ABHANDLUNGEN DER GEOLOGISCHEN BUNDESANSTALT
Abh. Geol. B.-A. | ISSN 0016–7800 | ISBN 3-85316-14-X | Band 57 | S. 69–78 | Wien, Februar 2002
Cephalopods – Present and Past | Editors: H. Summesberger, K. Histon & A. Daurer

The Pseudophallus of the Incirrate Octopoda: An Organ Specialized for Releasing Spermatophores Singly

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5 Text-Figures and 4 Tables

Octopoda Incirrata
Penis
Pseudophallus
Extensor Muscle
Terminal Organ

Contents

Der Pseudophallus der incirraten Octopoda – Ein auf Spermatophorenübertragung spezialisertes Organ

Zusammenfassung

Die incirraten Octopoda besitzen am Ende des männlichen Genitalapparates ein deutlich abgesetztes Organ, das bei Decabrachia und cirraten Octopoda kein Äquivalent besitzt. Der Terminus “Pseudophallus” wird als besser geeignet und die Morphologie und Funktion besser beschreibend den Termini “Penis” oder “Terminalorgan” vorgezogen. Die distale Spermatophorenleitung endet an ihrer Verbindung mit dem Pseudophallus, manchmal als eine mehr oder weniger deutliche Papille, die in das Lumen des Pseudophallus hineinragt. Es wird gezeigt, dass die Form des Pseudophallus bei der Bestimmung auf dem Art- und Gattungsniveau hilfreich sein kann, aber kein verlässlicher phylogenetischer Marker ist.

Das Kopulationsverhalten bei Kalmaren und Octopoden wird kurz behandelt. Es wird die Schlussfolgerung gezogen, dass der Pseudophallus der Octopoden die Funktion hat, die Einzelübertragung der Spermatophoren zu erleichtern, wahrscheinlich um den ökonomischen Einsatz der männlichen Reproduktionsressourcen zu gewährleisten. Das Vorhandensein eines Pseudophallusextensormuskels wird gezeigt. Seine wahrscheinliche Funktion ist es, die Abgabe der im Pseudophallus befindlichen Einzelspermatophore zu bewirken.

Abstract

There is a distinct organ at the end of the male reproductive system in the incirrate Octopoda that has no equivalent in the Decabrachia or the cirrate Octopoda. In preference to “penis” or “terminal organ”, the term “pseudophallus” is considered to be more appropriate and descriptive of this organ’s morphology and function. The distal spermatophoric duct terminates at its junction with the pseudophallus, sometimes as a more or less distinct papilla protruding into the lumen of the pseudophallus. The form of the pseudophallus is shown to be of some help with problems of identification at the level of species and/or genus but it is not a reliable phylogenetic marker.

Copulatory behaviour in squids and octopuses is briefly reviewed and it is concluded that the function of the octopod pseudophallus is to facilitate transfer of spermatophores one-by-one, probably ensuring more economical use of the male’s reproductive resources. The presence of a pseudophallus extensor muscle is demonstrated. Its probable function is to effect release of the single spermatophore lodged within the pseudophallus.

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1. Introduction

Characterizing cephalopod genera has long proved to be a difficult task: the genus *Octopus* CUVIER, for example, currently includes around 112 species (e.g. SWEENEY & ROPER, 1998) but among these are members of probably at least five other genera, which can be distinguished (in part at least) by the morphology of the distal region of the male reproductive tract. Although it is widely accepted that the morphology of this region is species-specific, it has rarely been described in sufficient detail to clarify the distinctions between species (but see MARCHAND, 1907), and in systematic descriptions is typically included as a small part of a standard diagram illustrating the entire dissected male reproductive system. Current work on redescriptions of octopus species in the Indo-Pacific has included a morphological study of the terminal region of the male reproductive tract in several different genera of the recent Octopodinae. In the present paper, a revised terminology for the terminal structures of the male reproductive tract is proposed, including some previously undescribed anatomical features.

The terminology used to describe the male reproductive system of cephalopods has often been based on comparisons with that of other animals such as mammals. However, there are functional and morphological differences that render some features of this comparison inappropriate. Firstly, cephalopod spermatozoa are not released freely but are packed into a specialized structure known as a spermatophore; and, secondly, the terminal region of the male system is not used as an intromittent organ during copulation (although this has yet to be confirmed for the cirrate Octopoda). Once the spermatozoa leave the testis and vas deferens, they become enclosed in spermatophore material, provision of which is the main function of the spermatophoric glands: two gland systems that at one time were given the inappropriate names “seminal vesicle” and “prostate” (see, for example, MARCHAND [1906]). This problem was discussed by MANN et al. (1970), who pointed out that many of these terms

> *“… are largely misnomers which fail to denote correctly either the morphological or the functional status of the cephalopod organs.”*

The more appropriate alternative terms spermatophoric glands I and II (replacing seminal vesicle and prostate, respectively) were provided by MARCHAND as long ago as 1907, and are widely known, but many subsequent authors seem to have found it difficult to let go of the more familiar terms borrowed from the mammalian model (see, for example, MANN et al. [1966, 1970, 1981]). The present account addresses the problem of terminology for an organ which, in the incirrate Octopoda, enables the controlled release of spermatophores one at a time at copulation. The term “pseudophallus” is introduced and it is pointed out that there is no analogue of this organ in the Decabrachia or the cirrate Octopoda. A stimulation experiment investigates the function of muscle tissue associated with the pseudophallus.

2. Methods

2.1. Dissection

The position in which the spermatophore in the pseudophallus is arranged in fixed specimens, and certain features of the junction with the distal spermatophoric duct, are characteristic of the species and genera of the incirrate Octopoda (i.e. excluding the cirrate Octopoda). These features can only be investigated by cutting open the pseudophallus. However, the reproductive organs are very delicate. Also, a number of Cephalopoda museum specimens have been damaged in recent years, and this has understandably contributed to a recent decision by the staff of the Natural History Museum, London (BMNH), to refuse permission for loans of preserved wet material from the Cephalopoda collection. This damage appears to be due to a lack of consideration and skill at dissection, so it is appropriate here to provide some details of the dissection techniques used in the present study.

With the aid of a binocular microscope and working with extreme care, the pseudophallus is opened with a slit along its lateral surface, beginning on a straight or gently curved section near the tip. This is best performed after first drawing the pseudophallus and reproductive system in situ, then removing the reproductive system from the specimen (assuming that permission for dissection of specimens on loan has been granted in writing). Insect pins (stainless steel “no. 2” [41 x 0.5 mm], or, for very small and fragile specimens, “no. 00” [41 x 0.3 mm]; Shiga Insect Pins, Japan) are used to fix the reproductive organs in position, submerged in preservative in a dissecting tray. It is emphasized that the pins are used only to gently buttress the organs with the shank of the pin and thereby hold them steady during dissection: neither the pseudophallus itself nor any other part of the reproductive system should be pierced with pins under any circumstances.

A brittle, double-edged razorblade (Feather Safety Razor Co., Osaka) is separated into two makeshift scalpel blades. Each of these is broken obliquely to form a sharp point and used to gently slit the pseudophallus, inserting the point just sufficiently to cut the pseudophallus wall without reaching (and therefore damaging) the spermatophore inside. Several blades are used for each dissection, discarding each blade after two or three small cuts, as they quickly become blunt and may then cause tearing, distortion or other damage to the pseudophallus and spermatophore. If removal of the spermatophore is required, the slit must be continued, following all the turns and folds of the pseudophallus.

When removing a spermatophore from the pseudophallus, great care is required, as often the spermatophore is poorly fixed and will easily break into fragments. Removal begins from the “oral” or “cap” end of the spermatophore (usually at the “diverticulum” end of the pseudophallus), by gently teasing free the cap filament which is often anchored in the surrounding tissue (MANN et al., 1970). The spermatophore itself is never held directly with forceps or any other instrument. Rather, the surrounding pseudophallus tissue is gently displaced, using a blunt seeker and blunt-ended forceps with non-serrated tips. After the spermatophore has been removed, the pseudophallus will return to its original shape (unless fixation was unusually poor) and, if all procedures have been performed skilfully, the incision in the pseudophallus will not be visible.

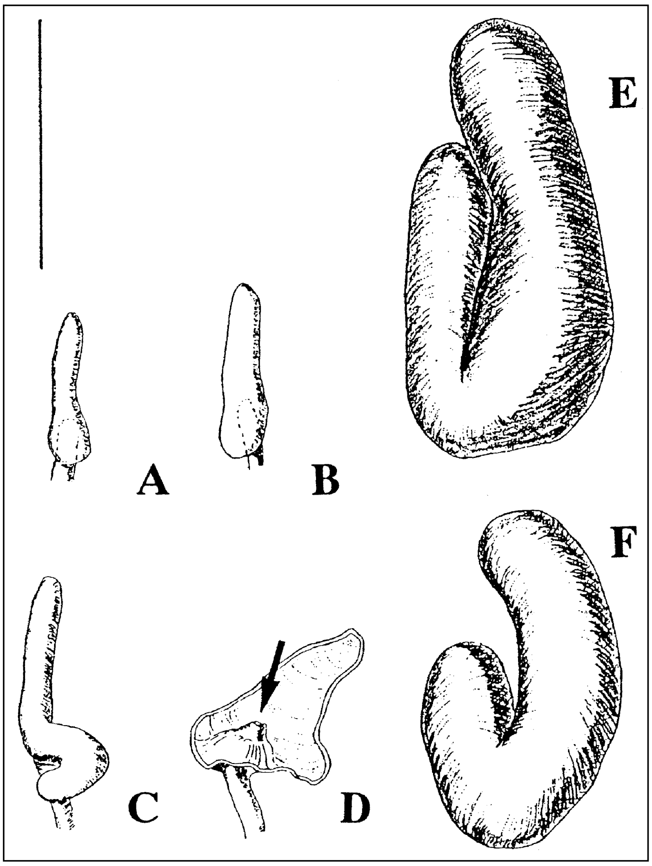
2.2. Electrical Stimulation

To investigate the action of muscle tissue associated with the pseudophallus, a stimulation experiment was performed on a young male *Enteroctopus dofleini*. Under anaesthesia with 2 % ethanol in seawater, the animal was laid ventral surface uppermost in a few centimetres of anaesthetic solution and the internal organs were exposed by opening the ventral mantle, severing the median mantle connective and folding the mantle outwards. The funnel was then slit open and part of its free tissue near the base removed on the left side to fully expose the target region. An indifferent electrode was placed in the solution bathing the animal, and the surface of the visceral sac (lying well above the level of the solution) was swabbed dry to prevent short-circuiting. Electrical stimulation was applied by gently touching the surface of different regions of the visceral sac with a sharp tungsten electrode, using a 20 Hz saw-tooth waveform at around 1V. Stimulation was first tested on the skin of one arm, where it produced a slight tightening of the skin in a discoid area of about 2 cm in diameter, which acquired a uniform pattern of tiny raised "granules".

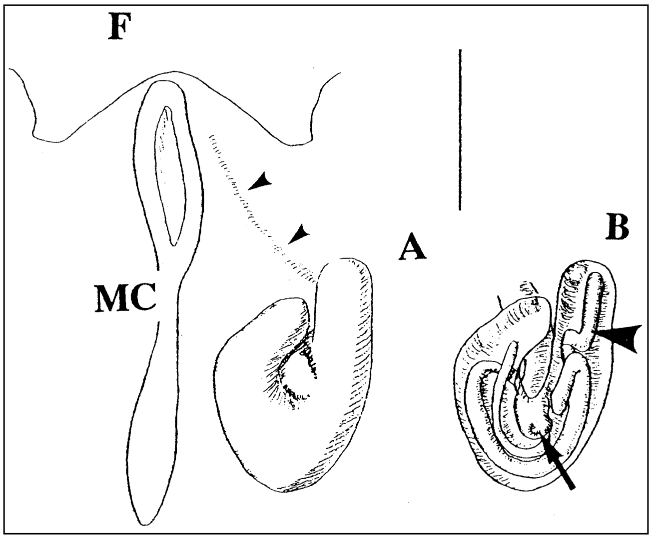
3. Results

3.1. Development of the Pseudophallus

The pseudophallus is derived from the most distal part of the distal spermatophoric duct, which is a narrowing of the exit from the spermatophoric sac (the organ of NEEDHAM, 1745). It develops from a diverticular expansion (Text-Fig. 1A–C). The rest (more proximal part) of the distal spermatophoric duct ends where it joins the pseudophallus (Text-Fig. 1D). This is sometimes in the form of a distinct papilla (Text-Fig. 1D; cf. fully grown adult pseudophallus in Text-Fig. 2B), which usually projects so as to direct the emerging spermatophore with its fatter ("aboral") end towards the anterior of the pseudophallus. Species in the genus *Amphioctopus* (the "*Octopus aegina* group" of ROBSON [1929]; see Appendix) have no well-defined papilla, but the angle at which the distal spermatophoric duct joins the pseudophallus still directs the spermatophore to lie with its aboral end lodged in the apex of the pseudophallus. In *Benthoctopus* and *Enteroctopus*, the pseudophallus has a more complex internal structure and the spermatophore is first directed posteriorly, into the so-called diverticulum, and is then looped back so that, again, the aboral end will emerge first. In all species encountered so far, the diverticulum is basically a more or less convoluted, more or less fused, tubular continuation at the opposite end of the pseudophallus from its (anterior) orifice to the outside.



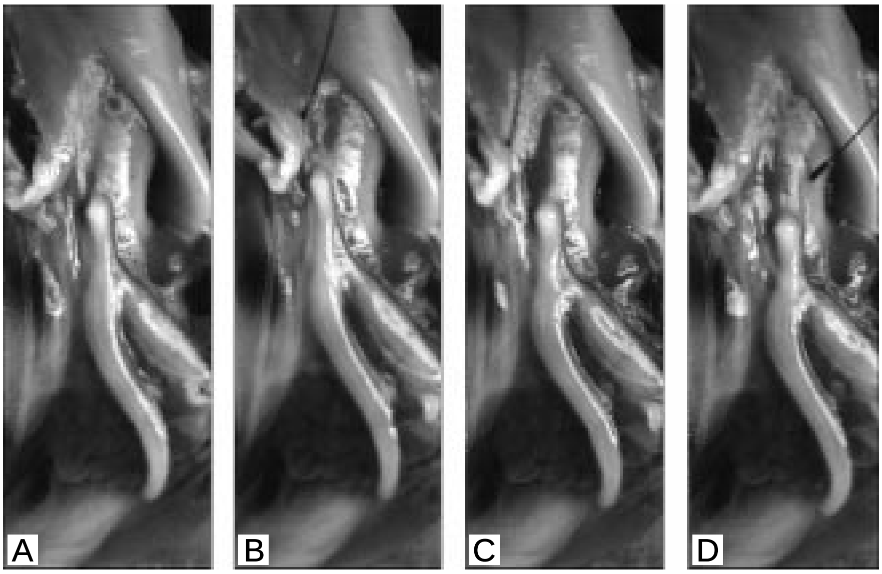
Text-Fig. 1.
Development of the pseudophallus.
A–C) Development of the pseudophallus in submature males of *Ptualoctopus kitaiensis* gen. et sp. nov. (see Appendix).
D) Opened pseudophallus (C) to show the developing papilla (arrow) of the distal spermatophoric duct.
E,F) Differences in the form of the pseudophallus of two adult specimens (cf. Text-Fig. 2).
Scale bar: 5 mm.



Text-Fig. 2.
Detail of the pseudophallus in *Ptualoctopus kitaiensis*.
A) Pseudophallus in situ to show its position relative to the funnel (F) and median mantle connective (MC).
Small arrowheads mark the pseudophallus extensor muscle.
B) Pseudophallus opened to show the position of the spermatophore (large arrowhead) and the distal spermatophoric duct papilla (arrow).
Scale bar: 5 mm.

3.2. Muscular Tissue Acting on the Pseudophallus

In all members of the incirrate Octopoda investigated so far (including the benthoctopodine genus *Benthoctopus*; the octopodine genera *Amphioctopus, Cistopus, Enteroctopus, Hapalochlaena, Octopus, Ptualoctopus* and *Scaeurgus*; and the eledonine genera *Eledone, Graneledone* and *Pareledone*), fixed specimens have a distinct bundle of muscle tissue attached to the pseudophallus by an ovoid insertion just posterior to the pseudophallus aperture. This tissue connects to a region near the base of the funnel, where it meets the tissue enclosing the anterior part of the digestive system and the anterior margin of the medial mantle connective (Text-Fig. 2A). However, in living and freshly dead specimens, no distinct muscle is visible. This is because, although there is a well-defined medial, subterminal insertion on the pseudophallus, its origin in the region at the base of the funnel appears to be more diffuse and is intimately associated with the connective tissue of the sac extending from the medial mantle connective to enclose the urogenital organs.



Text-Fig. 3.
The pseudophallus of an anaesthetized immature male *Enteroctopus dofleini* (Wülker) during an electrical stimulation experiment.
A) Pseudophallus prior to stimulation.
B) Stimulation of anterior part of urogenital sac causes muscular contraction, which pulls the pseudophallus tip anteriorly (towards top of page).
C,D) Stimulation of areas medial (C) or lateral (D) to the pseudophallus extensor muscle fails to cause any movements of the pseudophallus (cf. A).
The stimulating electrode is visible as a thin black line near the top of pictures B–D.

Stimulation applied to the region connecting the pseudophallus and the base of the funnel elicited a reproducible contraction pulling the pseudophallus antero-medially (Text-Fig. 3B). The tissue causing the pseudophallus to move was clearly seen to be attached a few millimetres from its tip. When stimulation was removed, the pseudophallus relaxed (over a period of 5–10 s.) back to its position prior to stimulation (Text-Fig. 3A). This could be repeated numerous times by stimulating at any point along a line between the pseudophallus tip and its apparent connection with the base of the funnel. However, placing the electrode slightly to the side (either medially or laterally) of this line produced no observable effects (Text-Fig. 3C, D). Stimulation of the pseudophallus itself caused it to constrict, reducing its diameter but with no apparent change in length. When stimulated more posteriorly, the posterior end (the tip of the so-called diverticulum) curled slightly towards the midline. Stimulating the region surrounding the pseudophallus or the spermatophoric sac produced little obvious effect (slight, localized contractions).

3.3. Variation in the Form of the Pseudophallus

The presence of the pseudophallus extensor muscle is a consistent feature of the Benthoctopodinae, Eledoninae and Octopodinae but the form of the pseudophallus shows a lot of variety. This is useful in identifying species which otherwise are difficult to tell apart, as in the genus *Amphioctopus*. In this genus, the posterior region of one type of pseudophallus turns acutely medially, then acutely dorsomedially. *Amphioctopus fangsiao, A. hummelincki* and *Amphioctopus* sp. 2 have this type (Text-Fig. 4A, B; type A, Table 1). *Amphioctopus robsoni* and *A. burryi* have a pseudophallus of similar appear-

Species	Distribution	Ocelli		Pseudophallus type	Egg size
		Annulus	Patch		
A. aegina	Tro IWP	absent	absent	?	small
A. burryi	Tro WA & EA	absent	present?*	B	small
A. exannulatus	Tro WP	absent	present	C?	small
A. fangsiao	NWP	gold or greenish	present	A	large
A. hummelincki	Tro WA	blue	present	A?	small
A. marginatus	Tro WP	absent	absent	C	?
A. membranaceus	Tro WP	violet?	present	?	small?
A. oculifer	Tro EP	blue	present	?	?
A. ovulum	Tro WP	violet	present	C	small
A. polyzenia	Tro WP	blue	present	A	large
A. robsoni	Tro IWP	violet	present	B	small
A. sp. 1	Tro WI	blue	present	?	?
A. sp. 2	Tro WP	violet	present	A	small
A. sp. 3	Tem WP	absent	absent	C	?
A. sp. 4	CP	absent	absent	?	small

*) Ambiguous in fixed specimens (Gleadall, redescription in prep.).

Table 1.
Summary of Species Characteristics in the Genus *Amphioctopus* (genus redescription in preparation; see Appendix.).
CP = Central Pacific; EA = Eastern Atlantic; EP = Eastern Pacific; IWP = Indo-West Pacific; NWP = Northern West Pacific; Tem = temperate; Tro = tropical; WA = Western Atlantic; WI = Western Indian Ocean; WP = Western Pacific; ? = unknown because only female or immature specimens have been observed.
For pseudophallus types A–C, refer to text Section 3.3. and Text-Fig. 4. Species 1, 2 are new species (Gleadall, in preparation); species 3 is of uncertain identification (cf. *Octopus kagoshimensis* Ortmann, 1888; *O. granulatus*: Sasaki, 1929); species 4 is a new species (Huffard & Hochberg, in preparation).

Table 2.
Comparison of terminology used to describe the terminal region of the male reproductive tract of the incirrate octopods.

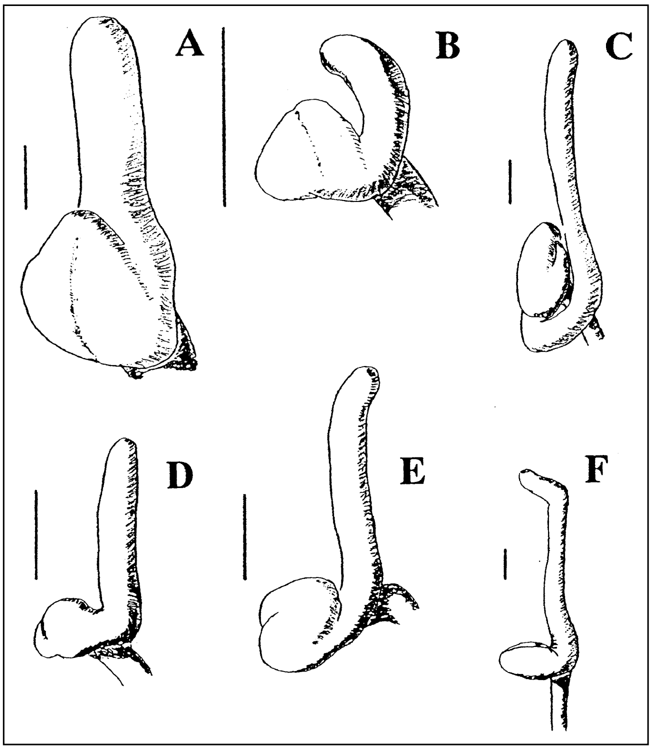
<table>
<tr><th>Author(s)</th><th>Spermatophoric Sac</th><th>Distal Spermatophoric Duct</th><th colspan="2">Pseudophallus</th></tr>
<tr><td rowspan="2">RACOVITZA, 1894</td><td rowspan="2">La poche de Needham</td><td colspan="3">Le canal excréteur</td></tr>
<tr><td colspan="2"></td><td>Papille</td></tr>
<tr><td rowspan="3">MARCHAND, 1906</td><td rowspan="3">(primärer) Spermatophorensack</td><td rowspan="3"></td><td colspan="2">Penis</td></tr>
<tr><td>Sekundärer Spermatophorensack</td><td rowspan="2"></td></tr>
<tr><td>Penisblindsack</td></tr>
<tr><td rowspan="4">MARCHAND, 1907</td><td colspan="4">Needhamsche Tasche</td></tr>
<tr><td rowspan="3"></td><td rowspan="3">Hals des Penis</td><td colspan="2">distaler Teil der Needhamschen Tasche</td></tr>
<tr><td colspan="2">Penis</td></tr>
<tr><td>Penisdivertikel</td><td></td></tr>
<tr><td rowspan="2">SASAKI, 1929</td><td rowspan="2">Needham's sac</td><td rowspan="2">Distal duct of Needham's sac</td><td colspan="2">Penis</td></tr>
<tr><td>Diverticle</td><td></td></tr>
<tr><td rowspan="3">ROBSON, 1929</td><td rowspan="3">Needham's organ</td><td rowspan="3"></td><td colspan="2">Penis</td></tr>
<tr><td>Diverticle</td><td></td></tr>
<tr><td>Appendix</td><td></td></tr>
<tr><td rowspan="2">BENHAM, 1942, 1943</td><td rowspan="2">Needham's sac</td><td rowspan="2">Penial duct</td><td colspan="2">Penis</td></tr>
<tr><td>Diverticulum</td><td></td></tr>
<tr><td rowspan="2">DELL, 1952</td><td rowspan="2">Needham's sac</td><td rowspan="2">Distal vas deferens</td><td colspan="2">Ejector</td></tr>
<tr><td>Diverticulum</td><td></td></tr>
<tr><td>PETERSON, 1959</td><td>Needham's sac</td><td>Distal part of the spermatophoric duct</td><td colspan="2">Penis</td></tr>
<tr><td rowspan="2">TAKI, 1963</td><td rowspan="2">Spermatophoric sac</td><td colspan="3">Penis</td></tr>
<tr><td>Proximal part of penis</td><td>Penis diverticle</td><td></td></tr>
<tr><td>TAKI, 1964</td><td>Spermatophoric sac</td><td>Penial duct</td><td>Penis diverticle</td><td>Penis</td></tr>
<tr><td rowspan="2">MANN, 1963</td><td rowspan="2">Spermatophoric Sac</td><td colspan="3">Penis</td></tr>
<tr><td></td><td>Diverticulum penis</td><td></td></tr>
<tr><td rowspan="3">HANSON *et al.* 1973</td><td rowspan="3">Spermatophoric Sac</td><td colspan="3">Terminal spermatophoric duct</td></tr>
<tr><td colspan="2" rowspan="2"></td><td>End portion of the terminal spermatophoric duct</td></tr>
<tr><td>Penis</td></tr>
<tr><td rowspan="3">MANN *et al.* 1966, 1970, 1981</td><td rowspan="3">Spermatophoric Sac</td><td colspan="3">Terminal spermatophoric duct</td></tr>
<tr><td rowspan="2"></td><td rowspan="2">Diverticulum of the terminal spermatophoric duct</td><td>Terminal organ</td></tr>
<tr><td>Penis</td></tr>
<tr><td rowspan="2">WELLS, 1978; NORMAN, 1993c; OKUTANI *et al.* 1987</td><td rowspan="2">Needham's sac</td><td rowspan="2"></td><td colspan="2">Penis</td></tr>
<tr><td>Diverticulum</td><td></td></tr>
<tr><td rowspan="2">NESIS, 1987</td><td rowspan="2">Spermatophoric (Needham's) Sac</td><td rowspan="2"></td><td colspan="2">Penis</td></tr>
<tr><td>Penial diverticulum</td><td></td></tr>
<tr><td>NORMAN, 1993a, b</td><td>Needham's sac</td><td></td><td>Diverticulum</td><td>Terminal organ</td></tr>
<tr><td>HANLON & MESSENGER, 1996</td><td></td><td></td><td colspan="2">Penis</td></tr>
<tr><td rowspan="2">NORMAN & SWEENEY, 1997</td><td rowspan="2">Needham's sac</td><td rowspan="2"></td><td colspan="2">Terminal organ</td></tr>
<tr><td colspan="2">Penis</td></tr>
</table>

ance, but with an extra turn to medial of almost 90 degrees before the tighter turns begin (Text-Fig. 4D, E; type B, Table 1). In other species of *Amphioctopus*, the pseudophallus is much longer, taking a long loop (which may cross the midline into the right side of the mantle cavity) before the tighter turns begin (Text-Fig. 4C; type C, Table 1). However, the form of the pseudophallus does not correlate well with other morphological characteristics such as the presence or absence of ocelli (Table 1), which suggests that pseudophallus morphology has only limited use as a phylogenetic marker. In some genera (e.g. *Enteroctopus* and *Hapalochlaena*), there is no apparent difference in pseudophallus morphology among species.

4. Discussion

4.1. Terminology

Previous descriptions of the terminal region of the male reproductive tract in the Cephalopoda have included "penis", "distal vas deferens", "terminal organ" and "distal spermatophoric duct" (summarized in Table 2). None of these terms are appropriate for the incirrate octopuses. Firstly, in both the Decabrachia and incirrate Octopoda no part of the male reproductive tract is inserted into the female during copulation, so the term "penis" is a misnomer. "Distal vas deferens" is inappropriate because it implies the flow of fluids and free spermatozoa, which in cephalopods are held within spermatophores and not released until after copulation. "Terminal organ" is void of any anatomical or functional significance and has also been used (e.g. by SASAKI, 1929) to describe the octopod ligula: the terminal organ of the hectocotylus (arm modified for transferring spermatophores). The term "distal spermatophoric duct" is inappropriate for the incirrate octopuses because in some genera the distal spermatophoric duct ends as a distinct papilla (Text-Figs. 1D, 2B) protruding into the pseudophallus. The latter appears to be a more suitable term for this discrete organ, with respect to its phallus-like shape and position at the distal end of the male reproductive tract.



Text-Fig. 4.
Variation in the form of the pseudophallus of mature males.
A) *Amphioctopus fangsiao* (D'ORBIGNY).
B) *A. polyzenia* (GRAY).
C) *A. marginatus* (TAKI).
D) *A. burryi* (VOSS).
E) *A. robsoni* (ADAM).
F) Japanese *Octopus vulgaris* (= *O. sinensis* D'ORBIGNY).
Drawn to the scale of a unit mantle length.
Scale bars: 2 mm.

Defining the pseudophallus and recognizing the termination of the distal spermatophoric duct at the junction with the pseudophallus also clarifies previous confusion over what exactly constitutes the "penis." As Table 2 shows, some authors have regarded only the tip of the organ as the "ejector" (DELL, 1952), "penis" or "terminal organ" (HANSON et al., 1973; MANN et al., 1966, 1970, 1981; NORMAN, 1993a, b). TAKI (1963) and MANN (1963) included the distal spermatophoric duct as part of the "penis." In the Decabrachia, there is no pseudophallus, so the male reproductive system terminates with the distal spermatophoric duct.

4.2. The Pseudophallus Extensor Muscle and Spermatophore Ejection

The only musculature associated with the pseudophallus was detected in the region corresponding to that observed in fixed specimens as an apparent connection from the median subterminal part of the pseudophallus to the antero-medial region of the visceral mass and mantle connective. Investigation of the movement of this musculature in vivo demonstrated that, as seems clear from its position in preserved specimens, it is a pseudophallus extensor muscle, the function of which is to draw the pseudophallus anteriorly towards the funnel, and in such a way as to manoeuvre the (subterminal) aperture of the pseudophallus to a more anterior (terminal) position. Normally, the pseudophallus holds a single spermatophore, the aboral ("fat") end of which is snugly located in the anterior end of the pseudophallus. It seems likely that, at copulation, contraction of the pseudophallus extensor muscle, combined with relaxation of the sphincter at the aperture of the pseudophallus (described from histological observations by PETERSON, 1959), will bring about ejection of the spermatophore.

Once the spermatophore has left the pseudophallus, another quickly takes its place (MANN et al., 1970), at which time the distal spermatophoric duct (papilla) will open to allow just one spermatophore to enter. One presumes that the hydrostatic forces (produced by muscular tension) within the fluid-filled reproductive organs act upon the elongated teardrop shape of the spermatophore to move it in the direction of its broad aboral end. Once freed from the glands that produce it, each spermatophore is transported firstly into the spermatophoric sac, and later into the pseudophallus, from which it is subsequently ejected aboral end first. Ejection is probably a combination of muscular constriction of the pseudophallus and the elastic energy released when the convoluted spermatophore (freed from being jammed in the anterior end of the pseudophallus) is allowed to assume its normal straightened or gently arcuate form (as seen when stored in the spermatophoric sac). In mature males, the pseudophallus is probably always charged with a spermatophore ready for mating to take place: mature fixed specimens invariably have a spermatophore in the pseudophallus (pers. obs. of many specimens); and MANN et al. (1970)

noted that, in *Enteroctopus*, following spermatophore transfer, the pseudophallus is recharged with another spermatophore within an hour.

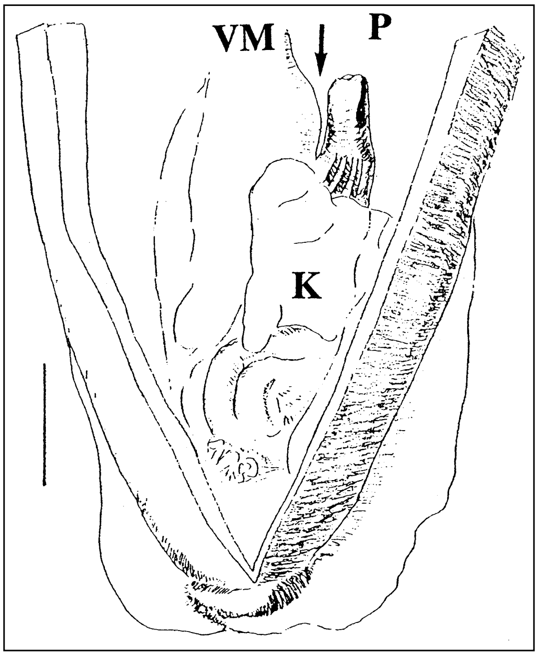
4.3. Variation in the Form of the Pseudophallus

There is clearly some individual variation in the shape of the pseudophallus within a given species (compare Text-Figs. 1E, 1F and 2A for *Ptualoctopus kitaiensis*; see also BURGESS [1966] for *Amphioctopus hummelincki*; and GLEADALL, 1993, for *A. fangsiao*). This variation is not wide enough to cause confusion, unless comparisons are attempted using immature and mature specimens (cf. Text-Fig. 1). However, an attempt in the present study to classify pseudophallus types based on size and shape encountered a number of difficulties. For example, the pseudophallus of *Scaeurgus unicirrhus* and *Hapalochlaena* deflects laterally towards its posterior end. However, in *Scaeurgus* the deflection is more acute (an angle of around 60 degrees), compared with a very shallow deflection in *Hapalochlaena*. In *Octopus salutii*, *Ptualoctopus kitaiensis* and *O. vulgaris*, the posterior part of the pseudophallus turns medially. However, in *O. salutii* the turn is acute, forming two tightly fused limbs, whereas in *P. kitaiensis* the turn is gentler and the two limbs can be separated. In *O. vulgaris* (Text-Fig. 4F), there is a short, abrupt turn of 90 degrees medially, then an acute turn in the dorso-lateral direction. Further complications arise within the genus *Amphioctopus*: species in this genus have a pseudophallus with one of three types of progressively complex morphology (Text-Fig. 4A–E) but this shows little correlation with other species characteristics (Table 1).

Evidently the grouping of species according to morphologically similar shapes of pseudophallus is of limited use in attempts to understand any evolutionary relationships. It is therefore recommended that species descriptions should always include a description of the pseudophallus, with detailed diagrams and close comparisons with related species, but that any assessments of evolutionary relationships must take into account a range of other morphological and molecular characteristics (cf. NESIS, 1996).

4.4. Comparison of the Incirrate Octopods with the Decabrachia

The present study has been concerned mostly with the incirrate octopods. For the Decabrachia, MARCHAND (1906, 1907) figured the reproductive systems of a number of genera and all appear to have a spermatophoric sac that releases spermatophores from a simple narrowing of the distal spermatophoric duct with little obvious difference among the genera. This is exemplified by *Sepia erostrata* SASAKI. Text-Fig. 5 shows the simple opening with three spermatophores visible in the subterminal region. The distal spermatophoric duct is a simple tube of relatively wide diameter (when fixed) from which the spermatophores can be removed manually with ease. The fact that the spermatophores are visible subterminally while the most terminal few millimetres of the distal spermatophoric duct are opaque, suggests that in the Decabrachia, too, there is some functional specialization distally (e.g. thicker layers of muscle). However, there is no morphological equivalent to the pseudophallus, neither is there any evidence of an extensor muscle (arrow, Text-Fig. 5). Superficial comparison of the reproductive systems of squids and octopuses (Table 3), and of their mating strategies (Table 4), suggests that the pseudophallus places more control over spermatophore release in the incirrate octopods. Perhaps this allows a more precise, economical use of reproductive resources by the male octopus, in comparison with his relatives in the Decabrachia.



Text-Fig. 5.
Opened ventral mantle of a mature male cuttlefish (*Sepia erostrata* SASAKI).
K = kidney; P = aperture of the distal spermatophoric duct, showing the absence of any organ equivalent to the octopod pseudophallus; arrow indicates gap between distal spermatophoric duct and visceral mass, VM.
Scale bar: 5 mm.

In squids, everything is fast and furious, with transfer of spermatophores taking a few seconds followed rapidly by the release of spermatozoa from the spermatophores (Table 4). In *Loligo pealeii*, three mating positions have been seen: the male may grasp the female from the side, or from a postero-dorsal position (either in mid-water or with the female resting her armtips and posterior mantle on the sea-bed) and pass the spermatophores to the mantle cavity in the vicinity of the oviducts; or meet the fe-

Table 3.
Comparison of the terminal region of the male reproductive tract in squids and octopuses.

Feature	Squids	Octopuses
Terminal region	Simple narrowing of spermatophoric sac - no pseudophallus	Well-defined chamber – the pseudophallus
Distal spermatophoric duct termination	Simple orifice into mantle cavity	At junction with pseudophallus
Special musculature	None (distal duct is free)	Funnel base (medial) to pseudophallus (subterminal)
No. of spermatophores released at one time	Many	One: pseudophallus holds only one

Table 4.
Comparison of events at copulation in squids and octopuses.
Squids represented by *Loligo pealeii* (DREW, 1911, 1919; ARNOLD, 1962; AUSTIN et al. 1964), *L. opalescens* (HIXON, 1983), *Dosidicus gigas* (NESIS, 1983), *Todarodes pacificus* (OKUTANI, 1983).
Octopuses represented by *Octopus vulgaris* (RACOVITZA, 1894; WELLS, 1978), *O. briareus* (HANLON, 1983a), *O. joubini* (HANLON, 1983b), *O. maya* (VAN HEUKELEM, 1983) and *Enteroctopus dofleini* (MANN et al. 1970; HANSON et al. 1973; GABE, 1975).

Feature	Squids	Octopuses
Mating location	Mid-ocean or with female resting on sea-bed	Both partners on sea-bed
Mating strategy	Fast, furious and messy	Slow, surreptitious and tidy
Mating position	Female grasped from below, from the side, from above & behind, or arms entwined "face-to-face"	Contact only with tip of hectocotylus, female mounted from above & behind, or partners facing with arms raised together
Copulation duration	<10s.	Several min. to >2hr.
Spermatophores transferred at a single mating	Up to 40 (in bunches)	1 or several (one at a time)
Spermatophore transfer speed	Around 1 second	Several seconds at least
Spermatophoric reaction	Very rapid (seconds)	Slow (c. 1 hr)

male head-on, entwine arms with her and pass the spermatophores to special receptacles in the buccal membrane (DREW, 1911; ARNOLD, 1962; AUSTIN et al., 1964). The rapidity of the mating process, with lightning-fast transfer of spermatophores and almost immediate ("messy") release of spermatozoa outside the relative protection of the mantle cavity (Table 4), is probably essential in view of the fact that mating occurs in open water (cf. the benthic habitat of most octopods), in full view of any lurking predators. In squids such as *L. pealeii*, the spermatophores are extruded from the funnel and grasped with the hectocotylized fourth left arm (DREW, 1911); in *Sepia officinalis*, the male removes spermatophores by reaching into the mantle cavity with the hectocotylus (BOLETZKY, 1983). In the sepiolid *Euprymna scolopes*, copulation takes place with the male swimming unseen beneath and behind the female, who is grasped from below with the male's two most dorsal pairs of arms (SINGLEY, 1983). The length of time spent in copulation in this species is similar to that for the octopuses. In *Sepietta oweniana* (another sepiolid), however, mating is fast, with the couple head-to-head after the female has been turned upside down by the male (BERGSTROM & SUMMERS, 1983).

Octopuses, being mostly benthic creatures, have a number of general differences from their relatives in the Decabrachia, including a tendency to escape predation by a combination of form changes and crypsis (HANLON et al., 1999), rather than relying more upon speed and shoaling. What is known of octopus mating behaviour suggests that coupling is a relatively long, slow process. Typically, the male sits at a distance from the female, caressing her with the tip of the hectocotylus, which is then inserted inside the mantle cavity to deposit one or two spermatophores. The latter are passed, by a peristaltic action, along a muscular groove in the arm web (e.g. WELLS & WELLS, 1972). Alternatively, the male may adopt a postero-dorsal "mounting" position or the partners may face each other with arms I and II raised and touching (ibid.). However, the process is generally rather slow and surreptitious in comparison with the squids, usually taking more than an hour to complete (although reportedly taking less than 30 min. in *O. joubini*; HANLON, 1983b). One supposes that, especially when using the "distant" mode of mating, both animals are able to quickly abandon copulation to make appropriate responses (to predatory threats, for example) at reaction speeds little different from those they would make when not mating. It is also interesting to note that in octopuses the spermatophoric reaction (whereby the spermatozoa are ejected) is much slower than in squids (around 1–2 hr. in *Enteroctopus*: MANN et al. [1970]; HANSON et al. [1973]) and usually occurs ("tidily") within the mantle cavity of the female.

In describing the reproductive systems of *Octopus bimaculoides*, PETERSON (1959) described the pseudophallus as a "penis-like organ which discharges the spermatophore" and DELL (1952) earlier described the pseudophallus as an "ejector". The observations and experiment reported here provide more evidence that the terminal part of the male reproductive system in the incirrate octopuses is indeed an organ specialized for the controlled discharge of spermatophores one at a time.

Acknowledgements

The term pseudophallus was first suggested to me by Mr. Fred NAGGS, in the Mollusca Section of the Dept. of Zoology at BMNH. I am most grateful to Fred and the staff of various other museums (Hokkaido University Fisheries Museum, Hakodate, Japan; the Musée National d'Histoire Naturelle, Paris; the National Rijksmuseum, Leiden, The Netherlands; the National Science Museum, Tokyo; Santa Barbara Museum of Natural History; Tokyo Fisheries University; the University of Miami Marine Laboratory; the Zoological Museum of the University of Copenhagen; and the Dept. of Zoology, Tokyo University Museum) for the loan of preserved specimens. I also thank Mr. K. WATANABE for obtaining a living specimen of *E. dofleini* (for the stimulation experiment); the staff of Sendai Morning Market for maintaining the octopus in their aquarium; and Profs. Yasuo TSUKAHARA and Hiroyoshi OHASHI for access to facilities at Tohoku University. This work was supported in part by a grant from the Fujiwara Natural History Foundation.

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Appendix

Identifications Used in the Present Study

Identification*)	Previous identification(s)
Amphioctopus membranaceus	*Octopus membranaceus* QUOY & GAIMARD
Amphioctopus aegina comb. nov.	*Octopus aegina* GRAY
Amphioctopus burryi comb. nov.	*Octopus burryi* VOSS
Amphioctopus exannulatus comb. nov.	*Octopus exannulatus* NORMAN
Amphioctopus fangsiao comb. nov.	*Octopus fangsiao* D'ORBIGNY (synonyms incl.: *O. areolatus* DE HAAN in D'ORBIGNY & *O. ocellatus* GRAY)
Amphioctopus hummelincki comb. nov.	*Octopus hummelincki* ADAM**)
Amphioctopus marginatus comb. nov.	*Octopus marginatus* TAKI
Amphioctopus oculifer comb. nov.	*Octopus oculifer* HOYLE
Amphioctopus ovulum comb. nov.	*Polypus [Octopus] ovulum* SASAKI
Amphioctopus polyzenia comb. nov.	*Octopus polyzenia* GRAY
Amphioctopus robsoni comb. nov.	*Octopus robsoni* ADAM
Enteroctopus dofleini comb. nov.	*Polypus [Octopus] dofleini* WÜLKER
Octopus vulgaris CUVIER	Japanese specimens also known by the synonym *Octopus sinensis* D'ORBIGNY
Ptualoctopus kitaiensis gen. et sp. nov.	*Octopus* sp. C VOSS & WILLIAMSON

*) *Amphioctopus* FISCHER, 1882. Type species by monotypy *Octopus membranaceus* QUOY & GAIMARD, 1832. *Enteroctopus* ROCHEBRUNE & MABILLE, 1889. Type species *Enteroctopus membranaceus* ROCHEBRUNE & MABILLE, 1889, by subsequent designation (HOYLE, 1910). *Ptualoctopus* is a new genus from Hong Kong, characterized by the presence of unusually large posterior salivary glands, a long distal spermatophoric duct papilla and a "limus": a raised red line passing around the ventral mantle (GLEADALL, in prep.).

**) *Octopus hummelincki* ADAM, 1936, was recognized by TOLL (1990) as a synonym of *O. filosus* HOWELL, 1867, although the latter name had not been used previously in the 20th century to identify this species. TOLL (1990) misrepresented a number of earlier identifications and argued in favour of replacing *O. hummelincki* as a junior synonym of *O. filosus*. The species name *hummelincki* has been used widely in most investigations of the biology of this species, so to preserve nomenclatural stability it should be retained (as a nomen protectum; ICZN Arts. 23.9.3 & 82). Pending a decision by the ICZN, the specific name *filosus* HOWELL (proposed nomen oblitum) should not be used (cf. ICZN Art. 23.9.2).

Manuskript bei der Schriftleitung eingelangt am 2. April 2001

Zeitschrift/Journal: Abhandlungen der Geologischen Bundesanstalt in Wien

Jahr/Year: 2002

Band/Volume: 57

Autor(en)/Author(s): Gleadall I.G.

Artikel/Article: The Pseudophallus of the Incirrate Octopoda: An Organ Specialized for Releasing Spermatophores Singly 69-78