

**Bangor University**

## **DOCTOR OF PHILOSOPHY**

**The biology of reproduction in two British pulmonate slugs.**

Nicholas, J.

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1984

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THE BIOLOGY OF REPRODUCTION IN TWO  
BRITISH PULMONATE SLUGS

by

Jane Nicholas

A thesis submitted in partial fulfilment of the  
requirements for the degree of Philosophiae Doctor in  
the University of Wales.

In three volumes

VOLUME III

School of Animal Biology,  
University College of North Wales,  
Bangor, Gwynedd,  
United Kingdom.



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KEY

a	acinus	agd	albumen gland ducts
ah	anterior, slender region of hermaphrodite duct	al	ascending limb of carrefour loop
alb	albumen gland	am	apical membrane
ap	apices	at	atrium
ax	axon		
b	bursa copulatrix	BM	basement membrane
br	brain	bs	blood sinus
bv	blood vessel	bw	body wall
C	carrefour	Ca	calcium cell
cc	cell cluster	CD	common duct
cg	carrefour gland	cil	ciliated cells
cl	clear vesicles	Cm	circular muscle
co	core vesicles	coll	collagen
CT	connective tissue	cy	cytoplasm
d	desmosome	div	carrefour diverticulum

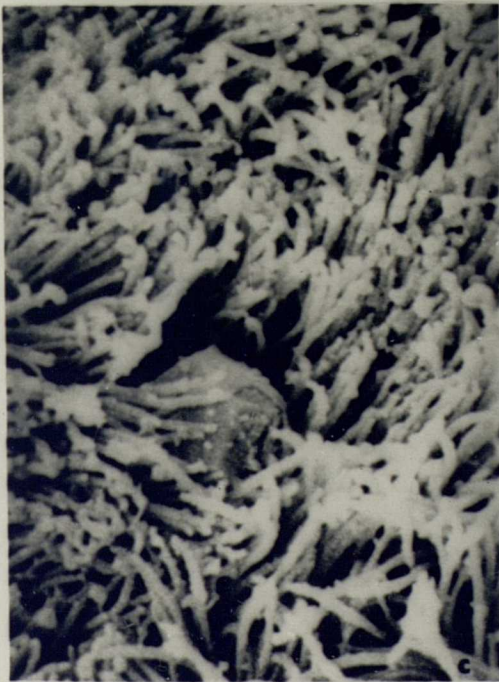
dl	descending limb of carrefour loop	du	ductule
ec	cone of epiphallus	ed	electron-dense granules
Ep	epithelium	epi	epiphallus
F	fibroblast	f	lateral foot
Fd	finger-like diverticulum	fo	focus of multiplication
foll	follicle		
g	granular connective tissue cells	gl	gland
Gly	glycogen	gr	granules
hd	hemidesmosome		
iv	intercellular vacuole	IV	intracellular vacuole
j	jelly layer		
L	duct lumen	LA	lower atrium
LM	longitudinal muscle	Ly	lysosome
M	mitochondria	mc	muscle
mf	microfibrils	mt	microtubules
mu	mucocytes	mv	microvilli

MVB	multivesicular body		
N	nucleus	Ne	neuron
nt	neurotransmitter granules	nu	nucleolus
Nv	nerve		
O	oviducal gland of common duct	oo	oocyte
Ov	oviduct		
P	polysome	pap	papilla
pb	polar body	Pd	pouched diverticulum
ph	posterior, slender region of hermaphrodite	pig	pigment
PM	penial mass	po	pore cell
pr	prostate gland	Ps	penial sac
Psp	phagocytosed sperm	pvf	perivitelline fluid
r	ciliary rootlet	rER	rough endoplasmic reticulum
S	sarcobellum	sc	secretory cells
sd	septate desmosomes	sER	smooth endoplasmic reticulum
Sg	sarcobellum gland cells	Sh	shell
sn	secretion	Sp	sperm

Sph	spermatophore	SR	sarcoplasmic reticulum
SV	seminal vesicle	Syn	synapse
t	tubule	ta	trifid appendage
tER	transitional endoplasmic reticulum		
UA	upper atrium	uncil	unciliated cells
V	vacuoles	Vd	vas deferens
za	zonula adhaerens		
♀	female duct	♂	male duct
I	type I secretory cell	II	type II secretory cell

Fig. 209 D.reticulatum, the surface of the sarcobellum.

- a. General view of ciliated ridges, S.E.M.  
(x130).
- b. Detail of (a), S.E.M. (x460).
- c. Detail of (b) showing the opening of a  
gland cell, S.E.M. (x6.5K).
- d. L.S. through ridges (x375).



**Fig. 209**

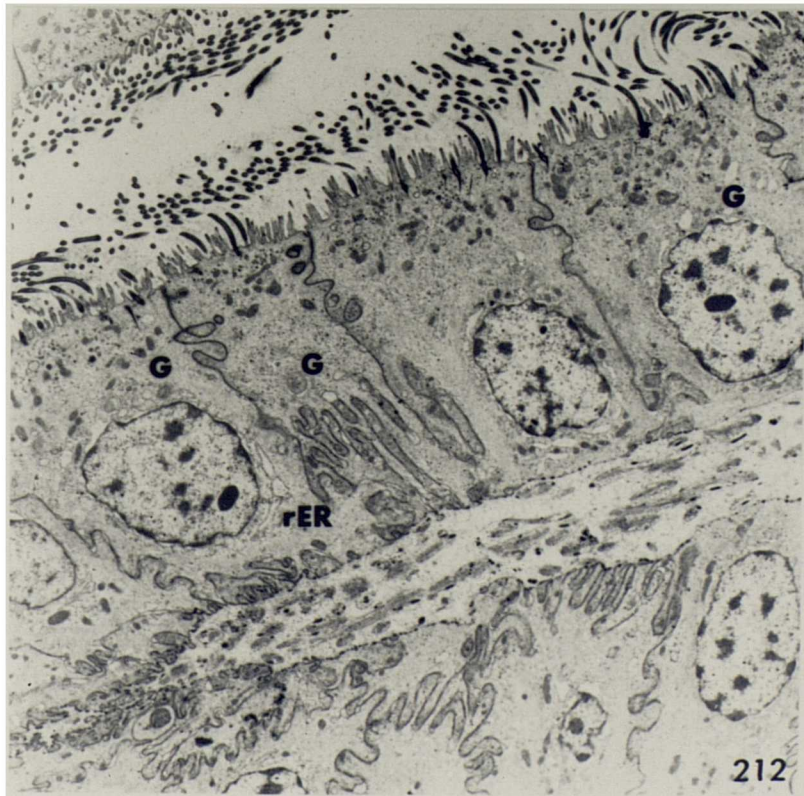
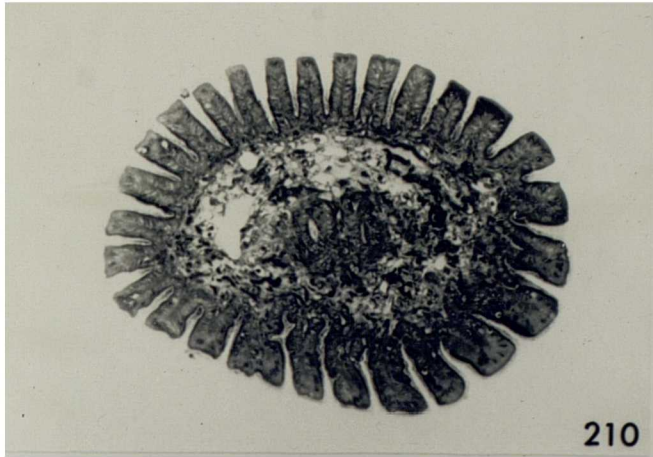


D.reticulatum, sarcobellum.

Fig. 210 T.S. through the tip of the sarcobellum  
(x110).

Fig. 211 Detail of the ciliated ridges (x450).

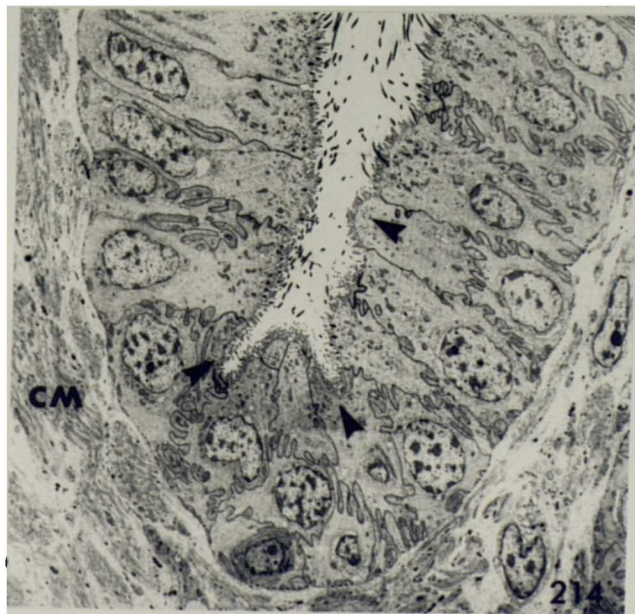
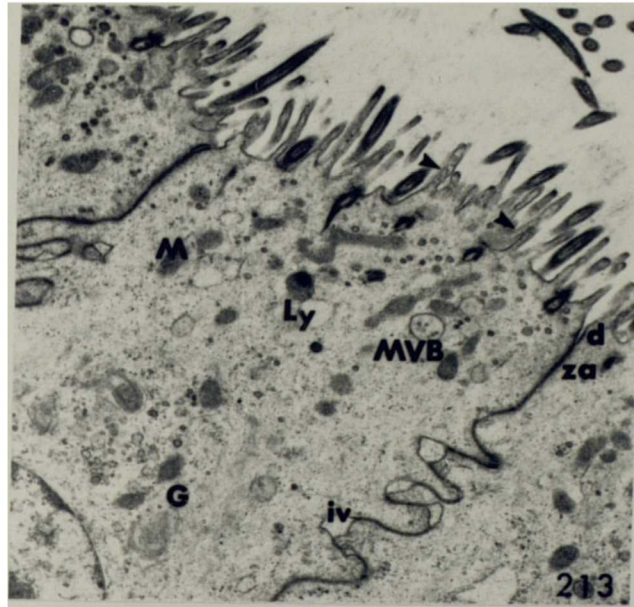
Fig. 212 General view of epithelial cells (x3K).



D.reticulatum, sarcobellum.

Fig. 213 Detail of a cell apex (x10.5K). Arrows indicate chains of vesicles.

Fig. 214 Unciliated epithelial cells (arrowed) at the bottom of the ridges (x1.5K).

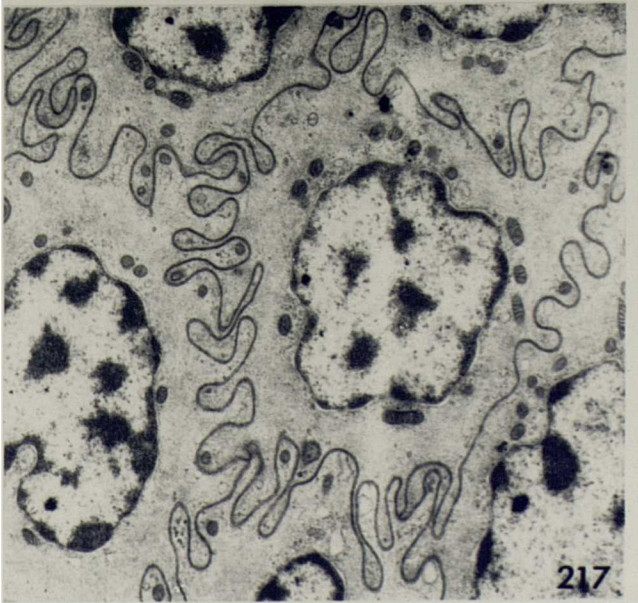
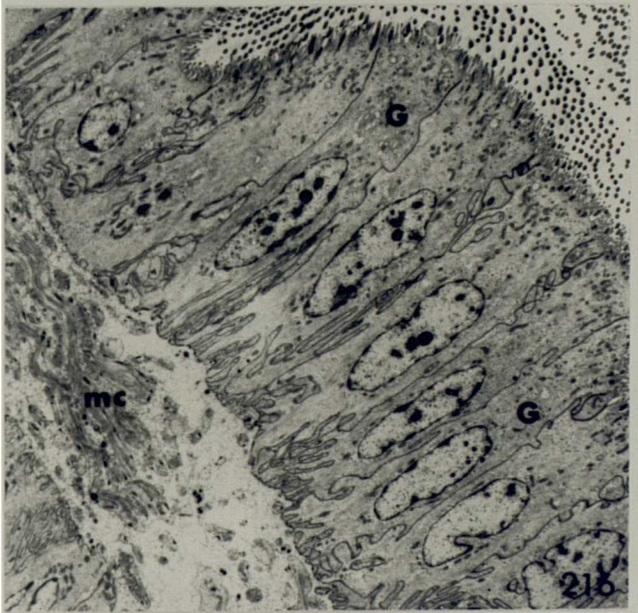


D.reticulatum, sarcobellum.

Fig. 215 T.S. through the base of the sarcobellum  
(x100).

Fig. 216 General view of epithelial cells (x2.25K).

Fig. 217 Horizontal section through the epithelium in  
the region of the nuclei (x9K).

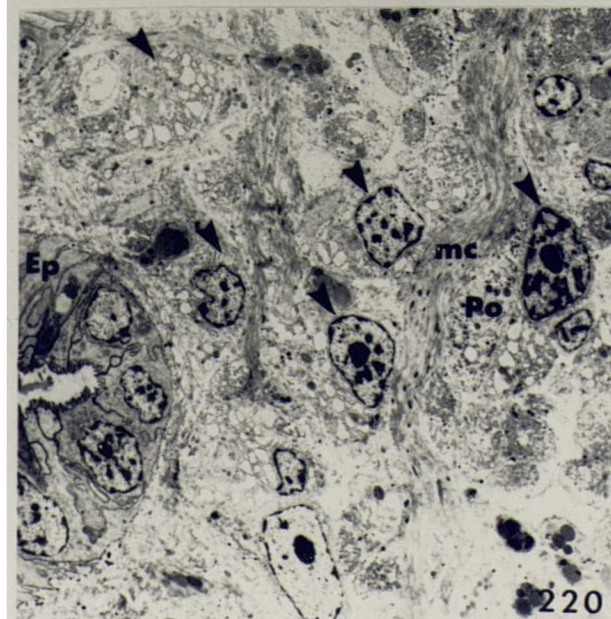
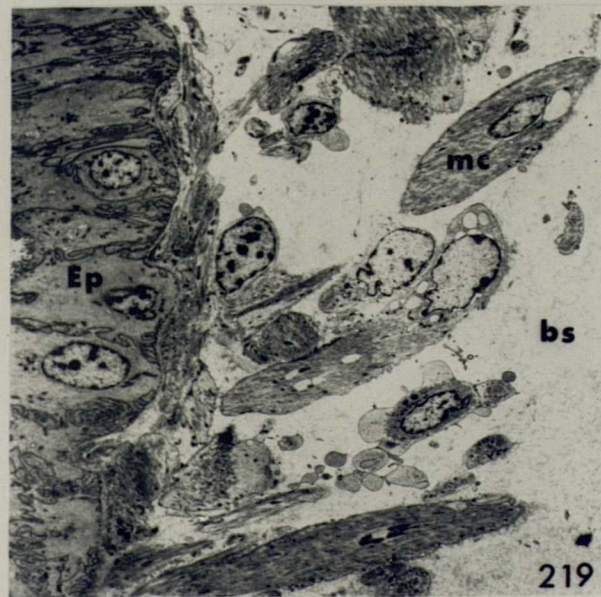
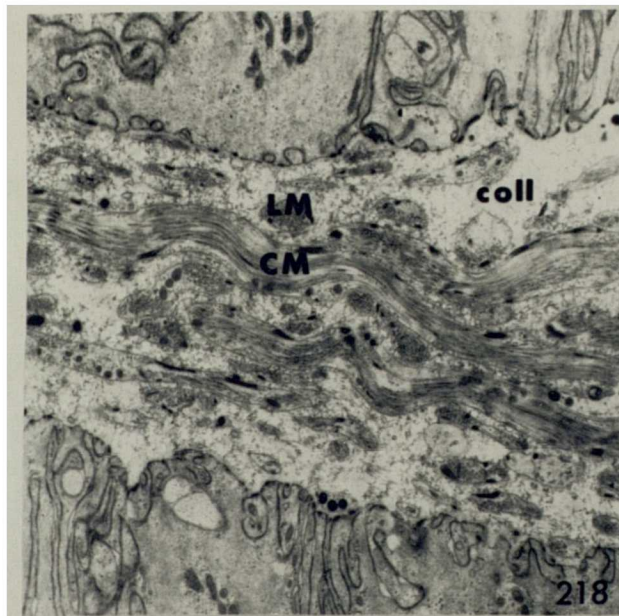


D.reticulatum, sarcobellum.

Fig. 218 Arrangement of the muscle within the ridges  
(x6K).

Fig. 219 Arrangement of the muscle in the core, at the  
tip of the sarcobellum (x1.5K).

Fig. 220 Arrangement of the muscle, gland and pore  
cells in the core, at the base of the  
sarcobellum (x2.25K). Arrows indicate the  
developing gland cells.



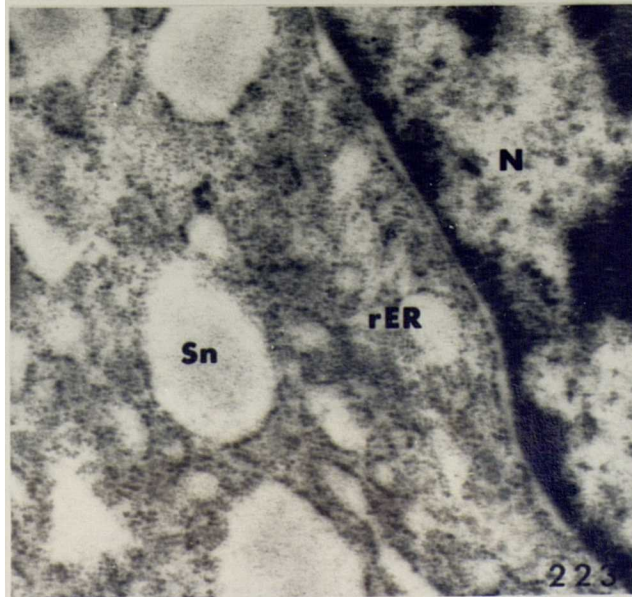
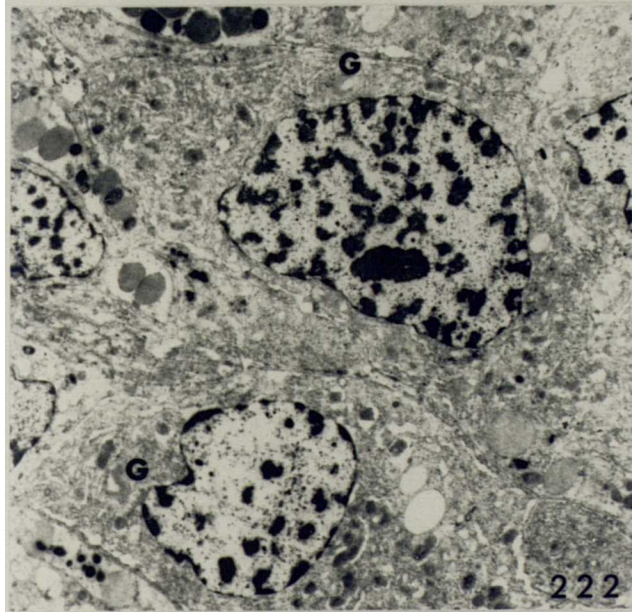
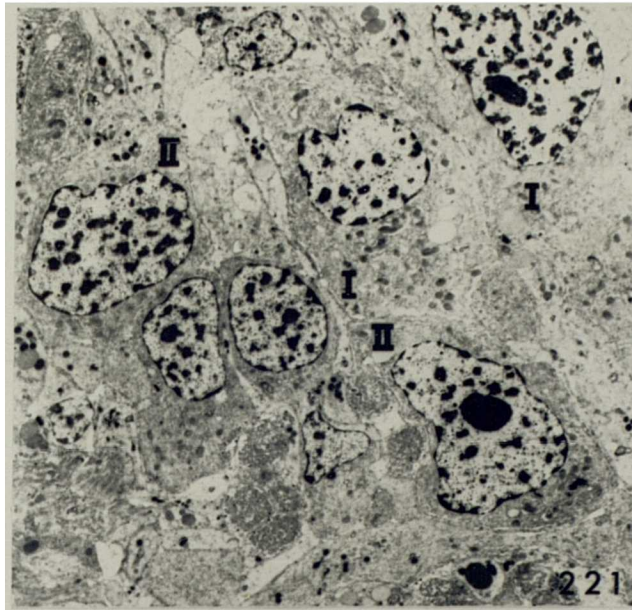


D.reticulatum, gland cells in the core of the sarcobellum.

Fig. 221 Developing gland cells, types I and II  
(x2.25K). Early C-stage.

Fig. 222 Type I gland cell (x4K).

Fig. 223 Type I, detail of the rER and secretion granules (x37.5K).

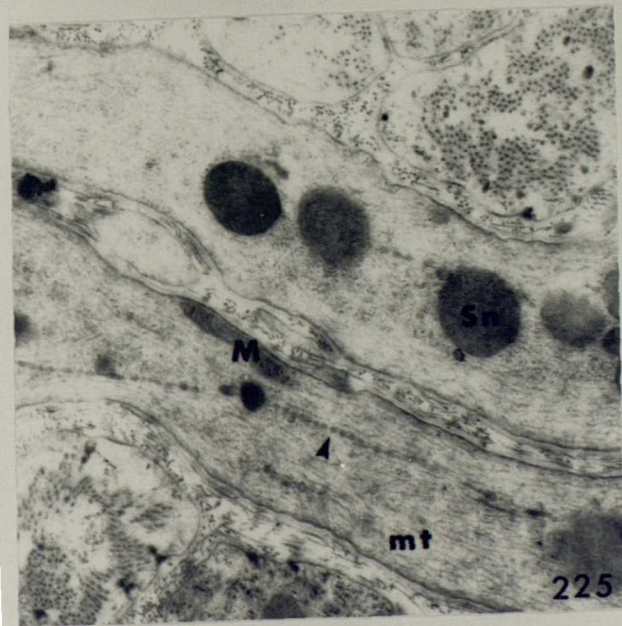
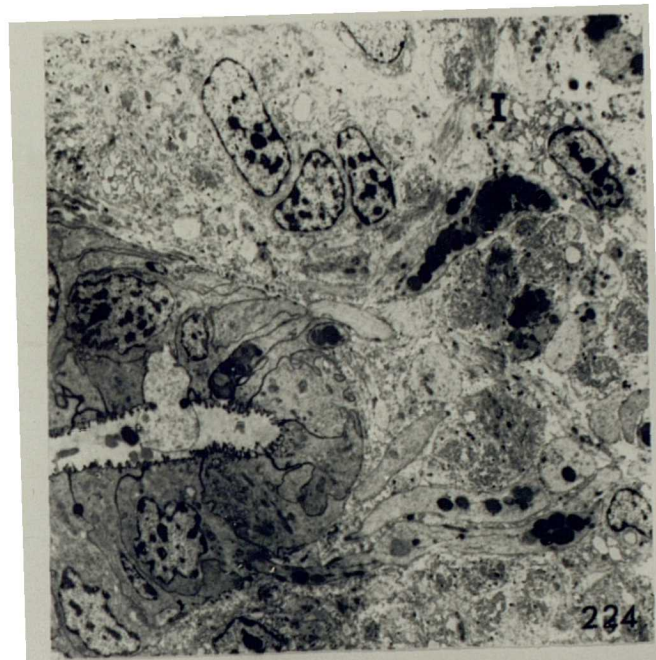


D.reticulatum, type I gland cells in the core of the sarcobellum.

Fig. 224 Accumulation of secretion granules in the tapering apices of the cells (x2.4K).

Fig. 225 Detail of the secretion granules and microtubules in the cell apices (x16K). The arrow indicates a chain of vesicles.

Fig. 226 Release of secretion into the unciliated region at the base of the ridges (x10K).

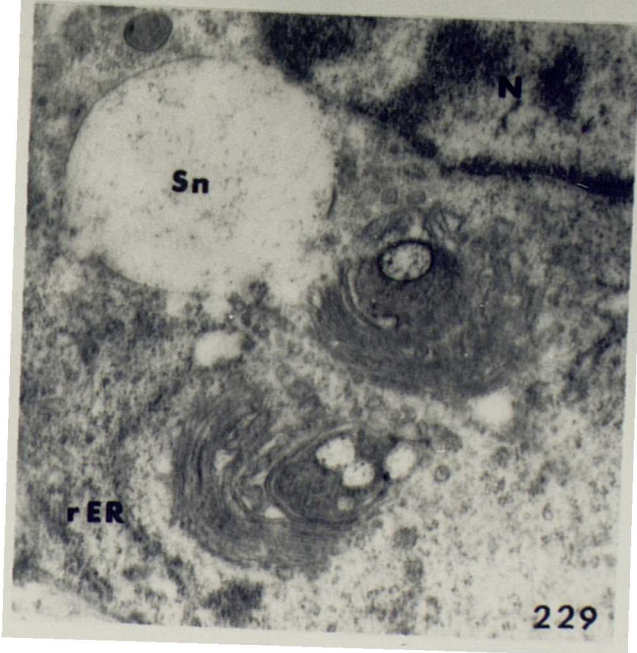
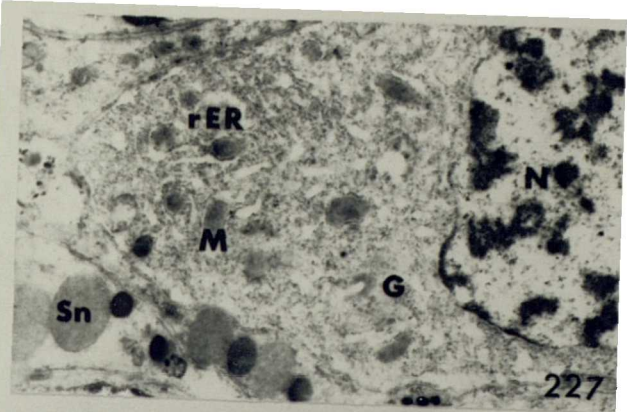


D.reticulatum, gland cells in the core of the sarcobellum.

Fig. 227 Type I, cytoplasmic detail (x9K).

Fig. 228 Type II, gland cell (x9K).

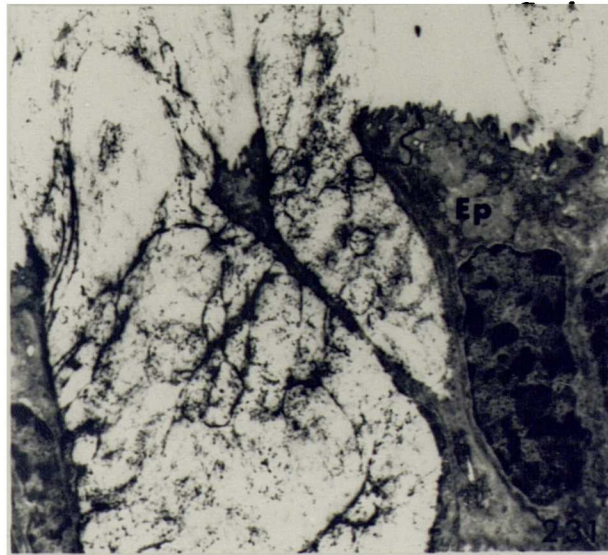
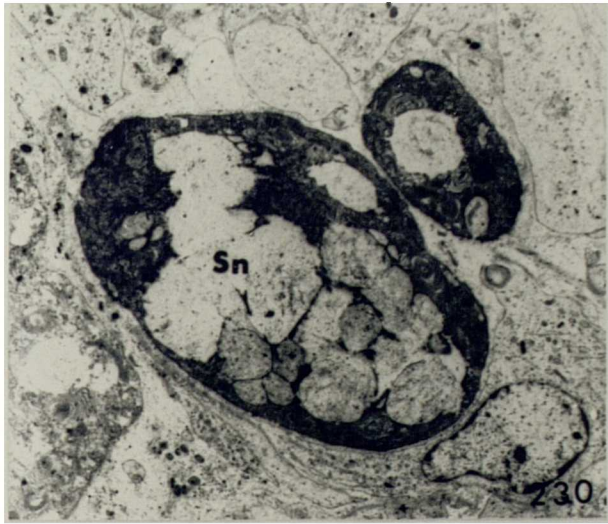
Fig. 229 Type II, detail of the Golgi region (x22.5K).



D.reticulatum, type II gland cells in the core  
of the sarcobellum.

Fig. 230 Mature gland cells (x3.8K).

Fig. 231 Release of secretion onto the surface of the  
sarcobellum (x6K).



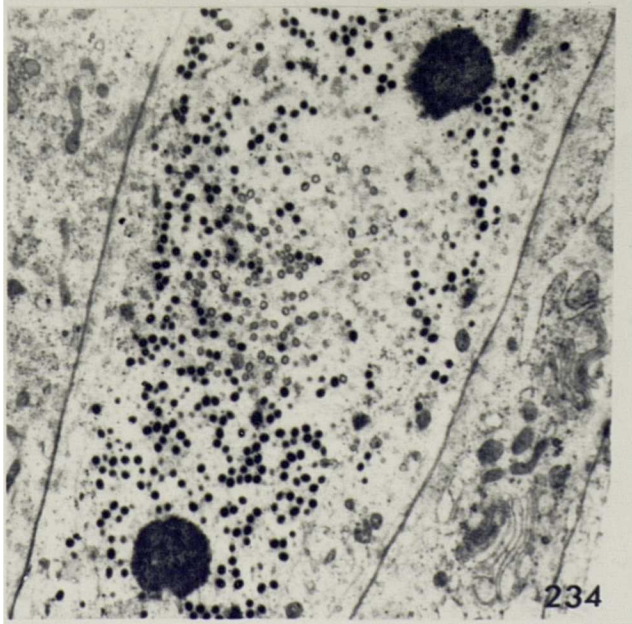
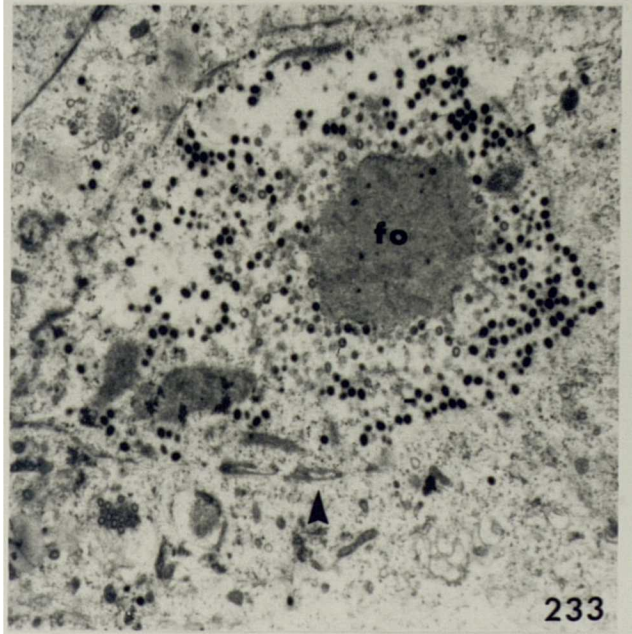
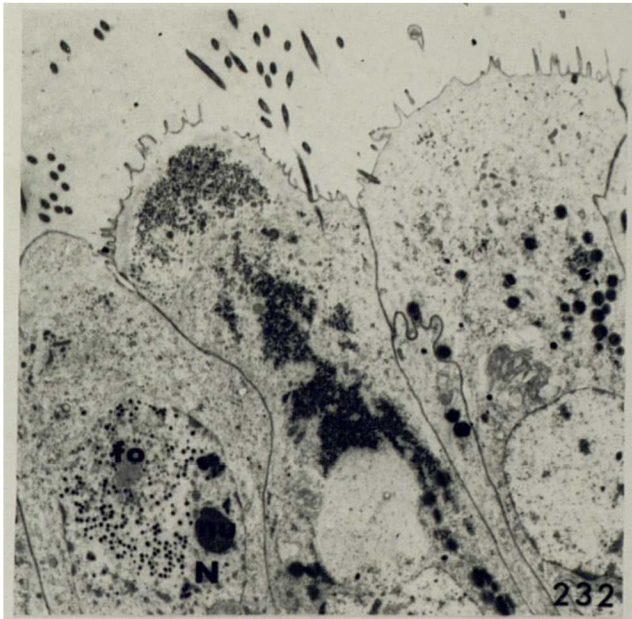


D.reticulatum, viral infection of the  
sarcobellum.

Fig. 232 Multiplication of viral particles in the  
nucleus of an epithelial cell (x3K).

Fig. 233 Breakdown of the nuclear membrane (arrowed)  
(x9K).

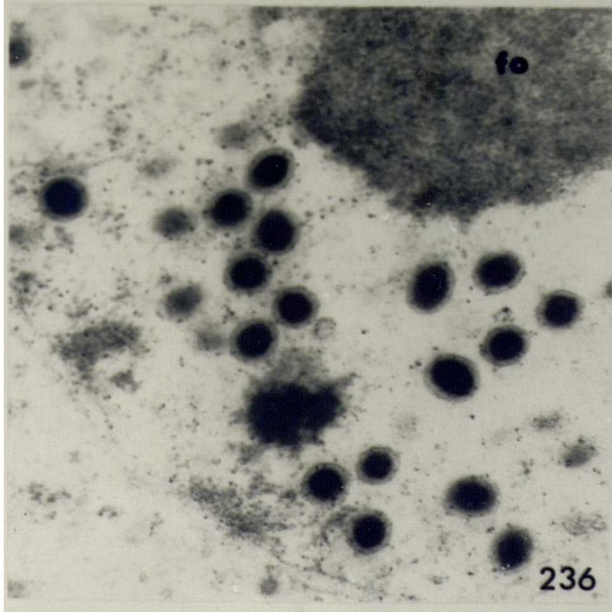
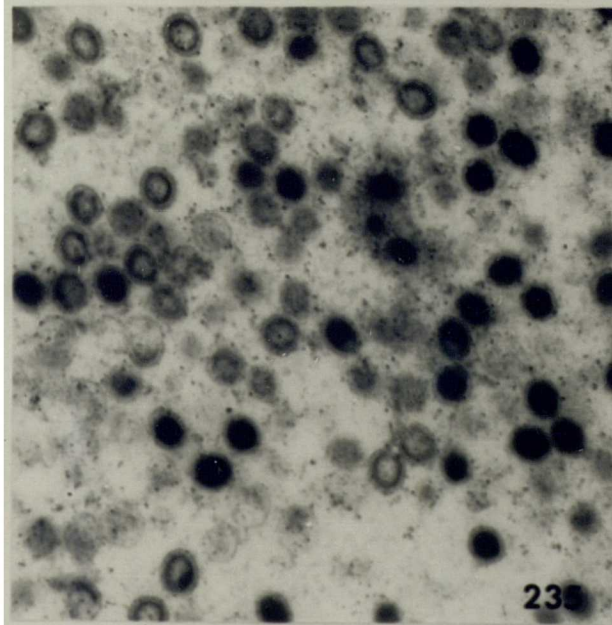
Fig. 234 Viral particles filling the cytoplasm (x9K).



D.reticulatum, viral infection of the  
sarcobellum.

Fig. 235 Viral particles in varying stages of  
maturation (x35K).

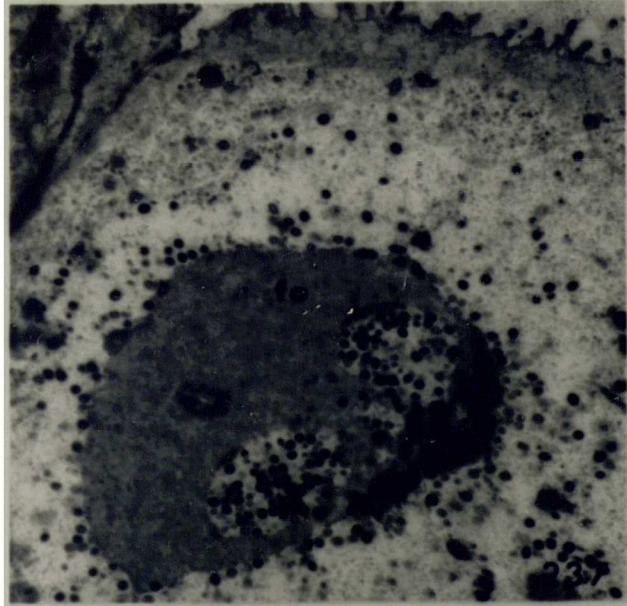
Fig. 236 Mature viral particles (x40K).



D.reticulatum, viral infection of the  
sarcobellum.

Fig. 237 Detail of the homogeneous material which  
accumulates at the focus of multiplication  
(x9K).

Fig. 238 Bleb of cytoplasm containing viral particles,  
released onto the surface of the sarcobellum  
(x20K).

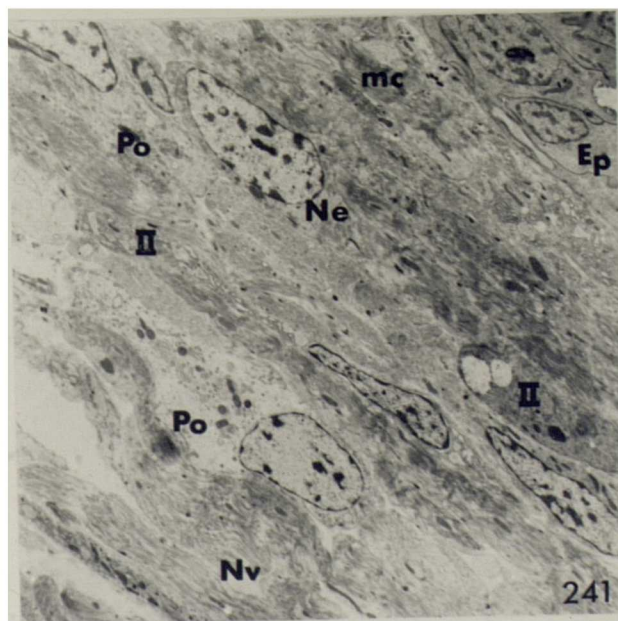
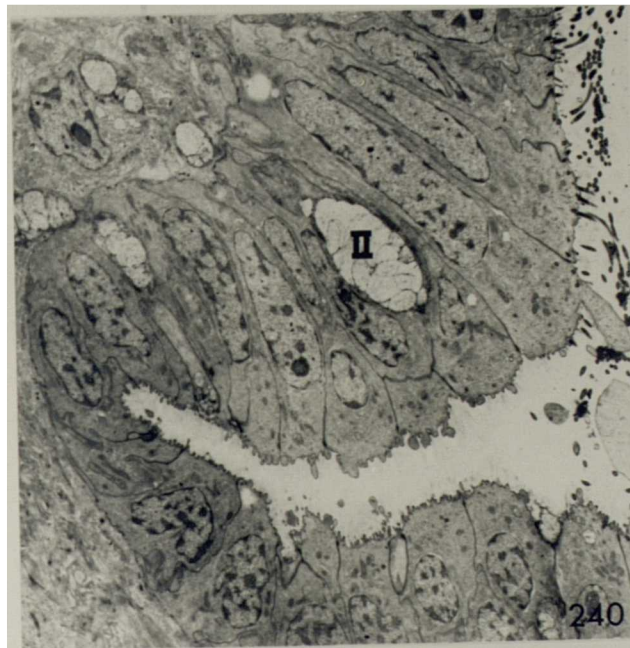
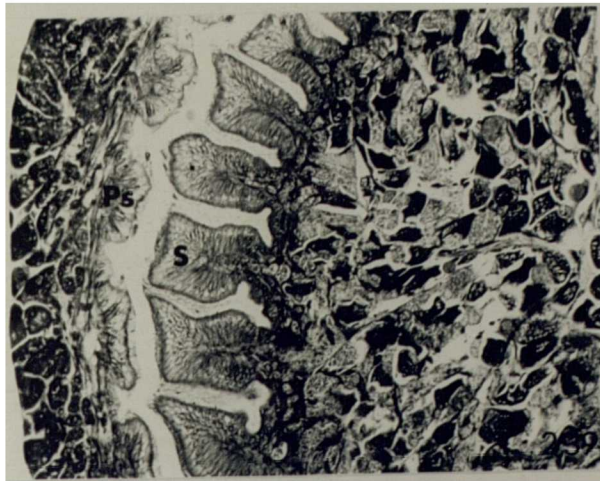


D.reticulatum, penial sac.

Fig. 239 T.S. through the wall of the penial sac  
(x160).

Fig. 240 General view of epithelium with isolated type  
II gland cell (x2.4K).

Fig. 241 Arrangement of the muscle, nerve, gland and  
pore cells in the connective tissue  
surrounding the penial sac (x2.4K).



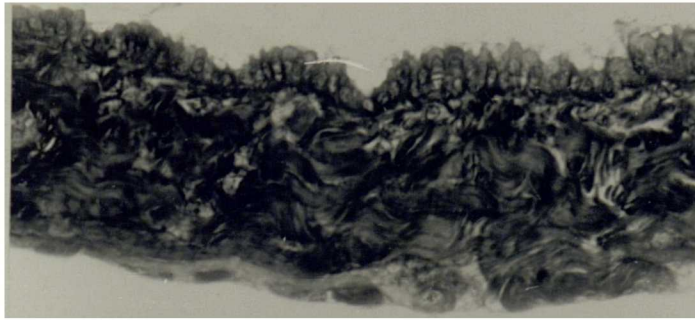


D.reticulatum, trifid appendage.

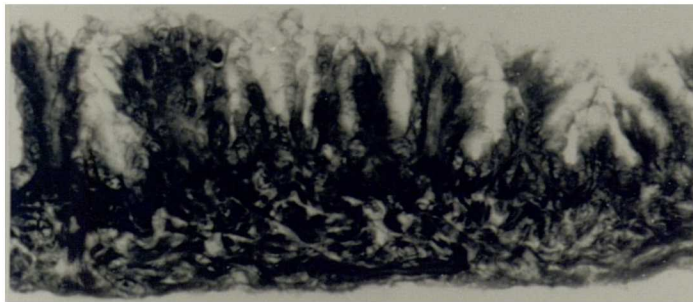
Fig. 242 L.S. through the penial sac near the trifid  
appendage (x255).

Fig. 243 L.S. through the base of the trifid appendage  
(x255).

Fig. 244 L.S. through the trifid appendage (x1.5K).  
C-stage.



242



243

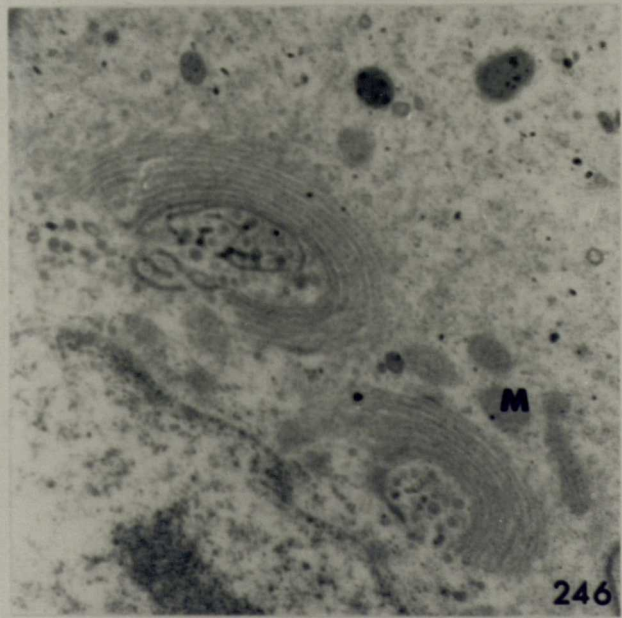
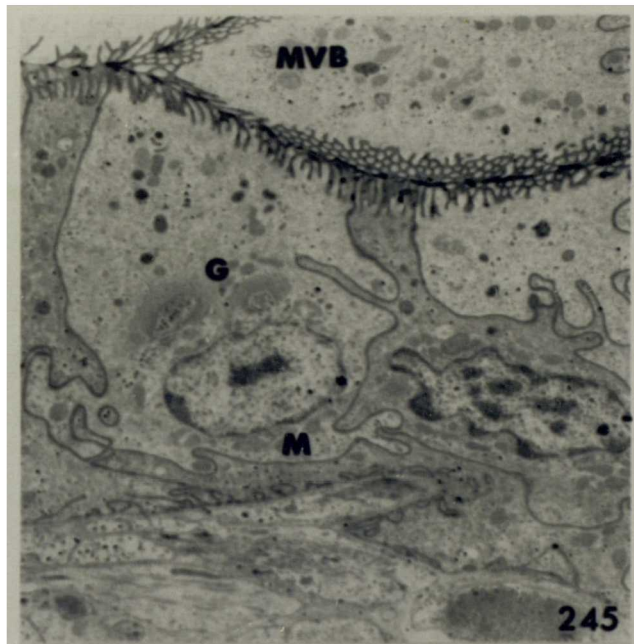


D.reticulatum, trifold appendage, C-stage.

Fig. 245 General view of epithelium (x6K).

Fig. 246 Detail of the Golgi region (x22.5K).

Fig. 247 Detail of the cell apices (x22.5K).

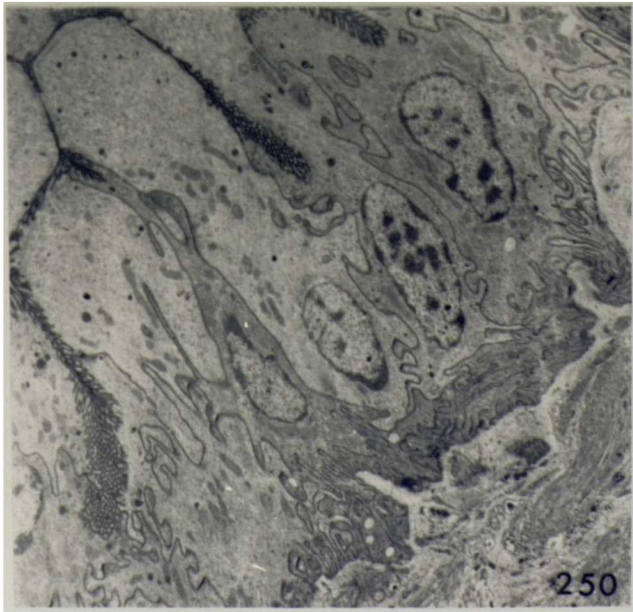
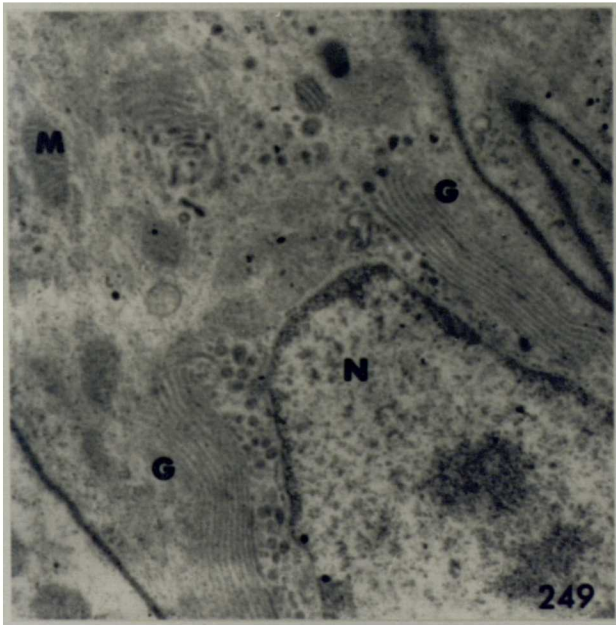


D.reticulatum, trifid appendage, E-stage.

Fig. 248 T.S. through the trifid appendage (x104).

Fig. 249 Detail of the Golgi region (x22.5K).

Fig. 250 General view of epithelium (x3.75K).

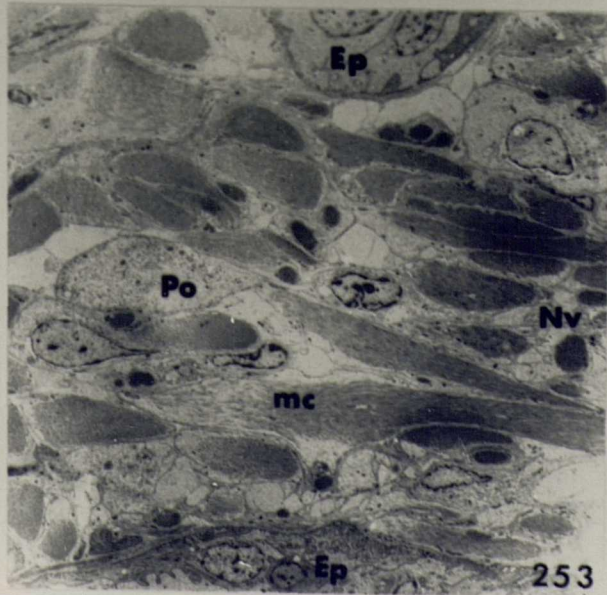
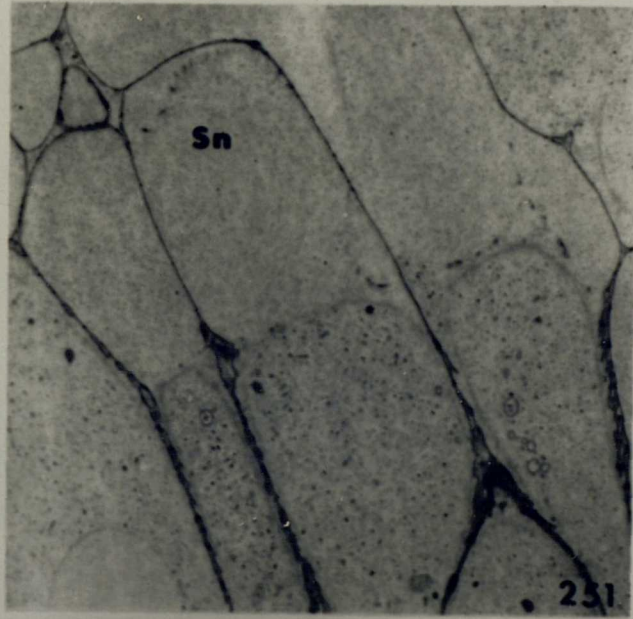


D.reticulatum, trifid appendage, E-stage.

Fig. 251 Detail of the cell apices (x6.5K).

Fig. 252 T.S. through a diverticulum with its lumen  
occluded by the swollen cell apices (x265).

Fig. 253 Arrangement of the muscle, nerve and pore  
cells in the connective tissue sheath (x1.5K).



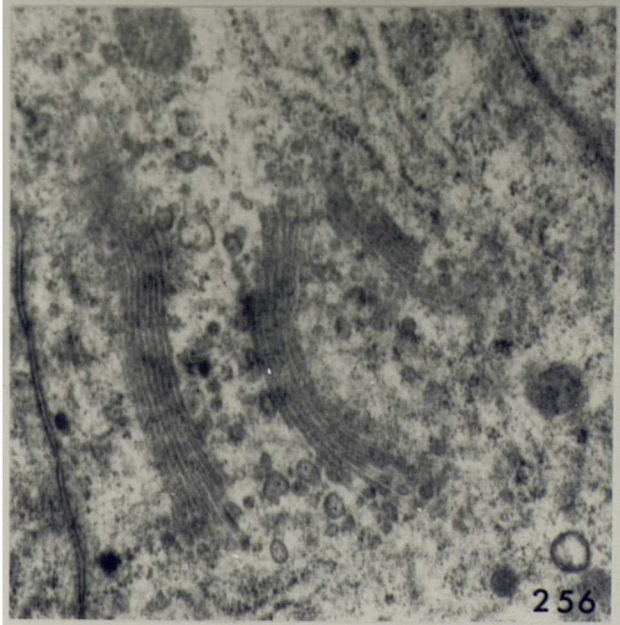
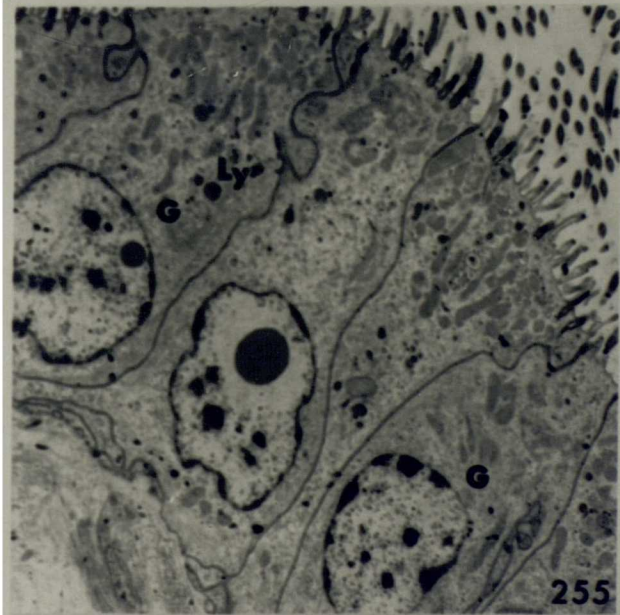
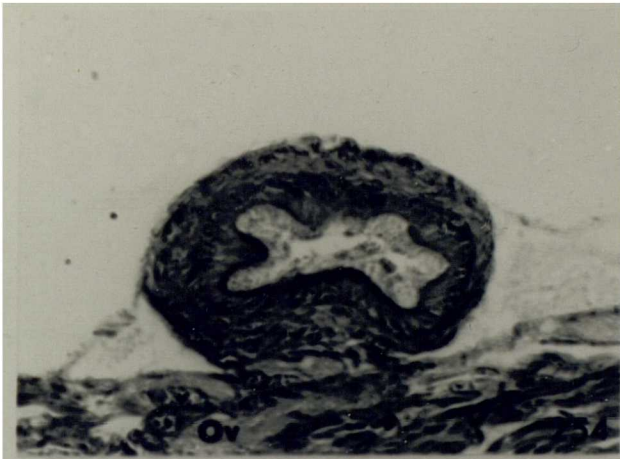


D.reticulatum, vas deferens.

Fig. 254 T.S.through the vas deferens (x260).

Fig. 255 General view of epithelium (x4.8K).

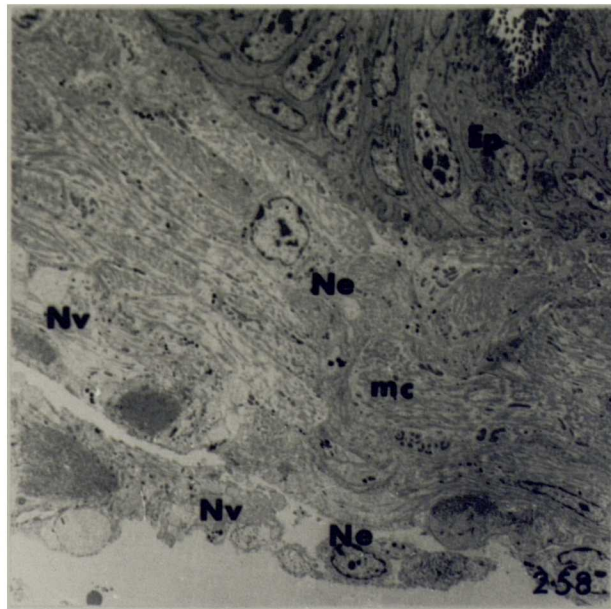
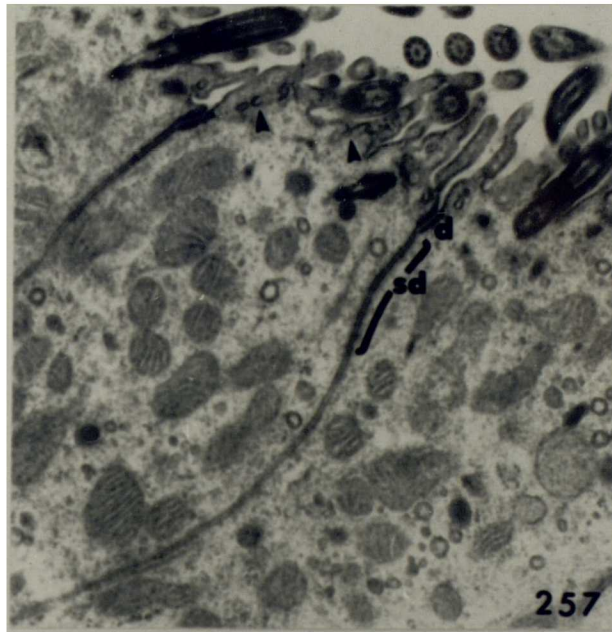
Fig. 256 General view of the Golgi region (x42K).



D.reticulatum, vas deferens.

Fig. 257 Detail of the cell apices (x22.5K). Arrows indicate vesicle chains.

Fig. 258 Arrangement of the muscle and nervous tissue in the connective tissue sheath (x1.5K).

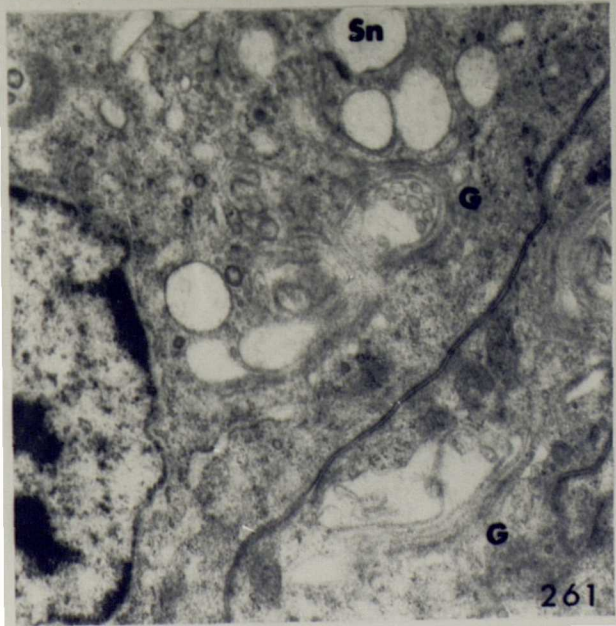
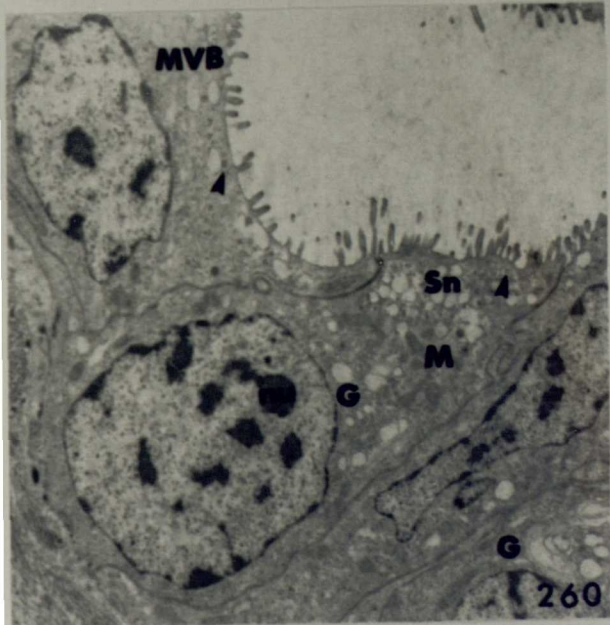
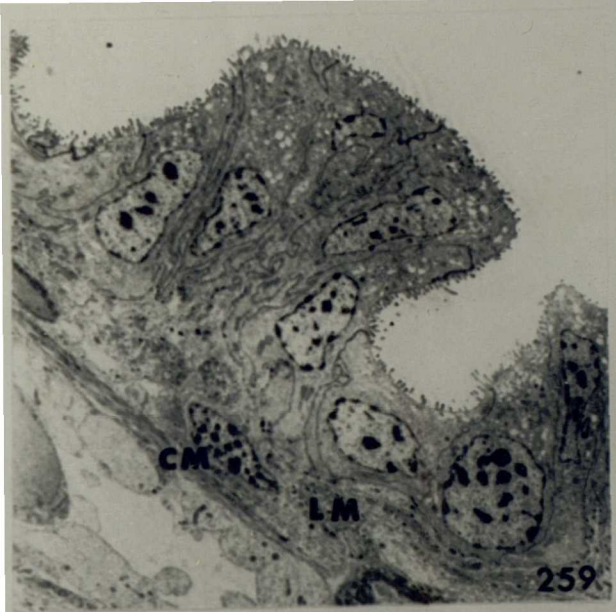


D.reticulatum, oviduct, epithelial cells.

Fig. 259 General view of epithelium (x2.5K).

Fig. 260 Detail of the epithelial cells (x6K). Arrows indicate small, possibly pinocytotic vesicles.

Fig. 261 Detail of the Golgi region (x20K).

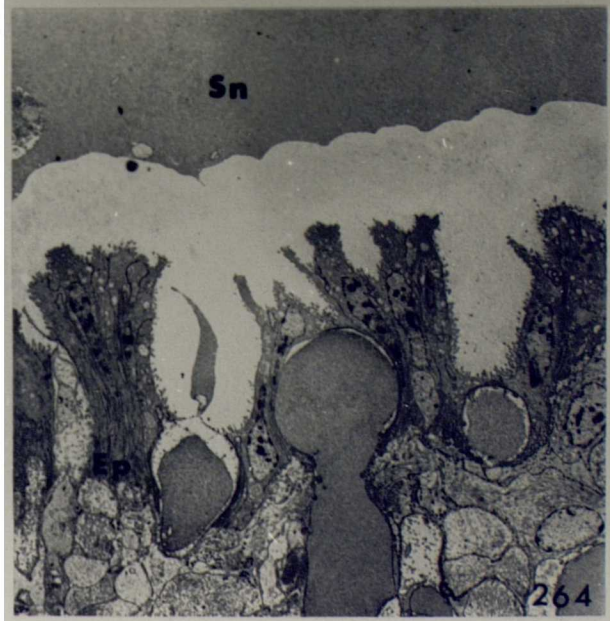


D.reticulatum, oviduct.

Fig. 262 Base of sub-epithelial oviducal gland cell  
(x2.5K).

Fig. 263 Oviducal gland cells (x1.5K).

Fig. 264 Gland cells opening into the lumen of the  
oviduct (x1.6K). The clear space is shrinkage  
artifact.

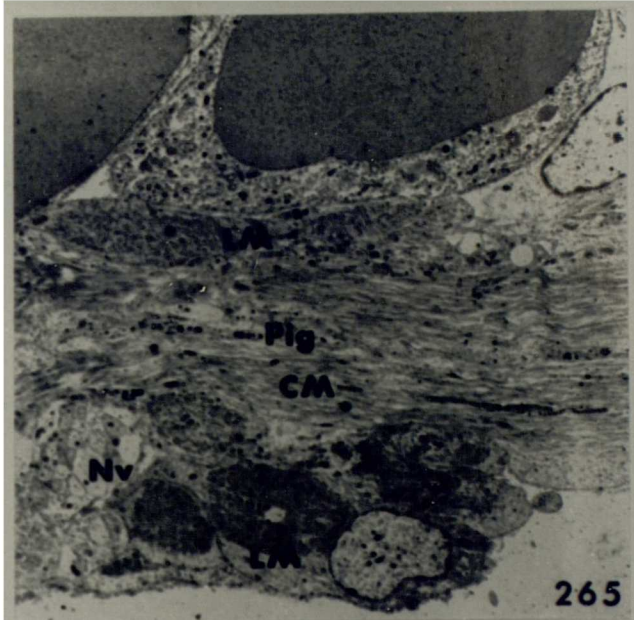




D.reticulatum, oviduct.

Fig. 265 Arrangement of the nerve and muscle in the connective tissue surrounding the oviduct (x2.4K).

Fig. 266 Arrangement of the nerve and muscle in the connective tissue near the epithelium (x6.4K). The arrow indicates the position of a possible neuromuscular junction.

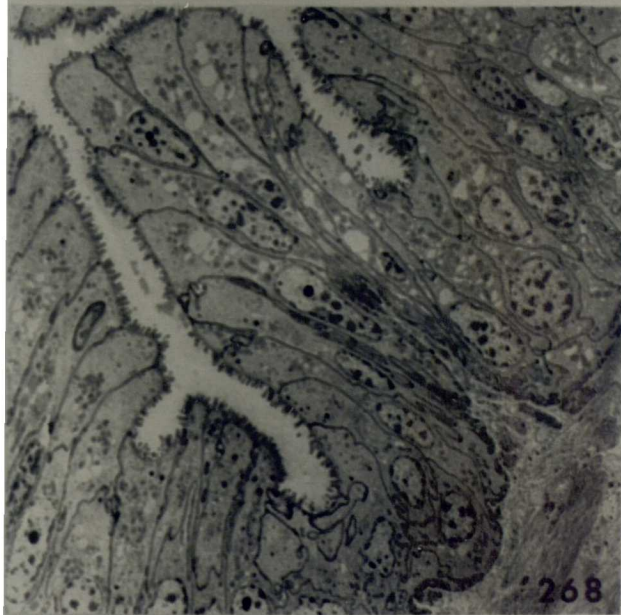
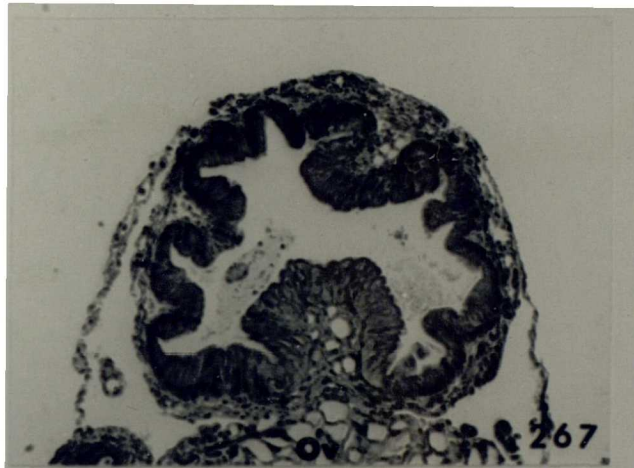


D.reticulatum, proximal region of the bursa  
copulatrix.

Fig. 267 Transverse section (x125).

Fig. 268 General view of the epithelium (x1.5K).

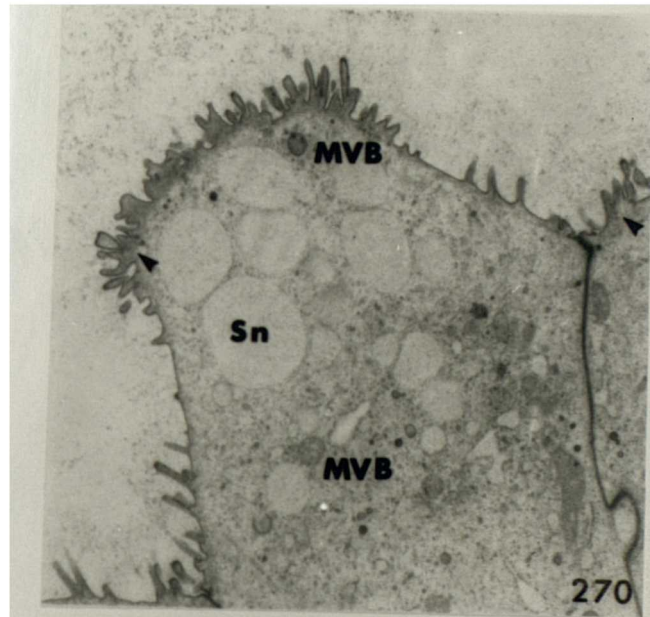
Fig. 269 Detail of the Golgi region in a typical  
epithelial cell (x37.5K).



D.reticulatum, mid-region of the bursa  
copulatrix.

Fig. 270 Detail of a cell apex swollen with accumulated  
secretion (x9K).

Fig. 271 Complex configuration of apical microvilli  
(x13.5K).



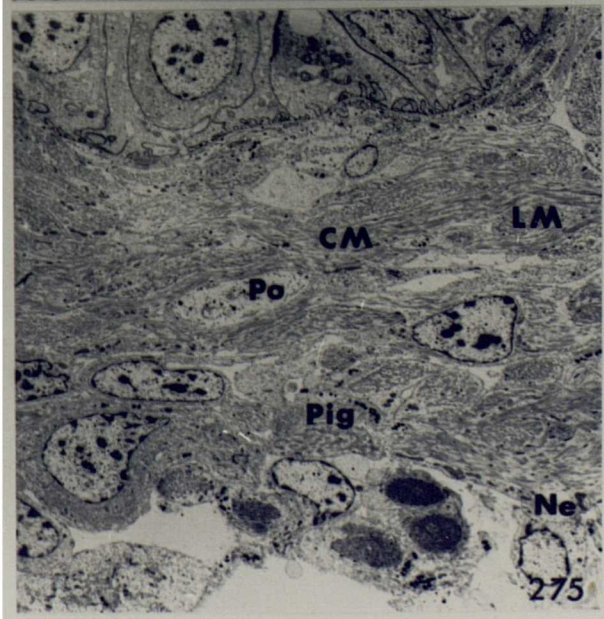
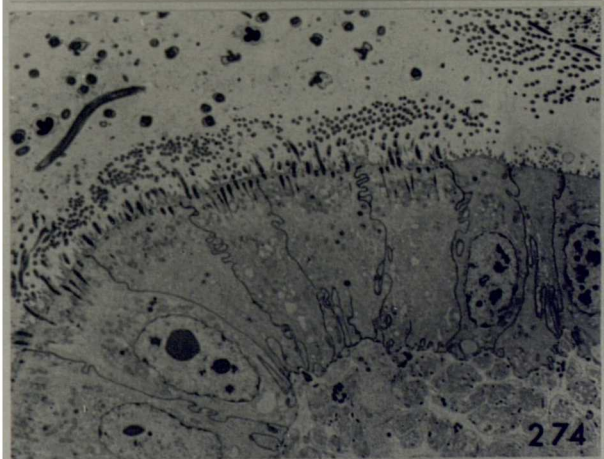
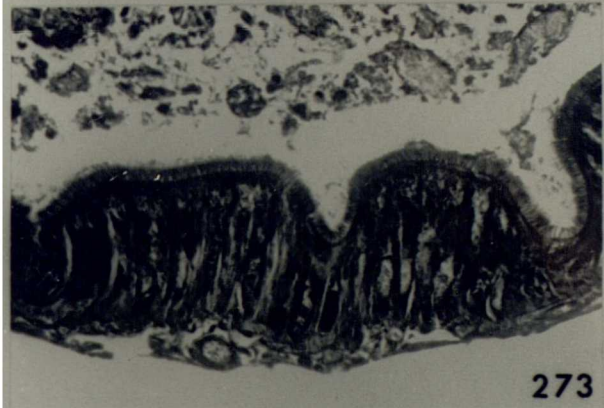
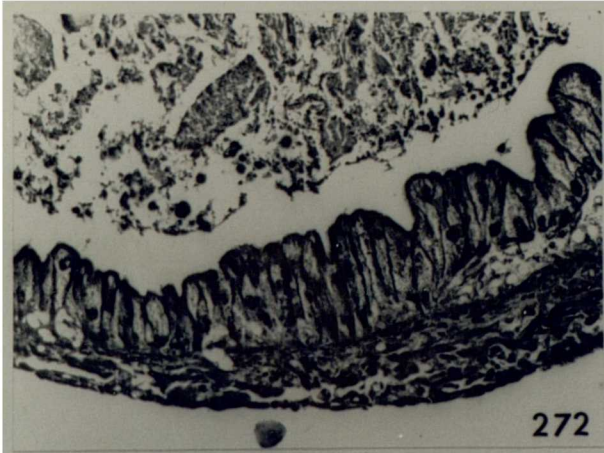
D.reticulatum, bursa copulatrix.

Fig. 272 Unciliated epithelium lining the mid-region of the bursa copulatrix (x160).

Fig. 273 Ciliated epithelium lining the distal region of the bursa copulatrix (x400).

Fig. 274 Transition from unciliated to ciliated epithelial cells (x2.2K).

Fig. 275 Arrangement of the muscle, nerve and pore cells in the connective tissue sheath (x 1.8K).



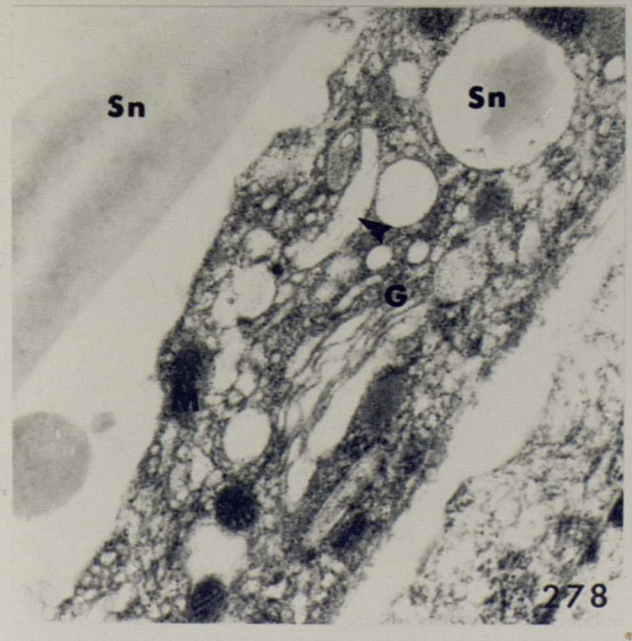
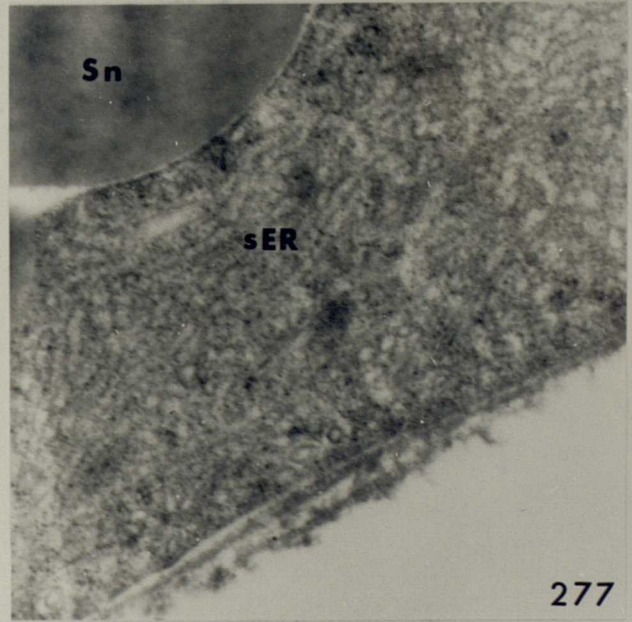
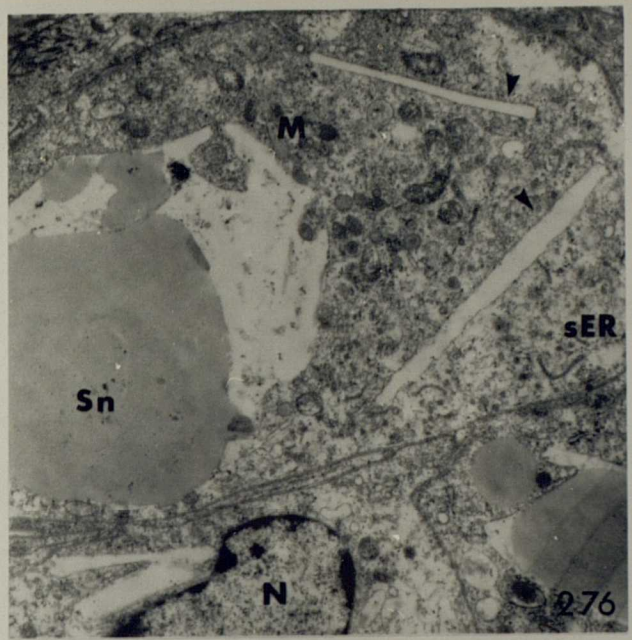


A. hortensis, lower atrium.

Fig. 276 Immature secretory cells (x 9K). Arrows indicate the rod or plate-like secretion granules.

Fig. 277 Detail of the smooth, tubular ER in the cytoplasm of a mature secretory cell (x 37.5K).

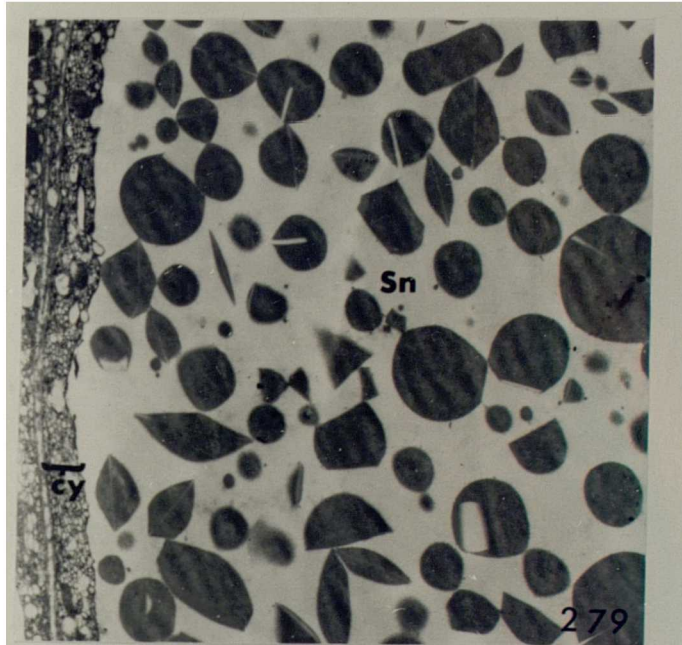
Fig. 278 Cytoplasmic detail of a mature secretory cell (x 22.5K). Arrow indicates a developing secretion granule.



A. hortensis, lower atrium.

Fig. 279 Accumulation of secretion in the centre of the gland cell (x 6K).

Fig. 280 L.S. through the lower atrium (x 160).

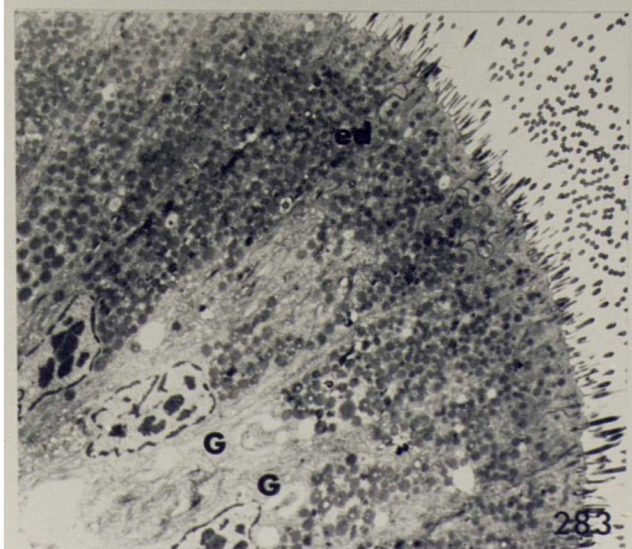
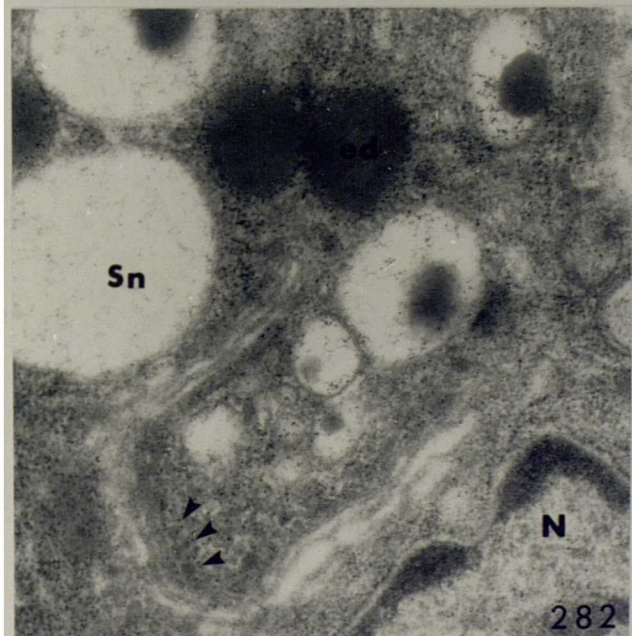
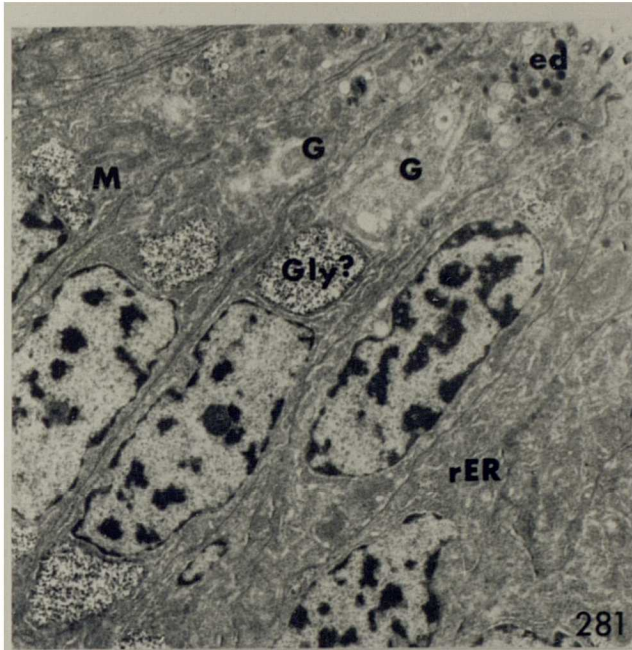


A.hortensis, vas deferens.

Fig. 281 Epithelial cells (x 6K). C-stage.

Fig. 282 Detail of a Golgi body and forming secretion granules (X 37.5K). E-stage. Arrows indicate electron-opaque vesicles.

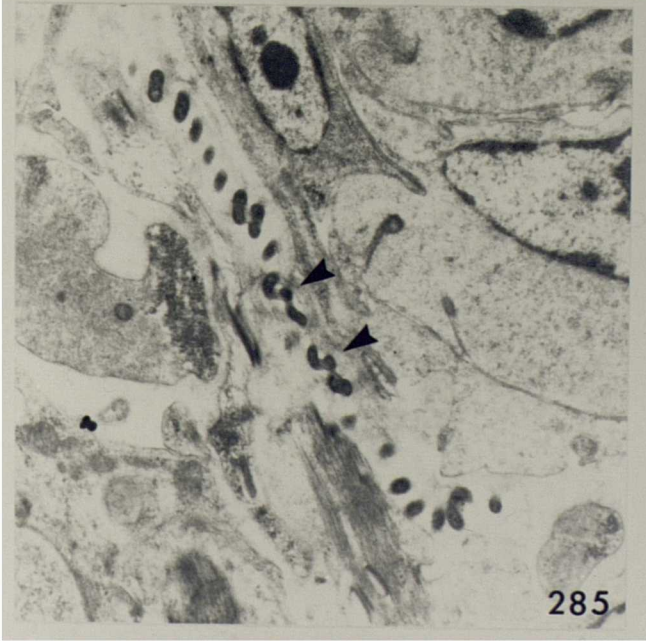
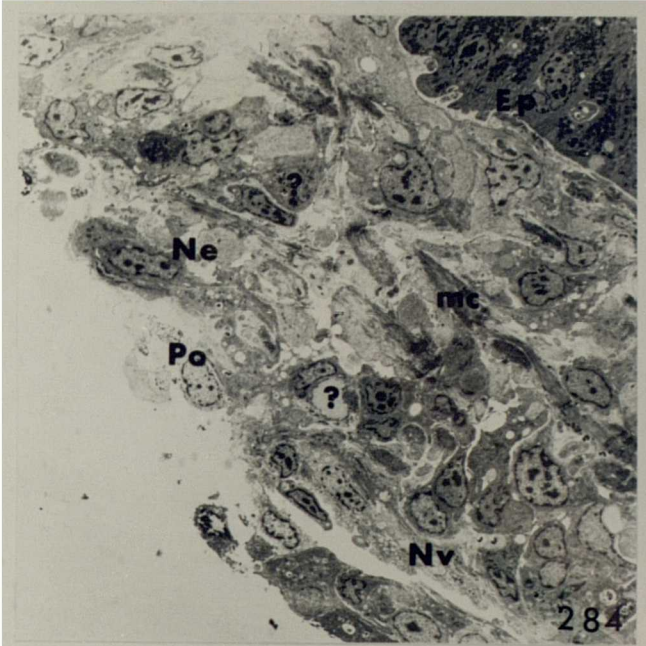
Fig. 283 Epithelial cells (x3.75K). E-stage



A.hortensis, vas deferens.

Fig. 284 Arrangement of the muscle, nerve and pore cells in the connective tissue sheath (x1.5K).  
? indicates unidentified cells with large inclusions.

Fig. 285 Spirochaetes in the connective tissue (arrowed) (x 22.5K).





A.hortensis, epiphallus.

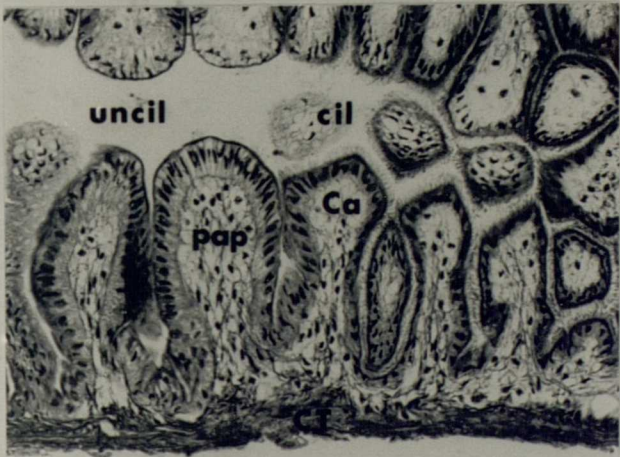
Fig. 286 Papillae lining the epiphallus, S.E.M.  
(x1.3K).

Fig. 287 L.S. through the epiphallus (x250).

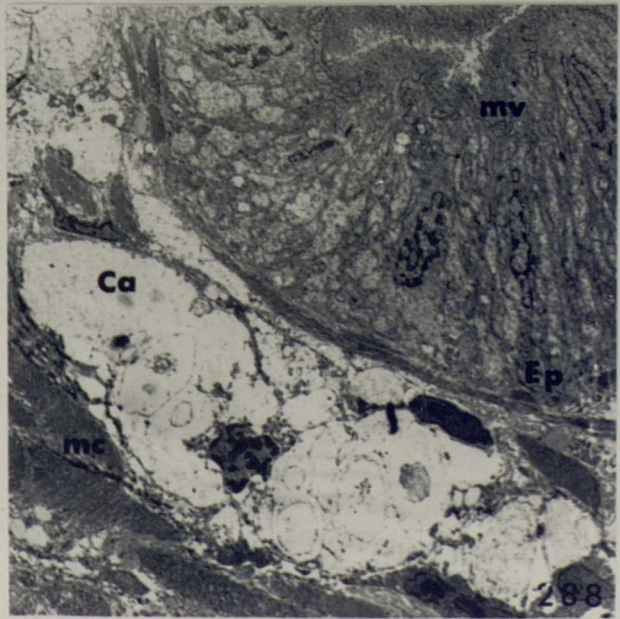
Fig. 288 General view of epithelium with underlying  
calcium cells (x2.25K).



286



287



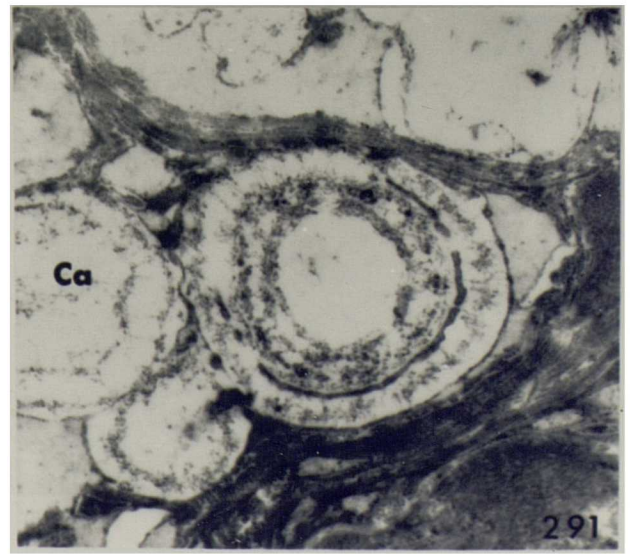
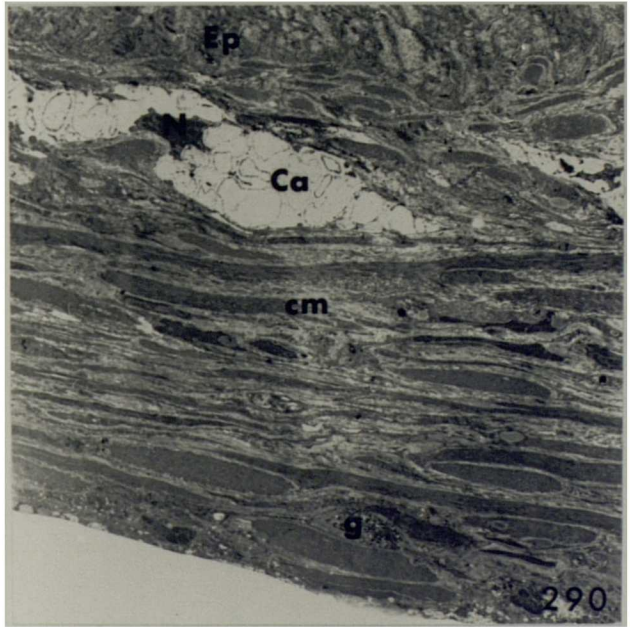
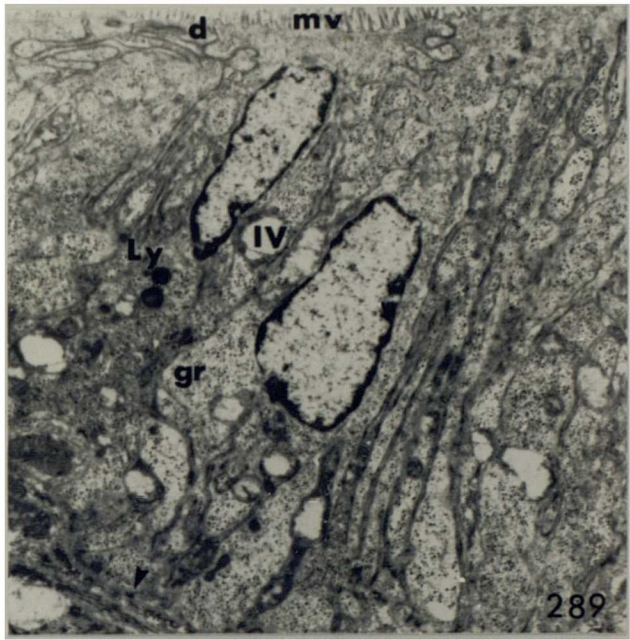
288

A.hortensis, epiphallus

Fig. 289 Epithelial cells (x6K). Arrow indicates hemidesmosome on basal membrane.

Fig. 290 Arrangement of muscle, granular cell and calcium cells in the connective tissue sheath (x2.25K).

Fig. 291 Detail of calcium concretions within the calcium cell (x15K).

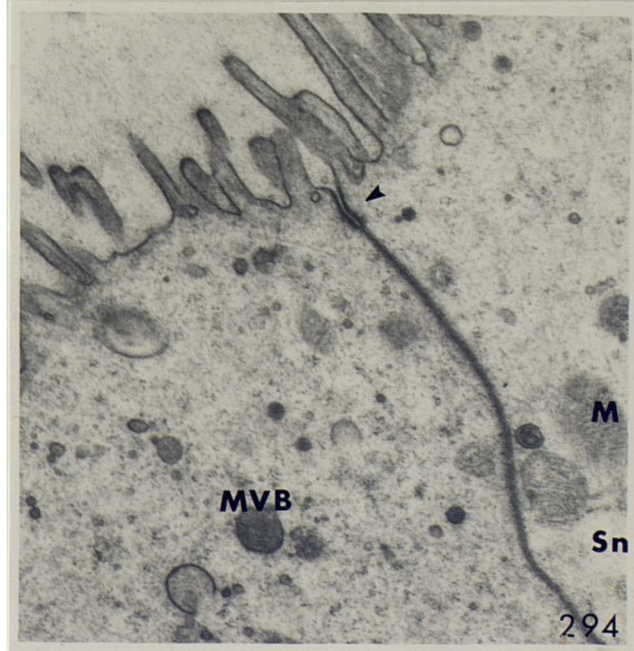
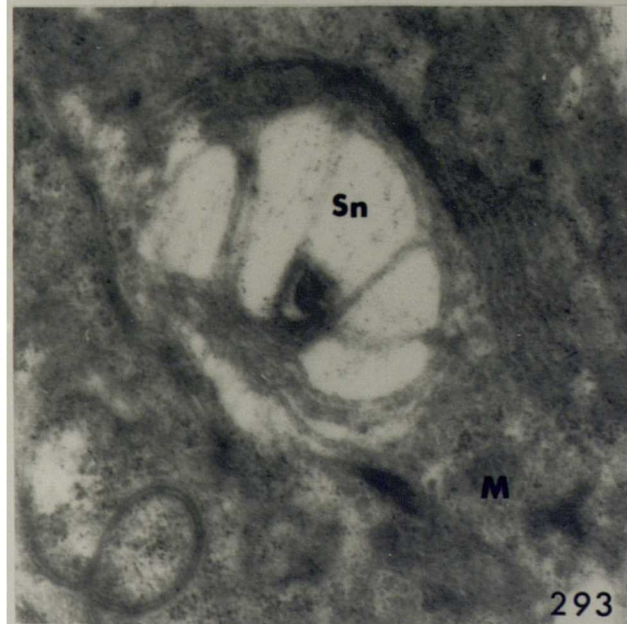
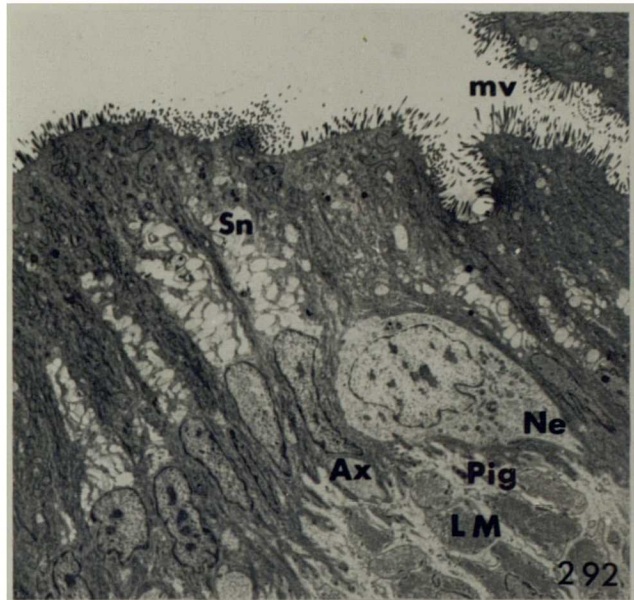


A.hortensis, thick oviduct.

Fig. 292 General view of epithelium (x2.25K).

Fig. 293 Detail of a Golgi body and forming secretory vesicles (x37.5K).

Fig. 294 Detail of cell apices (x22.5K). Arrow indicates the position of a desmosome.

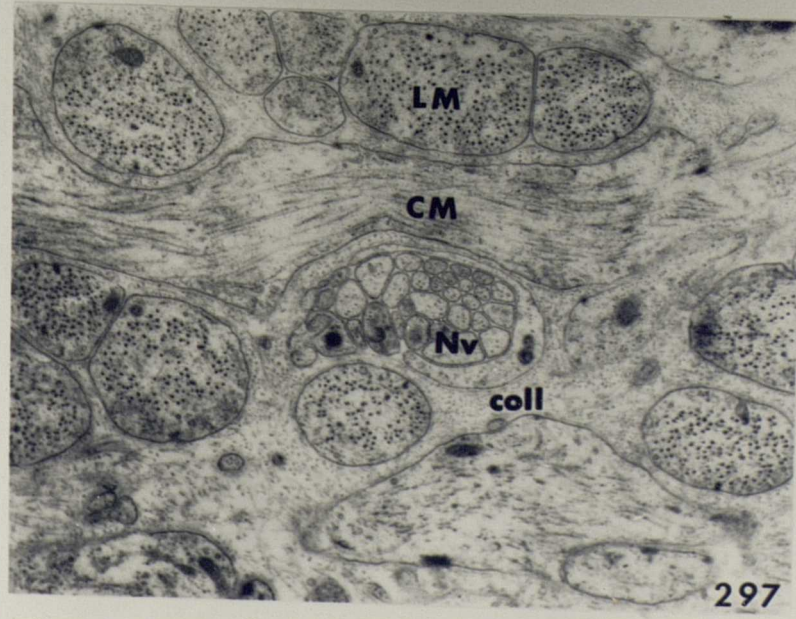
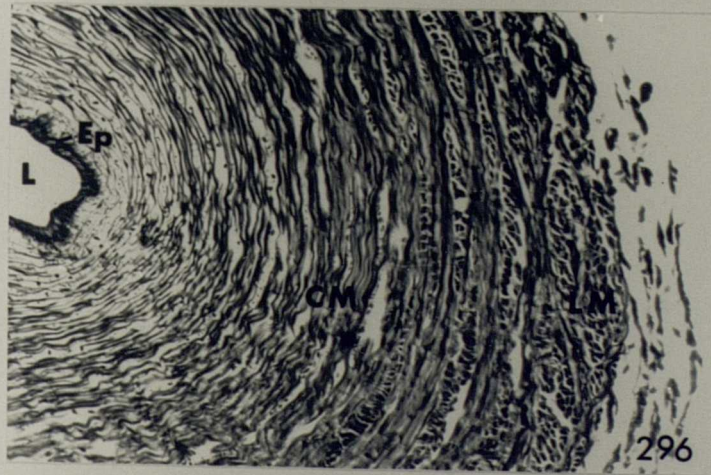
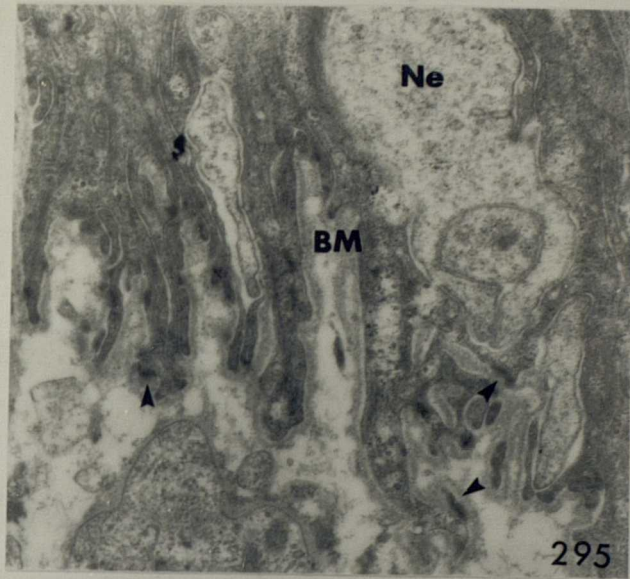


A.hortensis, thick oviduct.

Fig. 295 Detail of cell bases showing the relationship with the underlying nerve plexus (x15K).  
Arrows indicate hemidesmosomes in apposition to the thick basement membrane.

Fig. 296 T.S. through the thick oviduct (x164).

Fig. 297 Arrangement of the muscle and nerve cells in the inner region of the connective tissue sheath (x3.36K).



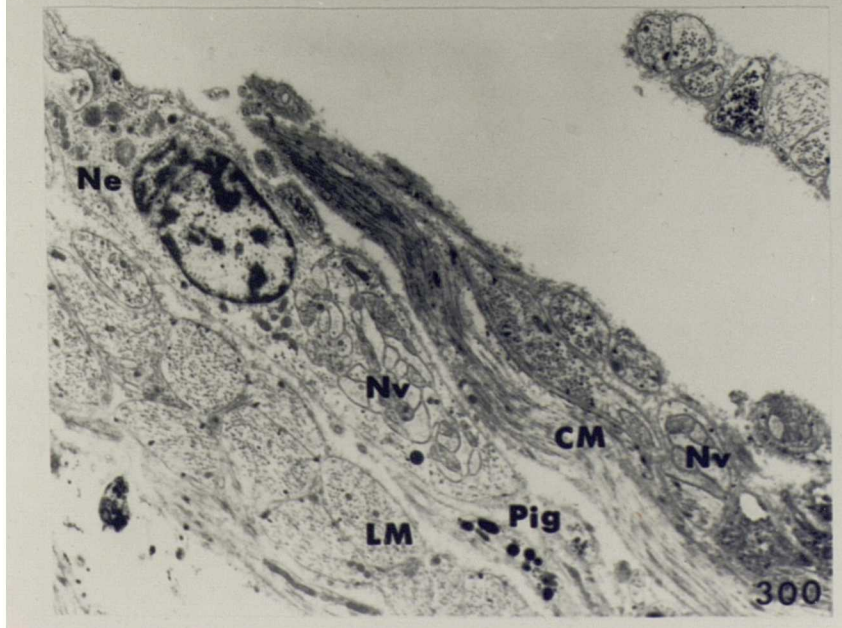
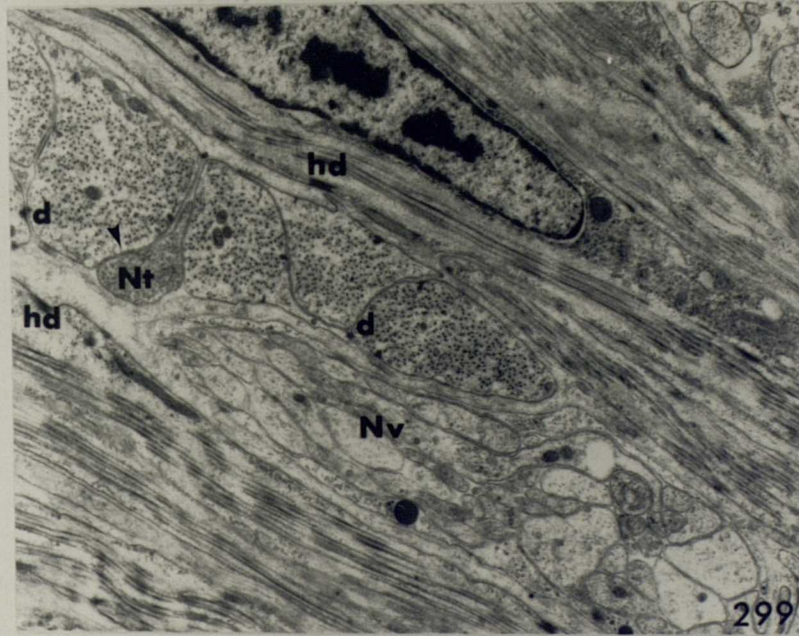
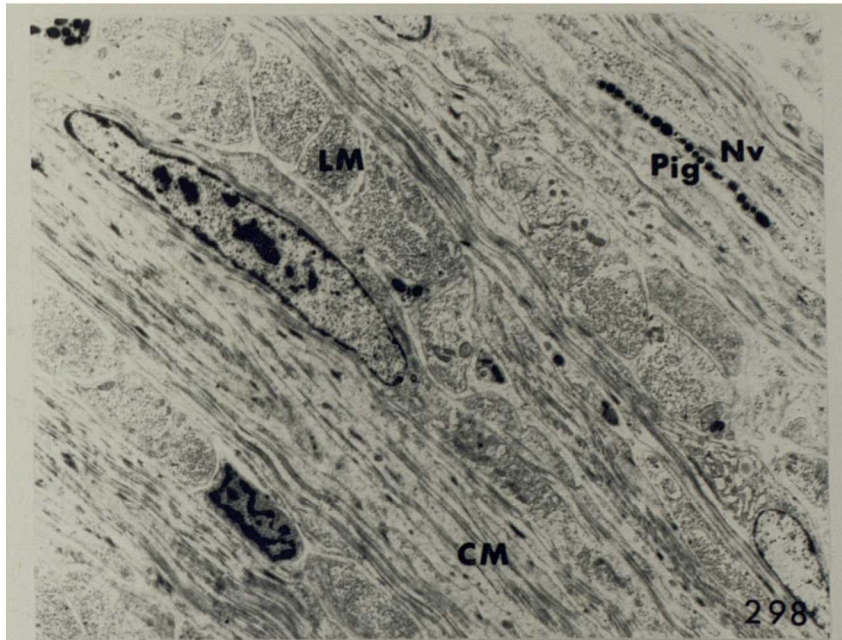


A.hortensis, thick oviduct.

Fig. 298 Arrangement of the muscle and nerve cells in the central region of the connective tissue sheath (x4.32K).

1  
Fig. 299 Detail of the muscle/nerve relationship (x9K).  
Arrow indicates possible neuromuscular junction.

Fig. 300 Arrangement of the nerve and muscle cells at the periphery of the connective tissue sheath (x5.16K).



A.hortensis, thin oviduct.

Fig. 301 General view of epithelium (x3.75K). Small arrows indicate granular accumulations in the cytoplasm, large arrows indicate lipid-like droplets.

Fig. 302 Detail of Golgi apparatus (x37.5K).

Fig. 303 Arrangement of muscle and nerve cells in the connective tissue sheath (x2.25K).

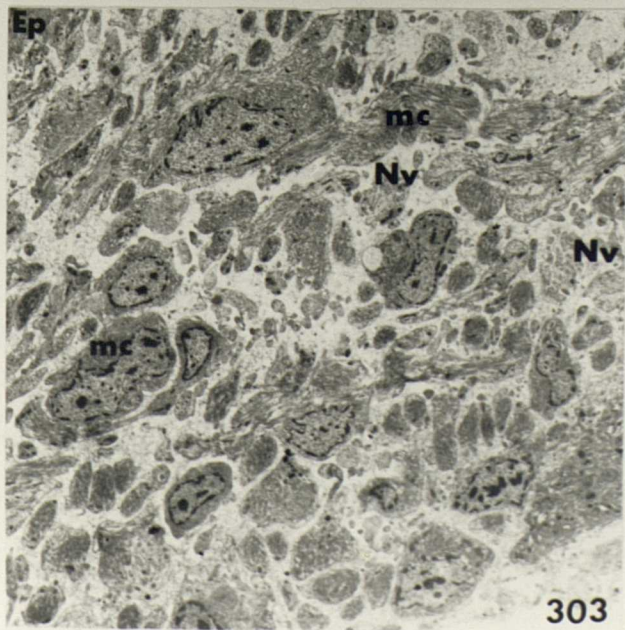
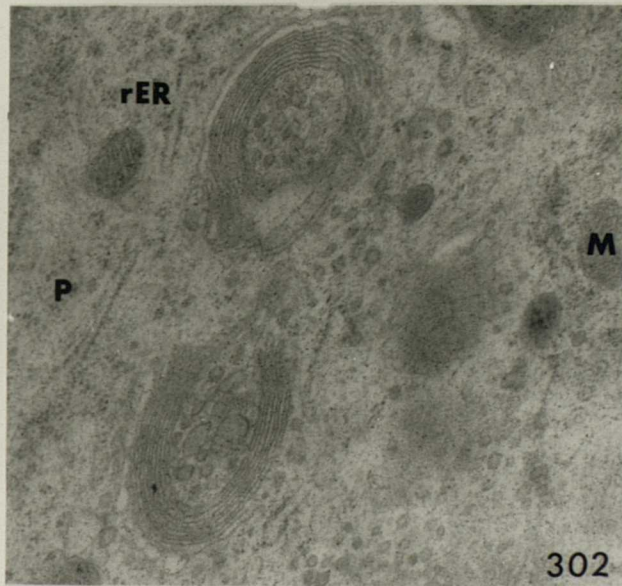
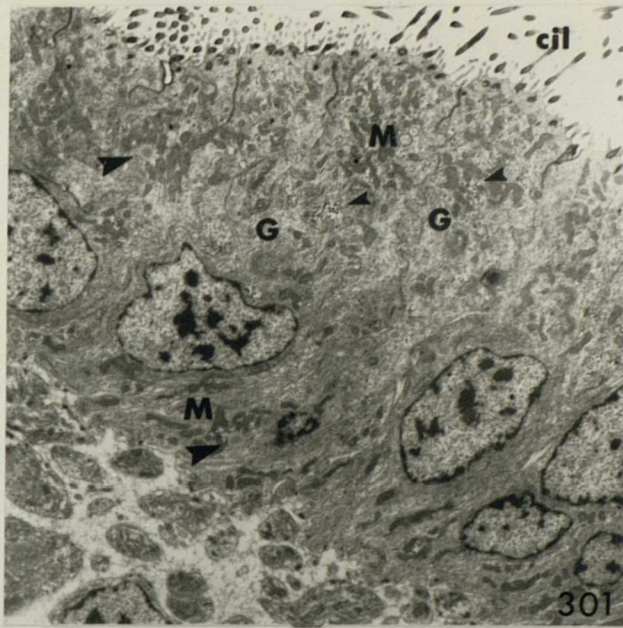


Fig. 304 Tracing of a thin layer chromatogram of lipid  
extracts from the lower atria of A.hortensis.

A. aqueous extract

B. first ether extract

C. second ether extract

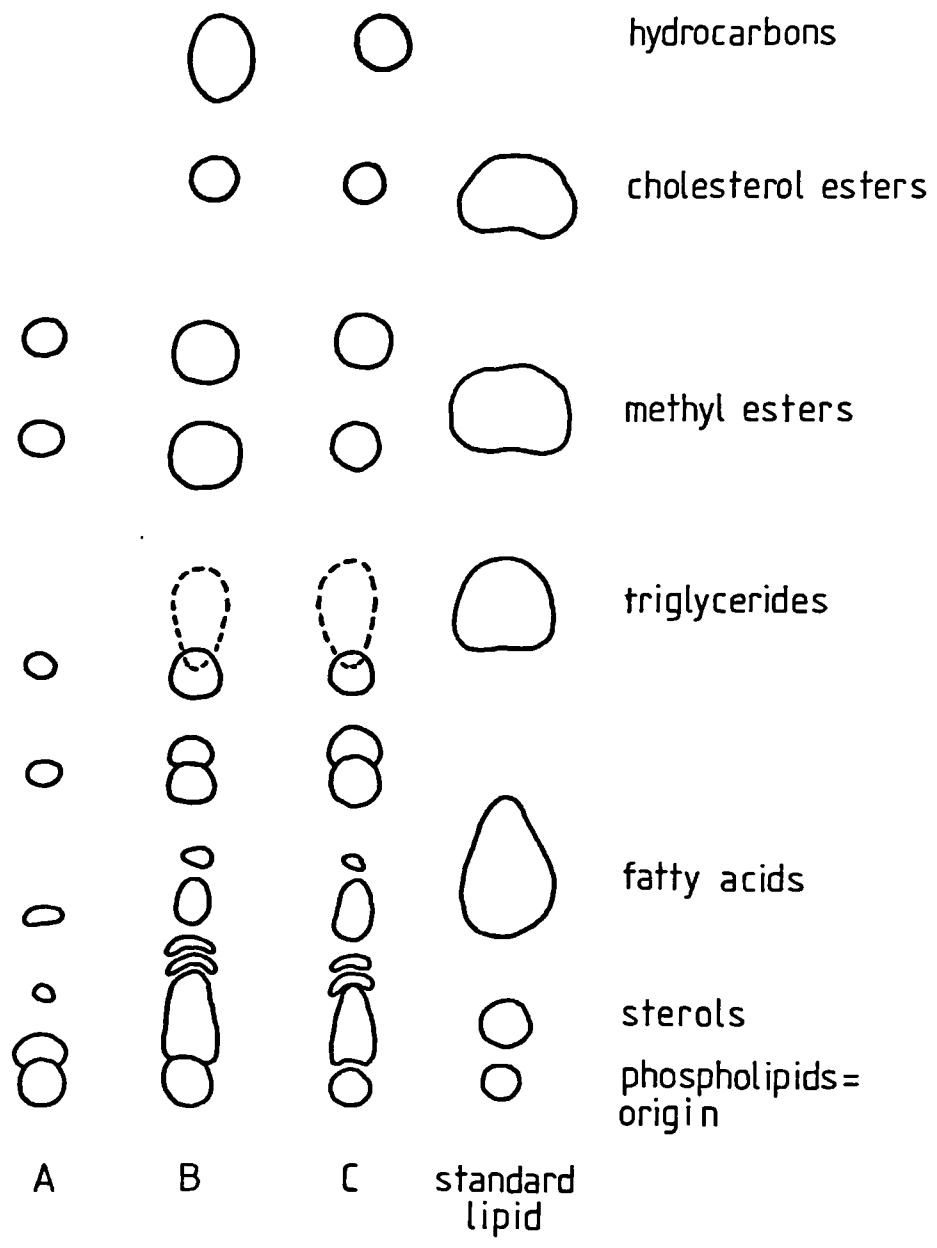


Fig. 304

Fig. 305 Diagram showing the variety of form of the anterior genital ducts in representative Stylommatophora.

- a. Generalized plan
- b. Helix aspersa
- c. Pellicula depressa
- d. Testacella haliotidea
- e. A.hortensis
- f. Milax budapestensis
- g. Limax maximus
- h. D. reticulatum
- i. Lehmannia marginata
- j. Philomycus carolinianus

Key: a, atrium; b, bursa copulatrix;  
c, caecum; CD, common duct; div,  
diverticulum; ds, dart sac;  
e, epiphallus; f, flagellum; lg, lobed  
gland; mg, mucous gland; o, oviduct;  
p, penis; pm, penial mass; ta, trifid  
appendage; vd, vas deferens.

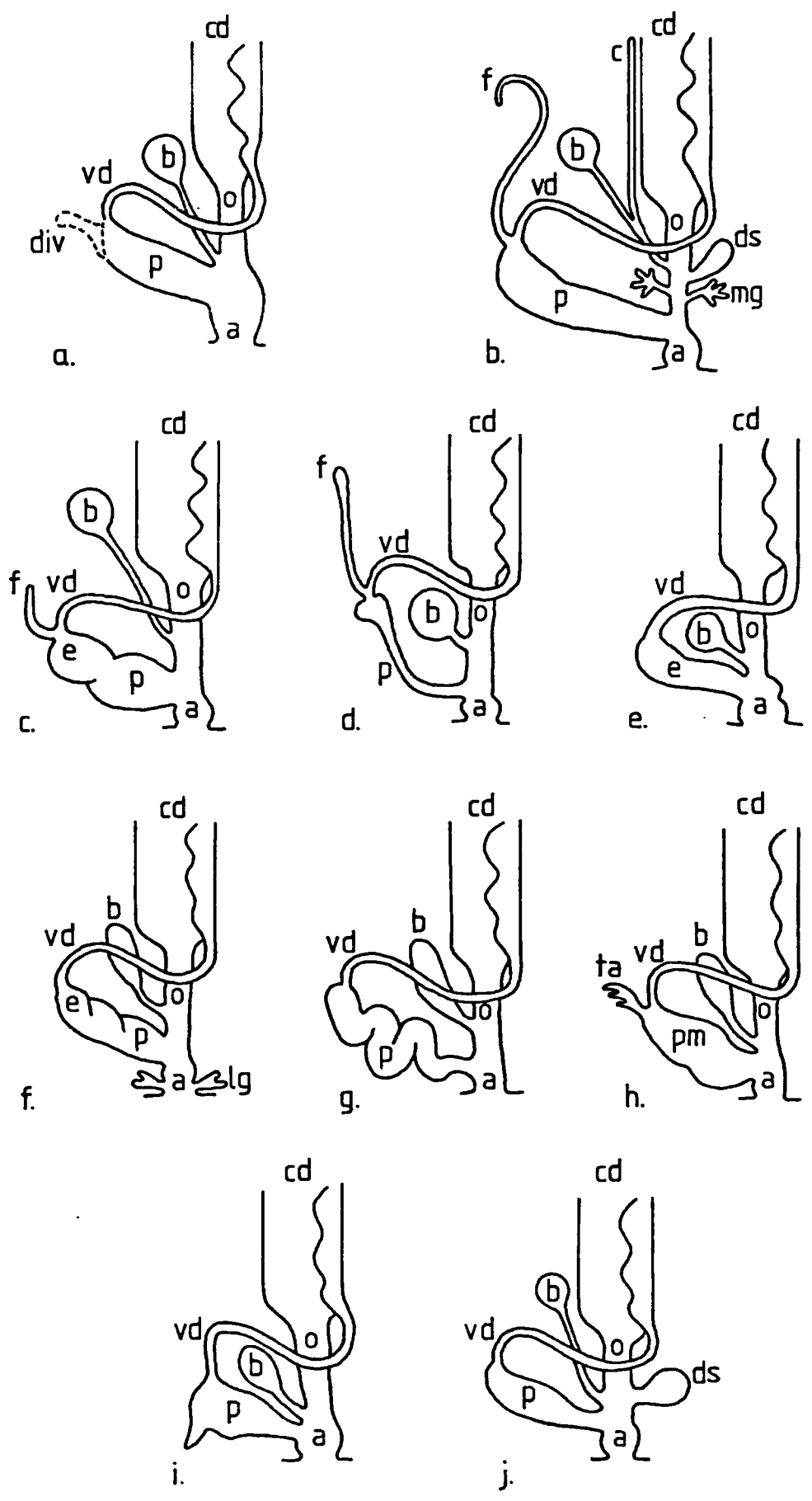


Fig. 305



Fig. 306 Variation in the origin of the bursa  
copulatrix at morphogenesis in representative  
*Stylommatophora*.

a. Helix pomatia

b. A. hortensis

c. D. reticulatum, Limax maximus

d. Arion ater

Key: cd, common duct; ga, genital atrium;

♀, female duct; ♂, male duct.

Bursa copulatrix, stippled.

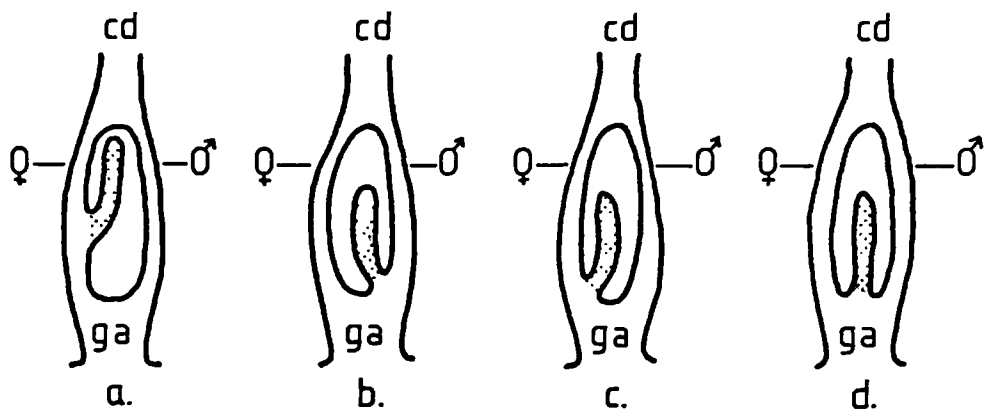


Fig. 306

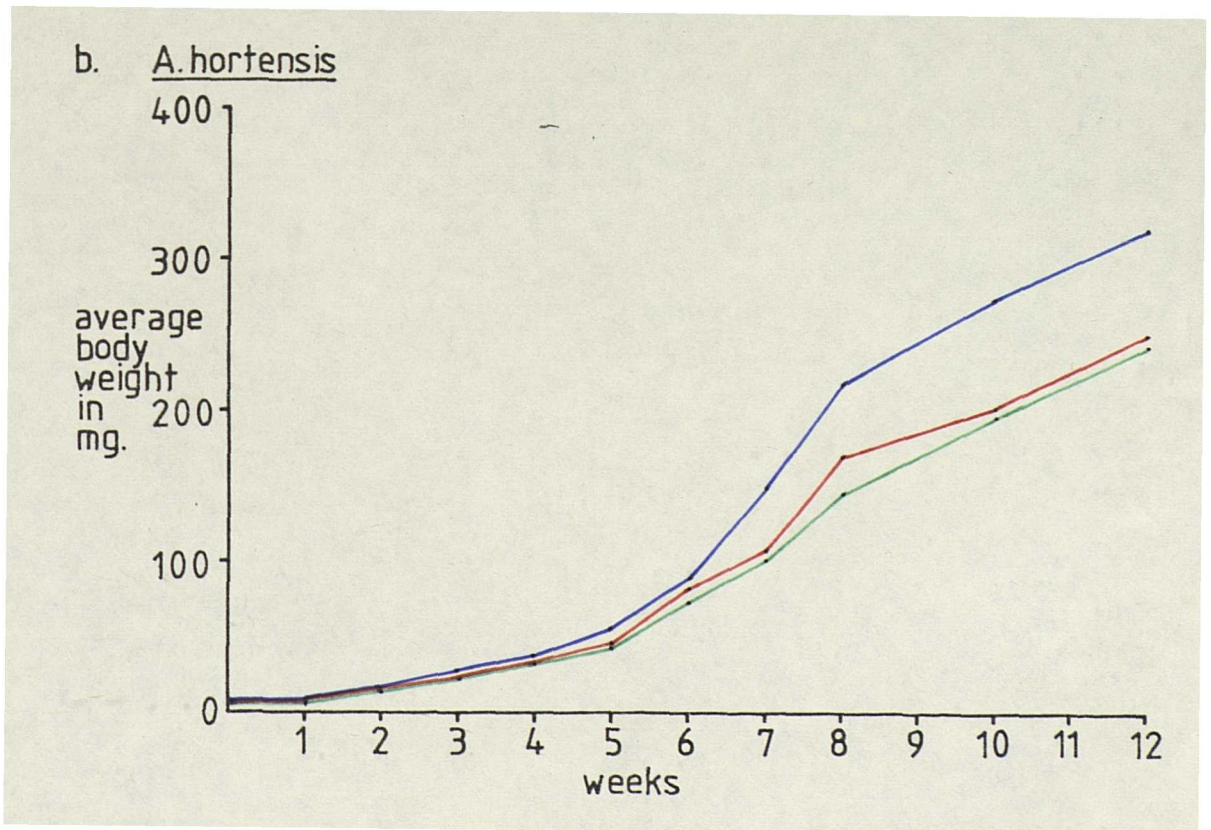
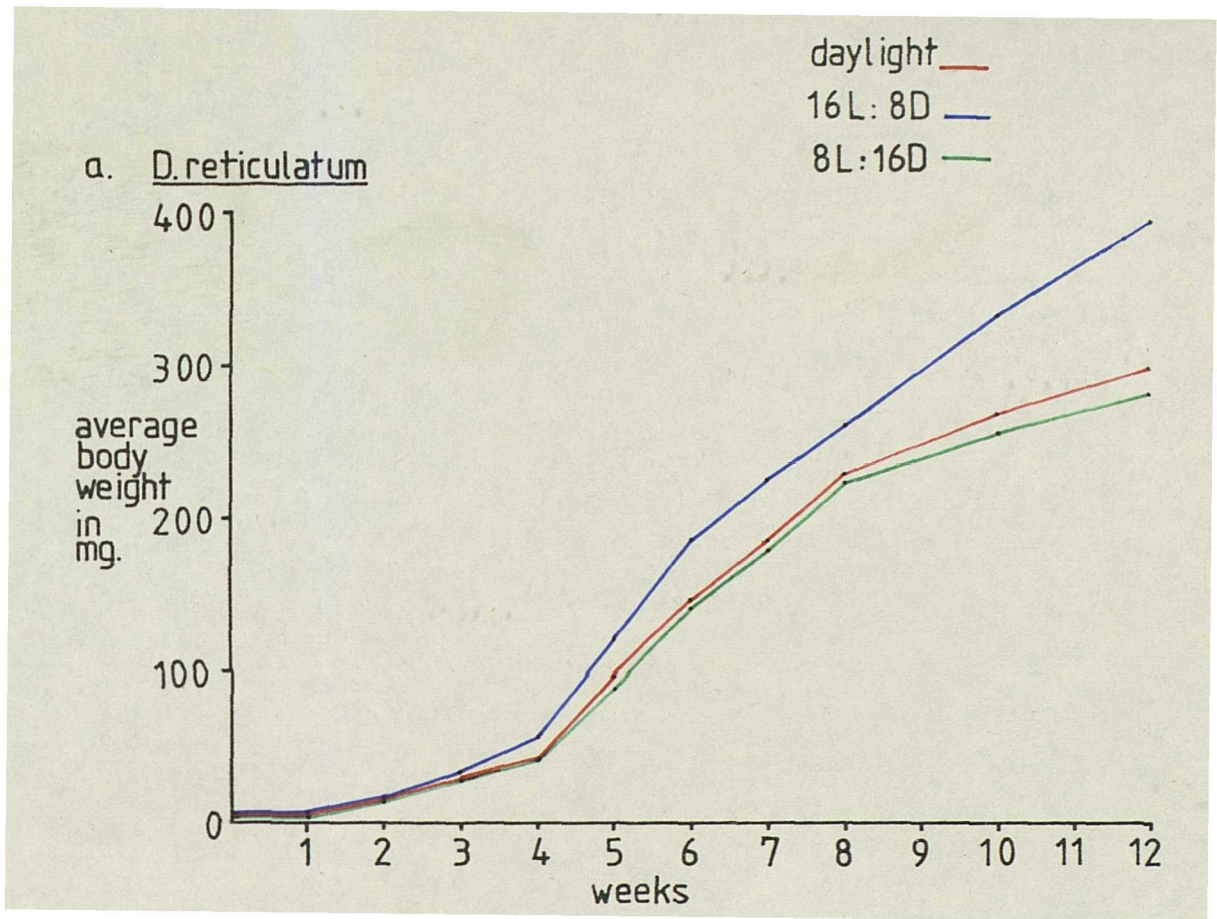
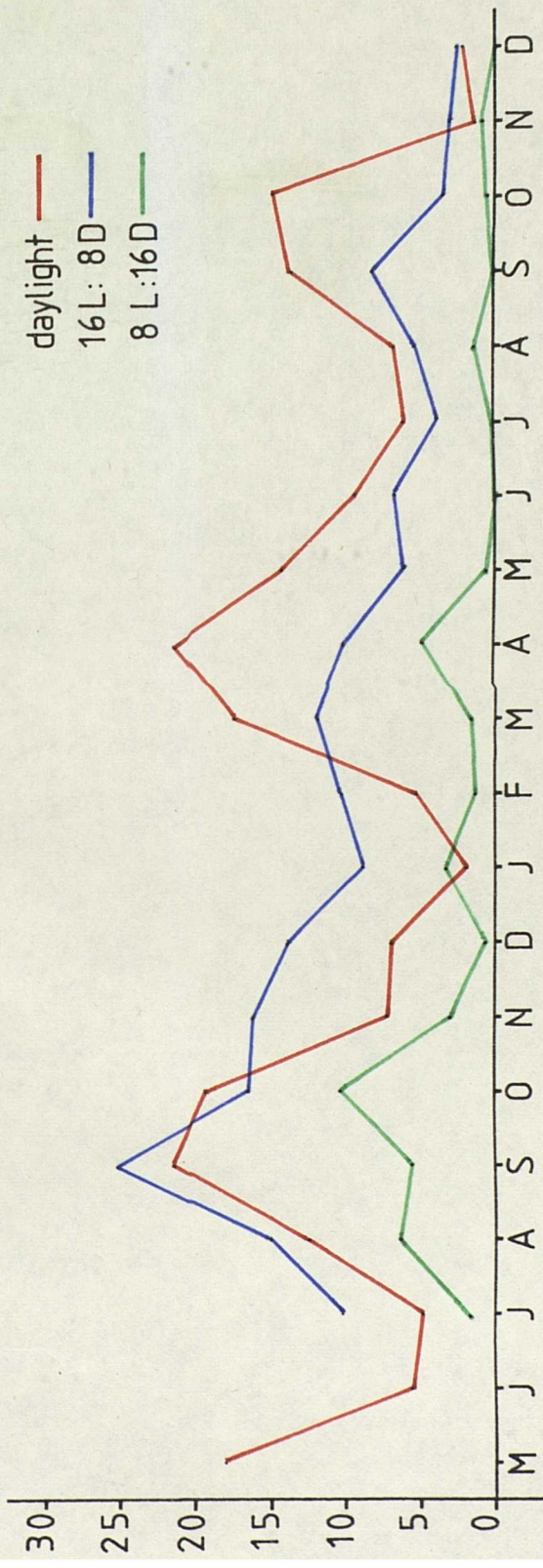


Fig. 307 The effect of photoperiod on growth

D.reticulatum

no. of eggs per animal



A.hortensis

no. of eggs per animal



The effect of photoperiod on egg production

Fig. 308

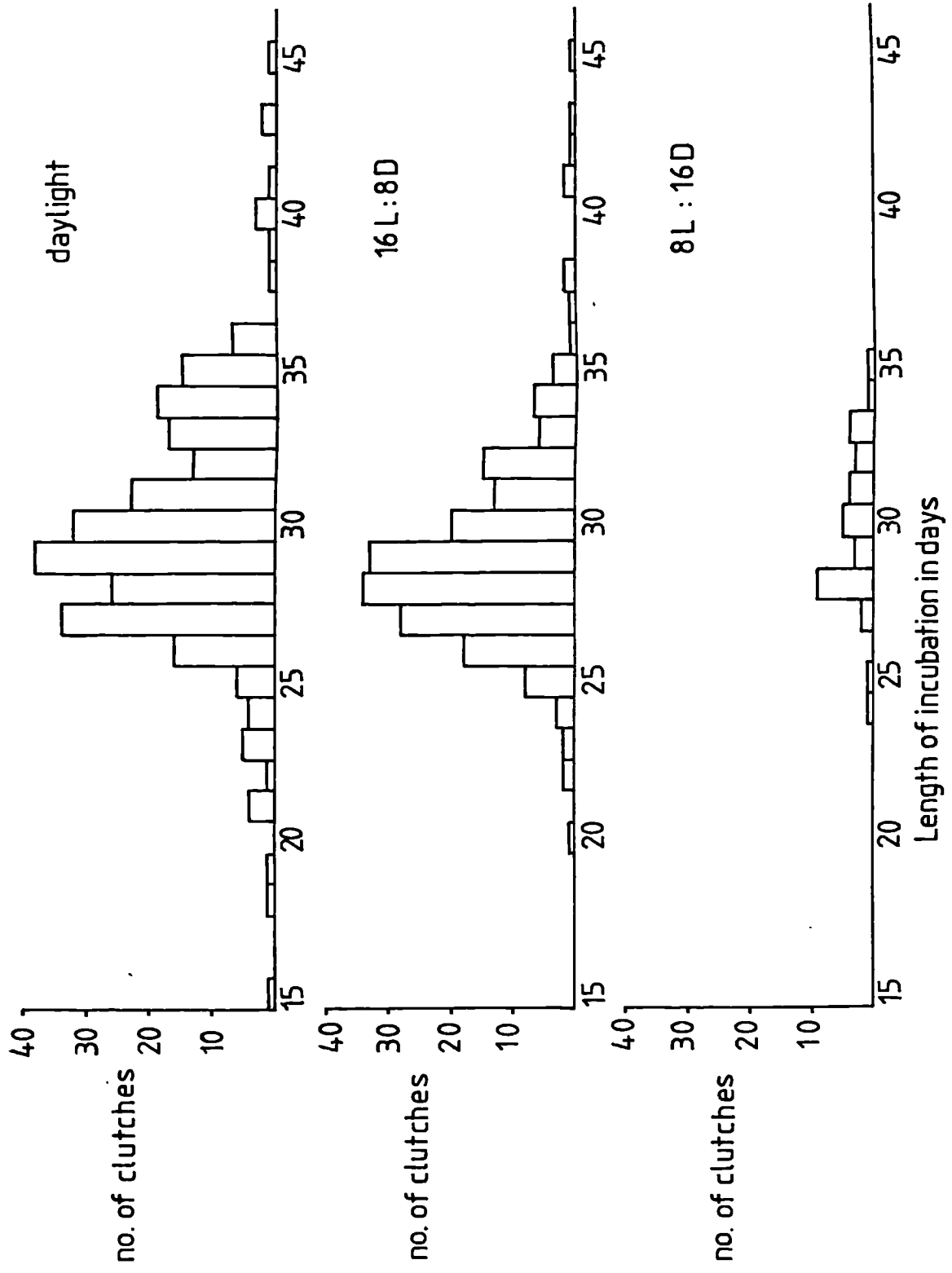


Fig. 309a The effect of photoperiod on the length of incubation in D. reticulatum

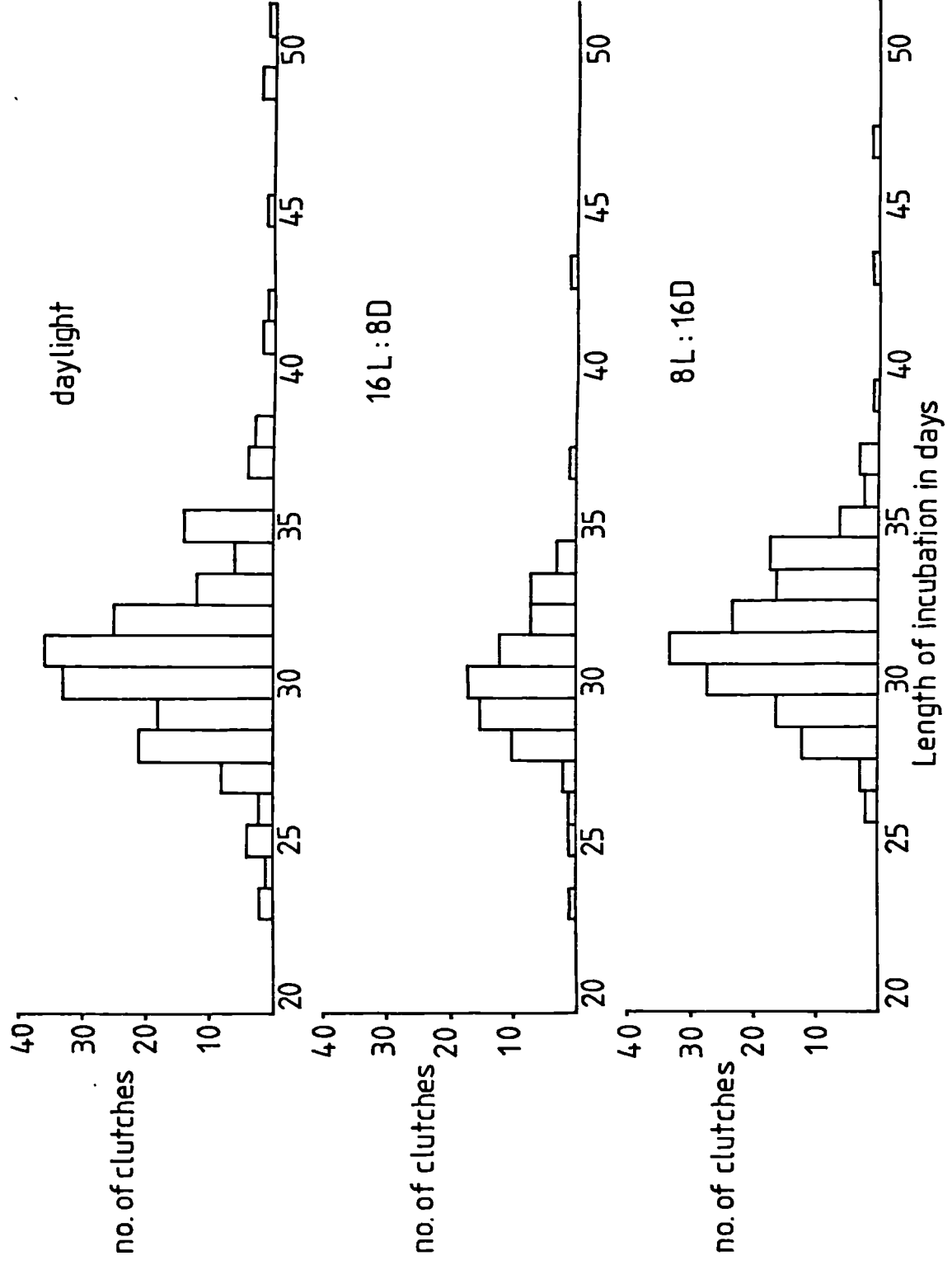


Fig. 309b The effect of photoperiod on the length of incubation in *A. hortensis*

Fig. 310 Abnormal development of A. hortensis , changes  
in pigmentation

- a. animal taken from the field.
- b. animal after six months in captivity.
- c. second generation animal.



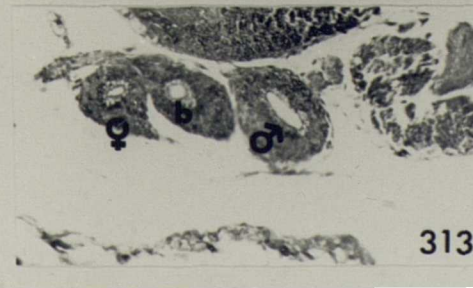
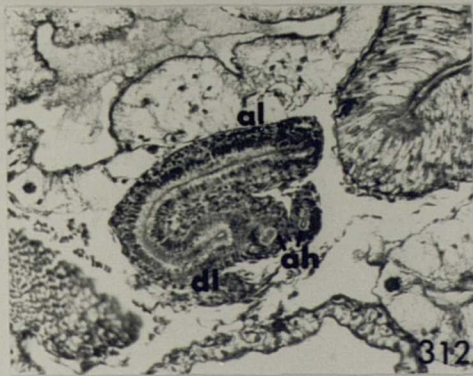
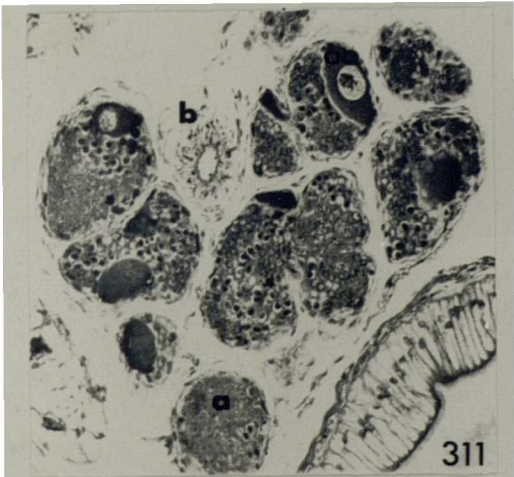


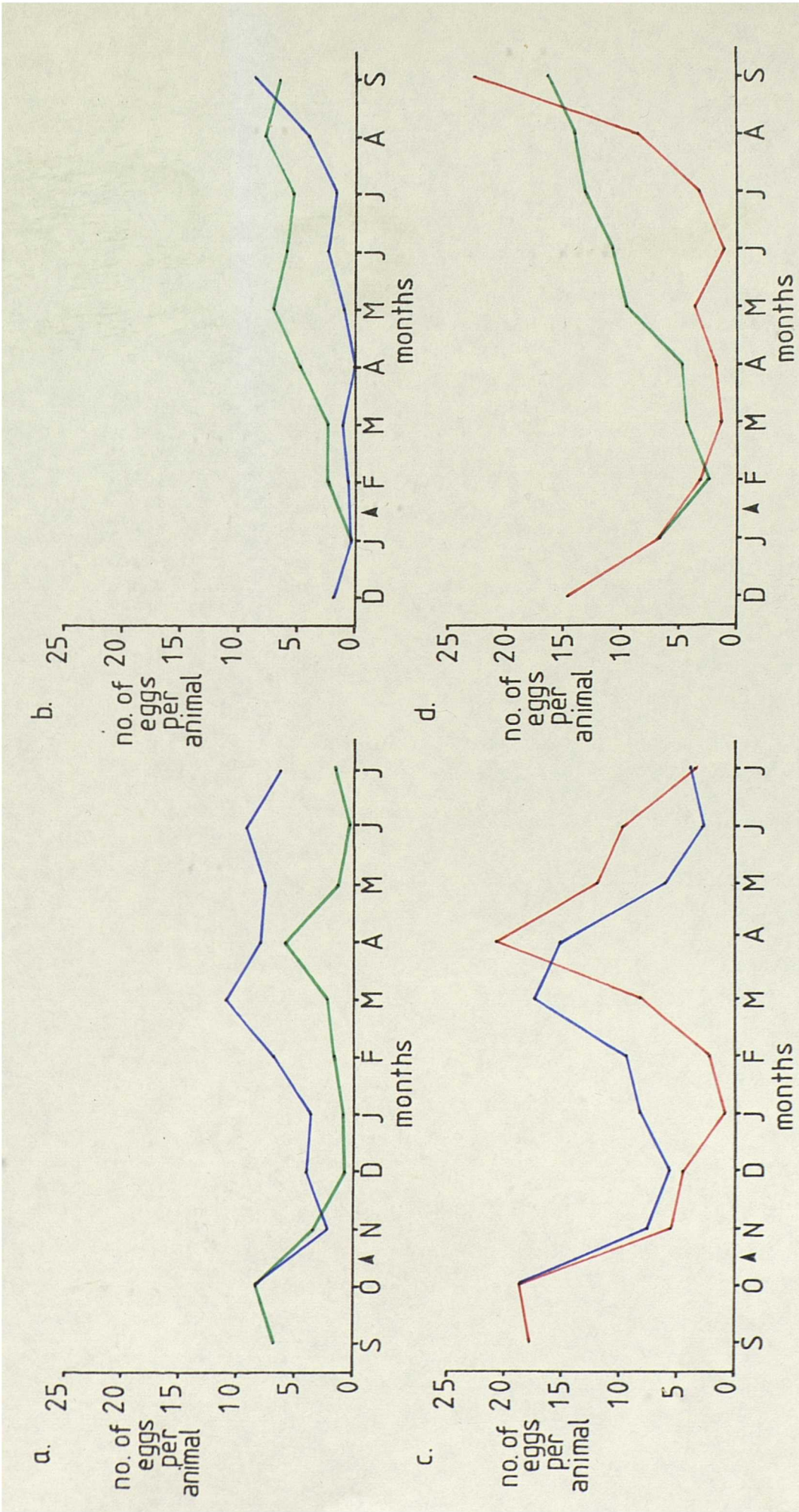
Abnormal development of A. hortensis.

Fig. 311 Gonad at 26 weeks (x160).

Fig. 312 Carrefour at 26 weeks (x160).

Fig. 313 Anterior genital ducts at 26 weeks (x160).





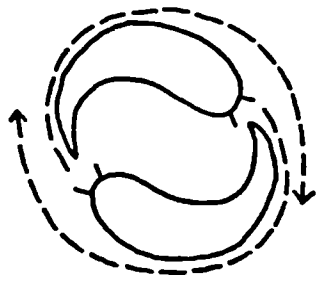
— Daylight  
 — 16L:8D  
 — 8L:16D  
 ▲ transferred to new light regime

Fig. 314 The effect of changing the photoperiod on egg production

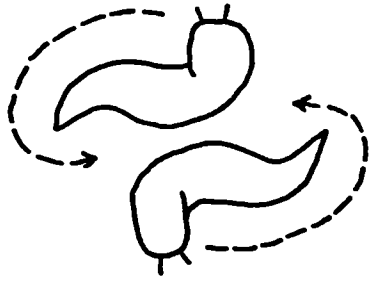
Fig. 315 Courtship behaviour of D. reticulatum .

- a. Position assumed during the early stages of courtship.
- b. Circling away from one another.
- c. Position assumed during the later stages of courtship.

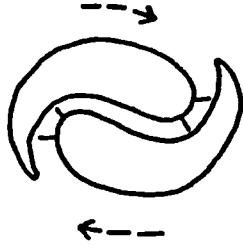
Broken arrows indicate the direction of movement.



a.



b.



c.

Fig. 315

Fig. 316 D. reticulatum, courtship and copulation under laboratory conditions.

- a. caressing with the tips of their sarcobella.
- b. pair moving closer together.
- c. sarcobella erected.
- d. penial sacs partially everted.
- e. penial sacs completely everted. The blue colouration is due to the blood pigment, haemocyanin.
- f. exchange of sperm packages.
- g. exchange of sperm packages. Arrows indicate the fully-everted trifid appendages.
- h. exchange of sperm packages.



**Fig. 316**

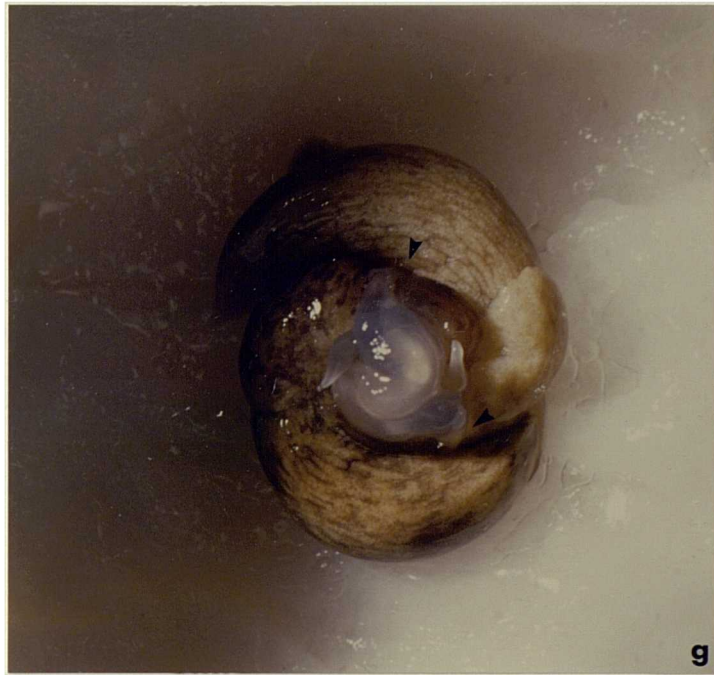


**Fig.316 cont.**





**Fig. 316 cont.**



**Fig. 316 cont.**

Fig. 317 D. reticulatum, courtship and copulation in the field.

a-b pair circling slowly while caressing with the tips of their sarcobella.

c. bases of the sarcobella apposed.

d. caressing with the sarcobella.

e. pair moving closer together.

f. genital openings apposed, sarcobella erected.

g. partial eversion of penial sacs, sarcobella displaced.

h. complete eversion of penial sacs. Arrows indicate the fully-everted trifid appendages.

i. exchange of sperm packages (arrowed).



**Fig. 317**



**Fig. 317 (cont.)**



**Fig. 317 (cont.)**



**Fig. 317 (cont.)**



**Fig. 317 (cont.)**



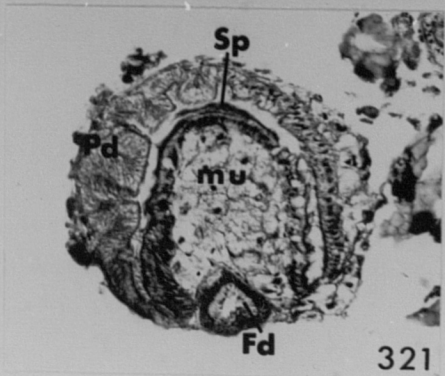
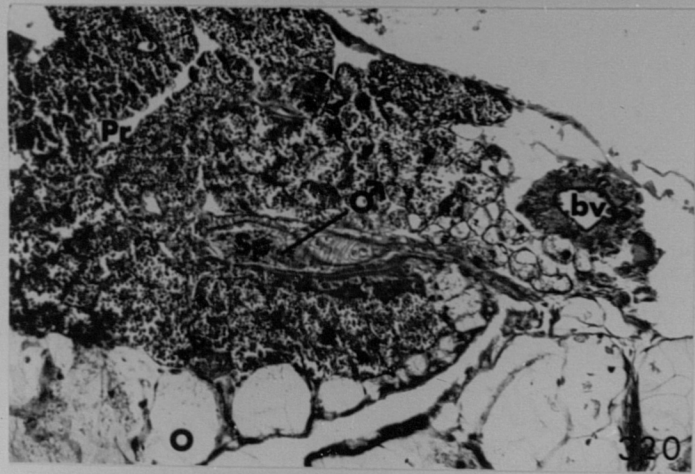
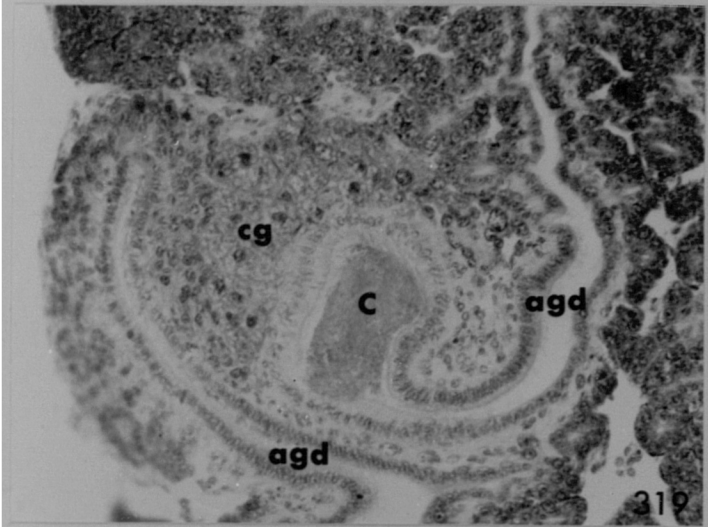
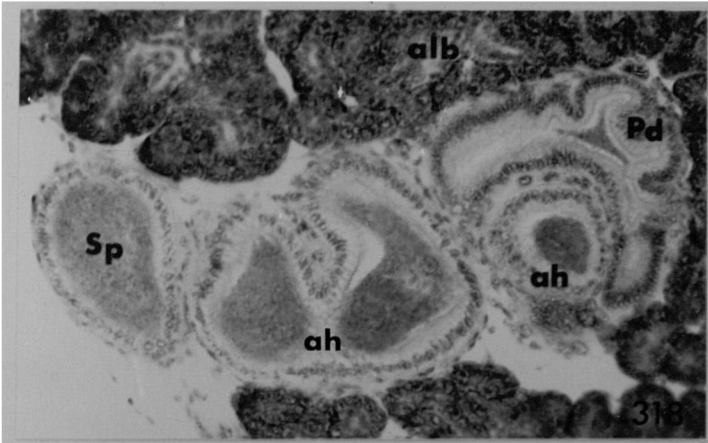
D, reticulatum, 10 minutes after protrusion of sarcobellum.

Fig. 318 Sperm in the anterior, slender region of the hermaphrodite duct and entering the pouched diverticulum of the carrefour (x240).

Fig. 319 Sperm filling the base of the carrefour (x240).

Fig. 320 Sperm entering the male groove of the common duct (x125).

Fig. 321 Increased activity of the sub-epithelial mucocytes associated with the carrefour diverticula (x240).



D. reticulatum, 15 minutes after protrusion of  
the sarcobellum.

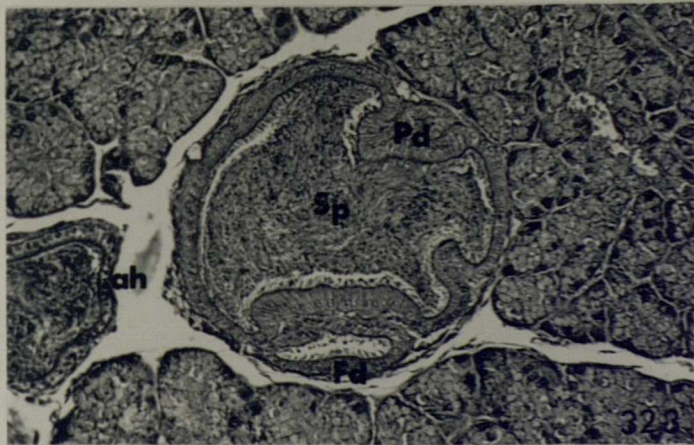
Fig. 322 T.S. through distal half of hermaphrodite duct  
(x160).

Fig. 323 T.S. through carrefour, pouched diverticulum  
swollen with sperm (x160).

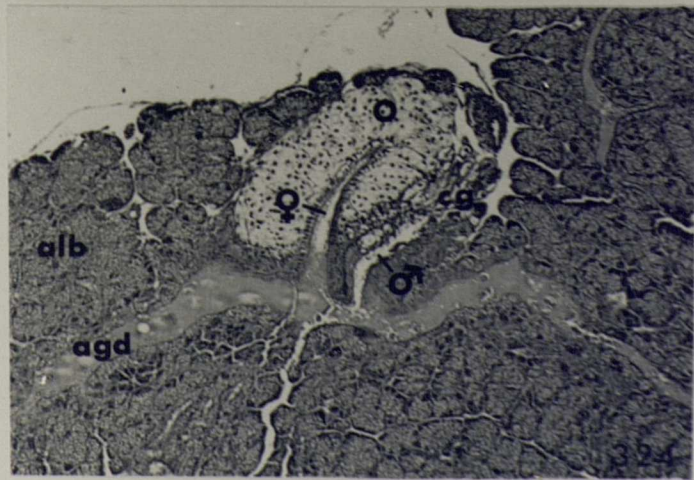
Fig. 324 T.S. through carrefour, albumen gland ducts  
filled with albumen, male groove filled with  
secretion from the carrefour gland (x125).



322



323

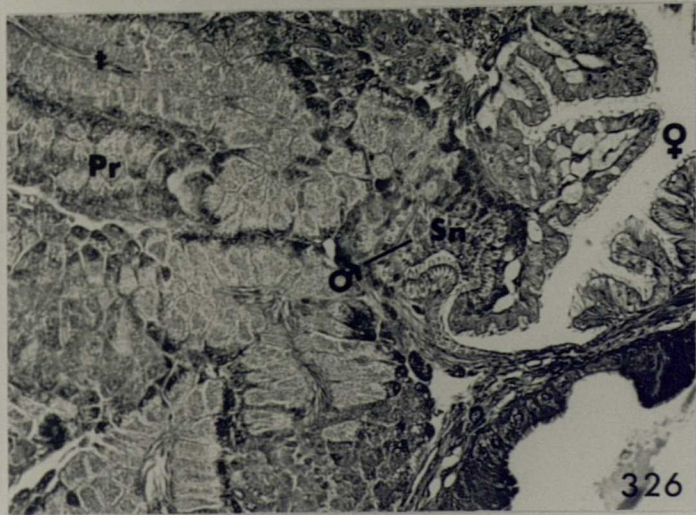
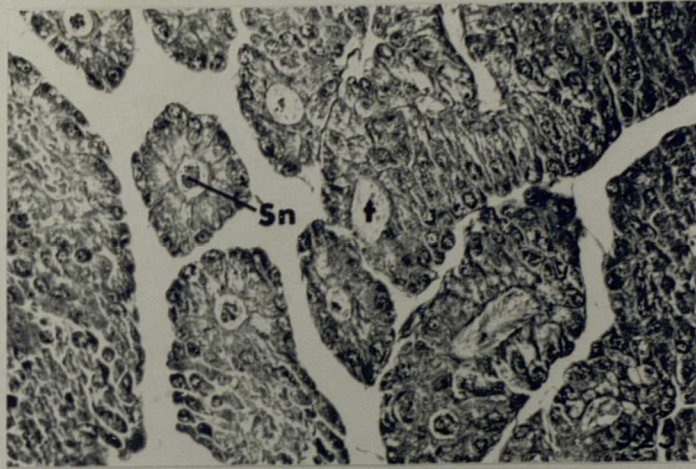


D. reticulatum, 15 minutes after protrusion of  
the sarcobellum.

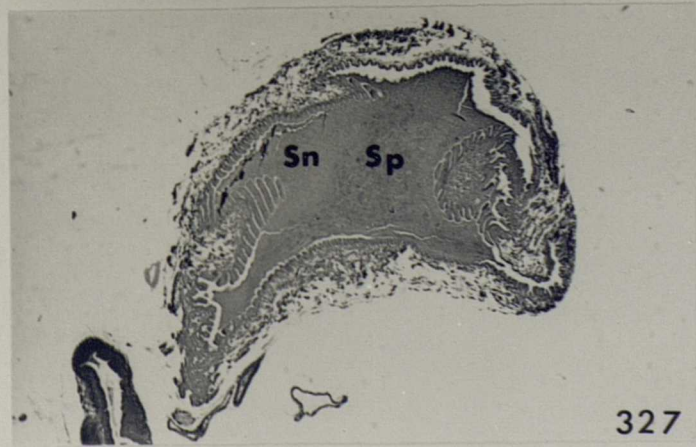
Fig. 325 Prostate gland, tubules containing prostate  
secretion (x160).

Fig. 326 Prostate secretion filling the male groove of  
the common duct (x155).

Fig. 327 Prostate secretion containing a small volume  
of sperm filling the penial sac (x25).



326



327

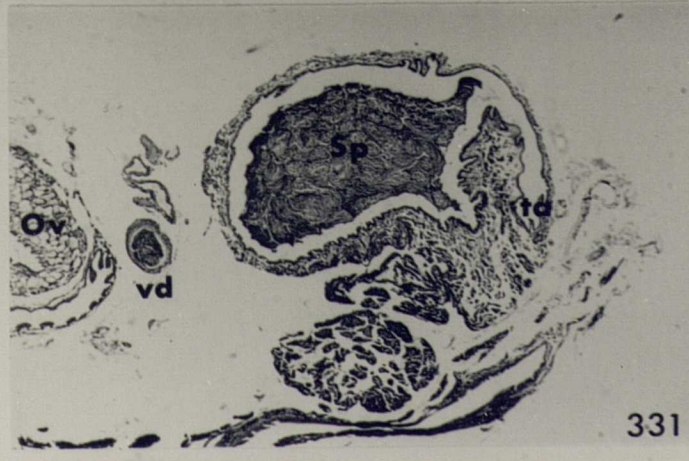
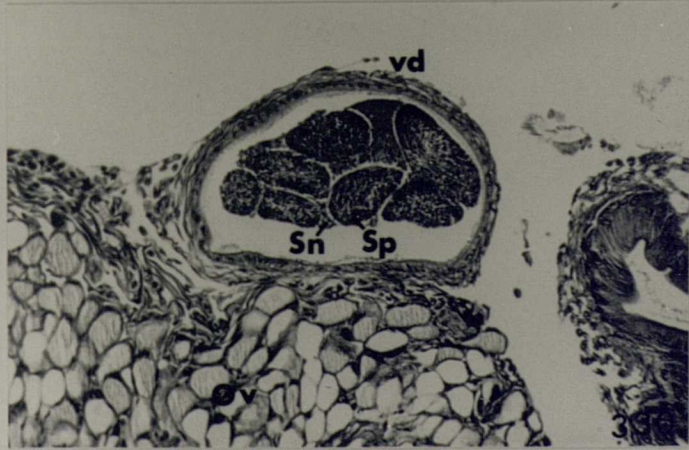
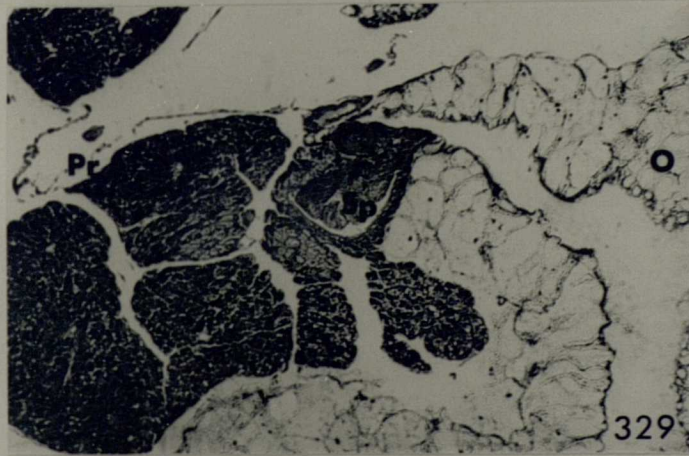
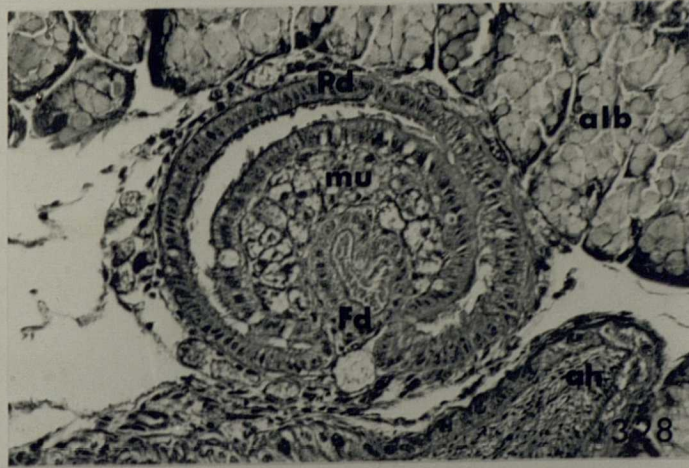
D. reticulatum, 20 minutes after protrusion  
of the sarcobellum.

Fig. 328 T.S. through four diverticula (x205).

Fig. 329 Sperm filling the male groove of the common  
duct (x100).

Fig. 330 T.S. through the vas deferens. Sperm arranged  
into discrete bundles and surrounded by  
prostate secretion (x160).

Fig. 331 Sperm and secretion filling penial sac and vas  
deferens (x40).



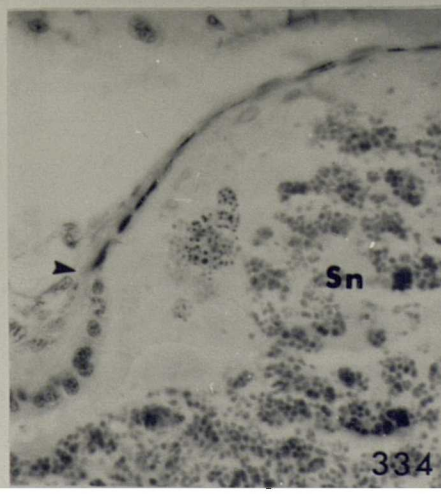
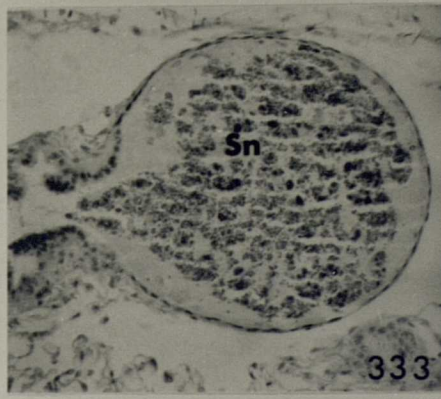
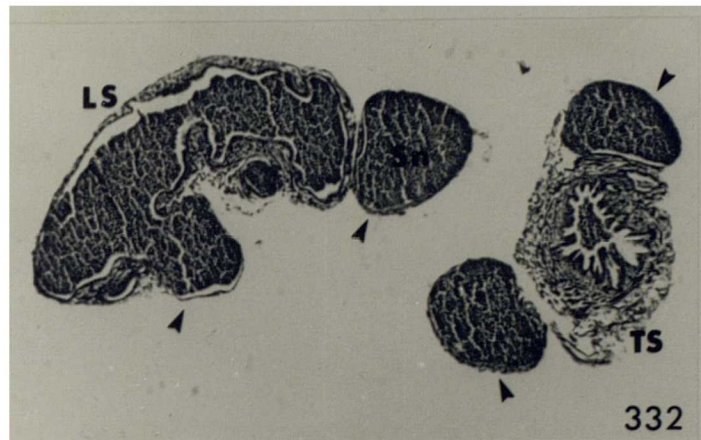


D. reticulatum, 20 minutes after protrusion  
of the sarcobellum.

Fig. 332 T.S. and L.S. through the diverticula of the  
trifid appendage (x125). Prostate secretion  
fills the side branches (arrowed).

Fig. 333 T.S. through a side branch of one of the  
trifid diverticula (x160).

Fig. 334 Detail of the epithelium lining the trifid  
appendage (x400). Arrow indicates the  
transition from cuboidal to squamous  
epithelium.

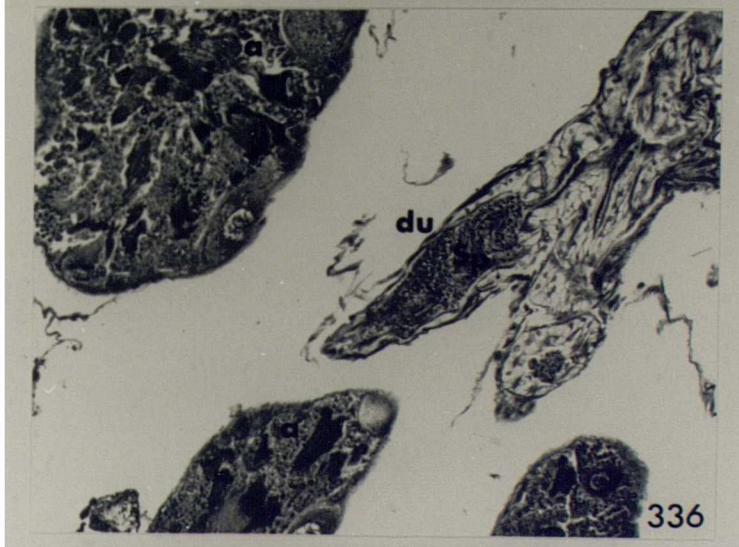
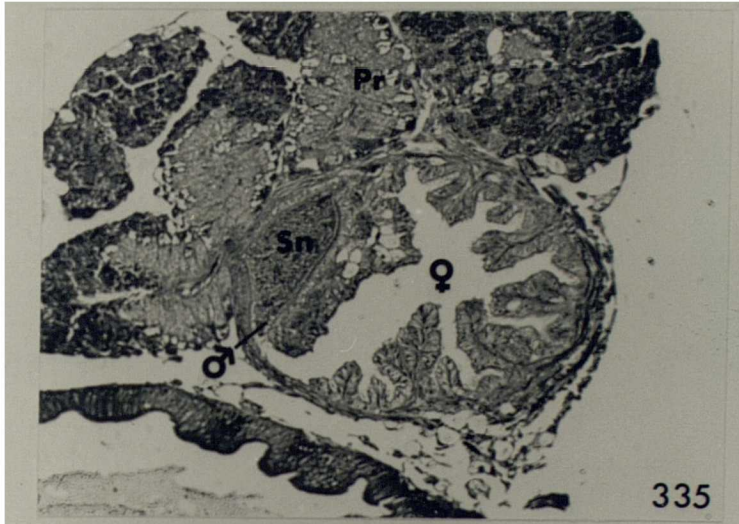


D. reticulatum, 30 minutes after protrusion of the sarcobellum.

Fig. 335 T.S. through the anterior region of the common duct (x125). Prostrate secretion fills the main groove.

D. reticulatum, 40 minutes after protrusion of the sarcobellum.

Fig. 336 Sperm entering the efferent ductules of the gonad (x160).

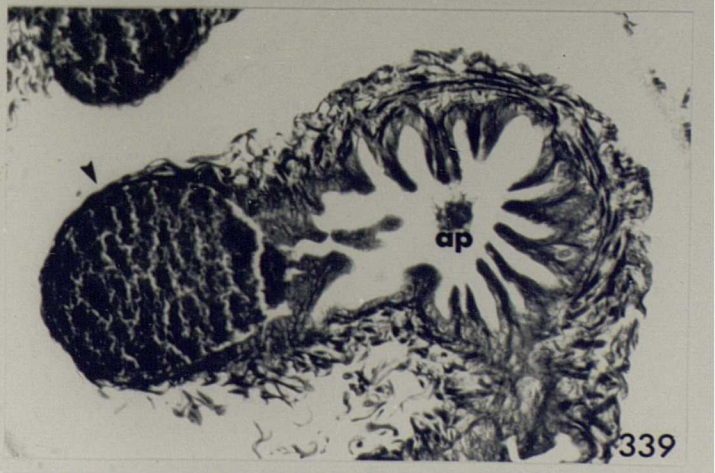
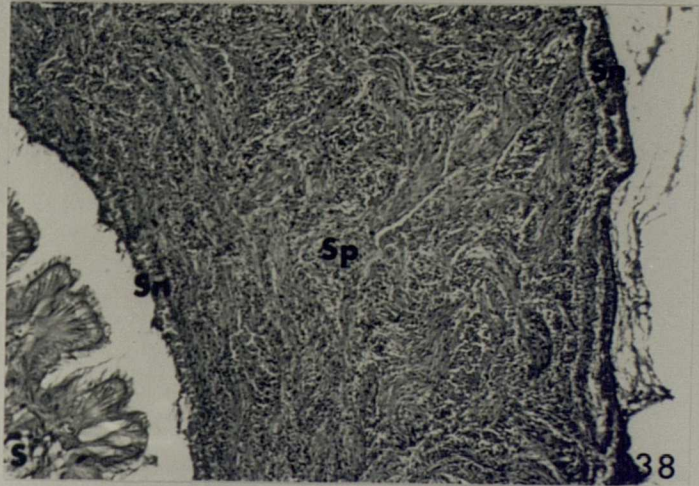


D. reticulatum, 40 minutes after protrusion of  
the sarcobellum.

Fig. 337 Sperm package filling the penial sac (x25).

Fig. 338 Detail of sperm package (x160).

Fig. 339 T.S. through one of the trifid diverticula  
(x250). Side branch filled with prostate  
secretion (arrowed).



D. reticulatum, prostate gland secretion.

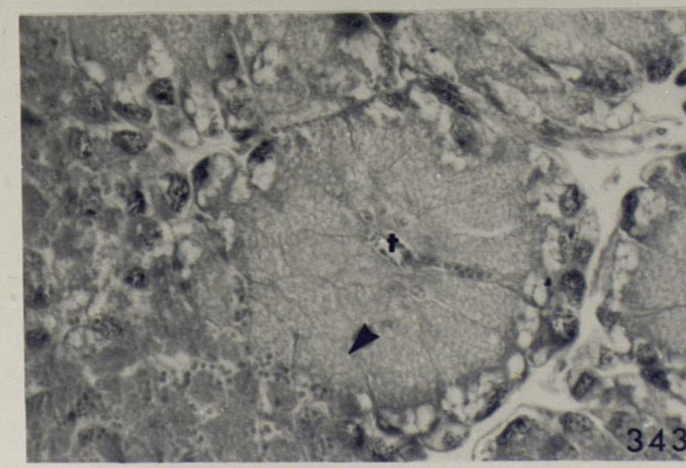
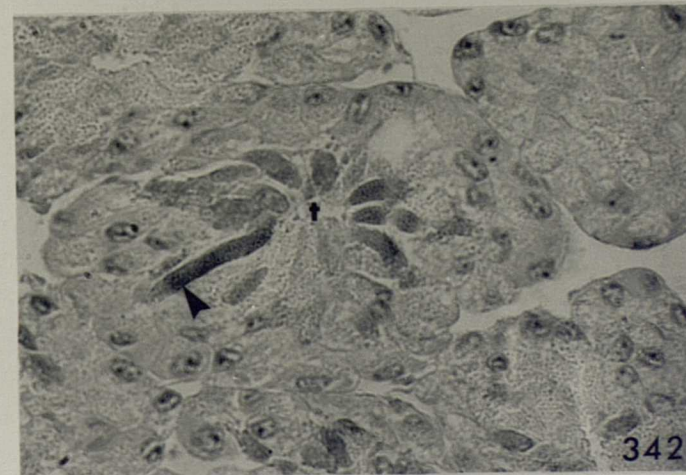
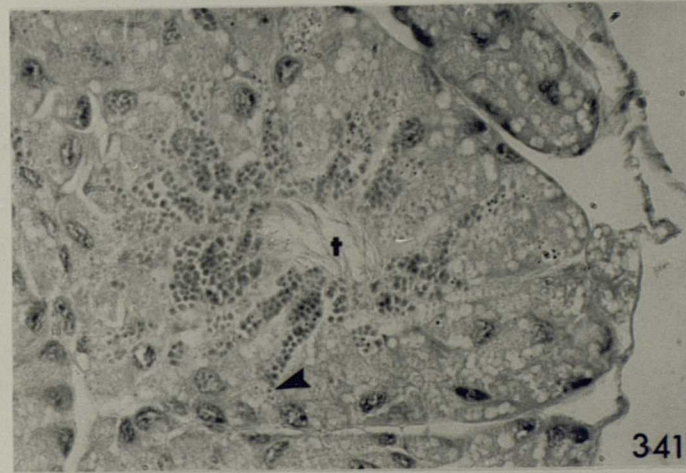
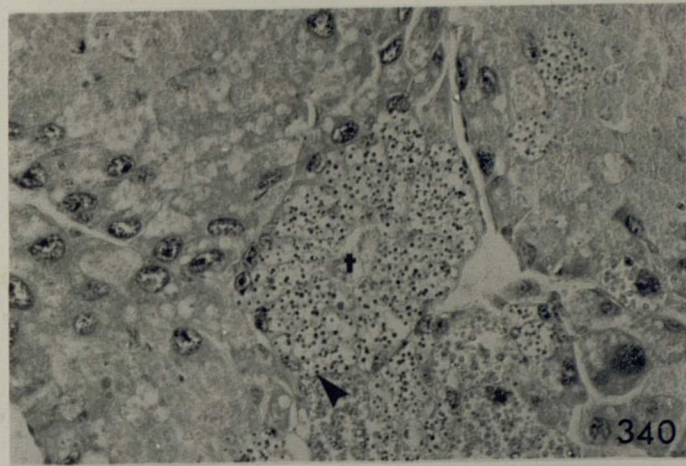
The granule types are arrowed.

Fig. 340 Type A (x250)

Fig. 341 Type B (x250)

Fig. 342 Type C (x250)

Fig. 343 Type D (x300)





D. reticulatum, prostate gland secretion.

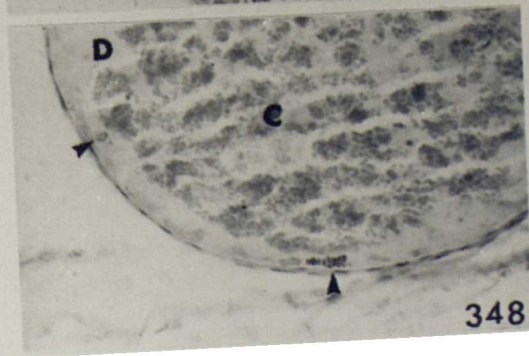
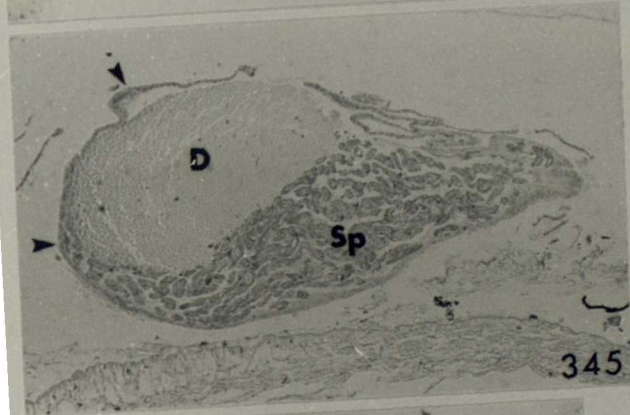
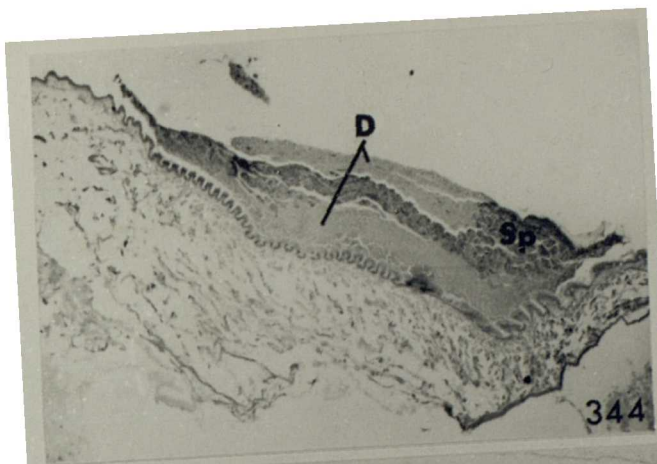
Granule types A, B, C and D.

Fig. 344 Sperm package on the surface of the everted penial sac (x30).

Fig. 345 Sperm package on the surface of the everted penial sac (x40). Arrows indicate the position of Figs. 346 and 347.

Fig. 346 } Detail of the prostate secretion surrounding  
Fig. 347 } the sperm package (x310).

Fig. 348 Detail of the prostate secretion within the trifid appendage (x310). Arrows indicate clusters of type A granules.



D. reticulatum, sperm package.

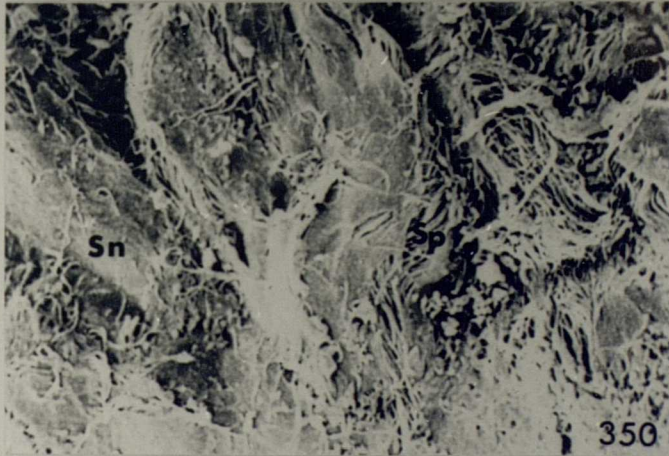
Fig. 349 Two sperm packages removed during copulation  
(x20).

Fig. 350 Surface detail of the sperm package, S.E.M.  
(x100).

Fig. 351 Surface detail of the sperm package, S.E.M.  
(x1.7K).



349



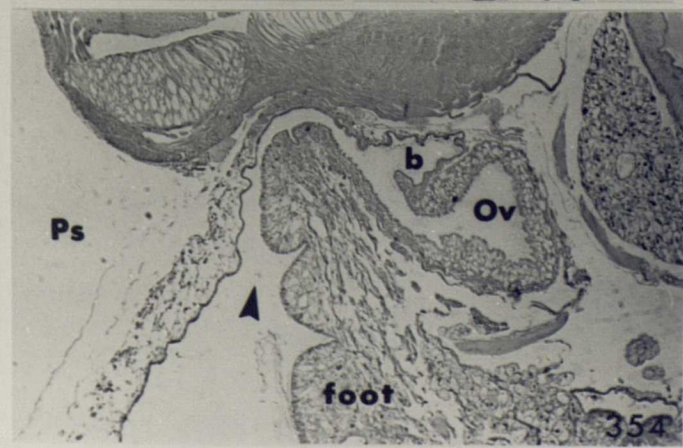
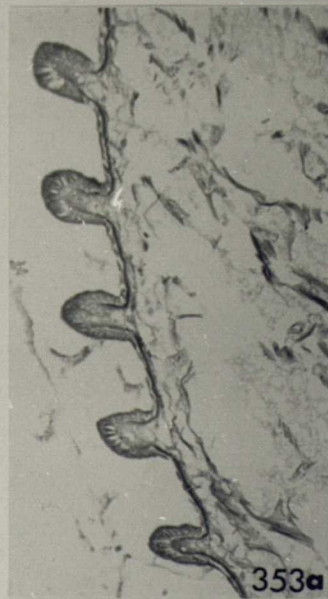
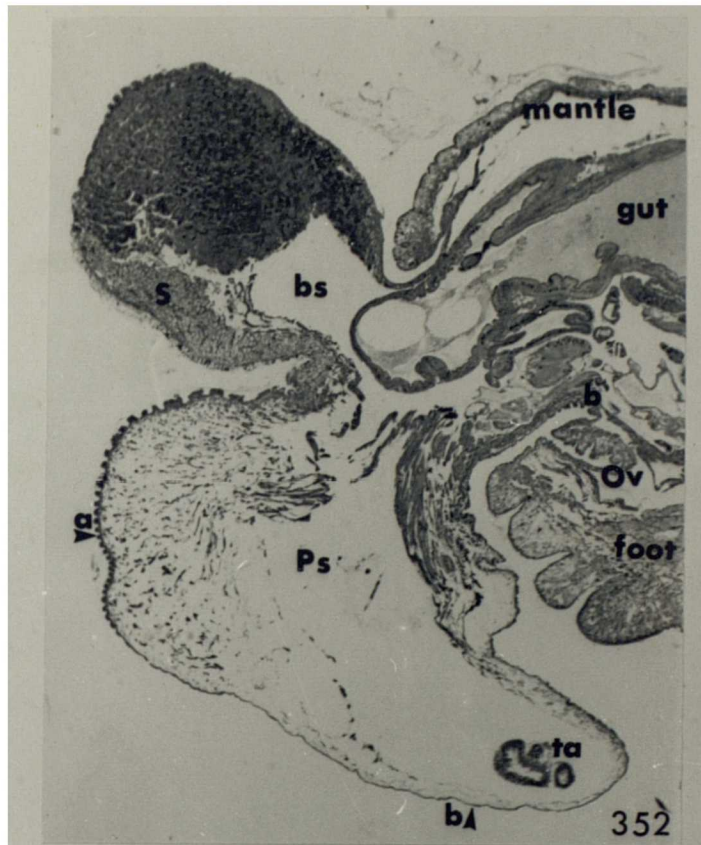
350



351

D. reticulatum, at copulation.

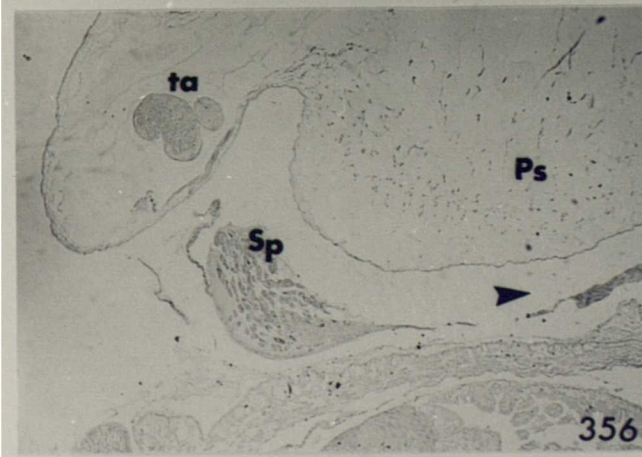
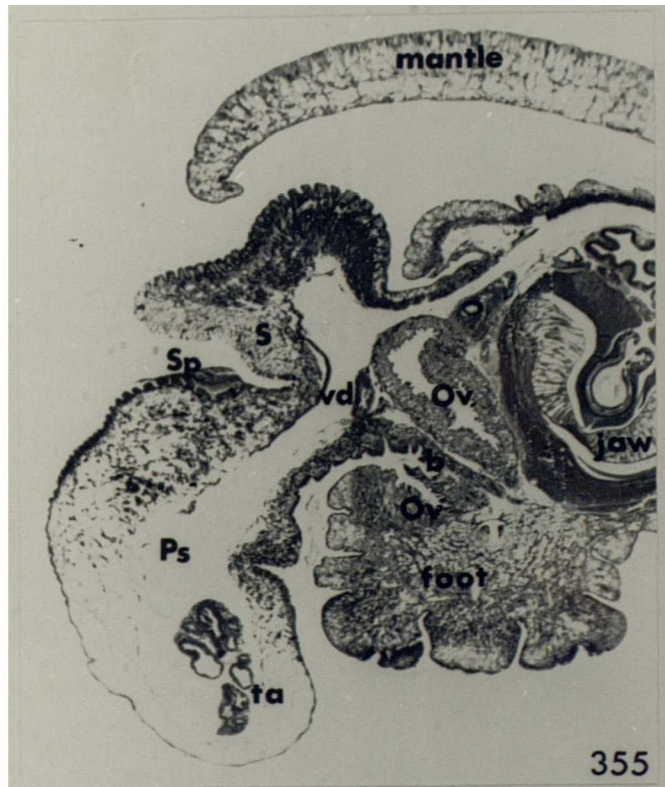
- Fig. 352 Penial mass everted at copulation (x18).  
Arrows a and b indicate the positions of Figs.  
353a and 353b respectively.
- Fig. 353 Detail of the epithelium of the everted  
penial sac at positions a (x160) and b (x400)  
in Fig. 352.
- Fig. 354 Groove formed between the everted penial sac  
and body wall, leading into the bursa  
copulatrix (x40). Arrow indicates the  
direction of movement of the sperm package.



D. reticulatum, at copulation.

Fig. 355 Penial mass everted at copulation (x18).

Fig. 356 Sperm package in the groove which develops between the everted penial sac and the body wall (x25). Arrow indicates the direction of movement.





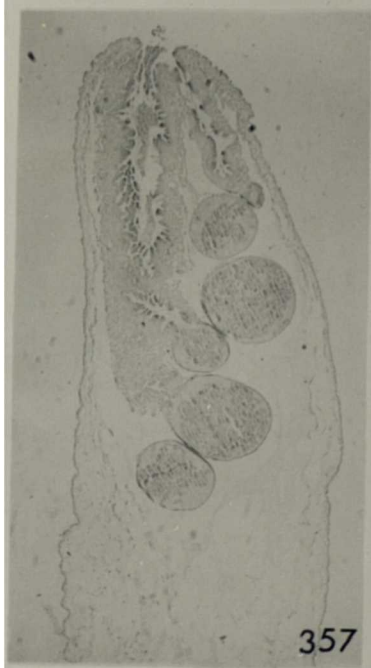
D. reticulatum, at copulation.

Fig. 357 L.S. through partially everted trifid appendage  
(x50).

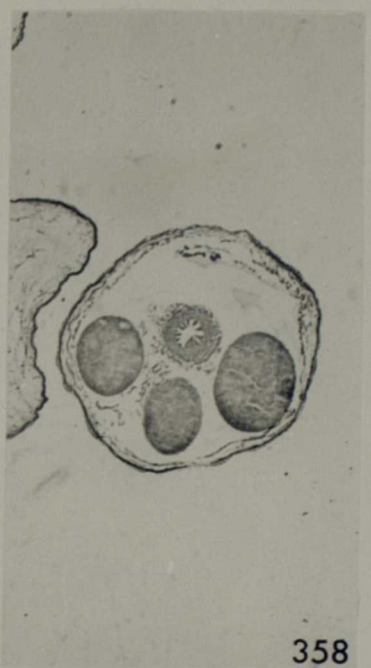
Fig. 358 T.S. through partially everted trifid  
appendage (x100).

Fig. 359 L.S. through fully everted trifid appendage  
(x25).

Fig. 360 T.S. through sarcobellum (x33).



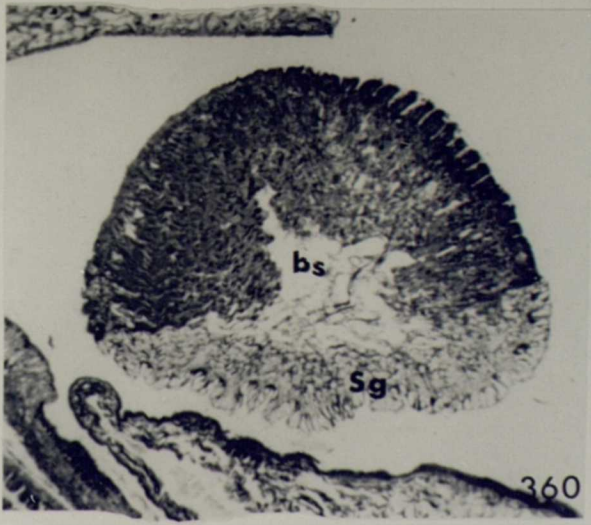
357



358



359



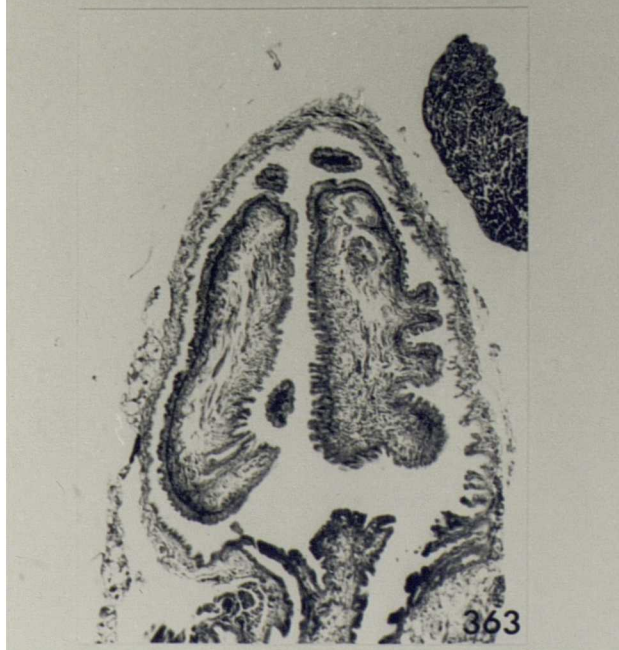
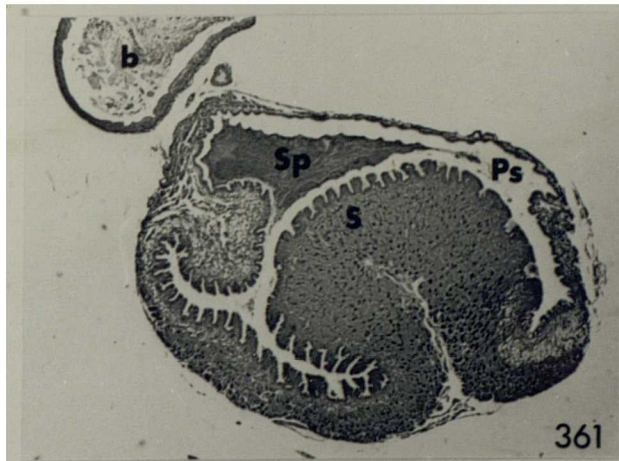
360

D. reticulatum, 10 minutes after copulation.

Fig. 361 Foreign sperm package in the penial sac (x25).

Fig. 362 Foreign sperm package entering the bursa  
copulatrix (x25).

Fig. 363 L.S. through the partially everted trifid  
appendage (x60).



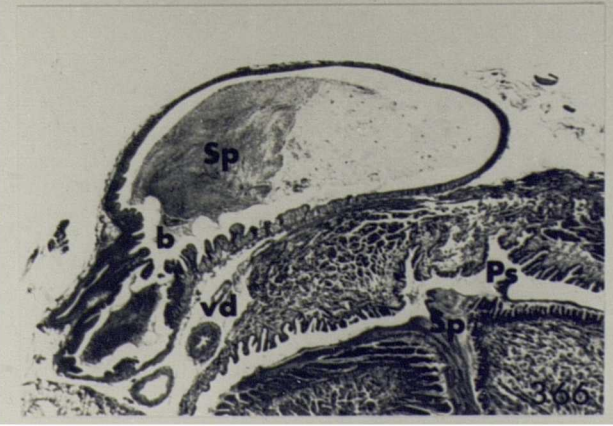
D. reticulatum, 30 minutes after copulation.

Fig. 364 Foreign sperm package entering the bursa  
copulatrix (x25).

D. reticulatum, 60 minutes after copulation.

Fig. 365 T.S. through bursa copulatrix (x25).

Fig. 366 L.S. through bursa copulatrix (x25).



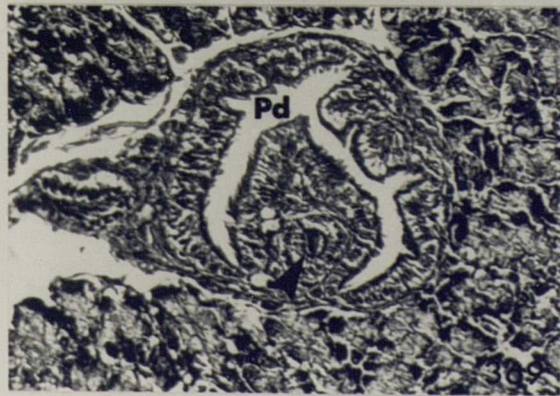
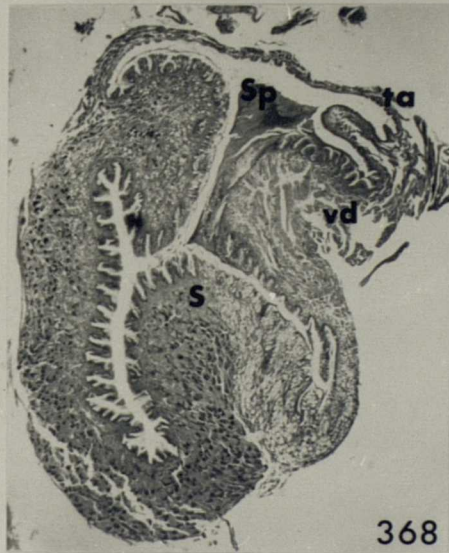
D.reticulatum, 75 minutes after copulation.

Fig. 367 T.S. through the bursa copulatrix (x30).

D.reticulatum, 90 minutes after copulation.

Fig. 368 Foreign sperm in the penial sac (x25).

Fig. 369 T.S. through the carrefour, sperm in finger-like diverticulum (arrowed) (x200).





D.reticulatum, 6 hours after copulation.

Fig. 370 T.S. through the carrefour, sperm in pouched diverticulum (x120).

D.reticulatum, 8 hours after copulation.

Fig. 371 T.S. through the carrefour (x200).

Fig. 372 T.S. through the anterior, slender region of the hermaphrodite duct (x300).

D.reticulatum, 24 hours after copulation.

Fig. 373 T.S. through the bursa copulatrix (x25).

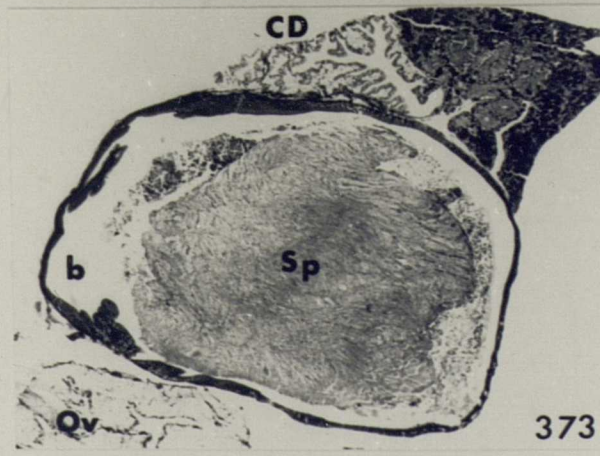
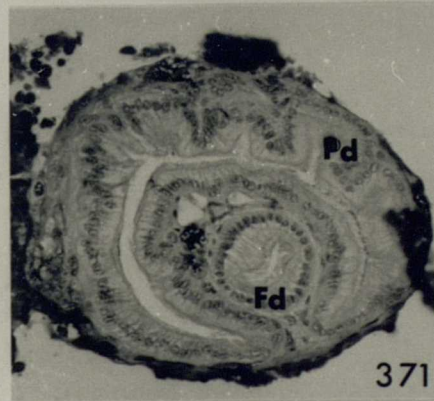
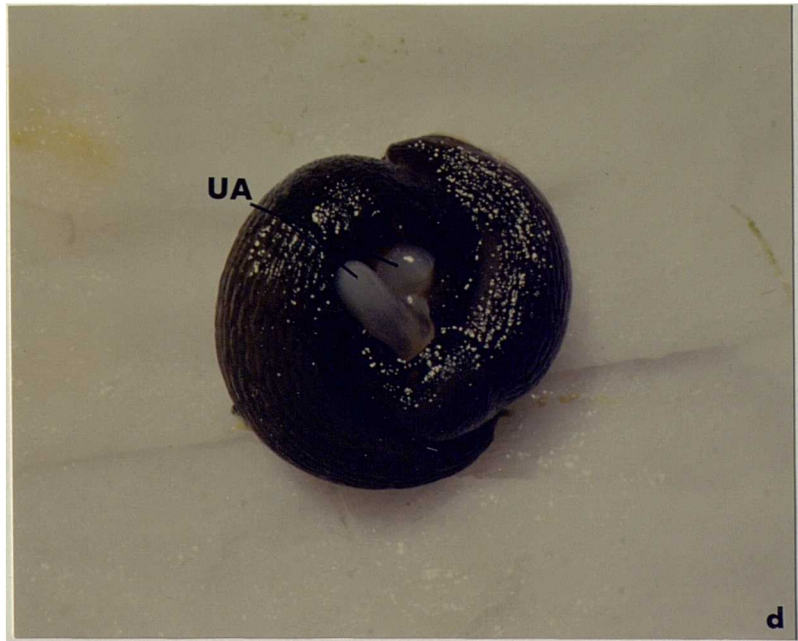


Fig. 374 A.hortensis, courtship and copulation under laboratory conditions.

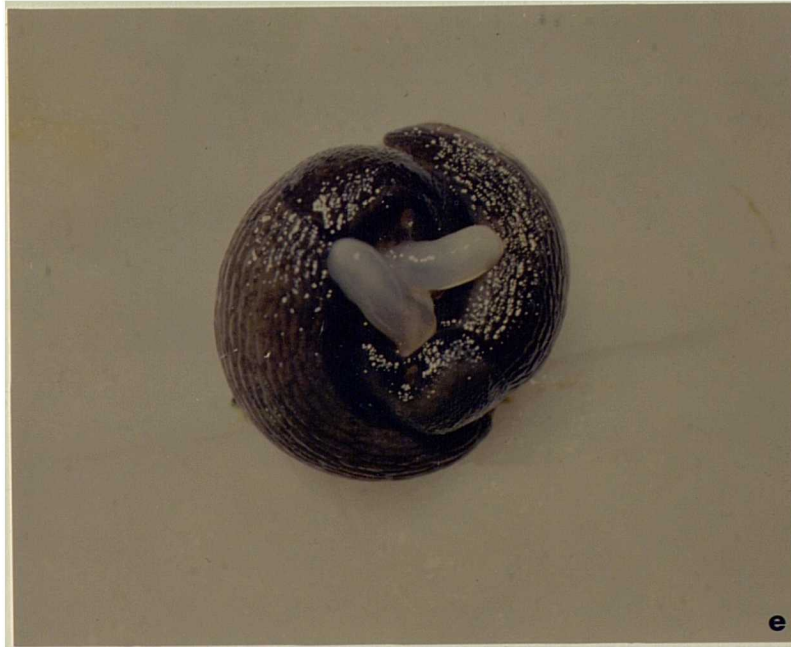
- a. courtship position.
- b. slight separation revealing the genital opening of one partner (arrowed).
- c. upper atrium partially everted by one partner (A) exposing the core of the epiphallus and the entrance to the bursa copulatrix (arrowed).
- d. eversion of the upper atria.
- e. upper atria completely everted.
- f. expansion of upper atria, the thick oviduct can be seen through the thin transparent wall.



**Fig. 374**



**Fig. 374 (cont.)**



e



Ov

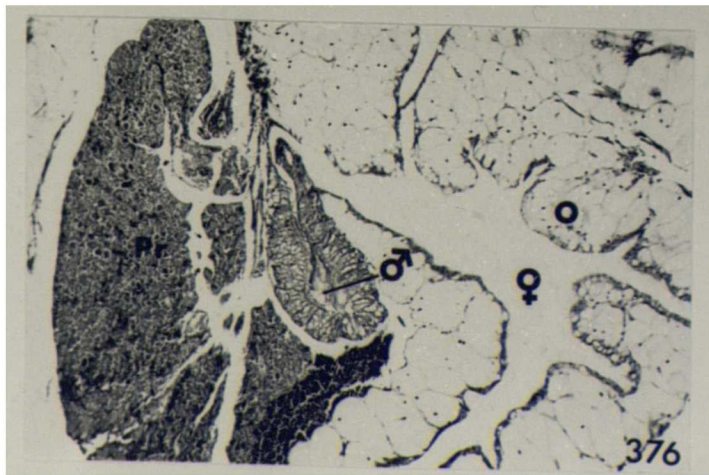
UA

f

**Fig. 374 (cont.)**

Fig. 375 A.hortensis, upper atria everted. The epiphallic cone of animal A has entered the channel leading to the bursa copulatrix of animal B (arrowed). The cone of animal B is about to enter the entrance to the bursa of animal A.

Fig. 376 A.hortensis, 30 minutes after the start of courtship. Carrefour gland secretion filling the proximal region of the male groove of the common duct (x63).

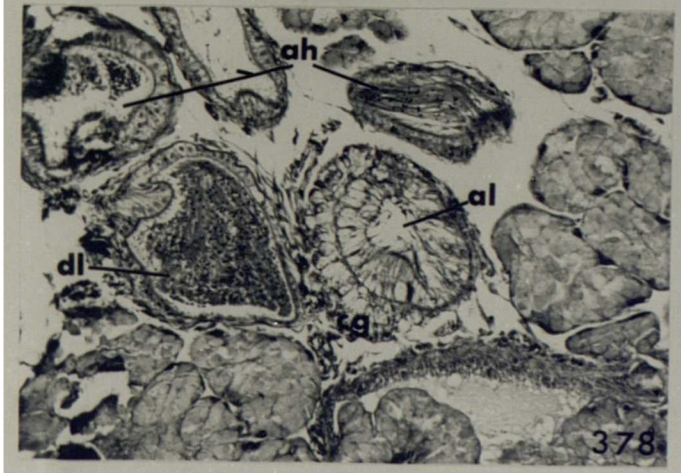




A.hortensis, 90 minutes after the start of  
courtship.

Fig. 377 T.S. through the carrefour loop (x160). Small  
amount of sperm has entered the base of the  
ascending limb.

Fig. 378 T.S. through the carrefour loop (x160). Mid-  
region.



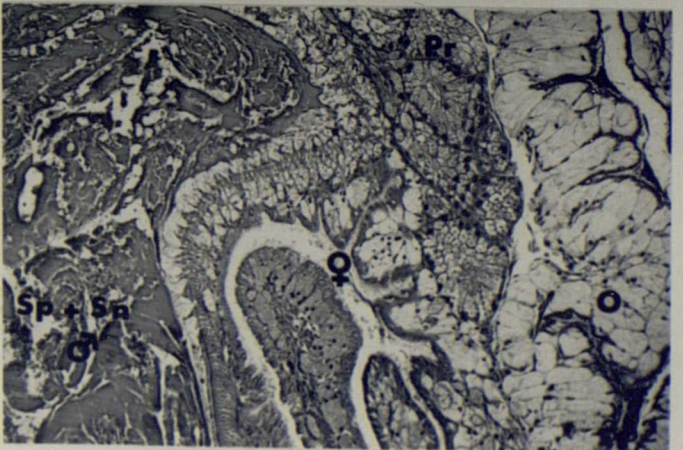
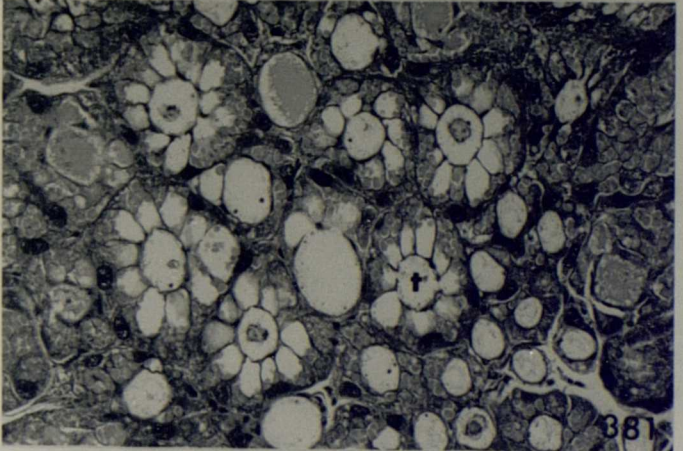
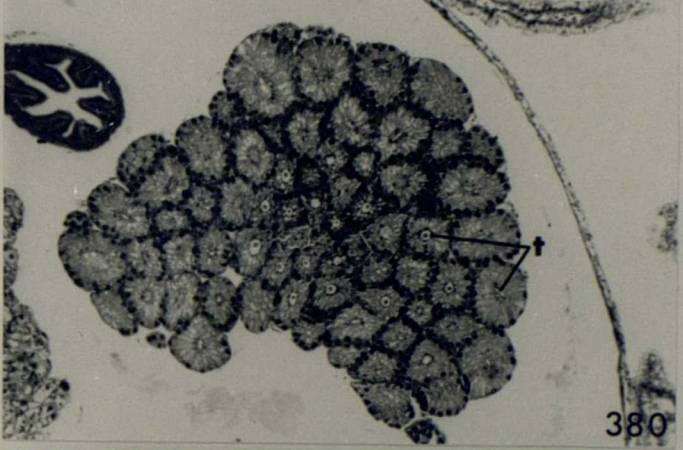
A.hortensis, 120 minutes after the start of courtship.

Fig. 379 Sperm filling the male groove at the anterior end of the common duct and the vas deferens (x40).

Fig. 380 T.S. through the prostate gland (x63). Secretion entering the tabules.

Fig. 381 T.S. through the prostate gland (x250). Cells depleted of secretion.

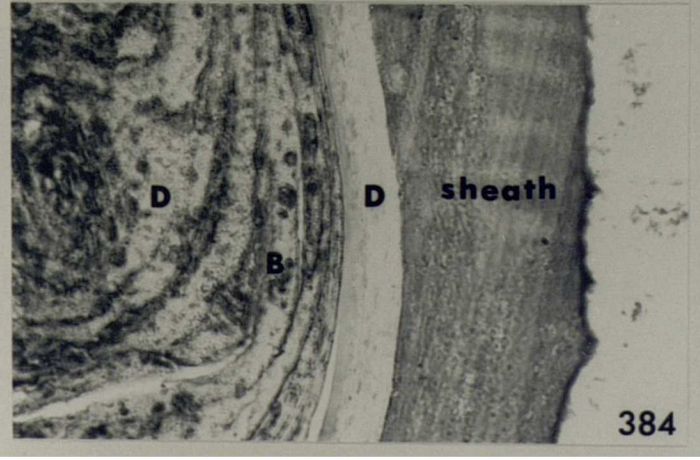
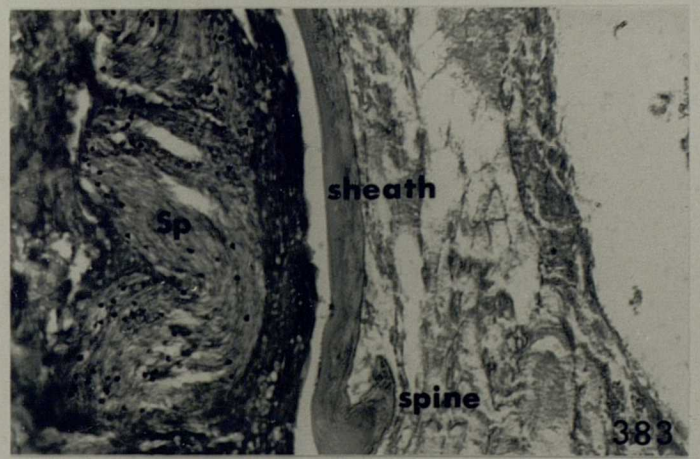
Fig. 382 Sperm and prostate secretion filling the male groove of the common duct (x100).



A.hortensis, spermatophore.

Fig. 383 T.S. through mid-region of spermatophore  
(x400).

Fig. 384 T.S. through anterior region of spermatophore  
(x400). Prostate granule types labelled B and  
D.



A.hortensis, at copulation.

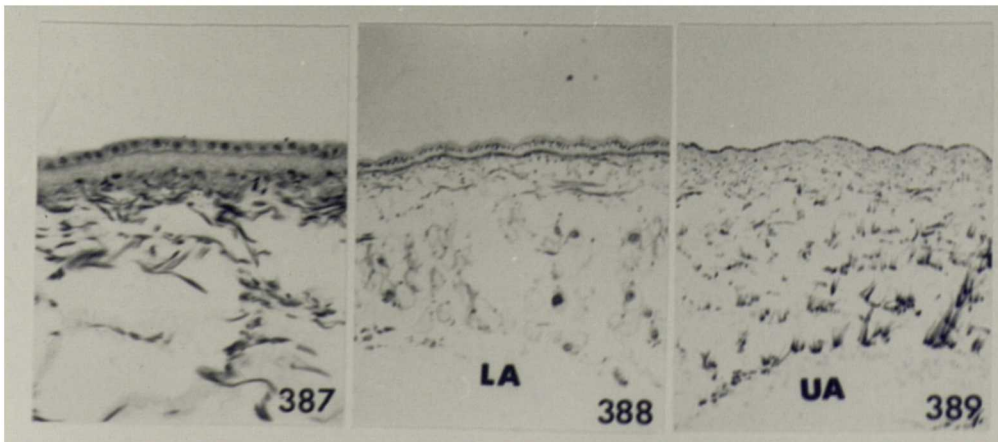
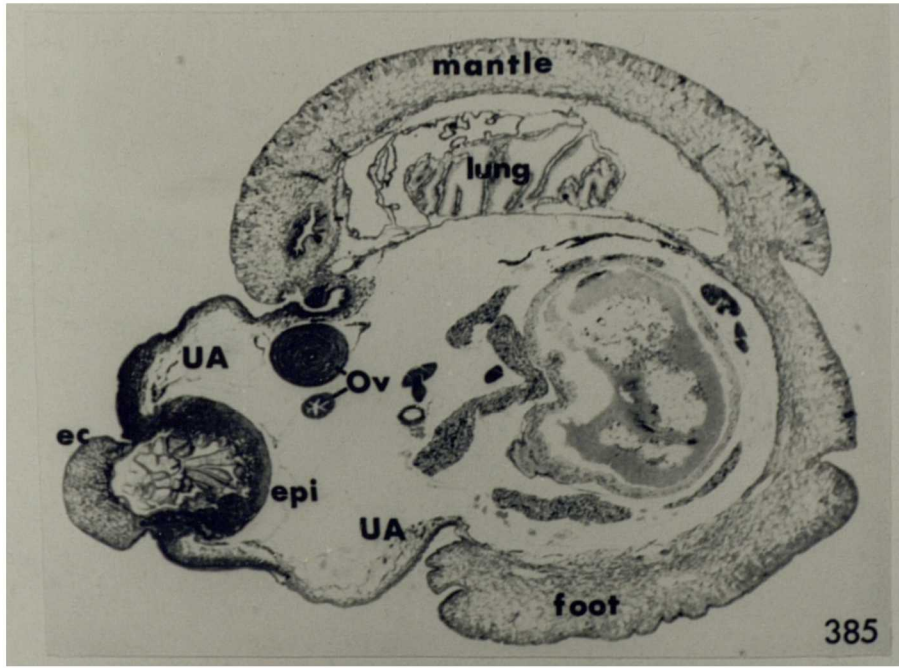
Fig. 385 Upper atrium everted exposing epiphallic cone  
(x18).

Fig. 386 Upper atrium completely everted (x25).

Fig. 387 Detail of the epithelium lining the everted  
upper atrium (x250).

Fig. 388 Detail of the epithelium lining the everted  
lower atrium (x125).

Fig. 389 Detail of the epithelium and muscle layers  
lining the everted upper atrium (x100).

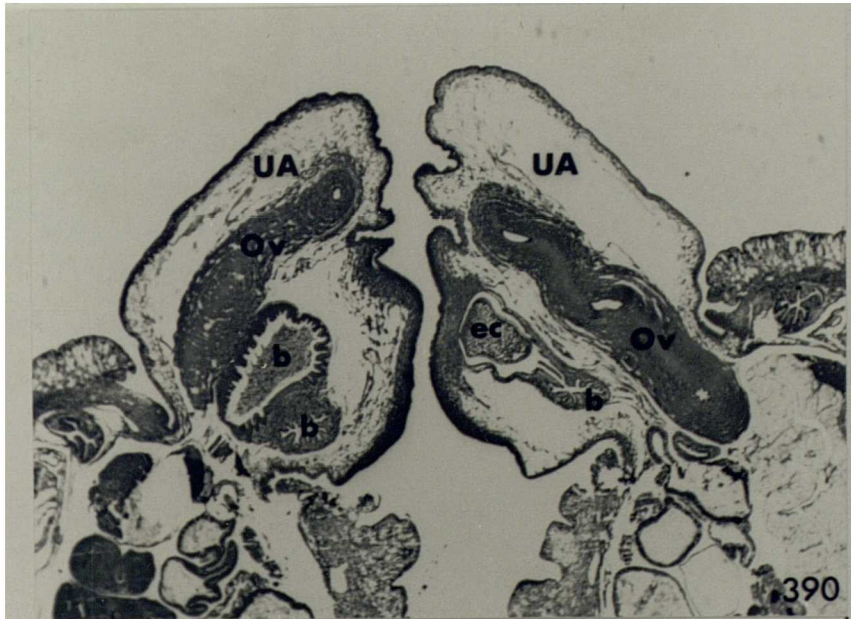




A.hortensis, at copulation.

Fig. 390 Upper atria everted (x18).

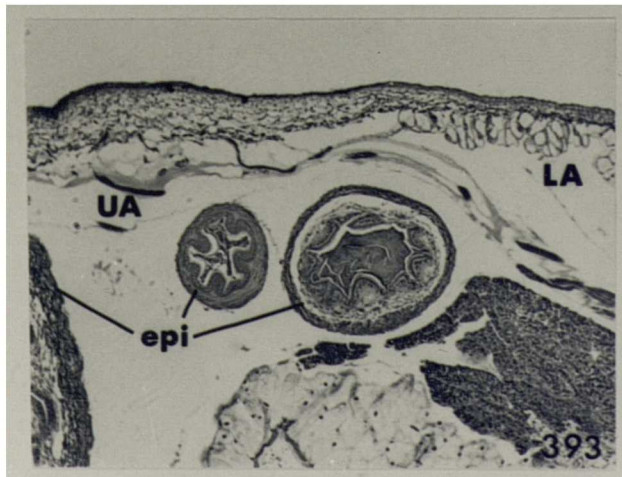
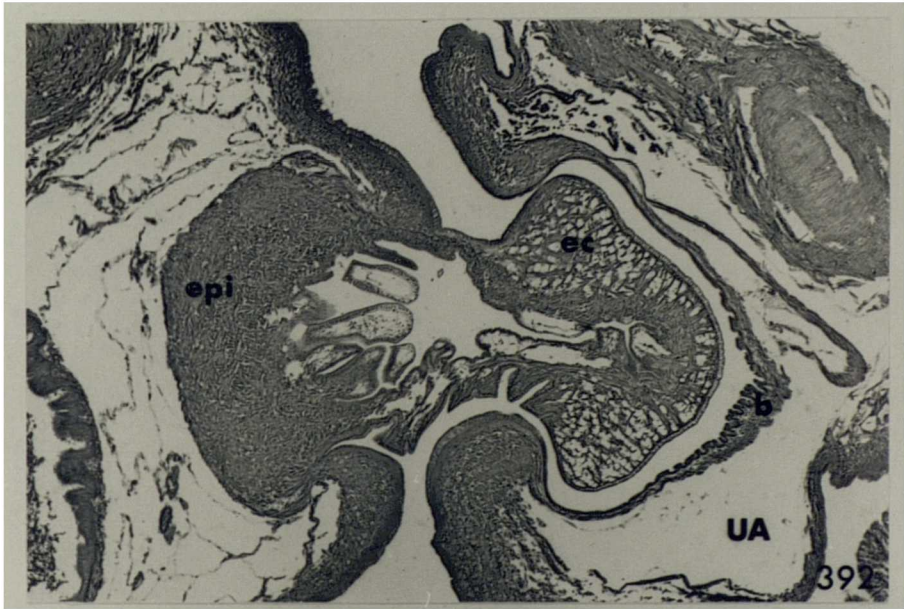
Fig. 391 Epiphallic cone engaged in the channel leading  
to the partner's bursa copulatrix (x18).



A.hortensis, at copulation.

Fig. 392 Epiphallic cone engaged in the channel leading to the partner's bursa copulatrix (x50).  
Detail of Fig. 391.

Fig. 393 Spermatophore material filling the posterior region of the epiphallus (x100).



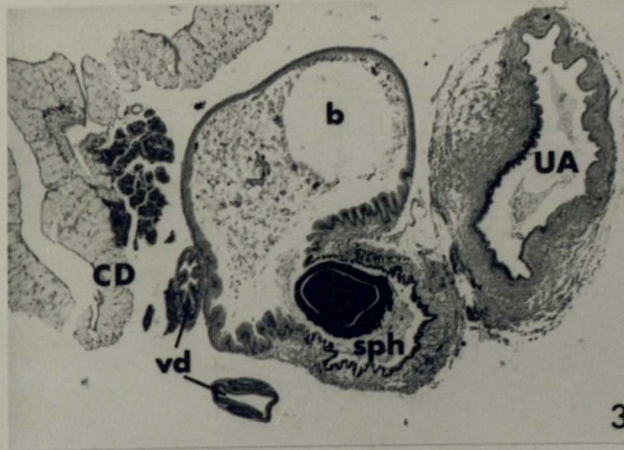
A.hortensis, immediately after copulation.

Fig. 394 Anterior region of the foreign spermatophore filling the entrance to the bursa copulatrix (x25).

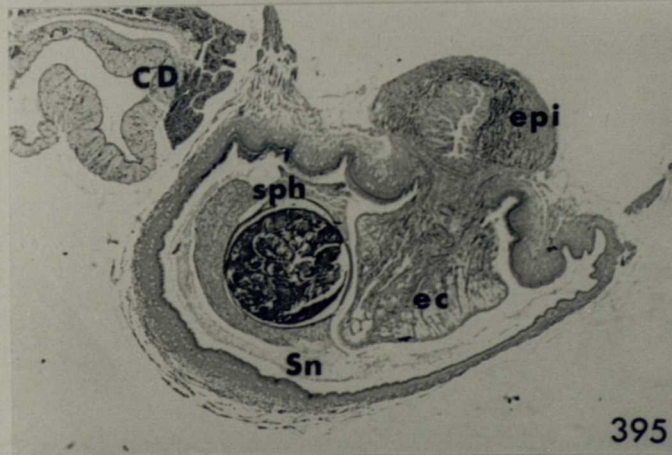
Fig. 395 Posterior region of the foreign spermatophore in the upper atrium (x25).

Fig. 396 L.S. through the lower atrium (x100).

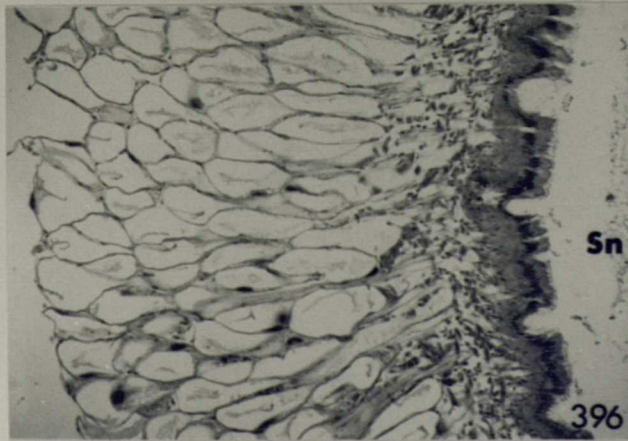
Fig. 397 T.S. through the oviduct (x63).



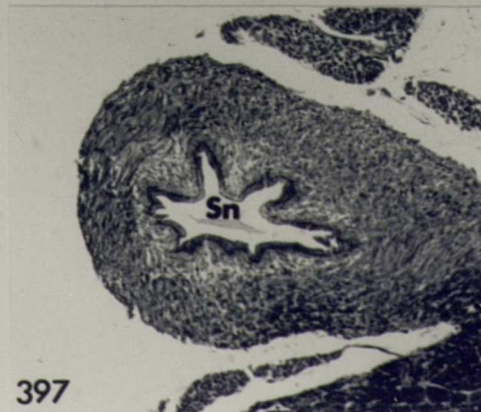
394



395



396



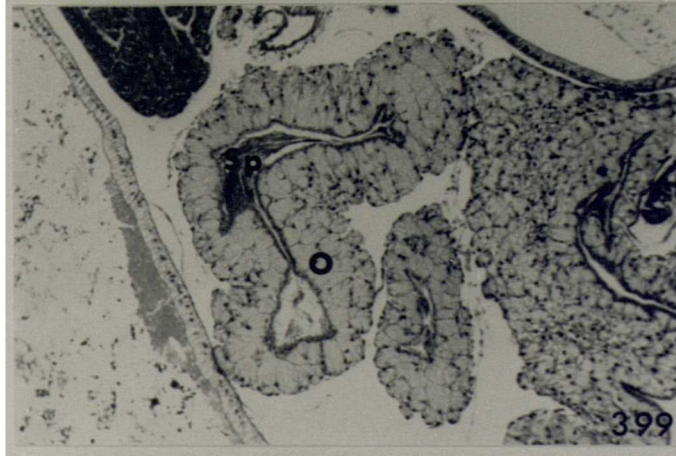
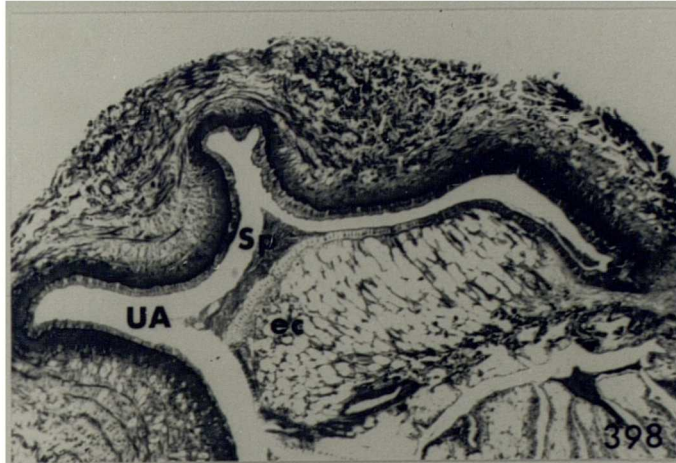
397

A.hortensis, 2 hours after copulation.

Fig. 398 Foreign sperm remaining in the upper atrium  
(x25).

A. hortensis, 4 hours after copulation.

Fig. 399 Foreign sperm in the oviducal side of the  
common duct near its junction with the  
carrefour (x63).



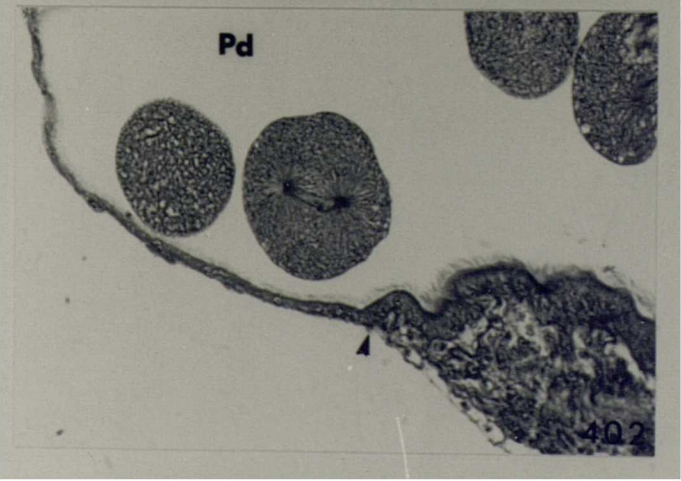
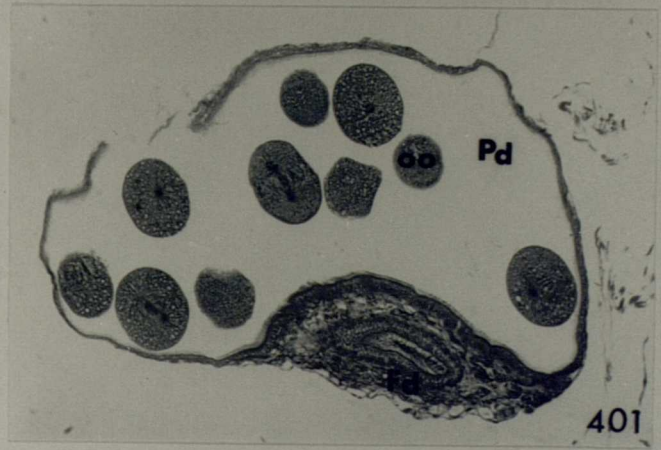
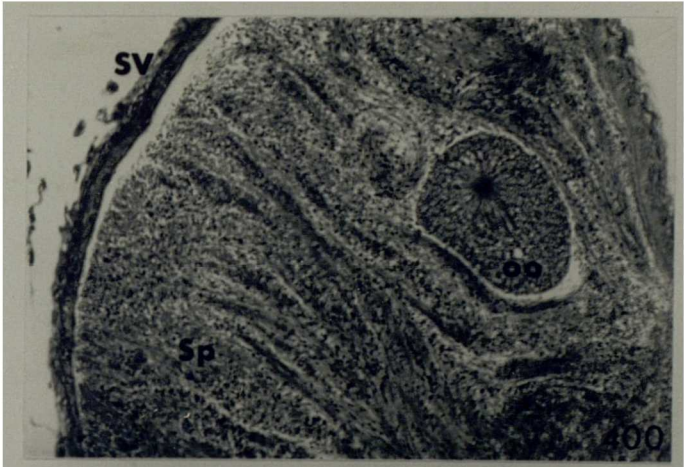


D.reticulatum, changes in the reproductive tract prior to egg-laying.

Fig. 400 Oocyte passing through the seminal vesicle (x250).

Fig. 401 Oocytes filling the pouched diverticulum of the carrefour (x125).

Fig. 402 Detail of oocytes in the pouched diverticulum (x250). Arrow indicates the transition from columnar to squamous epithelial cells (x250).



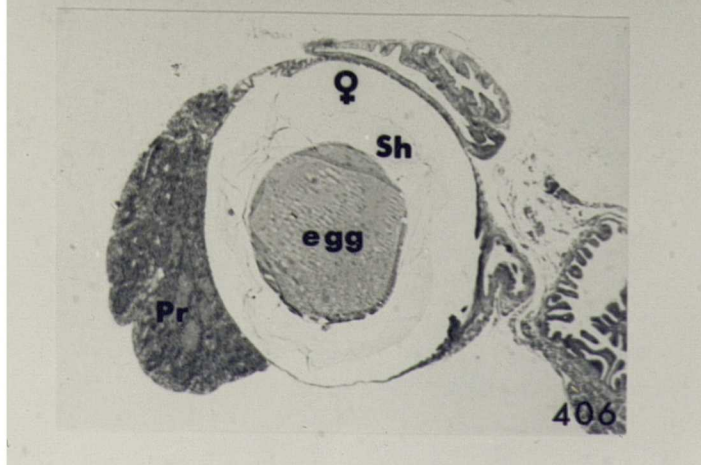
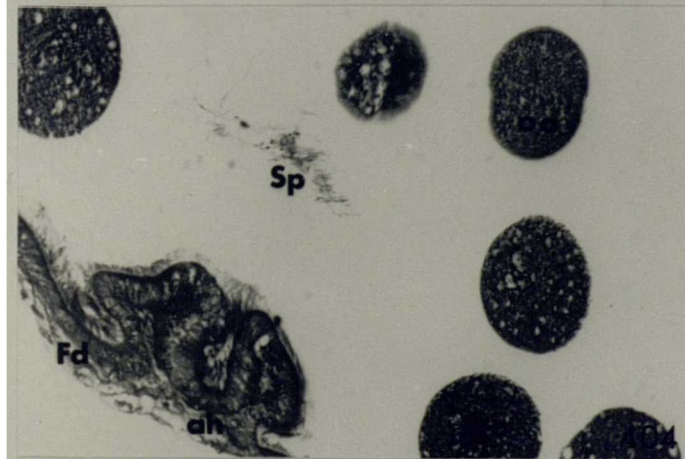
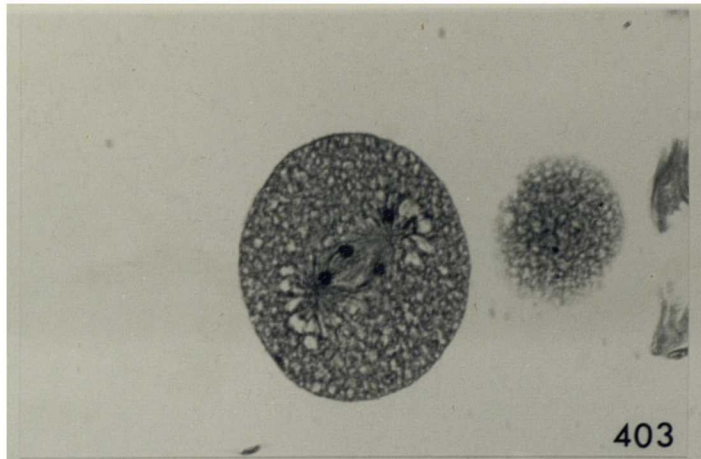
D.reticulatum, changes in the reproductive tract prior to egg-laying.

Fig. 403 Detail of oocyte containing spindle (x400).

Fig. 404 Sperm in the pouched diverticulum of the carrefour (x250).

Fig. 405 Albumen gland duct filled with secretion (x100).

Fig. 406 Egg receiving shell layers during its passage through the oviducal groove of the common duct (x30).

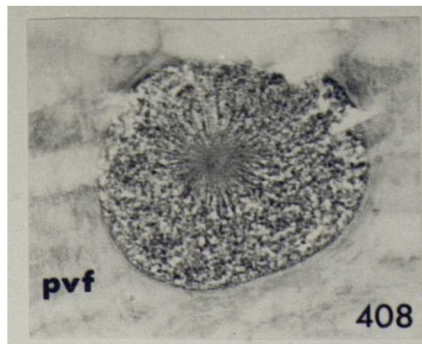
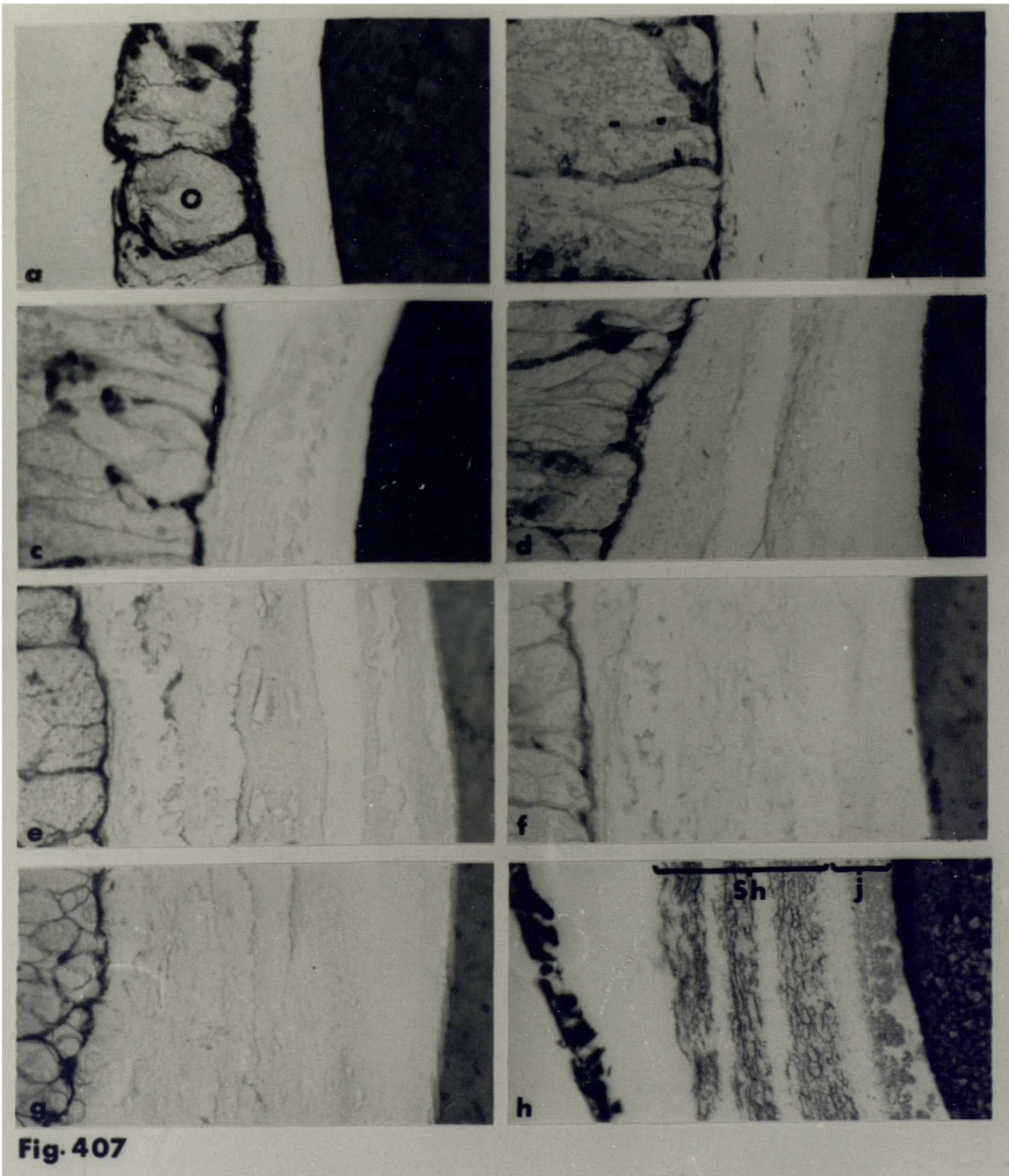


D.reticulatum, egg formation.

Fig 407 Eggs at different levels along the common duct showing the addition of successive jelly and shell layers (x250).

- a. formation of perivitelline membrane.
- b. addition of innermost, dense jelly layer.
- c-e. addition of jelly layer.
- f-g. addition of shell layer.
- h. fully-formed egg.

Fig. 408 Oocyte, with spindle, surrounded by perivitelline fluid (x400).



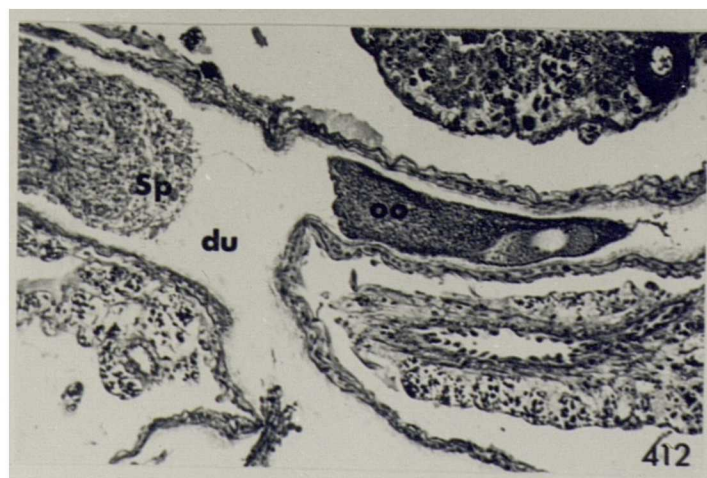
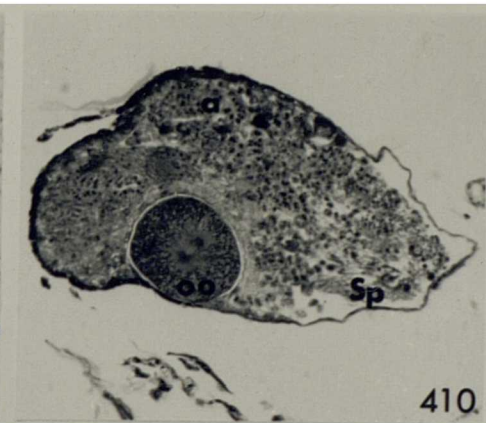
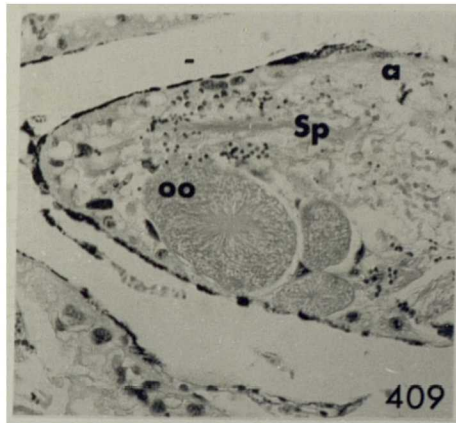
A.hortensis, changes in the reproductive tract  
prior to egg-laying.

Fig. 409 Oocytes with spindles in the gonad (x250).

Fig. 410 Oocyte with spindle in the gonad (x160).

Fig. 411 Oocyte leaving the follicle at ovulation  
(x250).

Fig. 412 Oocyte passing along an efferent ductule from  
an acinus into the posterior, slender region  
of the hermaphrodite duct (x160).



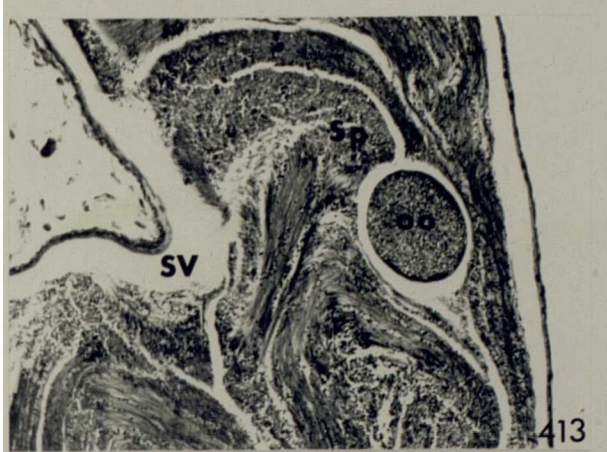


A.hortensis, changes in the reproductive tract  
prior to egg-laying.

Fig. 413 Oocyte passing through the seminal vesicle  
(x160).

Fig. 414 Perivitelline oocyte cluster (arrowed)  
entering the hermaphrodite duct (x160).

Fig. 415 Oocytes (arrowed) filling the ascending limb  
of the carrefour loop (x300).



A.hortensis, changes in the reproductive tract  
prior to egg-laying.

Figs. 416-418 Oocytes filling the ascending  
limb of the carrefour loop (x160).

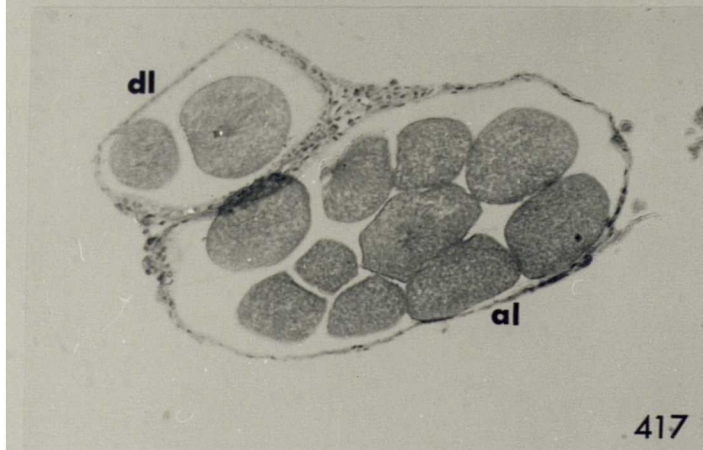
Fig. 416 T.S. through the mid-region of the  
carrefour loop.

Fig. 417 T.S. near the base of the carrefour  
loop.

Fig. 418 T.S. through the base of the  
carrefour loop.



416



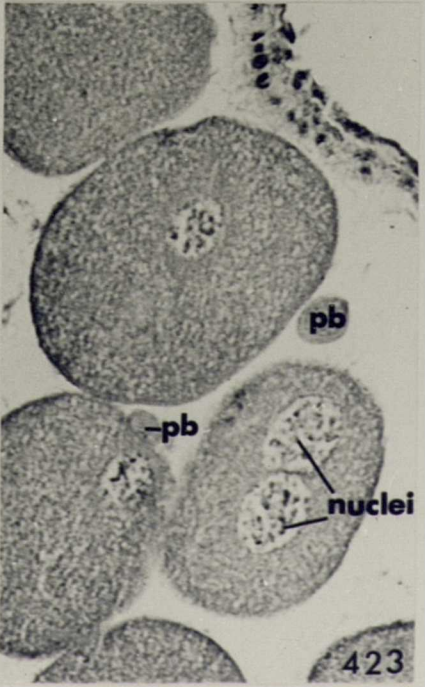
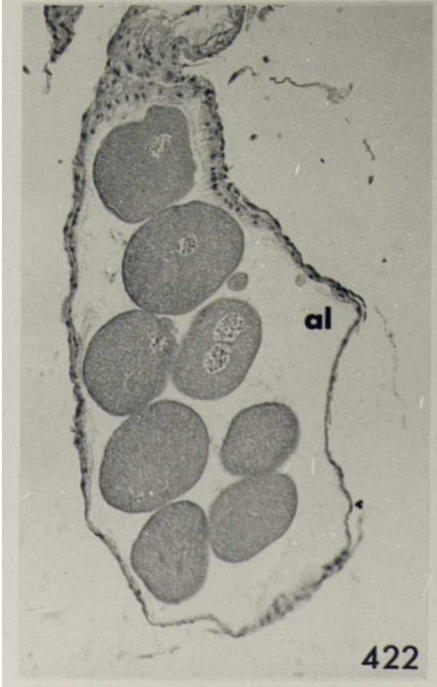
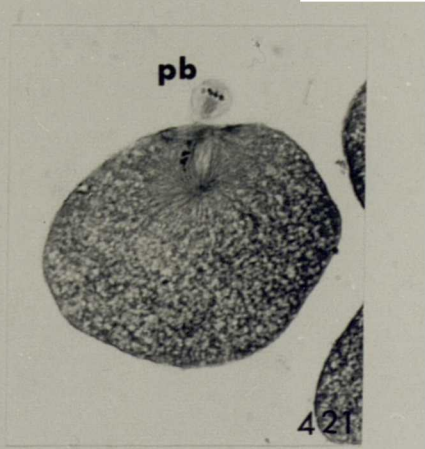
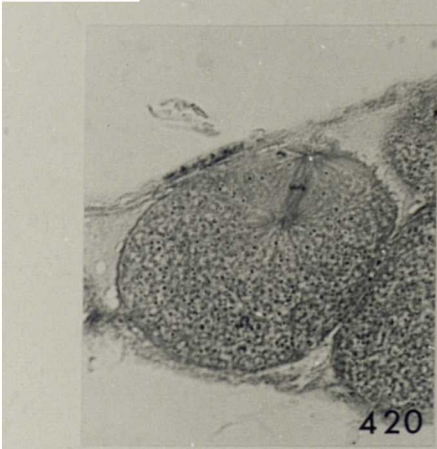
417



418

A.hortensis, changes in the reproductive tract  
prior to egg-laying.

- Fig. 419 Oocyte and sperm in the base of the carrefour  
loop (x160).
- Fig. 420 Detail of oocyte with spindle in the ascending  
limb of the carrefour loop (x400).
- Fig. 421 Detail of oocyte with polar body in the  
ascending limb of the carrefour loop (x400).
- Fig. 422 L.S. through the ascending limb of the  
carrefour loop (x200).
- Fig. 423 Oocytes containing the sperm and egg nuclei  
(x500). Detail of Fig. 422.

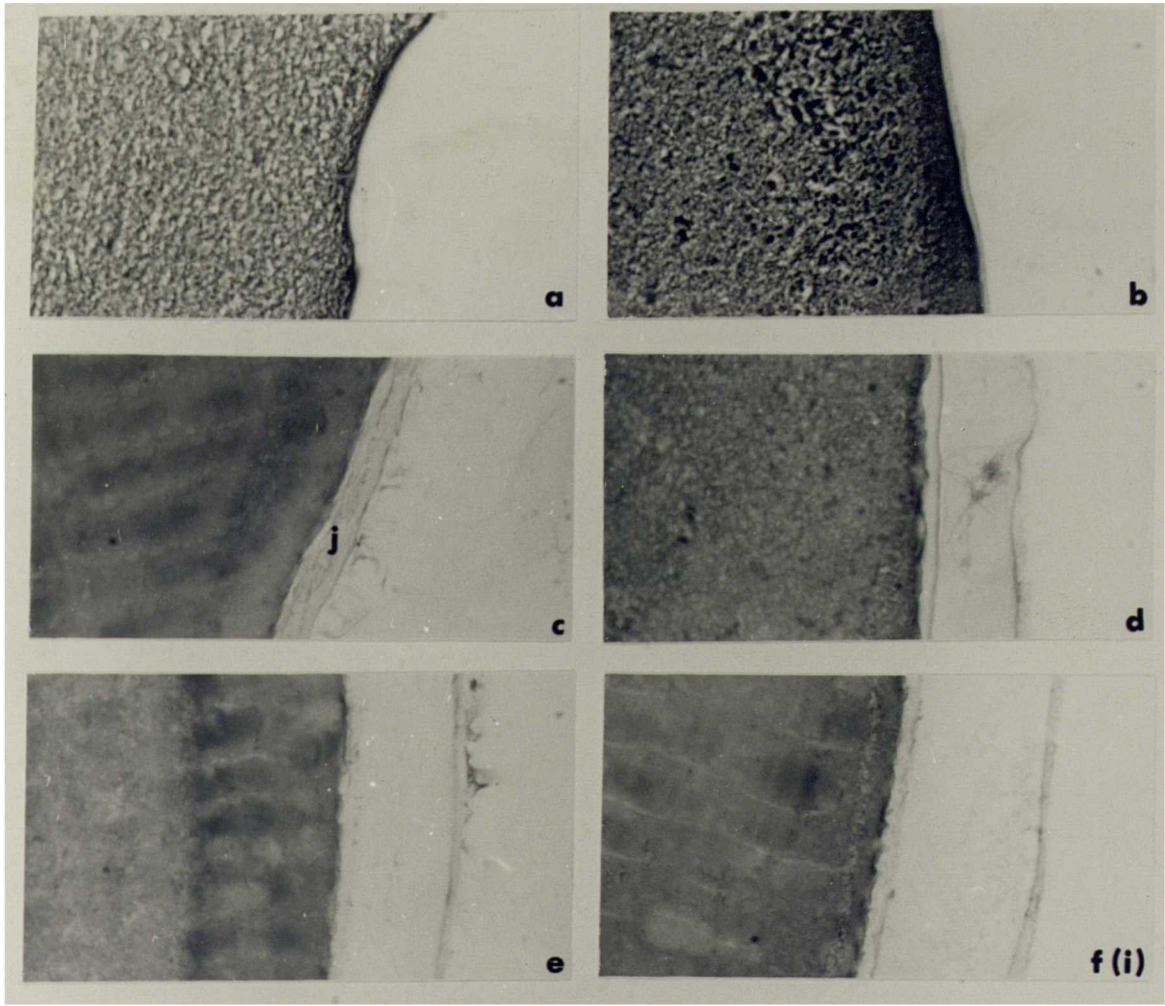


A.hortensis, egg-formation.

Fig. 424 Eggs removed at different levels along the common duct showing the addition of successive jelly and shell layers (x400).

- a. formation of perivitelline membrane.
- b. addition of innermost jelly layer.
- c-f. addition of jelly layer.

f(i) is a detail of the whole egg seen in f(ii) (x25).



**Fig. 424**



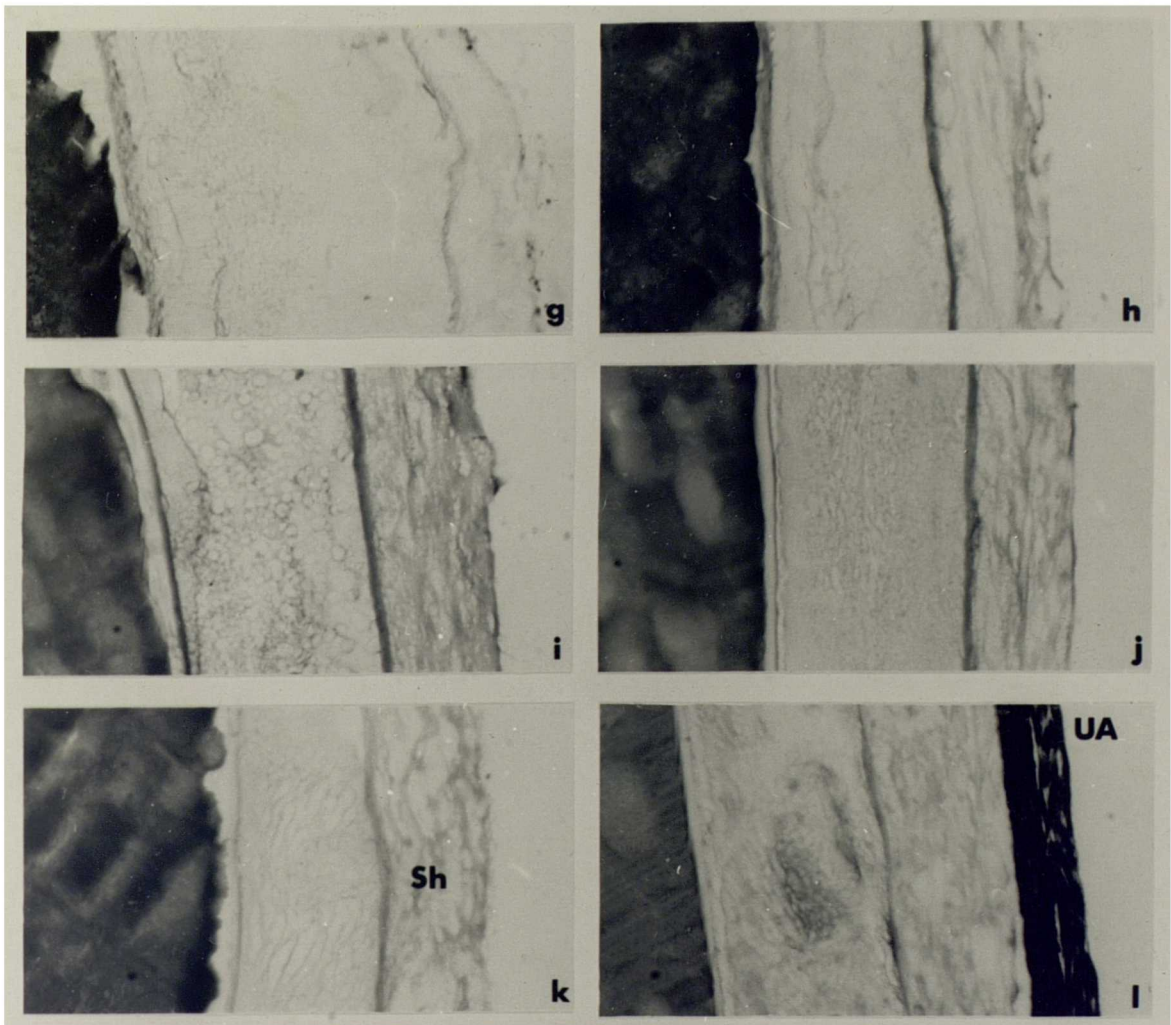
A.hortensis, egg formation.

Fig. 424 Eggs removed at different levels along the  
(cont.) common duct showing the addition of  
successive jelly and shell layers (x400).

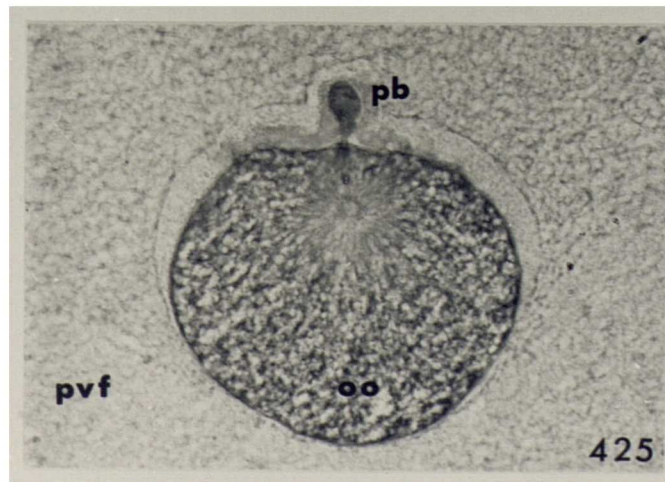
g-k. addition of outer shell layers.

l. fully-formed egg in upper atrium.

Fig. 425 Oocyte, with polar body, surrounded by  
perivitelline fluid.



**Fig. 424 (cont.)**



A.hortensis, egg-laying.

Fig. 426 T.S. of egg in the thin oviduct (x40).

Fig. 427 T.S. of egg in the thick oviduct (x25).

Fig. 428 Egg filling the upper atrium (x25).

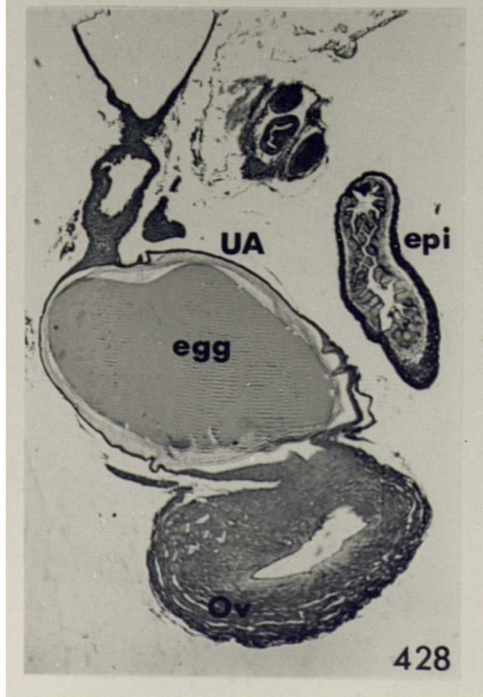
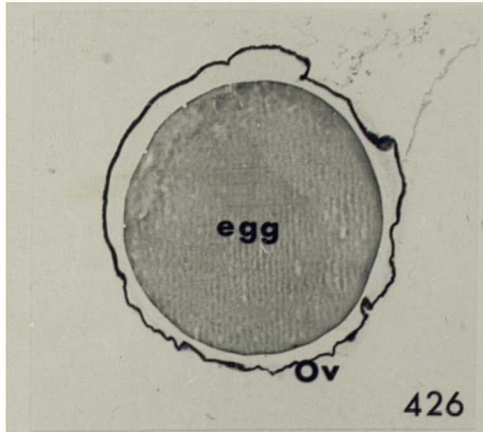
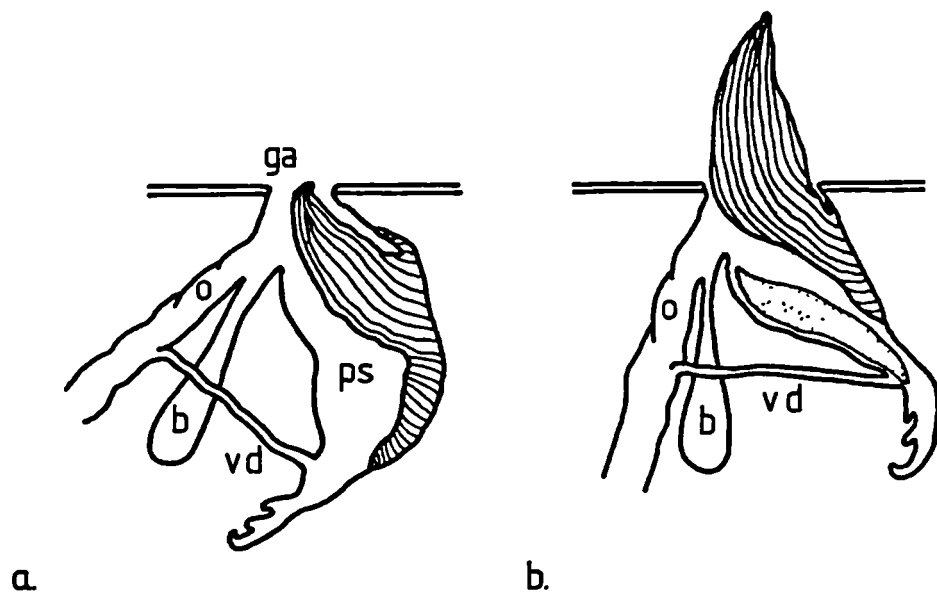


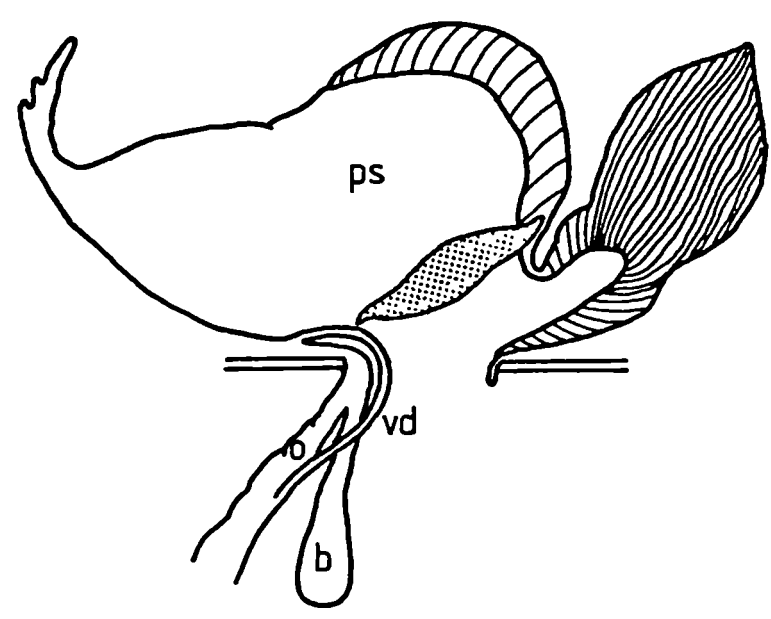
Fig. 429 Diagrams showing the position of the sperm package at intervals during courtship and copulation in D.reticulatum.

- a. at rest.
- b. during courtship, sarcobellum (striped) protruding through the genital opening. Sperm package (stippled) in penial sac.
- c. sperm package lying on the surface of everted penial sac.
- d. direction of movement of the sperm packages.
- e. immediately after copulation.
- f. 40 minutes after copulation.
- g. 75 minutes after copulation.



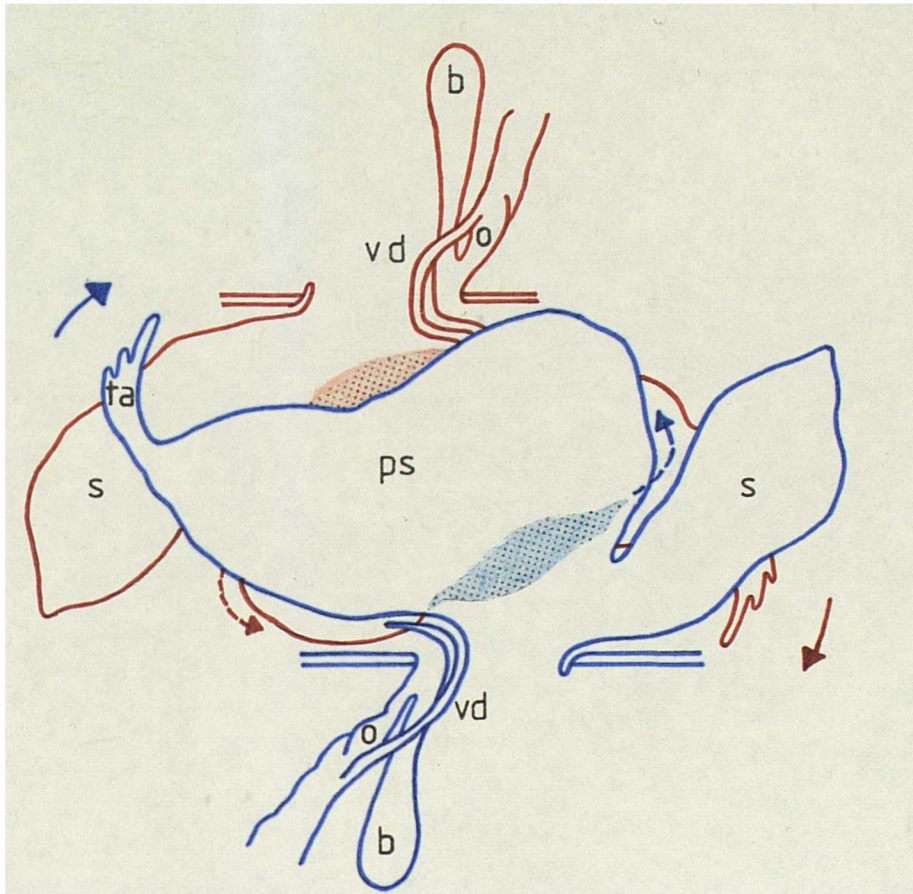
a.

b.



c.

Fig. 429



d.

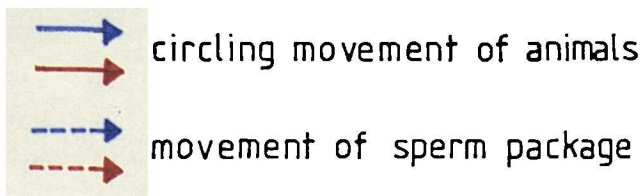
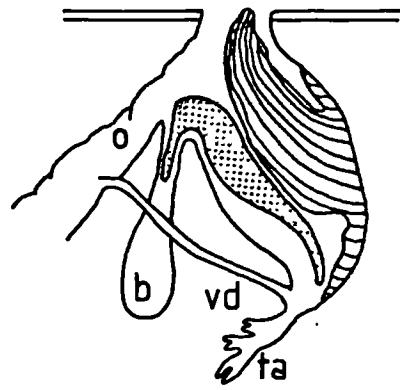
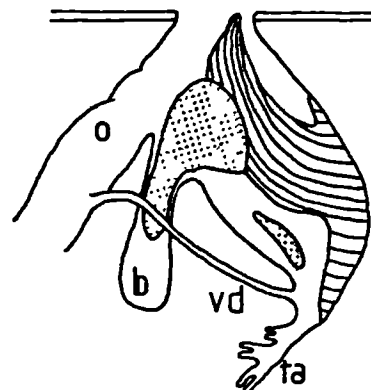


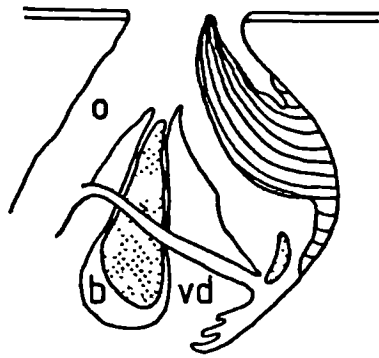
Fig. 429 (cont.)



e.



f.



g.

Fig. 429 (cont.)



Fig. 430 Diagram to show the variety of form of spermatophores produced by A.hortensis.

- a. elaborate, spined spermatophore.
- b. simple, smooth spermatophore  
(after Quick, 1960).

Fig. 431 Diagrams showing the position of the spermatophore at intervals during courtship and copulation in A.hortensis.

- a. 2 hours after the start of courtship.
- b. partial eversion of upper atrium.
- c. complete eversion of upper atrium.
- d. epiphallic cones engaged. Spermatophore transferred directly into the bursa copulatrix. (arrows show direction of movement).
- e. immediately after copulation.

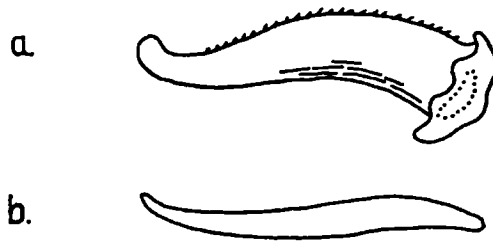


Fig. 430

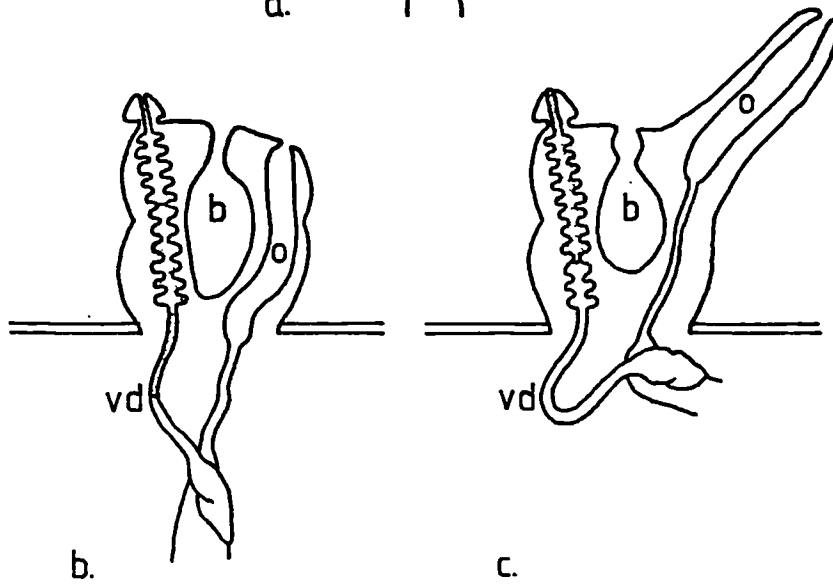
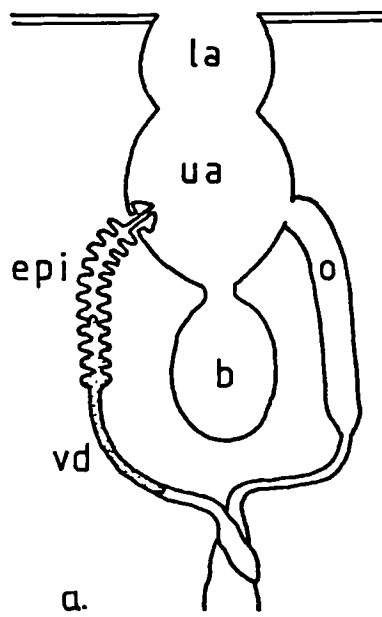
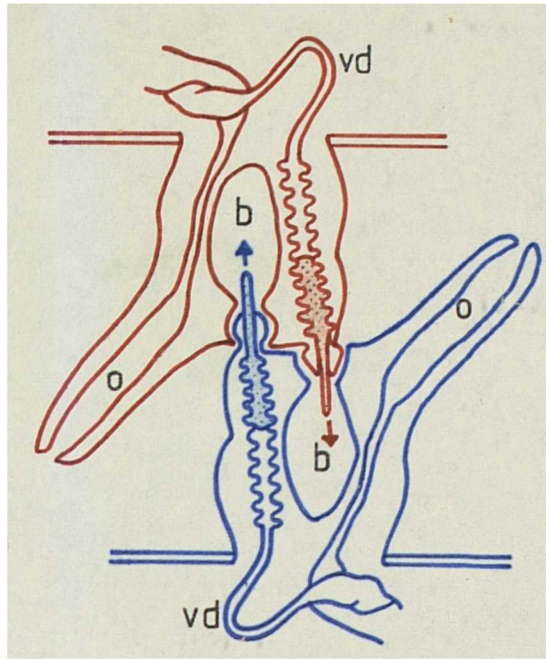
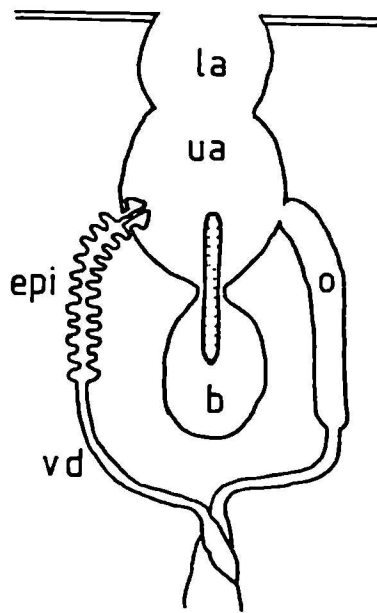


Fig. 431



d.



e.

Fig. 431 (cont.)