CIRROTHAUMA MURRAYI CHUN, A FINNED OCTOPOD

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[Plates 1–21; outrigger]

CONTENTS

Several specimens of the remarkable finned octopod *Cirrothauma* recently caught are described. The animal is taken at great depths, often near the bottom but sometimes away from it. The enormous arms and web can be spread to give a medusoid form but the animal also swims horizontally mainly using the fins, whose powerful muscles are attached to a large fin support. The animal is gelatinous and perhaps neutrally buoyant, and can almost certainly hover in the medusoid form. The mantle muscles are weak and the funnel very long. The arms are long and have a few small suckers in a single longitudinal row, only some of which have a minute suction chamber. The infundibula are small but the cuticle has small pegs with innumerable pores. The cuticle is closely similar to that of octopods and is capable of adhesion. In the base of each sucker peduncle, male and female, there is a possible light organ.

The beaks are large and black, the lower strongly pointed. There is a large tongue with vestiges of a radula. The salivary papilla carries the duct of the 'posterior salivary gland' which lies far forward within the buccal complex.

The male ducts are simple and produce simple packets of sperms. These are found in the oviducal gland (spermatheca), where the large eggs are fertilized. The heart has an accessory chamber presumably providing extra blood flow to the long arms and large fins.

The eyes are small open cups covered by a cornea but with no lens or iris. The rhabdomes are sometimes degenerate. The optic lobe is small with no granular layers of amacrine cells.

The suboesophageal lobes are close together and the superior buccal lobe is attached to the brain, as in incirrate octopods. There is a large fin lobe. The peduncle lobe and basal lobes are large, in spite of the small eyes, indicating their importance for locomotion. There are no giant fibres.

The supraoesophageal lobes are small, with development only of the tactile region (inferior frontal lobe) and reduction of the superior frontal and vertical lobe system. There are large epistellar bodies but no cranial photosensitive vesicles. The optic gland is clearly of neural origin.

The statocysts are very large and typically octopodan with a single macula and one anticrista, but the crista is not subdivided.

Cirrothauma, like other cirrates, thus shows some features that are present in *Vampyroteuthis*, and others that are found in decapods, as well as many present in the octopods without fins. These animals represent in some ways an early condition of the coleoid stock.

1. General introduction

1.1. *The* Cirromorpha

The cirrate octopods have aroused particular interest among teuthologists for two main reasons: first their unusual anatomy suggests that they are intermediate between the Decapoda and the main octopod group the Incirrata; and secondly their rarity in previous collections. It is now recognized that cirroteuthids favour the deep benthopelagic region and their supposed rarity is probably partly due to the difficulties of fishing this zone with suitable gear. Increased attention to the deep-sea has led to a steady rise in sightings and captures of cirrates in recent years. The use of submersibles, for example, has produced valuable first-hand observations of them as well as moving and still photographs (R. D. Ballard, personal communication). Similarly the recent expansion of interest in deep-sea benthos and the biology of total water columns, at the Institute of Oceanographic Sciences, has led to new techniques for fishing on or very close to the bottom at great depths. Consequently cirromorphs, although by no means abundant in the catches, are captured more regularly and the specimens of *Cirrothauma murrayi* Chun, 1913 (figure 1, plate 1) that form the basis of this study were caught as a direct result of the change in sampling emphasis.

Hoyle (1886), Chun (1913) and Robson (1926, 1932a) were the first to discuss the finned octopods in relation to their life in the abyssal depths. Robson (1932b) subsequently gave descriptions, in his monograph, of the specimens of cirrates known then as well as of eggs. More recently Berry (1949, 1952, 1955) reported on *Opisthoteuthis californiana* Berry, 1949, followed by Pereyra (1965), who described the actions of that animal while still alive and considered some aspects of its biology. During the past 15 years finned octopods have been photographed in the sea (Jahn 1971; Roper & Brundage 1972; Pearcy & Beal 1973; Ballard 1976). Roper & Brundage (1972) reviewed the literature, made a detailed analysis of the photographic evidence and discussed the biology of these animals in the light of their findings.

1.2. *Studies of the morphology of the* Cirromorpha

The first cirrate described was caught at Jakobshavn, Greenland and called *Cirroteuthis mülleri* by Eschricht (1836). This was followed by a memoir by Reinhardt & Prosch (1846). In 1886 Hoyle discussed the cirrates and described those taken by H.M.S. *Challenger*, as well as listing all the animals recorded to that time. Robson (1926, 1932a) considered the structure and function of the cirrates in relation to their deep-sea habitat, and later (1932b) compiled all the records to that time.

In view of the paucity of animals captured it is perhaps surprising that the anatomy of three of the finned octopods has been described in considerable detail. *Opisthoteuthis depressa* Ijima and Ikeda, 1895, was examined by Meyer in 1906 (a, b), and, *Cirroteuthis umbellata* Fischer, 1883 and *Stauroteuthis* sp. by Ebersbach in 1915. Chun (1913) made a microscopical examination of some internal features in the course of describing and naming the first specimen of *Cirrothauma murrayi*.

The nomenclature of the Cirrata, at present in disarray, is currently being revised by Dr G. L. Voss. To avoid further confusion we have retained the name *Cirroteuthis umbellata* Fischer, 1883 for the animals described by Ebersbach (1915) although the specimens were later identified as *Grimpoteuthis umbellata* by Robson (1932b, p. 139). The other cirrate, *Stauroteuthis* sp., also described by Ebersbach (1915), should be referred to *Chunioteuthis ebersbachi* (Robson 1932b, p. 139). The animal described by two of the present authors (J.Z.Y. and M.N.) in the Symposia of the Zoological Society of London (Young 1977a; Nixon & Dilly 1977) and referred to as *Cirroteuthis* sp. is now found to correspond to *Stauroteuthis syrtensis* Verrill, 1879 (G. L. Voss, personal communication).

The increase in the number of specimens of *Cirrothauma* captured in the last 15 years, with use of new methods, has resulted in a brief description of its morphology (Aldred *et al.* 1978). Other cirrates have been observed (Roper & Brundage 1972; Pearcy & Beal 1972; Ballard 1976) as well as those caught in recent times, and a new species has been described (G. L. Voss 1982). A monographic revision of the suborder Cirrata is also in progress (G. L. Voss, personal communication). There are new reports of cirrate eggs (Boletzky 1978, 1982). With additional *Cirrothauma* caught in the last few years it has been possible not only to dissect but also to make serial sections of the material to gain more information about these deep-living octopods.

1.3. *Distribution of* Cirrothauma

Cirrothauma murrayi was first caught in 1910 (Murray & Hjort 1912) and was probably the most valuable discovery of the Michael Sars Expedition. Chun (1913) described it as being completely gelatinous, semi-transparent, as delicate as a lobed ctenophore and unlike any known cephalopod. It has small eyes which are without dioptric apparatus and in this it is

TABLE 1. THE SPECIMENS OF *CIRROTHAUMA MURRAYI* SO FAR RECORDED

source	expedition vessel/station	date	position		sampling depth m	sounding m	gear	specimen	mantle length mm
Murray & Hjort 1912 } Chun 1913 } Voss 1967, p. 527 (and see Roper & Brundage 1972)	*Michael Sars*, 82	13.7.10	48° 24' N	36° 53' W	1500	4000	pelagic trawl		40
	Arliss II (Ice Island)		86° N	173° E	surface		dip-net		
Roper & Brundage 1972	*Eltanin*-175		40° 46' S	76° 48' W	2893	3700	IKMT 3 m		
	Eltanin-1514		57° 39' S	52° 02' W	3980–4136	4013–4136	10 Blake		
	Eltanin-878		55° 25' S	78° 28' W	3440–3705	4337	IKMT 3 m		
Nesis 1975	*Akademik Kurchatov* 1188	1973	Puerto Rico Trench (22° N 65° W)		3300	max. depth 8385	—		20
Ballard 1976	*Alvin*		Cayman Trough (18° N 82° W)		3660	3660	submersible		
Aldred *et al.* 1978	*Discovery* 8509, no. 43	1.5.74	43° 34' N	12° 58' W	1500–4650	5100	RMT 8 o.c.	A mat	155
	Discovery 9131, no. 23	23.9.76	20° 07' N	21° 46' W	3000–3500	3800	RMT 8 o.c.	B+eggs	130
present paper	*Discovery* 9541, no. 6	16.4.77	20° 10' N	21° 10' W	3929	3929	OTSB 14	C+eggs	220
	Discovery 9756, no. 5	12.4.78	49° 49' N	14° 06' W	4012–4020	4012–4020	OTSB 14	D	105
	Discovery 9756, no. 5	12.4.78	49° 49' N	14° 06' W	4012–4020	4012–4020	OTSB 14	E	21
	Challenger 50515	6.6.79	49° 44' N	15° 05' W	4505–4515	4505–4515	OTSB 14	F	—†
M. Okiyama, pers. comm.	*Kaiyo-Maru* KOC-13	23–24.5.81	40° N	150° E	0–4000	5250–0700	KOC-T net		150 (185)‡
	Soyo-Maru R53-7	25.6.81	30° 8' N	147° 14.5' E	0–6160	6160	beam trawl		70 (75)‡
	Soyo-Maru R53-9	26.6.81	29° 44.1' N 141° 5' E		0–6100	6100	beam trawl		70‡

Symbols and abbreviations: †, specimen too badly damaged to measure but of similar size to specimen A; ‡, measurements made when material fresh; est., estimated; IKMT 3 m, Isaacs Kidd midwater trawl; KOC-T net, rectangular midwater trawl with 9 m² effective mouth area, bearing catch-dividing bucket at cod end; mat, mature; o.c., opening–closing net used; OTSB 14, otter trawl semi-balloon benthic, with 14 m headline; RMT 8, rectangular midwater trawl with 8 m² effective mouth area.

unique among the Cephalopoda (Chun 1913). There were no further records of *C. murrayi* until one was dipped from an ice hole on Ice Island in the Arctic Ocean (G. L. Voss 1967, p. 527); three more were in the collection of the Institute of Marine Sciences, Miami, by 1972 (see Roper & Brundage) and a photograph taken from the submersible *Alvin* (Ballard 1976) has been identified (by R. G. A.) as *C. murrayi*. R.R.S. *Discovery* captured three specimens between 1974 and 1977 (Aldred *et al.* 1978), and since then has taken two more. These five animals, together with one captured by R.R.S. *Challenger*, form the basis of this paper.
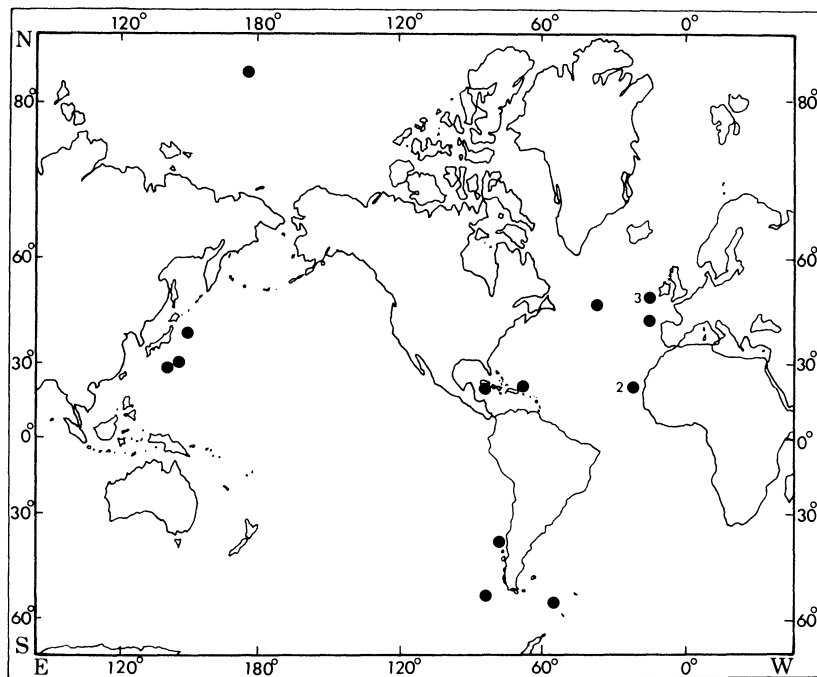

FIGURE 2. *Cirrothauma murrayi*. The localities from which the animals have been captured (see table 1 for details). The filled circles with accompanying number indicate more than one capture. The three recent captures are also included (M. Okiyama, personal communication).

The known distribution of *C. murrayi* is given in table 1 together with details of all the specimens so far captured. Even such sparse data provide much information; the positions in which these animals have been caught are remarkably widespread, being from within the Arctic Circle to close to the Antarctic Circle, in the North and South Atlantic Ocean and in the Pacific Ocean (figure 2). All except one have been taken at depths of more than 1500 m, and most below 3000 m. Six of the animals were near to the bottom but others were a considerable distance from it (table 1). The one taken at the surface in the Arctic Circle may be an example of polar emergence (Hoyle 1886; Roper & Brundage 1972).

2. MATERIAL AND METHODS

2.1. *The animals*

The material used in the present study was collected by the Institute of Oceanographic Sciences during cruises of R.R.S. *Discovery* and R.R.S. *Challenger* (table 1). The animals, mostly from great depths, were often found to be damaged and this has led to difficulties in measurement and in histological procedures. After capture all were preserved in formalin.

TABLE 2. THE MEASUREMENTS OF *CIRROTHAUMA MURRAYI* (ARRANGED IN ORDER OF SIZE)

specimen	C		A		B		D		E	
mantle length/mm	220		155		130		105		21	
total length/mm	940		660		560		535		67	
posterior to back of fin/mm	95		86		65		52		—	
funnel length/mm	185		47		61		38		5	
fin length/mm	210†		110		115		114		23	
fin width/mm	95†		65		78		50		11	
distance between eyes/mm	—		72		69		50		8	
eye diameter/mm	—		17		13		12		1.6	
arm length/mm										
I	R 685	L 685	R 465	L 445	R 420	L 430	R 400	L 405	R —	L 42
II	—	735	480	525	420	425	395	385	40	42
III	—	—	480	510	420	430	395	385	41	40
IV	650	670	470	470	420	420	425	400	—	—
number of suckers										
I	R —	L —	R 36	L 38	R‡	L —	R —	L —	R —	L —
II	—	—	37	38	—	—	—	58	—	—
III	—	—	38	38	—	—	58	58	—	—
IV	—	—	36	38	—	—	62	58	—	—
gill length (left)/mm	33		12		16		12.5		2.4	
gill width (right)/mm	25		10		12		10.5		1.4	
number of gill filaments	9		7		7		8		9	
sex	♀		♂		♀		♂ imm.		♂ imm.	
size of largest egg/mm	14.0 × 8.9				13.8 × 8.4					

Symbols and abbreviation: †, measurement estimated owing to damage or distortion; ‡, no arm with complete set of suckers but estimated to be in the upper thirties; imm., immature; R, right; L, left.

2.2. *Measurements*

The orientation of the animal is that adopted by a squid when swimming by jet propulsion; the funnel and mantle cavity being ventral and the apex of the mantle posterior (see Young 1971).

Each animal was subjected to a series of measurements although it was often difficult to be accurate because of the elastic and gelatinous nature of the tissues. In particular elasticity of the arms allowed them to be stretched considerably when being straightened for measuring: in consequence, with the exception of the smallest specimen, the arms were measured to the nearest 5 mm and other parameters were measured as accurately as the condition of the tissues permitted (table 2). The following measurements were taken:

mantle length, posterior of body to point midway between the eyes;

posterior to back of fin, posterior of body to the midpoint of a line joining the rear insertion points of the fins;

funnel length, ventral midline from apex of V at base to the tip;

fin length, from the insertion point into the mantle to the tip;

fin width, distance between the anterior and posterior edges at the widest point;

distance between eyes, measured to the outer edges of the eyes;

eye diameter, across the bulbus;

arm length, oral surface from the lips to the tip of the arm;

gill length, from the proximal filament to tip;

gill width, across widest point;

gill filaments, the number of demibranchs on one side of the left gill;

egg, the length and maximum diameter of the largest egg removed from the oviduct.

2.3. *Histological investigations*

The material available had all been fixed in formaldehyde (5 % in seawater). The tissues of specimen A were in good condition; those of B and C were less so. The eyes, optic lobes and central ganglia of A were stained by Cajal's method (Stephens 1971) and serially sectioned. Staining was only moderately successful but allowed some fibre tracts to be traced. Ganglia of animals B and C were serially sectioned and alternate slides were stained with the methods of Masson, Holmes (Drury & Wallington 1967) or Bodian (1936). These also were only moderately successful.

The statocysts were stained with Mayer's haemalum (Drury & Wallington 1967), injected into the cavity by a syringe. After study of the intact specimen the sac was cut open and the wall was laid flat, dehydrated and mounted in Canada balsam (figure 116, plate 20). Other specimens were left intact and cleared in glycerine (figures 113–115, plate 20). Serial sections of the buccal complex, the arms, cirri and suckers, the heart and the gonads were stained by one or more of the following methods: Cajal (Stephens 1971); Holmes, Masson's trichrome; haematoxylin and eosin; or Alcian blue (see Drury & Wallington 1967).

2.4. *Scanning electron microscopy*

A sucker was taken through graded ethanol, ethanol and Freon 113 before being critical-point dried (Anderson 1951; Boyde 1974). The specimen was attached to an aluminium rivet with Rapid Araldite, sputter-coated with gold and examined with a Cambridge Stereoscan Microscope (S4-10) at 10 kV.

3. ANATOMY

3.1. *General description*

The mantle is short, about 23 % of the total length, and narrow. Approximately half the length is taken up by a soft mass of gelatinous tissue posterior to the fins (figure 1, plate 1; figure 3). The mantle wall is also gelatinous, but rather firmer than the tissue filling the posterior extension. The exceptionally large fins are thickened along their posterior edge with dense supporting tissue, whereas the leading edge is much thinner and more gelatinous and transparent, forming a broad curve which narrows sharply at the base where it attaches to the mantle.

The head is the same width as the widest part of the mantle. The eyes are small but conspicuously dark and set deeply in the gelatinous tissue. Nevertheless the lack of lens and iris can be clearly seen (see p. 32).

The funnel is slender and extremely long, especially in the largest specimen (C, table 2), where it is 84 % of the mantle length. The funnel opening is a small round pore which looks capable of complete closure. There is no valve. The funnel organ is indistinct but there is a differentiated rectangular patch of tissue on the inner dorsal surface of the funnel, close to the base, which has a longitudinal ridge along its left and right edges. The mantle aperture surrounds the funnel closely (Robson 1932a; Bidder 1970); a small space remains, presumably serving for inhalation during respiration and jet propulsion inasmuch as this takes place. The olfactory organs are oval, slightly raised areas, paler than the surrounding tissue. Inside the mantle cavity the base of the funnel is considerably expanded (figure 7, plate 2), presumably
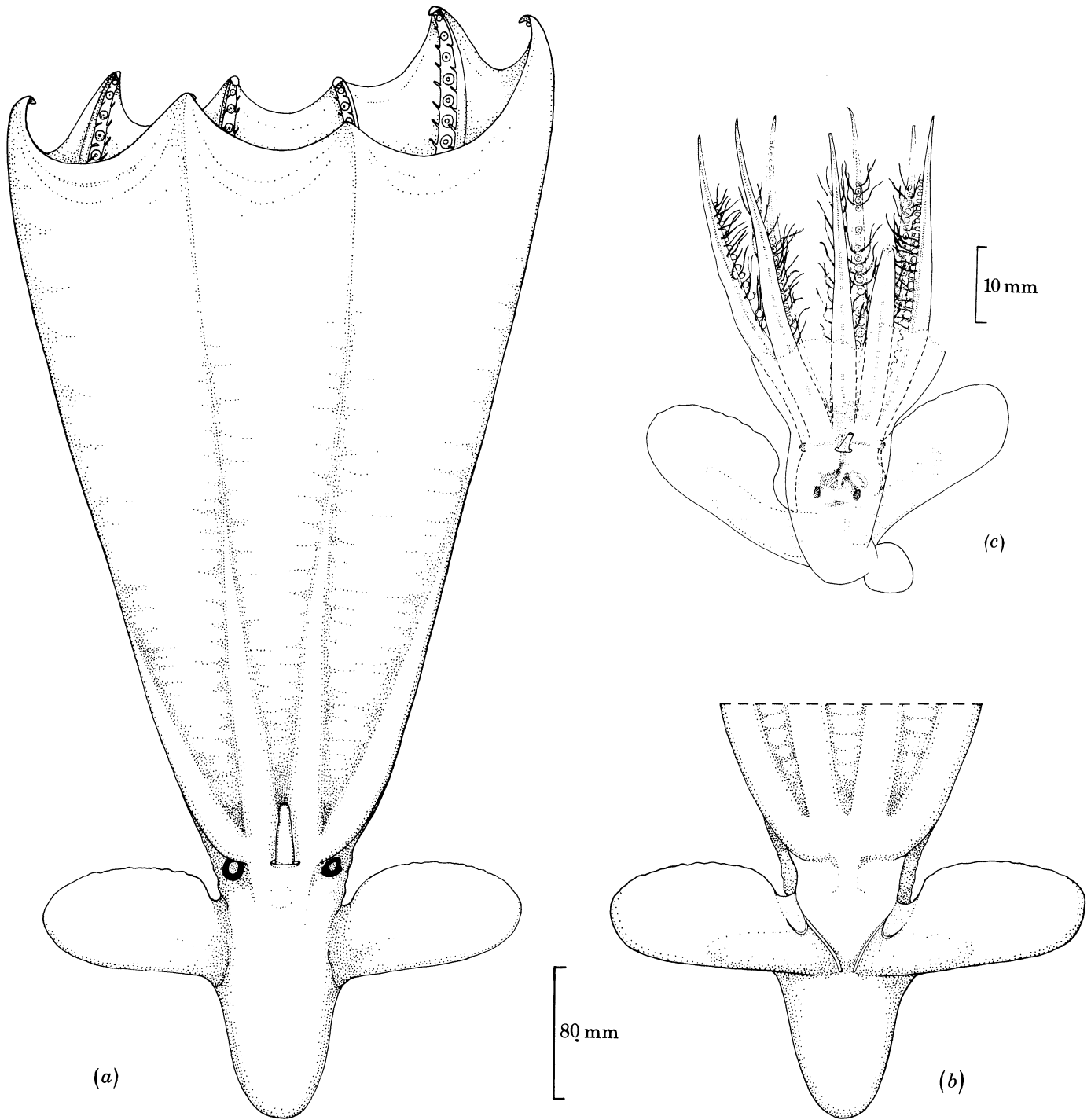
FIGURE 3. *Cirrothauma murrayi.* The ventral (*a*) and dorsal (*b*) view of specimen A and the ventral view of specimen E (*c*).

serving to block the mantle opening and ensure that water passes out of the funnel only during mantle contraction.

The arms are gelatinous, like the rest of the body, and sub-equal in length. However, LII in specimens A and C appear to be slightly longer than the rest (table 2). In the three largest specimens the arms are approximately three times the mantle length and in specimen E, the smallest, they are approximately twice this length. Specimen D is unusual in that the arms are four times the mantle length; this difference is reflected in the number of suckers, which is between 58 and 62 whereas in specimens A and B it is in the upper thirties. Specimens C, E and F are too badly damaged to allow meaningful counts. The appearance of the suckers, Chun's (1913) reason for establishing a new genus, differs considerably from that found in incirrate octopods. The proximal suckers (the first five or six on specimen A and the first eight in specimen D) are situated on rounded mounds. Distal to these the suckers consist of white convex discs on plump gelatinous stalks. A pair of cirri is situated between all but the most proximal suckers (p. 21). No hectocotylus was found (p. 18).

The web is delicate but well developed, extending the entire length of the arms, with a primary and secondary part as described by Robson (1932b, p. 117) for *Cirroteuthis* and *Chunioteuthis*. The primary web, occupying the brachial interspace, is joined directly to the arms for the proximal half and at the tip. The distal part of the arm, with the exception of the tip, is connected to the primary web by a thin segment-shaped secondary web. This arrangement is well illustrated by Roper & Brundage (1972) in their deep-sea photograph (figure 4, plate 2) and in the incirrate octopod *Pteroctopus tetracirrhus* (Boletzky 1976).

3.1.1. *Variation among the specimens*

With such limited material available it is difficult to know whether the observed differences between the specimens represents inter- or intraspecific variation. The appearance of all the *Cirrothauma* examined in this study is certainly very similar and separating them by variations in body proportions is difficult in such soft-bodied animals. The data are insufficient to reveal any sexual dimorphism. One such difference is the relative length of the arms and the numbers of suckers on them, which separates specimen D from others (see table 2). Specimens C, E and F are too badly damaged for sucker numbers even to be estimated, but the arm lengths of C ally it more closely to A and B. All the specimens in this study are from the northeast Atlantic but they could be split geographically into two groups: a northern group (A, D, E and F) from between the southwest of Ireland and just south of the Bay of Biscay, and a southern group (B and C) from north of the Cape Verde Islands. As there is one specimen with a sucker count in the upper thirties in each group (specimens A and B) the variation cannot be explained on geographical grounds.

3.2. *The skin*

Although *Cirrothauma* has no chromatophores the skin of the adult is coloured. *Cirrothauma* B (mantle length 130 mm), when freshly caught, was a red-brown colour virtually all over the body and arms. The small specimen (E), however, was nearly colourless and transparent with the exception of part of the alimentary canal which was deeply pigmented. The purplish colour described by Chun (1913) is a result of preservation. The colour of the five larger specimens is similar but the density of the pigment varies considerably on different parts of the body. It is deepest on the web and arms, particularly on the oral side, increasing in density
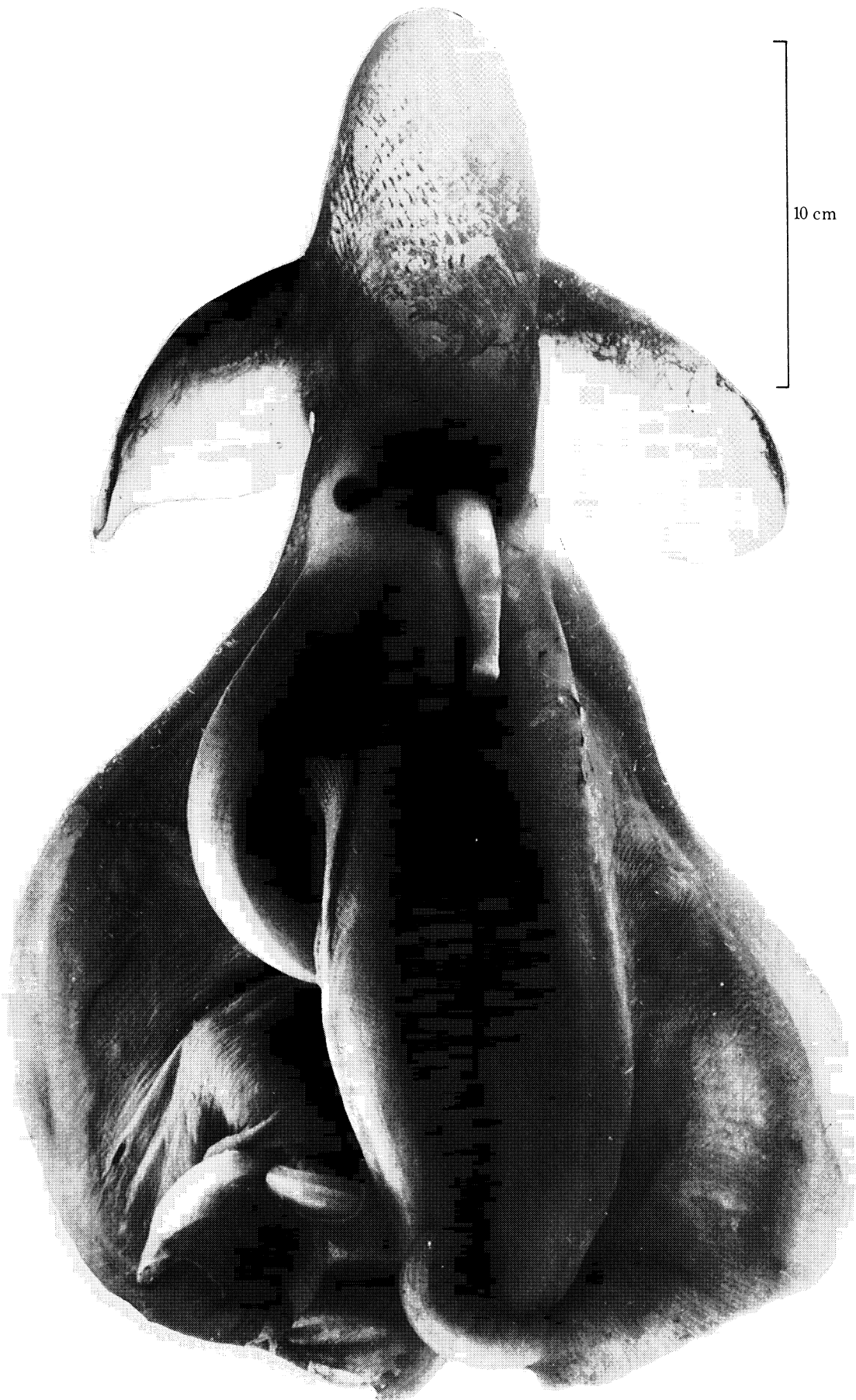
10 cm

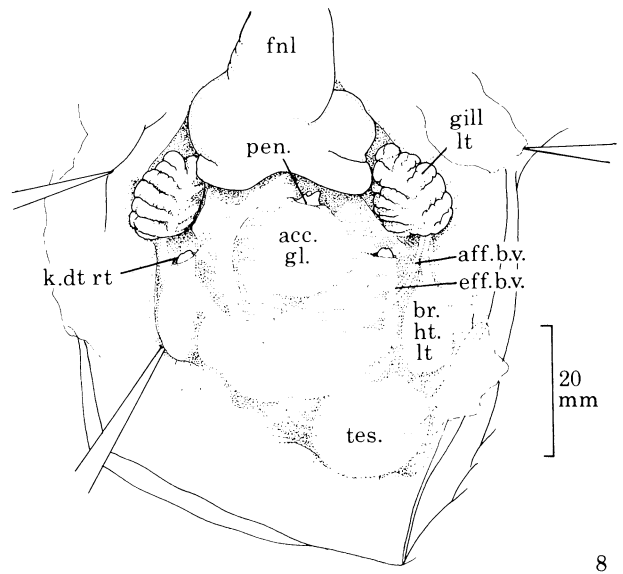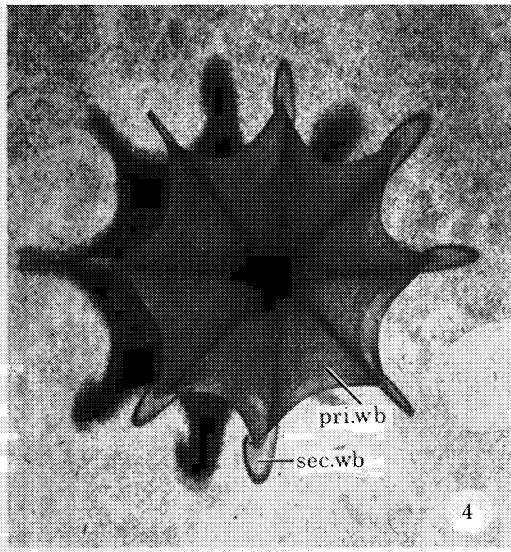FIGURE 1. *Cirrothauma murrayi.* Photograph taken immediately after capture (specimen B).

FIGURE 4. Cirrate octopod with intermediate web in drogue-like drifting configuration. Photograph taken with camera some 5 m above the octopod which was approximately 1 m above the floor of the sea (from Roper & Brundage 1972. fig. 20).

FIGURE 5. The transparency of the fin is demonstrated shortly after capture (specimen B).

FIGURE 7. The mantle cavity opened to reveal the main features.

FIGURE 8. A diagram showing the features of the mantle cavity seen in figure 7.

sept.

n.br.

5 mm

10

ins.
aur.

vent.

ins.
aur.

aur.

dor.
ch.

to
pal.art.

to
aor.a.

1 mm

12

mus.
ob.

mus.
long.

mus.
circ.

200 µm

11

200 µm

16

mus.
circ.

mus.
long.

40 µm

6

FIGURE 6. The mantle wall; transverse section.

FIGURE 10. The arm. A thick section from which the gelatinous layer has been removed.

FIGURE 11. The muscular wall of the arm in transverse section, taken from the inset on figure 10.

FIGURE 12. The heart, longitudinal section (Cajal).

FIGURE 16. Section through testis (*Cirrothauma* A).

FIGURE 17. Arrangement of sperms in sperm packet (*Cirrothauma* A).

FIGURE 18. The male ducts of *Cirrothauma* A.

FIGURE 19. The accessory gland, transverse section of *Cirrothauma* A.

FIGURE 20. Sperm packet in seminal vesicle (*Cirrothauma* A).

FIGURE 23. Oviducal gland showing sperm packet. (Longitudinal section, *Cirrothauma* B.)

FIGURE 24. Oviducal gland showing secretion of outer egg capsule (*Cirrothauma* B).

towards the mouth. The mantle and funnel are rather lighter. Pigmentation on the fins is of the same density as on the mantle but confined to the thickened posterior edge and a thin line round the remainder of the margin. The unpigmented anterior areas of the fins in a fresh specimen are almost perfectly transparent (figure 5, plate 2) and when folded around the body, as would sometimes occur during locomotion (figure 4, plate 2; figure 125; and see p. 19 in Roper & Brundage 1972) the transparent patches would lie directly over the eyes. The tissue overlying and surrounding the eyes is also without pigmentation; in specimen A this clear patch is 25 mm in diameter. Pigmentation is of two types: an outer layer with numerous single granules, beneath which is a layer containing pigment granules in well separated spherical clusters. No chromatophores were seen, and the rhomboid chromatophore described by Chun (1913) on the ventral side of the mantle between the fins could not be found on any of these specimens.

3.3. *Mantle cavity*

The mantle cavity is small and the mantle adductor muscle is very weak, consisting of a narrow membranous strip, 10 mm wide in specimen C, leaving the two sides of the mantle freely confluent posteriorly. The muscles of the mantle wall are in two thin layers separated by a thick gelatinous layer. Each muscle layer is divided into outer longitudinal fibres and inner circular fibres (figure 6, plate 3).

The gills are light brown and situated anteriorly, close to the mantle aperture (figures 7 and 8, plate 2). The number of filaments varies between seven and nine (see table 2) and they are arranged in the standard dibranchiate pattern, rather than the 'half orange' configuration found in some cirrates (Robson 1932b, p. 124).

Opening into the mantle cavity are the kidney ducts, one close to the base of each gill, and the single genital opening, in both sexes, just left of the midline at the base of the funnel, and the anus, inside the funnel. The viscera are covered by a thin layer of transparent tissue through which some of the internal organs are clearly visible; in particular the branchial heart, the gonad and associated glands and kidneys (figure 7, plate 2).

3.4. *Fin support*

The fin support, which is exceptionally large in the finned octopods, has been variously called a dorsal cartilage (Hoyle 1886; Ijima & Ikeda 1895), internal shell (Appellöf 1899), a shell-vestige (Robson 1932b) and gladius (see Donovan 1977). The fin support is used in classification of the Cirromorpha and is depicted in many descriptions.

The fin support is transparent and well developed. The shape in dorsal view resembles that of a butterfly with its wings open (figure 9). The 'wings', which form the attachment points for the fin musculature, are concave and slope downwards at an angle of approximately 45°. They extend mainly anteriorly from the very thick central region, curving outwards more from their inner than their outer edge and consequently tapering towards the tip. Posteriorly the edge of the 'wing' is bluntly rounded and extends only a short distance beyond the central thickening.

The fin supports were removed from all specimens with the exception of E. Although in outline they are similar to one another and considerably different from those of any other known species, they show individual variation, particularly with regard to the detailed shape of the central thickening.

The fin support of *Cirrothauma* is similar to that of *Cirroteuthis*, although the wings of the latter

are rather smaller. This feature separates these two genera from the other cirrates, in which the form of the fin support varies between a narrow horse-shoe shape (*Stauroteuthis*) and a nearly straight rod (*Opisthoteuthis*) (see Robson 1932*b*).
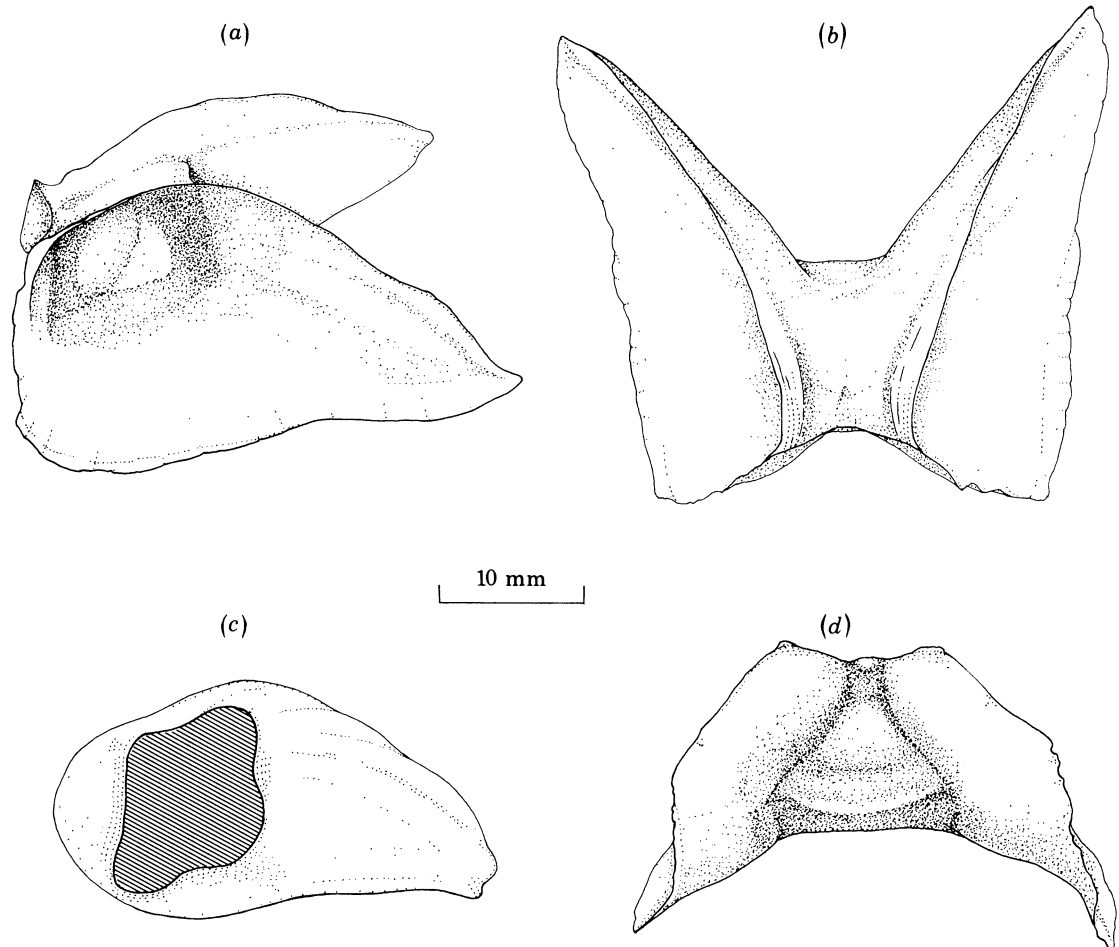
(a)

(b)

10 mm

(c)

(d)

FIGURE 9. Gladius of specimen A in dorsolateral view (a) from the right side; in dorsal view (b); the lateral view of left half cut to show central thickening (c); and posterior view (d).

3.5. Arm musculature

Under the fragile, pigmented skin the gelatinous tissue inside the arms is traversed by a variety of internal muscle bundles and is covered by a tough, multilayered outer wall or muscular sheath. In this description the sucker (oral) surface of the arms will be referred to as inner, and the opposite as outer.

3.5.1. Internal muscles

The arms are oval in cross section and each is divided into two distinct areas by a transverse muscular septum (figure 10, plate 3). On either side of the septum several branching bundles of muscle fibres connect the outer wall to the septum either directly or indirectly via branches to other muscle bundles. Muscles run diagonally inwards from the septum, forming two delicate curtains which cradle the brachial nerve cord and blood vessels by crossing beneath them and joining onto the wall of the oral surface. Also just below the nerve cord and blood

vessels fine muscles run across the arm from side to side strengthening the base of the cradle. All of these muscle bundles pass through the inner layers to connect with the outer layer of the muscular sheath (figure 11, plate 3).

3.5.2. *The outer wall*

Circular muscle fibres are only present laterally, where they form the outer layer of a thickened section, which is the attachment area for the bundles of large muscles running across the arm, below the septum (figure 10, plate 3). *Diagonal muscles* are present all round the arm orientated in two directions at approximately 45° to the arm's longitudinal axis. Above and below they are in a thin outer layer containing mixed fibres running in both directions; laterally they are separated into two thicker layers of unidirectional fibres, one in each direction, situated inside a layer of circular muscle (figure 11, plate 3). *Longitudinal muscle* separates the two unidirectional diagonal layers ventrolaterally but it is concentrated mainly above and below in the areas having the thin outer layer of two-directional diagonal fibres.

Separate muscle bundles run in various diagonal directions from the outside of the inner area and to a lesser extent from the lateral area adjacent to it, to secure and manipulate the sucker stalks.

3.5.3. *Presumed functioning of the arm muscles*

The gelatinous material in the arm constitutes a hydrostatic skeleton upon which the muscles operate. Rigidity is probably achieved by the action of the diagonal fibres, present in varying amounts all round the arm, the contraction of which will increase pressure on the jelly but have least effect on the arm's shape.

The transverse septum and the transverse bundles of fibres ventral to it form the most fully developed muscle group in the arm. These effectively divide the arm into two partially independent, flexible tapering tubes filled with gelatinous material. This division of the arm into two compartments will perhaps give a greater control over movement than would be possible if the arms were not divided in this way. The concentration of longitudinal muscles above and below indicates that the main arm movement is mainly in the oral–aboral plane. This would be important in extending and curving the arms to adopt the umbrella-like drifting position (figure 4, plate 2), in bringing the arms together at the onset of fin-swimming and possibly for medusoid-like pulsing movement, and in the capture of prey.

3.6. *Vascular system*

The blood vessels of some other cirrate octopods have been thoroughly described elsewhere (Ebersbach 1915; Meyer 1906a). Consequently, this description will be concentrated mainly on the most striking feature, the heart. It lies posteriorly in the visceral mass and is unusual in having two muscular chambers joined by a short narrow tube (figure 12, plate 3; figure 13). The first or ventral chamber is small and has a rounded, but somewhat triangular shape. Running into it are two auricles, essentially the very dilated, thin-walled basal portions of the long efferent branchial vessels. Arising from the ventral chamber is the single gonadial artery and two smaller vessels to the mantle organs. The dorsal chamber is crescent-shaped and gives rise, on the left side, to the two large pallial arteries, while on the right it narrows to become the anterior aorta. The vessel connecting the two chambers lies slightly to the right of the midline.

Examination of a variety of cirrates, kindly provided by Dr G. L. Voss, has shown the heart

of *Cirrothauma* to be similar to that of *Cirroteuthis* and has also allowed some speculation concerning this curious arrangement. The suggested line of development of the heart is not proposed as a guide to the phylogenetic development of the various species within the cirrate octopods, but merely considers *Cirrothauma* and *Eledone* to demonstrate two extreme conditions and shows other cirrates to form intermediate stages (figure 13).
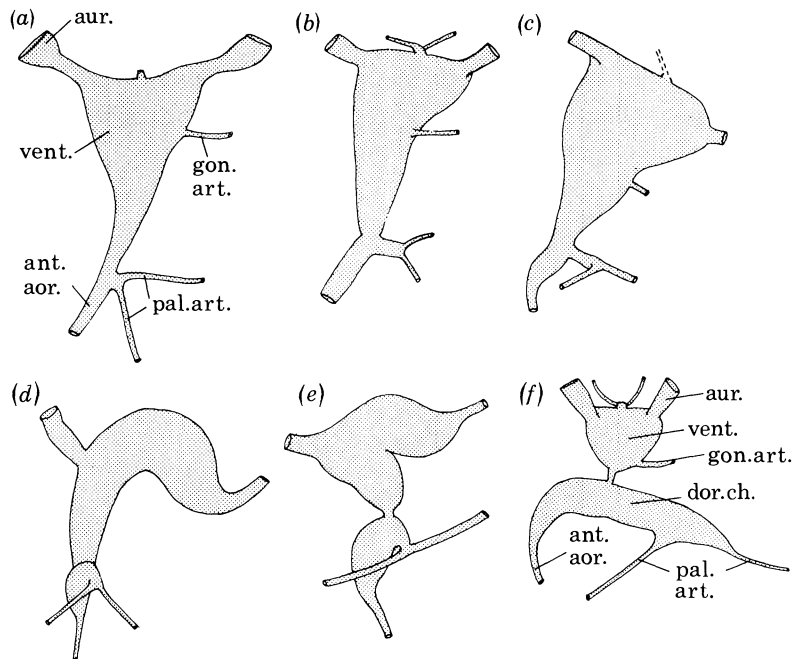

FIGURE 13. The hearts of cirrate octopods, shown in diagram. (*a*) *Grimpoteuthis glacialis*, (*b*) *Stauroteuthis* sp., (*c*) nov. sp., (*d*) *Opisthoteuthis agassizii*, (*e*) *O. californiana*, (*f*) *Cirrothauma murrayi*.

The ventral chamber appears to be equivalent to the ventricle in other octopods and undergoes little modification. The connecting vessel seems to be analogous with the proximal portion of the anterior aorta in octopodids such as *Eledone* (see Isgrove 1909) since it leaves the ventricle in the same relative position. The dorsal chamber appears to have been developed from a swollen part of the aorta together with the basal portion of the pallial arteries.

The simplest condition found within the Cirromorpha examined is that in *Grimpoteuthis glacialis*, Robson, 1930 which is very similar to the typical octopodid. There is no dorsal chamber, the triangular heart giving rise to a thick-walled aorta from which the pallial arteries have a common origin (figure 13). In a specimen of *Stauroteuthis* Verrill, 1879 the pallial arteries leave the aorta as a single vessel which later divides. This large artery joins with the aorta, forming a curved trunk, giving rise to the pallial arteries at one end and to the anterior aorta at the other. There is a slight constriction at the junction between the ventricle and the common trunk (figure 13*b*). An undescribed specimen (no. W.H. 97.11.76, University of Miami Collection) shows a condition similar to *Stauroteuthis*, but there is a slight swelling on the aorta close to its connection with the ventricle (figure 13*c*). This swelling of the aorta and combined pallial arteries is further developed in *Opisthoteuthis* to form a distinct curved chamber, with considerably more constriction at its junction with the ventricle. Of the three species of *Opisthoteuthis* studied, the dorsal chamber is most developed in *O. californiana* Berry, 1949 (figure 13*e*)

and although present in *O. depressa* (Meyer 1906*a*) and *O. agassizii* Verrill, 1883 (figure 13*d*), it is considerably smaller. From the condition found in *O. californiana* Berry, 1949 only a relatively small modification is required to achieve the type of heart found in *Cirrothauma* and *Cirroteuthis* (figure 13*f*).

The anterior aorta is also unusual in that it is much longer than appears necessary, forming several large curves across the dorsal side of the stomach and oesophagus (figure 14).
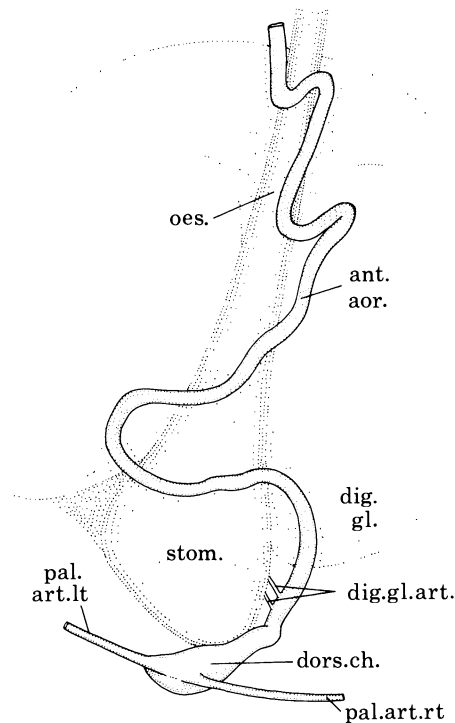

FIGURE 14. Dorsal aorta overlying the alimentary canal (*Cirrothauma* A).

One of the curious features of *Cirrothauma* is the addition of this extra chamber to the heart. Relative to the overall size of *Cirrothauma* the heart is rather small, and to deliver sufficient blood to some areas it may be necessary to have a method of improving the blood flow. The large fins, which are important organs of active locomotion, are supplied by the pallial arteries, substantial vessels leading directly from one end of the dorsal chamber. The other end of this crescent-shaped organ gives rise to the dorsal aorta which carries blood forward to the head and arms. The arms of *Cirrothauma* are particularly long and the musculature used to control them probably also requires a considerable blood supply. *Grimpoteuthis*, in which the heart is similar to the normal octopod type, is devoid of a dorsal chamber, and does not have the long arms or large fins of *Cirrothauma*.

3.7. *Reproduction*

3.7.1. *Male reproductive organs*

The oval testis is situated posteriorly in the mantle and in specimen A is 18 mm long. On its ventral side ridges radiate from a small central circular area (figure 15) and it is enclosed in a thin-walled sac. Sections through the testis of specimen A show it, by the presence of spermatozoa, to be mature (figure 16, plate 3).

The gonadial sac narrows anteriorly into the thin-walled, straight vas deferens which widens abruptly into a series of reflexed tubes, referred to by Ebersbach (1915) as seminal vesicles. The proximal section of the 'seminal vesicles' is thick-walled and highly folded internally (figure 18, plate 4). The duct turns sharply through 180° and for a short distance narrows. As it widens again the wall becomes very thin and through it numerous small structures are clearly visible (figure 19, plate 4). These prove to be packets of sperms. The seminal vesicle turns back again through 180° and gradually narrows, turning finally 90° and through a mass of accessory glands
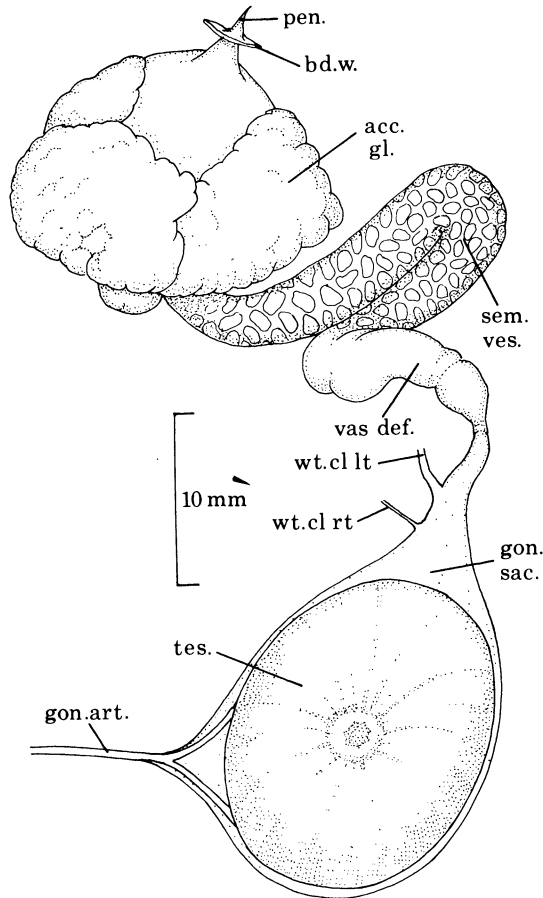
FIGURE 15. Male reproductive system (*Cirrothauma* A).

(figure 19, plate 4), where it expands slightly and curves into the small 'penis'. The part of the duct inside the accessory gland is also filled with sperm packets bound together by a transparent jelly. On the dorsal side of the accessory gland is a thin walled diverticulum, also containing sperm packets, less densely packed.

Sections through the seminal vesicles show the 'sperm packets' to be aggregations of spermatozoa with the heads arranged at the periphery and the tails towards the centre (figures 17 and 20, plate 4). *Opisthoteuthis depressa* has a similar arrangement with a reservoir of spermatozoa (Meyer 1906b). These structures are not present in the proximal section of the seminal vesicles. The small size and structural simplicity of the sperm packets explains the uncomplicated nature of the male reproductive tract of *Cirrothauma*. In *Octopus* it is of necessity more complex in order

to manufacture, manoeuvre and store their much larger and more intricate spermatophores (Mann *et al.* 1970).

Specimen E, with a mantle length of 21 mm, is obviously immature, but it can be seen to be male by the characteristic accessory glands visible through the ventral mantle wall.

3.7.2. *Female reproductive organs*

The mature eggs of cirrates are very large (Reinhardt & Prosch 1846; Verrill 1885; Meyer 1906a; Robson 1932b; Boletzky 1978, 1982). The ovaries in both female specimens (B and C) are packed with eggs of various sizes. Specimen B has approximately 200 eggs, the largest being 9 mm long (figure 21). The ovary is thin-walled and situated posteriorly in the mantle, below

5 mm

FIGURE 21. Egg mass from ovary of *Cirrothauma* B.

the gladius. Anteriorly it narrows, giving rise to the single, thin-walled oviduct (the right one being absent in cirrates). After a short distance the oviduct turns sharply through 180°, looping from dorsal to ventral around the kidney and efferent branchial vein (figure 22). After an almost straight section the oviduct turns once more through 180° and opens into the oviducal gland. The oviducal gland can be clearly divided into two sections by colour. Both are externally striated; the proximal, which is off white, is more coarsely striated than the distal, which is larger in diameter and pale brown. The oviduct narrows again and passes through the mantle wall, where it has a free length of approximately 20 mm, and opens into the mantle cavity.

Sections through the oviducal gland (specimen B) show both the distal and proximal sections to be highly folded internally. The proximal part of the gland functions as a spermatheca and contains numerous 'sperm packets' similar to those in the seminal vesicles (figure 23, plate 4). The oviducal gland also secretes a substance that forms the outer coating of the egg case as it passes through the central cavity (figure 24, plate 4) (see Boletzky 1978).
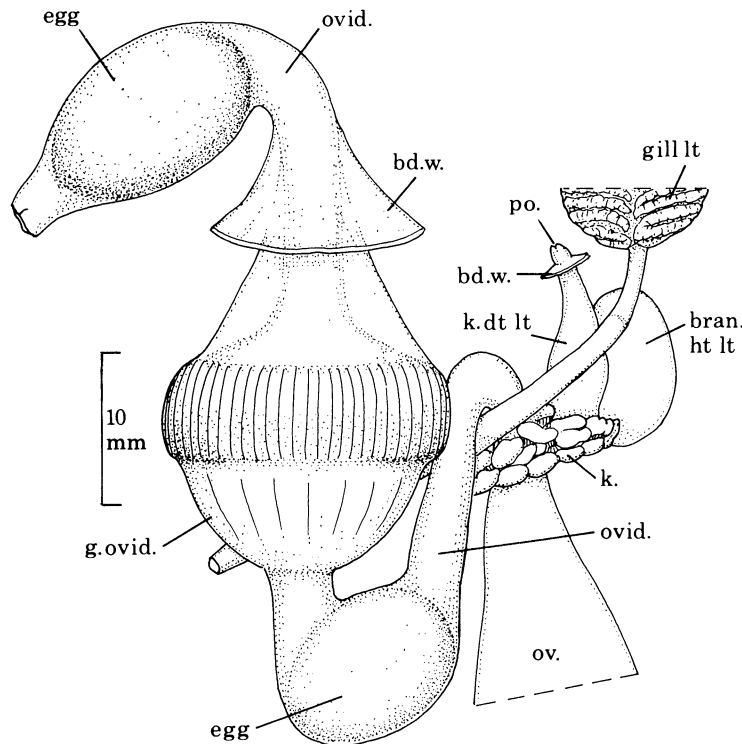
FIGURE 22. Female reproductive system (*Cirrothauma* B).

Two large oval eggs are present in the oviducts of B and C. In C they measure 14.0 mm × 8.9 mm and lie one behind the other just proximal to the oviducal gland. Specimen B has an egg either side of the gland (figure 22), the proximal one measuring 11.3 mm × 8.2 mm. The egg distal to the gland is 13.8 mm × 8.4 mm and has an additional tough, brown outer coating with the rudiments of a stalk on one end.

The large size range of eggs within the ovary (figure 21) and the relatively small number close to the maximum size indicates that the eggs only mature in small numbers or singly and egg laying could therefore be a continuous process once maturity is attained.

The presence of 'sperm packets' in the oviducal gland clearly demonstrates that fertilization is internal, but as there is no hectocotylus here or in *Opisthoteuthis depressa* Ijima and Ikeda, 1895 or other cirrates (see G. L. Voss in Voss & Voss 1983) the method of copulation remains a mystery. A possibility is that the 'sperm packets' are placed in the female mantle by the long thin funnel of the male.

3.8. *The coelom*

The coelom in cirrates like that of other octopods is limited to three cavities, those of the gonad and two branchial heart appendages. These are linked by water canals (aquiferous ducts),

which in *Cirrothauma* leave the gonadial sac where it narrows. In the male the left canal is short and stout whereas the right is long and thin. The female shows the same discrepancy in length, but the left canal is considerably thinner than its male counterpart. This is a condition similar to that found in *Eledone* (Isgrove 1909), while other cirrates show varying degrees of reduction. In *Grimpoteuthis umbellata* and *Opisthoteuthis*, for instance, the right duct has atrophied, so that it no longer communicates with the gonad (Robson 1932*b*, p. 126), while in *G. albatrossi* it is absent altogether (Sasaki 1920). *Chunioteuthis ebersbachii* shows a condition that Robson refers to as 'typical', presumably of the Octopodidae, and it will therefore be similar to *Cirrothauma*.

3.9. *The alimentary system*

The alimentary system is in the form of a short single loop, fitting closely around the digestive gland. The complete system was dissected out from specimen F and it is to this specimen that the general description applies (figure 25). The buccal mass is described later (p. 26).
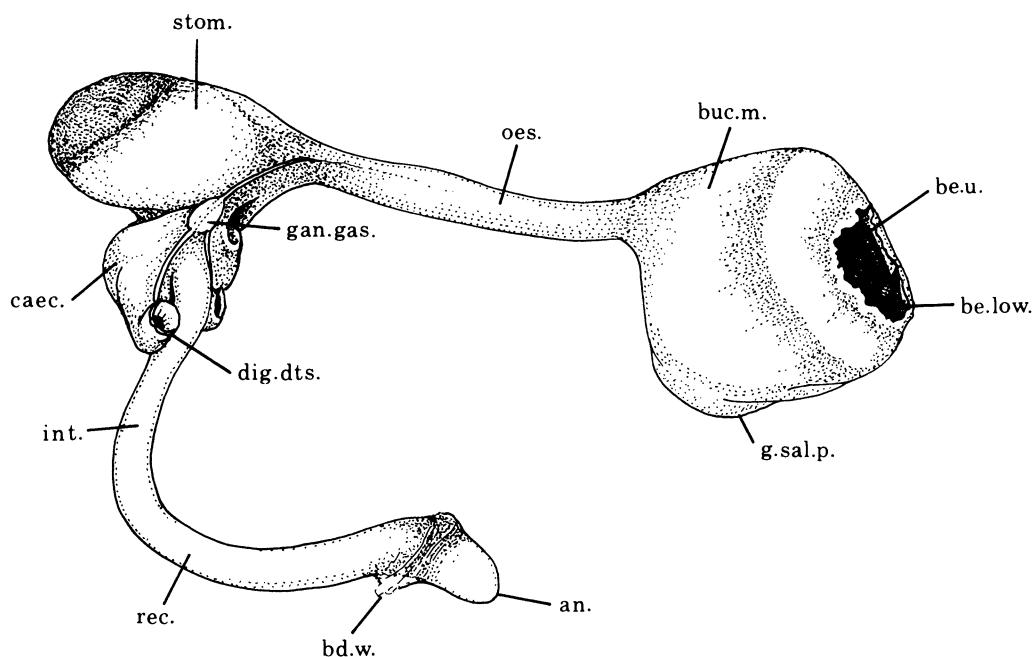
FIGURE 25. Alimentary canal (*Cirrothauma* F).

The oesophagus leaves the buccal mass dorsoposteriorly. It is initially 4 mm in diameter, widening to a maximum of 7 mm about half way along its length. The oesophagus wall is muscular and is highly folded into internal longitudinal ridges which have a thick cuticle. The slight swelling at the point of maximum diameter does not appear to be homologous with the crop, an organ absent or greatly reduced in all known cirrates, as there is no indication of a diverticulum.

The stomach is oval and lies on the digestive gland dorsoposteriorly, in a deep groove, displaced slightly to the right. It is 25 mm long and laterally the walls are very muscular attaining a maximum thickness of 8 mm. The stomach is lined with a thick cuticle and the cavity is laterally compressed, resulting in the dorsal and ventral walls being quite thin.

The caecum, into which the stomach leads via a narrow duct, is smaller and less muscular than the stomach and is not formed into a spiral as in the Octopodidae. It fits closely into the

bottom of the groove in the digestive gland (Bidder 1976), attached to it by the short, wide digestive ducts. The inner wall of the caecum is thrown into numerous folds. The gastric ganglion is attached to the right side of the caecum at the point where the duct joins it to the stomach.

The intestine is initially 5.5 mm in diameter, narrowing, after a distance of 12 mm, to 4 mm. The section of larger diameter is considered in some species, where the dilation is more pronounced, to be a 'third stomach' (Robson 1932b). The intestine is quite short and the rectum is not differentiated externally, the diameter remaining more or less constant to the anus. The rectum protrudes 8 mm from the body wall into the base of the funnel. The inner wall of the intestine and rectum are folded into longitudinal ridges. There are no anal valves or ink sac.

The oesophagus and dorsal side of the stomach are deeply pigmented, with a purple colour in preserved tissue, probably deep brick red in life, like the pigmentation of the skin (p. 10). The ventral side of the stomach, the caecum and a small area of the rectum where it passes through the body wall are lightly coloured and most of the intestine and the distal end of the rectum are devoid of pigmentation. The pigmentation presumably acts at certain depths to prevent light from luminous prey attracting the attention of other predators to the cirrate. The large epistellar body may have a similar function (p. 41).

No food fragments were found in any of the guts examined.

4. THE BABY CIRRATE

The young cirrate is a miniature adult (figure 3). It is largely translucent, even after fixation, except for the buccal mass, the pigmented oesophagus, the dense reddish branchial hearts which are somewhat like eye-spots, the eyes and the dense musculature of the base of the fins. There does not appear to be any reflective tissue such as is found in some other transparent cephalopods.

TABLE 3. THE NUMBER OF SUCKERS ON THE ARMS OF THE BABY CIRRATE

baby cirrate (E)	number of suckers	notes
left arm		
I	24	many lost
II	22	many lost
III	22	many lost
IV	10	many lost
right arm		
I	35	incomplete
II	27	some remained at tip but many lost
III	19	many lost
IV	14	many lost

The fins are relatively enormous (table 2) extending forwards beyond the buccal region (figure 3). The fin has a dense almost rectangular muscle at its base which occupies almost half its length, the distal part being quite transparent.

The arms are slender and delicate. They were damaged during capture especially at the tips, and in consequence we cannot be certain how many suckers and cirri were present (table 3). Suckers are present at the tip of one arm and so it is likely that they extend the full length of

each arm. The sucker peduncle is conical in form, about 800 μm in height, capped by a domed disc about 300 μm in diameter, only some of which have a small central orifice.

The cirri are especially well seen in this young cirrate (figure 3 and figure 26, plate 5). They are short until after the ninth sucker, when their length increases up to 10 mm, and they are of this length almost to the tip of the arm.

5. THE SUCKERS AND CIRRI

5.1. *The suckers*

The strange suckers of *Cirrothauma* were the unique feature that prompted Chun (1913) to found a new genus: he described them as 'minute suckers poised on long spindle-shaped and clumsy stalks of gelatinous substance.' He saw what he thought might be light organs in the base of the stalk of the suckers, each a 'whitish structure . . . to consist of a shell, . . . the aperture of the shell is filled by a ball-shaped cellular body which does not touch the edge of the shell. The latter is thickened towards the point, . . . and reminds one of the reflectors occurring in the light organs of many Oegopsidae.' The sucker peduncles are longest in the middle region of the arms and towards the tips and the buccal region they 'gradually assume the form of clumsy conical lumps' (Chun 1913). He also noted 'that the stalked suckers are evidently devoid of the sucking pit'. Indeed many are without an opening and those with an orifice have no suction chamber beneath it. Although so unusual they are indeed suckers since the infundibular cuticle is typical of that found in octopods (Nixon & Dilly 1977; Aldred *et al.* 1978). Their functioning is discussed on page 45.

Each arm bears a single longitudinal row of suckers alternating with paired cirri for most of its length (figure 27, plate 5). The number and size of the suckers and cirri are given in table 4. The small suckers are unlike those of most octopods; they are borne on conspicuous, large, stout peduncles, the first six or so being firm, round and plump with little space between them. The remaining ones have a longer peduncle which is soft and whose shape is easily altered. A small orifice, 1.9–3.1 mm in diameter, is present in the infundibulum of the first six or seven suckers but there is no suction chamber below. There is no orifice in the other suckers and the infundibulum resembles a small rounded cap. In some of the larger suckers the infundibulum becomes folded across its width. We cannot be certain if this occurs in life or whether it is an artefact of fixation. The narrow rim surrounding the infundibulum (figure 27, plate 5, and figure 28) is much folded and has a cubical epithelium.

The infundibulum of every sucker is small (table 4). The cuticular surface of the infundibulum has small, rounded pegs, each about 2 μm in diameter (figures 29 and 30, plate 5). These pegs are formed by aggregations of minute rods arranged so that there are spaces or pores, 0.1 μm in diameter, in the cuticle. This system of tiny pores may allow adhesion to a foreign surface followed by suction by capillarity. This mechanism has been postulated for the attachment of octopod suckers to a foreign surface (Nixon & Dilley 1977). The pores on the infundibular cuticle are closely similar in size to those of the sucker of *Octopus vulgaris*. However, the small infundibulum of *Cirrothauma* has few pegs and hence few pores when compared with the number present on the same area of infundibular cuticle of the shallow-living *Octopus vulgaris*. (see p. 45).

The peduncle is very large in relation to the sucker on its apex (figure 27, plate 5) and is formed mainly of connective tissue (figure 28 and figure 31, plate 5). There is a large inner core and a narrow outer layer of tissue with an amorphous matrix containing very fine fibrils.

Between there is a narrow cylinder of acid mucopolysaccharide-containing tissue, staining intensely with Alcian blue and consisting mostly of a dense mass of very fine branching fibrils (figure 32, plate 5). This tissue is not readily seen after any of the other stains used although it can be recognized by the nuclei along its limiting membrane.

TABLE 4. THE DIAMETER OF THE SUCKER INFUNDIBULA AND THE LENGTH OF THE CIRRI
OF TWO ANIMALS

	specimen A			specimen D		
sucker number	sucker infundibulum diameter mm	distance between suckers mm	length of cirrus mm	sucker infundibulum diameter mm	distance between suckers mm	length of cirrus mm
1	2.5	11.5	—	1.6	3.9	—
2	2.7	13.4	0.9	2.6	6.3	—
3	2.9	13.1	0.6	2.9	7.4	0.8
4	2.9	13.8	0.5	3.1	8.4	1.6
5	2.9	11.6	5.1	3.1	9.2	2.8
6	—	16.9	10.6	3.0	10.5	5.1
7	3.7	17.6	20.3	3.0	12.0	5.7
8	3.6	16.1	23.2	2.1	11.5	10.6
9	3.8	17.8	28.7	1.2	9.3	15.5
10	3.6	15.2	36	1.3	8.1	16.1
11	4.0	13.9	37	1.1	11.5	18.4
12	3.7	14.0	37	1.0	9.6	14.9
13	3.7	14.4	37	1.1	9.2	13.0
14	3.8	14.7	27	1.0	9.2	15.4
15	3.7	14.4	30	1.1	8.8	16.6
16	3.7	14.4	D	1.0	8.8	18.3
17	3.4	12.7	D	0.9	8.0	14.4
18	2.8	12.3	D	0.9	8.7	20.6
19	2.9	14.4	D	0.8	8.2	19.4
20	2.9	11.0	D	0.9	8.1	17.7
21	2.9	12.5	D	0.9	8.4	16.1
22	D	11.5	D	0.9	8.1	14.4
23	2.6	10.8	D	0.9	—	18.3
24	2.4	9.6	D	0.9	—	16.6
25	2.4	9.1	D	0.8	—	19.4
26	2.4	9.3	D	0.8	—	14.7
27	1.3	10.1	D	0.8	—	16.9
28	D	10.1	D	0.8	—	·13.9
29	1.4	10.6	D	0.8	—	—
30	1.3	10.8	D	0.8	—	—
31	D	10.0	D	0.9	—	—
32	1.1	9.3	D	—	—	—
33	0.9	8.5	D	—	—	—
34	D	6.6	D	—	—	—
35	D	4.2	D	—	—	—
36	D	—	—	—	—	—

D, damaged sucker.

A narrow band of circular muscle lies at the periphery of the inner core inside which are many small bundles of longitudinal muscle fibres. Within these layers of muscle fibres there are ten or more small, isolated, bundles of nerve fibres (Holmes's stain), arranged peripherally around the inner core. These bundles run the length of the peduncle to just below the sucker rim where each bundle bifurcates shortly before entering the radial muscles of the sucker. Here

the nerve fibres make an acute turn towards the periphery (figure **33**, plate **5**). The bundles divide and then emerge through a narrow band of circular muscles just below the rim of the sucker. Some of these bundles divide again in the rim but it has not been possible to trace their path further; presumably they are afferents.
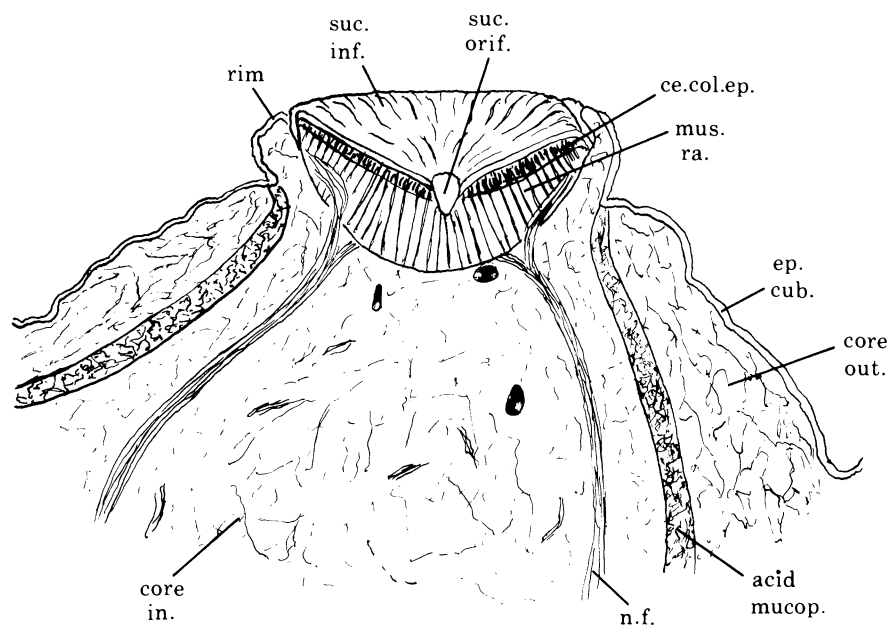
FIGURE 28. Drawing from a sagittal section of peduncle, and sucker with a small orifice.

5.2. *Possible light organs*

In the peduncle of each sucker, close to its junction with the arm, Chun described a possible photophore; he gave no illustration (Aldred *et al.* 1982) (figures **34***a* and **34***b*, plate **6**). Sections show that it consists of a bell-shaped shell in whose cavity lies possible luminous tissue (figure **34***c*, plate **6**). The shell is of collagen (stained green with Masson's technique). Transverse to the sucker axis strands of collagen radiate from the shell to hold the organ in place at the centre of the peduncle (figure **35***a*, plate **6**). Strands of another type are also attached. They stain red with Masson's stain and carry granules and nuclei along their length. They run straight or curved courses and may branch (figure **35***b*, plate **6**). The organ also receives many small arteries round its perimeter.

Inside the collagen shell is a layer of amoebocytes, each filled with granules stained an intense orange. The centre of the organ is filled with large cells, which may be photocytes, supported in a fine collagenous framework. Each cell has a large nucleus, acidic and basic nucleoli, and reticulated granular cytoplasm. There are also a few larger orange-stained inclusions (figure **36**, plate **6**).

Passing towards the base of the peduncle the photocytes form a ring surrounding a mass of tissue here labelled a lens but possibly photogenic. It contains a web of fine connective tissue, with many nuclei, enclosing in its meshes spheres of material stained pale grey-green with Masson's technique (figure **37**, plate **6**). At the base this mass is interspersed by a dense network of fine vessels entering from below and at the sides (figure **38**, plate **6**).

Below the level of the collagenous shell there is another ring of large cells, each isolated in its

own collagen sheath with a capillary (figure 39, plate 6). The cytoplasm of these cells is vacuo-
lated and they are accompanied by amoebocytes. Possibly they are degenerating photocytes.

Outside the bell is a thin strand of cells containing granules of pigment, but this does not
make the organ show up readily within the sucker.

5.3. The cirri

Cirri are present on the arms of the finned octopods and *Vampyroteuthis*. Photographs of finned
octopods in the sea show the cirri held outwards away from the arms, an ideal position to collect
information from the surroundings, when the animal is in the medusoid form. Meyer (1906a)
described the cirri of *Opisthoteuthis*. In *Vampyroteuthis* they carry abundant secretory as well as a
few 'olfactory-like' cells (R. E. Young, personal communication) and scanning electron
micrographs show cilia (Nixon & Dilly 1977).

Each cirrus is formed of an inner core of reticular tissue divided by septa (figures 40 and 41,
plate 7). This acid mucopolysaccharide-containing tissue (figure 42, plate 7) (staining brilliant
turquoise with Alcian blue) is divided into several compartments by transverse septa (figure 41,
plate 7). Each compartment is surrounded by a membranous sheath containing collagen (green
in Masson's stain). Surrounding the inner core is dense connective tissue with numerous blood
vessels (figures 41 and 42, plate 7) running from the tip to the base where they come together
to run into the arm. A few blood vessels also run the length of the cirrus through the inner core

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DESCRIPTION OF PLATE 5

FIGURE 26. The arms of the baby cirrate (E) to show the very long cirri.

FIGURE 27. A sucker, with a small orifice at the apex of its peduncle, and a pair of cirri.

FIGURE 29. Scanning electron micrograph of the cuticle of the infundibulum. (Field width 16 μm.)

FIGURE 30. Sagittal section through a sucker showing the new infundibular cuticle and, above, the old and almost
    detached cuticle, the sucker disc (Masson).

FIGURE 31. Sagittal section to show the domed disc of a sucker without an orifice. At the base of the peduncle is
    the bell-shaped organ shown in detail in figures 34–39.

FIGURE 32. Sagittal section through peduncle to show the vacuolated epithelium and the acid mucopolysaccharide-
    containing tissue stained brilliant turquoise with Alcian blue.

FIGURE 33. The bifurcation of a bundle of nerve fibres just before entering the radial muscles of the sucker.
    (Sagittal section, haematoxylin and eosin.)

DESCRIPTION OF PLATE 6

FIGURE 34a. The bell-shaped organ exposed at the base of the sucker peduncle (*Cirrothauma* A).

FIGURE 34b. The main features of the organ at higher magnification. Not stained.

FIGURE 34c. The organ in longitudinal section to show the collagenous shell stained green with Masson.

FIGURE 35a. The shell held in position in the peduncle by strands of collagen radiating from it (transverse section,
    Masson). Large cells at the centre.

FIGURE 35b. Other strands attached to the shell, which stain red with Masson and carry granules and nuclei
    along their length (transverse section).

FIGURE 36. At the centre of the organ are large cells, the presumed photocytes (transverse section, Masson).

FIGURE 37. Nearer the base of the peduncle a ring of large cells surround tissue presumed to act as a lens (trans-
    verse section, Masson).

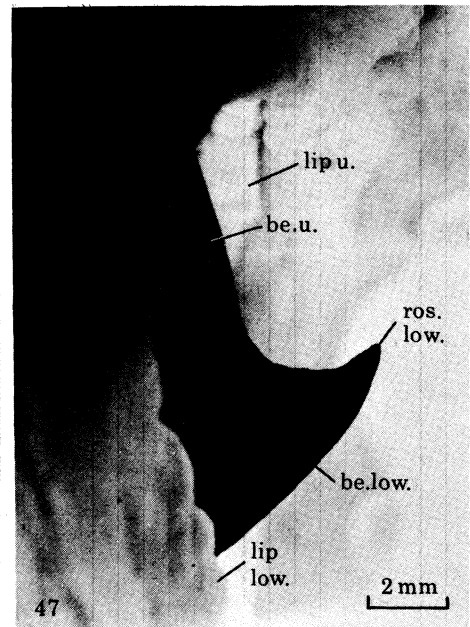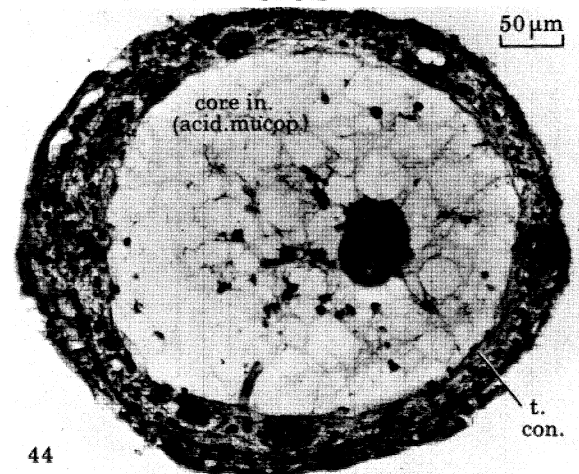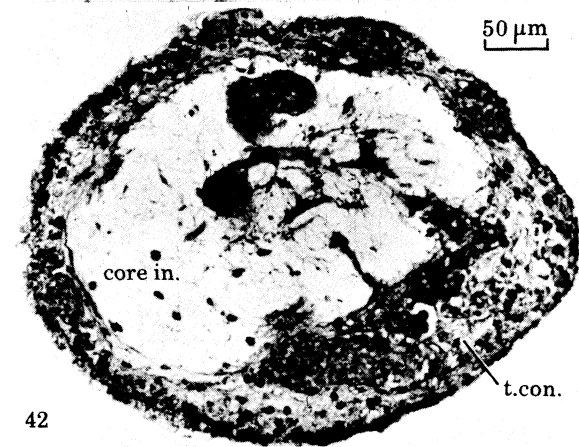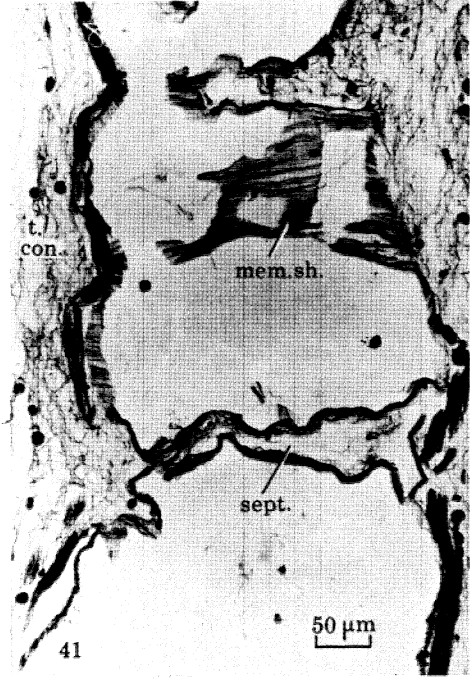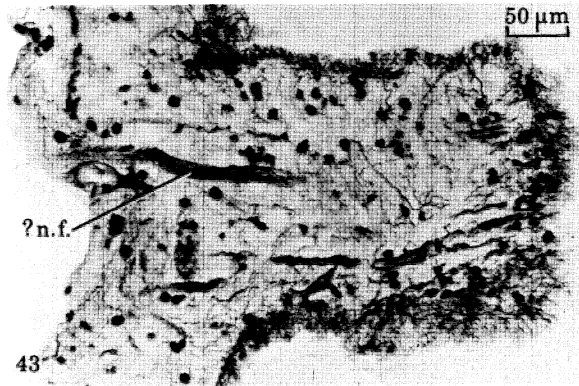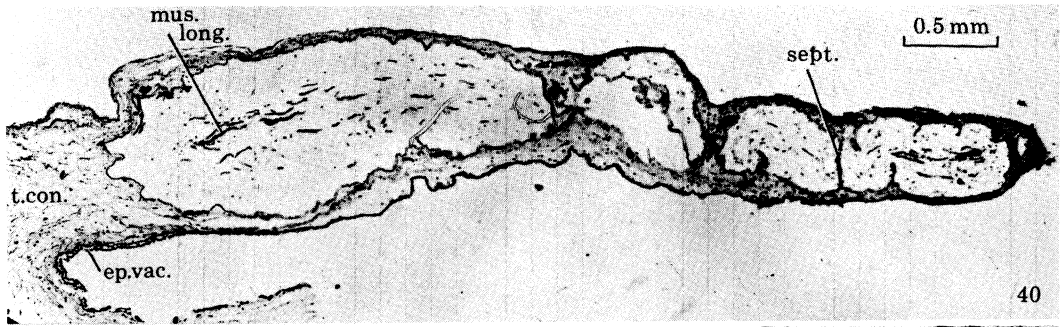FIGURE 38. The lens-like tissue (transverse section, Masson).

FIGURE 39. An outer ring of large cells, each in a collagen sheath with a capillary, lies below the lens (transverse
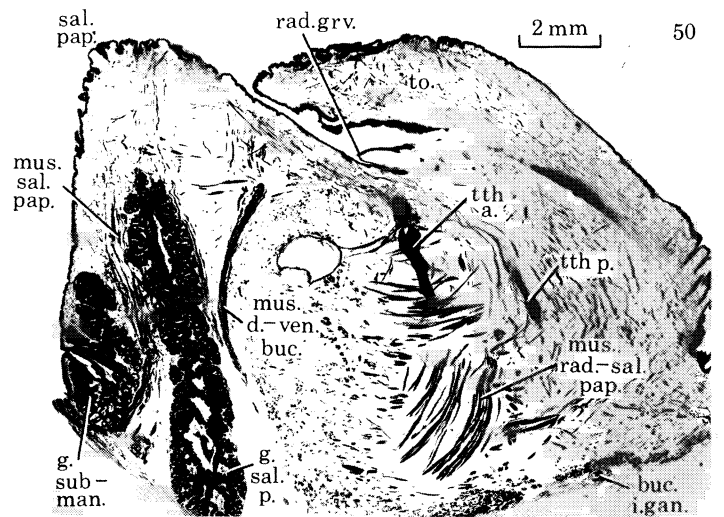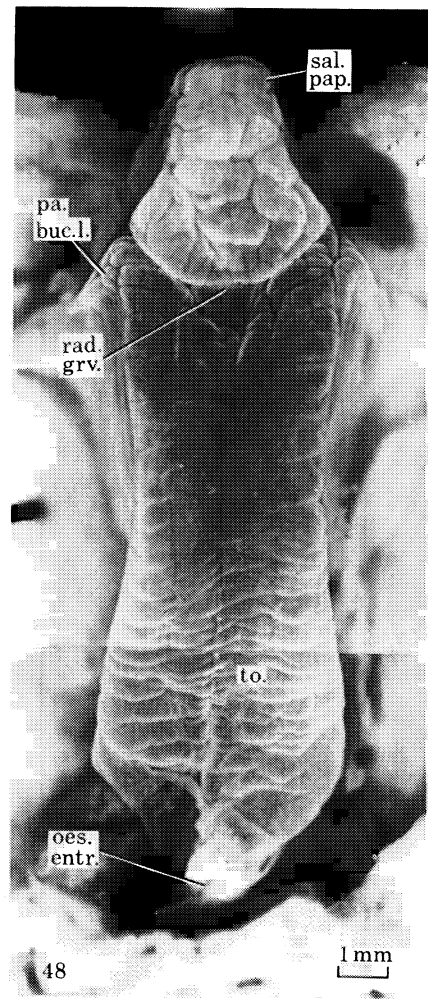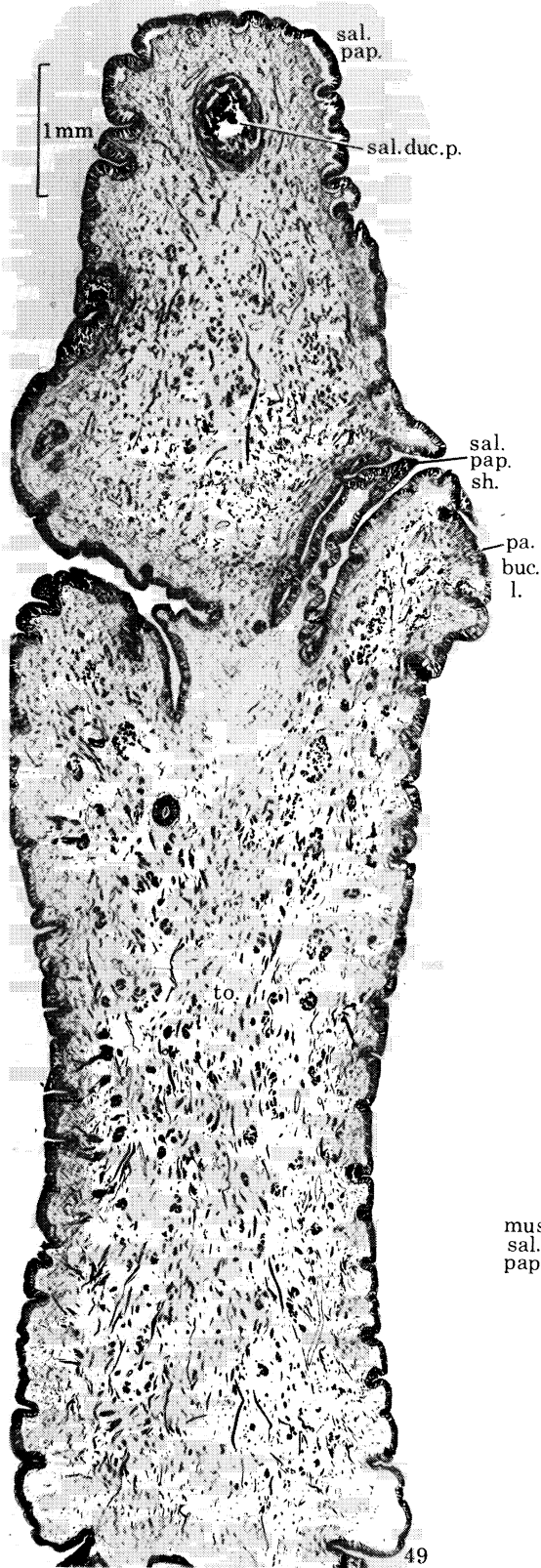   section, Masson).
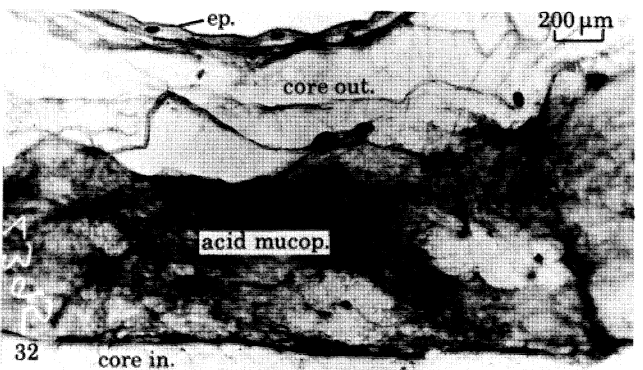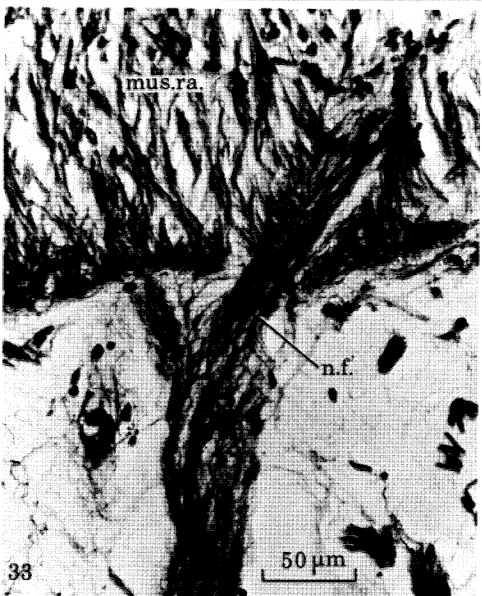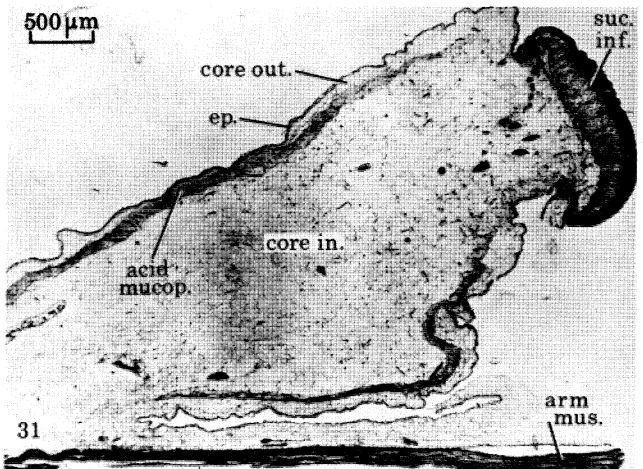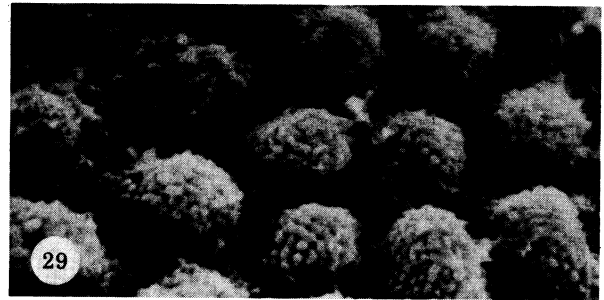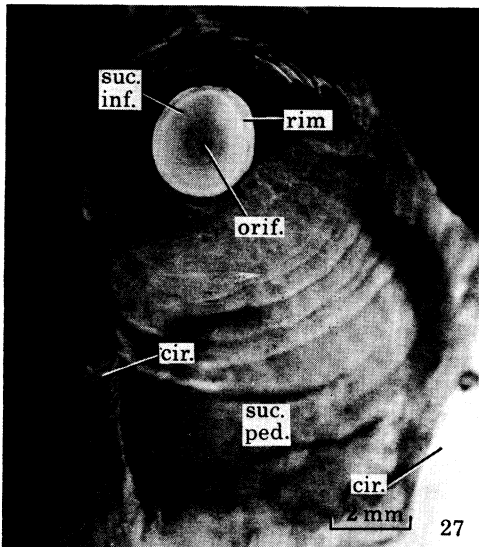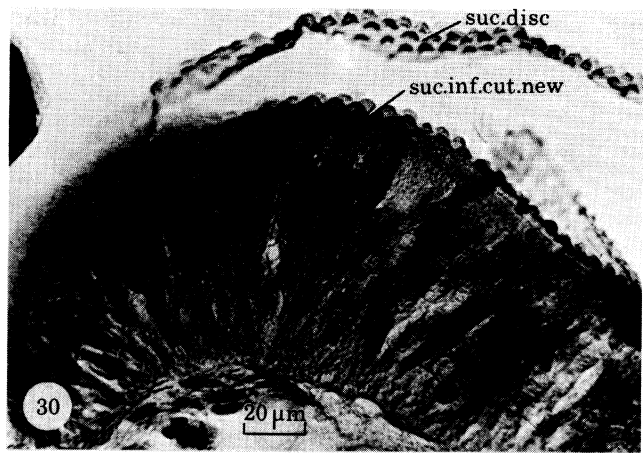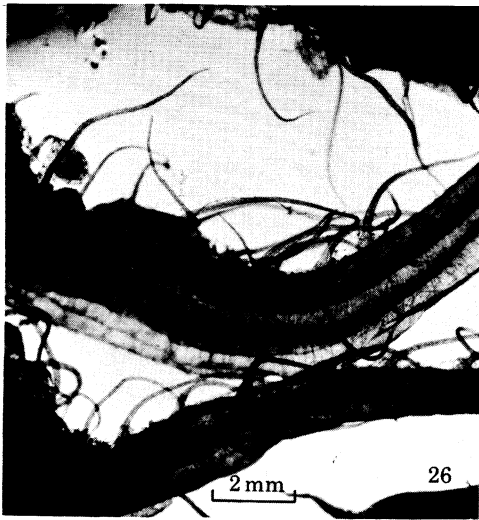
FIGURES 26, 27 AND 29–33. For description see opposite.
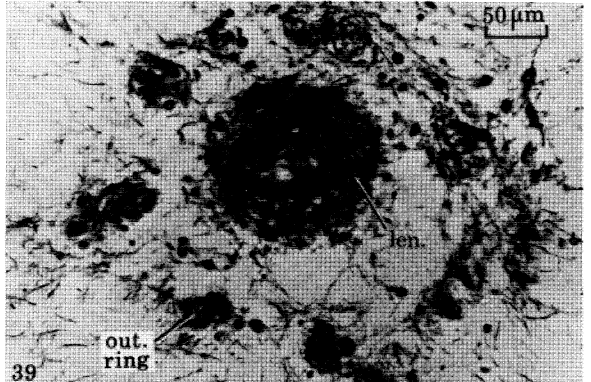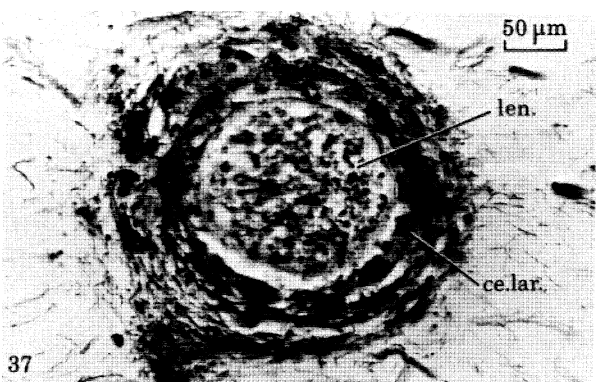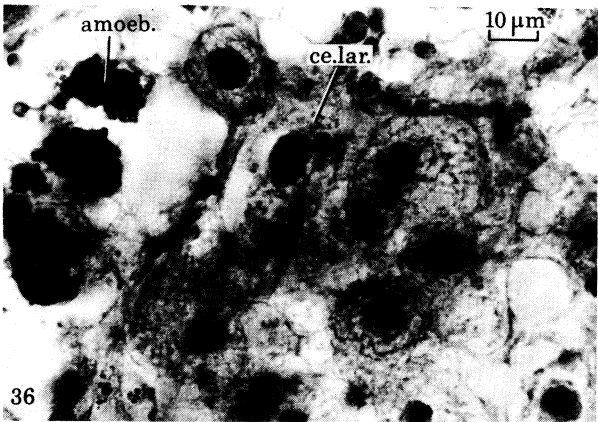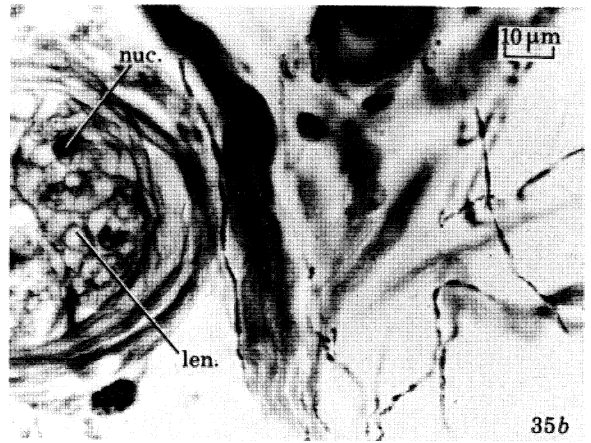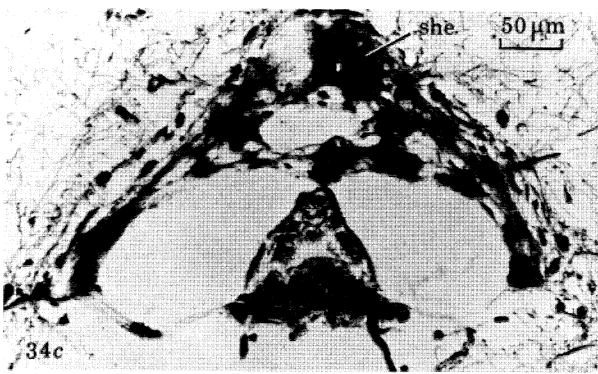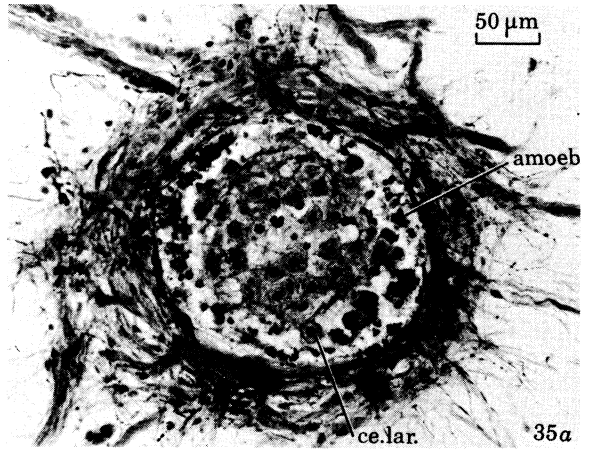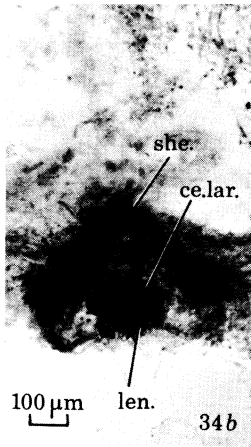
FIGURES 34–39. For description see p. 24.

FIGURES 40–44 AND 47. For description see p. 25.

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FIGURES 48–50. For description see opposite.

and the dividing septa (figure 42, plate 7). The blood vessels contain numerous amoebocytes (figure 41, plate 7).

Small bundles of nerve fibres were found near the base of the cirrus (figure 43, plate 7) (Holmes's stain) but it was not possible to trace these to their termination. The cirri would provide an extensive surface for receiving stimuli from potential prey: the longest cirri are 6 and 37 mm on animals of mantle length 21 and 155 mm respectively, forming a total length of 1300 mm in the smaller animal and 4400 mm in the larger one, even after fixation.

The core of reticular tissue is not distorted even after being brought up from great depths, followed by fixation and histological procedures. This acid mucopolysaccharide-containing tissue, its form so reminiscent of plant tissue, may provide a 'hydrostatic skeleton' (Chapman 1958) (figure 43, plate 7) to support the cirri when held outwards and away from the arms as in figure 4, plate 2 (Roper & Brundage 1972). The cirri are supplied by large blood vessels (figure 44, plate 7) while the surrounding collagenous membrane has associated small, flat bands of muscles. This arrangement is similar to that found in other soft-bodied invertebrates with a 'hydrostatic skeleton' (see Elder 1980).

6. The buccal mass, tongue and salivary glands

6.1. *The buccal mass*

The buccal mass is closely connected with the surrounding tissue, probably with little mobility when compared with some other cephalopods in which it lies in a sinus. In *Loligo* it is capable of rotation while feeding (Bidder 1950). The buccal mass contains large beaks encased by the thick muscles that move them, while anteriorly the lips surround the rostral regions of the upper and lower beaks (figure 45). Prey is received into the buccal cavity whose floor, formed by the salivary papilla in front and the tongue behind, leads to the oesophagus (figure 46). Minute toothed structures, possibly radulae, lie in an invagination between the salivary papilla and the tongue. The buccal mass also contains three sets of salivary glands.

DESCRIPTION OF PLATE 7

FIGURE 40. Sagittal section through a cirrus showing its division into compartments by septa. (Masson.)

FIGURE 41. Part of the same section as figure 40 at higher magnification. (Masson.)

FIGURE 42. Transverse section to show the large inner core of reticulate tissue, barely stained with Masson, and the outer one of connective tissue. Compare with figure 44.

FIGURE 43. Sagittal section at side of cirrus at its base, showing small bundles of nerve fibres. A fine network can also be seen but it is not certain that these are nerve fibres. (Holmes.)

FIGURE 44. Transverse section to show the reticular tissue containing acid mucopolysaccharide and staining brilliant turquoise with Alcian blue. Compare with figure 42.

FIGURE 47. The rostrum of the lower beak seen protruding beyond the surrounding lips, with the upper beak fitting closely within the lower one.

DESCRIPTION OF PLATE 8

FIGURE 48. The buccal complex. The dorsal surface, showing the recess between the salivary papilla and the tongue.

FIGURE 49. Horizontal section through the buccal complex, showing the salivary sheath, and the lateral buccal palps. The median duct of the posterior salivary gland lies near the front of the salivary papilla. (Masson.)

FIGURE 50. Sagittal section of the buccal complex, near the midline. (Masson).

6.2. The beaks

The rostrum of the lower beak protrudes from the lips in all the specimens (figure 47, plate 7). When closed the upper beak fits closely within the lower one, only a little of the hood being visible. In the baby cirrate the beaks are brown only along the edges of the rostra, the colour fading to pale brown posteriorly. The beaks of the large *C. murrayi* have dark brown rostra (figure 47, plate 7) paling to brown passing back over the hood, crest and lateral walls. The edge of the hood, crest and lateral walls is colourless and transparent. The lower beak has no clearly defined jaw angle and a ridge on the medial side of the lateral wall runs from near the curve of the jaw angle to the posterior corner of the lateral wall. These last two features are found in the beaks of Octopoda (Clarke 1962).
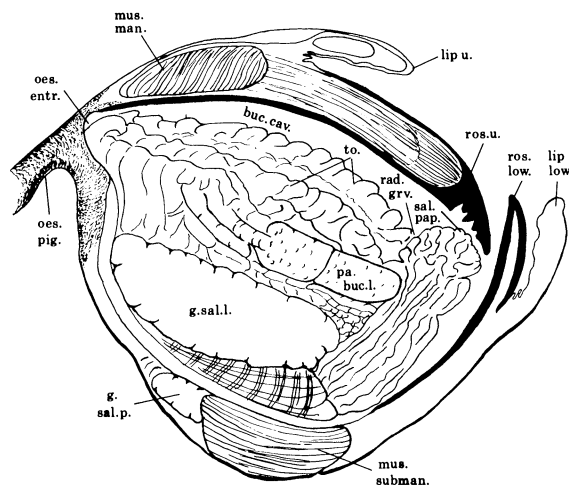
FIGURE 45. Drawing to show the features of the buccal complex within the buccal cavity after removing one side from both beaks.

6.3. The salivary papilla

This is the most anterior structure within the buccal mass, lying immediately behind the rostrum of the lower beak (figures 45 and 46). At its tip the salivary papilla carries the opening of the duct of the posterior salivary glands as in other cephalopods (p. 29). The surface of the papilla has rounded cushion-like folds (figure 48, plate 8) resembling that of *Octopus vulgaris* (M.N., unpublished). It is covered with a thick cuticle, hard after fixation, whose surface is smooth except around the opening of the duct (p. 31).

6.4. The tongue

The long tongue extends back to the oesophagus, from shortly behind the salivary papilla, and forms the floor of the buccal cavity (figure 45). Its surface carries a series of transverse folds (figure 48, plate 8). It has a thin, smooth cuticular coat, pliant after fixation and without teeth. At the sides of the tongue are two pairs of folds (figure 49, plate 8). The small, inner pair towards the front are analogous with the salivary papilla sheath in *Octopus* (Young 1965a). The outer folds are comparable with the lateral buccal palps of other octopods, but are relatively small and lack the teeth found in *Eledone* (Isgrove 1909), *Sepia* (Tompsett 1939) and *Octopus* (Nixon 1968).

6.5. *The radula*

There is a deep groove between the tongue and the salivary papilla, the radular groove, at the bottom of which lie structures that seem to correspond to the radula (figure 50, plate 8). They take the form of a pair of invaginations proceeding into the centre of the buccal complex. The invaginations have a high columnar epithelium covered by a thick cuticle (figure 51, plate 9). For part of the length this cuticle takes the form of a series of teeth (figures 52 and 53, plate 9) which are a bright, clear red after Masson's stain as are the radular teeth of *Eledone* and *Octopus*, whereas the underlying cuticle or radular ribbon stains green (figure 51, plate 9). Within and around each invagination is a mass of small cells, apparently amoebocytes. These give the impression that the lining tissues are continually being removed (figures 51–53, plate 9) (see p. 47).

6.6. *The radular support system*

In cephalopods with a well developed radula there is a muscular support system on either side of the ribbon. Distinct signs of this system are present in *Cirrothauma* (figures 54 and 55, plate 9). The supports are quite large, crescent-shaped in sagittal section and ovoid in horizontal sections, but apparently the sacs are empty except for very fine branching fibrils scattered in an amorphous matrix (figure 56, plate 10). This system has barely taken up the stains used. The radular support sacs are limited medially by a thin sheet-like muscle, the anteroposterior muscle, which separates the pair of radular supports (figure 55, plate 9).

6.7. *Muscles of the buccal complex*

Sagittal sections through the middle of the buccal complex show three dorsoventrally running muscles (figure 46).

(1) The *radular–salivary papilla muscle* is formed by a band of strands some 300 μm in width, and lies behind the radular support system. It inserts into connective tissue along the base of the buccal complex from whence it runs upwards. The more posterior strands are inserted into the dense connective tissue around the radula. Some of the anterior strands run forward into the salivary papilla where they end in the dense connective tissue below the epithelium just in front of the entrance to the radula. The most anterior strands run forward almost straight as far as the posterior salivary gland.

The radular–salivary papilla muscle thus runs to at least three parts of the buccal complex, (i) the radula, (ii) the salivary papilla in front of the entrance to the radula, and (iii) to the top of the posterior salivary gland and perhaps even to the front of the papilla. Thus the actions of this muscle must be complicated. It is probably concerned with the retraction of the radular groove at the upper end of which lie a few teeth. The teeth though very small could perhaps form roughened sites on the otherwise smooth surface, and aid the passage of the food towards the oesophagus.

(2) The *dorsoventral papillary muscle* consists of narrow but dense strands which, after sectioning, have a wave-like form. It runs from near the base of the radular–papillary muscle forwards, curving upwards behind the posterior salivary gland to just below the epithelium of the salivary papilla anterior to the entrance of the radular groove (figure 46).

(3) The *salivary papilla muscle* is large and complicated, associated with the posterior salivary gland and, to a lesser extent, with the submandibular gland. It runs from the floor of the buccal complex upwards between the lobes of the gland with a cross meshwork of fibres and continues
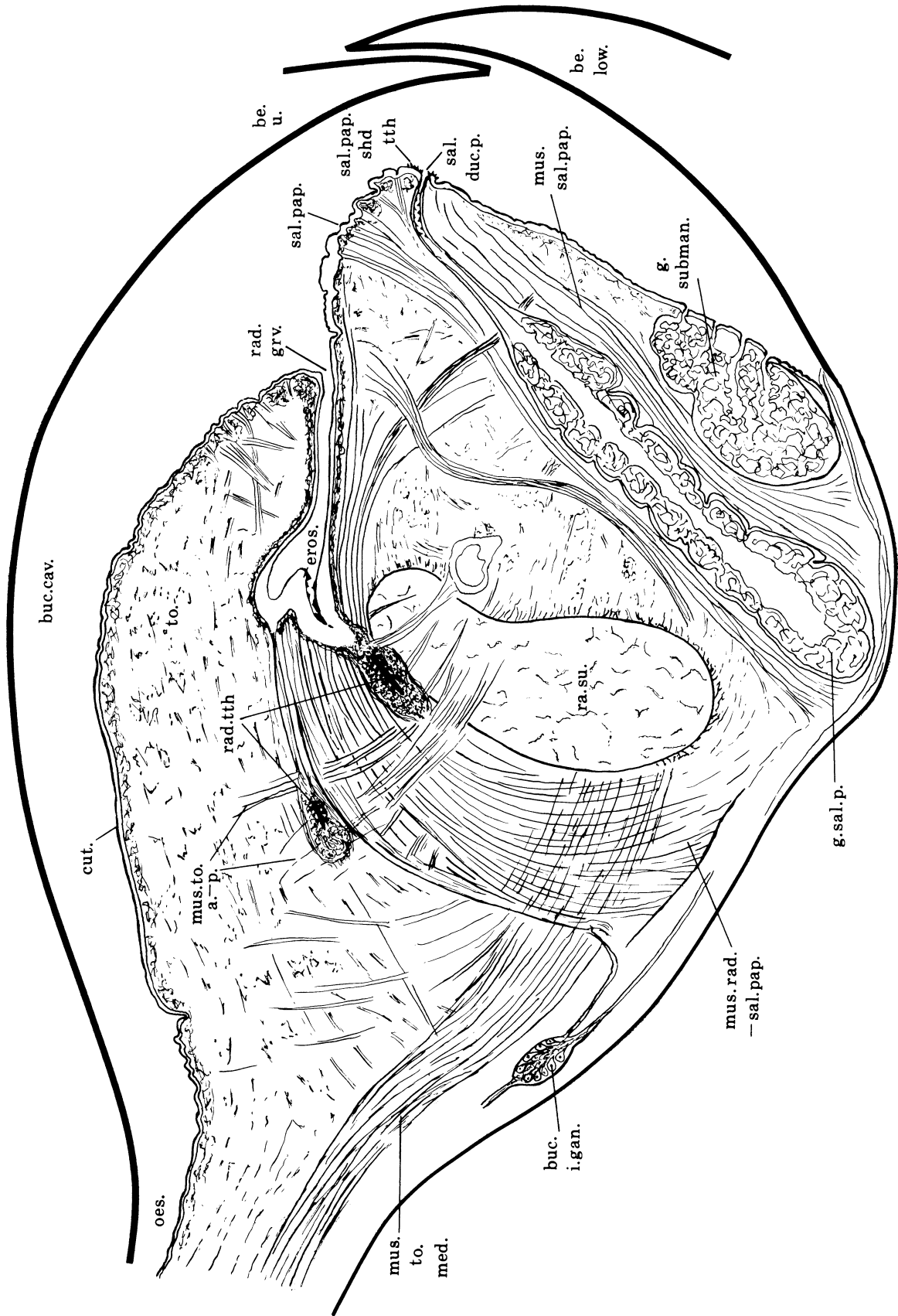
FIGURE 46. Drawing, reconstructed from serial sagittal sections near the midline, of the buccal complex showing its major features.

up to the apex of the salivary papilla. Some of the strands terminate around the opening of the duct of the gland itself, others run slightly posteriorly ending in the dense connective tissue on the upper surface of the salivary papilla (figure 46). Part of the muscle runs between the posterior salivary gland and the submandibular gland. The position and complicated course of this muscle suggests that it may be concerned in several actions: first in aiding the ejection of the salivary secretions, predominantly from the posterior salivary gland and probably, but to a smaller extent, the submandibular one; secondly, in everting the terminal, tooth-bearing, part of the duct from the posterior salivary gland to expose the teeth on the surface of the papilla; and lastly in everting the apical part of the salivary papilla where the cuticle is hard and presumably concerned with the passage of food items.

(4) The other muscles of the buccal complex are smaller and not so well organized as those just described. The median tongue muscle (figure 55, plate 9) runs across the radular–salivary papilla muscle (figure 46). There is a small anteroposterior tongue muscle which is also associated with the radular support system (figure 46). Several small muscles run from the lateral side of the radular support system forwards and laterally to the side of the complex. These muscles run between bundles of dorsoventrally running muscle strands. Posteriorly there is a muscle which runs across the back of the buccal complex and just in front of the inferior buccal ganglia (figure 55, plate 9).

6.8. Salivary glands

Within the buccal complex there are three sets of glands: a single submandibular, a pair of lateral and a single posterior salivary gland (figure 46, and figure 50, plate 8).

(1) The *submandibular gland* lies below the salivary papilla as in *Eledone* (Isgrove 1909). It has several lobes which join anteriorly partly to enclose the single, median, posterior salivary gland (figure 57, plate 10). The secretory products enter collecting ducts and expel their contents into the front of the buccal cavity through a number of pores (figure 58, plate 10). Serous and mucous cells are present. The serous cells have two populations of secretory granules, some 1–2 µm and others 7–11 µm in diameter (figure 59, plate 10). The submandibular gland has two features analogous with this gland in other cephalopods, namely that it lies below the salivary papilla and opens by many pores into the front of the buccal cavity. The name given to this gland has varied (table 5).

(2) The *lateral salivary glands*, sheathed in connective tissue, lie on either side of the tongue (figure 55, plate 9). Serous and mucous cells are present and secrete their products into the buccal cavity through two or three pores in the connective tissue sheath, on the labial surface (figure 60, plate 10). Two populations of granules are present in the serous cells, some 1–2 µm and others 6–9 µm in diameter (figure 61, plate 10). Each gland has two or three openings into the lateral buccal cavity. *Cirroteuthis umbellata* has glands in the same position, also opening by pores, and Ebersbach (1915) called them the anterior salivary glands. Table 5 lists the features of the salivary glands of several cephalopods; evidently the anterior salivary glands show great variation. Until morphological and functional affinities are demonstrated these glands in *Cirrothauma* will be called lateral salivary glands.

(3) The single *posterior salivary gland* is bordered on either side and in front by the submandibular gland (figure 57, plate 10). It extends from the floor of the buccal complex up towards the apex of the salivary papilla (figure 46). Horizontal sections show it to be a single gland surrounded by connective tissue and subdivided into lobules. In the sagittal sections of *Cirrothauma* the secretory granules are tightly packed and of almost uniform diameter 1–1.5 µm. The

cells are filled with dense, deep-staining granules in specimen A (figure 62, plate 10) but in B they are nearly devoid of granules (figure 63, plate 10) as though almost the entire contents had been voided at the same time. The products from the cells of the posterior salivary gland enter a large collecting channel from which a short, single duct runs almost to the apex of the salivary papilla where it opens at the front of the buccal cavity (figure 46). This is the *only* salivary gland of *Cirrothauma* that ends as a single duct. The subterminal part of the duct carries teeth 10–90 μm in height and then widens as it opens at the folded surface of the salivary papilla (figure 64, plate 11). These folds presumably open out by the action of the salivary muscle, so exposing the teeth at the end of the duct. There is another tooth-covered area around the opening of the duct, but these teeth are much smaller than those on the duct. This is the papillary shield (Nixon 1979*a*) (figure 65, plate 11).

TABLE 5. THE POSITION OF THE SALIVARY GLANDS AND DUCTS ASSOCIATED WITH THE BUCCAL
MASS OF VARIOUS CEPHALOPODS, AND THE NOMENCLATURE USED BY DIFFERENT AUTHORS

	anterior salivary		posterior salivary		other salivary		
	glands	duct	gland(s)	duct	gland	duct	
Cirrothauma murrayi	on side of tongue = lateral salivary gland	several pores	median	single	submandibular	pores	
Cirroteuthis umbellata	on side of tongue = anterior salivary gland, buccal or intrabulbar gland	pore	median	single	submaxillaris or submandibular	pores	Ebersbach 1915
Vampyrotheuthis infernalis	on posterior surface of buccal mass	duct from each gland	pair	single	sublingual	pores	R. E. Young 1961
Octopus vulgaris	on posterior surface of buccal mass	duct from each open on l.b.p.	pair	single	submandibular (subradular)	pores	J. Z. Young 1965, J. Z. Young 1977,
Eledone cirrosa	on posterior surface of buccal mass	duct from each opens on l.b.p.	pair	single	sublingual	pores	Isgrove 1909
Sepia officinalis	embedded in lateral buccal palps	duct from each opens on l.b.p.	pair	single	sublingual	pores	Tompsett 1939
Loligo pealei	between oesophagus and radula	each opens on l.b.p.	median	single	no mention		Williams 1909

Abbreviation l.b.p. stands for lateral buccal palps.

The posterior salivary glands of incirrate octopods are paired and lie behind the brain. Identification of the single, median gland lying far forward in the buccal mass as 'posterior' was possible because of three features: (*a*) the gland has a single duct which ends at the apex of the salivary papilla, (*b*) the terminal part of the duct bears teeth which can be everted so that they come to lie on the surface, and (*c*) around the opening of the duct is an area covered with much smaller teeth, the papillary shield. A single duct is found in *Eledone* (Isgrove 1909), *Sepia*

(Tompsett 1939) and *Octopus* (Young 1965a), although the glands are paired. Teeth on the terminal part of the duct and a toothed papillary shield are present in *Octopus* and *Eledone* (Nixon 1979a, b). Ebersbach (1915) found only a single posterior salivary gland within the subradular organ in *Cirroteuthis umbellata* Fischer, 1883 (table 5) (see p. 47).

6.9. *The cuticle of the buccal complex and digestive tract*

The lining of the buccal complex has an almost complete covering of smooth, colourless cuticle (green after Masson's stain). The cuticle of the salivary papilla is not of uniform thickness. On the dorsoposterior surface, near to the entrance to the radula, it is up to 100 μm thick (figure 66, plate 11), suggesting some role in feeding. Perhaps this is a region of wear and tear and the cuticle protects the underlying tissues. Just in front of this region there are patches which lie at the bottom of folds and stain red with Masson's stain. More anteriorly the cuticle becomes thinner and its surface is sculptured. The cuticle of the salivary papilla is quite hard, at least after fixation. Tall columnar cells secrete the cuticle and from the apical surface of these cells fine fibrils emerge arranged normal or parallel with the surface (figures 67 and 68, plate 11).

The cuticle is continuous from the buccal cavity into the oesophagus, covering the long, finger-like projections there (figure 69, plate 11). Where the oesophagus passes through the brain there are thickenings of the cuticle, which stain red in contrast with the green of the underlying cuticle (Masson's stain) (figures 70 and 71, plate 11). Further along the oesophagus the cuticle becomes thinner. The stomach cuticle is again thick and ridged on the two opposing walls which are covered with thick muscles and by their actions could squeeze any food present, freeing the prey's exoskeleton of tissue after digestion of its attachments, as does *Octopus* (Nixon 1983) (see p. 47).

7. THE NERVOUS SYSTEM

7.1. *General arrangement*

There is no cartilage around the central nervous system, which can therefore be completely revealed by simply cutting through the skin of the head (figure 72, plate 12). The eyes are directed laterally and the optic nerves are very long, passing through a massive orange 'white body' to the very small optic lobes, which lie close to the central nervous system. The statocysts lie at some distance from the brain, connected with it by long static nerves (figure 72, plate 12).

The central ganglia closely surround the deeply pigmented oesophagus. Their shape is very different from that of either decapods or non-cirrate octopods (figure 73). It is in the form of two rings, recalling the brain of *Nautilus* especially when seen from the side (Young 1965b) (figure 74, plate 12). There is a marked 'cerebral fissure' between the cerebro-brachial connective and the rest of the lateral part of the brain. The suboesophageal lobes are much larger than the supraoesophageal, the anterior and posterior suboesophageal masses being especially large. The lateral part of the brain is relatively very large, and the basal lobes, which are usually considered as supraoesophageal, here lie largely at the sides (figure 75, plate 12). A large lobe lying partly below the oesophagus has no exact parallel in other forms (figure 75, plate 12, and figure 97, plate 17). It corresponds approximately in position to the lateral pedal lobe of other cephalopods and is broadly connected above with the anterior basal lobe. Its connections suggest that it is a centre for the control of movement.

In the supraoesophageal lobes three regions can be recognized, but the divisions are barely obvious from the outside (figure 73, and figure 74, plate 12). In front there are joined superior buccal lobes, with labial nerves, of typically octopodan form. Behind this is a large inferior

frontal lobe, receiving the cerebro-brachial connective. This lobe is marked off by a groove from the tissue of the rest of the top of the supraoesophageal mass, which will be called the vertical lobe, though it differs from that of other cephalopods (p. 40). There is only a very vague hint externally of a superior frontal lobe; sections show that it consists only of a small lateral lobule (p. 40).

7.2. Eye

Cirrothauma was called 'ein blinder Cephalopod' by Chun in 1911 (see Robson 1932, p. 165) but it has complete eyes though they are reduced and have unique features. They are embedded within the jelly of the skin and are simple cups, with no lens (figures 72 and 76, plate 12). The back part of the cup is a pigmented retina and this is continuous in front with a transparent cornea (figures 77–79, plate 12). There is no trace of ciliary body or iris. The cells lining the inner surface of the cornea are continuous with those of the retina, whose peripheral cells cease to carry rhabdomes, become flattened and lose their pigment (figures 79 and 80, plate 12). The outer surface of the cornea is composed of very thin flat epithelial cells and there are a few cells and fibres but no blood vessels between the two layers (figure 80, plate 12). The front of the eye is thus a transparent, smoothly curved, window with a slightly irregular margin through which one looks directly onto the yellowish surface of the rhabdomes (figure 76, plate 12).

DESCRIPTION OF PLATE 9

FIGURE 51. Section through part of the radula at the bottom of the recess between salivary papilla and tongue, showing the tall columnar cells that secrete the cuticle (green with Masson's stain), the surface of which is being eroded by amoebocytes. (Cirrothauma A.)

FIGURE 52. Anterior part of the radula with the repeating tooth-like structures invaded by amoebocytes (Cirrothauma A, Masson).

FIGURE 53. Posterior part of the radula with larger tooth-like projections lying among amoebocytes (Cirrothauma A, Masson).

FIGURE 54. Sagittal section, lateral to midline, to show the crescent-shaped radular support system (Cirrothauma A, Masson).

FIGURE 55. The buccal complex to show the radular support system and the salivary glands (horizontal section, Masson).

DESCRIPTION OF PLATE 10

FIGURE 56. The tissue of the radular support, at higher magnification, showing the very fine fibrils scattered in the amorphous matrix (Masson, phase contrast).

FIGURE 57. The posterior salivary gland with the lobes of the submandibular gland enclosing it anteriorly (horizontal section, Masson).

FIGURE 58. The submandibular gland with two of the pores through which the secretory products are expelled (sagittal section, Masson).

FIGURE 59. The submandibular gland at higher magnification for comparison with the posterior and lateral salivary glands in figures 61 and 62 (sagittal section, Masson).

FIGURE 60. Lateral salivary gland showing one of the pores, on the labial surface of the buccal complex, through which secretory products are expelled (horizontal section, Masson).

FIGURE 61. Lateral salivary gland at the same magnification as figures 59 and 60 (sagittal section, Masson).

FIGURE 62. The posterior salivary gland of Cirrothauma A at the same magnification as figures 59 and 60, showing densely packed granules in the serous cells (sagittal section, Masson).

FIGURE 63. The posterior salivary gland of Cirrothauma B at the same magnification as figure 62. The granules are almost entirely absent from this gland when compared with Cirrothauma A. (Horizontal section, Masson.)
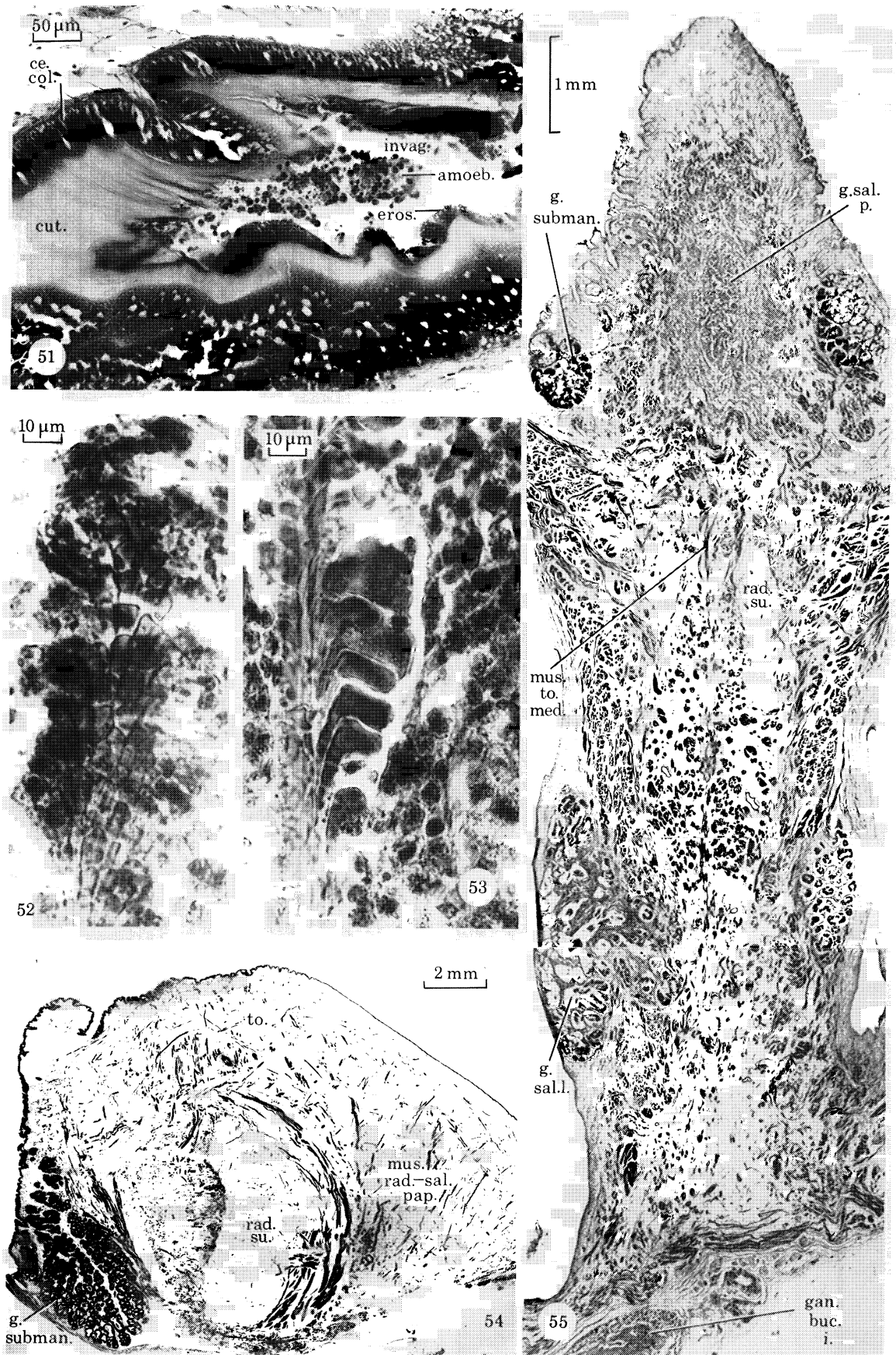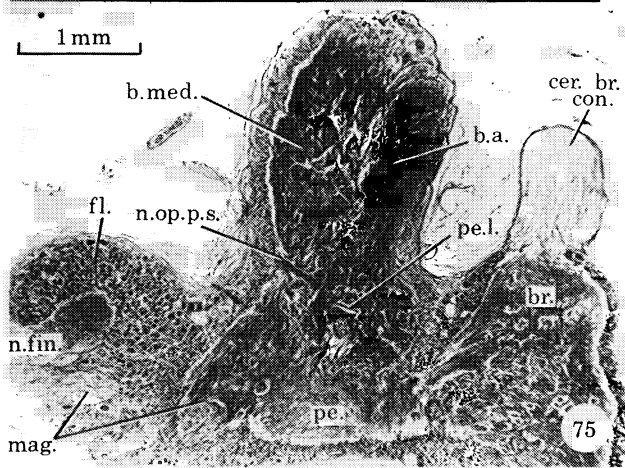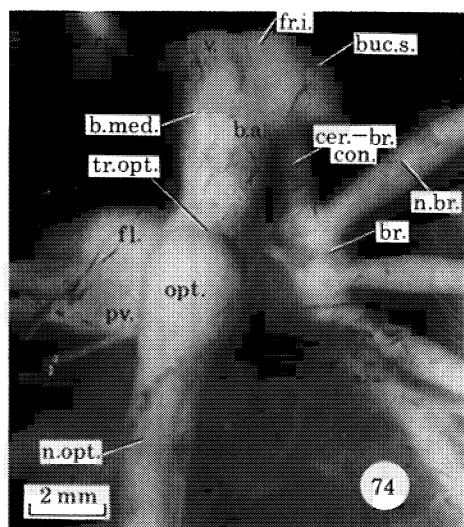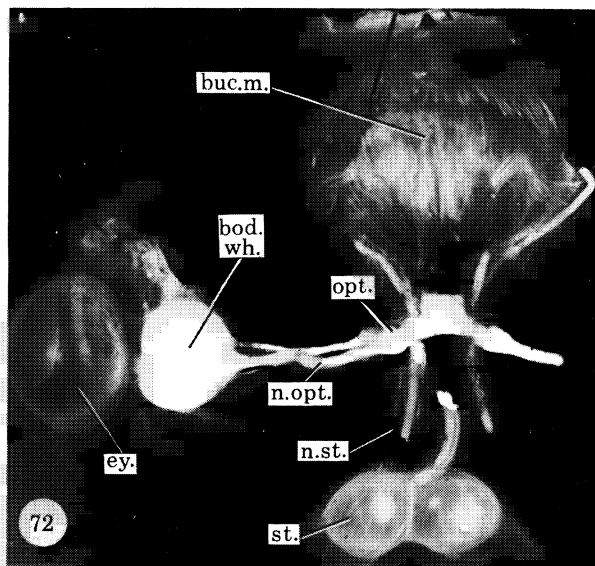
FIGURES 51–55. For description see opposite.
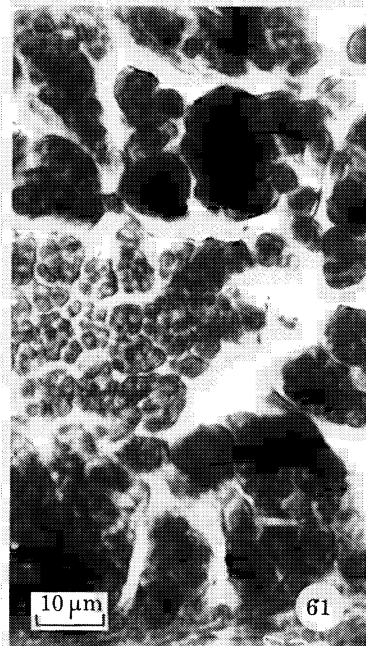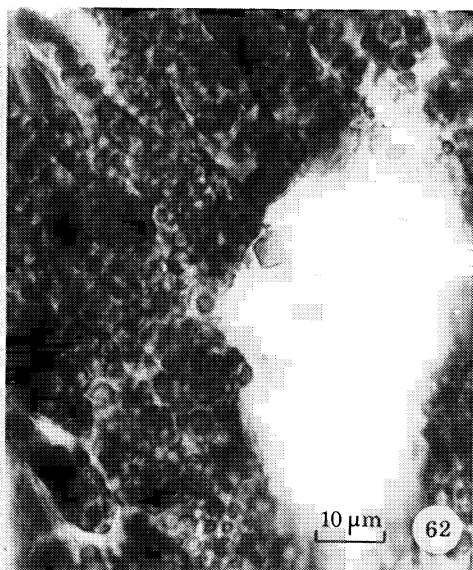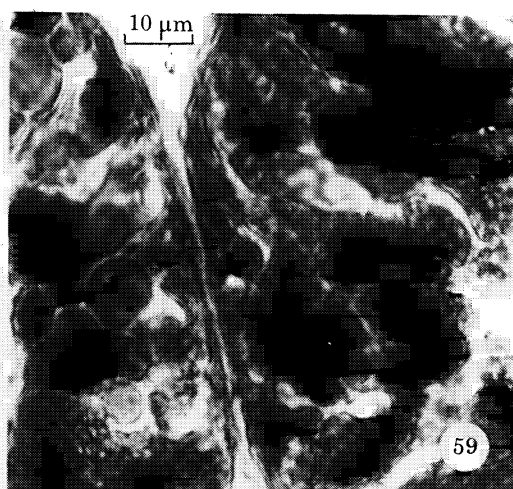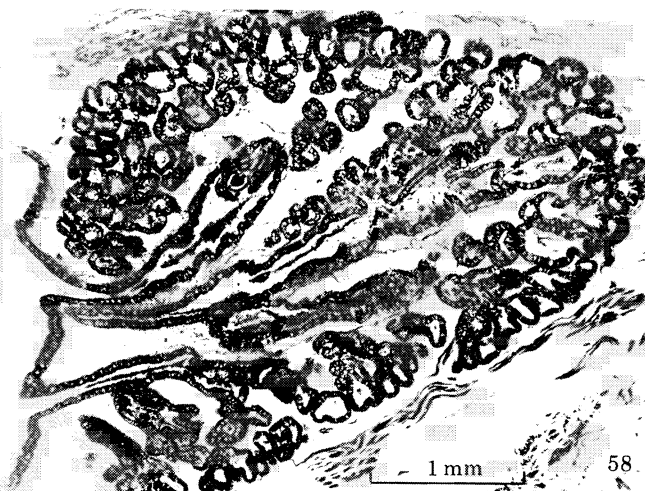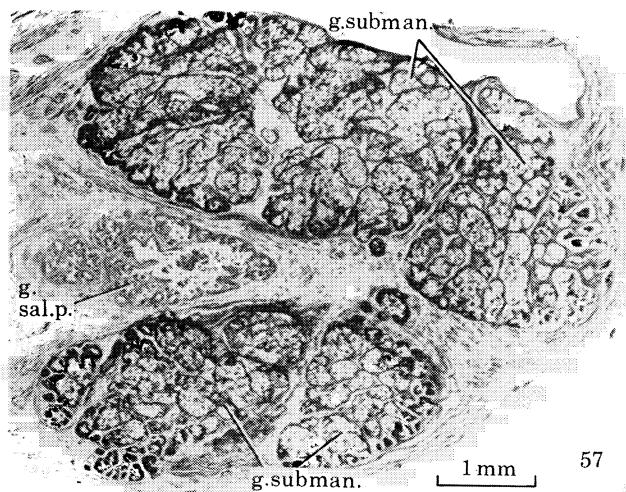
FIGURES 56–63. For description see p. **32.**
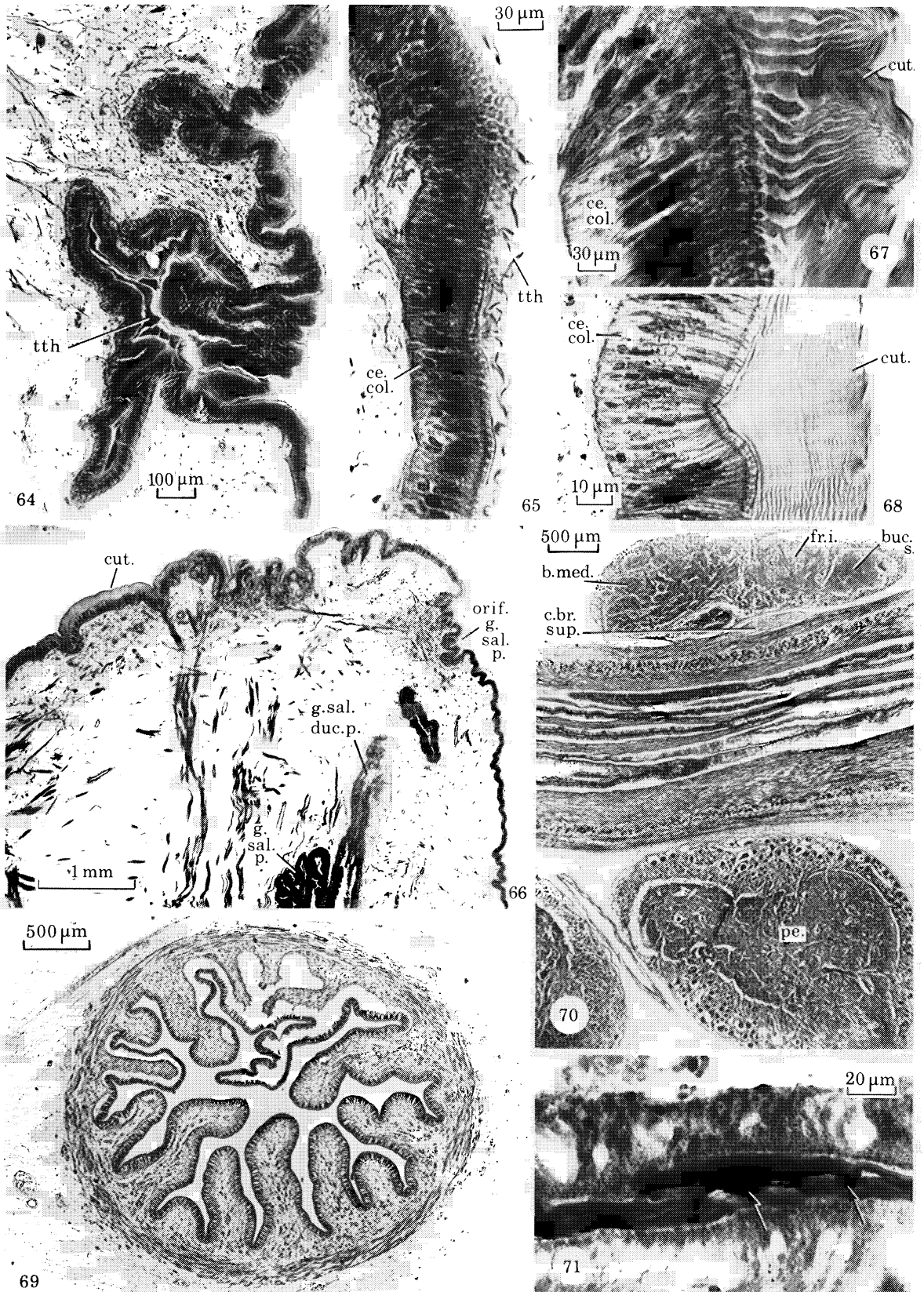
FIGURES 64–71. For description see p. **33.**
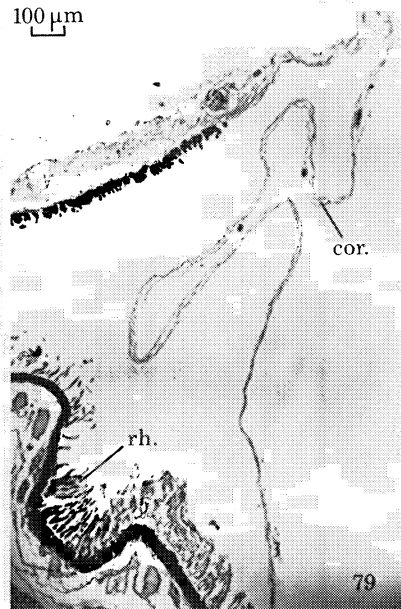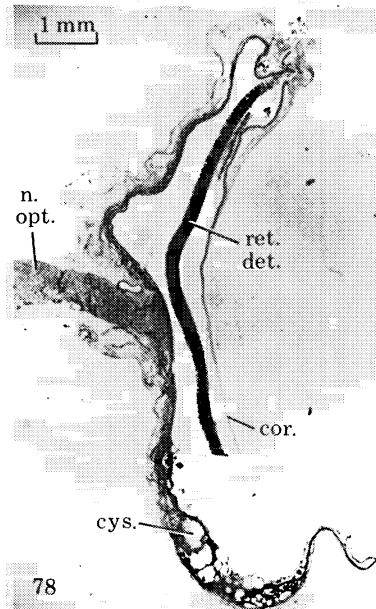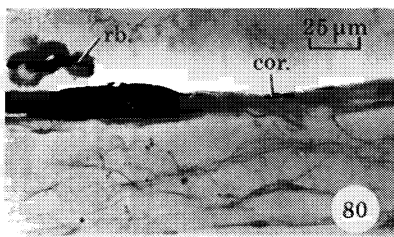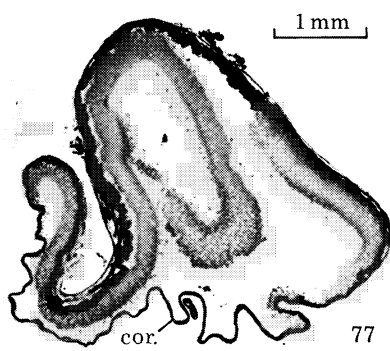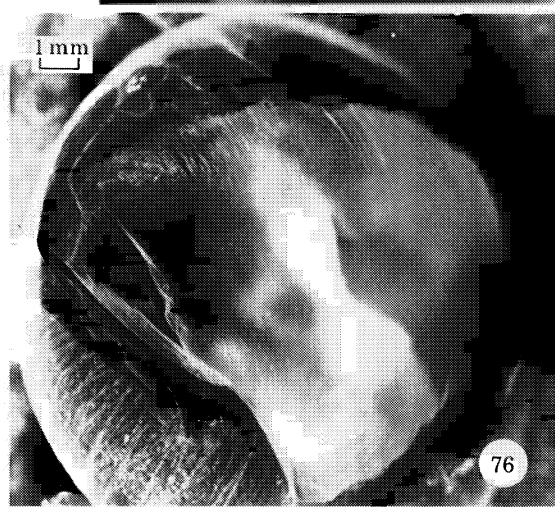
FIGURES 74–80. For description see opposite.

The eye cup is nearly spherical. In specimen A it is 14 mm in diameter in front and in specimen B it is 14.5 mm long by 12 mm dorsoventrally and 12 mm transversely. The clear pupil of B is also oval, 12 mm long and 9 mm dorsoventrally. There is thus no question of the eye forming an image by a pinhole.

The retina differs considerably in the sections of the three specimens examined. In the smallest eye examined (A) there is a rather regular set of rhabdomes, longest at the centre and decreasing towards the edges (figure 77, plate 12). In *Cirrothauma* B, however, a large part of the retina is broken up into a series of vesicles (figure 78, plate 12). In the largest eye, C, the centre is occupied by regular rhabdomes but at the periphery there are only pigmented support-ing cells (figure 79, plate 12). Moreover, in parts of the more central region and near the edges the rhabdomes become reduced to isolated individuals of the form described as 'flames' by Chun (1913) (figure 81, plate 13). However the greater part of the back of the eye is occupied by rhabdomes of more conventional form (figure 82, plate 13). They are of rather uniform length over most of the retina of this individual (300–400 µm). At their outer ends they form irregular narrow fingers and here the microvilli can just be resolved with the light microscope (figure 83, plate 13). The pigment is nearly all aggregated at the base of the retina, obscuring the inner segments (figure 82, plate 13). Bleaching reveals that there are two types of cell in

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DESCRIPTION OF PLATE 11

FIGURE 64. The posterior salivary gland duct opens on the apical surface of the salivary papilla. The surrounding toothed cuticle forms the papillary shield. At the bases of the folds the dark-staining teeth of the posterior salivary gland duct can be seen. (Masson.)

FIGURE 65. The cuticular teeth of the papillary shield and the very tall columnar cells below (Masson).

FIGURE 66. The salivary papilla showing the variations in the cuticle. Anteriorly is the duct opening from the posterior salivary glands. Moving back towards the entrance to the radular recess there is an area of especially thick cuticle. (Sagittal section, Masson.)

FIGURE 67. The salivary papilla where the surface is sculptured. The cuticle is formed by fibrils running normal to the surface, being laid down somewhat differently from that in the next figure. (Sagittal section, Masson.)

FIGURE 68. The salivary papilla showing part of the very thick cuticle, formed by fibrils running parallel with the cell surface, that lies just in front of the entrance to the recess leading to the radula (sagittal section, Masson).

FIGURE 69. The oesophagus, showing long, finger-like projections into the lumen. The cuticle is thin and colour-less. (Transverse section, Masson.)

FIGURE 70. The brain and the oesophagus. The projections into the oesophagus are in long, thin folds within the muscular walls. (Sagittal section, Masson.)

FIGURE 71. The oesophagus at higher magnification to show the cuticular surface where it is raised into small projections (arrowed). The projections have stained red in Masson's stain. (Sagittal section.)

DESCRIPTION OF PLATE 12

FIGURE 72. Eye, buccal mass, nervous system and statocyst from above (*Cirrothauma* B).

FIGURE 74. Central nervous system from the right side (*Cirrothauma* B).

FIGURE 75. The central nervous system of *Cirrothauma* B (sagittal section, Masson).

FIGURE 76. Eye of *Cirrothauma* A, looking through the cornea to the damaged retina.

FIGURE 77. Transverse section of eye of *Cirrothauma* A (Cajal).

FIGURE 78. Transverse section of eye of *Cirrothauma* B, showing cysts in part of the retina (Masson).

FIGURE 79. Section of eye of *Cirrothauma* C showing separate rhabdomes ('flames') and small rhabdomes and supporting cells at the edge of the retina (haematoxylin and eosin).

FIGURE 80. Section at edge of retina of *Cirrothauma* B showing the last retinal cells and beginning of the cornea (haematoxylin and eosin).

the lining of the retina, rhabdomes and supporting cells (figure 84, plate 13). It is characteristic of the retina that in many parts the supporting cells have rounded tops and do not send projections between the rhabdomes. This is why the latter are irregularly arranged as 'flames'. In some parts the lining is composed mainly of supporting cells, with only a few isolated rhabdomes (figure 81, plate 13).
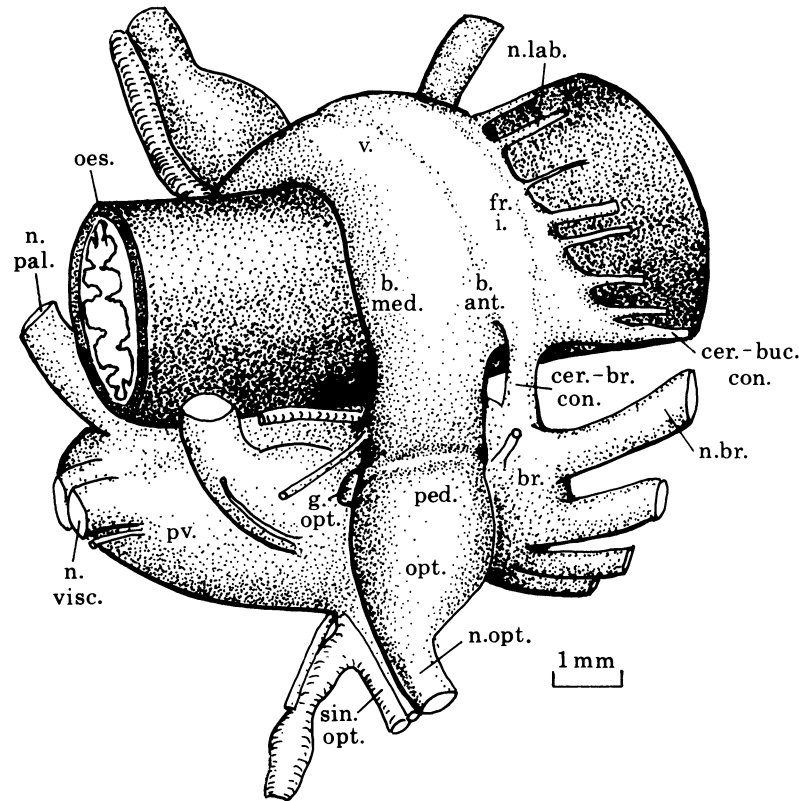

FIGURE 73. Drawing of central nervous system of *Cirrothauma* A.

The nuclei of the rhabdome cells are larger than those of the supporting cells and have more dispersed chromatin (figure 84, plate 13). Their cell bodies are round and the rhabdome is attached to the body by a very narrow neck. This is often broken in the sections or sometimes pulled out to a considerable length (figure 84, plate 13). The centre of the rhabdome contains filaments which continue into the neck.

In the better developed central part of the retina the adjacent rhabdomes are closely in contact with each other (figure 82, plate 13). There may, however, be some prolongations of the supporting cells, containing pigment, between groups of rhabdomes at least near the base (figure 85, plate 13).

These are the conditions of most of the retinae of three animals (A, B, C) but in a large region near the margin in specimen B the retina is broken up into vesicles (figure 86, plate 13). The rhabdomes here are of irregular shapes, some of them isolated 'flames' and some moniliform. Within the vesicles and between them are numerous amoebocytes, filled with pigment granules. Some of the vesicles are filled with rhabdomes and resemble photosensitive vesicles such as those of the epistellar body (p. 41) (figure 87, plate 13). Other vesicles are empty, as if the rhabdomes had been consumed by the amoebocytes. These vesicles are formed by folding

of the retina and the process can be seen to be at work, discontinuously along its length. These appearances seem to suggest a degeneration of the retina in this animal, but they may also be part of a sequence of regeneration of rhabdomes.

7.3. *Optic nerves and optic tract*

The back of the eye is attached to a large orange-yellow 'white body' by the walls of the optic sinus (figure 88, plate 14, and figure 89, plate 15). No obvious thickenings, or eye muscles, were seen during dissection. The sinus continues on towards the brain as a wide channel parallel to the optic nerve (figure 88, plate 14, figure 89, plate 15 and figure 90, plate 16). Centrally this optic sinus joins a sinus surrounding the brain and sends a large vessel downwards towards its fellow from the opposite side. These vessels carry swellings below the brain. They join large supra and suboesophageal sinuses and various smaller ones to run back as a vena cava (figure 89, plate 15). These sinuses are accompanied by large masses of neurovenous tissue (p. 37).

The optic nerves collect regularly from the back of the eyeball without any sign of twisting or chiasma formation such as is seen in the optic nerves of octopods with good vision (figure 88, plate 14, and figure 89, plate 15). The separate nerves join to make two strands, dorsal and ventral, which remain distinct all the way to the optic lobe, the trunks from the eyeball probably retaining their order in the nerves (figure 90, plate 16). The optic nerves are 19 mm long in specimen A. They run through the white body and then swell out slightly to form the optic lobe, which they enter without any sign of chiasma formation. They are accompanied by two thin strands but whether these are sensory (ophthalmic) or oculomotor nerves was not determined.

7.4. *Optic lobe*

The optic lobe is better developed than is implied by Chun (1913) but is only a small pear-shaped swelling (3.5 mm × 2 mm) lying close to the brain (figure 88, plate 14, and figure 89, plate 15). The lobe is attached to the brain by a broad optic tract and at this level is seen macroscopically to be crossed by two white ridges, the peduncle lobes, running around its hind end from dorsal to ventral (figure 73). Below them is the optic gland (p. 40). The optic and peduncle lobes are so closely continuous with the central brain that in a sense it can be said that there is no discrete optic tract.

The optic lobe has a very simple structure. The optic nerve fibres form a thick outer layer, within which an outer plexiform layer and central medulla can be distinguished (figure 91, plate 16). There are no well marked inner and outer granule cell layers, only scattered cells, little different from those forming the cell islands of the medulla (figure 92, plate 16). The very reduced plexiform zone presumably contains the endings of the optic nerve fibres, making contact with dendrites of the second order visual cells. The preparations do not show details, but there is no evidence of the tangential layers seen in other cephalopods (see p. 48). The reduction of the amacrine cells of the granular layers and absence of tangential layers in the plexiform zone suggests that the eyes of *Cirrothauma* are not used for form discrimination.

The cell islands of the medulla of the lobe are also simple. They are separated by tracts of neuropil and fibres leading to a central fibre mass at the hilum of the lobe. There is no sign of the arrangement into radial columns that is so conspicuous in the more developed optic lobes, for instance of *Loligo* (Young 1974).

In spite of their small size the optic lobes are the focus for many connections. Those presumed

to be afferent include a large brachio-optic tract arising from the brachio-palliovisceral con-
nective (figure 93, plate 16). Immediately after leaving the connective this bundle crosses the
static nerve and receives fibres from it (figure 93, plate 16).

Tracts presumed to be efferent run from the optic lobe to the lateral pedal 'movement centre'
and backwards to the palliovisceral and fin lobes (figure 95, plate 16). Large bundles run to the
anterior basal lobes and these may include fibres running in both directions (figure 93,
plate 16). At the dorsal surface the optic lobe neuropil, with fine fibres, is continuous with that
of the anterior basal lobe and may contain fibres running centrifugally.

Bundles of fibres run to the precommissural region (figure 96, plate 16) but no other con-
nections have been established with the vertical lobe system or with the posterior basal lobe. The
optic commissure is a thin bundle of fibres (figure 95, plate 16). It probably includes fibres
running between the peduncle lobes.

7.5. Suboesophageal lobes

These lie close together with no long intervening connections (figure 97, plate 17). The
anterior mass is very large, especially at the sides. It shows no clear division into prebrachial
and postbrachial parts but is crossed from front to back by irregular rows of cells between the
roots of the brachial nerves. An incomplete wall of cells separates it from the pedal lobe behind.
There is a large suprabrachial commissure (figures 105 and 106, plate 18). This is a feature of
octopods absent in decapods. In *Cirrothauma* it lies behind the cerebro-brachial connective, not
in front of it as in incirrate octopods.

The middle suboesophageal mass is the smallest of the three parts. It is difficult to compare
it with that of other cephalopods. A large region at the sides dorsally, marked off by a cell wall
from the rest, will be regarded as the lateral pedal lobe (figure 75, plate 12; figure 97, plate 17).
In other cephalopods the front part of this is an oculomotor centre and in *Cirrothauma* a bundle
of fibres could be traced from here to the posterior superior ophthalmic nerve (figure 75,
plate 12). The posterior part of this lobe in *Loligo* is a 'command centre' controlling movements of
arms and mantle and fins (Young 1976). This also seems to be the function of this large lobule
in *Cirrothauma*. Many fibres of the static nerves enter the lobule (figure 93, plate 16) and it
receives large bundles of fibres from the anterior and median basal lobes and probably from
the peduncle lobes. Its efferent connections are in tracts that pass forwards to the brachial
lobes, downwards and medially to the rest of the pedal lobe and backwards to the palliovisceral
lobe and fin lobe. The cells of this lateral pedal lobe are mostly small.

DESCRIPTION OF PLATE 13

FIGURE 81. Section of retina of *Cirrothauma* C (bleached and stained with haematoxylin and eosin).

FIGURE 82. Rhabdomes in retina of *Cirrothauma* C.

FIGURE 83. Tips of rhabdomes in *Cirrothauma* B, showing the microvilli (Holmes).

FIGURE 84. Bleached section of retina of *Cirrothauma* C showing the narrow necks of the rhabdomes and their
nuclei (bleached and stained with haematoxylin and eosin).

FIGURE 85. Section of retina of *Cirrothauma* C, showing pigment granules between the rhabdomes, presumably in
supporting cells.

FIGURE 86. Cysts near the edge of the retina of *Cirrothauma* B (haematoxylin and eosin).

FIGURE 87. Rhabdomes within the cysts (Holmes).
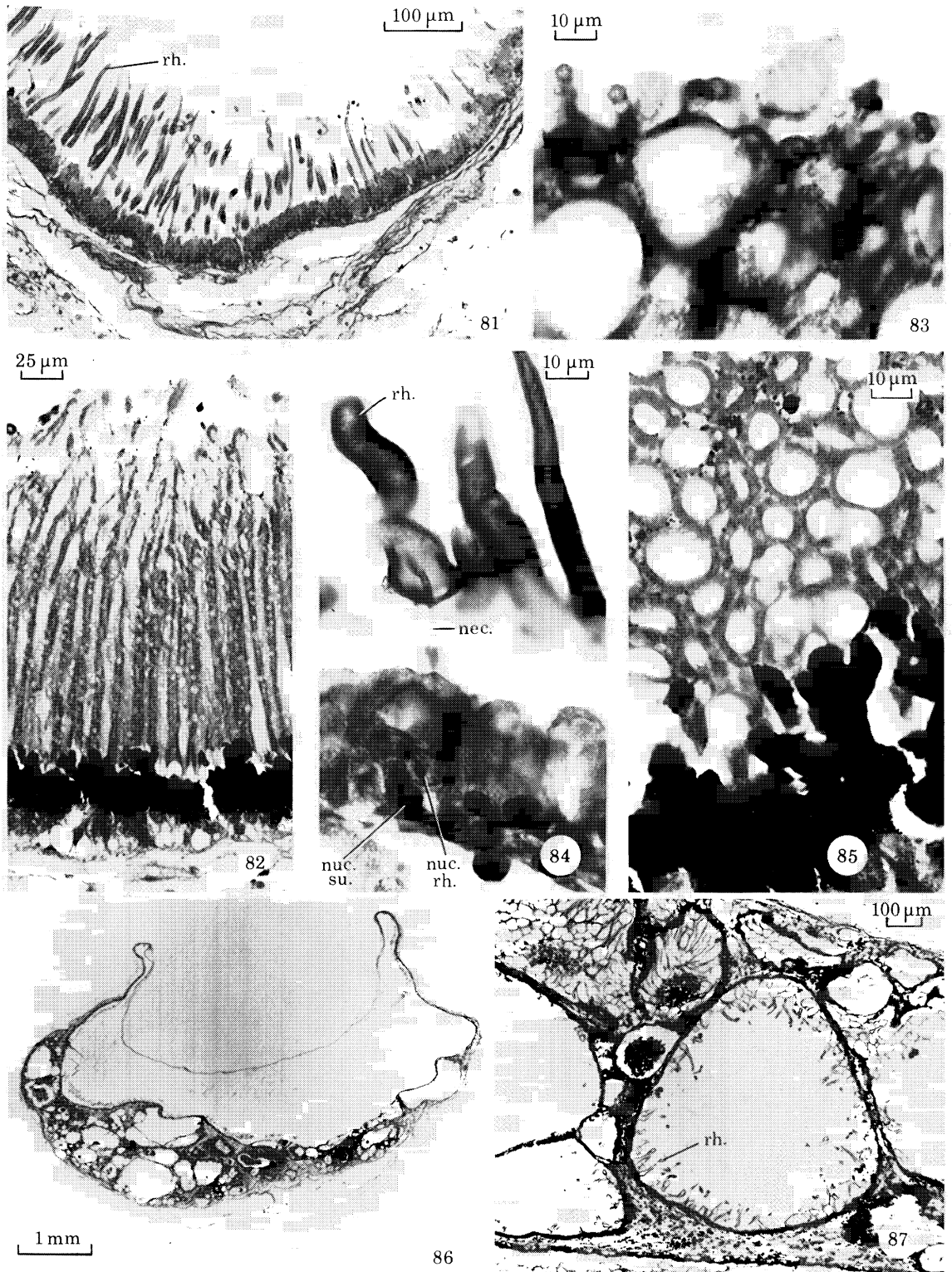
FIGURES 81–87. For description see opposite.
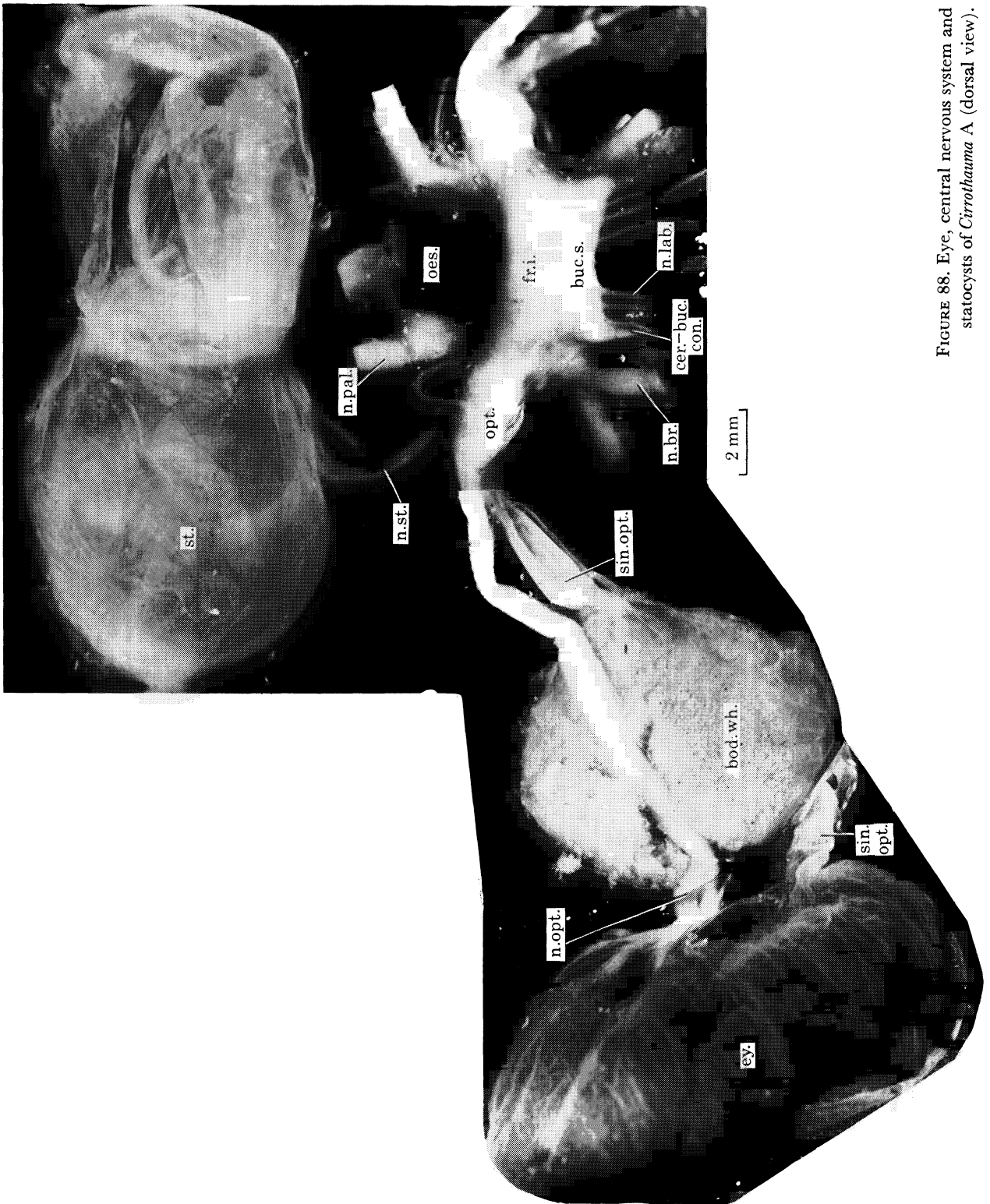
FIGURE 88. Eye, central nervous system and statocysts of *Cirrothauma* A (dorsal view).

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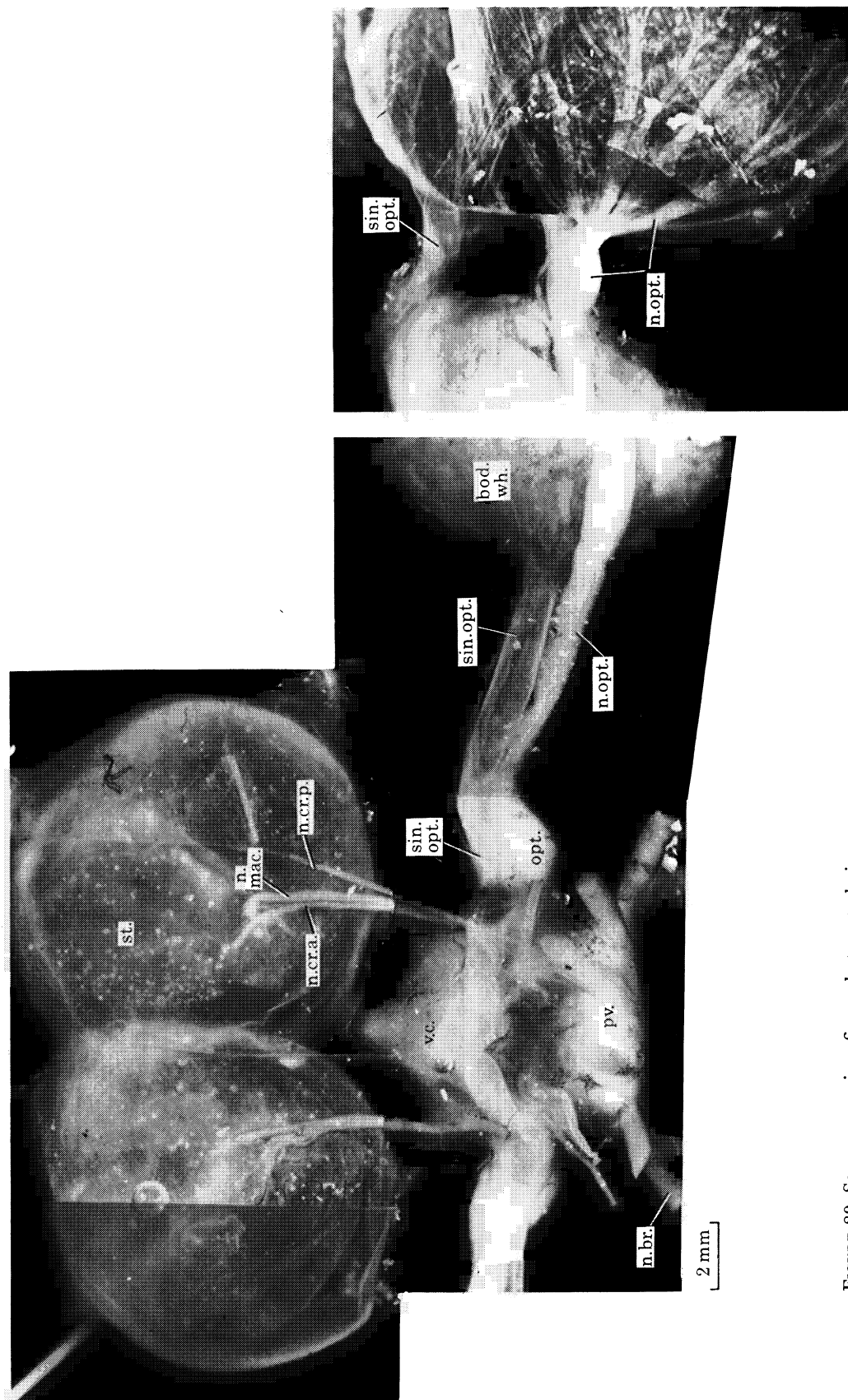
FIGURE 89. Same as previous figure, but ventral view.
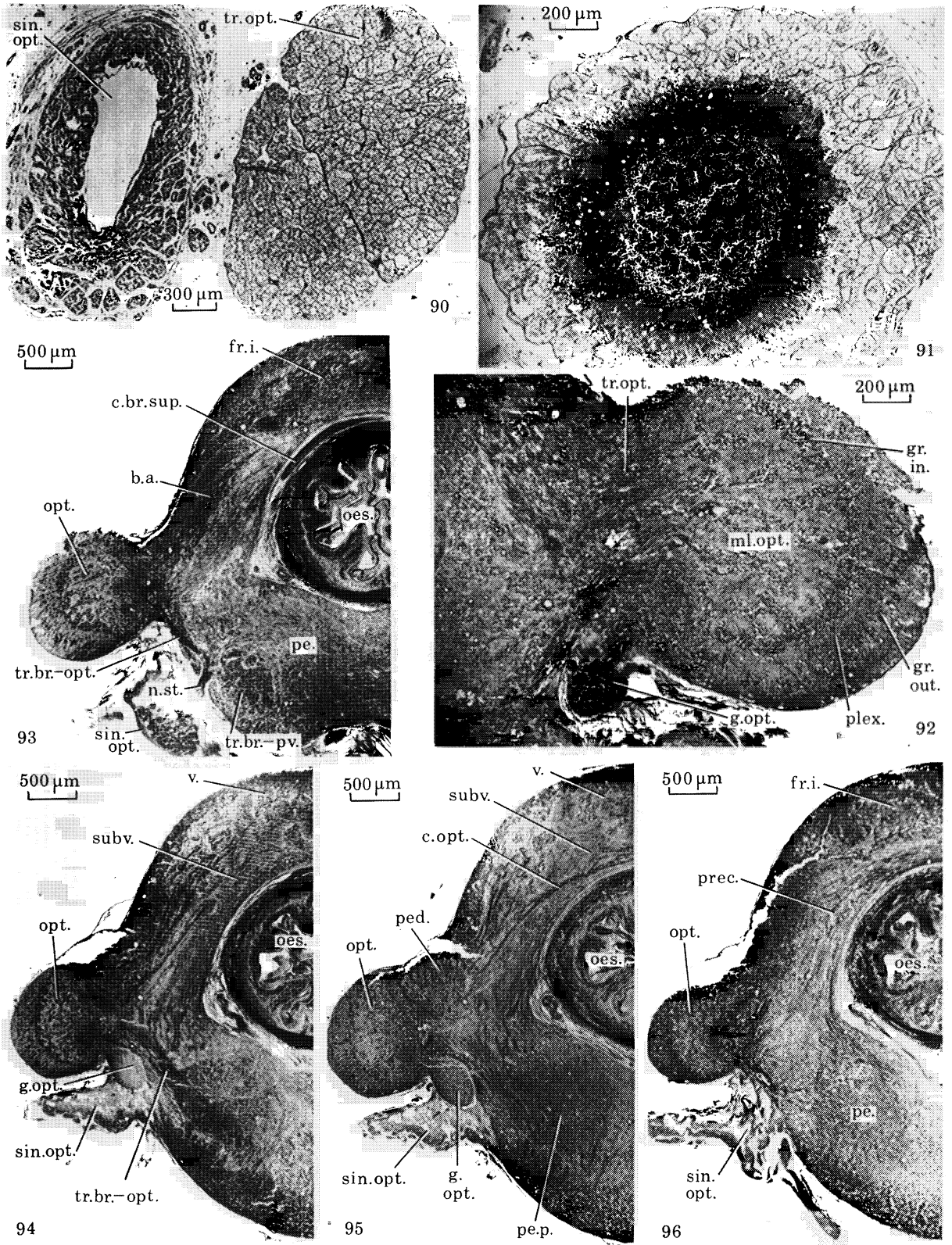
FIGURES 90–96. For description see opposite.

The rest of the middle suboesophageal mass consists of small anterior and posterior pedal regions, without clear separation. The middle pedal commissure, so conspicuous in many cephalopods, consists here only of scattered fibres, some perhaps from the static nerves. The small anterior funnel nerves arise in the posterior part immediately lateral to the pedal arteries. The median part of the posterior pedal lobe gives rise to a large tract running to the fin lobe. The region where this arises receives static nerve fibres and is continuous with the lateral pedal lobe. This whole area is evidently a centre for control of movement by the fins and arms. The walls of these parts of the middle mass are made up almost wholly of small cells.

Tracts of nerve fibres and nerve cells leave the wall to accompany the sinus that surrounds the optic nerves (figure 98, plate 17). This is an extensive system of presumably neurosecretory tissue found elsewhere in cephalopods but not usually connected with the pedal lobes (Boycott & Young 1956; Alexandrowicz 1961, 1965; Froesch & Mangold 1976).

In the posterior suboesophageal mass the parts are more nearly in the expected positions than in the other two regions. A very large brachio-palliovisceral connective sends fibres probably to all parts of the region (figure 99, plate 17). The fin lobe is very large and readily seen on the surface (figures 74 and 75, plate 12). It is almost completely cut off from the rest. It contains a uniform population of large cells, with no layers of microneurons next to the neuropil. The fin nerve arises directly from it (figure 75, plate 12). There are no signs of chromatophore lobes.

The mantle connective is smaller than the fin nerve and arises at the centre of the posterior suboesophageal mass. The outer layers of this region contain large cells at the outside and many smaller ones near the neuropil. Posterior funnel nerves arise ventrally from the front of the posterior suboesophageal mass. The large visceral nerves arise medially with roots above and below the magnocellular commissure (as in other coleoids). This part of the lobe contains many very small cells, presumably forming a vasomotor system. Some of these form an 'extracortical neuropil' around the exit of the nerve (Thore 1939). These small cells accompany the tracts of the visceral nerves for some distance.

7.6. *Magnocellular lobe*

This joins the median basal lobe dorsally and receives large tracts of fibres from this and from the optic lobes (figure 75, plate 12). The lobe passes obliquely and vertically down the side of the brain to the side of the palliovisceral lobe. There is no distinct ventral magnocellular lobe or commissure such as are present in decapods. Posteriorly the neuropil of the lobe is broadly continuous with that of the palliovisceral lobe. The cells of the wall are mostly small but there are a few large ones in the extreme anterior ventral region. These probably give rise to the several relatively large fibres (80 μm) that can be seen rather more dorsally (figure 98, plate 17). They can be followed back towards the palliovisceral lobe and are exactly in the position of the first order giant fibres of decapods. No giant fibres can be seen more posteriorly

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DESCRIPTION OF PLATE 16

FIGURE 90. Section of the optic nerves and optic sinus of *Cirrothauma* C (Bodian).

FIGURE 91. Sagittal section near the surface of the optic lobe of *Cirrothauma* B (Masson).

FIGURE 92. Sagittal section of the optic lobe of *Cirrothauma* A (Cajal).

FIGURES 93–96. Series of transverse sections through the central nervous system of *Cirrothauma* A. Figure 93 is the most anterior (Cajal).

(p. 41) but giant fibres are present in the stellar nerves of the cirroteuthid described in Young (1977 a).

The irregular strands of neurovenous tissue that accompany the ophthalmic vein are attached to the base of the magnocellular lobe (figure 98, plate 17). They continue all along its posterior part and even lie within it. The significance of this tissue is discussed by Froesch & Mangold (1976).

7.7. Basal lobe system

A remarkable feature of the brain is that the basal lobes are all large. This is very surprising since other evidence has suggested that these lobes are related largely to control of eye movements, which must be at most very weak in Cirrothauma (Young 1977 b). Indeed no eye muscles have been seen (p. 35). Obviously the basal lobes have some further functions that persist in this animal that has such poor vision. Their structure in this animal, as in others, is indeed consistent with the concept that they form a sort of cerebellum (Hobbs & Young 1973; Messenger 1979).

The peduncle and anterior and median basal lobes are closely interconnected and evidently form a single system, probably concerned with the control of movement (figure 102, plate 17, and figure 104 a, plate 18). They all receive large inputs from the static nerves as well as from the optic lobes. Their outputs go to the presumed movement centre in the lateral pedal lobe (p. 36), and to other parts of the suboesophageal lobes. They all contain the sets of parallel fibres characteristic of a cerebellum (Hobbs & Young 1973).

7.8. Peduncle lobes

These are surprisingly large considering the poor development of the eyes and the very small size of the optic lobes. As in other cephalopods they consist of a basal region and a 'spine', but only the latter is well developed. The basal region is very small and receives a few fibres from the optic lobes, whereas a large bundle from the statocysts passes directly to the spine. The spine consists of two long tracts of neuropil and one shorter one, all composed of very fine fibres and separated from each other by rows of small cells (figure 100, plate 17). The stain does not show the fibres of the neuropil clearly, but many certainly run parallel to the long axis. The lobes run up the whole length of the back of the optic tract and then forward over the top of it (figure 101, plate 17). The connections of the peduncle lobes have not been fully seen. They receive fibres from the optic lobes and from the static nerves (figure 102, plate 17). Their output probably goes to the lateral pedal lobe but there may be other connections.

Medial to the peduncle lobe lies a further lobe having a similar structure and running up lateral to the median basal to join the dorsal basal region (marked ped. ? in figure 103, plate 17). The connections of this lobe have not been determined and it is not clear whether it is also part of the parallel fibre system. It does not receive any of the large bundles of brachial and static nerve fibres. The similarity of this lobe to the peduncle lobes establishes that the latter are part of the posterior basal system.

The small olfactory nerve is seen in transverse sections. It passes up the back of the optic tract to a small olfactory lobule.

7.9. Anterior basal lobe

The three main parts of this lobe, anterior, posterior and lateral, seen in other coleoids can be recognized, but are not sharply separated. The parallel fibres that are characteristic of these cerebellum-like lobes are clearly marked. A bundle of them runs from the optic lobes

transversely and across the midline (figure 93, plate 16, and figure 104 c, plate 18). These parallel fibres thus lie in the horizontal plane, at right angles to those of the peduncle lobes (which are mostly transverse and vertical). Less compact bundles running in the third plane, sagittal vertical, are included in the lateral part of the anterior basal lobe (figure 75, plate 12).

The input to the anterior basal lobe comes mainly from the optic lobe (figure 102, plate 17, and figure 104 a, plate 18). No compact bundle from the static nerve has been followed to it. The main output pathway is to the lateral pedal movement centre, which is broadly continuous with the lateral anterior basal lobe (figure 75, plate 12). Fibres also pass forward to the anterior pedal and backwards to the posterior pedal regions. The anterior basal lobe is therefore presumably involved in the control of swimming movements, both by the arms and fins.

7.10. *Posterior basal lobes*

The region behind the optic commissure consists of a large median basal region at the sides, above which are islands of neuropil surrounded by groups of small cells, the dorsal basal lobes (figure 103, plate 17, and figures 104 b and 105, plate 18). This system makes a continuous series with the peduncle lobes and is the part of the cerebellum-like system that is mainly connected with the palliovisceral lobes. The more ventral part of it contains many fibres running transversely (figure 103, plate 17).

The input consists largely of bundles of fibres from the optic and peduncle lobes. Fibres passing down to the lateral pedal, magnocellular and palliovisceral lobes are probably mainly efferents but may include afferents from the mantle. The posterior superior ophthalmic nerve enters at the base of this lobe and may send afferents to it (figure 75, plate 12). There are bundles of fibres running between this region and the anterior basal lobe, which emphasize again that the members of the basal and peduncle lobe system probably act together in the control of movement.

7.11. *Superior buccal and inferior frontal systems*

The superior buccal lobe is attached to the rest of the brain in typical octopodan fashion. It is separated from the inferior frontal in the midline by a row of cells (figure 105, plate 18) but opens broadly to a posterior buccal lobe laterally (figure 106, plate 18). The inferior frontal system forms a broad band across the top of the supraoesophageal lobe (figure 73, and figure 88, plate 14). The very large cerebro-brachial connective enters at the side (figure 104 c, plate 18). It contains small fibres laterally which arise from the brachial nerves and are probably afferent. The larger efferent fibres medially run to the centre of the brachial lobe. The afferent fibres pass through a lateral inferior frontal (figure 107, plate 18) to a large median inferior frontal. This contains criss-crossing bundles of fibres similar to those of other octopods (figures 105 and 106, plate 18; figure 108, plate 19). Below and behind it in the midline lies an irregular system of small cells and fibres, the subfrontal lobe (figure 105, plate 18; figures 108 and 109, plate 19). Processes of the outer layer of cells of the median inferior frontal pass down across the incoming bundles from the arms and enter the subfrontal tissue. This is exactly the arrangement found in *Octopus*, but in *Cirrothauma* the subfrontal tissue is an irregular set of cells and islands of neuropil (figure 108, plate 19). The cells are smaller than any others in the brain and are probably amacrine microneurons, with no axon extending outside the lobe.

The posterior buccal lobe lies lateral and anterior to the subfrontal. It sends a large bundle to the cerebro-brachial connective, presumably containing descending fibres (figure 109, plate 19).

Posteriorly it opens widely to the subvertical lobe, from which it presumably receives the influence of the vertical lobe system (figure 106, plate 18). The posterior buccal lobe also receives a large inferior frontal to median basal tract from behind, running beneath the anterior basal lobe. As in other forms this tract is difficult to follow backwards but probably carries fibres in both directions, allowing integration of the tactile and palliovisceral systems.

7.12. *Vertical lobe system*

The superior frontal can be recognized as a very small lobule behind the median inferior frontal lobe, from which it receives fibres (figures 106 and 107, plate 18). It communicates behind with the vertical and subvertical lobes. No fibres have been traced to it from the optic lobes but it is impossible to be sure that there are none.

Behind this lobule follow a series of others that presumably represent the vertical lobes but are unlike those of any incirrate octopod. They consist of islands of cells separated by neuropil and with no clear division into vertical, subvertical and dorsal basal lobes (figure 106, plate 18). There are no external or internal signs of division into five regular lobules such as those of *Octopus*. Fibres enter the system from the front, some through the superior frontal and more from the posterior buccal lobe. Many fibres also run between these lobes and the optic lobes, but their direction cannot be determined (figures 94 and 95, plate 16).

Tracts also reach down to the suboesophageal lobes from this system through a precommissural region (figure 96, plate 16). Some pass forwards to the lateral pedal lobe and others pass backwards to the palliovisceral lobe.

7.13. *Optic glands*

These lie below the optic tract at the back (figure 95, plate 16) although in most, but not all, other cephalopods they lie dorsally. They were slightly yellowish brown in colour, and their structure is similar to that of other cephalopods. They are more clearly related to the neighbouring neural structures in *Cirrothauma* than in incirrates. This condition appears, especially in our large female, specimen C (figure 110, plate 19). Here the gland is a large mass closely connected with the peduncle lobe. A large tract of neuropil and nerve fibres spreads out as strands within this tissue. The central part is thus clearly nervous, the more peripheral part wholly glandular. In the two smaller animals the gland was smaller and less abundantly penetrated by nervous tissue but still not sharply separated from it. The glandular cells are larger than the nerve cells.

DESCRIPTION OF PLATE 17

FIGURE 97. Sagittal section of central nervous system of *Cirrothauma* B (Masson).

FIGURE 98. Horizontal section of magnocellular lobe, giant fibre and neurovenous tissue of *Cirrothauma* B (Masson).

FIGURE 99. Horizontal section of suboesophageal lobes of *Cirrothauma* B (Masson).

FIGURE 100. Sagittal section of the peduncle lobe of *Cirrothauma* A (Cajal).

FIGURE 101. Sagittal section of the optic tract, peduncle lobe and optic gland of *Cirrothauma* B (Holmes).

FIGURE 102. Horizontal section to show close relations of the peduncle and basal lobes (*Cirrothauma* B, Masson).

FIGURE 103. Transverse section to show lobule lying between the peduncle and median basal lobes (*Cirrothauma* A, Cajal).
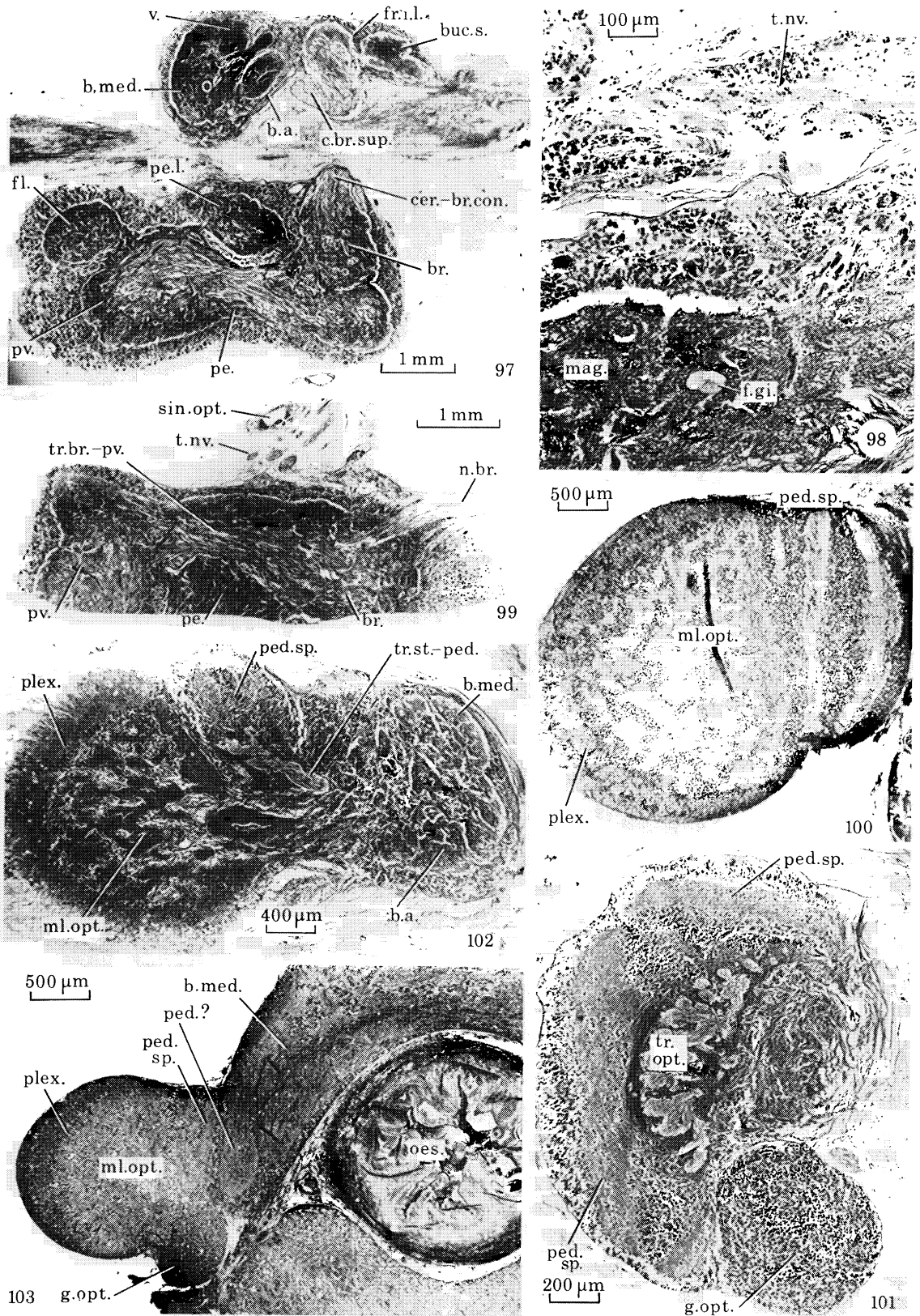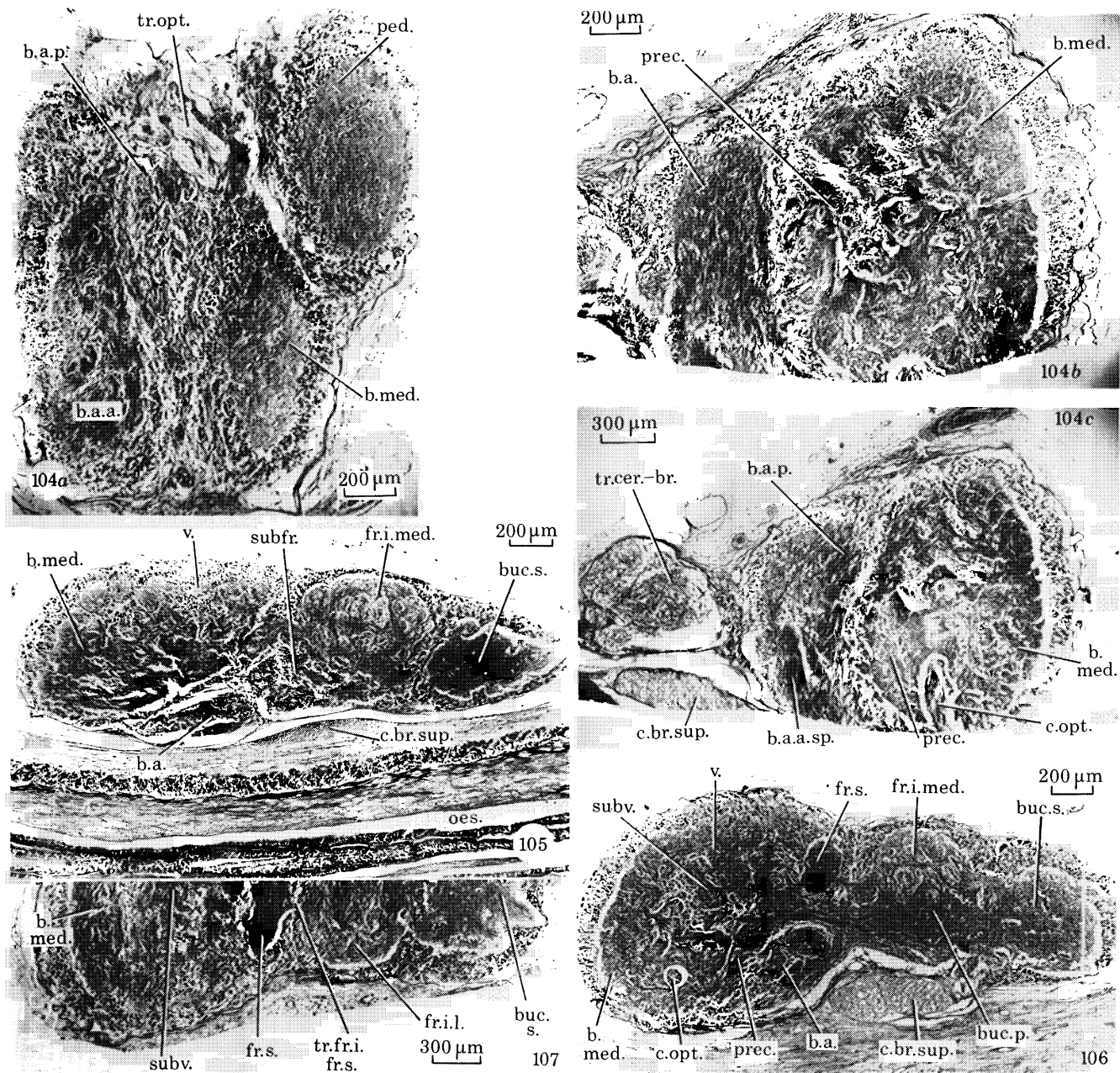
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FIGURES 97–103. For description see opposite.

FIGURE 104a. Sagittal section to show close relations between the peduncle lobe and basal lobes (*Cirrothauma* B, Masson).

FIGURES 104b AND 104c. Horizontal sections of the basal lobes; figure 104b is the more dorsal (*Cirrothauma* B, Masson).

FIGURES 105 AND 106. Sagittal sections of the supraoesophageal lobes. Figure 105 is nearer the midline. (*Cirrothauma* B. Figure 105 Holmes; figure 106 Masson.)

FIGURE 107. Horizontal section of the supraoesophageal lobes (*Cirrothauma* B, Masson).

DESCRIPTION OF PLATE 19

FIGURES 108 AND 109. Transverse sections of the inferior frontal system (*Cirrothauma* A, Cajal).

FIGURE 110. Transverse section to show the two parts of the optic gland in a mature male (*Cirrothauma* C, Bodian).

FIGURE 111. Stellate ganglion of *Cirrothauma* C.

FIGURE 112. Epistellar body of *Cirrothauma* A (Cajal).
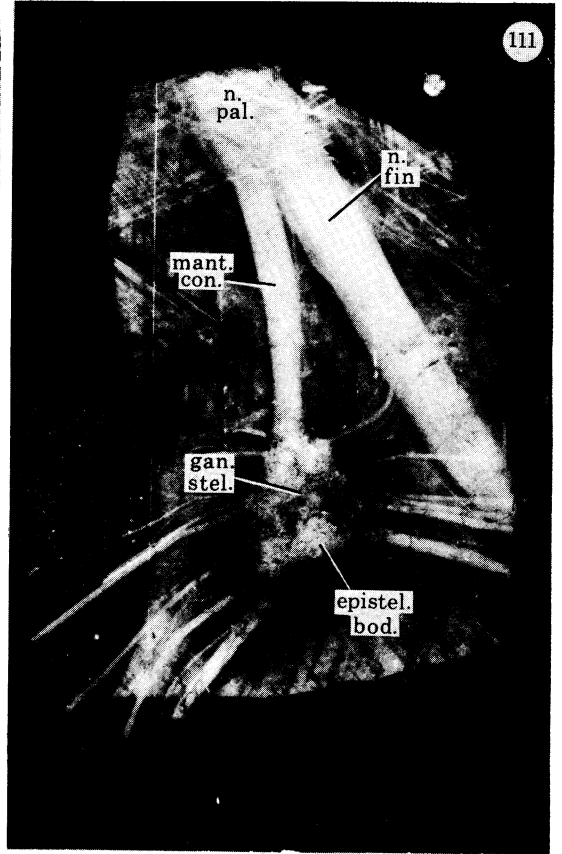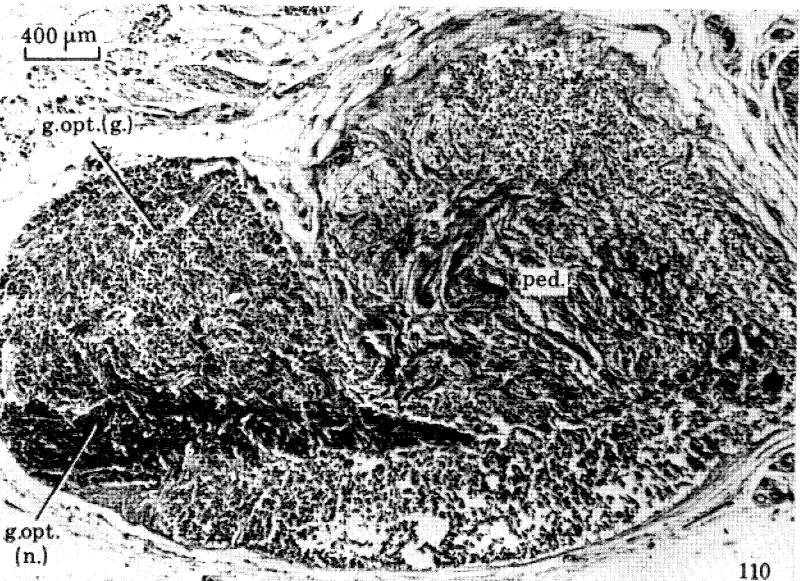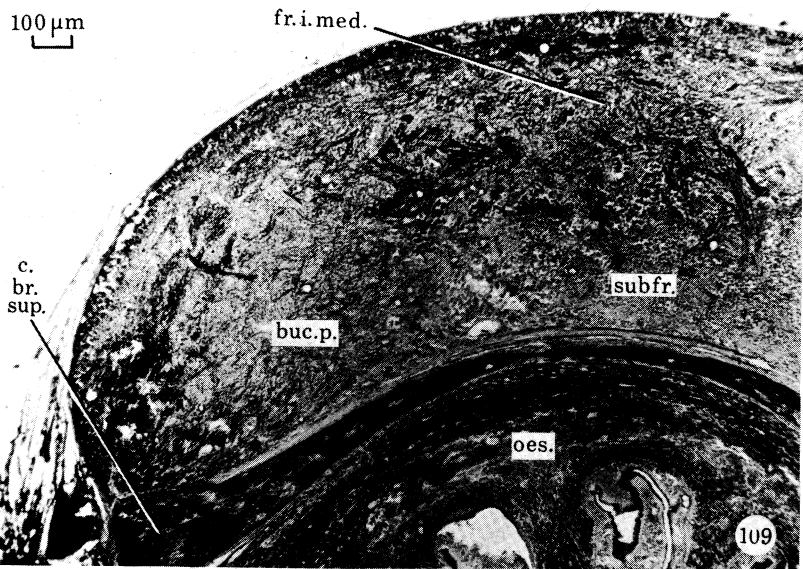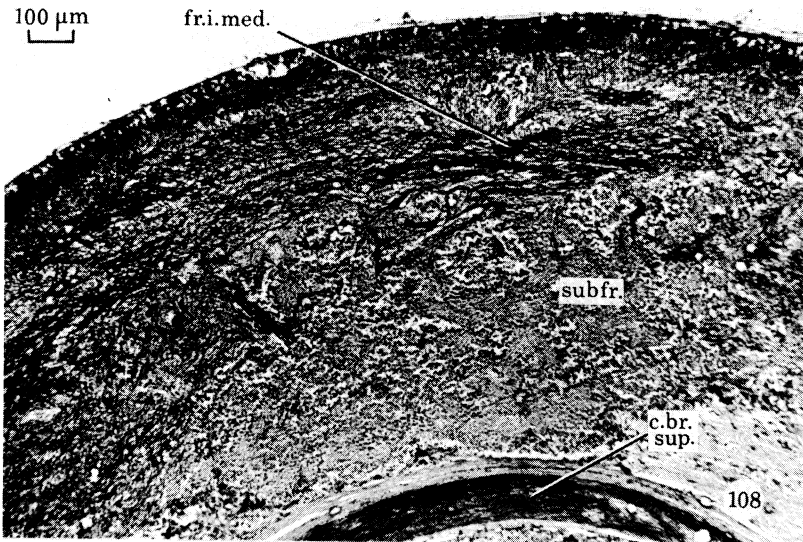
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Aldred et al., plate **19**
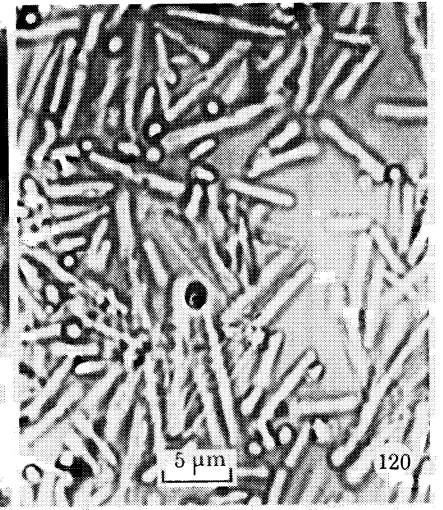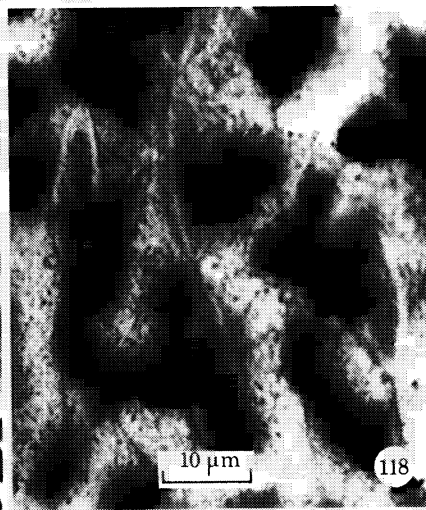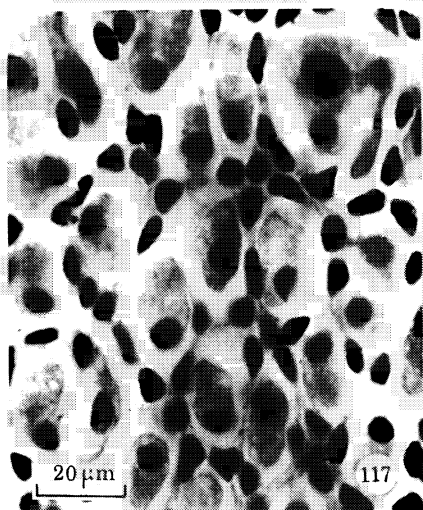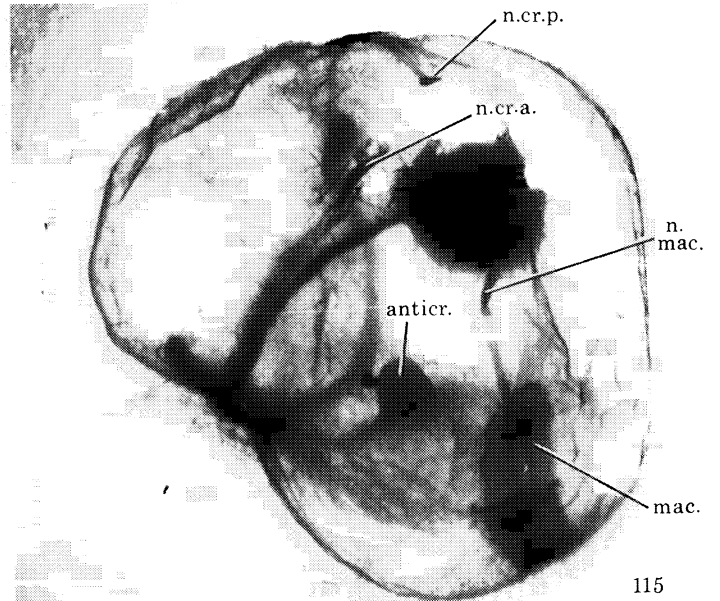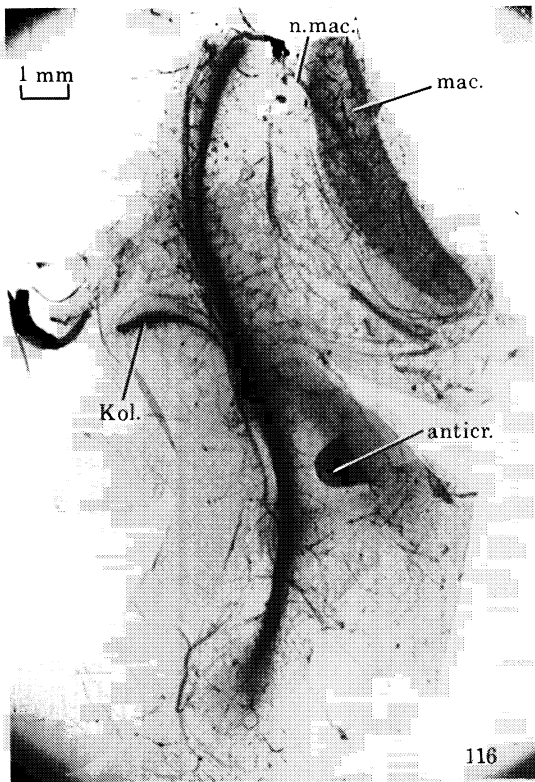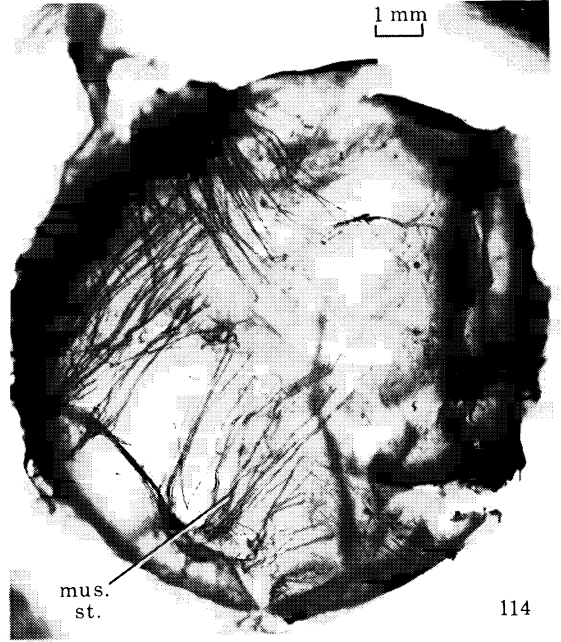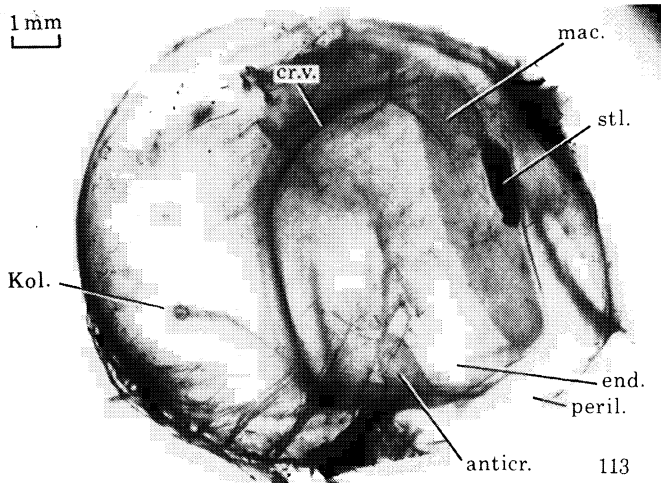
FIGURES 108–112. For description see opposite.

7.14. *Stellate ganglion and epistellar body*

The mantle connective and fin nerve have rather similar fibre contents. There are no out-standingly large fibres but a graded distribution from the smallest up to a few of 20 μm diameter. The arrangement of the stellate ganglion is similar to that of a decapod. The mantle connective leaves the fin nerve and the latter runs on past the ganglion (figure 111, plate 19). The stellar nerves arise from protuberances on the surface of the ganglion. Some of the nerves on the medial side appear to join the fin nerve.

The stellate ganglion has a thinner ventral wall of large cells and a thicker dorsal one includ-ing small and large cells, as in *Octopus* (Young 1972). There are no outstandingly large fibres in the neuropil, nor in the stellar nerves.

The epistellar body is a large irregular sac with several lobules and maximum diameter 1.5 mm, occupying the whole of the back of the ganglion (figure 112, plate 19). There are pigmented amoebocytes covering the tips of the rhabdomes and a mass of debris at the centre. The rhabdomes are up to 400 μm long and rather regularly arranged. This body is therefore much larger than in most octopods and evidently has an important function (p. 20).

7.15. *The statocysts*

The very large statocysts lie close together at a considerable distance from the brain, as isolated sacs, not enclosed in cartilage (figure 72, plate 12, figure 88, plate 14, and figure 89, plate 15). Externally they are almost spherical, each up to 10 μm diameter and of typical octopod form, with outer and inner sacs, separated by a perilymph crossed by strands (figure 113, plate 20). Large bundles of muscle fibres are attached laterally to the outer sac (figure 114, plate 20). Each sac is connected with the brain by long static nerves, each con-taining one macula nerve and anterior and posterior crista nerves. The inner sac is not quite spherical but has slightly larger medial and smaller lateral chambers, separated by a slight con-striction at the crista (figure 115, plate 20).

7.15.1. *Macula*

Each macula is an elongated oval area curved around the antero-median wall of the sac (figures 113 and 116, plate 20). The hair cells have oval bases surrounded by numerous support-ing cells (figure 117, plate 20). Their tops are drawn out to carry rows of hairs orientated along the long axis of the macula (figure 118, plate 20). Large cells around the edge are probably neurons. The macula nerve arises from the centre (figure 116, plate 20).

The edge of the macula is sharply marked and it is therefore easy to be sure that there is no trace of any areas of maculae neglectae with cells orientated in directions other than the vertical.

DESCRIPTION OF PLATE 20

FIGURE 113. Statocyst of *Cirrothauma* A, seen from the medial side after removal of the muscles.

FIGURE 114. Statocyst of *Cirrothauma* C, from above.

FIGURE 115. Statocyst of *Cirrothauma* A, showing the muscles attached to the lateral side.

FIGURE 116. Flattened wall of the statocyst of *Cirrothauma* A (Bodian).

FIGURE 117. Macula of *Cirrothauma* A, showing nuclei of hair cells and supporting cells (Bodian).

FIGURE 118. Surface of the same preparation showing the rows of cilia.

FIGURE 120. Statoconia of *Cirrothauma*.

Statoliths were preserved in two of our specimens, but they may be damaged by fixation. They were compact bodies, smaller than the maculae, and of differing shapes in the two animals (figure 119a, b, plate 21). The surfaces show numerous pits, perhaps points of attachment. The statolith is composed of a mass of elongated statoconia, crystals of various sizes and with some differences in shape. The largest are flattened plates, up to 13 μm long and 0.2 μm wide, with a constriction or clear space at the centre (figure 120, plate 20). Others are spindle-shaped or cylinders with flattened ends. The smaller ones have a similar range of shapes. In the statolith they are probably all lined up in parallel.

7.15.2. *Crista*

This runs as a continuous strand without any sharp division into sections (figure 116, plate 20). The greater part of it runs nearly in the sagittal plane around the centre of the sac (figure 113, plate 20). The anterior portion, however, closest to the macula, turns more dorsally and medially. This part thus lies approximately in the transverse plane and corresponds to the transverse horizontal crista of *Octopus* (Young 1960; Budelmann 1977). This section receives the anterior crista nerve. The next portion of the crista, lying in the lateral wall, corresponds to the longitudinal crista and the final part is approximately in the position of the vertical crista. A posterior crista nerve joins the end of the vertical crista, but it is uncertain where the division between innervation by the two nerves lies. Since the crista lies around such a large cavity each of these parts of it is suited for transducing slow movements. In the head-down position the animal presumably makes turning movements about a longitudinal axis. The greater part of the crista lies in a plane that would allow the cupulae to be activated by such rotations, the endolymph moving between the two major parts of the sac.

The crista contains a central row of large cells and several subsidiary rows, but the details have not been seen. Large cells beneath the crista are probably multipolar neurons (figure 121, plate 21). The presence of these cells shows that some of the hair cells are secondary sense cells, making contact with neurons. However, some of the hair cells undoubtedly carry axons. The crista nerve contains some large fibres (up to 10 μm diameter) and these show striking dilatations, up to 30 μm(figure 122, plate 21). These are present in specimens from two individuals and are not likely to be wholly artefactual. At the dorsal end of the vertical crista a fan of fibres spreads out over the wall of the sac (figure 116, plate 20). The fibres continue as a plexus, presumably of nerve fibres but containing also many cells of various shapes (figure 123, plate 21). Some of the cells are rounded, others branched or drawn out into long processes at either end of the nucleus. Similar cells have been seen in *Vampyroteuthis* but their nature is uncertain (Stephens & Young 1976). No undoubted hair cells were seen in the wall, but they may be present.

DESCRIPTION OF PLATE 21

FIGURES 119a AND 119b. Statoliths of *Cirrothauma* A and C respectively.

FIGURE 121. Part of the crista of *Cirrothauma* A, showing the large multipolar cells.

FIGURE 122. Varicose nerve fibres below the crista of *Cirrothauma* B (Holmes).

FIGURE 123. Elongated cells and fibres in the wall of the statocyst of *Cirrothauma* A (Bodian).

FIGURE 124. Kölliker's canal of *Cirrothauma* A (Bodian).
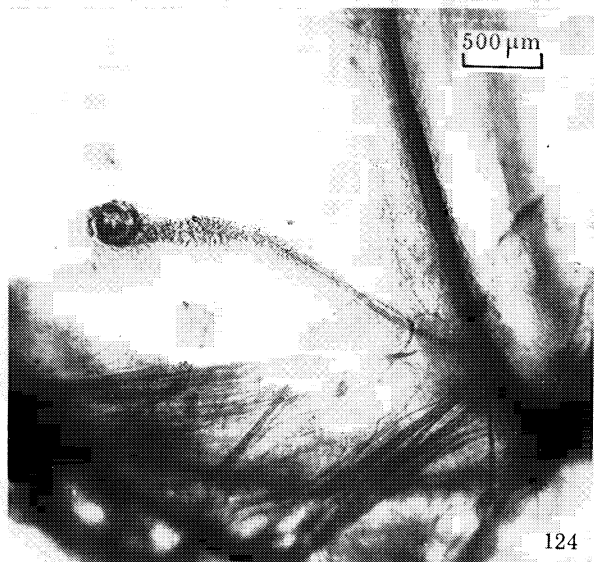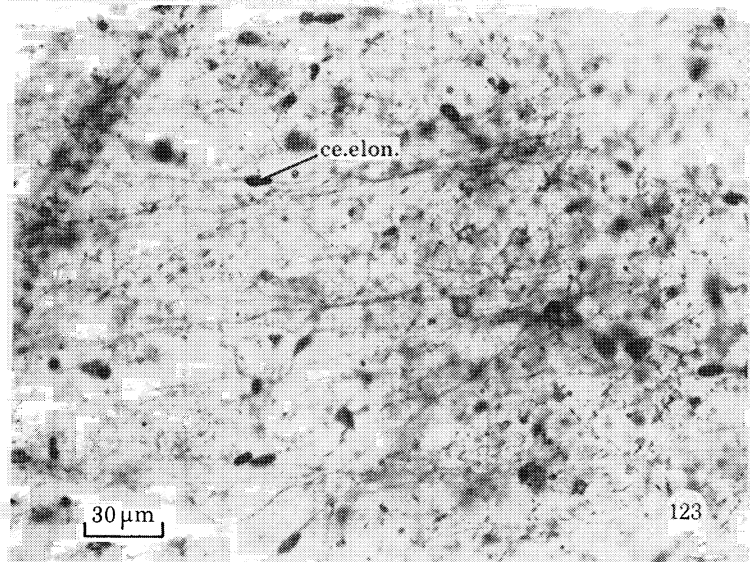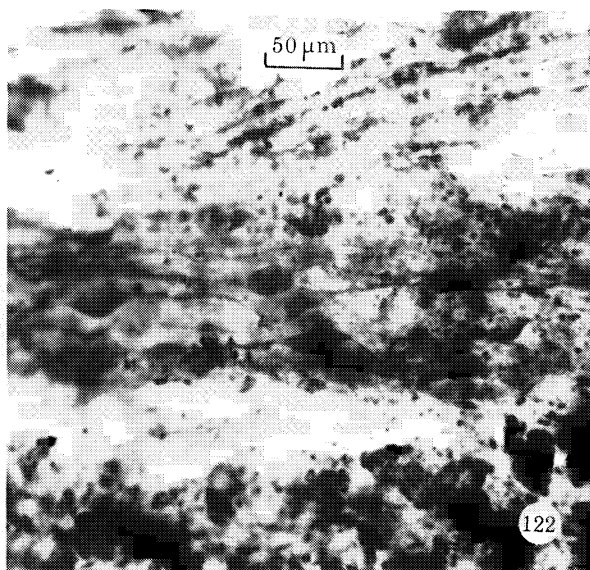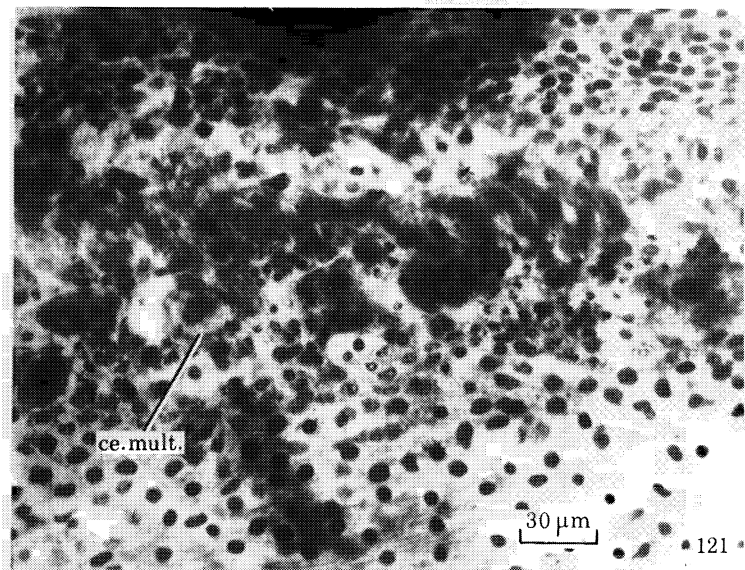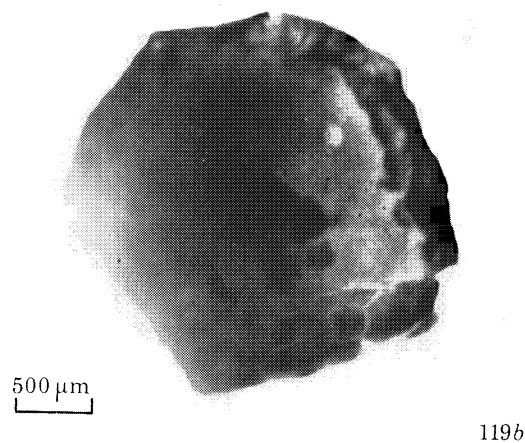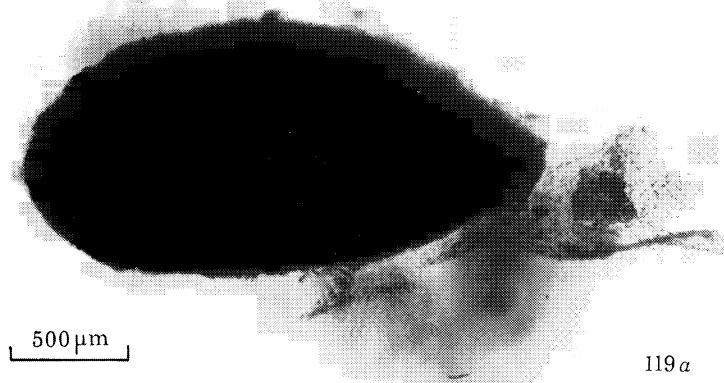
FIGURES 119 AND 121–124. For description see opposite.

The single anticrista is a large knob of cartilage standing on the medial side of the crista, close to the outer end of Kölliker's canal (figures 113, 115 and 116, plate 20). This is comparable to the position of the more expanded anticrista of *Octopus*. In *Cirrothauma* the peg is small in relation to the large sac and its function remains obscure (see p. 49).

Kölliker's canal is well developed in *Cirrothauma* as in all the cirrates. Its inner opening is a large funnel, surrounded by an area with long cilia (figure 124, plate 21). The proximal section of the duct is lined by very tall cells probably secretory. The terminal portion is a narrow canal, lined by cubical cells and ending close to the crista. It is not certain whether there is an opening at this point. The appearances suggest that this apparatus functions to keep the sac distended by endolymph.

8. GENERAL DISCUSSION

8.1. *Habitat and depth distribution*

The cirrates mostly live below 1000 m, many in excess of 2000 m (Robson 1926, 1932*b*; Voss 1967). Photographic records have shown them at 5145 m (Jahn 1971), at 3500–5200 m (Roper & Brundage 1972), and between 2360 and 3786 m (Pearcy & Beal 1973). One cirrate octopod has been captured at 7279 m, a world depth record for a cephalopod (G. L. Voss, personal communication). *C. murrayi* has been captured between 1500 and 4500 m (table 1), sometimes close to the bottom but often several hundred metres or more above it in open mid-water trawls at 1500–4050 m (Roper & Young 1975). It has been photographed at 3600 m (Ballard 1976; identified by R. G. A.). The only shallow-water record was the specimen dipped through an ice hole (see Voss 1967; Roper & Brundage 1972).

The photographs published by Roper & Brundage (1972) show cirrates to be suprabenthic, living close to the bottom but not actually in contact with it. *Opisthoteuthis* Verrill, 1883 was thought by Robson (1932*b*, p. 19) to be benthic as its shape seemed unsuitable for swimming or floating. Pereyra (1965) observed live *O. californiana* Berry, 1949 in an aquarium, where they exhibited quite efficient swimming, mainly using the pulsation of the web and arms (p. 45). However, these animals rested on their arms between bouts of swimming and Pereyra therefore described them as benthic.

Previous records (see table 1) suggest that *Cirrothauma* does not rigidly follow the suprabenthic habit either, but may be described as benthopelagic (i.e. migrating periodically into midwater from the benthic or suprabenthic environment). Of the five specimens previously recorded, three were captured with midwater nets, and one, despite being taken with a benthic trawl, was considered by Roper & Brundage (1972) more likely to have been captured during shooting or hauling. The R.R.S. *Discovery* catches confirm that *Cirrothauma murrayi* is found near the sea bed (bathybenthic) and in midwater (table 1).

Specimens A and B were captured in opening–closing midwater nets; A between 1500 and 4650 m and B between 3000 and 3500 m. The soundings at the stations where these animals were taken show that they were respectively at least 450 and 300 m off the bottom. Of the four specimens from otter trawls, C, D and E were captured in approximately 4000 m, D and E being in the same haul, while F was from approximately 4500 m. As the trawls used to catch specimens C–F were non-closing there is no certainty that they were taken close to the bottom. However, although the OTSB will fish in midwater if towed at a constant depth, during shooting and hauling the angle of the net appears to make the effective mouth area very small. Consequently, capture of anything but a small quantity of the more abundant groups is

unlikely (N. R. Merrett, personal communication). Several other cirrates, never previously taken in midwater were also present in the same catch as specimens D and E. Furthermore, only two *Cirrothauma* have been caught by boats of the Institute of Oceanographic Sciences in mid-water nets during many thousands of hours fishing, whereas four have been taken in benthic trawls with considerably less fishing effort. Additional evidence that *Cirrothauma* is suprabenthic for part of the time is given by the photograph taken from the submersible *Alvin* showing a cirrate octopus swimming just above the bottom in 3600 m (Ballard 1976). Although identification from photographs is difficult, there is little doubt in this case that the animal in the photograph is *Cirrothauma* (figure 125).

8.2. *Life cycle*

It is possible to say a little about the life cycle of this animal. In the period 12 April to 1 May four specimens of mantle length 21, 105, 155 and 220 mm have been taken, the largest was gravid while the two smallest were taken in the same haul, the size range being wide in one month of the year. This is not surprising as eggs of various sizes and stages of development were present in each of the two gravid females captured, large ones being in the oviduct (see p. 18). Eggs must be laid singly or in small numbers, and at intervals over quite a long period after reaching maturity since approximately 200 eggs (0.4–14 mm) were present in one female. Eggs of varying sizes are found in *Cirroteuthis mülleri* Eschricht, 1836 (Reinhardt & Prosch 1846), *Opisthoteuthis depressa* (Meyer 1906a) and *O. californiana* (Pereyra 1965).

TABLE 6. THE SIZE OF EGGS AND YOUNG OF VARIOUS CEPHALOPODS

	development	egg size mm	embryo mantle length mm	embryo fin length mm	
Stauroteuthis syrtensis		11 × 6			Verrill 1885
Grimpoteuthis meangensis		12.2 × 6			Robson 1932b
Opisthoteuthis californiana	all stages in female	9 × 5			Berry 1952, Pereyra 1965
unidentified cirrates					
A		12–15	3	3	
B		12 × 9	5	3	
C		24 × 11	9	4.5	Boletzky 1982
D		12.5 × 8	4	—	
E		*ca.* 12	9	4	
F		*ca.* 16 × 9	3	1.5	
Cirrothauma murrayi	all stages in female	14 × 8.9			this paper
Octopus vulgaris		1 × 3	2		Robson 1929, Boletzky 1977, 1978, Ambrose 1981
Octopus joubini		7	4		Bradley 1974
Vampyroteuthis infernalis	all stages in female	3.33			Pickford 1949

Verrill (1885) described eggs, presumably of cirrates, containing embryos with 'a well-developed body rounded behind with relatively large, rather broad lateral fins ... as long as the breadth of the body'. These eggs were attached to gorgonians and taken from depths of 900–2000 m. Robson (1932b, p. 145) found 'a few large elongate eggs measuring 12.2 mm' in a specimen of *Grimpoteuthis meangensis* (table 6). Boletzky (1982) has recently examined cirrate eggs collected from different parts of the world, taken at depths of 1218–4715 m, and all are large, being 12–24 mm in length (table 6). Thus the cirrate eggs so far known are large and similar in size to those of benthic incirrate octopods such as *Eledone*, which has an egg of

13 mm × 4.5 mm (Arnold 1971). They are quite different from the small, pelagic eggs of *Vampyroteuthis* (Pickford 1949*a*) and of the pelagic incirrates such as *Argonauta argo*, 0.6 mm × 0.8 mm, *Tremoctopus violaceus*, 0.9 mm × 1.5 mm, and *Ocythöe tuberculata*, 0.9 mm × 2.0 mm (Naef 1928, p. 71).

It is possible that the large eggs are laid, two at a time, on the bottom attached to the substratum. The descriptions of cirrate embryos have all included a comment on the large fins (table 6; Verrill 1885; Robson 1932*b*; Boletzky 1982) and are so in the baby cirrate (figure 3). This suggests an important role for the fins in the early part of the life cycle.

8.3. *Buoyancy and locomotion*

This gelatinous animal has many vacuolated cells and much reticulate tissue, an indication that probably it is neutrally buoyant (Denton 1974; Clarke *et al.* 1979). We do not know the mechanism involved and tests have not shown the presence of large quantities of ammonium ions. At the depths at which *Cirrothauma* lives the temperature is low and movement probably slow; indeed other cirrates have been observed to swim at 2.2 km h^{-1} (Roper & Brundage 1972) and at 0.46 km h^{-1} (Brundage *et al.* 1967). One cirrate, probably *Cirrothauma*, was seen and photographed while swimming past the submersible *Alvin* using power strokes of the fins. Dr R. D. Ballard, who made this observation, tells us that the animal 'was most definitely propelling himself with his fins with his hooded tentacles trailing passively behind'. The comment of the pilot of the *Alvin* at the time of sighting 'He flies with his ears' seems most apposite; and he also added 'when he opens, his webbed tentacles make him look like a big umbrella'. Another cirrate was pursued by Dr Ballard in the *Alvin* during a dive and a film made during the chase demonstrates again that the animal can move fastest by fin-swimming. Using long slow strokes the octopod swam only with its fins (figure 125). No contraction of the mantle, indicating jet propulsion, could be detected.

It is not likely that *Cirrothauma* moves by jet propulsion since the mantle-opening is minute (Robson 1932*a*; Bidder 1970), especially considering the size of the animal, and the very long, slender funnel has an extremely small orifice. There are no giant fibres and the mantle musculature is much reduced. The fins, however, are supported by a very large gladius and have a dense musculature; there is also a large fin lobe in the brain. The animal becomes streamlined during fin-swimming aided by the smooth skin. All these features strongly support the suggestion that locomotion is either by means of the fins or medusoid (Bidder 1970). There is some evidence that cirrates spend much if not most of their time in the medusoid form, suspended about a metre above the bottom (Roper & Brundage 1972). Movement in this position is achieved by the production of a jet of water from the bell, by contraction of the arms and web (Bidder 1970; and see Trueman 1975). Such medusoid swimming has been observed in *Opisthoteuthis* (Pereyra 1965; R. G. A., personal observation). We also know that the fins stroke horizontally when the mantle is perpendicular to the bottom and the animal moves sideways; this is evidenced from photographs taken at intervals of 15 s (Pearcy & Beal 1973).

8.4. *The suckers and cirri*

The hypothesis has been made that when the sucker takes an object it first forms a seal by means of the soft, folded rim, while the infundibulum becomes attached to the foreign surface by adhesion, followed by suction, the tiny pores acting like capillaries, each one a miniature sucker (Nixon & Dilly 1977). The effectiveness of such a system depends upon the surrounding

pressure and calculations have been made of the number of pores, each about 0.1 µm in diameter in octopods, needed for such a system to support 10 g at different depths. At 10 m depth 6×10^7 pores are needed, at 100 m 1×10^7 and at 1000 m 2×10^5, while at 4000 m only 5×10^2 pores would be needed. Thus, such a means of adhesion would be expected to require
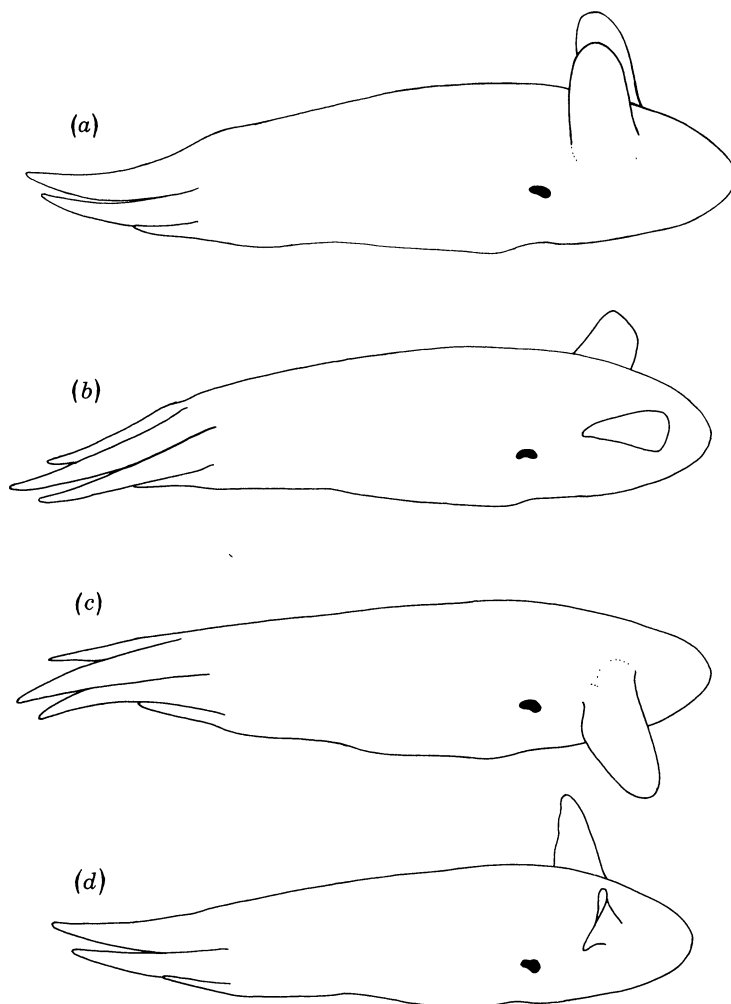
FIGURE 125. Outline drawings from a film of a cirrate to show the fin movements while swimming. The fins are fully raised (a), partway through a downstroke (b), at completion of downstroke (c) and partway through an upstroke (d). (Filmed from the *Alvin* by Dr R. D. Ballard.)

fewer pores the deeper the animal lives. This seems to be borne out by the conditions in *Cirrothauma* which has only some 320 small suckers with few pores in contrast with more than 1000 much larger suckers with many pores in *Octopus vulgaris* of similar body size but living in shallow water, the dimensions of the pegs and pores being similar in the two animals. The cuticular pores of the infundibula of the suckers of *Cirrothauma* thus almost certainly permit these structures to act as suckers, even in the absence of the suction chamber that is usually found in cephalopods.

The small 'light organs' in the base of the sucker peduncles are present in both males and females, and their function is presumably for mutual recognition for mating. The presence of

light organs in other octopods has recently been demonstrated (Robison & Young 1981). A bright yellow organ surrounds the mouth of large females of the bathypelagic *Eledonella pygmaea* and *Japetella diaphana* when sexually mature, but is resorbed during brooding. It is absent from the males of both species.

8.5. *Food and digestion*

The buccal complex of cirrate octopods has been described by Meyer (1906*a*), and Ebersbach (1915); their findings were summarized by Robson (1926, 1932*b*). Chun (1913, 1914) did not examine the digestive system of *Cirrothauma*. No radula was found in *Opisthoteuthis californiana* (Berry 1952). In *Cirroteuthis umbellata* Fischer, 1883 (Ebersbach 1915) it is reduced to a grinding plate with three simple teeth in each row. If the toothed structures of *Cirothauma*, eroded by amoebocytes, are the remnants of a radula then it must have developed and been retained through the early part of the life cycle. The reduction of the radula in cirrates may be connected with the fact that they swallow whole small prey. *Spirula spirula* has no radula (Kerr 1931) and small crustaceans have been found in its stomach (Young 1977*a*), some at least having been taken whole.

In *Cirrothauma* the large buccal cavity, the cuticular covering of the buccal complex, oesophagus and stomach strongly suggest that whole organisms, especially crustaceans, are important in the diet. The few records available of stomach contents of cirrates show that small and sometimes whole crustaceans are present (Scott 1910; Ebersbach 1915). Robson (1932*b*, p. 122) found large pieces of polychaetes in *Grimpoteuthis glacialis*. *Opisthoteuthis californiana* lives on the continental slope, and eats crustaceans, mostly small mysids (7 mm long), large copepods, amphipods and even shrimps of 22 mm length; most had been taken whole and not broken up during feeding; only one had been noticeably bitten.

The stomach of *Cirrothauma*, like that of *Eledone* (Isgrove 1909) has a ridged cuticle forming a gizzard. If whole crustaceans are taken then the two thick muscular walls over the ridged cuticle may exert pressure on the prey. If the musculo-skeletal attachments of the crustacean prey are separated by enzymatic action of the salivary secretions, as they are by *Octopus vulgaris* (M. Nixon 1983), then the tissue could be squeezed out, leaving the disorientated, separated pieces of the exoskeleton undamaged externally.

8.6. *The 'posterior' salivary gland*

The similarity between the features of the salivary papilla of *Cirrothauma* and that of *Octopus vulgaris* and *Eledone cirrhosa* (Nixon 1979*a, b*; Nixon *et al.* 1980) strongly suggests that the single, median salivary gland in *Cirrothauma murrayi* is comparable with the paired posterior salivary gland of these species. That the gland is so far forward in *Cirrothauma* (and also in *Grimpoteuthis umbellata* (Ebersbach 1915)) makes the name ambiguous but, in view of its otherwise close similarity with the posterior salivary gland of other octopods, this name should be retained. There is no evidence to show whether the gland produces a toxic or enzymatic secretion such as is found in coastal octopods (Ghiretti 1959, 1960; Cariello & Zanetti 1977) but this is likely since the contents appear to be expelled all at the same time (p. 30). The duct is ideally sited for ejecting the secretion.

The anterior position of the 'posterior salivary gland' may indeed be its original site in octopods since in *Octopus vulgaris* the nerve of the posterior salivary gland runs *forwards* to the base of the salivary papilla before turning back along the single duct to reach the paired glands (Pfefferkorn 1915; Young 1971) lying in the mantle cavity. Kerr (1931) says of this gland in

Spirula spirula that 'From the position in which its duct opens we may safely infer that it had primitively the form of a glandular involution of the epithelium covering the tip of the sub-radular organ . . . the gland is now far removed from its place of origin.'.

8.7. *Functioning of the receptors and brain*

The eyes of *Cirrothauma* are simple and having no lens presumably do not serve to discriminate between visual images. Yet they obviously function as photoreceptors perhaps to bioluminescent prey or enemies, or for orientation in relation to a mate, guided by the possible light organs which are present in males and females. The wide aperture of the cornea allows for detection of flashes over wide angles and for greater sensitivity. In this, of course, these eyes resemble those of *Nautilus*. Does this suggest the possibility that *Cirrothauma* represents a primitive state among coleoids? It is more likely to be a secondary loss in the deep-sea environment as *Cirrothauma* is the only cirrate octopod lacking a lens. The deep-sea teleost *Ipnops* has no lens and the eye is reduced to a cornea and retina spread out flat on the head (Munk 1959).

The visual system lacks several of the characteristic features of other cephalopods. The fibres from dorsal and ventral halves of the retina do not decussate. This absence agrees with the view of Young (1962) in which the presence of the chiasma was related to inversion by a lens (Scholes 1981). Without information about the use of the eye it is useless to speculate how a well formed chambered eye can have developed without a lens and chiasma. The granule cell layers and columnar organization of the optic lobes are greatly reduced, which suggests that these are necessary only for form discrimination. The small optic lobes and very small superior frontal lobe suggests that there is probably very little visual learning. On the other hand, the peduncle and basal lobes are very large, making up the greater part of the supraoesophageal lobes. This shows that the lobes are concerned with general orientation and not only with control of eye movement as in other cephalopods since this can hardly be an important activity in *Cirrothauma*. The peduncle and anterior basal lobes have sets of fine parallel fibres, indicating that they have a cerebellar-like function (Hobbs & Young 1973). This is interesting in an animal that is presumably rather sluggish in movement.

The large volume of the statocysts is clearly related to slow turning (Maddock & Young 1983). The unusual orientation of the crista round the middle of the statocyst in the sagittal plane is suitable to monitor accelerations when the head turns to right or left in either the yawing or in the rolling plane. These may well be common directions of turning if the animal hovers with the head downwards.

The eyes and statocyst may be largely responsible for control of orientation, but detection of food is probably a function of the arms, including the cirri. The well developed inferior frontal system is obviously well suited for chemotactile discrimination and perhaps learning the characteristics of suitable prey. The superior frontal and vertical lobes in this animal are probably exclusively related to the tactile system. In *Octopus* they participate in both visual and tactile learning (Bradley & Young 1975).

8.8. *Comparison of Cirrothauma with other cirrates*

Robson (1932*b*) divided the cirrate octopods into three families: the Cirroteuthidae, containing only *Cirroteuthis mülleri*; the Stauroteuthidae containing *Stauroteuthis*, *Grimpoteuthis*, *Chunioteuthis*, *Froekenia* and *Cirrothauma*; and the Opisthoteuthidae, containing two subgenera of *Opisthoteuthis*. The principal features of the Stauroteuthidae to which Robson assigned

Cirrothauma are: single web (i.e. no intermediate web), small mantle opening, median adductor present, gills of 'half-orange' type and shell vestige U- or V-shaped. *Cirrothauma* does, however, have an intermediate web, the gills are not of the 'half orange' type and the fin support is similar to the type described by Robson as 'saddle-shaped'. On the other hand, there is a median adductor muscle and the mantle opening is small. This last feature probably varies considerably among the various groups and the median adductor muscle may well prove to be present in all cirrates. Robson describes *Cirroteuthis* as not having a median adductor muscle but in the specimen of *C. mülleri* from Voss's collection at Miami the adductor, although small, is clearly present.

It seems therefore that *Cirrothauma* is much more closely related to *Cirroteuthis* than to the members of Robson's Stauroteuthidae, a view shared by G. L. Voss (1977, p. 578), who placed *Cirrothauma* together with *Cirroteuthis* in the Cirroteuthidae. Both have an intermediate web and a saddle-shaped shell vestige, features that Robson considers to be taxonomically important (1932b, p. 133). They also have in common a well developed 'dorsal chamber' to the heart, normal gills (i.e. not the 'half orange' type) and a similar body shape. The crop, which Robson lists as present in his diagnosis of the family Cirroteuthidae, he describes in the text as a 'moderate crop-like enlargement of the oesophagus' which could be similar to the slight non-diverticular swelling shown by *Cirrothauma*. The *Cirroteuthis* examined by Robson had a group of approximately 15 suckers in the middle of each arm, in which the cup had become a flat disc. This is a condition reminiscent of that found in *Cirrothauma*.

A full description of the external features of the nervous system of *Cirroteuthis umbellata* and *Stauroteuthis* was given by Ebersbach (1915) and there are some details of the internal structure of an unidentified cirroteuthid in Young (1977a). *Cirrothauma* shows a general resemblance to these forms, apart from its uniquely reduced eyes and visual system. The optic lobes of *Stauroteuthis syrtensis* are much larger and show better developed granule cell layers than in *Cirrothauma*. The vertical lobe system is also rather larger in the cirrates that have better eyes. In all the cirrates that have been studied the superior frontal lobe is small and the inferior frontal large, emphasizing the importance of the receptors of the arms to these animals.

Cirrothauma resembles other cirroteuthids in the arrangement of the fin lobes, fin nerves, stellate ganglion and epistellar body, but differs in the reduction of the giant fibres which, surprisingly, are quite conspicuous in the cirroteuthid described in Young (1977a).

In all cirrates the statocysts are very large, but in *Cirroteuthis* and *Stauroteuthis* they lie close to the brain, enclosed in cartilage, whereas in *Cirrothauma* they lie far away and are free. From these considerations of the statocyst it would seem that *Cirroteuthis mülleri* and *Stauroteuthis* (Ebersbach 1915) are the closest relatives of *Cirrothauma*.

The anticristae are very variable in cirroteuthids. Ebersbach (1915) reports no less than six in *Cirroteuthis umbellata* Fischer, 1883 but a specimen of *C. mülleri* Eschricht, 1836 shows only one (personal observation); *Stauroteuthis* apparently has only one (Ebersbach 1915) and *Grimpoteuthis* (Robson 1932b) two (J. Z. Y., unpublished observation). The significance of these differences may become clear with further study of the positions and functions of the anticristae.

8.9. *Comparison of Cirrothauma with Vampyroteuthis*

Vampyroteuthis resembles the cirrates in the presence of fins, extensive interbrachial web and cirri. However, there are many large differences. *Vampyroteuthis* has five pairs of arms (Young 1977a), two pairs of fins in the larva, a wide mantle opening, light organs scattered over the

arms and mantle (Pickford 1949*b*), a funnel valve, well formed spermatophores in the males, a sperm receptacle on either side of the head of the females and a right, as well as a left, oviduct (R. E. Young 1964). The wing-like fin support of *Cirrothauma* is quite unlike the rather flattened, boat-shaped gladius of *Vampyroteuthis* (Pickford 1949*b*).

Vampyroteuthis has a complex macula and many anticristae in the statocyst, and no epistellar body. The brain of *Vampyroteuthis* is in several ways better developed than that of cirrates and intermediate between them and decapods and octopods (Young 1977*a*). The fin lobes of the brain and pathways for the control of swimming are similar in *Vampyroteuthis* and cirrates. The vertical lobe and magnocellular systems are much more differentiated in *Vampyroteuthis* than in *Cirrothauma*, but in the inferior frontal system less so.

8.10. *Comparison of Cirrothauma with non-finned octopods*

Structures absent or reduced in *Cirrothauma* but generally present in the Incirrata are: chromatophores, chromatophore lobes, ink sac, a well developed radula, a hectocotylus and anal valves. Conversely, *Cirrothauma* has cirri, well developed fins and a massive gladius to support the fins, the first being totally absent from the Incirrata and the second either absent or reduced to two small stylets. The web of *Cirrothauma* is extensive, covering the entire length of the arm whereas in the incirrates it is usually less than 50 % of the length of the arm and only in *Pteroctopus* is there a primary and secondary element similar to that found in *Cirrothauma*. The male reproductive tract of *Cirrothauma* is simple, associated with the simple spermatophores (p. 15), and the female has only the left oviduct and associated glands.

The general form of the brain is octopodan and especially the union of the superior buccal ganglion with the main brain, presence of a suprabrachial commissure and the absence of a ventral magnocellular commissure. The inferior frontal system has the same general plan as that of *Octopus*, but the subdivisions of the subfrontal system seem to be in a primitive condition. The undeveloped superior frontal and vertical lobe system is hard to derive from that of known octopods. These lobes are still easily recognizable in aberrant incirrate octopods such as *Pteroctopus*. This suggests that the cirrates *have never possessed such a system*.

The stellate ganglion and epistellar body of cirrates are typically octopodan. The presence of photosensitive vesicles in the stellate ganglion and their absence from the head sharply differentiates octopods from decapods and shows the affinity of cirrates with the former. The multiplication of anticristae is a feature of the statocysts of decapods, whereas in all incirrate octopods examined there is only one anticrista. The inner and outer sacs of the statocyst are characteristically octopodan, as is the single macula and anticrista. The crista is simpler than that of the octopods with no sharp subdivisions even into the three main sections. This may be a primitive simplicity.

8.11. *Comparison of Cirrothauma with* Decapoda

The arrangements for control of the fins are very like those of decapods and also like *Vampyroteuthis*. Similarities extend even to the presence of a large tract from the posterior pedal region to the fin lobe. On the other hand the general arrangement of the brain is unlike that of decapods with their great elongation and separation of the superior buccal ganglion. In spite of the condition of the buccal ganglia in *Nautilus* (Young 1965*a*) it is difficult to avoid the suggestion that the elongated condition of decapods is secondary. The inferior frontal system of decapods shows at most very faint traces of the features that are present in cirrates and octopods.

It seems likely that the decapods diverged from the others before the development of this characteristic and important system.

Other features that are lacking in the cirrates and could be later acquisitions by the decapods are the ventral magnocellular lobes, photosensitive vesicles in the head region, and maculae neglectae in the statocyst.

8.12. *Conclusion: position of Cirrothauma and the cirrates*

Palaeoctopus from the Cretaceous was a finned octopod (Woodward 1896; Robson 1930; Donovan 1977) and it seems likely that the cirrates living today retain some features of the ancestral stock of the Octopoda. Other characteristics are similar to those of *Vampyroteuthis* and the decapods, for instance the fins themselves and the centres and nerves for control of them. The cirrates thus still keep features that were probably present in the ancestors of the whole coleoid stock, for example the simple male ducts and spermatophores. As in *Spirula* (Kerr 1931) the glands that open on the salivary papilla have not retreated behind the brain to their modern position as posterior salivary glands. The vertical lobe region shows no signs that it has been arrived at by reduction from that found in *Vampyroteuthis*, octopods or decapods. In spite of these retained ancestral characters the cirrates are probably closer to the line leading to the octopods than that leading to *Vampyroteuthis* and the decapods.

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ABBREVIATIONS USED ON FIGURES

acc.gl.	accessory gland	fr. s.	superior frontal lobe
acid mucop.	acid mucopolysaccharide-containing tissue	g. opt.	optic gland
		g. opt. (g.)	glandular region of optic gland
aff.b.v.	afferent branchial vein	g. opt. (n.)	nervous region of optic gland
amoeb.	amoebocyte	g. ovid.	oviducal gland
an.	anus	g. sal. a.	anterior salivary gland
anticr.	anticrista	g. sal. duc. p.	duct of posterior salivary gland
aor.a. (ant. aor.)	anterior aorta	g. sal. l.	lateral salivary gland
arm mus.	muscle of arm	g. sal. p.	posterior salivary gland
aur.	auricle	g. subman.	submandibular salivary gland
b.a. (b. ant.)	anterior basal lobe	gan. buc. i.	inferior buccal ganglion
b.a.a.	anterior anterior basal lobe	gan. stel.	stellate ganglion
b.a.a.sp.	spine of anterior anterior basal lobe	gast. gan.	gastric ganglion
b.a.l.	lateral anterior basal lobe	gill lt	left gill
b.a.p.	posterior anterior basal lobe	gon. art.	gonadial artery
b.med.	median basal lobe	gon. sac.	gonadial sac
be.low	lower beak	gr. in.	inner granular layer
be.u.	upper beak	gr. out.	outer granular layer
bd.w.	body wall	ins. aur.	insertion of auricles
bod.wh.	white body	int.	intestine
br.	brachial lobe	invag.	invagination
bran. ht lt (br. ht lt)	left branchial heart	k.	kidney
buc. cav.	buccal cavity	k. dt lt	left kidney duct
buc. i. gan.	inferior buccal ganglion	k. dt rt	right kidney duct
buc. m.	buccal mass	Kol.	Kölliker's canal
buc. p.	posterior buccal lobe	len.	lens
buc. s.	superior buccal lobe	lip low.	lower lip
c. br. sup.	suprabrachial commissure	lip u.	upper lip
c. opt.	optic commissure	mac.	macula of statocyst
caec.	caecum	mag.	magnocellular lobe
ce. col.	columnar cell	mant. con.	mantle connective
ce. col. ep.	columnar epithelial cell	mem. sh.	membrane sheath
ce. elon.	elongated cell	ml. opt.	medulla of optic lobe
ce. ep.	epithelial cell	mus. circ.	circular muscle
ce. lar.	large cell	mus. d.-ven. buc.	dorsoventral buccal muscle
ce. mult.	multipolar cell	mus. long.	longitudinal muscle(s)
cer.-br. con.	cerebro-brachial connective	mus. man.	mandibular muscle
cer.-buc. con.	cerebro-buccal connective	mus. ob.	oblique muscle
cir.	cirrus (cirri)	mus. ra.	radial muscle
cor.	cornea	mus. rad.-sal. pap.	radula-salivary papilla muscle
core in.	inner core of sucker peduncle	mus. sal. pap.	salivary papilla muscle
core out.	outer core of sucker peduncle	mus. st.	muscle fibres of statocyst
cr. v.	transverse horizontal crista	mus. subman.	submandibular muscle
cut.	cuticle	mus. to. a.-p.	antero-posterior tongue muscle
cys.	cysts in retina	mus. to. med.	median tongue muscle
dig. dts	digestive ducts	n. br.	brachial nerve
dig. gl.	digestive gland	n. cr. a.	anterior crista nerve
dig. gl. art.	arteries to digestive gland	n. cr. p.	posterior crista nerve
dor. ch.	dorsal chamber	n. f.	nerve fibres
eff. b. v.	efferent branchial vein	n. fin	fin nerve
egg case, out.	outer egg case	n. lab.	labial nerve
end.	endolymph of statocyst	n. mac.	macula nerve
ep.	epithelium	n. op. p. s.	superior posterior ophthalmic nerve
ep. cub.	cubical epithelium	n. opt.	optic nerve
ep. vac.	vacuolated epithelial cells	n. pal.	pallial nerve
epistel. bod.	epistellar body	n. st.	static nerve
eros.	erosion	n. visc.	visceral nerve
ey.	eye	nec.	neck of rhabdome cell
f. gi.	giant fibre	nuc.	nucleus
fl.	fin lobe	nuc. rh.	nucleus of rhabdome cell
fnl	funnel	nuc. su.	nucleus of supporting cell
fr. i.	inferior frontal lobe	oes.	oesophagus
fr. i. l.	lateral inferior frontal lobe	oes. entr.	entrance to oesophagus
fr. i. med.	median inferior frontal lobe	oes. pig.	pigmented oesophagus

opt.	optic lobe
or.	organ
orif.	orifice
out.	outer
out. ring	outer ring
ov.	ovary
ovid.	oviduct
pa. buc. l.	lateral buccal palp.
pal. art.	pallial artery
pal. art. lt	pallial artery, left
pal. art. rt	pallial artery, right
pe.	pedal lobe
pe. l.	lateral pedal lobe
pe. p.	posterior pedal lobe
ped.	peduncle lobe
ped.?	part of peduncle lobe?
ped. sp.	peduncle spine
pen.	penis
peril.	perilymph of statocyst
pig.	pigment
plex.	plexiform zone
po.	pore
prec.	precommissural lobe
pri. wb	primary web
pv.	pallivisceral lobe
rad. grv.	radular groove
rad. su.	radular support
rad. tth	'radular teeth'
rec.	rectum
ret. det.	detached retina
rh. (rb.)	rhabdome
ros. low.	rostrum of lower beak
ros. u.	rostrum of upper beak
sal. duc. p.	posterior salivary gland duct
sal. pap.	salivary papilla
sal. pap. sh.	salivary papilla sheath
sal. pap. shd tth	toothed shield of salivary papilla
sec. prod.	secretory product

sec. wb	secondary web
sem. ves.	seminal vesicle
sept.	septum
she.	shell
sin. opt.	optic sinus
sp. pkt	sperm packet
st.	statocyst
stom.	stomach
stl.	statolith
su.	support(ing)
subfr.	subfrontal lobe
subv.	subvertical lobe
suc. disc	sucker disc, shed cuticle
suc. inf.	infundibulum of sucker
suc. inf. cut. new	new cuticle of sucker infundibulum
suc. orif.	orifice of sucker
suc. ped.	peduncle of sucker
t. con.	connective tissue
t. nv.	neurovenous tissue
tes.	testis
to.	tongue
tr. br.-opt.	optic to brachial lobe tract
tr. br.-pv.	pallivisceral to brachial lobe tract
tr. cer.-br.	cerebro-brachial tract
tr. fr. i.-fr. s.	inferior frontal-superior frontal lobe tract
tr. opt.	optic tract
tr. st.-ped.	static nerve to peduncle lobe tract
tth	teeth (tooth)
tth a.	anterior teeth
tth p.	posterior teeth
v.	vertical lobe
vas def.	vas deferens
vc.	vena cava
vent.	ventricle
wt. cl lt	left water canal
wt. cl rt	right water canal

FIGURE 1. *Cirrothauma murrayi*. Photograph taken immediately after capture (specimen B).

FIGURE 4. Cirrate octopod with intermediate web in drogue-like drifting configuration. Photograph taken with camera some 5 m above the octopod which was approximately 1 m above the floor of the sea (from Roper & Brundage 1972. fig. 20).

FIGURE 5. The transparency of the fin is demonstrated shortly after capture (specimen B).

FIGURE 7. The mantle cavity opened to reveal the main features.

FIGURE 8. A diagram showing the features of the mantle cavity seen in figure 7.

FIGURE 6. The mantle wall; transverse section.

FIGURE 10. The arm. A thick section from which the gelatinous layer has been removed.

FIGURE 11. The muscular wall of the arm in transverse section, taken from the inset on figure 10.

FIGURE 12. The heart, longitudinal section (Cajal).

FIGURE 16. Section through testis (*Cirrothauma* A).

FIGURE 17. Arrangement of sperms in sperm packet (*Cirrothauma* A).

FIGURE 18. The male ducts of *Cirrothauma* A.

FIGURE 19. The accessory gland, transverse section of *Cirrothauma* A.

FIGURE 20. Sperm packet in seminal vesicle (*Cirrothauma* A).

FIGURE 23. Oviducal gland showing sperm packet. (Longitudinal section, *Cirrothauma* B.)

FIGURE 24. Oviducal gland showing secretion of outer egg capsule (*Cirrothauma* B).

FIGURES 26, 27 AND 29–33. For description see opposite.
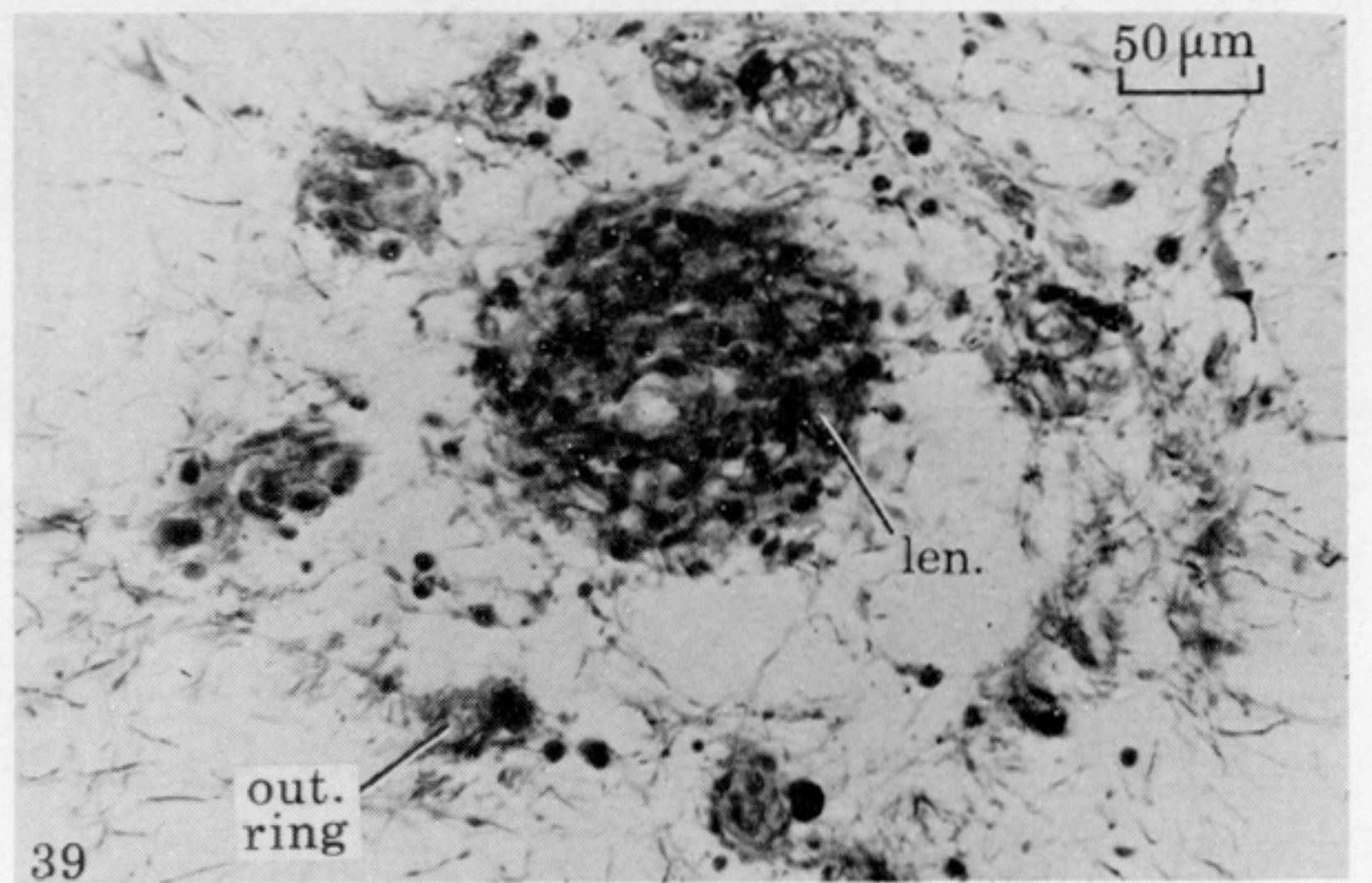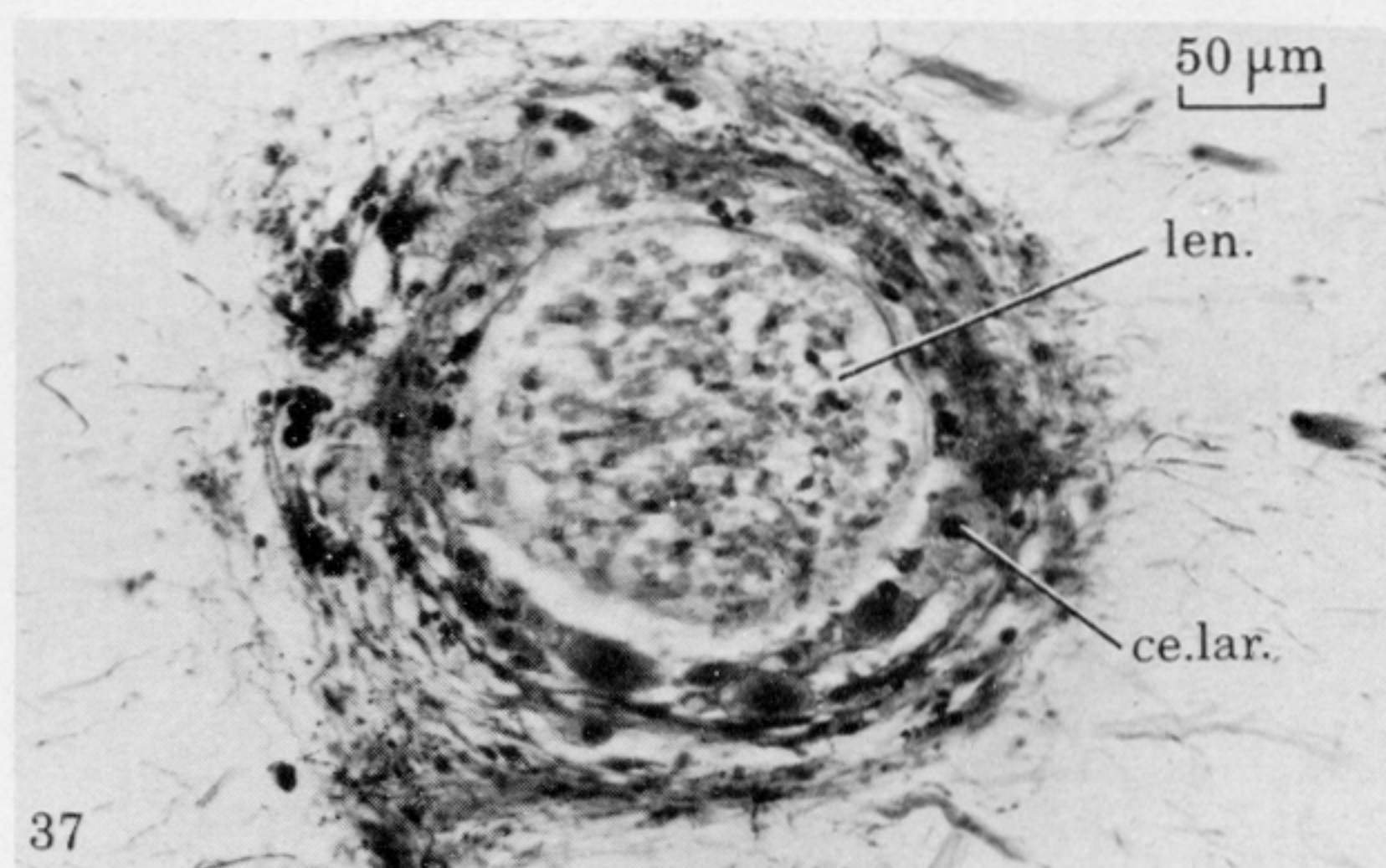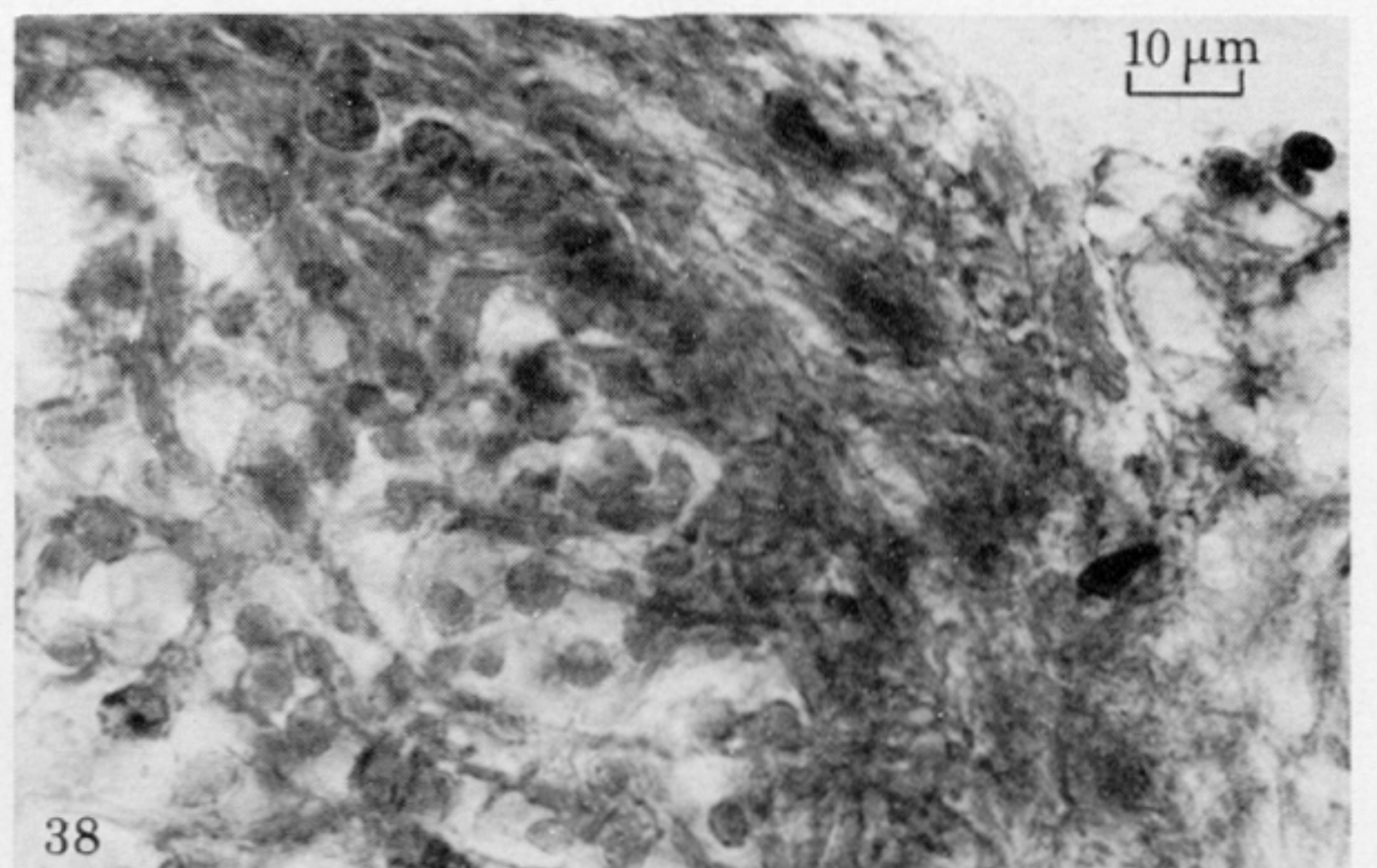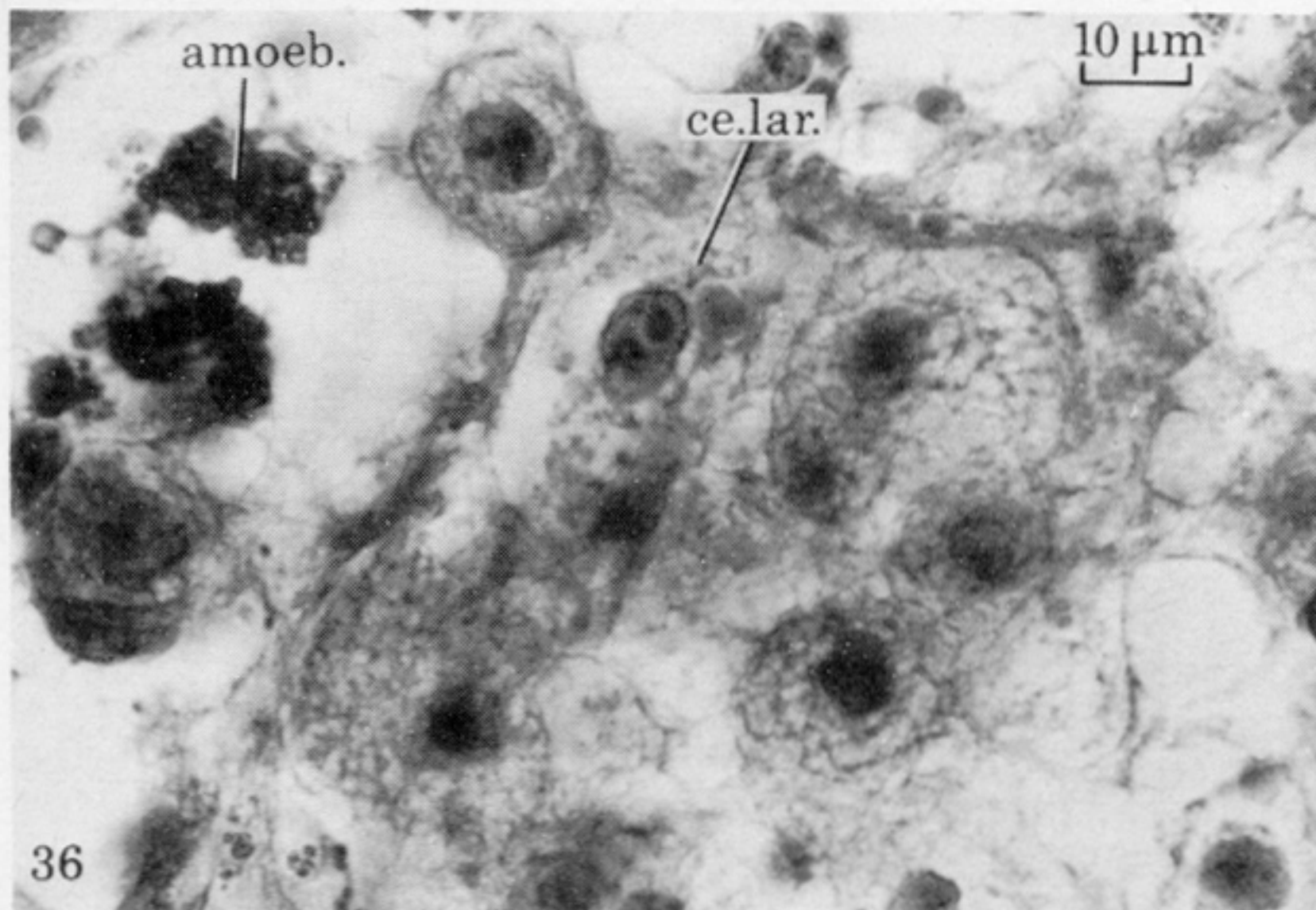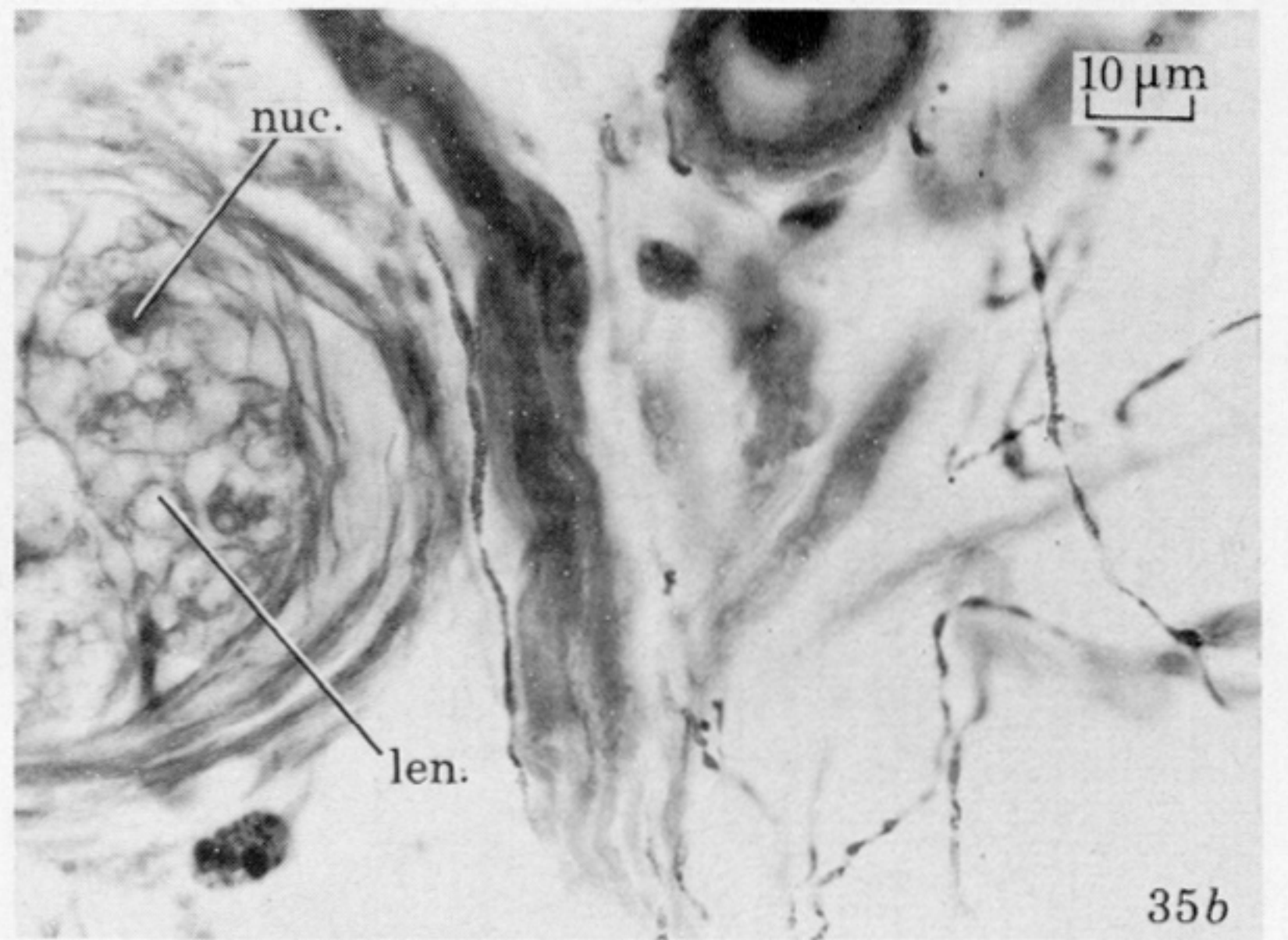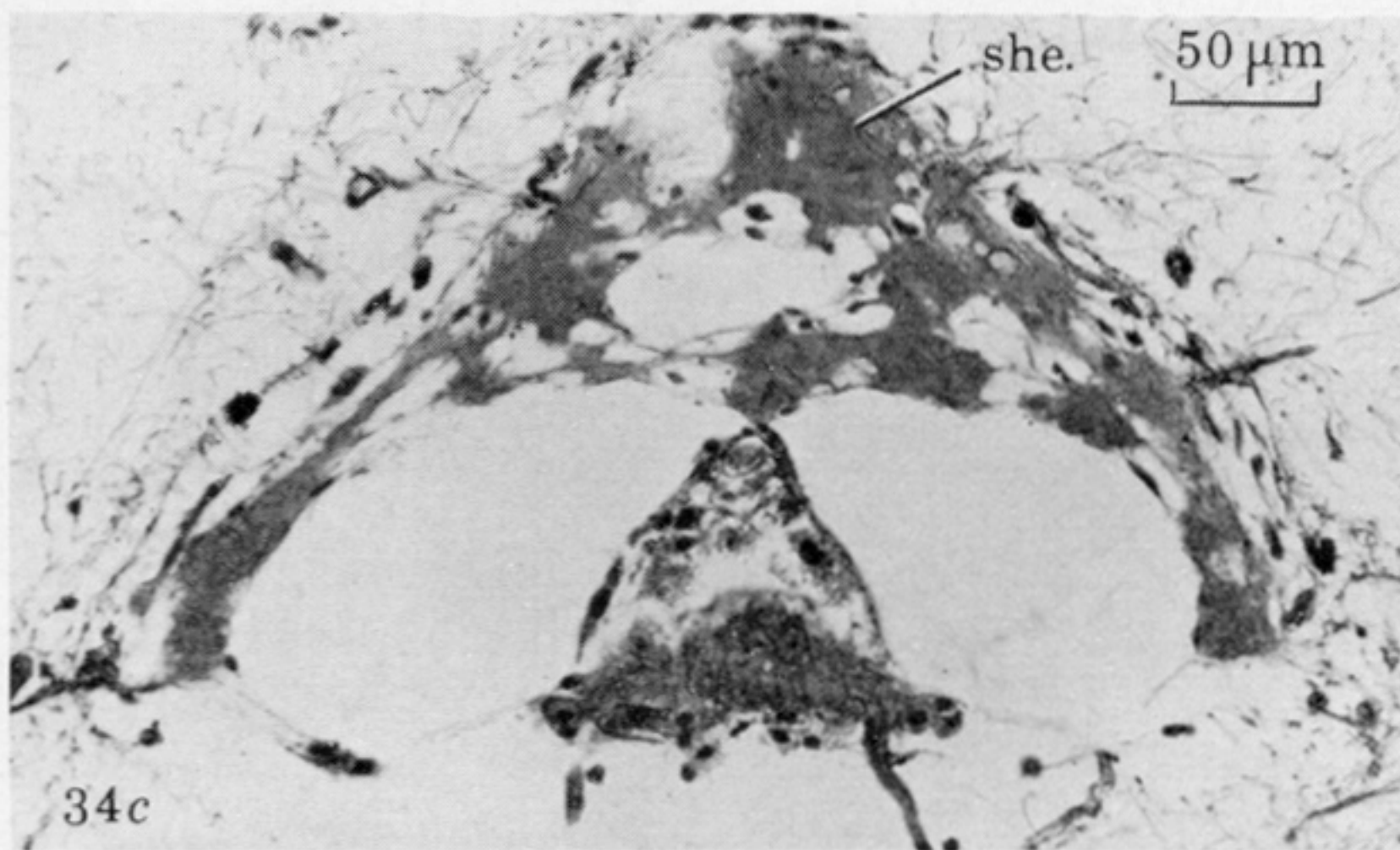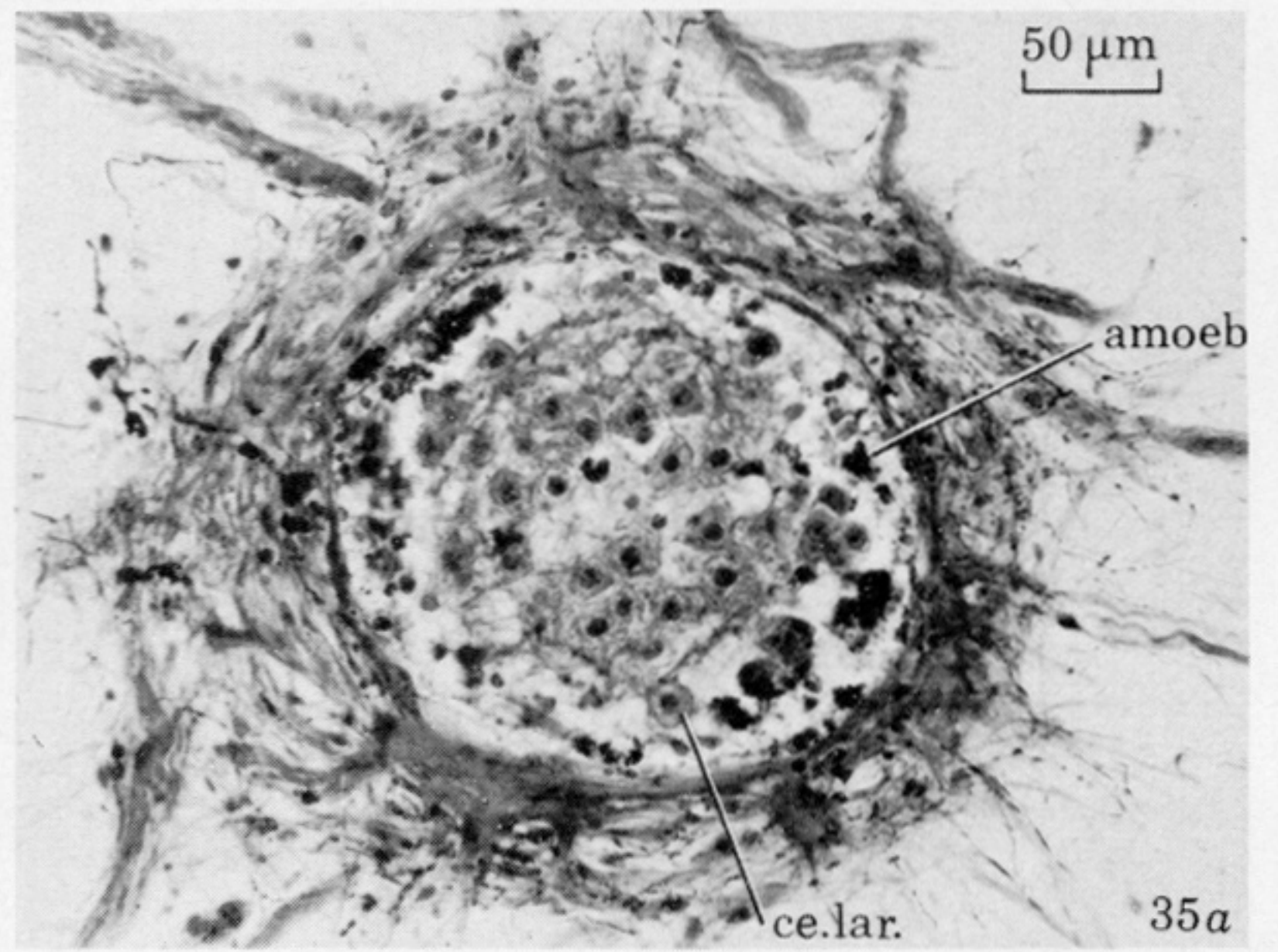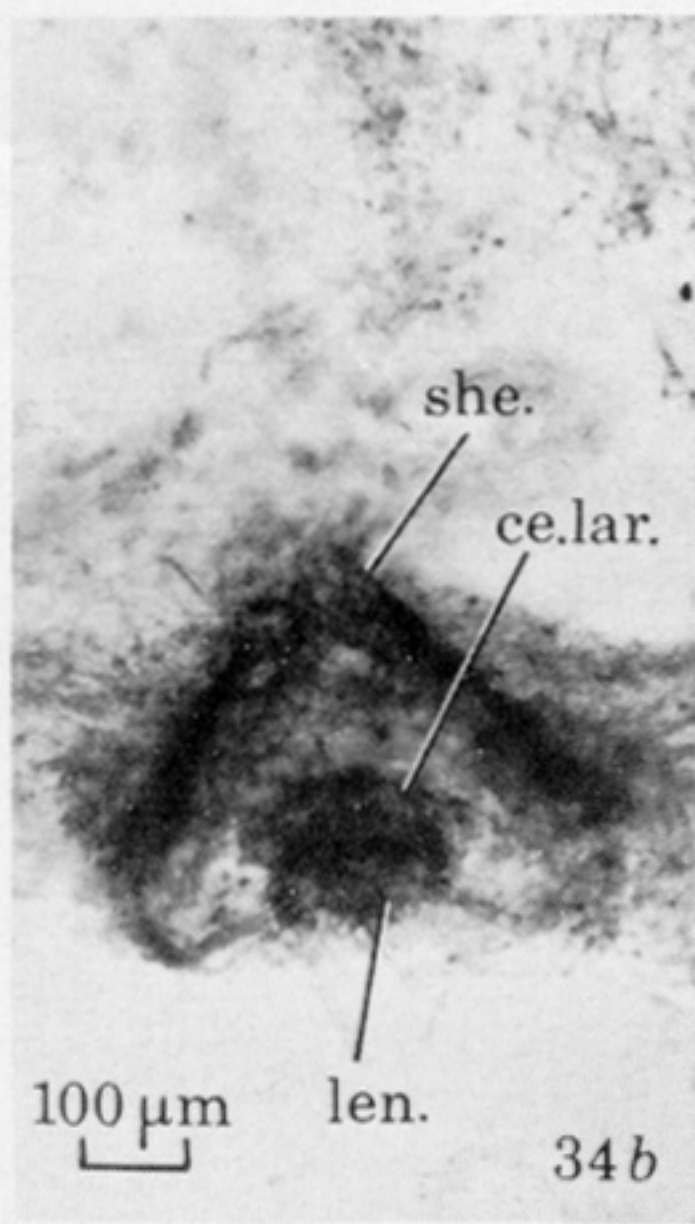
FIGURES 34–39. For description see p. 24.
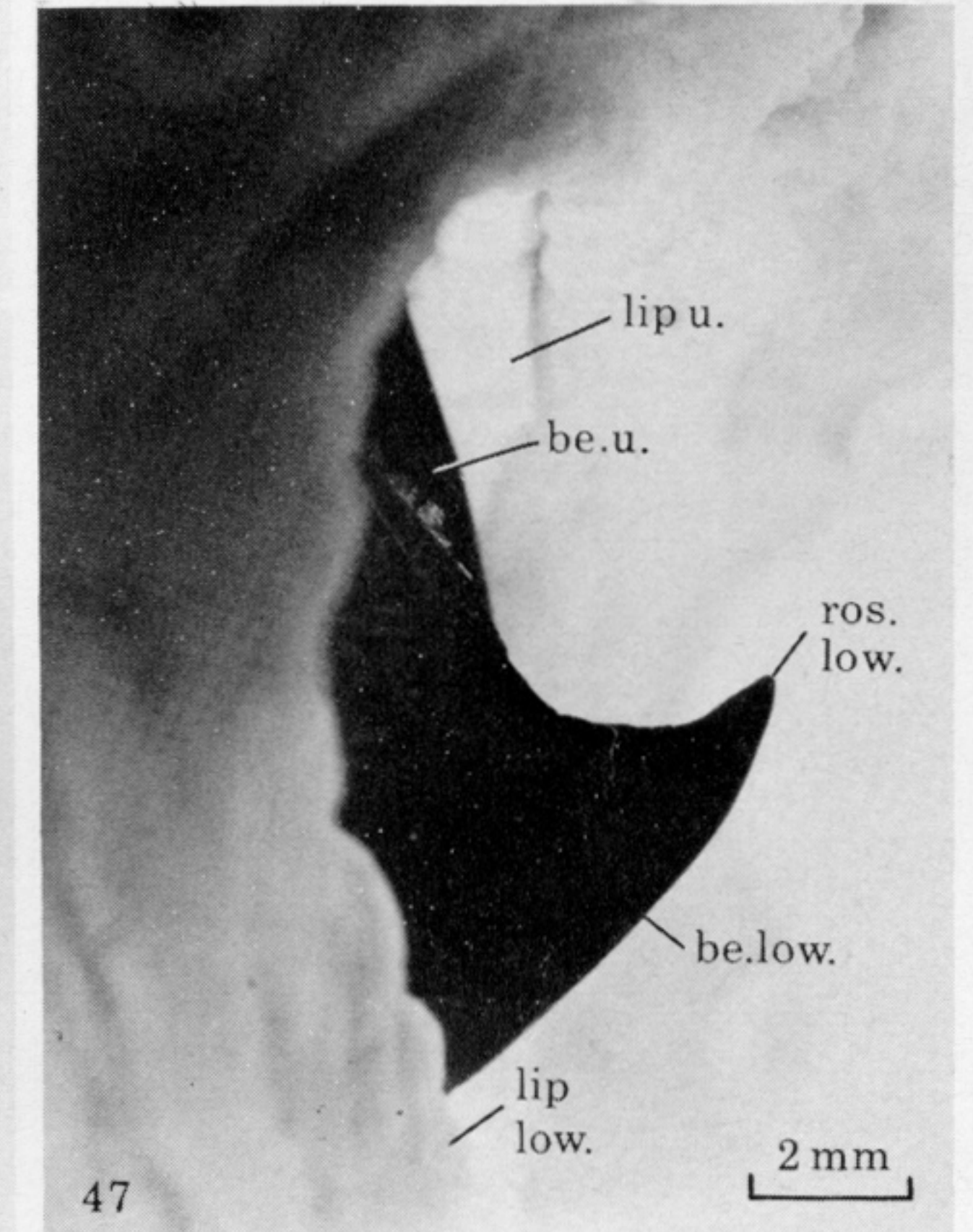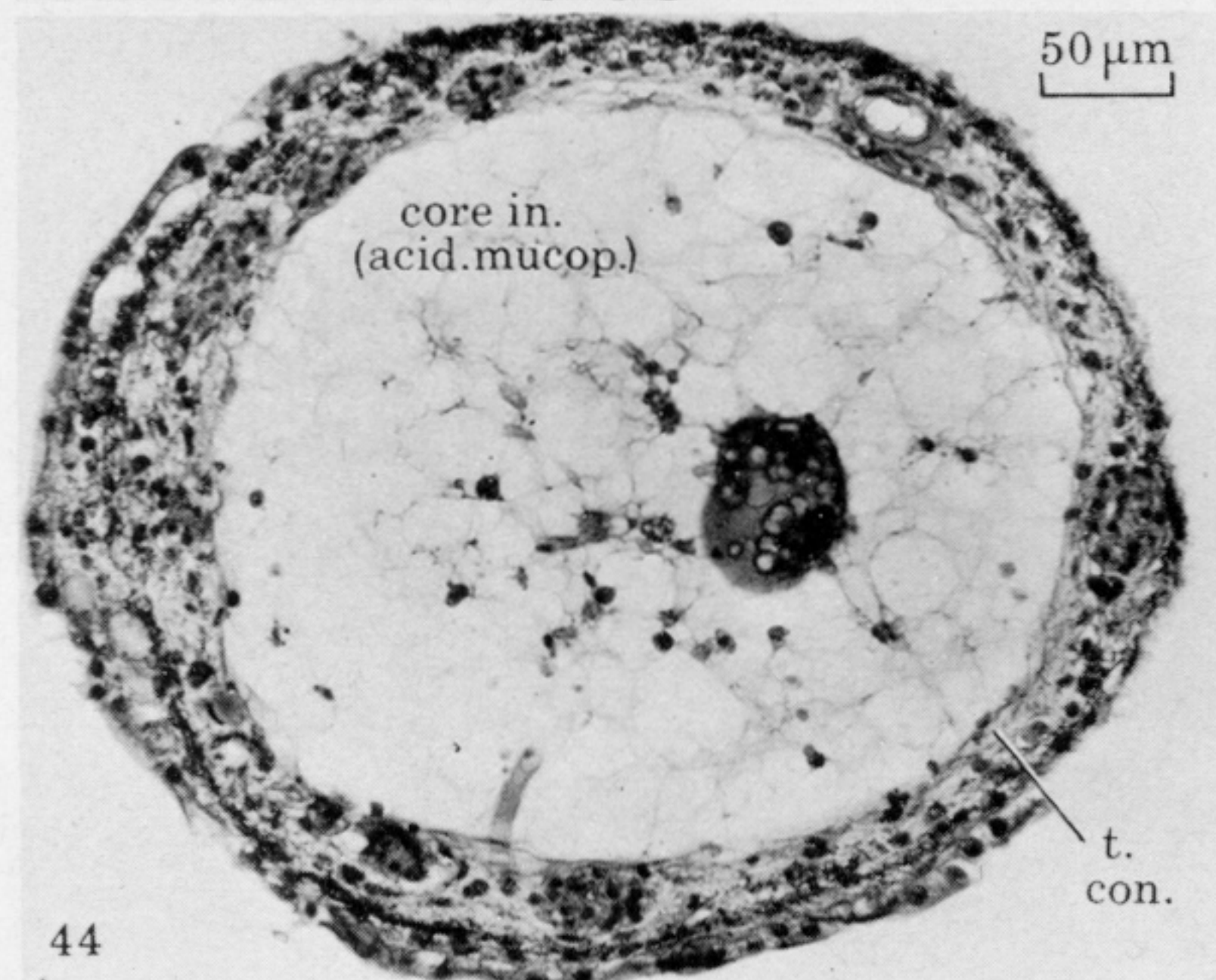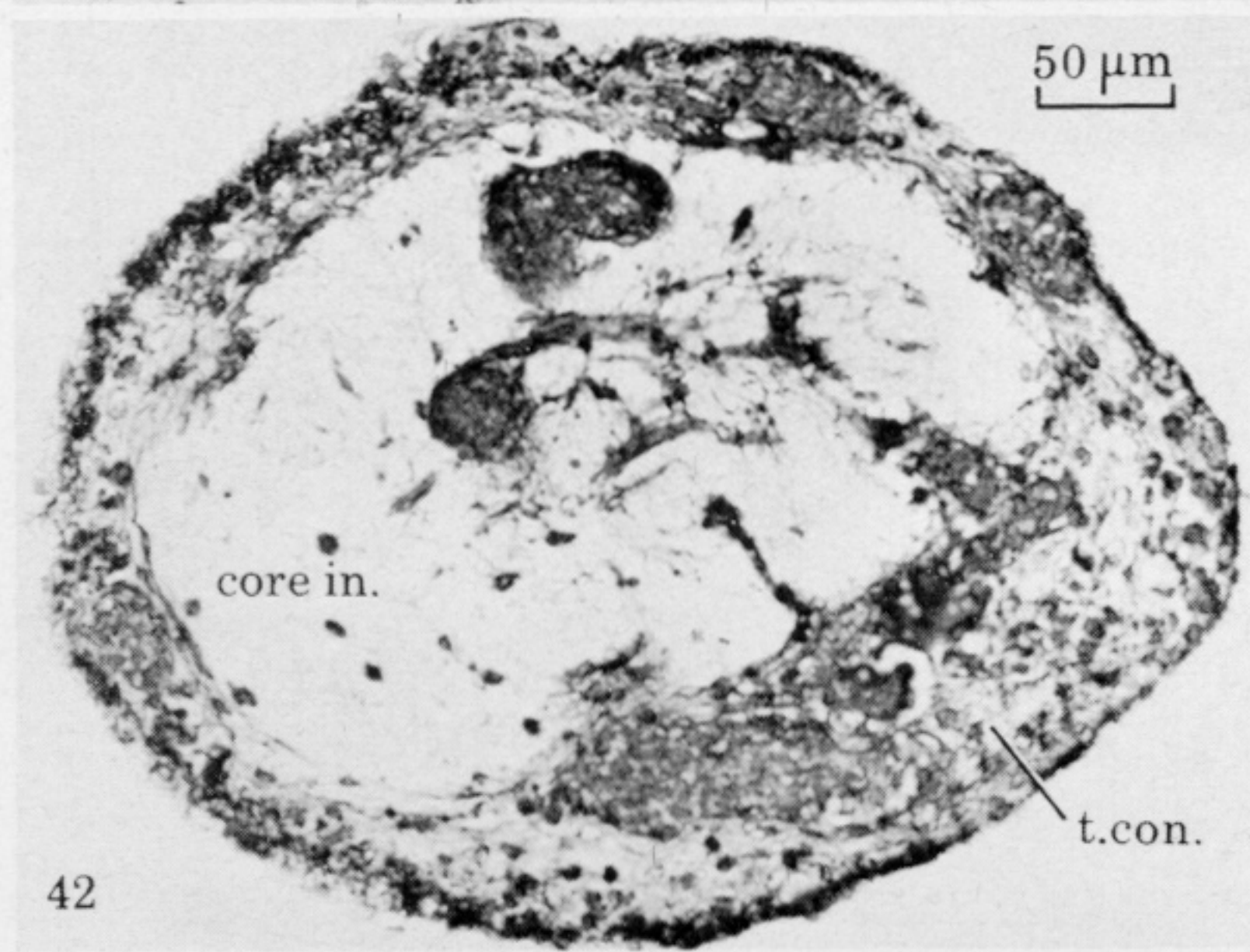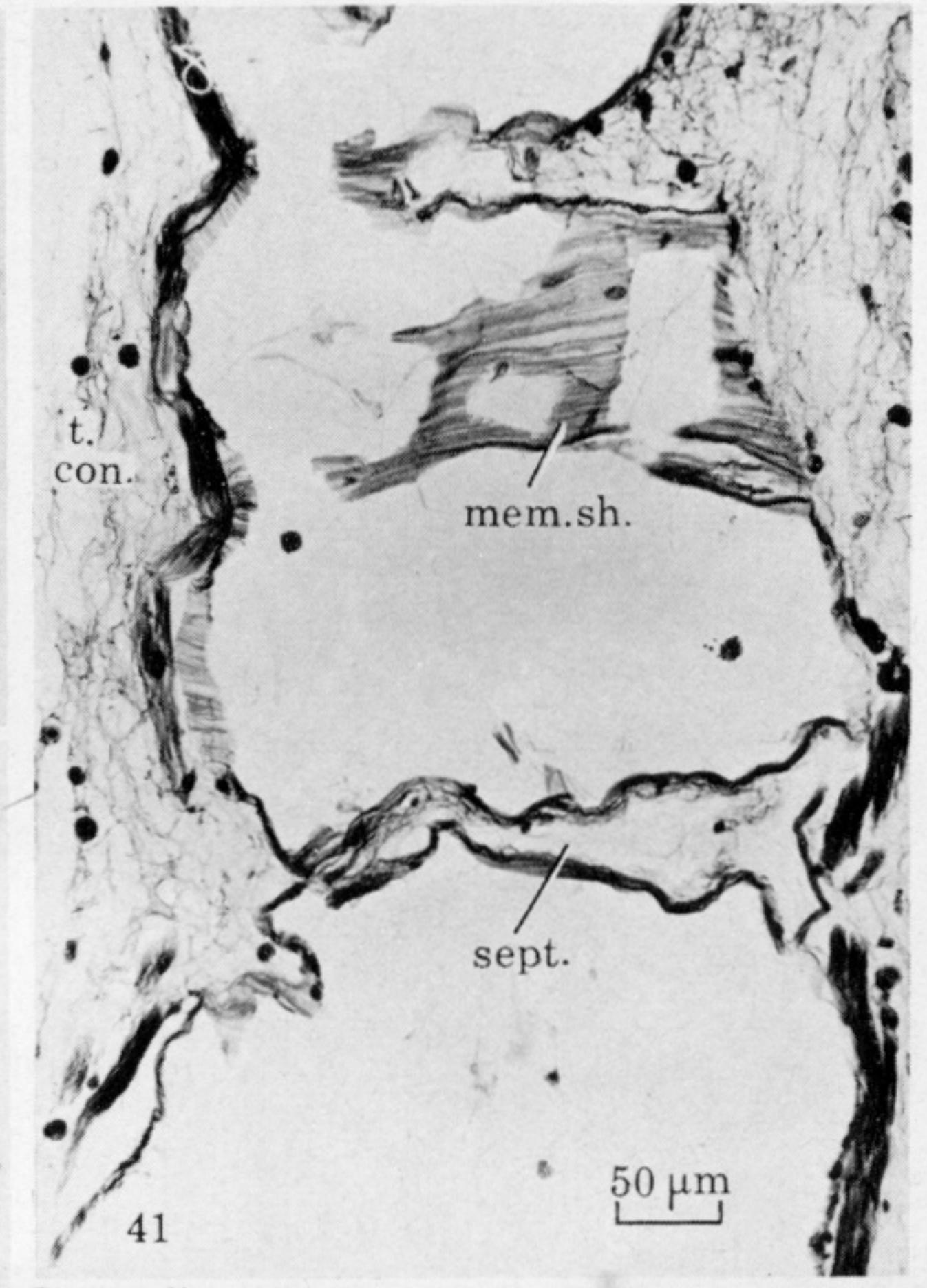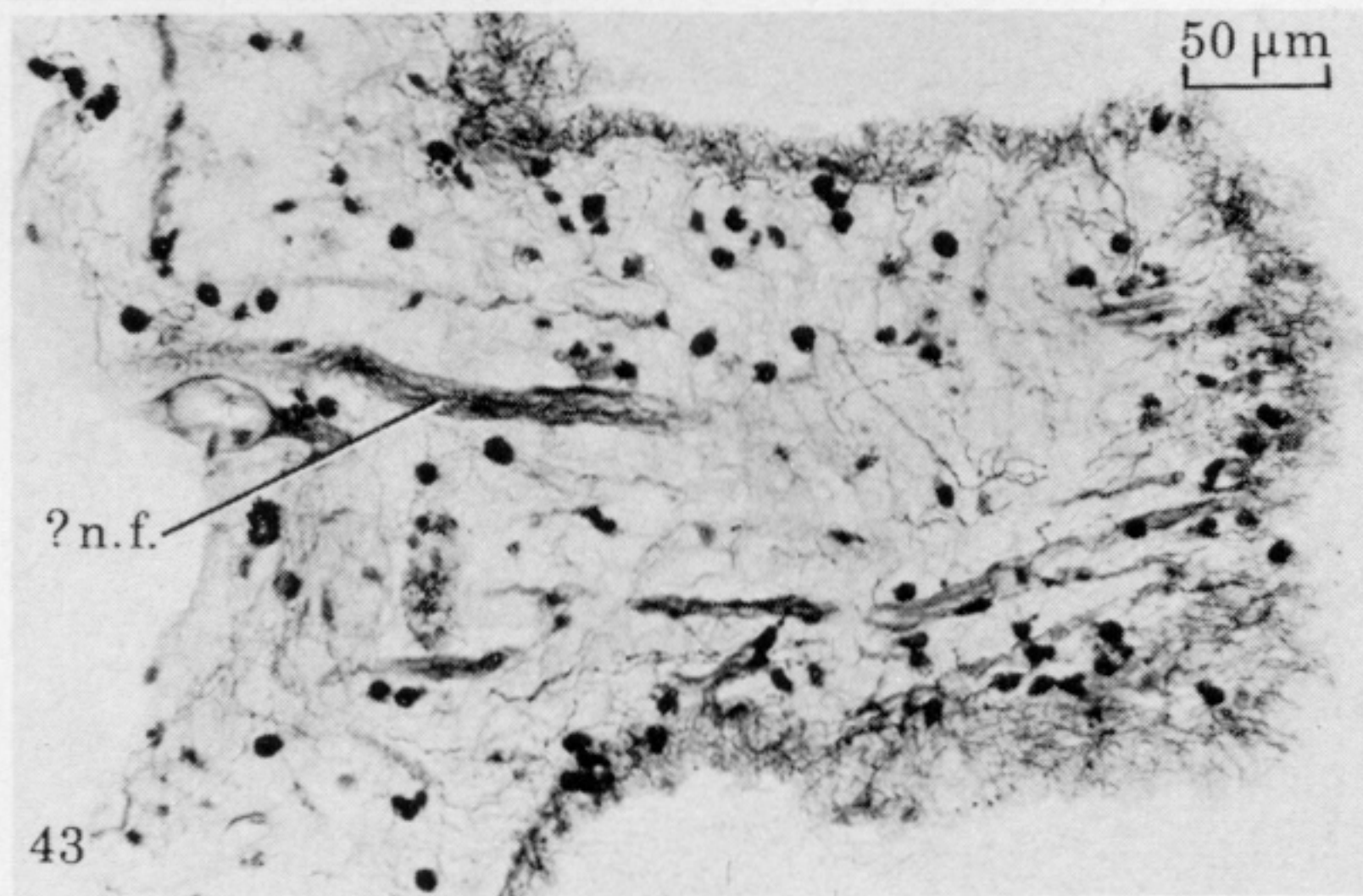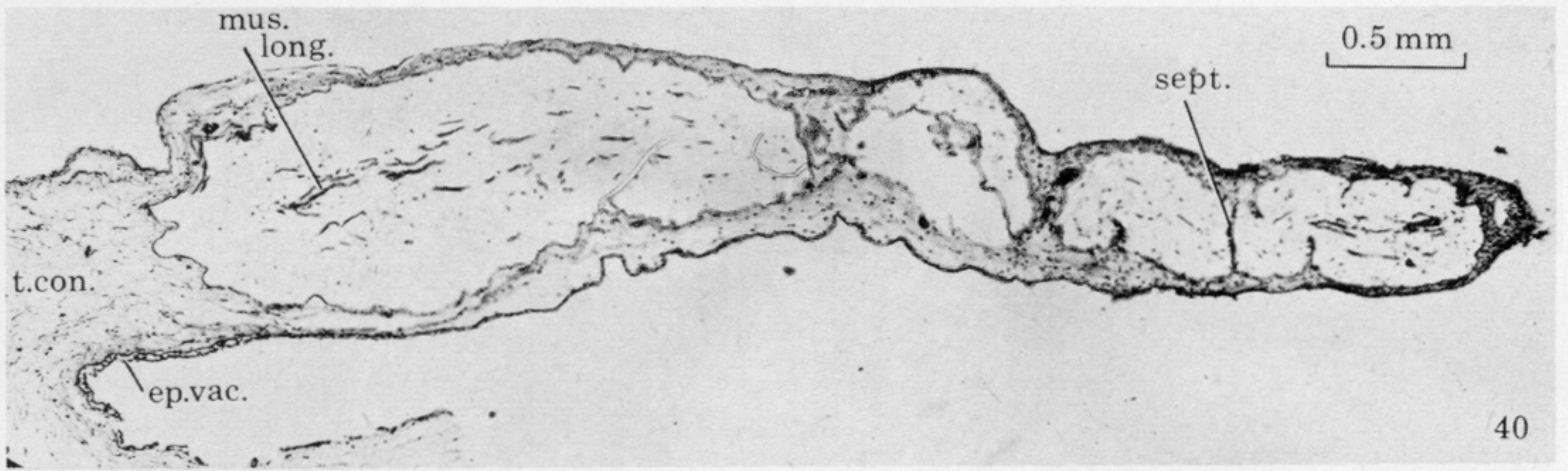
FIGURES 40–44 AND 47. For description see p. 25.
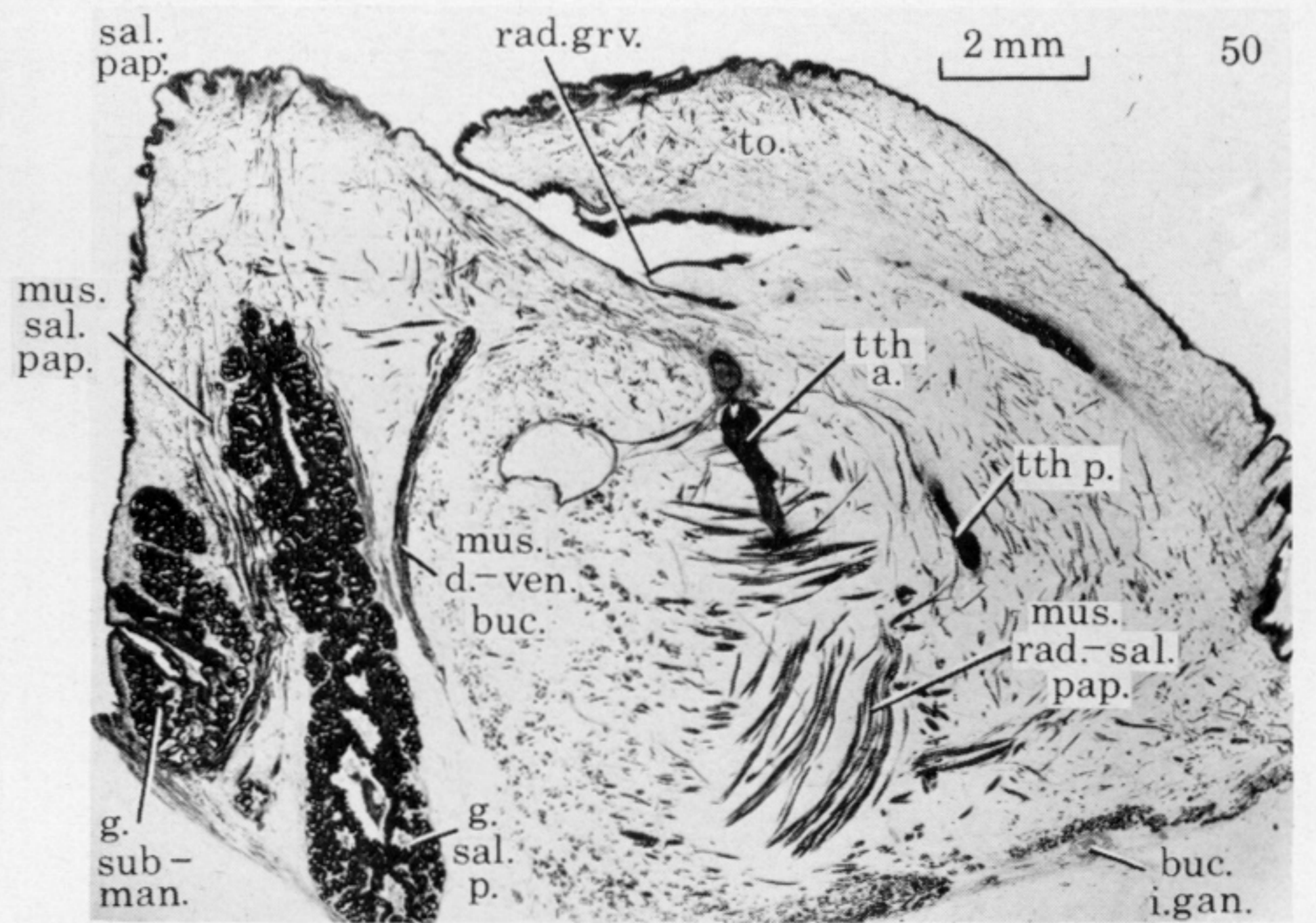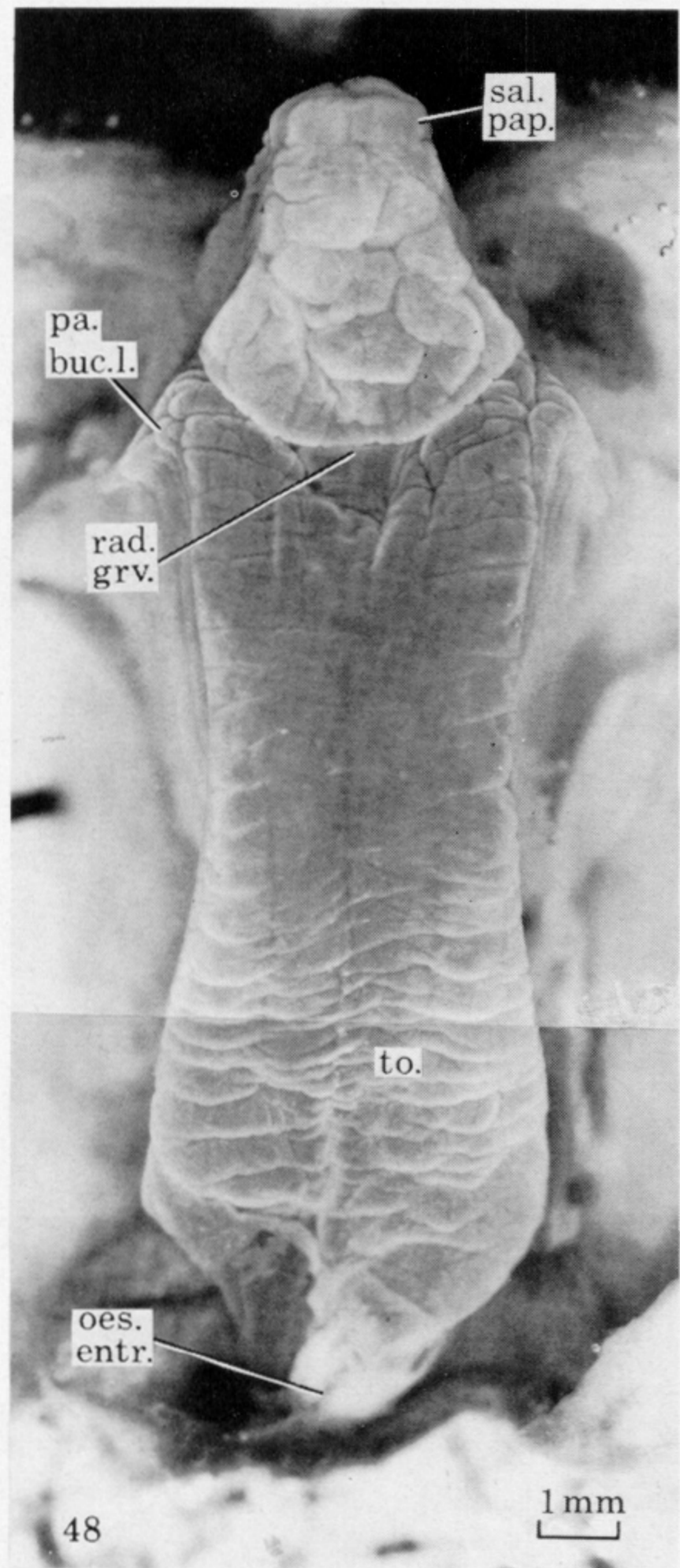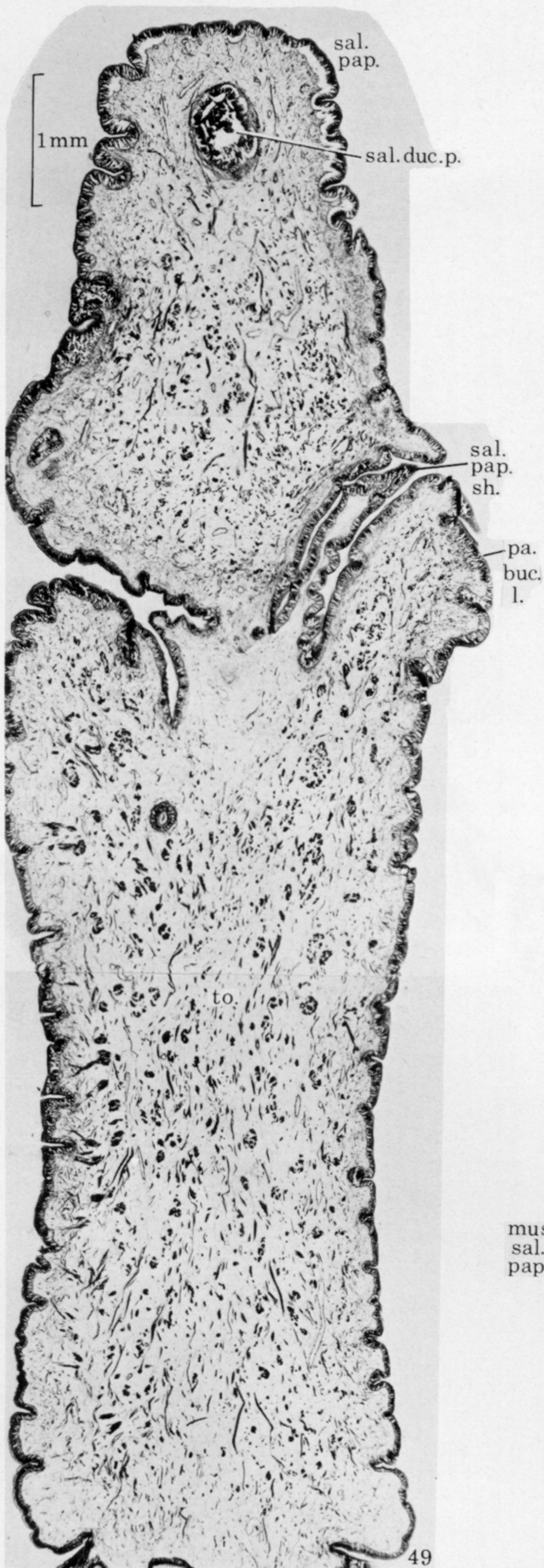
FIGURES 48–50. For description see opposite.
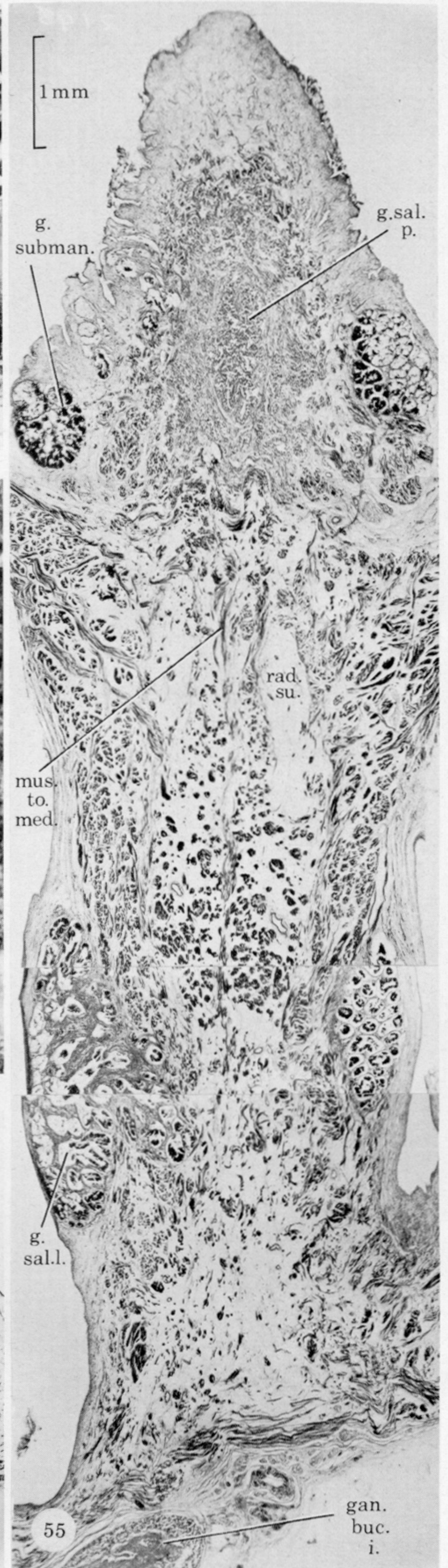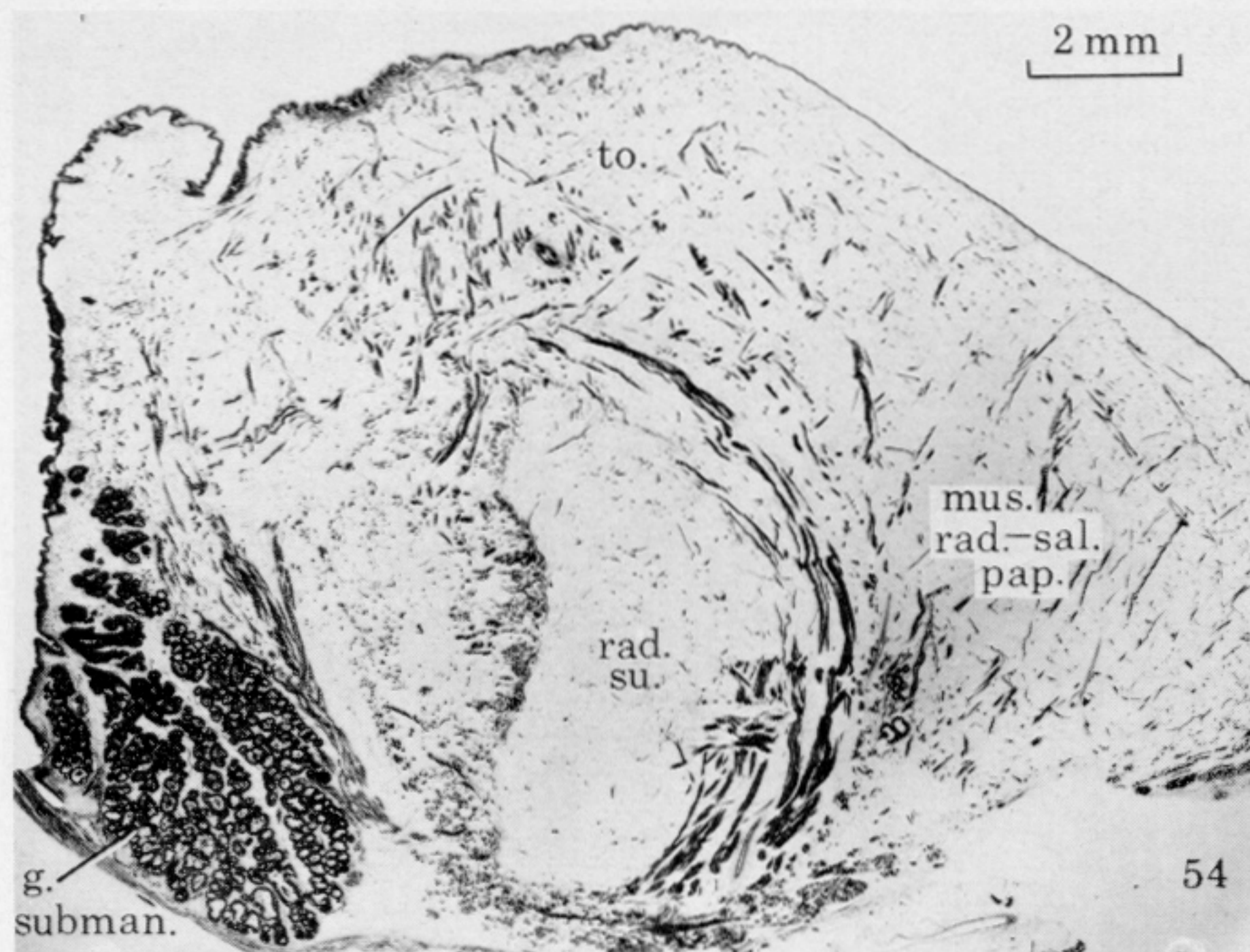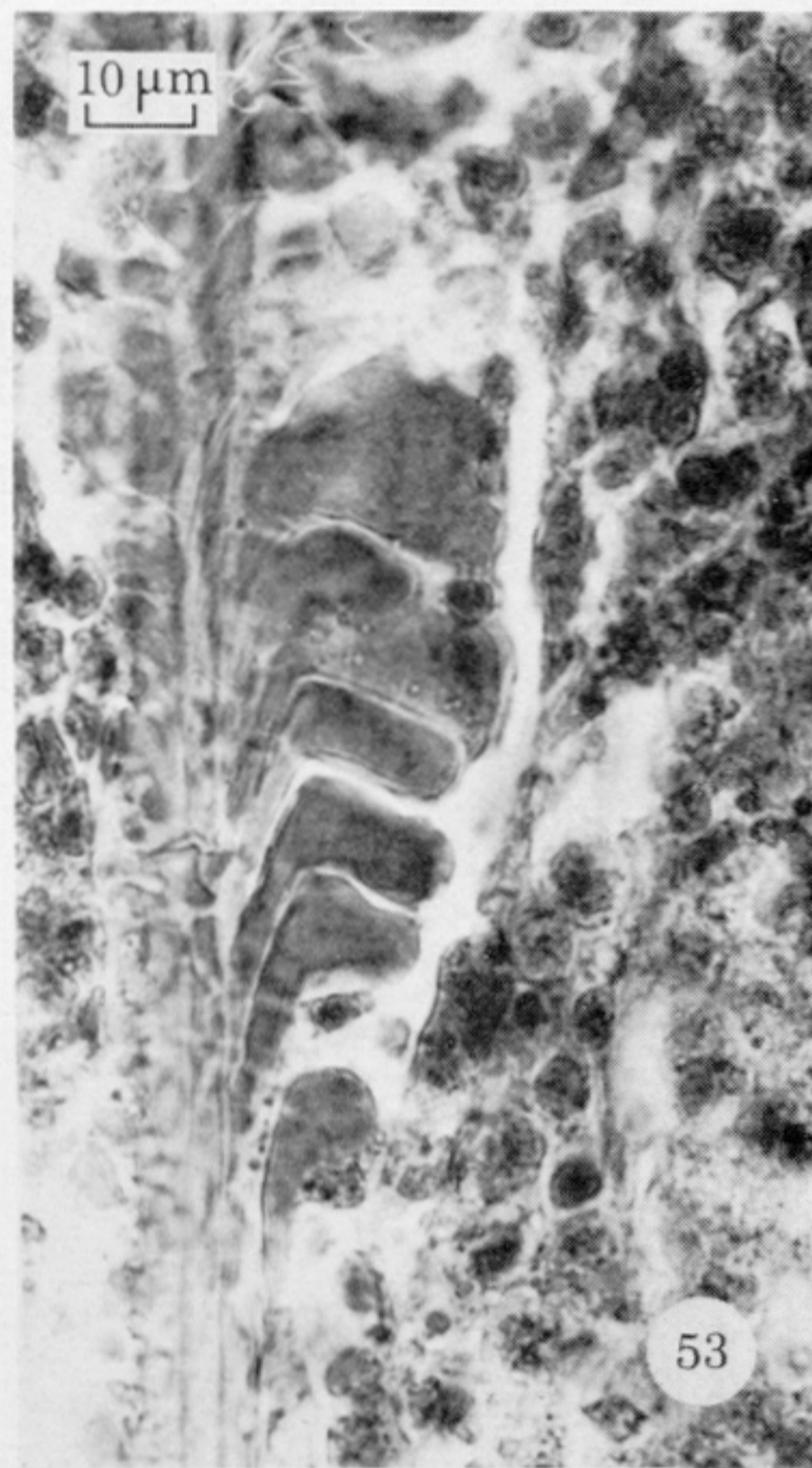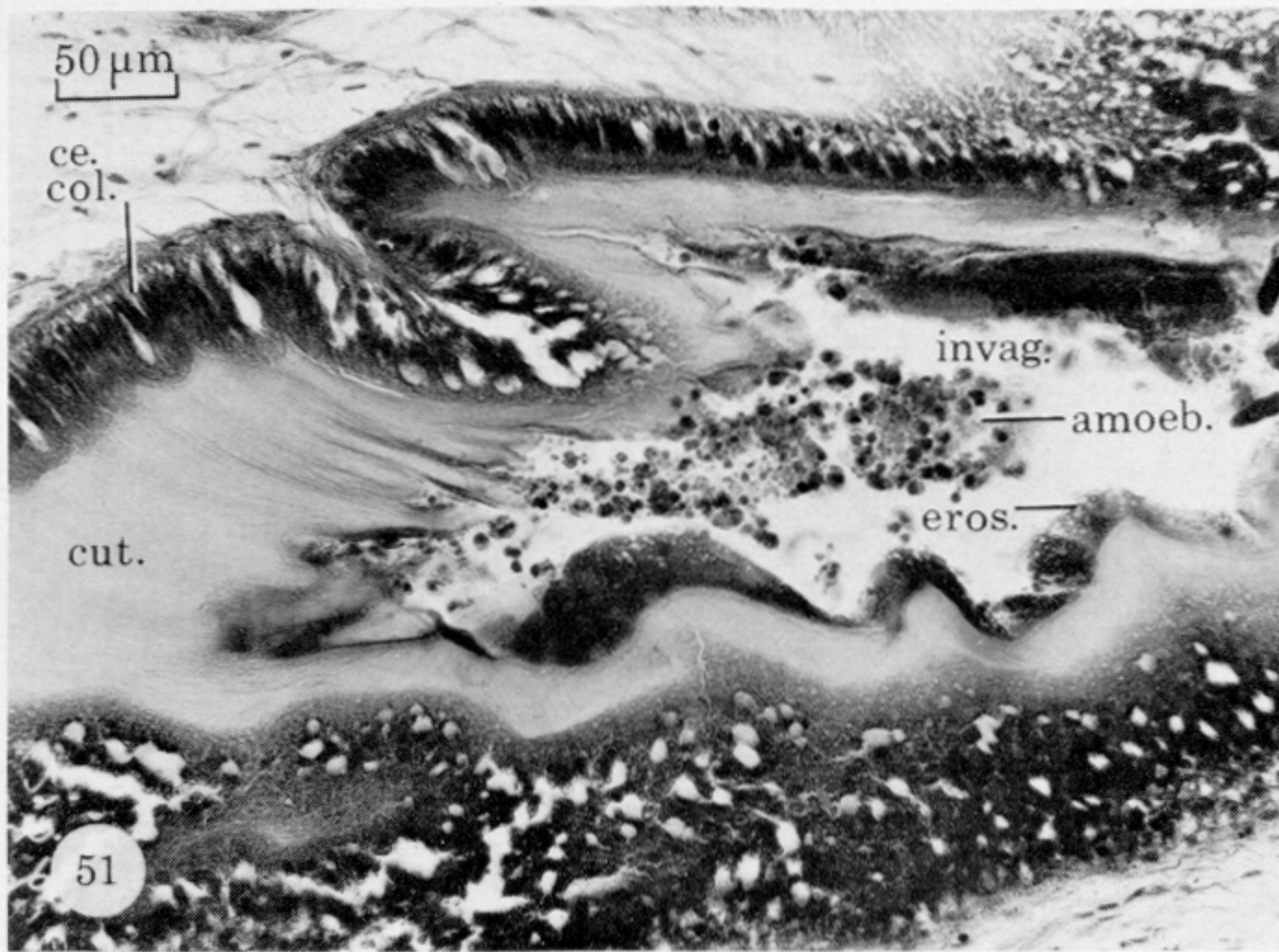
FIGURES 51–55. For description see opposite.
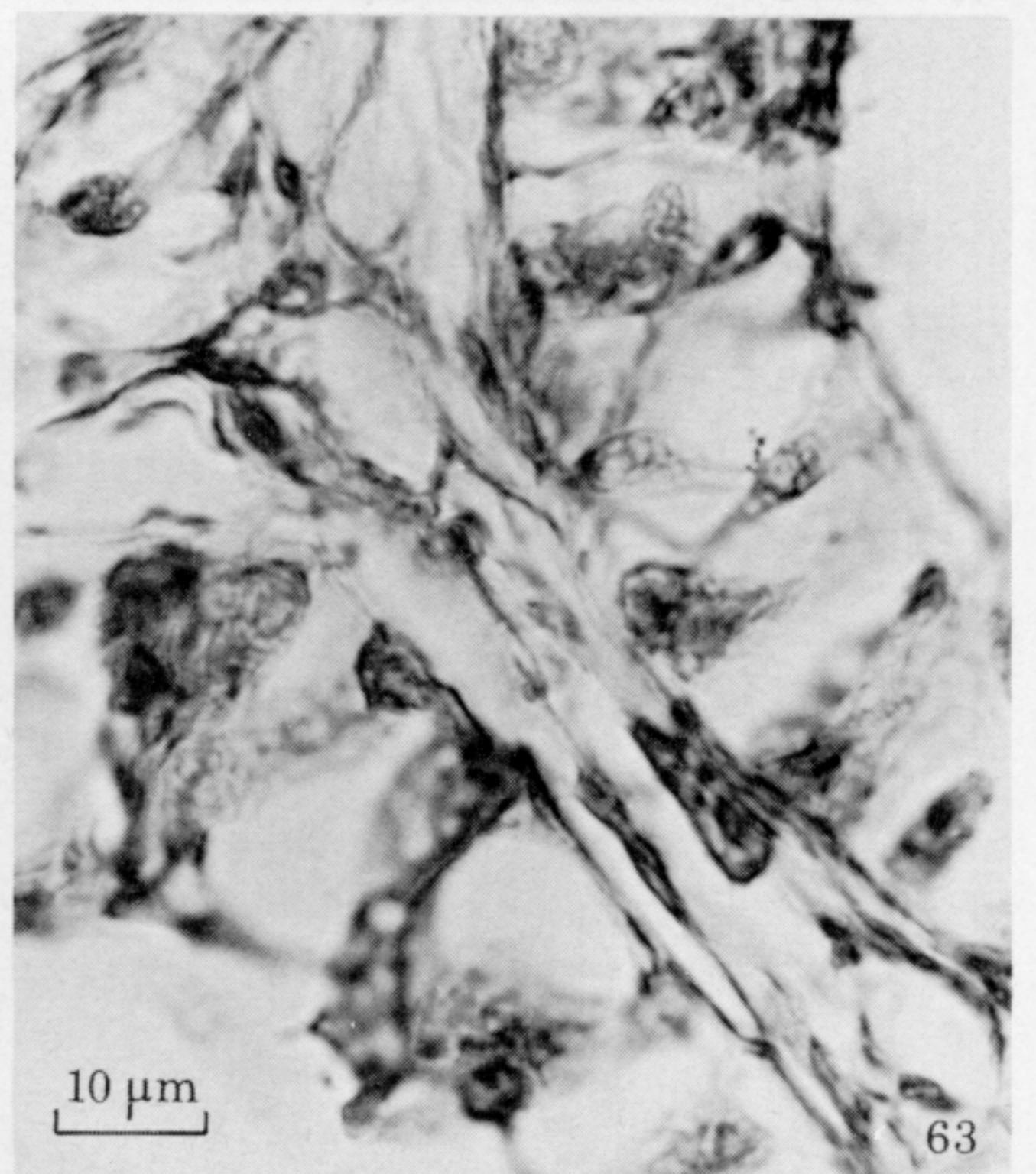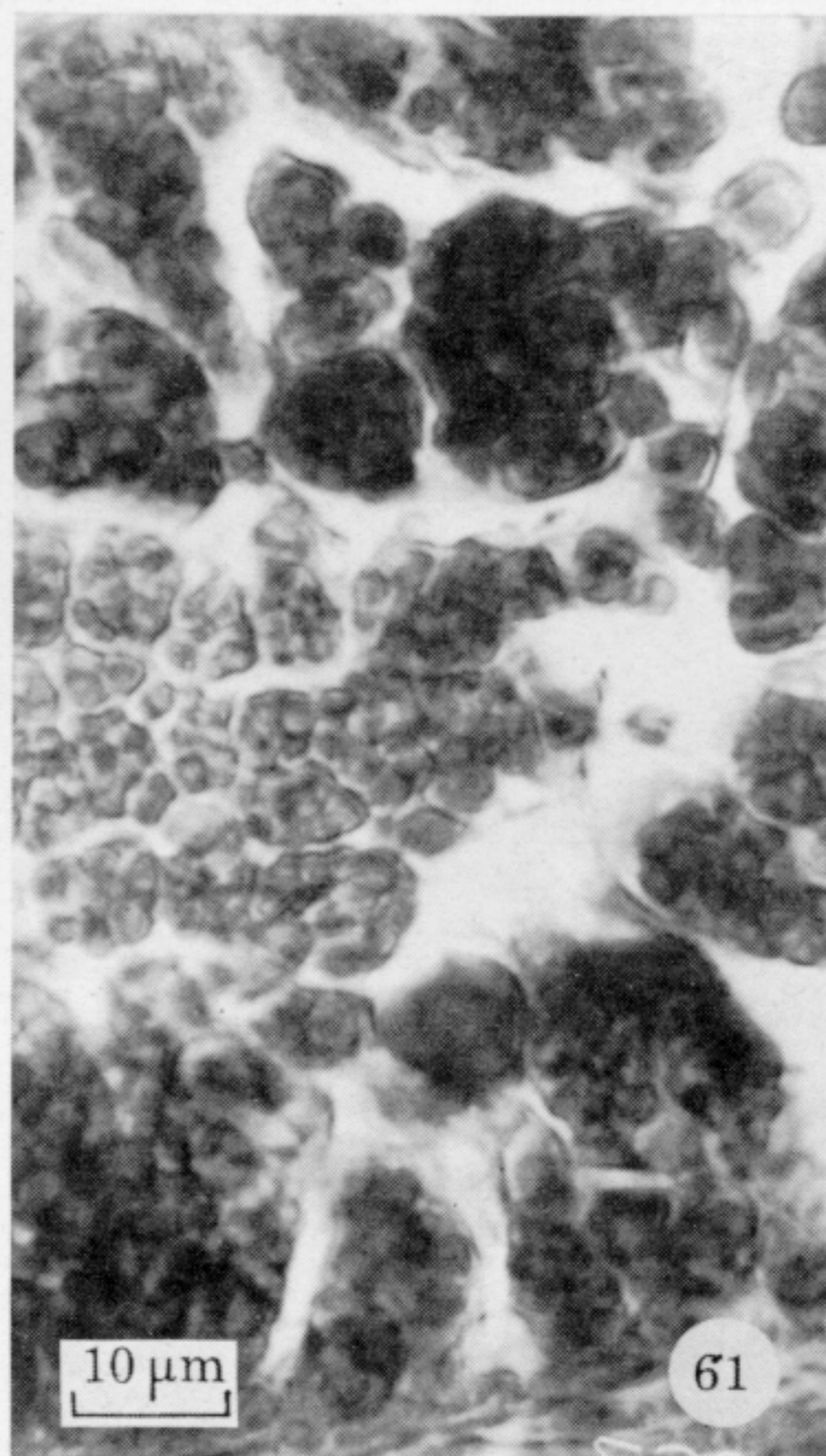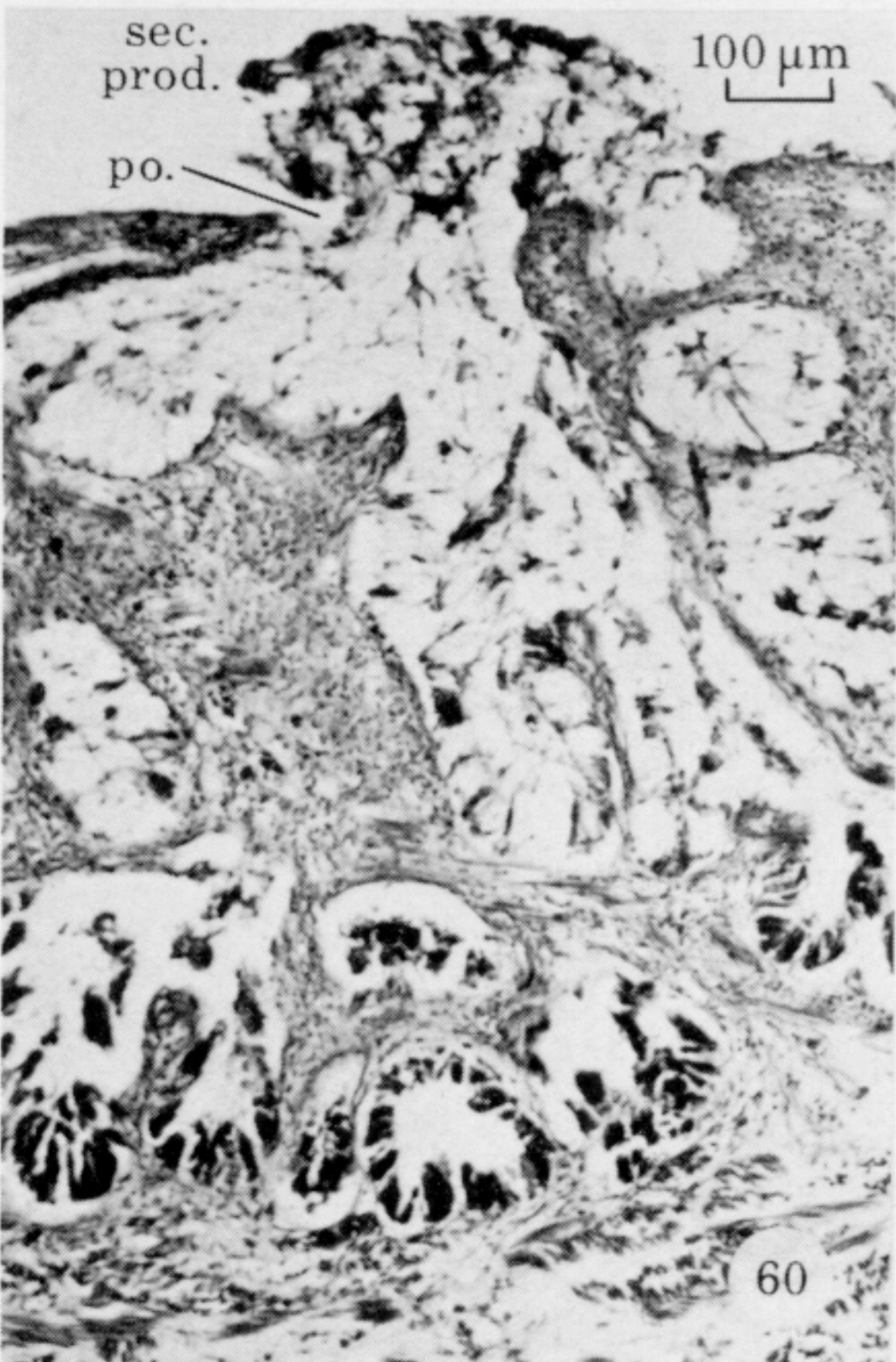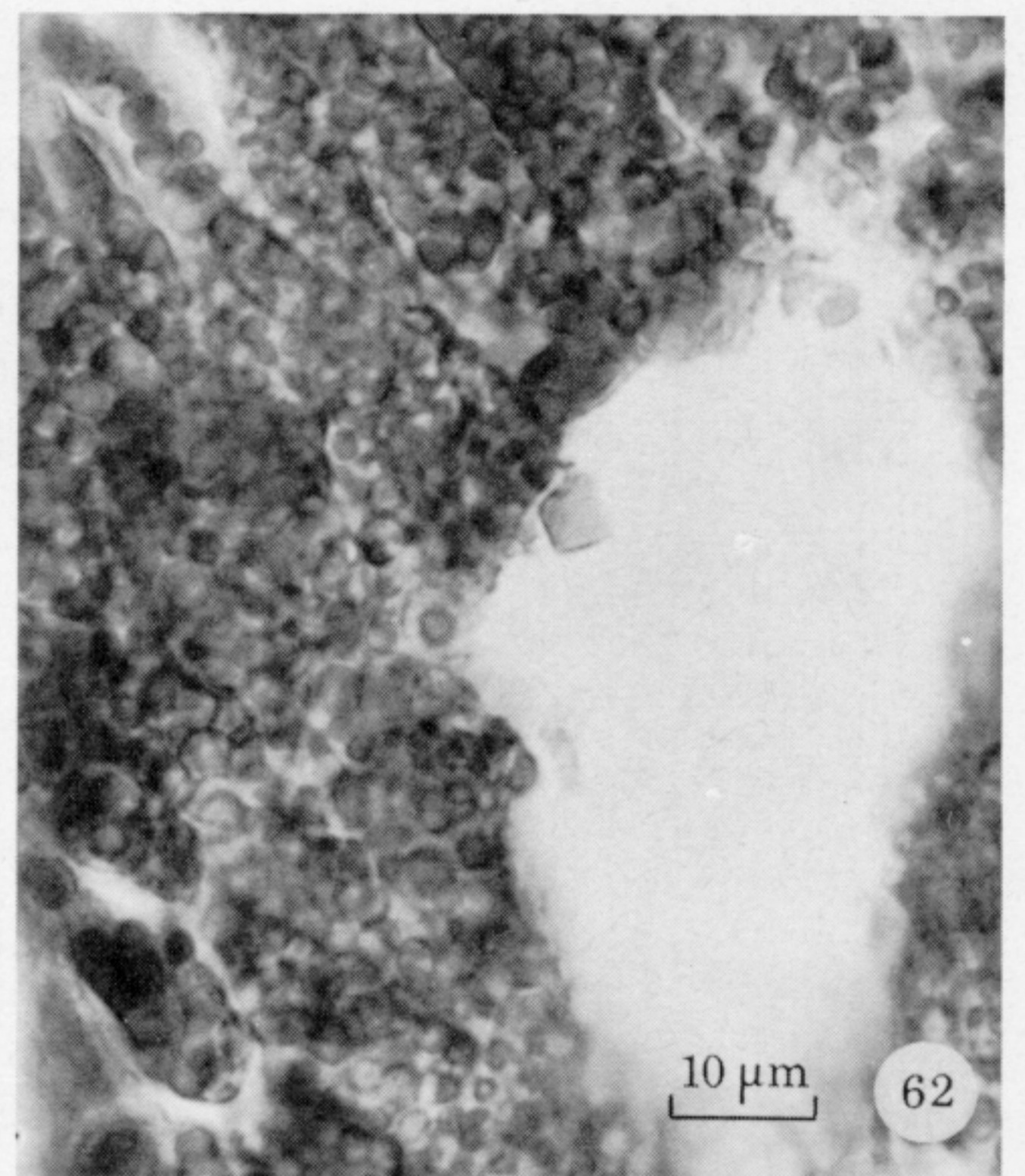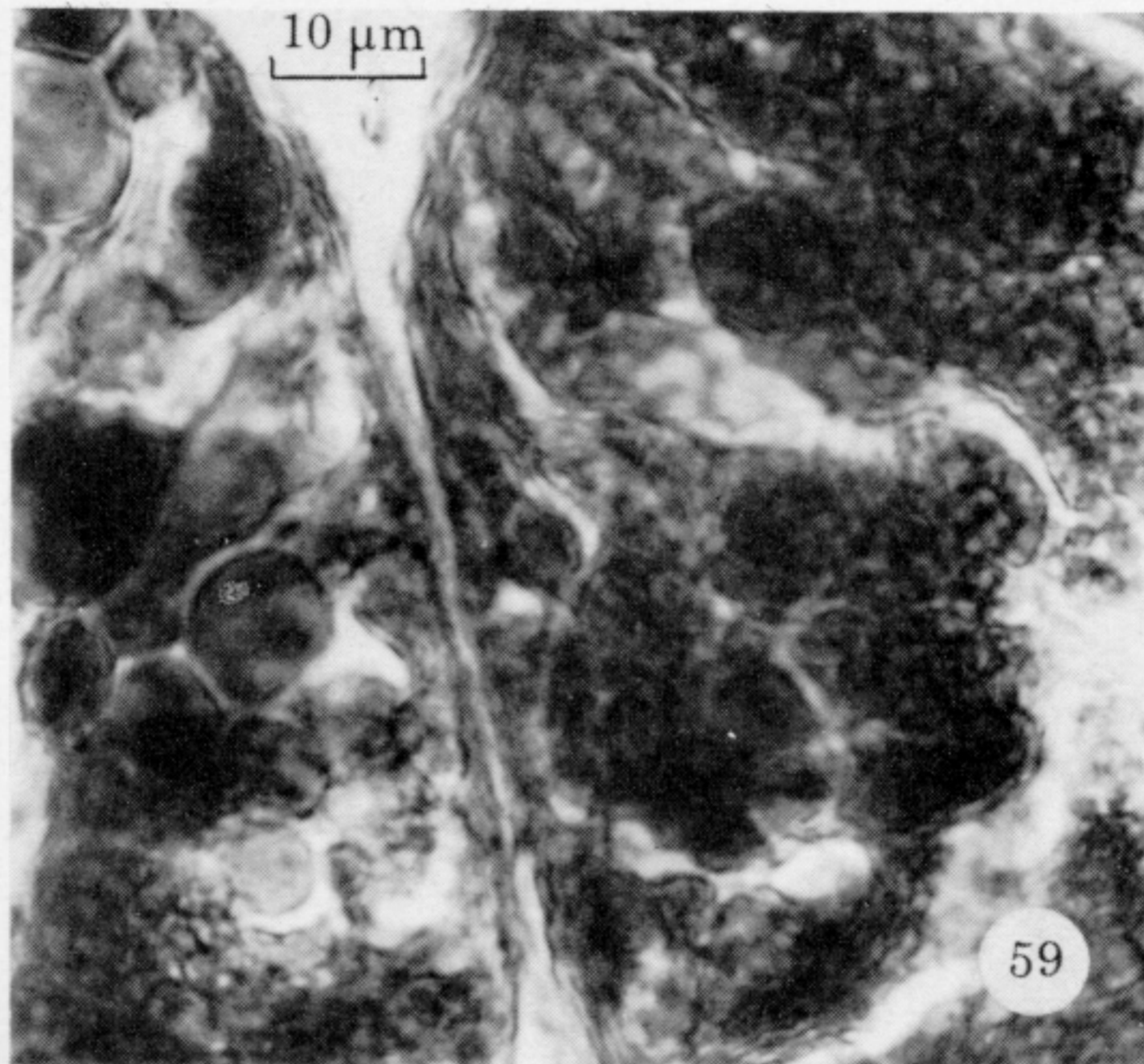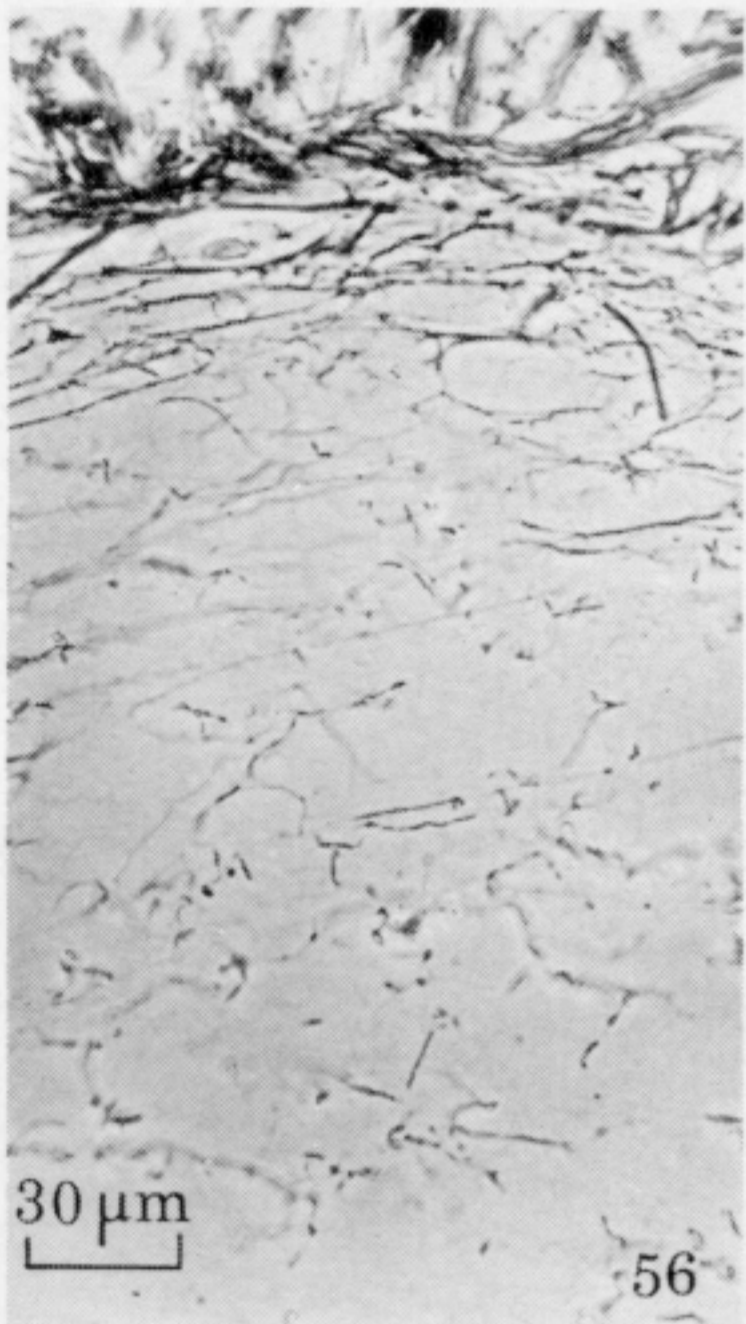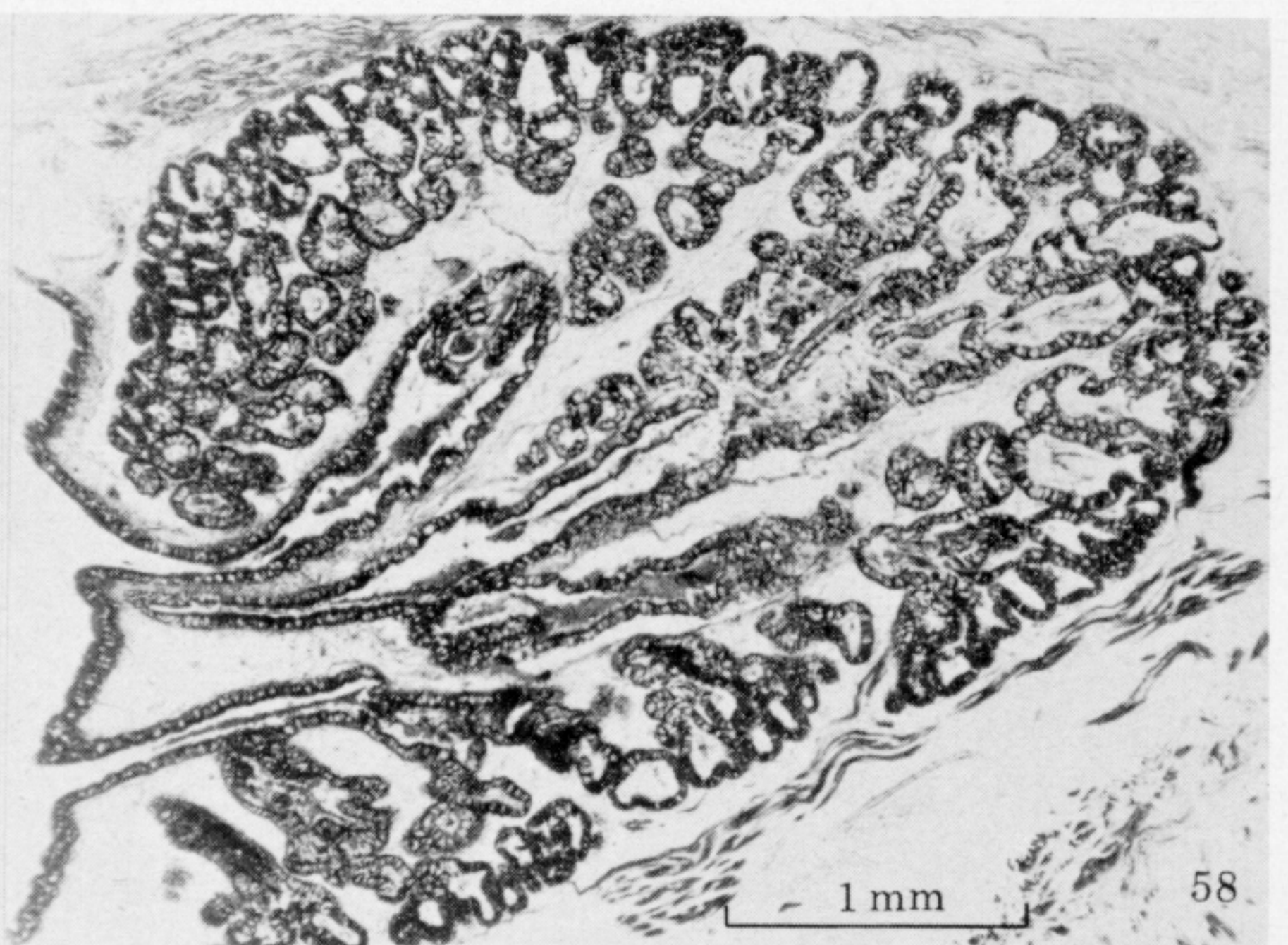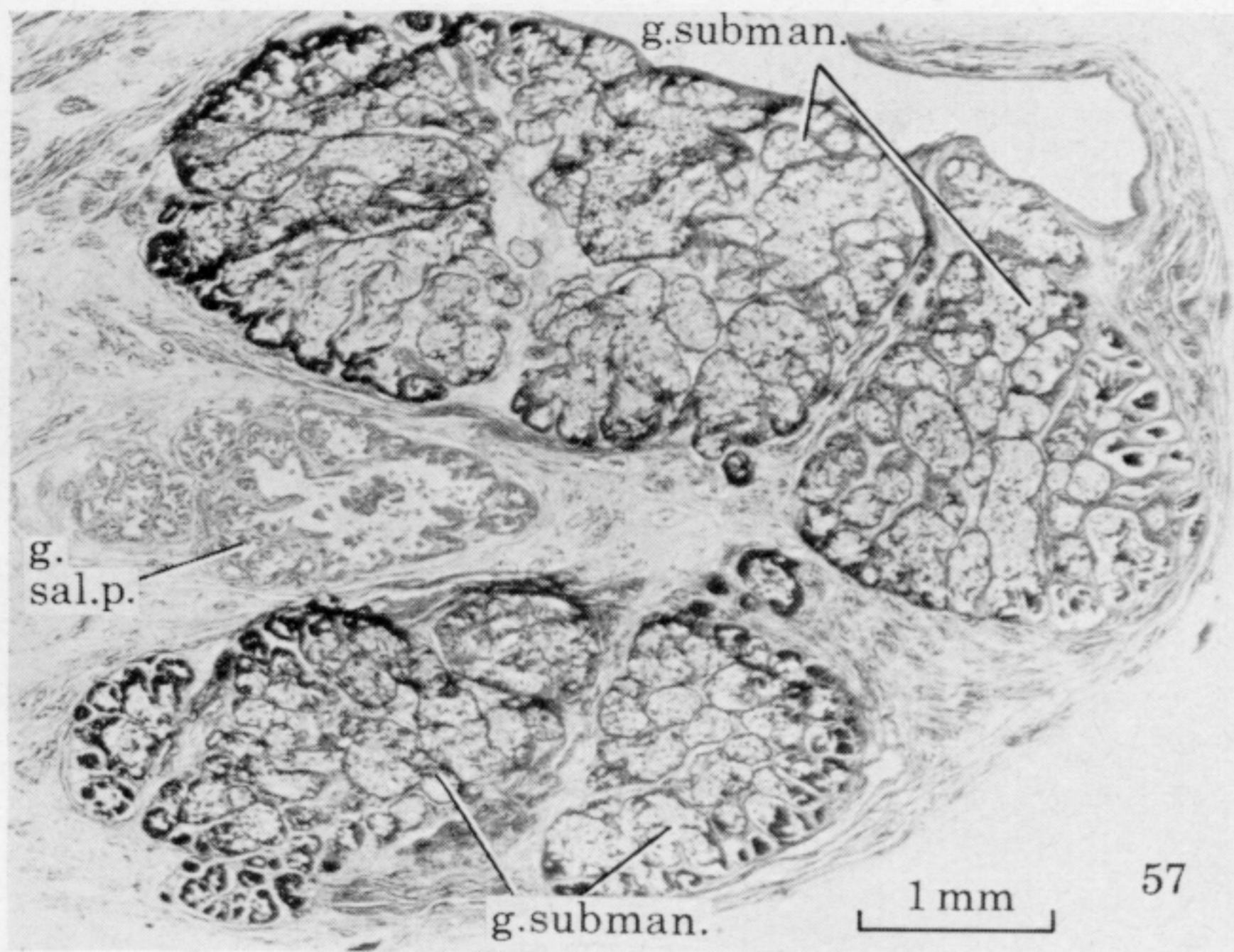
Figure 57 labels: g.subman., g.sal.p., g.subman., 1 mm

Figure 58 labels: 1 mm

Figure 56 labels: 30 μm

Figure 59 labels: 10 μm

Figure 62 labels: 10 μm

Figure 60 labels: sec. prod., po., 100 μm

Figure 61 labels: 10 μm

Figure 63 labels: 10 μm

FIGURES 56–63. For description see p. **32.**
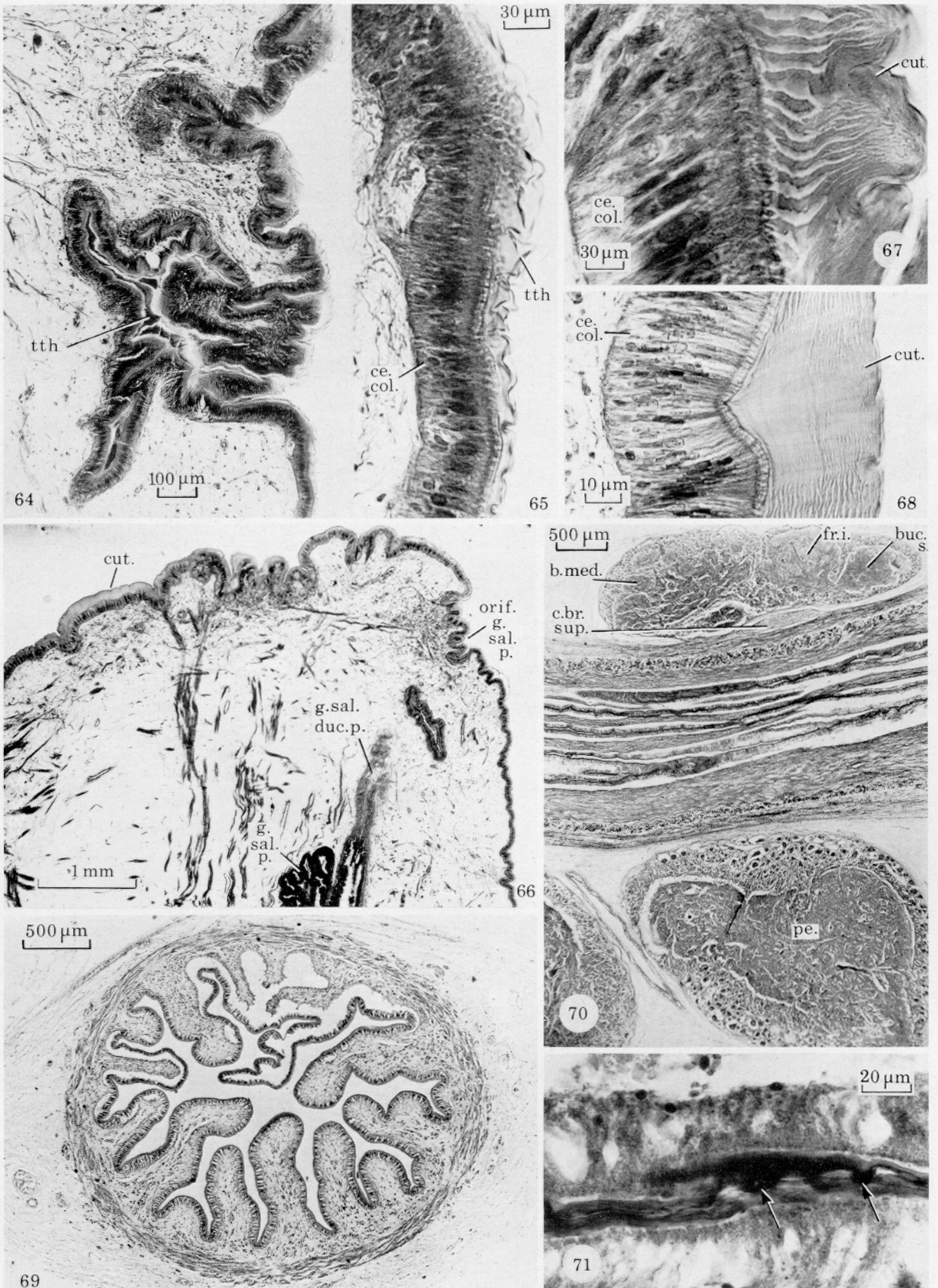
FIGURES 64–71. For description see p. **33.**
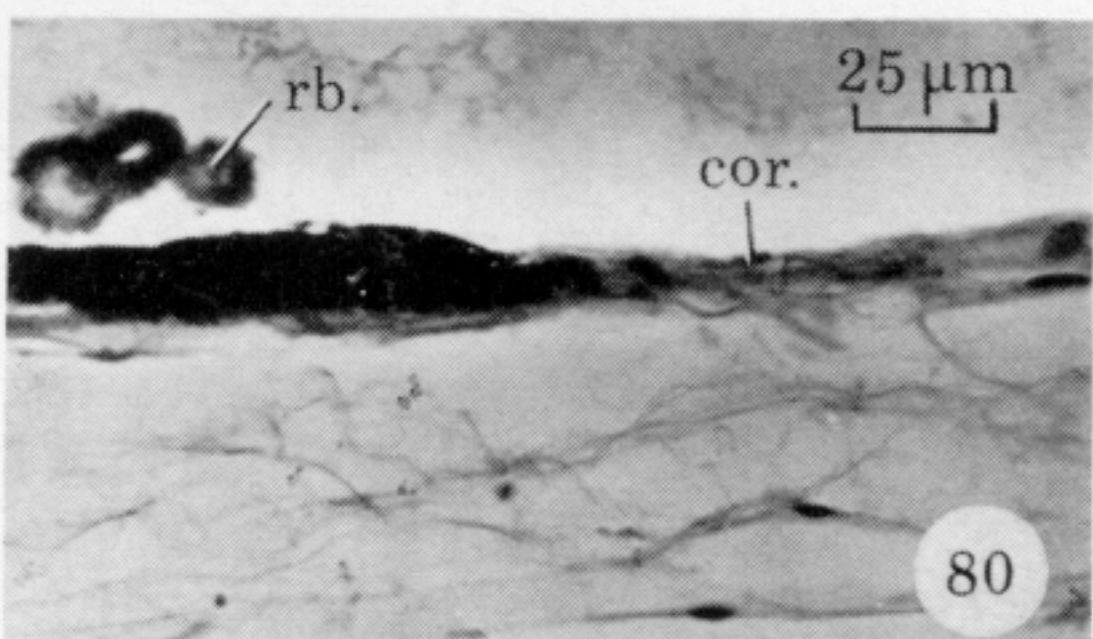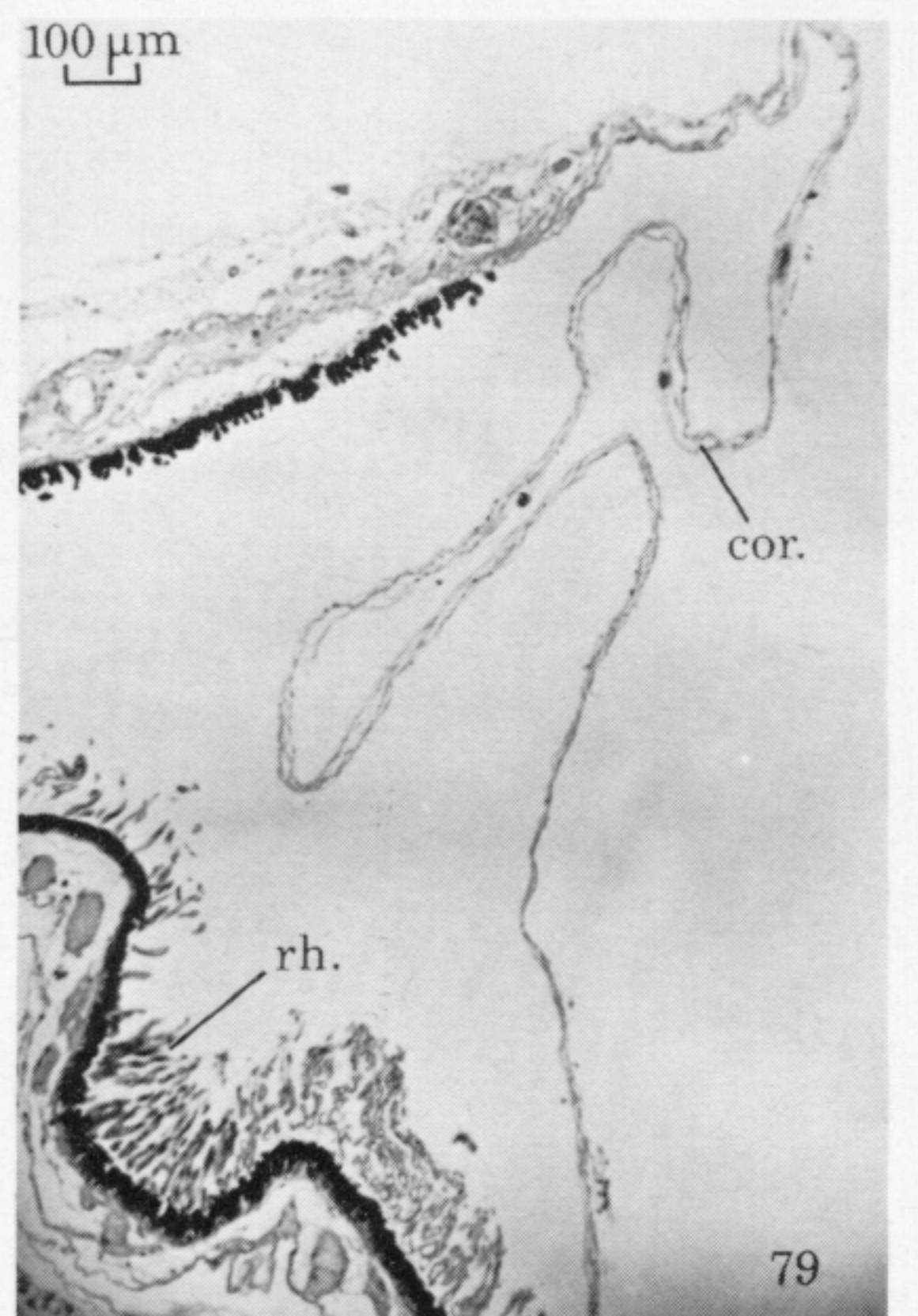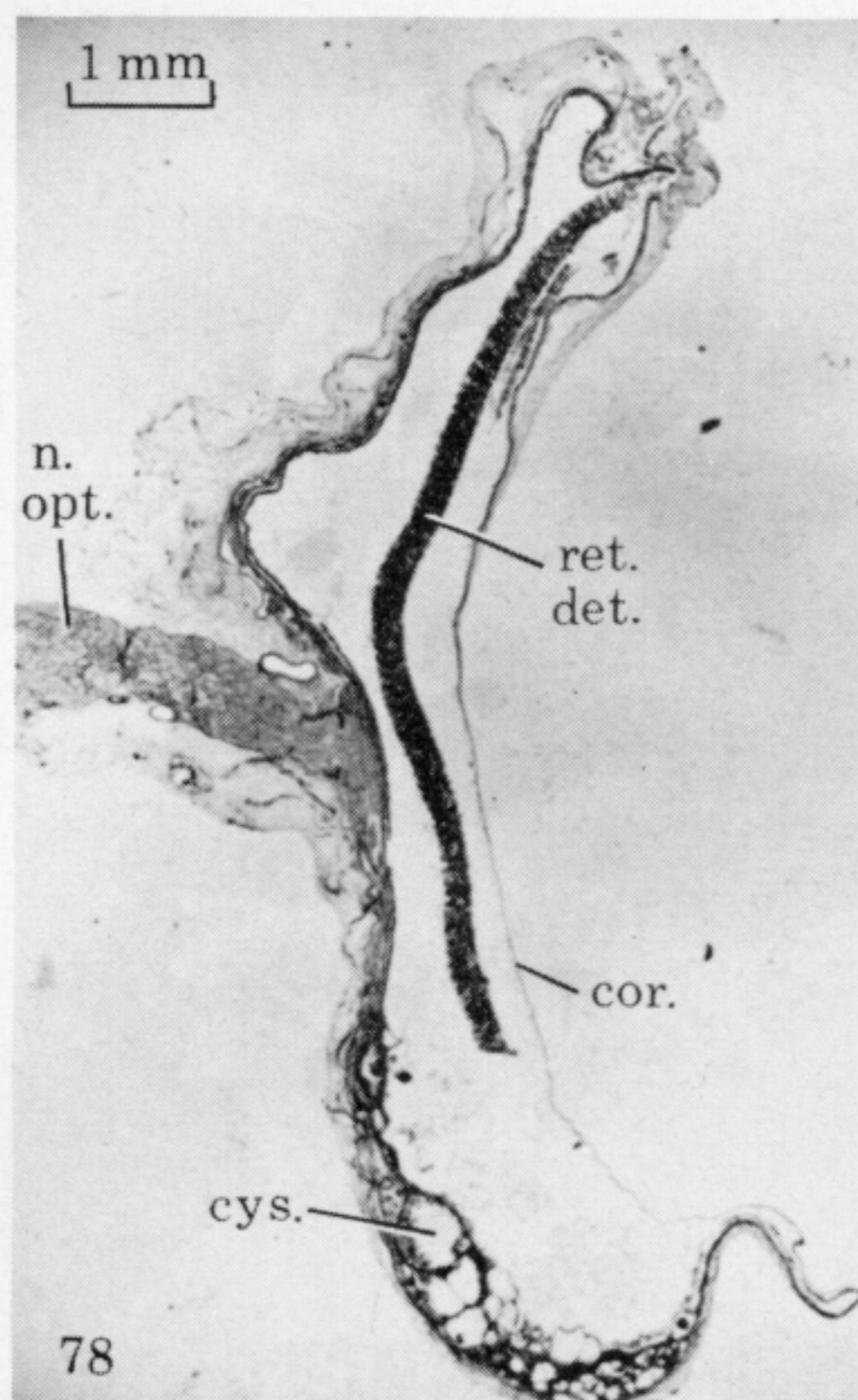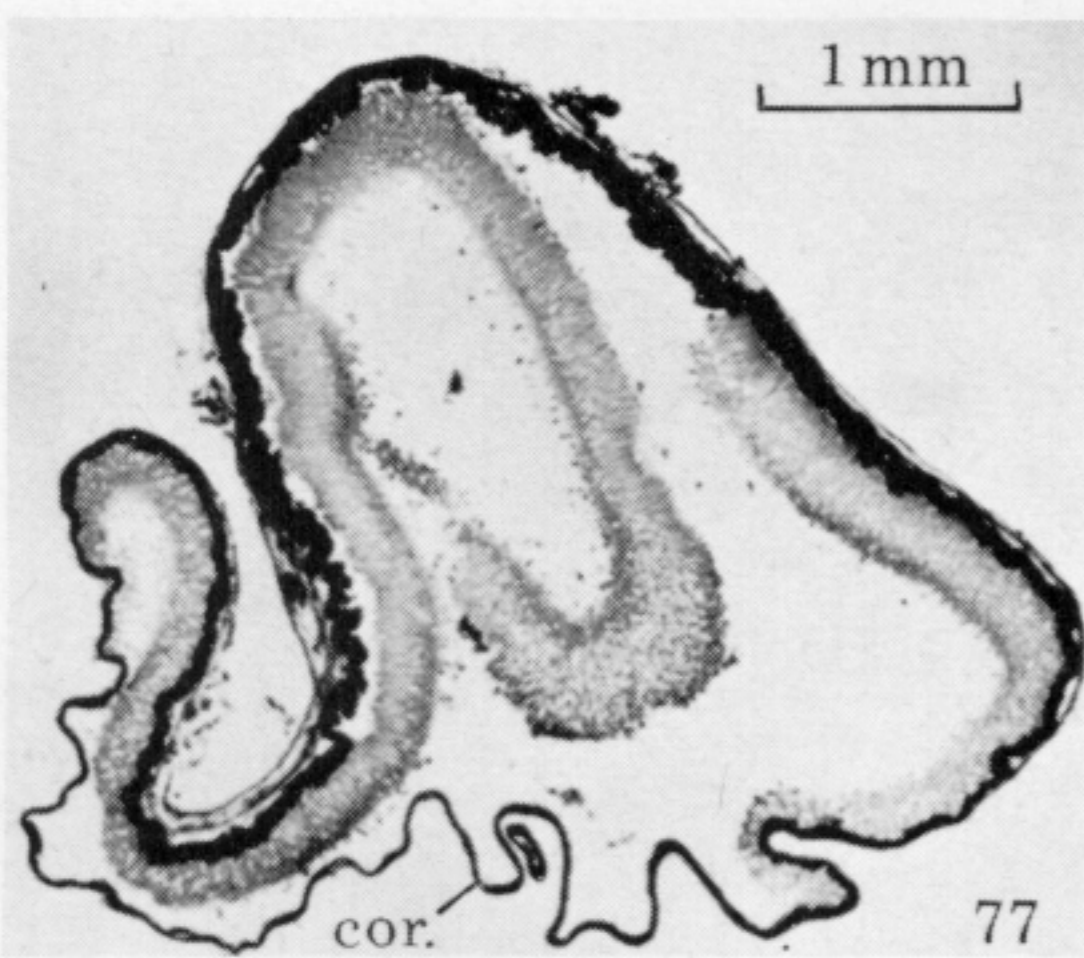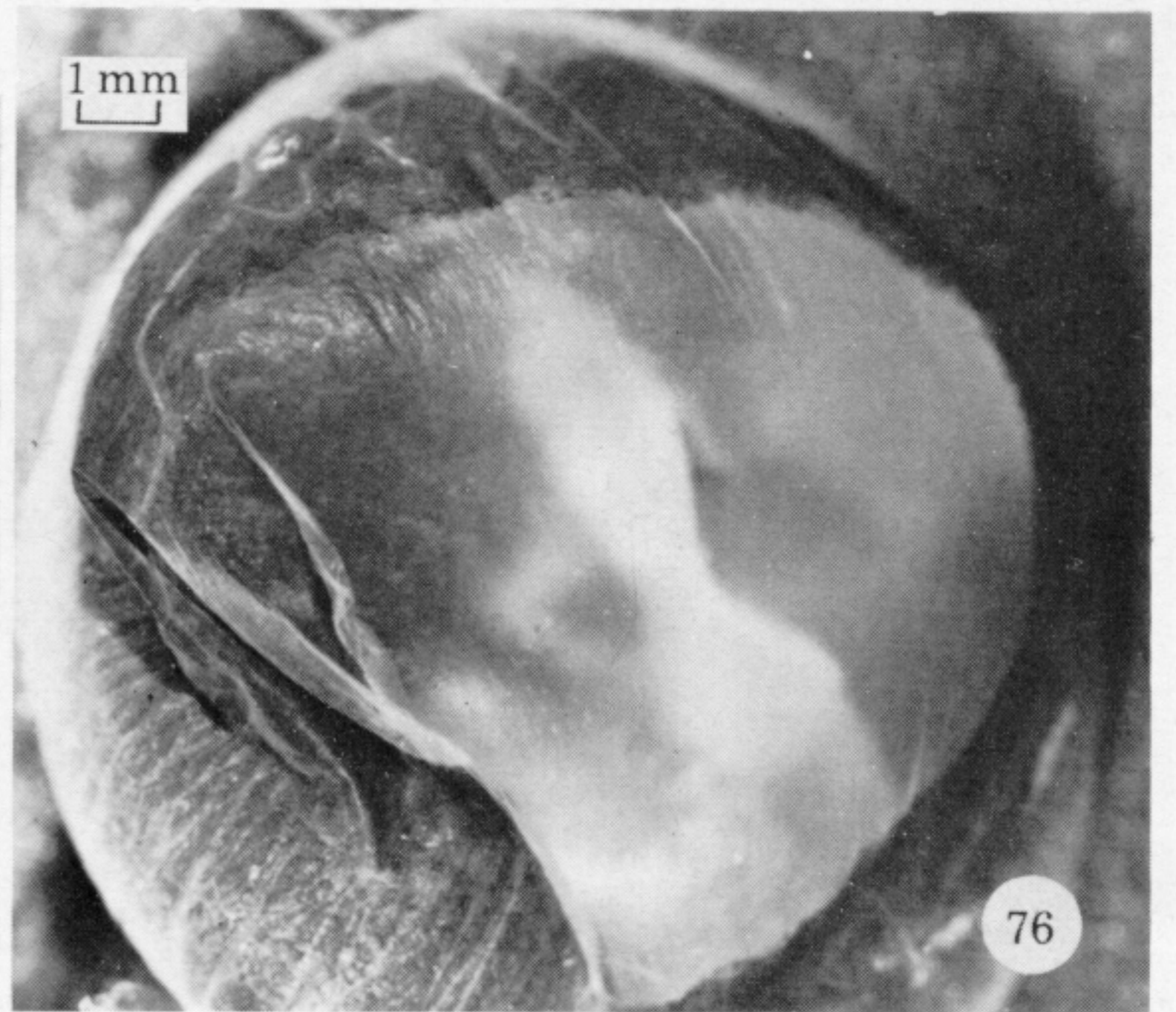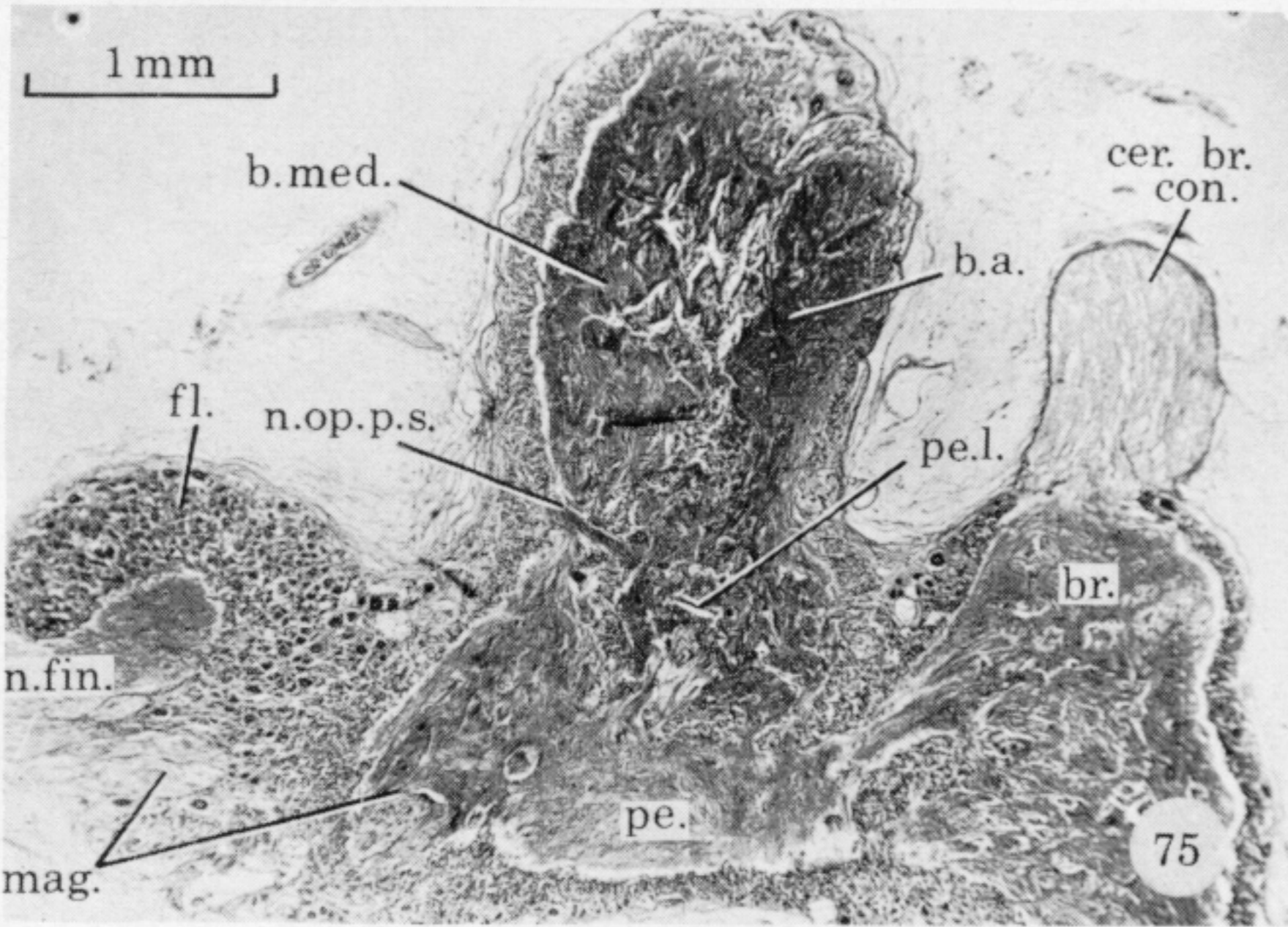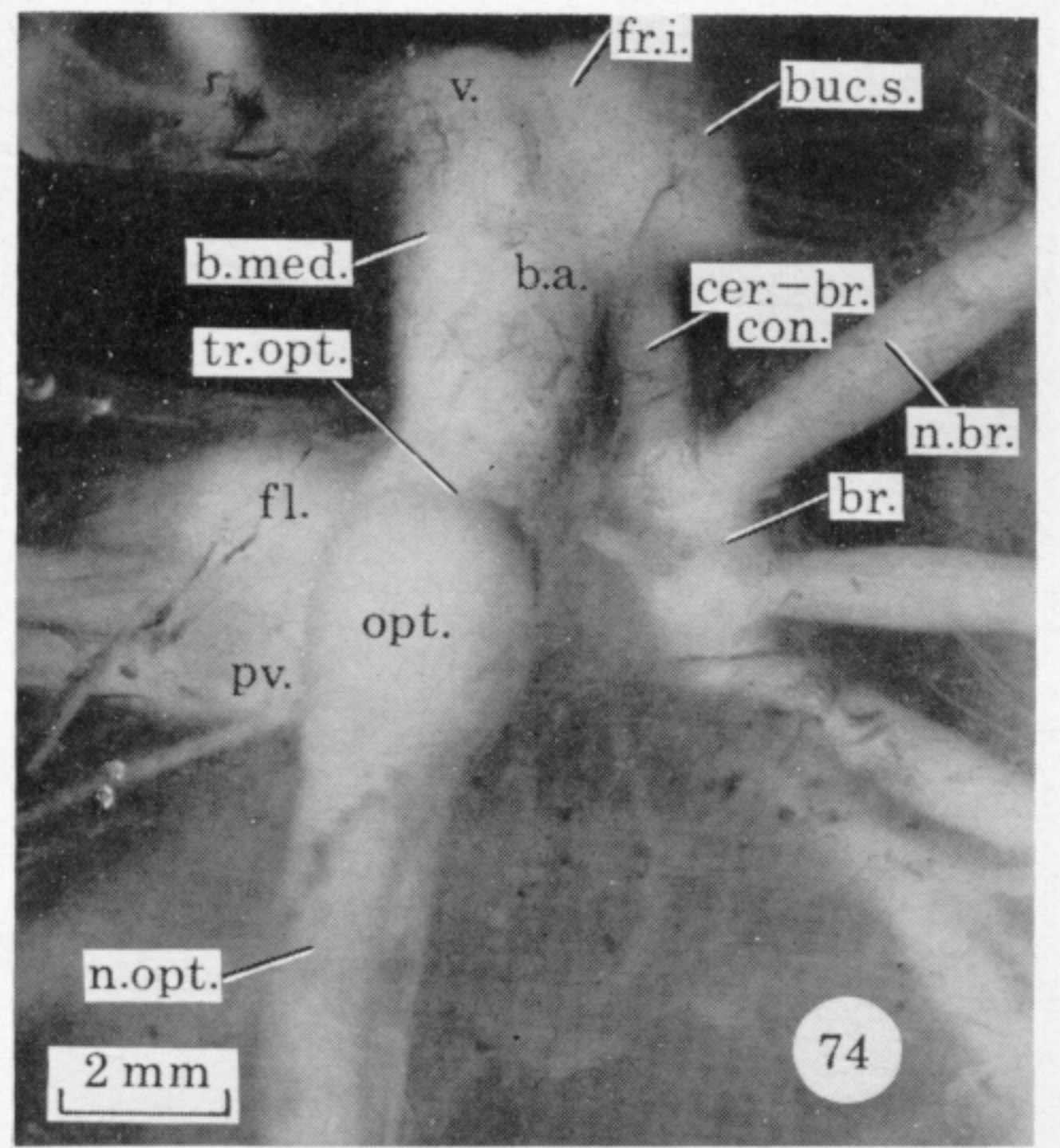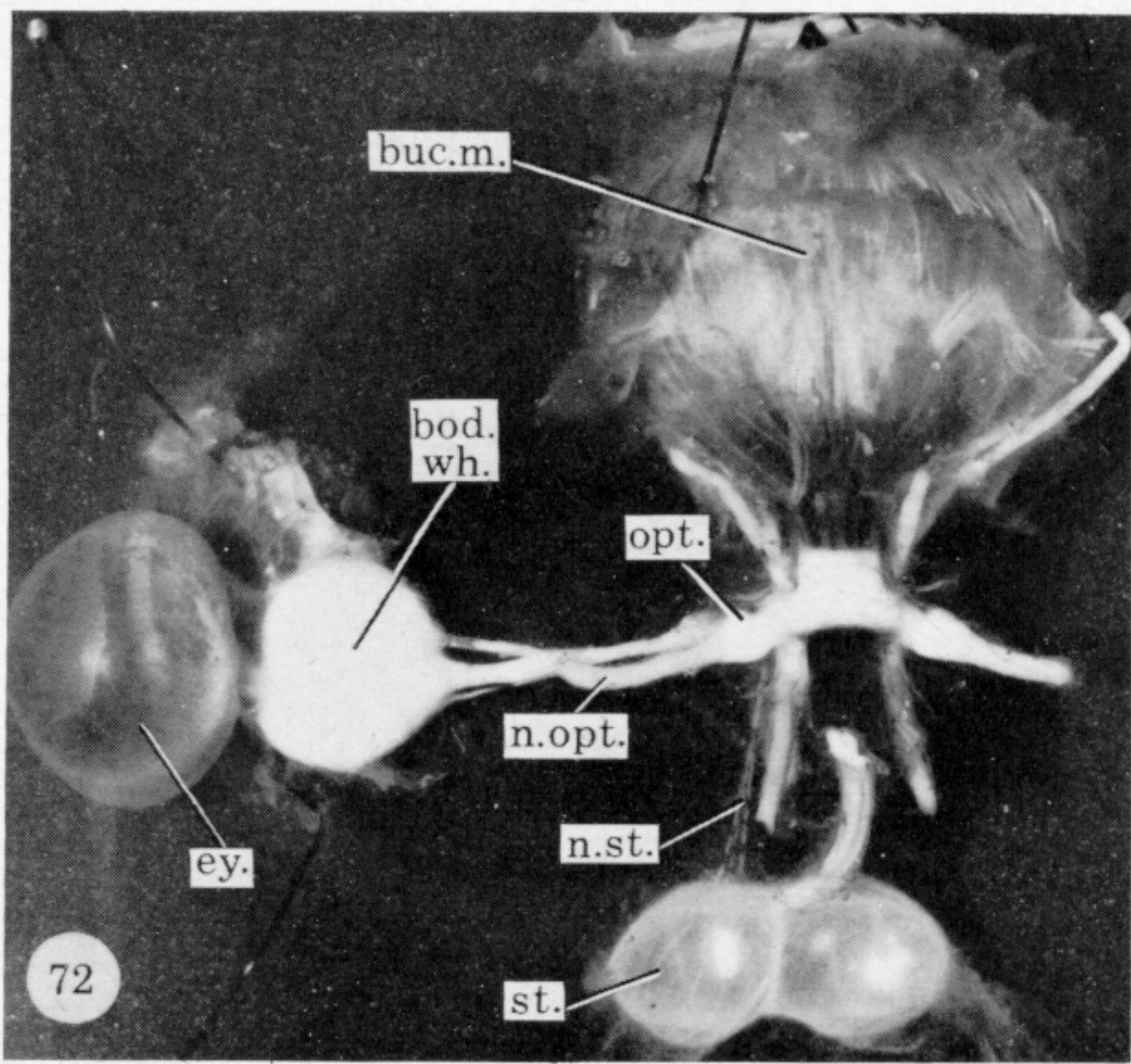
FIGURES 74–80. For description see opposite.
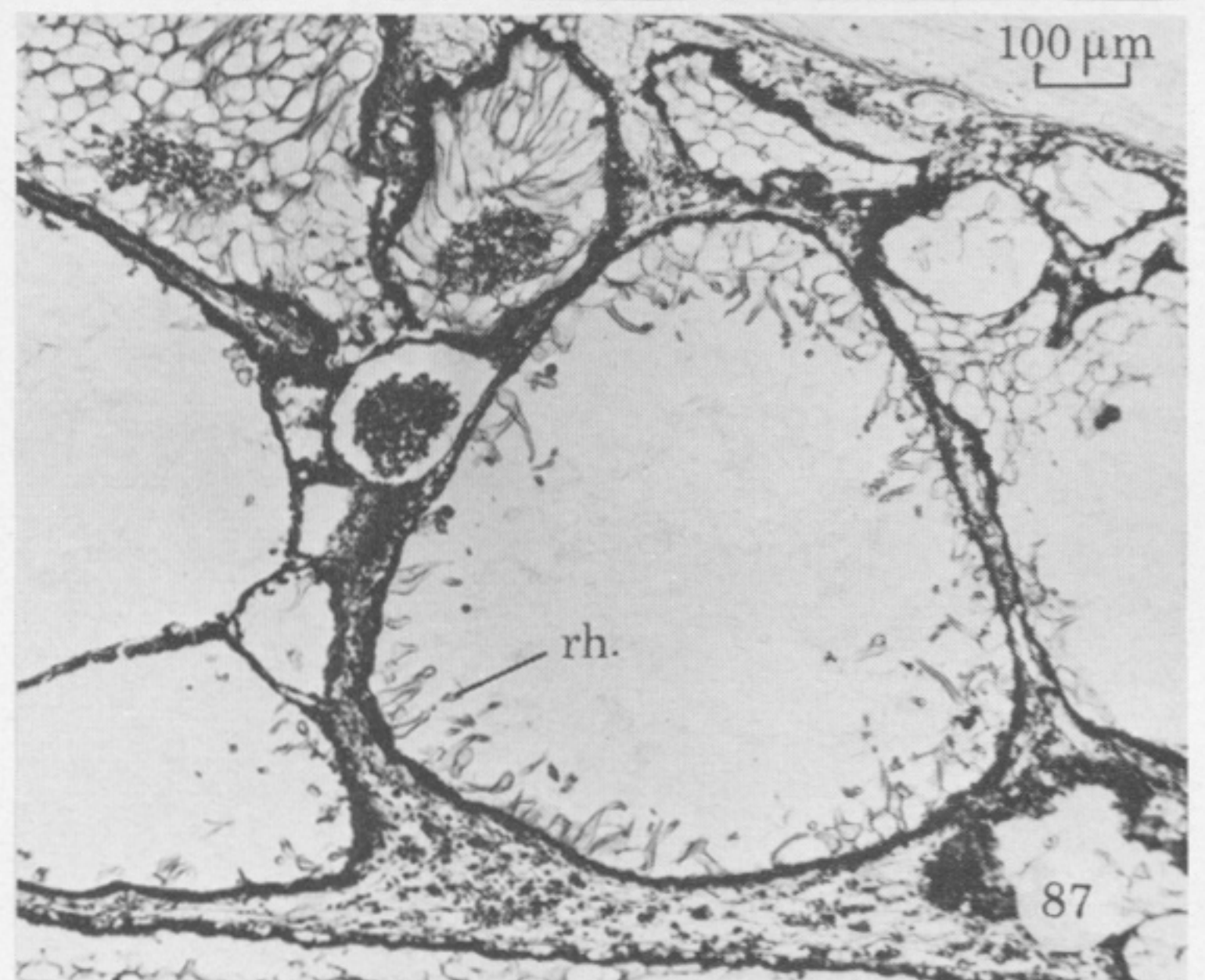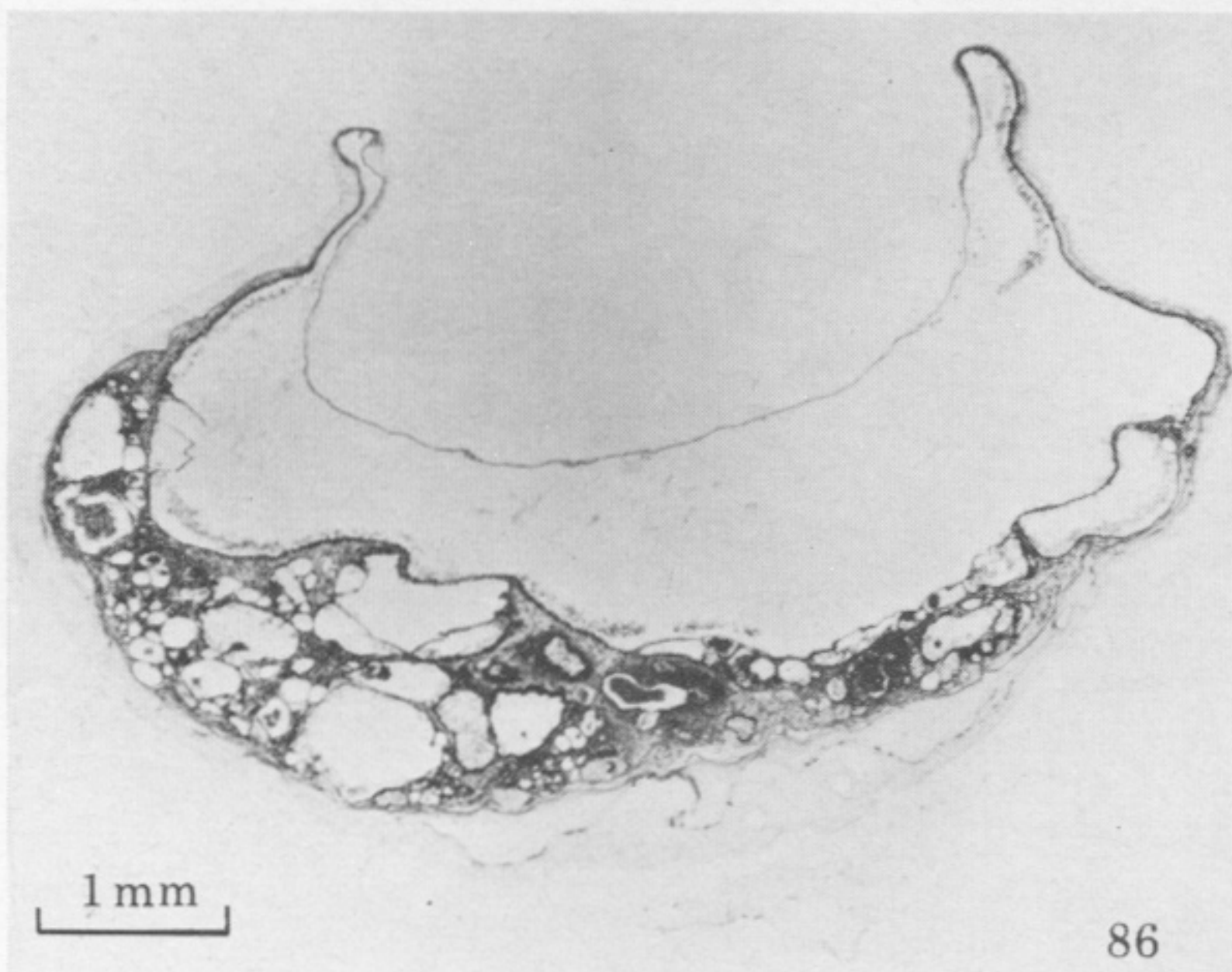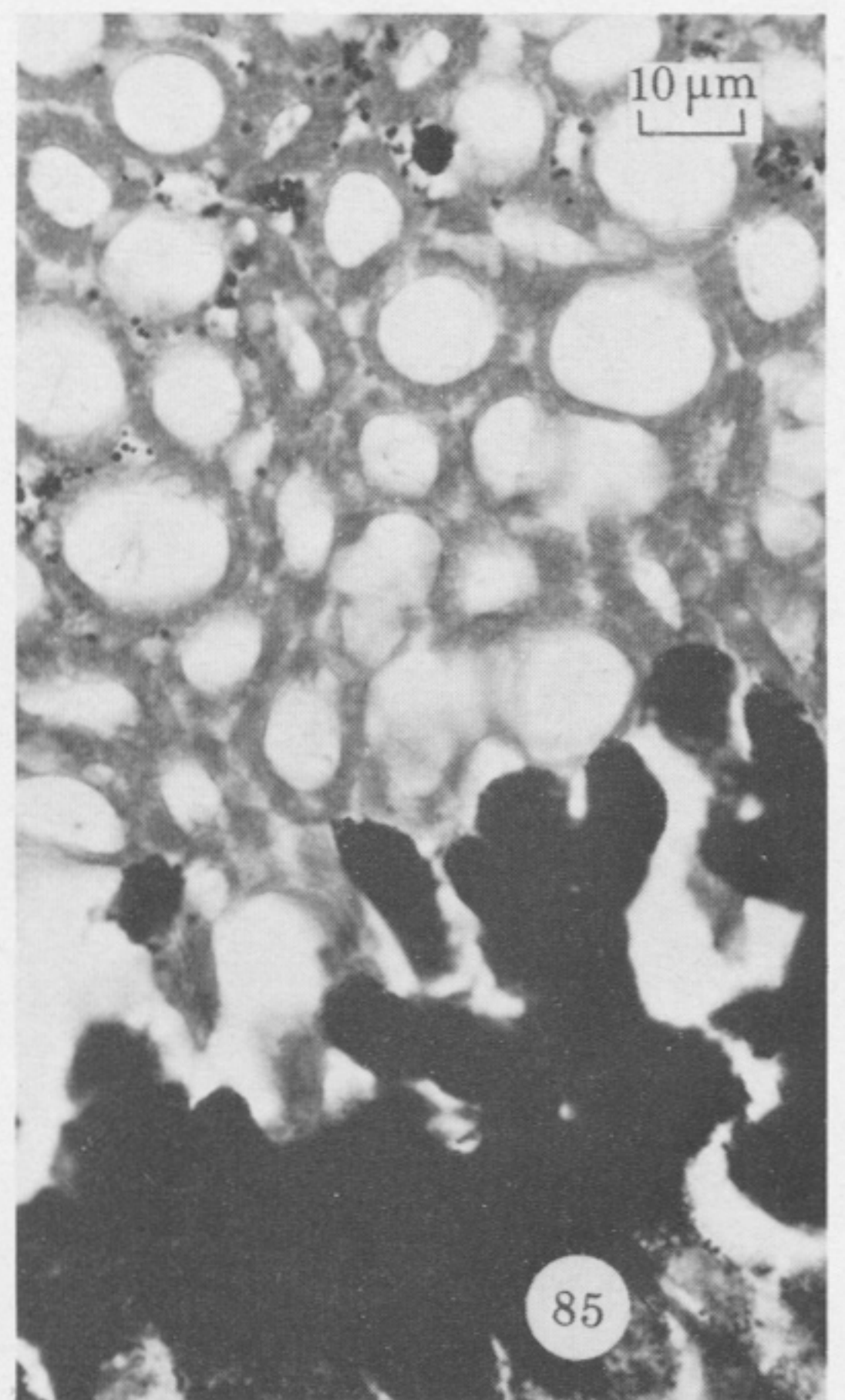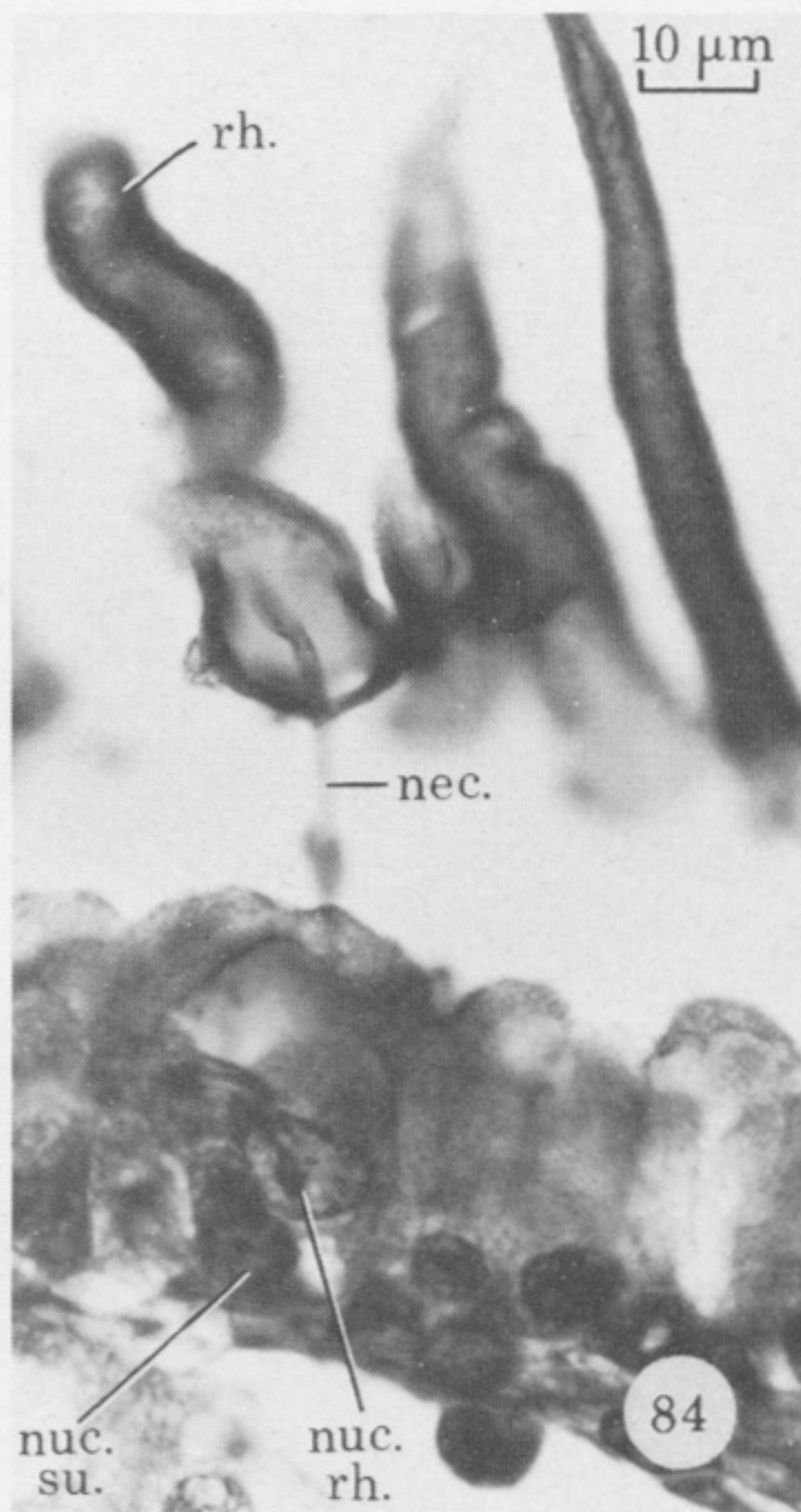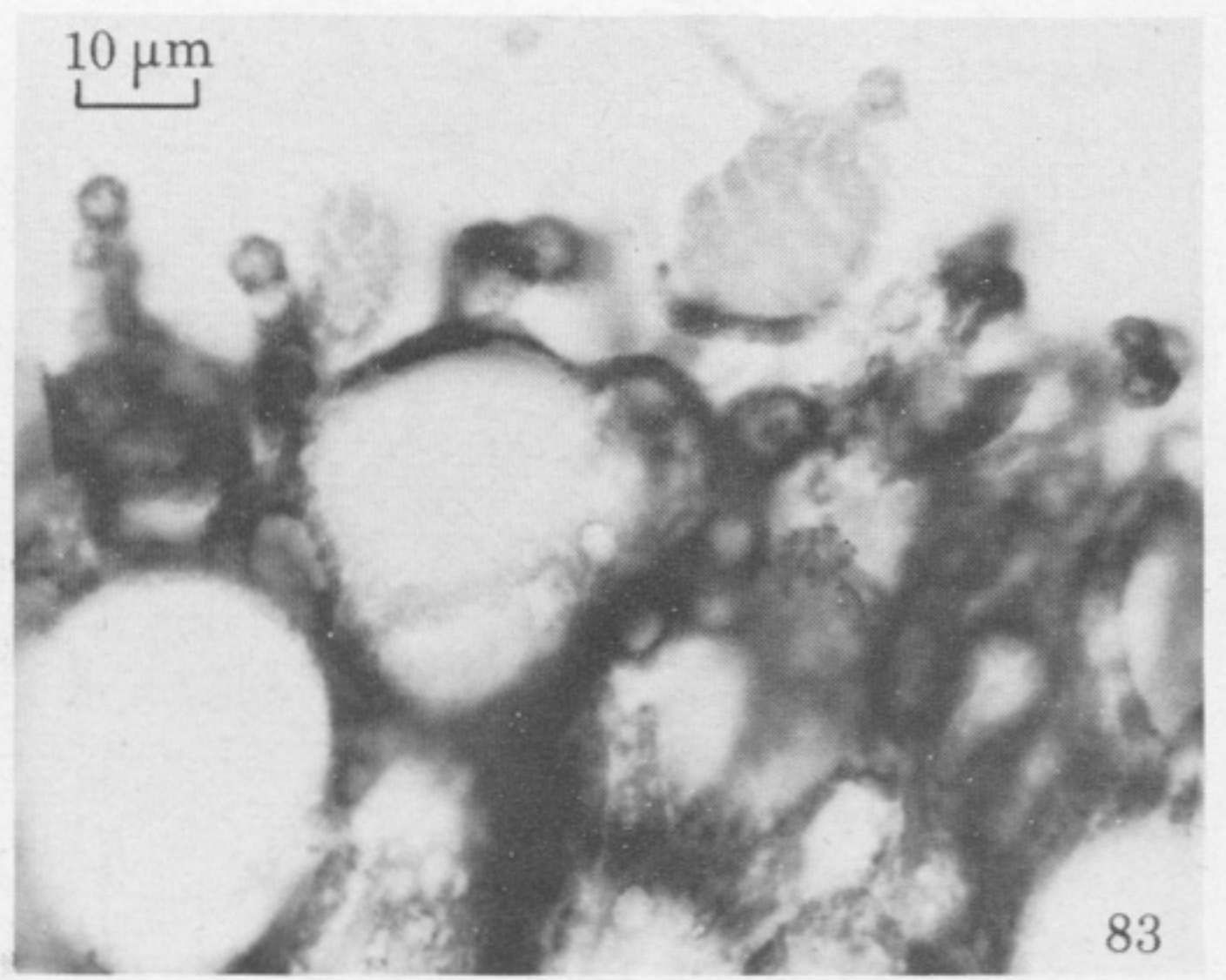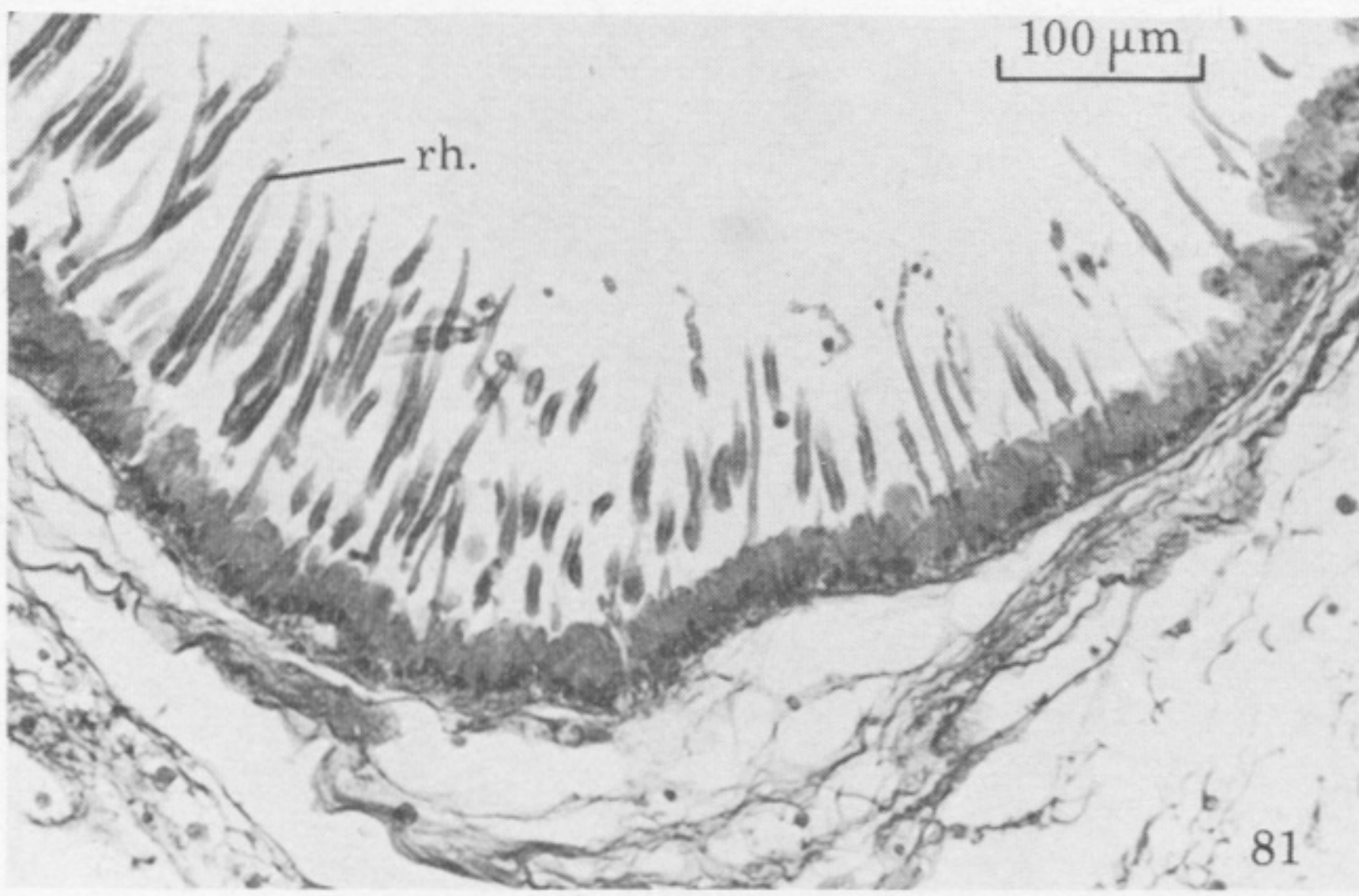
FIGURES 81–87. For description see opposite.
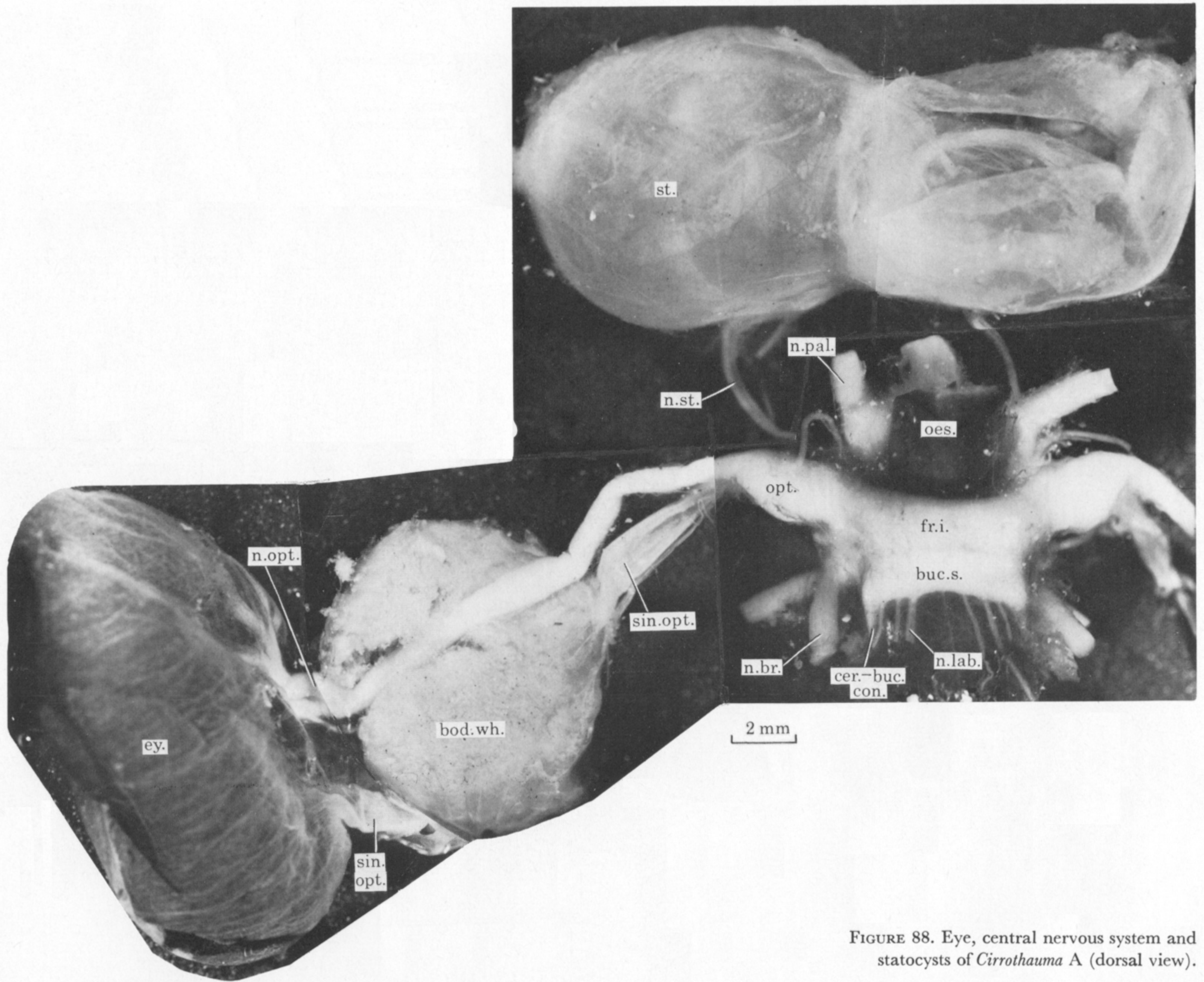
FIGURE 88. Eye, central nervous system and statocysts of *Cirrothauma* A (dorsal view).
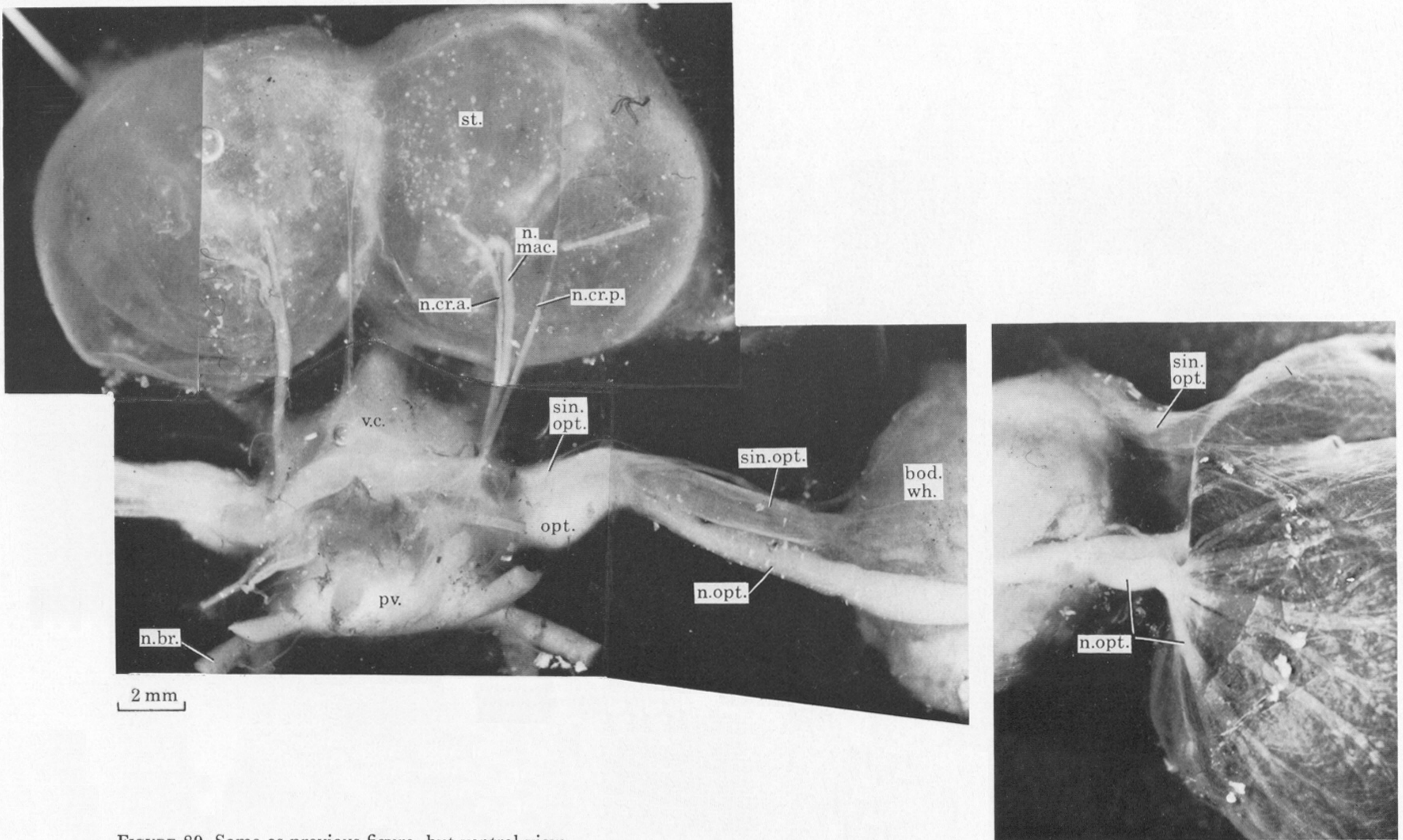
FIGURE 89. Same as previous figure, but ventral view.
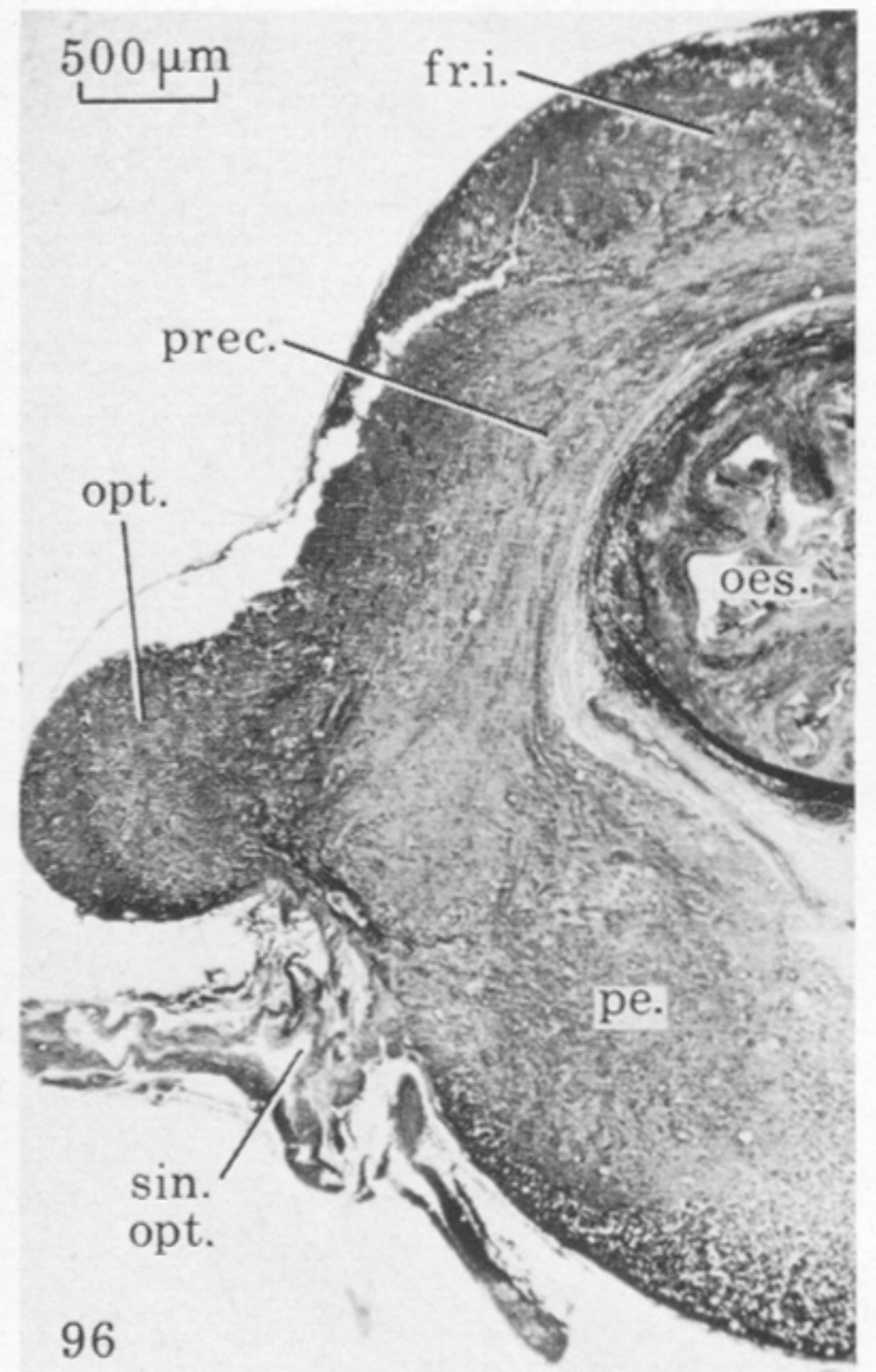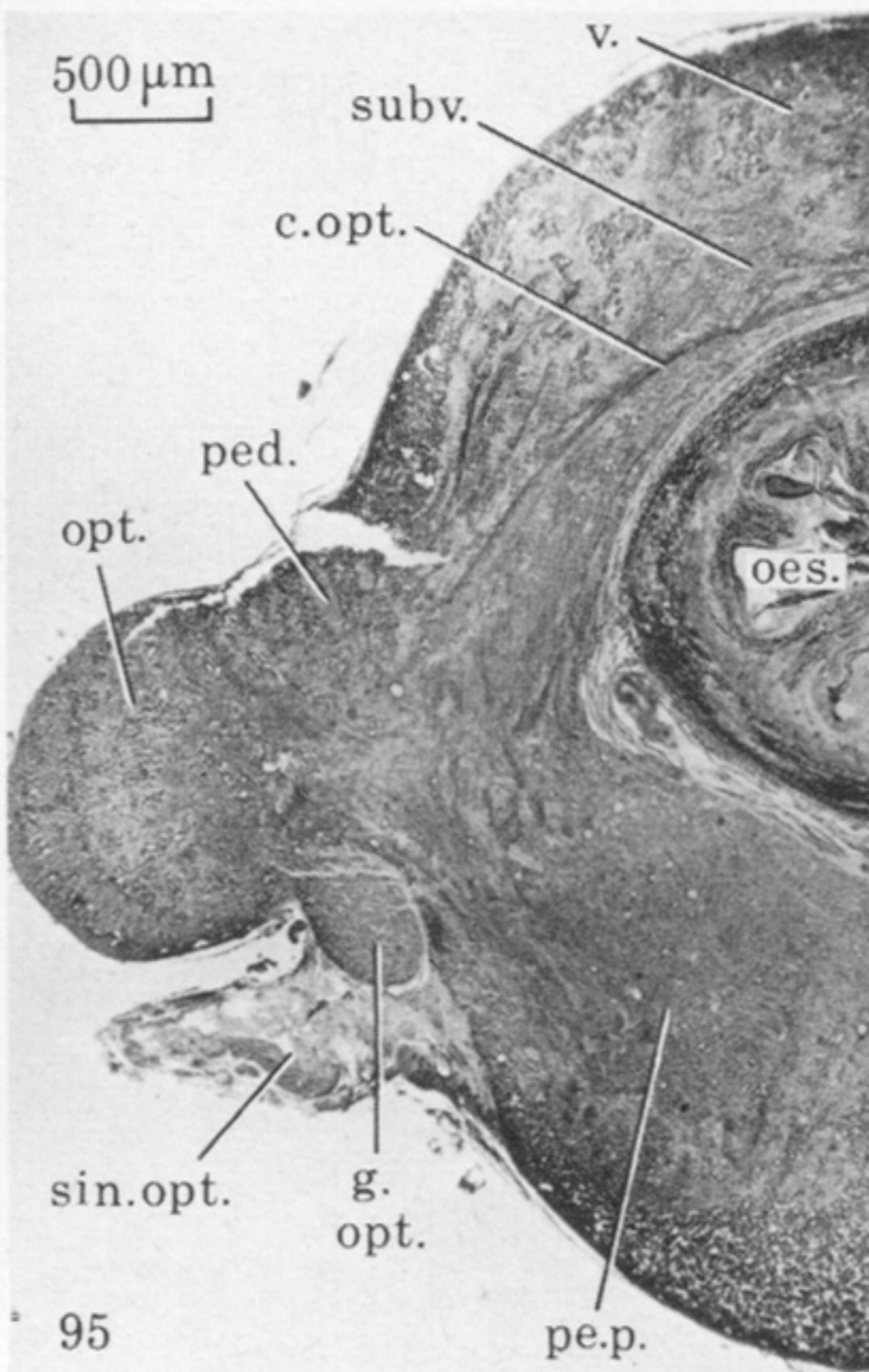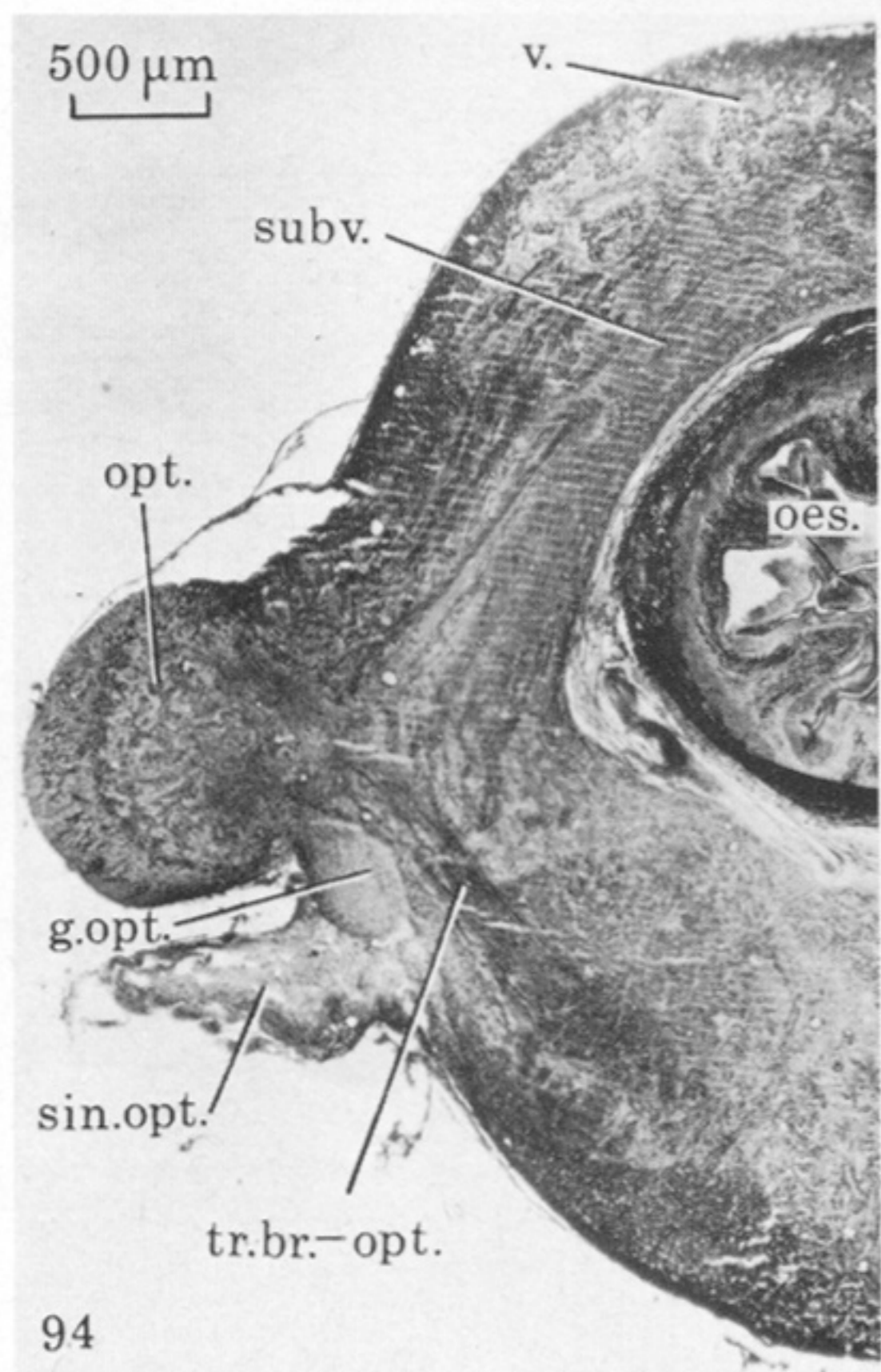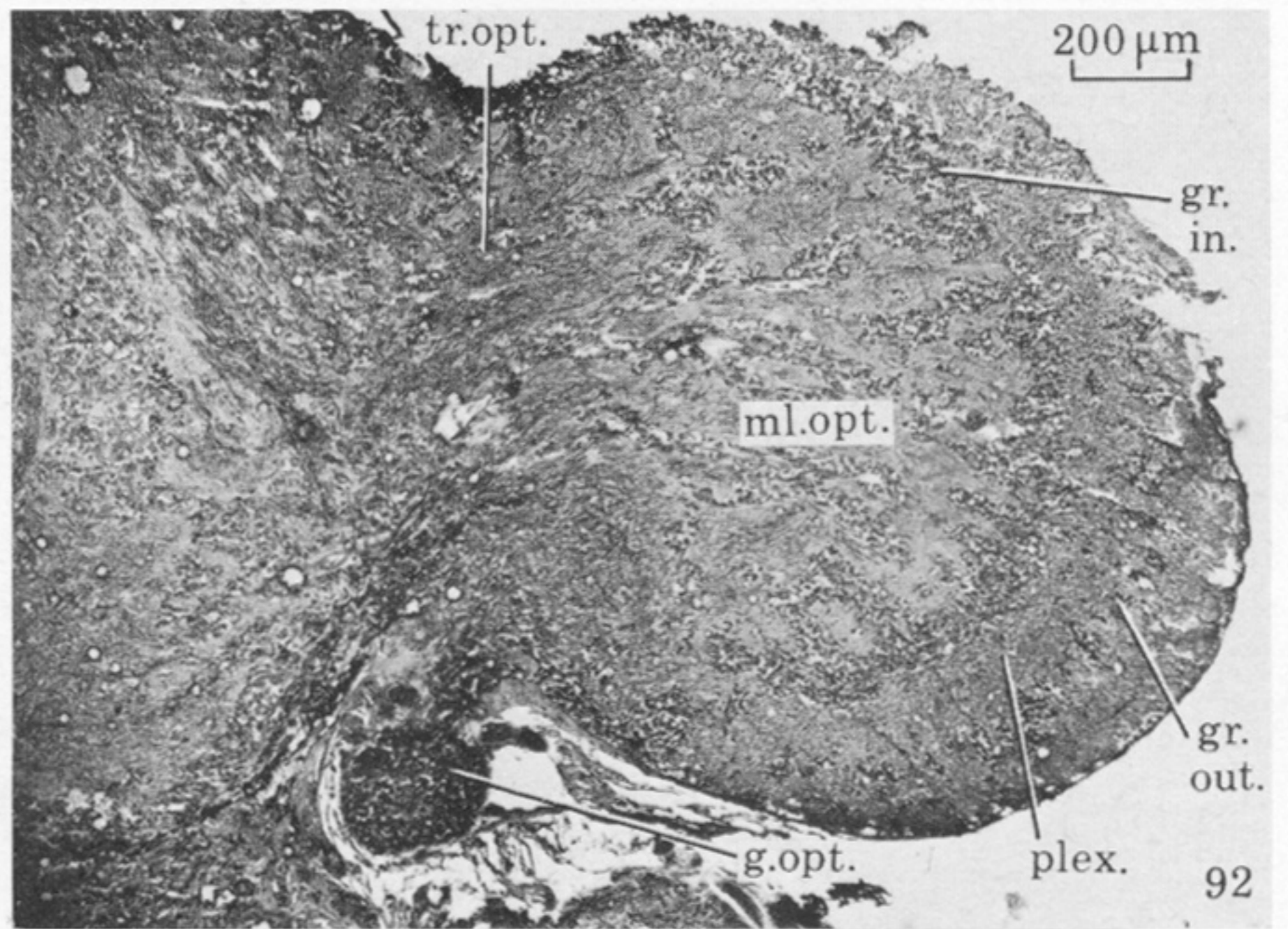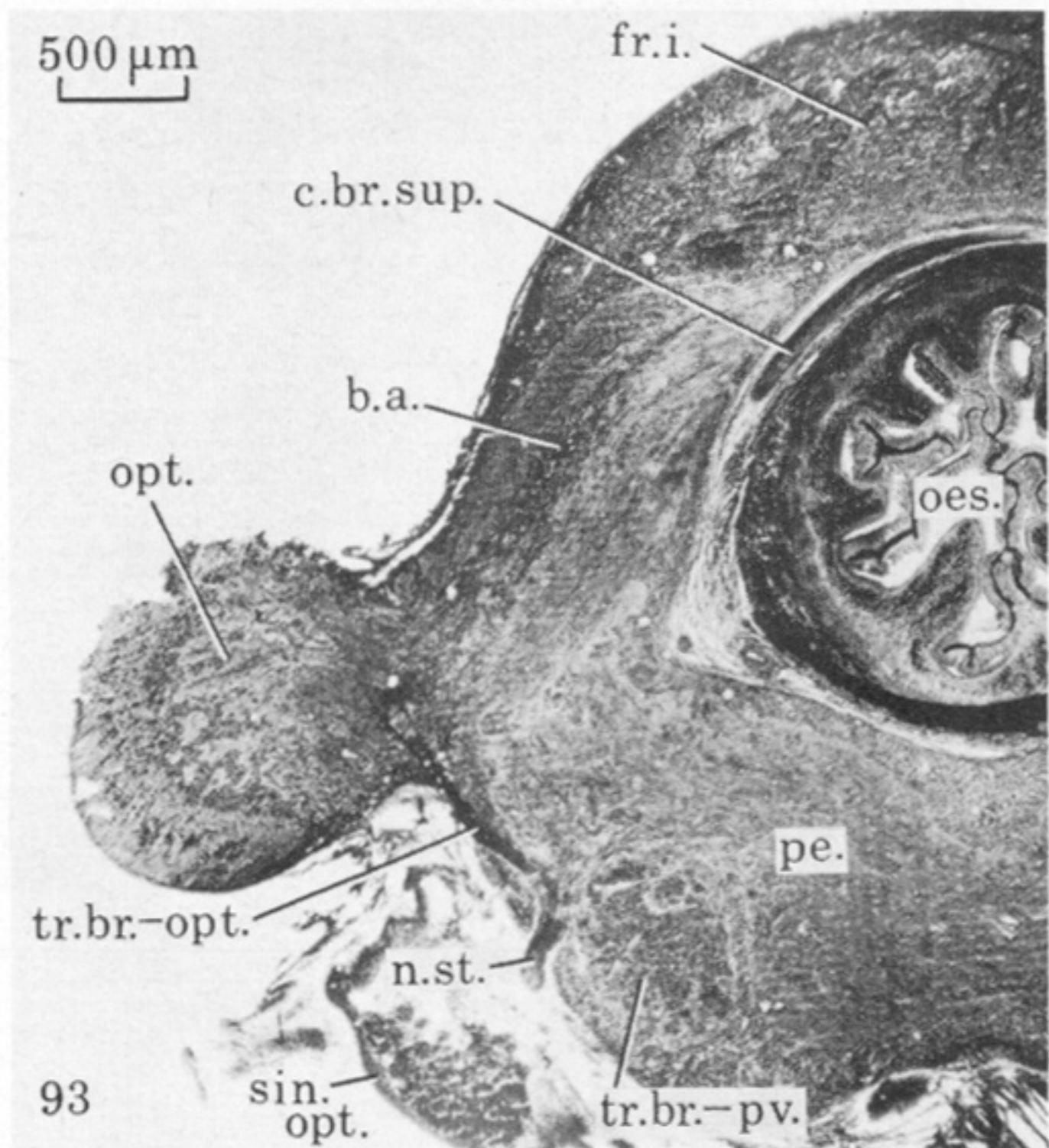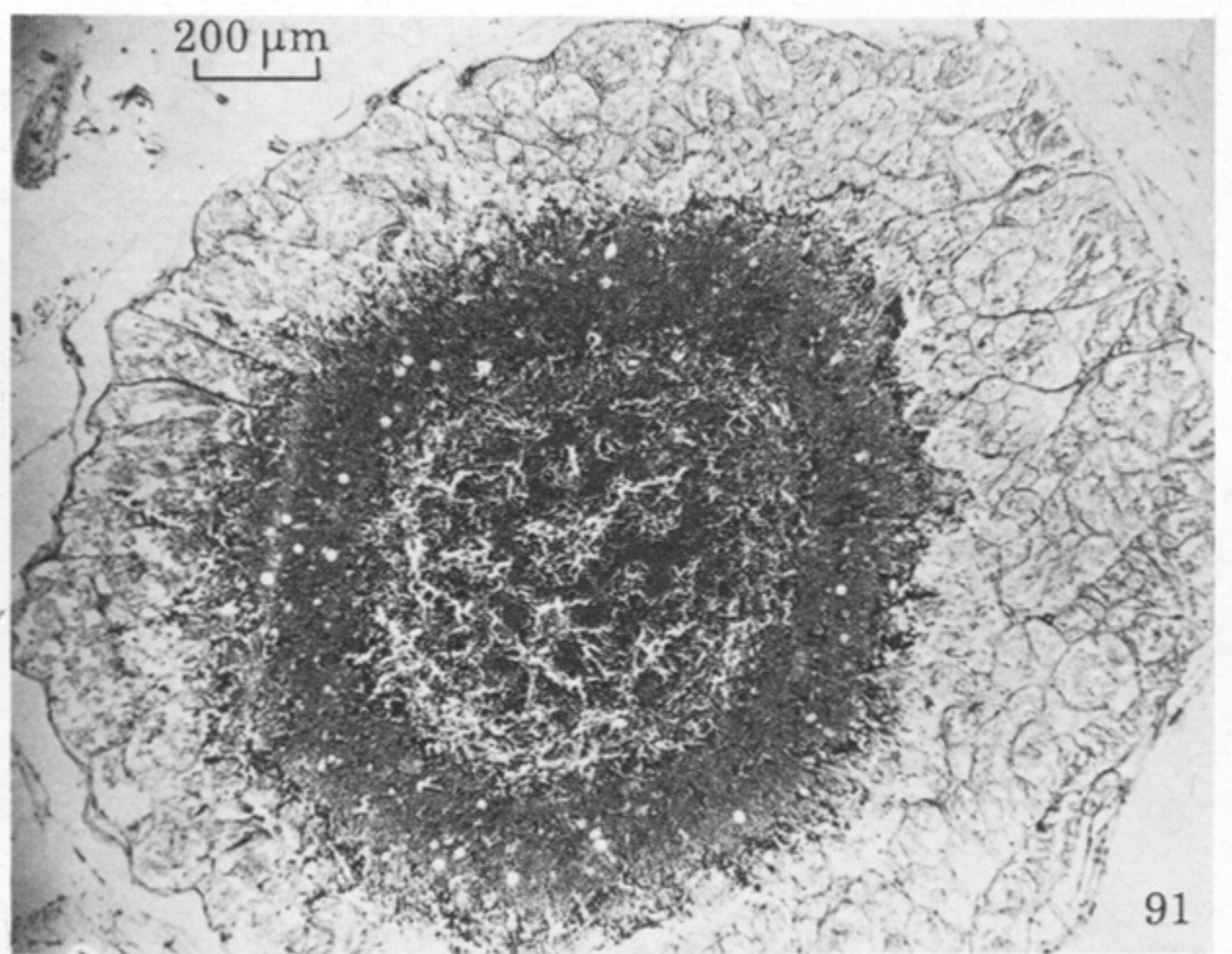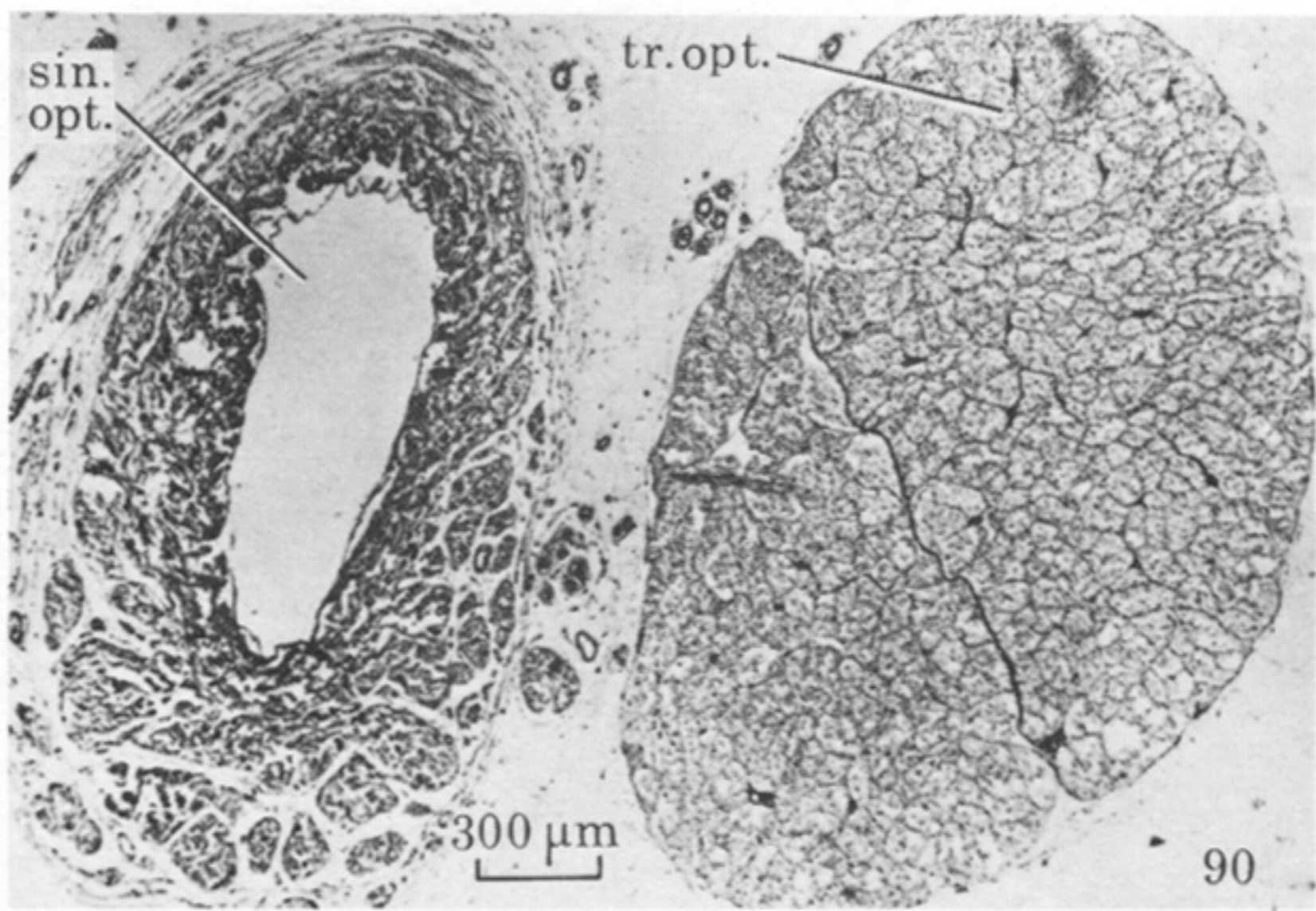
FIGURES 90–96. For description see opposite.
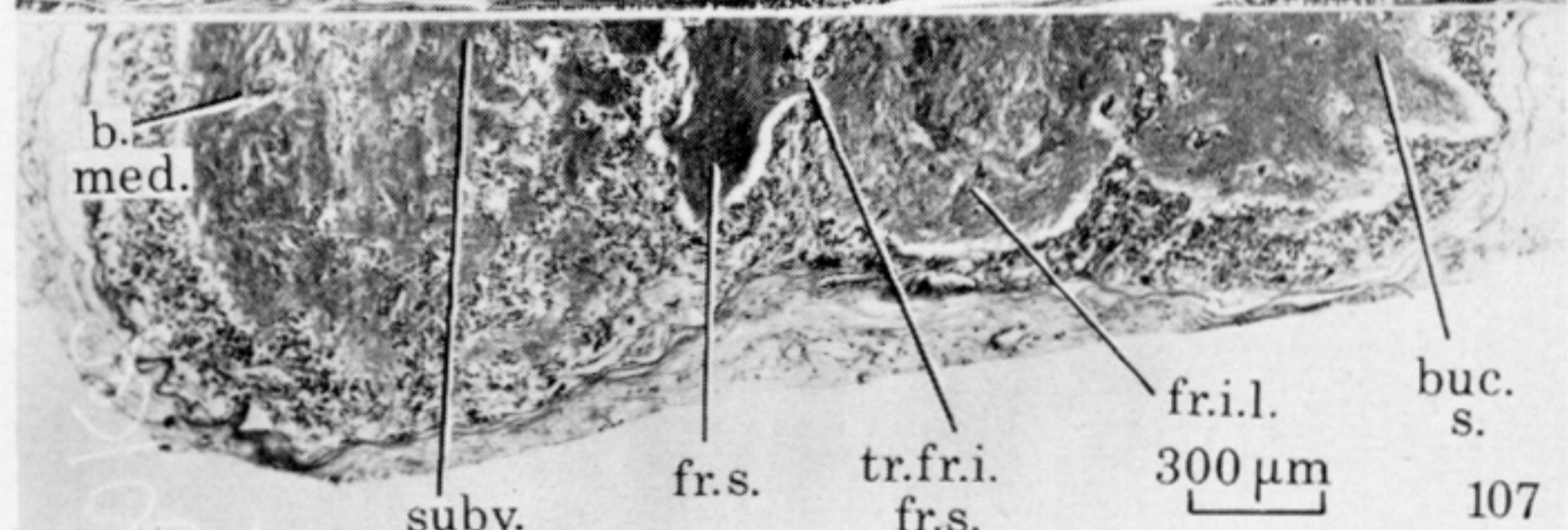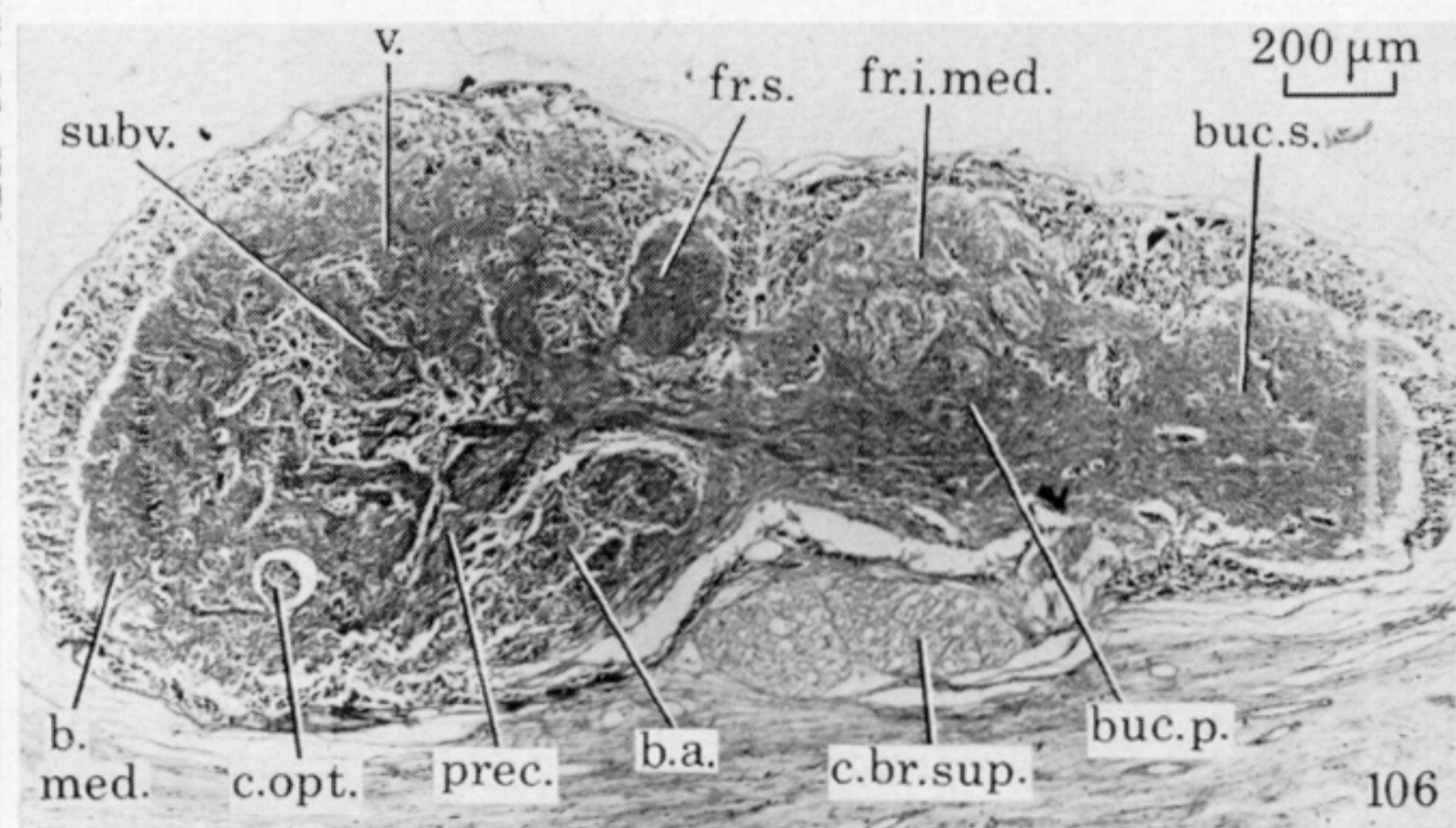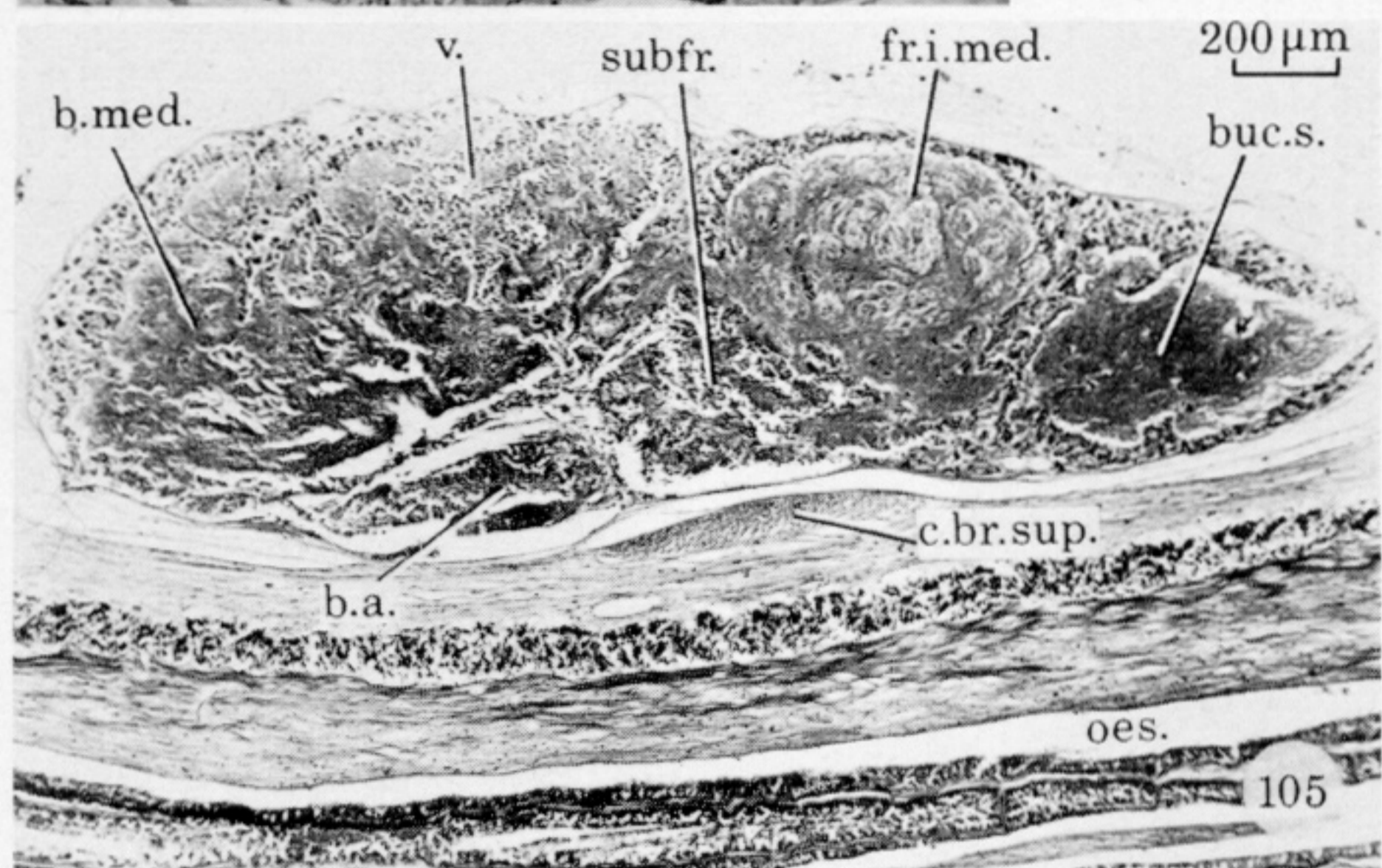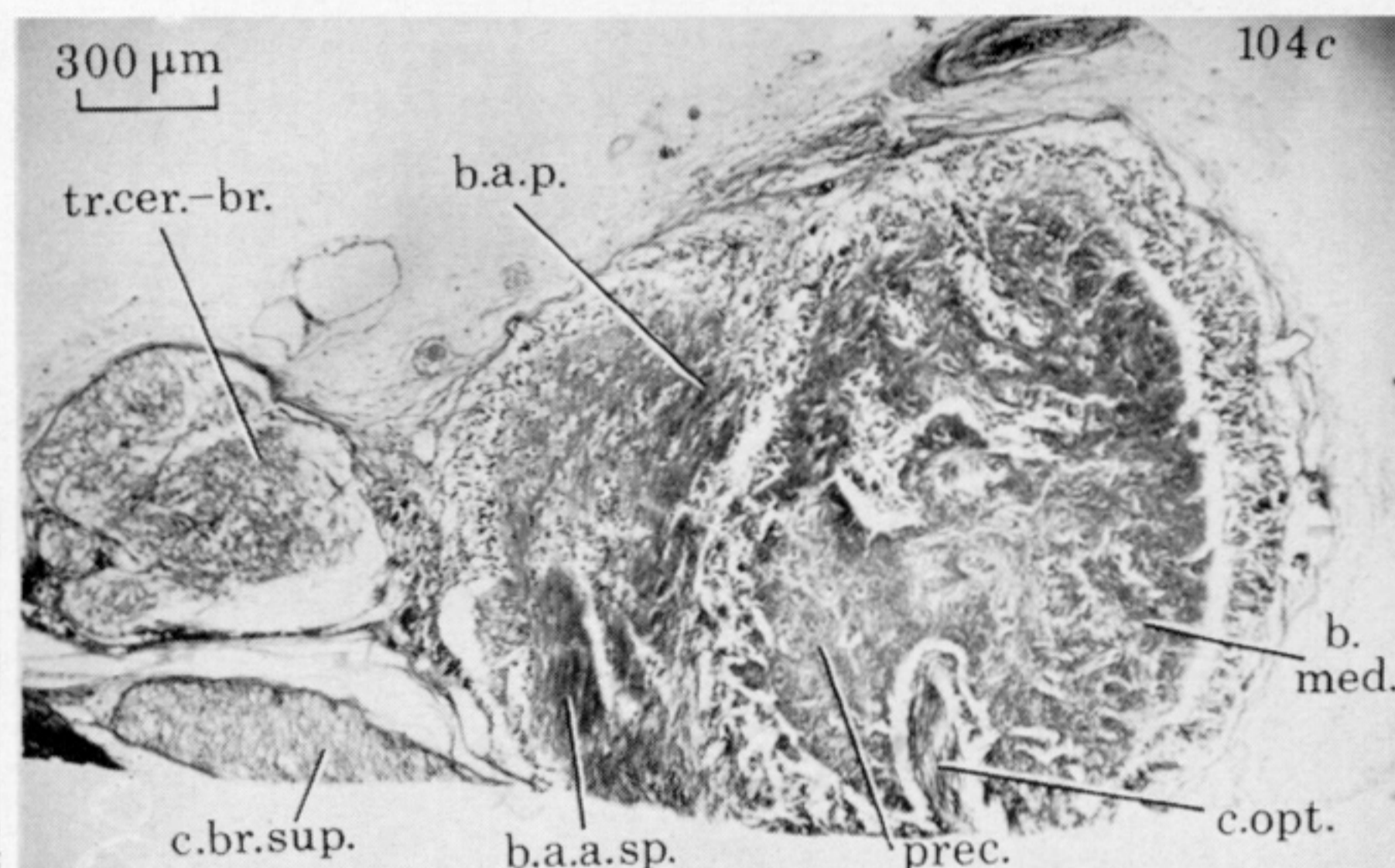
FIGURES 97–103. For description see opposite.
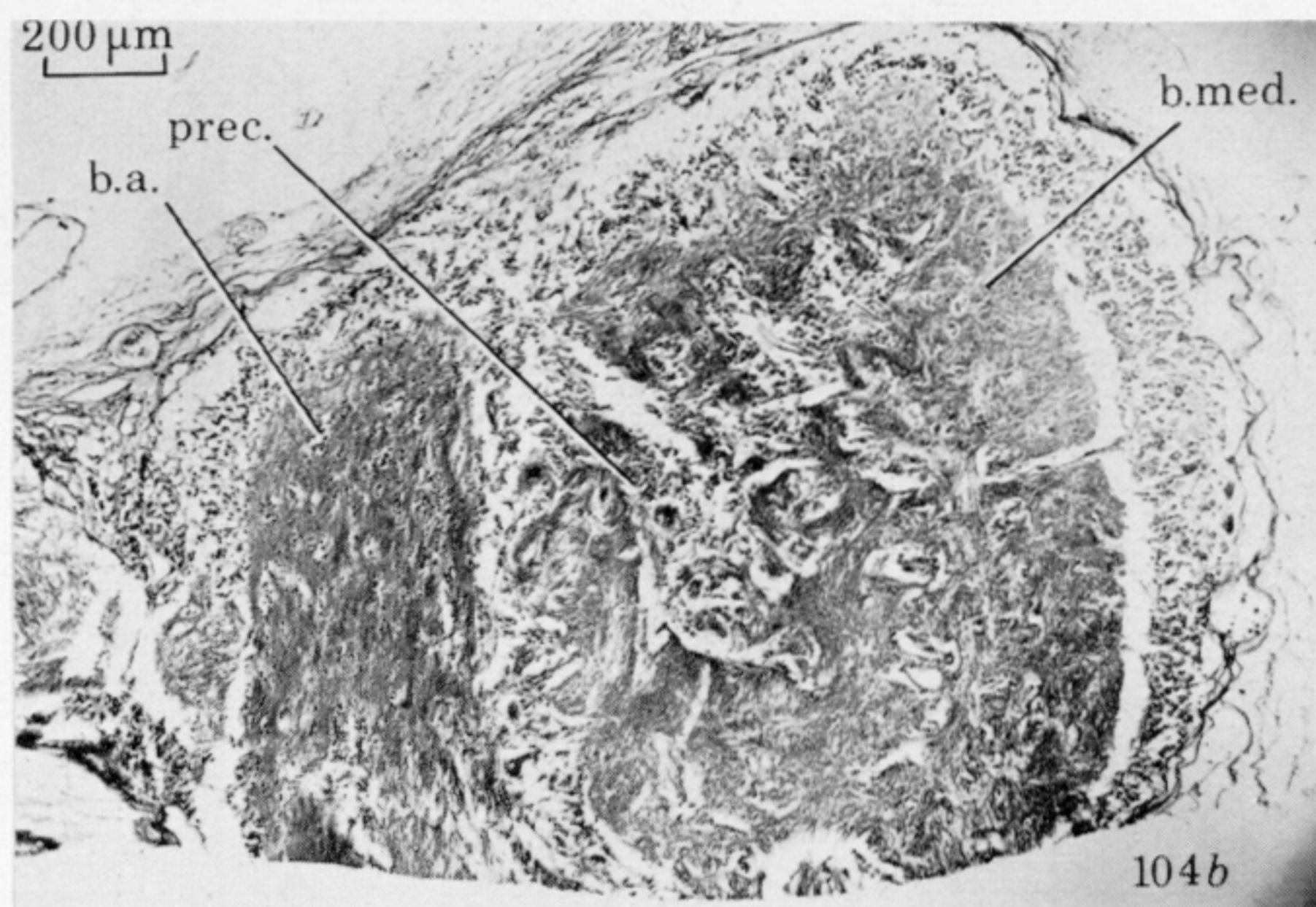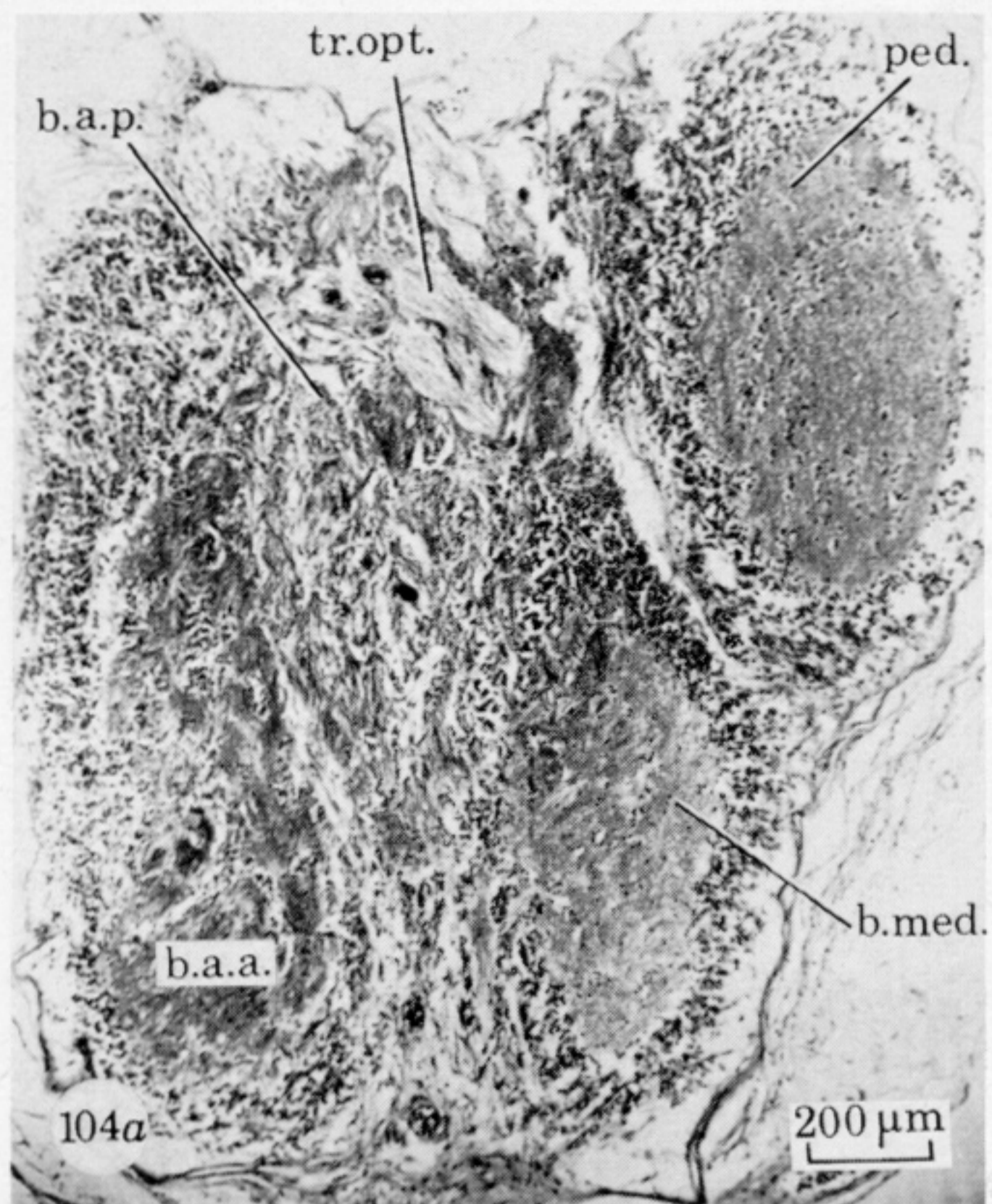
FIGURE 104a. Sagittal section to show close relations between the peduncle lobe and basal lobes (*Cirrothauma* B, Masson).
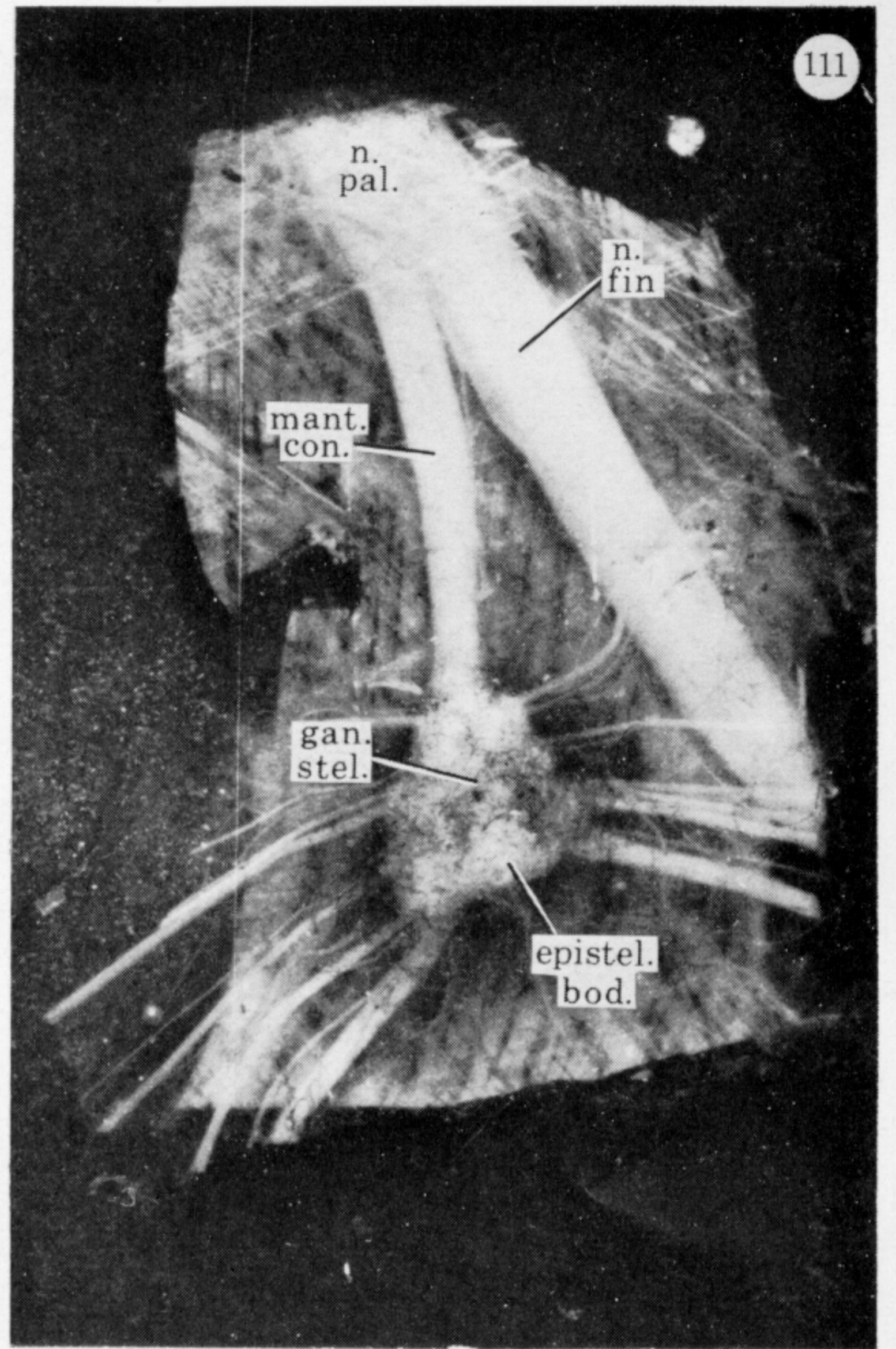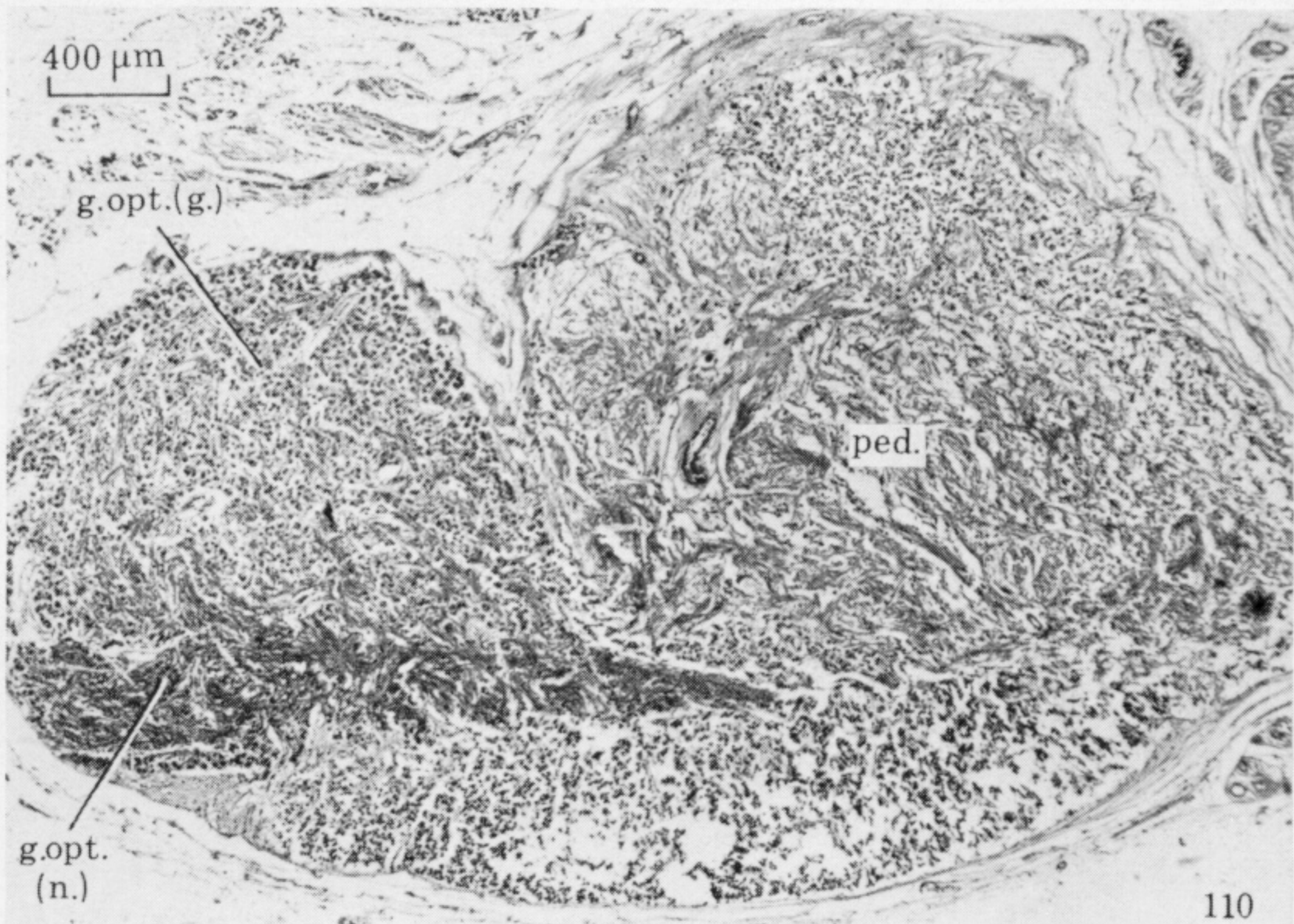
FIGURES 104b AND 104c. Horizontal sections of the basal lobes; figure 104b is the more dorsal (*Cirrothauma* B, Masson).

FIGURES 105 AND 106. Sagittal sections of the supraoesophageal lobes. Figure 105 is nearer the midline. (*Cirrothauma* B. Figure 105 Holmes; figure 106 Masson.)

FIGURE 107. Horizontal section of the supraoesophageal lobes (*Cirrothauma* B, Masson).
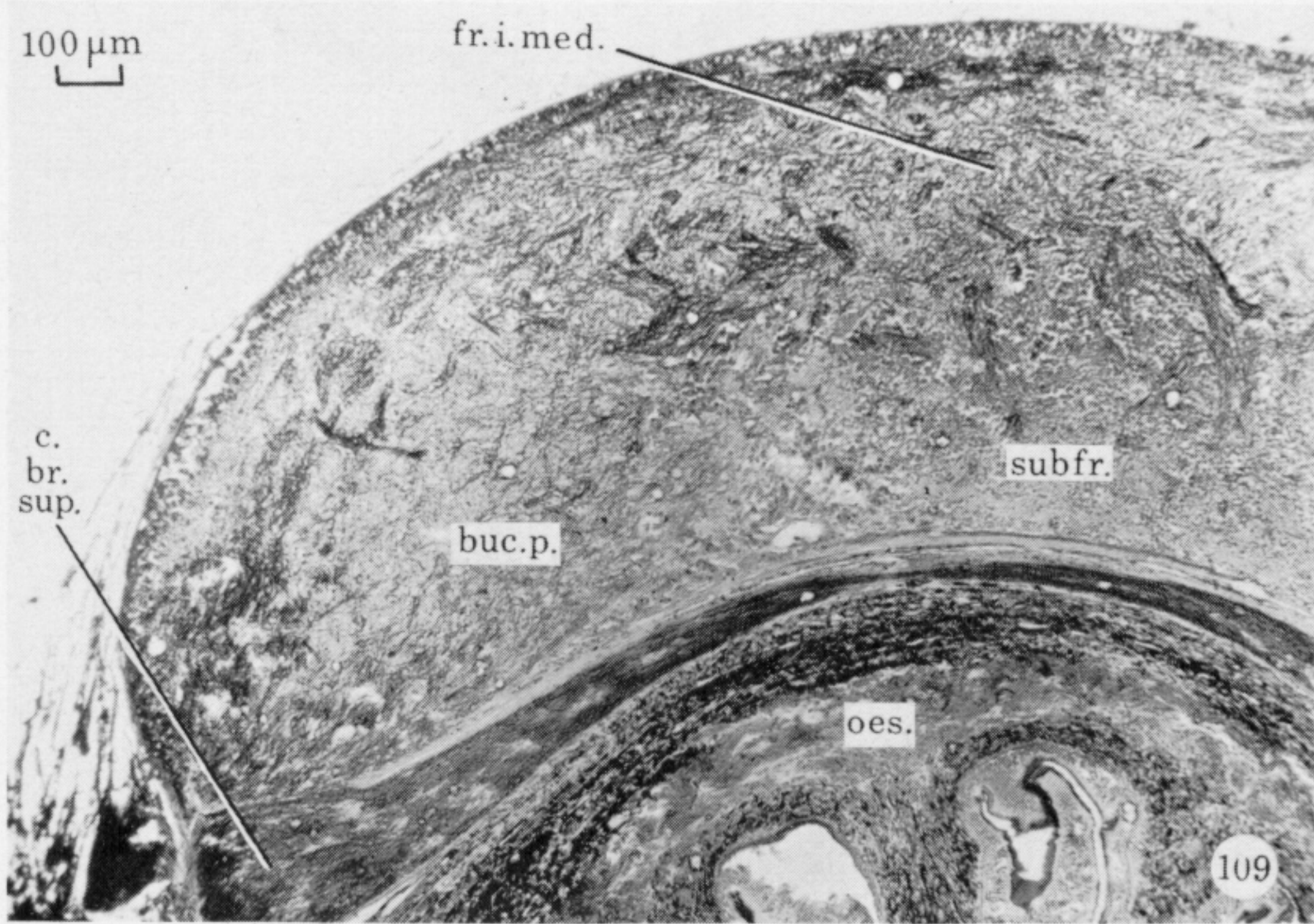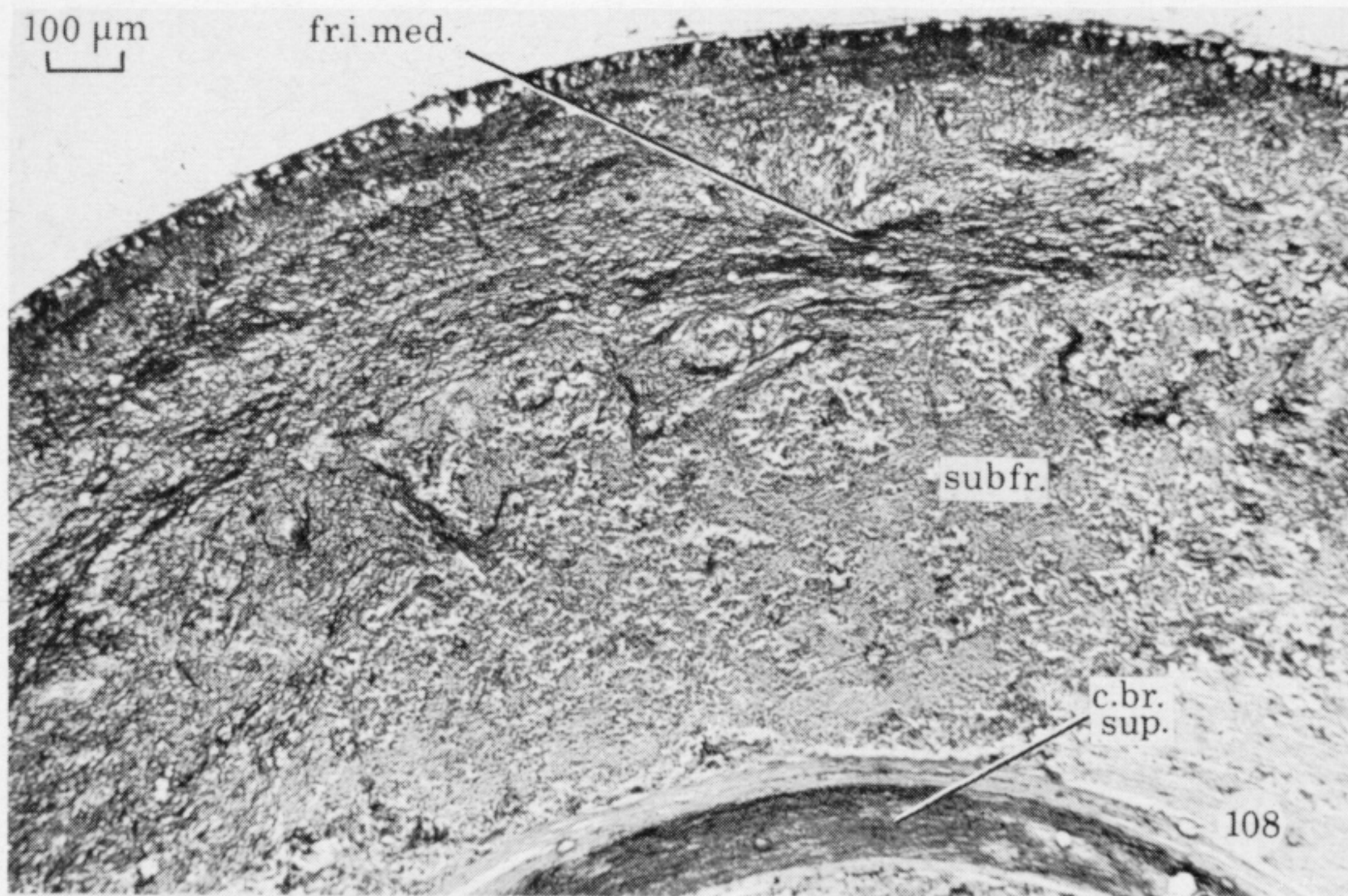
FIGURES 108–112. For description see opposite.
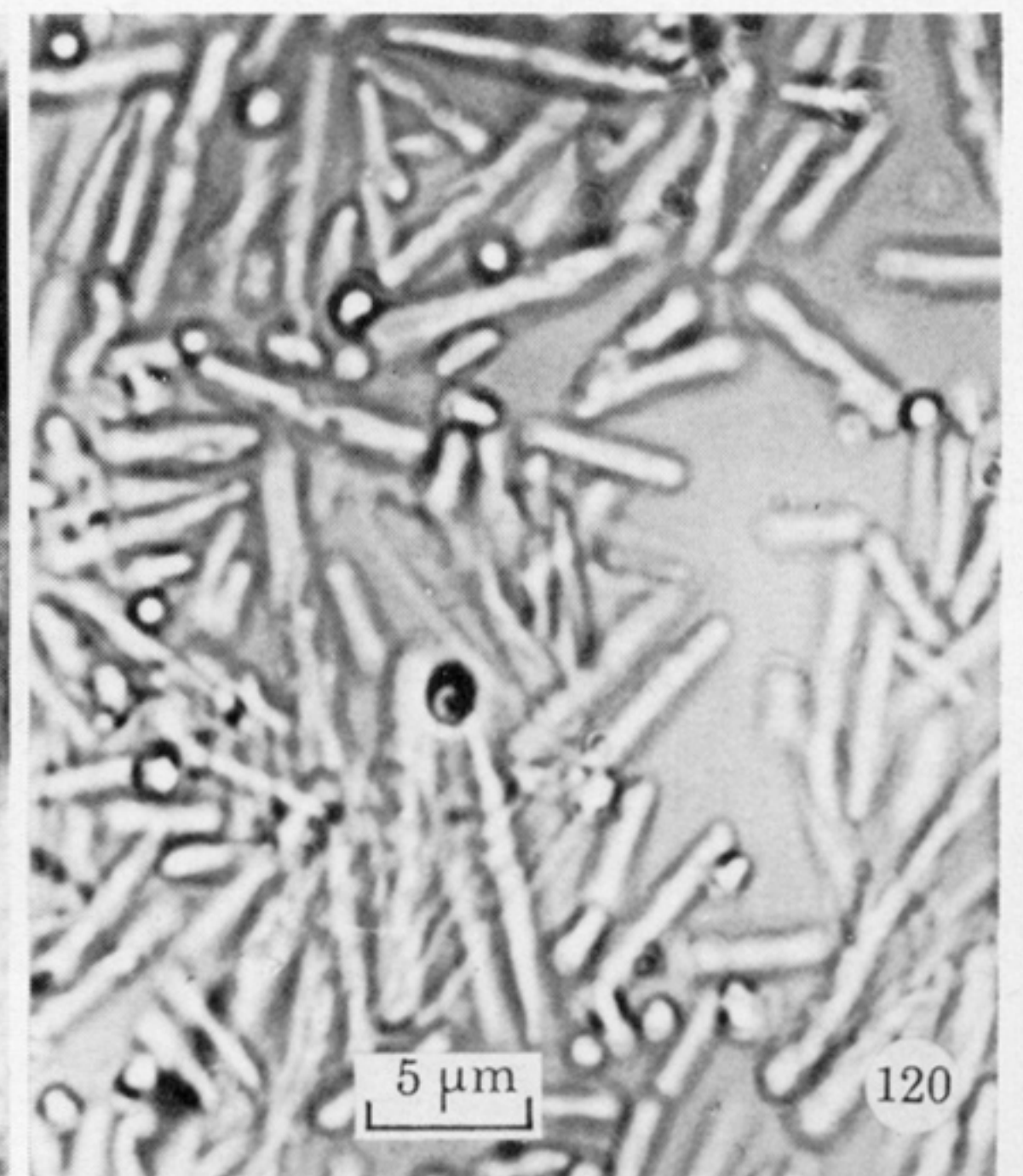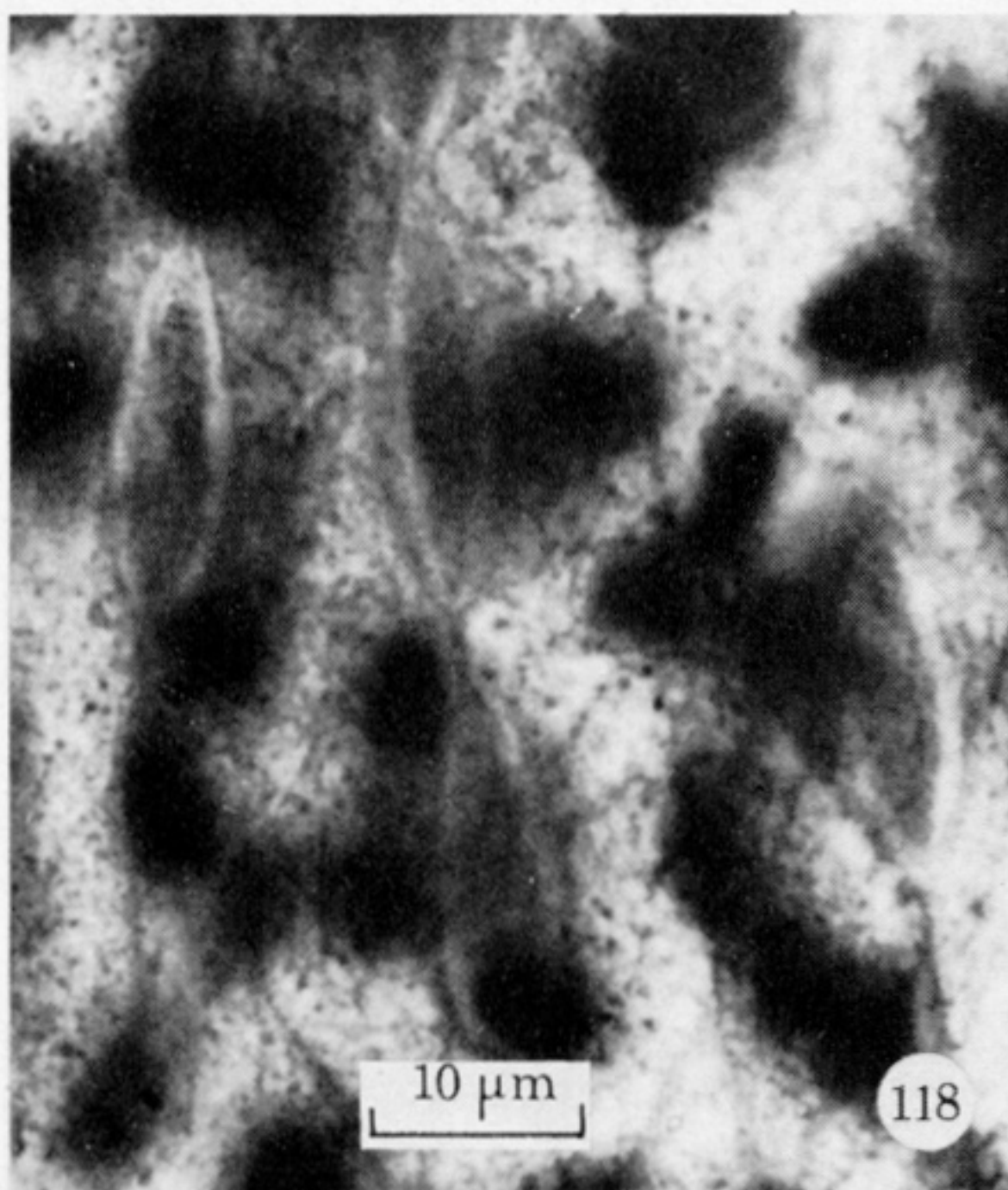
FIGURES 113–118 AND 120. For description see opposite.

FIGURES 119 AND 121–124. For description see opposite.

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Abbreviations used on figures

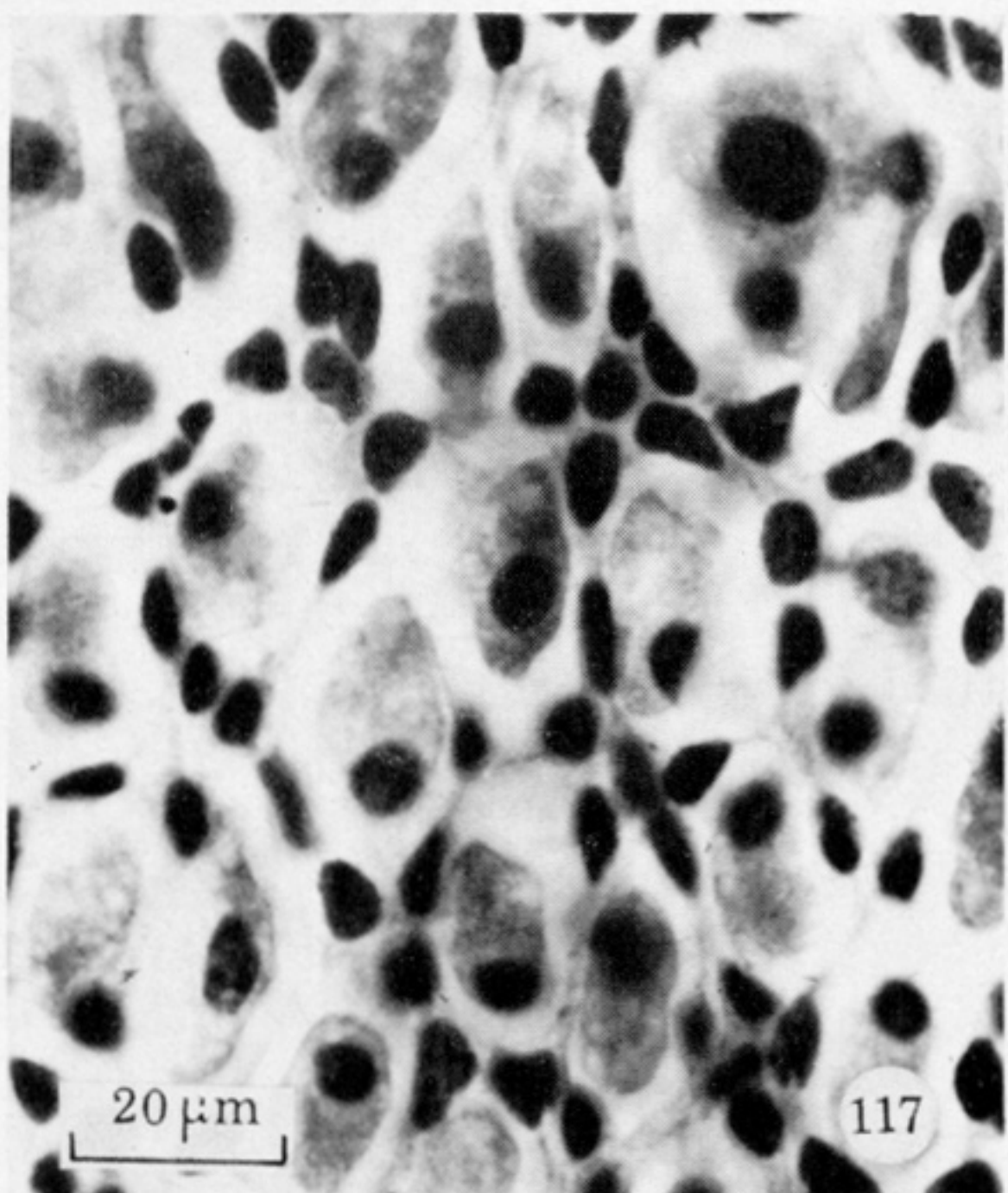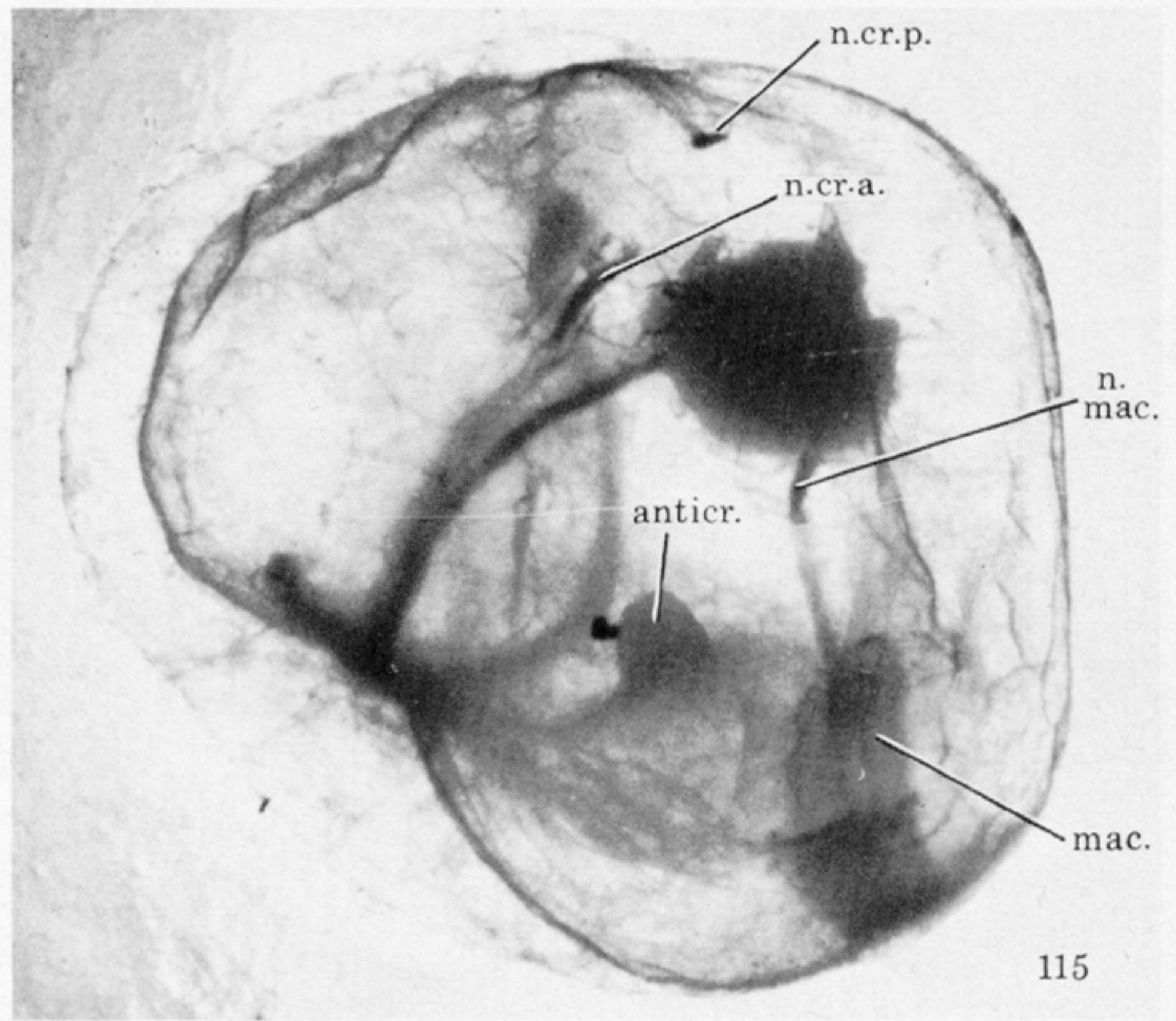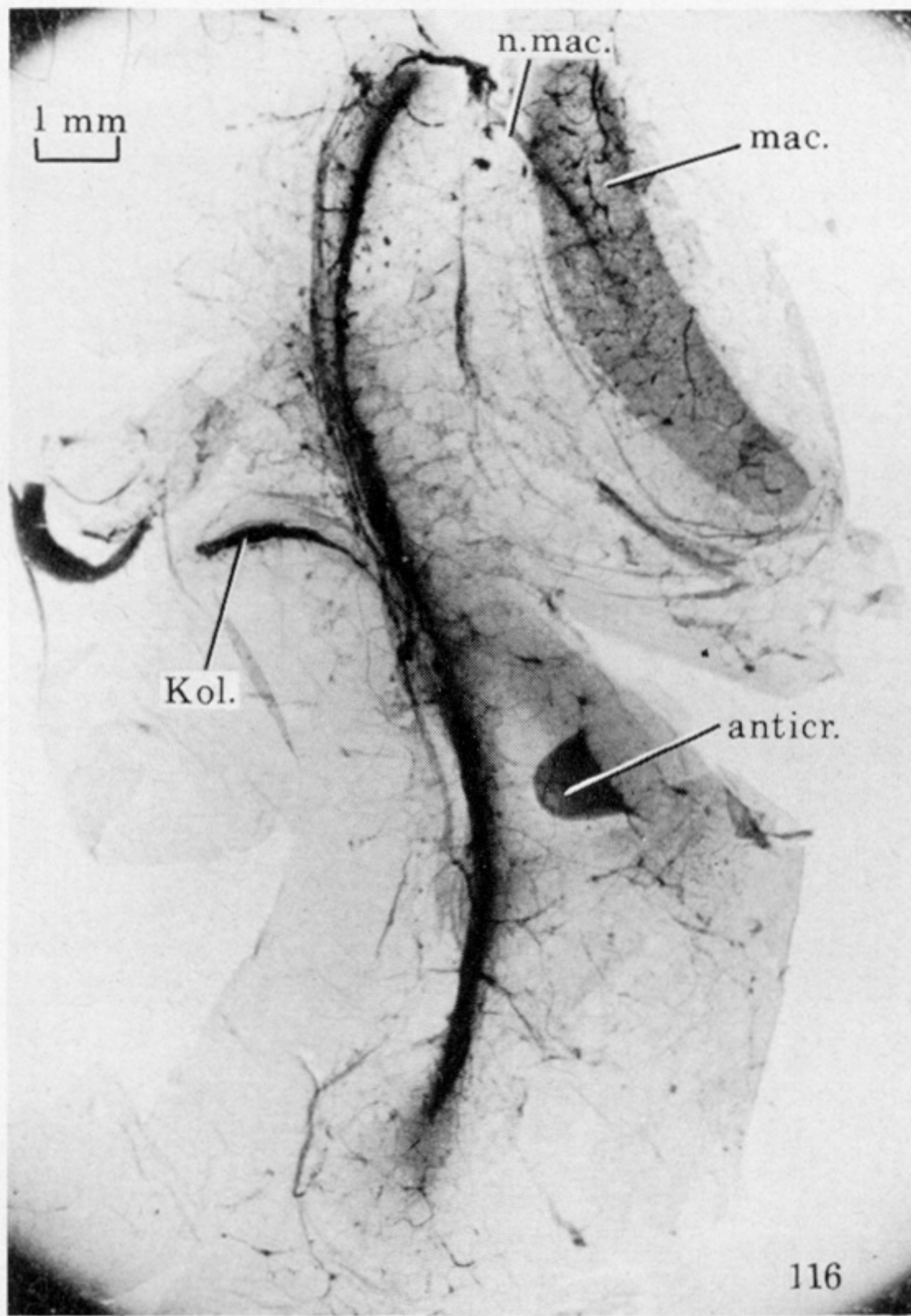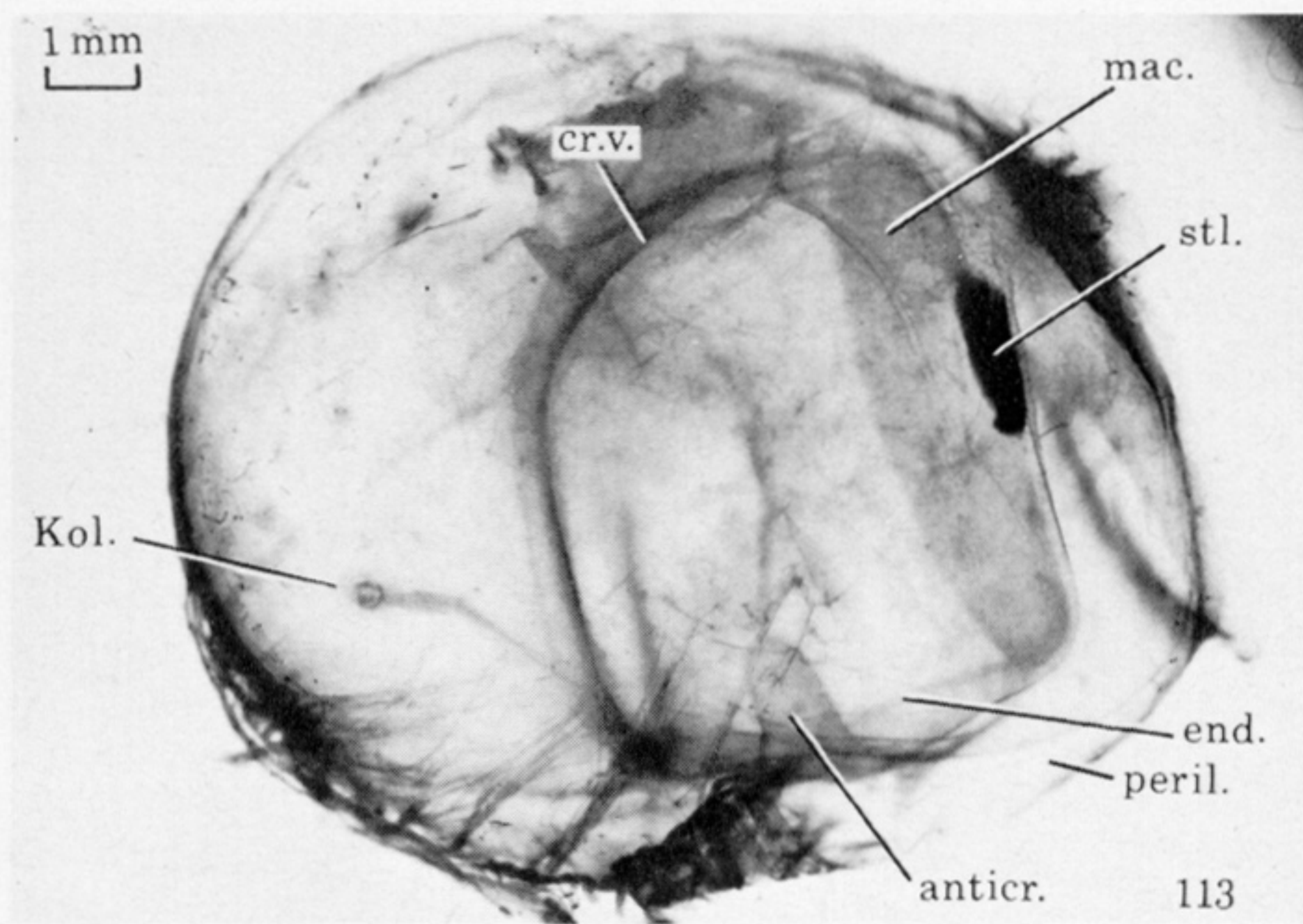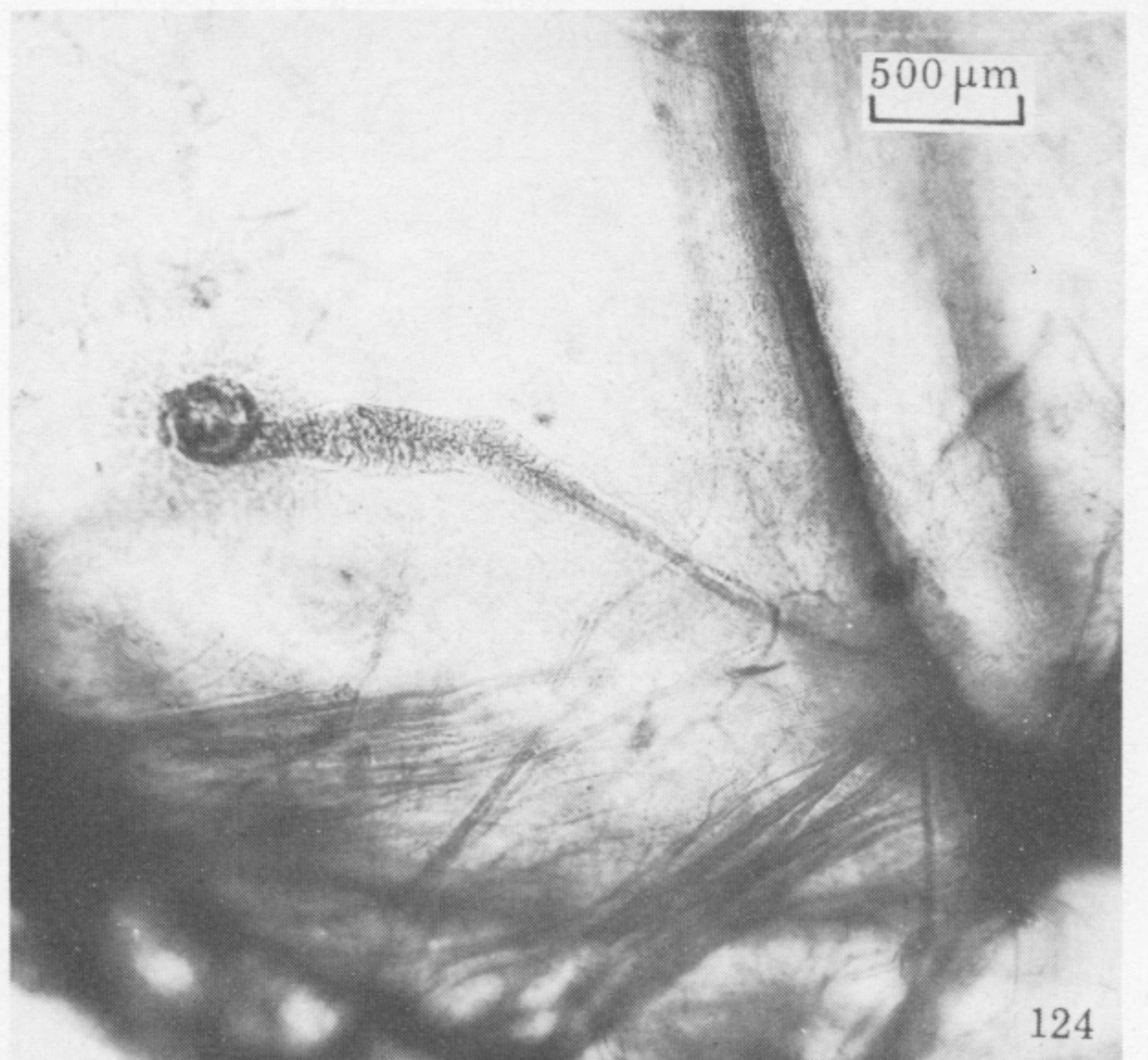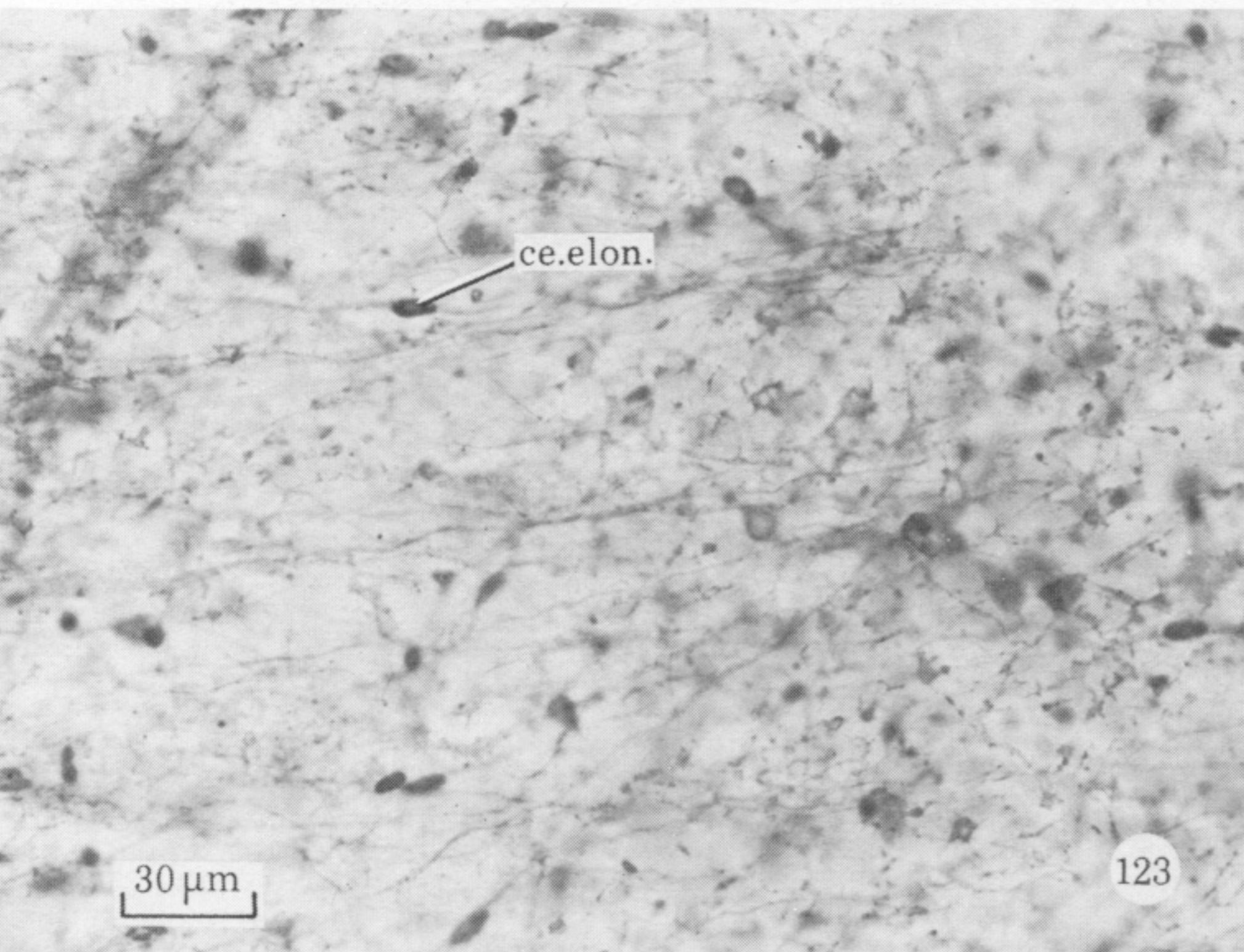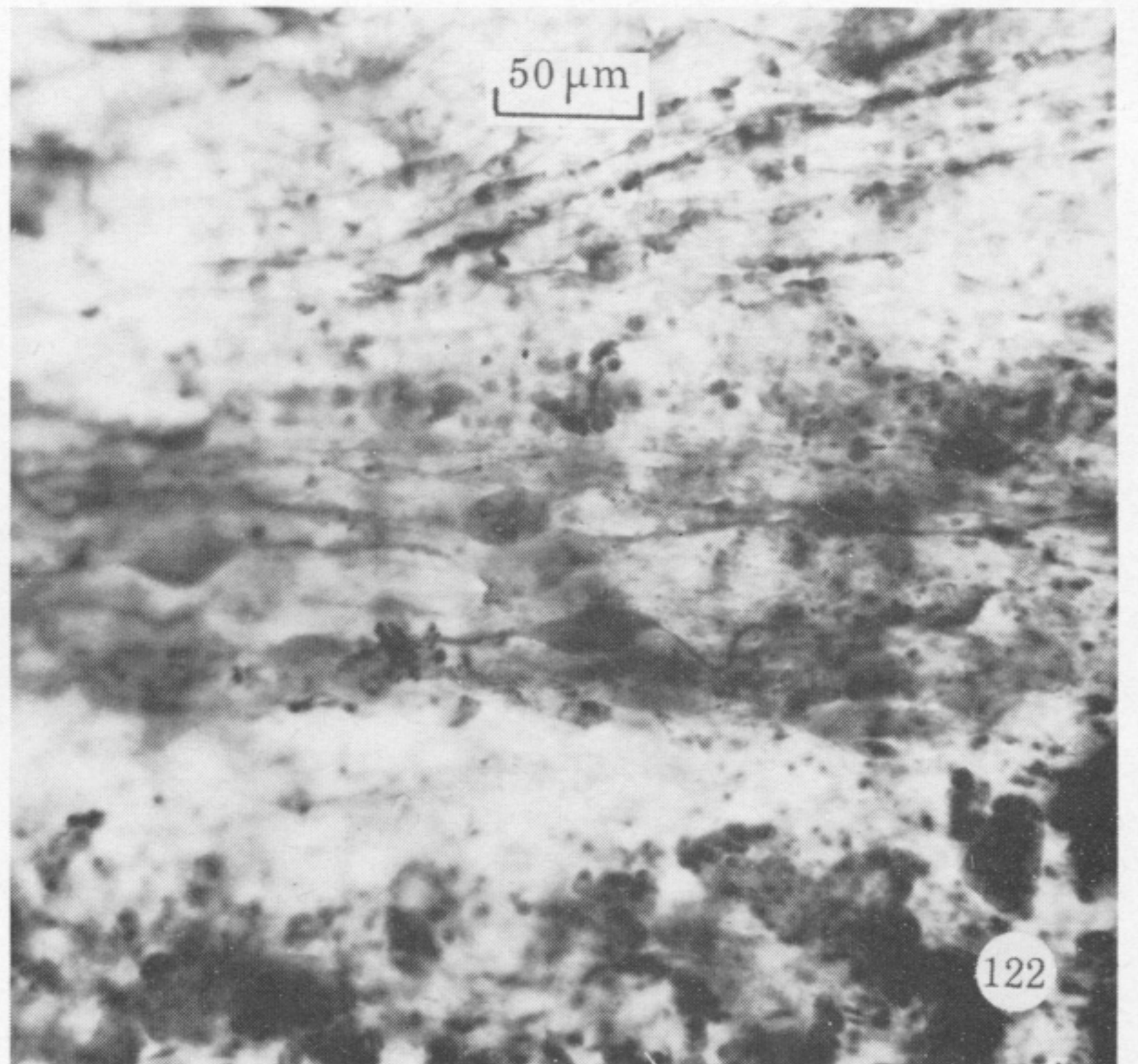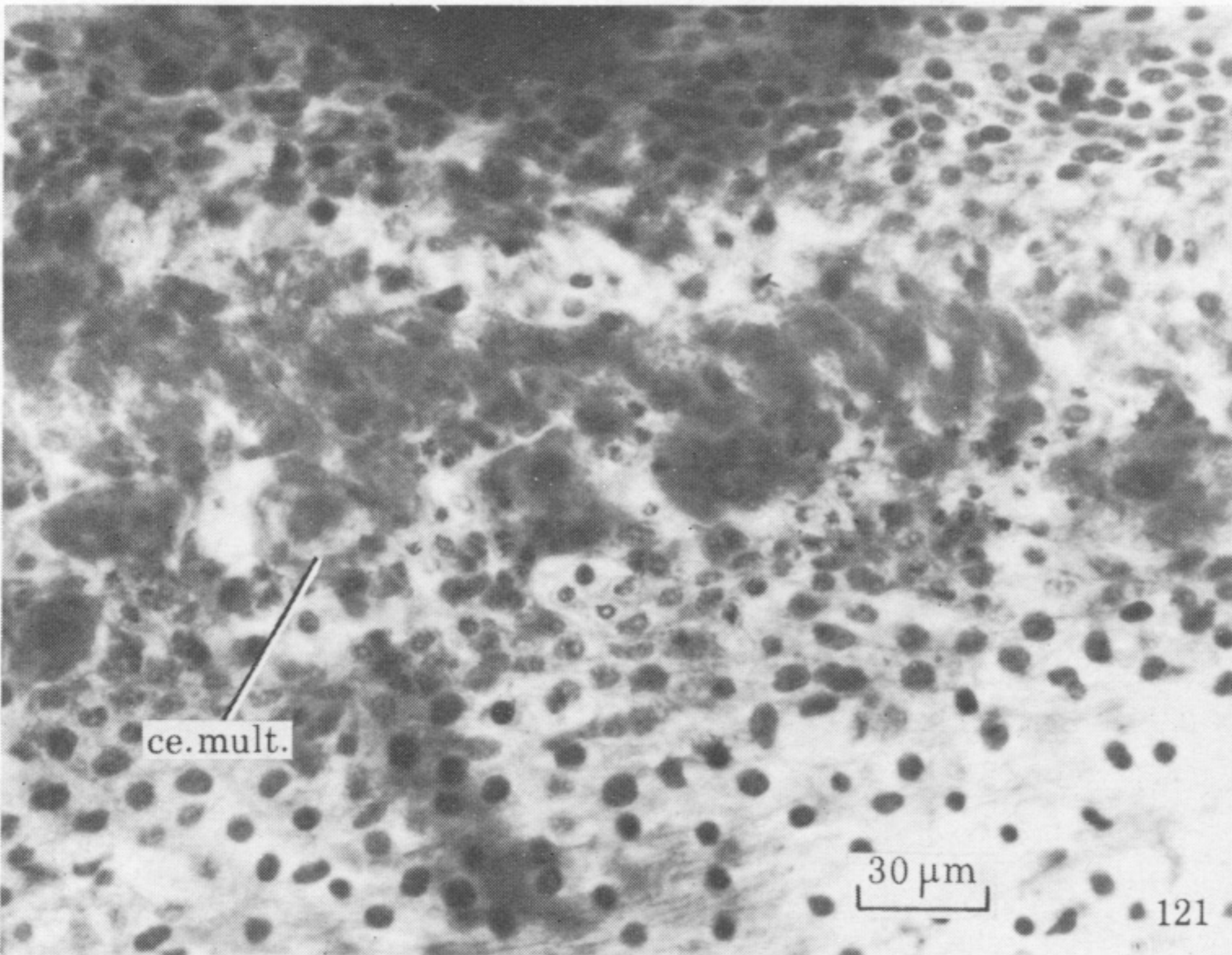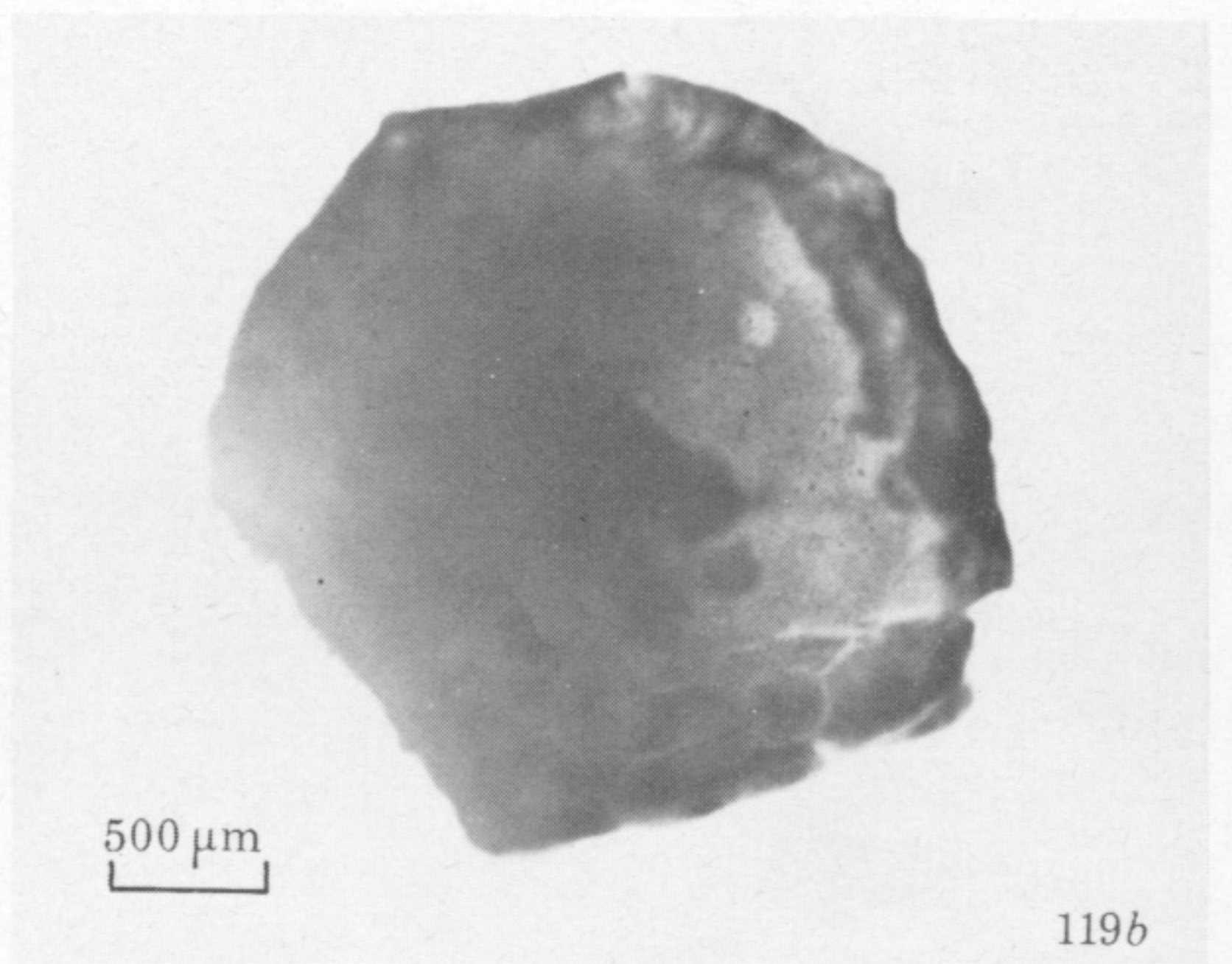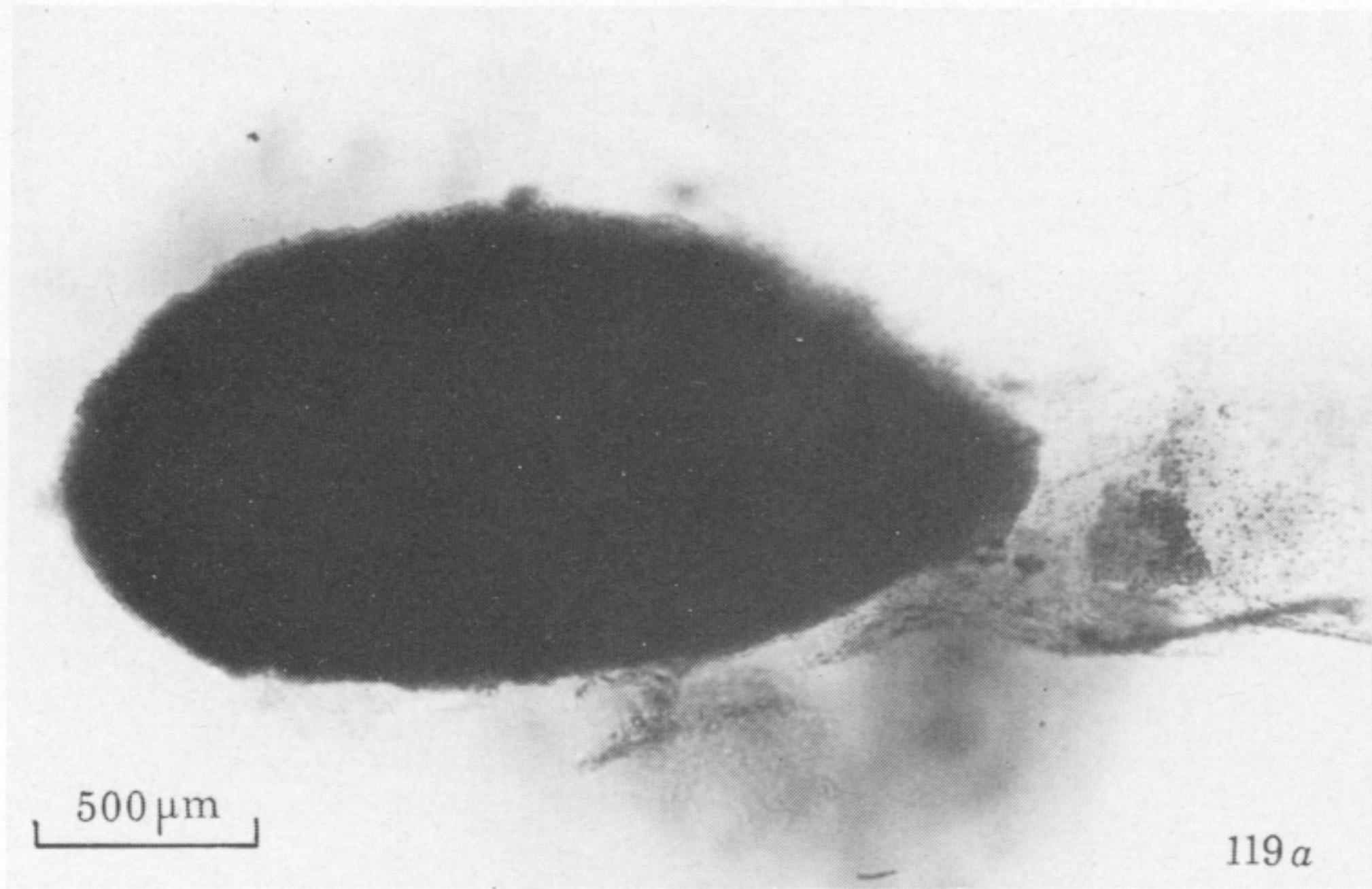|	
accgl.	accessory gland
acid mucopr.	acid mucopolysaccharides-containing tissue
afft.b.v.	afferent branchial vein
amoeb.	amoebocyte
an.	anus
antcrist.	anticrista
antrs. (ant. sor.)	anterior sorta
arm mus.	muscle of arm
aur.	auricle
b.a. (b. ant.)	anterior basal lobe
b.a.a.	anterior anterior basal lobe
b.a.a. sp.	spine of anterior anterior basal lobe
b.a.l.	lateral anterior basal lobe
b.a.p.	posterior anterior basal lobe
b.med.	median basal lobe
below	lower beak
be.u.	upper beak
bdw.	body wall
bodwh.	white body
br.	brachial lobe
brsn. l. (br. ht. l.)	left brachial heart
buc. cav.	buccal cavity
buc. i. gan.	inferior buccal ganglion
buc. m.	buccal mass
buc. p.	posterior buccal lobe
buc. s.	superior buccal lobe
c. br. sup.	suprabrachial commissure
c. opt.	optic commisure
caec.	caecum
ce. col.	columnar cell
ce. col. ep.	columnar epithelial cell
ce. clou.	clongated cell
ce. ep.	epithelial cell
ce. lar.	large cell
ce. mult.	multipolar cell
cer.-br. con.	cerebro-brachial connective
cer.-buc. con.	cerebro-buccal connective
cir.	cirrus (cirri)
cor.	cornea
core in.	inner core of sucker peduncle
core out.	outer core of sucker peduncle
cr. v.	transverse horizontal crista
cut.	cuticle
cys.	cysts in retina
dig. dts	digestive ducts
dig. gl.	digestive gland
dig. gl. art.	arteries to digestive gland
dor. ch.	dorsal chamber
eff. b. v.	efferent branchial vein
egg case; out.	outer egg case
end.	endolymph of statocyst
ep.	epithelium
ep. cub.	cubital epithelium
epi. ven.	encapsulated epithelial cells
epistel. bod.	epistellar body
eros.	erosion
ey.	eye
f. gi.	giant fibre
fl.	fin lobe
fnl	funnel
fr. i.	inferior frontal lobe
fr. i. l.	lateral inferior frontal lobe
fr. i. med.	median inferior frontal lobe
fr. s.	superior frontal lobe
g. opt.	optic gland
g. opt. (g.)	glandular region of optic gland
g. opt. (n.)	nervous region of optic gland
g. ovid.	oviducal gland
g. sal. a.	anterior salivary gland
g. sal. duc. p.	duct of posterior salivary gland
g. sal. l.	lateral salivary gland
g. sal. p.	posterior salivary gland
g. submt.	submandibular salivary gland
gan. buc. i.	inferior buccal ganglion
gan. stel.	stellate ganglion
gast. gar.	gastric ganglion
gill l.	left gill
gen. art.	gonadial artery
gon. sac.	gonadial sac
gr. in.	inner granular layer
gr. out.	outer granular layer
ins. aur.	insertion of auricles
int.	intestine
invag.	invagination
k.	kidney
k. d. lt	left kidney duct
k. dt. rt.	right kidney duct
Kol.	Kölliker's canal
len.	lens
lip low.	lower lip
lip u.	upper lip
mac.	macula of statocyst
msg.	magnocellular lobe
musc. con.	muscle connective
mem. sh.	membrane sheath
mi. o. st.	medulla of optic lobe
mus. circ.	circular muscle
mus. d.-ven. buc.	dorsoventral buccal muscle
mus. long.	longitudinal muscle(s)
mus. man.	mandibular muscle
mus. ob.	oblique muscle
mus. ra.	radial muscle
mus. rad.-sal. pap.	radula-salivary papilla muscle
mus. sal. pap.	salivary papilla muscle
mus. st.	muscle fibres of statocyst
mus. submn.	submandibular muscle
mus. to. a.-p.	antero-posterior tongue muscle
mus. to. med.	median tongue muscle
n. br.	brachial nerve
n. cr. a.	anterior crista nerve
n. cr. p.	posterior crista nerve
n. f.	nerve fibres
n. fin	fin nerve
n. lab.	labial nerve
n. mac.	macula nerve
n. op. p. s.	superior posterior ophthalmic nerve
n. opt.	optic nerve
n. pal.	pallial nerve
n. st.	static nerve
n. visc.	visceral nerve
nec.	neck of rhabdome cell
nuc.	nucleus
nuc. rh.	nucleus of rhabdome cell
nuc. su.	nucleus of supporting cell
oes.	oesophagus
oes. entr.	entrance to oesophagus
oes. pig.	pigmented oesophagus
opt.	optic lobe
or.	organ
orif.	orifice
out.	outer
out. ring	outer ring
ov.	ovary
ovid.	oviduct
pa. buc. l.	lateral buccal pulp
pal. art.	pallial artery
pal. art. lt	pallial artery, left
pal. art. rt	pallial artery, right
pe.	pedal lobe
pe. l.	lateral pedal lobe
pe. p.	posterior pedal lobe
ped.	peduncle lobe
ped. ?	part of peduncle lobe?
ped. sp.	peduncle spine
pen.	penis
peril.	perilymph of statocyst
pig.	pigment
plex.	plexiform zone
po.	pore
prec.	precommissural lobe
pri. wb	primary web
pv.	pallio-visceral lobe
rad. grv.	radular groove
rad. su.	radular support
rad. tth	'radular teeth'
rec.	rectum
ret. det.	detached retina
rh. (rh.)	rhabdome
ros. low.	rostrum of lower beak
ros. u.	rostrum of upper beak
sal. duc. p.	posterior salivary gland duct
sal. pap.	salivary papilla
sal. pap. sh.	salivary papilla sheath
sal. pap. shd tth	toothed shield of salivary papilla
sec. prod.	secretory product
sec. wb	secondary web
sem. ves.	seminal vesicle
sept.	septum
she.	shell
sin. opt.	optic sinus
sp. pke	sperm packet
st.	statocyst
stom.	stomach
sul.	statolith
su.	support (ling)
subfr.	subfrontal lobe
subv.	subvertical lobe
suc. disc	sucker disc, shed cuticle
suc. inf.	infundibulum of sucker
suc. inf. cut. new	new cuticle of sucker infundibulum
suc. orif.	orifice of sucker
suc. ped.	peduncle of sucker
t. con.	connective tissue
t. nv.	neurovenous tissue
tes.	testis
to.	tongue
tr. br.-opt.	optic to brachial lobe tract
tr. br.-pv.	pallioviseral to brachial lobe tract
tr. cer.-br.	cerebro-brachial tract
tr. fr. i.-fr. s.	inferior frontal superior frontal lobe tract
tr. opt.	optic tract
tr. st.-ped.	static nerve to peduncle lobe tract
tth	teeth (tooth)
tth a.	anterior teeth
tth p.	posterior teeth
v.	vertical lobe
vas def.	vas deferens
vc.	vena cava
vent.	ventricle
wt. cl. lt	left water canal
wt. cl. rt	right water canal