :5.

Family Tisbidae

1. *Tisbe varipes* Marcus, 1974a, to genus codon in KGG 100 (p.49).
2. For the genus *Scutellidium* (KGG 100, p.49 and General Notes, p.52) note this information :
   (a) Branch (1975) suggests—
   S. spinatum is a synonym of *S. ringueleti*,
   S. purpurocinctum is a synonym of *S. arthuri*,
   S. loureiroi and *S. deseadensis* possibly are synonymous with *S. lamellipes*, which itself may be a synonym of *S. longicauda*.
   (b) *S. arthuri* is redescribed by Ito, 1976.
   (c) *S. macrosetum* Branch, 1975, *S. caeneus* Ito, 1976, *S. hirutai* Ito, 1976, and *S. longicauda acheloides* Ito, 1976, all to genus codon in KGG 100.
   (d) *S. boreale* Ito, 1976 and *S. hippolytes akaba* Ito, 1976 to codon for *S. hippolytes* in KGG 100; amend footnote c) appropriately.

Family Peltidiidae

1. KGG 1 (p.53) :
   (a) *Neopeltopsis pectinipes* Hicks, 1976, new codon—
   1 / 2 / 0 :0 :0 / 1 :1 :1 / d :d.
   (b) *Eupelte acutispinis* Zhang & Li, 1976, new codon—
   2 / 2 / 0 :0 :0 / 2 :2 :1 / d :d.
2. KGG 100 : *Paralteutha minuta* Ramirez, 1971, to genus codon (p.55).
3. p.55 : Note that *Paralteutha villosa* is redescribed by Pallares (1975b).

Family Thalestridae

1. KGG 1 :
   (a) *Idomene cookensi* Pallares, 1975b, to codon for *I. scotti* (p.58).
   (b) *Dactylopodia pectenis* Pallares, 1975d to codon for *D. pontica* (p.59).
   (c) *Diarthrodes ponticus orientalis* Apostolov, 1975; add superscript[a] to species in footnote b) (p.60) and add the subspecies to item 2 in General Notes (p.69).
   (d) *Diarthrodes tetrastachyus* Yeatman, 1976, new codon—
   2 :3 / 7 :8 :8 / 2 :2 / 3 / p :f.

2. KGG 100 (p.61) :
   (a) *Dactylopodia decostata* Pallares, 1975d, to genus codon.
   (b) *Paradactylopodia hexiarticulata* Kunz, 1975, to genus codon.
3. KGG 400 : *Parathalestris patagonica, P. vinosa, P. aurantiaca,* all new species by Pallares, 1975d, to genus codon (p.64).
4. General Notes (p.69) :
   (a) Pallares (1975b) redescribes *Parathalestris ganio*.
   (b) Pallares (1975c) describes the male of *Paramenophia platysoma* (KGG 300, p.63).

Family Parastenhelidae

The description of *Parastenhelia reducta* Apostolov, 1975, requires a note of this new species in item 7 on p.12. Also, in the Key to Families, item 47 sub. 5 (p.10) now must read "with 4 :4-5 :4-5 . . . .", but note that this species will also key out in item 47 sub. 2 and then in item 49 sub. 2, to Thalestridae.

Family Diosaccidae

1. KGG 100 : *Robertgurneya soyeri* Apostolov, 1974 and *Robertgurneya* sp. Apostolov, 1973, to codon for *R. oligochaeta* (p.73).
2. KGG 110 : *Amphiascoides bulbiseta* Pallares, 1975e, to codon for *Amphiascoides*[d] (p.74).
3. KGG 210 (p.78) :
   (a) *Typhlamphiascus typhlops:* It is now known that P.4 Enp. 2 has an inner seta in populations from the Maldive Islands, Germany, Sweden and Spitzbergen (Becker, 1970). It is not known if Sars' original description is correct. Consequently the species must be added to footnote a).
   (b) *Typhlamphiascus lamellifer capensis* Kunz, 1975, new codon—
   5 / 5 / 5 :6 / ?
   (also, this species must be added to KGG 200 (p.76) where it keys out with *T. typhlops*).
4. KGG 230 and 240 : *Amphiascus elongatus* Ito, 1972 : The present codon in KGG 230 (p.80) applies to the female only. The species requires a new codon in KGG 240 (p.81)—
   tr / sw / 5-6 :6 / 2 :6.
5. KGG 240 : *Amphiascus longarticulatus* Marcus, 1974b, to codon for *A. tenuiremis* and *A. gracilis* (p.81).
6. KGG 260 : *Paramphiascopis triarticulatus* Moore, 1976, to genus codon (p.84).
7. KGG 400 (p.86) :
   (a) *Stenhelia (D.) oblonga* and *S. (D.) elisabethae:* Codons for these species are wrong. The correct codon for both is—
   4 / 7 :8 :8 / 8 / d :f / lss.
   (b) *S. (D.) normani:* Codon on p.86 applies only to subspecies *normani*. The codon for the other subspecies *(n. polluta* and *n. acutirostris)* is—
   4 / 7 :8 :8 / 8 / d :f / lss.
   (c) *S. (D.) bifida* Coull, 1976, new codon—
   5 / 6 :6 :7 / 8 / d :d / lss.

8. KGG 500 (p.88): *Stenhelia (D.) palustris bispinosa* Bodin, 1970, new codon—

    3:3:2 / 6:7:6 / 0:0:0.

    Also, indicate in KGG 400 (p.86) that the codon refers to the nominate subspecies only.

Family Ameiridae

1. *Leptomesochra* sp. Bodin, 1970 is identified by Bodin (1972) as *Mesochra pygmaea;* delete from KGG 1 (p.102).

2. KGG 1:
   (a) *Karllangia tertia* Kunz, 1975, to codon for *K. psammophila* (p.101).
   (b) *Parapseudoleptomesochra dubia* Kunz, 1975, new codon (p. 102)—

    3:3 / 3:3:3 / 3:3:2 / 4 / 0.

3. KGG 300 (pp.107-108):
   (a) *Sarsameira elegantula* Kunz, 1975, new codon—

    s / 1:1:1 / 1:1:1 / 4:4:4 / 2.
   (b) *Stenocopia longiseta:* Kunz (1975) describes the female (see footnote a).
   (c) *Nitocrella stygia* Apostolov, 1976 and *N. hibernica bulgarica* Apostolov, 1976, are not this genus but *Nitocra;* to codon for *Nitocra*[c].
   (d) *Psyllocamptus (Langpsyllocamptus) longisetosus* Kunz, 1975, new codon—

    s / 0:0:0 / 0:0:0 / 3:3:3 / 1-2.

4. KGG 330 (p.111): *Nitocra sewelli huntsmani* Kunz, 1976, new codon— 7:7:7 / 1:1:1 / 5:6 / 3:6,
    and indicate in KGG 500 (p.117) that the codon refers to the nominate subspecies only.

5. KGG 400 (p.114):
   (a) *Ameira usitata* is redescribed by Kunz (1975): delete from footnote b) (p.116) and add new codon—

    0:0:0 / 1:1:1 / 1:1:1 / 4:5:5 / 4:5 / 3(?) :5.
   (b) *Psyllocamptus (Langpsyllocamptus) quadrispinosus* Kunz, 1975, new codon—

    0:0:0 / 0:0:0 / 0:0:0 / 3:3:3 / 5:4 / ?.

6. *Psyllocamptus* is divided by Kunz (1975) into two sub-genera:

    Psyllocamptus s.str. for *monachus* (KGG 1) (p.101), *carolinensis* (KGG 1) (p.101), *propinquus* (KGG 100) (p.105), *minutus* (KGG 200) (p.106) and *bermudae* (KGG 200) (p.106);

    Langpsyllocamptus nov. for *quinquespinosus* (KGG 300) (p.108), *longisetosus* (KGG 300) (see note 3 above), *triarticulatus* (KGG 400) (p.114) and *quadrispinosus* (KGG 400) (see note 5 above).

7. *Ameiropsis australis* Kunz, 1975: Kunz states that P.1 Exp.2 has a very reduced, hair-like inner seta. As this is not a very obvious structure it may be best to place the species in both KGG 300 and 400, with an appropriate note. In KGG 400 (p.114) place a new codon—

    1:1:1 / 1:1:1 / 1:1:1 / 4:5:5 / 5:5 / 3:5.
    In KGG 300 (p.107) *A. australis* keys out with *Sarsameira exilis* and *S. peresi*, s / 1:1:1 / 1:1:1 / 4:5:5 / 2. This codon should now lead to KGG 350, a new KGG defined as follows—

KGG 350 — characters
   1. A.1 ♀
       n — number of segments.
   2. P.2 - P.4 Exp.3
       n:n:n — number of setae and/or spines on P.2, P.3 and P.4 respectively.
   3. P.5 ♀
       n:n — number of seteae on Benp. and Exp. respectively.
   4. P.5 ♂
       n:n — number of setae on Benp. and Exp. respectively.

KGG 350

A.1.♀ segs.	P.2-P.4 Exp.3 setae	P.5 ♀ setae	P.5 ♂ setae	
9	7:7:7	5:6	5:6	*Sarsameira exilis*
9	6:7:8	5:6	?	*S. peresi*
8	6:6:7	5:5	3:5	*Ameiropsis australis* Kunz, 1975

8. Petkovski (1976) has revised *Nitocrella*. He removes some species to *Parapseudoleptomesochra* and erects two new genera, *Nitocrellopsis* and *Stygonitocrella*. He describes three new species of *Nitocrella* s.str. and follows Borutzky (1969) in placing Sterba's (1968) species *Spelaeocamptus asiaticus* and *S. reductus* in *Nitocrella* s.str. However, it must be noted that Borutzky's renaming of *S. reductus* as *N. sterbai* is not valid. Borutzky apparently was unaware that Noodt (1957) has already returned *Nitocrella reducta* (Schäfer) to the genus *Nitocra*. Sterba's original name must be restored and *N. sterbai* lapse as a synonym of *N. reducta* (Sterba). Petkovski's revision requires the following amendments to the Keys—

   (a) KGG 1:
      (i) *Nitocrella*[d] (p.102) becomes *Parapseudoleptomesochra*[d] with consequent change to footnote d) (p.104).
      (ii) *Nitocrella*[g] and [h] (p.103) become *Stygonitocrella*[g] and [h] respectively, with consequent changes to the appropriate footnotes (p.104).
      (iii) On p.102 the species *Nitocrella tridens, botosaneanui, subterranea* and *heruridensis* are removed to *Parapseudoleptomesochra* and the species *Nitocrella intermedia, elegans* and *ionelli* are removed to *Nitocrellopsis*.

(iv) On p.103 the species *Nitocrella karamani, colchica, dubia, insularis, ljovuschkini* and *orghidani* are removed to *Stygonitocrella.*

(b) KGG 600 (pp. 118-119) : The following new codons are to be added—

     4:4:6 / 1:1:1 / 2:2:2 / 2-3:4 / 2:4   *Nitocrella caraioni*
                                                  Petkovski, 1976

     4:4:6 / 1:1:1 / 2:2:2 / 0:4 / 0:5   *N. motasi*
                                                  Petkovski, 1976

     4:4:5 / 1:1:1 / 2:2:2 / 3:4 / 2:5   *N. cubanorum*
                                                  Petkovski, 1976

     4:4:5 / 1:1:1 / 2:2:2 / 0:2 / ?   *N. asiatica*
                                                  (Sterba, 1968)

     4:4:5 / 1:1:1 / 2:2:2 / 4[b) / ?   *N. reducta*
                                                  (Sterba, 1968)

with the footnote—
     b) p.5 reduced to a single plate.

(c) General Notes item 6 (p.123) : This comment now applies to the four genera *Nitocrella, Nitocrellopsis, Stygonitocrella* and *Parapseudoleptomesochra.*

Family Paramesochridae

KGG 1 (p.124) :

(a) *Caligopsyllus primus* Kunz, 1975, new codon—
     2:0:0:0 / 1 / na / 5 / nf.

(b) *Kliopsyllus* sp. Apostolov, 1973, new codon—
     2:1:1:1 / 3 / 1 / 4 / ?.

(c) The species *K. minutus, K. pseudogracilis* and *K. runtzi* (p.125) are all species of *Kliopsyllus.*

Family Tetragonicipitidae

KGG 1 (p.131) :

(a) *Phyllopodopsyllus langi* Kunz, 1975, new codon—
     a / 2wd / 2 / 3:2:3 / 5:4:5.

(b) *Phyllopodopsyllus paraborutzkyi* Kunz, 1975, new codons—
     a / 2wd / 2 / 2:3:3 / 4:4:6 . . . . . . ♀
     a / 2wd / 2 / 2:3:2 / 4:4:6 . . . . . . ♂

Family Canthocamptidae

1. KGG 1 (p.135) : *Itunella intermedia* Apostolov, 1975, new codon—
     a / 1:4 / 2:1:1:1 / 1:1:1 / 7.
The existing codon for *Itunella* characterizes the other three species of the genus—*tenuiremis, muelleri* and *bacescui.*

2. KGG 100 (p.137) : *Mesochra bodini* Kunz, 1975, new codon—
     6 / 3 / 5-6:7:7 / 5:5 / 5:5 / 2:6.

Family Cylindropsyllidae

1. *Arenopontia stygia:* Lindgren (1976) considers that this species may be only an intra-population variant of *A. arenarida* (KGG 600) (p.149).
2. KGG 600: *Arenopontia riedli* Lindgren, 1976, to codon for *A. arenarida* (p.149).

Family Cletodidae

1. Error in KGG 500 (p.164) : Character 5 should read "P.3 ♂ Enp.".
2. Soyer (1975a) describes three new species of *Mesocletodes,* all of which can be included in KGG 1 (p.154)—
M. carpinei, new codon—
     3:2 / 3:3:3 / 2:2 / 7:7:7 / 4:4.
M. bodini, new codon—
     3:2 / 3:3:3 / 2:2 / 7:7:7 / 5:5.
M. ameliae, to codon for *M. commixtus* (p.157).
3. *Cletocamptus alburquerquensis:* This species is included in *Cletocamptus[e)* of KGG 1 (p.157) by mistake. Delete from footnote e) (p.159) and add new codon—
     3:2 / 3:3:3 / 2:1 / 5:5:4 / 3:2.
4. KGG 1 (p.154) :
(a) *Australonannopus aestuarinus* Hamond, 1974, new codons—
     3:2 / 3:3:3 / 2:0 / 4:4:5 / 2:na . . . . . ♀
     3:2 / 3:3:3 / 2:0 / 4:4:4 / 2:na . . . . . ♂
(b) *Paranannopus wellsi* Soyer, 1975b, new codon—
     3:2 / 3:3:3 / 3:2 / 7:8:8 / 5:6.
5. KGG 500 (p.165) : Pallares (1975e) notes some variation in *Enhydrosoma propinquum;* add a second codon for this species—
     2:2 / a / d:3:5 / d:2:2 / ♀.

Family Laophontidae

1. *Laophonte sinifer* Kunz, 1975, to codon for *Paralaophonte spinicauda* in KGG 1200- ♀ ♀ (p.182) and to codon for *Paralaophonte[a)* in KGG 1100- ♂ ♂ (p.197).
2. *Pseudocleta corbula:* Present codon in error; correct in KGG 1- ♀ ♀ (p.172) as follows—
     3:3:3 / 1:1:1 / 5:6 / 3 / 6.
3. *Heterolaophonte cambelliensis:* P.5 ♂ can have a total of 5 *or* 7 setae. Therefore this species must be added to footnote k) of KGG 1- ♂ ♂ (p.191).
4. *Microlaophonte trisetosa* Boxshall, 1976, new codons—
KGG 1- ♀ ♀ (p.172)—
     3:3:3 / 2:2:2 / 6:6 / 1 / 6.
KGG 1- ♂ ♂ (p.188)—
     3:3:3 / 2:2 / 0:4 / 1 / 3.
5. *Phycolaophonte insularis* Pallares, 1975a, new codons—
KGG 1400- ♀ ♀ (p.183)—
     5:5:5-6 / 0:0:0 / 0:0:0 / 2:3(4) :3(4)[b) / 0:0:0.
(with new footnote — "b) P.3 and P.4 Enp. 2 have 3 setae plus a fused spine").
KGG 1- ♂ ♂ (p.190)—
     3:3:3 / 2:2 / 2:5 / 2 / 2.

6. *Cletopsyllus bacescui* Marcus, 1976:
   KGG 1600-♀ ♀ (p.184) — to codon for *Pseudocletopsyllus spiniger*.
   KGG 1-♂ ♂ (p.188), new codon—
       3:3:3 / 2:2 / 3:4 / 3 / 2.

7. *Laophonte dinocerata:* The male is described by Pallares (1975b);
   to codon for *L. inornata* and *L. sima* in KGG 1300-♂ ♂ (p.198).

Family Ancorabolidae

1. p.203 item 1: Delete entirely; *A. s. spinifera* was described by Norman in 1911 and appears in Lang's Monograph.

2. *Laophontodes whitsoni* (p.202) is redescribed by Pallares (1975b) who describes P.4 Enp.2 with only 2 setae. Also, there is an error in the existing key which puts *L. whitsoni* in a codon with *L. bicornis* and *hamatus*. Remove from this codon and replace with this new codon—
       3:2 / 2:2 / 4 / 6:7:7 / 2:2 *or* 4.

Family Latiremidae

Bodin (1975) has formally proposed that *Latiremus* Bozic is a synonym of *Delamarella* Chappuis (see p.12 of the Keys). A simple key to the sole genus of the family can be constructed.

The relationships of the family are not at all clear, although it would appear to belong to the Suprafamily Ameiridimorpha Lang. Further research is required and until then it is best to treat the family as *incertae sedis* in Harpacticoida and thus to place it at the end of the sequence of families.

KGG 1 — characters

1. A.1♀
   n — number of segments.
2. P.1.
   n:n — number of segments in Exp. and Enp. respectively.
3. P.1 Exp., distal segment
   n — number of setae and/or spines.
4. P.2-P.3 Exp.2
   n:n — number of setae on inner border of P.2 and P.3 respectively.
5. P.2-P.3 Enp.3
   n:n — number of setae on P.2 and P.3 respectively.

KGG 1

A.1♀ segs.	P.1 segs.	P.1 Exp. distal seg. setae	P.2-P.3 Exp.2 inner setae	P.2-P.3 Enp.3 setae	
8	2:2	5	1:1	3:3	*Delamarella arenicola*
9	2:2	5	1:1	2:2	*D. karamani*
9	2:2	5	0:0	2:2	*D. galateae*
8	3:2	4	1:1	3:2	*D. eximia*

TYPOGRAPHIC ERRORS

A number of typographic errors have been brought to my notice. Corrections should be made as follows:

p.18   Scottolana bulbosa *(Por, 1964)*
p.18   Scottolana bulbifera
p.40   Danielssenia stefa*nss*oni (i.e. not stefa*nns*oni)
p.44   Perissocope li*t*oralis (i.e. not li*tt*oralis)
p.52   Tisbe bulbise*tos*a
p.58   Dactylopus*io*ides macrolabris
p.60   Diarthrodes campbell*i*ensis
p.69   Dactylopodia longyearbyen*ens*is
p.76   Robertgurneya (?) arabi*c*a
p.80   Amphiascus gauth*i*eri
p.88   Stenhelia longifurca (i.e. not longifurc*ata*)
p.94   Schizopera valid*i*or
p.99   Robertsonia tenuis kiel*i*ensis
p.101   Parapseudoleptomesochra reduc*t*a
p.104   Interleptomesochra euli*t*oralis (i.e. not li*tt*oralis)
p.127   Kliopsyllus spiniger Wells, Kunz & Rao, 1975 (bibliography requires consequent amendment)
p.128   Kliopsyllus longifurca*tus*
p.129   Apodopsyllus schulzi (i.e. not schul*tz*i)
p.132   Phyllopodopsyllus bahamensis (i.e. not baham*ae*nsis)
p.141   Sewellina reduc*t*a
p.145   Leptastacus walta*ir*ensis
p.146   Paraleptastacus suprali*t*oralis (i.e. not suprali*tt*oralis)
p.149   Arenopontia nesa*ie*
p.150   Arenopontia spinicauda*ta*
p.151   Ichnusella pasquin*ii*
p.151   Psammopsyllus lim*n*icola
p.155   Metahuntemannia spinos*a*
p.156   Eurycletodes ver*i*similis
p.158   Mesopsyllus ata*rg*atis (i.e. not ata*ga*rtis)
p.165   Enhydrosoma curticauda (i.e. not curticaud*ata*)
p.165   Enhydrosoma buc*h*holtzi
p.167   Cletodes carthagin*i*ensis
p.180   Laophonte recticauda*t*a
p.181 & 182   Esola spela*ea*
p.186   Heterolaophonte campbell*i*ensis
p.196   Laophonte longicauda*t*a

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Note that Bodin (1975, 1976) has published two further additional lists to supplement his catalogue of new species.

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