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THE ANGULAR ACCELERATION RECEPTOR SYSTEM OF DIVERSE CEPHALOPODS

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[Plates 1–8]

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The system for monitoring angular acceleration is described in 59 genera of cephalopods. The dimensions are measured and volumes calculated. The volume of the statocyst is always small relative to the size of the adult animal but is smallest in animals that move fast, such as ommastrephids, loliginids and sepiids; it is larger in neutrally buoyant squids and very large in cirroctopods.

In many genera the flow of endolymph is restricted by knobs, the anticristae, usually arranged on a standard plan. These reach their greatest extent in non-buoyant squids and sepiids, where some of them join to form incomplete semicircular canals in the horizontal plane, providing the lower sensitivity appropriate to rapid turning to right or left. In buoyant squids and octopods the cavity is less obstructed.

The system for adjusting sensitivity is not the same in all three planes: there are not three canals as in vertebrates. In the pitching and rolling planes the channels for endolymph flow are wide, presumably providing the higher sensitivity appropriate to slower movements. Sensitivity is perhaps also adjusted by variations in the cupulae, as it is in *Octopus*.

The crista of pelagic octopods such as *Argonauta* and *Japetella* is divided into nine sections, as in the typical benthic forms. In cirroctopods the crista is not divided in this way and indeed shows no interruption of the rows of hair cells, even at the turns.

In some cirroctopods and in *Vampyroteuthis* there are several anticristae, an apomorphic feature that they share with the decapods; but they have perilymph- and endolymph-like octopods.

In the more active cranchiid squids the anticristae are arranged on a helical course, perhaps serving to provide appropriate sensitivity during turns from the head-down position.

The statocyst of *Spirula* differs from both sepiids and teuthids.

1. Introduction

Cephalopods and crabs are the only invertebrates whose angular acceleration receptor systems sometimes involve canals. These statocysts show great variety, unlike the more nearly uniform semicircular canals of vertebrates. This paper attempts to illustrate that variety among cephalopods and to relate it to the lifestyle and environment of the animals. The only previous account of this variety is in the work of Ishikawa (1924, 1929), who described and figured the statocysts of various species of decapods but without relating them to their method of functioning or the way of life of the species.

The equilibrium receptor systems of cephalopods have several functions, including contribution to balance and to provide compensating eye movements for stabilization of the retinal image (see Budelmann 1970; Budelmann & Young 1984). For their purposes the angular acceleration receptors of the crista needs a range of sensitivity that is appropriate to the speed of locomotion, which varies greatly among cephalopods. The particular structures and dimensions of the statocyst, which are the subject of this study, presumably contribute to provide the bandwidth of sensitivity appropriate to each species.

The importance of a suitably defined range of sensitivity is shown in the only case where the responses of the cells of the crista is known, namely *Octopus vulgaris*, recently studied by Williamson & Budelmann (1985*a*). The crista is a ridge running approximately in three planes and carrying sensory hair cells of several types, provided with kinocilia (figure 1) (see Budelmann *et al.* 1987). Attached to the kinocilia are flaps, the cupulae, which move during acceleration as swinging doors under action of the endolymph. This causes the kinocilia to shear, which leads to either excitation or inhibition of the cells (Williamson & Budelmann 1985*b*). In such a hydromechanical system basic variables are the movement of the fluid (endolymph), its effective inertial mass and the properties of the cupula. These factors determine the sensitivity. An octopus uses a wide range of frequency of turning, from its slow walking on the arms to fast swimming with the jet. The crista meets this variety of speeds by division into nine sections, four carrying large cupulae attached to a narrow base and having higher sensitivity, and five with smaller cupulae with a broader base, responding only at higher rates of turning (figures 1 and 2*a*).

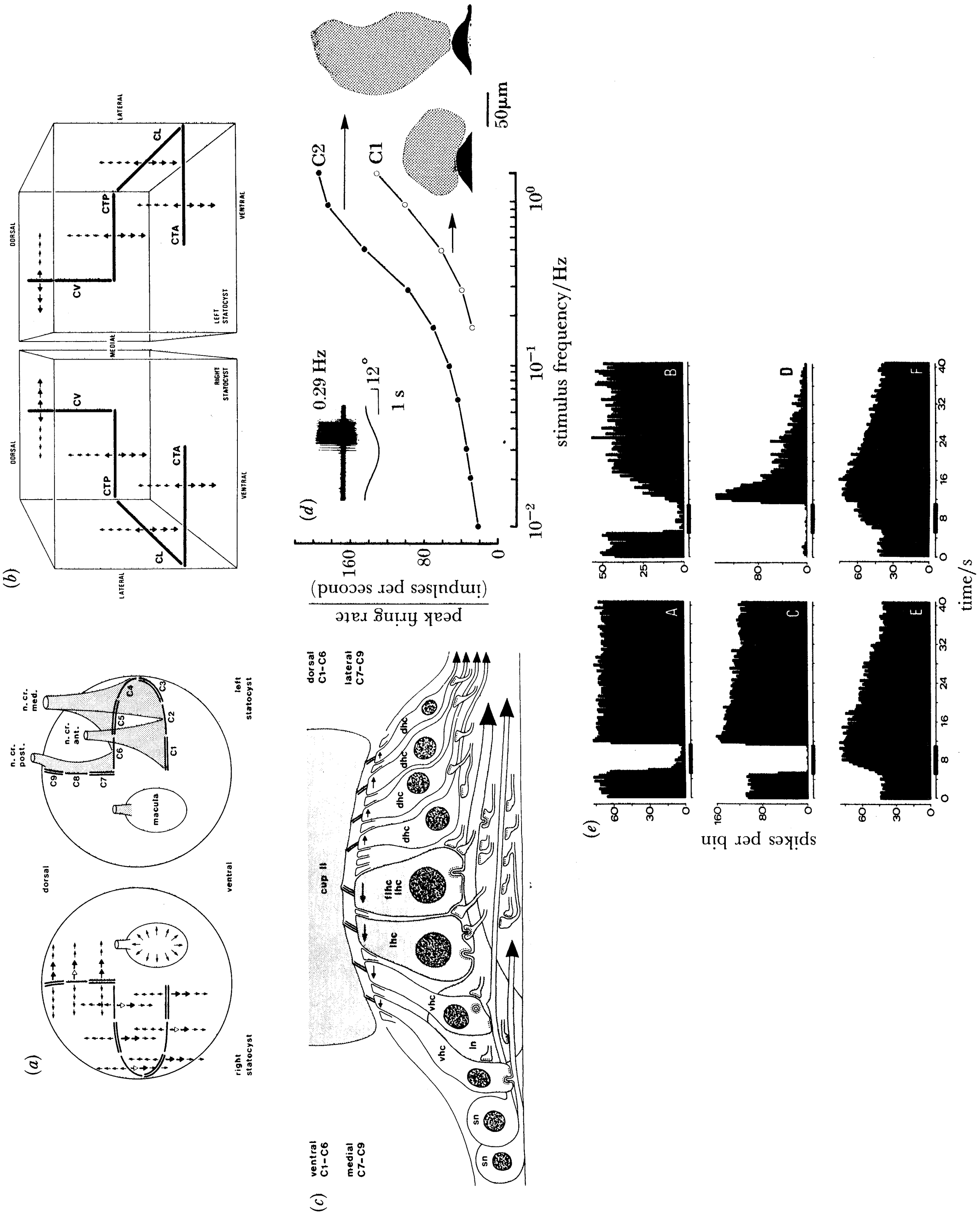
The experiments of Williamson & Budelmann involved recording nerve impulses generated by units of the first two sections, C_1 and C_2 of the crista, sensitive to acceleration in the pitching plane (p. 198). Units of section C_2, with a large cupula, gave a resting discharge, but units of C_1, with small cupula, did not: presumably the larger cupula with narrower more flexible attachment to the cilia is influenced by gravity (Budelmann & Wolff 1973; Williamson & Budelmann 1985*a*). During oscillation about the pitch axis both types showed increased activity in the head-up direction and a decrease in the down direction. The responses increased linearly with the amplitude of oscillation. With increasing frequency the C_2 units at first increased their response but at the higher frequencies (1.0–1.6 Hz) the response saturated. On the other hand C_1 units showed no response below 0.4 Hz but continued to increase their rate of firing up to and beyond 1.6 Hz (figure 1*d*). Thus it is clear that the units with large cupulae are suited for monitoring slow turning, as in walking, those with small cupulae have a ten times higher threshold and record the faster turns when swimming.

Calculation of the phase lag of the units showed that the maximum response occurs at the time of maximum velocity (figure 1*d*). Thus C_2 (large cupula) units showed a steady increase of phase lag with increasing frequency until 0.1–1.0 Hz, where there is a plateau in this 'Bode plot' between 80° and 90°, which is the phase position of peak angular velocity.

These important results show that the crista of *Octopus*, like the semicircular canals of vertebrates, serves to signal angular velocity. This is in spite of the fact that in an octopus the endolymph is not confined to canals. Presumably the hydromechanical analog conversion is here accomplished by the specific properties of the cupula–kinociliary system rather than by the viscous friction and other features of the canals of vertebrates. The relevant properties of a cupula in cephalopods are its area, length (i.e. distance from the fulcrum), and flexibility of attachment. These are probably the factors that influence the difference between C_1 and C_2 units and may, with others, determine the characteristic phase lags and hence the capacity to code for velocity over a wide range of frequency. There may of course also be integration steps within the sensory epithelium.

As a result of these discoveries about the properties of the cupulae in *Octopus* it is necessary to reconsider the situation in decapods, where the flow of endolymph is more highly regulated and takes place partly in canals (Stephens & Young 1978, 1982; Maddock & Young 1984). In decapods the statocyst cavity of many species is also interrupted by cartilaginous projections of two sorts: hamuli (hooks) at the ends of the four sections of the crista and labelled h1–h5; and anticristae, projections arranged in a pattern that is characteristic for the species and numbered 1–7. In the types that swim swiftly, such as *Loligo* or *Sepia*, the walls of the statocyst are shaped to form channels to convert them into semicircular canals (see figures 31 and 32*b*, plate 3, etc.). It is obvious that these may be compared with the semicircular canals of vertebrates, in which the system operates as an integrating angular accelerometer, giving signals proportional to the instantaneous angular velocity of the head over a wide range of frequency, 0.02–50 Hz in man (Wilson & Jones 1979).

The dynamics of the flow of endolymph in a toroidal semicircular canal have usually been


(a)
right statocyst
dorsal
ventral
left statocyst
macula
n.cr. post.
n.cr. ant.
n.cr. med.
C1
C2
C3
C4
C5
C6
C7
C8
C9
(b)
DORSAL
VENTRAL
LATERAL
MEDIAL
RIGHT STATOCYST
LEFT STATOCYST
CV
CTP
CTA
CL
(c)
ventral C1–C6
medial C7–C9
dorsal C1–C6
lateral C7–C9
cup II
sn
vhc
ln
lhc
fihc
dhc
(d)
0.29 Hz
12°
1 s
peak firing rate (impulses per second)
0
80
160
stimulus frequency/Hz
10^{-2}
10^{-1}
10^{0}
C1
C2
50µm
(e)
spikes per bin
time/s
A
B
C
D
E
F
0
8
16
24
32
40
60
30
50
25
160
80

described by the Steinhausen–Groen model, using analogy with a torsion pendulum. This provides an overdamped second-order equation of motion with two time constants, which define the frequency response. Improved models by Oman *et al.* (1987) and Muller & Verhagen (1988) may be relevant to cephalopods, especially the latter paper, which considers the response in all three channels together. These models are discussed later (p. 230).

Whichever model is considered, principal variables that determine the sensitivity are the moment of inertia of the endolymph, I, the moment of viscous friction per relative angular velocity of the canal, B, and the compliance and spring-restoring force of the cupula, K. It has to be remembered that the cupula may exert a greater (or lesser) effect on the fluid flow in cephalopods than in vertebrates. The first two of these variables are held by the Steinhausen theory to vary with the radius of curvature of the canal, R, and its internal radius, r. It was argued by Jones & Spells (1963) that the effective range of sensitivity between upper and lower angular velocities W_1 and W_2 is given by $W_1/W_2 \propto R/r^2$. They showed that this ratio increased only slightly, with a slope of 0.02 when plotted against the mass of the animal over 46 species of vertebrates: for instance, the internal radius of the canals in man is only twice that in a mouse.

It was shown by Maddock & Young (1984) that these considerations can be applied to cephalopods to a limited extent. In particular the statocyst cavities of decapods grow much more slowly than the body as a whole, whereas the anticristae grow faster (see p. 205). Evidently the restriction of the inertial mass of endolymph is an important factor. The radius of curvature (R) of the horizontal canal of squids is similar to that of fishes, whereas the internal radius (r) is twice as large in non-buoyant and four times as large in buoyant cephalopods. In trying to make the comparison in more detail there are various difficulties and we concluded that perhaps the system acts as an accelerometer rather than measuring angular velocity.† The subsequent findings of Williamson & Budelmann (1985*a*) make this unlikely. If the crista of

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† There is an unfortunate misprint in table 7 of Maddock & Young (1984): the last figure of the final column should be 10 not 1; see table 6 of the present paper.

FIGURE 1. (*a*) Innervation and pattern of polarization of the hair cells of the nine crista sections C1–C9 of *Octopus vulgaris*; seen from in front. Each arrow stands for a row of hair cells and shows the direction of polarization of the kinocilia. Large dark arrows refer to large hair cells, light arrows to fairly large hair cells, small arrows to small hair cells (after Budelmann 1977). (*b*) Pattern of polarization of the hair cells of the four crista sections of *S. officinalis* and *L. vulgaris*; seen from in front. CTA, crista transversalis anterior; CL, crista longitudinalis; CTP, crista transversalis posterior; CV, crista verticalis. Large arrows refer to rows of large hair cells, small arrows to small hair cells (after Budelmann 1977). (*c*) Diagram of a cross section of the crista of *Octopus vulgaris*. It represents both the odd-numbered (C1, C3, C5, C7, C9) and the even-numbered (C2, C4, C6, C8) crista sections, and demonstrates the different types of hair cell and first-order afferent neuron, as well as their afferent and efferent synaptic organization with finger-like and flat synaptic contacts. Some details have been enlarged for emphasis. In the middle (shaded): the large (lhc), and large or fairly large (flhc) secondary hair cells, together with their large first-order afferent neuron (ln). To the left: the rows of small ventral (C7–C9: medial) secondary hair cells (vhc), together with their small first-order afferent neurons (sn). To the right: the rows of small dorsal (C7–C9: lateral) primary hair cells (dhc). The arrows in the distal ends of the hair cells indicate the direction of their morphological polarization. Only the basal part of the large cupula type II (cupII) is shown; the small cupula type I has a larger area of attachment and extends further to the right. (*d*) Peak firing rates of the two types of crista–cupula system of *Octopus vulgaris* during sinusoidal oscillations (amplitude 12°) plotted against stimulus frequency. To the right: light microscope cross sections of the two types of crista–cupula systems. Upper left shows phase position of activity in a unit during sinusoidal oscillation (lower trace) (after Budelmann *et al.* 1988). (*e*) Effect of efferent stimulation on the resting activity of crista (C2) afferent units of *Octopus vulgaris*. Bin width 400 ms. (A, B) Stimulation with varying rates of recovery; (C, D) inhibition with post-stimulus facilitation; (E, F) excitation during stimulation (after Budelmann *et al.* 1988).

Octopus codes for velocity even at low frequency it is probable that this is also true for decapods. The curved canals and the anticristae of those animals presumably make special provision for the regulation of the effective inertial mass of endolymph.

The purpose of the present study is to examine this question further with new measurements including other species. In particular, consideration is given to the differences in the arrangements for control of sensitivity in three planes. Unlike the vertebrates, where there are three nearly similar canals, the cephalopods show partly enclosed canals only in the horizontal plane. Regulation of sensitivity in the other directions seems to be by the size of the channels and partial obstruction of them by suitably placed anticristae. No account has been taken of the possible contribution of the gravity receptor system to detection of angular acceleration, nor to possible susceptibility of the cristae to linear acceleration (Budelmann & Wolff 1975; Williamson & Budelmann 1985*a*).

The present paper describes the statocysts of 59 species, including representatives of almost every family of coleoid cephalopods. New measurements have been made to extend knowledge of the factors that may influence the sensitivity of the receptor systems according to the various modes of life of the animals.

2. METHODS

The specimens were whole statocysts prepared as described by Maddock & Young (1984). They were photographed in glycerol, from above and from in front. Drawings were made from the photographs, with further examination of the specimens. Measurements were made from these drawings, of the maximum length L, breadth B and depth D of the cavity, providing data on the shape and volume (table 1*a*). Such simple measurements can only vaguely define the shape of these complex objects. There are many possibilities for error and the results do not agree exactly with those of Maddock & Young (1984) made on the specimens themselves by projection, which are subject to different errors.

The major dimensions were normalized by reference to a scaling factor, V_1, obtained from the cube root of the product of the three dimensions: $V_1 = \sqrt[3]{(L \times B \times D)}$. Estimates of the total volume V were made from $V = \frac{4}{3}\pi\ (\frac{1}{2}L \times \frac{1}{2}B \times \frac{1}{2}D)$: this is obviously an overestimate of the volume of endolymph in species where much of the cavity is taken up by large anticristae and the statolith. Special attention was also given to the number, position and shape of the anticristae. These vary so much that no single measurement has been devised by which they may be compared. They are shown by the photographs and drawings and their possible influence on the endolymph is discussed.

An attempt has been made to estimate, in some of the species, the course of the relative movement of the endolymph during turning in the yawing plane, as indicated by shading on the drawings. New estimates R and r were made by measurement of these drawings, for comparison and in addition to the measurements made previously by Maddock & Young (1984) by projection from specimens in glycerol. The measurement of r was made at the level of the vertical crista and not between anticristae 6 and 7 as by Maddock & Young. The endolymph is confined to a closed canal for only a part of the circuit in the horizontal plane, mainly between anticristae 6 and 7. This tubular portion of the circumference is greater in the animals that move faster and an attempt has been made to estimate its extent in the last three columns of table 1*b*. The length of the whole circumference of the inner border of the horizontal channel was measured on the drawings with a map measuring wheel (circ. 1). Then the part of that circumference that is bordered by the anticristae was also measured (circ. 2). The ratio circ. 2/circ. 1 gives an estimate of the tubular part. It is certainly an overestimate, perhaps by 10% or more, because the channel is not completely closed ventrally except between anticristae 6 and 7. A better estimate might be the length of the outer edge of anticrista 7, but the strictly tubular section is even less than this (see p. 231).

An important problem in modelling the semicircular canals of vertebrates is the presence of a wider section, the utriculus. Its contribution to the system is debated, but it must serve to increase the inertial mass (Jones 1984). In cephalopods this open part is equally or more prominent, but no exact method has been devised for dealing with it (see p. 232). A similar problem has been examined experimentally in Crustacea by Fraser (1977) in the crab *Scylla*, where there are complete canals and these abstract the component of angular acceleration and integrate it to produce a signal proportional to angular velocity. Conversely, in *Carcinus* the canal is not completely closed and the 'interneurons are hence coding something between angular velocity and angular acceleration'.

The classification that has been used follows G. L. Voss (1977), with the addition of the following changes that will be suggested in Nixon & Young (1989).

- Class Coleoidea
  - Infraclass Octobrachia
    - Order Cirroctopoda
    - Order Octopoda
      - Suborder Benthoctopoda (*Octopus*, *Eledone*, etc.)
      - Suborder Epipelagoctopoda (*Argonauta*, etc.)
      - Suborder Bathypelagoctopoda (*Japetella*, etc.)
  - Infraclass Decabrachia
    - Order Teuthida
    - Order Sepiida
    - Order Sepiolida
    - Order Spirulida
  - Infraclass Vampyromorpha

With this classification the term 'octopod' is used only for members of the order Octopoda. I have continued to use 'decapod' for members of the Decabrachia.

3. The various types of statocyst in cephalopods

The statocysts of Coleoid cephalopods can be grouped into eight main types, corresponding to the habits of life and locomotion. The Octobrachia are different from all the rest with their capacity to walk on the arms, as well as swim with a jet produced by the mantle and funnel.

1. In the Octopoda (in the strict sense) the statocyst is a nearly spherical sac filled with endolymph and suspended within an outer space filled with perilymph and crossed by numerous strands containing blood vessels. The endolymphatic space is interrupted only by a single anticrista. The crista of octopods is divided into nine sections with alternately small and large cupulae (p. 199), suited to detect acceleration at large and small frequencies respectively, appropriate presumably for walking and jetting (Williamson & Budelmann 1985*a*). Octopods

TABLE 1*a*. DIMENSIONS OF THE STATOCYSTS OF VARIOUS INDIVIDUALS AND SPECIES OF *OCTOPUS* AND *ELEDONE*

(For calculation of volume (V) see table 1*b*.)

species	animal	mass/g	ML/mm	LS/mm	TS/mm	dep/mm	V/mm^3	V/ML	$V/^3\sqrt{M}$
O. vulgaris	UGA	0.001	1.0	0.25	0.25	0.25	0.082	0.008	0.082
O. digueti		12.5	26	1.95	1.55	1.50	2.37	0.09	1.02
O. bimaculoides	ULH	195	82	2.55	2.50	2.50	8.34	0.10	1.44
O. joubini	ULC	229	30	2.15	2.10	2.00	4.73	0.16	0.77
O. bimaculoides	ULE	272	105	2.70	2.40	2.50	8.48	0.08	1.31
O. vulgaris	ULB	300	115	2.69	2.60	2.64	9.67	0.08	1.44
O. briareus	ULF	771	80	2.60	2.50	2.60	8.85	0.11	0.97
O. maya	ULI	1136	155	3.00	2.60	2.75	11.23	0.07	1.08
O. maya	ULD	1675	160	3.45	3.05	2.95	16.25	0.10	1.37
O. vulgaris	ULA	4000	230	3.24	3.10	3.19	16.78	0.07	1.06
E. cirrhosa	DE	360	—	3.50	3.35	3.90	23.94	—	3.37
E. cirrhosa	DF	305	80	3.24	3.35	3.82	21.71	0.24	3.23
E. cirrhosa	DG	1186	—	4.33	4.20	4.93	46.94	—	4.43

TABLE 1*b*. DIMENSIONS OF THE STATOCYST IN THE LARGEST AVAILABLE SPECIMEN OF EACH GENUS, MEASURED ON THE DRAWINGS

(ML, mantle length; LS, length; TS, breadth; dep, depth. The volume is calculated as $\frac{1}{2}\text{LS} \times \frac{1}{2}\text{TS} \times \frac{1}{2}\text{dep} \times \frac{4}{3}\pi$. R is the maximum radius of the horizontal channel and r is its internal radius at the level of the vertical crista. Circ. 1 is the total circumference of the inner border of the horizontal channel and circ. 2 is the circumference of that portion of the channel whose walls form a tube (see p. 194).)

genus	ML/mm	LS/mm	TS/mm	dep/mm	vol/mm^3	R/mm	r/mm	R/r	circ. 1/mm	circ. 2/mm	circ. 2/circ. 1
Abraliopsis	39	2.40	1.72	2.50	5.41	0.76	0.14	5.43	2.64	0.76	0.29
Alloposus	100	4.15	4.46	4.62	44.89	—	—	—	—	—	—
Alloteuthis	45	2.46	2.74	2.29	8.12	0.80	0.16	5.00	3.95	1.00	0.25
Architeuthis	1610	19.54	9.20	12.31	1159.64	2.12	0.53	4.00	12.60	0.65	0.05
Argonauta	47	2.60	2.60	2.60	9.21	—	—	—	—	—	—
Bathothauma	195	5.60	7.00	5.69	116.99	—	—	—	—	—	—
Bathyteuthis	30	2.90	1.96	2.85	8.51	0.83	0.15	5.53	3.00	0.30	0.10
Brachioteuthis	52	1.68	1.63	1.58	2.28	—	—	—	—	—	—
Chiroteuthis	265	3.69	2.81	4.17	22.84	1.06	0.22	4.82	4.69	0.25	0.05
Cirroteuthis	75	8.00	8.00	8.00	268.00	—	—	—	—	—	—
Cirrothauma	155	7.00	9.97	7.78	284.58	—	—	—	—	—	—
Cranchia	125	4.07	3.07	4.50	29.62	—	—	—	—	—	—
Ctenopteryx	32	3.05	1.95	2.75	8.67	0.65	0.13	5.00	5.00	1.60	0.32
Discoteuthis	51	4.47	3.53	4.87	40.53	0.63	0.23	2.74	4.07	1.27	0.31
Dosidicus	1000	7.57	5.43	4.07	88.12	2.00	0.53	3.77	9.86	7.14	0.72
Egea	198	4.89	3.41	4.96	43.53	—	—	—	—	—	—
Eledone	80	3.24	3.35	3.82	21.71	—	—	—	—	—	—

Enoploteuthis	69	2.90	2.10	2.85	9.12	0.95	0.20	4.75	3.50	1.45	0.41
Galiteuthis	297	6.56	4.67	7.33	118.02	—	—	—	—	—	—
Gonatus	110	4.13	3.33	3.05	22.16	1.07	0.21	5.10	3.87	0.60	0.16
Grimalditeuthis	67	4.08	3.08	4.08	26.85	—	—	—	—	—	—
Grimpoteuthis	160	5.15	5.92	6.08	97.01	—	—	—	—	—	—
Helicocranchia	62	2.55	2.40	1.90	6.11	—	—	—	—	—	—
Heteroteuthis	11	1.20	1.36	1.28	1.09	—	—	—	—	—	—
Histioteuthis	60	3.91	2.96	3.00	18.23	1.00	0.30	3.33	4.27	0.39	0.09
Illex	270	5.17	4.43	4.61	56.12	1.58	0.30	5.27	5.25	4.67	0.89
Japetella	75	3.16	3.16	3.16	16.53	—	—	—	—	—	—
Joubiniteuthis	36	2.93	2.73	2.80	11.81	—	—	—	—	—	—
Leachia	126	3.10	2.67	3.70	16.10	—	—	—	—	—	—
Liguriella	138	3.76	3.36	4.56	30.17	—	—	—	—	—	—
Liocranchia	126	3.27	2.21	3.40	12.97	—	—	—	—	—	—
Loligo	500	5.80	4.60	5.00	69.87	1.70	0.40	4.25	6.80	2.20	0.32
Lycoteuthis	80	4.00	3.07	4.33	28.00	1.20	0.23	5.22	4.67	1.93	0.41
Mastigoteuthis	91	4.50	3.67	4.64	40.24	1.17	0.38	3.08	3.33	0.67	0.20
Megalocranchia	335	6.25	5.13	7.75	130.77	—	—	—	—	—	—
Mesonychoteuthis	1170	16.80	13.17	15.00	1739.55	—	—	—	—	—	—
Neoteuthis	104	6.00	4.58	5.08	73.11	1.58	0.38	4.16	5.83	0.83	0.14
Octopoteuthis	70	6.18	4.54	6.09	89.64	1.67	0.45	3.71	6.18	1.72	0.28
Octopus	230	3.24	3.10	3.19	16.78	—	—	—	—	—	—
Ommastrephes	850	6.00	4.66	5.00	73.22	2.16	0.52	4.15	7.76	4.83	0.62
Onycoteuthis	130	3.87	3.13	3.73	23.86	1.07	0.23	4.65	4.80	1.00	0.21
Opisthoteuthis	37	6.80	9.60	8.50	290.53	—	—	—	—	—	—
Pholidoteuthis	460	5.40	4.70	5.40	71.78	1.00	0.18	5.56	6.90	2.00	0.29
Pickfordiateuthis	13	1.54	1.10	1.44	1.28	—	—	—	—	—	—
Pterygioteuthis	23	2.00	1.56	2.06	3.37	0.68	0.13	5.23	2.75	0.47	0.17
Pyroteuthis	42	2.93	2.20	2.73	9.28	—	—	—	—	—	—
Neorossia	65	3.33	3.67	3.67	23.69	0.92	0.17	5.41	3.67	0.67	0.18
Sandalops	112	5.56	4.20	4.90	59.93	—	—	—	—	—	—
Sepia	230	5.58	4.00	5.08	59.39	1.33	0.42	3.17	3.50	0.83	0.24
Sepioteuthis	150	3.70	3.15	3.65	22.41	1.10	0.30	3.67	4.00	1.30	0.33
Sepiola	23	1.83	2.03	2.40	4.72	0.67	0.13	5.15	3.00	0.30	0.10
Spirula	38	3.50	3.10	3.18	18.07	1.00	0.28	3.57	3.05	0.40	0.13
Taonius	540	8.00	5.38	8.80	198.37	—	—	—	—	—	—
Teuthowenia	172	5.90	6.10	6.00	113.10	—	—	—	—	—	—
Thysanoteuthis	80	3.18	2.59	2.68	11.61	0.95	0.18	5.28	3.59	1.27	0.35
Todarodes	325	6.27	4.64	6.18	94.32	2.18	0.45	4.84	8.45	5.90	0.70
Tremoctopus	60	3.00	3.00	4.00	18.85	—	—	—	—	—	—
Vampyroteuthis	45	5.16	5.68	4.50	69.06	1.57	0.32	4.91	7.14	1.29	0.18
Vitreledonella	50	3.70	4.60	4.60	40.99	—	—	—	—	—	—

that have abandoned the benthic life retain this division of the crista, whether they are epipelagic (e.g. *Argonauta*) or bathypelagic (*Japetella*).

2. The Cirroctopoda possess statocysts of broadly the octopod type also with endolymph and perilymph, but without the provision of two types of cupula (so far as is known). In some of them the cavity of the statocyst is partly restricted by several anticristae, as in decapods.

3. The statocyst of *Vampyroteuthis* is in some ways similar to that of cirrates and strikingly intermediate between the Octobrachia and Decabrachia (see Stephens & Young 1976).

4. Non-buoyant teuthids. In the rapidly moving oceanic squids and in *Loligo* and its allies the flow of endolymph is greatly restricted in all three planes, especially horizontally. There is no outer perilymph space and the statocyst cavity is shaped by the cartilage to provide channels of flow in the various planes. The flow is further restricted by the growth of knobs or pegs of cartilage, the hamuli and anticristae. In the fastest-swimming squids some of these pegs become fused together to form canals comparable to those of vertebrates (see Stephens & Young 1978, 1982).

5. Buoyant teuthids. Many different families of squids achieve neutral buoyancy by replacement of sodium by lighter ions, especially ammonium (Clarke *et al.* 1979). This ability allows various postures and methods of locomotion to be adopted; many float with the head downwards. Discriminant analysis of 13 features of the statocysts shows that these buoyant forms are sharply distinct from the non-buoyant teuthids (see Maddock & Young 1984). The differences are mainly such as to provide greater sensitivity for monitoring of turns at lower frequencies. The cavity is large and little obstructed by anticristae. The hamuli are smaller than in non-buoyant forms and the gaps between them larger, indicating larger cupulae. The anticristae do not become joined together to make canals. However, some of these buoyant squids are hunters that move rapidly, and in these the statocyst cavity is more restricted.

6. In the family Cranchiidae the anticristae are placed quite differently from those of any other cephalopods (Young 1984). In some there are very few (none at all in *Bathothauma*); in others they are very numerous – 38 on each side in *Egea* and 22 in *Mesonychoteuthis*. These anticristae are arranged in a helix proceeding from the floor medially in front then up, laterally and backwards. It is suggested that these species have secondarily become active hunters and that the anticristae serve to provide friction to allow appropriate sensitivity as the squid turns from the head-down position upwards and forwards to attack (p. 227).

7. *Sepiida*. The statocyst of *Sepia* has a striking general similarity to that of *Loligo* but discriminant analysis shows that it is different from all the oegopsids, buoyant or non-buoyant. The differences are mostly at the front, probably providing for greater sensitivity in the dipping and rolling planes in *Sepia*. In particular there is a large hamulus at the first turn of the crista, thus restricting the length of the cupulae on the anterior transverse and longitudinal cristae. The statocyst of *Spirula* is unique but in some ways like that of *Sepia*.

8. Statocysts of the non-buoyant sepiolids are quite different from that of *Sepia* and in some ways like those of Octopoda.

4. OCTOPODA

The statocyst of *Octopus vulgaris* was described in Young (1960) but some corrections and much further detail are recorded by Budelmann *et al.* (1987). As in all Octobrachia there is an outer sac filled with perilymph and crossed by numerous strands containing blood vessels, which anchor the inner sac to the cartilage. The inner sac has a mainly thin membranous wall, supported by a cartilaginous framework below the crista. The sac is not spherical but bulges as a large posterior chamber (figure 2*a*).

The crista is divided into nine sections, carrying alternately small and large cupulae, which are fully described by Budelmann *et al.* (1987). Each crista section has large and small hair cells of several types, a total of 2100 for the whole crista. The large and the ventral smaller hair cells make synaptic contact with neurons, whose large axons proceed to the brain (figure 1*c* and figure 3, plate 1); these hair cells are ventrally (or medially) polarized (figure 1*c*). The smaller dorsal hair cells are primary receptor cells with axons, and they are all dorsally (or laterally) polarized. The odd-numbered crista sections, with small cupulae, have double rows of large hair cells; the even-numbered, with large cupulae, have single rows. Each hair cell has kinocilia, morphologically polarized as shown by their basal feet (figure 1*a*). There are no stereövilli such as occur in vertebrates. There are three crista nerves, which innervate unequal sections of the crista (not precisely as reported by Young (1960)).

The afferent fibres of the static nerves proceed to various central sites on both sides of the brain: (1) the magnocellular lobe; (2) the lateral pedal lobe; (3) the brachial lobe; (4) the pedal lobe; (5) the anterior basal lobe; (6) the median basal lobe; (7) the palliovisceral lobe; (8) the peduncle lobe. Details of their distribution are given by Budelmann & Young (1984) and Plän & Budelmann (1989).

There are numerous small efferent fibres in the crista nerves with synaptic endings on both the neurons and hair cells (figure 1*c* and figure 3, plate 1). These fibres have mostly an inhibitory influence on the resting activity of the crista afferent units (figure 1*e*) but a few are excitatory (Williamson 1985). The fibres run along the course of the crista rather than entering directly from the brain as do the afferents (figure 3, plate 1). The efferent fibres arise from three central sites, mostly on the same side: (1) the anterior lateral pedal (oculomotor) lobe; (2) the posterior pedal lobe and (3) the magnocellular lobe (Budelmann & Young 1984; Plän & Budelmann 1989).

The dimensions of the statocyst were measured on specimens of six species of *Octopus* and in three specimens of *Eledone cirrhosa* (table 1*a* and figure 2*b*). The measurements were of the length, breadth and depth and from them the volume was calculated as $V = \frac{1}{2}\mathrm{LS} \times \frac{1}{2}\mathrm{TS} \times \frac{1}{2}D \times \frac{4}{3}\pi$. This was plotted against the mass of the individual, ranging from 0.001 g at hatching to 4000 g in the largest *O. vulgaris*. The measurements were not easy to make but it is clear that the statocyst is relatively very large in the hatchling and then grows much less fast than the whole animal. The relative size of the statocyst is similar in the various species of *Octopus*, with perhaps

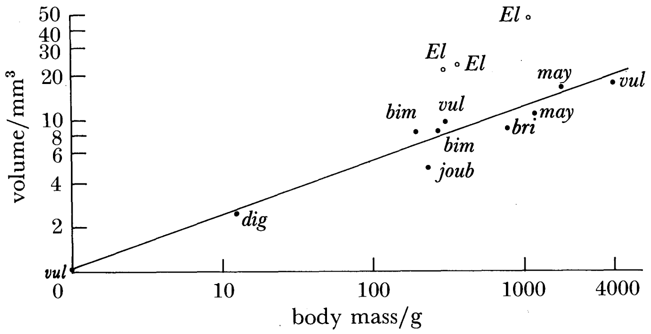

Figure 2*b*. Volumes of the statocyst plotted against body mass for various octopods. The line is drawn by eye to fit the species of *Octopus*. *bim*, *O. bimaculoides*; *bri*, *O. briareus*; *dig*, *O. digueti*; *El*, *Eledone cirrhosa*; *joub*, *O. joubini*; *may*, *O. maya*; *vul*, *O. vulgaris*.

a smaller volume in *O. joubini*. The statocyst of *Eledone* is relatively larger than that of *Octopus*, suggesting slower movement.

The volume of the statocyst of *Octopus* is small compared with that of most decapods. This is shown in table 4, using mantle length for comparison. This is, of course, not a good measure of size for an octopod; however, the absolute volumes are striking – only 17 mm^3 for the largest *Octopus* of 4000 g body mass, far less than the volume in much smaller squids. The smaller *Octopus* individuals of table 1*a* would still be low in table 4 relative to mantle length.

In Octopoda some restriction of the flow of endolymph is provided by the anticrista. This is a plate of cartilage standing up from the wall of the sac in front of the vertical crista (figure 2*a*, and figures 4 and 5, plate 1). This structure presumably serves to reduce the difference between the movement of endolymph and the wall during turns in the yawing plane, thus decreasing the effective mass of endolymph and lowering sensitivity. This is functionally similar to the situation in the horizontal channel in many decapods but the effect is produced by a different anatomical arrangement, probably produced by independent evolution. The dimensions are so different in octopods and decapods that no precise comparison can be made. However, it is interesting that in both groups the restriction of flow of endolymph occurs over a rather short part of the whole circumference (see p. 231).

An interesting feature of the anticrista of *O. vulgaris* is that its tip is divided into several fingers (figure 4, plate 1) and that the pattern of these differs between individuals but is similar on the two sides (Young 1960). This may be the result of genetic factors and/or of sculpturing by the particular pattern of flow of each individual or both, as also in *Alloteuthis* (p. 217).

The anticrista has a characteristic shape in each species of *Octopus*; presumably there are also variations within the species, as in *O. vulgaris*, but these have not been studied in detail. The forms shown in figure 5*a–f*, plate 1, are all quite different from any of the variants of *O. vulgaris*. It is not clear whether these differences of size and shape have any functional significance. The anticristae evidently occupy a larger proportion of the statocyst in *O. maya* (1675 g) and *O. briareus* (771 g) than *O. digueti* (12.5 g) and *O. joubini* (229 g), although all the individuals studied were adults.

The three-lobed anticrista of figure 5*c*, plate 1, is shown by Ishikawa (1929) for his '*Polypus bimaculatus*'. He also reports differences in the anticristae of various species.

In *Eledone* the anticrista is different from that in all the species of *Octopus*: it is a ridge with an irregular outline and a slight peak at its dorsal end (figure 7, plate 1). It slopes up gradually from the ventral end but falls off sharply dorsally. In the specimen shown in figure 7*b*, plate 1, the upper end showed a bifurcation.

5. EPIPELAGOCTOPODA

Argonautidae

Argonauta

The inner sac is approximately spherical (figure 9). The macula is oval with its long axis vertical in the anterior wall. The crista has nine sections, the last very short and indistinct. The sections have alternately single and double rows of large hair cells (figure 8, plate 2). The anticrista is an elongated flattened plate with six lobes (figure 9). The plate lies in the horizontal plane attached to the ventral wall in front of the base of the vertical section of the crista. It extends forwards almost to the macula in such a way as to provide a channel confining and restraining the flow during turning in the yawing plane. Kölliker's canal has a large ciliated funnel, broad proximal section and a long thin distal tube, ending apparently blindly, close to the base of the anticrista (figure 8, plate 2).

Tremoctopodidae

Tremoctopus

The best specimen is of the recently described *T. gelatus* (Thomas 1977) kindly sent from Miami by Dr G. Voss. The animal was caught by a dipnet at low tide and had a mantle length of 370 mm. The endolymphatic sac is pear-shaped with only a very slight suggestion of a posterior sac (figure 10, plate 2). The macula is a small oval area on the anterior face. The crista has nine sections (figure 11, plate 2). The anticrista is a small rounded knob close to the base of the vertical crista. This structure does not seem suitable for restraining the flow of endolymph across the vertical crista.

There are also statocysts from a specimen of *Tremoctopus violaceus* from Naples, of mantle length (ML) 84 mm. They lie far laterally behind the back of the orbits. The static nerves are long and enter the statocyst dorsomedially. The macula lies on the mediodorsal wall. The crista has nine sections with hair-cell rows alternately single and double, but the last is very short. The anticrista is like that of *T. gelatus*, a very small mass sloping upwards and ending as a rounded knob.

Alloposidae

Alloposus mollis

The statocyst is nearly round but is constricted by the crista cartilage; there are thus large sacs on both sides of all sections of the crista (figure 12). The macula is nearly round and lies on the anterior face. The crista is divided into nine sections and there are three crista nerves. The posterior crista nerve sends branches to the posterior sac, as in *Octopus*. The anticrista is a narrow ridge in front of the base of the vertical section of the crista; although small it may have some effect in diverting the horizontal flow of endolymph across the seventh section close to which it lies. Kölliker's canal is long, like that of *Argonauta* and *Tremoctopus*, but has an unusually wide ciliated section and a short final narrow portion.

6. BATHYPELAGOCTOPODA

Vitreledonella richardi

Statocysts from two animals of (ML) 66 mm (A) and 55 mm (B) are available. They are very large and lie apart from the brain (figure 14). The outer sac of A is oval and rather rigid: it measures 5.3 mm long, 6.0 mm broad and 5.1 mm deep; that of B measures 4.0 mm × 6.0 mm × 4.5 mm. The inner sac is less rigid and measures in A 3.7 mm from front to back, and equally 4.6 mm broad and deep: the volume is among the largest, 41 mm^3 (table 4). The macula is oval and lies on the anteromedial surface (figures 13 and 15, plate 2). The crista runs near the centre of the sac, with spaces on both sides of all parts. The crista has nine sections (figure 15, plate 2). The first, near the macula, has two rows of large hair cells, the second, one row. The other sections probably alternate, but the ninth is very short. There are anterior and posterior crista nerves. There is no sign of an anticrista, a feature that this genus shares with the other members of the suborder, but otherwise is found only in *Bathothauma*. Kölliker's canal has a short, broad inner section.

Amphitretus

I have a statocyst from a specimen of *A. pelagicus* of mantle length 32 mm. The sac was broken and no measurements were possible but the macula and crista were recovered intact; they are similar to those of *Vitreledonella* (figure 16, plate 2). The crista has the usual nine sections; the first has two irregular rows of hair cells and the second a single row. The first two sections are served by an anterior crista nerve in the form of distinct bundles. This is a somewhat different arrangement from that of *Vitreledonella*. Kölliker's canal has a wide outer section; there is no anticrista.

Japetella diaphana

The large statocysts from a specimen of ML 75 mm are placed as separate sacs on either side behind the brain (figure 17, plate 2). The inner sacs are approximately spherical with diameter 3.16 mm and volume 16.5 mm^3. The macula lies on the anteromedial wall and is oval. The crista is divided into nine sections, probably with alternating single and double rows of large hair cells. The first six sections are innervated by the anterior crista nerve, the last three by the posterior one. There is no anticrista.

7. CIRROCTOPODA

Introduction

The statocysts of the cirrates studied have many features in common, which can be described for all of them together. They are all large sacs standing away behind the brain and not enclosed in cartilage. There are inner and outer sacs but the outer is not much larger than the inner, so that there is little perilymph. The inner sac is approximately spherical but constricted by the crista cartilage to give a 'waist'. The volumes are the largest in any cephalopods and are about equal, except for *Grimpoteuthis*, which is somewhat smaller (table 4).

The crista runs approximately across the front, along the side, across the back and finally up dorsally. It can be said to have four sections and these are marked by rather sharp bends, especially in *Cirroteuthis* (figures 26 and 27, plate 3). However, there is no interruption of the crista at the bends and there is no division into nine sections as there is in Octopoda. There is no evidence about the condition of the cupulae. The crista has been described in detail in *Cirrothauma* (Aldred *et al.* 1983). There is probably only a single row of large hair cells and those have no axons but communicate with large nerve cells lying beneath. Some of the other hair cells of the crista are primary sensory cells with their own axons.

There are anterior and posterior crista nerves in all the cirrates. Kölliker's canal is large, with a large ciliated funnel. All these statocysts have one or more cartilaginous projections, presumably concerned with regulation of the flow of endolymph. Their positions are not exactly comparable to either the hamuli or anticristae of other cephalopods: for convenience they have all been labelled 'anticristae', but sometimes from their position at the turns of the crista they resemble the hamuli of decapods. The presence of multiple anticristae is extremely interesting evidence about the common stock that gave rise to both Octobrachia and Decabrachia (p. 235).

Opisthoteuthidae

Opisthoteuthis

In a specimen with ML 37 mm, taken by *Discovery* between 1007 and 1042 m, the outer sac is 15 mm broad and 13 mm long (figure 20, plate 3, and figure 21). The inner sac is not quite spherical, with diameters of 9.6, 6.8 and 8.5 mm, giving a volume of 290 mm^3. It is constricted by the crista at the waist. The crista is divided into four sections by rather sharp turns (figure 21). It runs across the front, along the side, across the back and then up vertically. There are no sharp constrictions at the turns. The details of the hair cells are not clear but they continue as an uninterrupted series at each turn. Near to the last turn there is an anticrista in the form of a spherical knob of cartilage, lying a short distance away from the crista and not bending over it, though it is in the position of hamulus 4 of decapods. Its effect must be to alter the flow across the posterior transverse and vertical sections of the crista, but only to a small extent. Kölliker's canal is small.

Grimpoteuthis glacialis

The statocyst is relatively smaller than in *Opisthoteuthis*: in a specimen of 160 mm ML given by Dr G. Voss the outer sac was 6 mm in transverse diameter and 8 mm deep. The inner sac was ovoid, with diameters 5.9, 5.1 and 6.8 mm, giving a volume of 107 mm^3 (figures 22–24, plate 3). The crista runs in a curve with three rather sharp bends. There is no sign of division into nine sections, nor are there constrictions at the bends. There are three cartilaginous knobs, two of them close together near the dorsal end of the crista, and a single one near the last turn. The knobs are thus approximately in the positions of hamuli 4 and 5 of decapods and they presumably serve to restrict the flow across the vertical section of the crista.

This is clearly a statocyst suited for slow turning, but perhaps adapted to a somewhat higher frequency than in *Opisthoteuthis*, especially in the yawing plane.

Cirroteuthidae

Cirrothauma

The statocysts have been described in detail by Aldred *et al.* (1983). They are separated from the brain at a distance of 15 mm and lie not in cartilage but apparently floating freely, attached by their nerves. They are nearly spherical and very large, the outer sac is 10 mm in diameter and the inner only a little less with diameters 9.97, 7.00 and 7.78 mm, giving a volume of 284 mm^3. There are muscle fibres running in the wall of the outer sac (figure 28). The crista runs on a continuous ridge of cartilage, lying almost in the sagittal plane, except for the anterior transverse first section. The crista does not show any division into sections or constrictions where it turns. There is probably a single row of large hair cells all along its length, with large nerve cells below, as in *Octopus*. There are also smaller hair cells, some of which are primary sense cells with axons.

There is a single anticrista in the form of a knob of cartilage standing on the floor of the statocyst at about 1 mm distant from the crista. In this position it is best considered as an anticrista rather than a hamulus. It presumably plays some part in distributing the flow of endolymph. Kölliker's canal is large, with large cilia. There are anterior and posterior crista nerves.

With its great size this is obviously the statocyst of an animal that moves slowly. If the animal lives head-downwards the greater part of the crista seems arranged to detect rotary movements about a longitudinal axis. The anterior section would respond in the pitching plane when swimming head-first.

Cirroteuthis muelleri

A statocyst from a specimen of 75 mm ML was kindly provided by Dr G. Voss. It is approximately spherical, with diameter 8 mm, giving a volume of 268 mm^3 (figures 26 and 27, plate 3). The crista shows four parts separated by bends. There are no divisions into shorter sections. There is a single anticrista in the form of a knob lying at a short distance from the hinder end of the crista but not bending over it. There are anterior and posterior crista nerves. The Kölliker's canal is large, with a conspicuous funnel at the inner opening.

Stauroteuthidae

Stauroteuthis syrtensis

Sections of the statocyst are available from a specimen identified by Dr G. Voss from photographs of the brain and optic lobes before sectioning. (This statocyst was described and figured in Young (1977) as a 'cirroteuthid'.) In spite of much distortion during sectioning it is clear that there are inner and outer sacs and several cartilaginous pegs, probably four. These anticristae are large knobs, three attached to the floor and one to the roof. The two most medial ones appear to lie on either side of the vertical section of the crista, but it is not easy to compare any of them with those of other cephalopods.

Ebersbach (1915) described a statocyst containing several anticristae, ascribing it to '*Cirroteuthis*' but it seems more likely that it was in fact *Stauroteuthis*. Figure 25 is a copy made from Ebersbach's drawing. It shows two knobs close to the crista, three on the ventral wall and a plate dorsally. With so many knobs this is an exceedingly interesting statocyst and further specimens are urgently needed.

The statocyst of '*Stauroteuthis*' described by Ebersbach (1915) as having a single anticrista was probably from *Cirroteuthis*. His figure and description show a plate in the position of the anticrista of *Octopus*.

8. VAMPYROMORPHA

Vampyroteuthis

The statocyst has already been described by Stephens & Young (1976). An excellent new specimen with ML 45 mm has been used to provide further details and new measurements (figure 18, plate 2, and figure 19). There are inner and outer sacs with perilymph between, as in Octopoda. The statocyst is very short, wide and shallow (table 2). Its volume of 69.27 mm^3 is greater relative to mantle length than in any other genus except among cirrates (table 4). The crista makes three turns, giving four sections, as in decapods, but there are no subdivisions such as those of Octopoda.

It is of great interest that there are hamuli and anticristae in approximately the positions found in decapods. Hooks occur only at the positions of h3 and h4 in the new specimen but in one of those previously described there was an h1. There are seven straight anticristae on each side in the new specimen. Four are on the medial wall, approximately in the positions of anticristae 2–5 in decapods, one is on the medial wall far back. A very large one, perhaps anticrista 7 hangs from the roof at the back, pointing towards a more ventral anticrista 6, which is penetrated by the Kölliker's canal. A similar distribution of the anticristae was seen in the specimens studied by Stephens & Young. In smaller animals only the very large one in the roof was prominent, some of the others were minute.

The large dorsal anticrista provides a medial border for the horizontal channel for 18% of its circumference (table 3).

With this extraordinary assemblage of characteristics the statocyst of *Vampyroteuthis* is shown by discriminant analysis to be far away from most other cephalopods (Maddock & Young 1984). In so far as it shows any similarities they are with the cirrates, which also have octopod-like inner and outer sacs and sometimes also several anticristae and a very large volume.

9. Non-buoyant oegopsids

The statocyst of all the squids that are heavier than water have rather similar dimensions. In a plot of the logarithm of the length of the statocyst against the mantle length they all fall along a single line with a slope of 0.42 (Maddock & Young 1984). The larger animals thus have relatively smaller statocysts. This, of course, also applies to growth during life in each species. In newly hatched *Loligo* the statocyst is very large – more than one quarter the length of the animal, providing for high sensitivity during slow turns. The statocyst then grows much more slowly than the whole animal, increasing by about 29 times against a 390-fold increase of mantle length. The relative growth of other features is also such as to increase sensitivity. Thus the length of the vertical section of the crista increases only 12 times and the gap between the 4th and 5th hamulus only five times. This is achieved by a very rapid growth of the hamuli themselves; for example, the fourth increases very fast at first, then more slowly, altogether by 83 times. The other hamuli also grow fast, though no measurements are available. Sensitivity is thus adjusted to suit higher frequencies in all three planes during growth, but probably most markedly for the vertical crista, because turning is most rapid in the yawing plane. It would be very valuable to have similar data for oceanic squids. A similar growth pattern occurs in *Sepia* (p. 223).

Ommastrephidae

In these oceanic squids the angular acceleration receptor system is organized to detect turns at a higher frequency than in any other squids. These animals can proceed at velocities up to 4 knots (≈ 206 cm s^{-1}) by their jets, but there are no data to show how fast they turn. The shape of the statocyst and its anticristae serve to form an almost complete horizontal circular tube, giving the vertical crista the sensitivity appropriate to rapid turning in the yawing plane. The statocyst cavity is shallow behind, but in front it is deeper, forming two channels, separated by the median row of anticristae and providing a restricted flow of endolymph across the three anterior sections of the crista.

The 'closed' portion of the horizontal channel occupies three quarters of the whole circumference, more than in any other squid (table 3). It has been difficult to obtain fully grown specimens of the largest ommastrephids, which may well show even more restriction of the channels than are illustrated.

TABLE 2. DIMENSIONS OF THE STATOCYST RELATED TO SCALING FACTOR V_1 CALCULATED AS $\sqrt[3]{(\text{LS} \times \text{TS} \times \text{DEPTH})}$

(The genera are listed in descending order of the magnitude of the relative dimension. B, buoyant squids; C, cranchiids; Ci, cirrates; NB, non-buoyant squids; O, octopods; S, sepiids, sepiolids and *Spirula*; V, *Vampyroteuthis*.)

LS/V_1		TS/V_1		depth/V_1	
Architeuthis	1.50 B	*Cirrothauma*	1.22 Ci	*Megalocranchia*	1.23 C
Dosidicus	1.37 NB	*Opisthoteuthis*	1.17 Ci	*Taonius*	1.23 C
Histioteuthis	1.20 B	*Bathothauma*	1.16 C	*Galiteuthis*	1.21 C
Ctenopteryx	1.20 NB	*Vampyroteuthis*	1.06 V	*Tremoctopus*	1.21 O
Gonatus	1.19 B	*Helicocranchia*	1.06 C	*Liguriella*	1.18 C
Neoteuthis	1.16 NB?	*Heteroteuthis*	1.06 S	*Leachia*	1.18 C
Ommastrephes	1.16 NB	*Grimpoteuthis*	1.04 Ci	*Chiroteuthis*	1.18 B
Bathyteuthis	1.15 NB	*Neorossia*	1.03 S	*Liocranchia*	1.17 C
Sepia	1.15 S	*Teuthowenia*	1.02 C	*Cranchia*	1.17 C
Sandalops	1.15 C	*Alloposus*	1.01 O	*Sepiola*	1.16 S
Pickfordiateuthis	1.14 NB	*Argonauta*	1.00 O	*Discoteuthis*	1.15 B
Loligo	1.14 NB	*Japetella*	1.00 O	*Abraliopsis*	1.15 NB
Thysanoteuthis	1.13 NB	*Vitreledonella*	1.00 O	*Lycoteuthis*	1.15 NB
Pyroteuthis	1.13 NB	*Cirroteuthis*	1.00 Ci	*Egea*	1.14 C
Helicocranchia	1.13 C	*Brachioteuthis*	1.00 NB	*Bathyteuthis*	1.13 NB
Mesonychoteuthis	1.13 C	*Dosidicus*	0.99 NB	*Pterygioteuthis*	1.11 NB
Liocranchia	1.12 C	*Sepiola*	0.98 S	*Enoploteuthis*	1.10 NB
Egea	1.12 C	*Eledone*	0.97 O	*Grimalditeuthis*	1.10 B
Enoploteuthis	1.12 NB	*Octopus*	0.97 O	*Octopoteuthis*	1.10 B
Octopoteuthis	1.11 B	*Joubiniteuthis*	0.97 B	*Eledone*	1.10 O
Todarodes	1.11 NB	*Alloteuthis*	0.96 NB	*Mastigoteuthis*	1.09 B
Taonius	1.11 C	*Gonatus*	0.96 B	*Todarodes*	1.09 B
Grimalditeuthis	1.10 B	*Spirula*	0.95 S	*Ctenopteryx*	1.08 NB
Abraliopsis	1.10 NB	*Illex*	0.93 NB	*Grimpoteuthis*	1.07 Ci
Illex	1.09 NB	*Thysanoteuthis*	0.92 NB	*Pickfordiateuthis*	1.07 NB
Onycoteuthis	1.09 NB	*Histioteuthis*	0.91 B	*Onycoteuthis*	1.05 NB
Pterygioteuthis	1.08 NB	*Pholidoteuthus*	0.91 B	*Pholidoteuthis*	1.05 B
Spirula	1.08 S	*Tremoctopus*	0.91 O	*Alloposus*	1.05 O
Galiteuthis	1.08 C	*Loligo*	0.90 NB	*Sepia*	1.05 S
Alloteuthis	1.08 NB	*Ommastrephes*	0.90 NB	*Sepioteuthis*	1.05 NB
Cranchia	1.08 C	*Sepioteuthis*	0.90 NB	*Pyroteuthis*	1.05 NB
Lycoteuthis	1.06 NB	*Onycoteuthis*	0.88 NB	*Neorossia*	1.03 S
Mastigoteuthis	1.06 B	*Neoteuthis*	0.88 NB?	*Opisthoteuthis*	1.03 Ci
Sepioteuthis	1.06 NB	*Mesonychoteuthis*	0.88 C	*Mesonychoteuthis*	1.01 C
Pholidoteuthis	1.05 B	*Sandalops*	0.87 C	*Octopus*	1.01 O
Chiroteuthis	1.05 B	*Liguriella*	0.87 C	*Sandalops*	1.01 C
Discoteuthis	1.05 B	*Mastigoteuthis*	0.86 B	*Vitreledonella*	1.00 O
Joubiniteuthis	1.04 B	*Leachia*	0.85 C	*Teuthowenia*	1.00 C
Brachioteuthis	1.03 NB	*Pyroteuthis*	0.85 NB	*Argonauta*	1.00 O
Octopus	1.02 O	*Pterygioteuthis*	0.84 NB	*Heteroteuthis*	1.00 S
Cirroteuthis	1.00 Ci	*Discoteuthis*	0.83 B	*Cirroteuthis*	1.00 Ci
Japetella	1.00 O	*Grimalditeuthis*	0.83 B	*Japetella*	1.00 O
Argonauta	1.00 O	*Sepia*	0.83 S	*Joubiniteuthis*	0.99 B
Vitreledonella	1.00 O	*Megalocranchia*	0.82 C	*Illex*	0.98 NB
Megalocranchia	0.99 C	*Todarodes*	0.82 NB	*Loligo*	0.98 NB
Leachia	0.99 C	*Octopoteuthis*	0.82 B	*Spirula*	0.98 S
Teuthowenia	0.98 C	*Lycoteuthis*	0.82 NB	*Neoteuthis*	0.98 NB?
Liguriella	0.97 C	*Enoploteuthis*	0.81 NB	*Brachioteuthis*	0.97 NB
Vampyroteuthis	0.96 V	*Chiroteuthis*	0.81 B	*Thysanoteuthis*	0.96 NB
Heteroteuthis	0.94 S	*Pickfordiateuthis*	0.81 NB	*Alloteuthis*	0.96 NB
Eledone	0.94 O	*Cranchia*	0.80 C	*Ommastrephes*	0.96 NB
Neorossia	0.94 S	*Abraliopsis*	0.79 NB	*Cirrothauma*	0.95 Ci
Alloposus	0.94 O	*Egea*	0.78 C	*Bathothauma*	0.94 C
Bathothauma	0.92 C	*Galiteuthis*	0.77 C	*Architeuthis*	0.94 B
Tremoctopus	0.91 O	*Ctenopteryx*	0.77 NB	*Histioteuthis*	0.92 B

Table 2 (*cont.*)

(The genera are listed in descending order of the magnitude of the relative dimension. B, buoyant squids; C, cranchiids; Ci, cirrates; NB, non-buoyant squids; O, octopods; S, sepiids, sepiolids and *Spirula*; V, *Vampyroteuthis*.)

LS/V_1		TS/V_1		depth/V_1	
Grimpoteuthis	0.90 Ci	*Bathyteuthis*	0.77 NB	*Gonatus*	0.88 B
Sepiola	0.88 S	*Liocranchia*	0.76 C	*Vampyroteuthis*	0.84 V
Cirrothauma	0.86 Ci	*Taonius*	0.74 C	*Helicocranchia*	0.84 C
Opisthoteuthis	0.83 Ci	*Architeuthis*	0.71 B	*Dosidicus*	0.74 NB

Table 3. Proportion of the horizontal canal that forms a partial tube, calculated as described on p. 194

(Abbreviations as for table 2.)

Illex	0.89 NB	*Sepia*	0.24 S
Dosidicus	0.72 NB	*Onycoteuthis*	0.21 NB
Todarodes	0.70 NB	*Mastigoteuthis*	0.20 B
Ommastrephes	0.62 NB	*Vampyroteuthis*	0.18 V
Lycoteuthis	0.41 NB	*Neorossia*	0.18 S
Enoploteuthis	0.41 NB	*Pterygioteuthis*	0.17 NB
Thysanoteuthis	0.35 NB	*Gonatus*	0.16 B
Sepioteuthis	0.33 NB	*Neoteuthis*	0.14 NB?
Loligo	0.32 NB	*Spirula*	0.13 S
Ctenopteryx	0.32 NB	*Sepiola*	0.10 S
Discoteuthis	0.31 B	*Bathyteuthis*	0.10 B
Pholidoteuthis	0.29 B	*Histioteuthis*	0.09 B
Abraliopsis	0.29 NB	*Chiroteuthis*	0.05 B
Octopoteuthis	0.28 B	*Architeuthis*	0.05 B
Alloteuthis	0.25 NB		

Dosidicus gigas

I have a large specimen (A) from Chile kindly provided by Dr G. Voss and reported to have had a mantle length of 1 m; there are also several others of up to 410 mm ML, which I picked up dead on the beach at Mazatlan, Mexico. In the large specimen A the statocyst is very long, rather broad but shallow (table 1, and figures 29 and 30, plate 3). The horizontal canal is a complete tube for three quarters of its circumference (table 3). The volume of the whole cavity is less relative to mantle length than in almost any other squid (table 4) and of course much of this volume lies in the anterior part: the horizontal canal has a very small volume. The lateral wall is curved and the posterior end of the statocyst cavity makes a shallow circular canal, leading to the vertical crista. The very large hamulus 4 completes the floor of the tube. Anticrista 7 is greatly elongated to make a roof to the canal and it is in contact for much of its length with anticrista 6, making the floor. Passing forwards the canal opens ventrally but is closed off by the four anticristae attached to the median wall, which are very large masses of cartilage. Anticrista 2 has an unusual form, with narrow base and expanded tip, which fits in to a groove in anticrista 7, making a complete roof to this part of the canal. Anticrista 2 carries a small round knob at its tip on both sides. Anticristae 3, 4 and 5 are all long with rounded tips, and very little space is left between them, so they make a medial wall to this part of the channel. Endolymph can flow forwards and downwards over their ends, but it is then obstructed in front by anticrista 1, which stands on a broad base medially and is very large and curved forwards so that its tip makes contact with the lateral wall, resting in a small depression.

TABLE 4. VOLUMES OF THE STATOCYST CALCULATED FROM THE DIMENSIONS AS $\frac{1}{2}\mathrm{LS} \times \frac{1}{2}\mathrm{TS} \times \frac{1}{2}\mathrm{DEP} \times \frac{4}{3}\pi$

	V/mm^3	ML/mm	V/ML	rank order	V/ML
Mesonychoteuthis	1740	1170	1.49	*Opisthoteuthis*	7.84 Ci
Architeuthis	1160	1610	0.72	*Cirroteuthis*	3.57 Ci
Opisthoteuthis	290	37	7.84	*Cirrothauma*	1.83 Ci
Cirrothauma	284	155	1.83	*Vampyroteuthis*	1.53 V
Cirroteuthis	268	75	3.57	*Mesonychoteuthis*	1.49 C
Taonius	198	540	0.37	*Octopoteuthis*	1.29 B
Megalocranchia	131	335	0.39	*Vitreledonella*	0.82 O
Galiteuthis	118	297	0.40	*Discoteuthis*	0.80 B
Bathothauma	117	195	0.60	*Architeuthis*	0.72 B
Teuthowenia	113	172	0.66	*Neoteuthis*	0.70 NB?
Grimpoteuthis	107	160	0.67	*Grimpoteuthis*	0.67 Ci
Todarodes	94	325	0.29	*Teuthowenia*	0.66 C
Octopoteuthis	90	70	1.29	*Bathothauma*	0.60 C
Dosidicus	88	1000	0.09	*Sandalops*	0.54 C
Neoteuthis	73	104	0.70	*Spirula*	0.47 S
Ommastrephes	73	850	0.09	*Alloposus*	0.45 O
Pholidoteuthis	72	460	0.16	*Mastigoteuthis*	0.44 B
Loligo	69	500	0.14	*Galiteuthis*	0.40 C
Vampyroteuthis	69	45	1.53	*Grimalditeuthis*	0.40 B
Sandalops	60	112	0.54	*Megalocranchia*	0.39 C
Sepia	59	230	0.26	*Taonius*	0.37 C
Illex	56	270	0.21	*Neorossia*	0.37 S
Vitreledonella	41	50	0.82	*Joubiniteuthis*	0.33 B
Alloposus	45	100	0.45	*Tremoctopus*	0.32 O
Egea	44	198	0.22	*Histioteuthis*	0.30 B
Discoteuthis	41	51	0.80	*Bathyteuthis*	0.30 NB
Mastigoteuthis	40	91	0.44	*Todarodes*	0.29 NB
Liguriella	30	138	0.22	*Ctenopteryx*	0.27 NB
Cranchia	30	125	0.24	*Sepia*	0.26 S
Lycoteuthis	28	80	0.24	*Eledone*	0.24 O
Eledone	28	115	0.24	*Cranchia*	0.24 C
Grimalditeuthis	27	67	0.40	*Lycoteuthis*	0.24 NB
Onycoteuthis	24	130	0.18	*Japetella*	0.22 O
Neorossia	24	65	0.37	*Liguriella*	0.22 C
Chiroteuthis	23	265	0.09	*Pyroteuthis*	0.22 NB
Gonatus	22	110	0.20	*Sepiola*	0.22 S
Sepioteuthis	22	150	0.15	*Egea*	0.22 C
Tremoctopus	19	60	0.32	*Illex*	0.21 NB
Histioteuthis	18	60	0.30	*Argonauta*	0.20 O
Spirula	18	38	0.47	*Gonatus*	0.20 B
Japetella	17	75	0.22	*Onychoteuthis*	0.18 NB
Octopus	17	230	0.07	*Alloteuthis*	0.18 NB
Leachia	16	126	0.13	*Pholidoteuthis*	0.16 B
Liocranchia	13	126	0.10	*Sepioteuthis*	0.15 NB
Thysanoteuthis	12	80	0.15	*Thysanoteuthis*	0.15 NB
Joubiniteuthis	12	36	0.33	*Loligo*	0.14 NB
Pyroteuthis	9	42	0.22	*Abraliopsis*	0.14 NB
Argonauta	9	47	0.20	*Pterygioteuthis*	0.13 NB
Enoploteuthis	9	69	0.13	*Leachia*	0.13 C
Ctenopteryx	9	32	0.27	*Enoploteuthis*	0.13 NB
Bathyteuthis	9	30	0.30	*Liocranchia*	0.10 C
Alloteuthis	8	45	0.18	*Helicocranchia*	0.10 C
Helicocranchia	6	62	0.10	*Pickfordiateuthis*	0.10 NB
Abraliopsis	5	39	0.14	*Heteroteuthis*	0.10 S
Sepiola	5	23	0.22	*Chiroteuthis*	0.09 B
Pterygioteuthis	3	23	0.13	*Dosidicus*	0.09 NB
Heteroteuthis	1	11	0.09	*Ommastrephes*	0.09 NB
Brachioteuthis	2	52	0.04	*Octopus*	0.07 O
Pickfordiateuthis	1	13	0.08	*Brachioteuthis*	0.04 NB

There is thus an almost complete circular tube in the horizontal plane. It has a nearly uniform diameter as seen from above, though slightly narrower at the level of the vertical crista. It opens out vertically in the space between the median row of anticristae and anticrista 1, but there is no single large 'utricular' space. The canal is almost completely obstructed medially by the row of four anticristae.

The relative movement of endolymph must be greatly limited in this horizontal plane, both by friction with the walls of the channel and by the blocking effect of the median row. Hamuli 4 and 5 are very large, restricting the flow across the vertical capula. The system is thus designed to allow sufficiently differentiated responses even during large accelerations produced by jetting. The dimensions of this system are discussed later (p. 232).

In our smaller specimens of *D. gigas* the statocyst is similar to that of the larger specimen A. In five animals between 310 and 410 mm ML the anticristae 2, 3, 4, and 5 are all in contact and anticristae 6 and 7 are fused. In a specimen of 210 mm ML, however, anticristae 2 and 3 and 6 and 7 are in contact but not fused.

The statocyst cavity of adult *Dosidicus* thus allows for very little flow of endolymph in the horizontal plane. In the other planes, however, movement of fluid is not so greatly limited and is appropriate to monitor slower turns. Thus hamulus 1 is small and there is no hamulus 2. The first three sections of the crista all lie close to the ventral surface, but the floor is deeply depressed at the centre of the length of the statocyst, allowing a considerable volume of endolymph to flow up and down across the anterior transverse and longitudinal cristae, monitoring dipping and rolling.

Ommastrephes

Four good specimens are available: one of 850 mm ML from *Discovery*, presumed to be *O. bartrami* and others of *O. pteropus* from Miami and Galveston, U.S.A., of 400, 350 and 250 mm ML. In the largest the statocyst is similar to that of *Dosidicus* but rather broader and deeper relative to the length (figure 31, and figure 32, plate 3). The anticristae are all large and smoothly rounded. In two specimens there is an extra anticrista, 4a, carrying an accessory knob.

Anticrista 7 is very large, extending the walls of the horizontal canal both forwards and backwards (figure 31). It makes close contact not only with anticrista 6 but also with several of those in the median row. These contacts are not fully fused and the cartilages often came apart during preparation (figure 32, plate 3). The members of the row also make contact with their neighbours, sometimes interlocking by means of a small knob fitting into a depression.

The horizontal channel is thus tubular for over 60 % of its circumference (see p. 194 and table 3). The volume of the cavity is very small relative to the mantle length, as in *Dosidicus* (table 4). The cupula on the vertical crista is shown moderately well preserved in figure 33, plate 3. It extends the full length of the section but is greatly expanded at the centre.

Illex coindeti

The statocyst of a specimen of 270 mm ML from Ischia, Italy, shows typical ommastrephid characters. It has very well-developed horizontal canals, tubular for 89 % of the circumference (figure 34 and table 3). Anticrista 7 is very large and extended backwards and forwards in contact with anticrista 6 below and anticrista 2 in front (figure 35, plate 4). The canal thus continues forwards in front of the median row of anticristae. It is completed in front by the statolith dorsally and more ventrally by anticrista 1, which is large and placed horizontally on a prominent base of cartilage. The anticristae of the median row have swollen tips and narrower bases, leaving small channels for endolymph between them (figure 35*b*, plate 4). The only slightly enlarged part of the circuit is thus in front of the vertical crista and behind the median row. The rest of the circuit provides for a flow of endolymph in an almost complete tube leading to the vertical crista.

The statocyst cavity is, however, enlarged ventrally, as in other ommastrephids, providing a large volume of endolymph to flow across the other three sections of the crista (figure 35*b*). The total volume of the statocyst is rather larger relative to mantle length than in *Dosidicus* (table 4). We also have statocysts from *Illex* at Naples of 33, 34, 55, 93, 100, 230 and 270 mm ML. In the smaller ones the anticristae are straight pointed rods (figure 36, plate 4), anticristae 6 and 7 do not meet and anticrista 7 is a simple knob. Even in the larger immature specimens the horizontal canal is not yet fully formed. Anticristae 6 and 7 are not in contact and anticrista 7 is a simple cone. The anticristae of the median row leave large spaces between them. The less restricted flow of endolymph presumably provides for the greater sensitivity at low rates of turning that are needed by smaller animals.

Todarodes sagittatus

Statocysts are available from animals of 460 and 330 mm ML from *Challenger* and two of 325 mm from Banyuls. They are similar to those of *Illex*, with a long narrow horizontal channel dorsally and deep vertical channels in front (figure 37, and figures 38 and 39, plate 4). Anticrista 7 is even more extended forwards and backwards than in *Illex*. In one specimen it is attached to anticrista 2 (figure 37*c*) and it has become separated after fixation in figure 38, plate 4. Anticristae 1 and 2 stand upon large cartilaginous bases. The members of the median row are less bulbous than in *Illex* and leave some spaces between them. The horizontal channel is thus complete for 70% of its circumference (table 3). The total volume of the statocyst is somewhat greater relative to mantle length than in other ommastrephids, but the functioning is probably similar.

Thysanoteuthidae

Thysanoteuthis rhombus

This oceanic squid has large fins. The statocyst shows adaptations for swift movement but considerable differences from those of ommastrephids. We have a fine specimen from the Pacific, of 800 mm ML (figure 40, and figure 41, plate 4). It is relatively long and broad but shallow, as in ommastrephids (table 2). The horizontal canal is well marked. Anticrista 7 is a large knob from which ridges extend forwards and backwards; it does not touch anticrista 6. The anticristae of the median row are not bulbous and have square ends; they are not in contact with each other. Anticrista 1 is a small knob, unlike the large rod of ommastrephids. The horizontal canal is thus complete for about one third of its circumference (table 3).

Another striking difference from ommastrephids is the presence of a large hamulus at the first turn of the crista. This is rather rare among oegopsids but is characteristic of *Sepia* and is possibly connected with the presence of a fin along the length of the mantle in *Thysanoteuthis* (see p. 236).

The cartilage around the statocyst is very dense and not vacuolated.

This statocyst is less well suited for rapid movement than in adult ommastrephids. It is likely that our specimen was close to maturity as its size approaches the maximum for the species.

Enoploteuthidae

These small active squids have statocysts suited for rapid movement. They are said to be non-buoyant, but the cartilage of our specimens is much vacuolated (Clarke *et al.* 1979). However, the statocysts are characteristic of fast swimmers.

Enoploteuthis leptura

In a specimen of 69 mm ML the statocyst is moderately long, but narrow and deep (figure 42, and figure 43, plate 4). The lateral wall is curved to make a horizontal canal. Anticrista 7 is a knob, tightly pressed against anticrista 6 to make a tunnel, and extended forwards and backwards (figure 42). The canal is thus tubular for about 13% of its circumference. The anticristae of the median row are all large but with pointed tips. They mostly lie close together, leaving very little space between them. Anticrista 1 is a short rod. There is no hamulus at the first turn but the others are well developed; hamulus 4 is especially large. The flow across the vertical crista must therefore be greatly limited by the restriction imposed by the walls of the canal and the median row of anticristae.

Enoploteuthis anapsis

My specimen of 39 mm ML is similar in shape to *E. leptura* but with anticristae shorter and less pointed (figure 44, plate 4). Anticristae 6 and 7 are in contact but anticrista 7 is not extended. These conditions may be due only to the smaller size of the animal.

Abraliopsis morrisi

The statocyst is very like that of *Enoploteuthis* but deeper and narrower (figure 45, and figure 46, plate 4). In a specimen of 39 mm ML the anticristae are large and rounded and fill up much of the cavity, but there is no anticrista 1. Anticristae 6 and 7 are large and are in full contact, making a tunnel for rather less than one third of the circumference (figure 46, plate 4). The cavity is shaped to make a clear horizontal canal leading to the vertical crista. Hamuli 1 and 5 are small and there is no hamulus 2, but 3 and 4 are large. Conditions are similar in the statocyst from a specimen of 36 mm ML; in one of 25 mm ML the anticristae are smaller and anticristae 6 and 7 are not in contact.

Onycoteuthidae

Onychoteuthis banksi

I have statocysts from five animals between 58 and 130 mm ML (figure 47, and figures 48 and 49, plate 4). The largest is typical of a rapidly moving squid. The cavity is rather rounded and about equal in length, breadth and depth. A transverse section across the front of the statocyst shows how the shape of the cavity provides for flow across the anterior transverse crista during movements in the dipping plane (figure 49, plate 4). The anticristae are large and rounded, but with some tapering. Anticrista 7 is elongated and in contact with anticrista 6, making a well-marked horizontal canal, about one fifth of which is tubular. There is a small anticrista 1 and the members of the median row are spread out and do not touch each other. There is no hamulus at the first turn and hamulus 1 is small, the others rather large, especially hamulus 4.

In the smaller animals of 121 and 88 mm ML the pattern is well developed and anticristae

6 and 7 in full contact. In an animal of 65 mm ML the anticristae are rather smaller and 6 and 7 do not meet. There is a small accessory anticrista 5a on one side. In one of 58 mm ML the anticristae are smaller still but yet already restricting the flow of endolymph.

Onychia caribbea

The statocyst from an animal of 20 mm ML is essentially like that of a small *Onycoteuthis* (figure 50, plate 4). The anticristae are rather small and the canals are wide. Anticristae 6 and 7 do not meet. No measurements were made.

Pterygioteuthidae

These active little squids are similar to the Enoploteuthidae but the statocysts show some clear differences. These animals are non-buoyant and the cartilage is not vacuolated.

Pterygioteuthis giardi

The statocyst of a specimen of 23 mm ML is of moderate length and breadth but rather deep (table 2). The volume is very small, 3 mm^3; the anticristae are large and flat and fill much of

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DESCRIPTION OF FIGURES 2*a* AND 3–19.

FIGURE 2*a*. Diagram of the statocyst of *O. vulgaris* Lamarck, 1798, lateral view.

FIGURE 3. *O. vulgaris*. Flattened preparation of the first sections of the crista after staining the nerve fibres with Bodian's stain.

FIGURE 4. (*a*, *b*) *O. vulgaris*. Flattened preparation from two individuals to show variations in the shape of the anticrista. Stained haematoxylin. (*c*) *O. macropus*.

FIGURE 5. Statocysts of five species of *Octopus* to show the anticrista, seen from the medial side except *bimaculoides*, which is lateral. Unstained preparations, in glycerine. (*a*) *O. maya*, 1675g; (*b*) *O. digueti*, 12.5g; (*c*) *O. bimaculoides*, 272g; (*d*) *O. briareus*, 771g; (*e*) *O. joubini*, 229g.

FIGURE 6. *Eledone cirrhosa* (Lamarck, 1798). Inner sac of statocyst seen from above, 360g.

FIGURE 7. (*a*, *b*) Anticristae from the statocysts of two individuals of *Eledone moschata* (Lamarck, 1798) stained haematoxylin.

FIGURE 8. *Argonauta argo* Linnaeus, 1758. Crista to show division into sections, also Kölliker's canal.

FIGURE 9. *Argonauta argo* outline drawings of statocyst. (*a*) From above; (*b*) dorsal–lateral to show position of the anticrista.

FIGURE 10. *Tremoctopus gelatus* Thomas, 1972. Statocyst seen from in front.

FIGURE 11. *Tremoctopus gelatus*. Flattened preparation of macula, crista and anticrista. Stained haematoxylin.

FIGURE 12. *Alloposus mollis* Verrill, 1880. Drawing of statocyst seen from above.

FIGURE 13. *Vitreledonella* Joubin, 1918. Anterior view.

FIGURE 14. *Vitreledonella*. Drawing of statocyst. (*a*) From above; (*b*) from in front.

FIGURE 15. *Vitreledonella*. Flattened preparation of macula and crista showing division into sections. Stained haematoxylin.

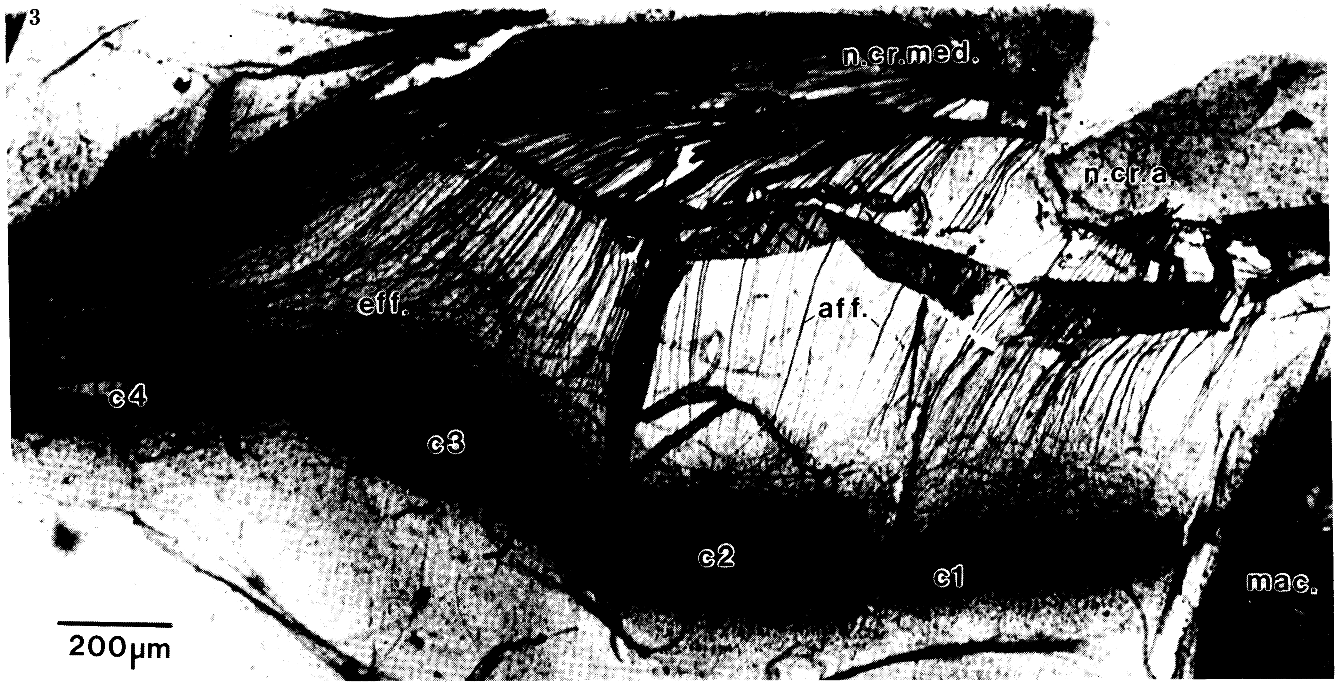
FIGURE 16. *Amphitretus* Hoyle, 1885. Flattened preparation of macula, crista and Kölliker's canal. Stained haematoxylin.

FIGURE 17. *Japetella diaphana* Hoyle, 1885. Central nervous system and statocyst, seen from above.

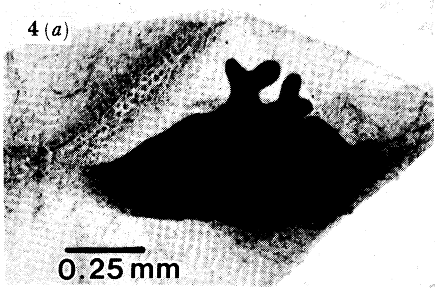
FIGURE 18. *Vampyroteuthis infernalis* Chun, 1903, 45 mm ML. (*a*) from in front; (*b*) from above.

FIGURE 19. *Vampyroteuthis*. Same animal as figure 18. (*a*) From above; (*b*) from in front.

3

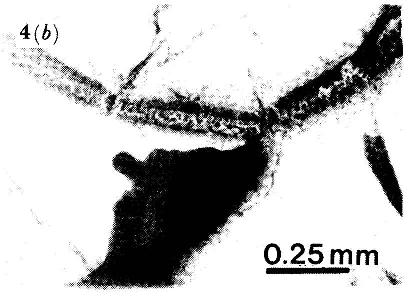


4(*a*)



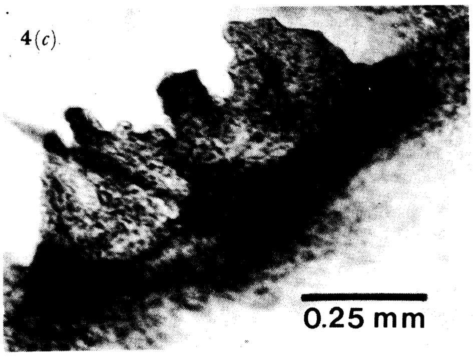
O. vulgaris

4(*b*)



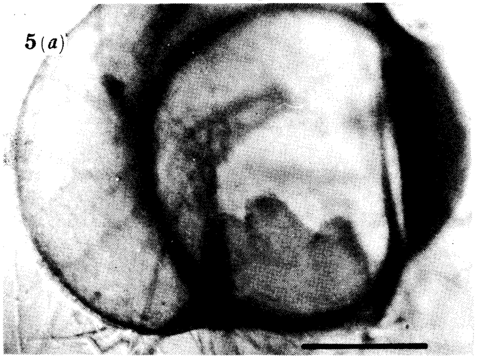
O. vulgaris

4(*c*)



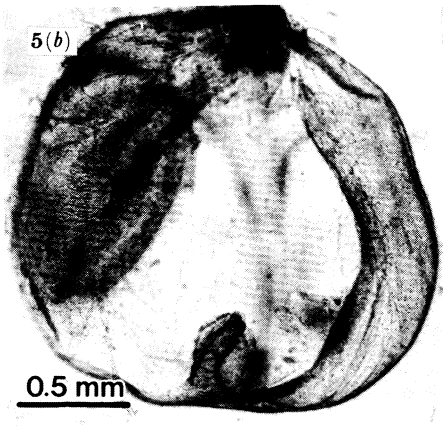
O. macropus

5(*a*)



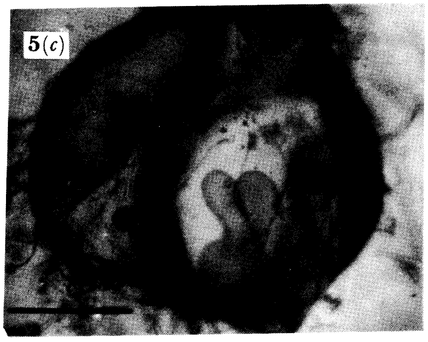
O. maya

5(*b*)



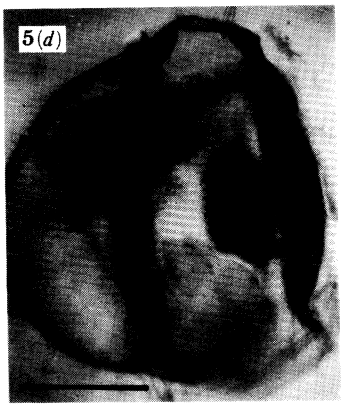
O. digueti

5(*c*)



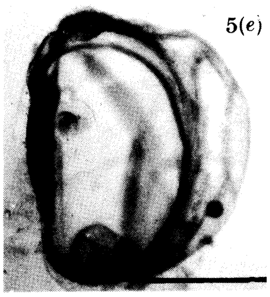
O. bimaculoides

5(*d*)



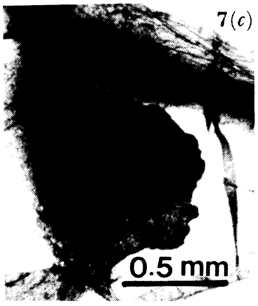
O. briareus

5(*e*)



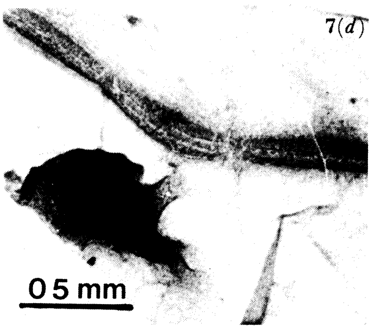
O. joubini

7(*c*)



E. moschata

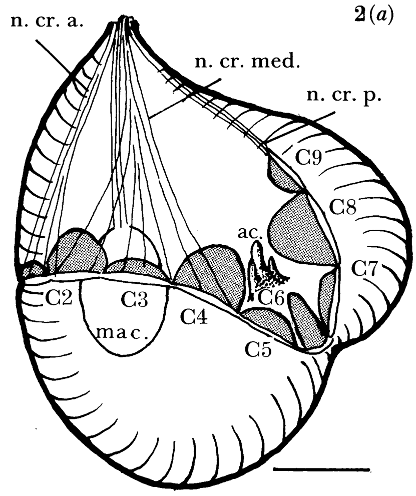
7(*d*)



E. cirrhosa

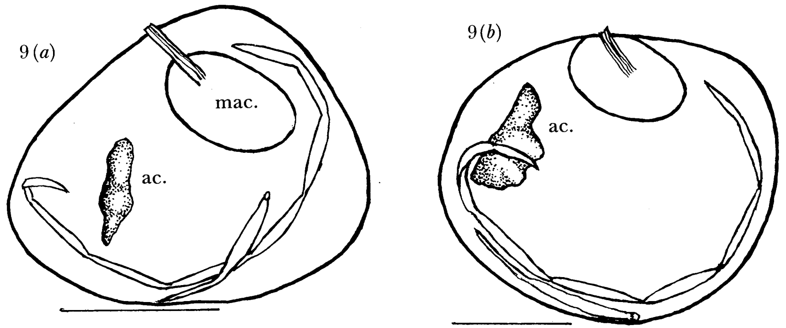
Figures 3–5 and 7. For description see opposite.

2(*a*)



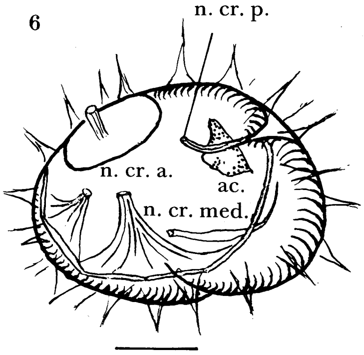
Octopus

9(*a*) 9(*b*)



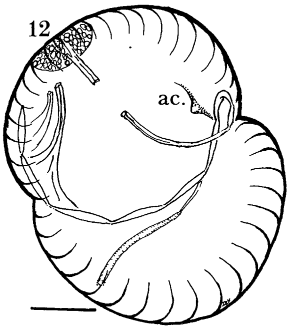
Argonauta

6



Eledone

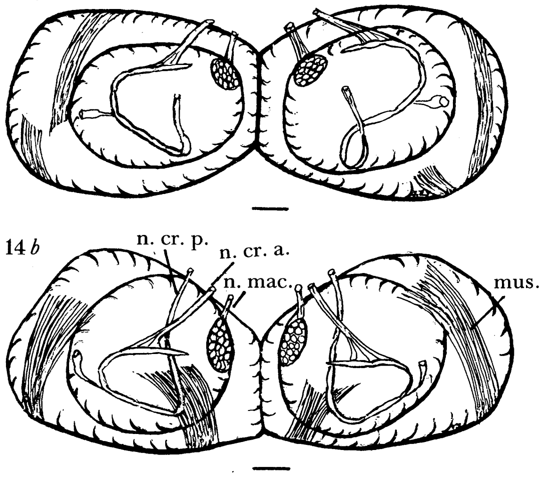
12



Alloposus

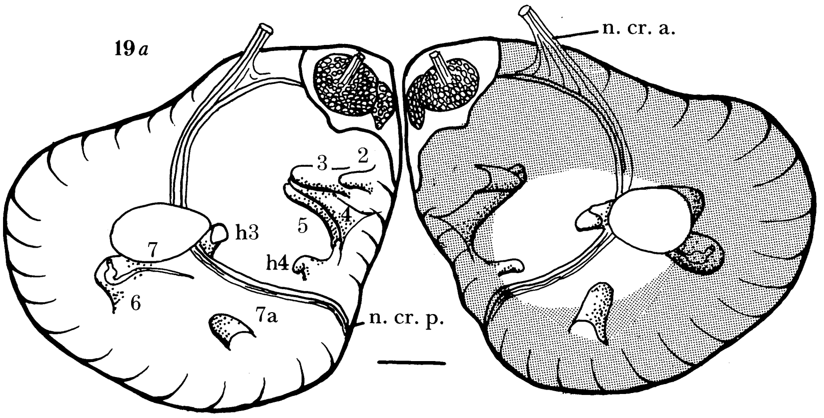
14 *a*

14 *b*

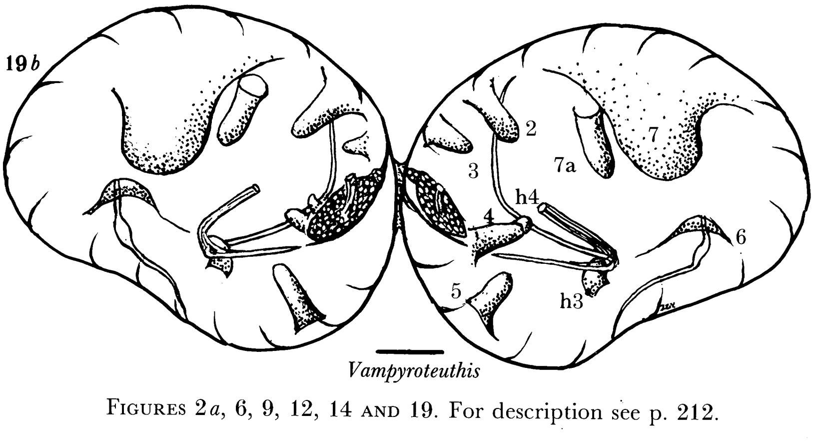


Vitreledonella

19 *a*



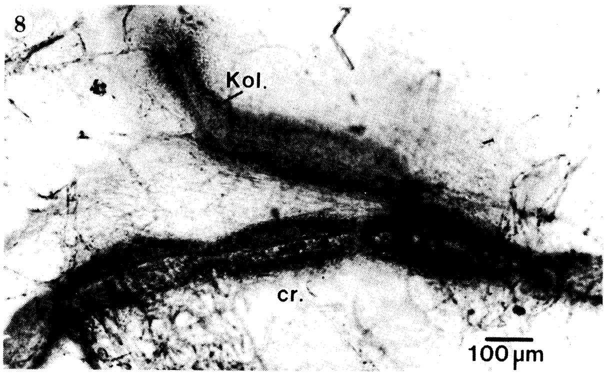
19 *b*



Vampyroteuthis

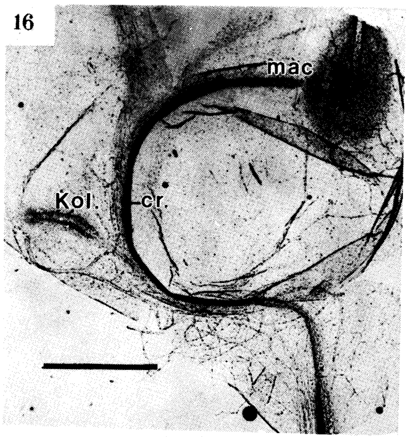
FIGURES 2*a*, 6, 9, 12, 14 AND 19. For description see p. 212.

8



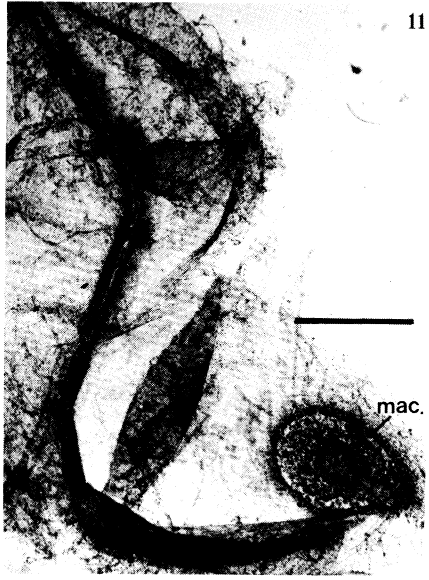
Argonauta

16



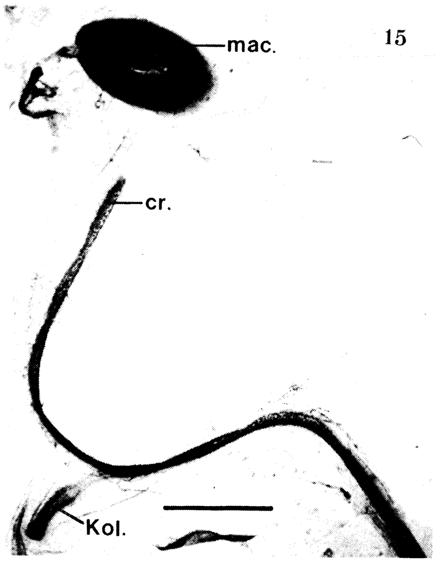
Amphitretus

11

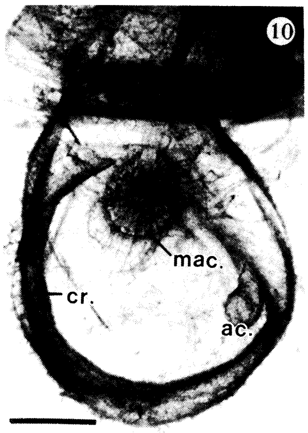


Tremoctopus

15

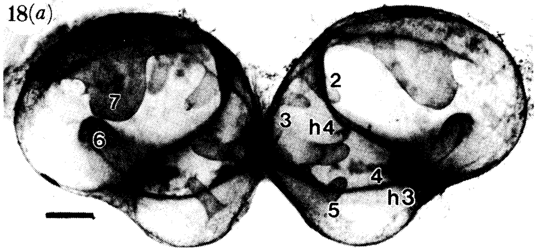


Vitreledonella

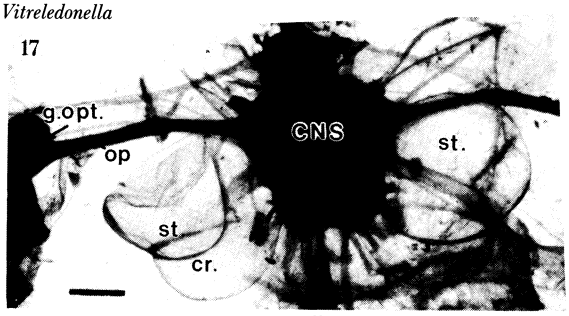


Tremoctopus

18(*a*)

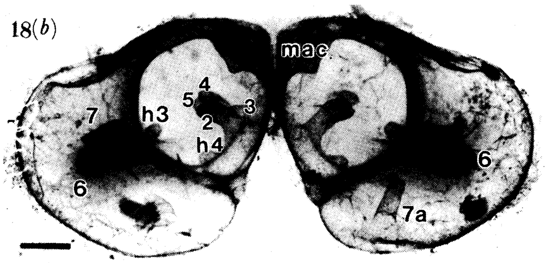


17



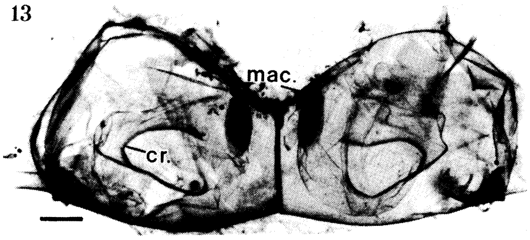
Japetella

18(*b*)



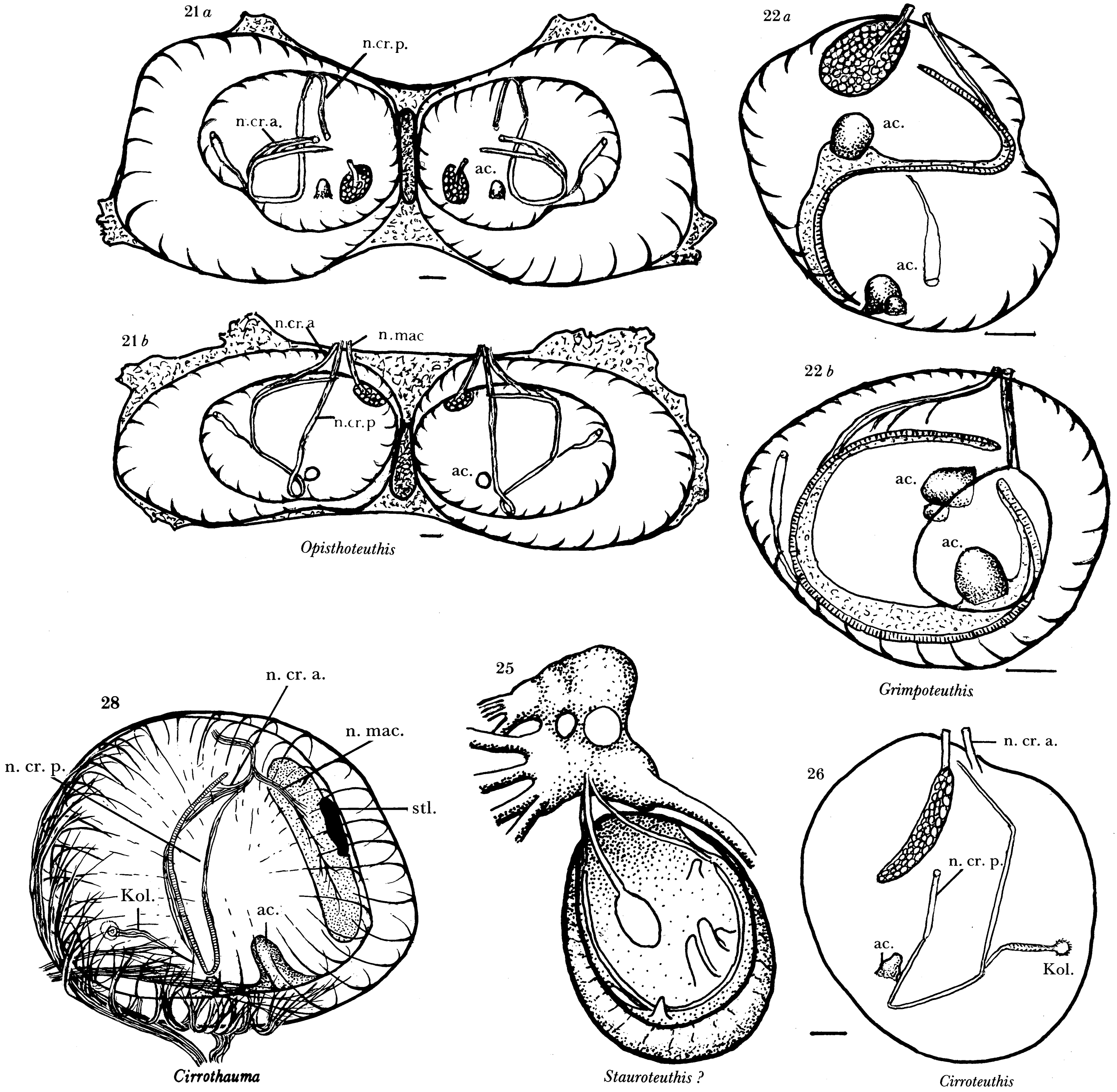
Vampyroteuthis

13



Vitreledonella

FIGURES 8, 10, 11, 13 AND 15–18. For description see p. 212.



Opisthoteuthis

Grimpoteuthis

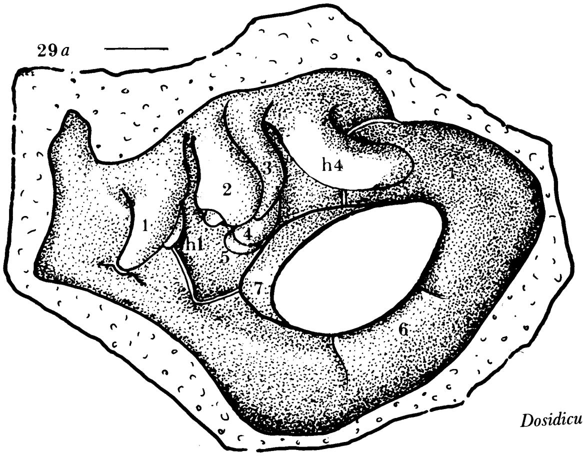
Cirrothauma

Stauroteuthis ?

Cirroteuthis

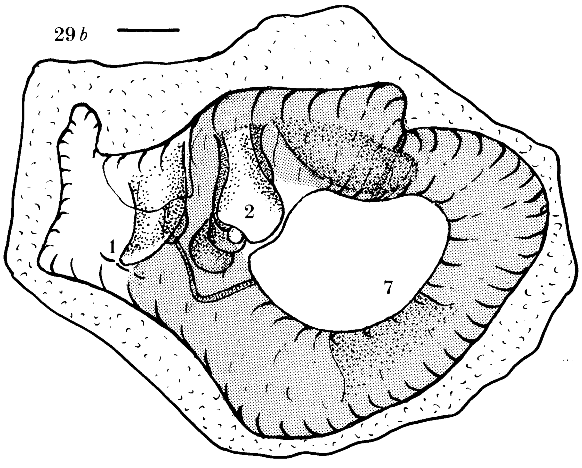
Figures 21, 22, 25, 26 and 28. For description see facing plate 3.

29 *a*

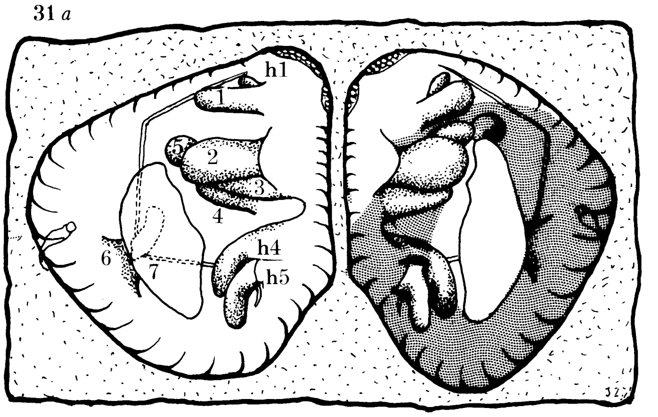


Dosidicus

29 *b*

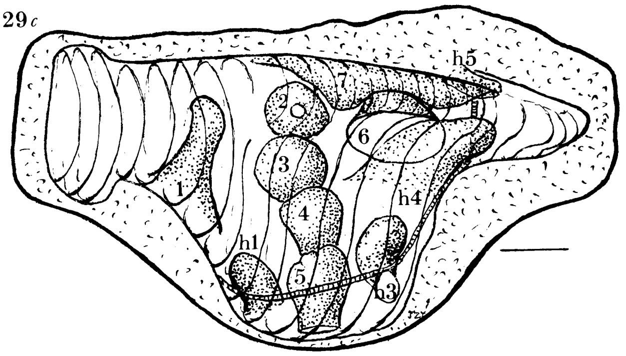


31 *a*



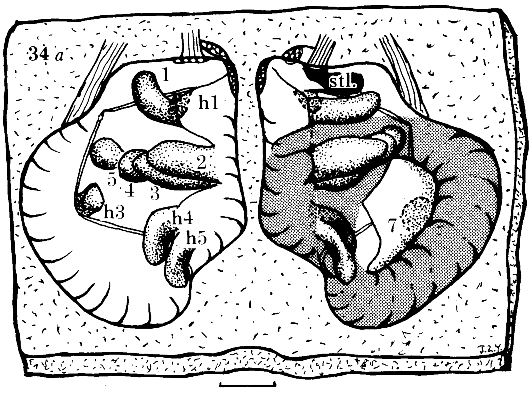
Ommastrephes

29 *c*

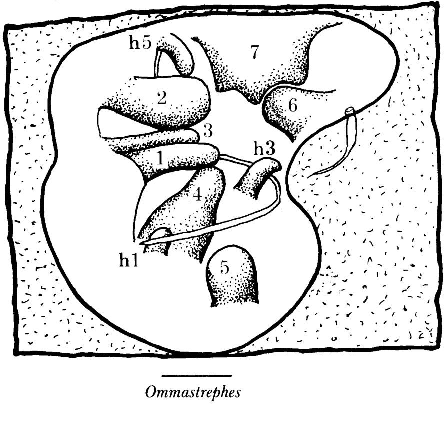


Dosidicus

34 *a*

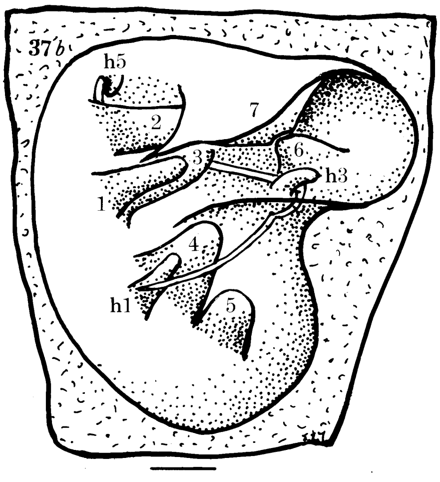


31 *b*



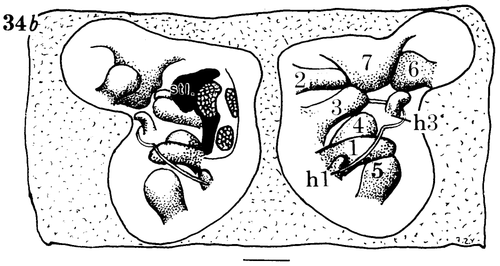
Ommastrephes

37 *b*



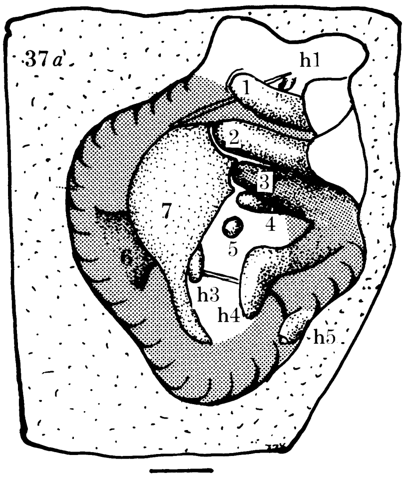
Todarodes

34 *b*



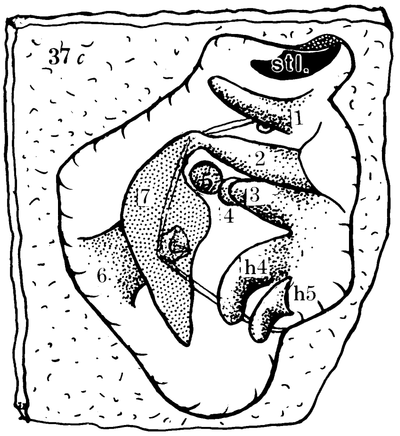
Illex

37 *a*



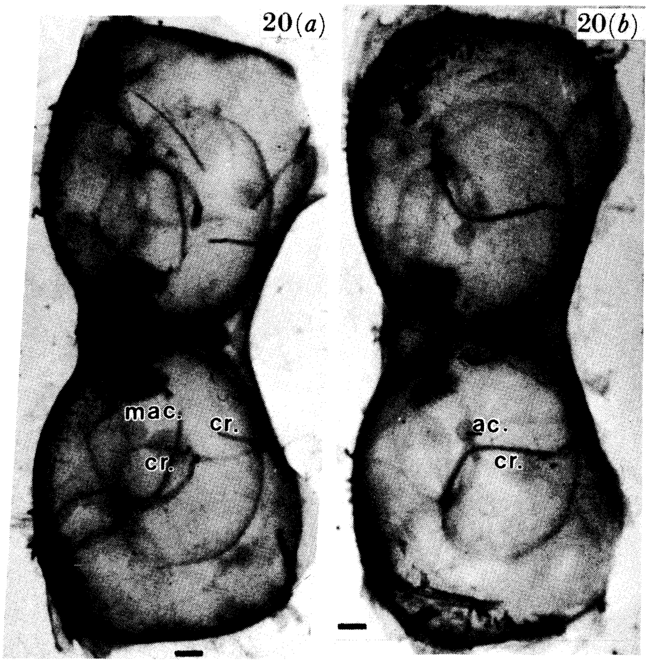
Todarodes

37 *c*

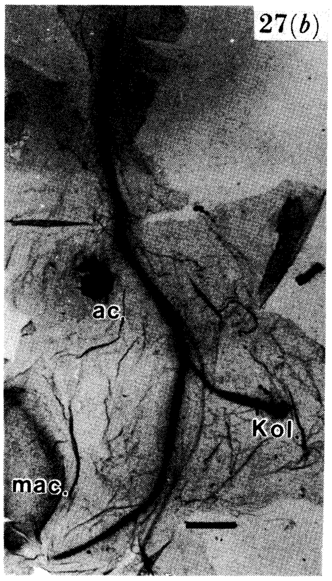


Todarodes

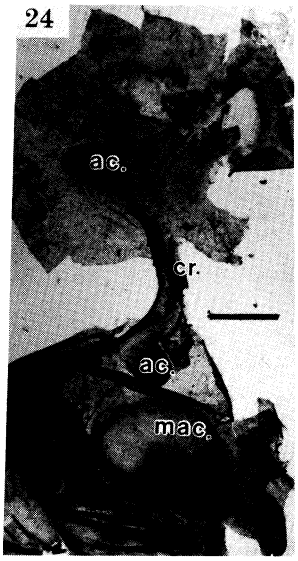
FIGURES 29, 31, 34 AND 37. For description see facing plate 3.



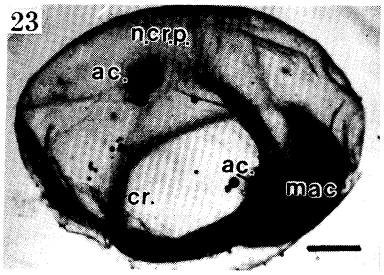
Opisthoteuthis



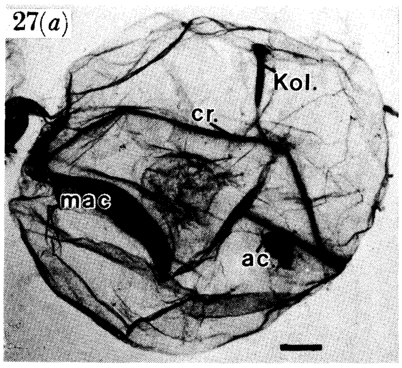
Cirroteuthis



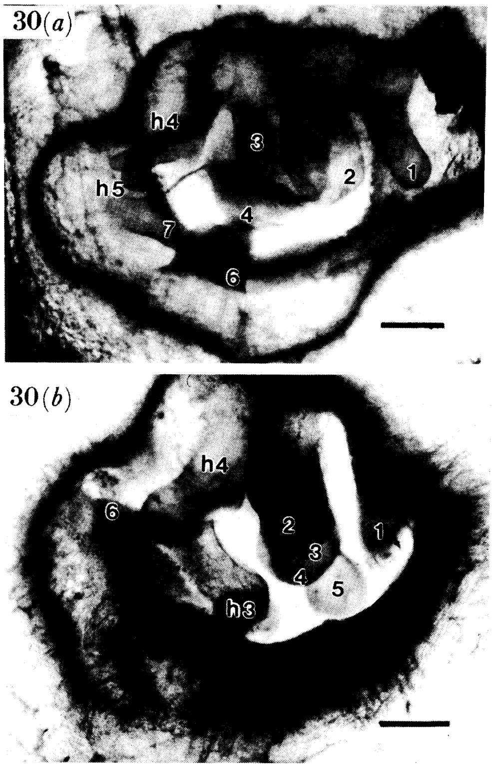
Grimpoteuthis



Grimpoteuthis

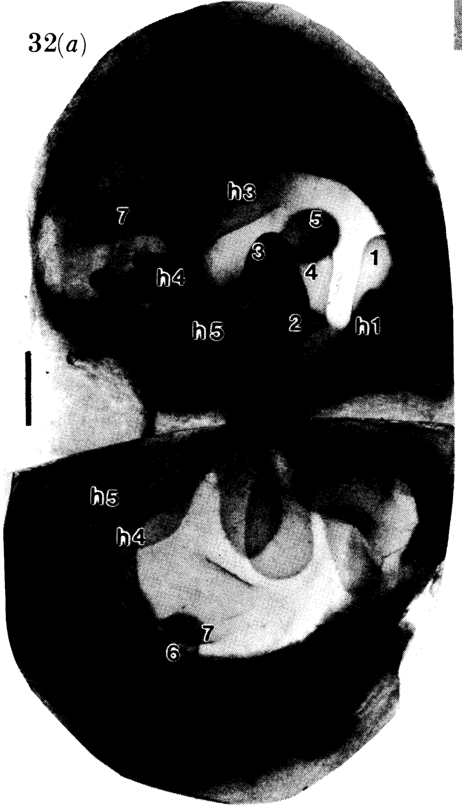


Cirroteuthis

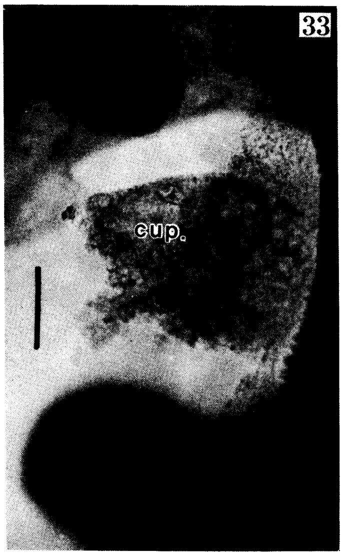


Dosidicus

32(a)

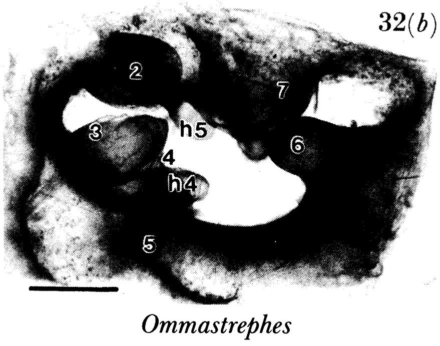


Ommastrephes



Ommastrephes

32(b)



Ommastrephes

FIGURES 20, 23, 24, 27, 30, 32 AND 33. For description see opposite.

DESCRIPTION OF FIGURES 20–34 AND 37.

FIGURE 20. *Opisthoteuthis* Verrill, 1883, 37 mm ML. (*a*) Anterior view; (*b*) posterior view.

FIGURE 21. *Opisthoteuthis*. Same animal as figure 20. (*a*) Dorsal view; (*b*) posterior view.

FIGURE 22. *Grimpoteuthis* Robson, 1931. 160 mm MM. (*a*) Dorsal view; (*b*) anterior view seen through the macula.

FIGURE 23. *Grimpoteuthis*. Same animal as figure 22, dorsolateral view.

FIGURE 24. *Grimpoteuthis*, flattened preparation of crista of the same animal (the smaller anticrista at the hind-end is hidden).

FIGURE 25. *Stauroteuthis*. Copy of the drawing of the statocyst by Ebersbach (1915), now presumed to belong to this genus (see text).

FIGURE 26. *Cirroteuthis*. Drawing of statocyst of same animal as figure 27.

FIGURE 27. *Cirroteuthis* Eschricht, 1838. 75 mm ML. (*a*) Lateral view, statocyst compressed; (*b*) flattened preparation of crista; note sharp turns but no division into shorter sections.

FIGURE 28. *Cirrothauma murrayi* Chun, 1911. 155 mm ML. Seen from medial side (after Aldred *et al.* 1984).

FIGURE 29. *Dosidicus gigas* (Orbigny, 1835). Specimen A, 1000 mm ML. (*a*, *b*) dorsal view, with horizontal canal shaded in (*b*). (*c*) Lateral view.

FIGURE 30. *Dosidicus gigas*. Dorsal views. (*a*) Specimen A; (*b*) specimen D, 410 mm ML.

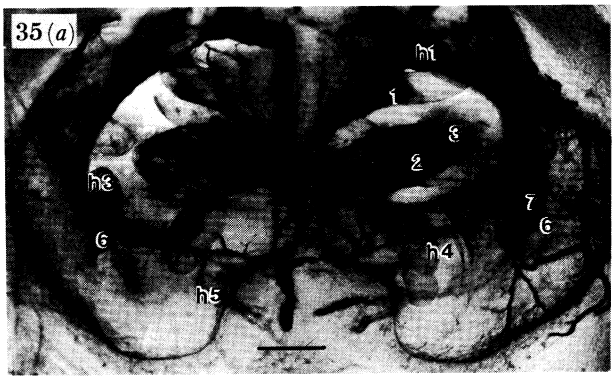
FIGURE 31. (*a*) *Ommastrephes caroli* Furtado, 1887. Dorsal view with the horizontal canal shaded on the right side. (*b*) Same specimen from in front, showing contact between anticristae 6 and 7 to make canal.

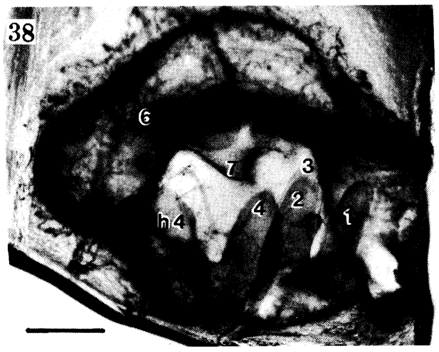
FIGURE 32. *Ommastrephes pteropus* Steenstrup, 1855. (*a*) From above; (*b*) from in front (after removal of the macula).

FIGURE 33. *O. pteropus*. Vertical crista with cupula.

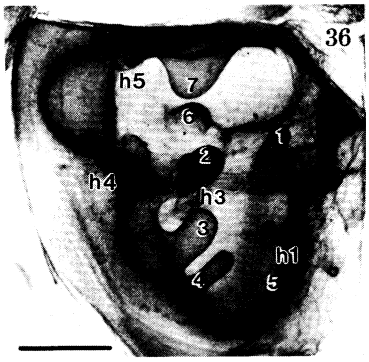
FIGURE 34. *Illex coindeti* (Vérany, 1837). Drawings from a specimen from Ischia of 270 mm ML. (*a*) From above; (*b*) from in front. Maculae removed on animal's left side.

FIGURE 37. *Todarodes sagittatus* (Lamarck, 1799). Drawings from a specimen of 325 mm ML from Banyuls. (*a*) dorsal view; (*b*) anterior view, with macula removed. (*c*) Another individual, 330 mm ML dorsal view showing union of anticristae 6 and 7.


35 (*a*)


38

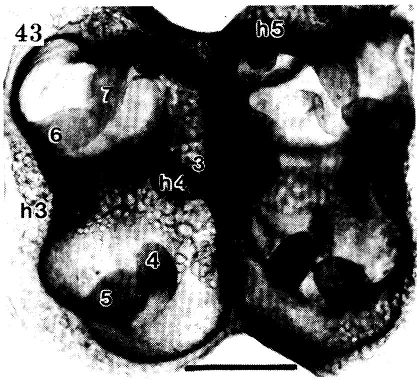
Todarodes


36

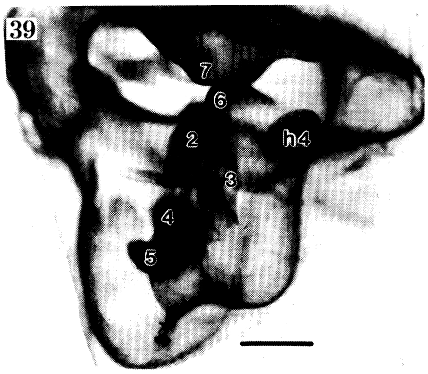
Illex


35 (*b*)

Illex

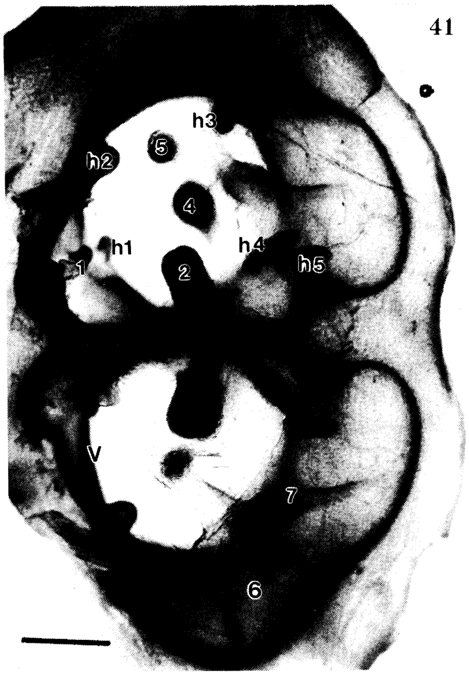

43

Enoploteuthis

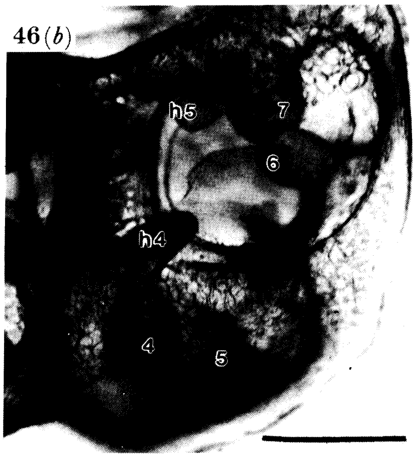

39

Todarodes

41

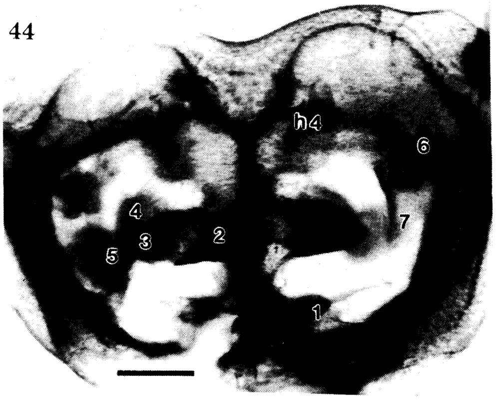


Thysanoteuthis

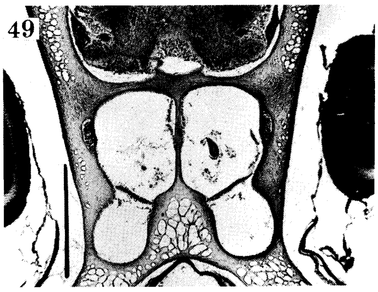

46 (*b*)

Abraliopsis

44

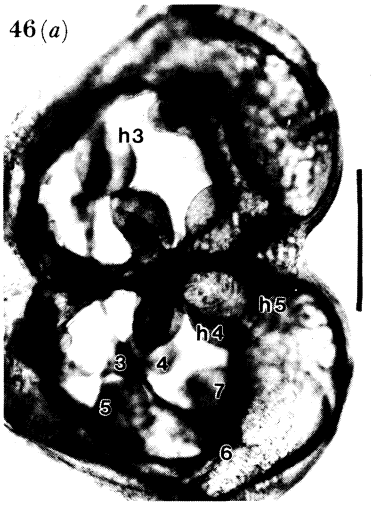


Enoploteuthis


49

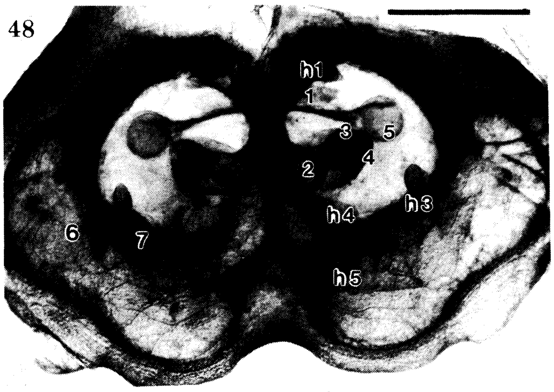
Onychoteuthis

46 (*a*)

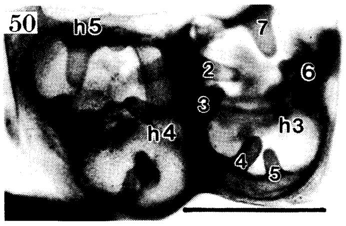


Abraliopsis

48



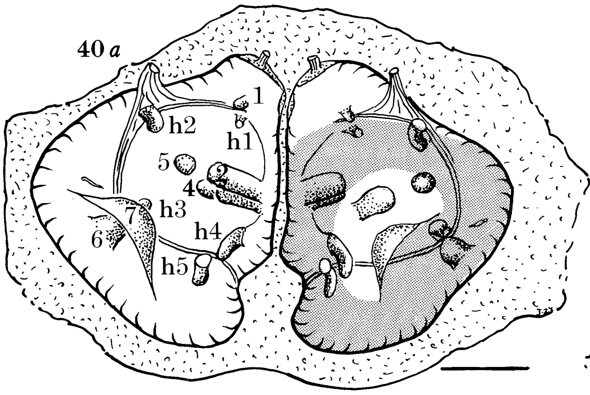
Onychoteuthis


50

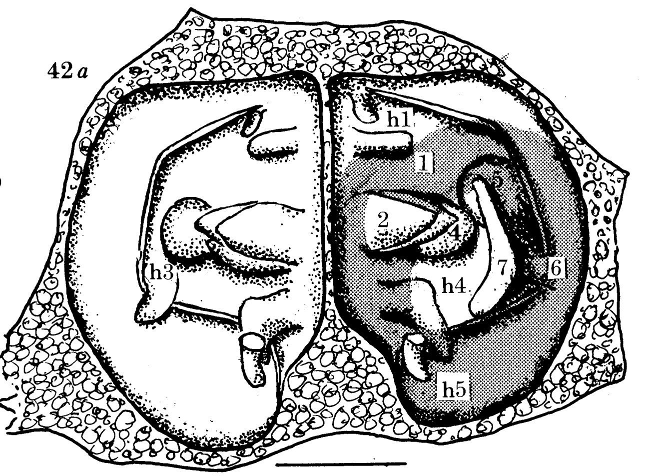
Onykia

FIGURES 35, 36, 38, 39, 41, 43, 44, 46 AND 48–50. For description see facing plate 5.

40 *a*

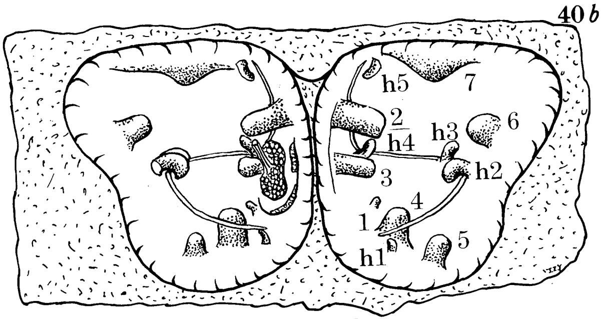


42 *a*



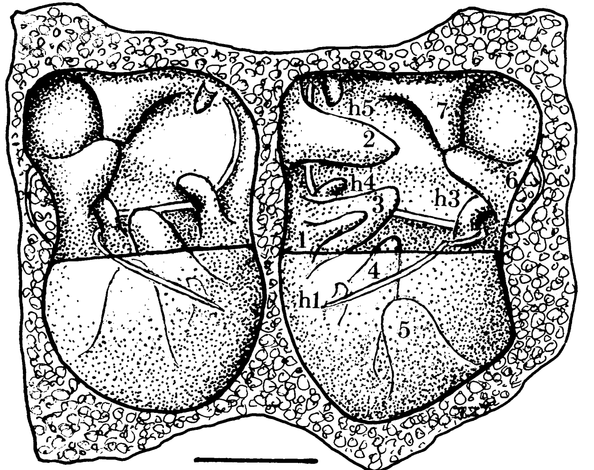
Enoploteuthis

40 *b*



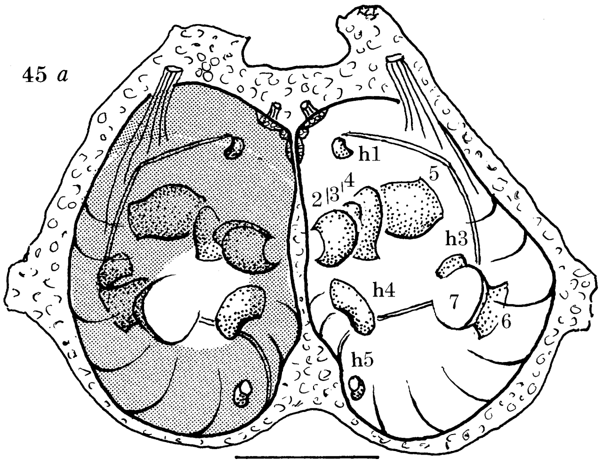
Thysanoteuthis

42 *b*



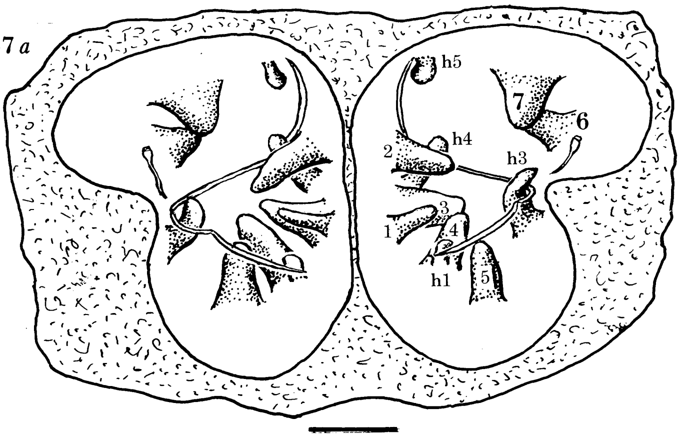
Enoploteuthis

45 *a*



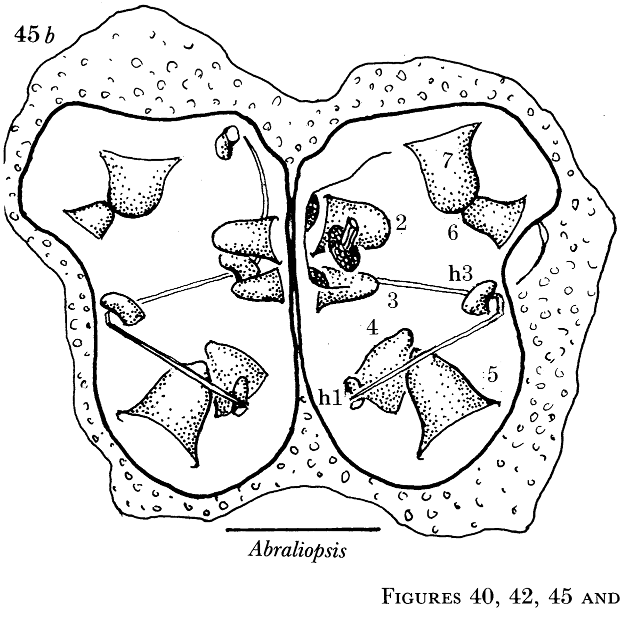
Abraliopsis

47 *a*



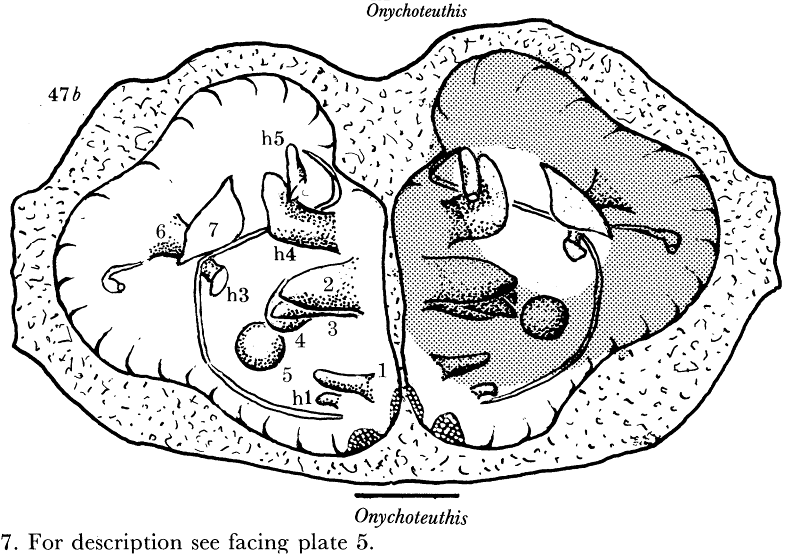
Onychoteuthis

45 *b*



Abraliopsis

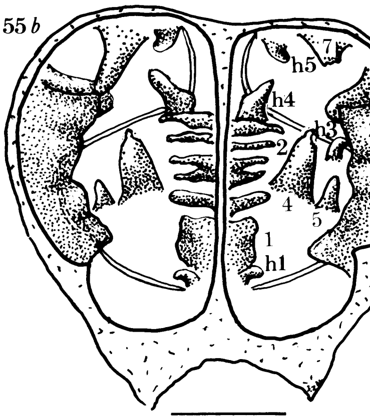
47 *b*



Onychoteuthis

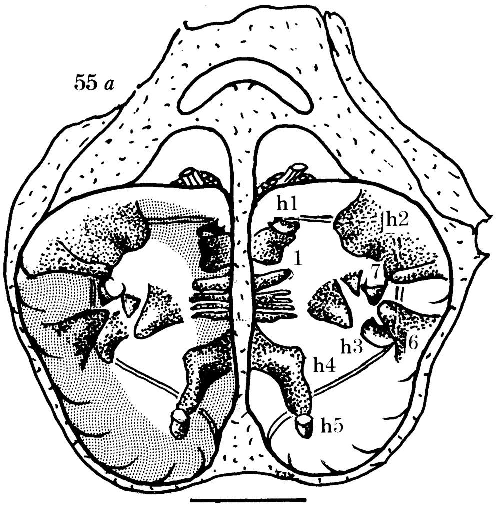
Figures 40, 42, 45 and 47. For description see facing plate 5.

55 *b*



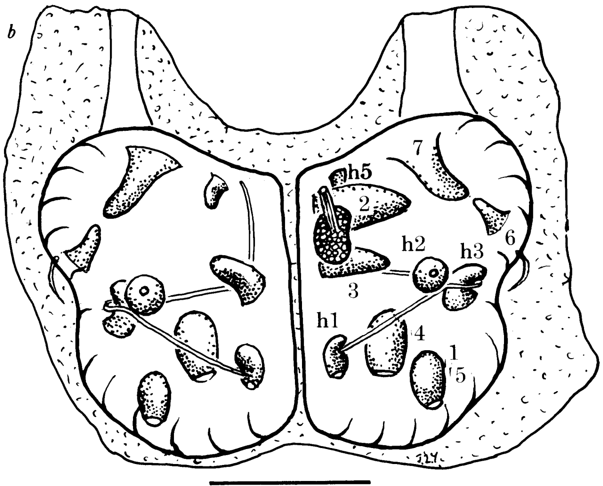
Ctenopteryx

55 *a*

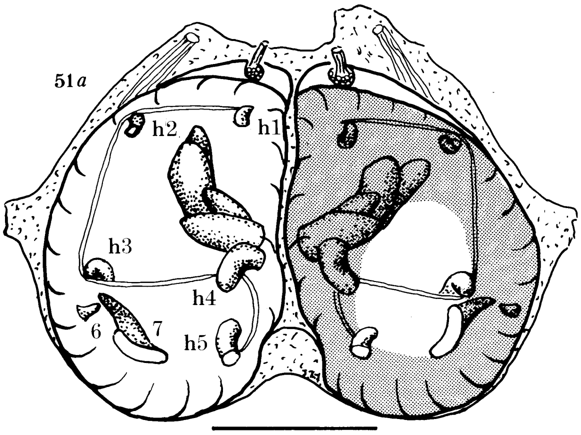


Ctenopteryx

51 *b*

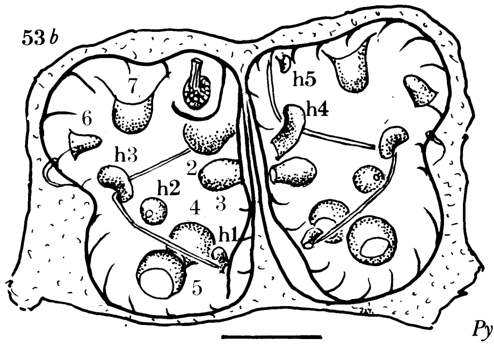


51 *a*

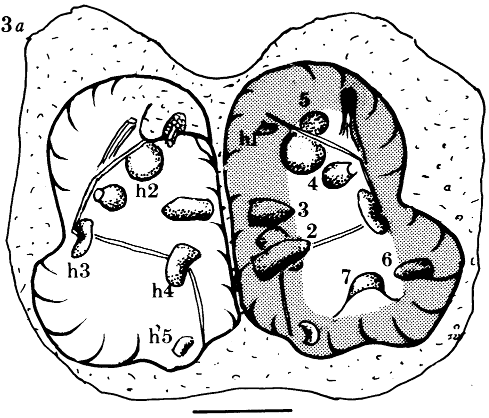


Pterygioteuthis

53 *b*

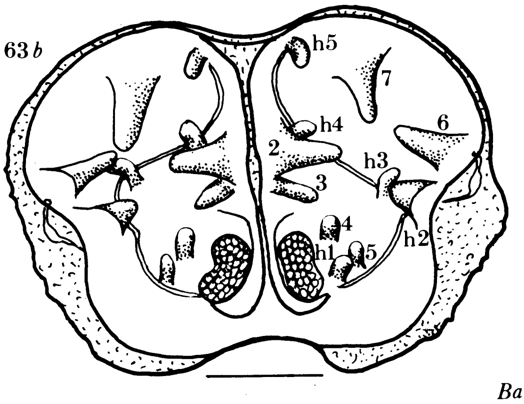


53 *a*

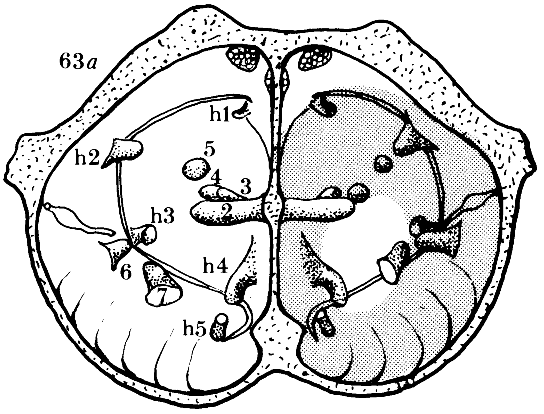


Pyroteuthis

63 *b*



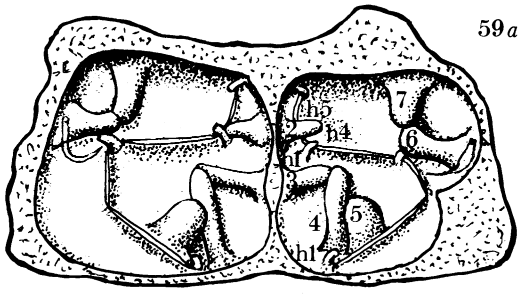
63 *a*



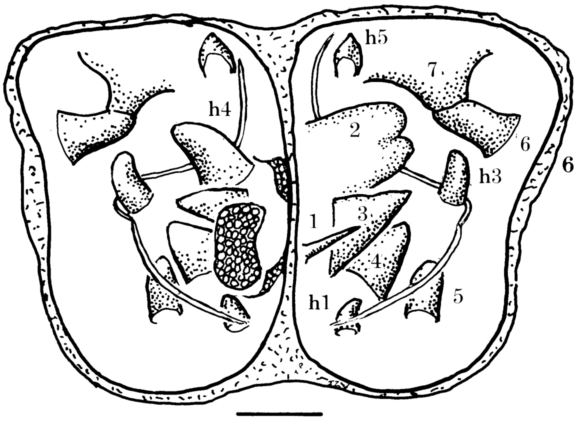
Bathyteuthis

FIGURES 51, 53, 55 AND 63. For description see facing plate 5.

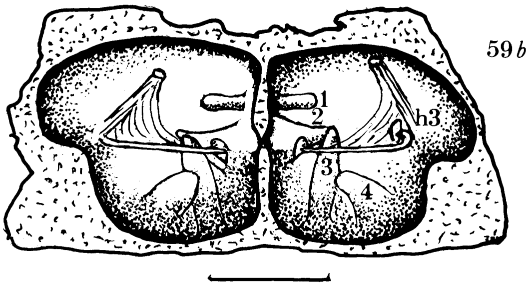
59*a*



61*b*

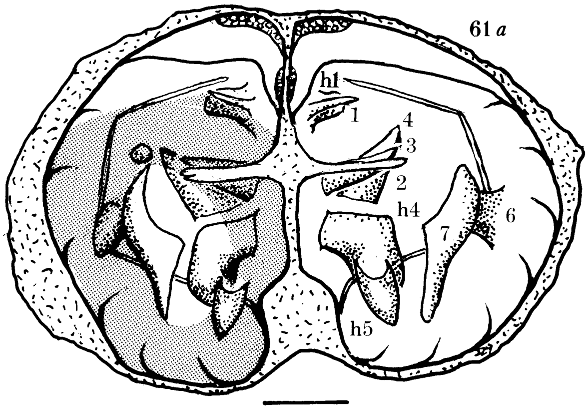


59*b*



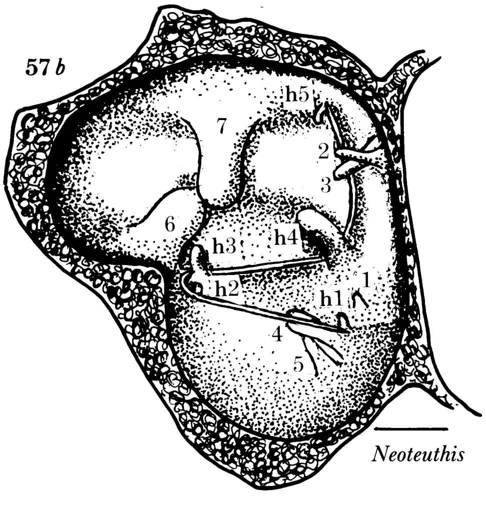
Brachioteuthis

61*a*



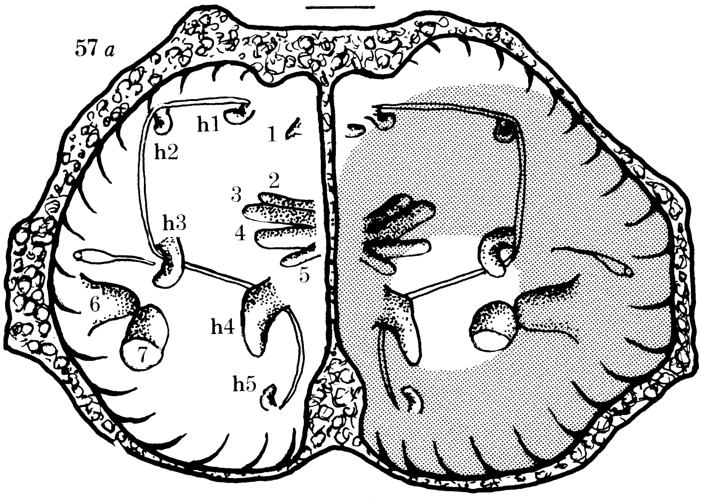
Lycoteuthis

57*b*



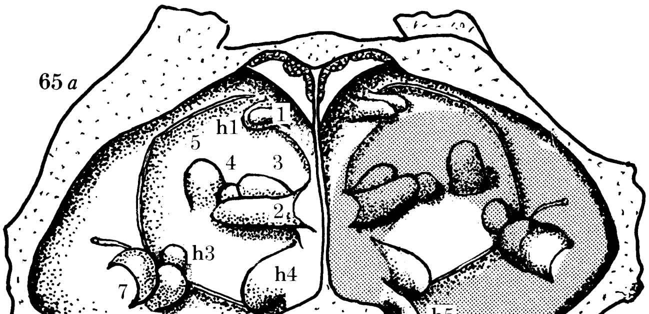
Neoteuthis

57*a*

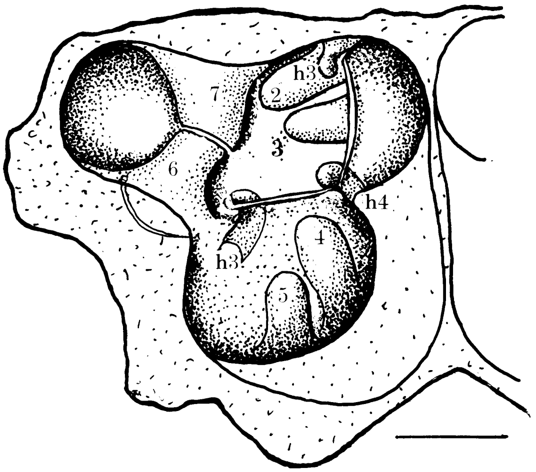


Neoteuthis

65*a*



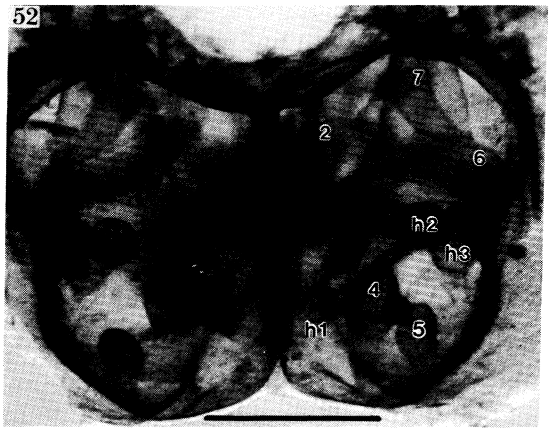
65*b*



Gonatus

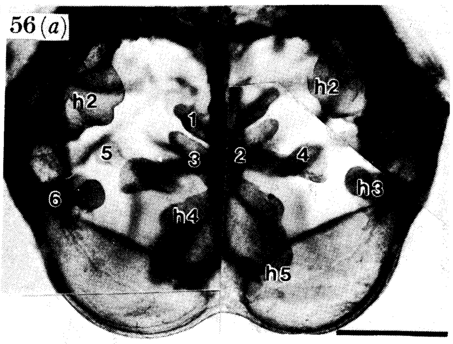
FIGURES 57, 59, 61 AND 65. For description see facing plate 5.

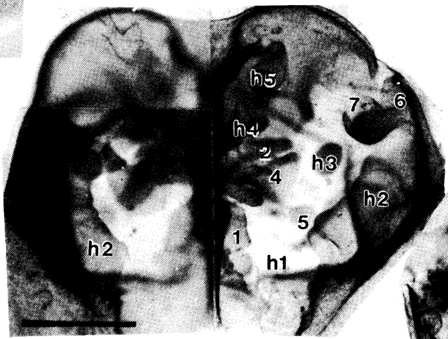
52



Pterygioteuthis

56(*a*)

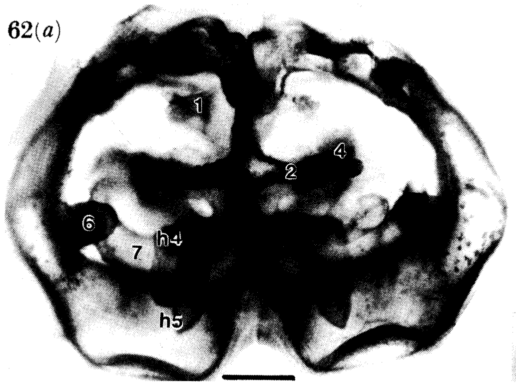




Ctenopteryx

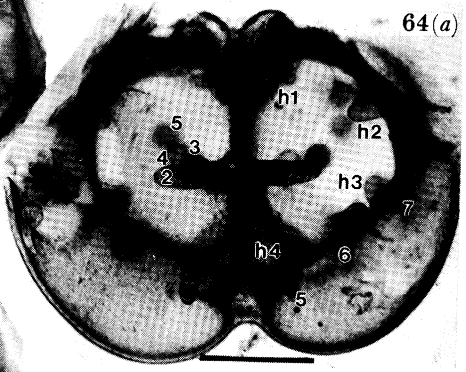
64(*b*)

62(*a*)



Lycoteuthis

64(*a*)



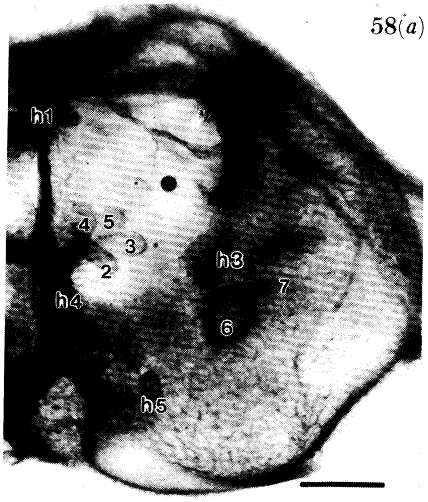
Bathyteuthis

60(*a*)

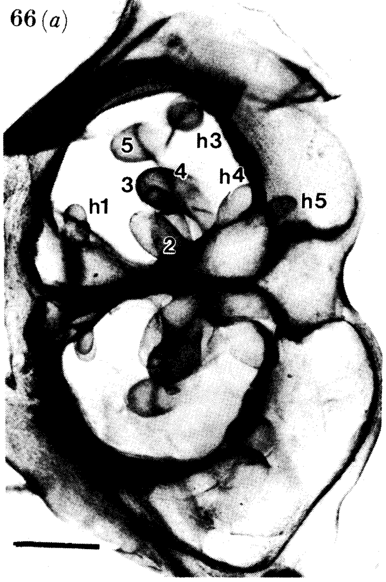
60(*b*)

Brachioteuthis

58(*a*)

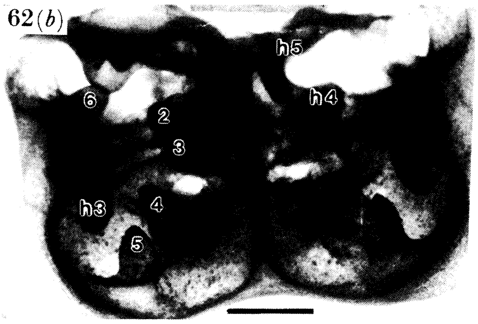


66(*a*)



Gonatus

62(*b*)

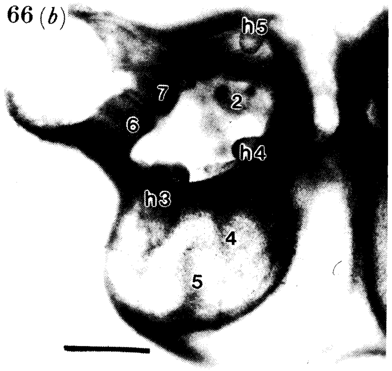


Lycoteuthis

58(*b*)

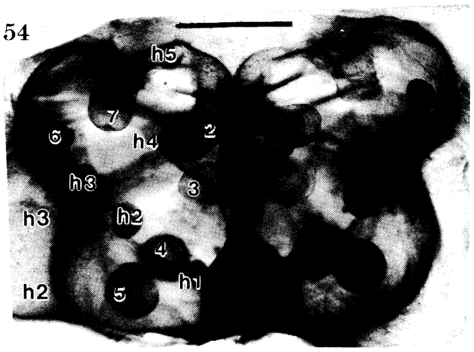
Neoteuthis

66 (*b*)



Gonatus

54



Pyroteuthis

FIGURES 52, 54, 56, 58, 60, 62, 64 AND 66. For description see opposite.

DESCRIPTION OF FIGURES 35, 36 AND 38–66.

FIGURE 35. *Illex coindeti.* Same specimen as figure 34. (*a*) From above; (*b*) from the front; statolith and anticrista 1 present on right side of animal (see figure 34*b*).

FIGURE 36. *I. coindeti.* Lateral view; 95 mm ML.

FIGURE 38. *Todarodes sagittatus.* Dorsal view of statocyst from an individual of 325 mm ML.

FIGURE 39. *Todarodes sagittatus.* Lateral view of specimen of 460 mm ML.

FIGURE 40. *Thysanoteuthis rhombus* Troschel, 1857. Drawings from specimen of 800 mm ML. (*a*) Dorsal views; (*b*) anterior view.

FIGURE 41. *Thysanoteuthis rhombus.* Dorsal view of the specimen of figure 40.

FIGURE 42. *Enoploteuthis leptura* (Leach, 1817). Drawings from a specimen of 69 mm ML. (*a*) Dorsal view; (*b*) anterior view.

FIGURE 43. *Enoploteuthis leptura.* Same specimen as figure 42. Anterior view.

FIGURE 44. *Enoploteuthis anapsis* (Roper, 1964). Anterior dorsal view; 39 mm ML.

FIGURE 45. *Abraliopsis morrisi* (Véranyi, 1837). Drawing of a specimen of 39 mm ML. (*a*) Dorsal view; (*b*) anterior view.

FIGURE 46. *Abraliopsis morrisi.* Specimen of figure 45. (*a*) Dorsal view; (*b*) posterior views.

FIGURE 47. *Onychoteuthis banksii* (Leach, 1817). Drawings from specimen of 130 mm ML. (*a*) Dorsal view; (*b*) anterior view.

FIGURE 48. *Onychoteuthis banksii.* Specimen of figure 47, dorsal view.

FIGURE 49. *Onychoteuthis banksii.* Transverse section at the front of the statocyst to show the large cavity below the first section of the crista.

FIGURE 50. *Onykia caribboea* Le Sueur, 1821. Anterior view; 20 mm ML.

FIGURE 51. *Pterygioteuthis giardi* Fischer, 1896. (*a*) Dorsal view; (*b*) anterior view.

FIGURE 52. *Pterygioteuthis.* Same specimen as figure 51. Anterior view.

FIGURE 53. *Pyroteuthis margaritifera* (Rüppell, 1844). (*a*) Dorsal view; (*b*) anterior view; 42 mm ML.

FIGURE 54. *Pyroteuthis.* Same specimen as figure 53. Dorsal view.

FIGURE 55. *Ctenopteryx sicula* (Véranyi, 1851). (*a*) Dorsal view; (*b*) oblique anterior view; 36 mm ML.

FIGURE 56. *Ctenopteryx.* Same specimen as figure 55. (*a*) Dorsal view; (*b*) oblique anterior view showing large h_2.

FIGURE 57. *Neoteuthis* Naef, 1921. (*a*) Dorsal view; (*b*) anterior view; 104 mm ML.

FIGURE 58. *Neoteuthis.* Same specimen; (*a*) dorsal view; (*b*) anterior view.

FIGURE 59. *Brachioteuthis* Verrill, 1881. (*a*) Dorsal view (tilted backwards); (*b*) anterior view; 52 mm ML.

FIGURE 60. *Brachioteuthis.* Same specimen as figure 59. (*a*) Anterior view; (*b*) posterior view.

FIGURE 61. *Lycoteuthis diadema* (Chun, 1900). (*a*) Dorsal view, anticrista 6 removed on right side of animal; (*b*) anterior view, anticrista 2 omitted on right side of animal; 80 mm ML.

FIGURE 62. *Lycoteuthis.* Same specimen. (*a*) Dorsal view; (*b*) anterior view.

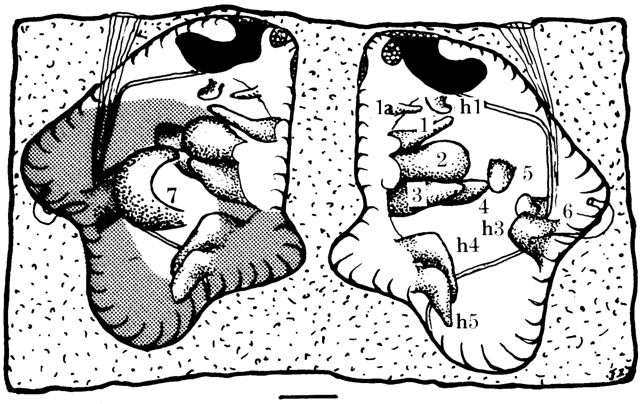
FIGURE 63. *Bathyteuthis abyssicola* Hoyle, 1855. (*a*) Dorsal view; (*b*) anterior view.

FIGURE 64. *Bathyteuthis.* Same specimen as figure 63. (*a*) Dorsal view; (*b*) anterior view (tipped forward).

FIGURE 65. *Gonatus steenstrupi* Kristensen, 1981. (*a*) Dorsal view; (*b*) view from behind; 110 ML.

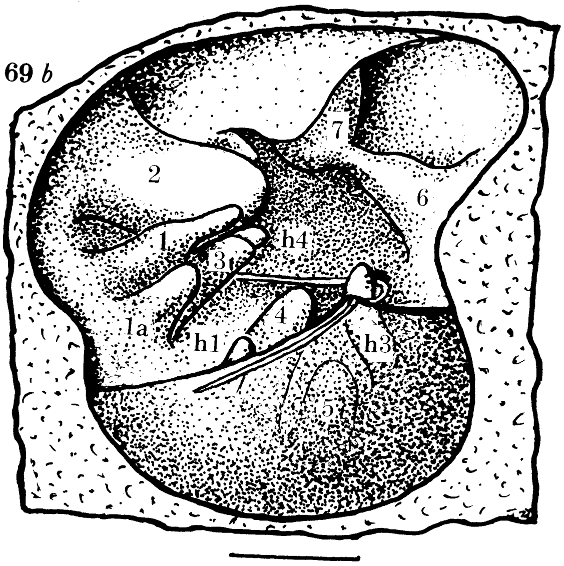
FIGURE 66. *Gonatus.* Same specimen as figure 65. (*a*) Dorsal view; (*b*) anterior view.

67



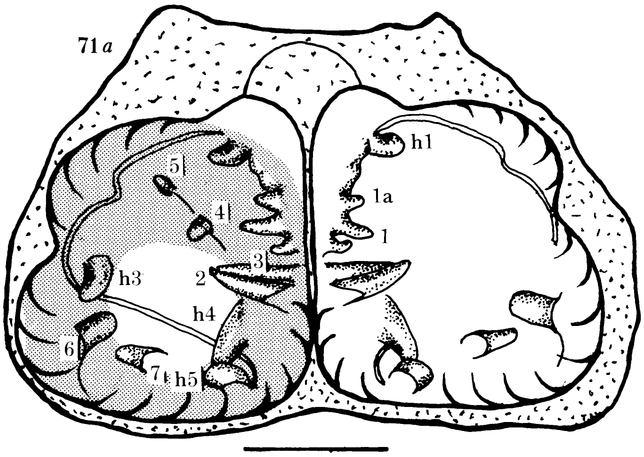
Loligo

69 *b*



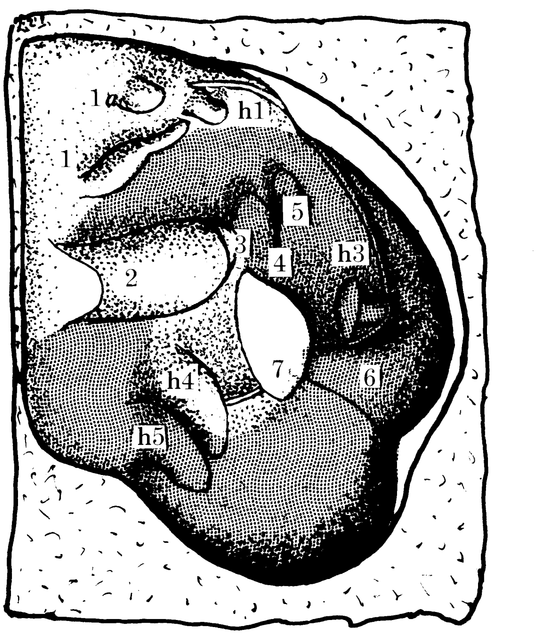
Sepioteuthis

71 *a*



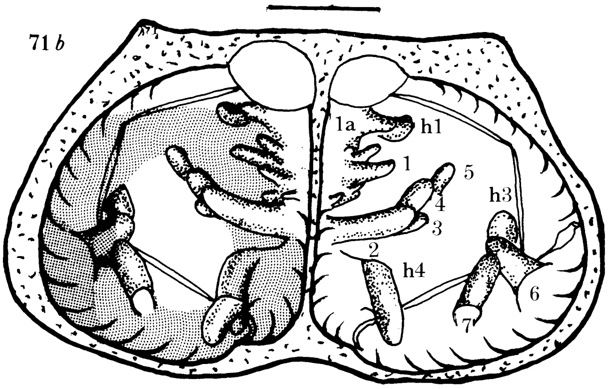
Alloteuthis

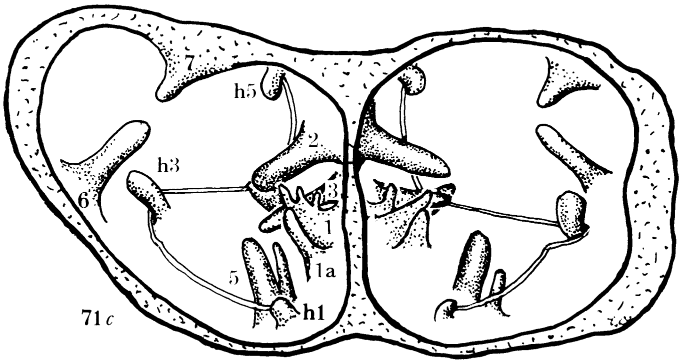
69 *a*



Sepioteuthis

71 *b*

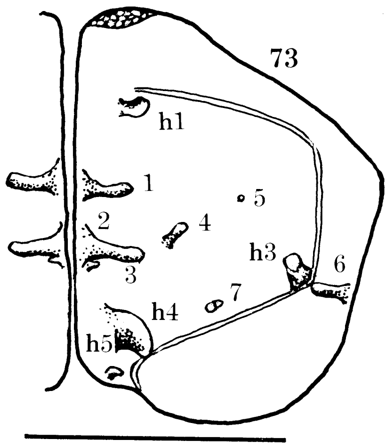




71 *c*

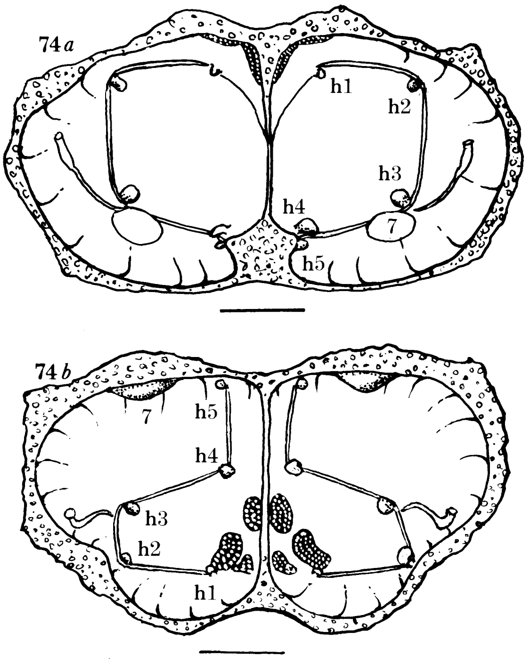
Alloteuthis

73

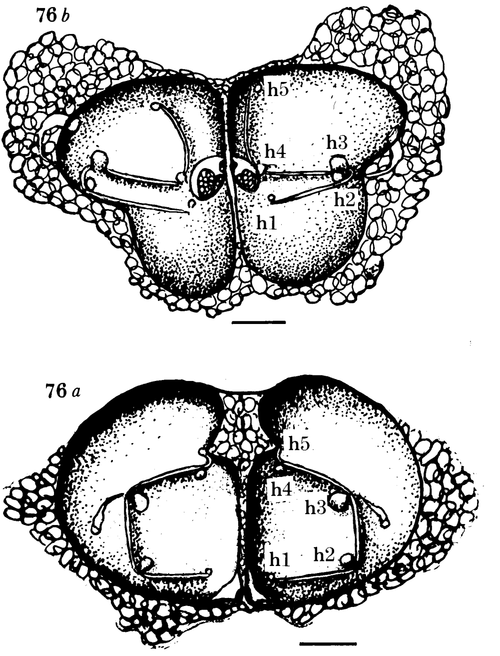


Pickfordiateuthis

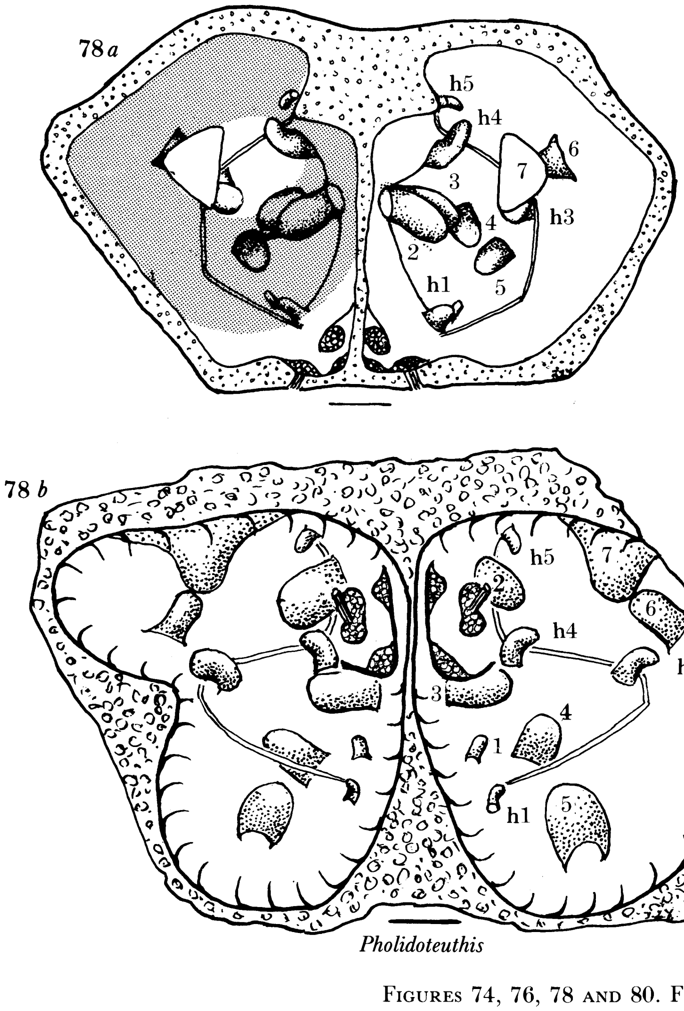
FIGURES 67, 69, 71 AND 73. For description see facing plate 6.



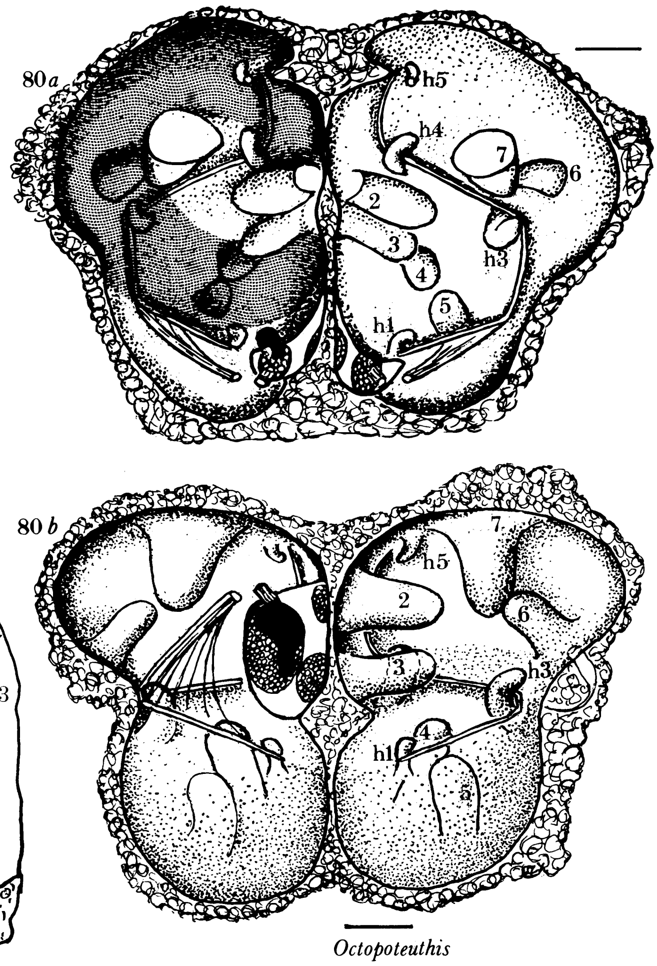
Joubiniteuthis



Grimalditeuthis

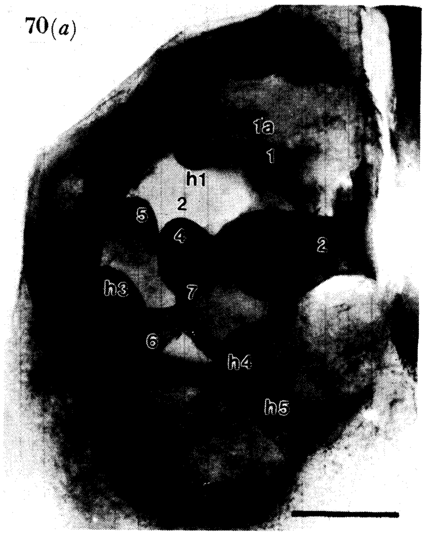


Pholidoteuthis

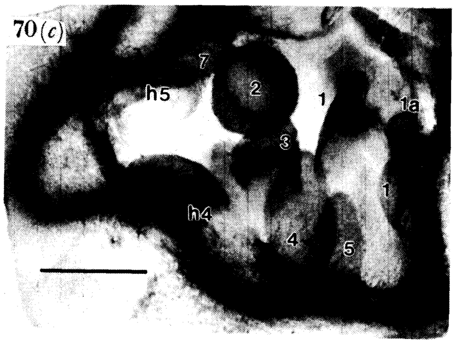


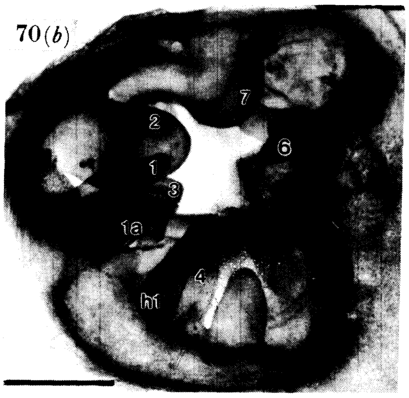
Octopoteuthis

Figures 74, 76, 78 and 80. For description see facing plate 6.

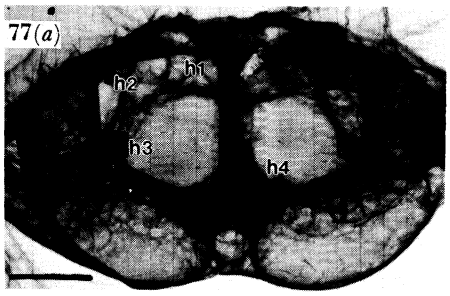


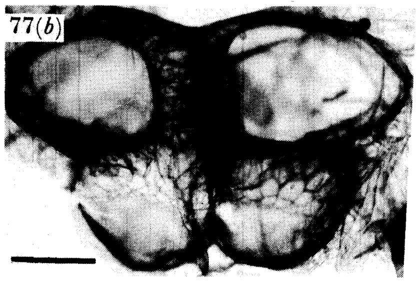
Sepioteuthis



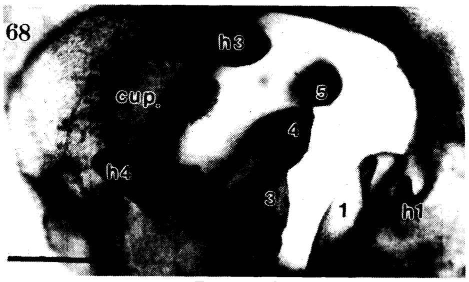


Sepioteuthis

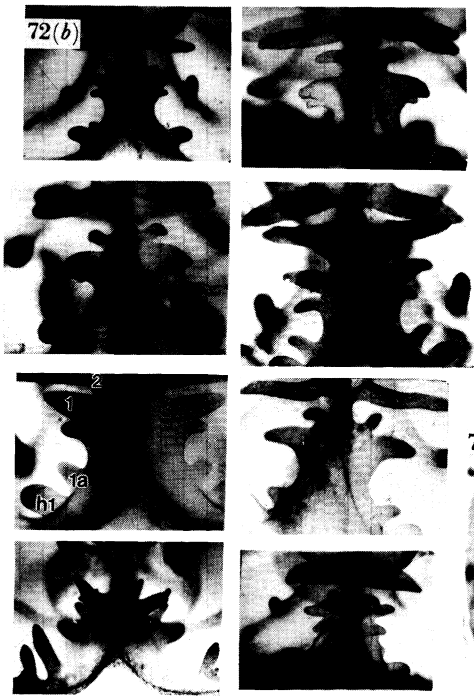




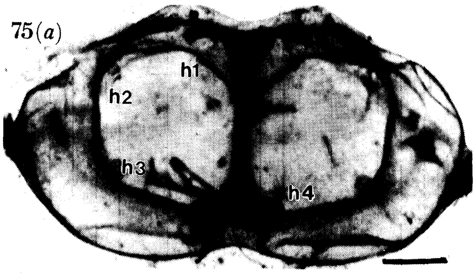
Grimalditeuthis

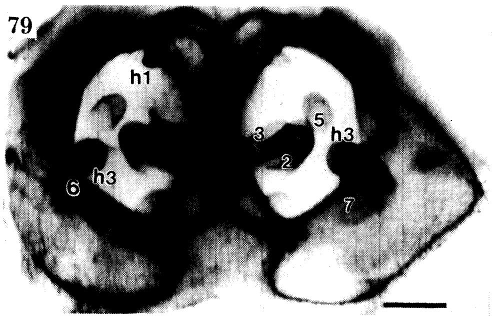


Doryteuthis

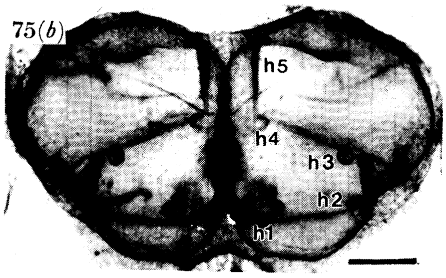


Alloteuthis

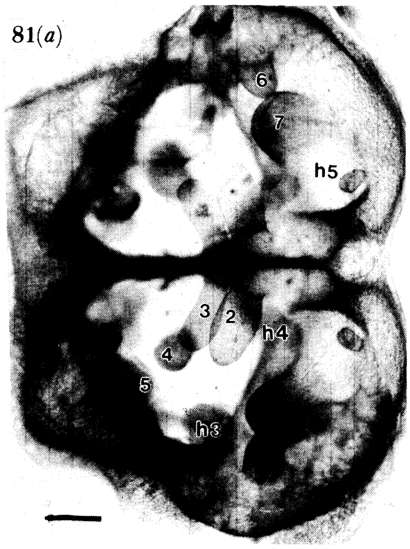




Pholidoteuthis

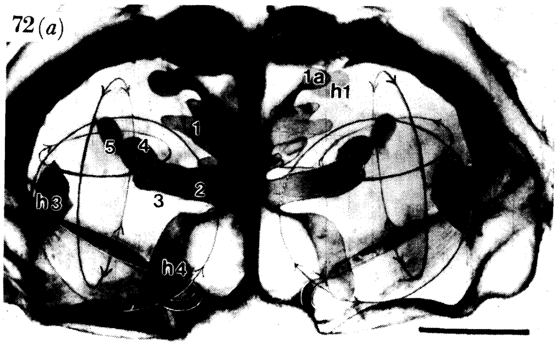


Joubiniteuthis



Octopoteuthis

Octopoteuthis



Alloteuthis

FIGURES 68, 70, 72, 75, 77, 79 AND 81. For description see opposite.

Description of figures 67–81.

Figure 67. *Loligo forbesi* Steenstrup, 1856. Dorsal view; 50 mm ML.

Figure 68. *Doryteuthis plei* Blainville, 1923. Dorsal view, showing cupula on posterior transverse crista.

Figure 69. *Sepioteuthis sepioidea* (Blainville, 1923). (*a*) Dorsal view; (*b*) anterior view; 150 mm ML.

Figure 70. *Sepioteuthis*. (*a*) Dorsal view; 150 mm ML, (*b*) same specimen as figure 73, anterior view; (*c*) view from medial side.

Figure 71. *Alloteuthis media* (Linnaeus, 1758). (*a*, *b*) Dorsal views; (*a*) 45 mm ML; (*b*) 105 mm ML; (*c*) anterior view, 70 mm ML.

Figure 72. (*a*) *Alloteuthis media*. Dorsal view; 105 mm ML. Arrows show the presumed direction of endolymph movement in the three planes. (*b*) *Alloteuthis media*. Anticristae 1 and 1a from eight specimens to show the variations and the symmetry on the two sides.

Figure 73. *Pickfordiateuthis pulchella* Voss, 1953. Drawing of statocyst seen from above; 21 mm ML.

Figure 74. *Joubiniteuthis portieri* Berry, 1920. (*a*) Dorsal view; (*b*) anterior view. 36 mm ML.

Figure 75. *Joubiniteuthis*. Same animal as figure 74. (*a*) Dorsal view; (*b*) anterior view.

Figure 76. *Grimalditeuthis bonplandi* (Véranyi, 1837). (*a*) Dorsal view; (*b*) anterior view; 67 mm ML.

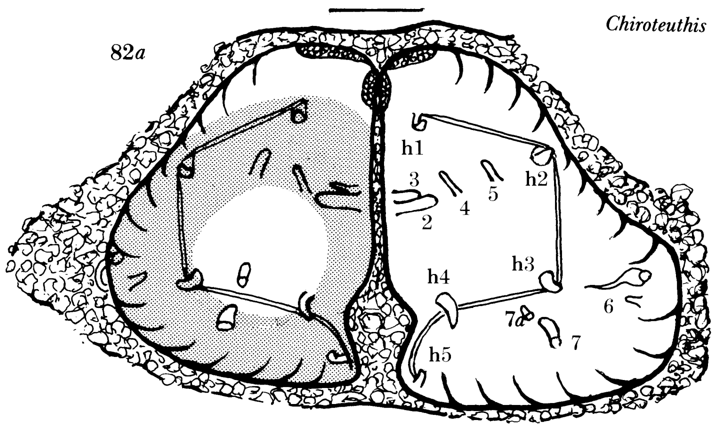
Figure 77. *Grimalditeuthis*. Same animal as figure 76. (*a*) Dorsal view; (*b*) anterior view.

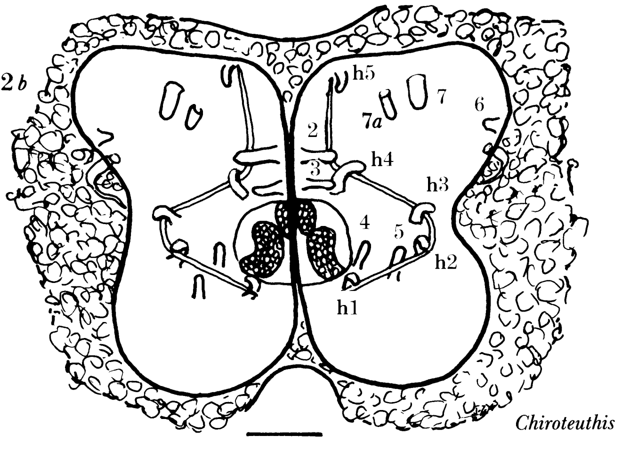
Figure 78. *Pholidoteuthis boschmai* Adam, 1950. (*a*) Dorsal view; (*b*) anterior view; 460 mm ML.

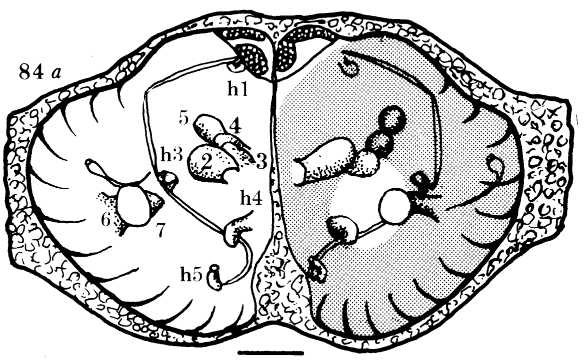
Figure 79. *Pholidoteuthis*. Same specimen as figure 78. Dorsal view.

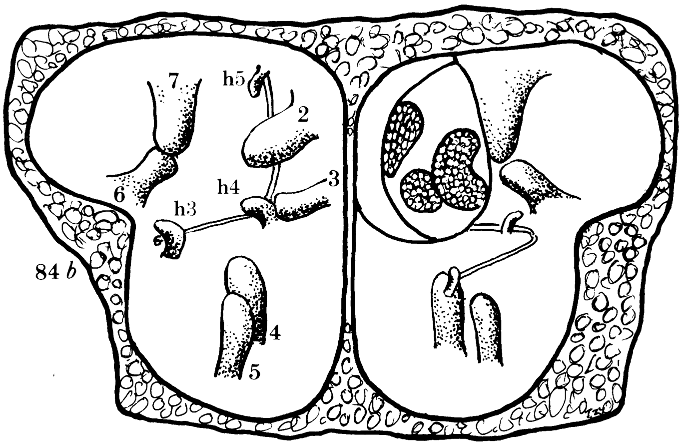
Figure 80. *Octopoteuthis danae* (Joubin, 1931). (*a*) Dorsal view; (*b*) anterior view; 70 mm ML.

Figure 81. *Octopoteuthis*. Same specimen as figure 80. (*a*) Dorsal view; (*b*) anterior view.

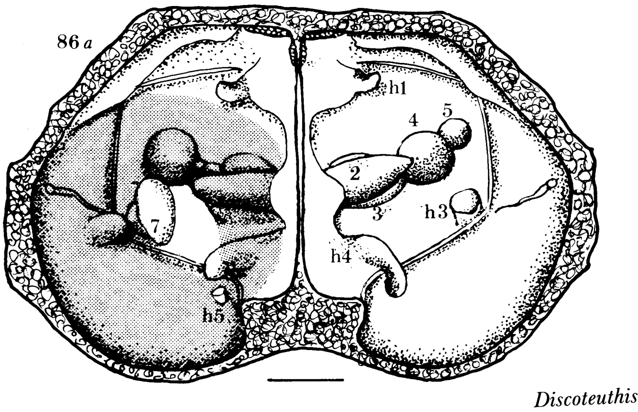


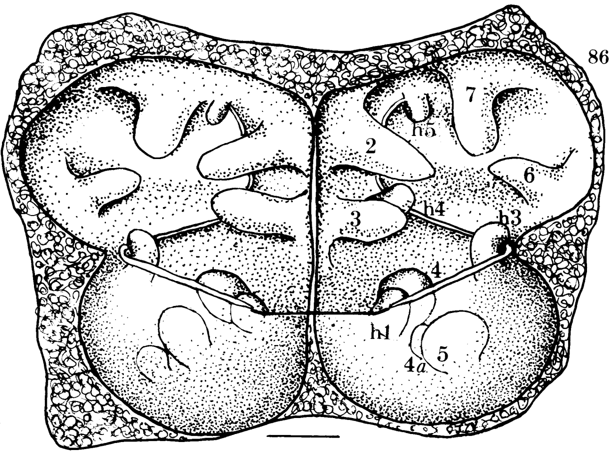






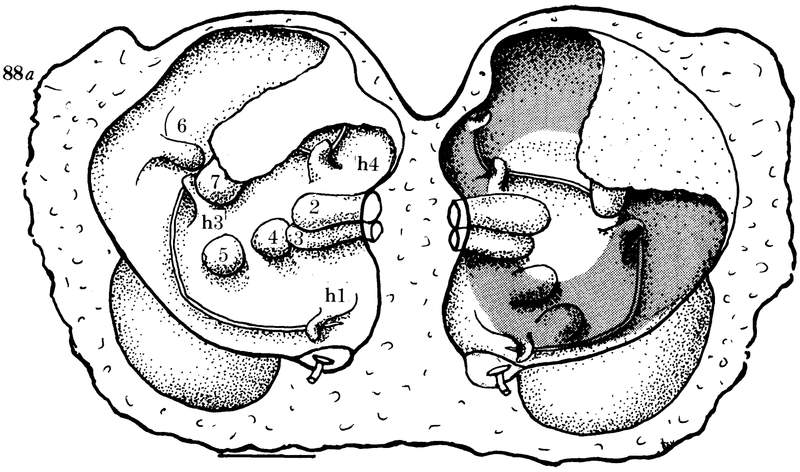
Mastigoteuthis



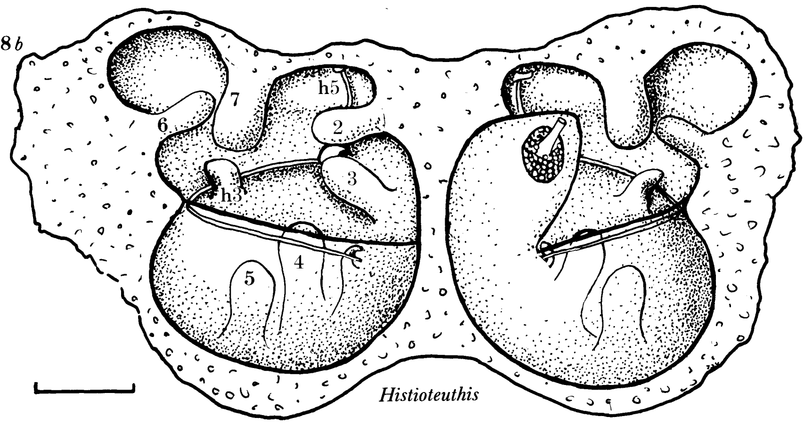


Figures 82, 84 and 86. For description see facing plate 7.

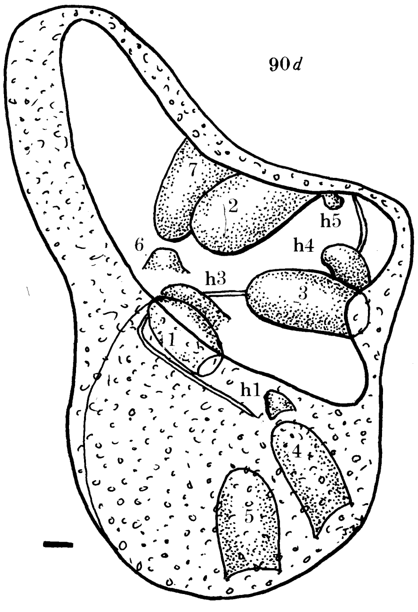
88*a*



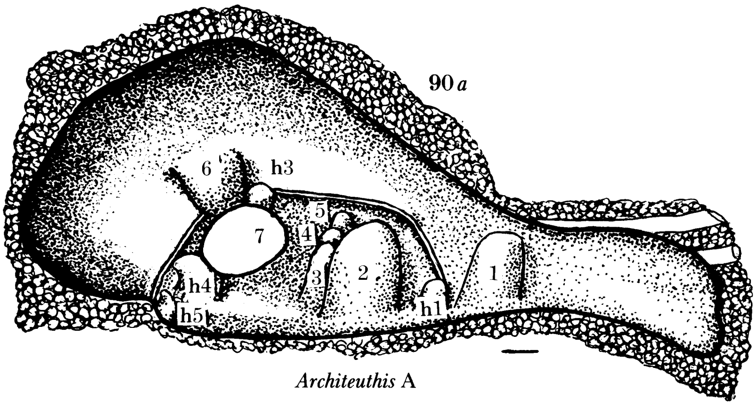
88*b*



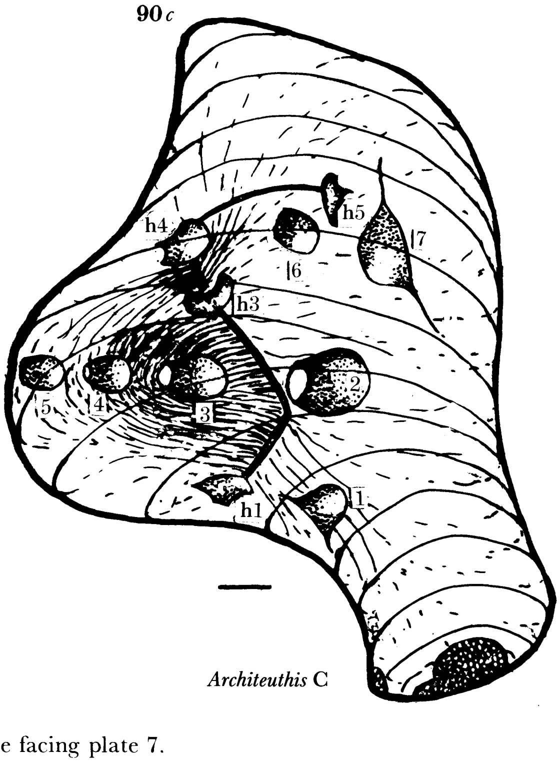
Histioteuthis



Architeuthis C



Architeuthis A



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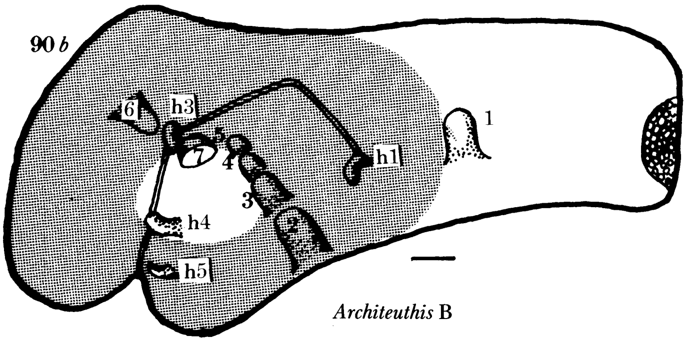
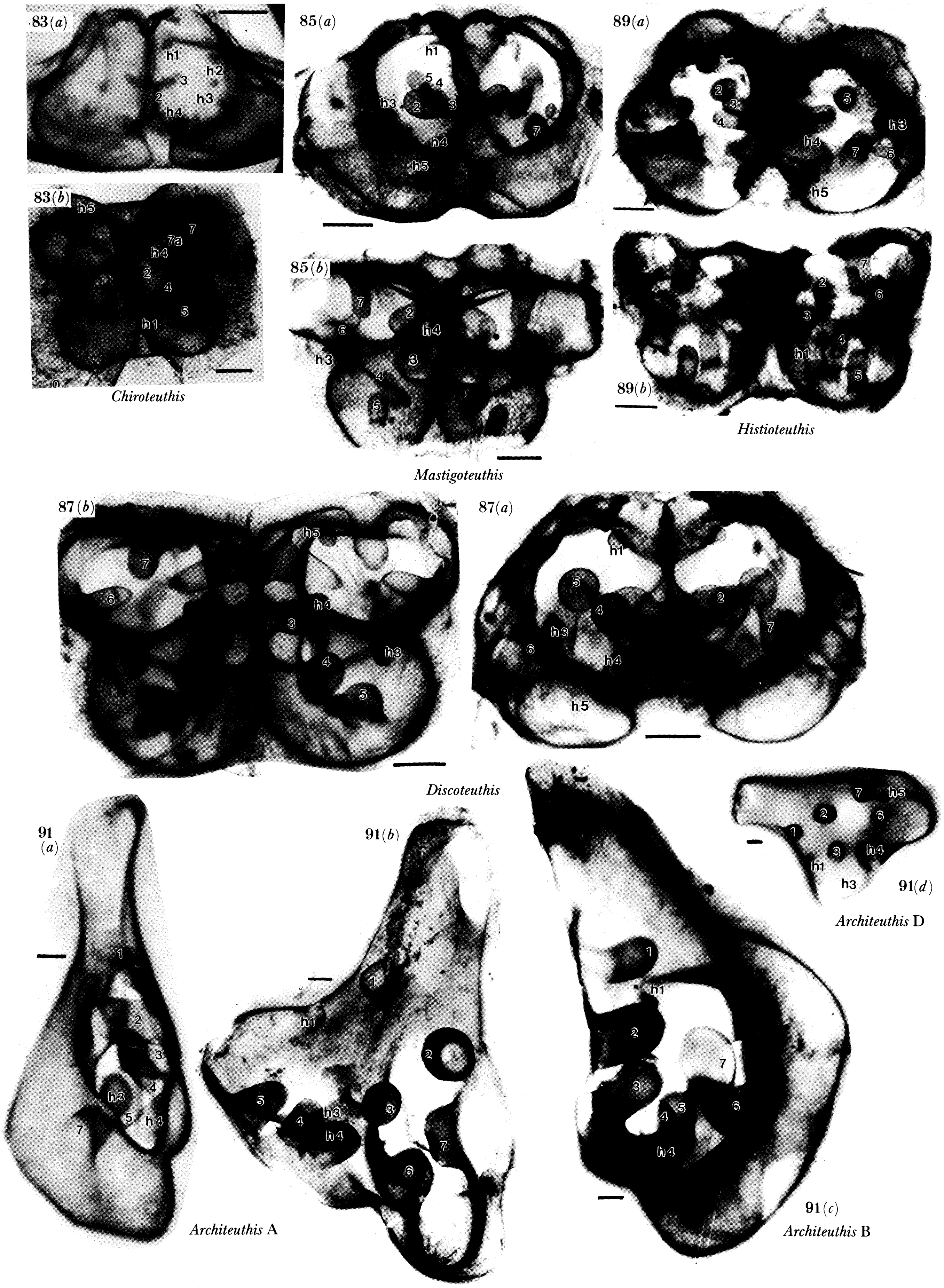


Architeuthis B

FIGURES 88 AND 90. For description see facing plate 7.



Chiroteuthis

Mastigoteuthis

Histioteuthis

Discoteuthis

Architeuthis A

Architeuthis B

Architeuthis D

FIGURES 83, 85, 87, 89 AND 91. For description see opposite.

DESCRIPTION OF FIGURES 82–91

FIGURE 82. *Chiroteuthis veranyi* (Férussac, 1835). (*a*) Dorsal view; (*b*) anterior view; 68 mm ML.

FIGURE 83. *Chiroteuthis*. Same specimen as figure 82. (*a*) Dorsal view; (*b*) anterior view.

FIGURE 84. *Mastigoteuthis schmidti* Degner, 1925. (*a*) Dorsal view; (*b*) anterior view; 60 mm ML.

FIGURE 85. *Mastigoteuthis*. Same specimen as figure 84. (*a*) Dorsal view; (*b*) anterior view.

FIGURE 86. *Discoteuthis laciniosa* Young & Roper, 1969. (*a*) Dorsal view; (*b*) anterior view; 51 mm ML.

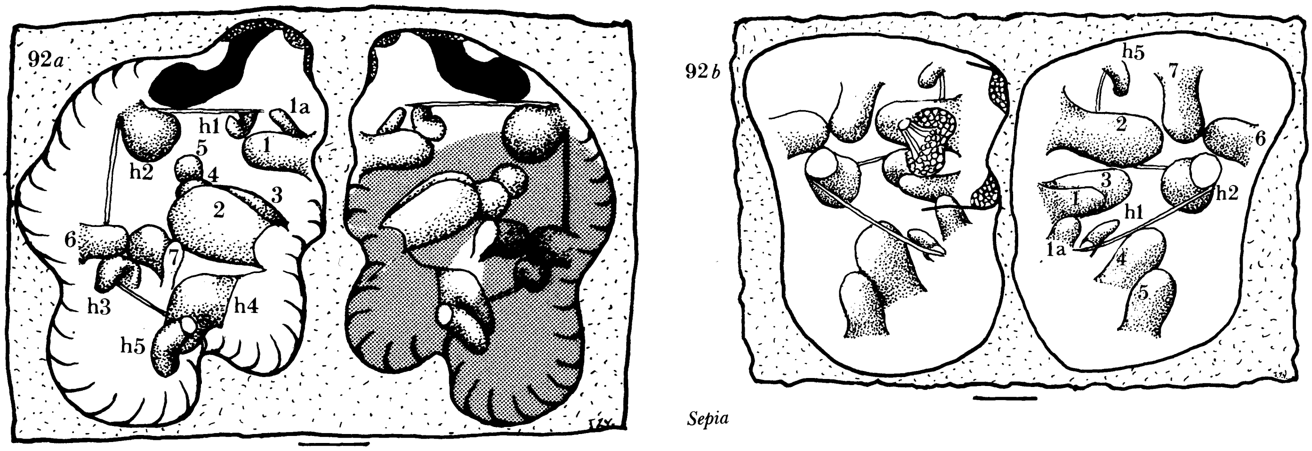
FIGURE 87. *Discoteuthis*. Same specimen as figure 86. (*a*) Dorsal view; (*b*) anterior view.

FIGURE 88. *Histioteuthis miranda* (Berry, 1918). (*a*) Dorsal view; (*b*) anterior view; 60 mm ML.

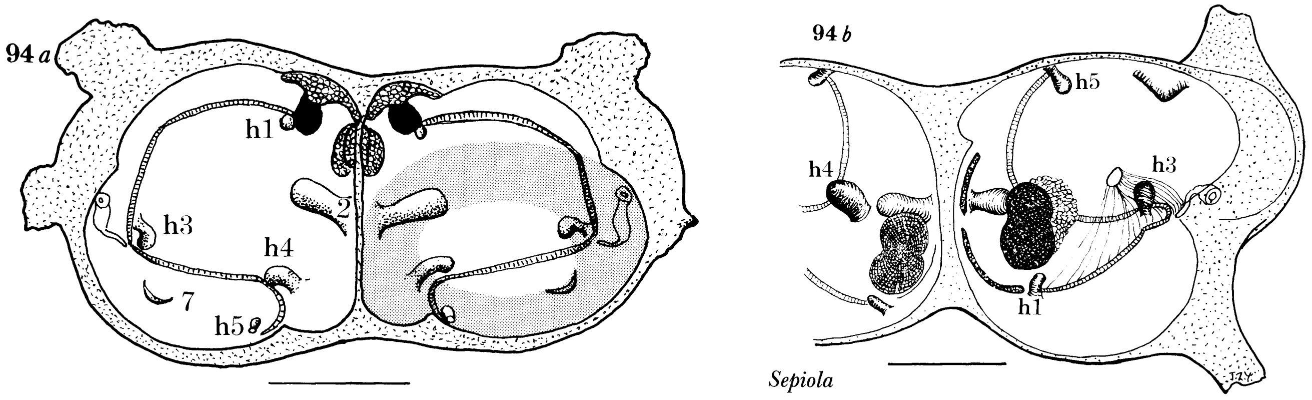
FIGURE 89. *Histioteuthis*. Same specimen as figure 88. (*a*) Dorsal view; (*b*) anterior view.

FIGURE 90. *Architeuthis dux* Steenstrup, 1857. Dorsal views: (*a*) A 162 cm ML; (*b*) B 161 cm ML; (*c*) D 157 cm ML; anteromedial view; (*d*) anterior view of (*c*) with macula removed.

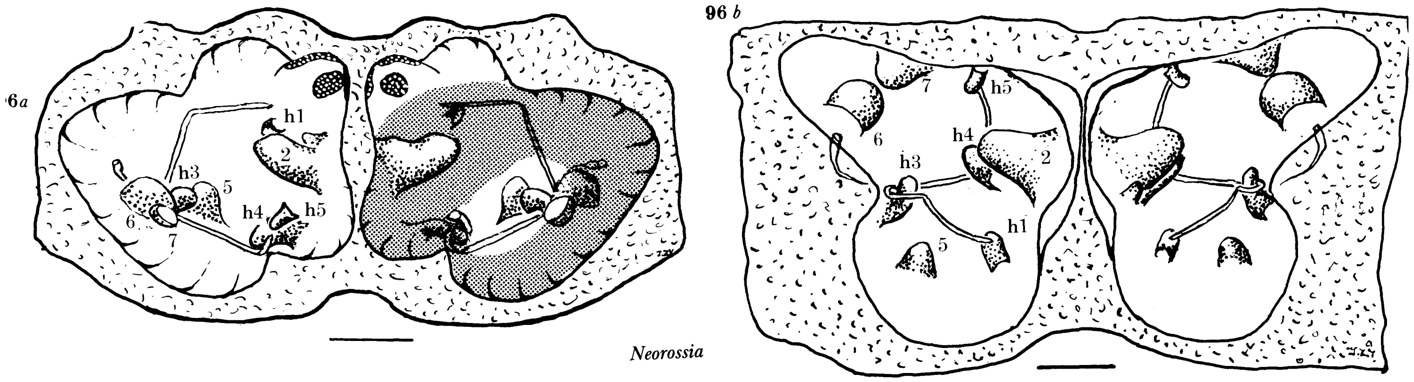
FIGURE 91. *Architeuthis dux*. (*a*) A Dorsal view; (*b*) A medial view; (*c*) B oblique dorsal view; (*d*) D medial view (anticristae 4 and 5 are missing).



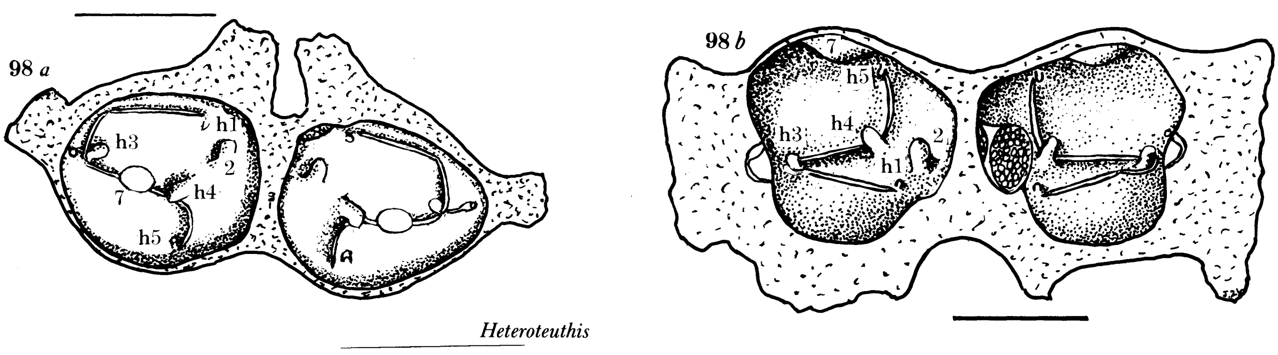
Sepia



Sepiola

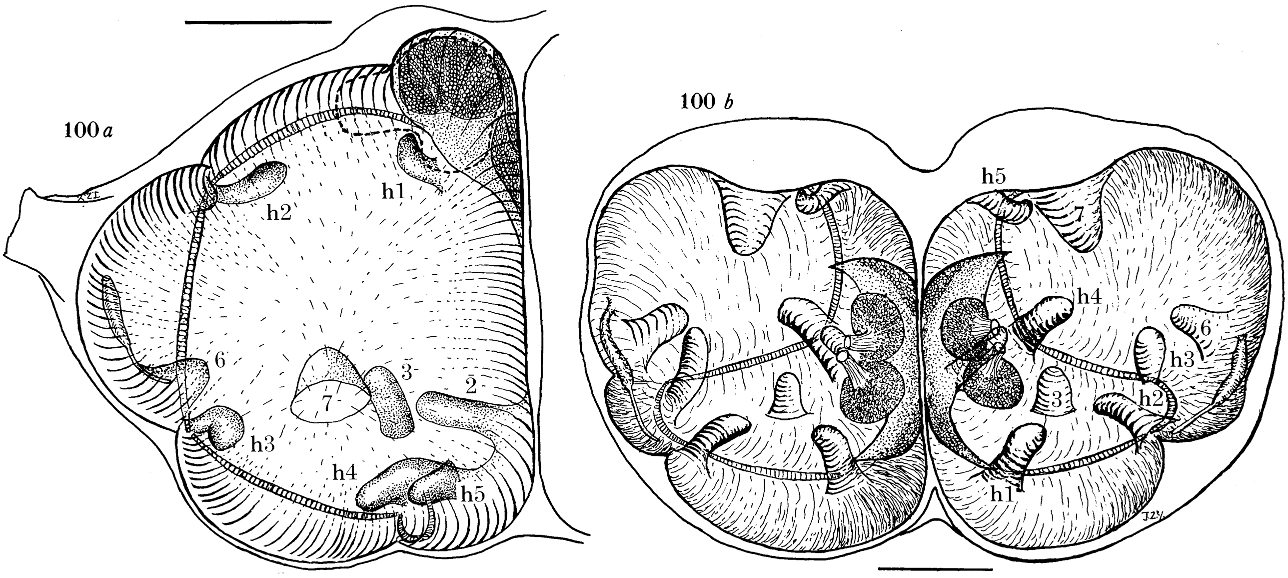


Neorossia



Heteroteuthis

FIGURES 92, 94, 96 AND 98. For description see opposite.



Spirula

Description of figures 92, 94, 96, 98 and 100.

Figure 92. *Sepia officinalis* Linnaeus, 1758. (*a*) Dorsal view; (*b*) anterior view; 230 mm ML.

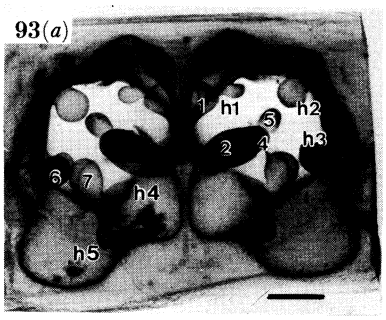
Figure 94. *Sepiola rondeleti* Leach, 1817. (*a*) From above; (*b*) from the front; 23 mm ML.

Figure 96. *Neorossia caroli* (Joubin, 1902), (*a*) From above; (*b*) from in front; 60 mm ML.

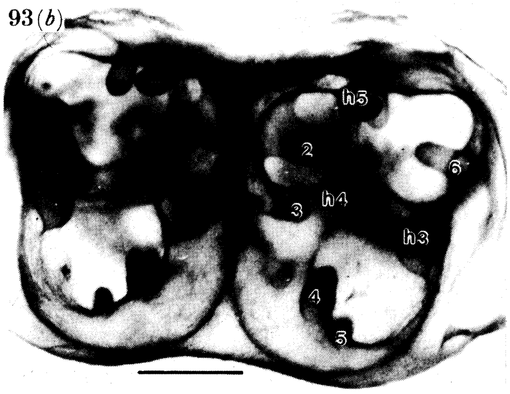
Figure 98. *Heteroteuthis dispar*. Gray, 1849. (*a*) Dorsal view; (*b*) anterior view; 11 mm ML.

Figure 100. *Spirula spirula* Linnaeus, 1758. (*a*) From above; (*b*) from in front; 21 mm ML.

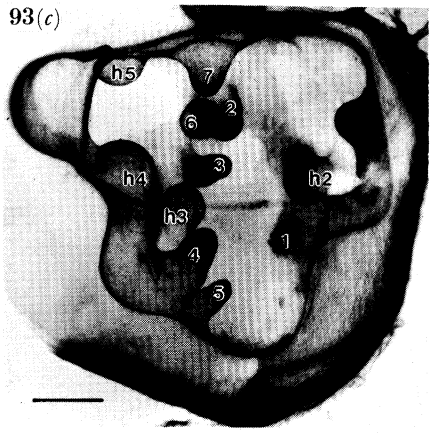
Figure 101. *Spirula*. Same animal as figure 100. Anterior view.



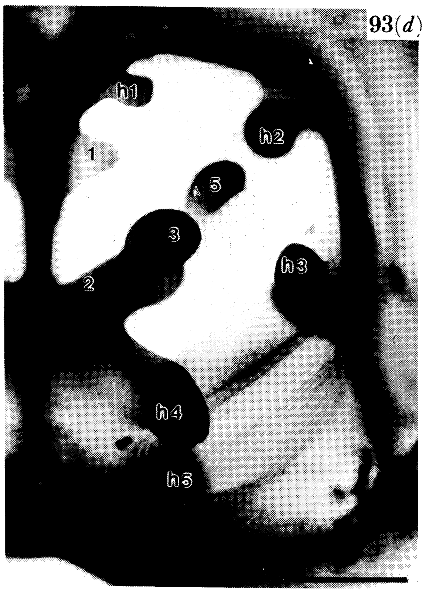
Sepia



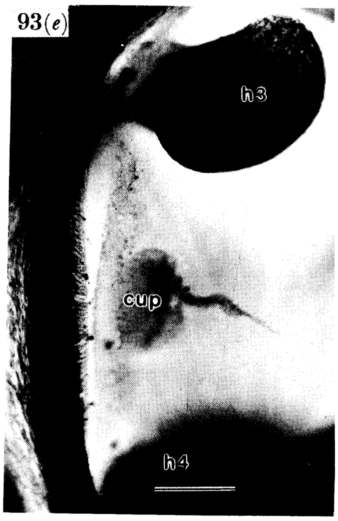
Sepia



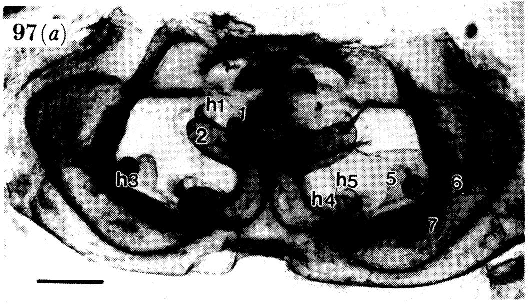
Sepia

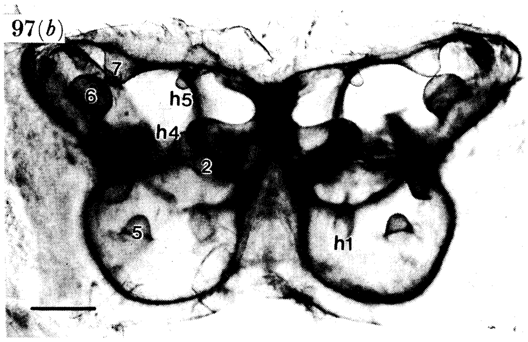


Sepia

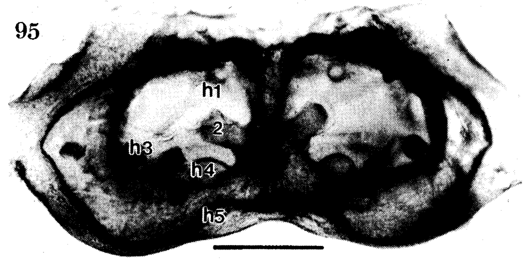


Sepia

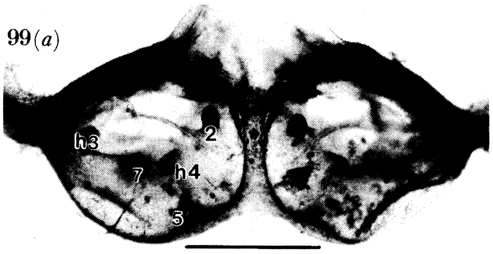


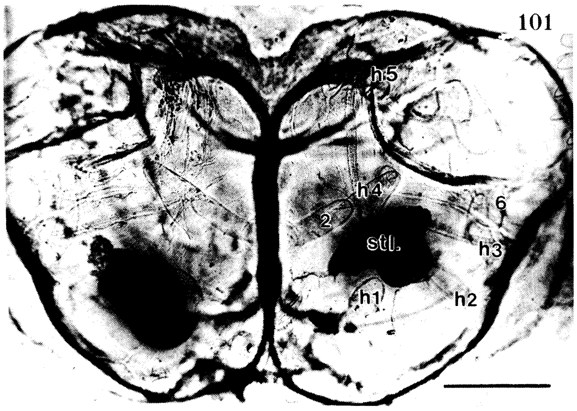


Neorossia

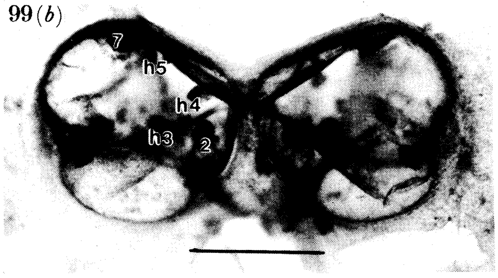


Sepiola





Spirula



Heteroteuthis

FIGURES 93, 95, 97 AND 99. For description see opposite.

the cavity (figure 51, and figure 52, plate 4). Anticrista 7 is unusually large and curved and tapers to a point that does not quite meet the small anticrista 6. There is a well-marked horizontal canal leading to the vertical crista and complete for 17 % of its circumference.

A clear difference from enoploteuthids is the presence of a large hamulus at the first turn of the crista, as well as all the other four hamuli. The anticristae of the median row are all large and form two groups, anticristae 2 and 3 lie close together dorsally, one across the other; They are thus related to the horizontal canal. Anticristae 4 and 5 are placed far ventrally and all four, with hamulus 2, divide the deep front part of the statocyst into an anterior canal related to the anterior transverse crista, and a more posterior one related to the longitudinal crista. The space between anticristae 2 and 3 and anticristae 4 and 5 forms a channel for flow across the transverse crista in the anterior–posterior direction.

The statocyst of *Pterygioteuthis* was found by discriminant analysis to be different from all other non-buoyant squids, even *Pyroteuthis* (Maddock & Young 1984). The method does not allow determination of which measurement produces this aberration: it is probably a combination of a rather long vertical crista and a large gap between hamuli 4 and 5.

Pyroteuthis margaritifera

The statocysts of animals of 42 and 40 mm ML are generally similar to that of *Pterygioteuthis* (figure 53, and figure 54, plate 5). The volume is small, 9 mm^3. The anticristae are all rounded, anticrista 7 is not curved and pointed as it is in *Pterygioteuthis*. There is a large hamulus at the first turn of the crista. The anticristae of the median row are divided into dorsal and ventral pairs and the upper pair are crossed as in *Pterygioteuthis*. The lower pair touch each other, making a complete wall to the canal. The statocysts of these small squids are probably able to monitor rapid turns in combinations of all three planes.

Ctenopterygidae

Ctenopteryx siculus is an unusual squid with fins extending the whole length of the mantle, as in *Sepia*. The statocyst from an individual of 36 mm ML is available and is so aberrant that it is only with difficulty that one sees that it is based on the pattern found in other non-buoyant oegopsids (figure 55, and figure 56, plate 5). The volume of 9 mm^3 is moderately large: 0.27 in relation to ML (table 4). The anticristae divide the cavity into distinct channels related to each of the four sections of the crista. The statocyst is one of the longest and narrowest of all the species examined and is of moderate depth (table 2).

The most unusual feature is an enormous hamulus at the first turn of the crista, continued upwards as a flat vertical plate, extending right to the roof. This wall divides the front part of the cavity into anterior and posterior channels related to the anterior transverse and

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DESCRIPTION OF PLATE 8

FIGURE 93. *Sepia officinalis*. (*a*) Dorsal view, 205 mm ML; (*b*) seen from behind, 63 mm ML; (*c*) lateral view, 180 mm ML; (*d*), dorsal view showing the two channels at the front of the statocyst and upward-facing posterior transverse crista, 82 mm ML; (*e*); remains of cupula on posterior transverse crista, 110 mm ML.

FIGURE 95. *Sepiola*. Same animal as figure 94. Dorsal view.

FIGURE 97. *Neorossia*. Same animal as figure 96. (*a*) From above; (*b*) from in front.

FIGURE 99. *Heteroteuthis*. Same animal as figure 98. (*a*) Dorsal view; (*b*) anterior view.

longitudinal cristae respectively. The more posterior of these two canals is especially narrow and is walled off in front by hamulus 2 and behind by large anticristae 6 and 7 and hamulus 3 (see figure 55*a*).

These two canals are also demarcated by the anticristae of the median wall, which are again highly unusual. Anticrista 1 is a vertical plate in the transverse plane above hamulus 1, jutting out towards hamulus 2 and thus helping to separate the two canals. Behind this are five thin anticristae in the position of anticristae 2 and 3 of other squids. They have broad bases and narrow tips and several of these are bent. Finally on the floor there are a very large anticrista 4 and smaller 5, completing the separation of the two anterior canals.

The horizontal channel is not strongly marked; anticristae 6 and 7 touch but are not fused. The vertical wall above hamulus 2 serves as an anterior wall to the horizontal canal, which may thus be nearly one third complete. Hamuli 4 and 5 are large and the vertical crista is probably tuned to rapid turns. Hamulus 4 has a markedly hooked shape and there are clear channels for flow across the posterior transverse crista both up and down and fore and aft. The large anticrista 4 delimits this vertical channel in front.

The statocyst thus provides for restricted flow in all three planes. The narrow channel for the lateral crista may be related to the need to monitor rolling during use of the long fins, which no doubt also contribute to rapid movements in all directions. This statocyst shows more specialization for sensitivity to high frequencies in several planes than in any other cephalopod (see p. 233). Some similarities with this condition can be seen in *Lycoteuthis* (p. 215).

Neoteuthidae

Neoteuthis

In a specimen of 104 mm ML, probably subadult, the statocysts are large cavities set in a strong capsule whose cartilage contains many small vacuoles. The volume of the statocyst is 104 mm^3, which is rather large relative to mantle length (table 4). It is relatively long, moderately broad and not deep (table 2) (figure 57, and figure 58, plate 5). The spacious cavity of the statocyst is little interrupted by the anticristae; only 6 and 7 are large and they are in contact and delineate a horizontal canal for about 14% of the circumference. The anticristae of the median row are small pegs, two lying dorsally and two ventrally. There is a minute anticrista 1. The hamuli are all small, but one is present at the first turn of the crista, a condition that may be associated with the presence of long, narrow fins (see p. 233).

Neoteuthis was reported to be non-buoyant by Clarke *et al.* (1979); however, there is much vacuolation in the cartilage. The structure of the statocyst suggests that movements are only moderately rapid. The volume of the statocyst is relatively larger than in any other supposedly non-buoyant squid (table 4).

Brachioteuthidae

Brachioteuthis

These are small active squids. The statocyst of a specimen of 52 mm ML (figure 59, and figure 60, plate 5) has a volume of only 2 mm^3 and is the smallest relative to mantle length of the whole series (table 4). It is nearly equal in all directions and is thus one of the relatively widest (table 2). Anticristae 6 and 7 are in contact but not fused, making only a short tubular section of the horizontal canal. The anticristae of the median row are of unusual sizes; anticrista 2 is smaller than anticrista 3; anticrista 5 is very broad. These shapes perhaps indicate special emphasis on the canals at the front of the statocyst, but there is no anticrista 1 and no hamulus at the first turn. All the other hamuli are small and equal. These facts suggest adaptation to turning equally in all planes, but not very fast. The cartilage is not vacuolated.

Lycoteuthidae

Lycoteuthis diadema

This remarkable little mesopelagic squid moves by strong mantle muscles and broad triangular fins, extending only for a short distance along the sides of the mantle. We have specimens from individuals of 80 and 82 mm ML. The statocyst is different from that of all other squids except perhaps *Ctenopteryx* (figure 61, and figure 62, plate 5). It is rather short and narrow but deep (table 2). The volume is 28 mm^3 (table 4). There is a well-marked horizontal canal, anticristae 6 and 7 are joined together and the latter has a remarkable crescent shape. This provides a canal with a medial wall for 40 % of its circumference; one of the most complete of all squids (table 3). Hamuli 4 and 5 are very large and the former has a very sharp angle. There is thus provision for sensitivity at high frequency in the yawing plane.

Anticrista 1 is thin and pointed, recalling the condition in *Loligo*. The anticristae of the median row are all sharply pointed and flattened in the transverse plane. Anticrista 2 is a very thin sheet, divided into two lobes in one of our specimens and three lobes in the other. Anticrista 3 is smaller and rod-like but anticrista 4 is a very large pyramid, flattened in the transverse plane. The four in the row together form a nearly complete wall, though with gaps between them laterally. This wall must provide an obstruction to flow in the horizontal channel and it divides the anterior part of the statocyst into two vertical channels related to the first and second sections of the crista.

This is evidently a statocyst suited for rapid movements. The flat plates in the median transverse plane are otherwise found only in *Ctenopteryx*, but this latter also has a broad hamulus 2, completely lacking in *Lycoteuthis*. The sharply pointed anticristae recall those of *Egea*. The anticrista 1 is like that of *Loligo*. *Lycoteuthis* is generally considered to be close to the Enoploteuthidae but its statocyst has unique features that are hard to relate to particular functional conditions, though evidently concerned with rapid turning.

Bathyteuthidae

Bathyteuthis

The statocyst of a specimen of 30 mm ML is of moderate volume (9 mm^3), is long, very narrow and deep (table 2, figure 63, and figure 64, plate 5). The anticristae and hamuli are broad and fill a large part of the cavity; this is evidently a squid that moves quite swiftly and turns rapidly in all planes.

The horizontal canal is well marked by the shape of the lateral wall; however, anticrista 7 is not elongated and does not meet anticrista 6: only 10 % of the circumference of the canal is complete. The anticristae of the median row are all large and make a wall dividing the deep anterior part of the cavity into two parts. Anticrista 2 is especially large and has a broad base. Anticrista 3 is thinner and lies across anticrista 2. There is an accessory anticrista, 5a, on one side. There is no anticrista 1. The striking feature is a very large hamulus at the first turn of the crista. It lies high up above the turn and is broad and not hooked. Its effect is to increase the division between the two anterior channels and perhaps it is not truly a hamulus 2 but a special development. It is larger than any of the other four hamuli, which are equal.

The statocyst thus shows unique features divergent from other squids, as are many other features of *Bathyteuthis*. It has been classed as neutrally buoyant on a basis of the interstitial spaces among the muscles of the arms and beneath the skin of the mantle (Clarke *et al.* 1979). However, it has thick mantle muscles innervated by giant nerve fibres and the cartilage is not vacuolated. Discriminant analysis of the statocyst places *Bathytheuthis* clearly among the non-buoyant squids, though some way from the centroid. It has therefore been included here in the tables as non-buoyant.

Gonatidae

Gonatus

This squid is neutrally buoyant because of a large content of oil in the digestive gland (M. R. Clarke & E. J. Denton, personal communication). It lives much of its life with the head down. Statocysts from specimens of 85 and 110 mm ML (of *G. steenstrupi*) show an organization suited to monitor quite rapid angular acceleration in all planes (figure 65, and figure 66, plate 5). The statocyst of our larger specimen is of rather small volume, 22 mm^3 (table 4) and is long, broad and shallow (table 2). It resembles that of *Histioteuthis* in dimensions and in having long anticristae with rounded tips. The horizontal canal is more fully developed than in *Histioteuthis*; anticristae 6 and 7 meet with flattened surfaces, a condition never seen in the ammoniacal squids; the canal is thus complete for 16% of its circumference. There is a small anticrista 1. There is no hamulus 2, but the others are all large and rounded. The cartilage is dense and not vacuolated.

This statocyst resembles those of non-buoyant rather than ammoniacal buoyant forms and discriminant analysis confirms this (Maddock & Young 1984).

10. LOLIGINIDAE

The statocysts of loliginids are similar to those of non-buoyant oegopsids and are suited to detect angular acceleration at high frequency in the yawing plane. Their special feature is the development of a large anticrista 1 at the front of the cavity.

Loligo forbesi

The statocyst has already been fully described by Stephens & Young (1978, 1982). It is of small volume, 69 mm^3, long and not very broad or deep (table 2). The anticristae are very large and fill much of the cavity; several of them are pointed (figure 67). The shape of the wall outlines a clear horizontal canal and two broad vertical canals at the front. Anticrista 7 is very large and fully fused with anticrista 6 in adults, making a tunnel. The anticristae of the medial row form a wall with little space between them; anticristae 2 and 3 are often joined. The horizontal canal is thus complete for at least one third of its circumference (table 3).

Anticrista 1 is characteristic and different from all the others. It is very long and pointed and bends forwards. It is rather flexible and moves easily when touched; it is possible that it is moved under the pressure of the endolymph during yawing. It is covered with nerve fibres and may possibly serve as a transducer of the movement (Stephens & Young 1982). A small anticrista, 1a, lies in front of anticrista 1 and has the same form. These conditions are not seen in any oceanic squids.

There is no hamulus at the first turn of the crista but the other four hamuli are all present. Hamulus 4 is especially large and bent backwards; its surface probably has an effect in directing the flow of endolymph medially across the vertical crista.

Lolliguncula brevis (Blainvill, 1923)

The statocyst is very like that of *Loligo*. In a male of 115 mm ML the anticristae are all rounded except anticrista 1, which is very long, thin and pointed; there is a small anticrista, 1a. Anticristae 6 and 7 touch but are not fused.

Doryteuthis

The statocyst is indistinguishable from *Loligo* (of which *Doryteuthis* is a subgenus). In our specimen of *D. plei* from Japan the cupula on the posterior transverse crista is preserved on both sides (figure 68, plate 6). It appears as a rounded mass at the centre of the gap, tapering sharply towards the ends. Hamulus 4 is bent down firmly over the crista but the cupula is not attached to it. The cupula is attached to the crista so as to point upwards and backwards: it cannot even be moved into a position pointing forwards.

Sepioteuthis

The statocyst is similar to that of *Loligo* and is of similar relative volume (22 mm^3) but it is considerably shorter and deeper (table 2, figure 69, and figure 70, plate 6). There are, however, distinct differences from *Loligo*, some of them in the direction of *Sepia*. Thus all the anticristae and hamuli are rounded at the tips rather than pointed (figure 70*a*, plate 6). Anticristae 4 and 5 are shorter and blunter than in *Loligo* and on one side they are joined, whereas anticristae 2 and 3 are in contact at their tips (figure 70, plate 6). The horizontal canal is thus complete for about one third of its circumference and is also much restricted by the anticristae of the median row. On one side there is an accessory anticrista, 4a. Anticrista 1 is strikingly narrower than all the others and bent forward. There is a small anticrista 1a.

There is a slight ridge at the first turn of the crista, but no hamulus. Hamulus 4 is very short and blunt (compared with *Loligo*) and hamulus 5 is large. The crista is thus evidently tuned to detect angular acceleration at relatively high frequency in the horizontal plane and perhaps at higher frequencies in the other planes than in *Loligo*.

Alloteuthis

The statocyst is similar to that of *Loligo* in shape and relative volume (8 mm^3) but is shorter and also broader (table 2). The horizontal canal is less well defined than in *Loligo* (figure 71, and figure 72, plate 6); anticristae 6 and 7 touch but are not fused together even in larger individuals. The canal is thus enclosed for 25% of its circumference. The anticristae of the median row are long and do not completely obstruct the horizontal canal; anticristae 4 and 5 are widely separated ventrally from the others.

The characteristic feature of the statocyst is the great development of the anticristae at the front, especially anticristae 1 and 1a. Several specimens of different sizes have been examined and show a remarkable variety of the knobs in this region, the complexity increasing with age. Anticristae 1 and 2 stand upon a horizontal ridge of cartilage, lying at an angle to the median row of anticristae. These anticristae form a system of projecting knobs apparently serving to restrict the flow of endolymph during turning in any plane. The simplest situation is seen in animals of 40 and 50 mm ML, where anticrista 1 is a flat plate with two or three projections, lying in front of anticrista 2, whereas anticrista 1a is a small knob further forwards above hamulus 1 (figure 72, plate 6). This seems to be the basic pattern, but has many variants. The knobs of anticrista 1 may be broad plates or subdivided, giving several points on each side (figure 72). They may be separate projections, not arising from a plate.

In larger animals these anticristae become further complicated by the development and lengthening of secondary knobs. There may also be addition of extra anticristae to the median row. The statocyst of figure 72, plate 6, was from a mature, female *A. media* of 105 mm ML with a tail, showing a very complex situation not easily derived from division of a plate. The oblique horizontal ridge carries three large spikes of various shapes and several smaller ones. However, not all ripe individuals with long tails showed such complex knobs.

It seems likely that these variations reflect contributions of both genetic and behavioural factors. Figure 72*a*, *b*, plate 6, shows that the pattern of the knobs is usually similar on the two sides, as was shown also in the variable anticristae of *Octopus* (p. 200) (Young 1960). The development of these anticristae is probably related to the performance of fast turning movements in the forward pitching and rolling planes. It is not clear why these anticristae develop in *Alloteuthis* in a way so different from *Loligo* or *Sepioteuthis*, whereas those in turn are different from anticrista 1 in ommastrephids and other non-buoyant squids.

Pickfordiateuthis

The statocyst is like that of a juvenile *Loligo* (figure 73). The proportions are similar and the volume of only 1 mm^3 is very small, both absolutely and relative to mantle length (table 4). The hamuli and anticristae are all present (except at the first turn) but are mostly small. Anticrista 5 is placed far back.

11. BUOYANT SQUIDS

Neutral buoyancy allows economy of muscular effort and buoyant squids mostly have weak mantle muscles. They often live at considerable depth and move and turn rather slowly. The statocysts are accordingly mostly suited to monitor angular acceleration at rather low frequencies. They are usually larger, relative to mantle length, than in non-buoyant forms, providing a greater inertial mass of endolymph (table 4). The anticristae and hamuli are smaller and provide less restriction of flow.

Buoyancy may be so distributed as to lead the animals to live largely head-up (i.e. *Mastigoteuthis*) or head-down (cranchiids) and turning may occur easily in any direction (*Histioteuthis*). The statocysts accordingly do not show the special features that give high sensitivity in the yawing plane. They are often nearly equal in length, breadth and depth (table 2). The anticristae 6 and 7 seldom meet to form a complete tunnel and the proportion of the horizontal channel that is enclosed is mostly lower in buoyant than in non-buoyant squids (table 3). The conditions in cranchiids are different from the rest and are considered in p. 227.

Joubiniteuthidae

Joubiniteuthis

This is a most unusual squid, with a very long tail and extremely long thin arms and tentacles. The statocyst in our specimen of *J. portieri* of 36 mm ML is a large sac approximately equal in all directions and the volume of 11.8 mm^3 is large relative to the size of the animal (table 4). There is a less-clear division into dorsal and anterior chambers than in the statocyst of *Grimalditeuthis*, which is otherwise similar (figure 74, and figure 75, plate 6). As in that genus, the cavity is very little obstructed, but the hamuli are all present, including one at the first turn. There are no other obstructions except for a slight swelling in the roof, recalling that in *Helicocranchia* (p. 227). The similarity to *Grimalditeuthis* may be connected with the long tail, and the genera are usually considered to be related, though placed in distinct families. Both probably make slow turns in all planes.

Grimalditeuthidae

Grimalditeuthis

This squid has the unusual features of two pairs of fins and a long tail. The tentacles are lost in the adult. The statocyst has a large cavity with little obstruction, even in my specimen of *G. bomplandi* of 67 mm ML, which is nearly the maximum size (figure 76, and figure 77, plate 6). The volume of 26.9 mm^3 is large relative to the size of the animal, nearly one half that of a *Loligo* of more than five times the mantle length (table 4). The statocyst is set in cartilage containing very large fluid-filled spaces. It is about equal in all directions but broad at the back and deep in front, making large clear anteroposterior and dorsoventral chambers. The crista is set at the centre with large spaces around it, except anteriorly. It is significant that the walls of the cavity are shaped to form channels even when, as in this animal and *Joubiniteuthis*, the statocyst is adapted to slow turning. All five hamuli are present, but they are small and there are no other anticristae.

This is clearly a statocyst suited to monitor slow turning in all planes, which is presumably accomplished by the two pairs of fins.

Pholidoteuthidae

Pholidoteuthis

These are large, possibly buoyant squids with broad fins. We have the statocyst from a specimen of 460 mm ML, kindly provided by Dr M. R. Clarke, from the stomach of a shark. The volume of 72 mm^3 is rather small relative to ML (table 4). The statocyst is short, broad and deep (table 2, figure 78, and figure 79, plate 6). There is a well-marked horizontal canal and a deep channel at the front. The hamuli and anticristae are large and fill up much of the cavity; they are all blunt and rounded at the tips. Anticristae 6 and 7 are large and are in contact but not fused. Anticrista 7 has an unusual triangular form and the horizontal canal is completed for rather less than one third of its circumference. The anticristae of the median row are massive and they obstruct the horizontal canal and delineate a vertical one.

This statocyst is evidently suited for monitoring angular acceleration in the horizontal plane that is rapid but somewhat slower than in ommastrephids or loliginids. It is surprising to find these conditions in neutrally buoyant squids, which emphasizes the doubt of Clarke *et al.* (1979) as to their buoyancy.

Octopoteuthidae

Octopoteuthis

These squids have weak mantle muscles and long fins, and in this they are somewhat like *Discoteuthis* and *Mastigoteuthis*, though they differ from those in losing the tentacles after the juvenile stage. In our specimen of *O. danae* of 70 mm ML the statocyst is rather long, narrow and shallow. Its volume of 89.6 mm^3 is one of the largest of any squid relative to its size (table 4). It is broader behind and deeper in front, giving a marked horizontal canal and a deep anterior chamber (figure 80, and figure 81, plate 6). In spite of its great volume the statocyst has considerable internal subdivisions. The hamuli and anticristae are all plump and rounded at the tips, as in *Sepia* and other animals with long fins. They occupy a large part of the cavity, suggesting quite a high rate of turning in all directions. However, there is no hamulus at the first turn. Anticristae 6 and 7 are large and touch in our specimen, but are not fused. The horizontal canal is thus complete for rather less than a third of its circumference.

Chiroteuthidae

Chiroteuthis

This is a mesopelagic or bathypelagic squid with large arms and extremely long, thin tentacles. They may live head upwards. The mantle is weak and there are large fins. We have the statocyst from a large specimen of *C. veranyi* of 265 mm ML. It is rather short and narrow but very deep (table 2). It is broad and shallow at the back but deep at the front, thus having major dorsal and ventral chambers (figure 82, and figure 83, plate 7). The volume of 23.3 mm^3 is rather large for the mantle length (table 4).

All five hamuli are present along the crista but they are small. There is no anticrista 1 and the anticristae 2–5 are present in the usual positions but are small. Anticrista 6 is minute but there are two large knobs in the roof, labelled 7 and 7a. There is thus no enclosed horizontal canal and the conditions somewhat resemble those in cranchiids and suggest that the crista provides a high sensitivity for slow turns equally in all directions. This seems likely because of the strange proportions of the animals. The statocyst is very different from those of *Mastigoteuthis* and *Discoteuthis*, which also have very large fins (in some species).

Mastigoteuthidae

Mastigoteuthis

These bathypelagic squids have large buoyant arms and probably live head up, with their very long whip-like tentacles moving around to catch prey with their minute suckers (Dilly *et al.* 1977). Propulsion is mainly by the very large fins (in many species), and the mantle is weak. The statocyst is of about the same extent in all directions. It is wider at the back than the front, making a clear horizontal canal (figure 84, and figure 85, plate 7). It is also much deeper at the front than the back, making large channels across the anterior transverse and longitudinal cristae. The volume of 40.2 mm^3 is among the largest of all squids relative to mantle length (table 4).

The hamuli are all rather small, especially 1, 3 and 5, with hamulus 4 only a little larger. There is no hamulus 2. There are therefore large gaps for large cupulae in all three planes. The anticristae are much larger than the hamuli and all are blunt and rounded. Anticristae 6 and 7 touch but are not fused. Those of the median wall make a large obstruction. There is no anticrista 1. The horizontal canal is estimated to be complete for one fifth of its circumference (table 5). This is clearly a statocyst suited for turns at moderately high frequency.

The blunt rounded anticristae recall those of *Sepia*, *Octopoteuthis* and *Discoteuthis*, which also have very long fins and a deep sac in front of the statocyst. The Kölliker's canal of *Mastigoteuthis* is very large and its cilia are joined to form plates, whose significance is not known (Dilly *et al.* 1977).

Cycloteuthidae

Discoteuthis

These squids have fins reaching the whole length of the mantle, which itself is weak. In our specimen of *D. laciniosa* of 51 mm ML the statocyst is rather short and narrow but is very deep, like that of *Chiroteuthis* (table 2). It is wider at the back than the front, making a broad horizontal channel (figure 86; figure 87, plate 7). It is deepened at the front to make a broad anterior vertical channel. The volume of 40.4 mm^3 is among the largest (table 4).

The characteristic feature of the statocyst is that the anticristae and hamuli are all large, but there is no hamulus 2. Anticristae 6 and 7 do not quite meet in our specimen (ML 51 mm) but anticrista 7 is expanded longitudinally, making a channel calculated to be complete for one third of the circumference. There are extra anticristae in the median rows; on the left a 4a between 4 and 5 and on the right a 5a ventrally. There is no anticrista 1. Kölliker's canal is large.

This statocyst is obviously suited to detect turns at rather high frequency in all directions. The short, deep shape and rounded projections recall the condition in *Mastigoteuthis* and *Sepia* and is probably related to the large fins.

Histioteuthidae

Histoteuthis miranda

With its two unequal eyes *Histioteuthis* probably adopts a variety of postures, with the head and arms sometimes upwards, at others downwards or forwards. The statocyst seems to be suited to monitor quite rapid turns in various planes. In our specimen of 60 mm ML it is relatively long and broad but shallow (table 2). Its volume of 18.2 mm^3 is rather small for a buoyant squid (table 4, figure 88, and figure 89, plate 7).

The anticristae are large and fill much of the cavity. They are elongated and rounded rather than bulbous. Anticristae 6 and 7 are in contact but not fused. There is a clear horizontal canal but less than 10% of it is complete. There is no anticrista 1 and no hamulus at the first turn. The statocyst is thus clearly that of an active animal, not one that drifts passively.

Architeuthidae

Architeuthis

The tissues of the giant squid float in water and contain ammonium and it is therefore probably near to neutral buoyancy (Clarke *et al.* 1979). No one has yet reported on its behaviour when adult. We have been able to secure the statocyst of five large specimens thanks to the kindness of several donors (table 5). All the animals were stranded, four on North Sea beaches and one in Newfoundland and we assume that all were *Architeuthis dux* Steenstrup, 1857. Specimens A, C and E had been preserved in formalin for a long time: in specimen C the statocysts were hardly recognizable. Together, the five provide a consistent picture of the organization. The statocysts of the large animals show strikingly similar dimensions, the smaller animal (E) is deeper than the others (table 5).

TABLE 5. DIMENSIONS OF THE STATOCYSTS FROM FOUR SPECIMENS OF *ARCHITEUTHIS*

(In animal C no reliable measurements could be made.)

specimen	ML/cm	length	statocyst breadth (mm)	depth	source	donor
A	162	19.54	9.20	12.31	Scarborough, stranded	British Museum
B	161	18.46	9.08	12.62	North Berwick, stranded	A. Packard
C	118	—	—	—	British Museum, Newfoundland	British Museum
D	157	20.00	12.46	12.34	Aberdeen, stranded	P. Boyle
E	95	16.92	10.50	13.50	Aberdeen, Zoology Department	P. Boyle

The statocysts lie close together at their front ends, but diverge backwards, as in the other very large squid *Mesonychoteuthis* (figure 102). They lie in dense cartilage with some fine vacuolation. The statocyst is longer in relation to its volume than in any other cephalopod and it is also the narrowest and is very shallow (table 2). The great length is due to the presence of a long 'macula chamber' in front.

The estimated volume of 1160 mm^3 is larger than in any other squid except *Mesonychoteuthis*; even related to the mantle length it is also among the largest (table 4). The statocyst has been difficult to illustrate except by dorsal and lateral views (figure 90, and figure 91, plate 7). The view from in front by transmitted light is very confused and an interpretation is given in figure 90*d*. Dorsal views show the extraordinary shape (figure 90*a*, *b*, and figure 91*a*, plate 7).

The statocyst is shallow at the front and back and deep at the centre, there is thus a long horizontal channel dorsally and transverse channels at the centre. The horizontal channel is tubular in front and well marked by the shape of the wall behind. It is limited to a canal by anticristae 6 and 7, which fit closely together but are not fused in our specimens (figure 91*b*, plate 7). Anticristae 2 and 3 provide partial obstruction to the channel anterior to the vertical crista. The large anticrista 1 does not project dorsally and the horizontal channel provides a very large mass of endolymph to act on the vertical crista. Hamuli 4 and 5 are moderately large. The possible course of the flow during yawing movements is shown in figure 90*b*. There is a very large unobstructed mass of endolymph at the front of the cavity. The horizontal channel is 20 mm long laterally. It is 4 mm in diameter between anticristae 6 and 7, narrowing to 3 mm at the vertical crista and widening again behind anticristae 2 and 3. Anticristae 6 and 7 provide a complete wall for the canal for about 18% of its circumference. This channel presumably produces the required high sensitivity for the slow turns of these large creatures.

The first three sections of the crista lie in a horizontal plane in a groove below the horizontal canal. Here they are crossed by movement of the endolymph in the two deep transverse channels, which are separated by the large anticristae of the median row. Anticrista 1 contributes to the more anterior of these channels, which is related to the anterior transverse section of the crista, running from a small hamulus 1 upwards, laterally and backwards. The first turn is sharp and there is no hamulus 2.

The longitudinal section of the crista is also in relation to the more anterior transverse channel, running in the horizontal plane. It ends in a large rounded hamulus 3, which completely overhangs it. The posterior transverse crista runs medially and backwards, therefore not parallel to the anterior transverse crista. The great depths of the vertical channels provide large volumes of endolymph for transducing slow accelerations in the pitching and rolling planes.

The statocyst thus shows a general similarity to those of other moderately active buoyant oegopsids and discriminant analysis places it clearly in the centre of the buoyant group (Maddock & Young 1984). The peculiar feature related to the great size of the animal is the extreme length of the horizontal channel. The only other comparably large squid, the cranchiid *Mesonychoteuthis*, also has a very long statocyst, though this may be associated with the peculiar arrangement of all cranchiids (p. 228). The statocyst is also very long in *Dosidicus* and other large ommastrephids (p. 207).

12. SEPIIDA

Sepia

A cuttlefish is both buoyant and fast moving: the statocyst differs from that of both buoyant and non-buoyant oegopsids but is more like the latter (figure 92, and figure 93, plate 8). The cavity is similar to that of *Loligo* in length relative to volume but is narrower and rather deeper (table 2). The volume of a specimen of *S. officinalis* of 80 mm ML is 59.4 mm^3, larger relative to mantle length than in *Loligo* (table 4). The chamber extends backwards as a long dorsal horizontal canal and is deeper in front as a transverse canal (figure 93*c*, plate 8). The dorsal channel is well marked by the shape of the outer wall, which takes a characteristic sinuous course, being very narrow at the vertical crista but wide elsewhere. The circular cross section of the channel is well seen in figure 93*b*, plate 8. Anticristae 6 and 7 meet and touch in adult *Sepia* but have not been seen to fuse. Anticrista 7 is somewhat extended backwards and the channel thus has an inner wall for about 25% of its inner circumference (figure 92*a*).

The conspicuous difference from *Loligo* is the presence of a large hamulus at the first turn of the crista. This limits the effective length of the anterior transverse and longitudinal sections, presumably giving reduced sensitivity appropriate to high frequency in the pitching and rolling planes. This large hamulus is in line with the anticristae 2–5, thus dividing the anterior part of the statocyst into two channels (figure 93*d*, plate 8). The more anterior of these is related to the anterior transverse section, the more posterior to both the longitudinal and posterior transverse sections. Anticrista 1 has a blunt pyramidal shape (quite different from that of *Loligo*) and also contributes to the wall of the most anterior chamber. All the anticristae and hamuli have blunt, rounded shapes.

We have followed the growth of the statocyst in a series of specimens (see Maddock & Young 1984). *Sepia* begin immediately after hatching to hunt like adults and the statocyst already shows much differentiation. The pattern of subsequent growth is surprisingly like that of *Loligo* (p. 205): the increase in length and breadth is much slower than that of the body as a whole. Conversely, the fourth hamulus grows faster than the rest of the statocyst, so that the gap along the vertical crista becomes relatively shorter, as in *Loligo* (p. 205). Throughout growth the gaps between the hamuli on the anterior transverse and longitudinal cristae are shorter in *Sepia* than in *Loligo*.

Vestiges of the cupulae have been preserved in a few specimens (figure 93*e*, plate 8). They are probably somewhat distorted but show that the cupula is much longer at the centre of each crista section and tapers towards the hamuli. Dr B.-U. Budelmann has suggested that perhaps the central part of the cupula moves readily whereas the terminal portions respond only at higher frequencies (personal communication): this would provide separate systems to monitor slow turns with the fins and fast jet responses as in *Octopus*.

The plexus on the walls of the sac has been stained in some specimens. It extends all over the surface, including the anticristae, and has a complex mesh, with few nerve cells and hair cells.

The statocyst of *S. elegans* is similar to that of *S. officinalis*.

The statocyst of *Sepia* is thus clearly suited to monitoring rapid angular acceleration in all three planes. The horizontal channel is not quite so complete as in *Loligo* and the ommastrephids but is partly tubular. On the other hand, the channels for the other sections of the crista are very distinct (figure 93*d*, plate 8).

13. SEPIOLIDA

The Sepiolida are now placed in an order distinct from the Sepiida (Fioroni 1981). They are all short, rounded animals moving largely by means of large round fins. *Sepiola* and *Rossia* live close to the bottom and often bury, as perhaps also does *Heteroteuthis*, though in deeper water over seamounts. In spite of these differences the statocysts are all alike. They are the three shortest among all cephalopods relative to volume (table 2). The cavity is thus rounded, rather little obstructed and probably suited to monitor angular acceleration in all three planes. Only in *Rossia* is there some emphasis on the horizontal channel to monitor turning in the yawing plane. Discriminant analysis places these statocyst well away from that of *Sepia* and close to those of non-buoyant teuthoids; *Rossia* stands rather apart from the others (see Maddock & Young 1984).

Sepiola

Specimens of these small animals were obtained from the fish market at Portici (Naples) and may have included both *Sepietta* and *Sepiola*. The walls of the statocyst sac are very thin, especially at the back, where the posterior sac readily collapses. The statocyst is the shortest relative to volume of any decapod and is very broad and rather deep (table 2). Its volume in an animal of 23 mm ML of 4.01 mm^3 is rather small even relative to the small size of the animal (table 4). The cavity is smoothly rounded as seen from above but shows large anteroventral and dorsal–lateral sacs (figure 94, and figure 95, plate 8). The crista runs round the centre of the cavity, with large spaces above and below it. All sections thus encounter large inertial masses of endolymph and presumably have a rather high sensitivity, suited to moderately slow turns.

Hamuli 1, 3, 4 and 5 are present and are rather large knobs, mostly with narrow bases. There are only two anticristae, a large blunt one on the medial wall in the position of anticrista 2 and an anticrista 7 in the roof. This anticrista is broad and blunt in two of our specimens (figure 94*b*) and longer in another: with hamulus 3 it delimits a broad horizontal canal, as shown dotted in figure 94*a*. There is very little tubular canal; at the most 10 % of the circumference.

Kölliker's canal is large with a wide opening into the dorsolateral sac.

Neorossia

The statocyst has a form somewhat similar to that of *Sepiola* but with more obstructions of the cavity, probably related to rather faster turning (figure 96, and figure 97, plate 8). The cavity is relatively very short, very broad and rather shallow (table 3). The volume of 23.69 mm^3 is rather large relative to mantle length (table 4). The crista runs round near to the centre, leaving large spaces above and below. There are large anteroventral and laterodorsal sacs. Hamuli 1, 3, 4 and 5 are present and are rather large. There is a large anticrista 2 with an extra knob at its base. There are no anticristae 3 or 4 and anticrista 5 lies far laterally and posteriorly. There is thus no marked median row. Anticrista 6 is very large and nearly meets the smaller anticrista 7, making a clear horizontal canal occupying 18 % of the circumference. This is clearly a statocyst suited for rapid movement. There is no sign that it is like that of *Octopus*, which *Neorossia* is said to resemble when moving.

Heteroteuthis

This occupies with *Rossia* and *Sepiola* the place of the shortest statocyst among all decapods (table 2). It is also one of the broadest and is moderately deep (table 2). Its volume of only 1.09 mm^3 is one of the smallest even relative to mantle length (table 4). The cavity is almost round in the horizontal plane and shows slight anteroventral and laterodorsal sacs (figure 98, and figure 99, plate 8).

The cavity is very little obstructed. Hamuli 1, 3, 4 and 5 are present but only 4 is large. There is an anticrista at position 2 on the median wall, recalling that of *Sepiola*. The only other anticrista is a ridge in the roof, perhaps comparable to anticrista 7, and again like that of *Sepiola*. It may serve to direct flow in the horizontal plane, but there is no definite channel. This is clearly a statocyst suited to slow movements in a deep-sea habitat. It is remarkable that it shows some similarity to the other sepiolids but it lives above seamounts and may bury like the others.

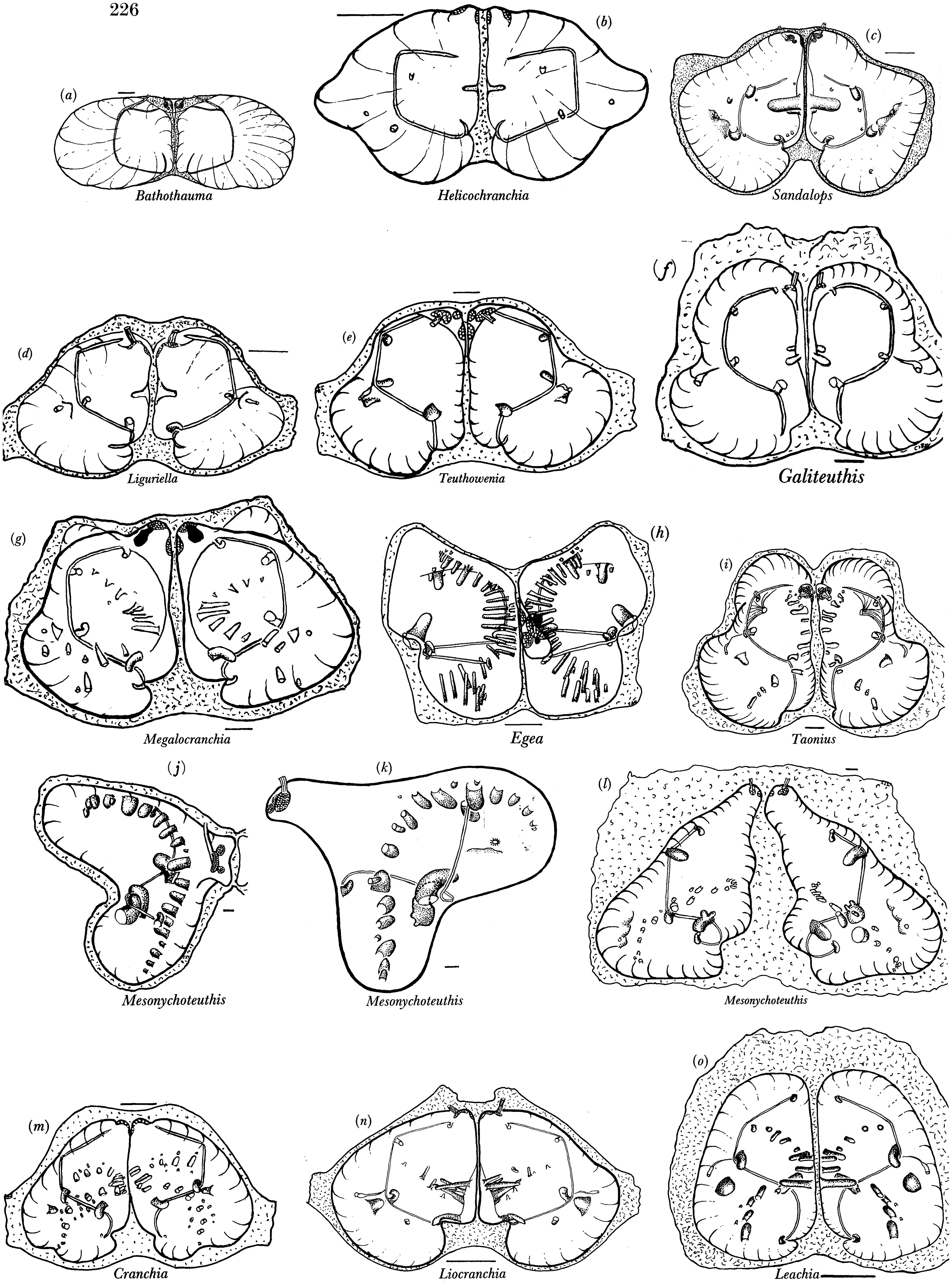
14. SPIRULIDA

Spirula

The statocyst shows marked differences from *Sepia*, sepiolids and teuthoids. It is stoutly built, with thick cartilage at the sides and midline but thinner at front and back. It is about equal in all directions (table 2) but the cavity is shaped to form small sacs anteroventrally and posteriorly and large ones dorsally (figures 100 and 101, plate 8). The volume of 12.91 mm^3 is rather large relative to mantle length (table 4). All five hamuli are present and are unusually large and long. The second stands *below* the crista and there is also a small ridge above the crista. The third hamulus bends closely over the crista and ends in a point. The fourth is particularly large, with a broad base.

There are only four anticristae, which are in somewhat different positions from those of other cephalopods. They all lie very far back, leaving a large unobstructed anterior chamber, which provides a large mass of endolymph to act across the anterior transverse crista and longitudinal crista. A large knob on the medial wall might be compared to anticrista 2 or 3 of *Sepia*, and one below it, standing on the floor, is in the position of anticrista 6, with the opening of Kölliker's canal at its base. In the roof there is the largest of the anticristae, corresponding perhaps to anticrista 7 and pointing towards anticrista 6 to make a very broad horizontal channel (figure 100*b*).

All four anticristae thus seem to be concerned with regulating the flow around the horizontal channel, which seems to be the one concerned in more rapid turning, in spite of the head-down position that is usually adopted. The flow in this channel involves a very large inertial mass of


(a)
Bathothauma
(b)
Helicochranchia
(c)
Sandalops
(d)
Liguriella
(e)
Teuthowenia
(f)
Galiteuthis
(g)
Megalocranchia
(h)
Egea
(i)
Taonius
(j)
Mesonychoteuthis
(k)
Mesonychoteuthis
(l)
Mesonychoteuthis
(m)
Cranchia
(n)
Liocranchia
(o)
Leachia

endolymph in the more anterior region and the anticristae 6 and 7 provide only a partly closed channel for at most 13 % of the circumference. The provision is thus for rather slow turning even in the yawing plane. Appropriate sensitivity in the other planes is presumably ensured by the characteristics of the cupulae. The large hamuli present at each of the turns suggest that rotation is at about the same speed in all directions.

The statocyst of *Spirula* is thus different from that of all other cephalopods. This is not surprising because of the peculiarities of shell, posture and locomotion, and its isolated systematic position. Discriminant analysis places it close to *Sepia*, probably because of its second hamulus and the lengths of the first and second crista gaps that result from it (Maddock & Young 1984). Yet the general shape and other features are not at all like those of *Sepia*.

15. CRANCHIIDAE

The statocysts of cranchiids have been described recently (Young 1984). Here we shall notice those features that are relevant for comparison with other squids and for discussion of the functioning of the statocyst (figure 102). The hamuli resemble those of other cephalopods and often all five are present. The special characteristic of cranchiids is the large number and unusual position of the anticristae in some genera. These features are probably related to the adoption by the cranchiids of a head-down position, which is determined by the buoyancy of the coelomic sac, filled with ammonium, at the hind-end of the body.

The statocysts of many cranchiids are large, as in other buoyant squids, indeed several of them are among the largest relative to mantle length (table 4). However, in *Liocranchia*, *Leachea* and *Helicocranchia* they are small, both absolutely and relatively. Our specimen of *Mesonychoteuthis* of ML 1170 mm, caught by *Discovery*, has the largest statocyst of any cephalopod studied, with a calculated volume of 1.74 ml.

The shapes of the statocysts of cranchiids are very varied (table 2). The most characteristic feature is that many are very deep, indeed seven of them are among the first nine places in the list of depths in table 2; only *Bathothauma* is among the shallowest. Many are broader dorsally than ventrally, giving a butterfly shape when seen from the front, as shown by *Egea* in figure 102.

An understanding of these conditions can be obtained by considering the degree of mobility of the various genera, as suggested by N. A. Voss (1988). In three genera of the subfamily Taoniinae shown in the top row of figure 102 all the animals have small fins and weak muscles and are slow movers. The statocyst cavity is little obstructed, indeed *Bathothauma* is the only cephalopod, except the bathypelagic octopods, with no internal divisions at all. In this group the anticristae are few and small except for rather large ones in the position of 2 and 6 in *Sandalops*. The hamuli are absent, again except for small ones in *Sandalops*; presumably the cupulae are large and the statocysts are typical of animals with slow movements.

Of the three taoniine genera in the second row of figure 102, *Liguriella* has small fins and a leathery mantle and slight mobility, the other two have larger fins and a more muscular

FIGURE 102. Statocysts of the thirteen genera of the Cranchiidae, arranged to show the difference in mobility (after N. A. Voss 1988). Those in the top row have low mobility, in the second row moderate mobility, in the third and fourth rows high mobility. The three in the bottom row are the members of the subfamily Cranchiinae all with moderate mobility. All the views are from above except *Egea* (*h*) from the front and *Mesonychoteuthis* (*j*) from the front and (*k*) from the medial side.

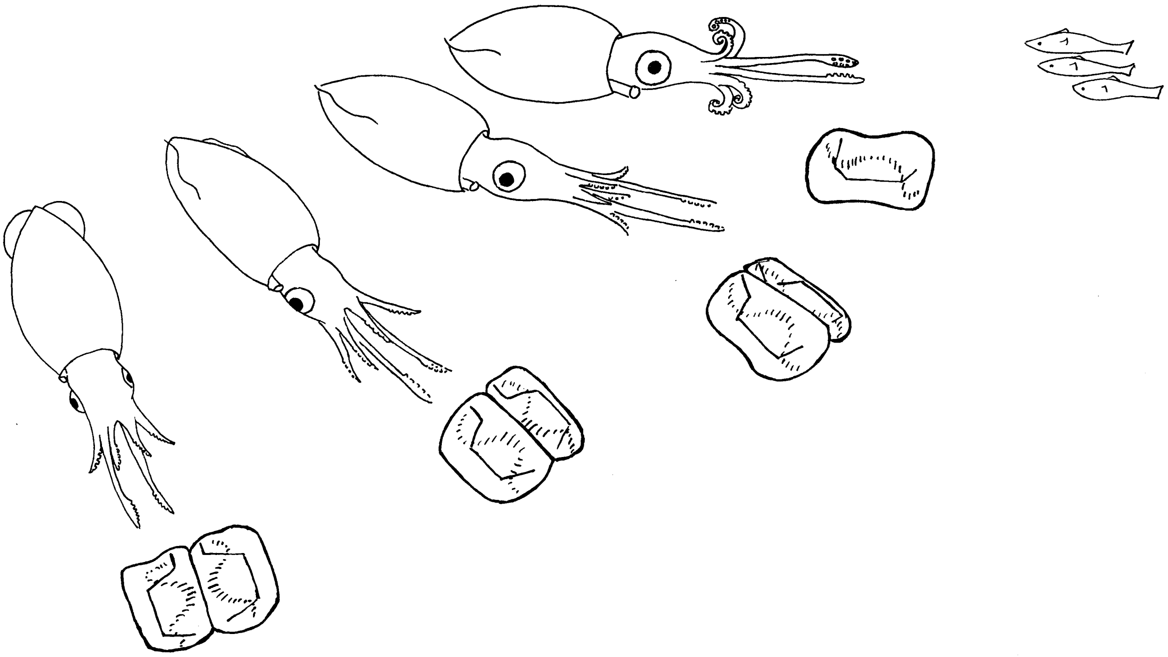


FIGURE 103. The attack of a cranchiid squid on prey above and lateral to it, showing the rotation of the statocyst, seen first from above and then finally from the side. The crista and helical row of anticristae are indicated.

mantle. The statocysts of all three are similar, with few, small anticristae but well-developed hamuli, all five in *Teuthowenia* and *Galiteuthis*; presumably this signifies smaller and less sensitive cupulae in this group, associated with moderate mobility.

The remaining four genera of taoniines shown in the third and fourth rows of figure 102 have statocysts with much greater subdivisions and the animals are all active. None of them has a very thick mantle but all are large animals with long fins and they are probably active predators. *Mesonychoteuthis* is a huge formidable creature with a mantle length of over a metre and the suckers of the tentacles carry hooks, which are also present in *Taonius* and *Galiteuthis*. In these four genera all five hamuli are present. There are numerous anticristae but they are not grouped as they are in other squids. They do not seem to be related particularly to any one of the four sections of the crista. The only projection that can be definitely compared with any of the usual set lies close to Kölliker's canal and is similar to anticrista 6. The remainder are aligned as a helical row, beginning in front ventrally and proceeding up medially, then backwards across the roof, ending lateral to the vertical section of the crista. Precisely the same spiral arrangement of anticristae is seen in the three genera of the subfamily Cranchiinae, which are shown in the bottom row of figure 102. These are smaller, active animals in which the resting position is with the head partly downwards.

The common factor in all these cranchiids with numerous anticristae is that in attacking prey that moves above them they must first turn upwards and often laterally. This would involve a spiral course of relative movement of the endolymph, influencing all four sections of the crista, whose signals would then provide the required information (figure 103). The multiplicity of the anticristae suggests that they serve to provide frictional resistance to the flow, allowing sensitivity appropriate to a higher frequency of turning.

The helical plan of the anticristae can be seen in the drawing of *Mesonychoteuthis* viewed from the front (figure 102*j*) and medial side (figure 102*k*). The frictional effect is at its maximum in *Egea*, where there are 38 anticristae on each side (figure 102*h*). Here the spiral consists of two parallel rows of thin, pointed spikes, of varying length. These, with the five hamuli and large knobs lying in the position of anticrista 6, must reduce the relative movement of the endolymph considerably. Unfortunately there are no reports of the behaviour of *Egea*: they are rather large animals with long bodies and large fins.

The unusual position of the anticristae in these cranchiids suggests that they may have been independently acquired. On the other hand the reduction of the anticristae in the other six genera suggests a paedomorphic condition. *Bathothauma* is the extreme case and N. A. Voss (1988) has considered that this genus shows a secondary paedomorphosis from a primitive cranchiid statocyst, perhaps like that of *Liguriella*. An alternative possibility is that the whole family is derived from a paedomorphic ancestor, so that *Bathothauma* most nearly represents the primitive condition (Young 1984). The new row of anticristae would then have been secondarily developed as the animals became active predators, needing to turn rapidly upwards and sideways on a spiral course.

16. Discussion

Differing arrangements in the three planes

The great variety in the structure of the statocyst among cephalopods presumably reflects widely differing needs for information about angular acceleration. To find a model with which to analyse the conditions in the various species it is important to recognize that the optimum sensitivity may not be the same in all planes. In cephalopods the systems for measuring angular acceleration are different in the three planes and in this way they are unlike the three canals of vertebrates. This arrangement allows for the provision of structures specifically suited to give signals at the frequency appropriate to each plane. This is probably the explanation for the curious irregular shape of the statocysts of the more active decapods; they are designed to measure acceleration over distinct ranges of frequency. In the upper and hinder parts of the statocyst the narrow horizontal canal allows measures at higher frequencies in the yawing plane, whereas the anterior and lower parts of the statocyst have larger cavities suited to lower frequencies in the rolling and pitching planes. The resultant shape is well seen in the lateral view, for instance in *Dosidicus* (figure 29*c*), *Todarodes* (figure 39, plate 4) or *Sepia* (figure 95*c*, plate 8). In buoyant squids on the other hand there is provision for similar sensitivity in all planes, with less emphasis therefore on canals (p. 218). In an octopus there are no canals and major influences on the sensitivity to angular acceleration are shown to be the area of the cupula and breadth of its attachment to the crista (p. 191). These factors no doubt vary among decapods as well as octopods, and in different planes; but unhappily there is no further information available about them.

In vertebrates in different species the angles between the planes of the ducts may deviate from 90 % and there are variations in the size and shape of the ducts and of the utricle. Some of these differences in dimensions are obviously appropriate to provide the required sensitivity. Thus the canals of fishes are relatively larger than those of mammals and the horizontal canal in fishes may be of smaller radius than the others to allow for more rapid turning in the yawing plane (Howland & Masci 1973).

New models

It is obviously difficult to find exact means for description of the movement of the endolymph in the complex cavities of the cephalopod statocyst but recent models devised for vertebrates may provide some help. Oman *et al.* (1987) have extended the classic torsion pendulum model of a semicircular canal to include the case where the size, shape and curvature of the canal lumen change continuously through the duct, utricle and ampulla. The parameters that they use are: (1) the length of the central streamline of the lumen; (2) the area enclosed by this streamline as projected into the plane of rotation; (3) the average inverse cross-sectional area; and (4) the average inverse squared cross-sectional area weighted by a local 'wall-shape factor'.

This procedure makes proper allowance for the wider portions of the circuit and would therefore be appropriate for treatment of the cephalopod statocyst, but the parameters would be hard to measure. Oman *et al.* (1987) show that the chief effect of the wider part of the circuit is on the long time constant of their equation.

A different approach is used by Muller & Verhagen (1988), who describe the flow in the entire labyrinth, including all the three semicircular ducts, with the common crus and utriculus. They show that the flow in each duct is not independent of the others and requires description by six terms, with three short and three long time-constants. This system also has attractions for application to cephalopods, allowing for influence of flow in the channels on each other. It does not deal specifically with the problem of the utricle, though the authors claim that it provides a solution equivalent to that of Oman *et al.* (1987).

Volume and moment of inertia

Although it is difficult to find a model that is entirely satisfactory it is clear that a factor that must be relevant in both octopods and decapods is the moment of inertia of the endolymph, I. This is the product of the mass of endolymph (m) and the square of the distance from the centre of rotation. Both of these increase with R, the radius of the sac ($I = R^2m$), so that larger statocysts provide greater sensitivity, appropriate to slow rotation. Table 4 shows the volumes of the statocysts of various species calculated from the radii.

In no cephalopod is the endolymph constrained into canals as completely as it is in a vertebrate. Therefore in any cephalopod the mass of the total volume of endolymph is to some extent effective on each section of the crista and bears some relation to I, even in animals where the endolymph is partly confined to a canal. The volumes are given in table 4 as a function of the mantle length. All the larger volumes are in buoyant animals or cirrates. The relatively smallest volumes include the large pelagic ommastrephids. The actual volume of fluid will be even smaller in these animals because the 'volume' as calculated from a product of the overall dimensions is in fact largely occupied by the large anticristae. There are only three non-buoyant forms in the upper half of table 4 and only two buoyant forms in the lower half (excluding cranchiids). This is a striking result considering the uncertainties of measurement and the unsatisfactory use of mantle length for comparisons. The cranchiids show no consistent pattern, having statocysts with wide variation in volume; evidently the factors involved are somewhat different from those in other squids (p. 227).

The absolute volumes as given in table 4 for the largest specimens emphasize the relatively small size of the statocysts, especially in large cephalopods. The largest volumes are 1740 mm^3 for *Mesonychoteuthis* and 1160 mm^3 for *Architeuthis*, both from individuals that must have weighed over 100 kg. The smallest volumes were 100 times smaller: 1.09 mm^3 for *Heteroteuthis* and 1.28 mm^3 for *Pickfordiateuthis*; animals weighing only a few grams, 100000 times less than the giants.

In young animals the statocysts are relatively very large; in freshly hatched *Loligo* they are more than one quarter the length of the whole animal (Maddock & Young 1984). Then they grow more slowly than the rest of the body, increasing by 29 times in length between hatching and the largest squid, in which mantle length had increased by 390 times. These figures emphasize that proper regulation of size of the statocyst and hence of mass of endolymph and radius of its action is essential for the functioning of the angular acceleration receptors.

Acceleration in the yawing plane

In all decapods the rounded lateral and posterior internal surfaces of the statocyst make a semicircular channel, which directs the relative movement of endolymph that activates the vertical crista. The presumed course of the horizontal flow is shown shaded on many of the drawings. These assumed flows are, of course, speculative, but may help discussion. They show at once that the canal is never a complete regular tube of constant internal radius. The outer wall of the channel differs strikingly in the lateral and medial sections, as shown for instance in the ommastrephids of figures 29–39. The lateral section is a smooth semicircular canal and this contains the inertial mass that is effective for excitation during the yaw to the same side (see figure 1*b*). The medial section is less smoothly curved and is obstructed by the dorsal members of the medial row of anticristae, which may be partly joined, though there are spaces between them. The inner face of the channel is enclosed to various extents. In the lateral 'pre-excitatory' section the wall is completed by the anticristae 6 and 7, which touch and form a complete tube in adult ommastrephids, enoploteuthids, onychoteuthids, *Lycoteuthis*, *Neoteuthis*, *Gonatus* and most loliginids. In ammoniacal squids these two anticristae are never joined but they come close together in the presumably more active forms such as *Pholidoteuthis* or *Octopoteuthis* (if these are indeed buoyant).

Anticrista 7 acquires remarkable extensions both forwards and backwards, especially in ommastrephids and enoploteuthids. This increases the length of the tube, for instance in *Todarodes* (figure 37*a*). There is always a gap between the closed section and the crista itself, which seems to be a defect of design in the system but may have some specific effect.

The medial portion of the channel, anterior to the vertical crista, is so irregular that it is difficult to estimate its likely effect on the flow. The circuit has been represented in the diagrams as more nearly complete than it probably is in reality. It is difficult to judge how far the endolymph in this medial region contributes to the inertial mass acting on the vertical crista during a yaw turn in either direction.

An attempt to estimate the extent of the horizontal canal has been made by measuring what is considered to be the total inner circumference of the canal and the proportion of it that is closed on its inner face (see p. 194). The result is shown in table 3 for all the statocysts where it could be estimated. Nearly all the non-buoyant squids appear in table 3, mostly in its upper half. The buoyant squids are all low in the table, none in the first ten. In the cranchiids the anticristae do not form a canal, and the octopods, of course, are also excluded. The canal is only strictly tubular between anticristae 6 and 7; over the rest of the circuit it is open ventrally. Nevertheless, its walls seem to influence the sensitivity of the system somewhat as they do in vertebrates.

Comparison with vertebrates

The presumed course of the horizontal channel as shown in the figures allows new measurements of the values of R and r for comparison with the condition in vertebrates, such as was attempted by Maddock & Young (1984). Table 6 shows these figures for ommastrephids, taken from the minimum diameters as seen from above and shown by shading in the figures. The previous estimates were made from projections with the microscope of the transverse diameter of the statocyst (R) and the distance between anticristae 6 and 7 (r). The values in table 6 are somewhat lower for both R and r than those in table 7 of the previous paper. This brings r closer to the value for fishes and R even further away. The difficulty in interpreting these figures is that the 'canal' has no strict inner boundary at the level of the cupula, though it is evidently narrowed here (see e.g. figure 29*b*). The values are therefore rather arbitrary and certainly too low as a measure for the whole circuit. In the fast-moving ommastrephids the canal is about twice as wide over most of its circumference as it is at the crista. There is, however, no large open space and anticrista 1 extends forwards to close the channel in front, though it remains open below (figure 29*c*). With these difficulties it is hard to make exact estimates but it is clear that the system is designed to decrease I, the effective moment of inertia and increase B, the moment of viscous friction acting on the circuit.

Table 6. Dimensions of the horizontal channel in four ommastrephid squids, together with the comparable dimensions in vertebrates as quoted in Maddock & Young (1984)

	R/mm	r/mm	R/r			
Ommastrephes	2.16	0.52	4.15			
Dosidicus	2.00	0.53	3.77			
Illex	1.58	0.30	5.27			
Todarodes	2.18	0.45	4.84			
Mean	1.98	0.45	4.40			
				W_1/Hz	W_2/Hz	W_1/W_2
human	3.15	0.14	23	50	0.017	2941
mammals	2.30	0.12	19	70	0.023	3043
fish	5.99	0.23	26	19	0.013	1461
Ommastrephidae	1.98	0.45	4.4	6	0.410	15

According to the theory developed by Wilson & Jones (1979) as explained on page 193, these values influence the upper and lower frequencies, W_1 and W_2 respectively, over which the canal provides a reliable measure of angular velocities. The low value of r in cephalopods is especially important because it raises the likely upper-frequency value, $W_1 = B/I \propto R/r_2$. In other words, the narrower channels are suited to higher frequencies. This of course agrees with the presence of narrow horizontal channels in the faster squids.

These new values do not alter the qualifications that must be considered in using this model to compare cephalopods and fishes. The fundamental assumption is that r is much less than R and with the new figures this clearly is no nearer true than with the old figures. Moreover, no account is taken of the fact that the canal is a complete tube only for a part of its circumference. With these considerations Maddock & Young (1984) suggested that perhaps the horizontal canal system in cephalopods does not measure angular velocity but acts as an angular accelerometer. The work of Williamson & Budelmann (1985*a*) showed that the crista of *Octopus* signals velocities and it seems likely that this is so also in other cephalopods, perhaps by the properties of their cupulae. If so the horizontal canal of squids presumably serves to ensure reliable response at the appropriate (high) level of frequency. This channel is obviously constructed in non-buoyant squids so as to limit the volume of endolymph and hence the moment of inertia I, and also to add a moment of viscous friction B by enclosure in a canal and obstruction by anticristae. According to the torsion pendulum model both of these effects would tend to raise the upper limit of frequency of coding for velocity because $W_1/W_2 \propto B^2/KI$. It seems clear that similar factors are operating in cephalopods and fishes, together with differing factors, perhaps especially those concerned with the cupulae. Table 6 shows the upper and lower frequencies in the velocity transducing range as calculated from the constants used by Wilson & Jones (1979) for man. The 'canals' of the ommastrephids approach those of vertebrates more closely than in other squids but the differences are still great. The frequencies suggested by the calculations seem reasonable, but many assumptions are involved. Direct experimental observations are urgently needed to show whether the decapod cristae code for velocity or acceleration. The restrictions on the endolymph imposed by the partial canals of decapods apparently serve to raise the upper limit W_1 above that in *Octopus*, which appears to be about 2 Hz. The fact that R/r is lower in squids than in fishes suggests that the upper limit is lower than 19 Hz.

Angular acceleration in the rolling plane

In most squids rolling is perhaps rather slow except for sudden unexpected jerks. The endolymph does not flow across the lateral crista in a closed canal but moves in a deep pocket made by a ventral sac, which increases the inertial mass acting in this plane. The cavity is often partly divided into deeper anterior and shallower posterior parts, with the medial row of anticristae between, for example in *Todarodes* (figure 39, plate 4). It is not clear whether these two regions are separately related to the first and second sections of the crista. The anticristae of the medial row 2–5 presumably have some effect on the flow (see *Doryteuthis*: figure 68, plate 6). In *Alloteuthis* (figure 72*a*, *b*, plate 6) the complex anterior anticristae 1 and 1a also lie in this plane and perhaps provide some friction to adjust the sensitivity to a high level of frequency of rolling in these animals, which often have long tails.

Unusual features of this vertical channel are seen in *Ctenopteryx* (p. 214), where the high hamulus 2 and large anticrista 6 make a narrow vertical channel, interrupted on its medial side by numerous pointed anticristae (figure 55*a*, *b*, and figure 56, plate 5). This suggests suitability for a rather high range of frequency, which may be connected with the curious fin running along the sides of the body and supported by cartilages (hence the name, 'comb fin'). Restriction of this channel in animals with long fins is also suggested by *Sepia*, where the channel is narrowed by a large hamulus 2 and the large anticristae of the median row. In most squids there is no hamulus at the first turn, but it is present in a curiously restricted set of genera: *Neoteuthis*, *Joubiniteuthis*, *Grimalditeuthis*, *Chiroteuthis*, *Bathyteuthis*, *Pyroteuthis*, *Pterygioteuthis*, *Thysanoteuthis*, many cranchiids and *Spirula*. Some but not all of these have long fins, like *Ctenopteryx* and *Sepia*. *Discoteuthis* and *Octopoteuthis* have long fins but no hamulus 2. So there is no obvious functional or phylogenetic significance for its presence (see p. 236).

Angular acceleration in the pitch plane

The more anterior part of the sac at the front end of the statocyst serves for the passage of endolymph across the first section of the crista. This is well seen in the section of *Onycoteuthis* on figure 49, plate 4. The possible course of the circulation in this plane is shown for *Alloteuthis* in figure 72*a*, plate 6: in this way it would act upon both the anterior and posterior transverse cristae. The anticristae of the median row probably partly obstruct and disturb this circulation (see, for instance, *Enoploteuthis*, figure 42*a*, *b*. This is usually a broad channel tuned to a lower frequency than the horizontal canal. The anterior and posterior transverse cristae presumably give complementary signals during positive and negative pitching, although they do not run precisely parallel to each other.

Statocysts and buoyancy

The similarity of the statocyst in *Sepia* and *Loligo* shows that its form is related to speed of movement rather than to buoyancy. However, many buoyant cephalopods have weak muscles and move and turn slowly; correspondingly their statocysts are large and relatively little interrupted by anticristae, providing high sensitivity at low frequency. Thus cirrates, pelagic octopods and *Vampyroteuthis*, as well as buoyant oegopsids, mostly appear higher in the list of relative volumes than the non-buoyant forms (table 4). Again, the buoyant squids mostly show a smaller proportion of the horizontal channel enclosed by anticristae (table 3). Probably these animals live with the body oriented in varying directions and the statocysts are correspondingly suited for turning in all planes.

Unfortunately no evidence is available to show whether with these conditions the statocysts of buoyant cephalopods provide signals of angular acceleration or velocity. Because these neutrally buoyant animals have imperfect canals the measurements of R and r are not perhaps of great value but they show a still further departure from the vertebrate condition than do the non-buoyant forms (Maddock & Young 1984). Possibly also the endolymph behaves differently under the conditions of temperature and pressure at great depths.

The condition of the cranchiidae has already been considered. Those that have weak muscles, like *Bathothauma*, have relatively large statocysts and few anticristae (figure 102). However, the volumes are very varied, as seen in table 4. Where there are many anticristae they are set in a helix, whose possible relation to the method of attack is shown in figure 103.

Differences between the statocyst in Octobrachia and Decabrachia

It is not easy to understand the wide difference between the statocysts of these two main groups, especially because it seems likely that the octopod condition was derived from something more like that of decapods (p. 235). In *Octopus*, locomotion involves both walking and swimming and the two types of cupulae have been evolved to provide cover for a wide range of frequencies (p. 191). The orientation of the crista is less sharply restricted to three planes than in decapods. This may possibly be connected with the use of only one eye for attack. Perhaps all the sections of the crista signal to some extent during turning in any plane, although the anticrista seems to limit the flow across the vertical section, providing greater sensitivity in the yawing plane, as in decapods.

Variations in sensitivity among some Octobrachia

The ranges of sensitivity provided by the two types of cupula in *Octopus* are presumably appropriate to its various speeds of movement. Although these seem to be set largely by the properties of the cupulae themselves, the moment of inertia, I, of the endolymph must be another important factor. Table 4 shows that this varies considerably among Octobrachia. The length of the statocyst of *Octopus* relative to mantle length is smaller than that of any of the pelagic Octobrachia except *Argonauta* and much smaller than in cirroctopods. In these last the larger radii and volumes presumably provide the greater moment of inertia and hence greater sensitivity appropriate to slow turning in deep water by these animals with weak muscles (see Aldred *et al.* 1983).

It is striking that both types of pelagic Octopoda show a division of the crista into nine sections in spite of the fact that they do not 'walk' on the bottom. It will be interesting to discover whether these animals have two sorts of cupulae. In the cirrates in the absence of any sharp subdivision of the crista it is difficult to know how the cupulae are placed and further study is needed.

The anticristae of Octopoda

The only restriction to the flow of endolymph in Octopoda is provided by the single anticrista. From its position its action seems to be to limit the flow across the vertical section of the crista. This may serve like the horizontal canal of decapods to limit sensitivity to levels appropriate to high frequency in the yawing plane, but this has not been examined experimentally. The anticrista is relatively larger in *Octopus vulgaris* and *Eledone* than in other species of *Octopus* examined, but further data on its variations are needed. The anticrista is probably relatively smaller in all the epipelagic octopods than in the benthic forms, though no detailed measurements are available. It is altogether absent in *Japetella* and other Bathypelagoctopoda, which probably turn very slowly.

The multiple anticristae in *Vampyroteuthis* and some cirroctopods provide a functional and evolutionary puzzle (p. 204). Their presence in these animals, as in decapods, is possibly connected with the need to monitor movements in various planes during swimming with the fins. Reduction to a single anticrista in Octopoda may thus be a consequence of life on the bottom and swimming only by a jet.

The presence of a perilymph in Octobrachia and *Vampyroteuthis* is another functional and evolutionary mystery that remains unexplained. Indeed, it has never been investigated. The perilymph may have some effect on the movement of endolymph, as has been suggested in vertebrates (see Wilson & Jones 1979). However, in both groups it is interrupted by numerous supporting strands and blood vessels, which must greatly restrict movement of the perilymph.

Evolutionary considerations

The statocysts provide some striking evidence of evolutionary affinities lying behind the strong functional forces by which they have been moulded. The presence of a perilymph sac in Octobrachia and *Vampyroteuthis* is perhaps a new apomorphic character acquired after they diverged from the Decabrachia, perhaps in the later Triassic. The presence of several anticristae in *Vampyroteuthis* and in some cirrates is evidently a very ancient feature, which they share with the ancestors of the decapods. The division of the crista into nine sections is a unique apomorphic feature of the order Octopoda; it is not present in Cirroctopoda, which presumably never possessed it. The feature was possibly developed to provide for the wide range of frequency of turning during walking and swimming. It is surprising to find that the crista is still so divided in all the pelagic octopods examined.

The pattern of arrangement of the hamuli and anticristae is strikingly constant throughout the Decabrachia, except in cranchiidae. It is clearly recognizable in most teuthoids and in *Sepia*, *Spirula* and sepiolids; it must be a very ancient feature. The pattern can be recognized also in *Vampyroteuthis*, but it is not clear in the cirrates. The common pattern must be based on a common genetic background, which allows modification in all the various directions required to monitor the different movements needed for life in the various parts of the sea that have been colonized by decapod coleoids.

The pattern is constant within each family of teuthids, for instance Ommastrephidae or Loliginidae, but the statocyst is not much help in identifying relationships between families. The presence or absence of hamulus 2 has been mentioned (p. 233). This hook is present in *Joubiniteuthis*, *Grimalditeuthis* and *Chiroteuthis*, which are thought to be related (Clarke 1988) but absent from *Mastigoteuthis*, usually placed in the same group. It is present also in *Thysanoteuthis*, sometimes suggested as belonging to the above group; but it is absent from the Cycloteuthidae. The presence of hooks at each turn of the crista might be supposed to be the ancestral condition, and they are all present in *Spirula*. The presence of a hamulus at the first turn in many cranchiids suggests that the family diverged early, perhaps from ancestors common to the *Chiroteuthis* group mentioned above.

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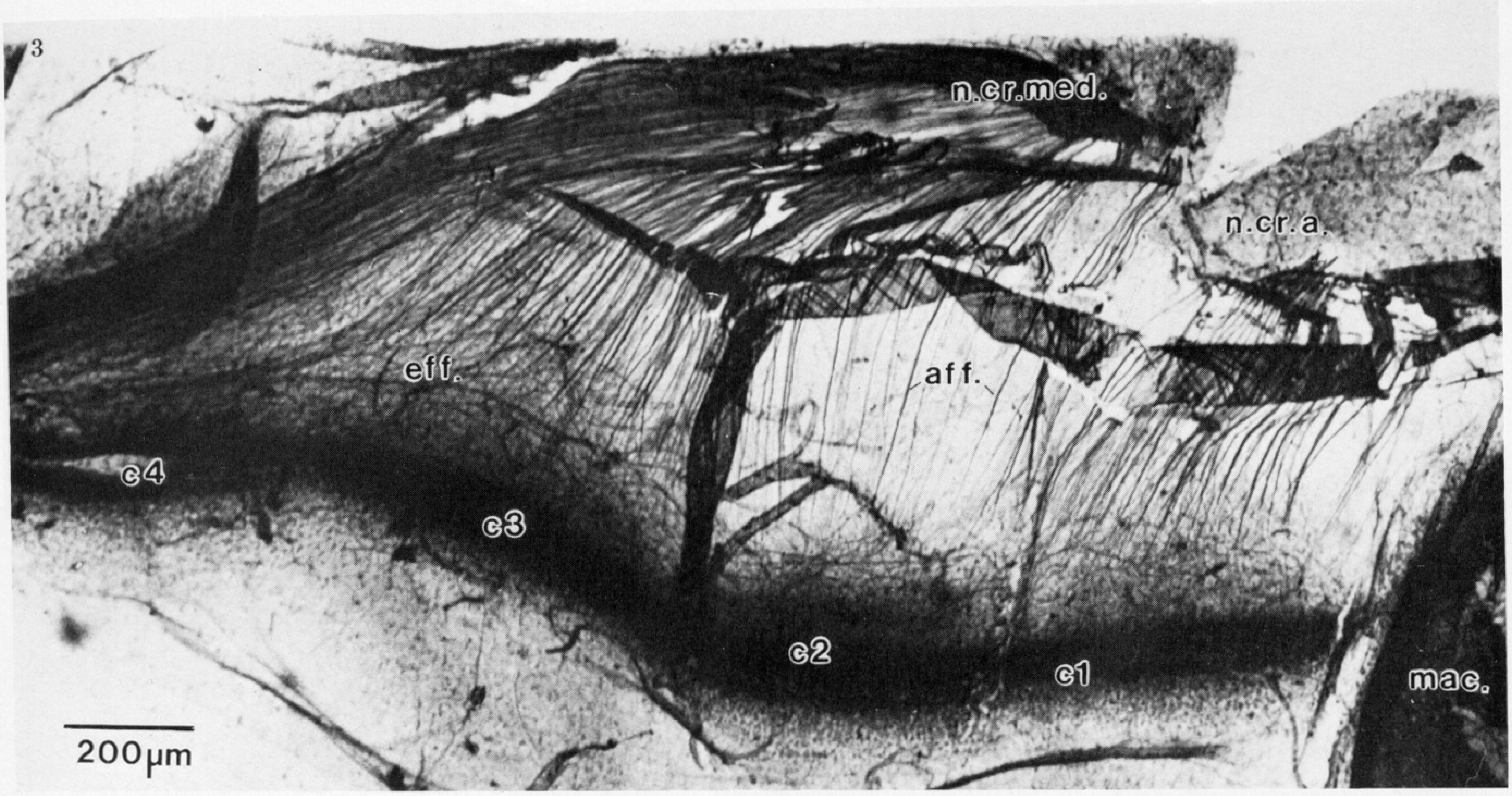
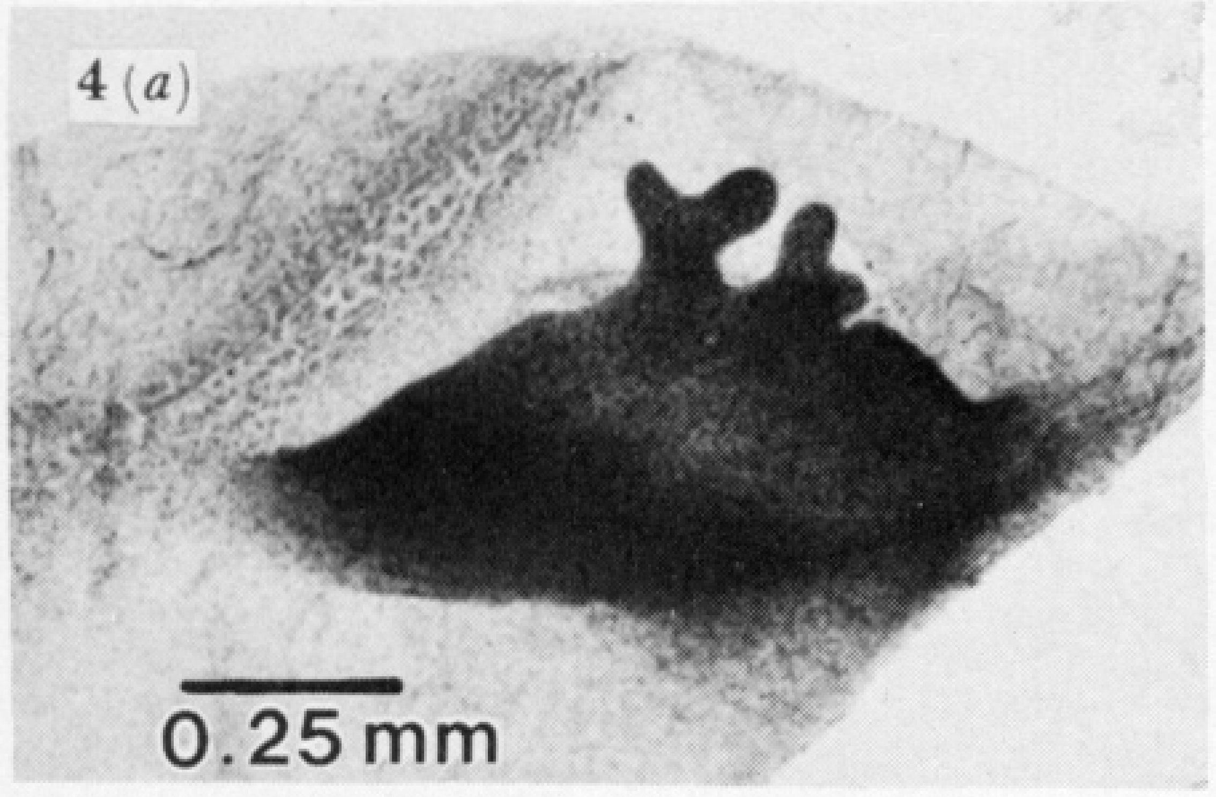
ABBREVIATIONS USED ON THE FIGURES

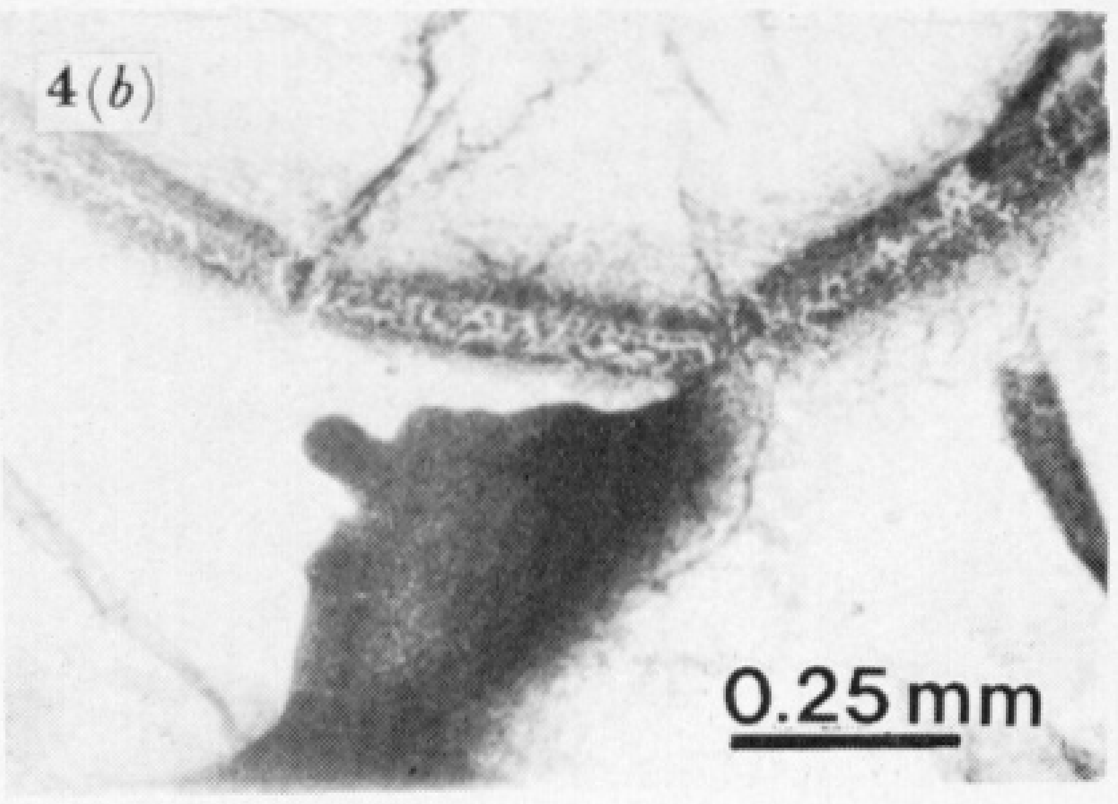
ac.	anticrista (also numbered 1–7)	Kol.	Kölliker's canal
aff.	afferent nerve fibres	mac.	macula
C_1, C_2, C_3, etc.	sections of the crista	n.cr.a.	anterior crista nerve
cr.	crista	n.cr.med.	medial crista nerve
cup.	cupula	n.cr.p.	posterior crista nerve
eff.	efferent nerve fibres	n.mac.	macula nerve
g.opt.	optic gland	st.	statocyst
h1, h2, h3, h4, h5	hamuli	stl.	statolith

The size indicated on the figures is always 1 mm, except where indicated.

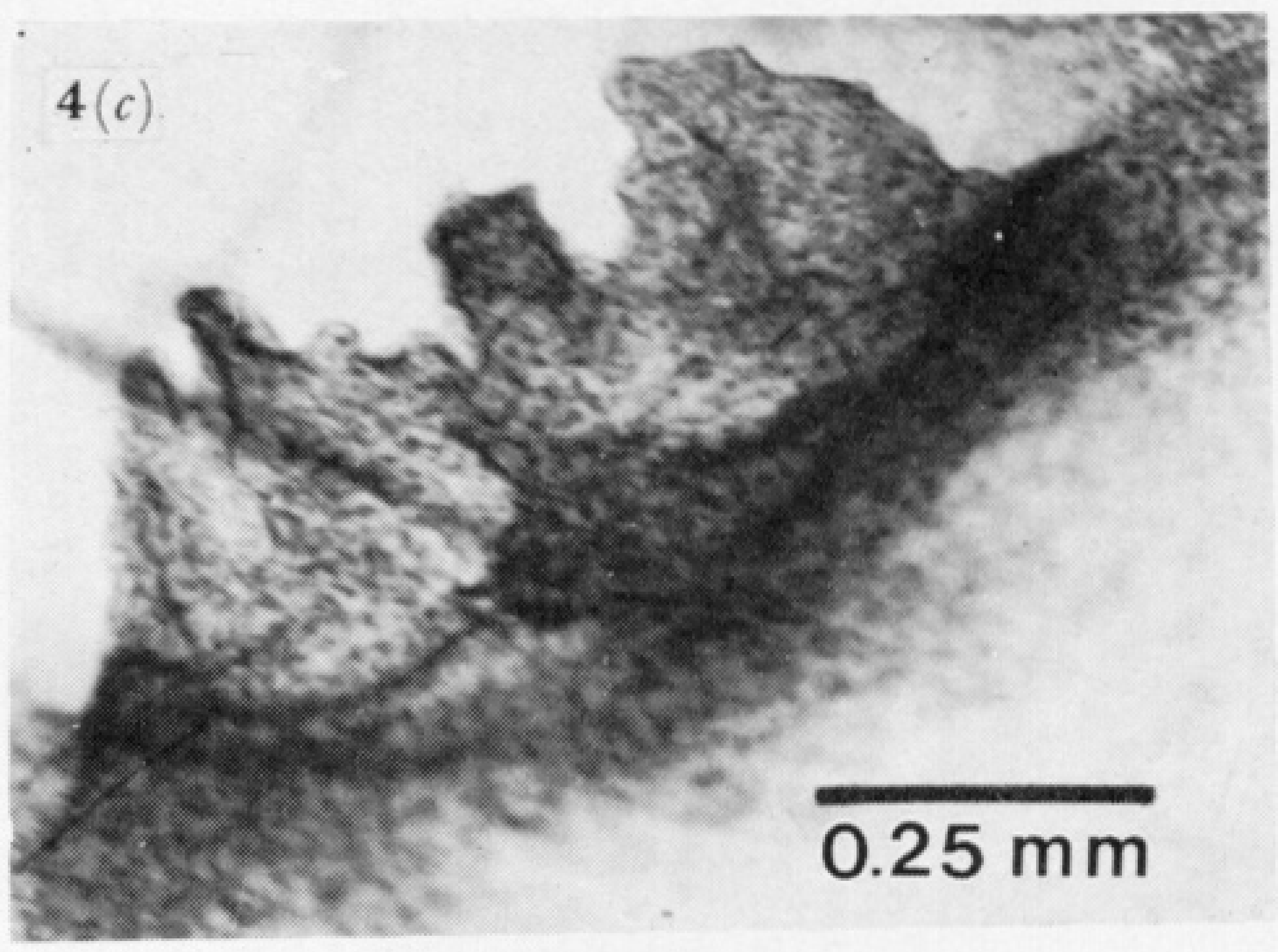




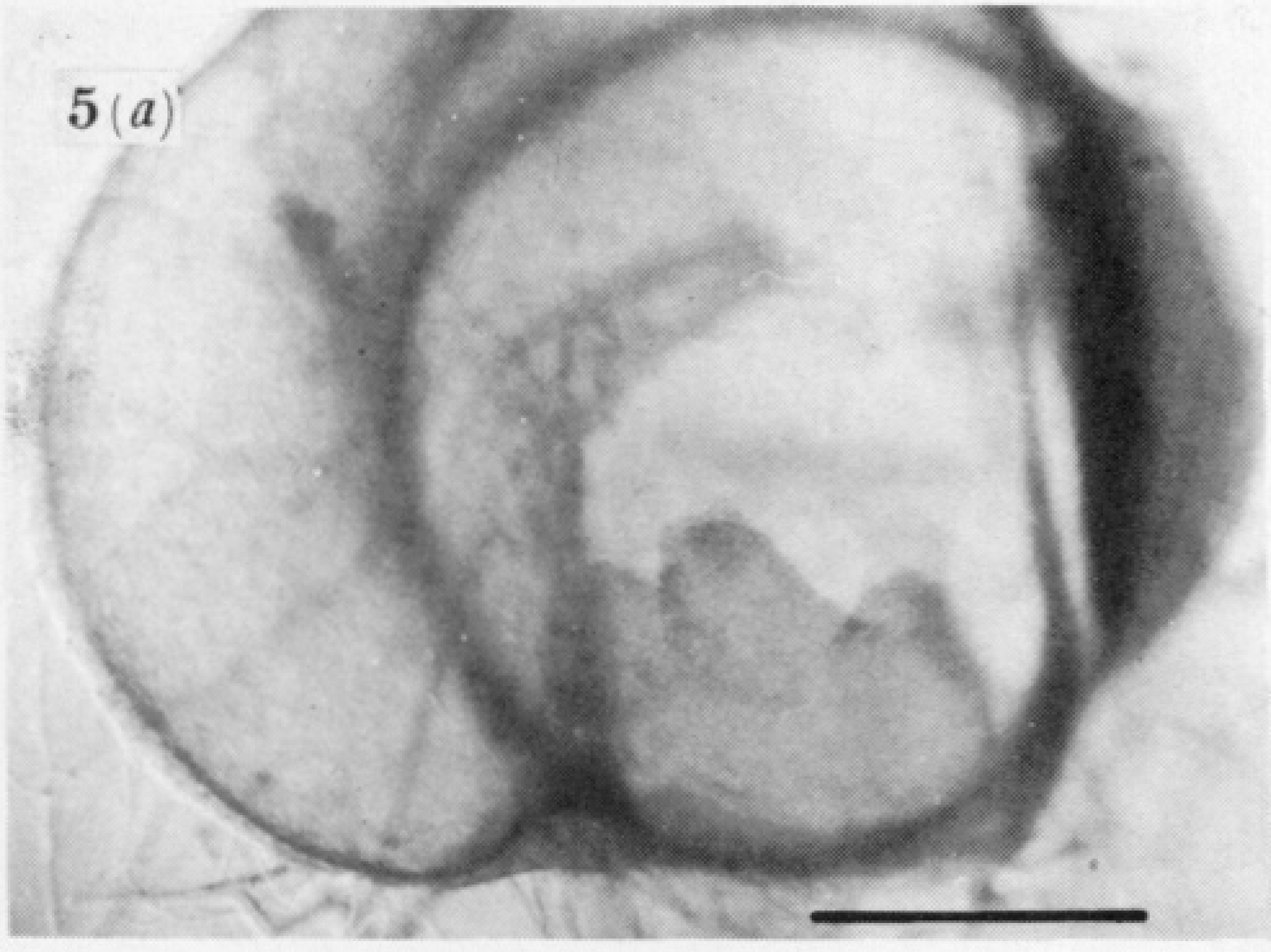
O. vulgaris



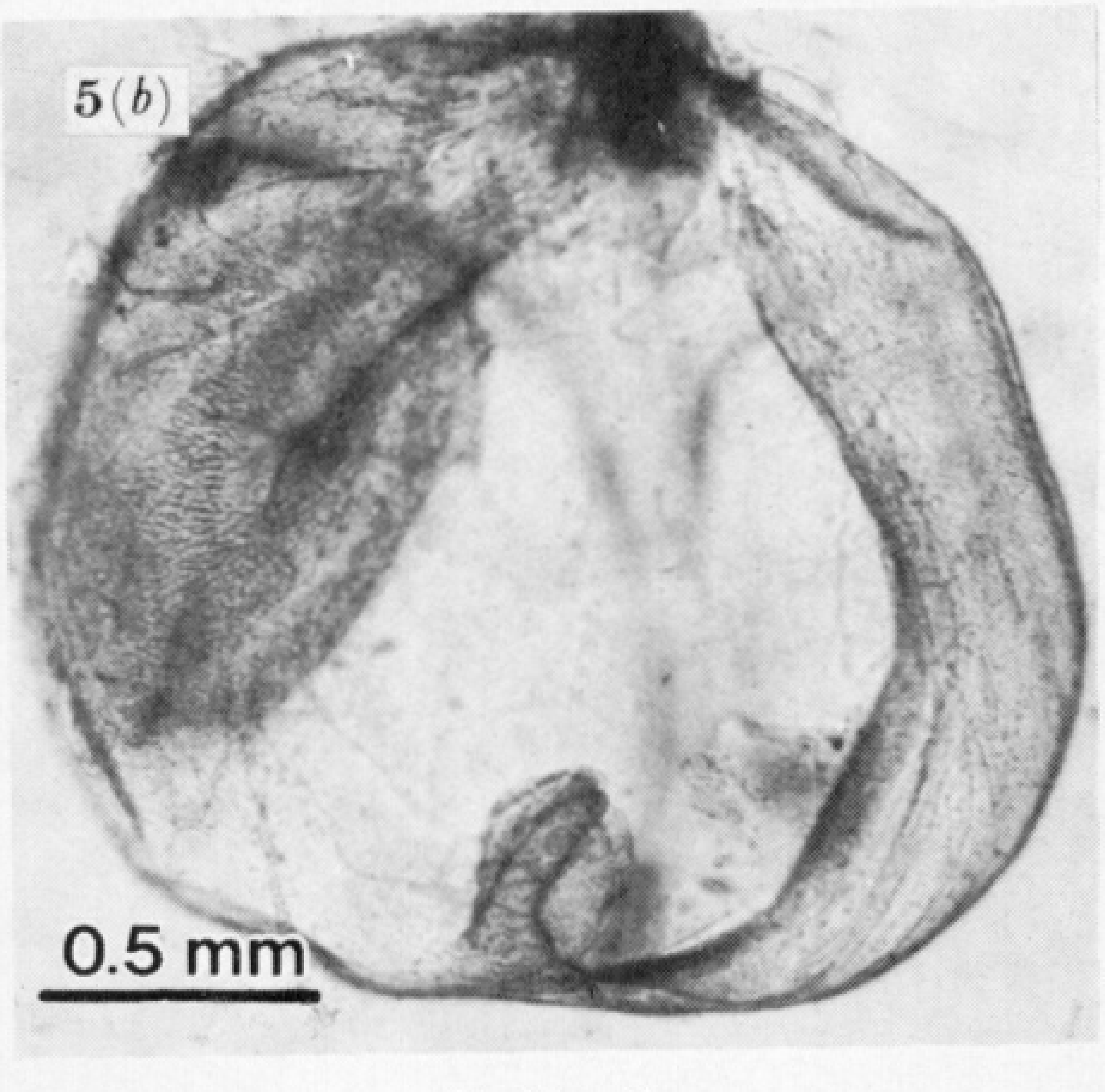
O. vulgaris



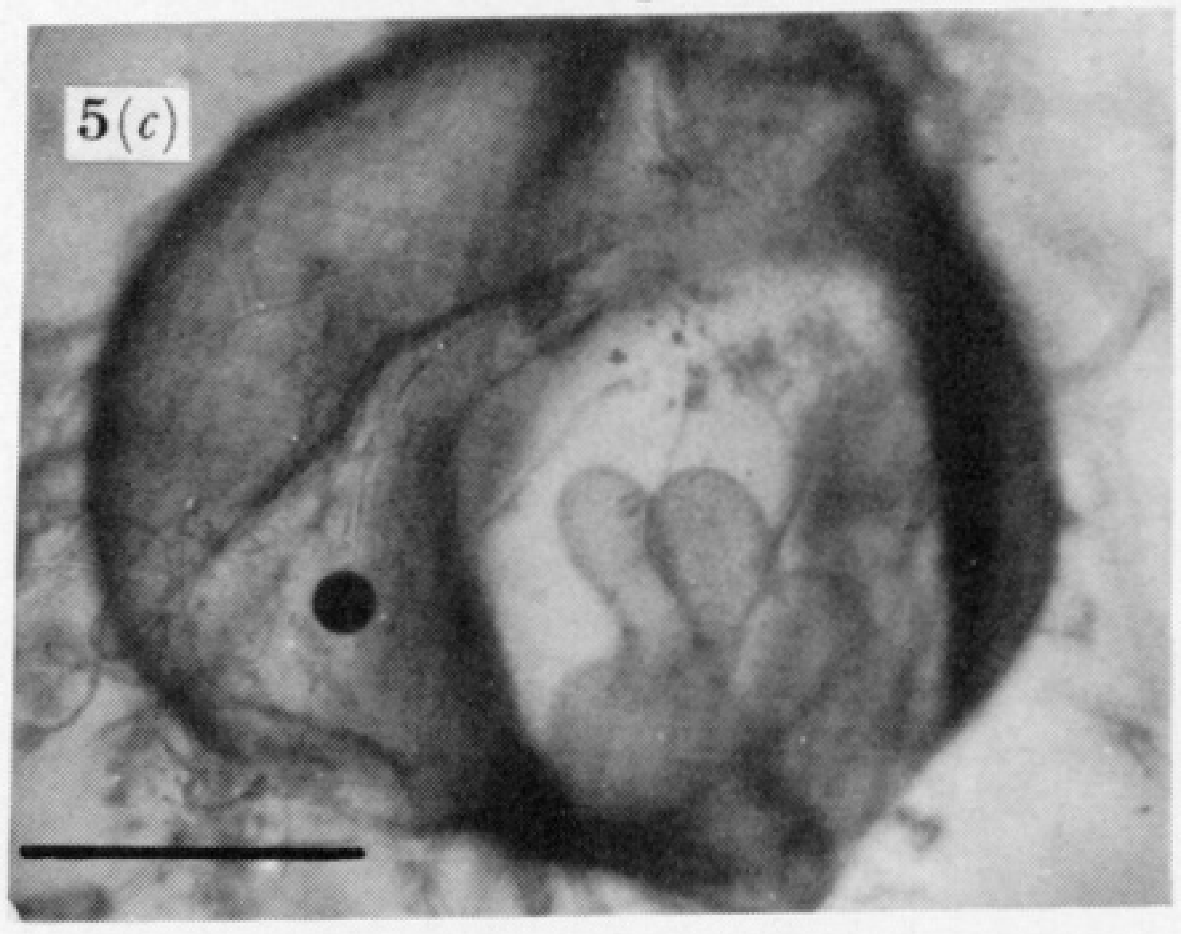
O. macropus



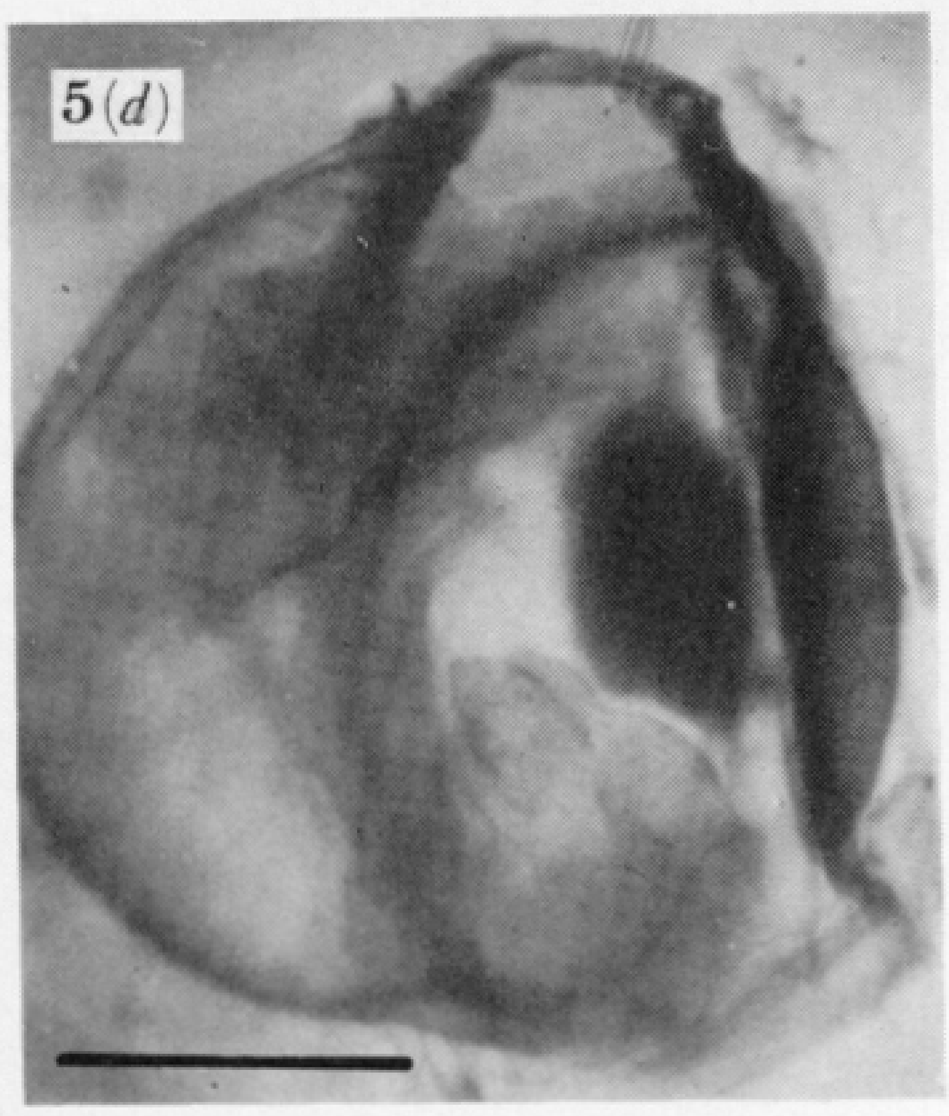
O. maya



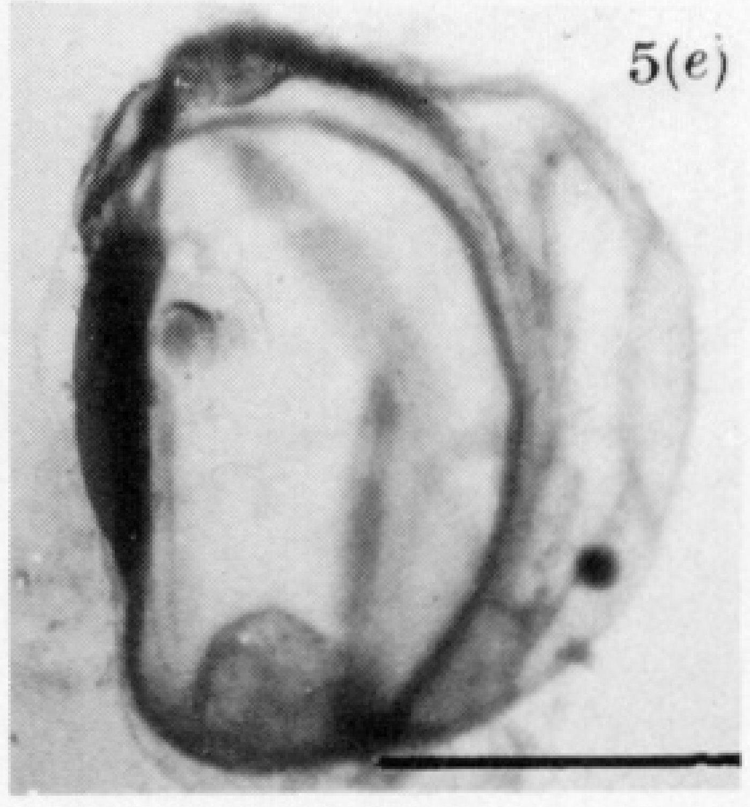
O. digueti



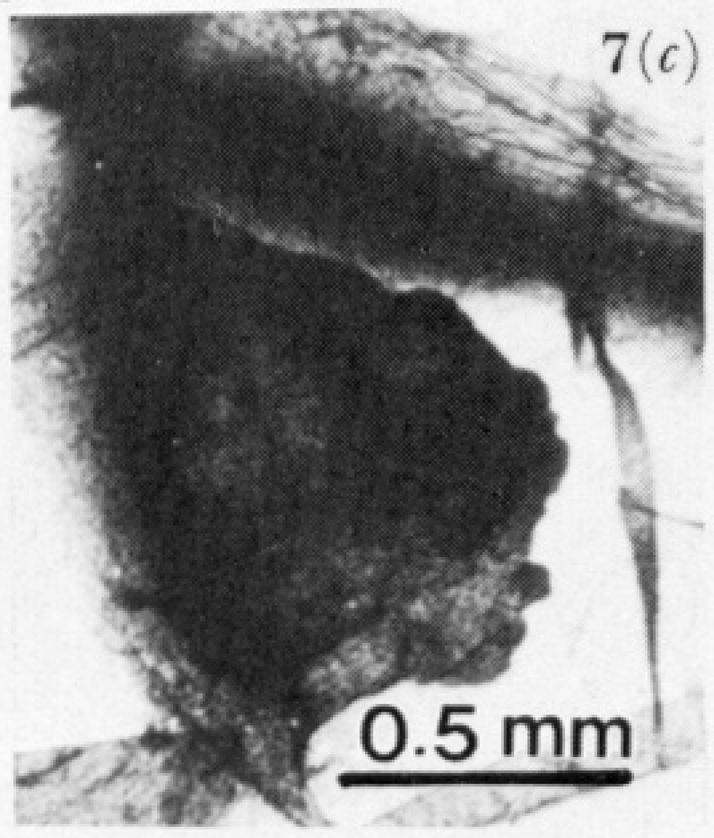
O. bimaculoides



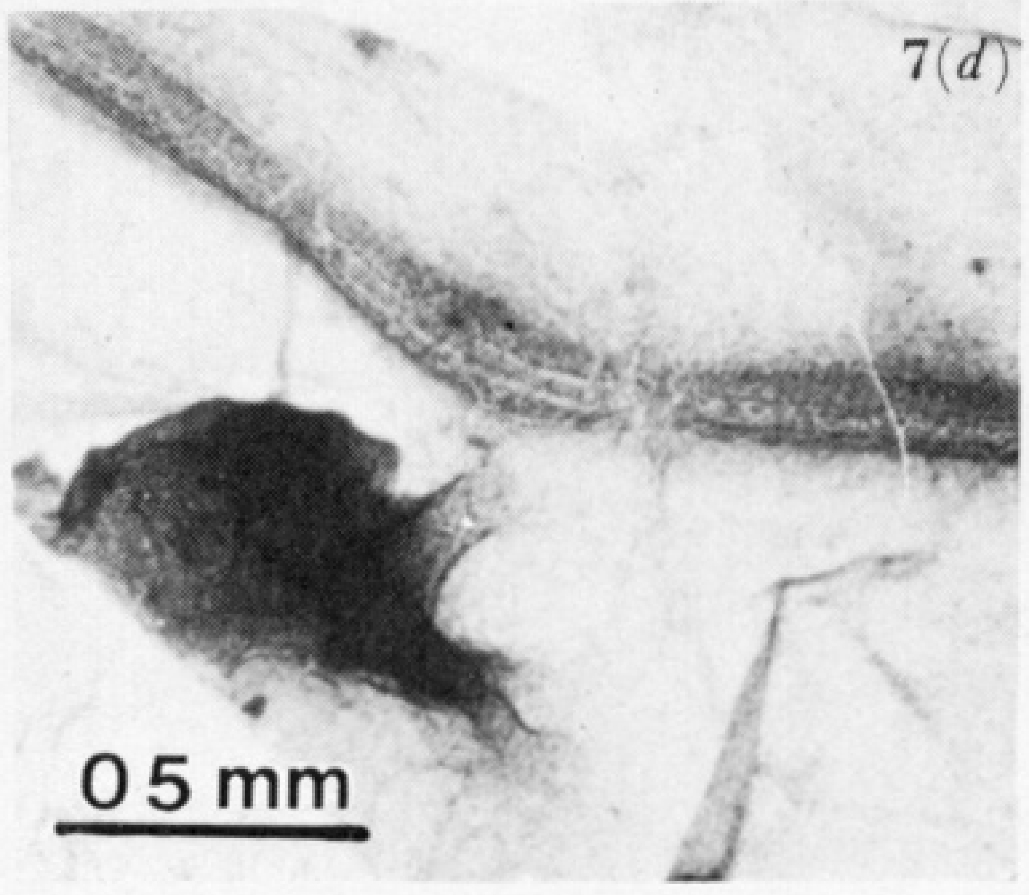
O. briareus



O. joubini

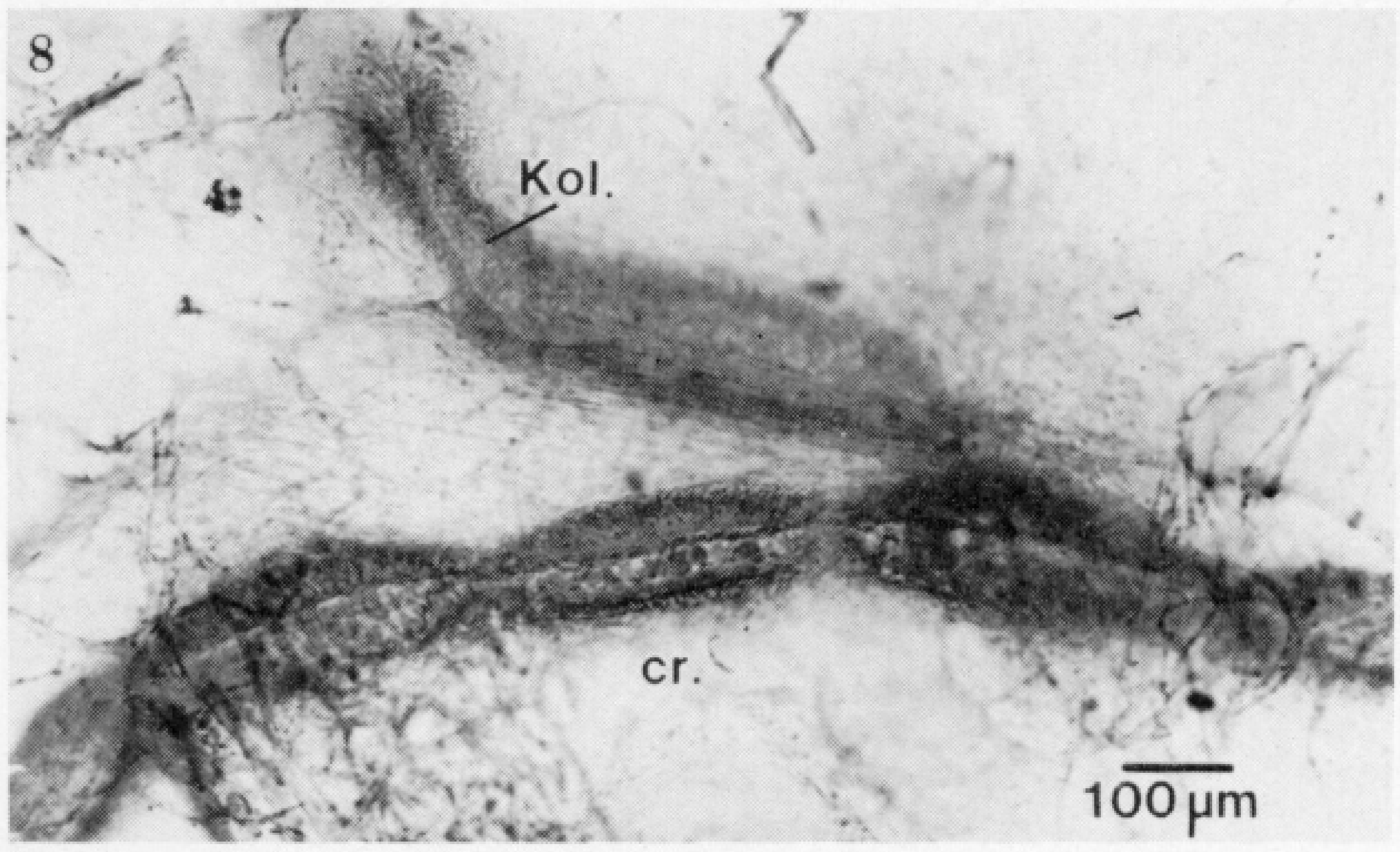


E. moschata

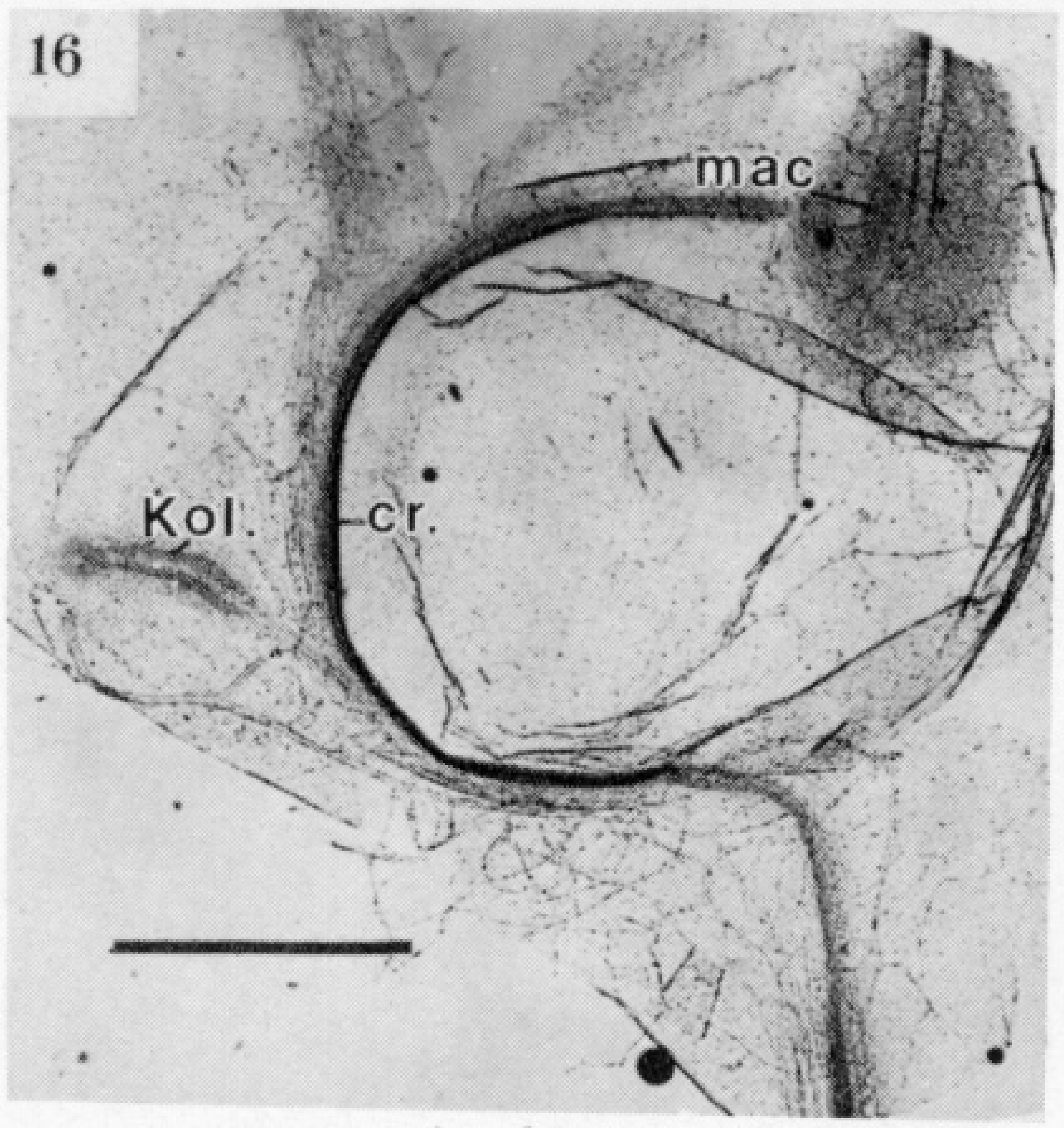


E. cirrhosa

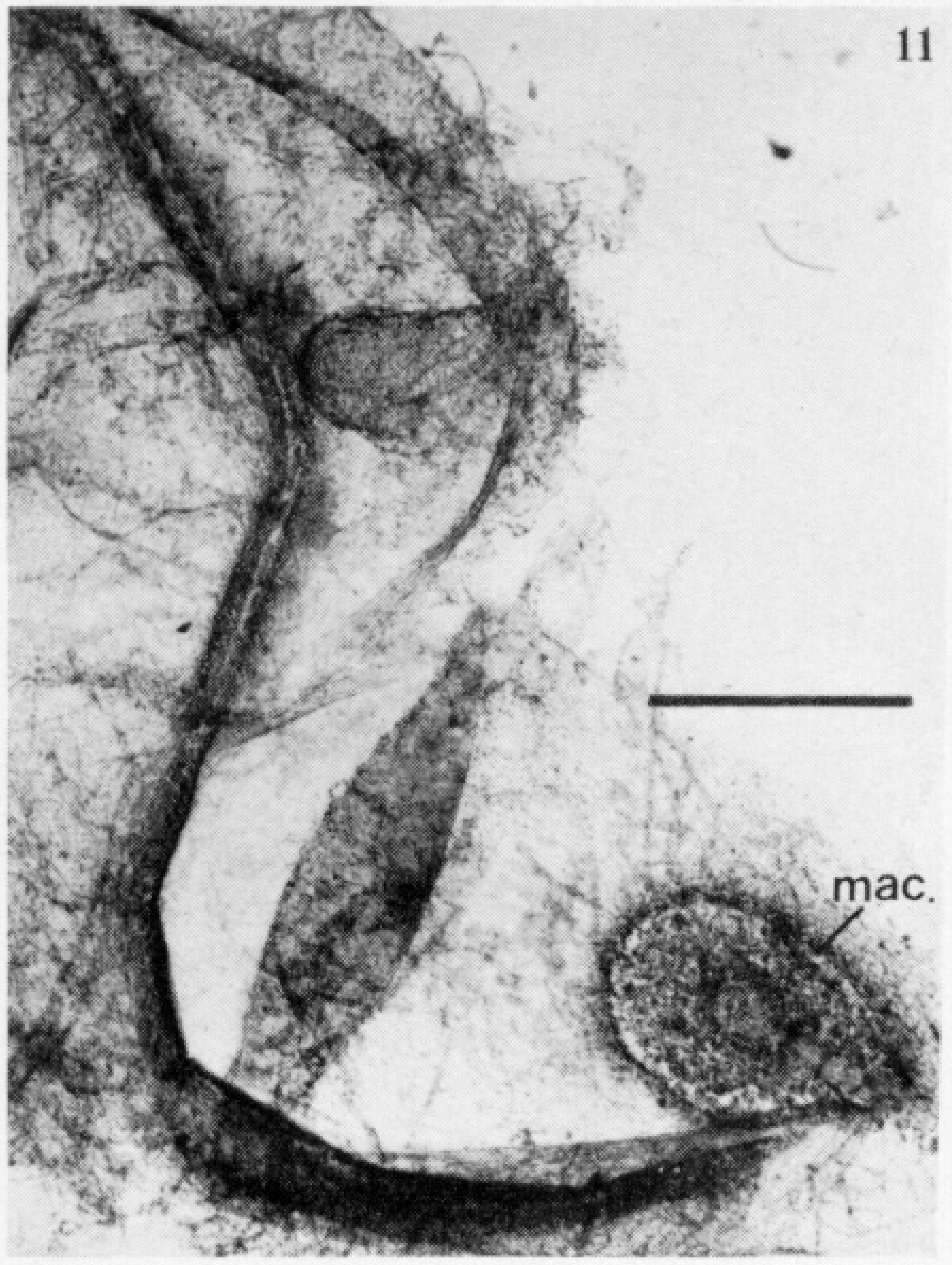
FIGURES 3–5 AND 7. For description see opposite.



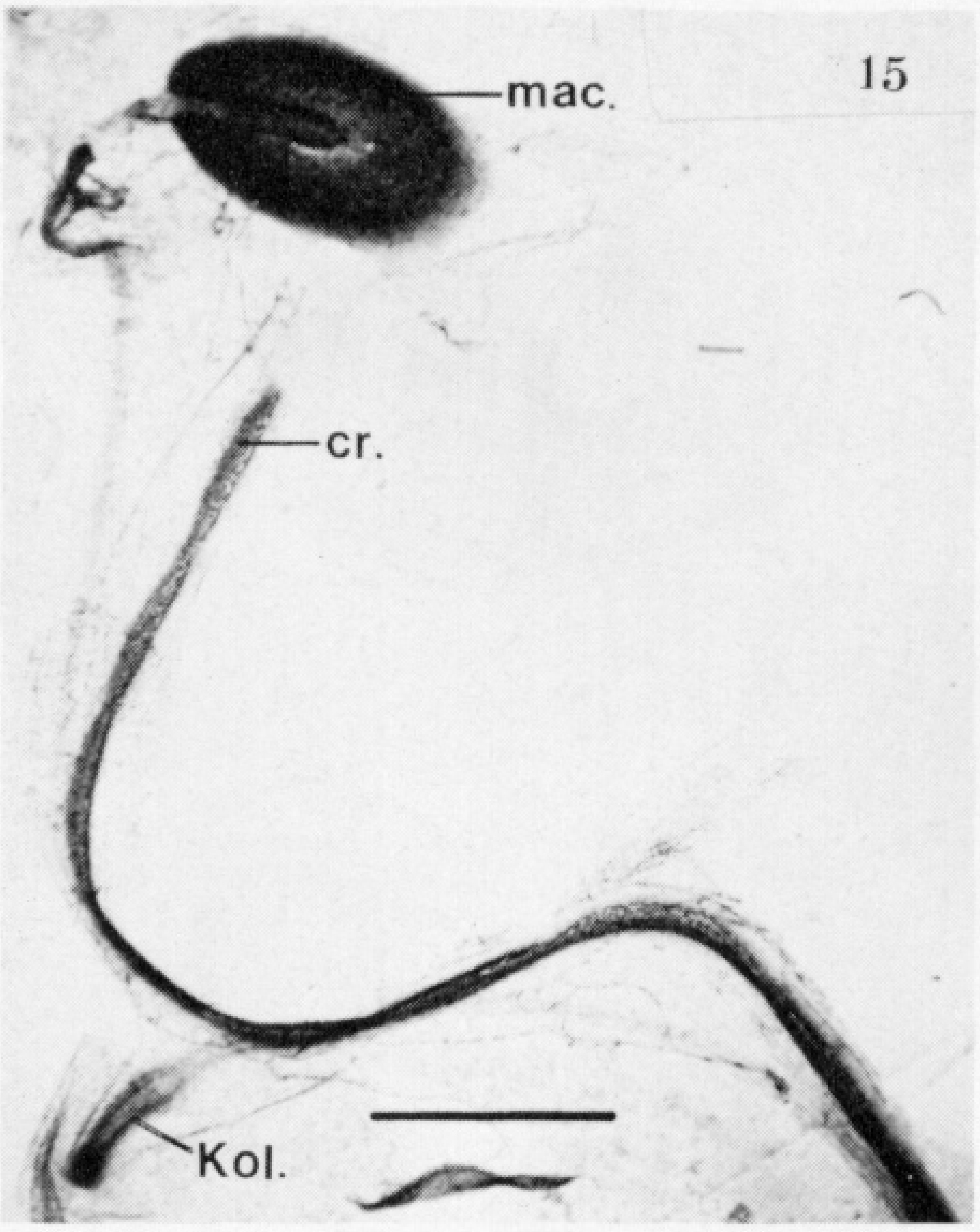
Argonauta



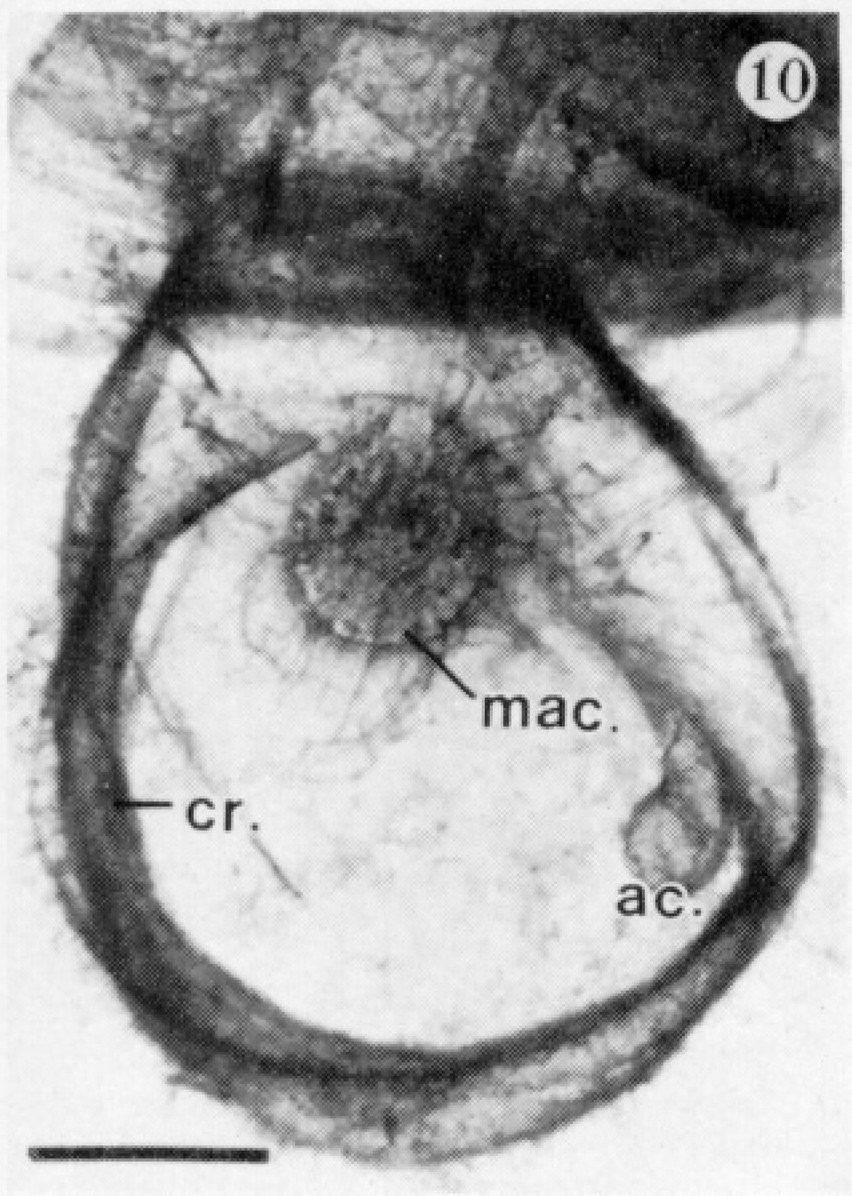
Amphitretus



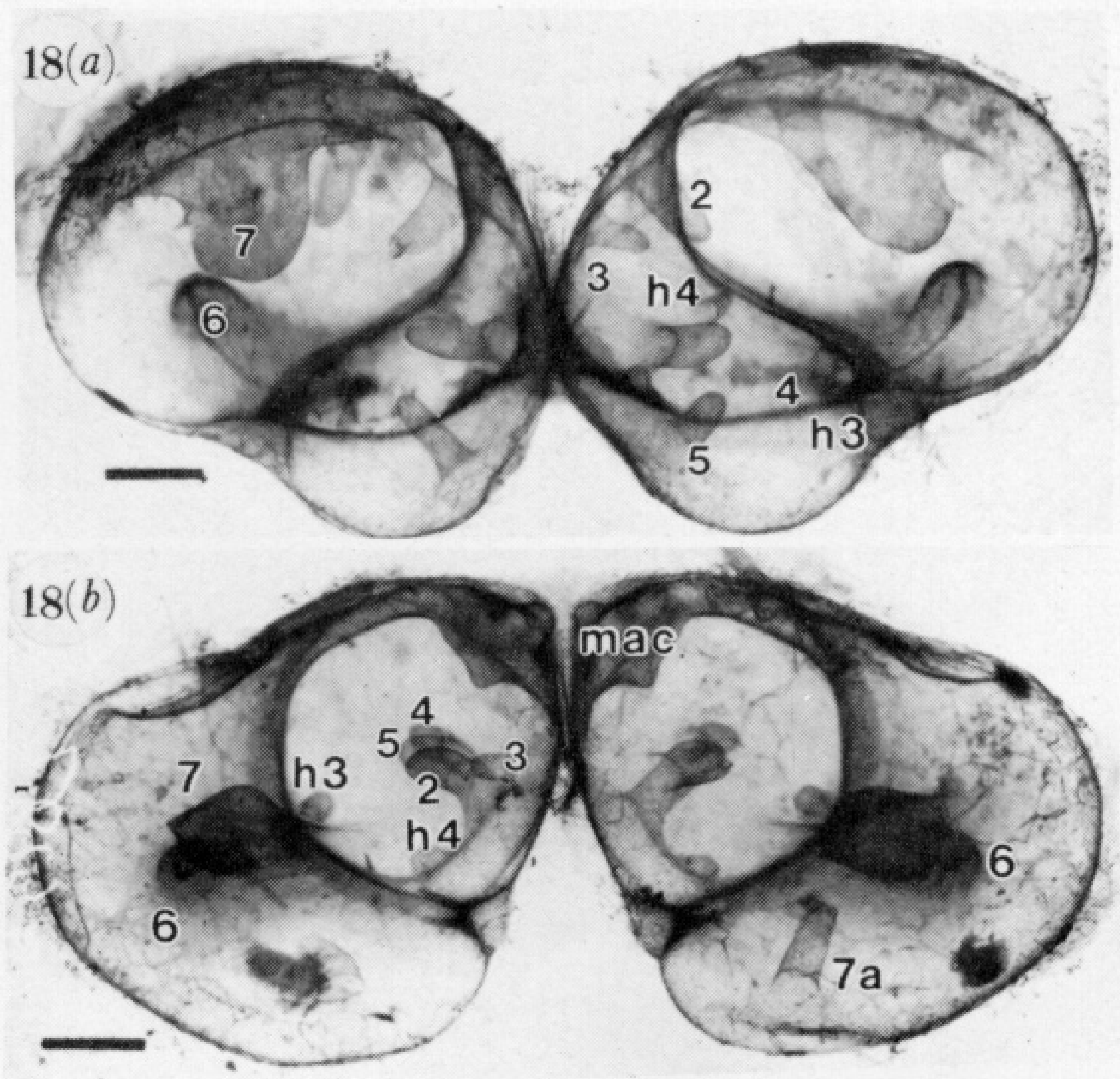
Tremoctopus



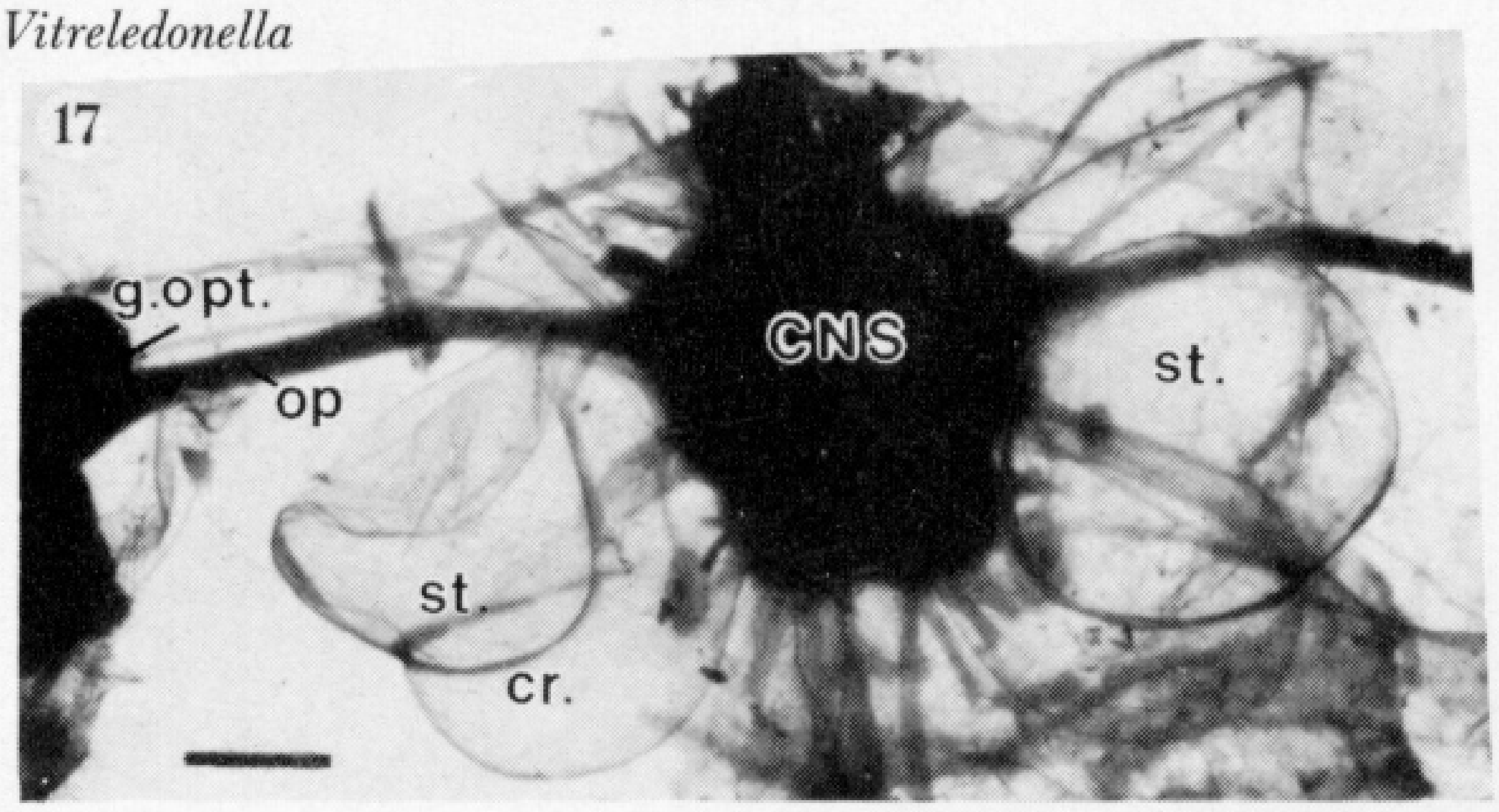
Vitreledonella



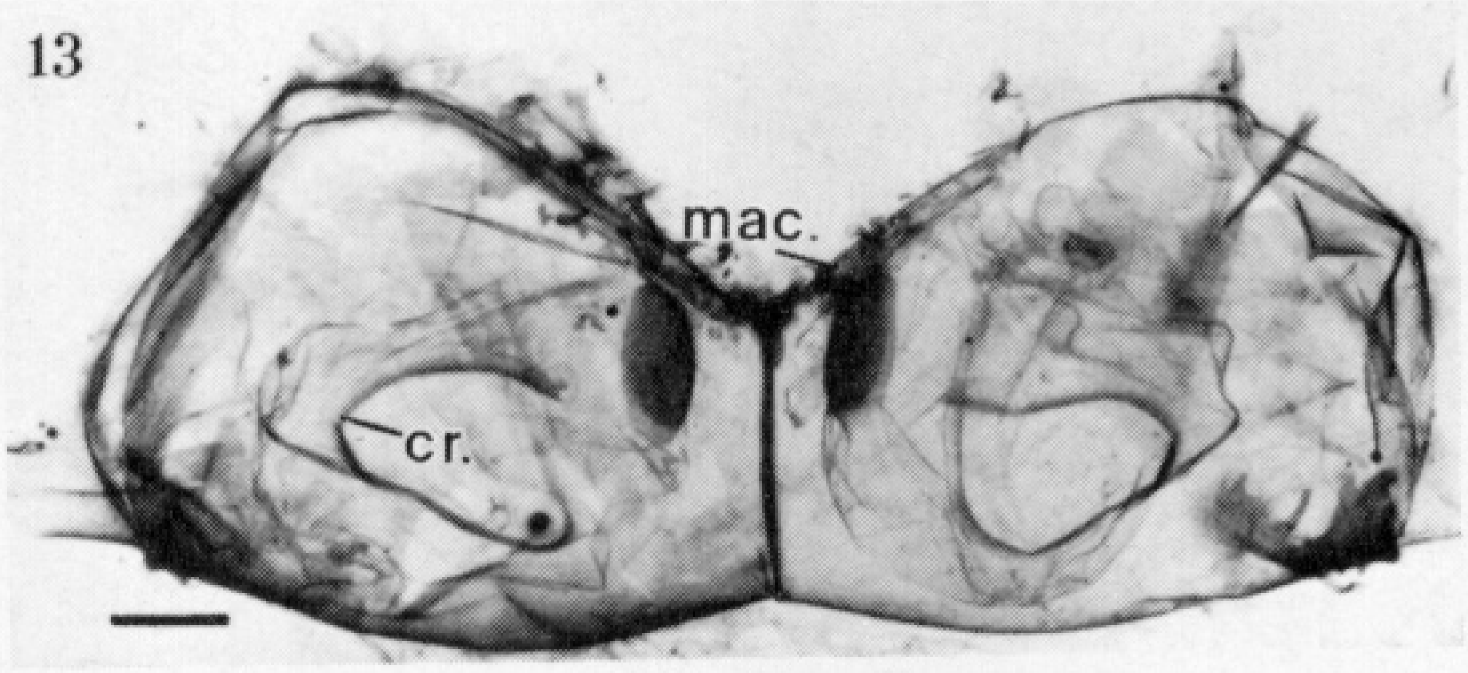
Tremoctopus



Vampyroteuthis

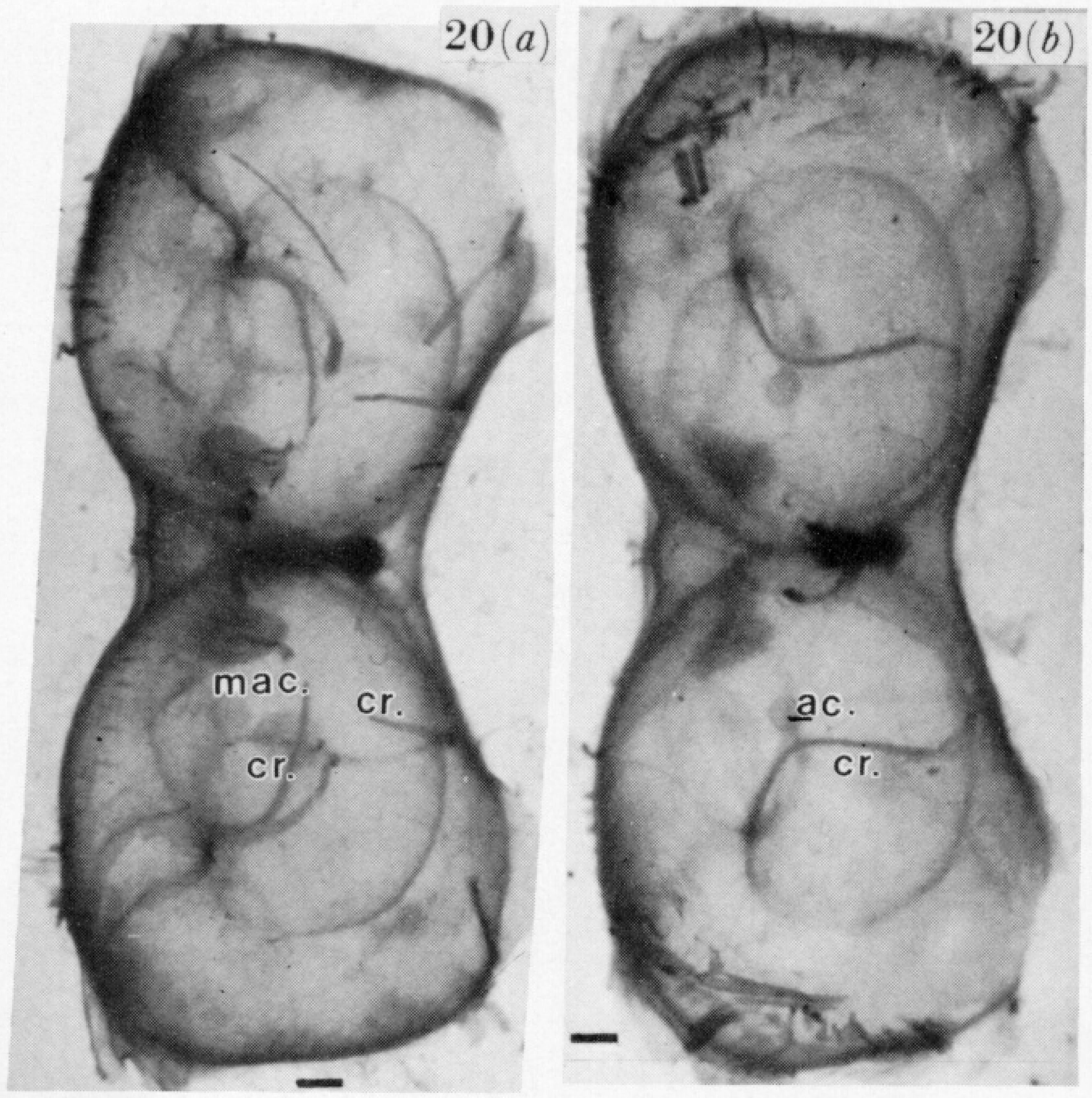


Japetella

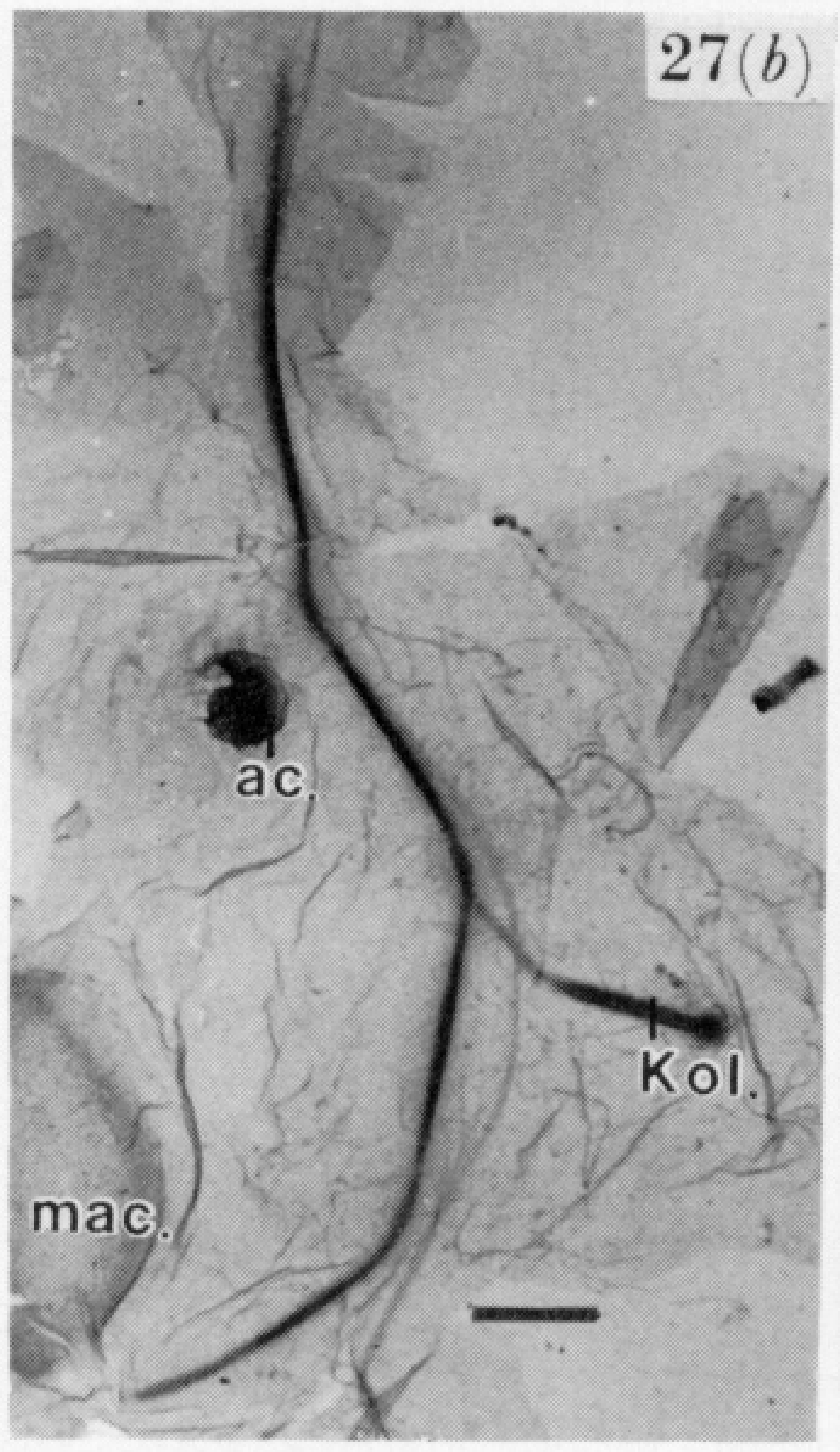


Vitreledonella

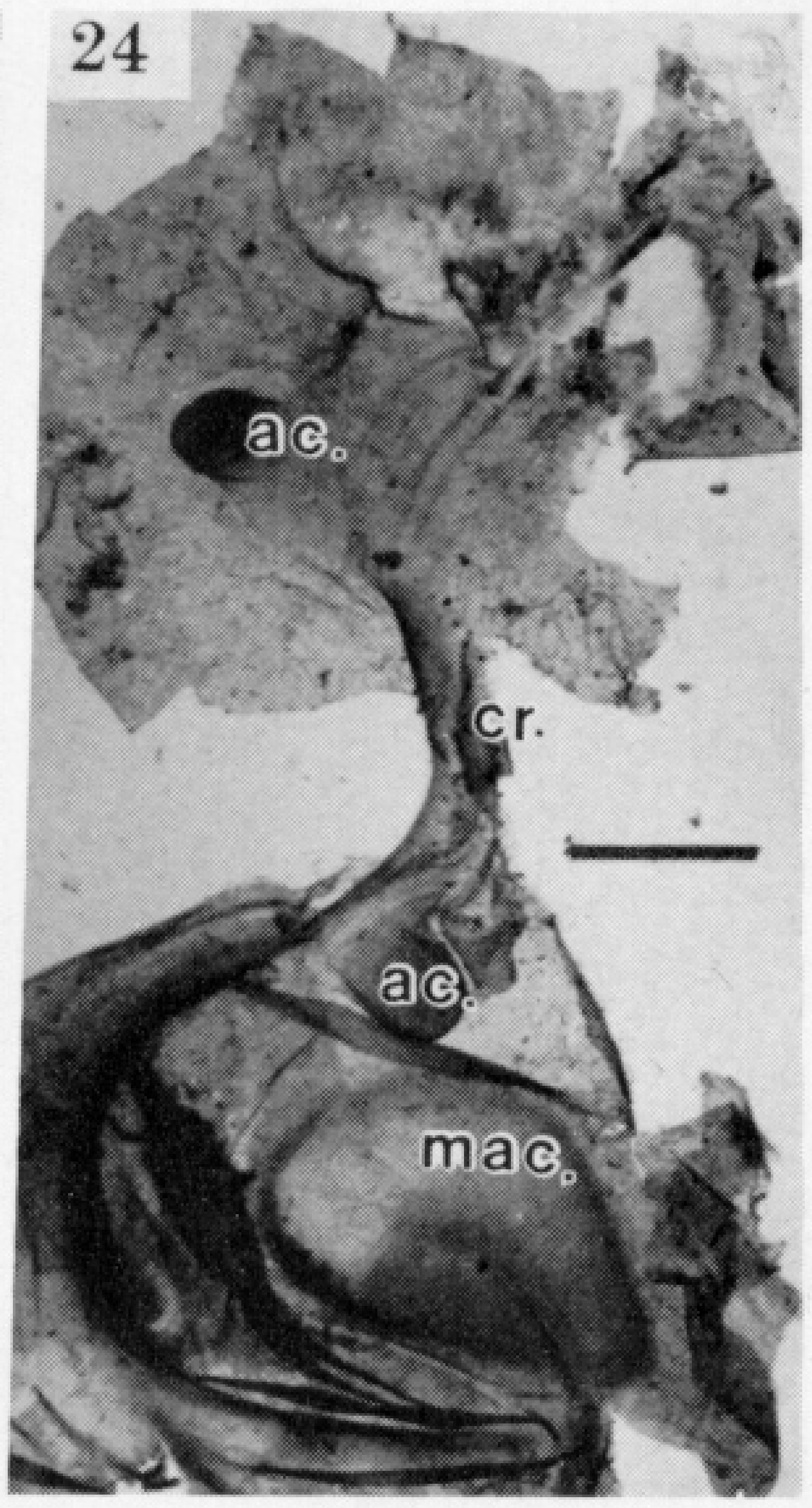
FIGURES 8, 10, 11, 13 AND 15–18. For description see p. 212.



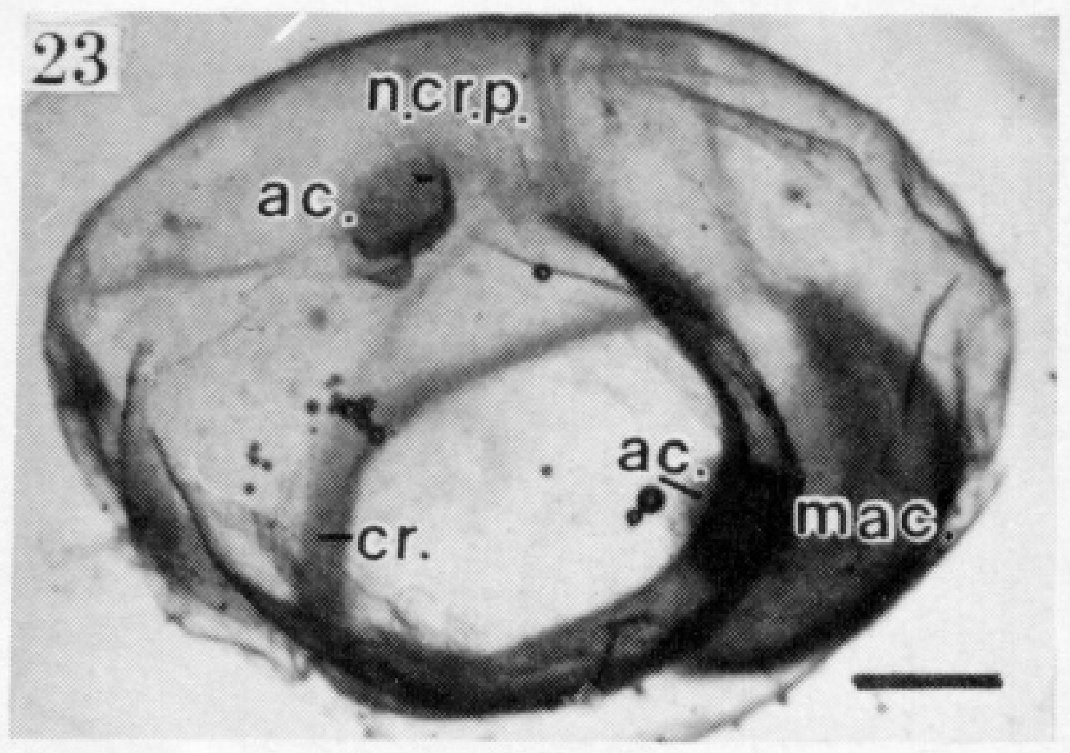
Opisthoteuthis



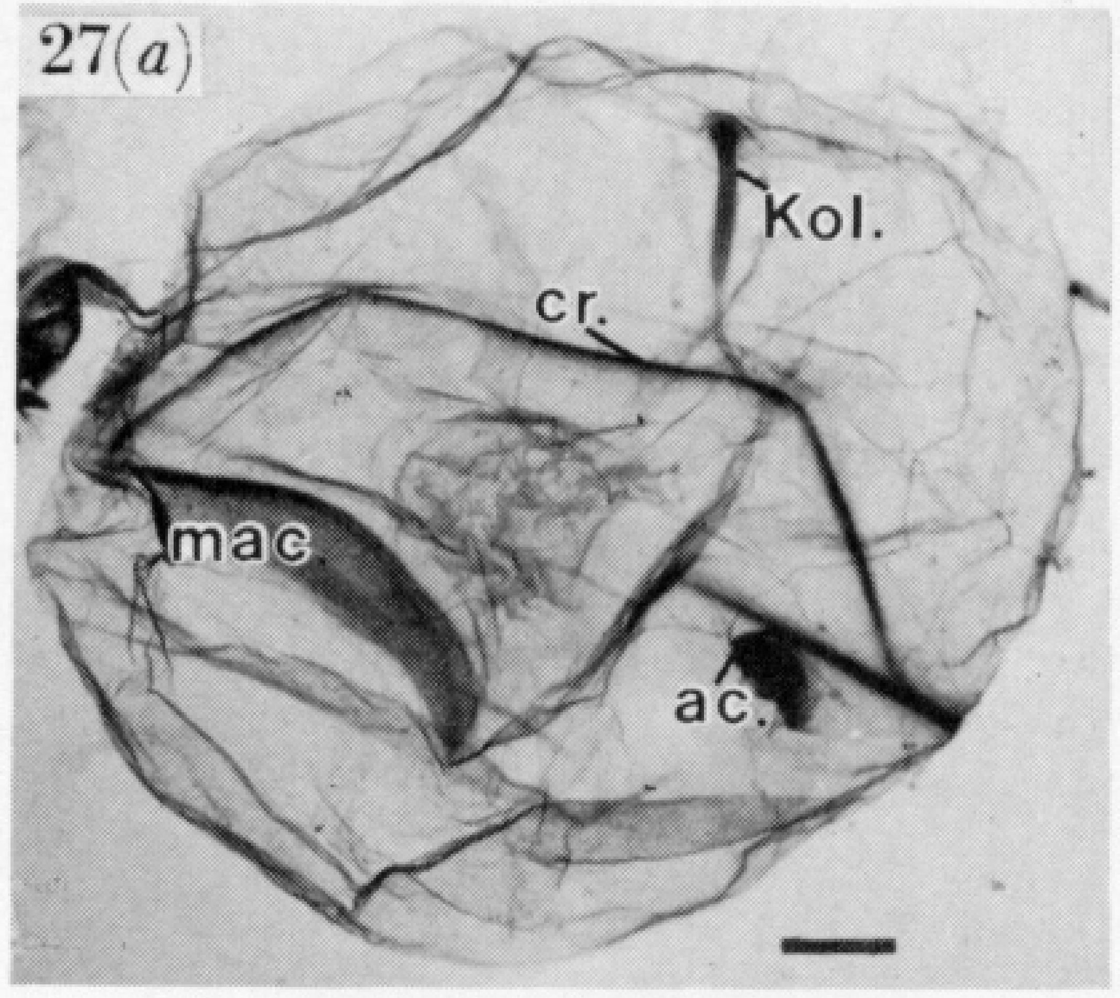
Cirroteuthis



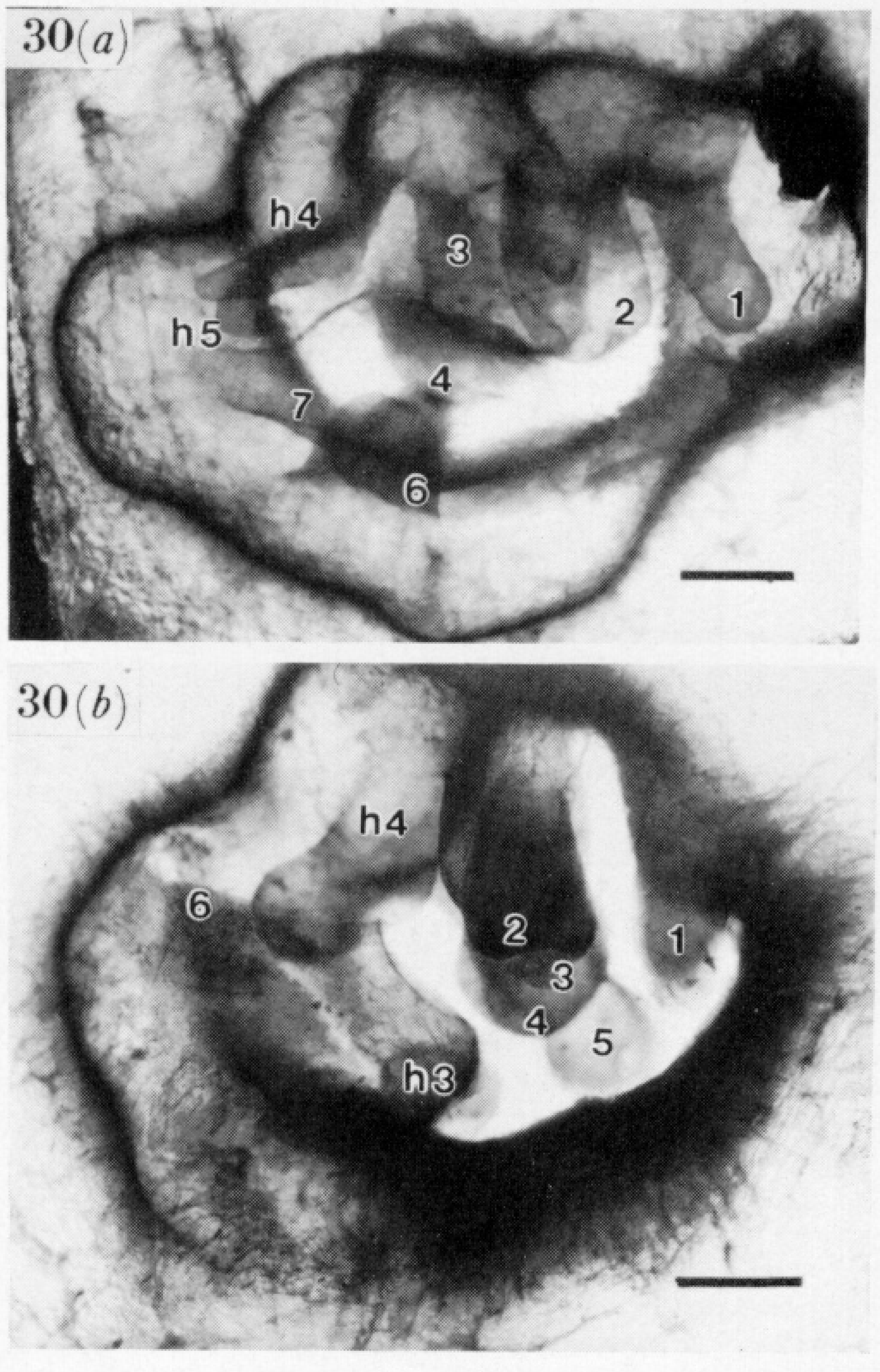
Grimpoteuthis



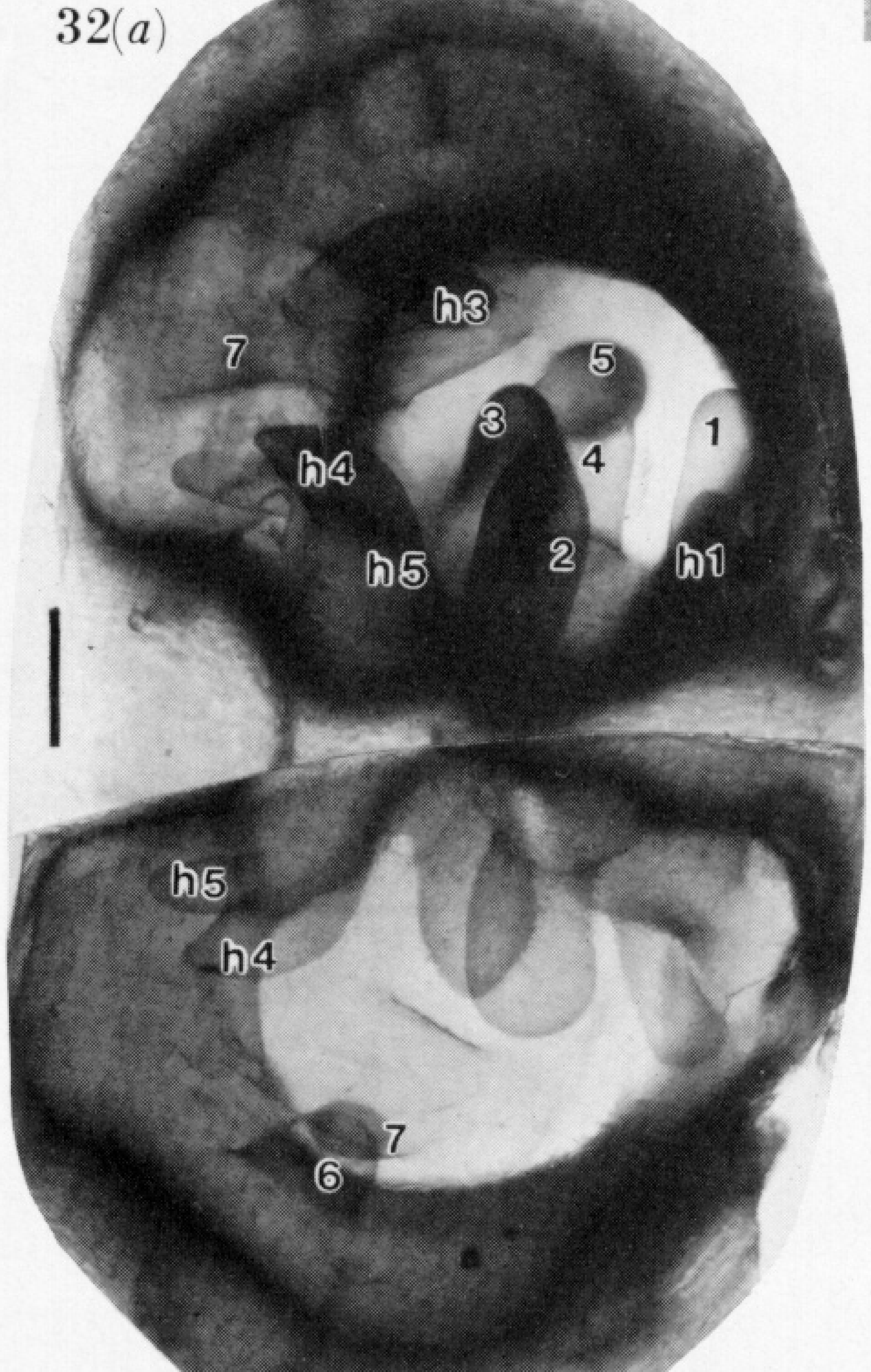
Grimpoteuthis



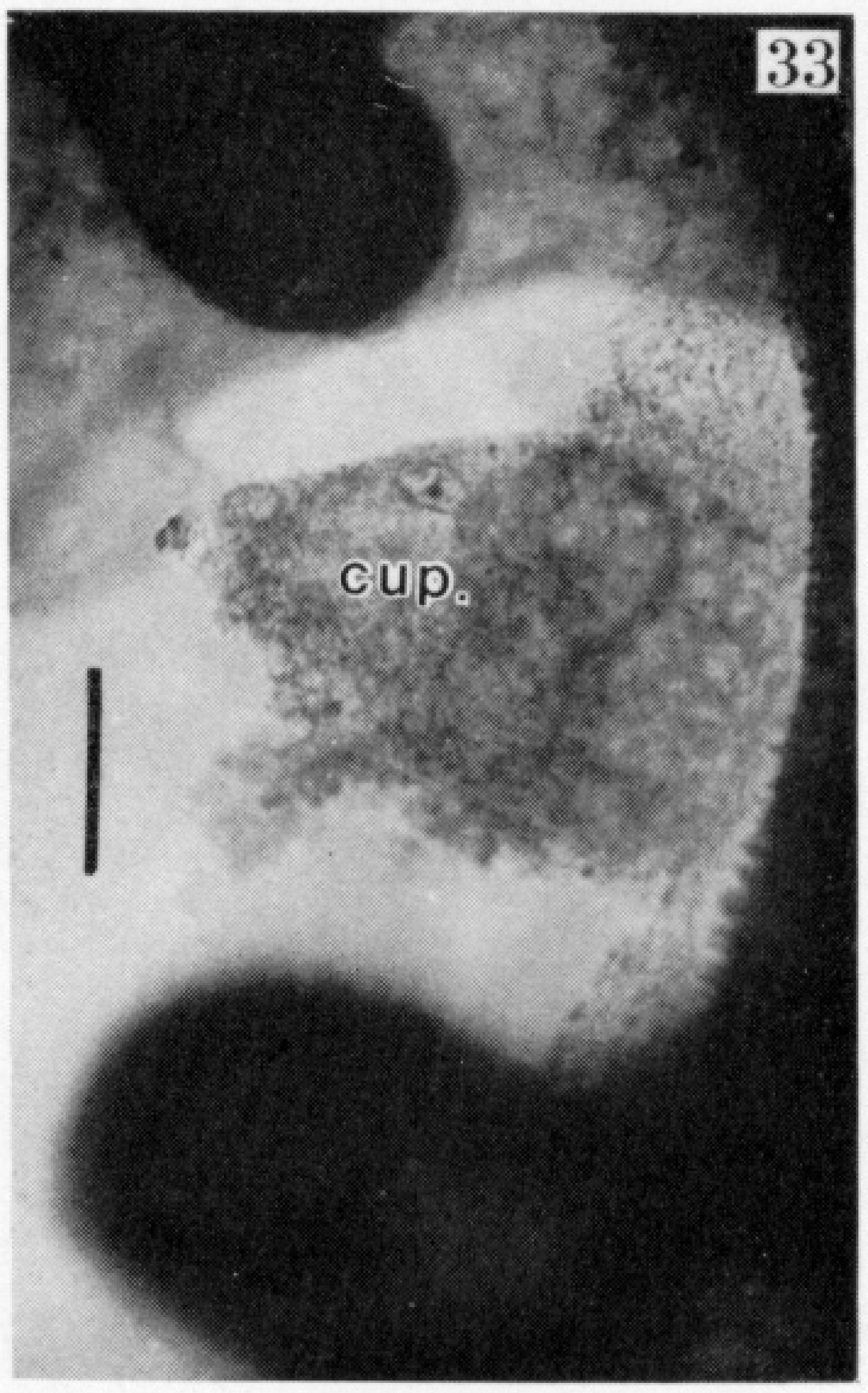
Cirroteuthis



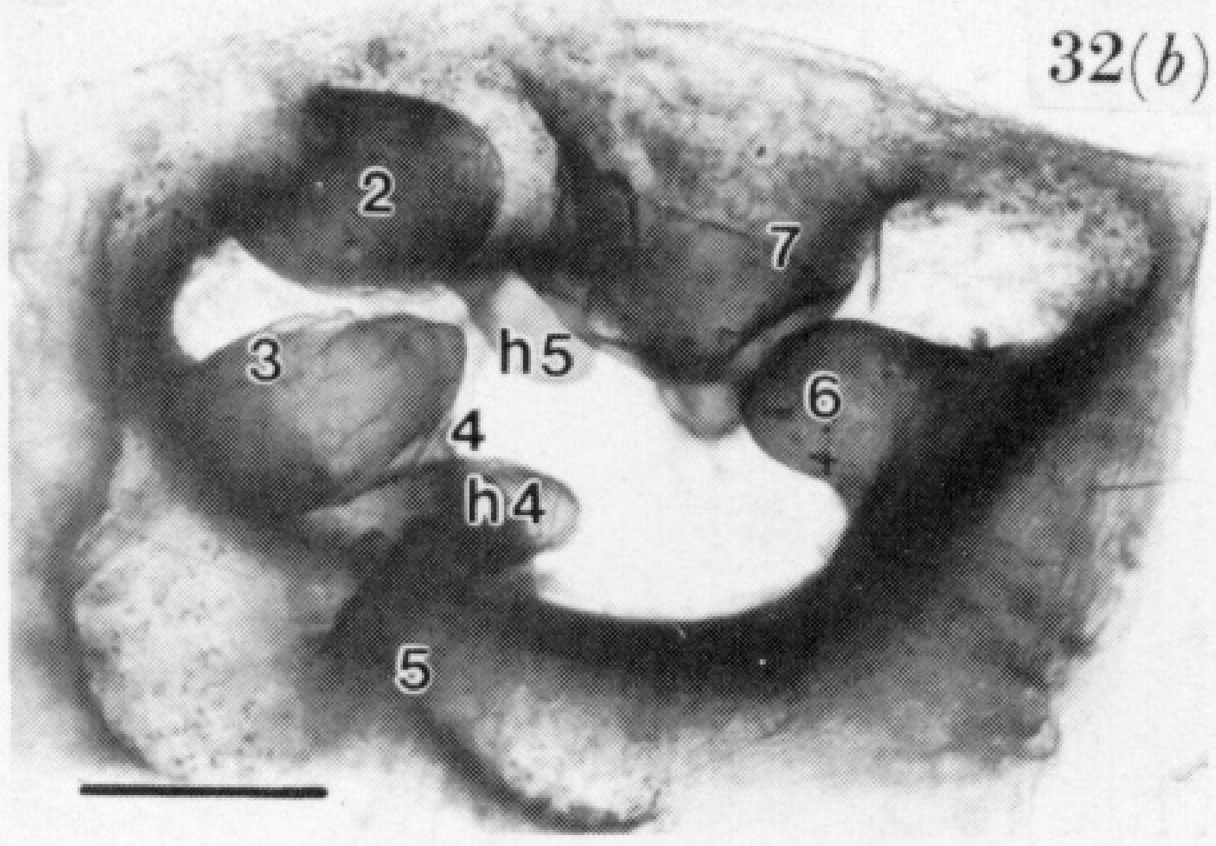
Dosidicus



Ommastrephes

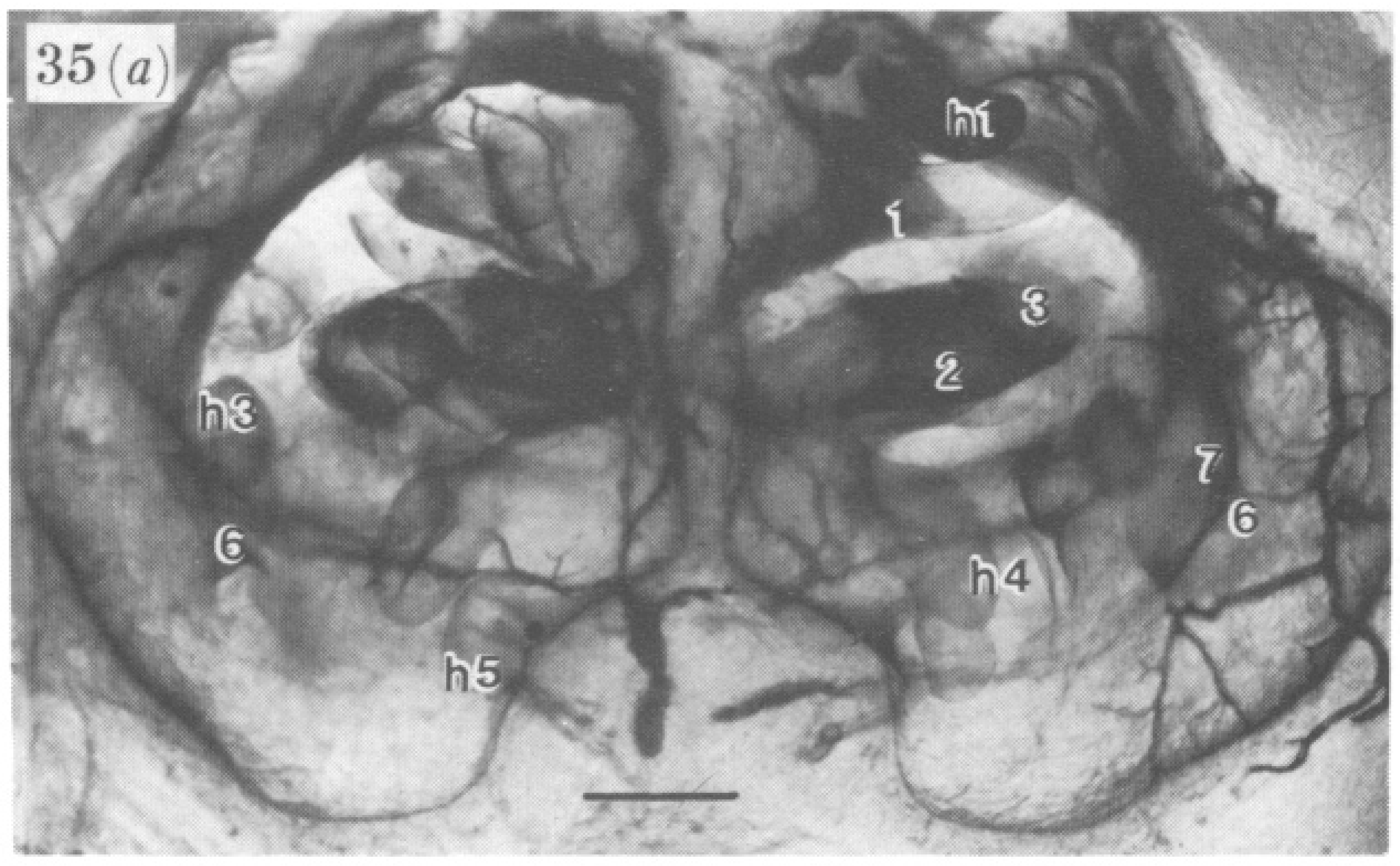


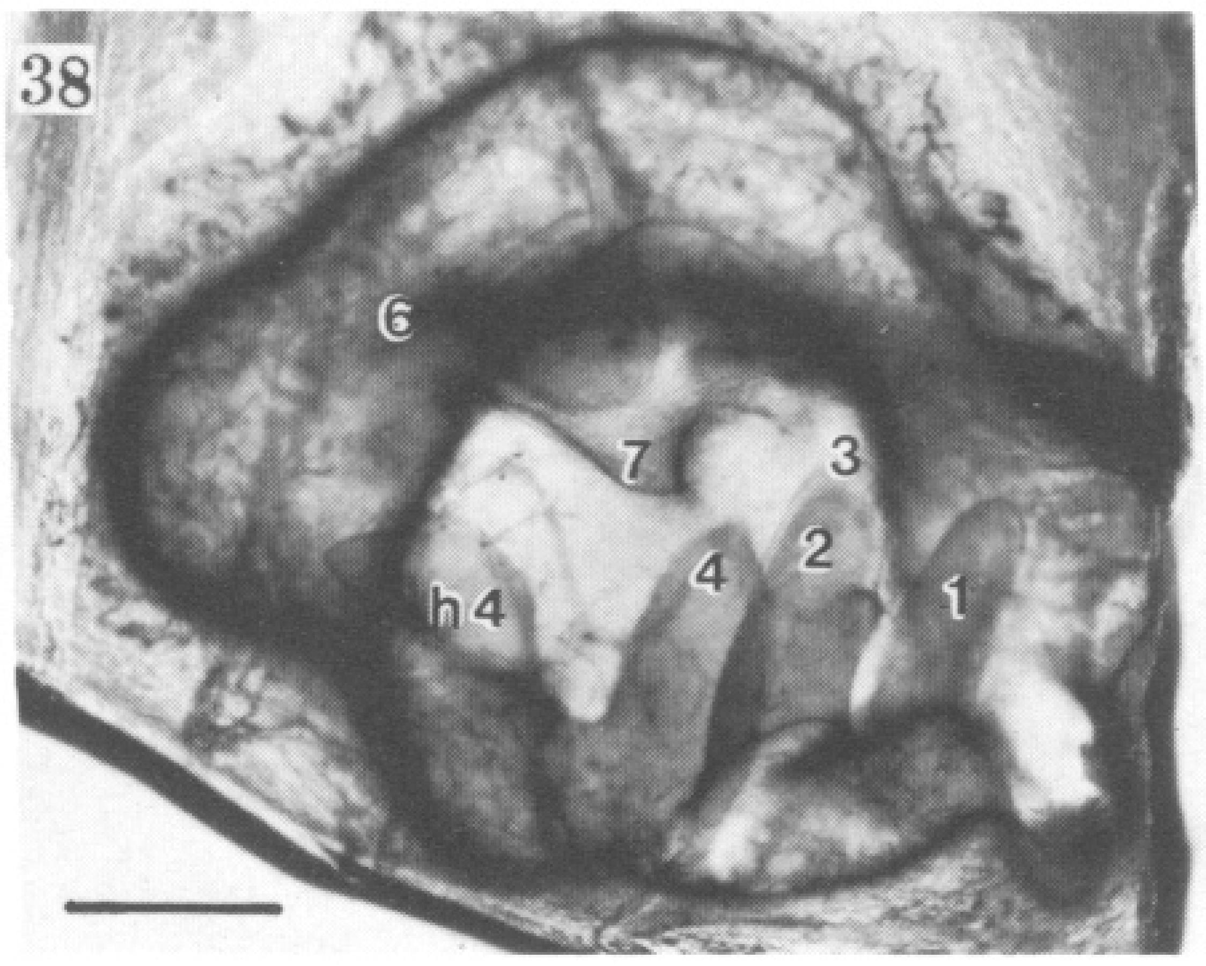
Ommastrephes



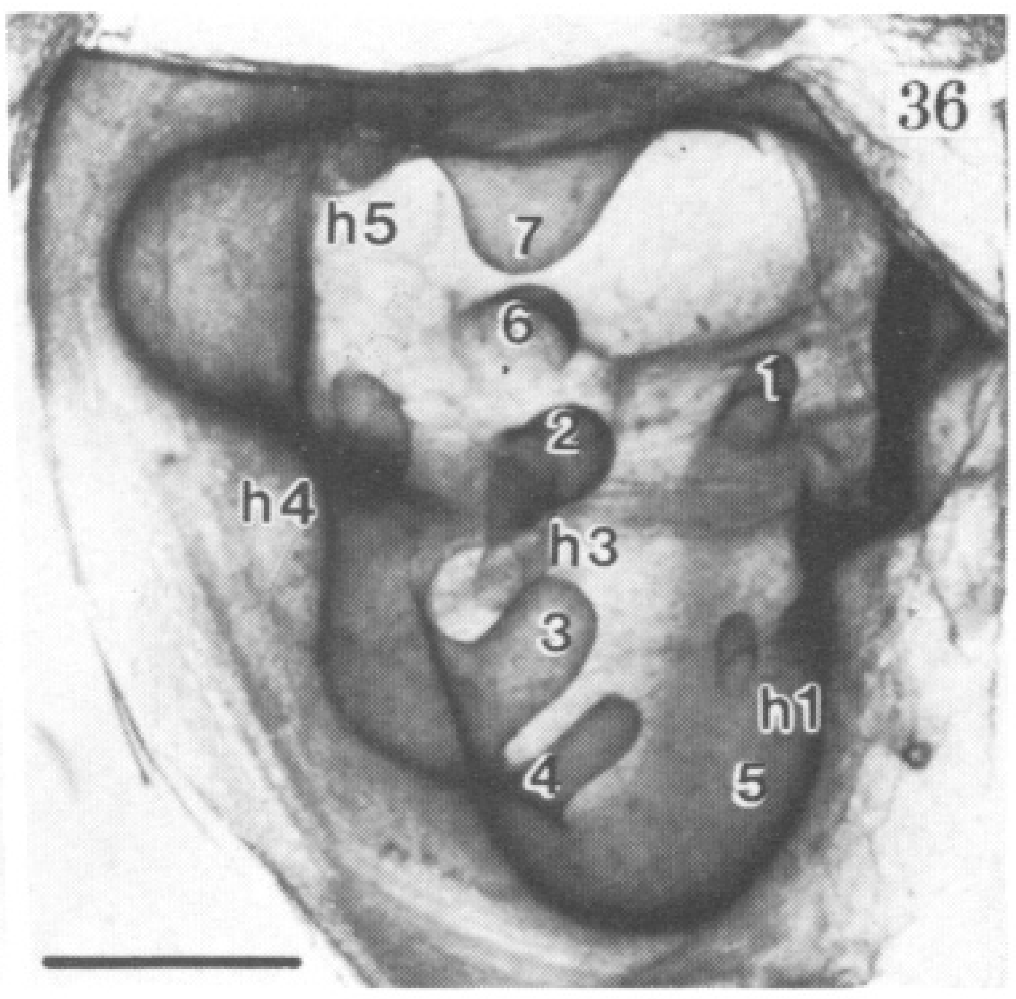
Ommastrephes

Figures 20, 23, 24, 27, 30, 32 and 33. For description see opposite.

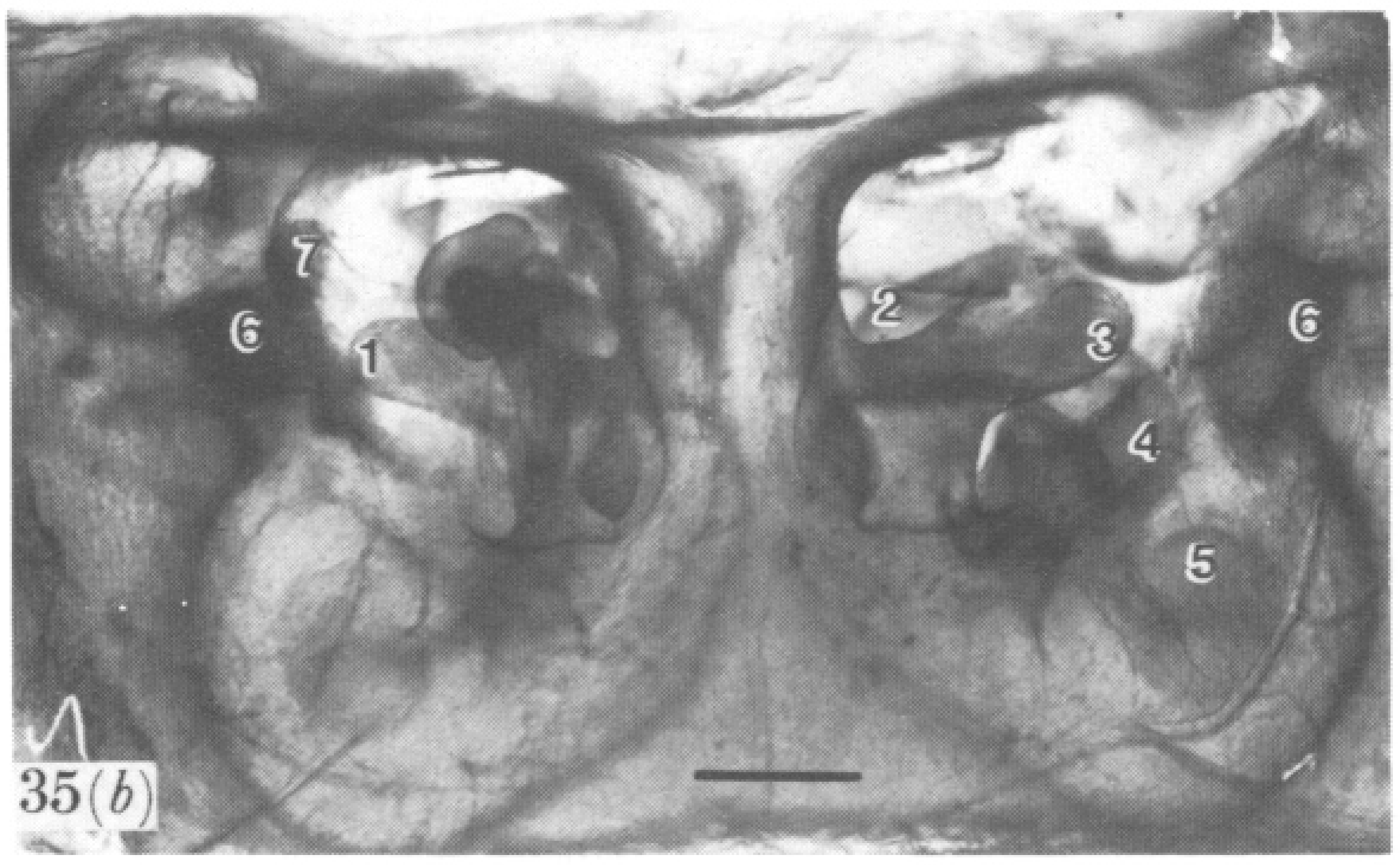




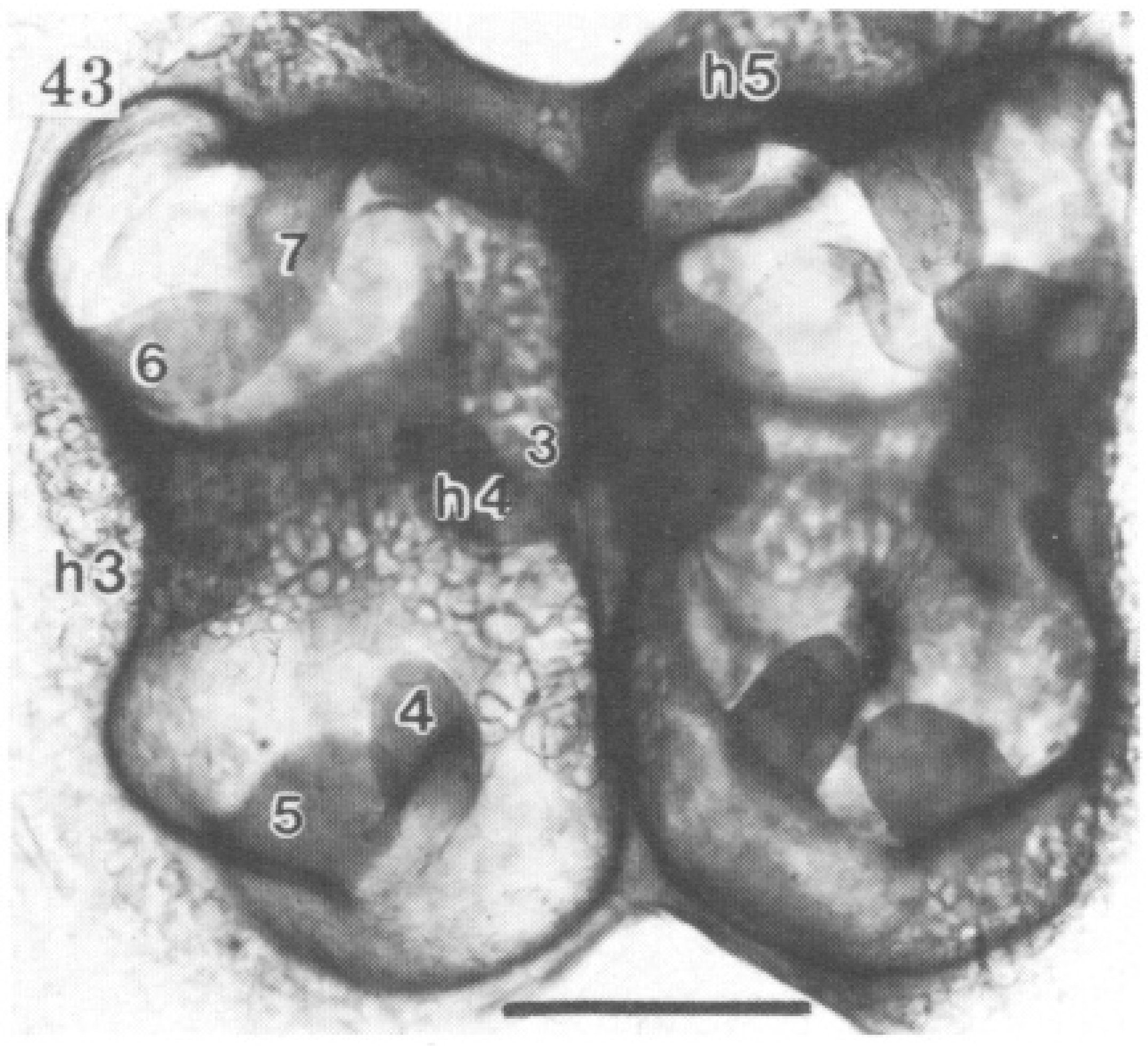
Todarodes



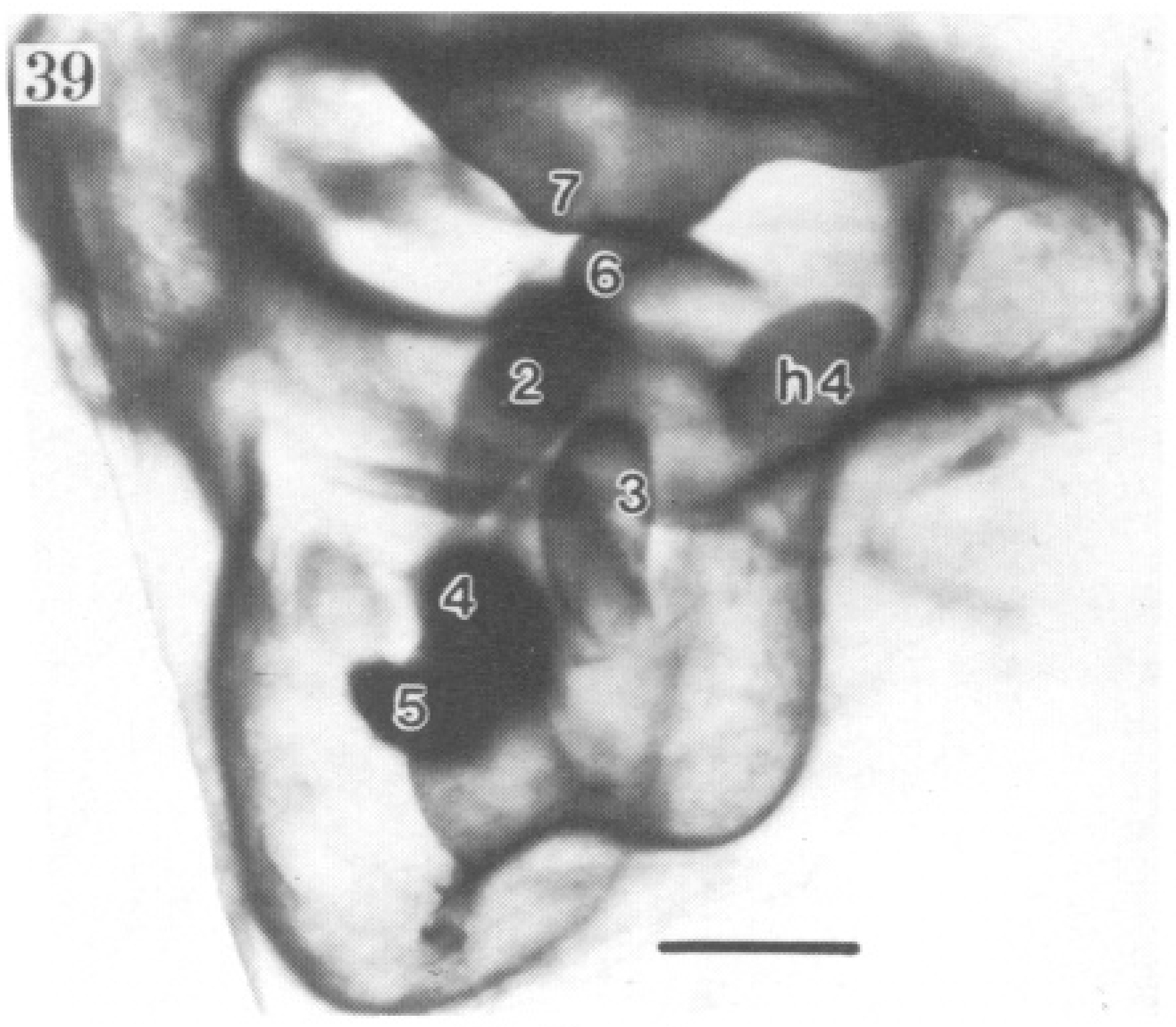
Illex



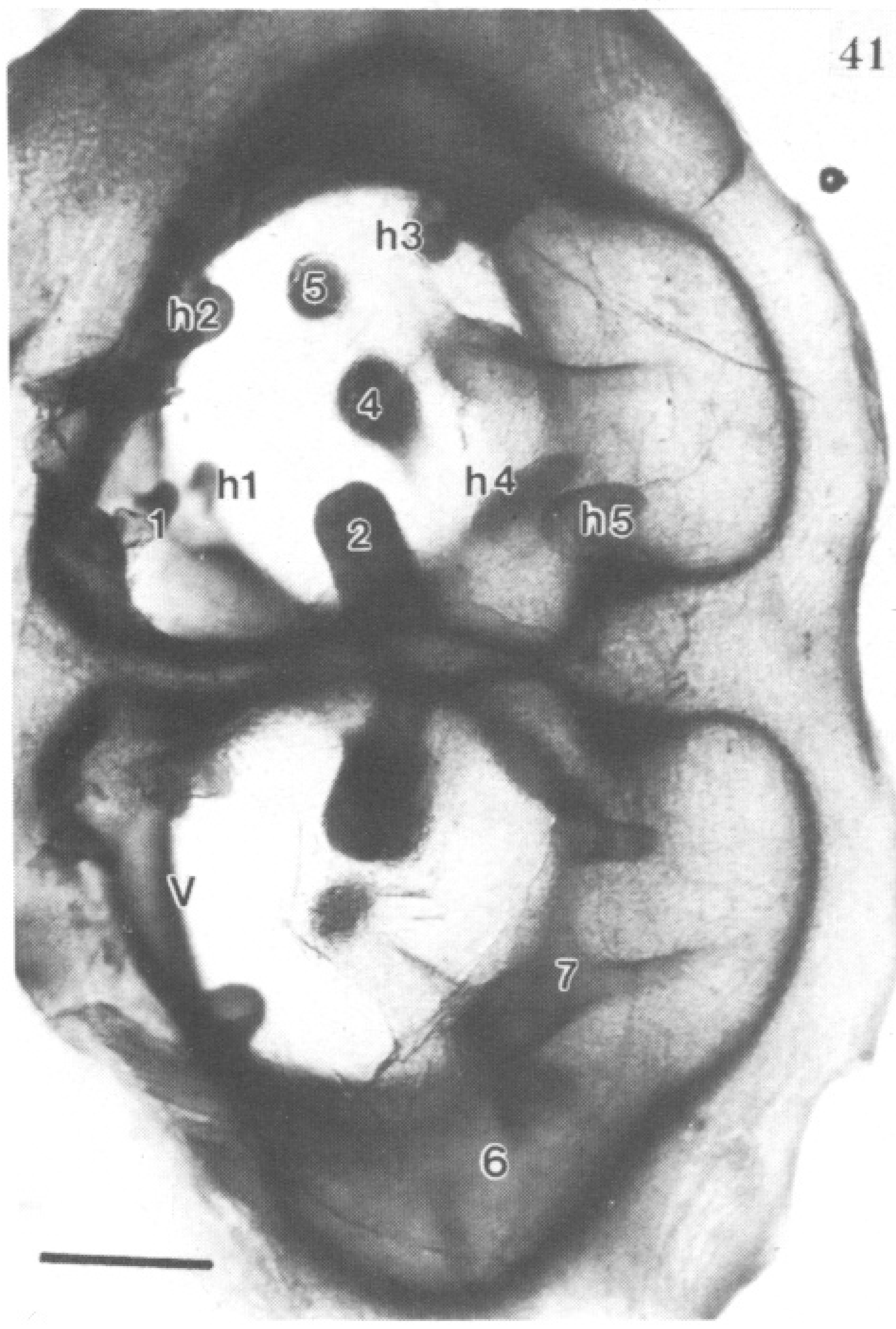
Illex



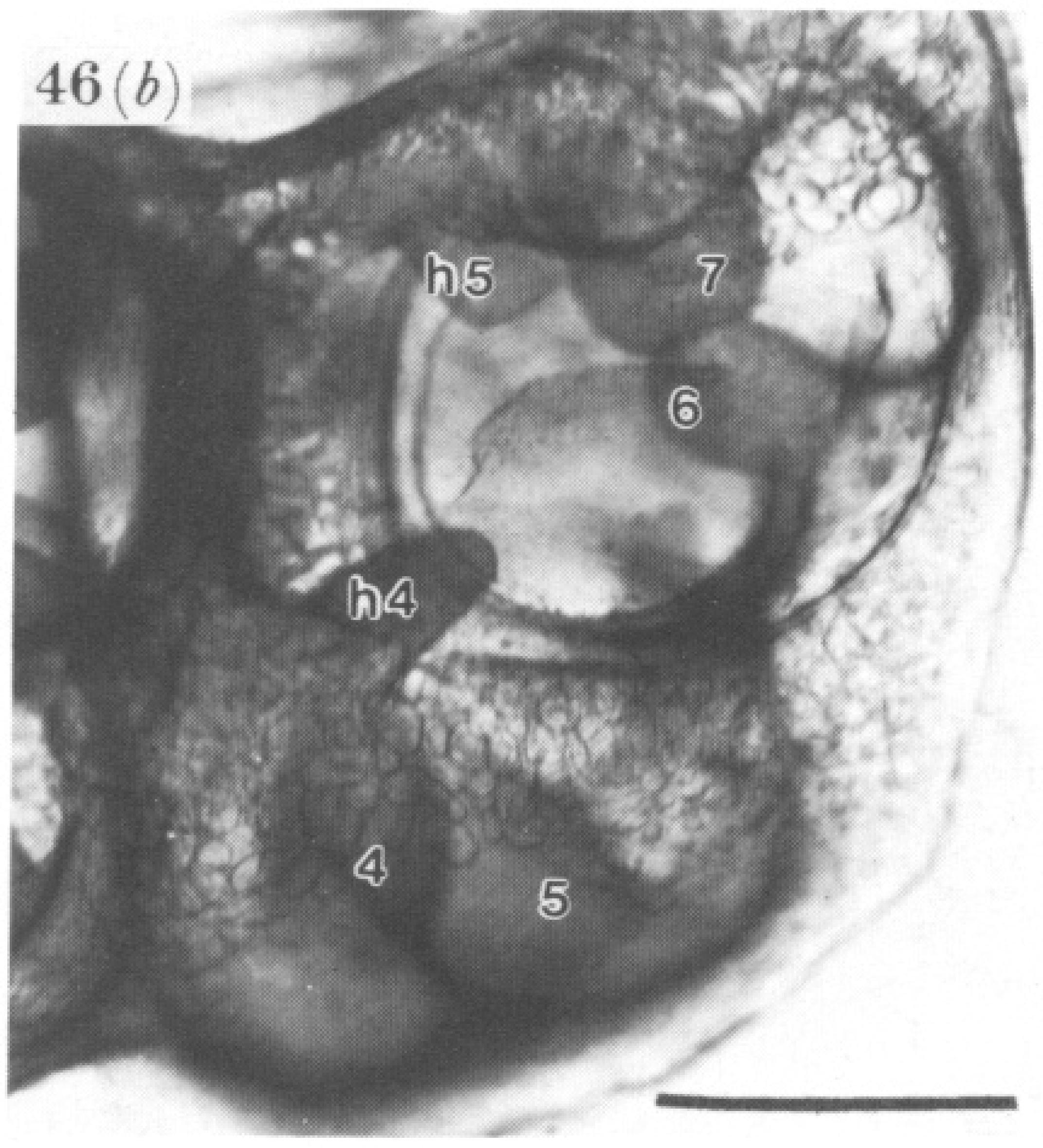
Enoploteuthis



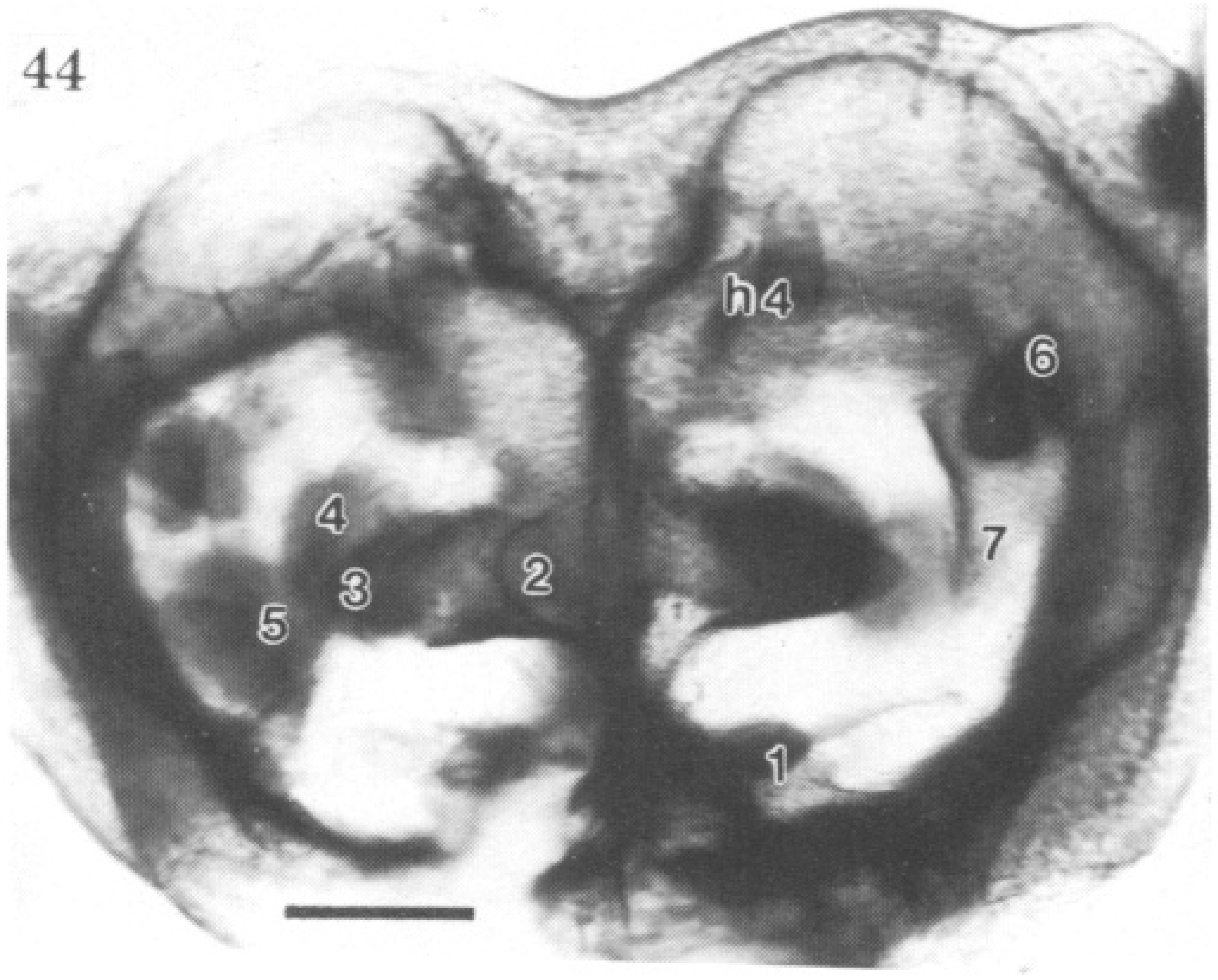
Todarodes



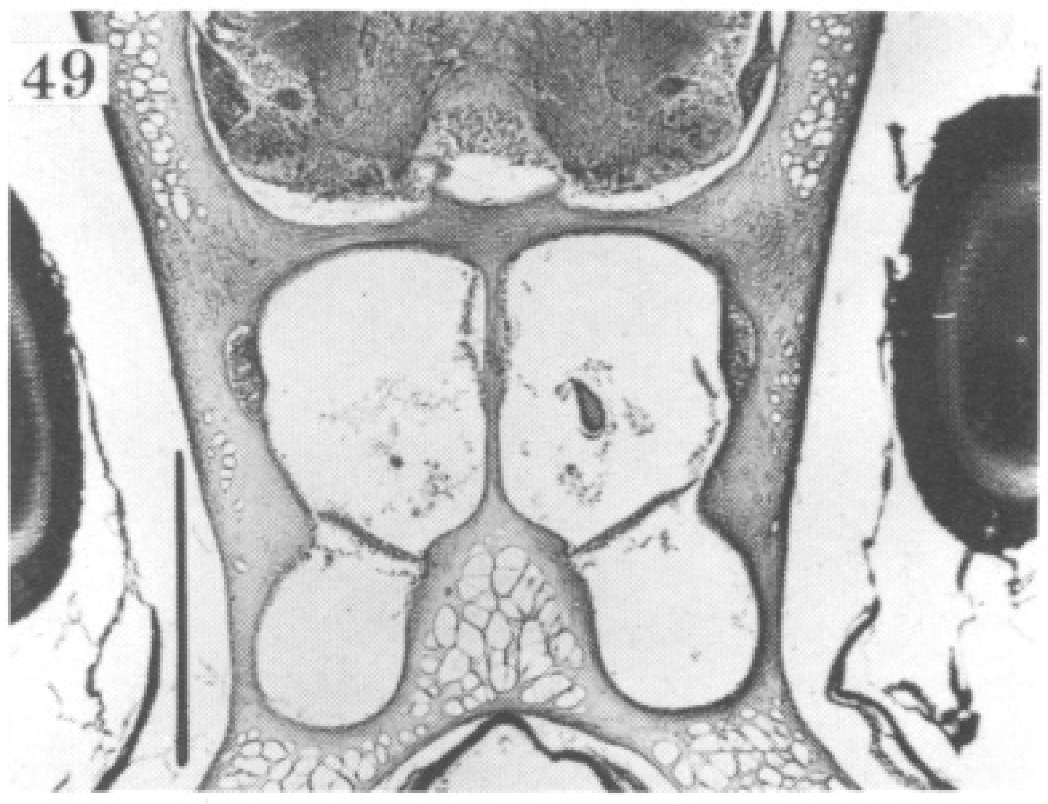
Thysanoteuthis



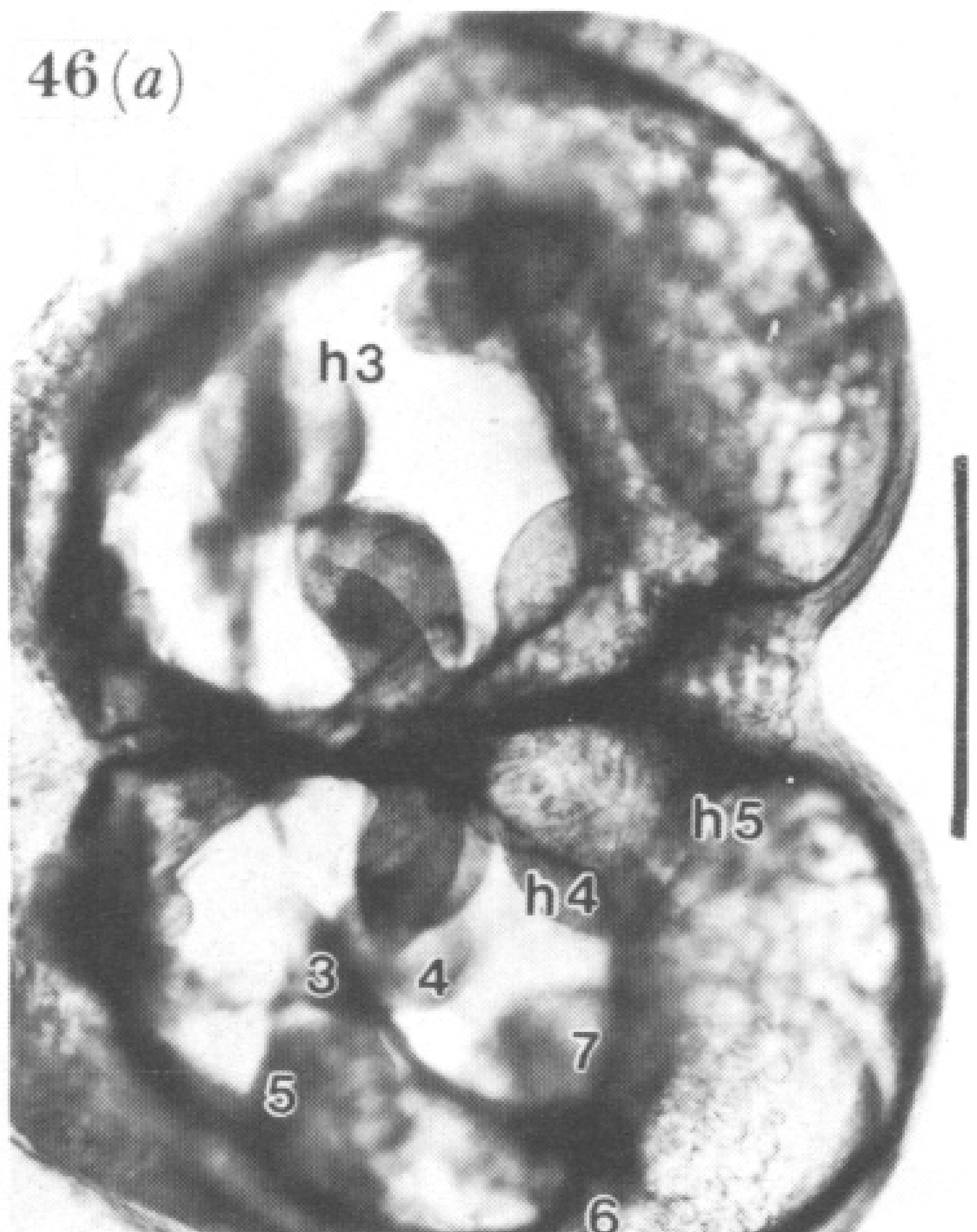
Abraliopsis



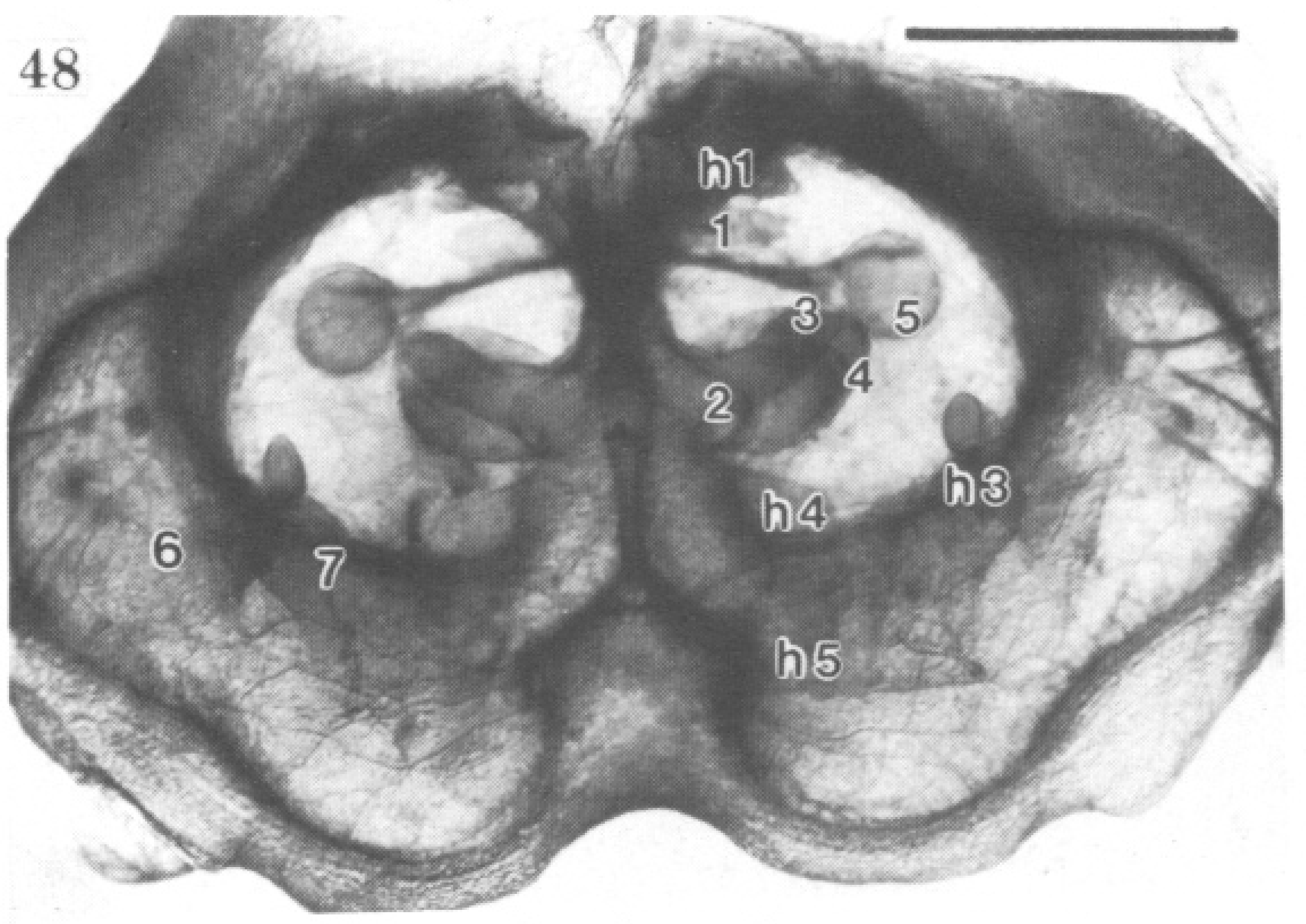
Enoploteuthis



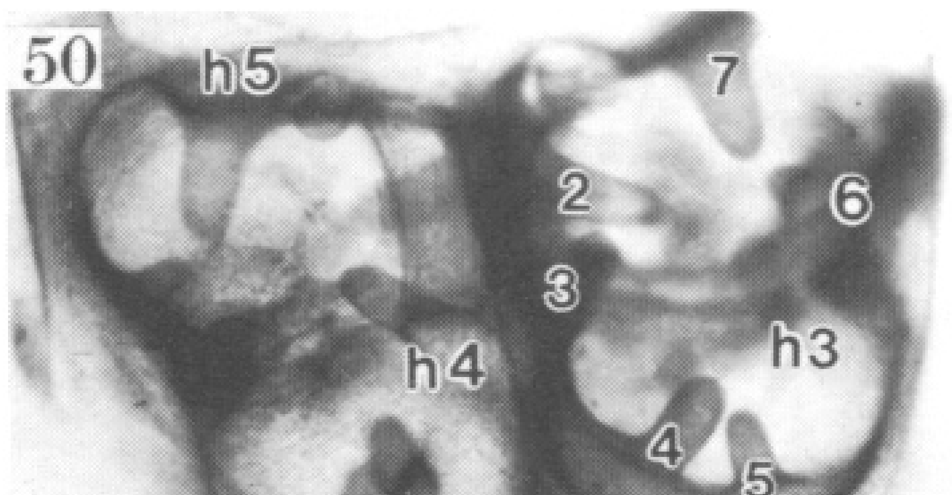
Onychoteuthis



Abraliopsis



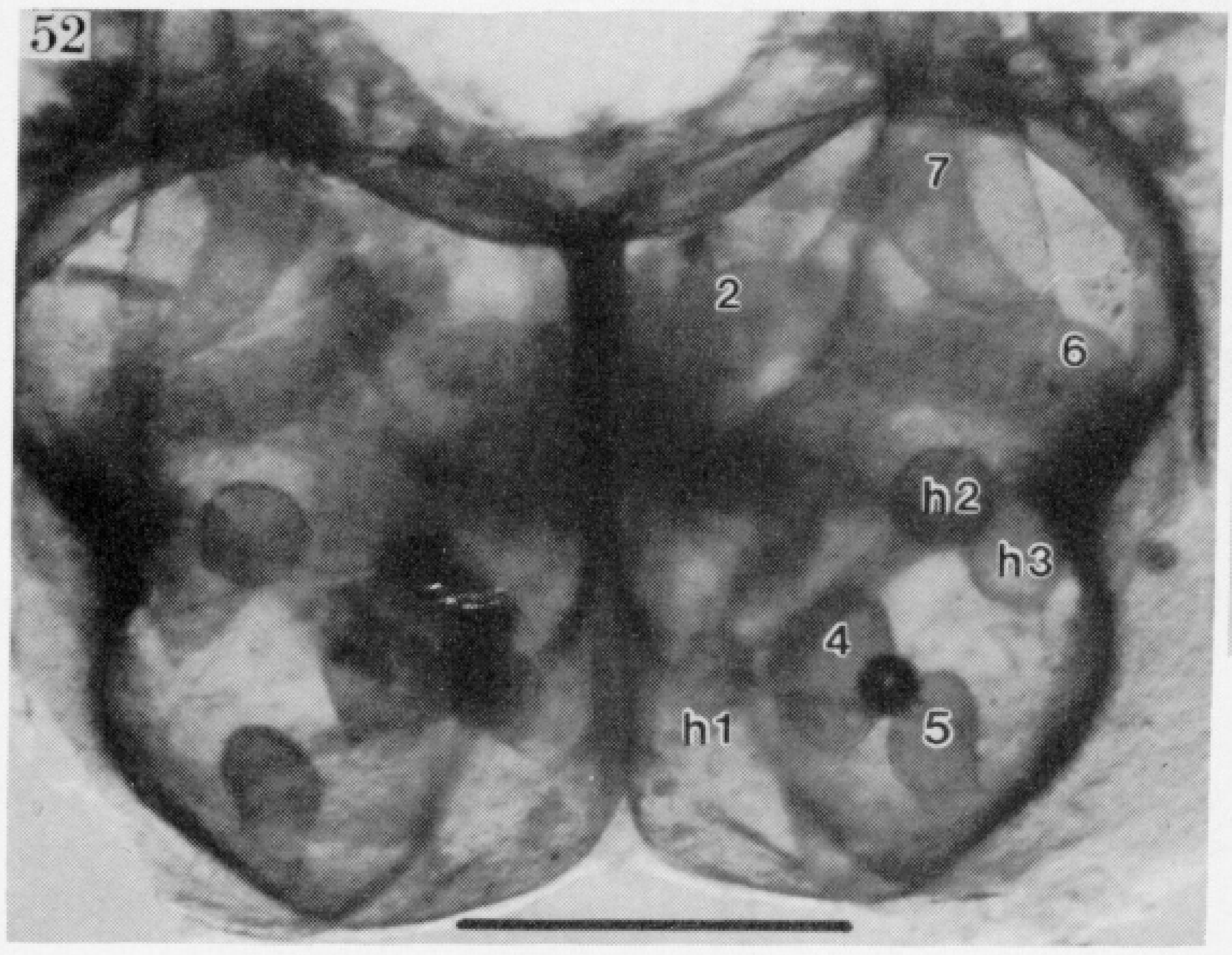
Onychoteuthis



Onykia

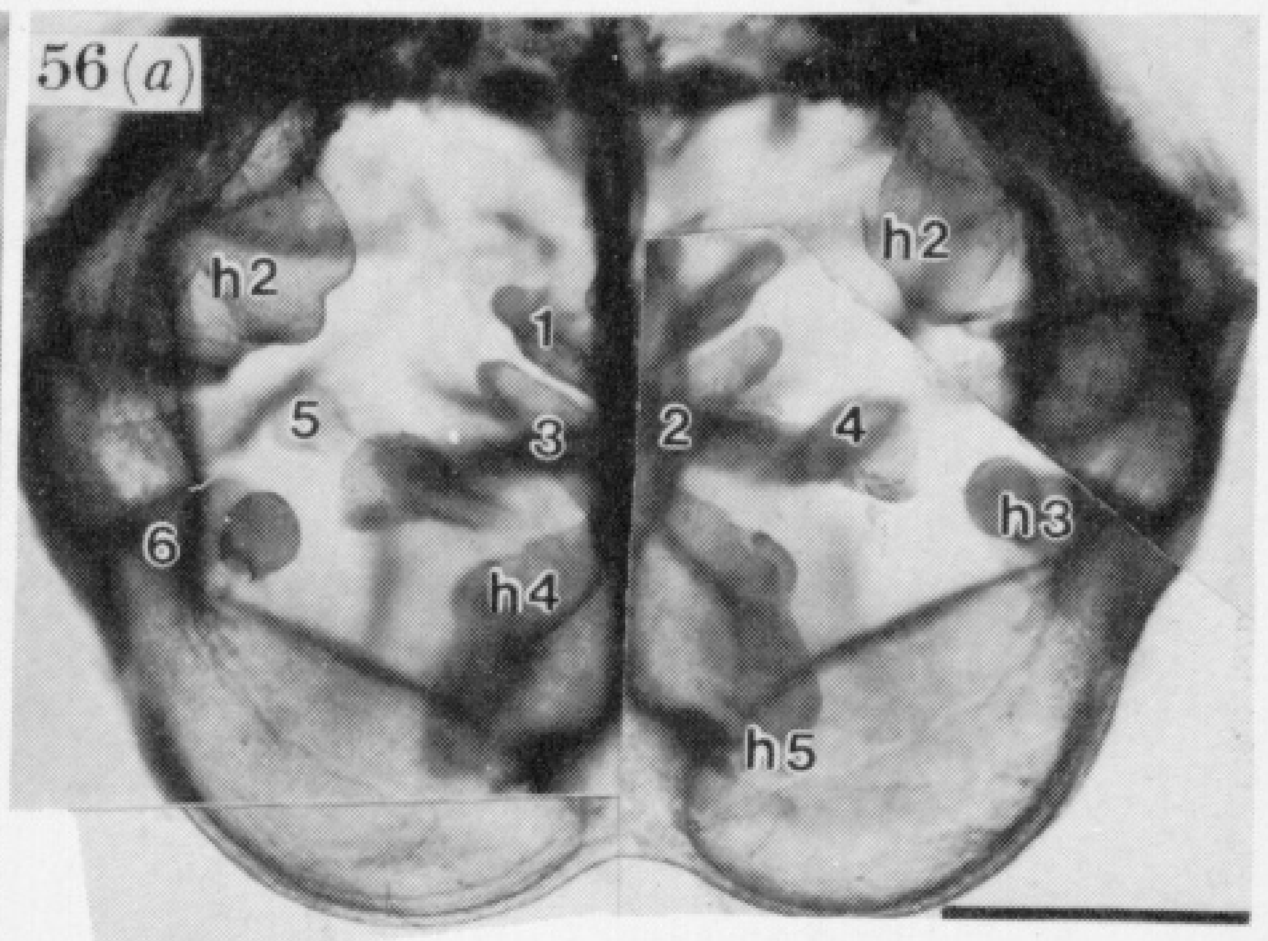
FIGURES 35, 36, 38, 39, 41, 43, 44, 46 AND 48–50. For description see facing plate 5.

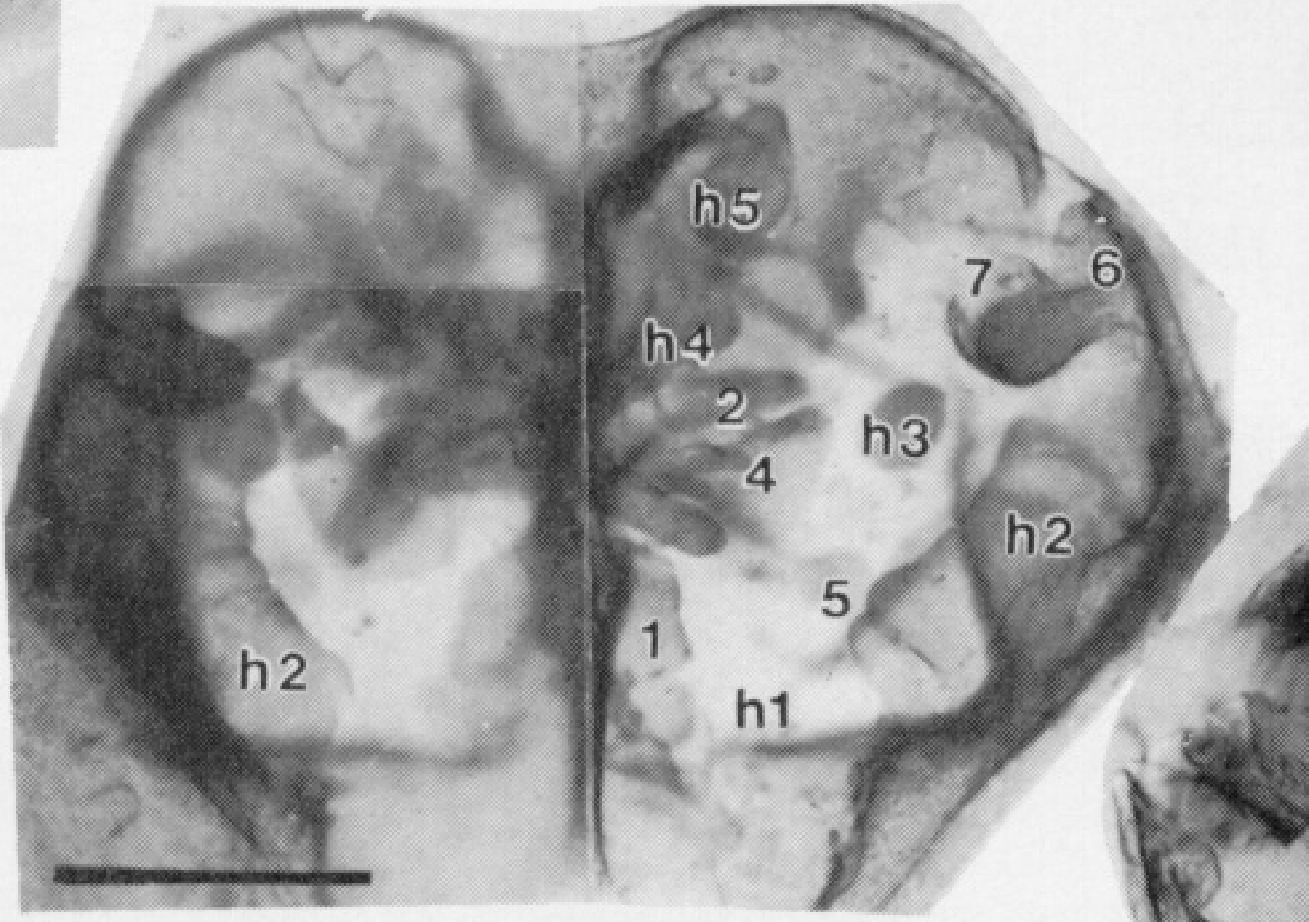
52



Pterygioteuthis

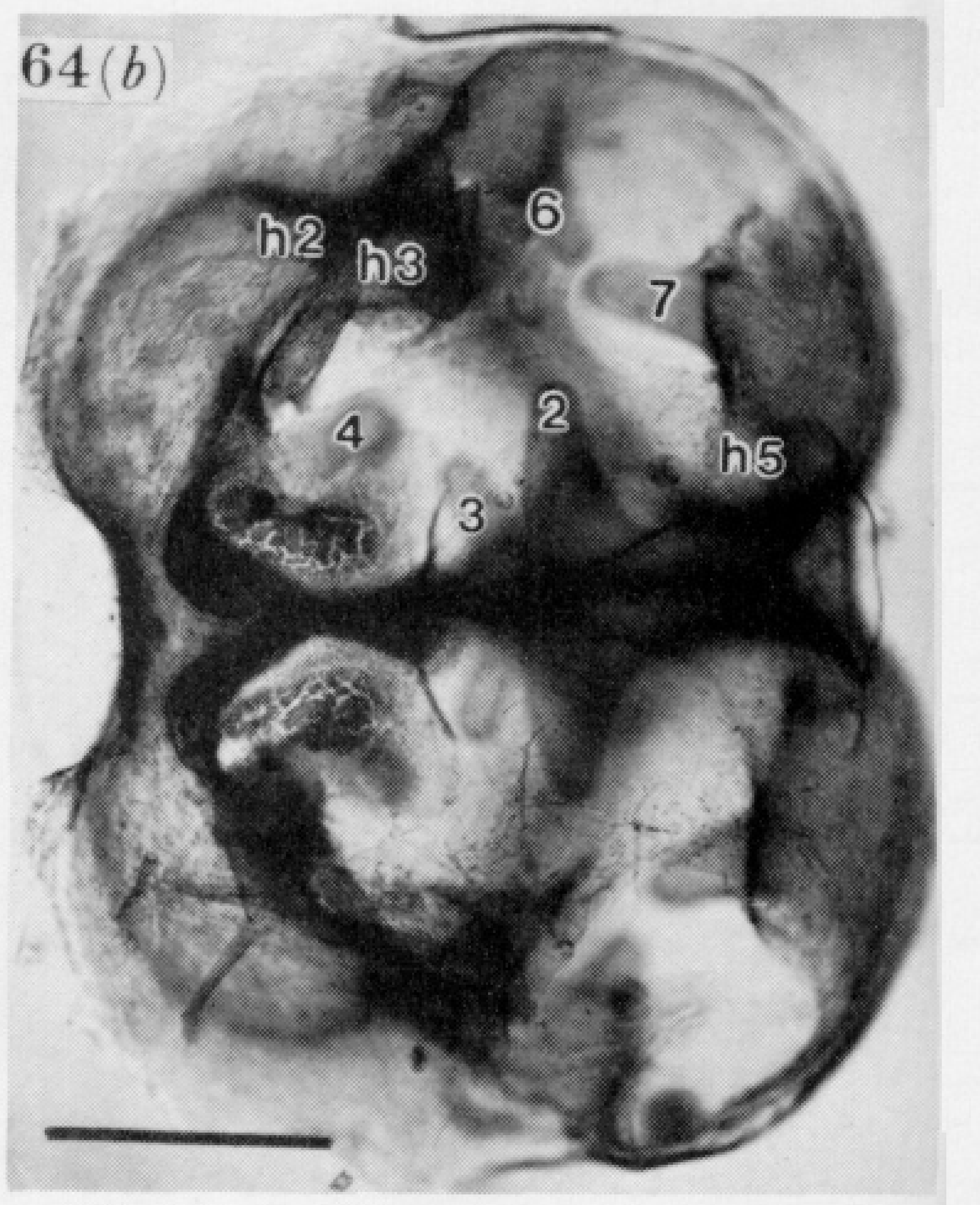
56(*a*)



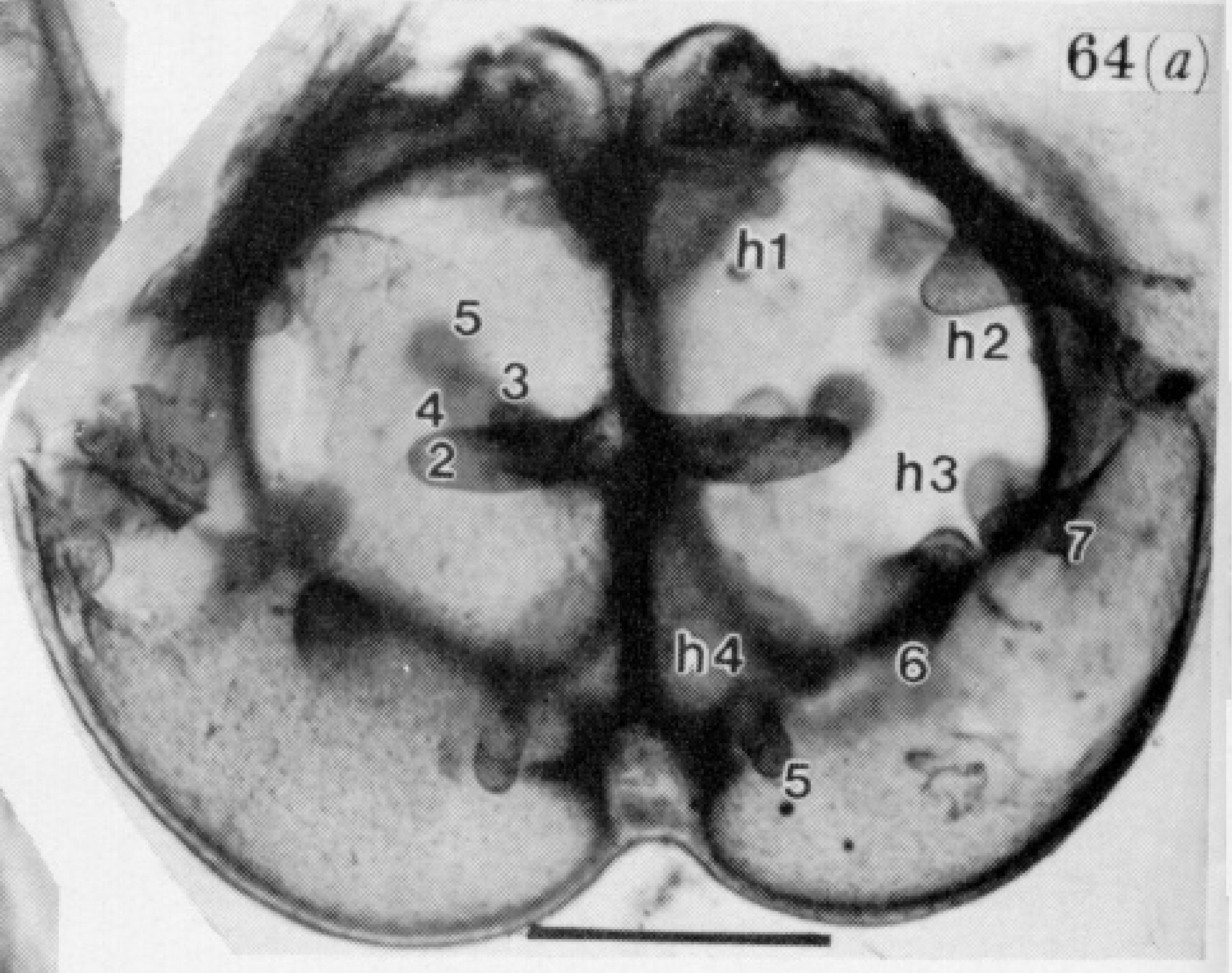


Ctenopteryx

64(*b*)

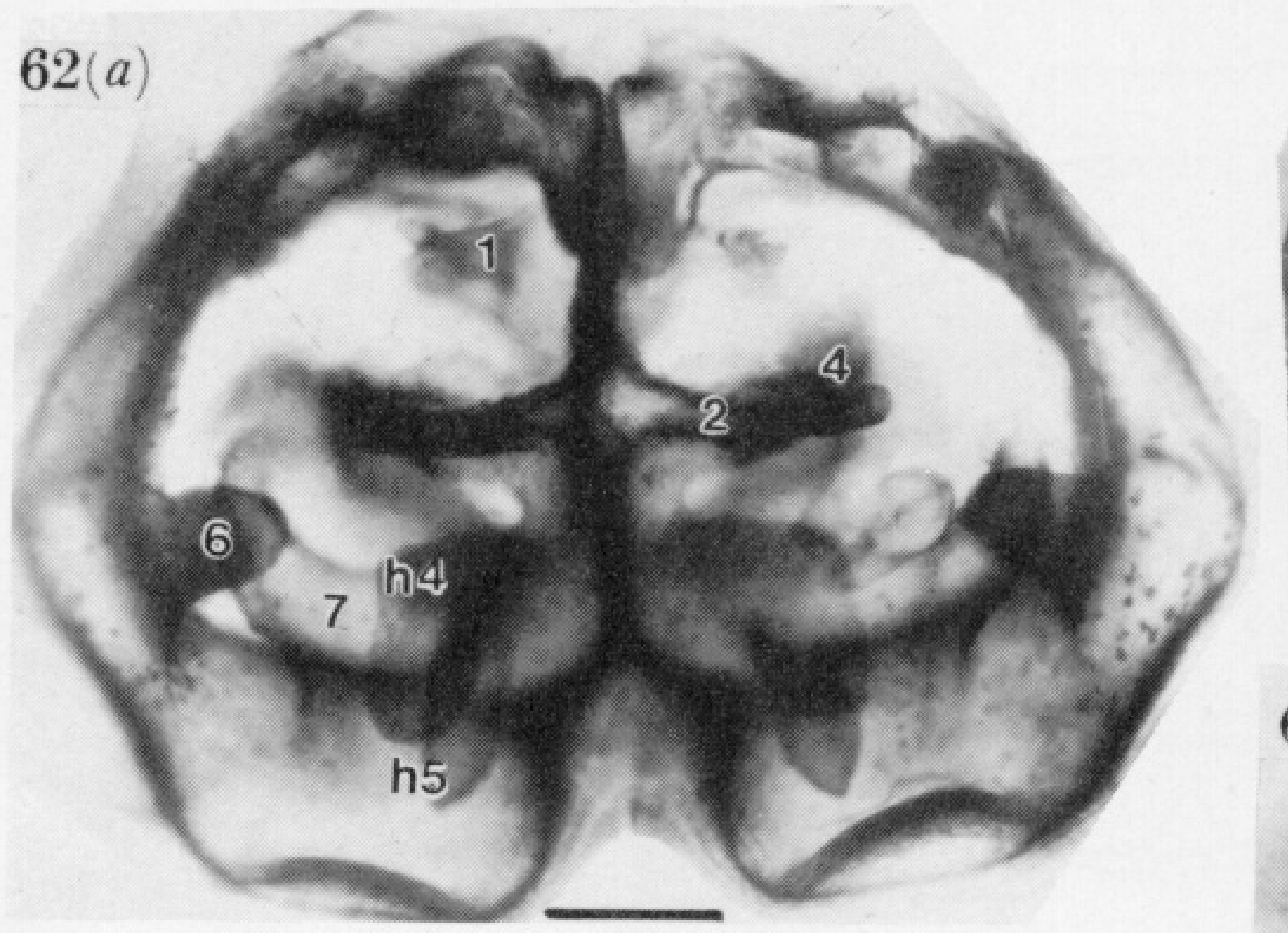


64(*a*)



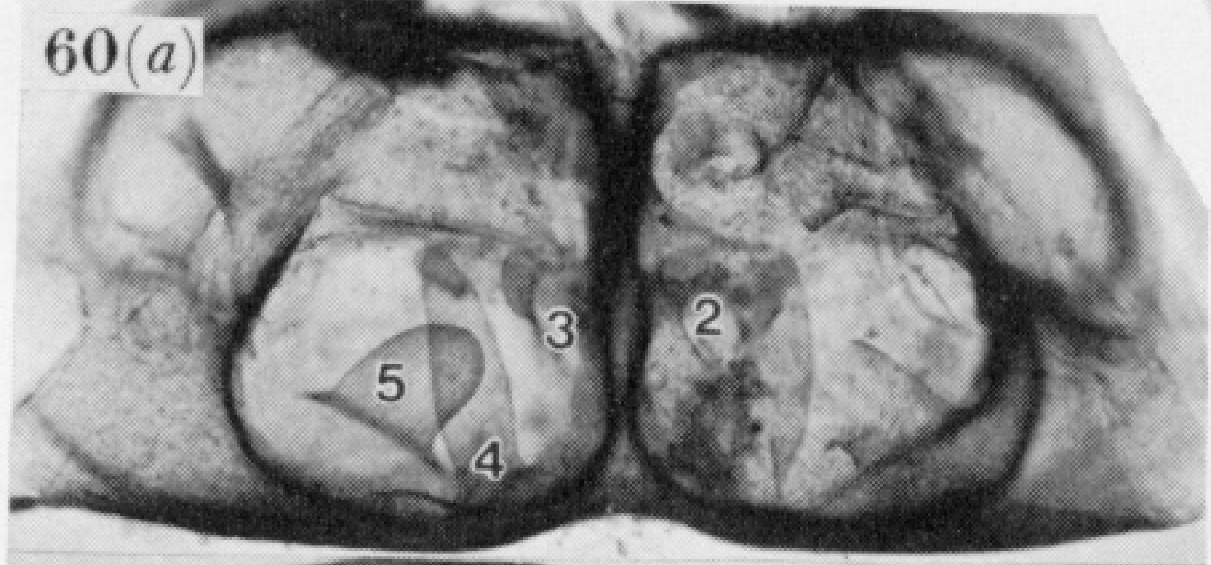
Bathyteuthis

62(*a*)

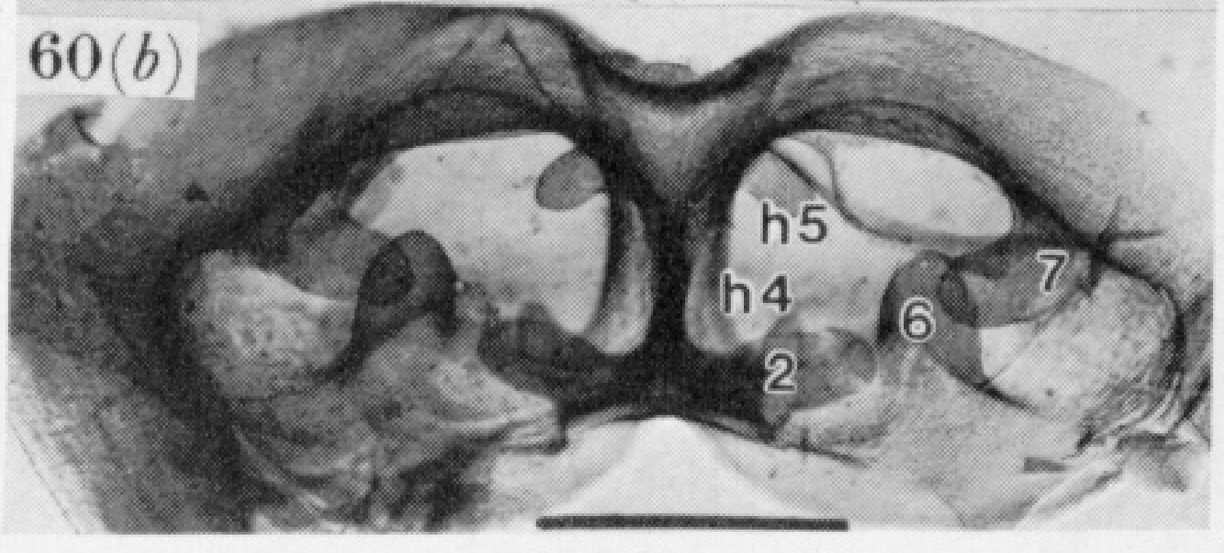


Lycoteuthis

60(*a*)

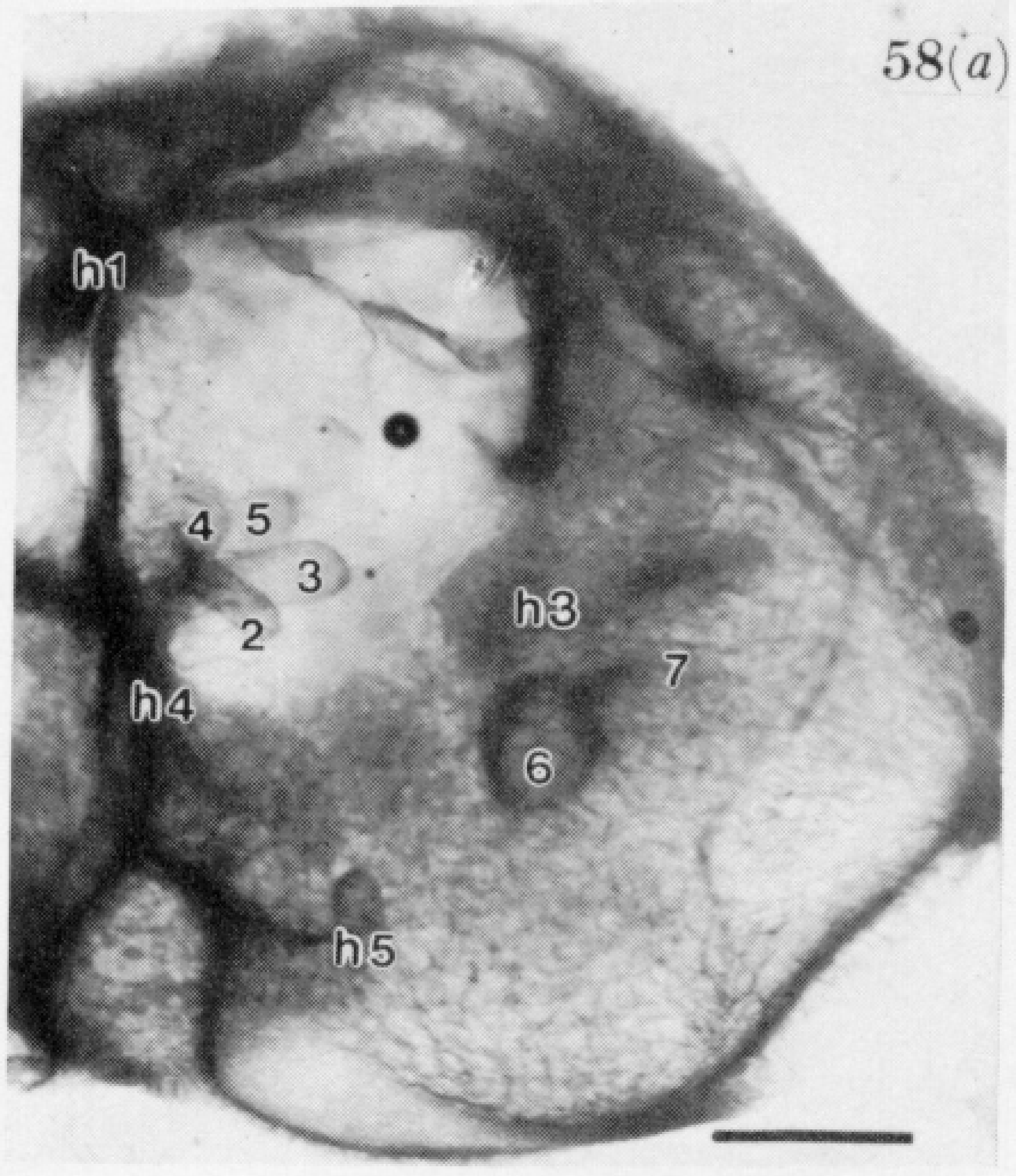


60(*b*)



Brachioteuthis

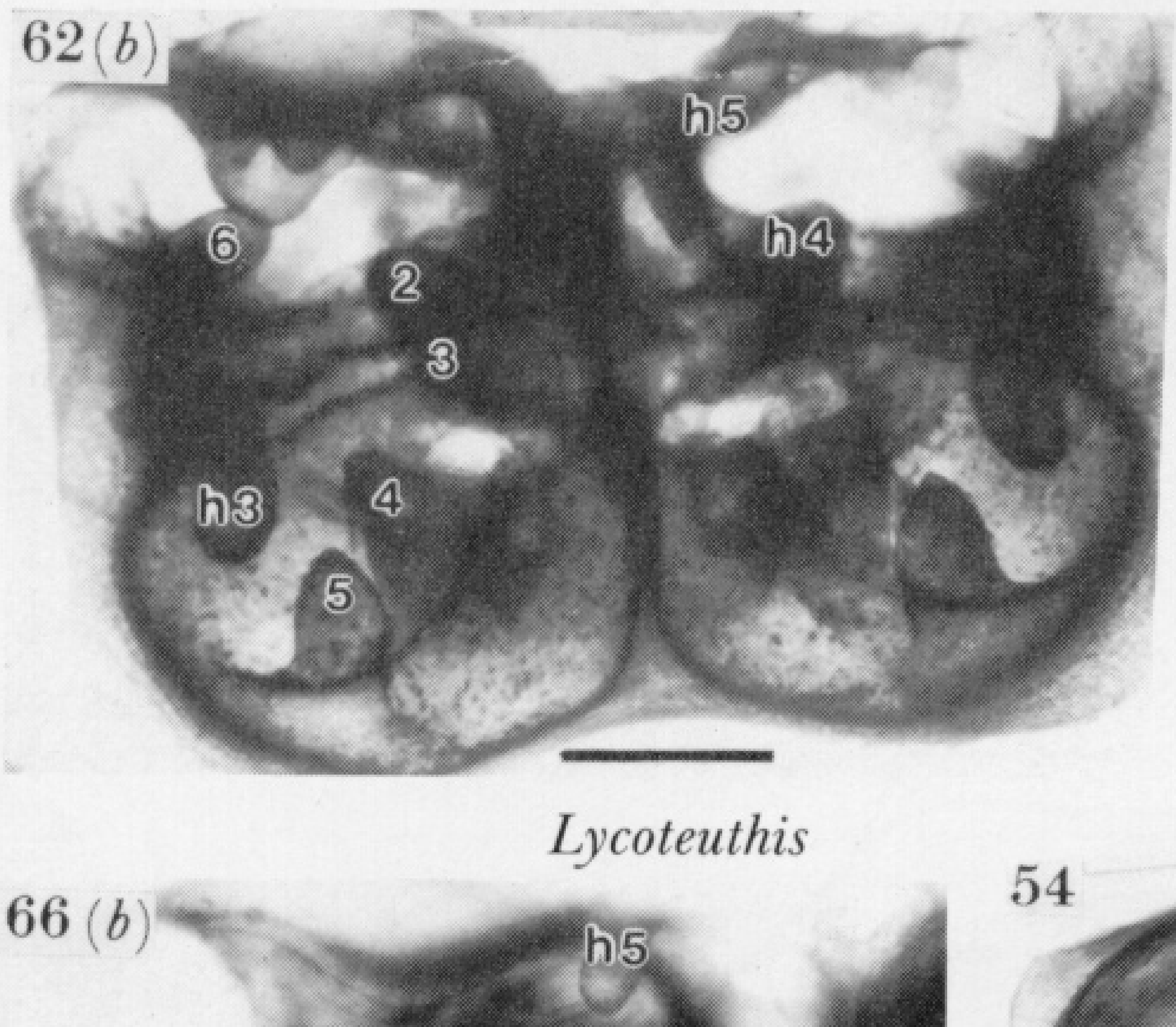
58(*a*)



58(*b*)

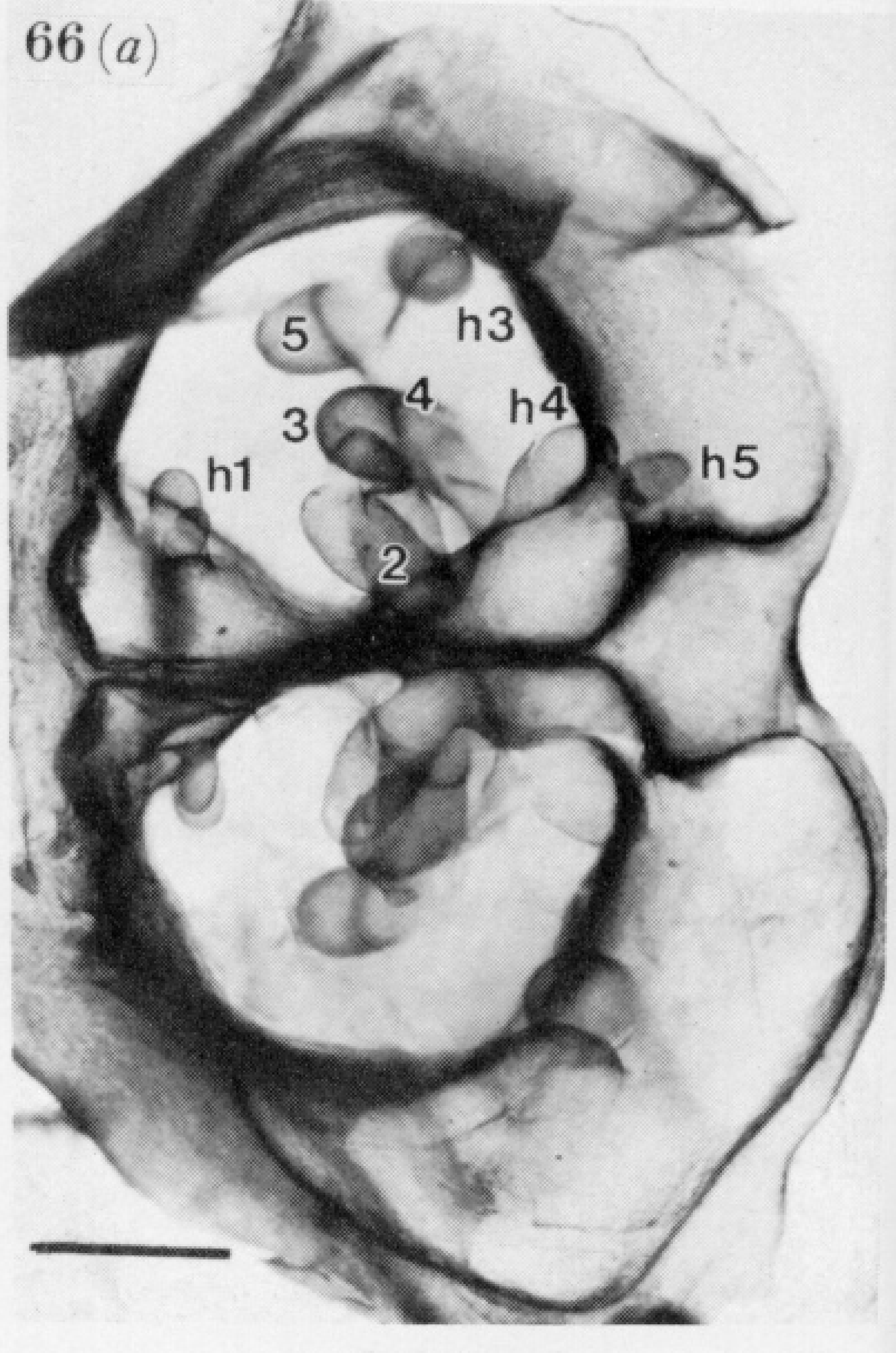
Neoteuthis

62(*b*)



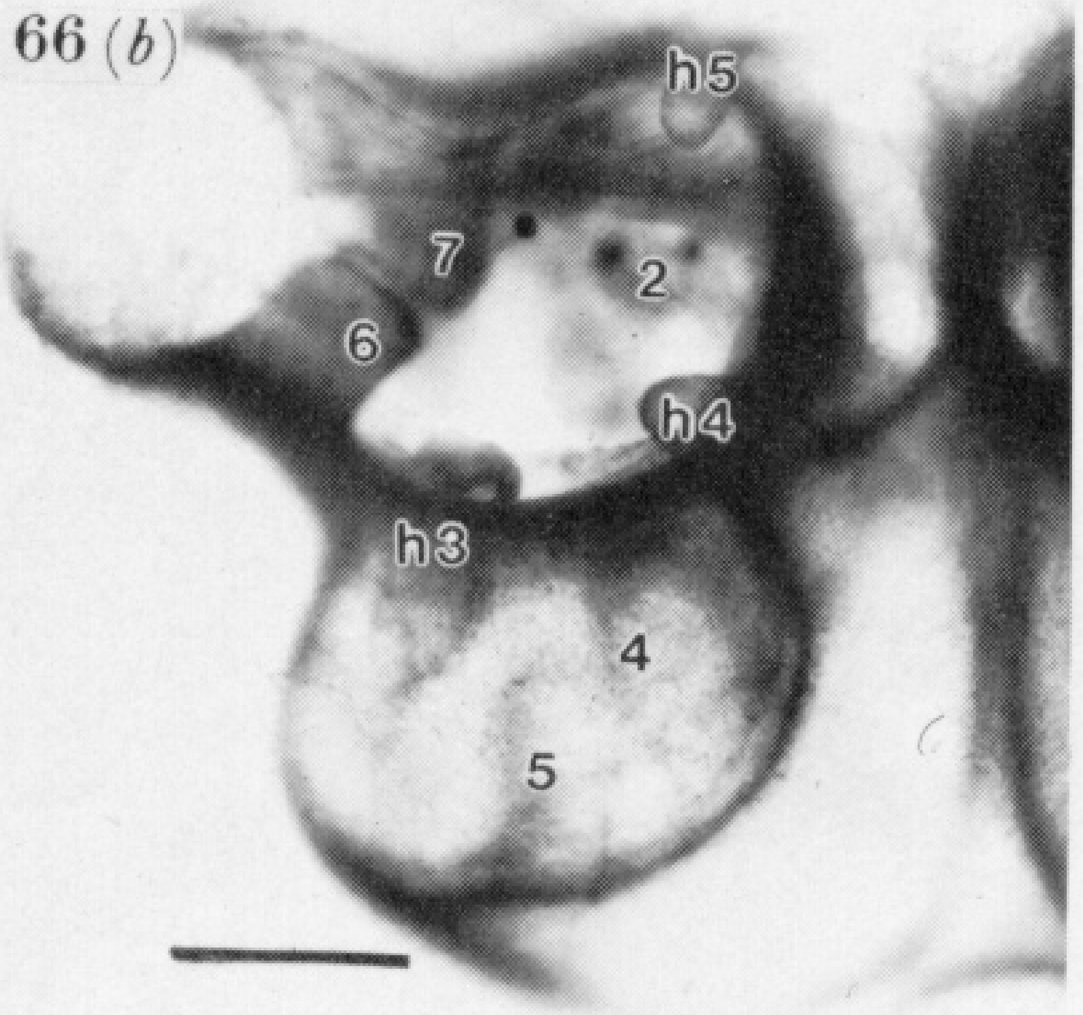
Lycoteuthis

66 (*a*)



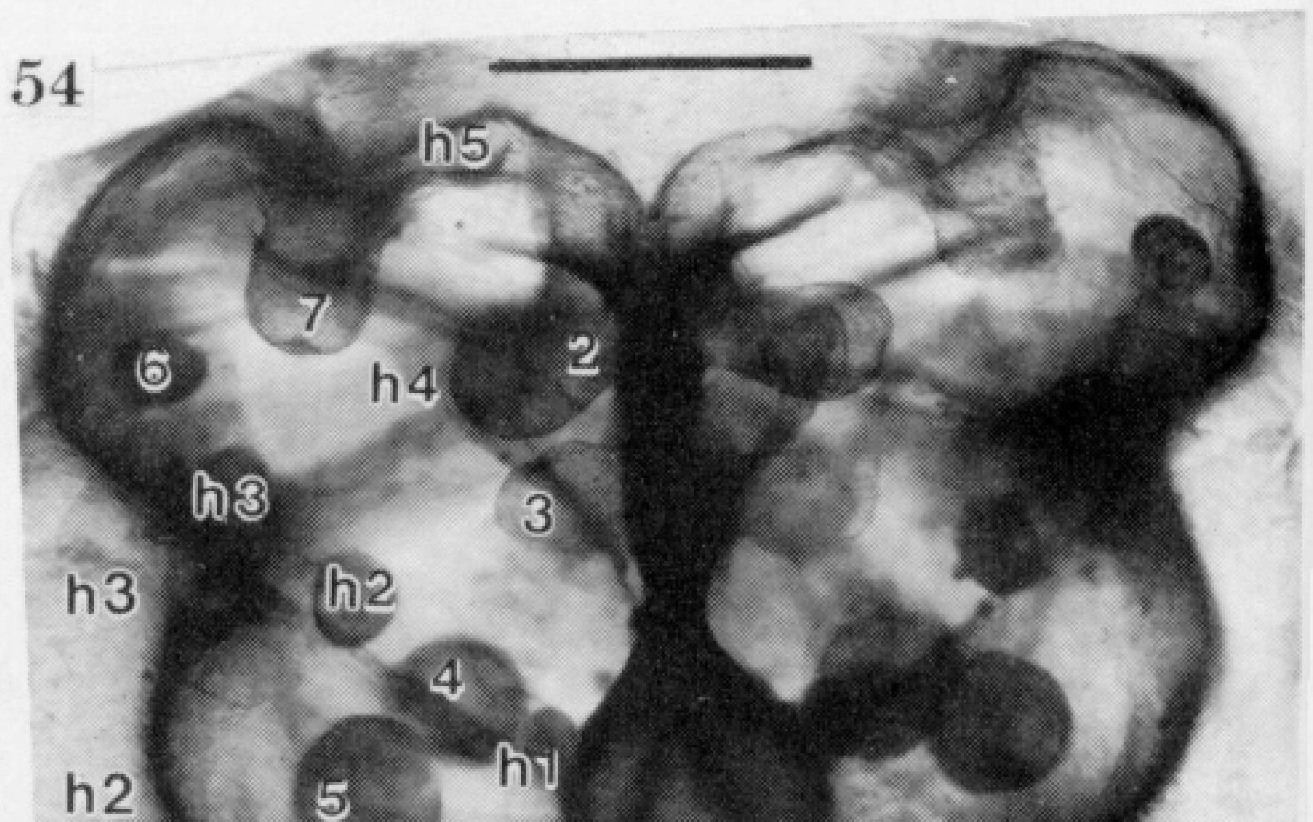
Gonatus

66 (*b*)



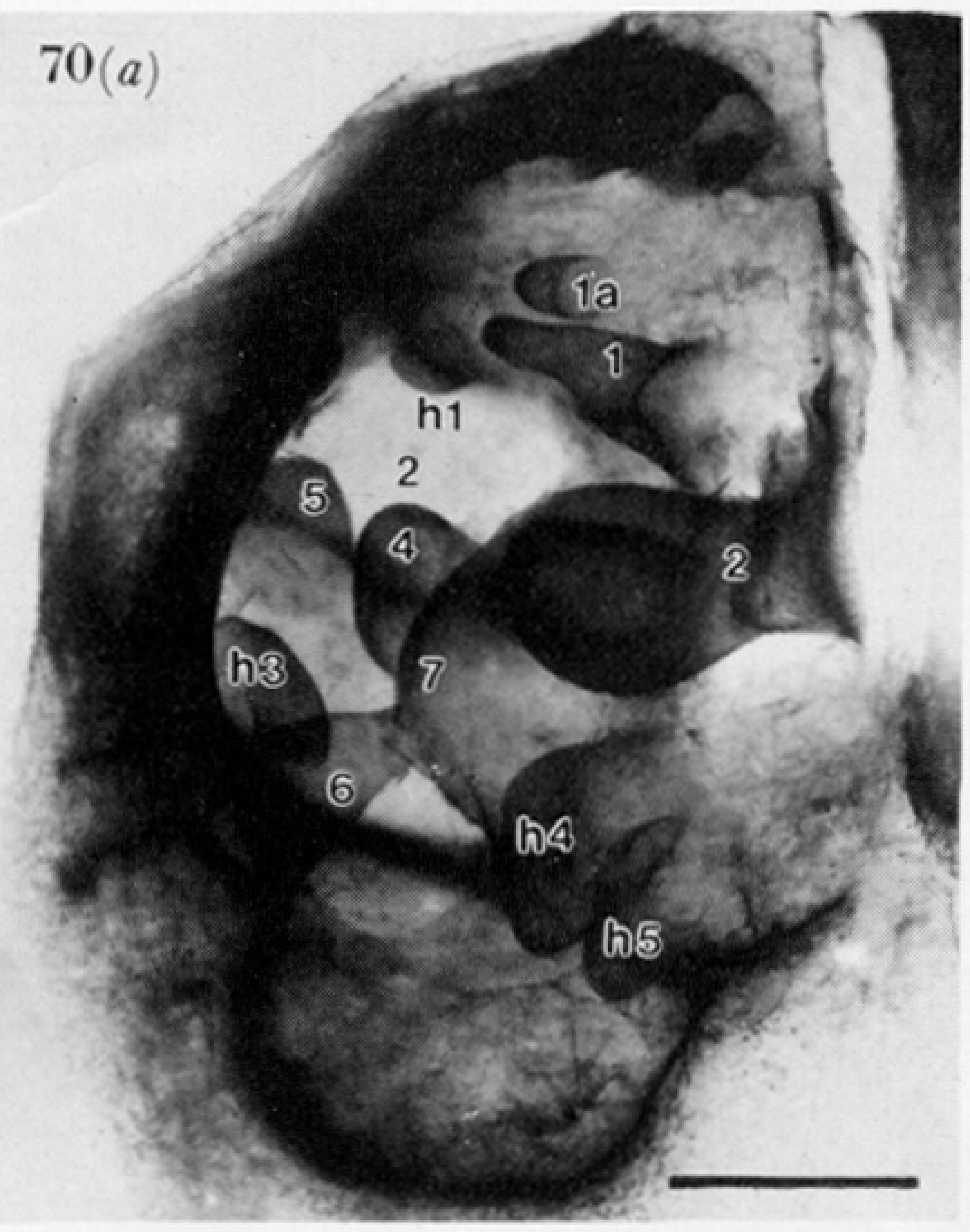
Gonatus

54

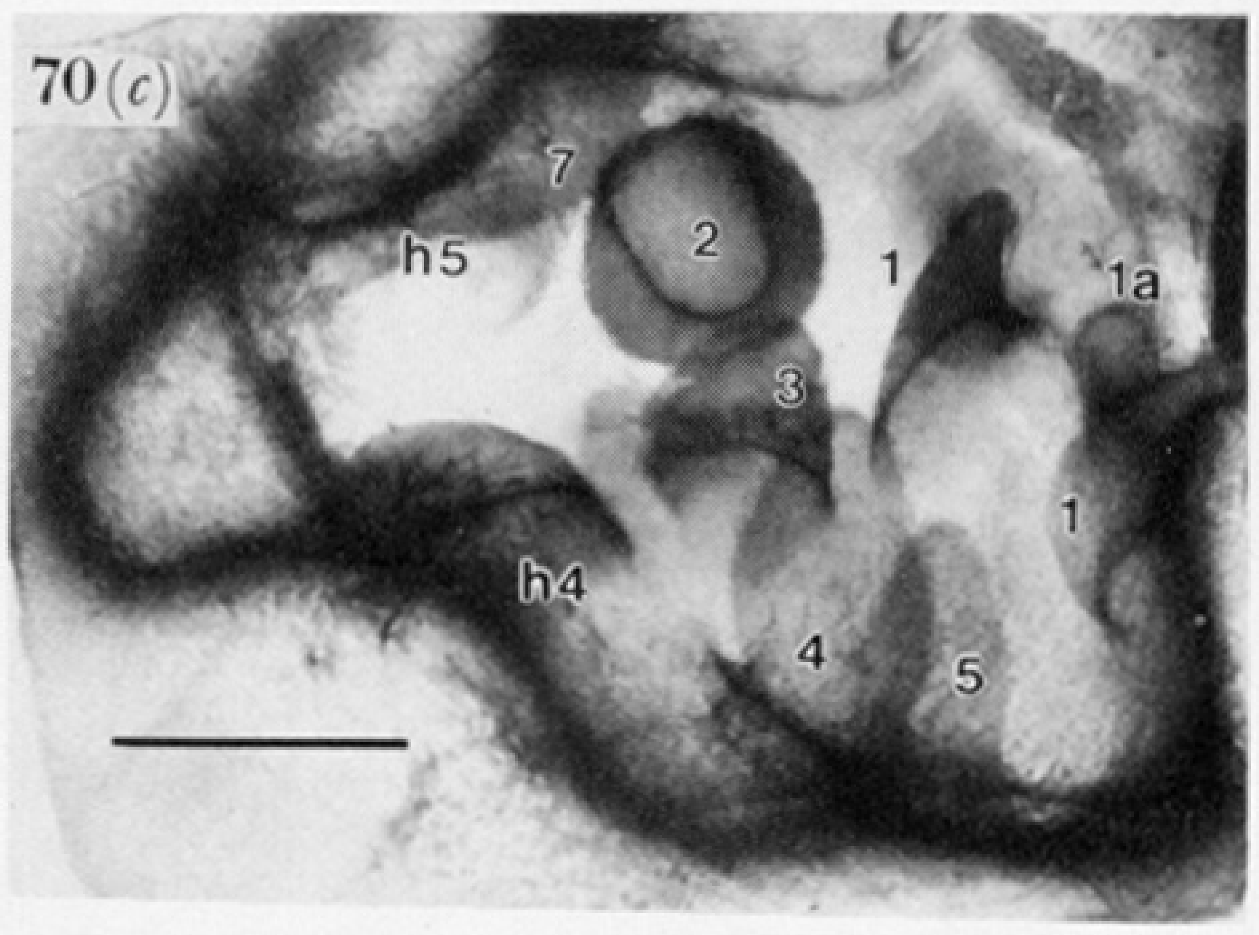


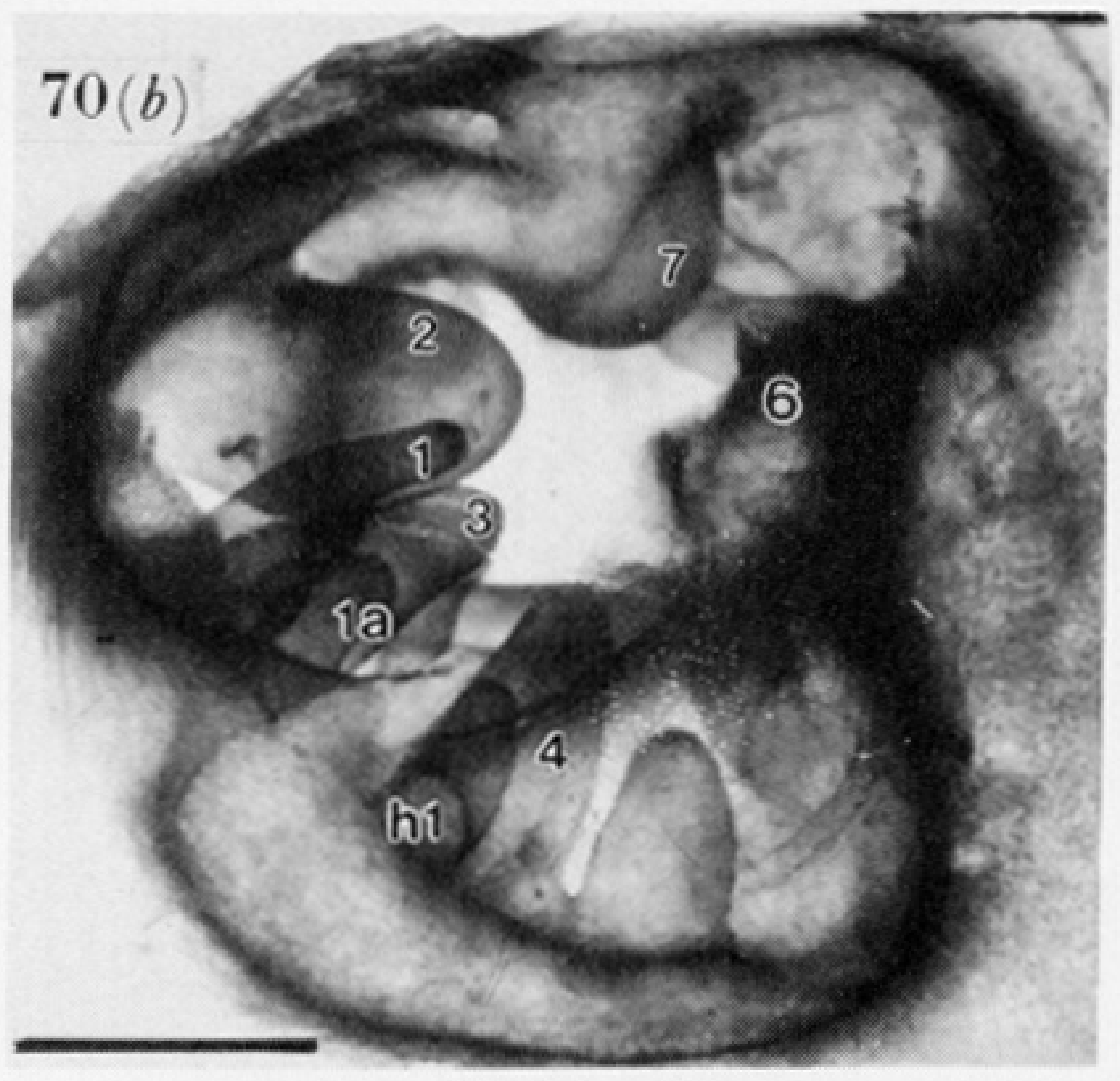
Pyroteuthis

FIGURES 52, 54, 56, 58, 60, 62, 64 AND 66. For description see opposite.

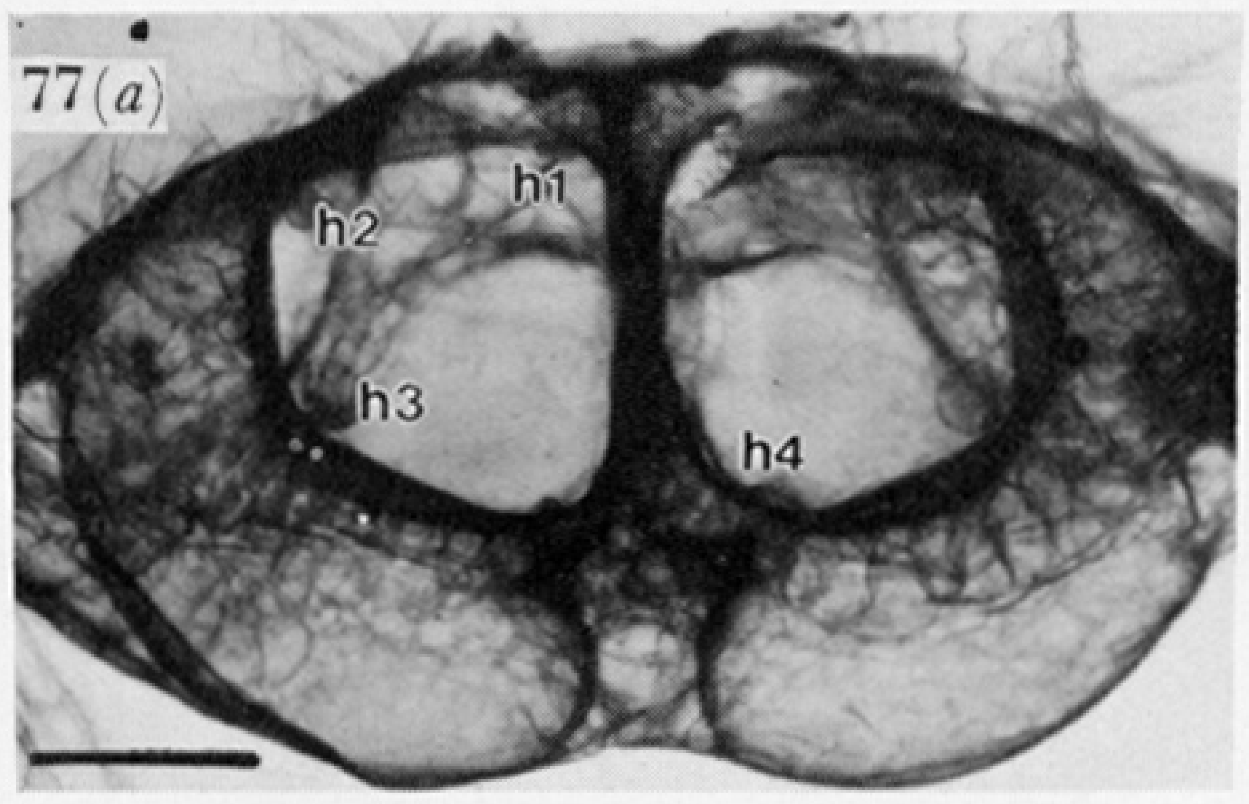


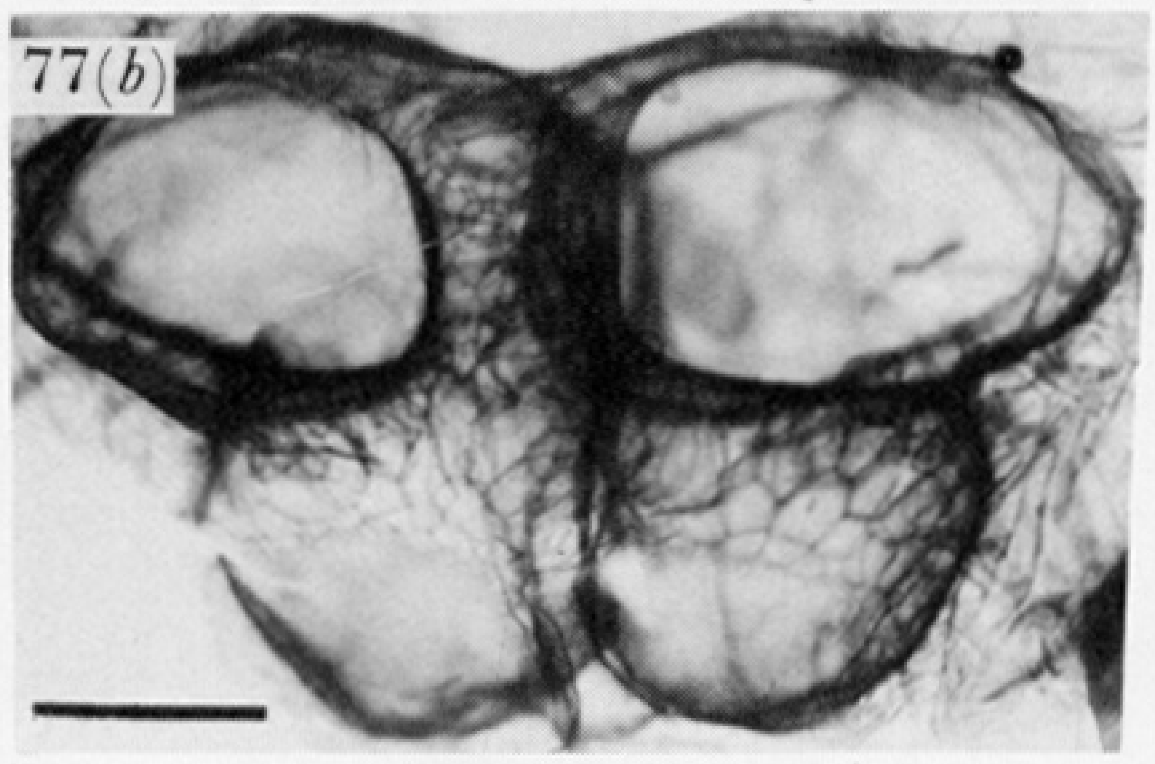
Sepioteuthis



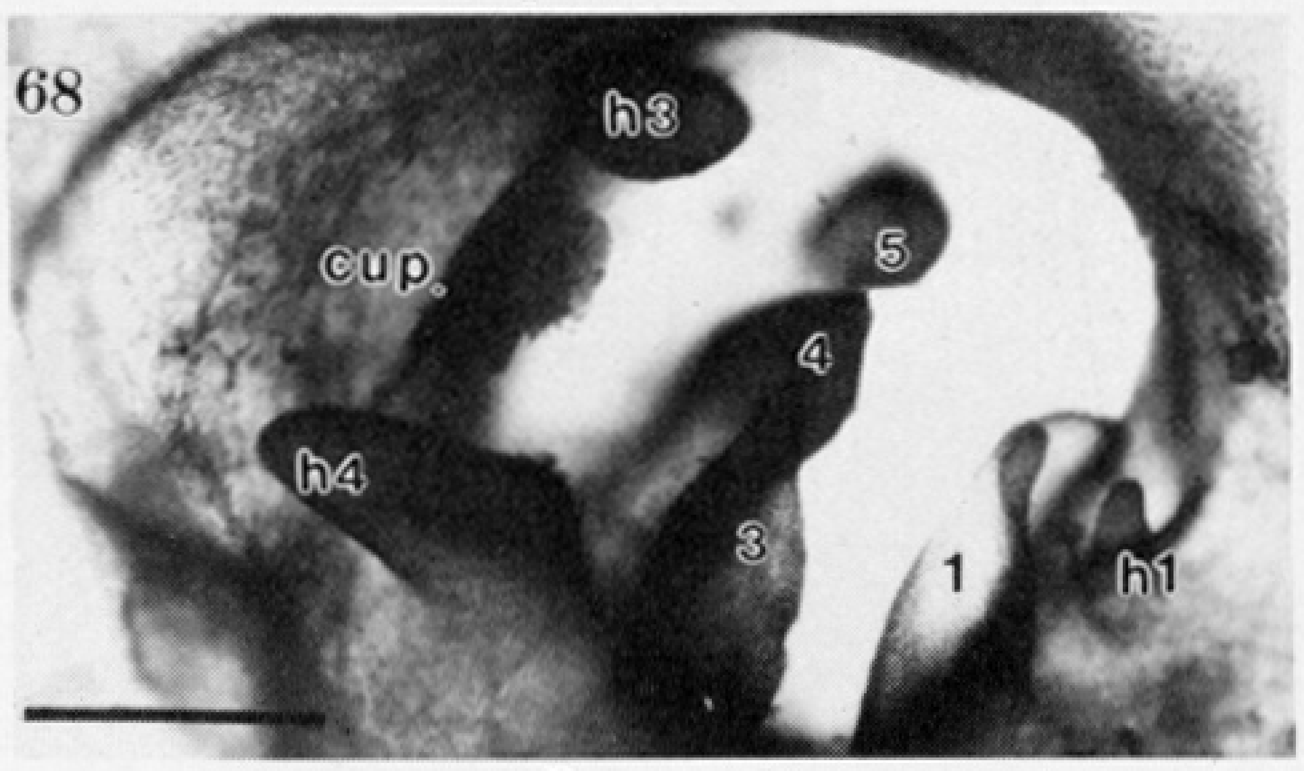


Sepioteuthis

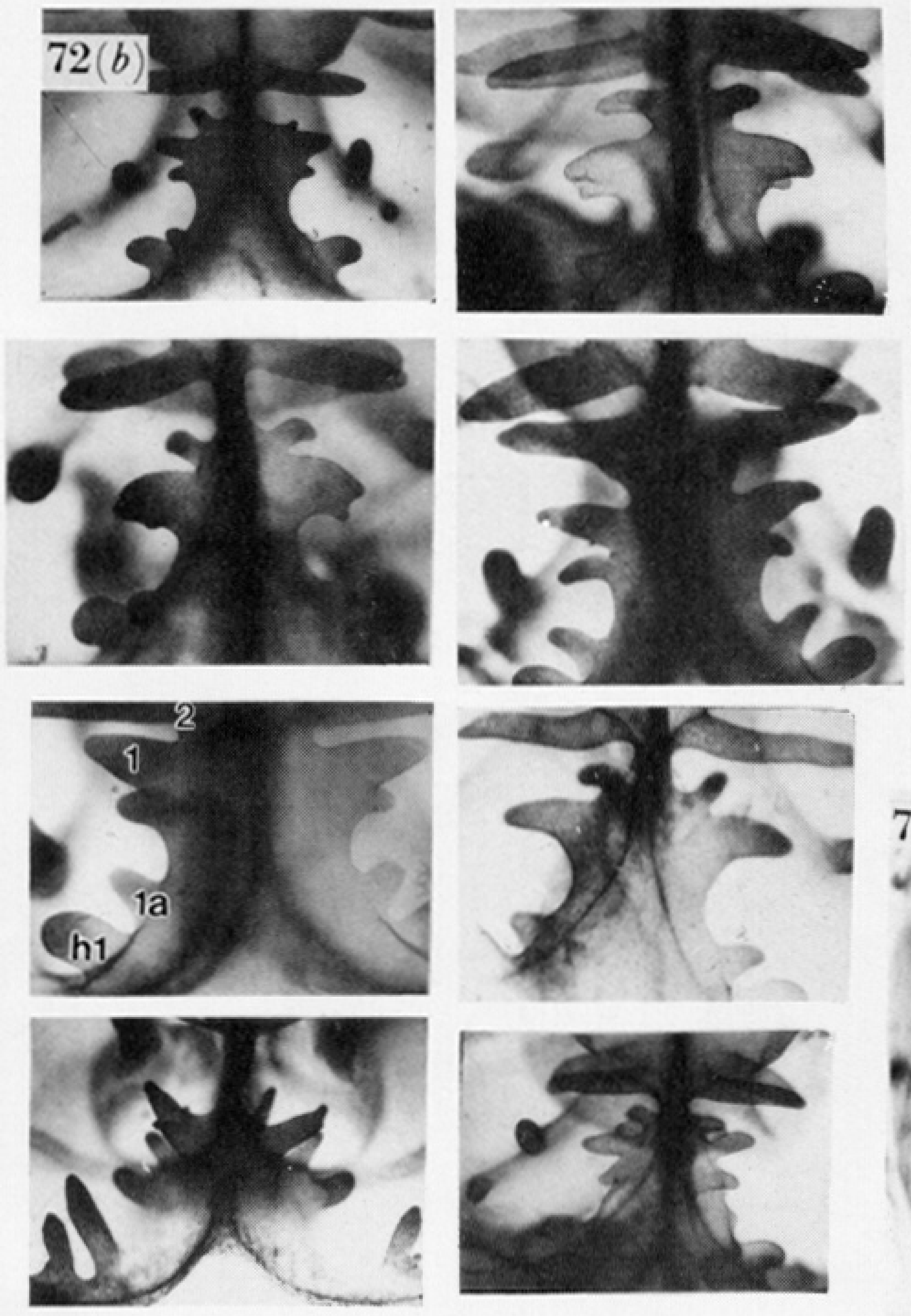




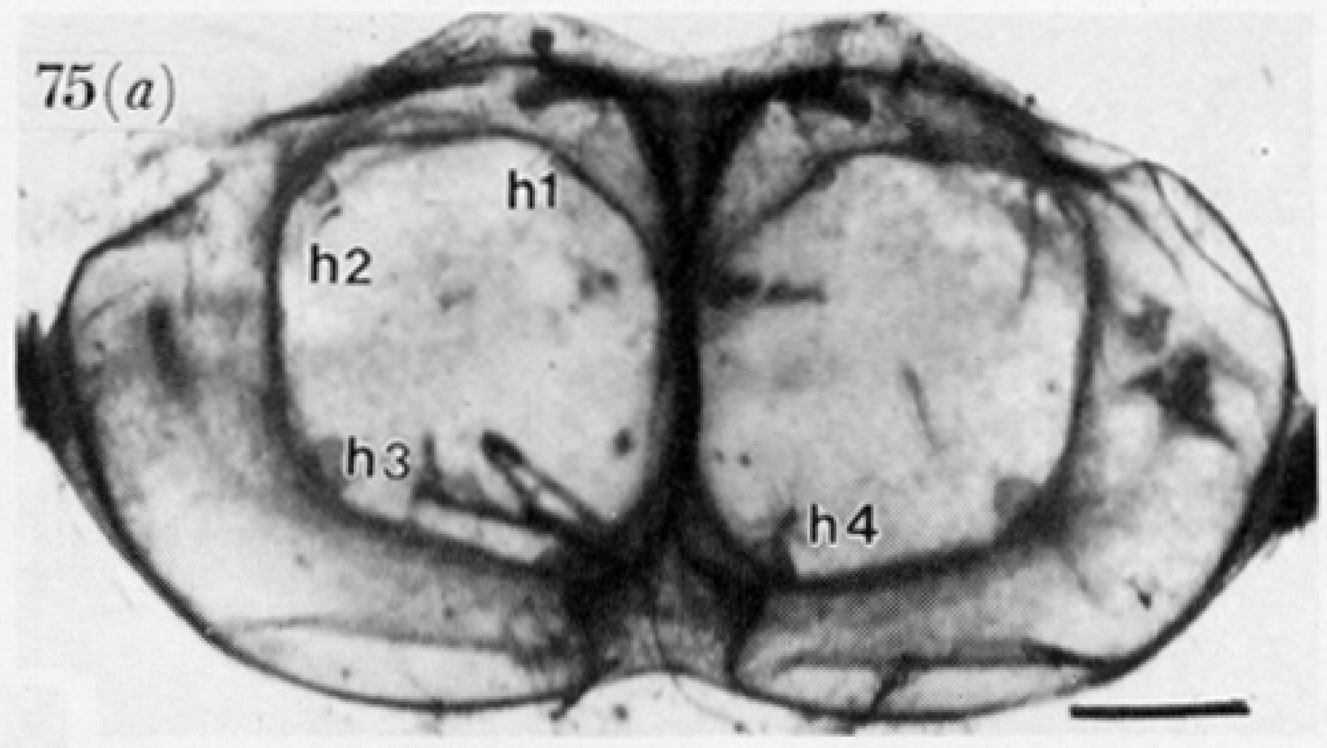
Grimalditeuthis

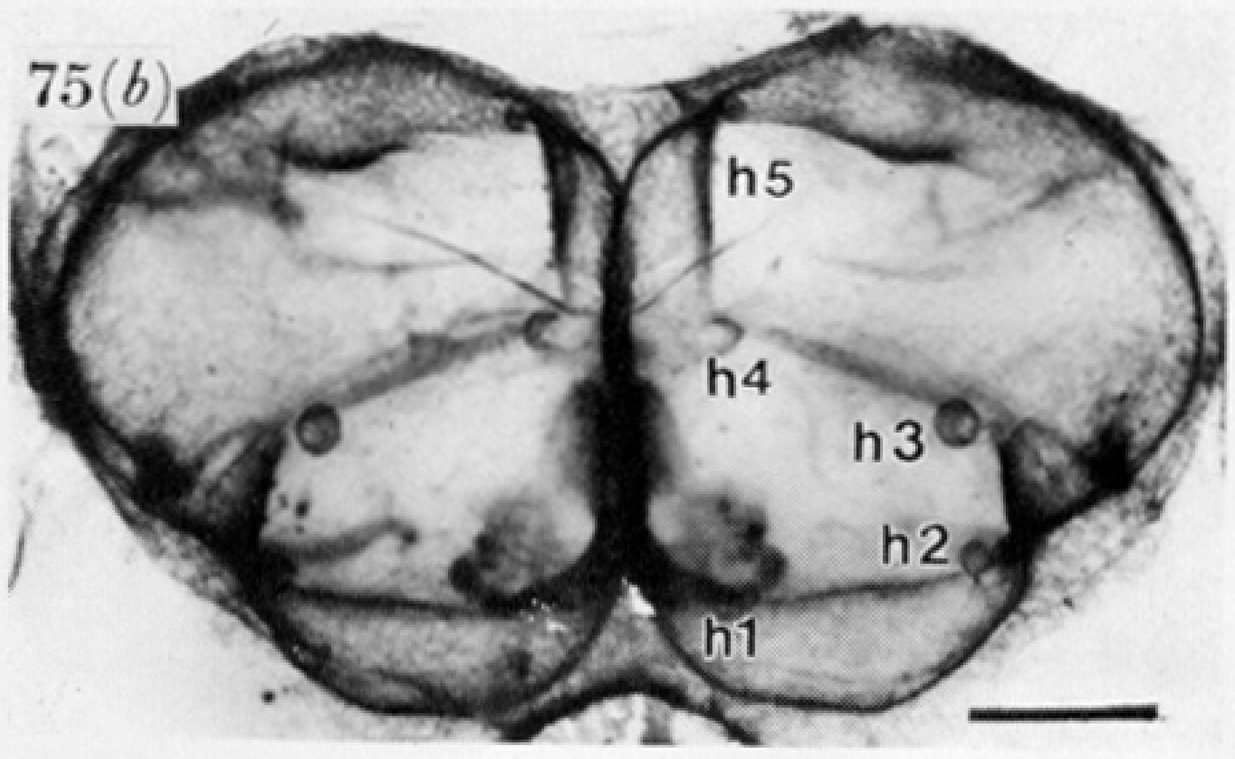


Doryteuthis

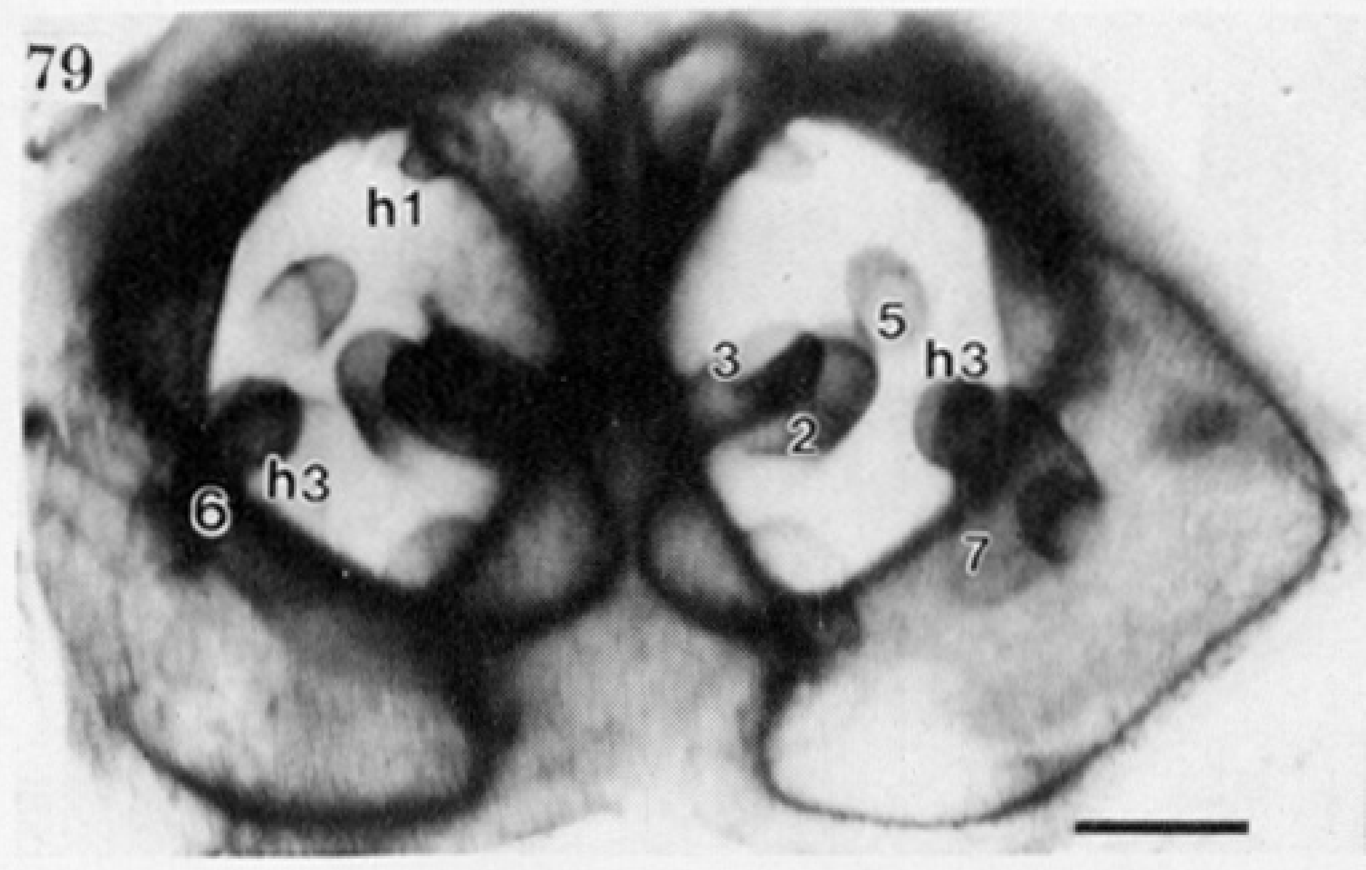


Alloteuthis

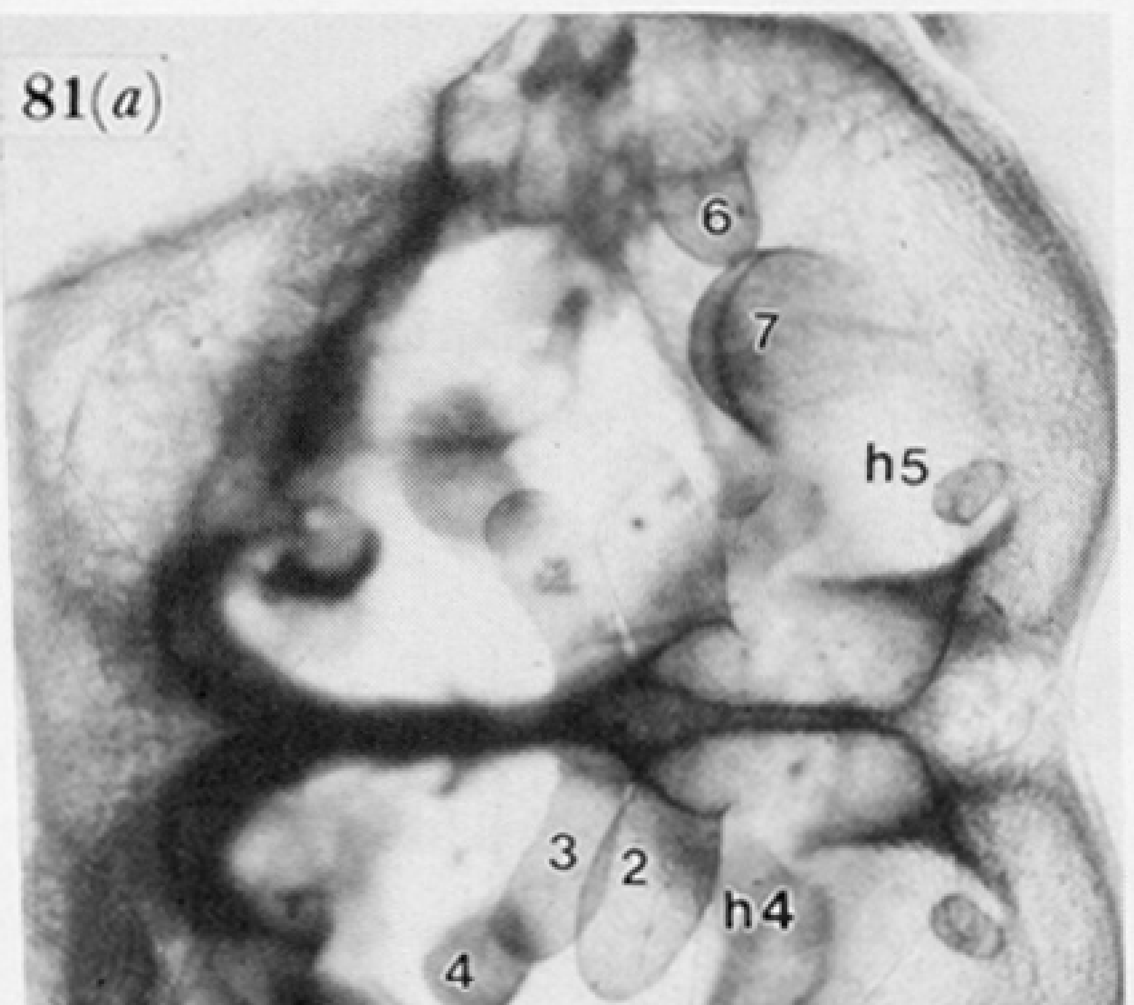




Joubiniteuthis

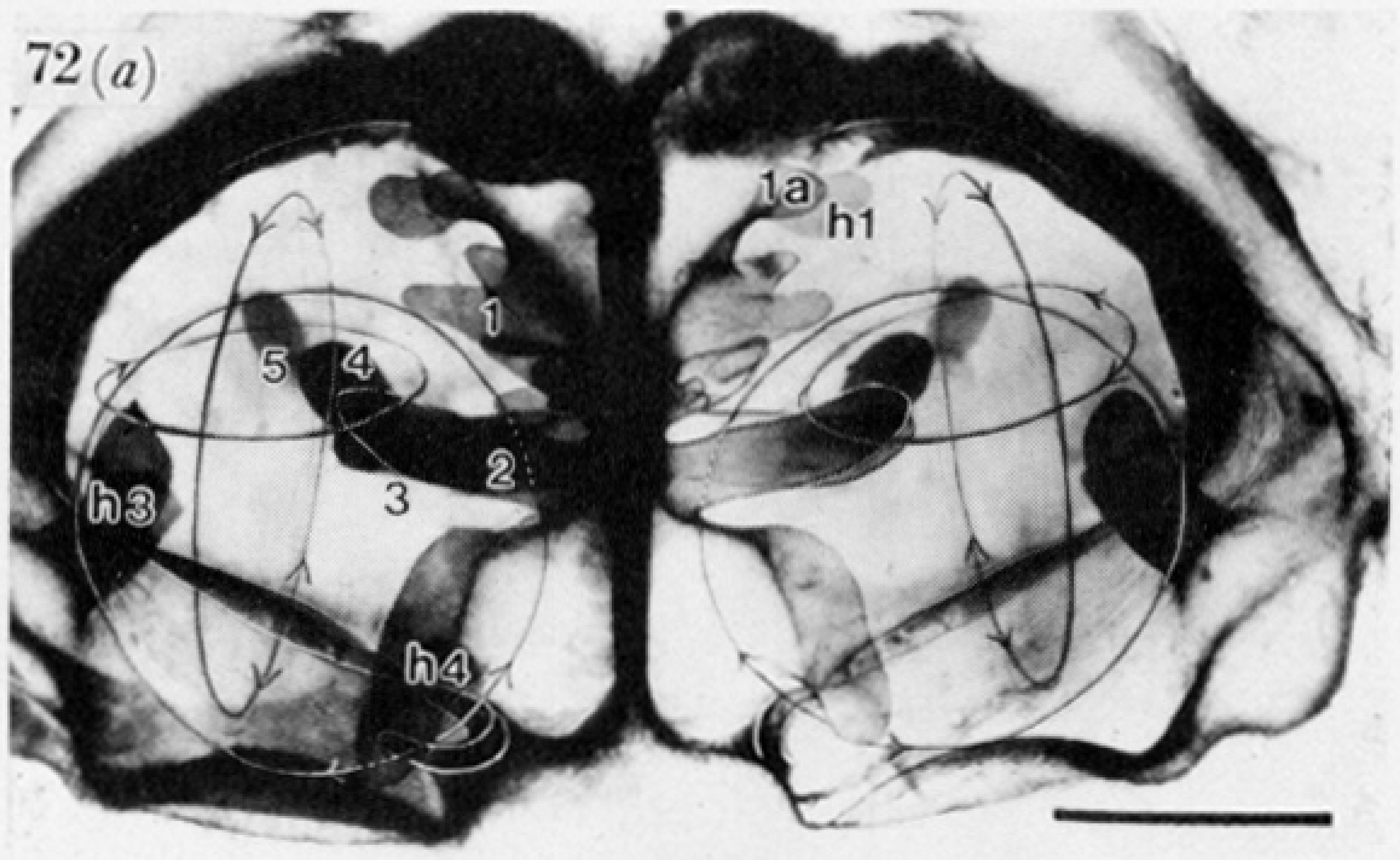


Pholidoteuthis



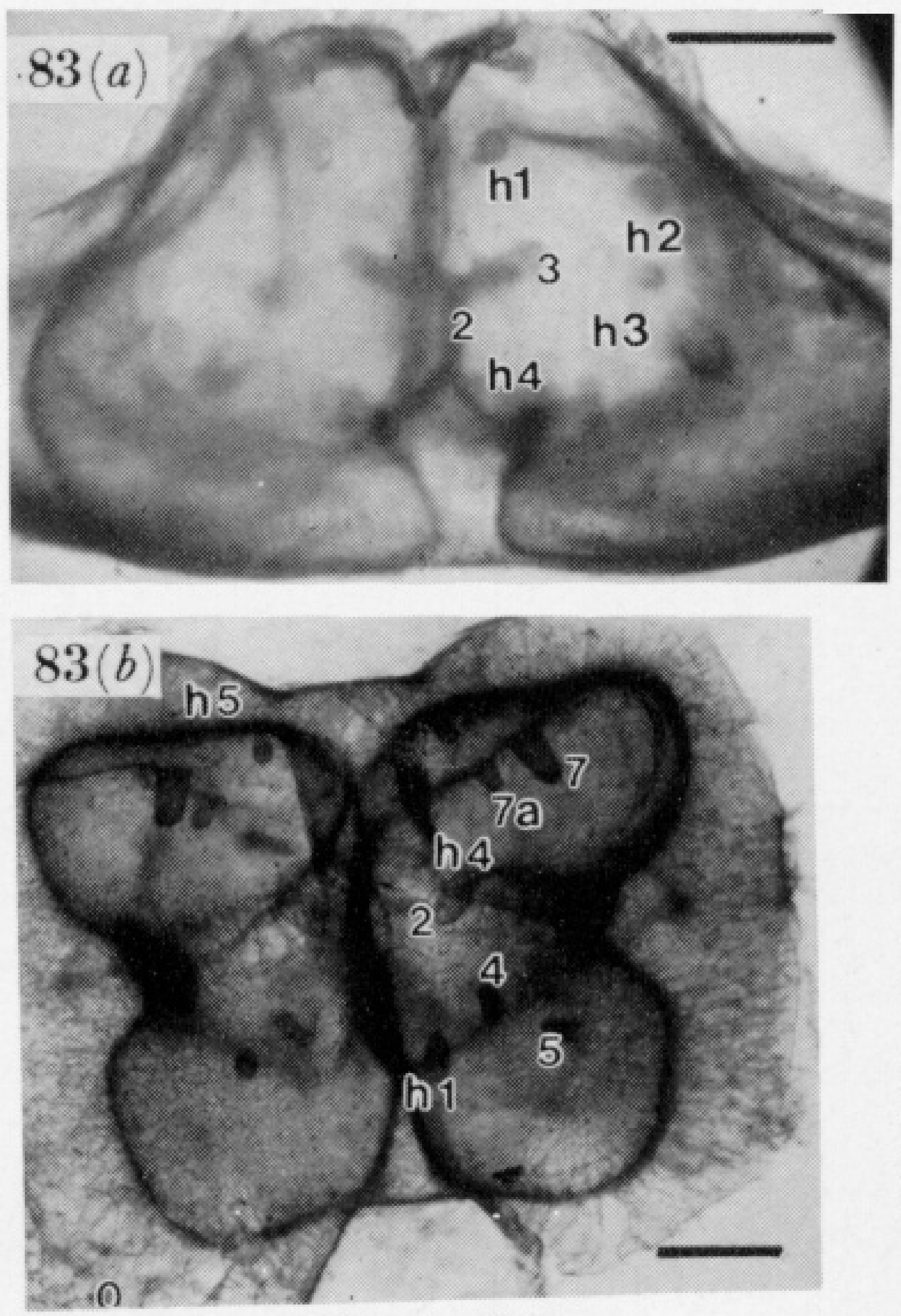
Octopoteuthis

Octopoteuthis

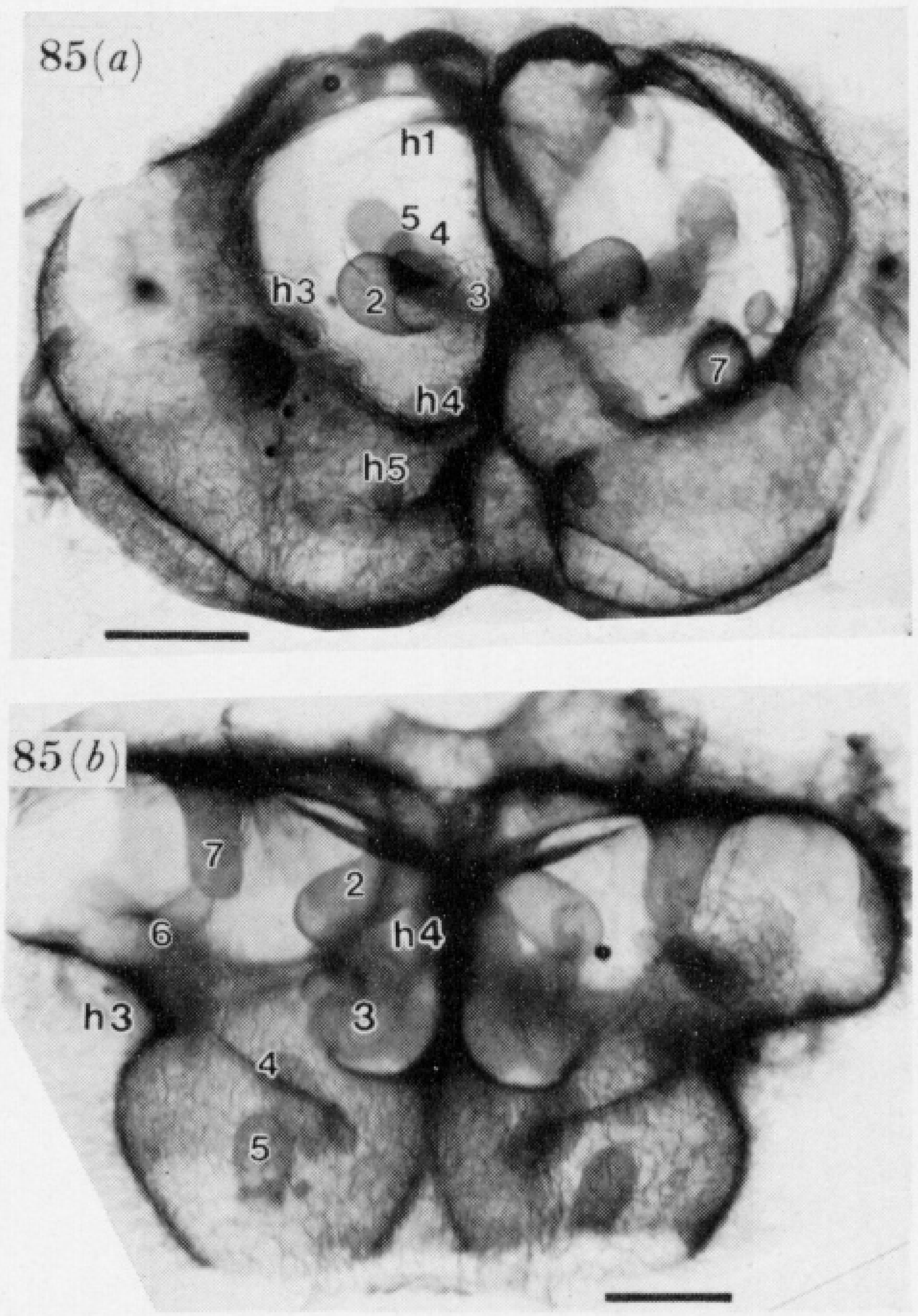


Alloteuthis

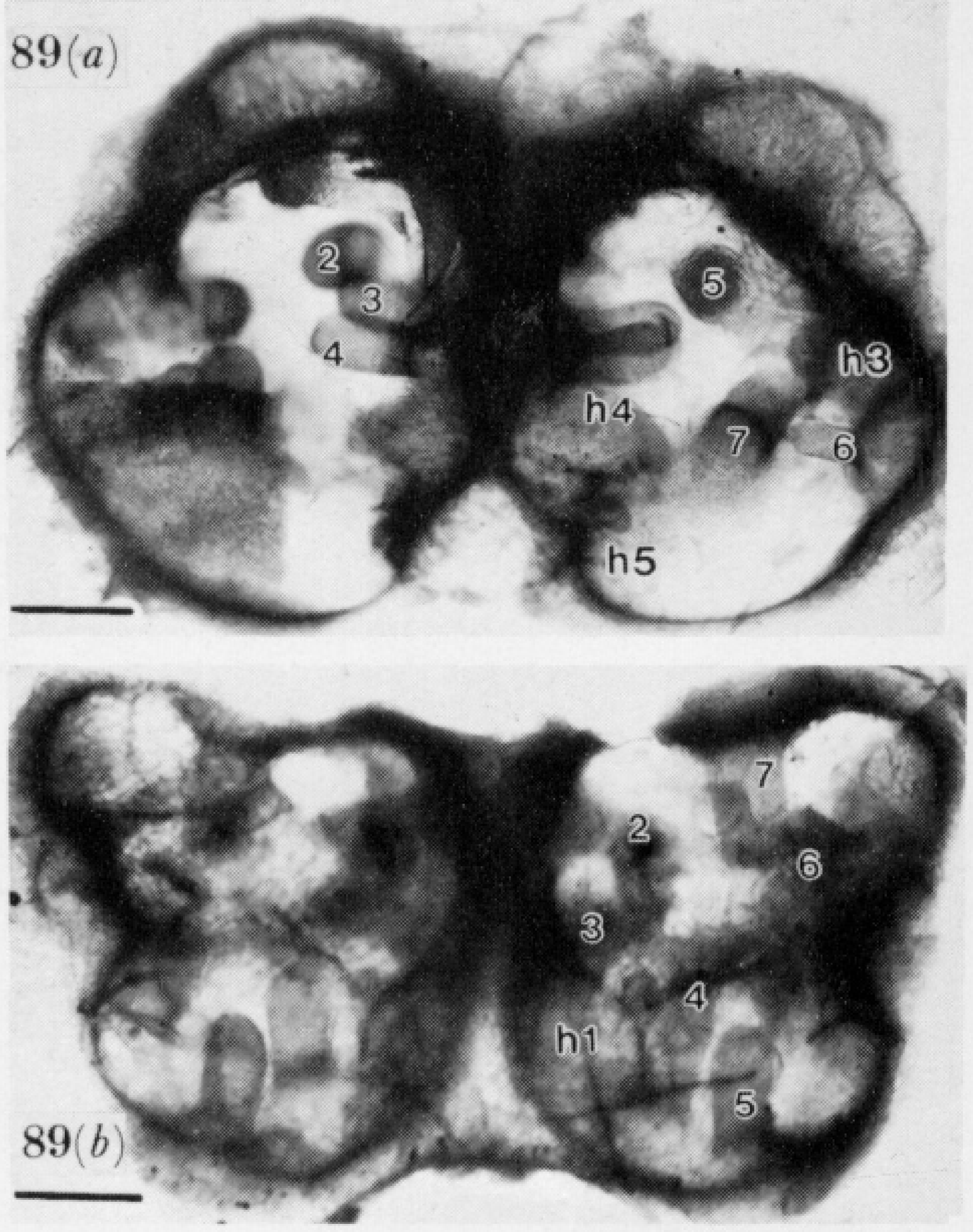
FIGURES 68, 70, 72, 75, 77, 79 AND 81. For description see opposite.



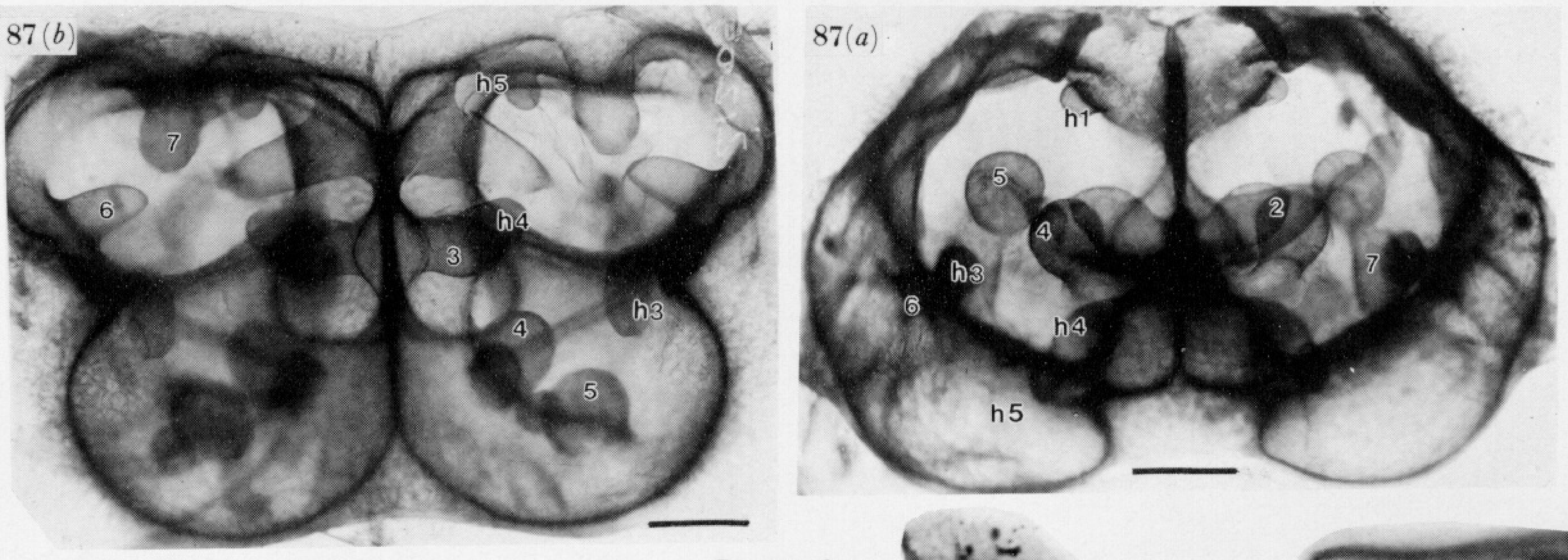
Chiroteuthis



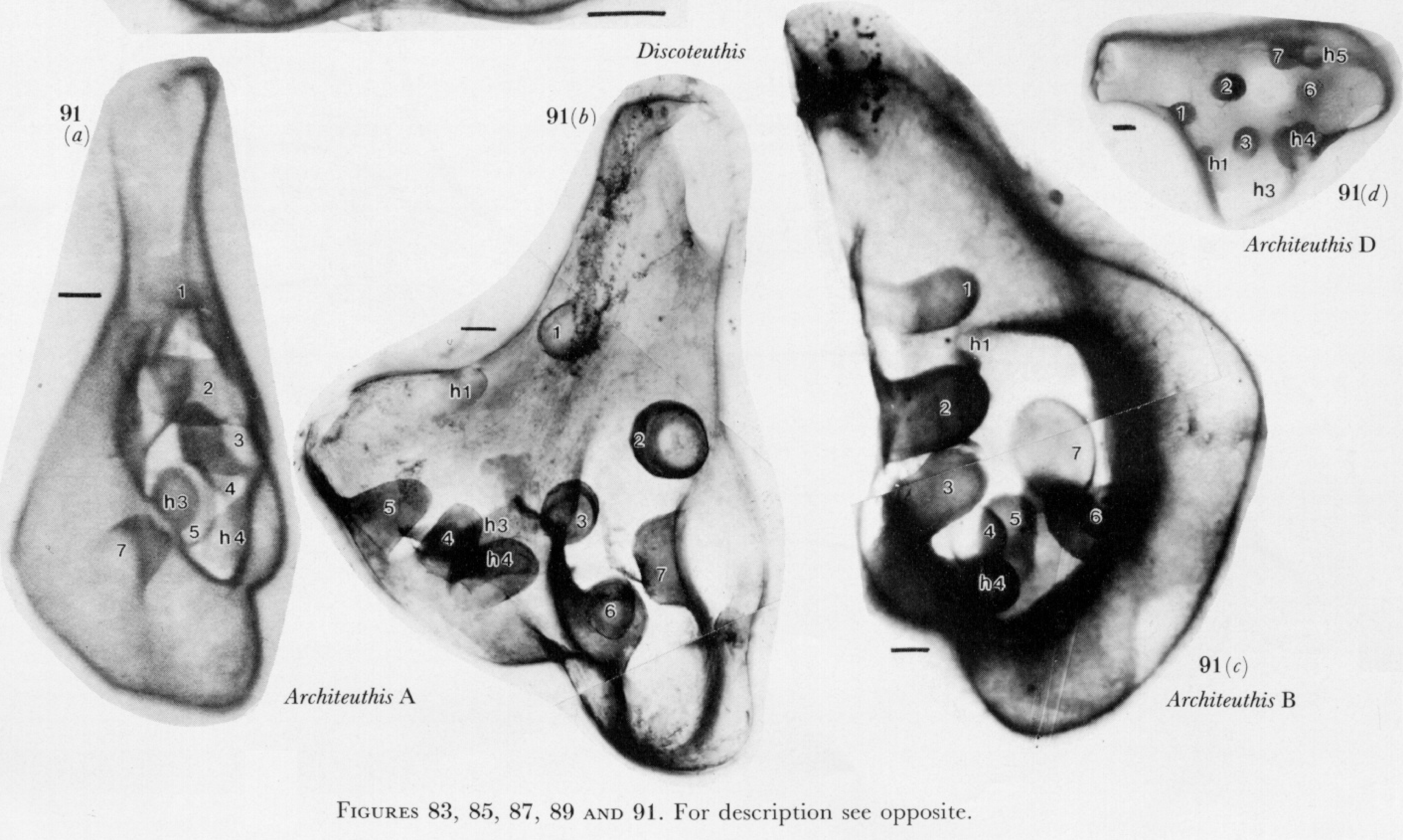
Mastigoteuthis



Histioteuthis



Discoteuthis



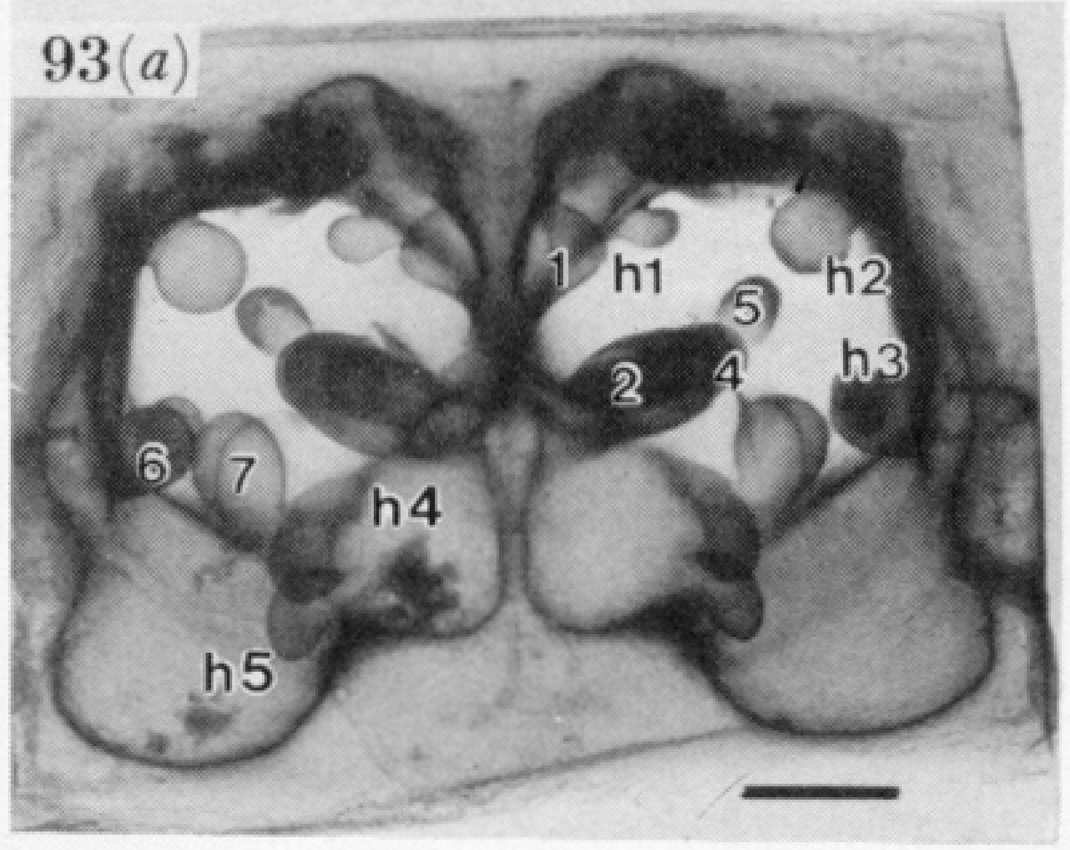
Architeuthis A

Architeuthis B

Architeuthis D

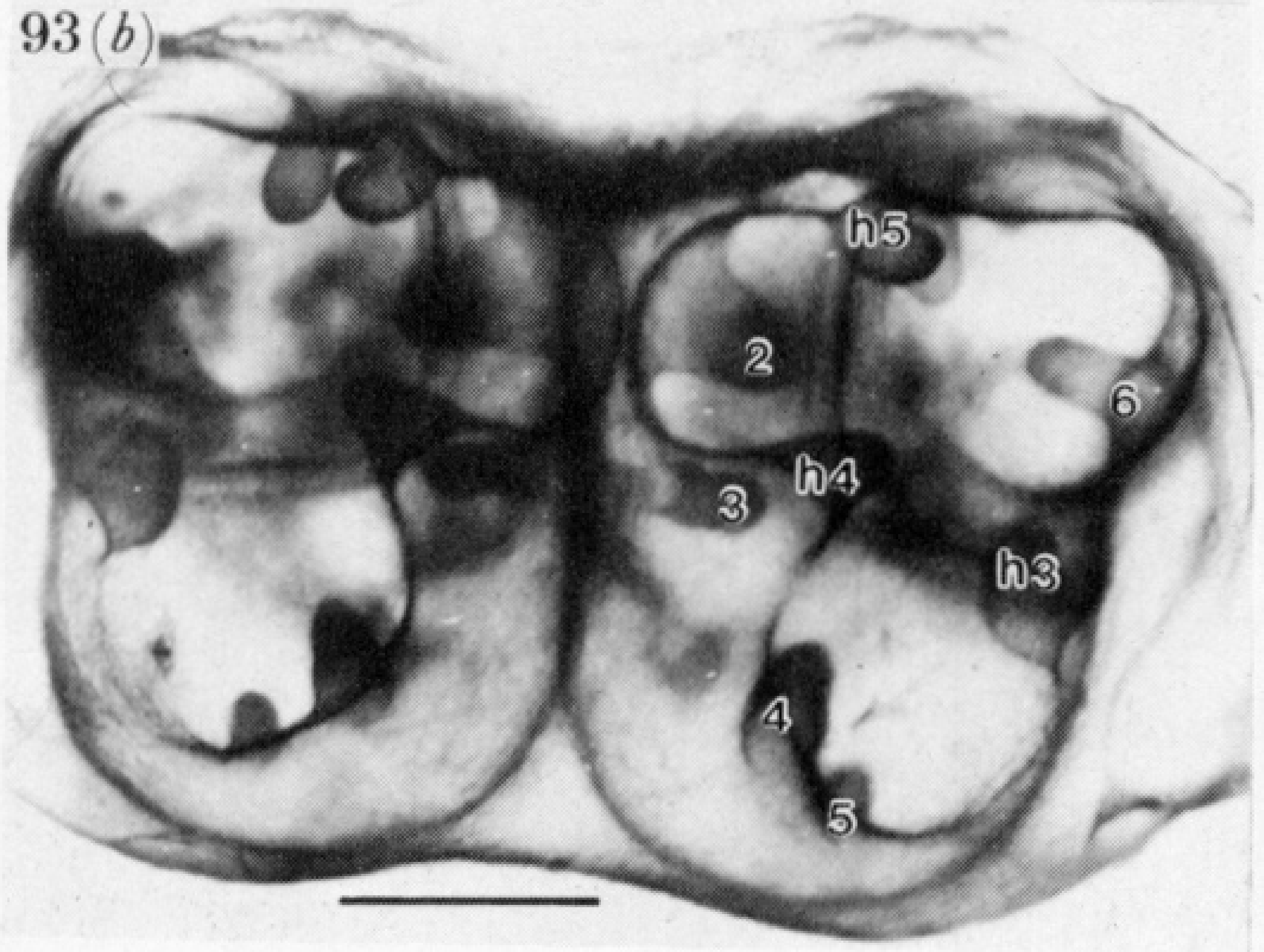
FIGURES 83, 85, 87, 89 AND 91. For description see opposite.

93(*a*)



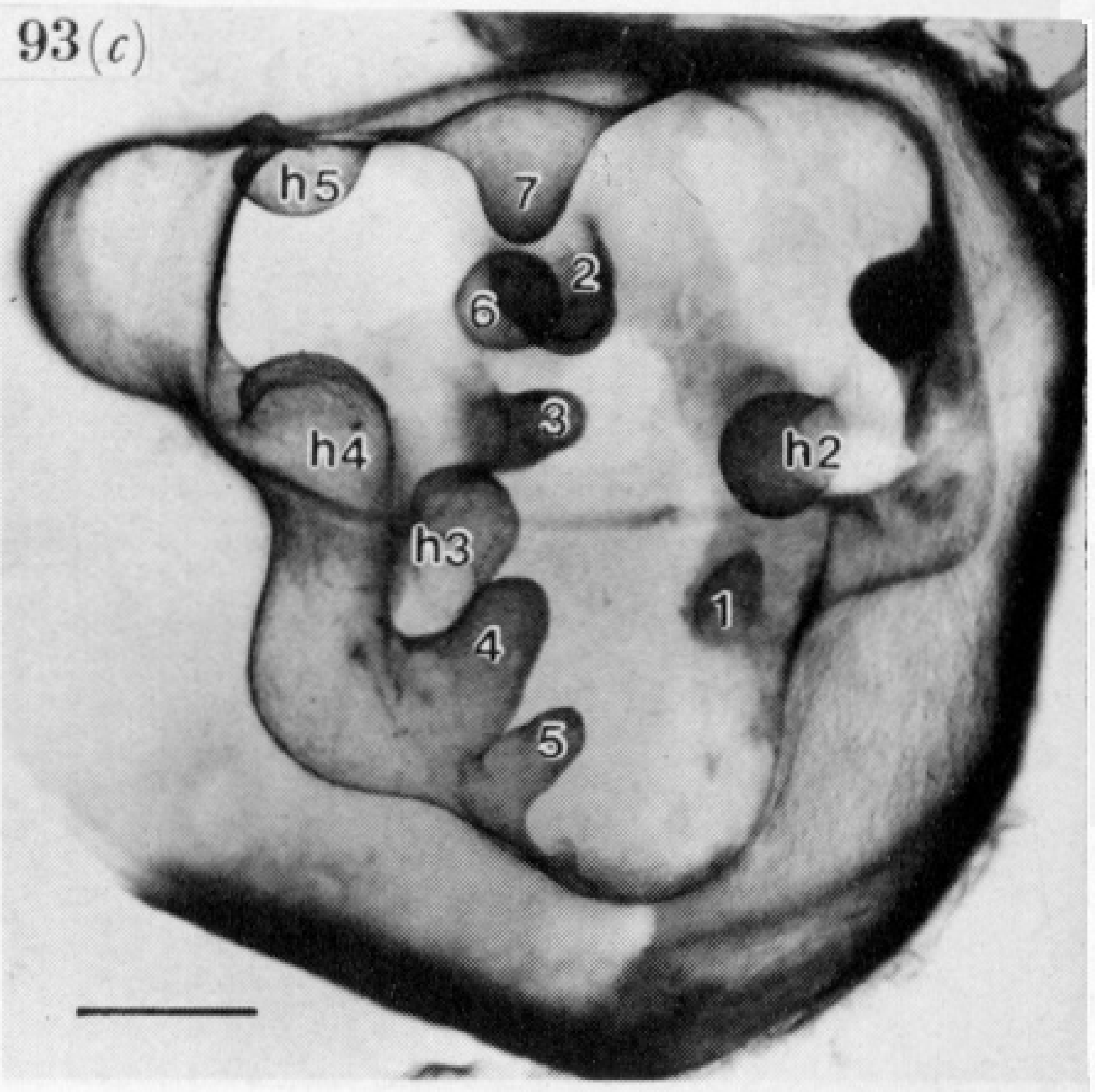
Sepia

93(*b*)



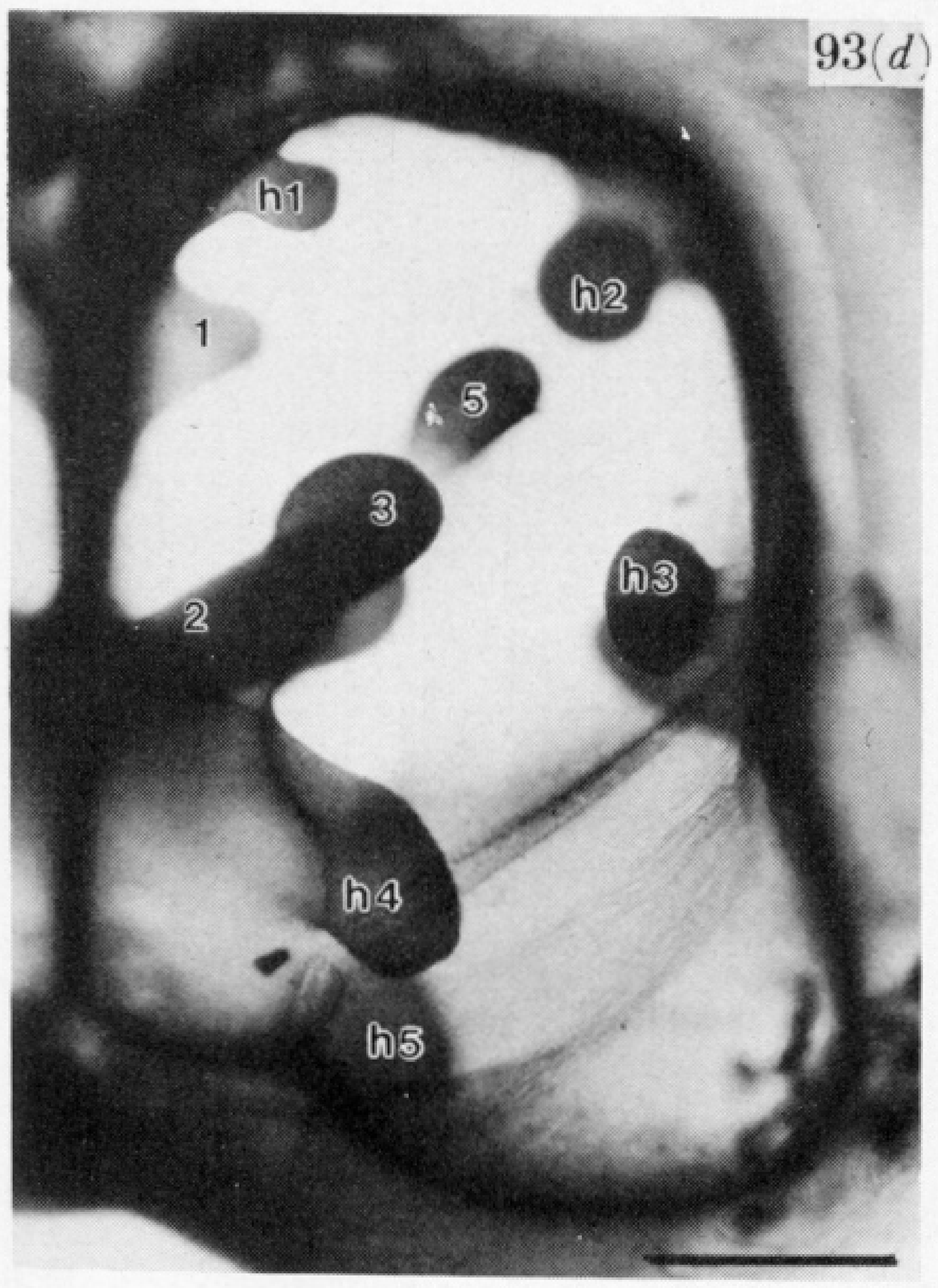
Sepia

93(*c*)



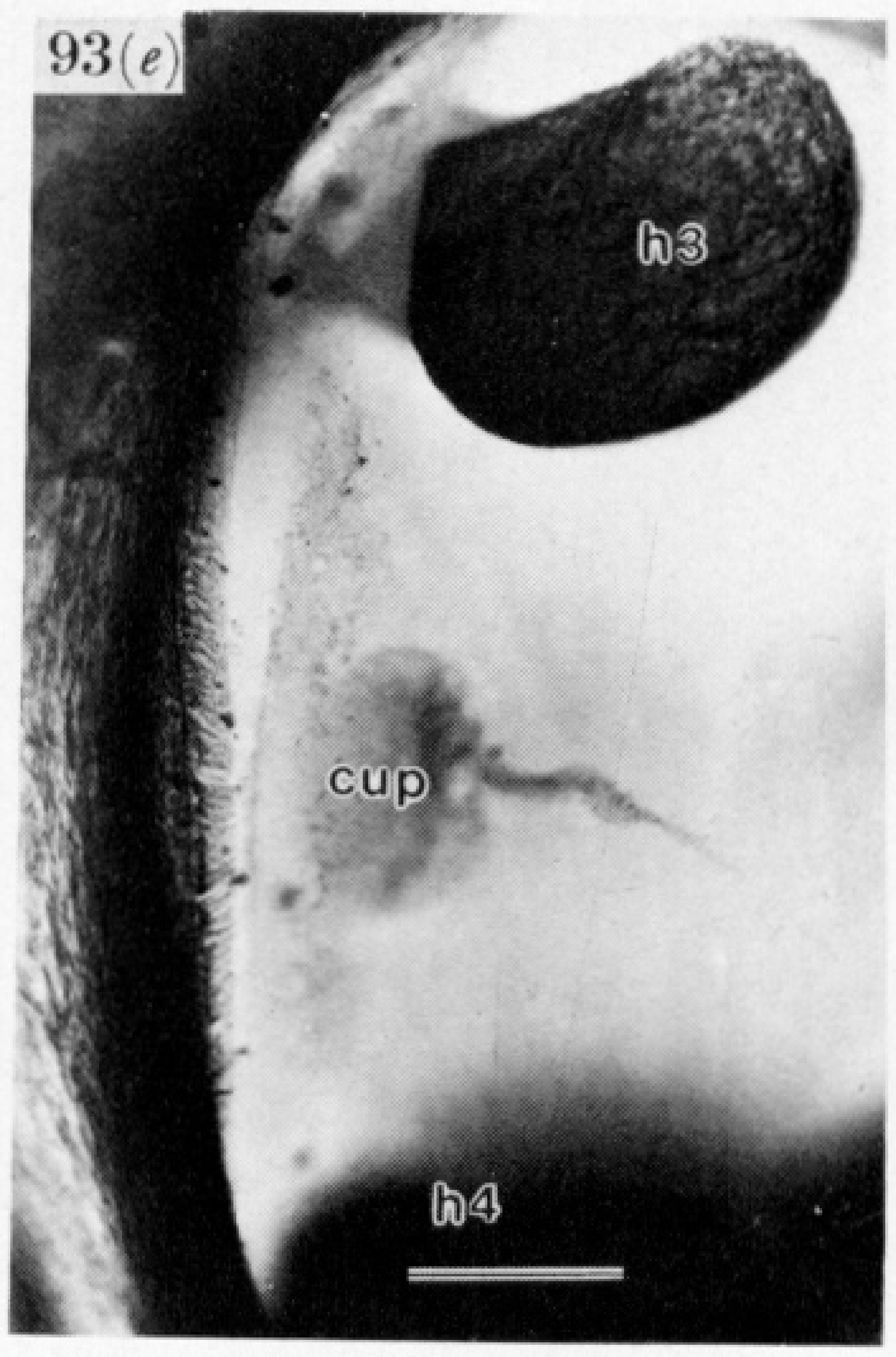
Sepia

93(*d*)



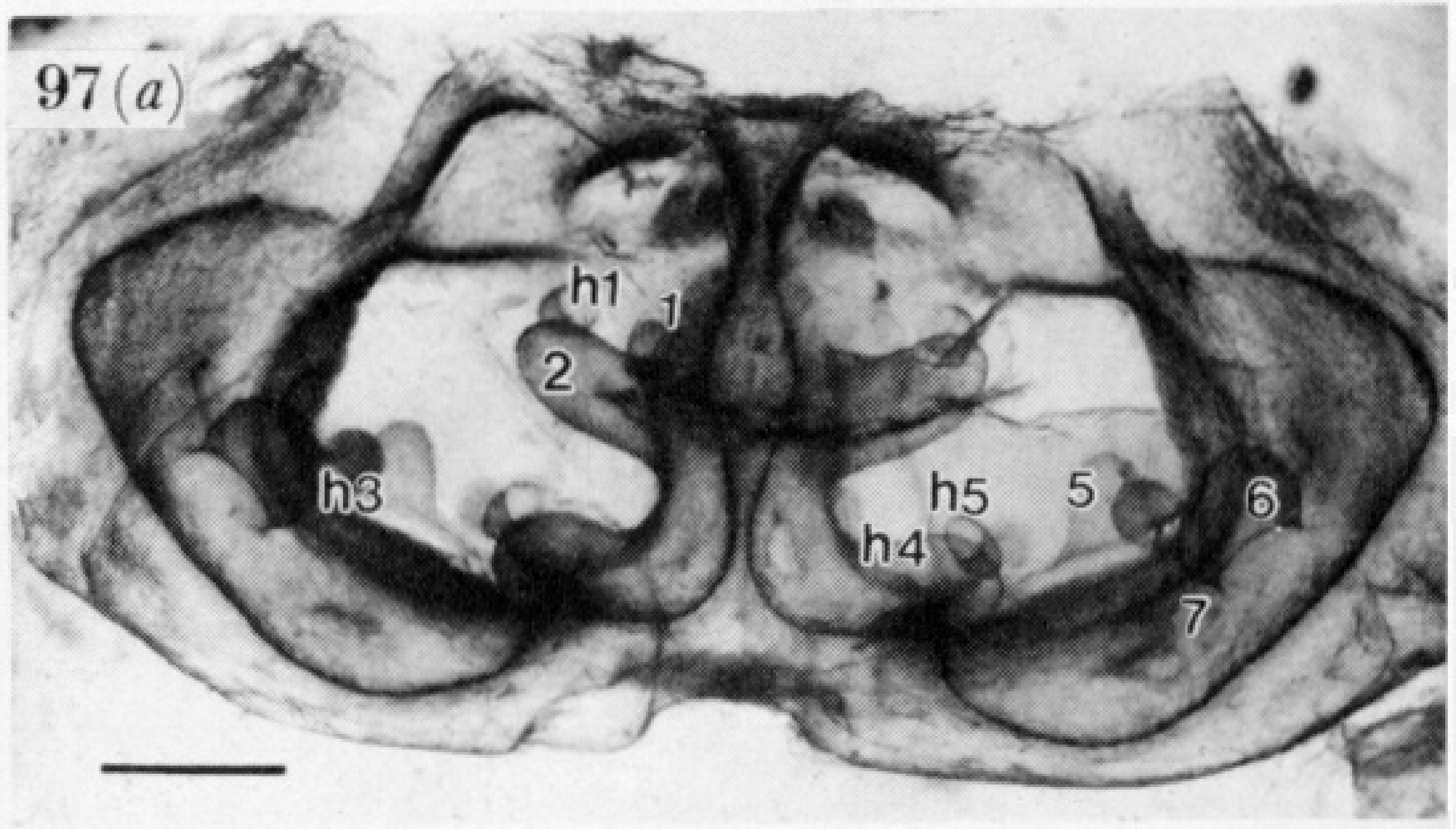
Sepia

93(*e*)

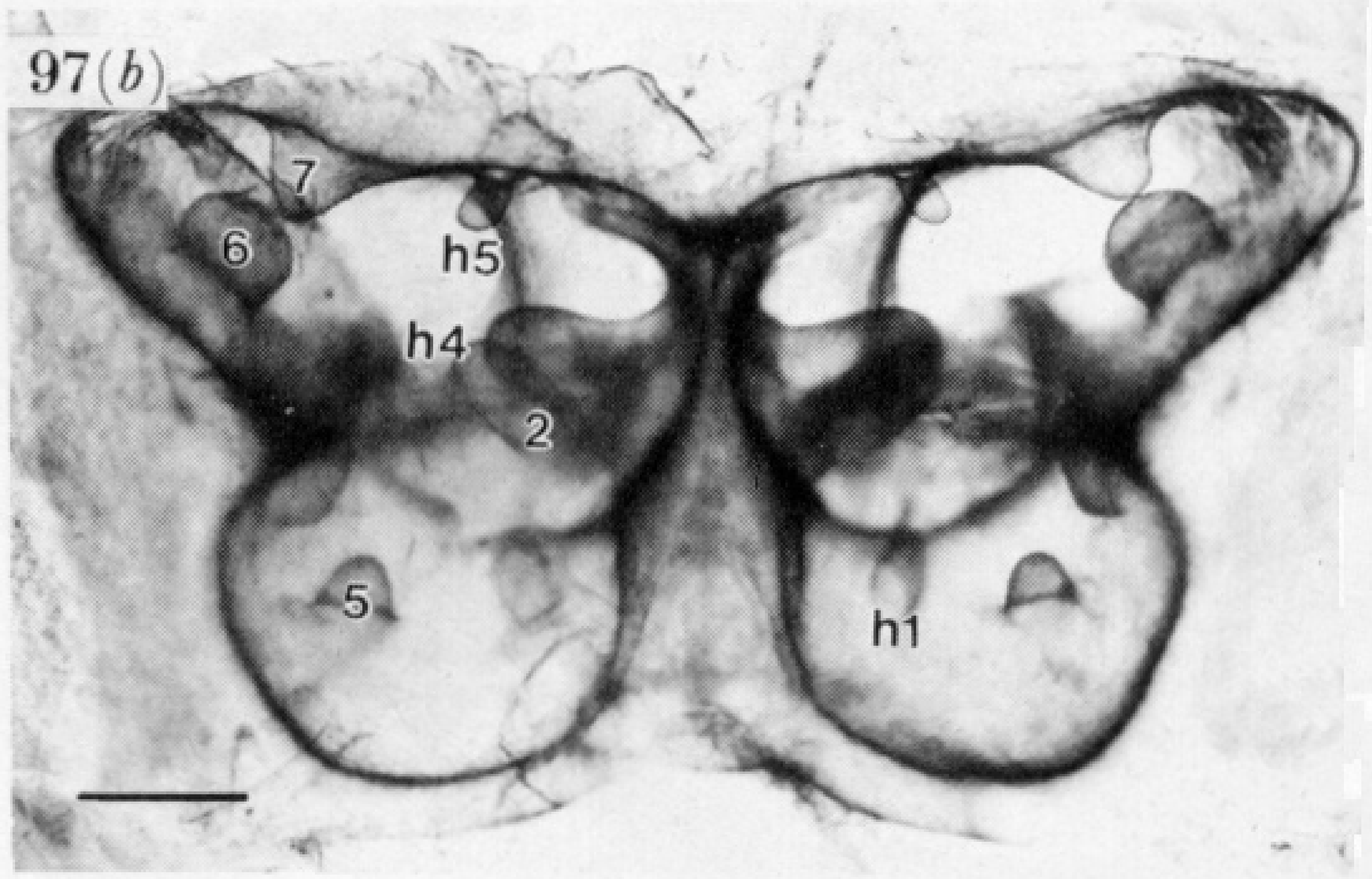


Sepia

97(*a*)

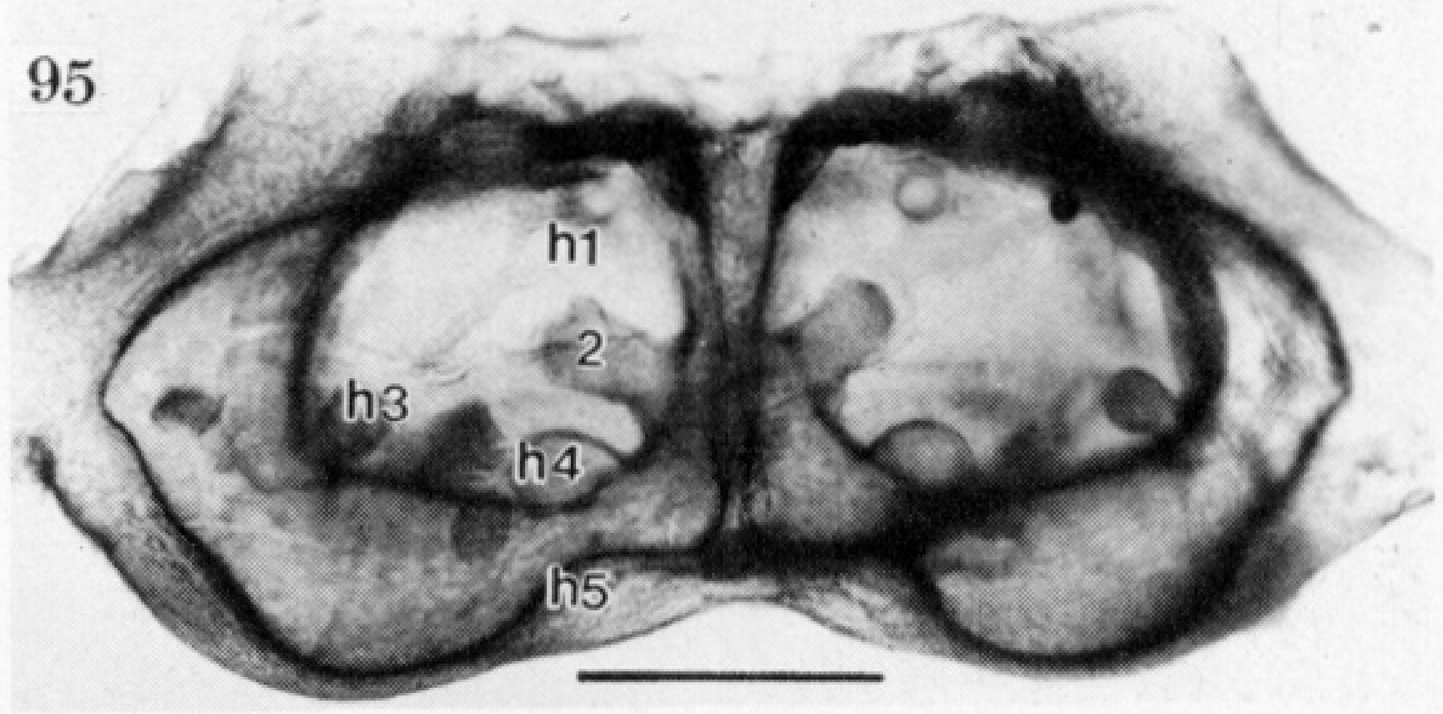


97(*b*)



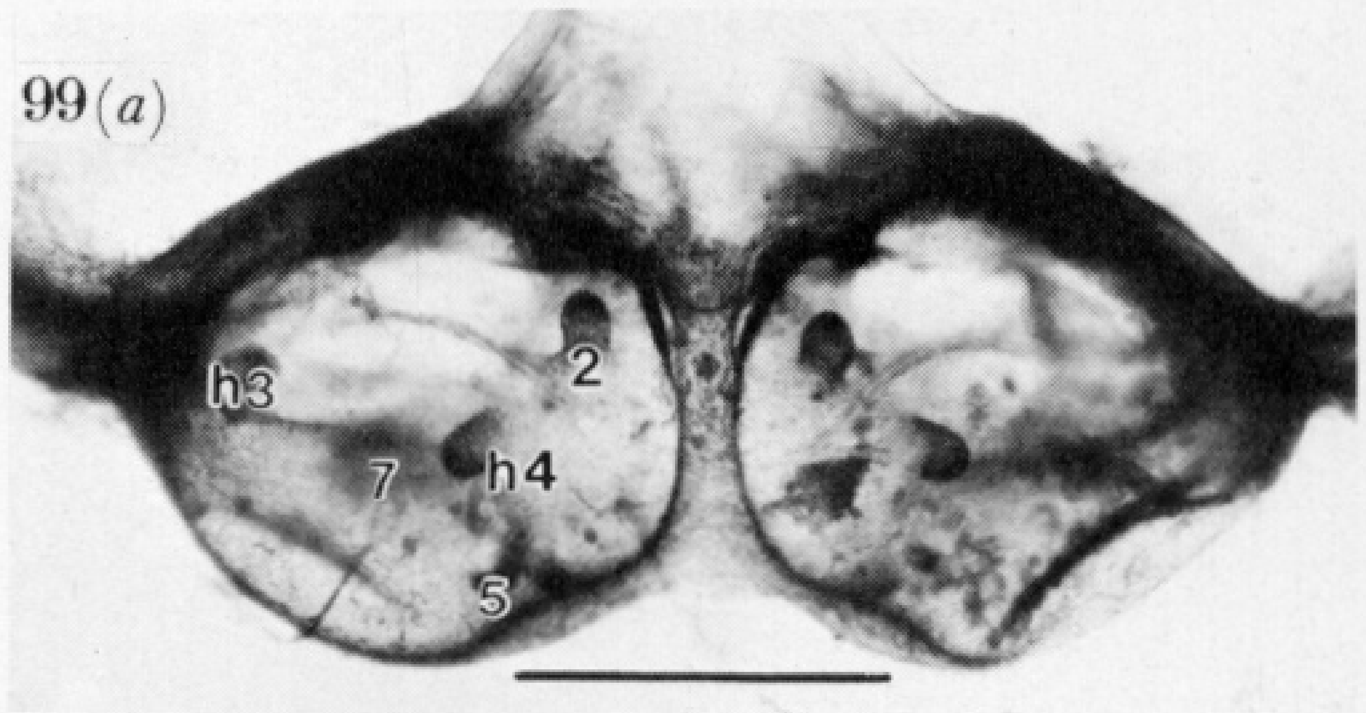
Neorossia

95

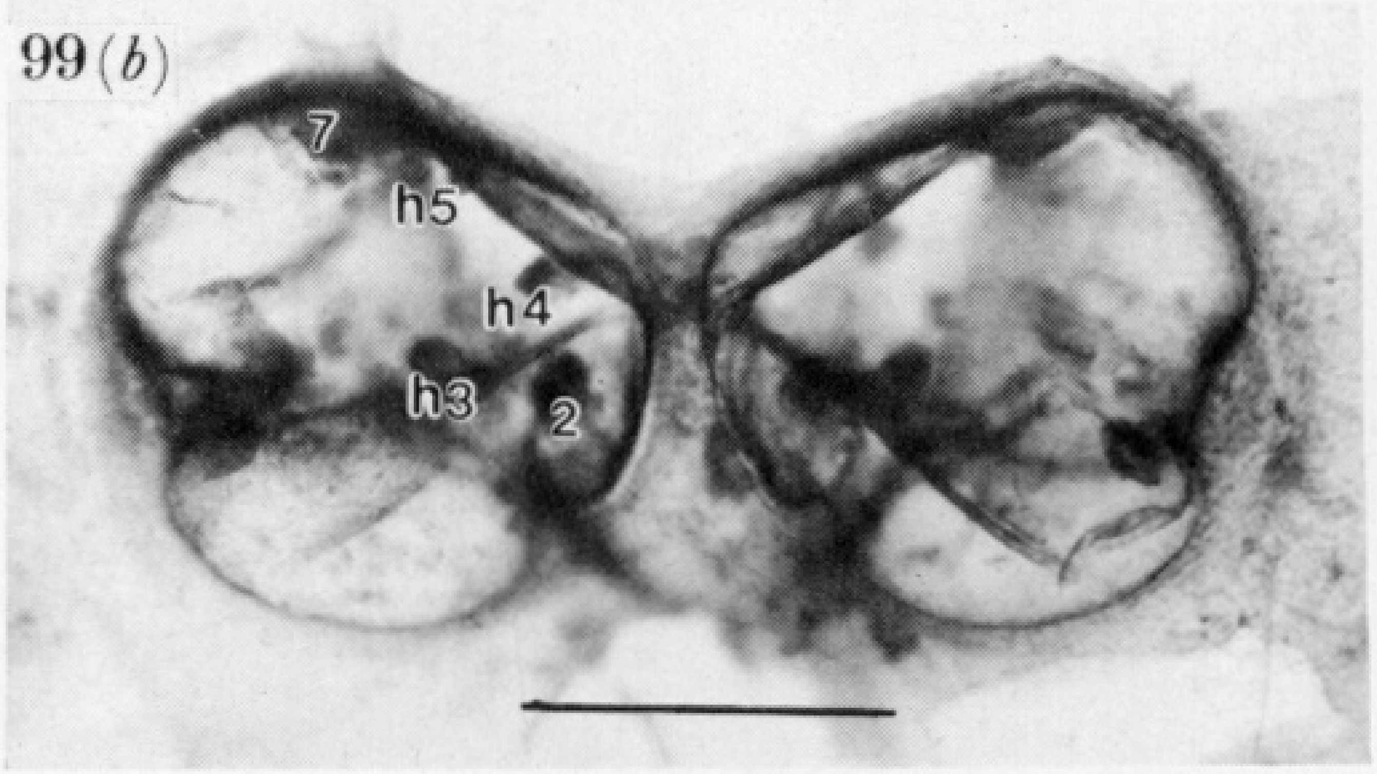


Sepiola

99(*a*)

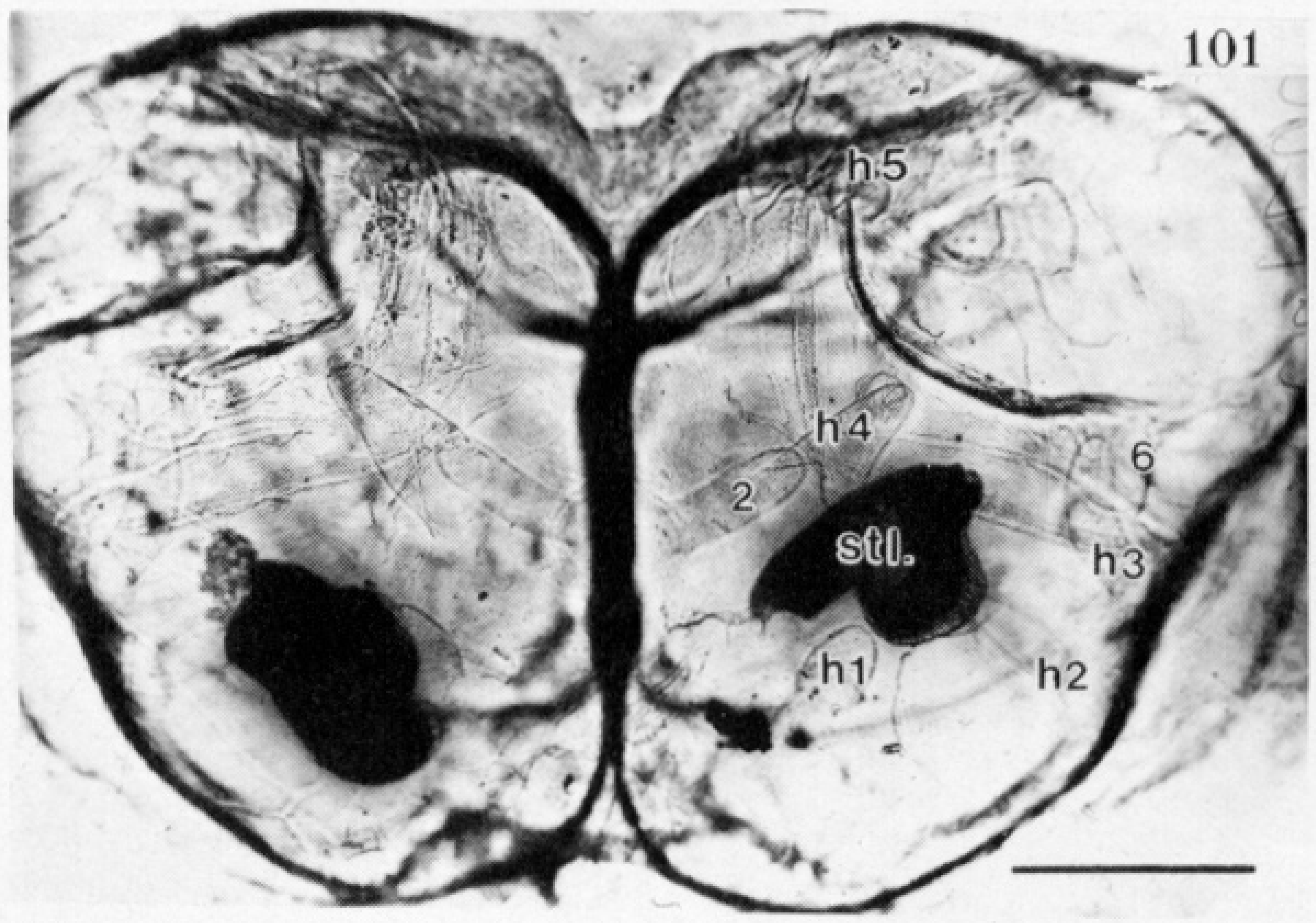


99(*b*)



Heteroteuthis

101



Spirula

FIGURES 93, 95, 97 AND 99. For description see opposite.