Phil. Trans. R. Soc. Lond. B **320**, 437–487 [437]
Printed in Great Britain

ADAPTIVE COLORATION IN YOUNG CUTTLEFISH (*SEPIA OFFICINALIS* L.): THE MORPHOLOGY AND DEVELOPMENT OF BODY PATTERNS AND THEIR RELATION TO BEHAVIOUR

By R. T. HANLON[1] and J. B. MESSENGER[2]

[1] *The Marine Biomedical Institute, and Department of Psychiatry and Behavioral Sciences, The University of Texas Medical Branch, Galveston, Texas* 77550–2772, *U.S.A.*
[2] *Department of Zoology, The University of Sheffield, Sheffield S*10 2*TN, U.K.*

(*Communicated by J. Z. Young, F.R.S. – Received* 15 *December* 1986 – *Revised* 25 *June* 1987)

[Plates 1–15]

CONTENTS

[Published 12 August 1988

Young *Sepia officinalis* (0–5 months) were studied in the laboratory and in the sea, and their appearance and behaviour compared with that of adult animals.

Cuttlefish lay large eggs and the hatchlings are miniature replicas of the adults. From the moment of hatching they show body patterns as complex as those of adults and far more elaborate than those shown by most juvenile cephalopods. There are 13 body patterns: 6 of these are 'chronic' (lasting for minutes or hours) and 7 are 'acute' (lasting for seconds or minutes). The patterns are built up from no fewer than 34 chromatic, 6 textural, 8 postural and 6 locomotor components, used in varying combinations and intensities of expression. Nearly all these components occur in young animals: 26 of the chromatic, all the textural and locomotor, and 6 of the postural components. Nevertheless, patterning does change with age and we have recorded this and correlated the changes with behaviour.

The components are built up from units, which themselves comprise four elements organized in precise relation to one another: chromatophores, iridophores, leucophores and skin muscles. The chromatophores are always especially important: they are muscular organs innervated directly from the brain and controlled ultimately by the highest centres (optic lobes). The areas in the *Sepia* brain that control patterning are already well developed at hatching, for the appearance of the skin is as much part of the brain's motor program as is the attitude of the arms or fins, or the posture of the entire animal. The iridophores and leucophores develop later and are especially important constituents of many adult patterns, notably the Intense Zebra of the mature male.

Experiments confirm that patterning is neurally controlled and apparently mediated exclusively by the visual system. Young cuttlefish use patterning primarily for concealment, utilizing such strategies as general colour resemblance, disruptive coloration, obliterative shading, shadow elimination, disguise and adaptive behaviour. Older animals also conceal themselves but increasingly use patterns for signalling, both interspecifically (warning or 'deimatic' displays) and intraspecifically (sexual signalling).

Laboratory-reared cuttlefish were released in the sea and observed underwater. They quickly and effectively concealed themselves on the substrate; it was easy for the human observer to lose them and many passing fish behaved as if they were not there. One local predator, *Serranus cabrilla*, was observed to attack them and no fewer than 35 attacks were recorded, only six of which were successful. Laboratory-reared cuttlefish apparently distinguished between these predators and other, non-predatory, fish the first time they encountered them in nature.

1. INTRODUCTION

The ability of cephalopods to change colour has been known since antiquity and recently several workers have concerned themselves with the physiological, neurological and behavioural aspects of this phenomenon, especially in the more common littoral octopuses and squids (see, for example, Boycott 1953; Florey 1969; Packard & Sanders 1969, 1971; Packard & Hochberg 1977; Andrews *et al.* 1981; Boyle & Dubas 1981; Hanlon 1982; Moynihan & Rodaniche 1982; Dubas & Boyle 1985; Florey *et al.* 1985; Dubas *et al.* 1986*a*, *b*).

The common cuttlefish, *Sepia officinalis*, has also received considerable attention because it is a common European species and its repertoire of colour patterns is so remarkable. Bott (1938) and L. Tinbergen (1939) described the courtship patterns, and Holmes (1940) described several of the other patterns in a paper that has remained the standard work on this species for nearly 50 years. Boycott (1958) has summarized these findings and gives a good general account of cuttlefish behaviour. None of these workers studied young cuttlefish, however, and because their chromatic behaviour differs in several important respects from that of adult animals, we set out to describe this and to record changes in patterning during ontogeny.

By rearing the cuttlefish from the egg, by studying them in the laboratory and underwater in their natural habitat, and by using modern photographic equipment we have been able to document the patterns more fully than Holmes and, in addition, we could describe the various components of the patterns according to the recent classification of Packard and his collaborators (Packard & Sanders 1969; Packard & Hochberg 1977). We also relate changes in patterning to changes in behaviour as the animal grows, and consider the neural correlates of such a complex system of patterning. The many illustrations, selected from over ten times that number of slides and photographs, are necessary to give some idea of this complexity. They form the substance of this paper and may also, we hope, serve as a baseline for future studies on the neural control of chromatic behaviour in this and other cephalopod species.

2. MATERIALS AND METHODS

The principal subjects were more than 50 individuals of the common cuttlefish, *Sepia officinalis* L., hatched from eggs taken in the Catalan Sea (Mediterranean) and reared in the Laboratoire Arago, Banyuls-sur-Mer, France, at temperatures of between 16 and 21 °C during the spring and summer of 1981. Young animals were followed in the laboratory for 5 months, but our studies concentrated on 'hatchlings' (less than 1 week old: dorsal mantle length (ML) 7–10 mm), 'early juveniles' (animals 7 weeks of age: 16–20 mm ML) and on 'late juveniles' (animals 17 weeks of age: 35–45 mm ML). Representative animals of all these age groups (32 in all) were released into the sea and observed underwater at depths of less than 10 m in their natural environment; a total of 39 h underwater observation time was recorded at Banyuls. Different groups of animals from Banyuls were studied (1) in the laboratory in Galveston, Texas during 1982 from hatching to 7 months, and (2) in the sea near Banyuls during the summer of 1985. These observations were supplemented by data obtained at different times at laboratories in Plymouth (U.K.), Naples (Italy) and Luc-sur-Mer (Normandy, France) as well as by data on adults filmed by the late D. M. Maynard and by M. Zahn of the Düsseldorf Aquarium, F.R.G. (see Zahn 1979*a–c*, 1983).

The animals were photographed with a Nikon F camera body and 24, 35, 55 (macro) and 105 mm lenses, sometimes in conjunction with a Nikon bellows for high magnification. Underwater photographs were taken with the same system enclosed in an Ikelite housing or a Nikonos II camera with a 21 mm Seacor lens. Small Rollei E27 electronic flashes were used in varying combinations both above and below water. Kodachrome 64, Kodacolor II and Ilford FP4 film was used.

To determine the size, spatial arrangements and densities of chromatophores in the skin, wholemounts of live skin (minus the epidermis) were flattened by a cover slip and photographed with compound microscope at magnifications of 20× and 50×. All measurements were taken directly from the photographs. Frozen sections of skin from different regions of the body were cut in cryostat, stained wtih toluidine blue and basic fuchsin, and mounted in gelatine or Eukitt mounting media for examination and photography with a compound microscope. The ultrastructure of the skin was studied after fixation by immersion in either buffered glutaraldehyde (2.5% by volume) in Sorensen's reagent or a modified Karnovsky's solution and staining with lead citrate. For histology of the central nervous system

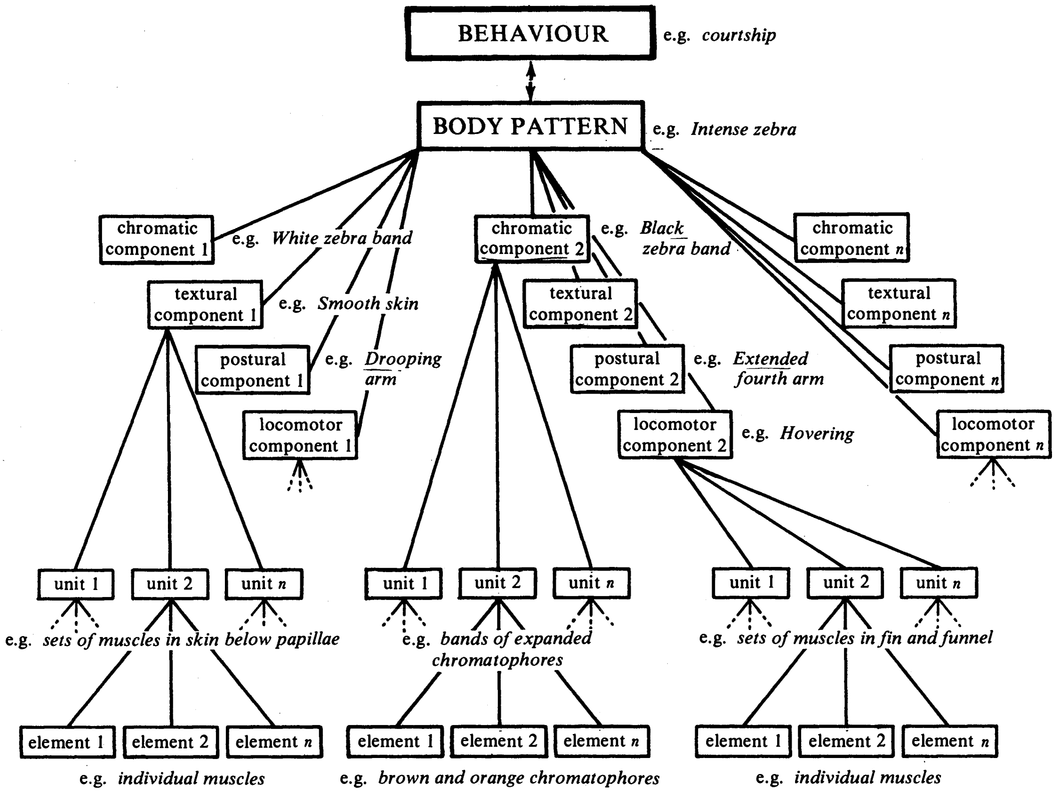


FIGURE 1. Hierarchical classification of body patterning. See text and figure 9.

DESCRIPTION OF PLATE 1

The colours of elements, units, components and patterns.

FIGURE 2. Dorsal mantle skin of a 17 mm ML cuttlefish showing the standard morphological array of chromatophores. Figures 2, 3 and 4 incident light. (Magn. × 87.)

FIGURE 3. Dorsal mantle skin of a 220 mm ML cuttlefish showing pink and green iridophores subjacent to chromatophores. Note reduced density of chromatophores compared with the young animal in figure 2. (Magn. × 74.)

FIGURE 4. Ventral mantle skin of a 17 mm ML cuttlefish. (Magn. × 26.)

FIGURE 5. Dorsal mantle skin of a 21 mm ML (9 weeks old) juvenile showing details of the first (anterior) set of Paired mantle spots (component 21), composed mainly of expanded brown and orange chromatophores. (Magn. × 7.7.)

FIGURE 6. White and Black zebra bands (components 9 and 26) on dorsal mantle of a female, 205 mm ML. (Magn. × 5.)

FIGURE 7. White fin spots (component 5). Note flecks of green iridophores and the overlying chromatophores. Compare figures 14 and 15 (Magn. × 8.)

FIGURE 8. A young cuttlefish (12 mm ML) half buried in gravel showing a Disruptive body pattern (no. 5) resulting particularly from White arm triangle (component 14), Anterior head bar (component 29), White head bar (component 13) and White square (component 2). Note colour resemblance.

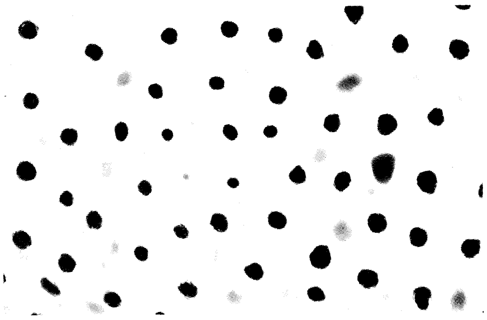
FIGURE 9. Sexual display in a mature male 180 mm ML. See figure 1 and text for details. Note Pink iridophore arm stripe (component 15).

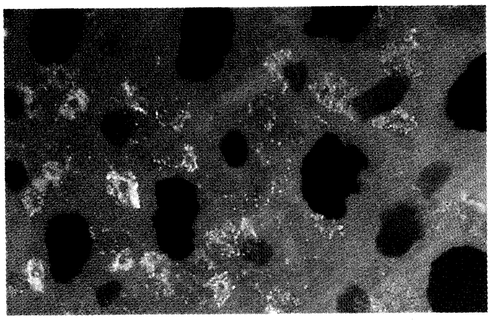
FIGURE 10. Iridescent ventral mantle (component 8) in the same individual.

FIGURE 11. Where is it? Clue: look for Major lateral papillae (component 40). Underwater photograph of a hatchling aged 2 weeks (10 mm ML).

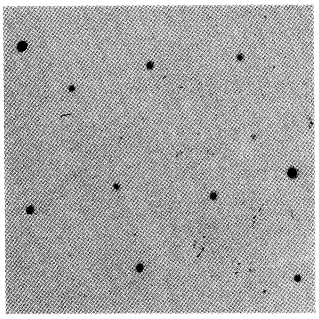
FIGURE 12. Concealment by general colour resemblance and a weak Disruptive pattern on a 33 mm ML cuttlefish underwater.

2, 3

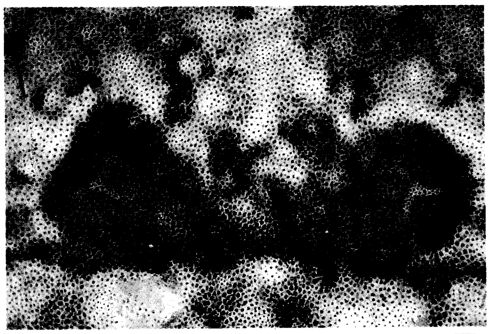


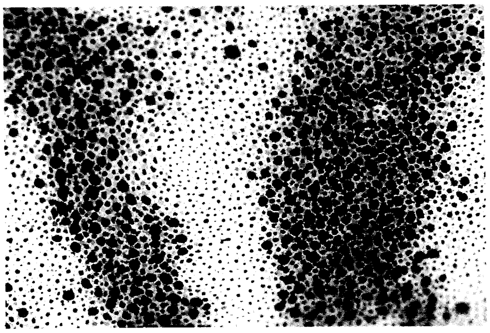


4

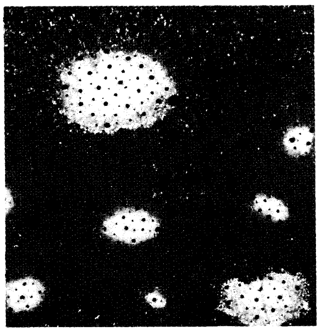


5, 6

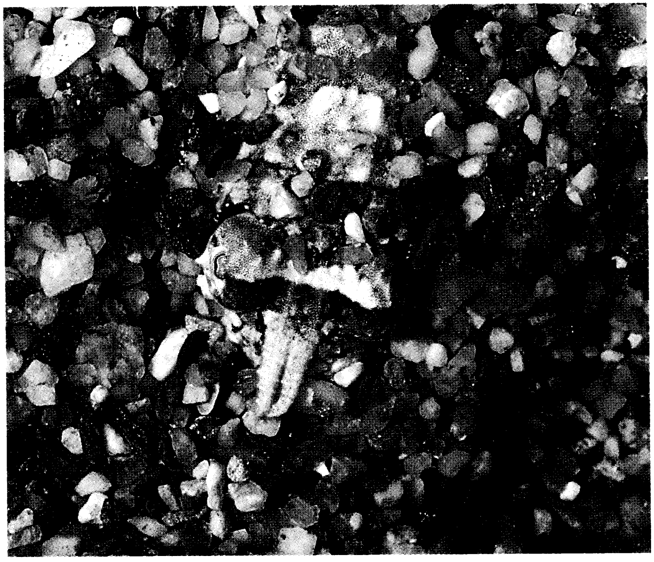




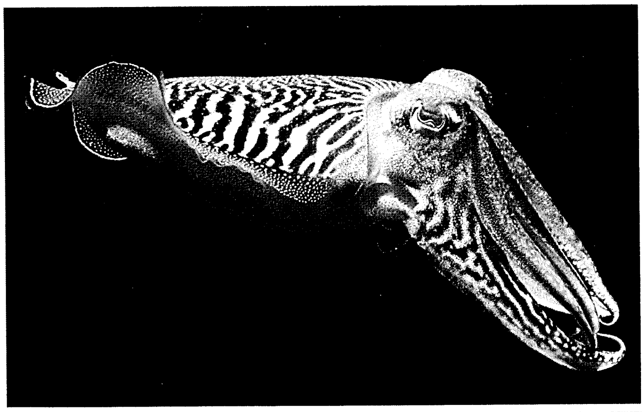
7



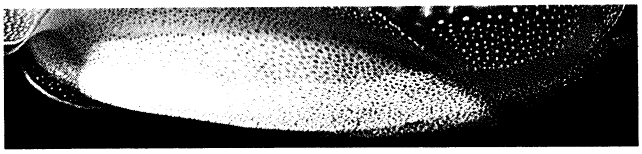
8



9



10



11

12

Figures 2–12. For description see opposite.

(CNS), the brains were fixed in neutral formalin (10% by volume) in seawater, stained with the block Cajal method (Stephens 1971) and cut serially at 7 μm for young animals and 14 μm for adults. Measurements of cell sizes, chromatophore lobe size and mantle area were made by using a Kontron Videoplan image-analyser in conjunction with a Reichert–Jung Polyvar microscope.

Details of particular experimental procedures are given in the appropriate section.

3. HIERARCHICAL CLASSIFICATION OF BODY PATTERNS IN CEPHALOPODS

To describe the body patterns of *Sepia* we have followed the hierarchical classification that Packard and his collaborators have devised during their studies of *Octopus* (see, for example, Packard & Hochberg 1977). According to this a 'body pattern' comprises several 'components' each comprising 'units' that are in turn made up from diverse 'elements'. This classification is illustrated in figure 1, and reference to plate 1† should help make it clearer.

Figure 9 shows a male cuttlefish hovering in mid-water with its fourth right arm extended towards the observer. This animal is showing the 'body pattern' we term 'Intense Zebra'. The pattern is the result of four different types of component: chromatic, textural, postural and locomotor. Conspicuous 'chromatic components' in this individual are the White and Black zebra bands on the mantle and arms and the White fin spots; the chief 'textural component' is the Smooth skin; the main 'postural component' is the Extended fourth arm; the most conspicuous 'locomotor component' is the gentle swimming we term 'Hovering'. If we were to examine a particular chromatic component under a low-power microscope, we would find that it contains numerous morphological units, each comprising differently coloured chromatophores and reflecting structures organized precisely with respect to each other (figures 2–4). These units, which differ in different parts of the body, are not obvious to the naked eye so that in *Sepia* we do not name them. Finally, it is possible to recognize that each chromatic unit may comprise up to three classes of 'elements': chromatophores, leucophores and iridophores.

For textural, postural and locomotor components the subordinate units and elements are muscles. Thus the muscles in a small area of skin may be organized to form a small papilla (unit) and several papillae may be erected simultaneously to form a component, e.g. White square papillae or Major lateral papillae.

Despite some inadequacies (see §7) this hierarchical classification of body patterns is very useful and we have not hesitated to follow it, although, in the detailed analysis that follows, we find it appropriate to start by considering the elements and then proceeding upwards to the body patterns. It is the body pattern that the cuttlefish shows to its prey, predators and conspecifics, and it is these that we discuss in relation to behaviour (§5) and development (§6)

4. MORPHOLOGY OF THE BODY PATTERNS

4.1. *Chromatic elements and units*

The chromatic elements of patterning in *Sepia officinalis* consist of chromatophore organs, and two types of reflecting elements: leucophores and iridophores. We emphasize from the outset that these elements are not uniformly distributed and that although the chromatophores are

---

† Figures 2–12 and 14–106 appear on plates 1–15.

the elements contributing most to patterning because they are most subject to transformation, reflecting elements are equally important in certain areas.

4.1.1. *Chromatophores*

The chromatophores are of three broad colour classes – yellow, orange and dark brown – with gradations of colour within each class. The browns range from very pale to a very dark chocolate and the orange often appears reddish. Kühn & Heberdey (1929) reported that the yellow chromatophores are shallowest in the dermis, oranges intermediate in depth and dark browns, which they termed 'black', deepest; we have confirmed this layering with cryostat sections.

The chromatophores of this species are between 10 and 30 μm in retracted diameter (browns 25–30 μm, oranges 18–21 μm and yellows 10–18 μm) and are densely packed over most of the dorsal surface. The density of dorsal mantle chromatophores of both sexes changes dramatically from hatching to adult size: hatchlings (7 mm ML) have approximately 400–500 chromatophores mm^{-2}; animals of approximately 15–20 mm ML have between 200 and 500 mm^{-2}; animals of 40 mm ML have about 150 mm^{-2}; animals of 150 mm ML have about 60–70 mm^{-2}; adults (e.g. of 220 mm ML) have only 35–50 mm^{-2}: a tenfold difference from hatching. A hatchling has in the order of 12×10^3 chromatophores on the dorsal mantle, whereas an adult of 220 mm ML has in the order of 2×10^6.

Most of the chromatophores of the dorsal mantle, head and arms are arranged regularly in a static morphological array that is characterized by a single, central, brown chromatophore surrounded by smaller yellow and orange chromatophores (figures 2 and 3). The skin of *Sepia officinalis* contains no macroscopically distinct 'morphological units' such as are found in *Octopus vulgaris* (Packard & Hochberg 1977) or *Loligo plei* (Hanlon 1982; formerly *Doryteuthis plei* (see Boycott 1965)) so that we refrain from naming morphological units in this species. Nevertheless, it is possible to recognize microscopically that the ratio of brown chromatophores to yellows plus oranges is about 1:1.44. All chromatophores are fairly uniformly spaced from one another: the mean nearest-neighbour distance on the dorsal mantle of an early juvenile (17 mm ML) is 37 μm (range 20–50 μm; $n = 92$). By using the method of Clark & Evans (1954), the R value is 1.37 where 1.00 is random and 2.15 the maximum for perfect uniformity. The distribution of mantle brown chromatophores, relative to other browns, is more uniform, with an R value of 1.67; an example of mean nearest-neighbour distance is 75 μm (range 65–100 μm; $n = 88$). Yellow chromatophores are spaced fairly regularly around browns but the oranges are not found in any particular arrangement with respect to other oranges, yellows or browns. When fully expanded, chromatophores of each colour class overlap with chromatophores of all colour classes (e.g. browns overlap with all adjacent browns, yellows and oranges). The density of chromatophores on the fin is slightly less than on the dorsal mantle, especially towards the edge. It is also slightly less on the posterior head region in the vicinity of the dark Posterior head bar (component 30), under the eyes and on the fourth arms.

Chromatophore density and arrangement are quite different on the ventral mantle (figure 4). The main difference is the much lower density of chromatophores per unit area; density is about 20 mm^{-2} in an early juvenile, or roughly $\frac{1}{10}$ to $\frac{1}{20}$ the value for the dorsal surface. An example of the mean nearest-neighbour distance among all chromatophores in the area of the Latero-ventral patch (see §4.2) in an animal of 17 mm ML is 160 μm (range 50–220 μm; $n = 50$).

There are areas on the ventral mantle just under the fin where all three colours are present, whereas only yellow chromatophores occur in some areas, and there is a small area anteriorly where no chromatophores occur at all.

There are several other areas where chromatophore arrangement is different, such as the funnel and the oral surfaces of the arms, but these do not make a strong contribution to patterning and they are not described here. The tentacular clubs have a particularly unusual arrangement in that there are about 15 single rows of brown and yellow chromatophores oriented transversely on the aboral surface. The significance of this is unknown.

The chromatophores of *Sepia* have not been subjected to detailed physiological study (but see Hill & Solandt 1935) but all the evidence suggests that they are similar to the chromatophores of squids and octopuses (Sereni & Young 1932; Florey 1966; Cloney & Florey 1968; Florey & Kriebel 1969; Young 1971; Dubas & Boyle 1985; Florey *et al.* 1985; Dubas *et al.* 1986*a*). That is, the organ comprises pigment granules in a cytoelastic sac and a set of radial muscle fibres that are innervated directly from the brain, by excitatory fibres only. Contraction of the radial muscles leads to chromatophore expansion; in the absence of excitation the cytoelastic sac causes chromatophore retraction.

4.1.2. *Reflecting elements*

Leucophores, which have been described in the skin of *Octopus vulgaris* (Packard & Sanders 1971; Messenger 1974; Froesch & Messenger 1978) and *O. dofleini* (Brocco 1975; Brocco & Cloney 1980; Cloney & Brocco 1983) make a major contribution to the appearance of the adult cuttlefish (figure 9). They are highly branched cells, bearing 1000 to 2000 electron-dense clubs all over the surface (figures 16 and 17), that scatter light of all wavelengths and thus appear white in white light, yellow in yellow light and so on. Figures 14 and 15, which are of the same area of mantle skin in reflected and transmitted light, show how the islands of leucophores in an otherwise translucent skin contribute to the characteristic white spots, bands and forks at the edge of the mantle (cf. Packard & Sanders 1971).

In *Sepia* we have ultrastructural evidence that there are leucophores in the White fin spots, the White fin line and the White zebra bands. The outward manifestation of their presence in these regions is shown in figures 6, 7, 9 and 24–27, but the photographs reveal many other white areas (the light chromatic components, §4.2.1) that might be expected to contain leucophores (e.g. figures 61–65). They are probably also present on the other white components listed in table 1 and also the Major lateral papillae. In those skin regions so far examined in the electron microscope, the leucophores are very closely associated with iridophores (figures 16 and 17); the optical significance of this arrangement is unclear, but it may serve to maximize reflection. Leucophores develop with age and become very important in some adult light chromatic components, notably the White zebra bands on the fourth arm and the mantle of mature males.

Iridophores (figure 17), the other important reflecting element, have been described in *Sepia esculenta* by Kawaguti & Ohgishi (1962) and in *S. officinalis* by Denton & Land (1971), who give an excellent account of the physics of the colour produced by these multi-layered stacks of thin platelets (see also Land 1972). They produce interference colours when viewed from the appropriate angle and in *S. officinalis* are responsible for the conspicuous pink stripes running longitudinally down arms 1, 2 and 3 (figure 9), the less distinct pink and green iridescent areas around the head (figure 3), eyes and fourth arms and the bright green or blue uniform

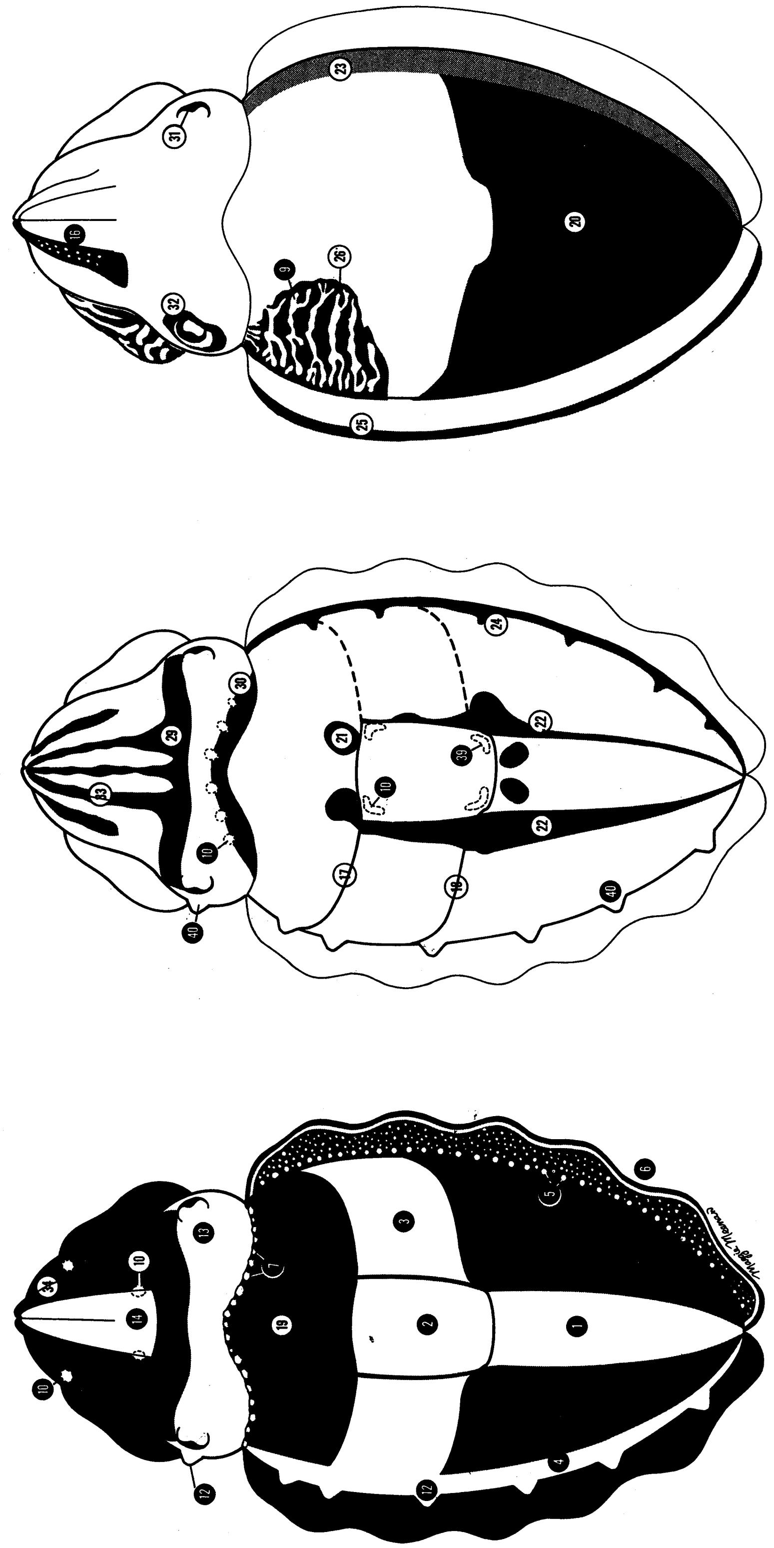


FIGURE 13. Diagrammatic representation of the components of patterning. See table 1 and text (§4.2).

TABLE 1. BODY PATTERNS AND THEIR COMPONENTS IN *SEPIA OFFICINALIS* L.
(See figure 13.)

chromatic components

light		dark
(1) White posterior triangle		(17) Anterior transverse mantle line
(2) White square		(18) Posterior transverse mantle line
(3) White mantle bar		(19) Anterior mantle bar
(4) White lateral stripe		(20) Posterior mantle bar
(5) White fin spots		(21) Paired mantle spots
(6) White fin line		(22) Median mantle stripe
(7) White neck spots	mantle	(23) Mantle margin stripe
(8) Iridescent ventral mantle		(24) Mantle margin scalloping
(9) White zebra bands		(25) Dark fin line
(10) White landmark spots		(26) Black zebra bands
(11) White splotches	head	(27) Mottle
(12) White major lateral papillae	or	(28) Latero-ventral patches
(13) White head bar	arms	(29) Anterior head bar
(14) White arm triangle		(30) Posterior head bar
(15) Pink iridophore arm stripes		(31) Pupil
(16) White arm spots (males only)		(32) Eye ring
		(33) Dark arm stripes
		(34) Dark arms

textural components	postural components	locomotor components
(35) Smooth skin	(41) Raised arms	(49) Sitting
(36) Coarse skin	(42) Waving arms	(50) Bottom suction
(37) Papillate skin	(43) Splayed arms	(51) Buried
(38) Wrinkled first arms	(44) Drooping arms	(52) Hovering
(39) White square papillae	(45) Extended fourth arm (males only)	(53) Jetting
(40) Major lateral papillae	(46) Raised head	(54) Inking
	(47) Flattened body	
	(48) Flanged fin	

body patterns

chronic patterns	acute patterns
1. Uniform Light	7. Uniform Blanching
2. Stipple	8. Uniform Darkening
3. Light Mottle	9. Acute Disruptive
4. Dark Mottle	10. Flamboyant
5. Disruptive (weak, strong)	11. Deimatic
6. Weak Zebra	12. Intense Zebra (males only)
	13. Passing Cloud

iridescence of the ventral mantle (figure 10). Iridophores are distributed widely in the skin below the chromatophores (figures 3, 7; see also 16). Schäfer (1937) has suggested that some of the iridophores (= iridocytes (see Cloney & Brocco 1983)) diffract light as from a grating but this hypothesis remains to be tested. Recent evidence indicates that some cephalopod iridophores are physiologically active, i.e. iridescence is seen only during particular intraspecific agonistic bouts (Hanlon 1982) and acetylcholine causes iridescence *in vitro* in certain cell types in squids (Cooper & Hanlon 1986). Thus *Sepia* and other cephalopods may actively control some of their iridescence.

4.1.3. *Physiological units*

The chromatic 'units' discussed above are 'morphological' (Packard & Sanders 1971); that is, they are based upon a static array of chromatophores, leucophores and iridophores. But the patterns we describe below are transient phenomena resulting from the activity of cells in the CNS. According to the motor program currently in operation, some of the chromatophores in the static array will be expanded at any one moment, whereas others will remain retracted. A few minutes later the program may change and with it the appearance of a particular patch of skin, resulting in a pattern change of the whole animal.

An example of how physiological units can be activated to produce discrete chromatic components in areas of skin with uniformly distributed morphological units of chromatophores is illustrated in figures 30 and 31. Normal excitation (by the animal) of selected motorneurons in the CNS expands well-delineated groups of chromatophores resulting in dark components; areas with unexpanded chromatophores become light components with their reflecting elements enhanced. Figures 20–23 show how the changing activity of physiological units can transform a Mottle pattern into a Weak Zebra pattern and emphasize that any one chromatophore can participate in two or more different patterns because chromatophores may receive multiple innervation (Maynard 1967; Florey 1969; see also figure 25).

Conventional neurophysiological stimuli can also be used to activate these 'physiological' (motor) units in the skin, which are, of course, selected from among the morphological units (for a discussion of the relation between physiological and morphological units see Packard 1982)). When the chromatophore nerves in the skin at the base of the fin are stimulated directly with a silver electrode the result is local expansion of specific groups of chromatophores, organized into elongate, oval motor fields whose long axis may exceed 50 mm. By moving the electrode it is possible to find and stimulate a unit covering several white spots so that they become obliterated (figure 19); it is equally possible to position the electrode so that it activates units between and at the edge of several white spots so that the spots become enhanced (figure 18). These observations emphasize that the chromatophores and reflecting elements complement one another in the production of certain patterns.

4.2. *Chromatic components*

Chromatic components, which are very conspicuous and easily defined, occur repeatedly in the same relative position. They may be 'light' (when the dark chromatophores are retracted, or the yellow ones are expanded, or when local aggregations of reflecting elements are revealed) or 'dark' (when the darker chromatophores are expanded and reflecting elements are concealed). Light components include whites, yellows and pale oranges. Dark components include dark oranges, reds and browns. Throughout we define a 'bar', 'band' or 'line' as being

DESCRIPTION OF PLATE 2

Reflecting elements.

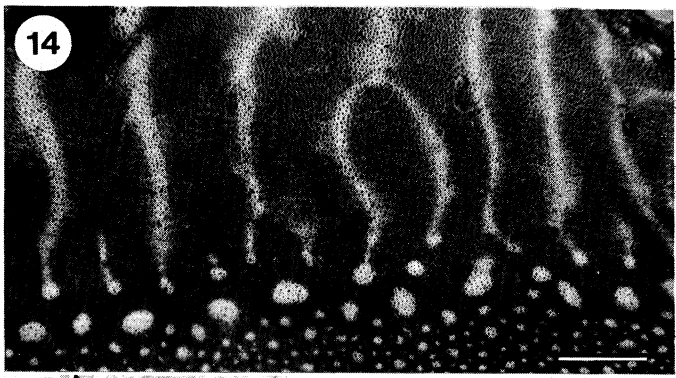
FIGURES 14 AND 15. White zebra bands (component 9) and White fin spots (component 5) seen in a skin preparation in reflected and transmitted light to point out the morphological arrangement of leucophores that contribute to these components. Scale 4 mm.

FIGURE 16. White fin spot seen in transmission electron microscopy. Below the chromatophore (torn at top) note the complex arrangement of iridophores (thin platelets) and leucophores (clubs; see arrows) (cf. figure 17). Scale 10 μm.

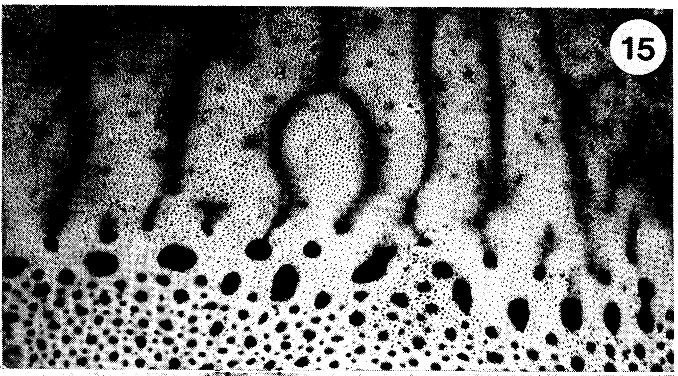
FIGURE 17. Details of iridophore platelets and leucophore clubs (arrows). Scale 10 μm.

FIGURES 18 AND 19. Physiological units that emphasize (left) or conceal (right) a group of White fin spots. Direct stimulation of the skin through a silver electrode at just suprathreshold strength (20 Hz, 0.5 ms). At higher voltages increasingly larger motor fields appear. Scale 3 mm.

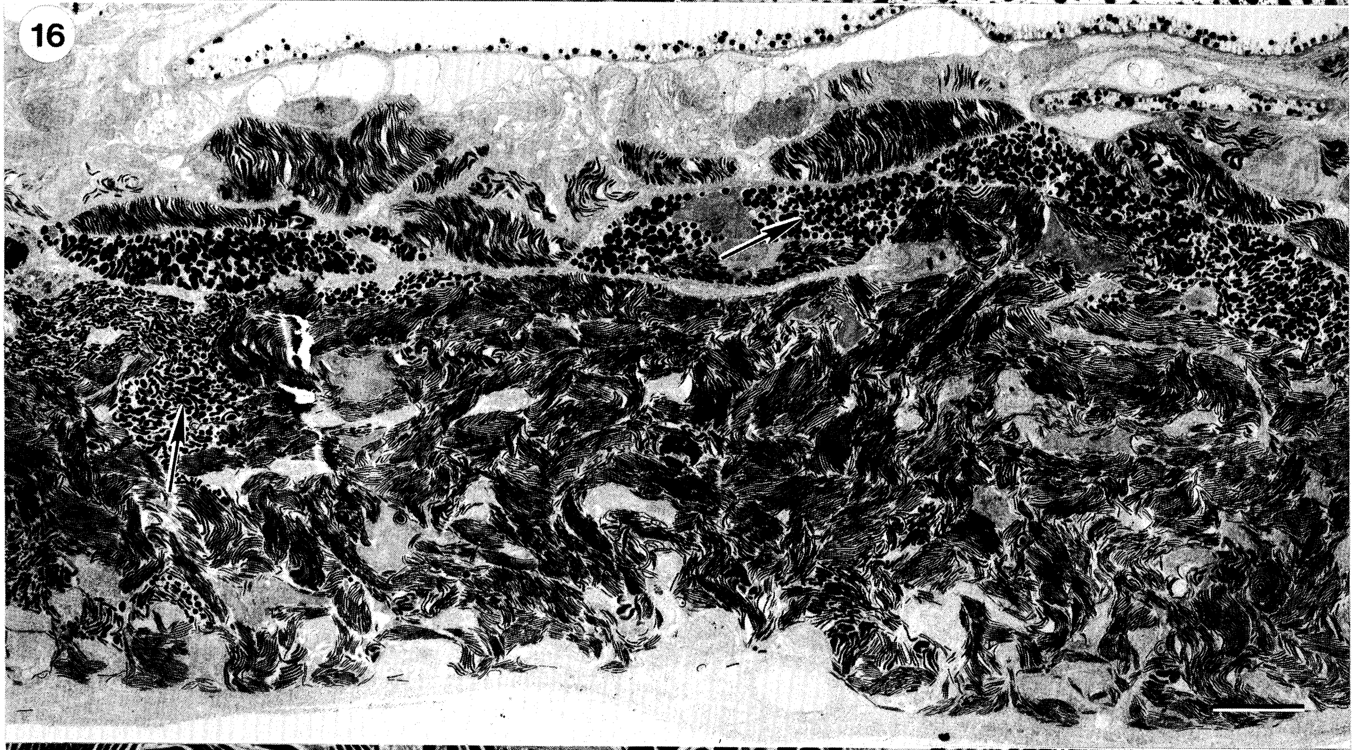
14



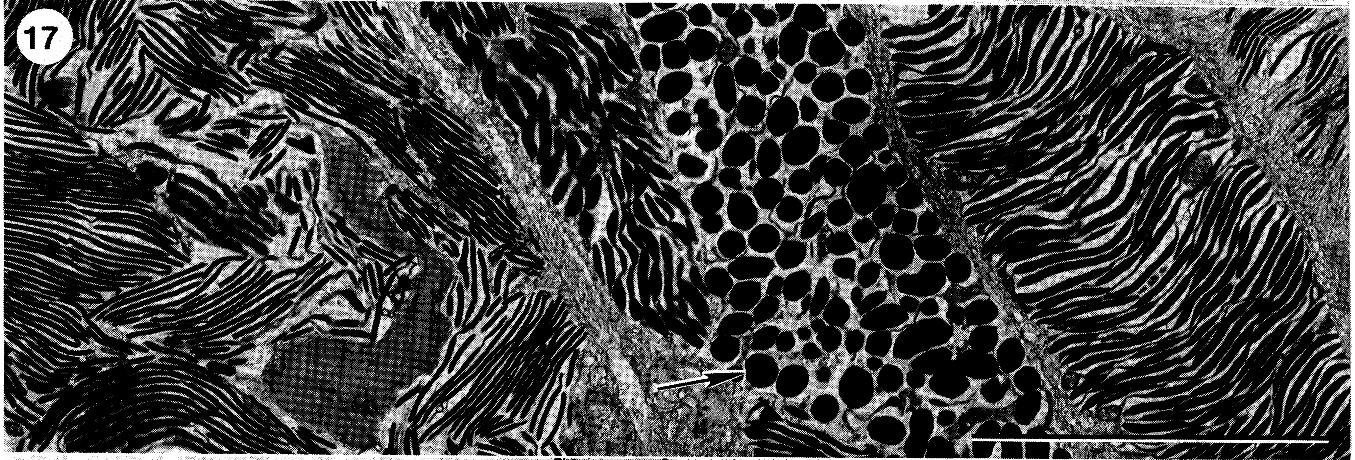
15



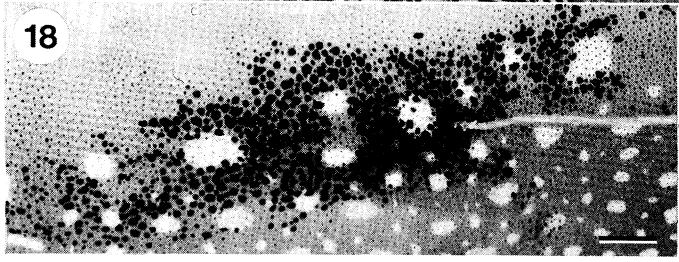
16



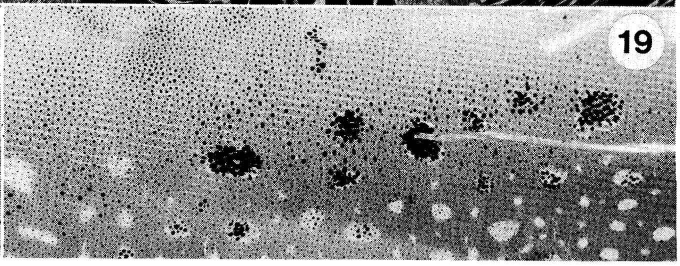
17



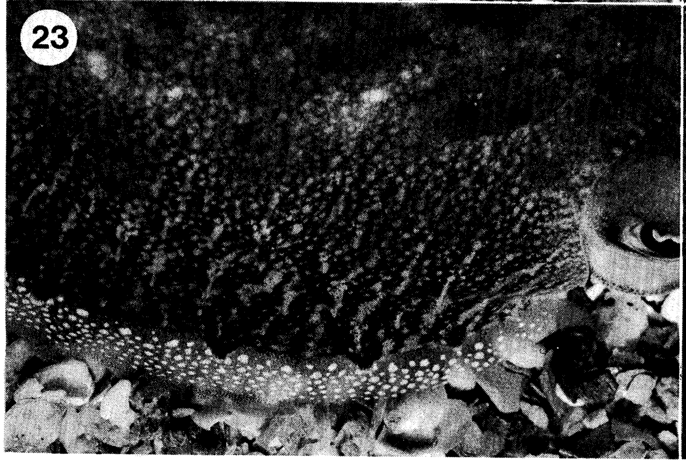
18

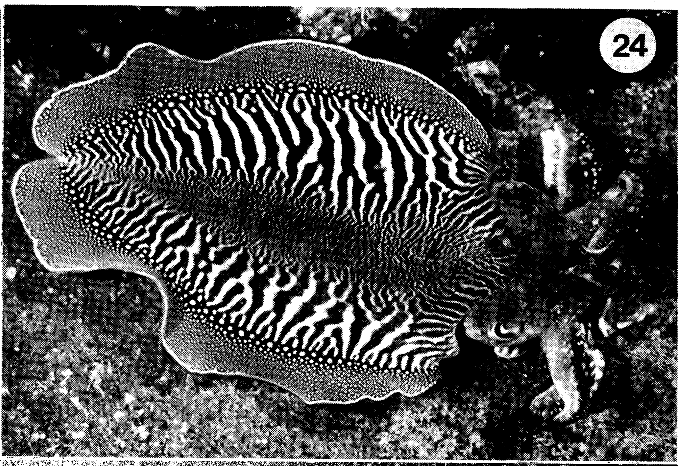


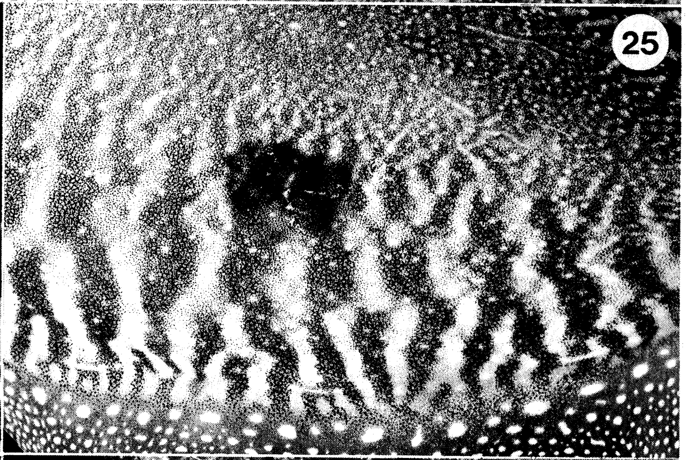
19

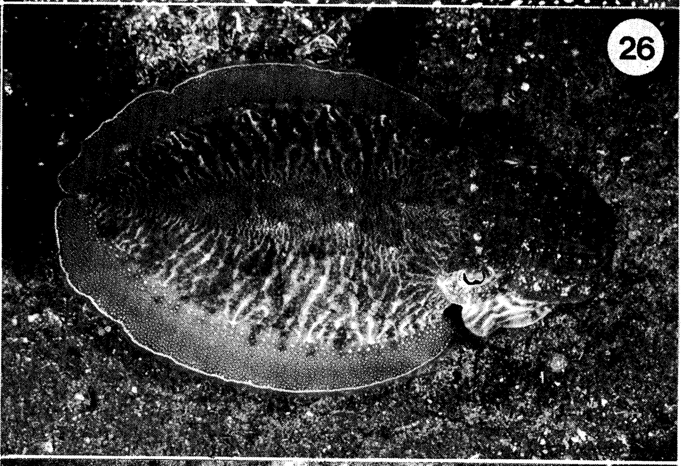


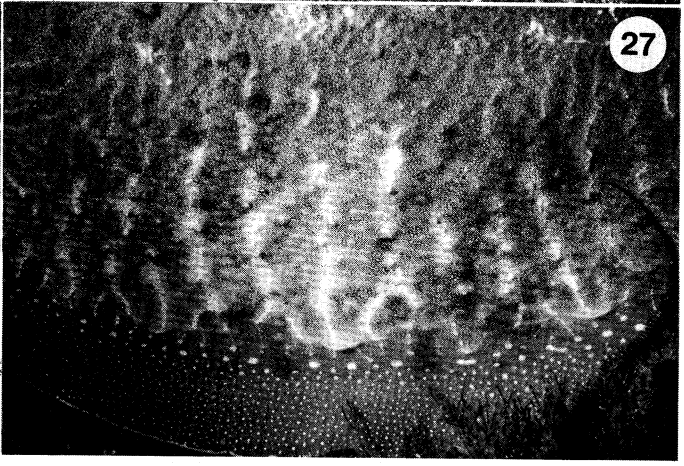
FIGURES 14–19. For description see opposite.











FIGURES 20–27. For description see opposite.

Description of plate 3

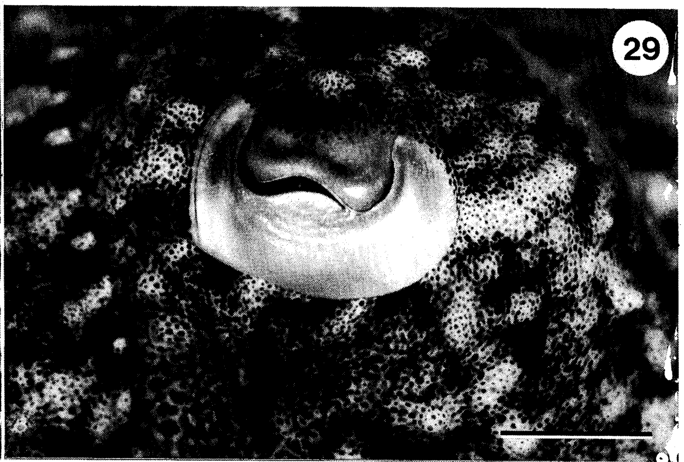
Dynamic aspects of patterning.

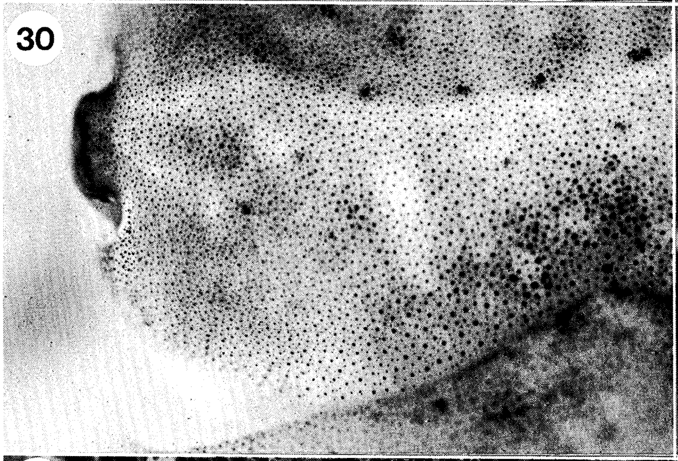
Figures 20–23. Sequence of the same individual (75 mm ML) over a 1 min period. The gradual change from a Mottle pattern to a weak Zebra pattern is brought about by the activity of different physiological units. The components Mottle (27), White square (2), and all four Paired mantle spots (21) gradually fade out and are replaced by increasingly intense White and Black zebra bands (9 and 26). Note too the progressive darkening of the Major lateral papillae (40).

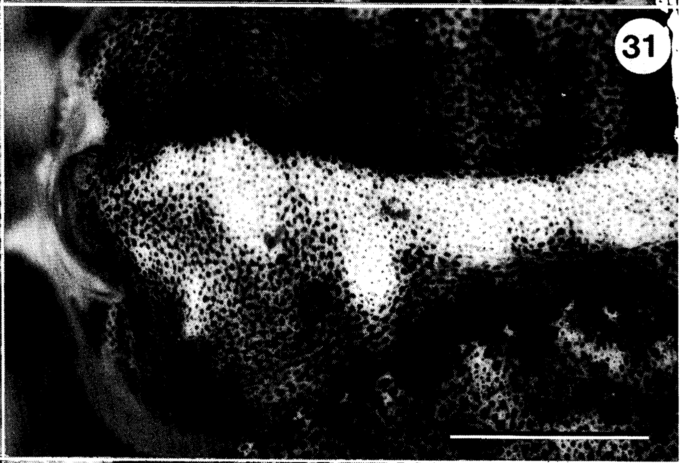
Figures 24 and 25. Intense Zebra pattern in a male (220 mm ML) eating a crab. Note in figure 25 how one of the third Paired mantle spots (component 21) is beginning to be expressed. This illustrates how the same morphological units can participate in different physiological units (see text §4.1.3 & figures 98 and 99).

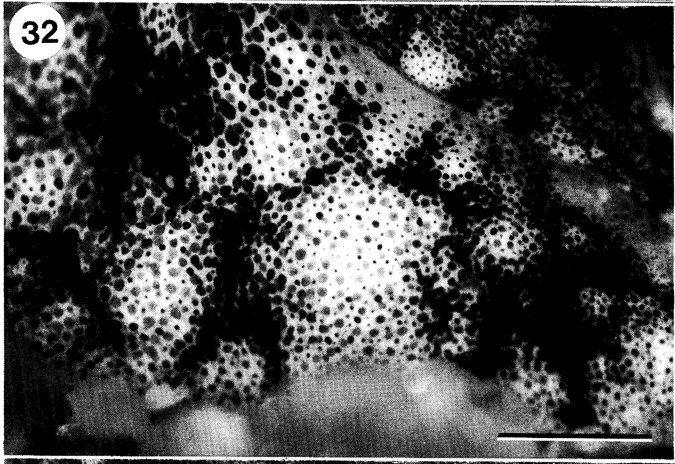
Figures 26 and 27. Weak Zebra pattern in the same male. Compare the intensity and width of the White and Black zebra bands (components 9 and 26) with figures 24 and 25. Note the weak enhancement of White fin spots (component 5) and the presence of many White landmark spots (component 10) in this concealment pattern.

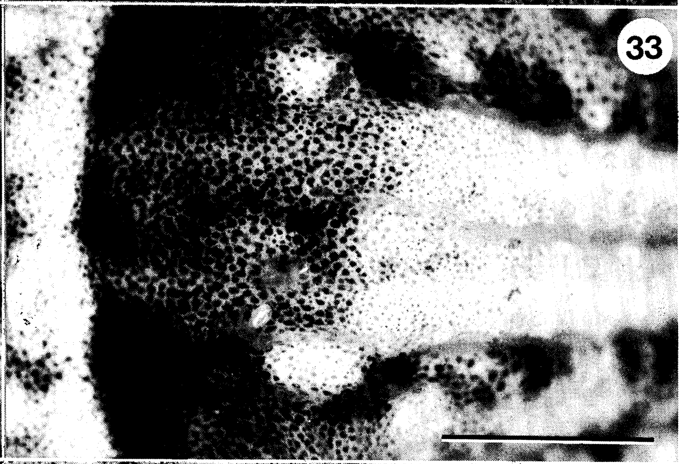

28

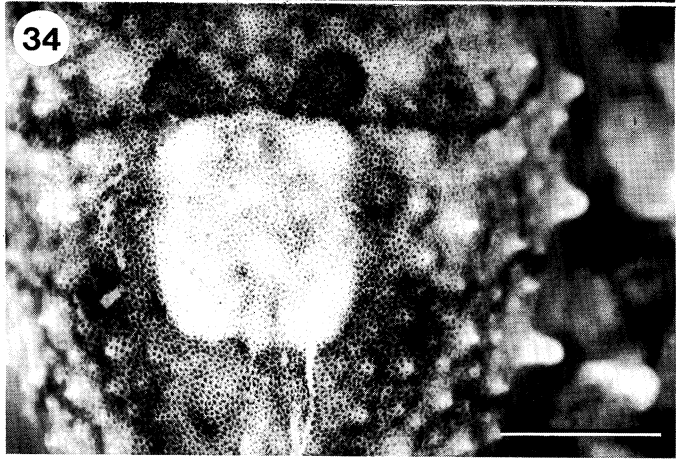

29

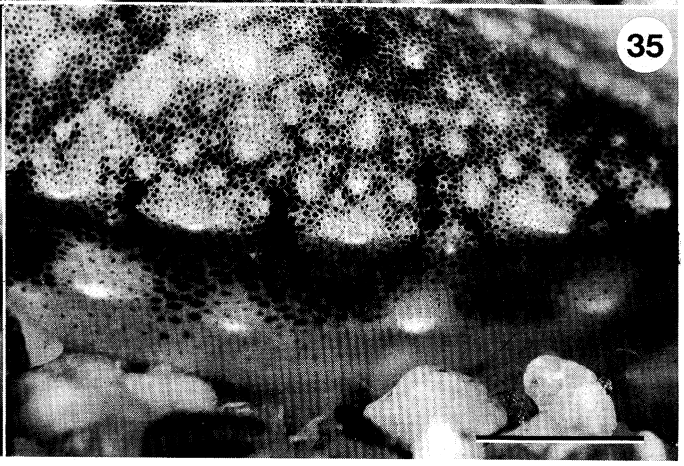

30


31


32


33


34


35

FIGURES 28–35. For description see opposite.

oriented transversely on the body, whereas 'stripes' run longitudinally. Most of the chromatic components are shown on the dorsal surface of the animal. Some components have been described or were figured by Holmes (1940).

4.2.1. *Light chromatic components* (*see figure* 13)

1. White posterior triangle (figure 61). A roughly triangular area situated on the midline of the posterior mantle, with the base of the triangle formed by the posterior edge of the White square (component 2) and the opposing apex formed by the mantle tip. The extreme posterior part of the triangle may be especially bright. (See also figures 59, 65 and 89.)

2. White square (figure 34). A rectangular area centred on the dorsal mantle. This area is delineated by a single large white papilla at each corner. It may be tapered posteriorly. The anterior margin is particularly distinct. (See also figures 12, 61, 63–66, 75 and 89.)

3. White mantle bar (figure 62). Transverse bar across roughly the middle third of the mantle. Component 2 forms the middle third of the bar. Near the mantle margin the bar curves slightly forward, which makes it crescent-shaped when viewed from above. May be expressed unilaterally. (See also figures 57, 60, 89, 91 and 98.)

Components 1, 2 and 3 may be expressed together, so forming a white T.

4. White lateral stripe (figure 59). A stripe that runs along the mantle just medial to the fin; it is slightly broader posteriorly.

5. White fin spots (figure 39). Spots of different size, composed of reflecting elements, extending across the fin, with the larger spots situated medially. May be seen unilaterally. (See also figures 9, 12, 22–27, 56, 57, 60, 66, 70 and 84.)

6. White fin line (figure 72). Very narrow strip of reflecting elements along the outer edge of the fin. It is usually wider and more conspicuous in mature males. Components 5 and 6 can be especially dazzling when fully revealed by retraction of the overlying chromatophores

Description of plate 4

The contribution of elements to the expression of components in hatchling cuttlefish.

Figure 28. Light Mottle pattern: principal components are White splotches (11) and Mottle (27). This lateral view reveals the Latero-ventral patches (component 28) below the fin and on the fourth arms. An example of coincident disruptive coloration (Cott 1940). 12 mm ML.

Figure 29. Closed Pupil (component 31) with surrounding Mottle (component 27) and White neck spots (component 7) enhanced by surrounding expanded chromatophores. Scale 2 mm.

Figures 30 and 31. The head in Uniform Light pattern (no physiological activity) and in strong Disruptive pattern. Physiological units are active in forming the dark components Anterior and Posterior head bars (29 and 30). The White head bar (component 13) is presumably so conspicuous because of underlying leucophores. Scale 2 mm.

Figure 32. The components Mottle (27) and White splotches (11) on the base of the fourth arm. Scale 2 mm.

Figure 33. The arms and head region showing (left to right) the components White head bar (13), dark Anterior head bar (29), two conspicuous White landmark spots (18), White arm triangle (14) and Wrinkled first arms (38). Scale 2 mm.

Figure 34. Dorsal mantle (top is anterior) in a weak Disruptive pattern showing first Paired mantle spots (component 21), Anterior transverse mantle line (17), White square (2), Mottle (27), Papillate skin (37) and the White major lateral papillae (12). Note white streak of damaged skin at bottom right of White square. Scale 2 mm.

Figure 35. Lateral view of posterior mantle showing the components Mottle (27), White splotches (11), White major lateral papillae (12, both above and below fin), Mantle margin scalloping (24) and, below the nearly transparent fin, the Latero-ventral patches (28). Scale 2 mm.

and enhanced by dark surrounds. May be expressed unilaterally. (See also figures 24, 26 and 66.)

7. White neck spots (figure 29). A series of 15–20 small white spots, often enhanced by surrounding dark chromatophores, along the anterior mantle margin just behind the head (hence the term neck). (See also figures 50, 59, 63, 75, 79, 89 and 106.)

8. Iridescent ventral mantle (figure 10). Uniformly widespread green or blue iridescence seen over the entire ventral mantle, and also on the lateral edge of the fourth arms. Visible only from the side or below.

9. White zebra bands (figure 72). Distinctive pale bands, sometimes forked, on the dorsal mantle of mature males and females and on the fourth arms of mature males. They contain aggregations of reflecting elements. They are arranged transversely on the proximal part of the arm, and longitudinally distally. Often expressed unilaterally. (See also figures 9 and 24–27.)

10. White landmark spots (figures 46 and 56). Conspicuous, well-defined white spots localized on specific body parts. On the arms, one at the base of the first and second arms on each side, and one midway down the third arm medial to the Pink iridophore arm stripe (component 15). On the head, a series of white spots (some elongate) arranged transversely on the posterior half of the head within the area defined by the White head bar (component 13). On the mantle, one each at the corners of the White square. (See also figures 31, 54, 58, 62, 70, 75 and 84.)

11. White splotches (figure 35). Numerous irregularly shaped and variously sized splotches found all over the dorsal surface of the animal. (See also figures 28 and 40.)

12. White major lateral papillae (figure 65). Along the edge of the mantle are five to seven very large, prominent papillae, both above and below the fin. In addition, less commonly expressed, there may be a large, conspicuous papilla under each eye, extending laterally. (See also figures 11, 12, 37, 43, 47, 66, 79, 90 and 97.)

13. White head bar (figure 89). An area shaped like a dumbbell extending from eye to eye, and occupying the posterior half of the head. It is sharply defined laterally by the cornea and anteriorly by the transverse line of pink iridophores. (See also figures 12, 41, 63–66, 75, 78, 85, 87 and 104.)

14. White arm triangle (figure 85). A more or less triangular area formed by the dorsal surface of the first pair of arms when the chromatophores are retracted. (See also figures 5 and 33.)

15. Pink iridophore arm stripes (figure 9). A thin stripe of distinctly pink iridophores extending the length of arms 1, 2 and 3 up to a transverse line of pink iridophores that coincides with the anterior edge of the White head bar. The stripe on arm 4 is similar but not distinct. (See also figure 12.)

16. White arm spots (figure 72). In the mature male only, large spots (formed by reflecting elements) arranged along the medial surface of arms 1, 2 and 3 in two longitudinal rows. The medial row is very regularly arranged. On arm 4 there are spots distally, decreasing in size towards the arm tip. Proximally these merge with the White zebra bands (component 9). May be expressed unilaterally.

4.2.2. *Dark chromatic components* (*see figure* 13)

17. Anterior transverse mantle line (figure 61). A well-defined thin line of expanded dark chromatophores traversing the mantle approximately a quarter of the way back from the anterior mantle margin. It forms the anterior demarcation of the White mantle bar. It may be expressed as a series of dark dots rather than as a continuous line. (See also figures 34, 58, 60, 63, 65, 75, 85, 87, 89, 90 and 104.)

18. Posterior transverse mantle line (figure 89). A thin line of expanded dark chromatophores, less well-defined than component 17, traversing the mantle approximately two thirds of the way back from the anterior mantle margin. It forms the posterior margin of the White square and the anterior margin of component 20. (See also figures 60–65 and 96.)

19. Anterior mantle bar (figure 65). A broad dark bar constituting the anterior quarter of the mantle. It is defined posteriorly by component 17, and anteriorly by the mantle margin itself. (See also figures 12, 60, 63, 75, 85, 91 and 98.)

20. Posterior mantle bar (figure 79). A less well-defined component: it can include the entire posterior third of the mantle, and so be shield-shaped, or more commonly be restricted to a bar posterior to component 18 (figure 37). It may be partly expressed as a complex configuration that we term the 'head-in-reverse'. (See also figures 37 and 98.)

21. Paired mantle spots (figure 61). Four pairs of spots around the White mantle square, numbered from the anterior. Pairs 1 and 3 are especially large and very conspicuous. Pair 1 lies anterior to the square, within a forward extension of its lateral margins, and pair 3 lies posterior to the square and outside a backward extension of its lateral margins. It is pair 3 that persists into maturity (§6) and forms the prominent eye-spots of the full Deimatic pattern (Acute body pattern no. 11; figures 25, 71 and 78). Pair 2 is more conspicuous than pair 4, which comprises a pair of medium dark oval spots with a posterior dark spot in each. All the spots may be expressed unilaterally. (See also other figures in plates 8 and 12.)

22. Median mantle stripe (figure 74). A conspicuous stripe on either side of the midline, extending along the posterior three quarters of the mantle. Each stripe borders the lateral edge of components 1 and 2. May be expressed unilaterally. (See also figures 61, 73, 76, 85 and 89.)

23. Mantle margin stripe (figure 42). A stripe along the extreme lateral edge of the mantle, just medial to the fin. (See also figure 41.)

24. Mantle margin scalloping (figure 35). A complex arrangement of expanded chromatophores in the same area as component 23 between and below the White major lateral papillae (component 12). (See also figures 28 and 57.)

25. Dark fin line (figure 71). A line of expanded chromatophores along the outside margin of the fin, sometimes continuing along the outside margin of the fourth arm. (See also figure 70.)

26. Black zebra bands (figure 24). A distinct arrangement of dark bands of chromatophores on the dorsal mantle and, in males, on the fourth arms (where they run transversely proximally but longitudinally distally). May be expressed unilaterally. (See also figures 9, 25–27 and 72.)

27. Mottle (figure 32). Broad generic term for patches of dark chromatophores of irregular shapes and varying sizes. Sometimes expressed only with yellow chromatophores, resulting in a lighter Mottle.

28. Latero-ventral patches (figure 44). A series of four to five dark patches on the lateral aspect of the ventral mantle, directly below the fins. Visible only from the side or below, these patches are conspicuous against the white ventral mantle skin. A similar patch may be shown on the fourth arm (figure 28). (See also figure 35.)

29. Anterior head bar (figure 89). A dark bar across the head extending from the base of the arms to component 13, where it terminates abruptly. (See also figures 8, 12, 31, 33, 54, 57–59, 61–66, 75, 78, 85 and 98.)

30. Posterior head bar (figure 58). A less well-defined component limited to the centre posterior region of the head. The anterior edge may be irregular and interdigitate with the White landmark spots on the head (component 10). (See also figures 8, 31, 56, 59 and 89.)

31. Pupil (figure 71). The pupil is W-shaped when closed, but may be dilated to become almost circular and very conspicuous. May be expressed unilaterally. (Compare figures 29 and 54.)

32. Eye ring (figure 71). A dark ring around the eye that is often associated with pupil dilation. May be expressed unilaterally. (See also figure 70.)

33. Dark arm stripes (figure 103). Dark stripes running longitudinally down the dorsal surface of the arms; especially prominent on arms 1, 2 and 3. May be expressed unilaterally. (See also figures 74, 85 and 105, and figure 3 in Messenger (1977*a*).) There may also be a very narrow dark stripe along the outer margin of arm 4 (both sexes).

34. Dark arms (figure 59). General darkening of the arms, mostly 1, 2 and 3 forming a triangle. May be expressed unilaterally. (See also figure 58.)

4.3. *Textural elements, units and components*

The dermal muscles responsible for texture are numerous and are organized physiologically into the units we term papillae. These are present in great numbers all over the dorsal surfaces of the arms, head and mantle, and on the periphery of the ventral mantle. Papillae are usually round, although some may become spatulate; they can vary greatly in height. They probably always contain iridophores that will lie at the tip of the papillae when they are erect.

35. Smooth skin (figure 36).

36. Coarse skin (figure 40).

37. Papillate skin (figure 37).

DESCRIPTION OF PLATE 5

Textures and postures.

FIGURE 36. Smooth skin (component 35) in a cuttlefish (15 mm ML) underwater. Uniform Light pattern. Note fin folded against body in an animal that is Jetting (component 53).

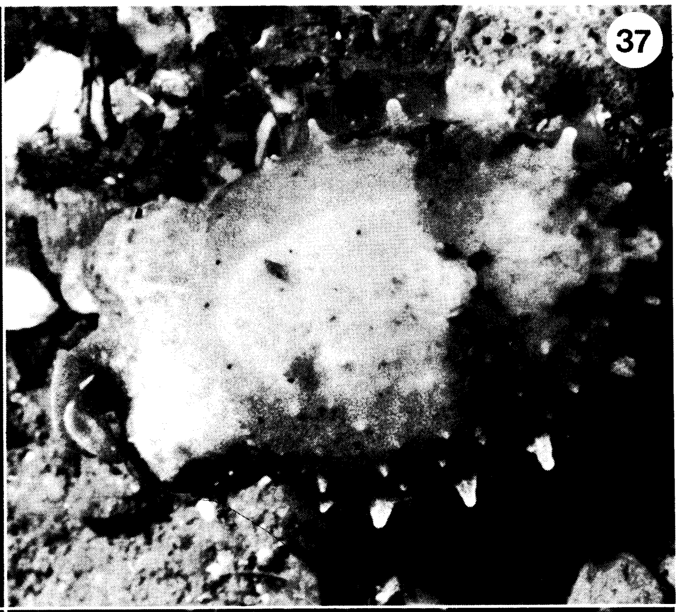
FIGURE 37. Papillate skin (component 37) featuring very spatulate Major lateral papillae (40) and White square papillae (39). The dark Posterior mantle bar (20) is expressed weakly and the arms are raised (41). Underwater photograph (13 mm ML).

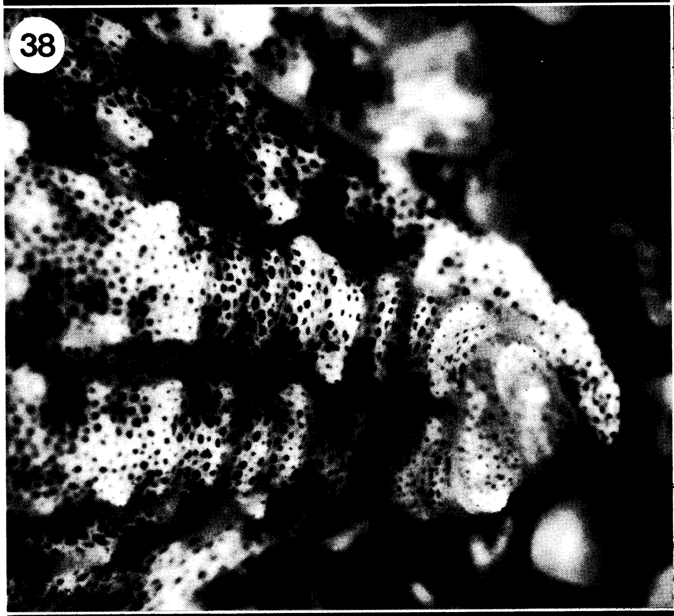
FIGURE 38. The component Wrinkled first arms in a hatchling (10 mm ML).

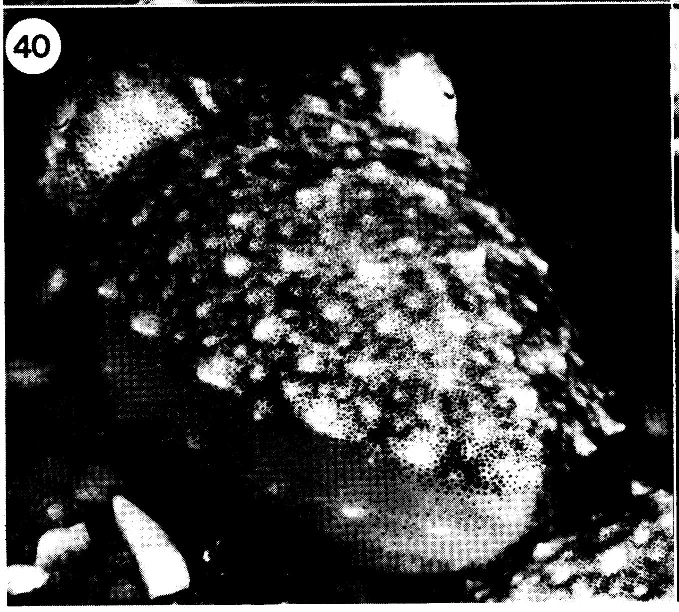
FIGURE 39. Mottle pattern in an animal aged 17 weeks (45 mm ML) Sitting (component 49) on a gravel plain underwater. Flanged fin (component 48) blends with the fourth arm to help eliminate shadows at edge of animal.

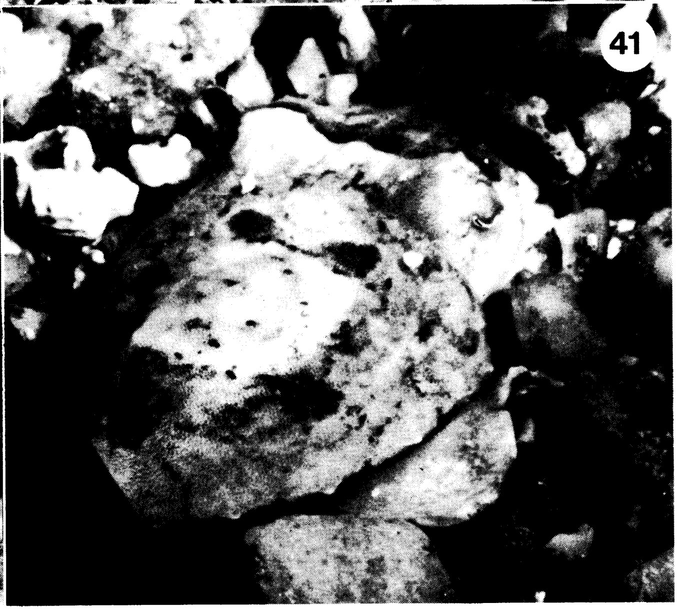
FIGURE 40. Light Mottle pattern with the Raised head posture (component 46) and Coarse skin (component 36) while Sitting (component 49). 12 mm ML.

FIGURE 41. Weak Disruptive pattern underwater (25 mm ML). Flattened body posture (component 47), Smooth skin (component 35) and the dark Mantle margin stripe (component 23) are prominent.









FIGURES 36–41. For description see opposite.

All over the body the skin may grade from being glassy smooth to heavily papillate. We define smooth as the absence of any projections, and coarse as a rugose condition where there are numerous small, equally sized projections. In the papillate condition there are fewer, longer projections (papillae) giving a spiky appearance. (See also plates 5 and 6.)

38. Wrinkled first arms (figure 38). Transverse grooves sometimes appear on the first pair of arms, generally when the arm tips are curved upward.

39. White square papillae (figure 61). Four large, conspicuous papillae at the corners of component 2. They are distinctive in being angled (**L**-shaped or almost **U**-shaped).

40. Major lateral papillae (figure 89). See component 12. (See also figures 11, 34, 37, 61, 79 and 97.)

4.4. *Postural and locomotor elements, units and components*

The various muscle groups of the arms, head, eyes, mantle, collar, funnel and fins constitute the units responsible for posture and locomotion.

We recognize eight distinct postural components of body patterning (numbers 41–48) and five distinct types of movement (numbers 49–53) that we designate locomotor components. Arbitrarily we include the ejection of ink as a locomotor component (number 54). Other common locomotor activities (e.g. feeding, attack) are not listed as separate components.

41. Raised arms (figure 43). The first pair of arms is raised vertically upwards and usually slightly parted. Often the second pair of arms is raised at a slight angle so that from the side the first two pairs of arms appear at right angles to each other. The arms are sometimes dark. This posture has been described in adults by Sanders & Young (1940), Boycott (1958) and Messenger (1968).

42. Waving arms (figure 48). The first pair of arms is held high and parted, each in an **S**-shaped curve; they may sway gently from side to side and are usually dark. This posture has been described in adults by Messenger (1968).

43. Splayed arms (figure 42). All arms held apart, often irregularly curved. This posture is shown while hovering.

44. Drooping arms (figure 53). Arms held together and down, pulled back towards the body so that their dorsal surface is nearly vertical.

45. Extended fourth arm (figure 72). Adult animals only. The fourth lateral arm, which has a broad, curved base and tapers to a long point, is extended laterally from the body towards an adjacent animal. This posture is always accompanied by components 9, 16 and 26. It has been described by Bott (1938), L. Tinbergen (1939) and Boycott (1958).

46. Raised head (figure 40). In the sitting position the head is raised up so that the eyes appear very prominent.

47. Flattened body (figure 41). In the sitting position the head and mantle are pressed to the substrate, in direct contrast to Raised head. In adults this is often associated with the Deimatic pattern (Holmes 1940; Boycott 1958, 1961).

48. Flanged fin (figure 46). Fin angled down onto or into the substrate when the animal is sitting or slightly buried.

49. Sitting (figure 40). Animal resting on the substrate, with the fin, arms and ventral mantle visible and in contact with the substrate.

50. Bottom suction (figure 47). On a smooth substrate, in the sitting position, small animals attach themselves to the substrate apparently by using the entire ventral mantle and arms to form a sucker (Bather 1895; see also Boletzky 1974).

51. Buried (figure 94). There are graded degrees of burying (Boletzky 1974), in the most complete of which the animal is almost entirely covered by the substrate with only the eyes protruding.

52. Hovering (figure 43). Maintaining a position in the water column mainly by use of the fins (Boycott 1958), although aided by the neutrally buoyant cuttlebone.

53. Jetting (figure 36). Swift travel by rapid jets of water from the funnel, with the fins folded down and the arms pointed together in the midline (Boycott 1958, 1961).

54. Inking (figure 49). Ejection of ink through the funnel. Ink may be discharged either as one or several discrete packets, or repeatedly to form a dense cloud (Boycott 1958).

4.5. *Body patterns*

Chromatic, textural, postural and locomotor components combine to produce body patterns. As Packard & Hochberg (1977) observed, individual components usually appear

Description of plate 6

Postural and locomotor components.

Figure 42. Underwater photograph of a late juvenile aged 16 weeks (30 mm ML) Hovering (component 52) with Splayed arms (component 43) and prominent Mantle margin stripe (component 23).

Figure 43. Uniform Blanching pattern with Raised arms (component 41) and Papillate skin (component 37). Major lateral papillae (component 40) are especially prominent. Underwater photograph. 15 mm ML.

Figure 44. Flamboyant pattern of a 13 mm ML cuttlefish, highlighting the Latero-ventral patches (component 28) on the ventral mantle and the Papillate skin (component 37).

Figure 45. Head-on view of Flamboyant pattern with dark Splayed arms (component 43) while Hovering (component 52). 13 mm ML.

Figure 46. Very young cuttlefish (11 mm ML) Sitting (component 49) with the first and second arms slightly raised (component 41). Note the Flanged fin (component 48) and the White landmark spots on the third arms (component 10).

Figure 47. A hatchling (10 mm ML) showing Bottom suction (component 50) with the ventral mantle and arms.

Figure 48. Underwater photograph of a 33 mm ML cuttlefish with Waving arms (component 42), while Sitting (component 49) in a light Mottle pattern. Note the Flanged fin (component 48).

Figure 49. Escape from attack by *Serranus cabrilla* underwater. The small cuttlefish (13 mm ML) is Jetting away (component 53) after Uniform blanching (pattern 7) and Inking (component 54).

Description of plate 7

Chronic body patterns, illustrating gradations from Uniform Light to weak Disruptive.

Figure 50. Uniform light pattern. 15 mm ML.

Figure 51. Stipple pattern with Papillate skin (component 37) and White landmark spots (component 10). 22 mm ML.

Figure 52. Very fine Stipple pattern and Papillate skin (component 37) in a partly Buried (component 51) position. Some light and dark components expressed weakly. 40 mm ML.

Figure 53. A hatchling (11 mm ML) in a Light Mottle pattern with Drooping arms (component 44).

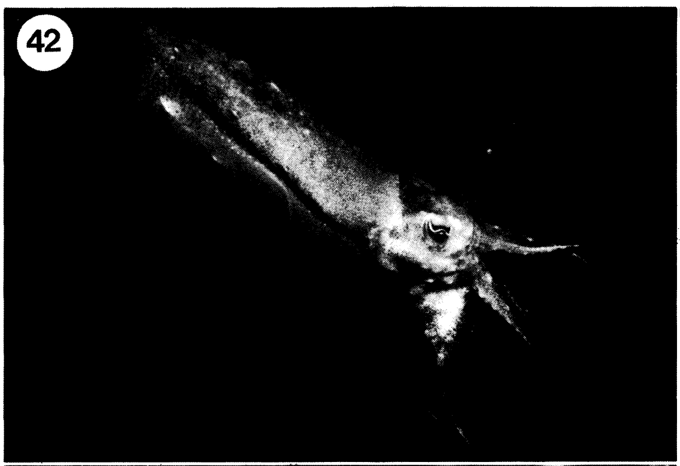
Figure 54. Light Mottle pattern (20 mm ML) with the Mottle component (component 27) and White head bar (component 13) expressed faintly. Note the dilated Pupils (component 31).

Figure 55. Dark Mottle pattern (28 mm ML). Note how fourth arm is light to match the substrate.

Figure 56. Dark Mottle pattern expressed so coarsely that it appears spotted. White landmark spots (component 10) very conspicuous on the head. Underwater photograph, 33 mm ML.

Figure 57. Weak Disruptive pattern. There are fewer mantle spots than in figure 56 and the White mantle bar (component 3), Anterior head bar (component 29) and White head bar (component 13) are expressed weakly to create the disruptive effect. Note the Flanged fin (component 48). Underwater photograph, 35 mm ML.

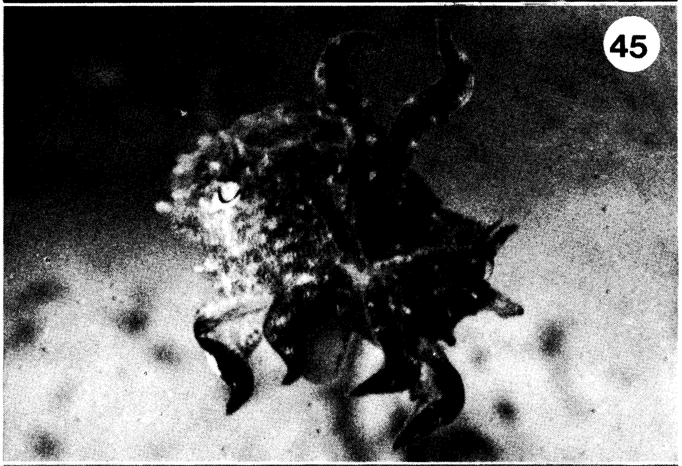
42



43

44

45

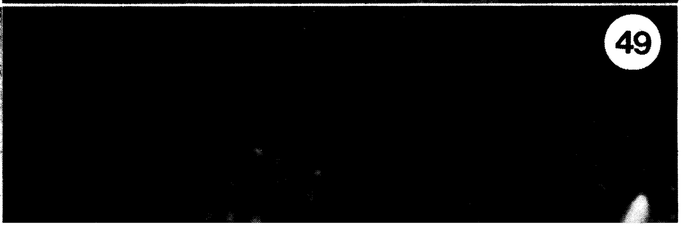


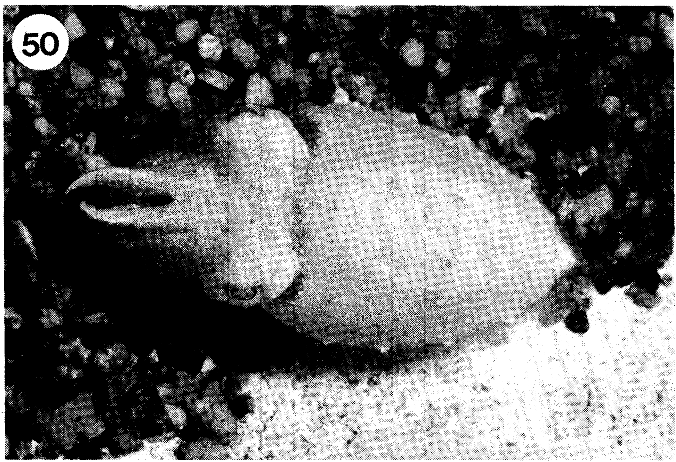
46

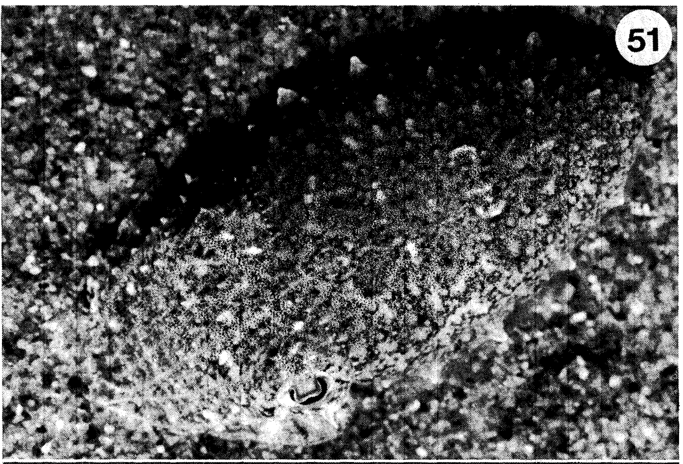
47

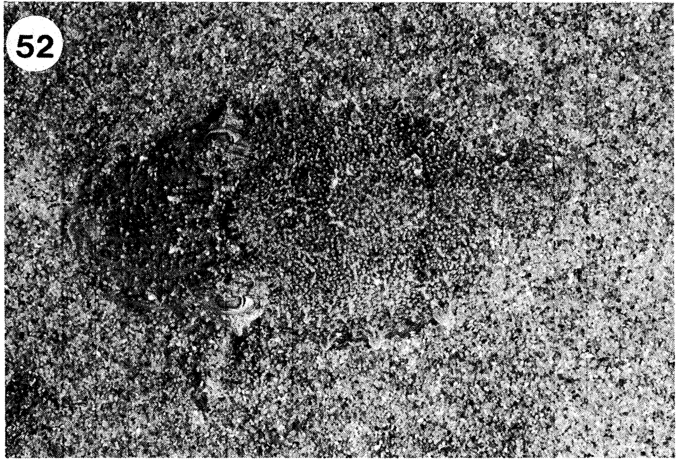
48

49

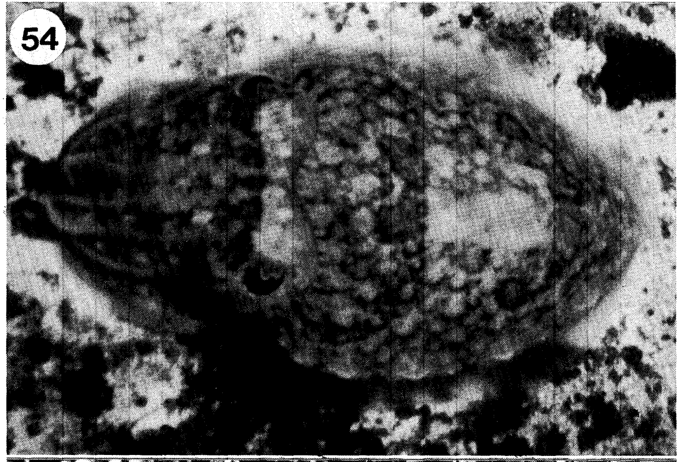


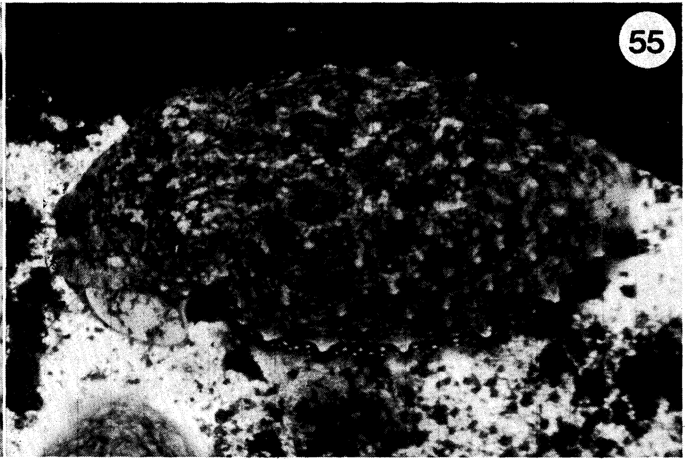

50


51


52


53

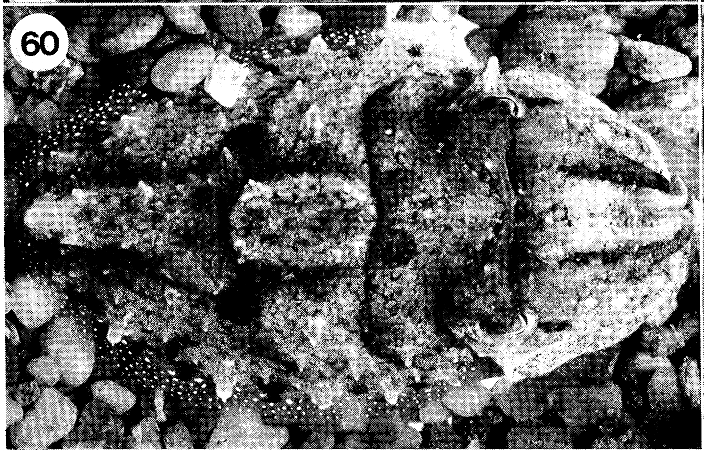

54

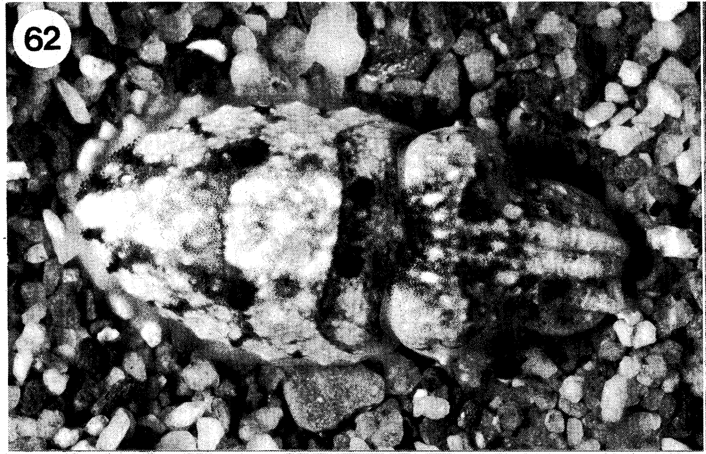

55

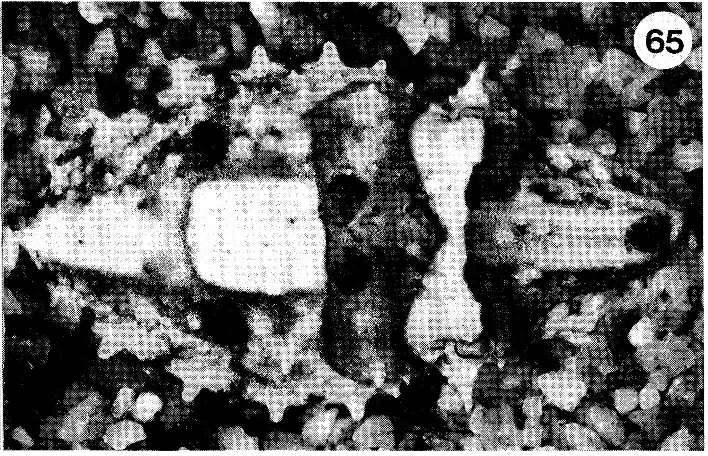

56


57

FIGURES 50–57. For description see p. 452.







FIGURES 58–65. For description see facing plate 9.

DESCRIPTION OF PLATE 8

Disruptive body patterns.

FIGURES 58–65. These illustrate eight expressions of disruptive patterns, which comprise mainly bold transverse and longitudinal components, both light and dark. For example, study the head and eye region of each animal. Note the pebble on the edge of the White square in figure 58, an example of Cott's (1940) 'adventitious' concealing coloration.

DESCRIPTION OF PLATE 9

Acute body patterns.

FIGURE 66. Adult (215 mm ML) showing Acute Disruptive with prominent White head bar (component 13), White square (component 2) and part of the White posterior triangle (component 1).

FIGURES 67 AND 68. Young juvenile (25 mm ML) showing the Flamboyant pattern to a predatory fish *Serranus cabrilla*. Figure 68 is a fish-eye view of the same individual.

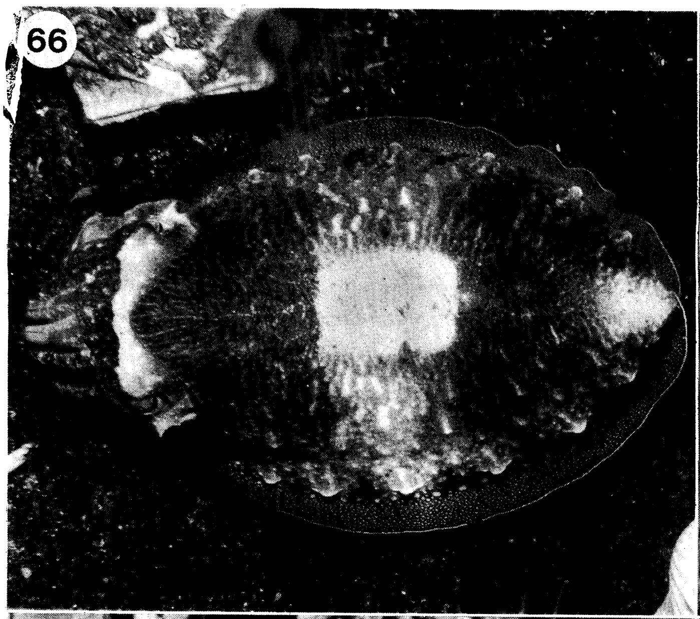
FIGURE 69. Passing Cloud pattern in a juvenile aged 3 weeks (13 mm ML). Broad transverse bands of expanded chromatophores are passing rapidly from the posterior mantle to the arm tips; pattern caused by the photographer's close presence. Underwater photograph.

FIGURE 70. Deimatic pattern in a late juvenile (40 mm ML). Flattened body (component 47) is characteristic as well as Dark fin line (component 25) and dark Eye ring (component 32).

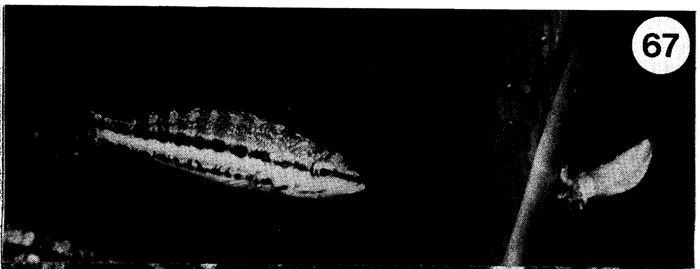
FIGURE 71. Nearly full adult Deimatic pattern with dilated Pupil (component 31), Eye ring (component 32), Dark fin line (component 25) and Paired mantle spots (component 21). Female 140 mm ML.

FIGURE 72. Intense Zebra pattern in a mature male (205 mm ML) showing sexual display to an adjacent cuttlefish. Extended fourth arm (component 45) with its bands and spots (components 9, 16 and 26) is an integral part of this behaviour.

66



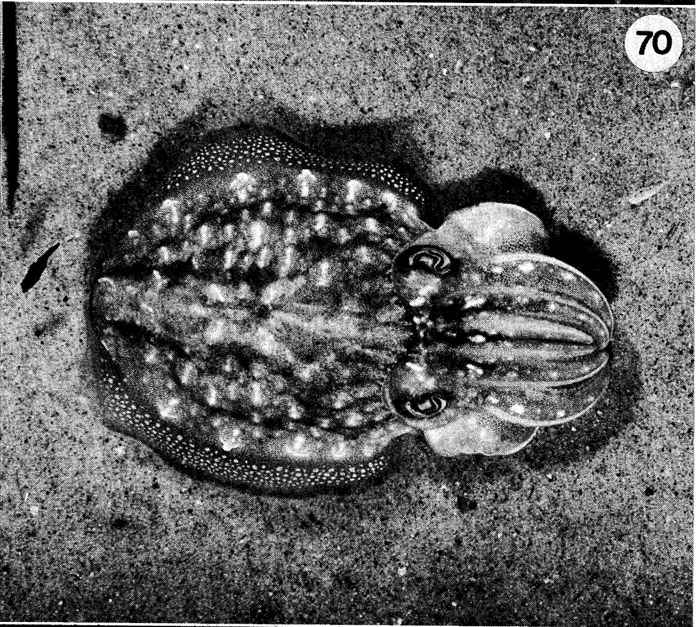
67



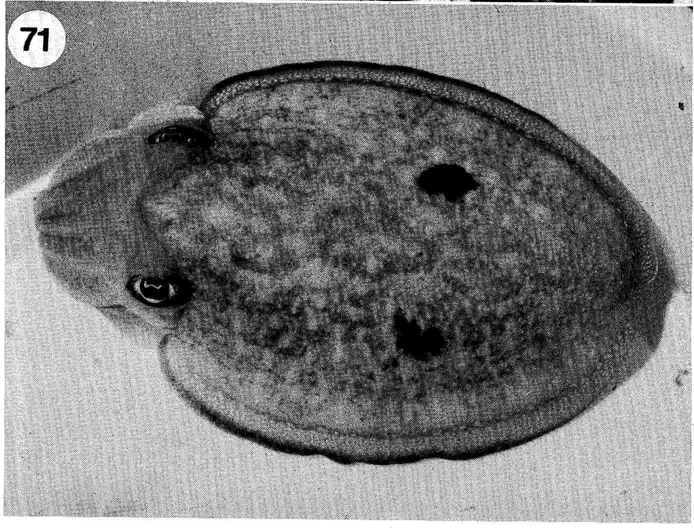
68

69

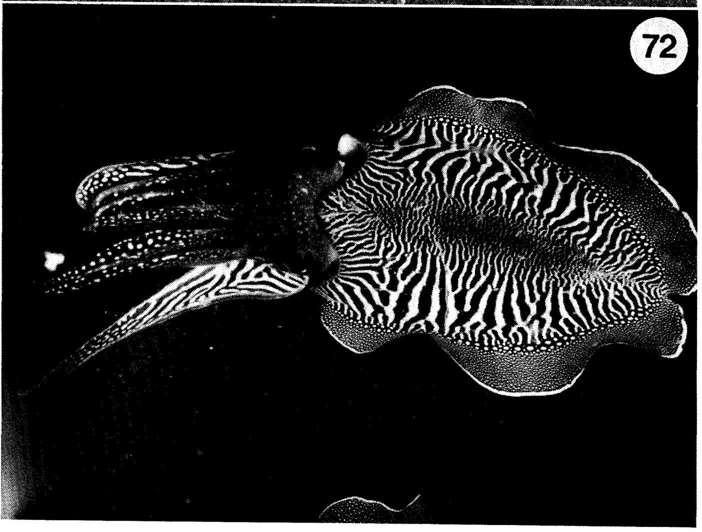
70



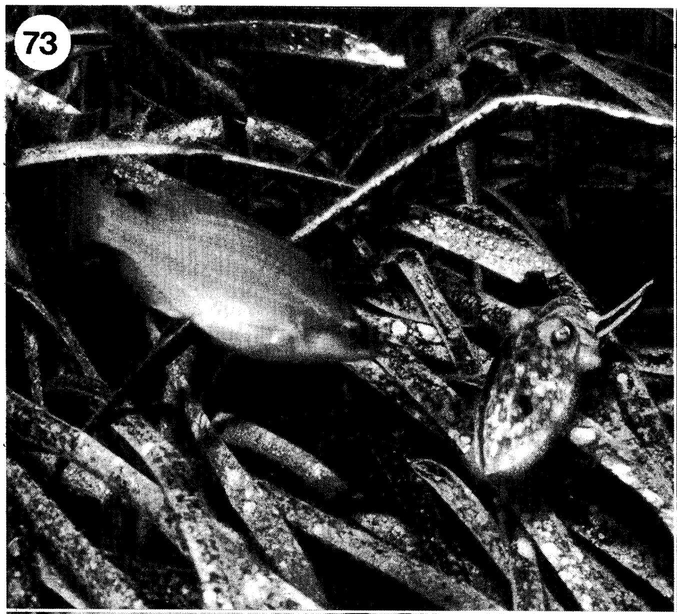
71

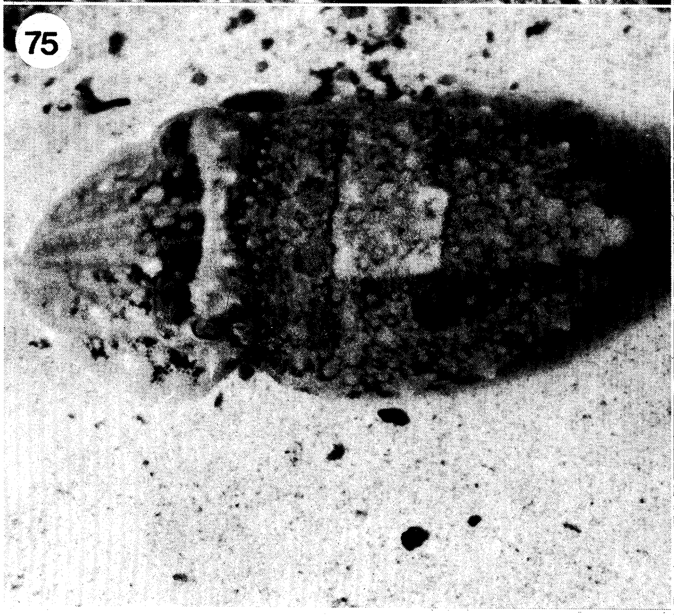


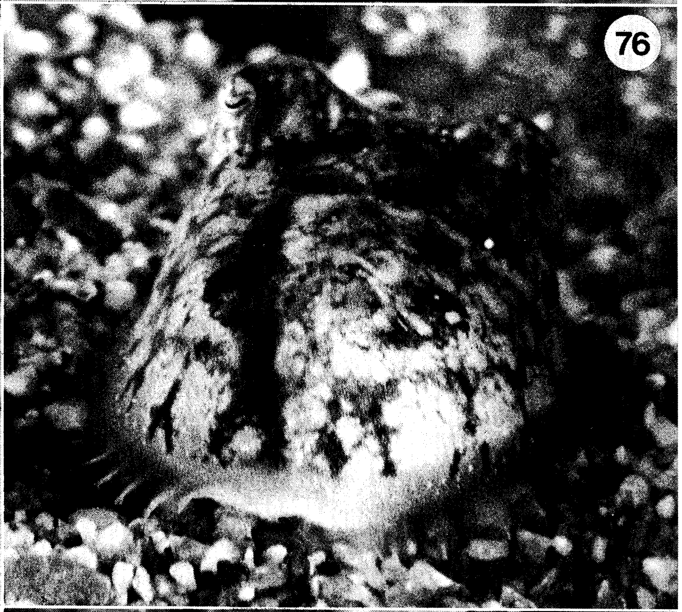
72

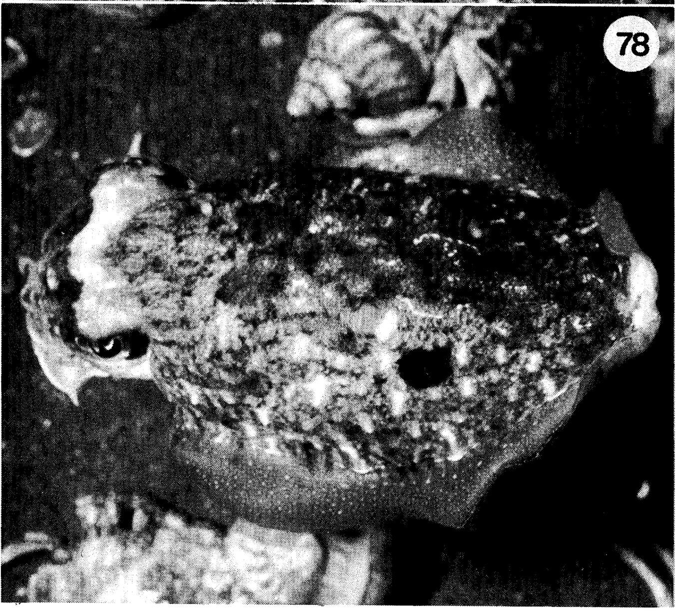


Figures 66–72. For description see opposite.









Figures 73–78. For description see opposite.

DESCRIPTION OF PLATE 10

The unilateral expressions of patterning.

FIGURE 73. Young cuttlefish (33 mm ML) showing Median mantle stripe (component 22) strongly on the side toward the approaching (non-predatory) fish. The cuttlefish is showing a mild form of the Deimatic pattern.

FIGURE 74. Young cuttlefish (14 mm ML) Jetting (component 53) rapidly to the right after being attacked by fish *Serranus cabrilla*; it is showing Median mantle stripe (component 22) strongly toward the photographer, who approached rapidly and closely for the underwater photograph.

FIGURE 75. Weak Disruptive pattern with Median mantle stripe (component 22) expressed weakly on left side, and White mantle bar (component 3) absent on the left side. 12 mm ML.

FIGURE 76. Hatchling (10 mm ML) Sitting (component 49) with unilateral expression of Raised head (component 46) and Median mantle stripe (component 22). Note the Flanged fin (component 48).

FIGURE 77. Late juvenile (75 mm ML) with Weak Zebra pattern expressed more strongly on the left.

FIGURE 78. Adult female (205 mm ML) showing weak Deimatic pattern with only the third Paired mantle spots (component 21) expressed more strongly on the left.

DESCRIPTION OF PLATE 11

FIGURE 79. Young juvenile (22 mm ML) in a Stipple pattern showing partial Posterior mantle bar (component 20) that could be interpreted as a 'Head-in-reverse'.

FIGURES 80–83. Young cuttlefish (32 mm ML) matching the bottom rather than the surroundings in the tanks shown in figures 82 and 83. See text §5.2.3.

DESCRIPTION OF PLATE 12

Concealment strategies of differently sized cuttlefishes on the same substrate.

FIGURE 84. Montage of three individuals photographed at different times on the same substrate (small variegated stones). For left to right: hatchling, late juvenile, early juvenile.

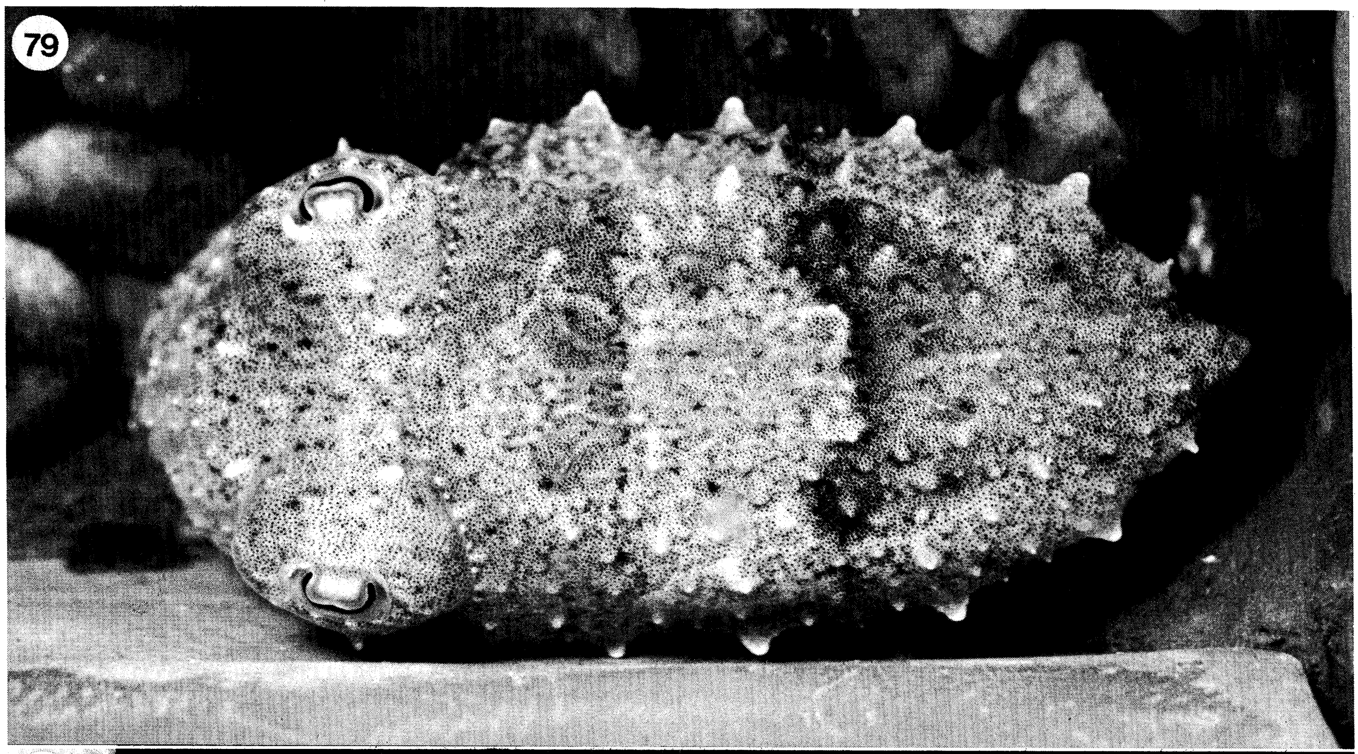
FIGURE 85–87. The same three individuals printed so that their mantle lengths are approximately equal. The smallest individual (10 mm ML) shows a strong Disruptive pattern; the intermediate-sized one (8 mm ML) a less-pronounced Disruptive; and the largest one (35 mm ML) a Light Mottle. See text §5.2.3.

DESCRIPTION OF PLATE 13

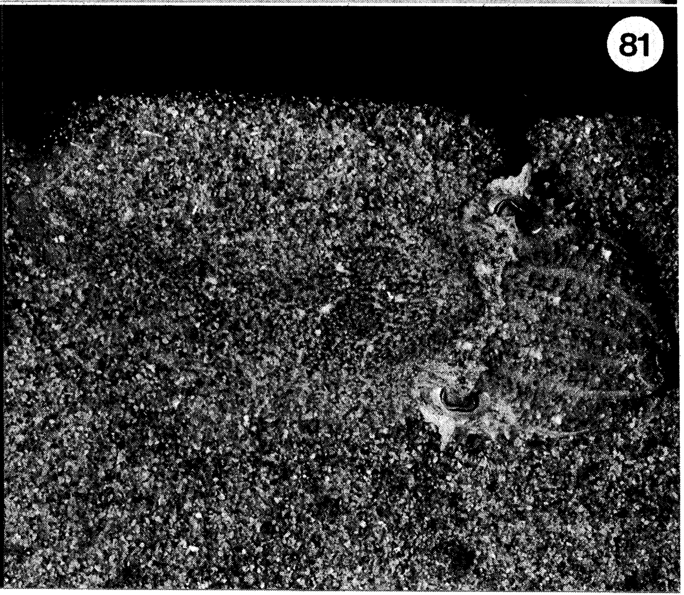
Different concealment strategies by hatchlings.

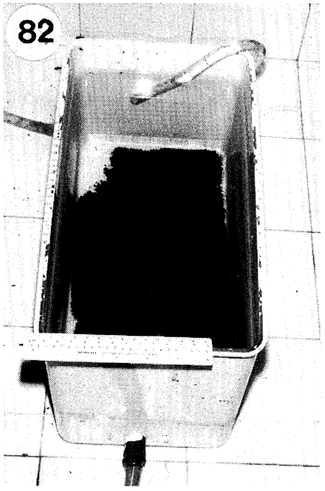
FIGURE 88. Stipple pattern in a 10 mm ML hatchling.

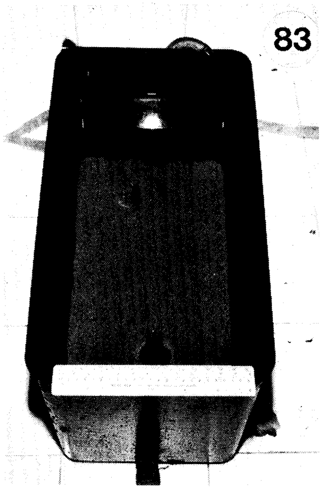
FIGURE 89. Strong Disruptive pattern in a 10 mm ML hatchling. See text §5.2.1.

79


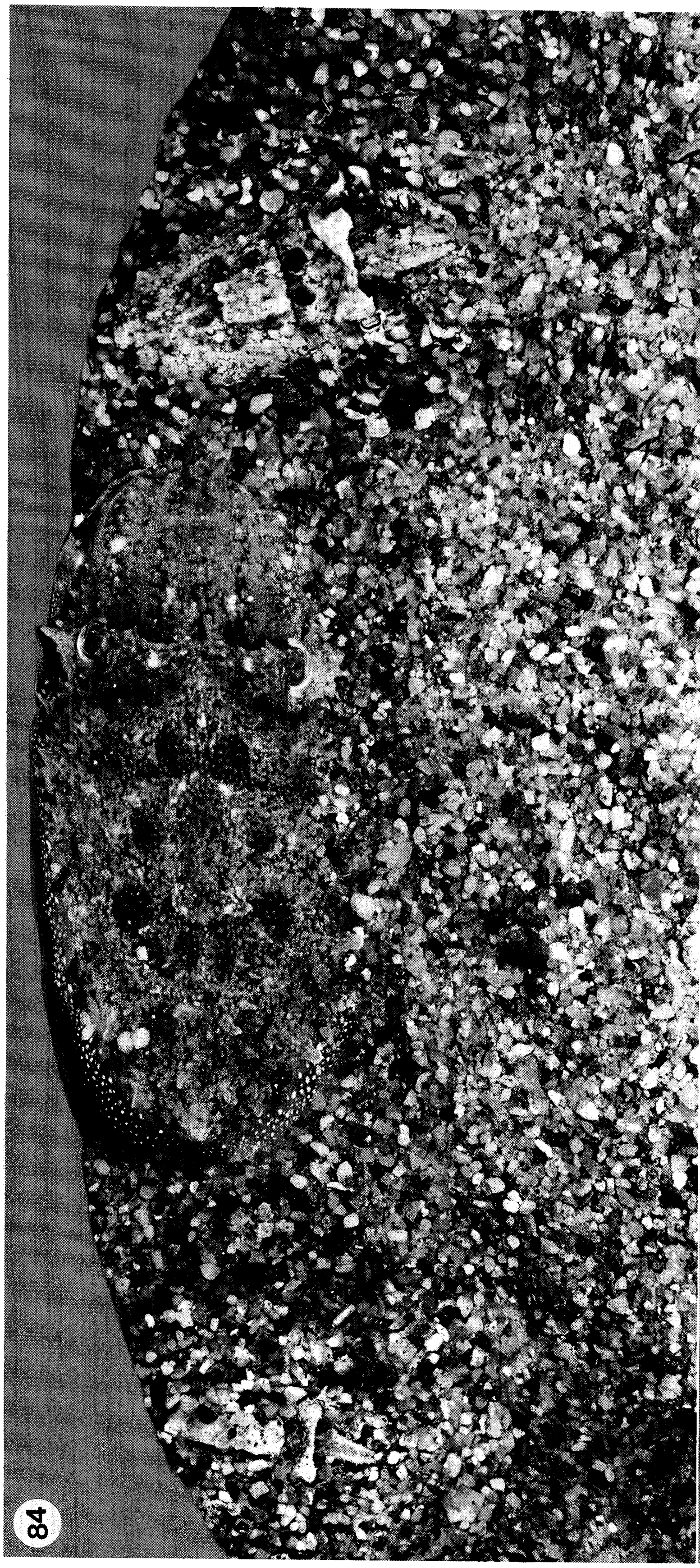
80

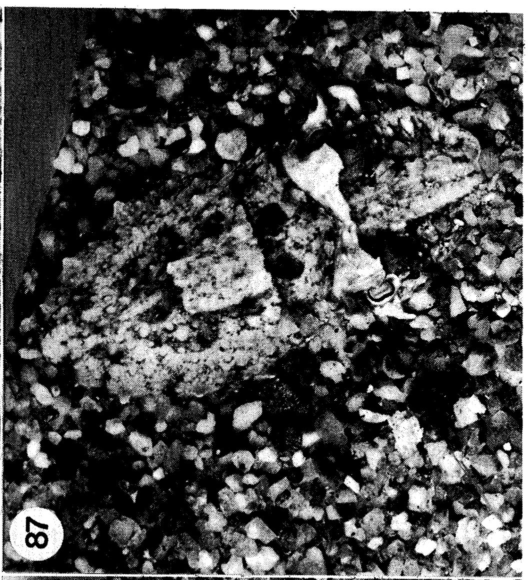

81


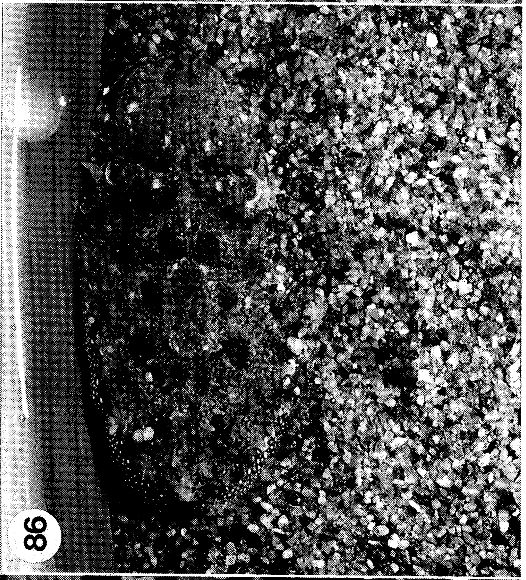
82


83


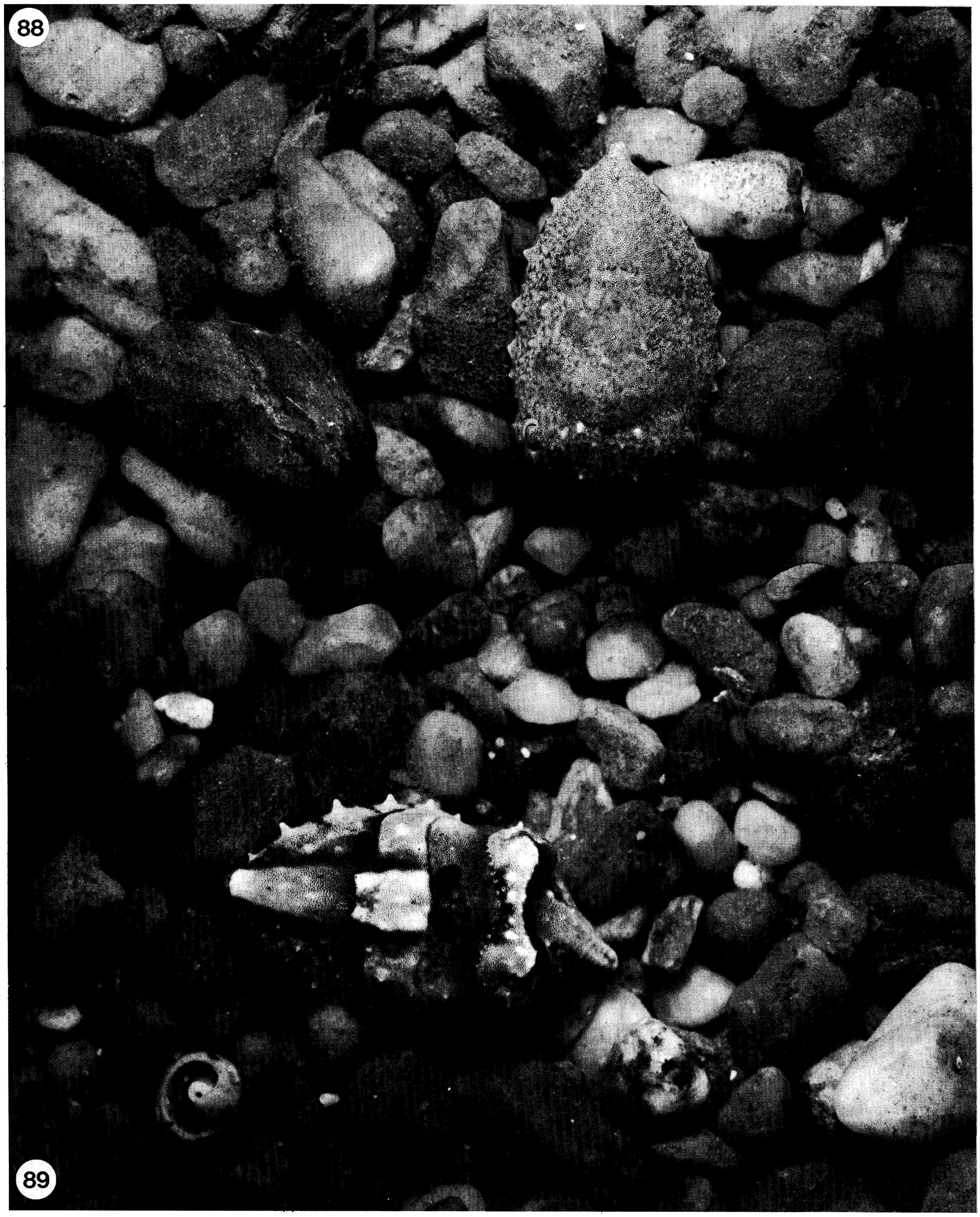
FIGURES 79–83. For description see facing plate 10.


84


87


86


85



FIGURES 88 AND 89. For description see facing plate 10.

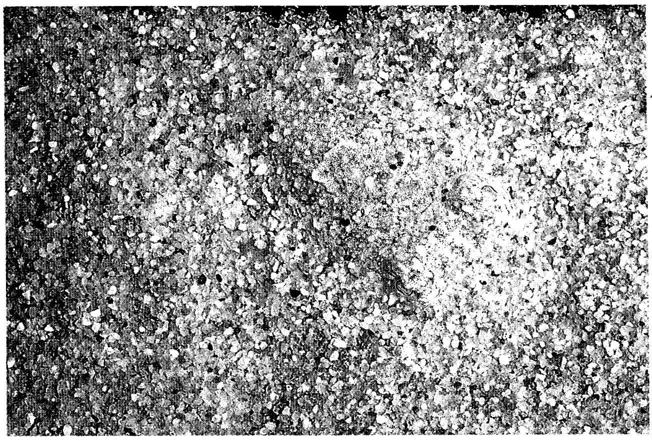
90

91

92

93

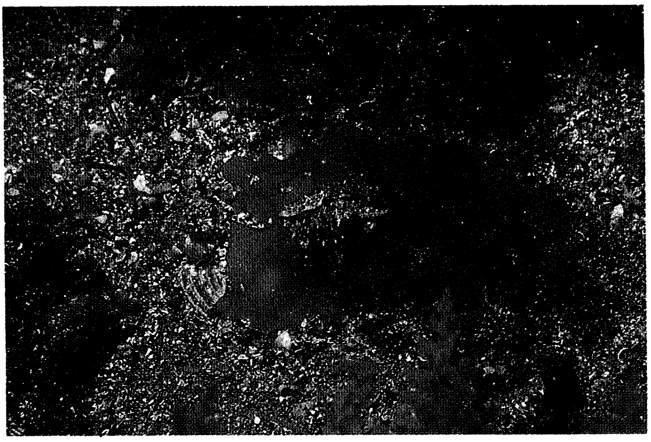
94



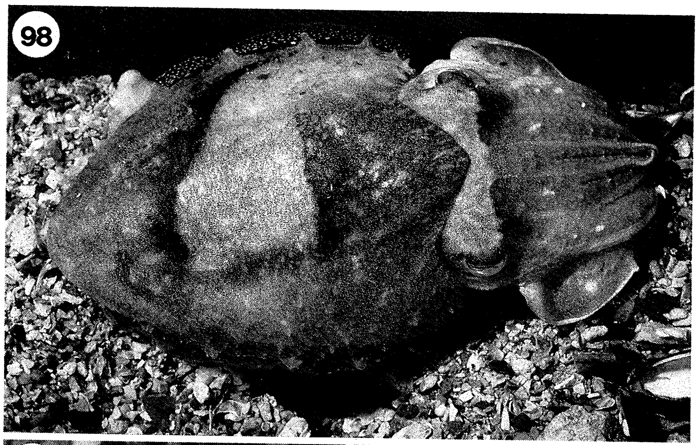
95

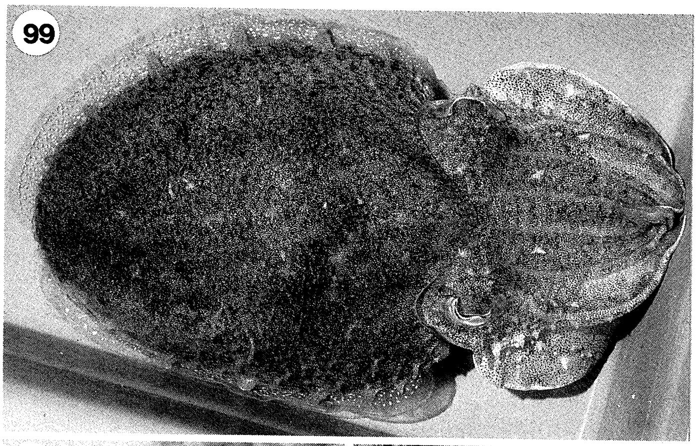
96

97



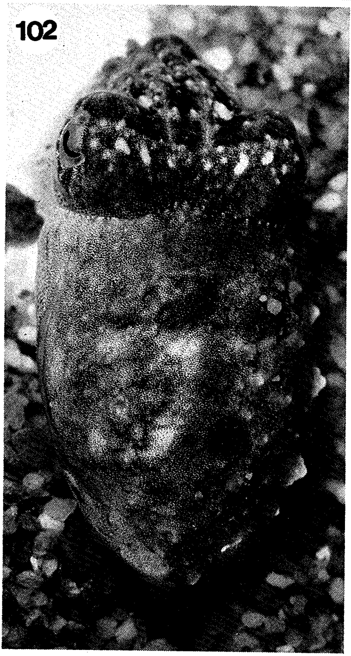
FIGURES 90–97. For description see facing plate 15.

98


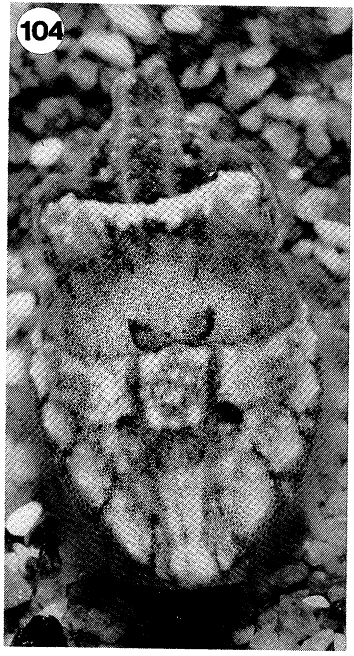
99


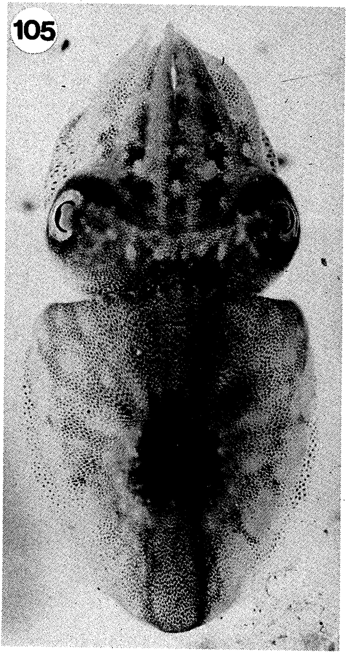
100

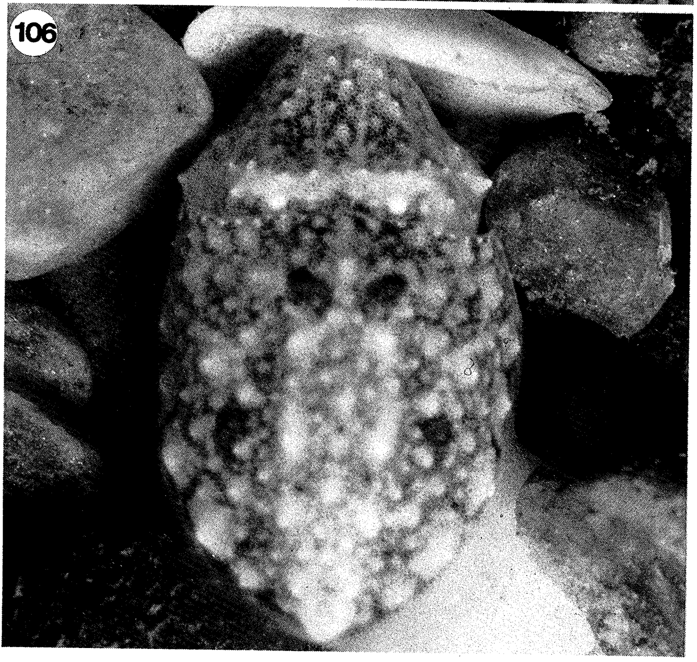

101


102


103


104


105


106


FIGURES 98–106. For description see opposite.

together with other components of the same or different class, and any particular component may vary from the barely visible to the fully expressed. Obviously it is difficult to categorize patterns arising from as many as 54 components. Nevertheless, we can recognize 13 basic patterns: six chronic and seven acute. The six chronic patterns exhibit considerable variation (see §4.5.3) because they are used for concealment on highly diverse substrates in the natural habitat; they are usually seen while the animal is stationary and on the substrate. Acute patterns, which are usually seen while the cuttlefish is off the substrate or while moving, are less variable.

4.5.1. *Chronic body patterns*

The following body patterns are shown for hours at a time.

1. Uniform Light (figure 50). The overall tone is light, irrespective of hue, and there are no dark chromatic components present. This body pattern can occur with any textural, postural or locomotor component. Countershading (by means of the Iridescent ventral mantle, component 8) is an important variant of this pattern during Hovering or Jetting (components 52 and 53).

Description of plate 14

General colour resemblance in the natural environment.

Figure 90. Light Mottle pattern in a young cuttlefish of 22 mm ML. Skin is very Papillate (component 37) and notice how the Raised arms (component 41) resemble the algae to the right.

Figure 91. Late juvenile (33 mm ML) Sitting (component 49) with Raised arms (component 41) in a Mottle pattern. The raised arms mimic the form of the algae.

Figure 92. Juvenile aged 3 weeks (12 mm ML) Sitting (component 49) among stone rubble in a Light Mottle pattern with dark components Anterior and Posterior head bars (29 and 30) and Paired mantle spots (21). Cuttlefish is in centre of photograph.

Figure 93. Uniform Light pattern in a late juvenile (25 mm ML) Sitting (component 49) in an empty bivalve shell.

Figure 94. Stipple pattern shown by a hatchling aged 1 week (10 mm ML) partly Buried (component 51) in fine sand (head is toward bottom right). White square (component 2) and White square papillae (component 39) are visible.

Figure 95. Early juvenile aged 8 weeks (21 mm ML) Sitting (component 49) with a Light Mottle pattern. Note how the first Paired mantle spots (component 21) coincide with the holes in the *Haliotis* shell.

Figure 96. Light Mottle pattern shown by a juvenile aged 2 weeks (11 mm ML) among rocks and pebbles.

Figure 97. Flamboyant pattern in a juvenile aged 3 weeks Hovering (in the exact centre of the photograph) in front of algae. It is very Papillate (component 37) and the White square (component 2) is recognizable (head is toward the right).

Description of plate 15

Abnormal patterns.

Figures 98 and 99. Photographs of the same young adult (70 mm ML) taken within a few minutes of each other 19 weeks after right pallial nerve had been crushed. The deficit in patterning is obvious in figure 98, but not in figure 99, emphasizing that the same morphological units can be part of different physiological units.

Figures 100–103. Same juvenile (18 mm ML) photographed (left to right) on days 1, 12, 19 and 22 after the left pallial nerve had been crushed. Note in figures 102 and 103 how the skin in pulled over to the left during the healing process.

Figures 104 and 105. Starved young animals (13 and 11 mm ML). Left animal is only slightly starved and White square (component 2) is shrunken slightly. Right animal is badly starved and shows dark, permanently expanded chromatophores in area of White square.

Figure 106. Eye-less hatchling (blinded in embryo) showing Light Mottle pattern. See text §6.2.

2. Stipple (figure 51). The overall tone is uniform and slightly darker than in pattern 1, owing to the expansion of numerous small dark chromatophores across the body surface. The chromatic components 10 and 12 are often present. This pattern can occur with any textural, postural or locomotor component.

3. Light Mottle (figure 54). The overall tone is light, but not uniform as in pattern 2. The major chromatic components that define this pattern are numbers 11, 24 and 27, but numbers 10 and 21 may also be present. Again, this pattern can occur with any textural, postural or locomotor component.

4. Dark Mottle (figure 55). Similar to pattern 3, except that the overall tone is darker. Patterns 2, 3 and 4 intergrade; the mottles are coarser-grained than the Stipple, and Dark Mottle is higher in contrast than Light Mottle or Stipple.

5. Disruptive (weak, strong) (figure 57 and plate 8). This pattern is characterized by bold transverse or longitudinal chromatic components. The chromatic components that contribute most to this pattern include numbers 1, 2, 3, 13, 14 (light) and numbers 17, 18, 19, 22, 29 and 30 (dark). This pattern can be expressed in widely differing strengths (plate 8) according to the degree of contrast between the light and dark chromatic components, and different components may sometimes predominate. This pattern subsumes the White square pattern of Holmes (1940), for this is merely one form of Disruptive pattern. The pattern is associated with postural components 49, 50 and 51 and can occur with any of the textural components.

6. Weak Zebra (figure 26). This pattern results from chromatic components 9 and 26 being weakly expressed on the mantle only, resulting in the low-contrast zebra patterning that Holmes (1940) called 'sandy stripe'. Chromatic components 5 and 6 may also be expressed weakly in this pattern. Textural components 35, 36, 39 and 40 and locomotor components 49 and 52 may be associated with it. The pattern is shown by males and females but in males it can be intensified (and complemented by zebra bands on the fourth arm to become pattern 12).

4.5.2. *Acute body patterns*

The following patterns are shown for seconds or minutes.

7. Uniform Blanching. Instant retraction of all chromatophores.

8. Uniform Darkening. Instant expansion of all chromatophores.

9. Acute Disruptive (figure 66). The sudden appearance of pattern 5 in any of its guises, usually expressed very strongly.

10. Flamboyant (figure 68). A pattern shown while Hovering (component 52) in midwater, with the arms splayed (component 43), the skin papillate (component 37) and darkly mottled (component 27), and lateroventral patches (component 28) present. The term was coined by Packard & Sanders (1969).

11. Deimatic (figure 71). A complex pattern that is fully expressed only in adult cuttlefish. The body flattens (component 47) and becomes pale except for the intense expression of dark chromatic components 25, 32 and, above all, 21, which really characterizes the pattern. The pupil may also be dilated (component 31). The skin texture is generally smooth (component 35). In the adult and older juveniles it is the third pair of spots that are shown, but in young animals the first and second pair of spots and component 33 are often shown too. This pattern, first described by Holmes (1940), is shown to a potentially threatening stimulus, such as a large human figure in the laboratory or a fish, and often the cuttlefish re-orient to that stimulus so that the dark mantle spots are presented towards it, thus maximizing the effect (figure 73).

Warning or 'frightening' displays of this kind were termed 'dymantic' by Young (1950), a word coined from a Greek root meaning 'terrifying', and this word has been used widely in the cephalopod literature. Nevertheless, the word 'deimatic' from the same root (Maldonado 1970) seems now to be more widely used for arthropods and vertebrates, and to have gained general acceptance (see, for example, Edmunds 1974; McFarland 1981) so that we prefer to use that term here.

Holmes (1940: p. 27; see also Edmunds 1974) described another 'warning' pattern in adult *Sepia* as Deimatic. It consisted of four longitudinal dark stripes on the mantle (i.e. the components Median mantle stripes plus Mantle margin stripes) while the animal was otherwise pale. We have not observed this pattern.

12. Intense Zebra. Adult males only (figure 72). This pattern is much stronger than pattern 6 and, in addition, the Extended fourth arm (component 45) also bears White and Black zebra bands (components 9 and 26) as well as White spots (component 16). Skin texture is usually smooth (component 35) and this pattern is normally shown during Hovering (component 52). Although females can heighten the contrast of Weak Zebra on the mantle they lack aggregations of leucophores on the fourth arm, which therefore never bears light components 9 or 16 (or dark component 26). This pattern, which is for sexual display, has been described and illustrated by Bott (1938) and L. Tinbergen (1939); it can become chronic during male–male interactions and persist for tens of minutes at least (J. B. Messenger, unpublished results).

13. Passing Cloud (figure 69). A kinetic pattern, lasting only a second or two, characterized by broad transverse bands of chromatophore expansion moving rapidly forward from the posterior mantle tip across the dorsal body surface to the anterior tip of the arms (see also Boycott 1958).

4.5.3. *Variations on a theme*

We emphasize that patterning in *Sepia* is a dynamic process subject to immediate change and countless gradations. Having just listed 54 components and 13 body patterns we must now qualify this and describe some of the variations frequently encountered within the broadly defined categories of body patterns. Such gradations and variations may be seen in figures 50–65. The sequence begins with a Uniform Light pattern (figure 50) and proceeds through Stipple patterns, Light and Dark Mottle patterns into weak and strong Disruptive patterns showing how quite subtle changes in the types and intensities of individual components can affect the patterns. There is a progression from few to many components in this sequence, and from subtle and low-contrast components to bold spots (figure 56) or transverse and longitudinal components (figure 61), especially the white components. Figures 88 and 89 show the extremes of this continuum. Plate 14 illustrates not only variations within the chronic pattern categories but also their effectiveness in providing camouflage in the natural environment.

Some variations in the acute body pattern Flamboyant may be seen in plates 6 and 9. It may vary in the degree of arm splaying, overall darkness and degree of Mottle, and the amount of skin papillation (figures 42, 43, 44, 45, 48, 67 and 68). The Deimatic and Intense Zebra patterns can also be expressed with varying degrees of intensity and it is possible to state an important general principle: *the intensity of an acute body pattern varies directly with the stimulus evoking it* (usually a predatory fish or a mating rival). Chronic patterns, on the other hand, vary mainly in relation to the surrounding substrate because they are used principally for camouflage.

It is very common indeed for chromatic and textural components to be expressed with different degrees of intensity on the two sides. In its extreme form this leads to the unilateral expression of the component and we have frequently observed the following dark chromatic components being shown unilaterally: numbers 21, 22, 26, 31, 32, 33 and 34. Although potentially other dark components could be shown unilaterally, we have not observed them. Holmes (1940: plate D) showed the left half only of the White square (component 2) in an adult animal being expressed, but we have not observed this. The unilateral white components that we have seen are numbers 2, 3, 5, 6, 9 and 16. Extended fourth arm (component 45) is the only unilateral postural component. Both Zebra patterns can be shown unilaterally and it is not uncommon for part of the Deimatic pattern to be shown unilaterally toward the stimulus, specifically one of the third pair of spots in adult animals (component 21; figure 78).

Starved laboratory-reared cuttlefish exhibit abnormal patterns. Very young starving animals show a characteristic pattern (figures 104 and 105) in which the skin of the dorsal mantle is drawn taut toward the mid-dorsal mantle in the vicinity of the White square component. This area is usually very dark owing to the fixed expansion of damaged chromatophores.

5. BEHAVIOUR AND THE FUNCTION OF BODY PATTERNS

5.1. *Overview of behaviour during the life cycle*

The life cycle of *Sepia* has been described by Boletzky (1983) and various aspects of adult behaviour by Bott (1938), L. Tinbergen (1939), Holmes (1940), Wilson (1946), Boycott (1958) and Messenger (1968). The prey-catching behaviour of young *Sepia* was described by Wells (1958, 1962).

The common cuttlefish lays large eggs in shallow, well-lit waters (Mangold-Wirz 1963). The hatchlings, which resemble the adult in habit and in appearance, receive no parental protection. They appear to be solitary animals: only single individuals were ever observed underwater in their natural habitat. Whenever a group of hatchlings or juveniles from the laboratory was released underwater, its members always moved away in different directions, showing no tendency to school or move in pairs as adults sometimes do. In the laboratory, young *Sepia* tolerated fairly crowded rearing conditions; sometimes they aggregated beneath an incoming jet of water but usually their distribution in a tank was random. They showed no signs of intraspecific behaviour, in contrast to mature cuttlefish whose remarkable sexual displays are well known.

The young are epibenthic and during the daytime they bury themselves in, or sit in, the substrate, only leaving it to pursue prey (Bather 1895). They occur on sandy or muddy bottoms associated with seagrass (*Zostera*) or algae beds (Ferussac & d'Orbigny 1835–1848; Lo Bianco 1909; Cuénot 1917, 1933; Burton & Burton (eds) 1969; this study) and, in the laboratory and in the sea, the young come off the bottom at dusk and generally remain active in the water column all night. Adult *Sepia* are also essentially crepuscular or nocturnal (Denton & Gilpin-Brown 1961), although they may be active during the daytime.

Young *Sepia officinalis* feed mostly on small crustaceans such as mysids, which commonly swarm in large schools just above the bottom. Small fish are also taken but the mysids are so abundant that they probably constitute the main diet, at least in the Banyuls area. Feeding, which is essentially visual (Wells 1958, 1962; Messenger 1968, 1977*a*), brings the cuttlefish off the bottom so that the attack takes place in the water column: we have consistently observed that on the rare occasions when young cuttlefish feed in the daytime they immediately return to the bottom, often reverting to their previous buried position. Occasionally, we have observed young animals in the sea grasping mysids with the tentacles without leaving the substrate; sometimes they even remained partly buried.

There appear to be no studies of adult *Sepia officinalis* in the sea. From analysis of stomach contents we know that they feed on all kinds of crustaceans and fish, or smaller *Sepia* (Guerra 1985) and, more rarely, on polychaetes (B. Gonzales-Castro, personal communication 1985). This is similar to their diet in the laboratory (Messenger 1968).

The predators of young cuttlefish include other cuttlefish and, especially, teleost fish, which have excellent vision, swift, accurate movements and a capacious terminal mouth (Bone & Marshall 1982). Such predators are abundant in the clear water in which cuttlefish hatch. Cuttlefish avoid predation in three ways: (1) by being active mainly at night and by otherwise remaining concealed (primary defence); (2) by flight or by showing threatening patterns (secondary defence); and (3) by misdirecting a predator's attack (which we term tertiary defence). Adult cuttlefish are preyed upon by sharks (Clarke & Stevens 1974) and by dolphins (Clarke & Pascoe 1985).

Table 2 summarizes the antipredator adaptations of young *Sepia officinalis*. For convention of terminology we mainly follow Cott's (1940) thorough treatise on concealment, although the more recent and appropriate behavioural terminology of Edmunds (1974), Curio (1976) and Hailman (1977) is used to describe active defence against predators.

5.2. *Mechanisms of concealment*

5.2.1. *Chromatic responses of cuttlefish on different substrates*

Twelve hatchlings, twelve early juveniles and six late juveniles were each observed and photographed on four different substrates in a specially designed tank (round, 46 cm diameter, divided into four equal quadrants) that enabled us to transfer individuals gently from one compartment to another. The animals were viewed through a slot in a screen and allowed 5 min to settle down before observations were made.

The substrates were: (1) pale grey plastic; (2) fine brown sand (figure 52); (3) coarse yellow sand (1 mm, see plate 12); and (4) small variegated stones (4–9 mm, see plate 13). Attempts made to quantify the chromatic match with the substrates were unsatisfactory but, as it turned out, unnecessary. For only a direct demonstration (or a photograph) could show the extraordinary way cuttlefish concealed themselves against these different backgrounds. Some measure of this can be gauged by the fact that a human observer frequently had great difficulty in locating a cuttlefish in one of the compartments, and this on the laboratory bench, in broad daylight, and through only a few centimetres of clear seawater!

How is this matching achieved? First by what Cott (1940) terms 'general colour resemblance', which includes matching the substrate in brightness, colour, texture and pattern. In *Sepia*, brightness is controlled by the degree of expansion of chromatophores. The colours derive from the chromatophores, used in different combinations, to reflect yellow, orange, red and black; from the iridophores, which produce cyans and greens by structural interference;

TABLE 2. VISUAL ANTIPREDATORY ADAPTATIONS

(See table 1 and §4.5.)

adaptive coloration and behaviour	body pattern	effect
primary defence‡: concealment from predators		
nocturnally active	all patterns	harder to see at night
remain motionless	all chronic patterns	predator is not attracted by motion
general colour resemblance†	all chronic patterns	match substrate
deceptive resemblance†	Flamboyant	disguise by resembling algae
	Uniform Light Stipple Light Mottle	disguise by resembling a stone
countershading†	Uniform Light	blend with water column
disruptive coloration†	chronic Disruptive	obliterate body form
coincident disruptive coloration†	all chronic patterns	visually join different body parts
concealment of shadow†	all chronic patterns	blend body outline with substrate
secondary defence‡: make a predator hesitate		
flash behaviour†	Flamboyant	shape, posture and colour change startle predator
	Inking	predator is startled and loses sight of prey
	Deimatic	pattern, posture change and apparent size increase bluff predator
	Uniform Blanching + *Raised arms*	pattern, posture change confuse predator
	Passing Cloud	rapid colour change confuses predator
	Acute Disruptive	bold pattern change confuses predator
flight†	Uniform Blanching + *Jetting*	predator loses sight of prey
tertiary defence: misdirect a predator's attack		
deflective marks†	Deimatic	misdirect predator's attack with false eyespots
	'Head-in-reverse'	misdirect predator's attack with false head
diversion behaviour‡	Uniform Blanching + *Inking* + *Jetting*	predator attacks ink blob, becomes disoriented and loses sight of prey
protean display §	erratic *Jetting*	upset target prediction by predator; obviate predator's improvement of capture techniques

† Terminology of Cott (1940).
‡ Terminology of Edmunds (1974).
§ Terminology of Humphries & Driver (1971).
Italic type indicates components of patterns.

and from the leucophores, which reflect ambient light, whatever its wavelength, provided the overlying chromatophores are retracted sufficiently for incident light to reach them (Messenger 1974, 1979; Packard & Hochberg 1977; Froesch & Messenger 1978). Textural resemblance is achieved with papillae, and pattern resemblance is achieved by regulating the combination of chromatic components that are shown. Plate 14 should convey something of the effectiveness of cryptic coloration in *Sepia*.

Secondly by the development of 'disruptive coloration'. The principles of this are set out fully by Cott (1940) and could hardly be better exemplified than in young cuttlefish, as many of our photographs show (figures 8 and 12, and plate 8). The essence of disruptive coloration is that it breaks up the outline of the whole animal by drawing the observer's attention to selected areas of the body. In effect, it no longer looks like a cuttlefish when its bold transverse and longitudinal components are shown (figure 89).

Table 3. Responses of young cuttlefish to four substrates

(All age groups, $n = 30$.)

substrate	body patterns	main concealment strategy
I. pale grey plastic	Uniform Light	general colour resemblance
	Stipple	
II. fine brown sand	Stipple	general colour resemblance
	Dark Mottle	
III. coarse yellow sand	Stipple	general colour resemblance
	Light Mottle	—
	Disruptive	disruptive coloration (hatchlings and early juveniles only)
IV. small variegated stones	Disruptive	disruptive coloration
	Uniform Light (some hatchlings)	

Table 3 and figure 107 summarize the way cuttlefish used these two techniques on the substrates studied. Disruptive patterns were more frequently used when the substrate particle size was large (i.e. small variegated stones), but 3 of the 12 small hatchlings used the general colour resemblance tactic effectively on the variegated stones (plate 13). These individuals were hardly larger than the individual stones, so that by exhibiting a Uniform Light pattern or Stipple they became, to a human observer, another stone (figure 88). The Disruptive pattern, however, provided equally effective concealment (figure 89). In both patterns, the eyes were obliterated well and the hatchlings used Bottom suction (component 50) to remain stationary. Viewing this plate from a distance illustrates how effective both methods are; if one eliminated the strong shadows caused by the electronic flash, the animals would be nearly invisible.

When cuttlefish were placed on completely unnatural, uniform substrates, their responses were often quite inappropriate, especially among younger animals. For example, on pale grey plastic, some animals showed Disruptive patterns, which rendered them highly conspicuous. Figure 107 shows that hatchlings and early juveniles were more likely to display inappropriate disruptive patterns on this pale artificial substrate than older animals.

In another experiment (done in 1982 in Galveston), we placed each of eight early juvenile cuttlefish (11–20 mm ML) on a series of seven different substrates inside a large plastic bucket: white plastic, black plastic, fine sand, light natural gravel (2 mm), dark green gravel (5 mm), light oyster shell (6 mm) and variegated stones (16 mm). A video camera recorded patterning responses, and the whole set-up was screened off to minimize disturbance to the animals. In this experiment the animal was always placed on the substrate in a glass dish. The animals consistently revealed perfect substrate matching through general colour resemblance or disruptive coloration, emphasizing that skin patterning can be controlled entirely by visual pathways. Cuttlefish were not apparently stressed by being in a glass dish but they consistently

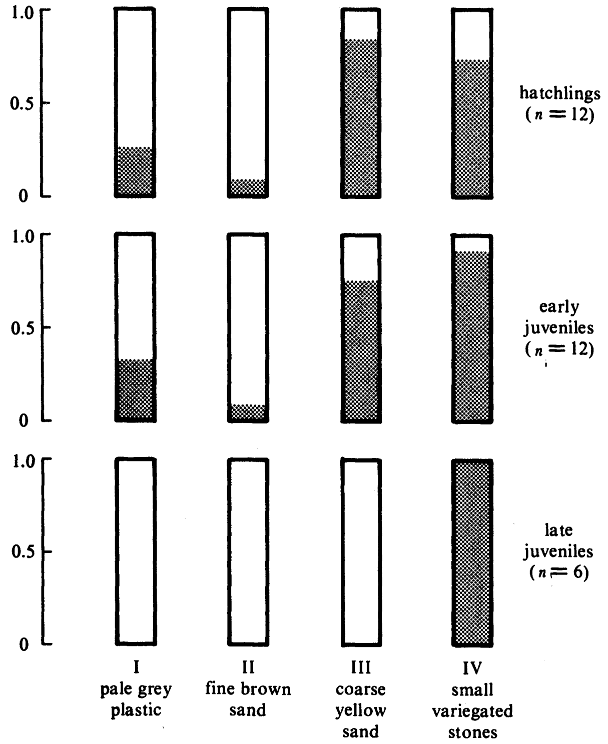


FIGURE 107. Proportion of animals showing Disruptive patterns on various backgrounds. See text (§5.2.1).

swam to the side of the dish and settled close to the wall (as they often do in opaque walled tanks); they also made occasional burying movements.

5.2.2. *Textural responses of cuttlefish on different substrates*

Attempts to correlate skin texture (smooth, coarse, papillate) with substrate roughness in the previous experiments (§5.2.1) were inconclusive. Although there was some evidence that coarse sand elicited coarse or papillate skin rather than smooth skin, more data (and a more careful system of measurement) are needed. In particular, the hypothesis that substrate texture could influence skin texture via tactile receptors in the skin need rigorous testing, for in the second experiments, in which we placed cuttlefish on varying substrates in glass dishes, the animals showed all grades of skin texture, and sometimes coarser textures were shown on substrates with large particles. This suggests that visual information alone could determine skin texture in young cuttlefish. Certainly it is apparent from observations in the laboratory and underwater (figures 11, 68, 90 and 97) that algae fronds elicit the most papillate appearance and it seems highly unlikely that this could be a tactile effect when the animals are swimming.

5.2.3. *Do cuttlefish match the bottom or the surroundings?*

In Banyuls, young cuttlefish of all three age groups were placed in a white tank with a light substrate (pale yellow sand) and in a dark tank with dark substrate (charcoal grains or black plastic). Each tank measured 35 cm × 19 cm × 22 cm deep.

As table 4*a* shows, the animals adjusted the luminance of their skin to match these uniform surrounds. Ninety percent of the 30 animals become pale in the uniformly pale tank; none was dark. Seventy-three percent of the 30 animals turned dark in the uniformly dark tank; none was pale. Thus the general luminance clearly exerts a strong influence on the luminance of the skin, as would be expected. For some reason young cuttlefish were much slower to settle in the all-black environment; they exhibited signs of stress and eight of the 24 young showed disruptive patterns.

To assess the relative importance of the substrate against the surrounds for luminance matching, we placed the same cuttlefish consecutively in white and black plastic tanks containing contrasting substrates: dark charcoal grains and very pale yellow sand, respectively (figures 80–83). The results (table 4*b*) show unequivocally that in this situation cuttlefish adjust their skin to match the luminance of the bottom, not the sides. Three times in the sea, young cuttlefish were observed to swim down and settle on a patch of sand surrounded by dark algae-covered rocks: each time they became a pale sandy colour.

Table 4. The influence of substrate on luminance of skin

(See plate 11 for example of (*b*).)

(*a*) Uniformly pale surrounds (bottom and sides) versus uniformly dark surrounds ($n = 30$).

		surrounds	
		pale	dark
animal	pale	27	0
	dark	0	22
	disruptive	3	8

Difference between scores not significant ($\chi^2 = 2.78$; d.f. = 1; $p < 0.05$).

(*b*) Contrasting surrounds: bottom versus sides ($n = 30$).

		surrounds	
		dark sides pale bottom	pale sides dark bottom
animal	pale	30	0
	dark	0	26
	other	0	4†

† Three hatchlings showed Disruptive; one early juvenile would not settle.

These experiments and observations suggest that cuttlefish are primarily concerned with matching the bottom substrate.

5.3. *Concealment in the natural environment*

For comparison with the laboratory substrate tests, a total of 11 hatchlings, 10 early juveniles and 5 late juveniles that had all been reared in the laboratory were taken underwater and released in July 1981 (by R.T.H.). Six more hatchlings were taken underwater in June 1985 for comparison. Their patterning was observed for more than 1 h each on various natural substrates. A total of 39 h underwater observation time was recorded. Wild, free-living cuttlefish of various ages and sizes (about 20 in total) were also observed during day and night dives between June and September 1981 and in June 1985 along the coastline near Banyuls.

There were no differences in the way animals reacted to different substrates in the laboratory and underwater. They were able to adapt to every substrate encountered (sand, algae and rocks) and underwater it was nearly impossible to find animals again if the observer glanced away even momentarily. Taking the *Sepia* underwater also gave us direct evidence that their concealment patterns were effective against fish as well as ourselves, because motionless cuttlefish were repeatedly overlooked by passing fish (including predatory fish: more than 40 observations) even when they were not buried in the substrate. It must be stressed that the photographs tend to highlight the cuttlefish because they frame the animal, and our artificial light from the flash created shadows that were not present under natural illumination.

More patterns were seen underwater simply because the substrates were far more diverse. The underwater photographs (e.g. plates 1, 6, 9, 10 and 14) clearly illustrate the wide range of patterns that young *Sepia* use to conceal themselves on natural substrates. We shall consider these in terms of the classifications of Cott (1940) and Hailman (1977).

'General colour resemblance' in the sea is illustrated in plate 14. The efficacy of patterning in these circumstances is remarkable. Not only are brightness and hue in accordance with surroundings, but the skin texture and posture blend in as well. The body patterns in figures 92, 93 and 95 are very light, but they are in harmony with other light objects on the substrate. The eye is always very well concealed, an important feature because this precludes rapid assessment of body orientation. In figure 95 observe how the first Paired mantle spots (component 21) coincide with the holes in the *Haliotis* shell. In figure 97 note that the cuttlefish has no obvious body form and closely resembles the substrate and dark algae seen nearby. Many other details may be extracted from the photographs.

'Deceptive resemblance', or concealing imitation (Hailman 1977), is a form of disguise in which the cuttlefish resembles another object in its environment and is thus of no interest to a predator. Young cuttlefish often use the Uniform Light, Stipple or Light Mottle patterns to resemble small stones (figures 88, 92 and 93) or algae (figures 90 and 91). Sometimes young cuttlefish use Flamboyant to resemble small bits of floating algae (figures 11 and 97).

'Obliterative shading', or countershading, is used by cuttlefish swimming in midwater. We consider this a chronic Uniform Light pattern and it is illustrated in figure 36, where the dorsal chromatophores are slightly expanded and the ventral chromatophores retracted to counter the shaded underbody. When viewed laterally by a human observer underwater, the young animals were extremely difficult to see from even one metre away; the brightness of the body appeared uniform from top to bottom and closely matched that of the water column. The iridophores of the ventral mantle contribute to its whiteness and undoubtedly aid in lightening this shadowed area during mid-water swimming.

'Disruptive coloration' is exhibited at its fullest in *Sepia*. Cuttlefish have a large arsenal of components to achieve it: five light (numbers 1, 2, 3, 13 and 14) and six dark (numbers 17, 18, 19, 22, 29 and 30). Figures 8, 12, 57–66 and 89 illustrate the effectiveness of disruptive patterns. The form of the animals is not evident in any of these photographs. Several of the optical principles of disruption mentioned by Cott (1940) are found in *Sepia*. The principle of differential blending, achieved by some chromatic components blending with the substrate whereas others contrast sharply with it, allows some body parts to stand out and others to fade away. Figures 61–65 show how the prominence of the head varies according to this principle. The dark components Mottle and Mantle margin scalloping (numbers 27 and 24) also help disruption in *Sepia*. The principle of maximum disruptive contrast operates when adjacent components of the pattern have great tonal contrast and thus provide greatest disruptive function; the bright White square (number 2), White head bar (number 13) and White major lateral papillae (number 12) surrounded by components of lower tonal contrast in figure 89 are a good example. The principle of adjacent contrast emphasises that a broken visual pattern made up of sudden transitions of colour, sharply contrasted passages of tone and of irregular shapes of all kinds results in an image of multiple objects rather than parts of one form; the maximum effect is when tones of greatest contrast occur adjacent to one another in a pattern and when their demarcation is most sharply defined. Figures 61, 65 and 89 illustrate this principle; note the juxtaposition of dark components around the White square and White head bar: thin and thick intensely dark lines, bars and stripes that run both transversely and longitudinally. Gradations of tone within individual components such as White square can also produce the visual illusion of relief, giving the impression that the square is elevated or depressed, making it seem even more separate from the body.

'Coincident disruptive coloration' has the function of joining together separate and easily identifiable parts of the body so that they are not recognizable to predators. *Sepia* conceals its eyes, for example, by connecting them optically with the dark Anterior head bar (component 29; figure 89); the W-shaped pupil and the chromatophores and iridescent cells on the eye further enhance concealment. The mantle and head are joined optically by (1) the natural curve of the anterior mantle, (2) the dark Anterior mantle bar (component 19) plus Posterior head bar (component 30; figure 56), (3) the general confluence of Black zebra bands (component 26; figure 26), (4) general colour resemblance (figures 55, 79 and 94), (5) complementarity of Major lateral papillae (component 40; figure 65), and (6) continuity between the lateral mantle margin and the fourth arms (figures 28 and 72) seen in such components as the Latero-ventral patches (number 28), Mantle margin scalloping (number 24) and White and Black zebra bands (numbers 9 and 26). Concealment of the contour is achieved with lateral papillae (figures 37 and 65), Mantle margin scalloping (component 24; figure 63) and White fin spots (component 5) together with Flanged fin (component 48; figures 55, 76 and 84). The Weak Zebra pattern (figures 25 and 26) is interesting because it radiates out from a central region of the mantle and cuts across the contour of the animal in much the same way as in zebras; this pattern is remarkably effective in concealing adult cuttlefish when they are amidst the common seagrass beds (Boycott 1958). The Intense Zebra, of course, has a signalling function (see §5.6).

'Concealment of the shadow' is achieved in *Sepia* by combinations of the Flattened body posture (component 47; figure 41), Flanged fin with White fin spots (figures 39, 48, 57, 60 and 84), the natural flange on the outside portion of the fourth arms (figures 12, 47, 55, 63 and 96) and by partial burying (figure 94). Finally, partial burying is most effective in effacing the contour.

5.4. *Reactions to disturbance in the laboratory*

Young *Sepia* in the laboratory react quickly to disturbances such as a large moving object near them (e.g. a hand, camera or net), a sudden movement or a light switched on at night. They show various combinations of all seven acute body patterns. The following components are most commonly associated with these responses: light components 2 and 3; dark components 21, 22, 25, 31, 32 and 33; textural component 37; postural components 41, 42, 43 and 47; and locomotor components 53 and 54. It is noteworthy that dark chromatic components and postures predominate in these responses; in particular, it is the longitudinally oriented dark components and the arm postures that are most frequently used and the responses are often expressed unilaterally on the side of the stimulus.

In hatchling *Sepia* there is a general sequence of acute patterns seen in response to a threatening object moved towards it. The first response of a sitting cuttlefish to a distant, moving object is to raise and darken the first pair of arms and become papillate (figure 43). This is a variation of the Flamboyant pattern and appears to function as 'flash behaviour' (table 2) (Edmunds 1974), which quickly changes the shape, posture and colour of the cuttlefish. An equally seen response is the Passing Cloud pattern (figure 69) that functions similarly. Upon further approach of the object, the *Sepia* shows a full Flamboyant pattern (figure 68), often with the unilateral expression of the Median mantle stripe (component 22) and Dark arm stripes (component 33) on the side of the stimulus. If the object approaches closely or suddenly the cuttlefish shows Uniform Blanching, then inks, jets away sometimes erratically (as in protean behaviour; Humphries & Driver (1967, 1971)) and shows Flamboyant or Uniform Darkening with Splayed arms (component 43). Hatchlings that are completely buried will, without moving themselves, occasionally puff a cloud of ink at a large object approaching too closely or swiftly.

Early and late juvenile cuttlefish show slightly different responses to disturbance. They may show the same general first responses as hatchling *Sepia*, but they are equally liable to show a partial Deimatic pattern (or one of its unilateral variations) in place of the Flamboyant pattern when the object approaches closely. Presumably the Deimatic pattern serves as a bluff to increase apparent size and alter the shape. The large third pair of spots (component 21) characteristic of the adult Deimatic pattern may also be shown by late juveniles: these may function as 'deflective marks' by appearing as false eye spots (table 2) (Cott 1940; Holmes 1940). On a few rare occasions juveniles were seen sitting on the substrate with the third pair of mantle spots merged with part of the Posterior mantle bar to form an image resembling a 'head-in-reverse' (figure 79); this may serve to misdirect a predator's attack (table 2). Upon close, sudden approach juveniles respond just like hatchlings (i.e. Uniform Blanching, Inking, Jetting, Flamboyant or Uniform Darkening) except that they tend to move quickly onto the substrate and show an Acute Disruptive pattern, which is another form of flash behaviour. Juveniles that are completely buried before any object approaches usually jet straight away from the buried position; they do not ink from the buried position but will sometimes ink during jetting.

The responses of adult cuttlefish to disturbance have been described by Holmes (1940). To a mild disturbance they may erect papillae, including the White major lateral papillae. To a strong stimulus, they show the full Deimatic pattern comprising Dark fin line, Eye ring, Paired mantle spots (3rd only) and a Flattened (pale) body (figure 71). We have never observed this full Deimatic pattern in hatchlings or early juveniles (table 8) either in the laboratory or underwater in the natural habitat, although Boycott (quoted in Thorpe 1963) reports having seen this on the seashore. According to Holmes (1940) they may, upon further approach, show four longitudinal stripes on the mantle (see page 455). They may also jet about erratically and then ink profusely (see also Boycott 1958).

5.5. *Reactions to predatory fishes in the natural environment*

Thirty-two young *Sepia* (the same as in §5.3) were taken underwater in plastic bags and released onto a sand plain (10 m in diameter and 5 m below the surface) surrounded by seagrass beds and large rocks, a site typical of the Banyuls coastline. The hunting territories of two *Serranus cabrilla* (Teleostei: Serranidae) approximately 14 and 20 cm standard length overlapped on this particular sand plain so that the cuttlefish encountered one of the foraging fish within periods ranging from 5 min to 1 h after release. Many other fish inhabited this sand plain but all were either herbivorous or not primary predators of *Sepia*. Several were as large as *Serranus cabrilla*.

A typical sequence of events from release to attack by *Serranus* was as follows. The *Sepia* swam to the substrate and first showed a Light Mottle concealment pattern (figure 92). It sometimes fed on mysids. Within minutes the abundant and long, thin labrid fish *Coris coris* would inspect the cuttlefish. This was the first fish the laboratory-reared *Sepia* had ever seen and almost invariably animals of all age groups would assume a Flattened body posture and then display the incomplete Deimatic pattern (see §6.1) at varying intensities. The *Sepia* would do this during its first few encounters with *Coris* as well as with other fishes (e.g. figure 73) except *Serranus cabrilla*, but thereafter the cuttlefish would not show special reaction to these fishes unless they came extremely close in a head-down attack posture. The Passing Cloud pattern was occasionally shown to closely approaching fishes other than *S. cabrilla*. If the cuttlefish was startled by sudded movement by a nearby fish or other object, it oriented towards the stimulus and showed Uniform Blanching with Splayed arms (component 43) for a few moments before returning to its original pattern and posture. When young cuttlefish were moving they frequently showed Passing Cloud, especially just when they settled on the substrate as well as before and after feeding on small mysids.

Serranus cabrilla detected young *Sepia* only as a result of movement (e.g. swimming or burying). Cuttlefish that were buried or sitting motionless in a normal concealment pattern were not detected, even when the fish swam directly over them (more than 40 observations). When *S. cabrilla* detected the cuttlefish and moved directly towards it in an attack posture, the cuttlefish responded at distances of up to 3 m, even when other fishes were nearer. Hatchlings and early juvenile cuttlefish did not show any kind of Deimatic pattern to *S. cabrilla* and typically responded in the following sequence. First they oriented directly towards the fish and displayed a dark Flamboyant pattern (flash behaviour) with maximally expanded papillae (component 37). Some hatchlings, however, showed Uniform Blanching plus Raised arms (figure 43). Late juveniles (33–45 mm ML) began to show a Deimatic pattern to *S. cabrilla* (see §6.1.2) although dark Flamboyant was also used. Upon the forward rush of the attacking fish, the young *Sepia* instantly changed to Uniform Blanching, inked and jetted 1 to 2 m backwards (figure 49); this form of diversion behaviour (table 2) (Edmunds 1974) left the fish with a mouthful of ink and its vision obscured. The cuttlefish then either resumed the dark Flamboyant pattern (presumably a disguise to resemble algae) or continued swimming upwards to the surface (table 5).

Serranus never pursued the *Sepia* more than 1 m above the substrate, nor was any second attack ever performed. Most of the successful attacks by *Serranus* occurred when the cuttlefish appeared to have been distracted by the observer. On two occasions a *Sepia* was partly caught in the jaws of the fish but escaped. Excluding captures in which the observer had obviously distracted the young *Sepia*, the cuttlefish were successful in avoiding capture 29 out of 36 times (table 6). Full details of these field observations will be the subject of a future publication.

5.6. *Intraspecific behaviour*

The use of body patterning in sexual and agonistic behaviour in adult *Sepia officinalis* is well documented (Grimpe 1926; Bott 1938; L. Tinbergen 1939; Boycott 1958; Zahn 1979*c*). Although we have little to add to these descriptions it is appropriate to summarize this work in the present context.

Adult males, in the presence of other cuttlefish or a mirror (J. B. Messenger, unpublished results), show the acute pattern Intense Zebra (figure 72). This comprises chromatic components 5, 6, 9 (on the fourth arm as well as on the mantle), 16, 26, 31 and 32; textural

Table 5. Responses of cuttlefish to attacks by the predatory fish *Serranus cabrilla*

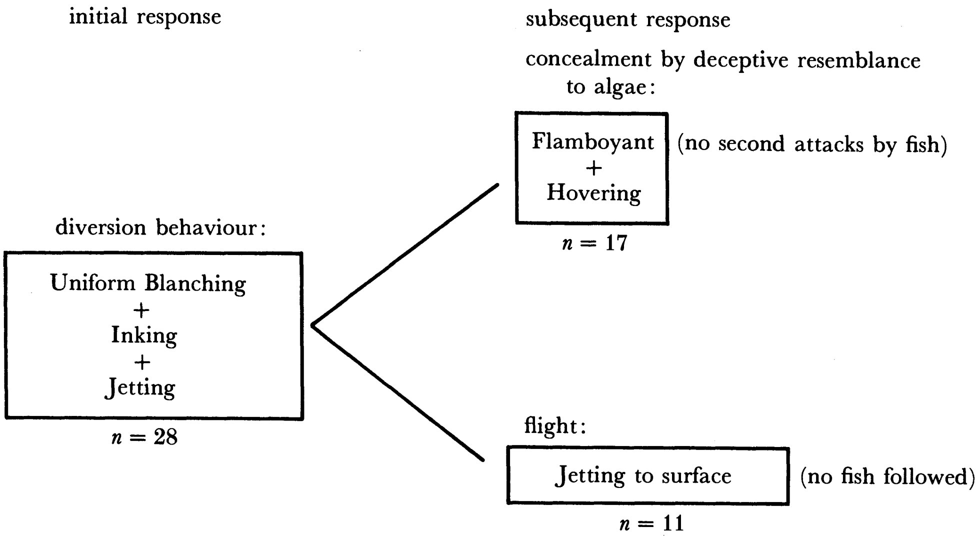


Table 6. Effectiveness of escape from fish attacks

	cuttlefish released	attacks made	successful attacks
1 week old	17	18	6 (33%)
7 weeks old	10	14	1 (17%)
17 weeks old	5	4	0
totals	32	36	7 (19%)

component 35; postural component 45; and locomotor component 52. The Extended fourth arm (component 45) is especially characteristic, but the essence of this pattern is low frequency, black and white contrast, not only along the fourth arm and the sides of the mantle but also along the fin, where the spots and line are maximally enhanced (figure 9). It may be significant that this intraspecific signal is intensity-modulated because *Sepia*, like other cephalopods, may be colour-blind (Messenger 1981).

A male cuttlefish displayed to in this way will show the same pattern, often turning parallel with the first male, and the pair may circle for many minutes, each head-to-tail with the other in this agonistic display. Male cuttlefish separated from one another by glass will behave in exactly the same way. A female cuttlefish, although she may be showing the Weak Zebra pattern on the mantle, rarely intensifies this when displayed to; but she may extend the fourth arm to the male although this lacks leucophores and never bears White and Black zebra bands (components 9 and 26) or White arm spots (component 16). It is the absence of this body pattern that signals 'female-ness' to the male, and unless the female swims away she will be grasped by the male and copulation with ensue. A unilaterally blinded male *Sepia* will show the Intense Zebra to a male that approaches on his seeing side and an agonistic display will ensue, but if approached on the blind side he will not show Intense Zebra and attempted copulation will ensue, with subsequent fighting and inking (Messenger 1970). During copulation the male may maintain the Intense Zebra pattern for many minutes, intensifying it if another male approaches.

Young cuttlefish, up to an age of about 4 months, show no kind of visual intraspecific communication. Mature females when placed together in a confined space generally sit motionless, often close together, showing one of the chronic patterns. Brief anti-parallel displays between females have been observed but never with the Intense Zebra pattern, and although the fourth arm is extended towards the other animal it is unpatterned.

6. DEVELOPMENT AND CONTROL OF PATTERNING AND BEHAVIOUR

6.1. *Changes in patterning and behaviour from hatching to adult*

6.1.1. *Morphological changes*

Of the three chromatic elements contributing to patterning, leucophores are absent at hatching, iridophores are few and sparsely distributed, whereas chromatophores are numerous. The chromatophores are small and densely packed, and although no specific measurements were made, their colours appear to be similar to those of the adult. Their morphological arrangement is probably the same as in the adult and the only gross difference we have observed between the chromatophores of a hatchling and an adult *Sepia* is in the density of packing. This is far greater in the young animal and although new chromatophores arise during growth their density declines dramatically with age (§4.1.1).

Despite these density differences, the size that individual chromatophores attain is roughly equal in hatchlings and adults. One result of this is that nearly all chromatic components, but especially dark ones such as Paired mantle spots, are less well-defined in hatchlings because the individual chromatophores are relatively large compared to the size of the component and the size of the animal. During the first few months of growth, as new chromatophores are 'recruited' into each dark component, the component becomes more distinct and well-defined. Close inspection of the plates will reveal many examples of this.

The chromatophores of young *Sepia* are not only numerous: they are already organized neurally so that they can participate in a large number of components, which can in turn contribute to complex patterns. Table 7 demonstrates that hatchlings and young *Sepia officinalis* are comparable to adults in their ability to produce complex patterns: 64 % of components and 69 % of patterns are seen throughout the young and adult stages, with little noticeable difference in their form or degree of expression.

TABLE 7. COMPONENTS AND PATTERNS USED BY CUTTLEFISH THROUGHOUT THE LIFE CYCLE

chromatic components			patterns
light:	8 out of 16	chronic:	5 out of 6
dark:	12 out of 18	acute:	4 out of 7
textural components	4 out of 6		
postural and locomotor components	11 out of 14		
total:	35 out of 54 (64 %)	total:	9 out of 13 (69 %)

Table 8 lists separately those components and patterns that are shown in different form or expression at different stages of the life cycle. It is noteworthy that relatively few of the 19

Table 8. Development of patterning in *Sepia officinalis* L.

(Only those components and patterns that are not present throughout the life cycle are listed (except 3rd pair of mantle spots for comparison). Numbers of components and patterns correspond to table 1.)

	hatchling 1–3 weeks (7–10 mm ML)	early juvenile 4–10 weeks (16–20 mm ML)	late juvenile 11–20 weeks (35–45 mm ML)	adult
components				
chromatic				
light:				
White neck spots (7)	———	———	——— – – –	
White posterior triangle (1)	———	———	———	– – –
Iridescent ventral mantle (8)	– – –	– – –	– – –	———
White lateral stripe (4)		———	?	
White fin spots (5)		———	———	———
White zebra bands (9)				———
White fin line (6)				———
White arm spots (16)				———
dark:				
Paired mantle spots (21)				
3rd pair	———	———	———	———
1st pair	———	———	———	– – –
2nd pair	———	– – –	– – –	– – –
4th pair	———	– – –	– – –	– – –
Mantle margin scalloping (24)	———	———	———	– – –
Pupil (31)	– – –	———	———	———
Eye ring (32)		———	———	———
Dark fin line (25)			– – – ———	———
Black zebra bands (26)				———
textural				
Wrinkled first arms (38)	———	– – –		
Major lateral papillae (40)	———	———	———	– – –
postural and locomotor				
Bottom suction (50)	———	———	– – –	
Splayed arms (43)	? – –	———	———	———
Extended fourth arm (45)				———
body patterns				
chronic:				
Weak Zebra (6)				———
acute:				
Flamboyant (10)	———	———	———	?
Deimatic (11)	– – –	– – –	– – – ———	———
Intense Zebra (males only) (12)				———

———, Presence of the component or pattern in its full, normal expression.

– – – –, Presence in an altered or less-complete expression.

?, Lack of information.

components and 4 patterns in this table are actually absent or strikingly different in form or expression between young *Sepia* or adults. More commonly there occurs a gradation in the emphasis with which a component or pattern is expressed through time, either during its development or extinction. In some cases this is due to the changing densities of chromatophores in the skin (§4.1.1). Some examples follow.

First, components and patterns that are conspicuous at hatching and then gradually disappear. The White neck spots (number 7), the second and fourth pairs of Paired mantle spots (number 21), Mantle margin scalloping (number 24), Major lateral papillae (number 40), Wrinkled first arms (number 38) and Bottom suction (number 50) are used for concealment by hatchlings. The first three are chromatic components that merge into the Mottle component as the cuttlefish grow. The Paired mantle spots (pairs 2 and 4) and the papillae can be seen in the adult but are seldom distinct. Wrinkled first arms fill out with growth and lose their transverse grooves, and Bottom suction becomes unnecessary in large animals that weigh more, have better buoyancy control and are less affected by water surge. White posterior triangle (number 1) is strongly expressed in all three young stages. We have not seen it in adults but Holmes (1940) refers to it.

The Paired mantle spots (number 21) deserve separate comment. In hatchlings all four pairs are common (figure 65), usually expressed two pairs at a time (especially the common 4-spot appearance of pairs 1 and 3 together), whereas in late juveniles and adults usually only a single pair (especially pair 3) is expressed. Pair 1 is conspicuous and common in younger stages (figure 89) but not in adults. Pair 2 is relatively inconspicuous throughout the life cycle. Pair 3 is highly conspicuous and common throughout life and it is this that forms the major component of the well-known adult Deimatic pattern (figure 71) (see also Cott 1940; Packard 1972; Messenger & Miyan 1986). Pair 4 is usually inconspicuous and is most common in hatchlings one to two weeks old. All these spots may be expressed unilaterally throughout the life cycle.

Second, components and patterns absent or barely evident at hatching but conspicuous in late juvenile or adult stages. Iridescent ventral mantle (number 8) is present at hatching but only as small indistinct patches of pink or green, whereas in adults it is expressed as a striking bright green over the entire ventral mantle (figure 10). White lateral stripe (number 4), which contributes to Disruptive patterns, has been documented only during the juvenile stages, but it is possible, and even likely, that it occurs both in younger and older animals. White fin spots (number 5) definitely do not appear before about 20 weeks and 37 mm ML (i.e. the leucophores are not present morphologically); similarly, White fin line (number 6) first appeared at 85 mm ML and White zebra bands (number 9) on the mantle and on the Extended fourth arm (number 45) at 72 mm ML. In males especially, the leucophores must develop considerably with the onset of sexual maturity, but mature females also develop the components 5 and 6. The component Black zebra bands (number 26) was first recorded in a late juvenile male *Sepia* 26 weeks old and of 75 mm ML. The dark chromatic components Pupil (dilated form; number 31), Eye ring (number 32) and Dark fin line (number 25) are constituents of the Deimatic pattern and none of these appears until the early juvenile stage. The Deimatic pattern gradually becomes simpler and more boldly expressed by the late juvenile stage. Before this only one or two of its components are expressed, or at the same time other dark components like Mottle (number 27) or Dark arm stripes (number 33) are expressed weakly (figure 70), thus diminishing the high contrast between the dark components and white background of the mantle that are so characteristic of the fullest expression of the Deimatic pattern.

6.1.2. *Behavioural changes*

Several changes in behaviour deserve special mention. The most obvious is that hatchlings and juveniles are almost wholly concerned with concealment and predator evasion (i.e.

interspecific interactions) whereas adults may be also concerned with courtship (i.e. intraspecific interactions). Table 9 shows how juveniles and adults use specific components and patterns for each of these classes of behavioural interactions; juveniles use more concealment components than adults, and adults use more 'display' or 'advertisement' components (in the terminology of Cott (1940)).

For concealment, three changes are noteworthy. The first is the change of chromatic behaviour with age on coarse yellow sand (substrate 3 in our experiments, §5.2.1). The chronic Disruptive patterns shown by young animals disappear in late juveniles to be replaced with such cryptic patterns as Light or Dark Mottle. As table 10 shows, the change from Disruptive patterns to Mottle involves a reduction from four to one bold white component and an increase in the dark mottle components. The explanation of this change in tactics lies, we believe, in the actual physical size of the chromatic components in smaller cuttlefish. Reference to figures 84–87 should make this point clearer. The composite photograph (figure 84) shows a background of coarse sand on which can be seen a late juvenile (centre), early juvenile (right) and a hatchling (left). All are fairly inconspicuous, but close inspection reveals that the largest animal is showing a Light Mottle, the next a weak Disruptive and the smallest a strong Disruptive pattern. This can be seen more clearly in figures 85–87 where the photographs are printed at such magnification that the mantle lengths of the animals are roughly equal. Inspection of plate 12 will reveal that the dimensions of some of the light and dark components in the hatchling are close to those of the sand grains, so that the Disruptive pattern is

TABLE 9. COMPONENTS AND PATTERNS USED EXCLUSIVELY BY JUVENILE OR EXCLUSIVELY BY ADULT CUTTLEFISH FOR DIFFERENT CATEGORIES OF BEHAVIOUR

	juveniles (< 50 mm ML)	adults (> 50 mm ML)
concealment:		
components	11	8
intraspecific:		
components	0	7
patterns	0	1

TABLE 10. CONCEALMENT STRATEGIES OF DIFFERENTLY SIZED CUTTLEFISH ON THE SAME SUBSTRATE

(See plate 12.)

1 week (10 mm ML) $n = 12$	7 weeks (20 mm ML) $n = 12$	17 weeks (35 mm ML) $n = 6$
strong Disruptive pattern	weak Disruptive pattern	Light Mottle pattern
components:	components:	components:
White square†	White square†	White fin spots†
White head bar†	White head bar†	Flanged fin
White arm triangle†	White arm triangle†	Mottle
White posterior triangle†	Mottle	Paired mantle spots
Median mantle stripe	Paired mantle spots	
Dark arm stripes		

† Reduction in bold white components.

appropriate; the dimensions of the late juvenile are already such that these components, were they expressed, would far exceed the grains in size and thus render the animal conspicuous. This illustrates a most important feature of concealment strategy in this species: *the most effective means of concealment on a given background is related to the size of the cuttlefish*. The coarse sand substrate on which this change was observed is the commonest one in the sea near Banyuls, and there is an obvious adaptive advantage for the growing animal to make this important adjustment for concealment as its size increases.

The second change is when young adults (approximately 75 mm ML) begin to show chronic Weak Zebra for concealment in addition to Mottle patterns. Figures 20–23 illustrate a single cuttlefish implementing this change, and figure 26 gives an impression of how the pattern provides concealment. Not until this size, apparently, do the animals have the morphological equipment (full complement of leucophores) and physiological development (motor units for dark chromatophore bands) to produce the components White and Black zebra bands (numbers 9 and 26).

A third important change is that late juveniles are better able to match diverse substrates compared with hatchlings and early juveniles (figure 107); indeed, in these experiments the youngest animals occasionally showed inappropriate (Disruptive) patterns that rendered them conspicuous on uniform substrates such as pale grey plastic and fine brown sand.

Accompanying these concealment 'patterns' are appropriate concealment 'behaviours'. Nearly all the concealment patterns illustrated in this paper were being displayed when the young cuttlefish were either Sitting (locomotor component 49), showing Bottom suction (component 50) or lying Buried (component 51) and hatchlings and juveniles spend far more time motionless than adults.

By contrast, older animals are often found swimming in the water column (Hovering: locomotor component 52). This is because they are less vulnerable to attack (see Discussion) and also because they engage in courtship while Hovering (Intense Zebra pattern: number 12). One pattern shown by hatchlings, although not by older animals, in mid-water is Flamboyant (number 10): this may be for concealment ('deceptive colour resemblance' in table 2) with the textural, postural and locomotor components and the behaviour all contributing to make a small cuttlefish look like a piece of floating alga.

Changes in concealment behaviours (primary defence) with age are not as marked as changes in secondary defence behaviours. For example, once a cuttlefish has been detected by a predator it may resort to escape by rapid backward jetting, but adults tend to follow a direct pathway ('flight' in table 2) whereas young animals move erratically ('protean behaviour' in table 2), presumably because they cannot achieve such high speeds as adults (see Discussion).

Inking is another form of secondary defence, but in aquaria adults are more likely to emit their ink as a dense cloud, obliterating visibility in all directions for more than a metre, whereas hatchlings and juveniles usually eject small discrete blobs of ink-plus-mucus that stand in the water and attract the predator's attention to a false cuttlefish while the real cuttlefish escapes. Of course adults can also eject blobs of ink: for a fuller description of inking behaviour see Boycott (1958).

The response to predators that changes most is the Deimatic pattern. This familiar, well-documented pattern (Holmes 1940; Packard 1972; Messenger & Miyan 1986) is shown in its complete form (figure 71) only by older animals. Hatchlings do not show the Deimatic response at all and juveniles show a weak form of it to approaching fish, even if they are not predatory.

This comprises two or even three pairs of mantle spots (component 21) but the body does not completely flatten (component 47) nor does the mantle become pale all over. Only in the adult is the pattern expressed at its boldest and simplest, with just the third pair of mantle spots being shown (see Discussion).

Most interesting of all are the field observations that hatchlings first encountering *Serranus* show the Flamboyant or Uniform Blanching patterns rather than the Deimatic pattern. These kinds of 'flash' behaviours (Edmunds 1974) are presumably utilized because of the ineffectiveness of the Deimatic pattern in such small animals (see Discussion).

In summary, young *Sepia* (up to 20 weeks) generally show a slightly greater diversity in patterning than adults mainly because of their need for concealment. The important point is that the chromatic potential of young *Sepia* is extremely well-developed at hatching, and the animal can show a wide range of complex patterns such as Flamboyant, Passing Cloud and Disruptive.

6.2. *The neural control of patterning and its development*

Patterning in cephalopods is controlled hierarchically by four pairs of lobes in the brain: the optic, lateral basal, anterior chromatophore and posterior chromatophore lobes (Boycott 1953, 1961; see also Boycott & Young 1950; Young 1971; Chichery & Chanelet 1976). The available data, anatomical and physiological, suggest that the principal neural control pathway is:

eye → optic lobe → lateral basal lobe → chromatophore lobes → skin,

although, of course, this pathway is open to other influences.

The importance of vision in the life of cephalopods is well known but we report here two new experiments that demonstrate its role in the control of patterning in young *Sepia*. In the first (reported in §5.2) we showed that cuttlefish produce the appropriate concealment pattern with a glass dish between them and the environment, eliminating the possibility of tactile feedback. In the second, we unilaterally or bilaterally blinded some *Sepia* early in embryonic development (stages 13–18 according to Naef (1928)). Animals so treated hatched normally 2–3 weeks later. The four unilaterally blinded animals behaved like normal hatchlings; they had the full complement of patterns and employed then for concealment in a way appropriate to all four substrates (§5.2.1). Four bilaterally blinded animals survived long enough to be tested on a variety of substrates: they were then the equivalent of hatchlings in age (i.e. 1–2 weeks). They were extremely difficult to feed and spent an unusual amount of time swimming. The chromatophores functioned, and at least some of the chromatic components were expressed: paired mantle spots, transverse mantle lines and bars, Mottle or Uniform Darkening were also shown to mechanical stimuli (such as tapping the tank or blowing on the water) and, interestingly, to bright light or a discharge from an electronic flash. The patterns were usually quite inappropriate to the background. Thus figure 106 shows an animal exhibiting a mottle on small variegated stones, although such stones never elicit such a response from normal animals (table 3). When the animals were tested on the series of different substrates they showed no chromatic change whatever as they passed from substrate to substrate. This blinding experiment shows that the neural machinery for generating patterns can function in the absence of visual input, although the patterns will be inappropriate.

The optic lobes contain the sets of cells ultimately responsible for each motor program (i.e.

each body pattern) and the lateral basal lobes somehow help execute these programs. Cursory inspection of these lobes in sections of young and adult *Sepia* brains revealed no gross differences during ontogeny. The final motorneurons innervating the chromatophores lie in the chromatophore lobes, and we therefore examined these lobes in more detail in young and adult cuttlefish and compared them with those in *Octopus vulgaris* (tables 11–13).

The chromatophore lobes of adult *Sepia* are like those of adult *Octopus*: they are more or less spherical projections on the laterodorsal surface of the suboesophageal brain. Around the central neuropil is the cell layer: this has cells of different sizes, the small cells lying next to the neuropil, the large ones lying peripherally. These cells are organized into columns, groups of which are separated by canals, intruding from the neuropil and carrying afferents. This highly characteristic arrangement is also present in the chromatophore lobes of hatchling *Sepia* and, at the level of the light microscope using silver or trichrome stains, their gross appearance is identical to those in the adult brain.

TABLE 11. CELL DIAMETERS IN POSTERIOR CHROMATOPHORE LOBE

			mean diameter/μm			
age/days	ML/mm	*n*	smallest cells	*n*	largest cells	*n*
7	8.00	1	9.9	20	18.3	20
112	31.00	1	12.3	20	26.9	20

TABLE 12. SIZE OF CELL LAYER IN POSTERIOR CHROMATOPHORE LOBE

age/days	ML/mm	*n*	area of cell layer/μm^2	area of whole lobe†/μm^2	ratio
7	8.00	1	54884	126904	0.43
112	31.00	1	178277	365555	0.49

† At maximum diameter of posterior chromatophore lobes (PCL).

TABLE 13. RELATIVE SIZE OF POSTERIOR CHROMATOPHORE LOBE DURING GROWTH

age/days	7	14	28	56	112
ML/mm	8	9	11.5	19	31
n	2	2	2	2	2
ratio of PCL to total suboesophageal mass	0.09	0.075	0.13	0.07	0.07

TABLE 14. NUMBERS OF CHROMATOPHORES AND THEIR NEURONS

age	ML/mm	total mantle chromatophores	cells in PCL†	ratio
hatchling	7	12000	12000	1.00
adult	200	2000000	78000	0.04

† Bilateral.

Measurement of cell size in the posterior chromatophore lobe show that in hatchlings the cells are considerably smaller (table 11). Measurements of the total area of the lobe and the area of the cell layer suggest that the ratio of the cells to neuropil is roughly the same in a hatchling and an adult (table 12). And finally, measurements of posterior chromatophore lobe size relative to the entire suboesophageal brain in a series of cuttlefish fixed at known times after hatching show that the proportions of the brain devoted to controlling the mantle chromatophores and skin remains almost identical over 4 months (table 13). In two individuals we made estimates of cell numbers, based upon counts made on photographs of sections, corrected by the method of Abercrombie (1946; see also Young 1963). In a hatchling aged 7 days there were about 6000 cells in each posterior chromatophore lobe; in an adult there were about 39000 cells (table 14). Despite the great increase in numbers of chromatophore neurons with growth, the ratio of neurons to mantle chromatophores decreased markedly, agreeing with our photographic data that hatchlings are capable of very sophisticated patterning.

All this contrasts strongly with the situation in *Octopus vulgaris*. Examination of sections through the brain of newly hatched 'larvae', which have only 70 chromatophores *in toto* (Packard & Sanders 1969) and cannot produce any kind of patterning, reveals no trace of chromatophore lobes in the suboesophageal brain (see Discussion).

7. Discussion

7.1. *The morphological and neural bases of patterning*

The morphology of the skin and the repertoire of patterning and behaviour demonstrate that *Sepia officinalis* is among the most richly endowed of cephalopods. However, quantitative data are required before the analysis of patterning and its maturation can proceed further, and we hope future workers will extend these preliminary descriptions accordingly.

An important finding in this work is that hatchling cuttlefish are equipped morphologically (both in the skin and neuroanatomically) to produce body patterns and behaviour that, in general, are as complex as those of the adult. The well-developed ability of young cuttlefish to fixate and capture prey has been known for some time (Wells 1958, 1962; Messenger 1968, 1977*a*) time but hitherto it has not been realized how diverse, complex and adaptive are the body patterns and associated behaviour of young animals.

To describe patterning in *Sepia* we have followed the hierarchical classification of Packard and his associates (1969, 1971, 1977); it is ideally suited for comparative studies (§7.5) for several reasons but principally because of its consistent and functional terminology. However, we have not found it useful to name morphological units in *Sepia* because they are so inconspicuous, compared with those of *Octopus*, that we do not believe it would serve any useful purpose.

Any classification is open to criticism and ours is no exception so that it is necessary, especially for workers coming new to this or other cephalopods, to list some of its more obvious limitations. The quality of light reflected from a particular patch of skin can be varied almost infinitely because there are three independent colour classes of chromatophore and the degree of expansion of individual chromatophores can be varied considerably so that they can even overlap. Also, the chromatophores are controlled neurally, not hormonally, so that different numbers of physiological units can be recruited to form a particular component with varying size and intensity. For example, Posterior transverse mantle line (component 18) may be expressed as a thin line (low intensity) or a thicker line (higher intensity). Finally, there is the problem that any classification of patterns embodies the limitations of perceptual mechanisms in the human visual system (Casey & Nagy 1971).

We can only claim that we have studied many individuals that have been exposed to a wide range of backgrounds and situations in the laboratory and in their natural habitat, and we have described only those patterns that are expressed frequently and can usually be associated with a particular type of behaviour. Although in our analysis we consistently tried to restrict the number of patterns and components, we were forced to recognize 13 basic body patterns in *Sepia officinalis*, based upon no fewer than 54 components. This large number is, of course, directly related to its behaviour and ecology (table 16); body patterns are categorized as chronic or acute, and there are behavioural correlates to this scheme (§7.2).

Chronic patterns are used for concealment and may be highly diverse depending upon the substrate (plates 7, 8 and 14). Our somewhat arbitrary choices of names for the chronic patterns (from uniform through stipples, mottles and disruptives) were derived from the photographs and were meant to draw attention to general features of the patterns and not to specific details. It is evident that hatchling cuttlefish need only visual input from the substrate, and not experience, to produce the correct body pattern for concealment. It is also apparent from our substrate tests that young cuttlefish do slightly improve their match of the substrate with age, but we know nothing about the basis for this 'fine tuning'. Although the 'correct' general category of pattern (e.g. Mottle) is always shown on the appropriate natural substrate, there are variations in the patterns (especially in intensity). Given the great diversity of natural substrates, it is not surprising that the chronic patterns for concealment are not totally 'fixed' in their appearance, but are adaptable to a range of substrates. Considering the high mobility of cuttlefish as well as the wide distribution of *Sepia officinalis* (Boletzky 1983) one might expect concealment patterns to be somewhat 'plastic' and even for clinal variations to occur.

Conversely, the acute patterns and their components are more discrete and stereotyped. Indeed, Deimatic and Intense Zebra are so discrete that they may ultimately be useful in providing some clues as to how the nervous system that controls the chromatophores is organized. Boycott (1953, 1961), Maynard (1967) and Packard & Hochberg (1977) have all provided potential schemes for the innervation of the chromatophores, and Messenger & Miyan (1986) have now shown that one component of the adult Deimatic pattern (i.e. one of the third Paired mantle spots: component 22) can be elicited by direct electrical stimulation in the ipsilateral posterior chromatophore lobe. It is also possible to produce this spot by stimulating the appropriate nerve bundle in the mantle, emphasizing that the nerves in the skin are organized precisely with regard to parts of chromatic components (see Maynard 1967; Packard 1974). This is illustrated in the present work for the White fin spots (figures 18 and 19). Their 'whiteness' depends not just upon the leucophores they contain but also upon their being uncovered (as a result of retraction of the overlying chromatophores) and on their being surrounded by dark areas. A motor unit responsible for darkening the surrounds of several white spots is being stimulated in figure 18 and a separate unit, for darkening the centres of a group of white spots, is being stimulated in figure 19. These motor fields are contiguous with little or no overlap, but what complicates any analysis of the neural correlates of patterning is that many chromatophores receive multiple innervation so that any one chromatophore can participate in two or more different components (Maynard 1967; Florey 1969). This is illustrated in figure 25 and it can also be shown by lesion and degeneration experiments (figures 98–103).

It is relatively simple to denervate the mantle chromatophores unilaterally in a young cuttlefish by cutting or crushing a pallial nerve. Such an operation causes loss of tone and retraction of the chromatophores on the ipsilateral mantle so that the lesioned side appears pale or shows marked deficits in patterning (figures 100–103). After some days the isolated chromatophores become hyperexcitable and dark waves of chromatic activity pass across the denervated skin. After weeks or months, however, this spontaneous activity decreases as the lesioned chromatophores come under the influence of the CNS once more, and parts of the pattern or even the whole pattern become restored (see also Sanders & Young 1974). Figures 98 and 99 show the result of one particular experiment and are of interest in showing not only that the chromatophores receive multiple innervation, but that in this experiment those on the right side of the mantle were only partly re-innervated at the time the photographs were taken. Thus although the cuttlefish shows a perfect Stipple, its Disruptive pattern is defective: components 3, 17, 18 and 19 are all poorly expressed or absent on the lesioned side while, most unusually, only a part of component 22 is expressed on that side, flanking the White square.

It is inappropriate here to comment further on the neural basis of patterning in *Sepia* but it is worth drawing attention to possible parallels between the hierarchical chromatophore control system demonstrated by Boycott (1953, 1961), the hierarchical body patterning model developed by Packard and more general theories for the organization of behaviour developed by such ethologists as Lorenz (1950), N. Tinbergen (1950), Hinde (1953), Barlow (1968, 1977) and Nelson (1973), all of whom consider behavioural output to be organized hierarchically. In particular, more data are needed before we shall know how profitable it may be to analyse a body pattern as a Modal Action Pattern and a chromatic component of the pattern as one of its 'acts' (Stokes 1960; Barlow 1977).

7.2. *The function of patterning: behaviour and ecology*

All our observations as well as the published literature indicate that *Sepia officinalis* is generally a solitary animal until sexual maturity, at which time courtship and reproduction occur. Although adult males develop sexual displays, for the majority of the life cycle *Sepia* is concerned with predator evasion and prey capture and most of those patterns are directed towards these ends; our study concentrated most upon predator evasion and did not address adaptive coloration relative to prey.

A summary of what we term 'visual antipredatory adaptations' is given in table 2. The available evidence suggests that all chronic patterns are shown by stationary animals and are used for concealment, which we term primary defence (Edmunds 1974). Animals that are moving or are in the water column use acute patterns for threat or misdirection: these, which we term secondary or tertiary defences, are shown once the cuttlefish has been detected by the predator. The primary defence of concealment was remarkably effective (see also next section) as was borne out by our field observations with natural predators, the first of their kind with *Sepia*. Among the secondary defences, it was surprising that the youngest *Sepia* did not show the early form of the Deimatic pattern to the predator *Serranus cabrilla*, but only to other non-predatory fishes that approached very closely. Passing Cloud seems mainly a pattern for distracting prey and to be used while moving in the open. The dark Flamboyant pattern was shown to *S. cabrilla* by all three size groups of young *Sepia*, but it was not clear if the pattern was functioning as deceptive resemblance (to algae) or as flash behaviour. Nevertheless, ensuing attacks were evaded effectively (81%) by the diversive technique of Uniform Blanching plus Inking plus Jetting. Several cuttlefish avoided attack after detection by moving with the surge of waves, then intermittently attaching to the bottom, thus resembling other bottom debris moving with the surge. The tertiary defences of deflective marks and protean display were not observed in underwater observations. Finally, it appeared as though predator recognition (Hirsch & Bolles 1980) might not require learning, for young *Sepia* were well-equipped to detect and react at least to *S. cabrilla* in a systematic, efficient manner.

The diversity of colour change, patterning and accompanying behaviour in *Sepia officinalis* allows for a wide range of visual antipredator responses. One function of this diversity may be to prevent predators from building up a 'perceptual set' or 'search image' (Uexküll & Kriszat 1934; L. Tinbergen 1960; Hailman 1977; Krebs 1978). Future work on other predators of *Sepia* must be done before clearer conclusions can be formulated. In Banyuls *Serranus cabrilla* is a major nearshore predator on small *Sepia*, but other fishes (as well as other cephalopods) prey on juvenile cuttlefish and adaptive responses to these predators may be different. One reason for the high quality of camouflage in *Sepia* is its benthic habit, and our experiments showing that young animals match the bottom, not the sides, of their environment (§5.2.3) are important in this context. It is no coincidence that flatfish (Pleuronectidae) have the most elaborate colour change mechanisms of teleosts and can also show patterning (Cunningham & MacMunn 1893; Mast 1914; Burton 1981).

7.3. *Adaptive coloration in action*

In studying the patterning of young cuttlefish and its significance we have referred repeatedly to Cott's (1940) classic book and in §5.3 we described how *Sepia* uses many of the techniques employed by vertebrates and insects to escape detection. General colour resemblance (which includes brightness matching), obliterative shading and disruptive coloration are all used by cuttlefish to conceal their colour, relief, contour and shadow (see plate 14).

General colour resemblance in *Sepia* is brought about by a combination of chromatophores, iridophores and leucophores: its chromatophore pigments can only reflect light of longer wavelengths: yellow, orange, red as well as black, but greens and blues can be produced structurally by the iridophores, and incident light of all wavelengths can be reflected from areas of skin rich in leucophores. All the available evidence suggests that cephalopods are colour-blind (Messenger 1977*b*, 1981; Messenger *et al.* 1973) so that it seems probable that *Sepia*, on the basis of information about brightness, uses its chromatophores to match the reflectance of the background rather than its hue and many of our halftone photographs bear this out. In bright light, when the screen of overlying dark chromatophores retracts, the leucophores will be exposed to reflect more of the ambient light, whatever its wavelength. Thus 'general colour resemblance' is brought about by a combination of an active brightness-matching process (using the chromatophores) and a largely passive reflecting process (using leucophores and iridophores) (Messenger 1974, 1979; Froesch & Messenger 1978). However, there is recent evidence that the thickness of platelets in some squid iridophores may be controlled actively to change the hue of iridescence (Hanlon 1982; Cooper & Hanlon 1986).

Disruptive patterns are frequently used by cuttlefish (e.g. plate 8) and we have described in detail in §5.3 how these (and coincident disruptive coloration) are used for camouflage. Cott (1940) also outlines the principles of 'disguise', or 'deceptive resemblance', when an animal is an 'impostor' rather than a 'self-effacer': we have noted resemblances to algae (figures 11, 90, 91 and 97), to stones (figures 88, 92 and 93) and even to an empty *Haliotis* shell (figure 95) by young cuttlefish. Some of the disguises illustrated by Cott involve striking morphological modifications that would render their owner very conspicuous in another environment; for example the frogfishes and *Phyllopteryx*, which resemble *Sargassum* seaweed. *Sepia*, however, is able by its dermal musculature and chromatophores to match a variety of special environments and this versatility, like that of *Octopus* (Packard & Sanders 1969; Packard & Hochberg 1977), must contribute considerably to its success in shallow inshore waters.

The neurally controlled chromatophores are eminently suited to the sudden production of what Cott terms 'deflective' or 'directive' marks (table 2). Deflective marks include the Paired mantle spots, especially the third pair often shown in isolation (figure 78) and also the 'Head-in-reverse' (figure 79), an example of what Hailman (1977) terms symmetry-deception. Flash behaviour can also be regarded as deflective: the display of a pattern during retreat and its sudden disappearance as the cuttlefish comes to rest must confuse the predator's search image very effectively (Cott 1940; Edmunds 1974). Among directive marks, which are specifically directed at prey, are the dark-striped first and second arms waved at prawns during the attack (Holmes 1940; Messenger 1968). However, it is worth recalling that the effects of such marks on predators have never been subject to rigorous testing in the field or in the laboratory.

The colour change mechanisms we have been describing not only permit patterning, they are also very fast. Such changes are termed physiological by workers on vertebrates (Brown 1961; Bagnara & Hadley 1973). They contrast with morphological changes, which operate over periods of days or weeks and involve an actual change in the numbers of chromatophores in the skin. Although such morphological changes have been shown experimentally to occur in the skin of adult flatfish (Cunningham & MacMunn 1893) there is no evidence for them in any adult cephalopod maintained for long periods on a particular substrate.

7.4. *The development of patterns, behaviour and the* CNS

The body patterns shown by a cuttlefish change during ontogeny just as its behaviour changes when it becomes large and sexually mature.

The most remarkable feature of *Sepia officinalis* is its capacity for showing many complex patterns from the moment of hatching. This is because most of the chromatic components (26 out of 34), all the textural and locomotor components and all but two of the postural components are already present and functional (compare tables 1 and 8). These components are used mainly for concealment, which is the primary defence of a small unprotected animal that for the most part stays still and hides.

The density of chromatophores is very high in hatchling cuttlefish so that patterns with very fine resolution may be generated: many of our photographs illustrate this feature, which is entirely appropriate to the small size of the animal (figures 28, 31, 61, 88, 89 and 97). It is significant that several of the components used in such patterns are dropped from the repertoire as the cuttlefish ages and grows (e.g. White neck spots, Mantle margin scalloping in table 8).

Such precocious chromatic behaviour contrasts markedly with that of young, planktonic *Octopus vulgaris* and is clearly related to habit and life style. More importantly, it is accompanied by early development of the chromatophore lobes and lateral basal lobes, whose gross morphology and organization appear to be identical to those of an adult cuttlefish; in *O. vulgaris* hatchlings, the chromatophore lobes are undifferentiated and all the basal lobes poorly developed.

'Threat' patterns such as Flamboyant and Deimatic can also be shown very early in life; indeed, in *Sepia latimanus*, Corner & Moore (1980) have a photograph of Flamboyant being shown in the egg. Such patterns can be thought of as secondary defence (Edmunds 1974), to come into operation after detection by a predator. They are characterized by the strong expression of certain postural components and by the appearance of bold, low-spatial-frequency chromatic components (figures 44, 71, 74 and 78). The organization of the postural components depends upon lower motor centres in the suboesophageal brain, on higher motor centres (notably anterior and median basal lobes) and on the optic lobes (Boycott 1961); all these are well developed in hatchling *Sepia* (Wirz 1954; Messenger 1973) so that, again, the neural machinery for generating such behaviour is present and appears to be fully functional. In constrast to this we should note that those lobes associated with setting up memories are poorly developed in young cuttlefish, with consequent deficits in learning performance (Wells 1958, 1962; Messenger 1973). It is clearly more important that hatchling *Sepia* can match their background or threaten a predator than that they can learn!

It is interesting that there is no evidence for any maturation of the response to a background in the first two or three days of life, such as is shown in the visual response to its prey animal, *Mysis* (Wells 1962). All the available evidence is that visual cues continue to be a major influence on the chromatophore system throughout life. The observations in the sea on the initial responses of naive cuttlefish to *Serranus cabrilla* (§5.5) suggests that they were almost certainly detected visually; animals kept in plastic bags underwater reacted just the same. It has also been demonstrated experimentally that the sexual displays shown by mature males can be established or maintained through glass (J. B. Messenger, unpublished results).

As cuttlefish grow the density of chromatophores (§4.1.1) and the relative number of chromatophore motorneurons declines (table 14). There is no need for them to maintain the same spatial frequency of patterns, however, because such body patterns as Stipple or Mottle are much more effective in concealing a large animal. The photographs in figures 84–87 illustrate this and emphasize that cuttlefish of all ages, like flatfish (Mast 1914), must be able to estimate in absolute terms the substrate particle size so that they display the appropriate patterns for concealment.

Yet as *Sepia* become larger they become vulnerable only to the largest of predators: for example, sharks, sparids, large demersal fish and various kinds of dolphins, narwhal, sperm, bottlenose and pilot whales (Clarke & Stevens 1974; Clarke & Pascoe 1985; Clarke 1986; Roper *et al.* 1984; P. L. Pascoe, personal communication) so they can more safely abandon concealment and indulge in conspicuous sexual displays. Yet presumably there has to be a balance here between pressures to hide and pressures to advertise and it must be significant that the adult display pattern derives from a chromatic pattern effective for camouflage in sunlit water, especially among beds of *Zostera*. The body pattern used in sexual displays has a very low spatial frequency, i.e. it is a bold, black-and-white affair designed for visual signalling rather than concealment and it relies heavily upon leucophores, which are not present at hatching but which develop in the male during the late juvenile stage and into adulthood. Because of the probability that *Sepia* is colour-blind, it is surely significant that this most important of intraspecific signals is couched in terms of brightness, not hue.

One very conspicuous change with age occurs in the Deimatic pattern. Initially this comprises no fewer than eight components, one of which (Paired mantle spots) comprises four pairs of black spots. Fully grown adults may reduce the number of components to two (Flattened body and Paired mantle spots) and there will only be one pair of spots shown. This change in behaviour is especially interesting for its own sake and also because it may be possible to discover some of its neural correlates. The change from complex to simple suggests that the patterns derive from Mottle; and comparison with Packard's (1963) data in *Octopus* suggests it may come from the Mottle (shown in an ambivalent situation) that he terms Conflict Mottle (compared our figure 71 and his figure 2). The gradual simplification of the pattern must be related to size. An animal only a few centimetres long cannot make itself big by flattening, paling and showing two spots; but an animal sufficiently large can increase its apparent size more effectively and 'bluff' a potential predator. The maturation of this pattern in *Sepia* is similar to that of *Octopus vulgaris* (Packard & Sanders 1969) perhaps for this very reason and it can be no coincidence that very young *O. vulgaris* also use Flamboyant patterns and that these largely disappear in adult life.

7.5. *Towards a comparative ethology of cephalopods*

There are, regrettably, very few ethological studies of cephalopods, so that it would be premature to give a detailed comparative account of patterning. Yet it may be helpful to assess current knowledge and predict future trends. Packard (1972), Moynihan (1975, 1985) and Moynihan & Rodaniche (1977) have provided behavioural examples of parallel, divergent and convergent evolution of cephalopods. It is clear from our work and theirs that cephalopod body patterns are inextricably linked with cephalopod behaviour so that study of body patterns becomes central to cephalopod ethology. We believe that Packard's (see, for example, Packard & Hochberg 1977) hierarchical classification will facilitate future work in this direction (table 15).

TABLE 15. CEPHALOPOD BODY PATTERNS ANALYSED BY THE HIERARCHICAL SYSTEM OF PACKARD & SANDERS (1971)

Order Sepioidea		Order Octopoda‡	
Sepia officinalis†	present paper	*Octopus vulgaris*†	Packard & Sanders (1969, 1971)
S. papuensis	Roper & Hochberg (1988)	*O. burryi*†	Hanlon & Hixon (1980); Forsythe & Hanlon (1985)
Metasepia pfefferi	Roper & Hochberg (1988)	*O. briareus*†	Hanlon & Wolterding (1989)
		O. bimaculoides	Forsythe & Hanlon (1988); Packard & Hochberg (1977)
Order Teuthoidea		*O. cyanea*	Roper & Hochberg (1988)
Lolliguncula brevis	Dubas *et al.* (1986*a*)	*O. ornatus*	Roper & Hochberg (1988)
Loligo plei	Hanlon (1978, 1982)	*Eledone cirrhosa*	Boyle & Dubas (1981)
L. pealei	Hanlon (1988)	*Hapalochlaena maculosa*	Roper & Hochberg (1988)
L. vulgaris	Hanlon (1988)		
L. forbesi	Hanlon (1988)		

† Ontogeny of patterning reported.
‡ Packard & Hochberg (1977) reported aspects of patterning in *Octopus dofleini*, *O. rubescens* and *O. californicus*.

Hanlon (1988) has recently provided a framework for behavioural taxonomy based upon aspects of patterning in live cephalopods. The main argument is that components, not patterns, may yield as much, or more, comparative information not only in taxonomy and ontogeny but eventually in phylogeny and higher-order systematics. Moynihan (1975, 1985) and Moynihan & Rodaniche (1977) have taken a different approach by focusing on the use of signals in communication (i.e. acute body patterns and related stereotyped displays). In this paper we have approached these issues by beginning with morphological or neural bases of patterns and smaller units of behaviour.

Table 16 represents a first attempt towards comparing the behavioural ecology of species based upon morphological characteristics of their skin, body patterns and general habits. These three species represent each of the major orders of living cephalopods: Sepioidea, Teuthoidea and Octopoda. As in comparative anatomy, skin structure and even brief obervations of a living cephalopod can provide clues to body patterning complexity, activity cycle, habitat and social behaviour. For example, many cephalopods (of all orders) have relatively simple skin with large chromatophore organs of low density and few iridescent (or leucophore) cells. These species will have a limited repertoire of patterning and are likely to be exclusively nocturnal or reclusive and/or live in monotonous environments (e.g. mud or sand substrates, deep water, open ocean). Examples are *Sepia elegans* (deeper water), the teuthoid squid *Lolliguncula brevis* (estuarine, murky water) and *Octopus joubini* (strongly nocturnal and reclusive). Cephalopods living on or near diverse substrates in clear water (e.g. coral reefs), or species that swim or school and encounter numerous predators, are more likely to have evolved complex skin structure and patterning repertoires. Examples are *Sepia officinalis*, the teuthoid squid *Sepioteuthis sepioidea* (Caribbean reef squid) and *Octopus vulgaris* (worldwide tropical and temperate nearshore distribution). Moynihan & Rodaniche (1982) review some of these correlations as well. The guiding principle is that each species will have adapted to its specific environment. Thus body patterning can be expected to be better developed in some species than others and its usefulness in systematics will vary considerably across the class Cephalopoda.

TABLE 16. BODY PATTERNING RELATED TO ECOLOGY IN THREE NERITIC CEPHALOPODS

	Sepia officinalis	*Octopus vulgaris*	*Loligo plei*
mode of life	solitary, benthic	solitary, benthic and reclusive	schooling, pelagic
activity cycle and habitat	nocturnal–crepuscular; shallow seagrass and rock reefs	diurnal–crepuscular; crevices in shallow seagrass and rock reefs	nocturnal; near coral reefs
chromatophore density (mm^{-2})	high: 200–500	high: 300	low: 8
number of components	54	42	27
patterns for concealment	many	many	few
patterns for advertisement (intraspecific signals)	few	few	many
references	present paper	Packard & Sanders (1971) Packard & Hochberg (1977)	Hanlon (1982)

Sepia officinalis L. has a rich patterning repertoire compared with other cephalopods, but among sepioids, *Sepia latimanus* (of tropical Indo-Pacific coral reefs) appears to be equally diverse in its patterning and behavioural repertoires (Corner & Moore 1980; R. T. Hanlon & B. A. Carlson, unpublished results). In addition, many of the patterns and behaviours used in response to predators, prey and conspecifics seem to be similar in both species (Corner & Moore 1980; R. T. Hanlon & B. A. Carlson, unpublished results). *Sepia esculenta* (Yamamoto 1941: figure 3), *Sepia papuensis* and *Metasepia pfefferi* (Roper & Hochberg 1988) appear also to have diverse patterning capabilities, although they have been observed only cursorily; *Euprymna scolopes* and *Idiosepius pygmaeus* are small sepioids with moderate patterning repertoires (Moynihan 1983*a*,*b*). It is interesting that *Sepia*, with its rigid cuttlebone (and thus rigid mantle shape), has evolved a wide range of chromatic components used in disruptive patterning. Octopuses, of course, can change their body outline easily and thus do not need specific chromatic components to break up the outline of their 'typical' body form.

Compared with teuthoid squids, *Sepia officinalis* is far more diversified than any of the *Loligo* spp. or *Lolliguncula* spp. (table 15), or any of the oceanic (oegopsid) squids, which have a limited patterning repertoire (R. T. Hanlon, personal observation). Among loliginids, only *Loligo plei* (Hanlon 1982) has a moderately diverse patterning repertoire, but most of its components are used during encounters with schooling conspecifics (table 16). Only one loliginid, *Sepioteuthis sepioidea*, has a repertoire of patterning and behaviour comparable to that of *Sepia officinalis*. Moynihan & Rodaniche (1982) have provided a valuable account of the behaviour and patterning of *Sepioteuthis sepioidea* in the most exhaustive ethological study of a cephalopod thus far. Unfortunately, it is difficult to compare their species with *Sepia officinalis* because they used the terms pattern and component interchangeably. However, Moynihan (1985: tables 2–4) compared 'ritualized patterns' of sepioids, teuthoids and octopods, and his tables are useful in highlighting homologous and conservative body patterns seen across species and genera. *Sepioteuthis sepioidea* lives near coral reefs and has a particularly rich pattern repertoire for interactions with predators; *Sepia officinalis*, on the other hand, has the capability of sitting or burying in the substrate and thus has more disruptive and concealment patterns. In general, there is remarkable convergence in body shape (Boycott 1965) and pattern richness in these genera belonging to different orders, and it surely has to do with similar habitat diversity and predator pressures.

Compared with octopods, *Sepia officinalis* has a pattern repertoire surpassing even the most complex octopod studied thus far, *Octopus vulgaris* (table 16) (Packard & Sanders 1969, 1971; Packard & Hochberg 1977). These species co-occur in the eastern Atlantic and are subject to similar predator pressures, but *O. vulgaris* is reclusive, avoiding the open seabed and living in crevices. Both species have densely packed chromatophores, a large number of components and a wide range of concealment patterns against the substrate (table 16). Mottle patterns and papillae are used extensively by both genera to achieve general resemblance to the substrate. As mentioned previously, *Sepia* requires more chromatic components to achieve disruptive patterns on its rigid mantle, which is constantly exposed to predation from above.

Analysis of adaptive coloration as a comparative behavioural tool will be most useful with species that inhabit diverse habitats in shallow, clear water and thus use body patterning for concealment and predator avoidance. It will also be useful in species that use patterning for sexual signalling or prey capture. Only Moynihan (1985) has so far attempted comparative ethological analyses and we agree that field studies are necessary to complement the wealth of data available on laboratory behaviour of cephalopods (see Young 1971; Wells 1978; Boyle (ed.) 1983). Recently there has been increased interest in ecological studies of cephalopods (see, for example, Ambrose 1982, 1988; Ambrose & Nelson 1983; Hartwick *et al.* 1984, 1988; Aronson 1986) and we hope field researchers will begin to record systematically ethological data such as adaptive coloration, with the long-term goal of providing a more comprehensive view of their behaviour and life style.

We are indebted to Dr S. v. Boletzky of the Laboratoire Arago in Banyuls, France (C.N.R.S.) for sharing his considerable knowledge of *Sepia officinalis*, for providing eggs and young in Banyuls in 1972 and 1981, and in Galveston in 1982; and also for helping rear some of the animals in Banyuls. It is a pleasure to thank Dr K. Mangold for laboratory space in 1981 and

Dr H.-J. Marthy at Banyuls for his expert assistance in removing primordial eye tissue from developing embryos. We also wish to thank the director of that Laboratory and those at Naples and Plymouth for placing their facilities at our disposal. Drs R. and M.-P. Chichery of the University of Caen were also very helpful: they not only supplied us with eggs and young animals in 1982, but also reared the animals in figures 98 and 99. Dr M. Zahn (Düsseldorf) kindly showed us his films on young *Sepia officinalis* behaviour. We are grateful for the expert technical assistance given us by John Forsythe, Margarita Ackerson, Janice Sheldon, Kay Cooper, Laura Beall Koppe and Arlene Hanlon in Galveston, and Pauline Gaitens, David Hollingworth and Roger Webb in Sheffield.

We benefited from encouragement and helpful suggestions by Dr M. J. Wells, Professor J. Z. Young, F.R.S., Dr Raymond F. Hixon, Dr Sigurd Boletzky and especially from Dr Andrew Packard, who reviewed a late draft.

This work was supported by a NATO Postdoctoral Fellowship held in the Department of Zoology, Cambridge University (R. T. H.), by the Sheffield University Research Fund (Grant numbers 615 and 667) and the Browne Fund of the Royal Society (J. B. M.). Additional support was received from the Marine Medicine General Budget of The Marine Biomedical Institute, The University of Texas Medical Branch at Galveston.

REFERENCES

Abercrombie, M. 1946 Estimation of nuclear population for microtome sections. *Anat. Res.* **98**, 239–247.

Ambrose, R. F. 1982 Shelter utilization by the molluscan cephalopod *Octopus bimaculatus*. *Mar. Ecol.* **7**, 67–73.

Ambrose, R. F. 1988 Population dynamics of *Octopus bimaculatus*: influence of life history patterns, synchronous reproduction and recruitment. *Malacologia* **29**, 23–39.

Ambrose, R. F. & Nelson, B. V 1983 Predation by *Octopus vulgaris* in the Mediterranean. *Mar. Ecol.* **4**, 251–261.

Andrews, P. L. R., Messenger, J. B. & Tansey, E. M. 1981 Colour changes in cephalopods after neurotransmitter injection into the cephalic aorta. *Proc. R. Soc. Lond.* B **213**, 93–99.

Aronson, R. B. 1986 Life history and den ecology of *Octopus briareus* Robson in a marine lake. *J. exp. mar. Biol. Ecol.* **95**, 37–56.

Bagnara, J. T. & Hadley, M. E. 1973 *Chromatophores and color change: the comparative physiology of animal pigmentation.* Englewood Cliffs: Prentice-Hall.

Barlow, G. W. 1968 Ethological units of behavior. In *The central nervous system and fish behavior* (ed. D. Ingle), pp. 217–232. University of Chicago Press.

Barlow, G. W. 1977 Modal action patterns. In *How animals communicate* (ed. T. A. Sebeok), pp. 98–135. Indiana University Press.

Bather, F. A. 1895 The habits of the young *Sepia*. *J. Malacol.* **4**, 33–34.

Boletzky, S. v. 1974 The 'larvae' of Cephalopoda: a review. *Thalassia Jugosl.* **10**, 45–76.

Boletzky, S. v. 1983 *Sepia officinalis*. In *Cephalopod life cycles: species accounts*, vol. 1. (ed. P. R. Boyle), pp. 31–52. London: Academic Press.

Bone, Q. & Marshall, N. B. 1982 *Biology of fishes*. Glasgow: Blackie.

Bott, R. 1938 Kopula und Eiablage von *Sepia officinalis* L. *Z. Morphol. Ökol. Tiere* **34**, 150–160.

Boycott, B. B. 1953 The chromatophore system of cephalopods. *Proc. Linn. Soc. Lond.* **164**, 235–240.

Boycott, B. B. 1958 The cuttlefish–*Sepia*. *New Biol.* **25**, 98–118.

Boycott, B. B. 1961 The functional organization of the brain of the cuttlefish *Sepia officinalis*. *Proc. R. Soc. Lond.* B **153**, 503–534.

Boycott, B. B. 1965 A comparison of living *Sepioteuthis sepioidea* and *Doryteuthis plei* with other squids, and with *Sepia officinalis*. *J. Zool.* **147**, 344–351.

Boycott, B. B. & Young, J. Z. 1950 The comparative study of learning. *Symp. Soc. exp. Biol.* **4**, 432–453.

Boyle, P. R. (ed.) 1983 *Cephalopod life cycles: species accounts*, vol. 1. London: Academic Press.

Boyle, P. R. & Dubas, F. 1981 Components of body pattern displays in the octopus *Eledone cirrhosa* (Mollusca: Cephalopoda). *Mar. Behav. Physiol.* **8**, 135–148.

Brocco, S. L. 1975 The fine structure of the frontal and mantle white spots of *Octopus dofleini*. *Am. Zool.* **15**, 782.

Brocco, S. L. & Cloney, R. A. 1980 Reflector cells in the skin of *Octopus dofleini*. *Cell Tissue Res.* **205**, 167–186.

Brown, F. A. Jr 1961 Chromatophores and color change. In *Comparative animal physiology* (ed. C. L. Prosser & F. A. Brown), pp. 502–537. Philadelphia: W. B. Saunders.

Burton, D. 1981 Physiological responses of melanophores and xanthophores of hypophysectomized and spinal winter flounder, *Pseudopleuronectes americanus* Walbaum. *Proc. R. Soc. Lond.* B **213**, 217–231.

Casey, R. G. & Nagy, G. 1971 Advances in pattern recognition. *Scient. Am.* **224**, 56–71.

Chichery, R. & Chanelet, J. 1976 Motor and behavioural responses obtained by stimulation with chronic electrodes of the optic lobe of *Sepia officinalis*. *Brain Res.* **105**, 525–532.

Clark, P. J. & Evans, F. C. 1954 Distance to nearest neighbor as a measure of spatial relationship in populations. *Ecology* **35**, 445–453.

Clarke, M. R. 1986 Cephalopods in the diet of odontocetes. In *Research on dolphins* (ed. M. M. Bryden & R. Harrison), pp. 281–321. Oxford: Clarendon Press.

Clarke, M. R. & Pascoe, P. L. 1985 The stomach contents of a Risso's dolphin (*Grampus griseus*) stranded at Thurlestone, South Devon. *J. mar. biol. Ass. U.K.* **65**, 663–665.

Clarke, M. R. & Stevens, J. D. 1974 Cephalopods, blue sharks and migration. *J. mar. biol. Ass. U.K.* **54**, 949–957.

Cloney, R. A. & Brocco, S. L. 1983 Chromatophore organs, reflector cells, iridocytes and leucophores in cephalopods. *Am. Zool.* **23**, 581–592.

Cloney, R. A. & Florey, E. 1968 Ultrastructure of cephalopod chromatophore organs. *Z. Zellforsch. mikrosk. Anat.* **89**, 250–280.

Cooper, K. M. & Hanlon, R. T. 1986 Correlation of iridescence with changes in iridophore platelet ultrastructure in the squid *Lolliguncula brevis*. *J. exp. Biol.* **121**, 451–455.

Corner, B. D. & Moore, H. T. 1980 Field observations on the reproductive behavior of *Sepia latimanus*. *Micronesica* **16**, 235–260.

Cott, H. B. 1940 *Adaptive coloration in animals*. London: Methuen.

Cuénot, L. 1917 *Sepia officinalis* est une espèce en voie de dissociation. *Arch. Zool. exp. gén.* **56**, 315–346.

Cuénot, L. 1933 La seiche commune de la Méditerranée: étude sur la naissance d'une espèce. *Arch. Zool. exp. gén.* **75**, 319–330.

Cunningham, J. T. & MacMunn, C. A. 1893 On the coloration of the skins of fishes, especially of Pleuronectidae. *Phil. Trans. R. Soc. Lond.* B **184**, 765–812.

Curio, E. 1976 *The ethology of predation*. Zoophysiology and Ecology, vol. 7. Berlin: Springer-Verlag.

Denton, E. J. & Gilpin-Brown, J. B. 1961 The buoyancy of the cuttlefish. *J. mar. biol. Ass., U.K.* **41**, 319–342.

Denton, E. J. & Land, M. F. 1971 Mechanism of reflexion in silvery layers of fish and cephalopods. *Proc. R. Soc. Lond.* B **178**, 43–61.

Dubas, F. & Boyle, P. R. 1985 Chromatophore motor units in *Eledone cirrhosa* (Cephalopoda: Octopoda). *J. exp. Biol.* **117**, 415–431.

Dubas, F., Hanlon, R. T., Ferguson, G. P. & Pinsker, H. M. 1986*a* Localization and stimulation of chromatophore motoneurons in the brain of the squid, *Lolliguncula brevis*. *J. exp. Biol.* **121**, 1–25.

Dubas, F., Leonard, R. B. & Hanlon, R. T. 1986*b* Chromatophore motoneurons in the brain of the squid, *Lolliguncula brevis*: an HRP study. *Brain Res.* **374**, 21–29.

Edmunds, M. 1974 *Defence in animals. A survey of anti-predator defences.* London: Longman.

Ferussac, M. & d'Orbigny, A. 1835–1848 *Histoire naturelle des céphalopodes acétabulifères.* Paris: Chez J.-B. Baillière, Libraire de l'Académie Nationale de Médecine.

Florey, E. 1966 Nervous control and spontaneous activity of the chromatophores of a cephalopod, *Loligo opalescens*. *Comp. Biochem. Physiol.* **18**, 305–324.

Florey, E. 1969 Ultrastructure and function of cephalopod chromatophores. *Am. Zool.* **9**, 429–442.

Florey, E., Dubas, F. & Hanlon, R. T. 1985 Evidence of L-glutamate as a transmitter substance of motoneurons innervating squid chromatophore muscles. *Comp. Biochem. Physiol.* **82** C, 259–268.

Florey, E. & Kriebel, M. E. 1969 Electrical and mechanical responses of chromatophore muscle fibers of the squid, *Loligo opalescens*, to nerve stimulation and drugs. *Z. vergl. Physiol.* **65**, 98–130.

Forsythe, J. W. & Hanlon, R. T. 1985 Aspects of egg development, post-hatching behavior, growth and reproduction of *Octopus burryi* Voss, 1950 (Mollusca: Cephalopoda). *Vie Milieu* **35**, 273–282.

Forsythe, J. W. & Hanlon, R. T. 1988 Behavior, body patterning and reproductive biology of *Octopus bimaculoides* from California. *Malacologia* **29**, 46–56.

Froesch, D. & Messenger, J. B. 1978 On leucophores and the chromatic unit of *Octopus vulgaris*. *J. Zool.* **186**, 163–173.

Grimpe, G. 1926 Biologische Beobachtungen an *Sepia officinalis*. *Verh. dt. Zool. Ges.* 31, (2. Suppl. Band Zool. Anz.), pp. 148–153.

Guerra, A. 1985 Food of the cuttlefish *Sepia officinalis* and *S. elegans* in the Ria de Vigo (NW Spain) (Mollusca: Cephalopoda). *J. Zool.* **207**, 511–519.

Hailman, J. P. 1977 *Optical signals*. Indiana University Press.

Hanlon, R. T. 1978 Aspects of the biology of the squid *Loligo* (*Doryteuthis*) *plei* in captivity. Ph.D. dissertation, University of Miami.

Hanlon, R. T. 1982 The functional organization of chromatophores and iridescent cells in the body patterning of *Loligo plei* (Cephalopoda, Myopsida). *Malacologia* **23**, 89–119.

Hanlon, R. T. 1988 Behavioral and body patterning characters useful in taxonomy and field identification of cephalopods. *Malacologia* **29**, 247–263

Hanlon, R. T. & Hixon, R. F. 1980 Body patterning and field observations of *Octopus burryi* Voss, 1950. *Bull. mar. Sci.* **30**, 749–755.

Hanlon, R. T. & Wolterding, M. R. 1989 The behavior, growth and life history of *Octopus briareus* cultured in the laboratory. *Stud. trop. Oceanogr.* (In the press.)

Hartwick, E. B., Ambrose, R. F. & Robinson, S. M. C. 1984 Den utilization and the movements of tagged *Octopus dofleini*. *Mar. Behav. Physiol.* **11**, 95–110.

Hartwick, E. B., Robinson, S. M. C., Ambrose, R. F., Trotter, D. & Walsh, M. 1988 Inshore–offshore comparison of *Octopus dofleini* with special reference to abundance, growth and physical condition during winter. *Malacologia* **29**, 57–68.

Hill, A. V. & Solandt, D. Y. 1935 Myograms from the chromatophores of *Sepia*. *J. Physiol., Lond.* **83**, 13–14*P*.

Hinde, R. A. 1953 Appetitive behaviour, consummatory act, and the hierarchical organisation of behaviour, with special reference to the great tit (*Parus major*). *Behaviour* **5**, 191–224.

Hirsch, S. M. & Bolles, R. C. 1980 On the ability of prey to recognize predators. *Z. Tierpsychol.* **54**, 71–84.

Holmes, W. 1940 The colour changes and colour patterns of *Sepia officinalis* L. *Proc. zool. Soc. Lond.* **110**, 17–35.

Humphries, D. A. & Driver, P. M. 1967 Erratic display as a device against predators. *Science, Wash.* **156**, 1767–1768.

Humphries, D. A. & Driver, P. M. 1971 Protean defence by prey animals. *Oecologia* **5**, 285–302.

Kawaguti, S. & Ohgishi, S. 1962 Electron microscopic study on iridophores of a cuttlefish. *Sepia esculenta*. *Biol. J. Okayama Univ.* **8**, 115–129.

Krebs, J. R. 1978 Optimal foraging: decision rules for predators. In *Behavioural ecology, an evolutionary approach* (ed. J. R. Krebs & N. B. Davies), pp. 23–63. Sunderland: Sinauer Associates.

Kühn, A. & Heberdey, R. F. 1929 Über die Anpassung von *Sepia officinalis* L. an Helligkeit und Farbton der Umgebung. *Verh. dt. Zool. Ges.* **33**, 231–237.

Land, M. F. 1972 The physics and biology of animal reflectors. *Prog. Biophys. molec. Biol.* **24**, 75–106.

Lo Bianco, S. 1909 Notizie biologiche riguardanti specialmenti il periodo di maturità sessuale degli animali del golfo di Napoli. *Mitt. zool. Stn Neapel* **19**, 645–657.

Lorenz, K. Z. 1950 The comparative method in studying innate behaviour patterns. *Symp. Soc. exp. Biol.* **4**, 221–268.

Maldonado, H. 1970 The deimatic reaction in the praying mantis *Stagmatoptera biocellata*. *Z. vergl. Physiol.* **68**, 60–71.

Mangold-Wirz, K. 1963 Biologie des céphalopodes benthiques et nectoniques de la Mer Catalane. *Vie Milieu* **13** (suppl.). (285 pages.)

Mast, S. O. 1914 Changes in shade, color, and pattern in fishes, and their bearing on the problems of adaptation and behavior, with especial reference to the flounders *Paralichthys* and *Ancylopsetta*. *Bull. Bur. Fish., Wash.* **34**, 173–238.

Maynard, D. M. 1967 Organization of central ganglia. In *Invertebrate nervous systems. Their significance for mammalian neurophysiology* (ed. C. A. G. Wiersma), pp. 231–255. University of Chicago Press.

McFarland, D. 1981 *The Oxford companion to animal behaviour*. Oxford University Press.

Messenger, J. B. 1968 The visual attack of the cuttlefish, *Sepia officinalis*. *Anim. Behav.* **16**, 342–357.

Messenger, J. B. 1970 Optomotor responses and nystagmus in intact, blinded and statocystless cuttlefish (*Sepia officinalis* L.). *J. exp. Biol.* **53**, 789–796.

Messenger, J. B. 1973 Learning performance and brain structure: a study in development. *Brain Res.* **58**, 519–523.

Messenger, J. B. 1974 Reflecting elements in cephalopod skin and their importance for camouflage. *J. Zool.* **174**, 387–395.

Messenger, J. B. 1977*a* Prey-capture and learning in the cuttlefish, *Sepia*. In *The biology of cephalopods* (ed. M. Nixon & J. B. Messenger) (*Symp. zool. Soc. Lond.* **38**), pp. 347–376. London: Academic Press.

Messenger, J. B. 1977*b* Evidence that *Octopus* is colour blind. *J. exp. Biol.* **70**, 49–55.

Messenger, J. B. 1979 The eyes and skin of *Octopus*: compensating for sensory deficiencies. *Endeavour* **28**, 92–98.

Messenger, J. B. 1981 Comparative physiology of vision in molluscs. In *Handbook of sensory physiology*, vol. VII/6c (ed. H. Autrum), pp. 93–200. Berlin: Springer-Verlag.

Messenger, J. B. & Miyan, J. A. 1986 Neural correlates of colour change in cuttlefish. *J. exp. Biol.* **125**, 395–400.

Messenger, J. B., Wilson, A. P. & Hedge, A. 1973 Some evidence for colour-blindness in *Octopus*. *J. exp. Biol.* **59**, 77–94.

Moynihan, M. 1975 Conservatism of displays and comparable stereotyped patterns among cephalopods. In *Function and evolution in behaviour. Essays in honor of Niko Tinbergen* (ed. G. Baerends, C. Beer & A. Manning), pp. 276–291. Oxford: Clarendon Press.

Moynihan, M. 1983*a* Notes on the behavior of *Euprymna scolopes* (Cephalopoda: Sepiolidae). *Behaviour* **85**, 25–41.

Moynihan, M. 1983*b* Notes on the behavior of *Idiosepius pygmaeus* (Cephalopoda: Idiosepiidae). *Behaviour* **85**, 42–57.

Moynihan, M. 1985 *Communication and noncommunication by cephalopods.* Indiana University Press.

Moynihan, M. & Rodaniche, A. F. 1977 Communication, crypsis, and mimicry among cephalopods. In *How animals communicate* (ed. T. A. Sebeok), pp. 293–302. Indiana University Press.

Moynihan, M. & Rodaniche, A. F. 1982 The behavior and natural history of the Caribbean reef squid *Sepioteuthis sepioidea* with a consideration of social, signal and defensive patterns for difficult and dangerous environments. In *Advances in ethology*, vol. 25, pp. 1–125. Berlin: Parey.

Naef, A. 1928 Die Cephalopoden. Embryologie. *Fauna Flora Golfo Napoli*, **35** (1), pt 2.

Nelson, K. 1973 Does the holistic study of behavior have a future? In *Perspectives in ethology* (ed. P. P. G. Bateson & P. H. Klopfer), pp. 281–328. New York: Plenum.

Packard, A. 1963 The behaviour of *Octopus vulgaris. Bull. Inst. Oceanogr., Monaco*, **1** D, 35–49.

Packard, A. 1972 Cephalopods and fish: the limits of convergence. *Biol. Rev.* **47**, 241–307.

Packard, A. 1974 Chromatophore fields in the skin of the octopus. *J. Physiol., Lond.* **238**, 38–40*P*.

Packard, A. 1982 Morphological and physiological units of chromatophores in cephalopods: are they the same? *Malacologia* **23**, 193–201.

Packard, A. & Hochberg, F. G. 1977 Skin patterning in *Octopus* and other genera. In *The biology of cephalopods* (ed. M. Nixon & J. B. Messenger) (*Symp. zool. Soc. Lond.* **38**), pp. 191–231. London: Academic Press.

Packard, A. & Sanders, G. 1969 What the octopus shows to the world. *Endeavour* **28**, 92–99.

Packard, A. & Sanders, G. D. 1971 Body patterns of *Octopus vulgaris* and maturation of the response to disturbance. *Anim. Behav.* **19**, 780–790.

Roper, C. F. E. & Hochberg, F. G. 1988 Behavior and systematics of cephalopods from Lizard Island, Australia based on color and body patterns. *Malacologia* **29**, 153–193.

Roper, C. F. E., Sweeney, M. J. & Nauen, C. E. 1984 Cephalopods of the world. *F.A.O. Fish. Biol. Synop.* (125) 3.

Sanders, F. K. & Young, J. Z. 1940 Learning and other functions of the higher nervous centres of *Sepia. J. Neurophysiol.* **3**, 501–526.

Sanders, G. D. & Young, J. Z. 1974 Reappearance of specific colour patterns after nerve regeneration in *Octopus. Proc. R. Soc. Lond.* B **186**, 1–11.

Schäfer, W. 1937 Bau, Entwicklung und Farbenentstehung bei den Flitterzellen von *Sepia officinalis. Z. Zellforsch. mikrosk. Anat.* **27**, 222–245.

Sereni, E. & Young, J. Z. 1932 Nervous degeneration and regeneration in cephalopods. *Pubbl. Staz. zool. Napoli* **12**, 173–208.

Stephens, P. R. 1971 Histological methods, appendix II. In *The anatomy of the nervous system of Octopus vulgaris* (ed. J. Z. Young), pp. 646–649. Oxford: Clarendon Press.

Stokes, A. W. 1960 Agonistic behaviour among blue tits at a winter feeding station. *Behaviour* **19**, 118–138.

Thorpe, W. H. 1963 *Learning and instinct in animals*, 2nd edn. London: Methuen.

Tinbergen, L. 1939 Zur Fortpflanzungsethologie von *Sepia officinalis* L. *Archs néerl. Zool.* **3**, 323–364.

Tinbergen, L. 1960 The natural control of insects in pine woods. I. Factors influencing the intensity of predation in song birds. *Archs Néerl. Zool.* **13**, 265–343.

Tinbergen, N. 1950 The hierarchical organization of nervous mechanisms underlying instinctive behaviour. *Symp. Soc. exp. Biol.* **4**, 305–312.

Uexküll, J. v. & Kriszat, G. 1934 *Streifzüge durch die Umwelten von Tieren und Menschen.* Berlin: Springer-Verlag.

Wells, M. J. 1958 Factors affecting reactions to *Mysis* by newly hatched *Sepia. Behaviour* **13**, 96–111.

Wells, M. J. 1962 Early learning in *Sepia. Symp. zool. Soc. Lond.* **8**, 149–169.

Wells, M. J. 1978 *Octopus: physiology and behaviour of an advanced invertebrate.* New York: John Wiley & Sons.

Wilson, D. P. 1946 A note on the capture of prey by *Sepia officinalis* L. *J. mar. biol. Ass. U.K.* **26**, 421–425.

Wirz, K. 1954 Études quantitatives sur le système nerveux des Céphalopodes. *C.r. hebd. Séanc. Acad. Sci., Paris* **238**, 1353–1355.

Yamamoto, T. 1941 Observations on the habits of the squid larvae, *Sepia esculenta* Hoyle, with special reference to the change of colour pattern on the mantle. *Shokubutsu oyobi Dobutsu* **9**(3), 31–35. (In Japanese.)

Young, J. Z. 1950 *The life of vertebrates.* Oxford: Clarendon Press.

Young, J. Z. 1963 The number and sizes of nerve cells in *Octopus. Proc. zool. Soc. Lond.* **140**, 229–254.

Young, J. Z. 1971 *The anatomy of the nervous system of Octopus vulgaris.* Oxford: Clarendon Press.

Zahn, M. 1979*a* *Sepia officinalis* (Sepiidae) – Ruheverhalten, Tarnung, und Fortbewegung. Publikationen zu Wissenschaftlichen Filmen – E 2271, Biologie vol. 12 no. 2, pp. 1–17. Göttingen.

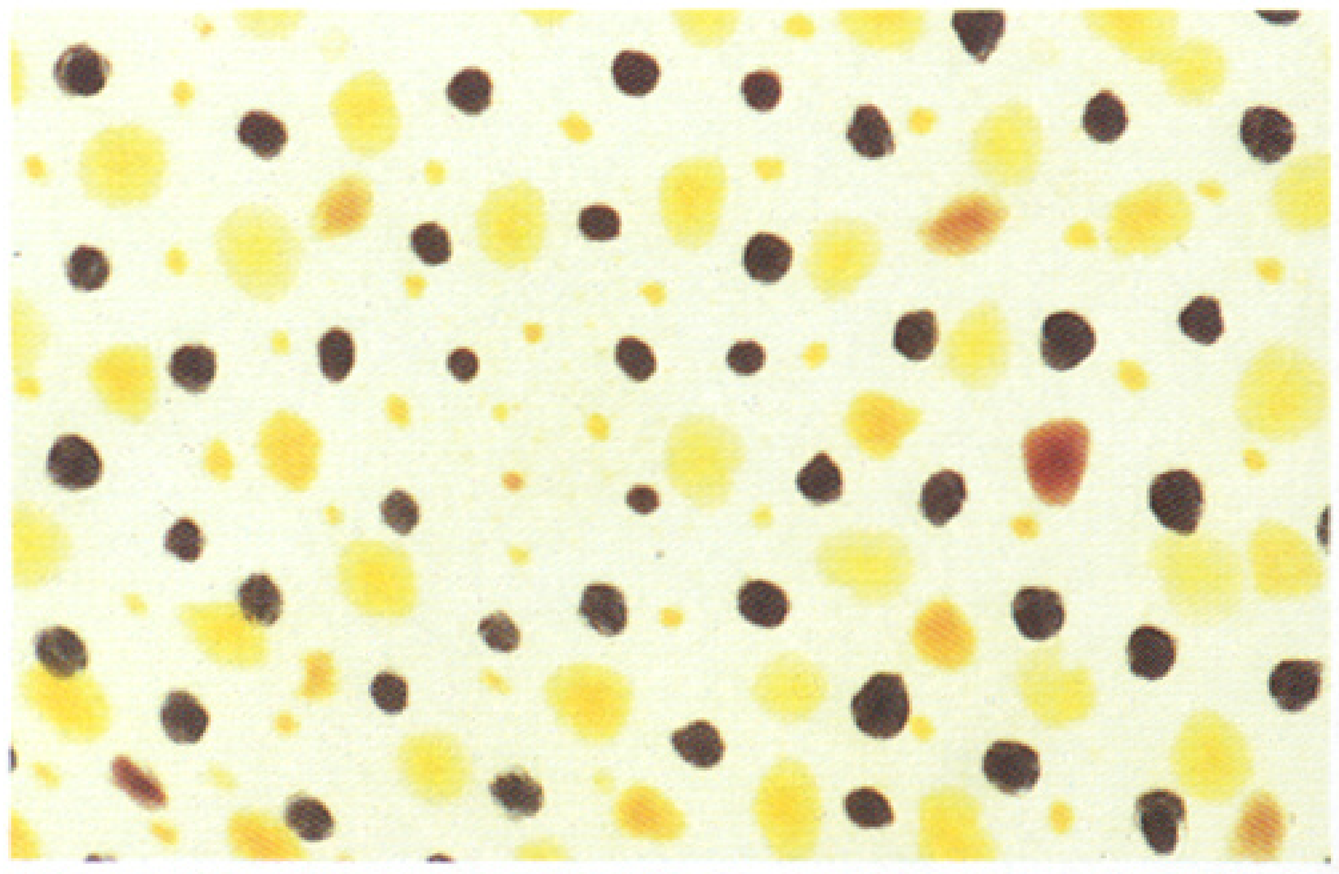
Zahn, M. 1979*b* *Sepia officinalis* (Sepiidae) – Beutefang. Publikationen zu Wissenschaftlichen Filmen – E 2272, Biologie vol. 12 no. 3, pp. 1–18. Göttingen.

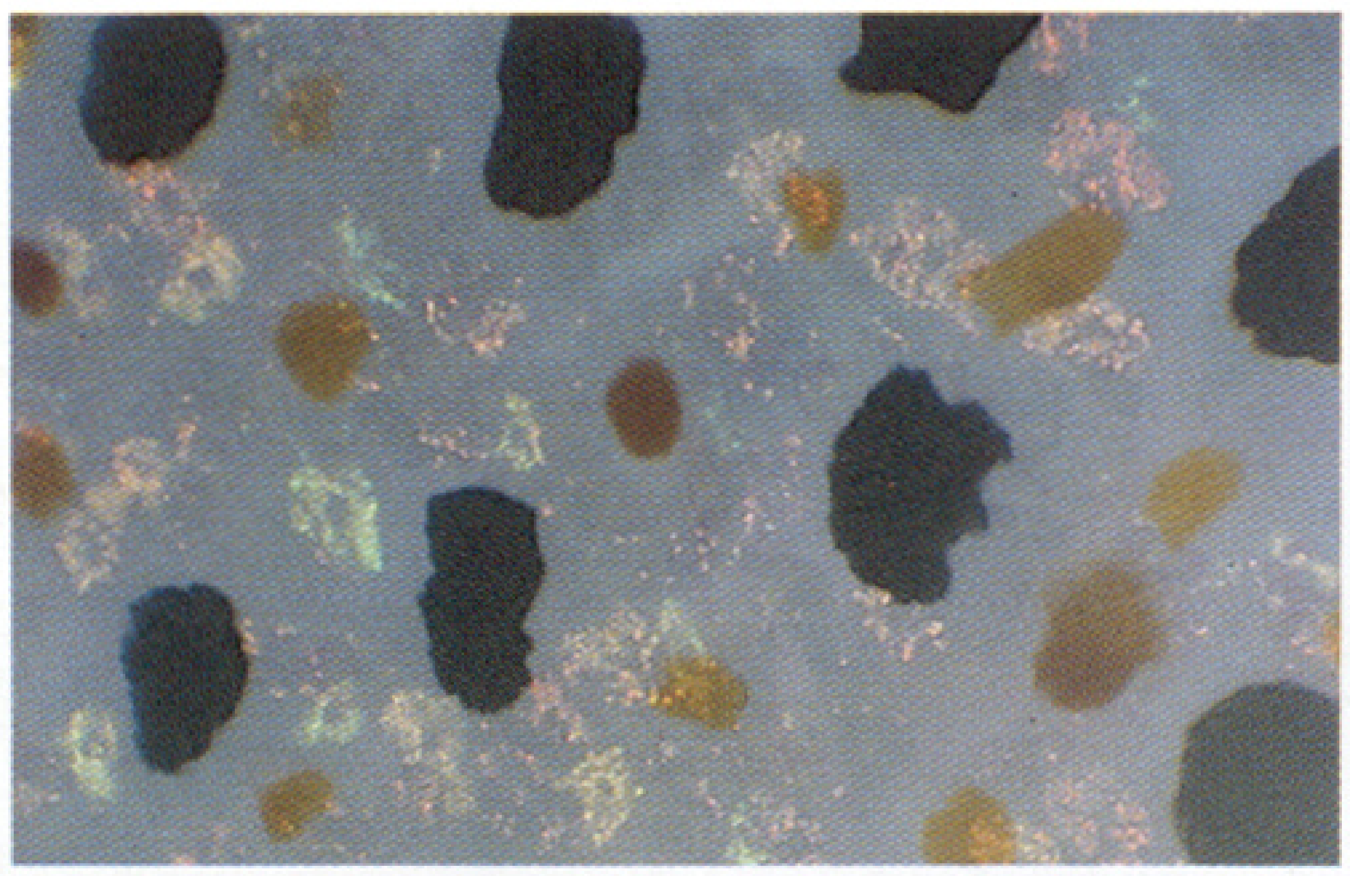
Zahn, M. 1979*c* *Sepia officinalis* (Sepiidae) – Balz, Paarung und Eiablage. Publikationen zu Wissenschaftlichen Filmen – E 2273, Biologie vol. 12 no. 4, pp. 1–26. Göttingen.

Zahn, M. 1983 *Sepia officinalis* (Sepiidae) – Schlüpfen und Jugendentwicklung. Publikationen zu Wissenschaftlichen Filmen – E 2505, Biologie vol. 16 no. 15, pp. 1–17. Göttingen.

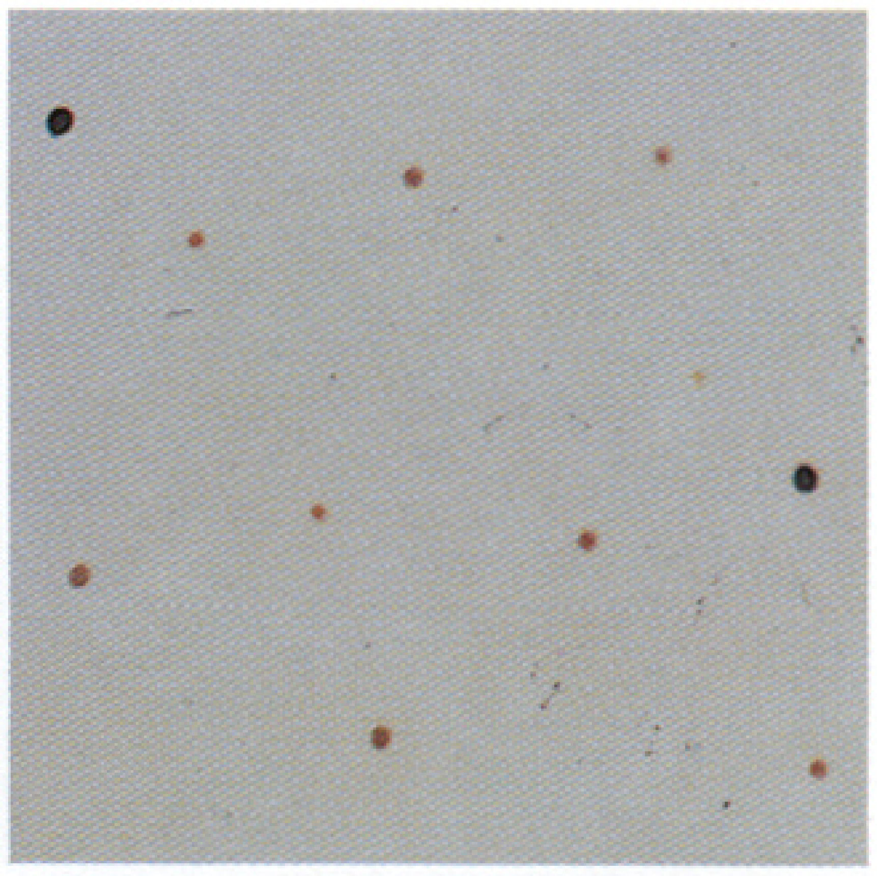
Plates 1, 14 and 15 were printed by George Over Limited.

2, 3

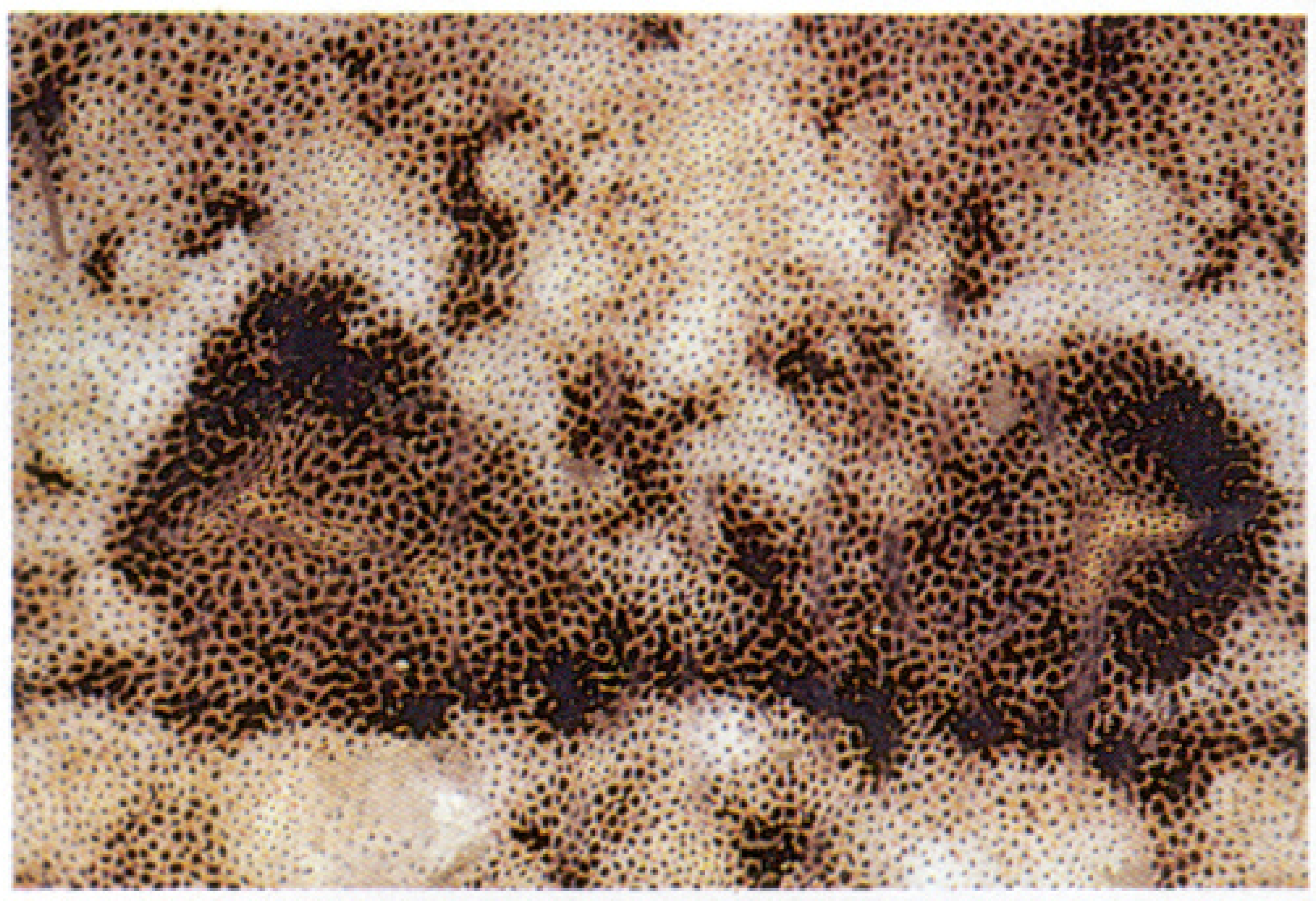


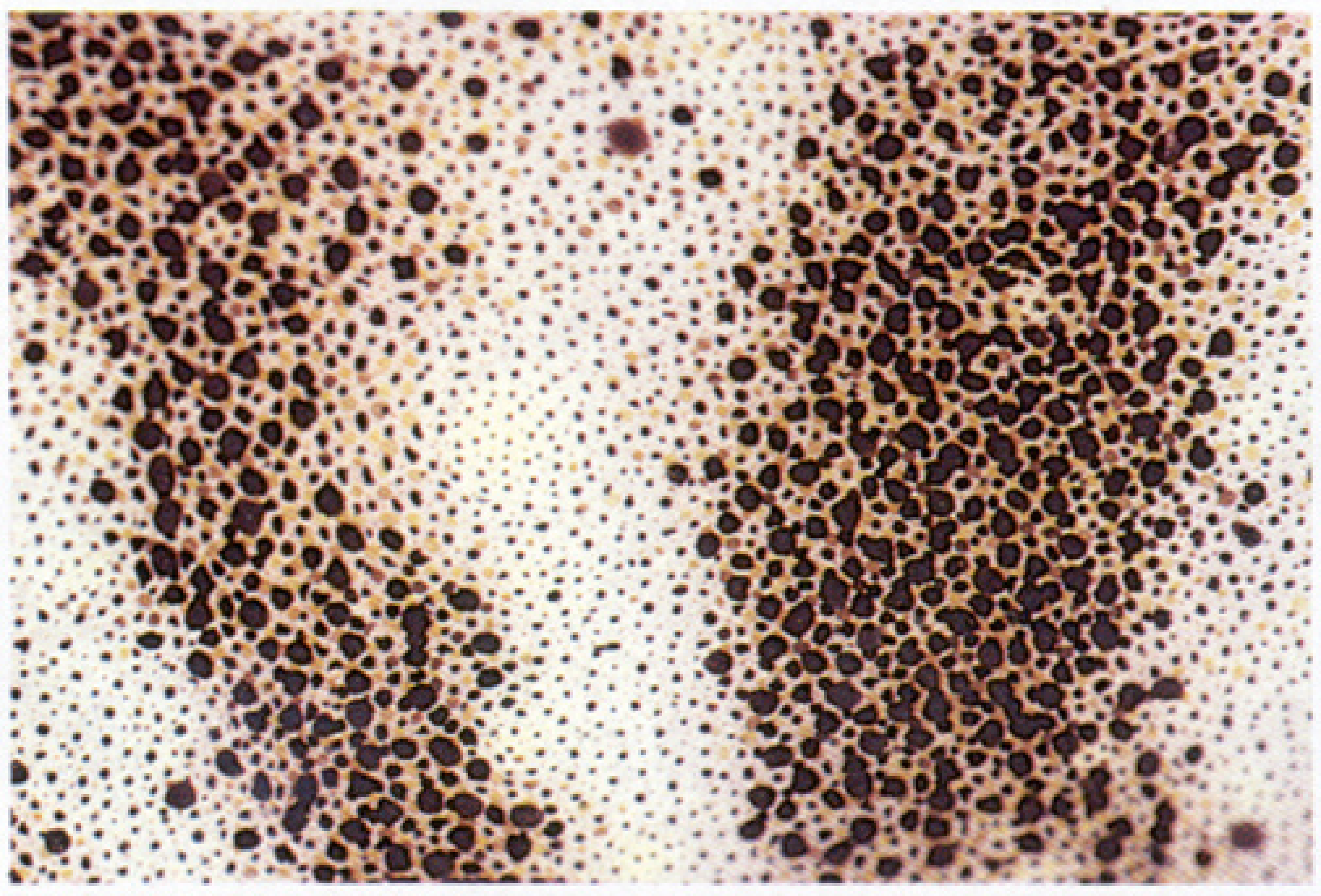


4

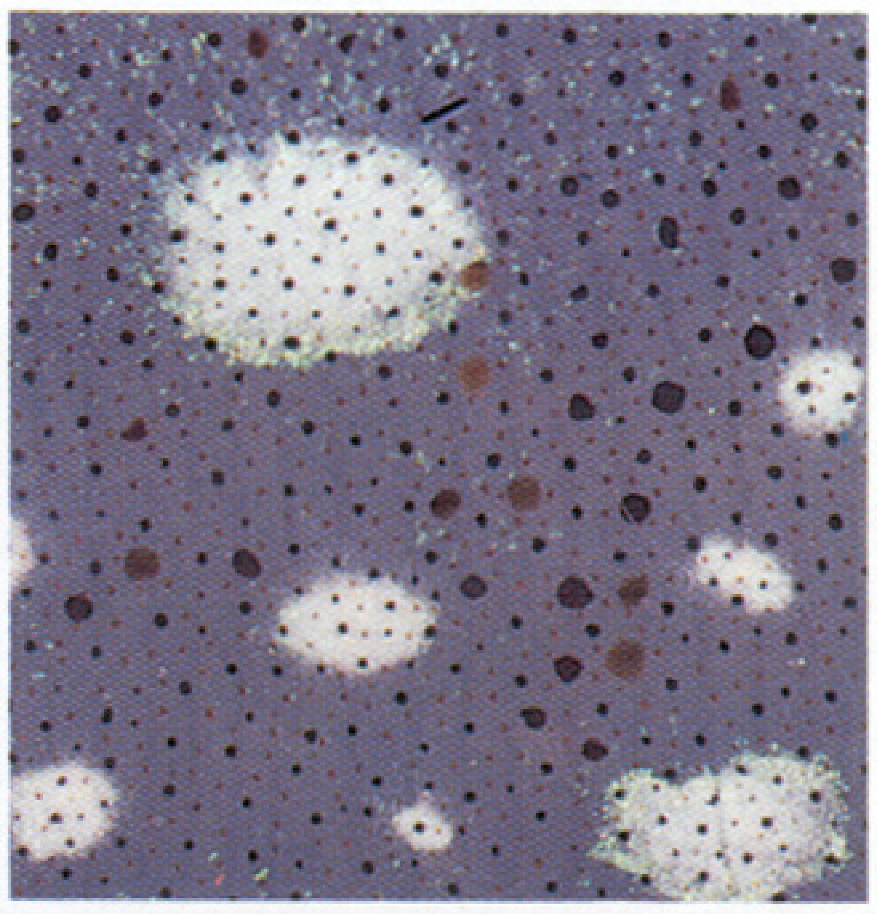


5, 6



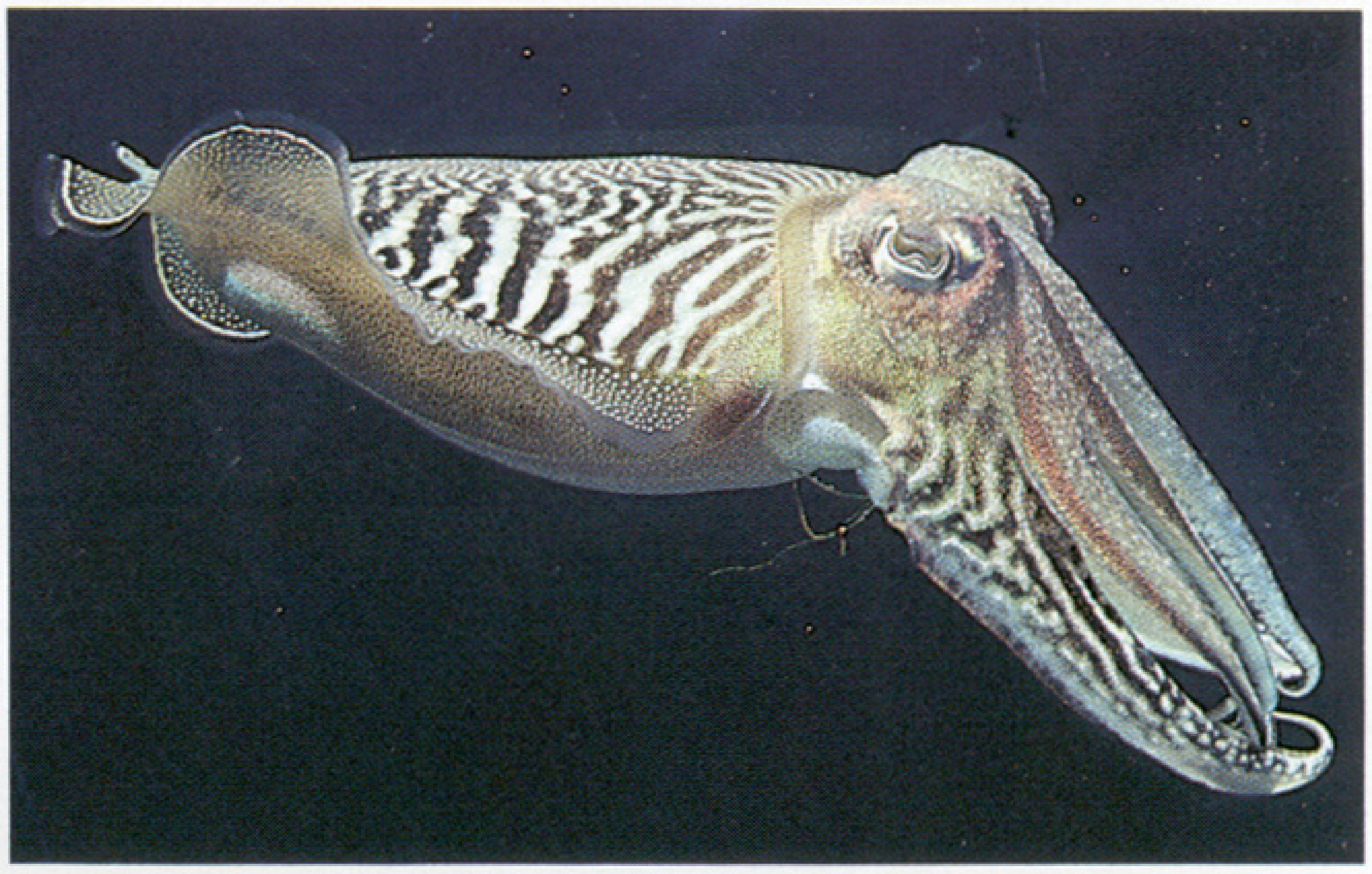


7

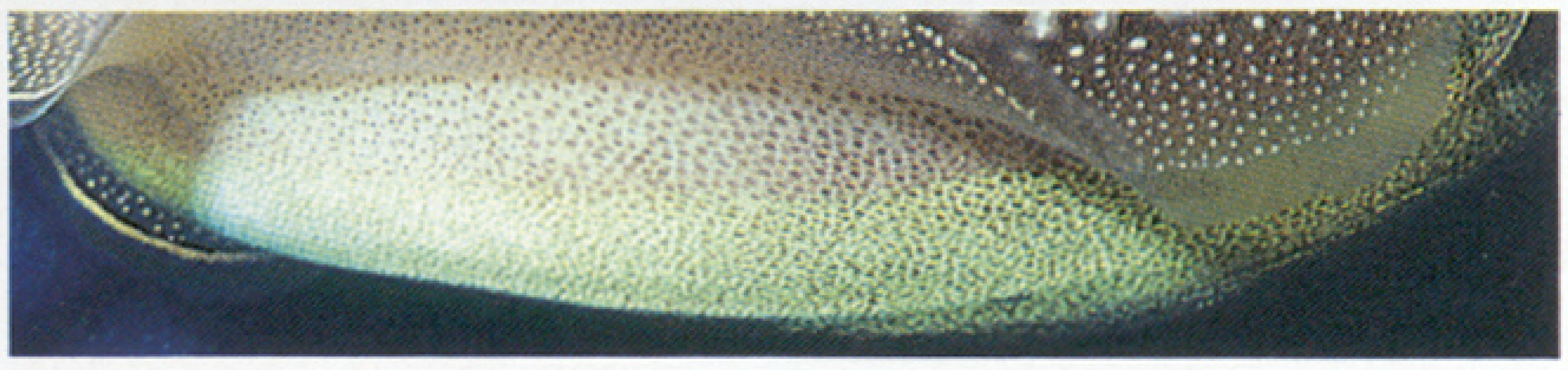


8

9



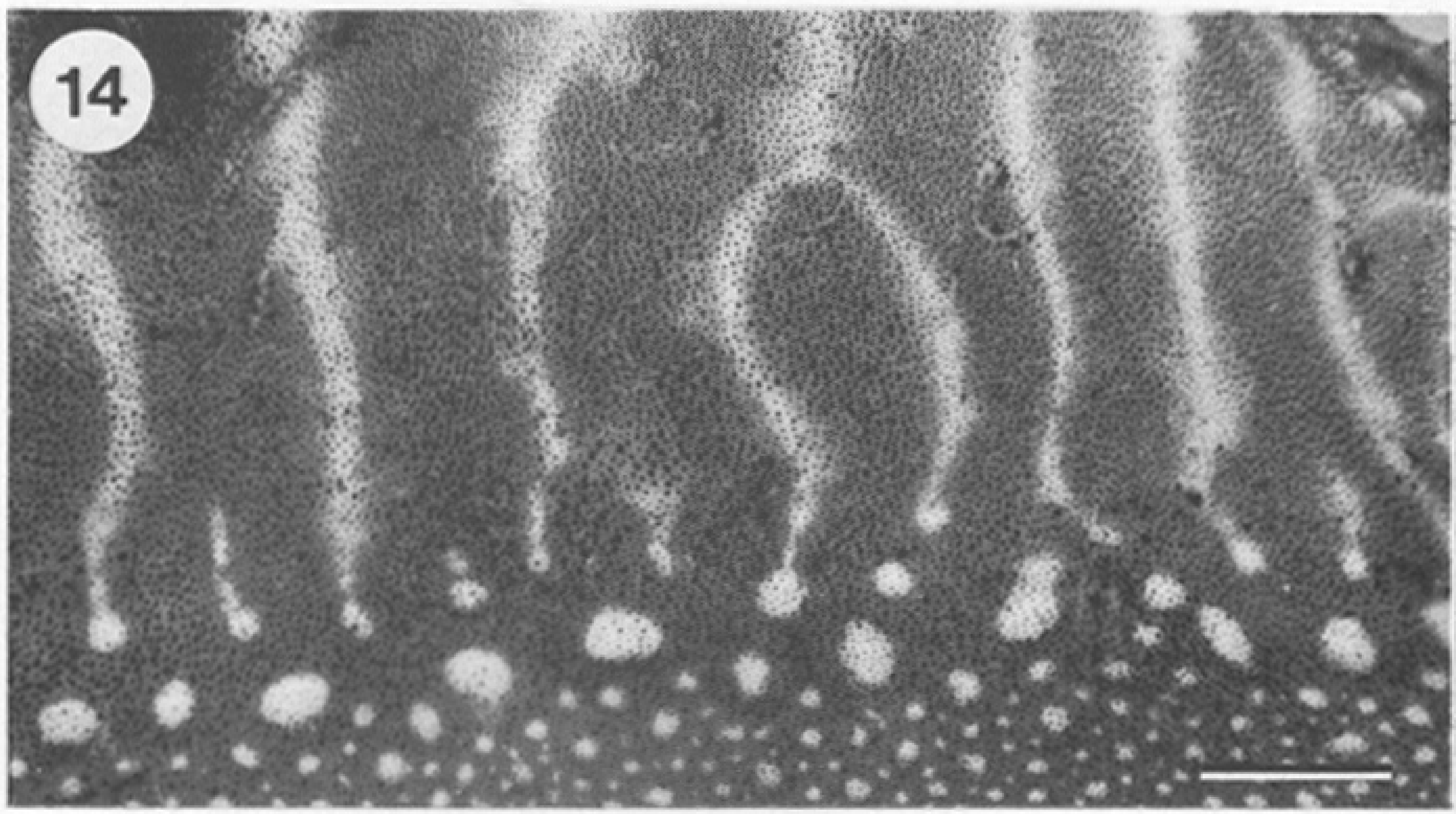
10

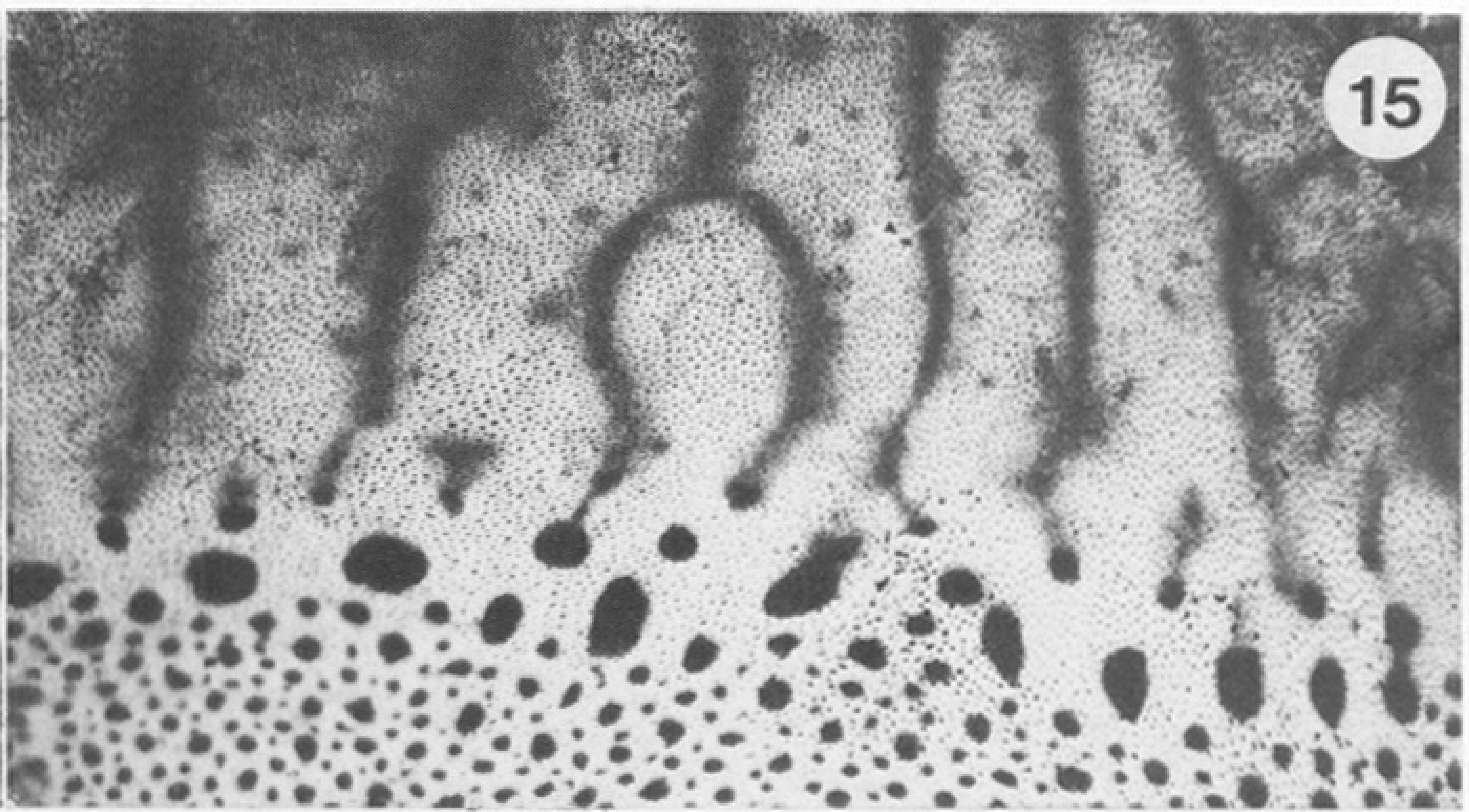


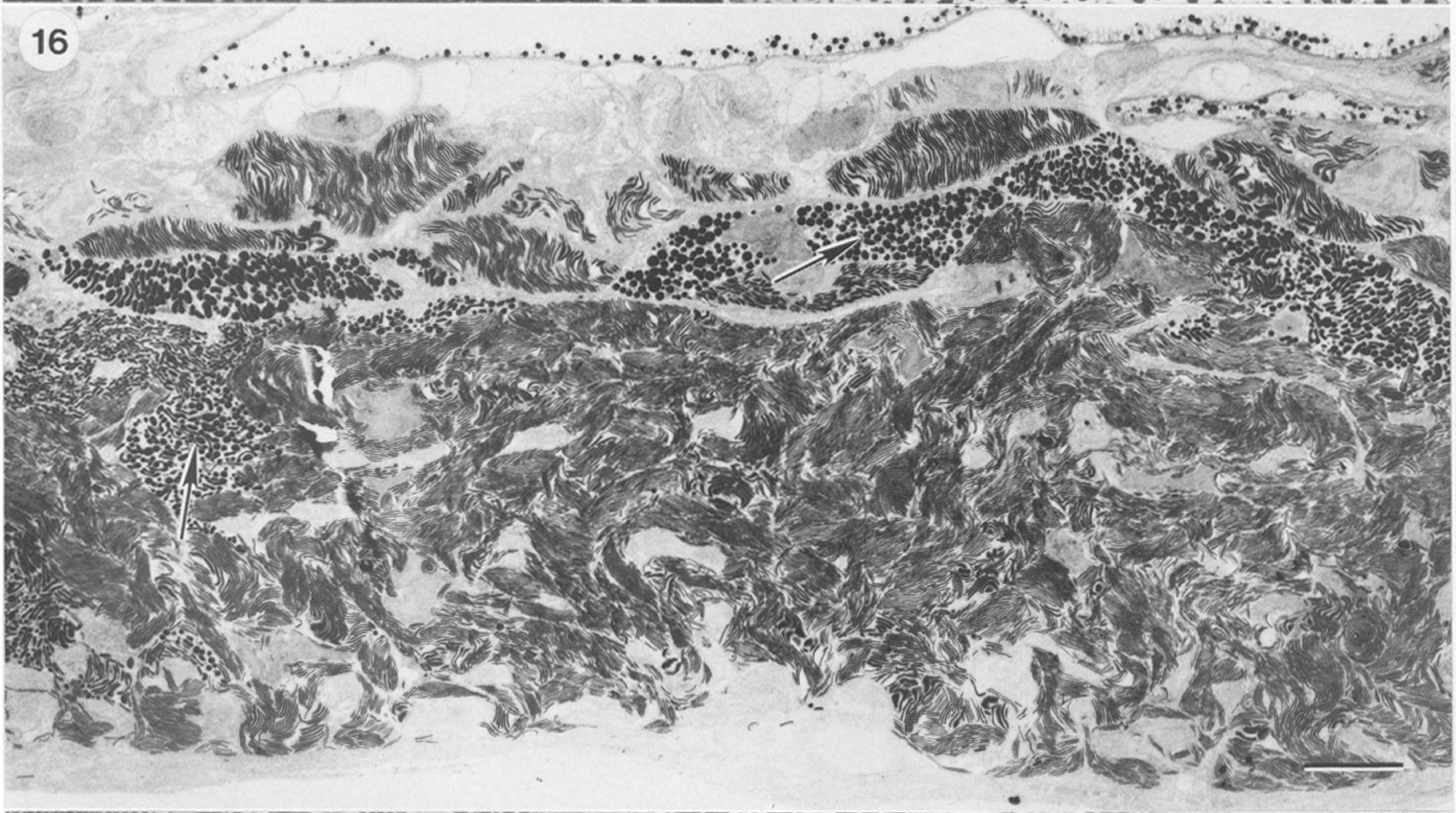
11

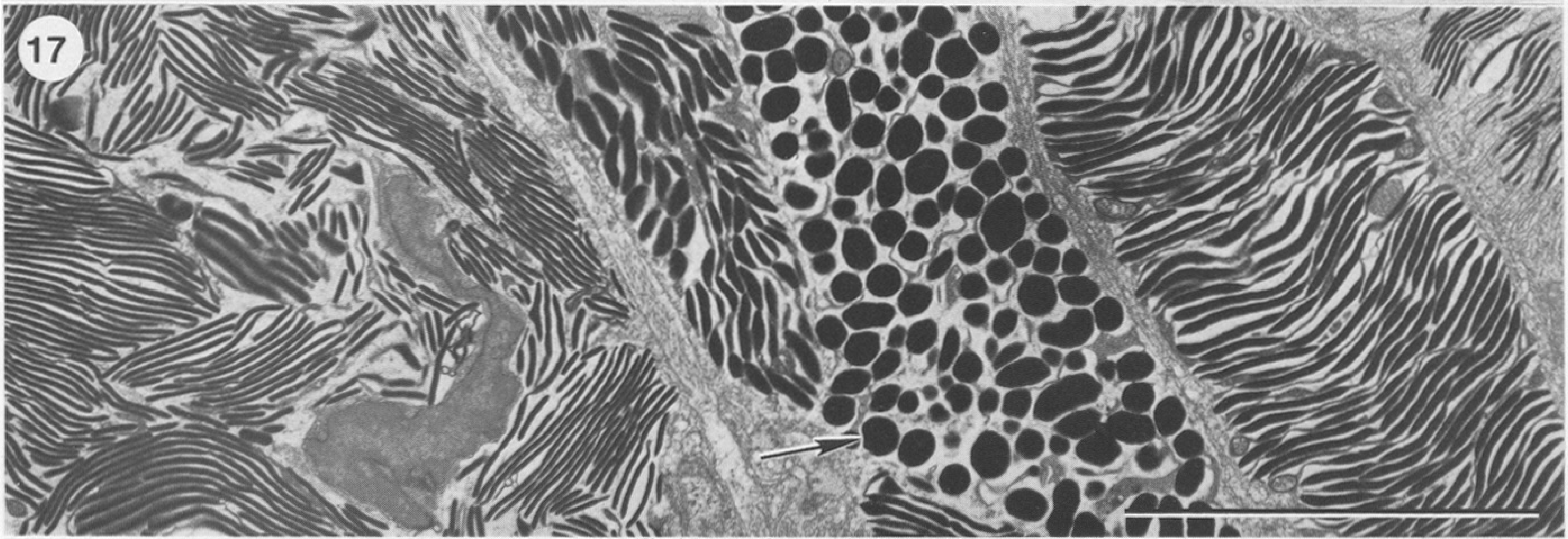
12

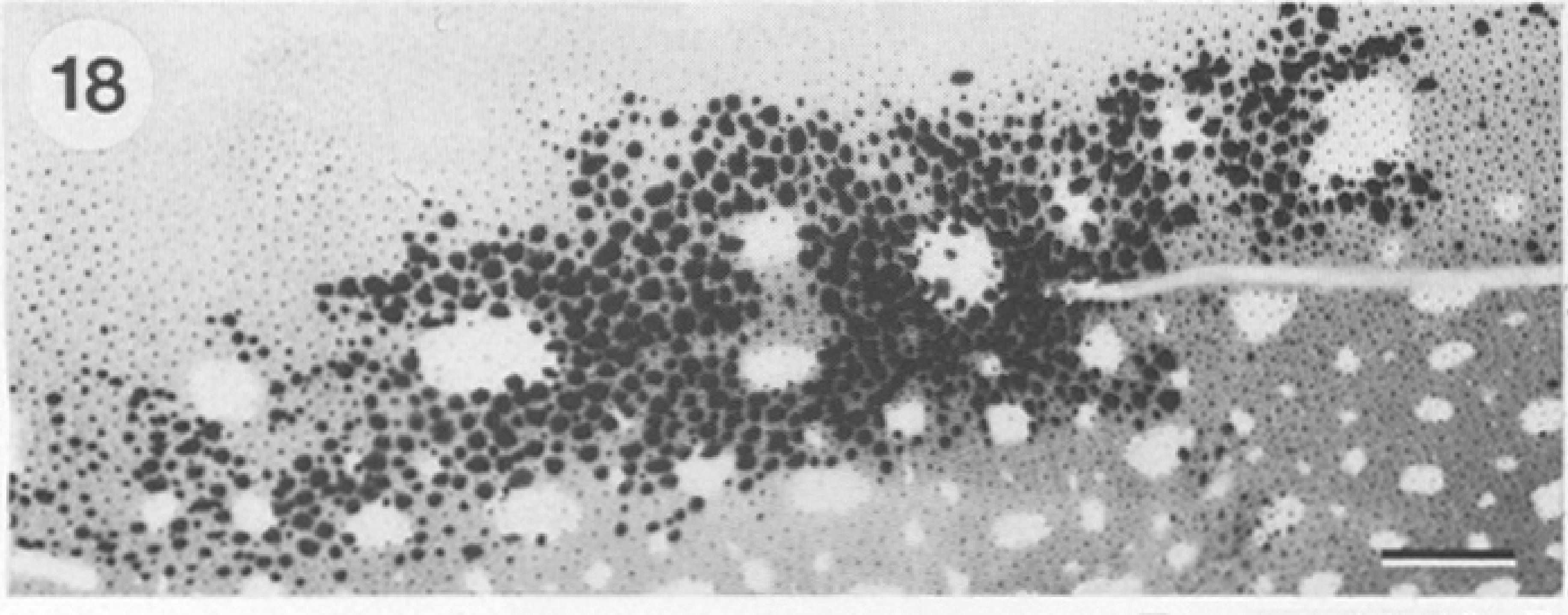
Figures 2–12. For description see opposite.

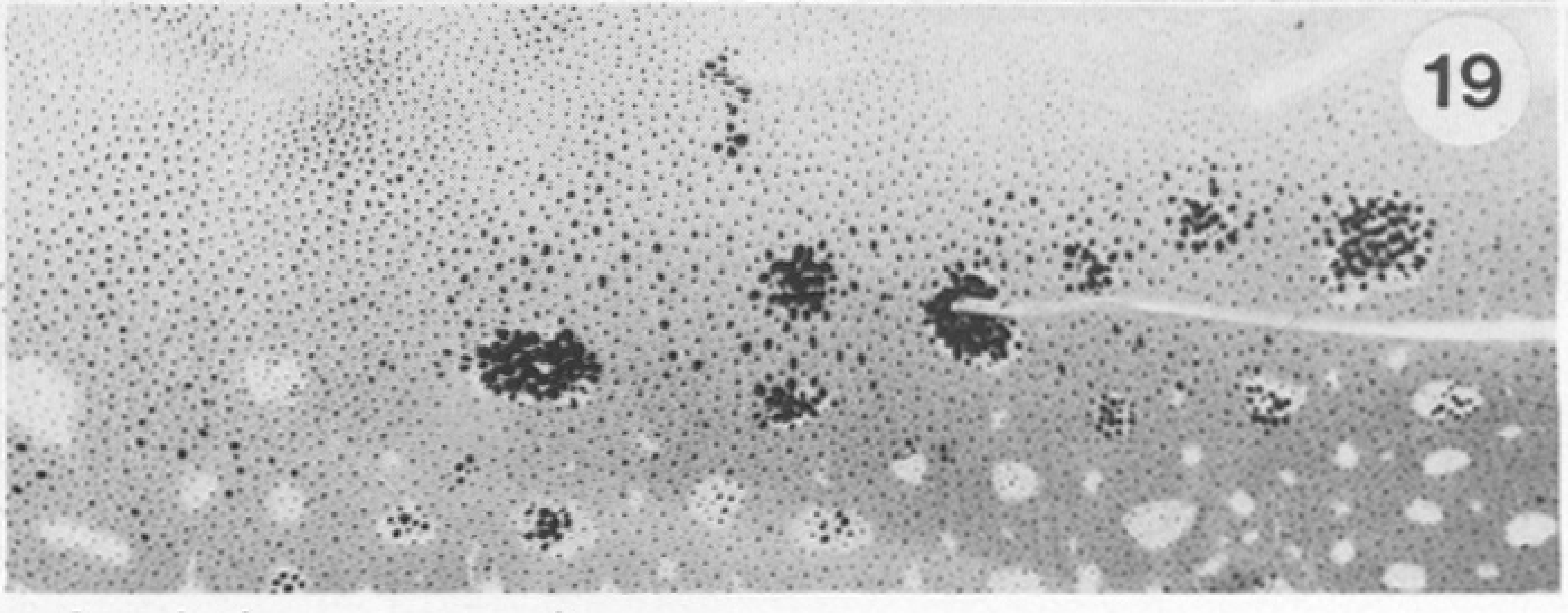






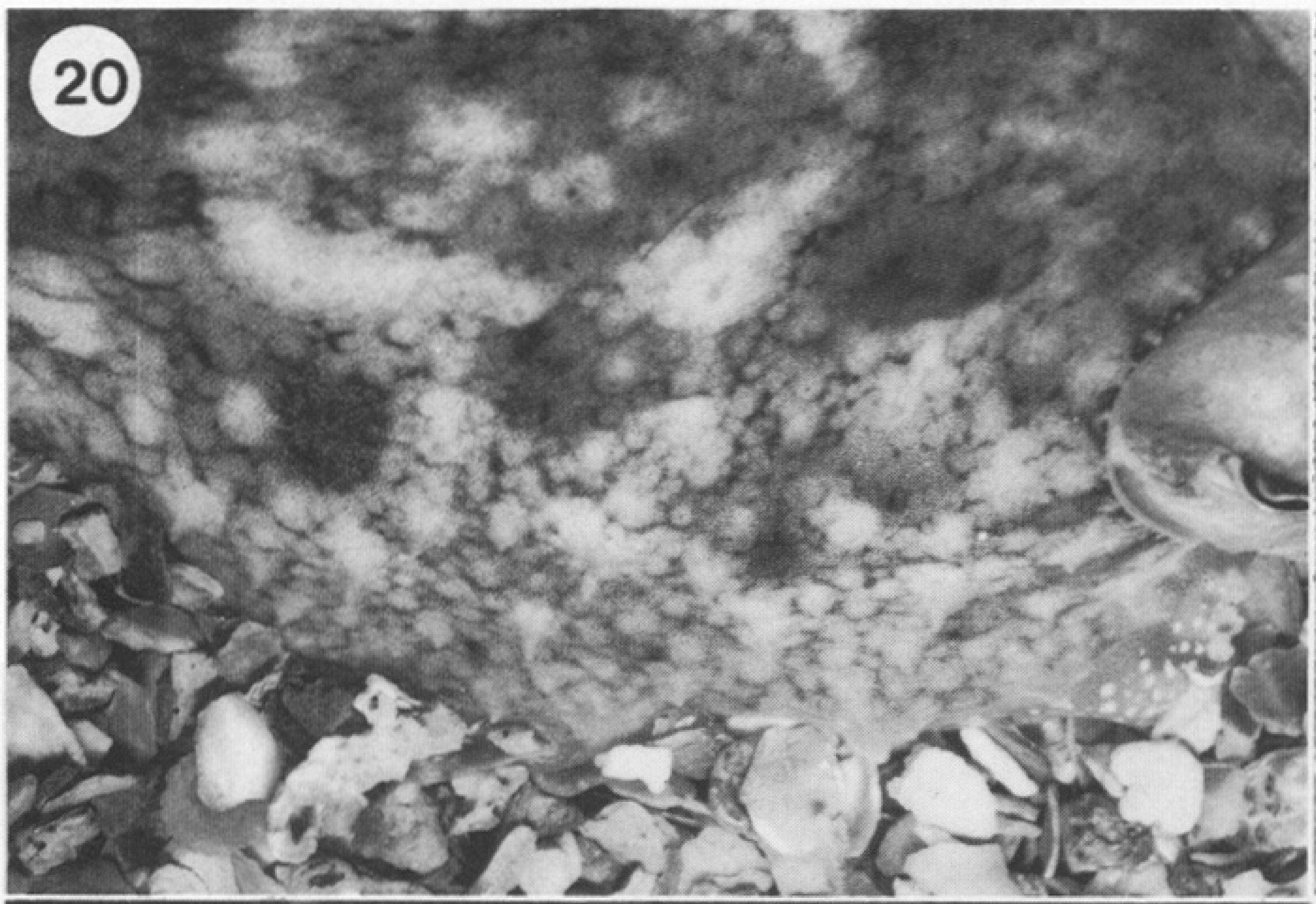




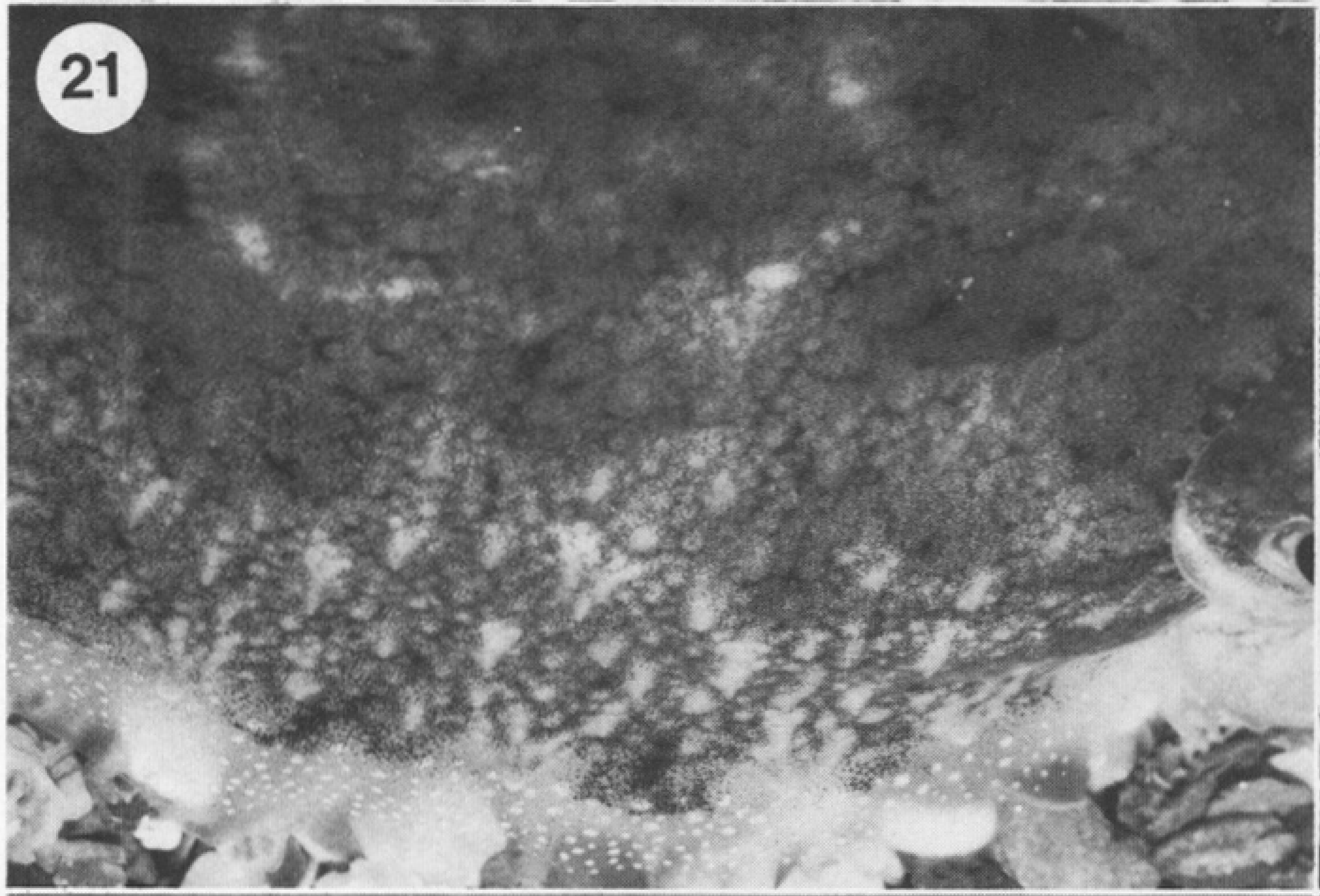


FIGURES 14–19. For description see opposite.

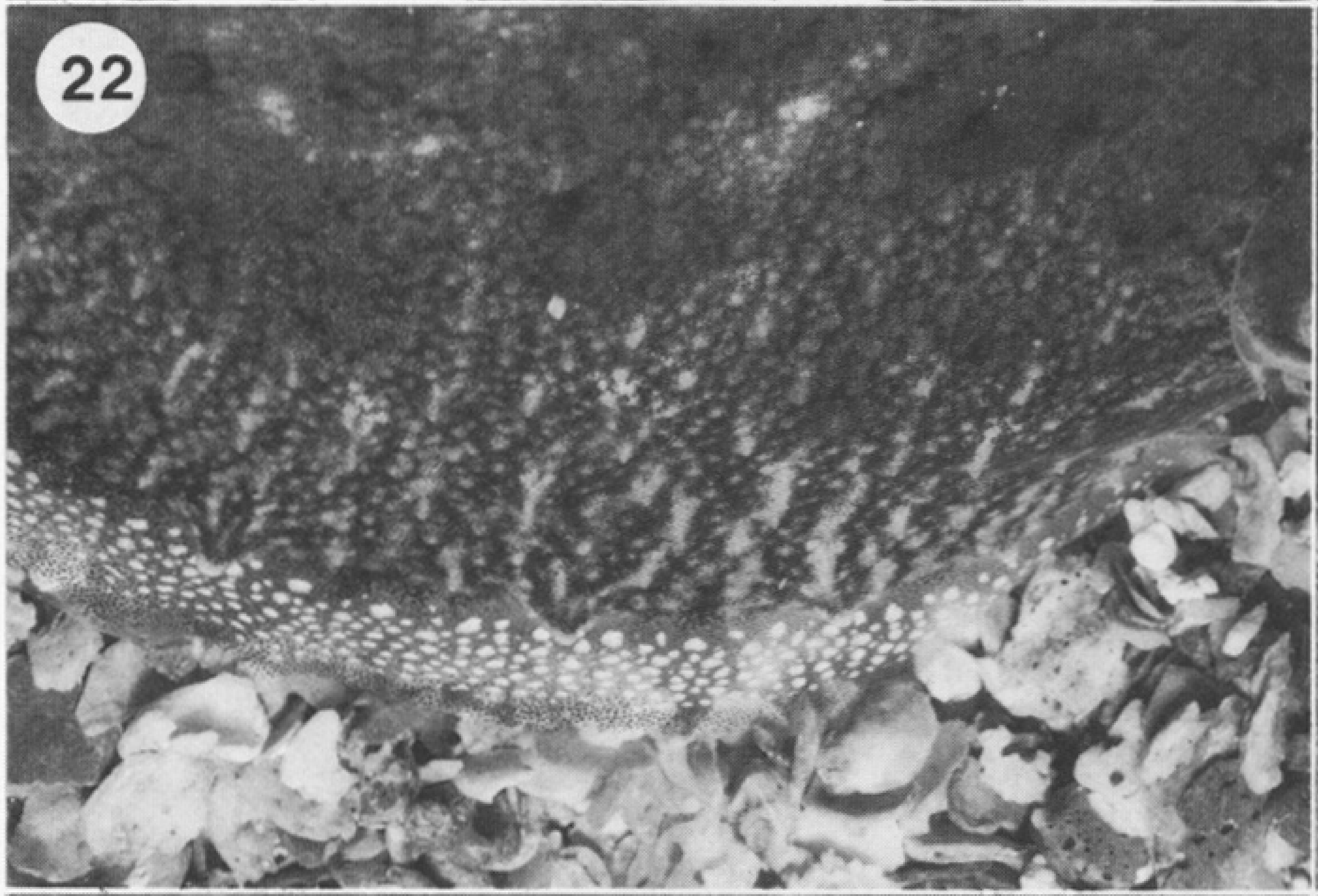
20



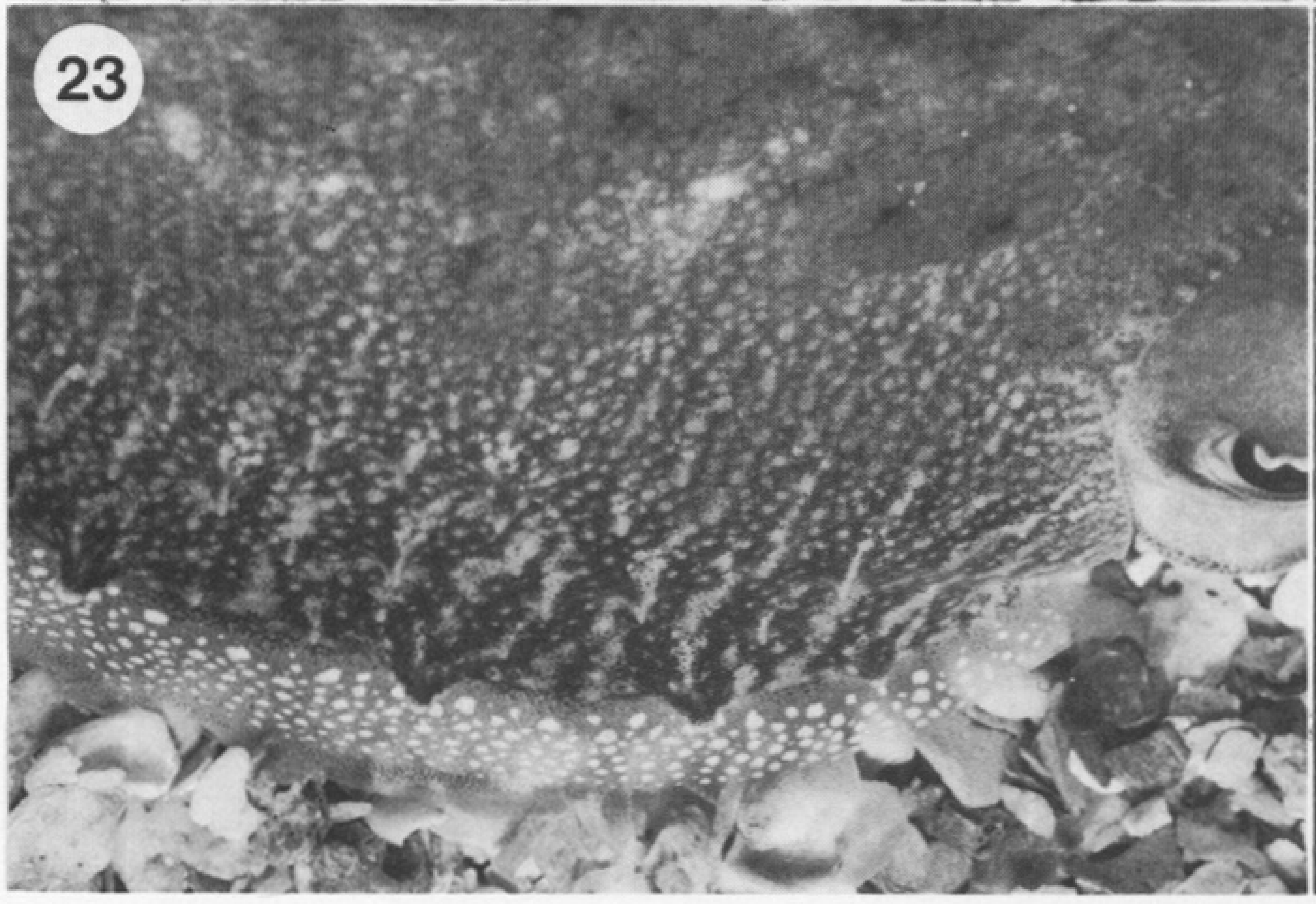
21



22

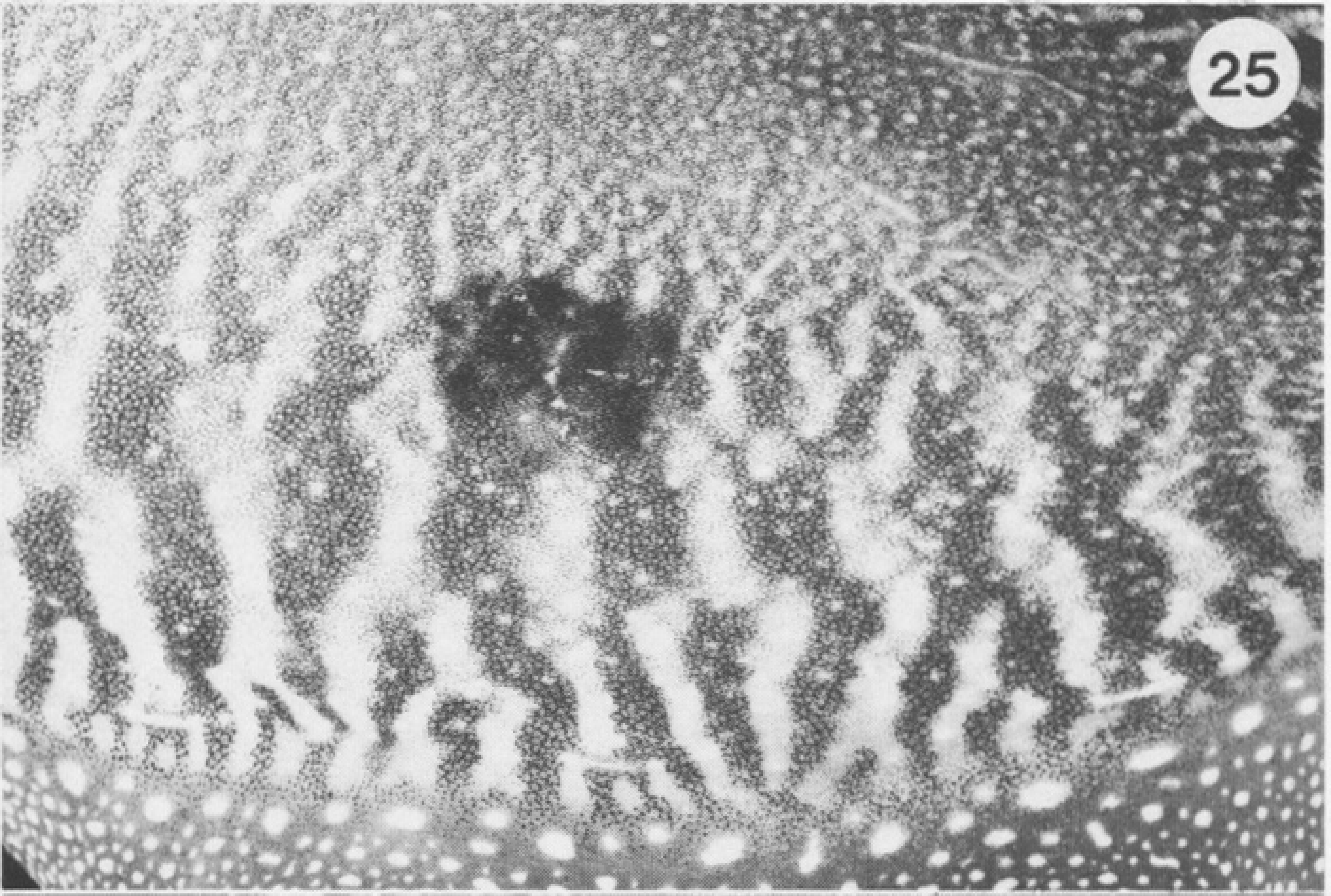


23

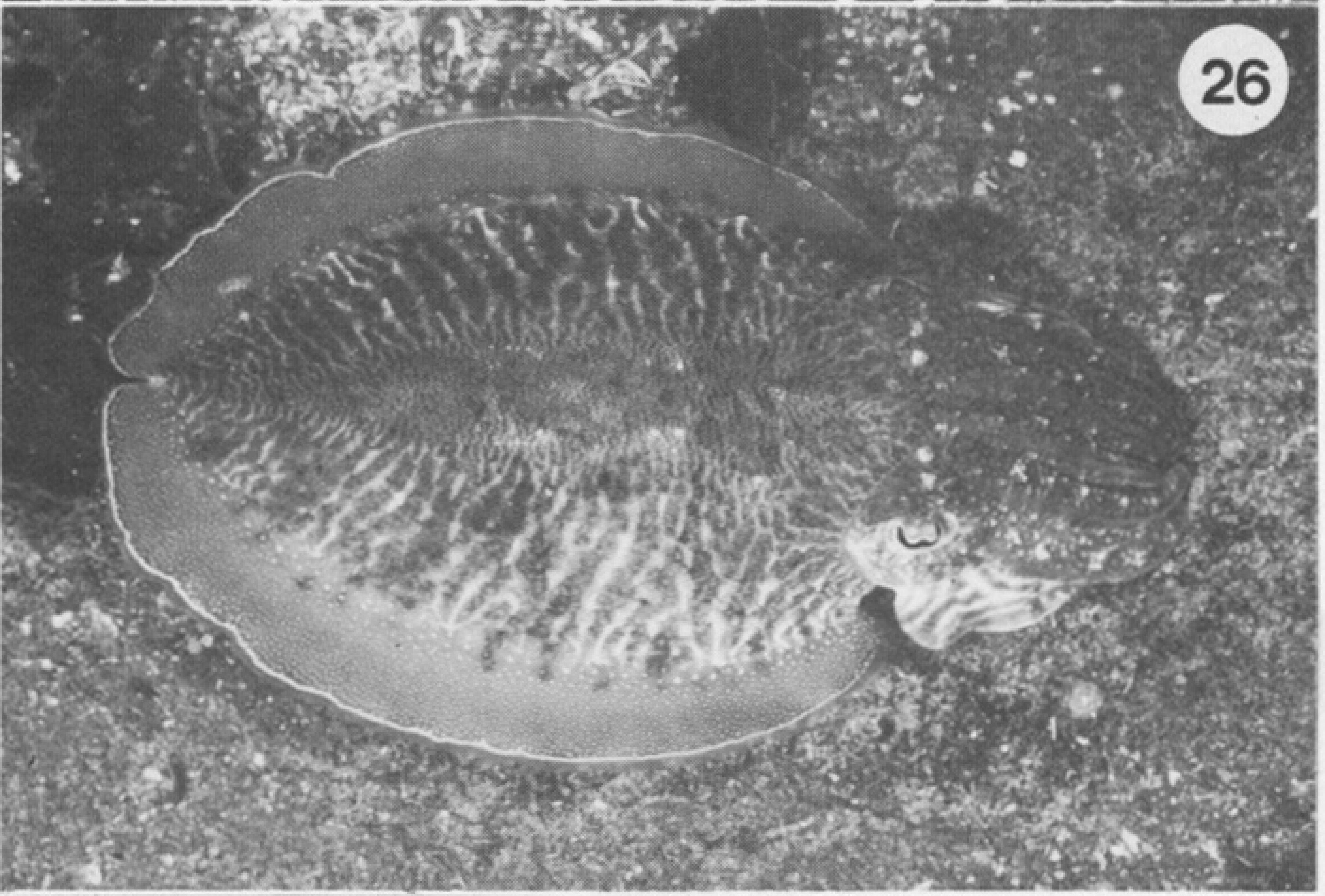


24

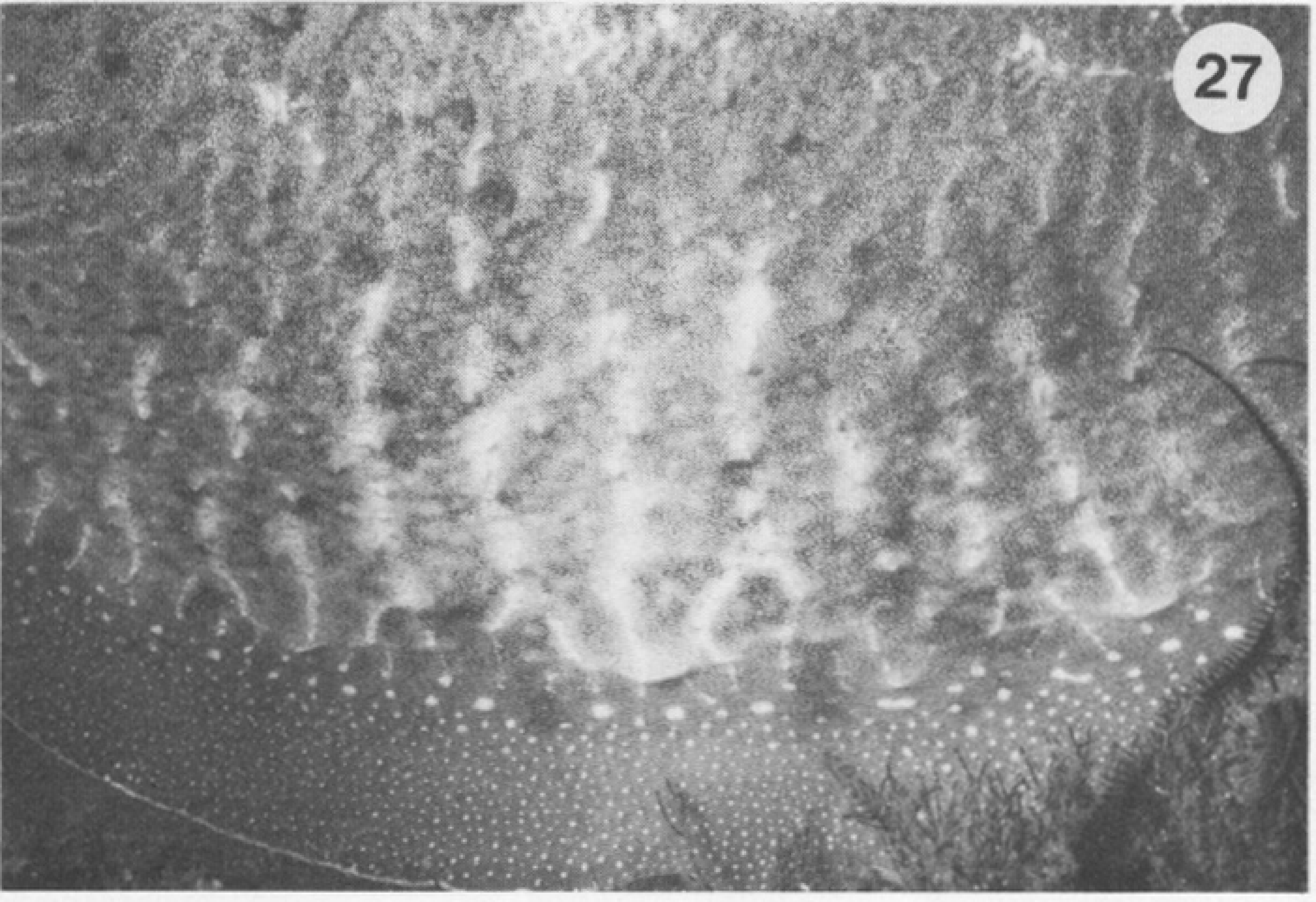
25



26



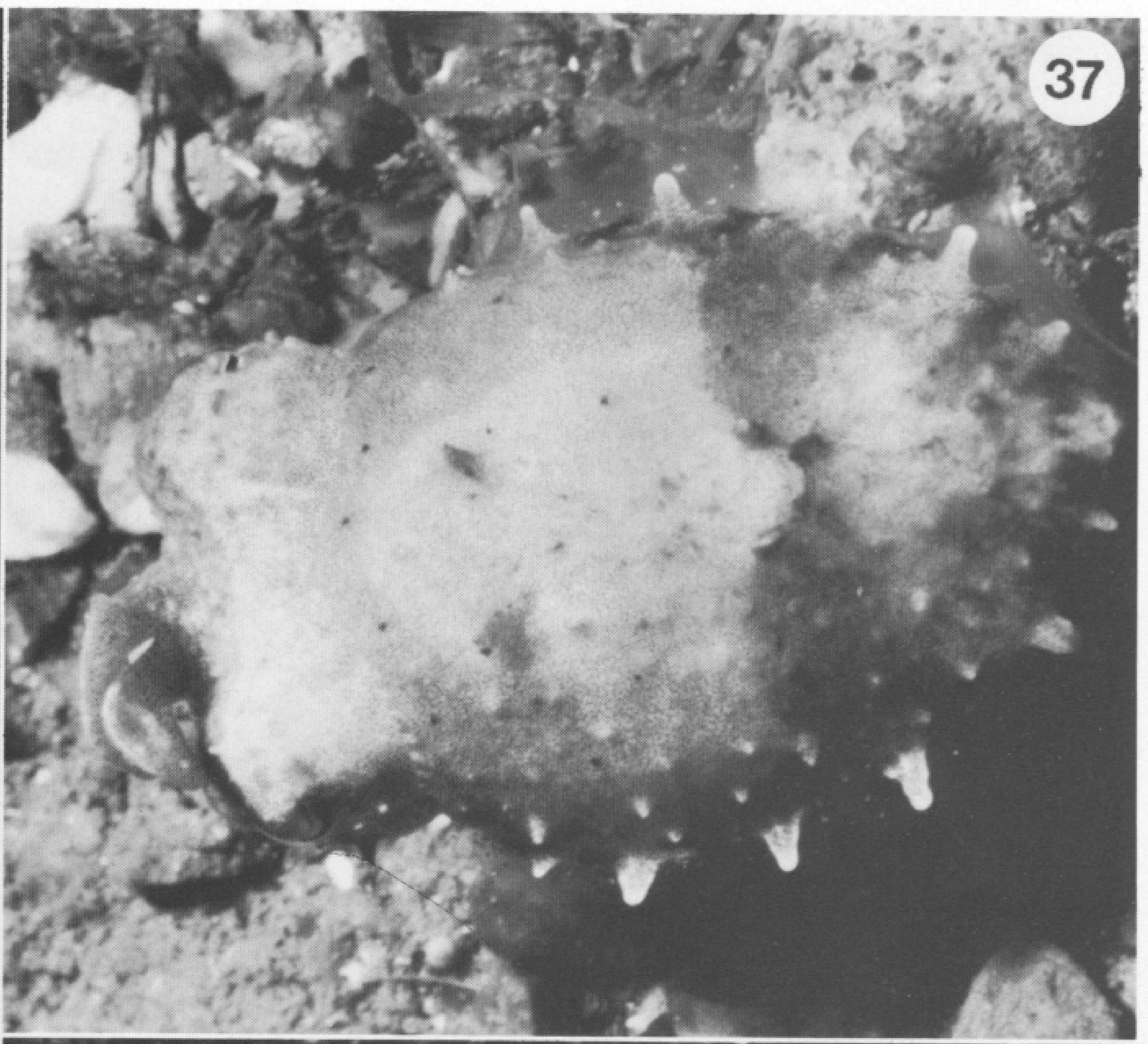
27

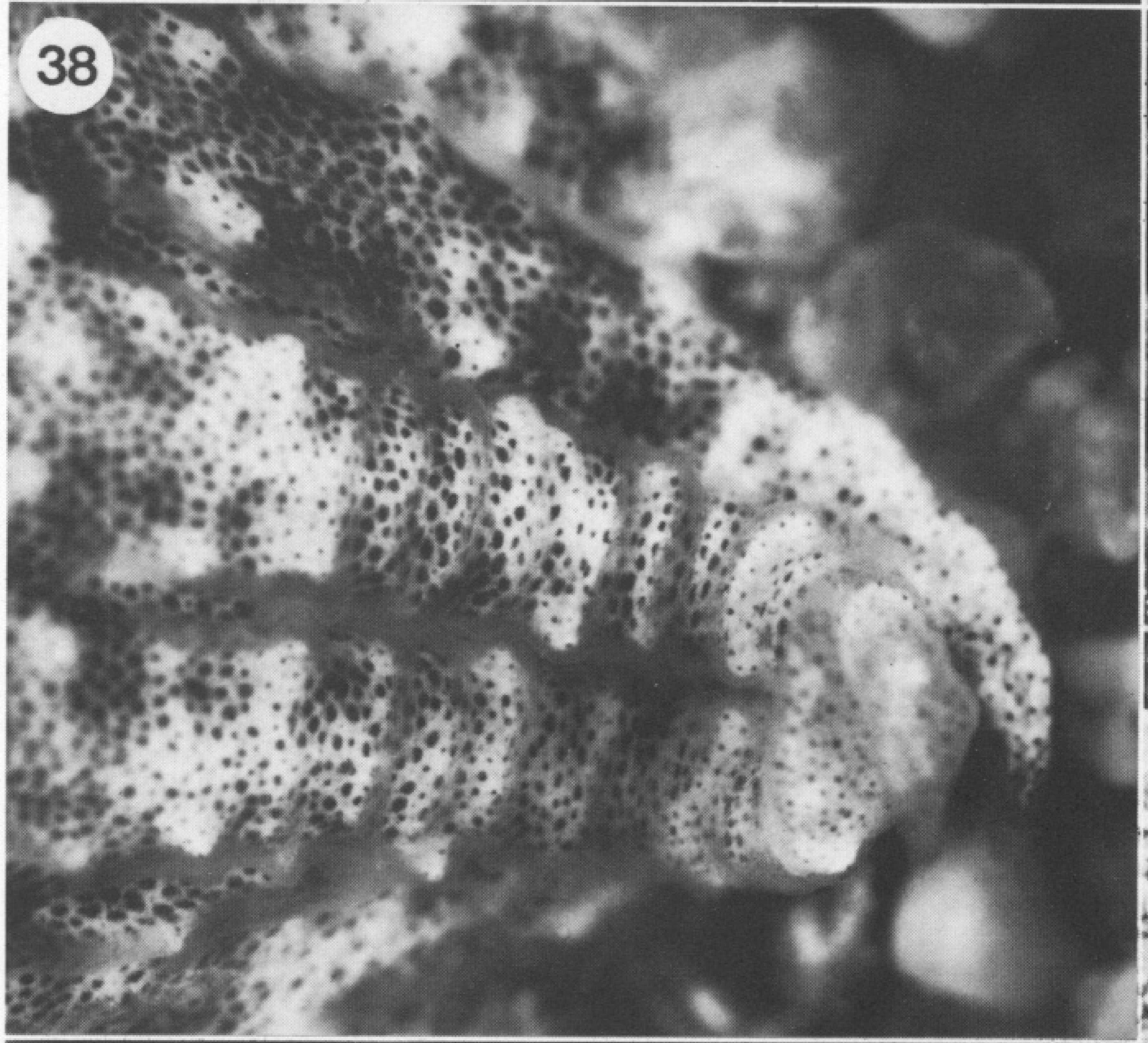


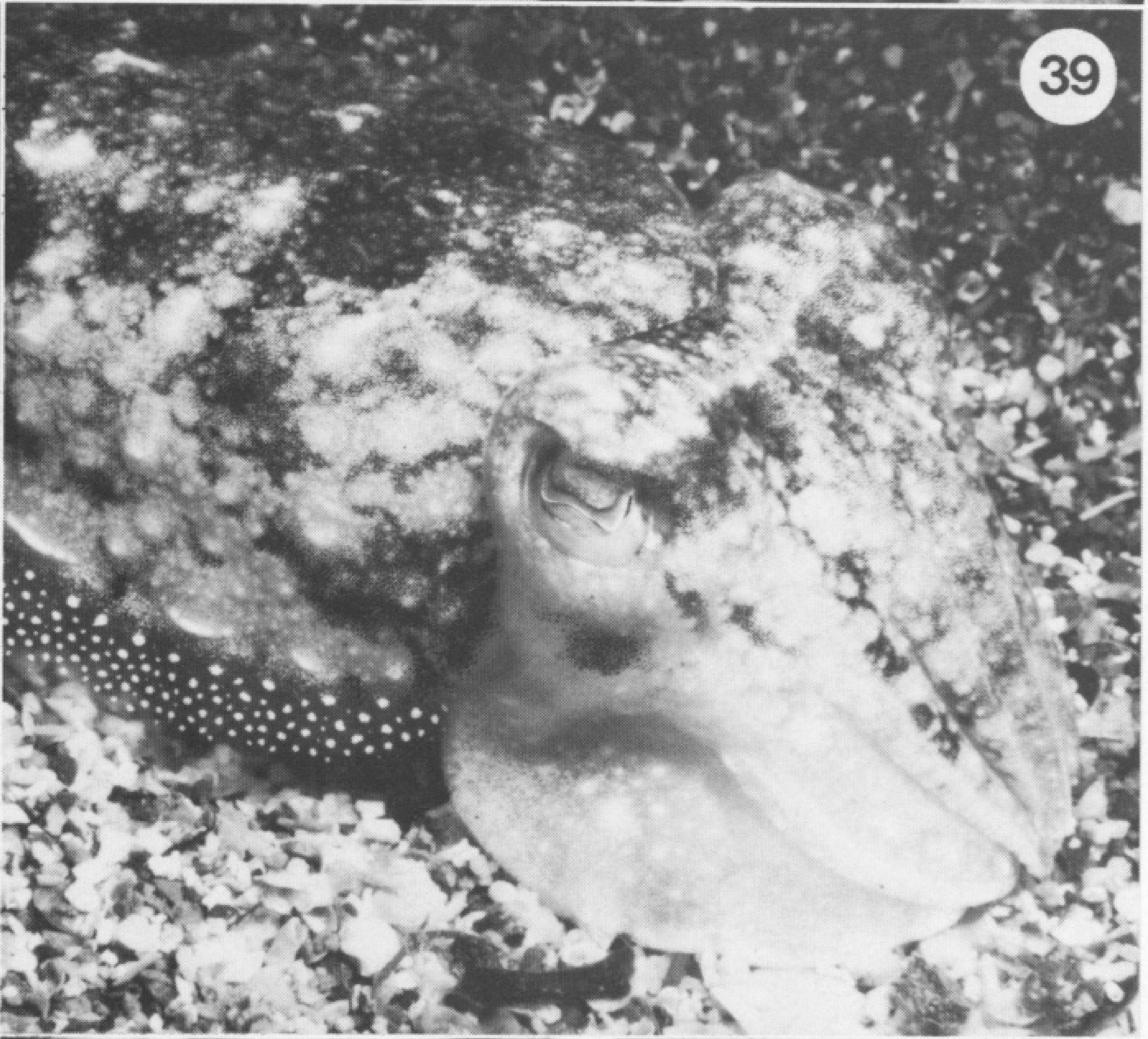
FIGURES 20–27. For description see opposite.

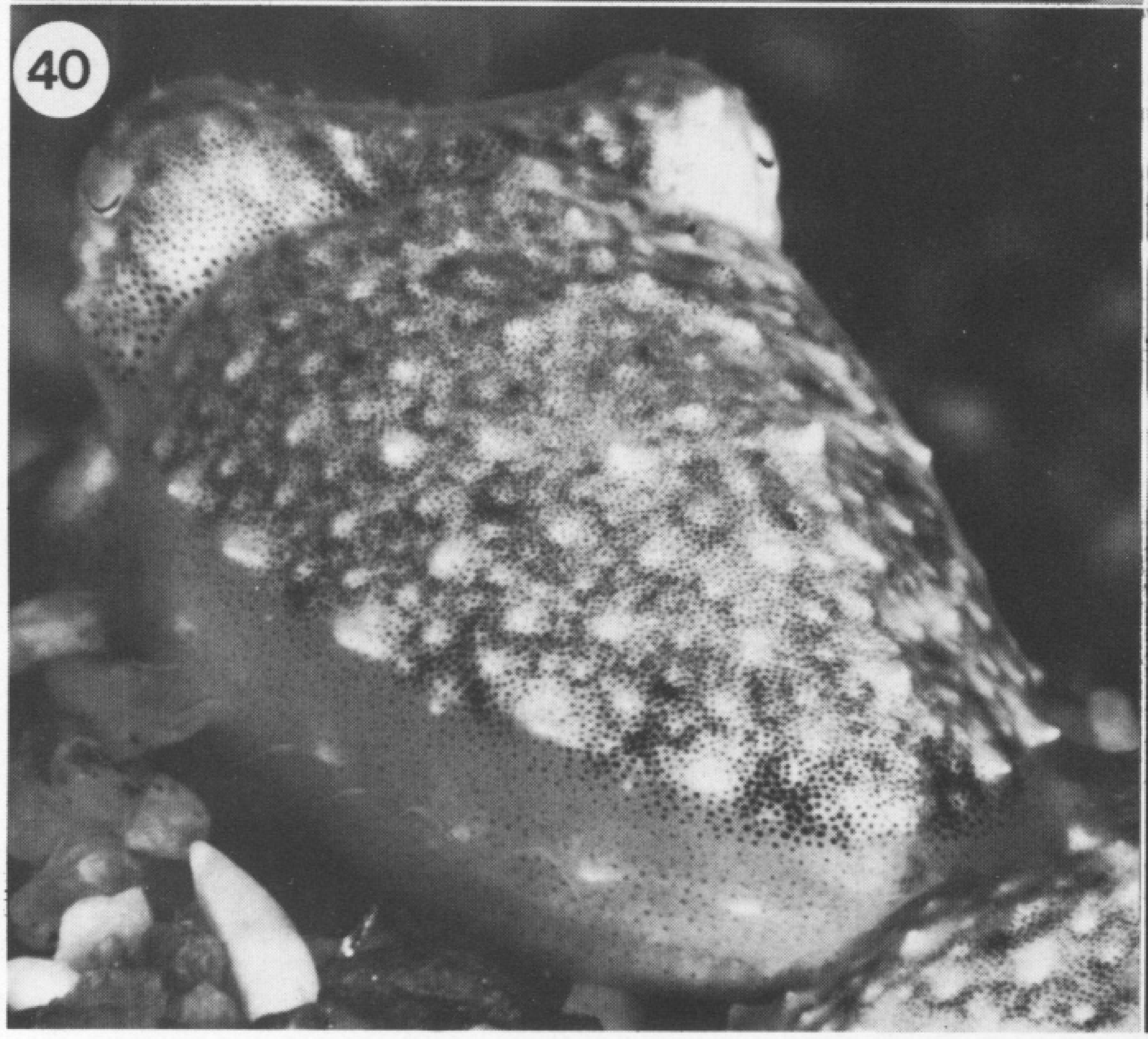
FIGURES 28–35. For description see opposite.

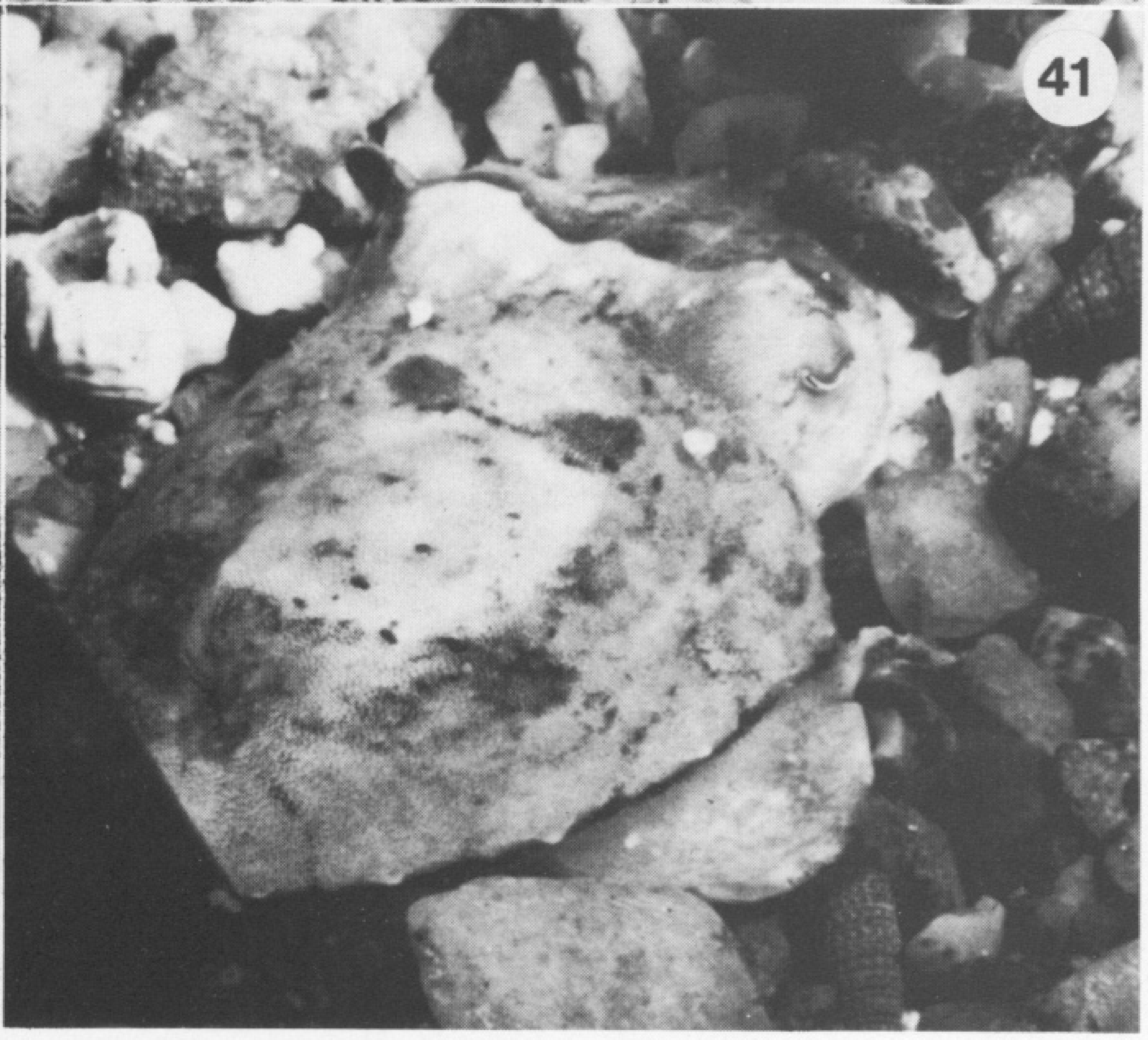

36


37


38

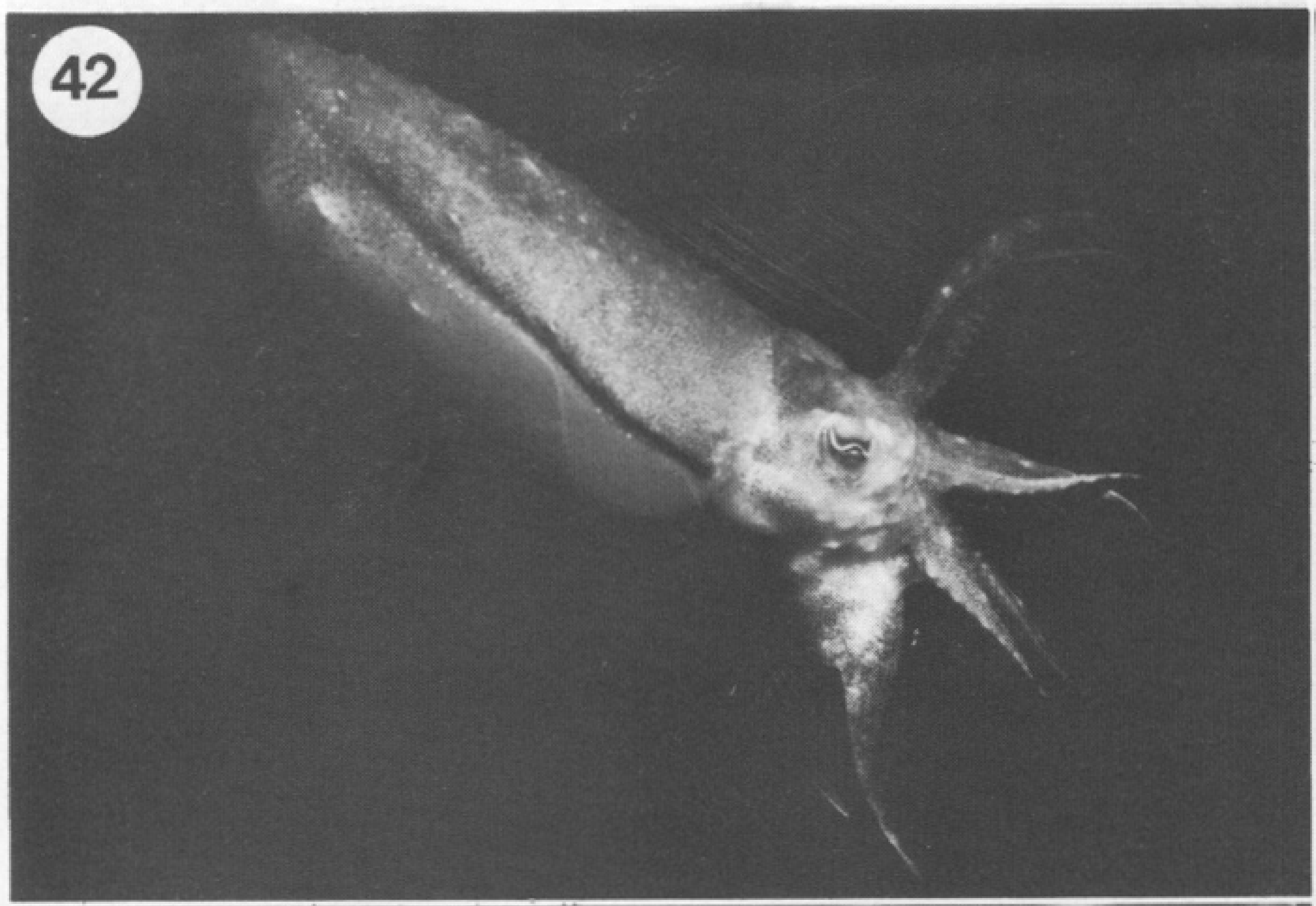

39


40

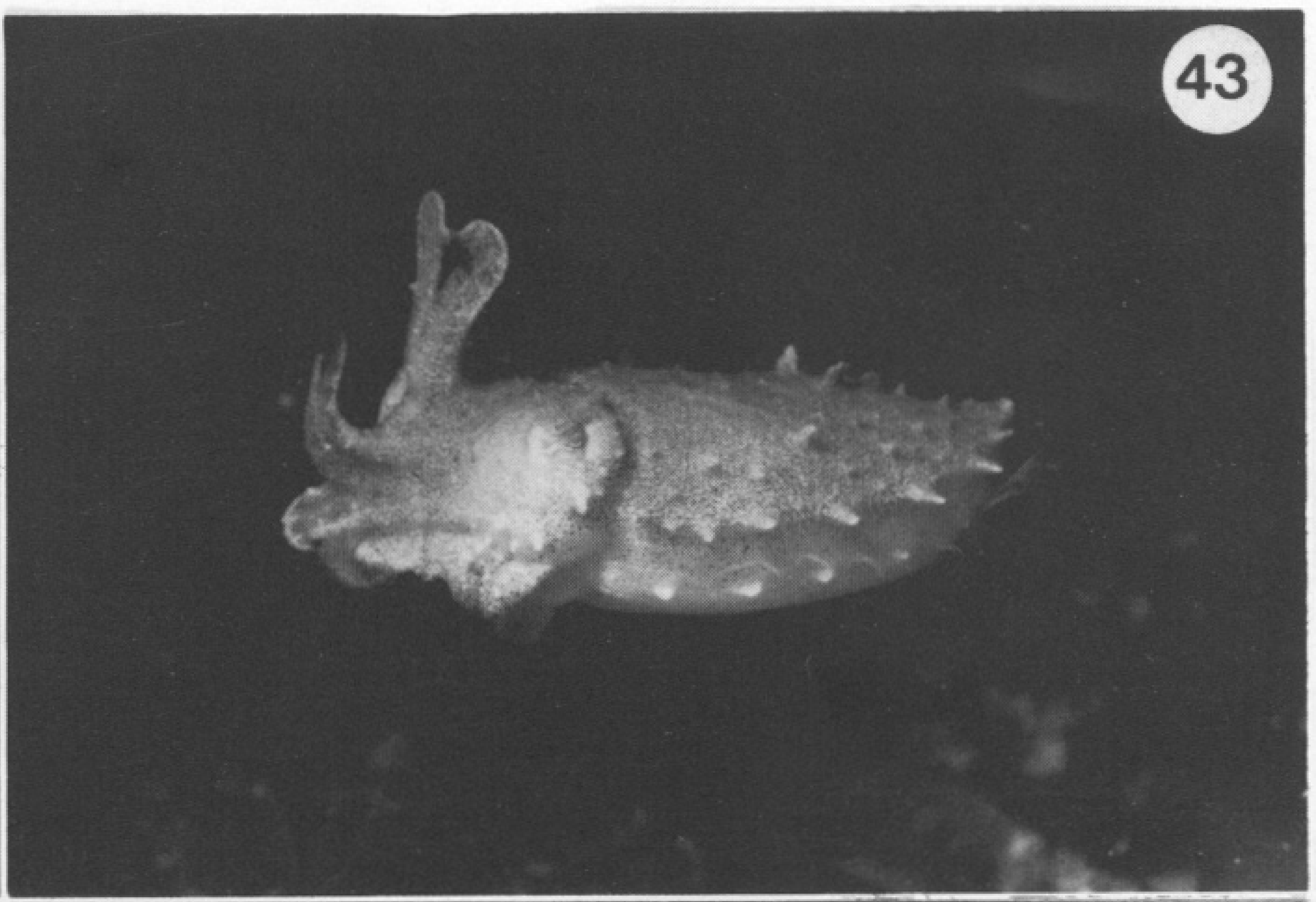

41

FIGURES 36–41. For description see opposite.

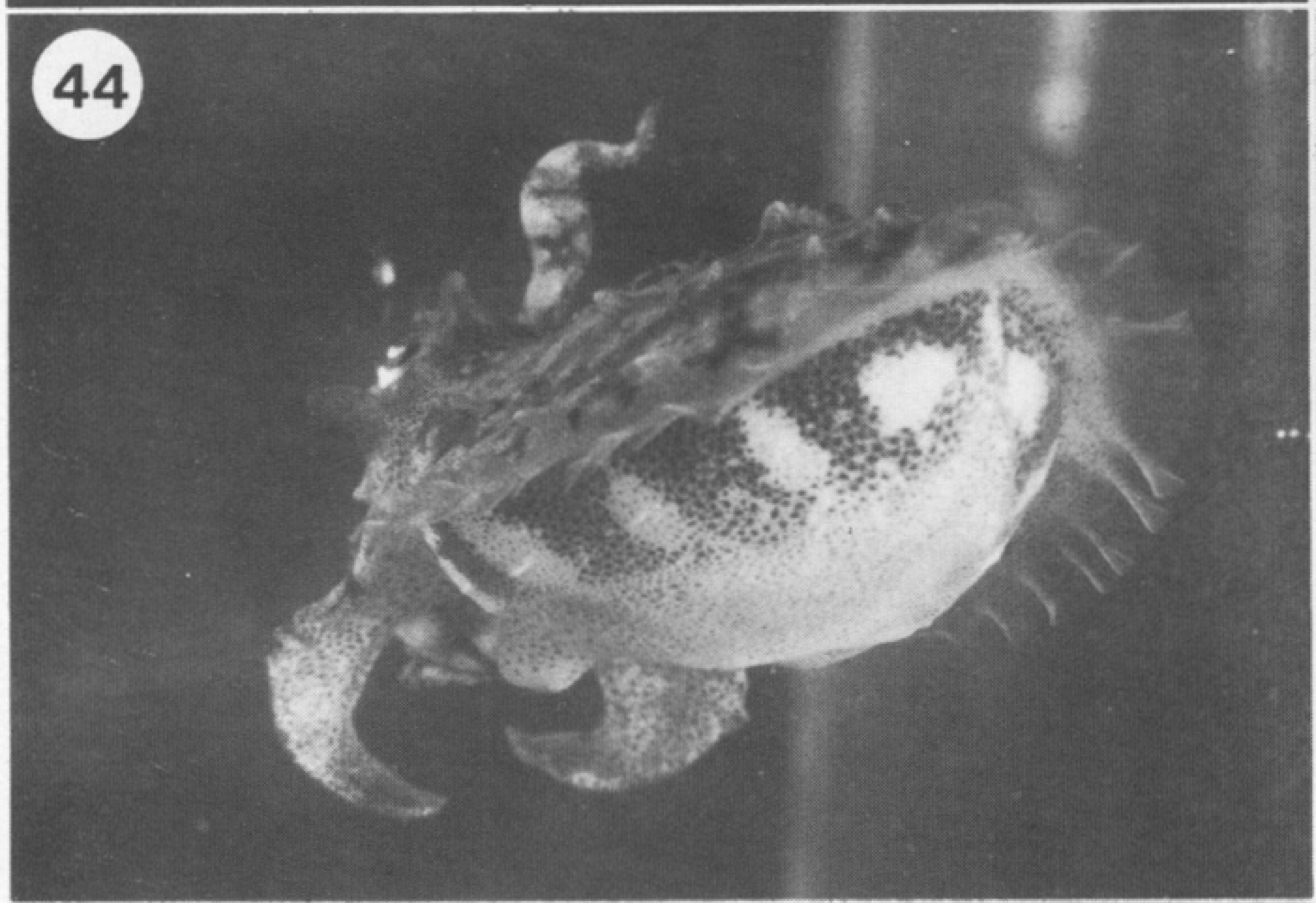
42



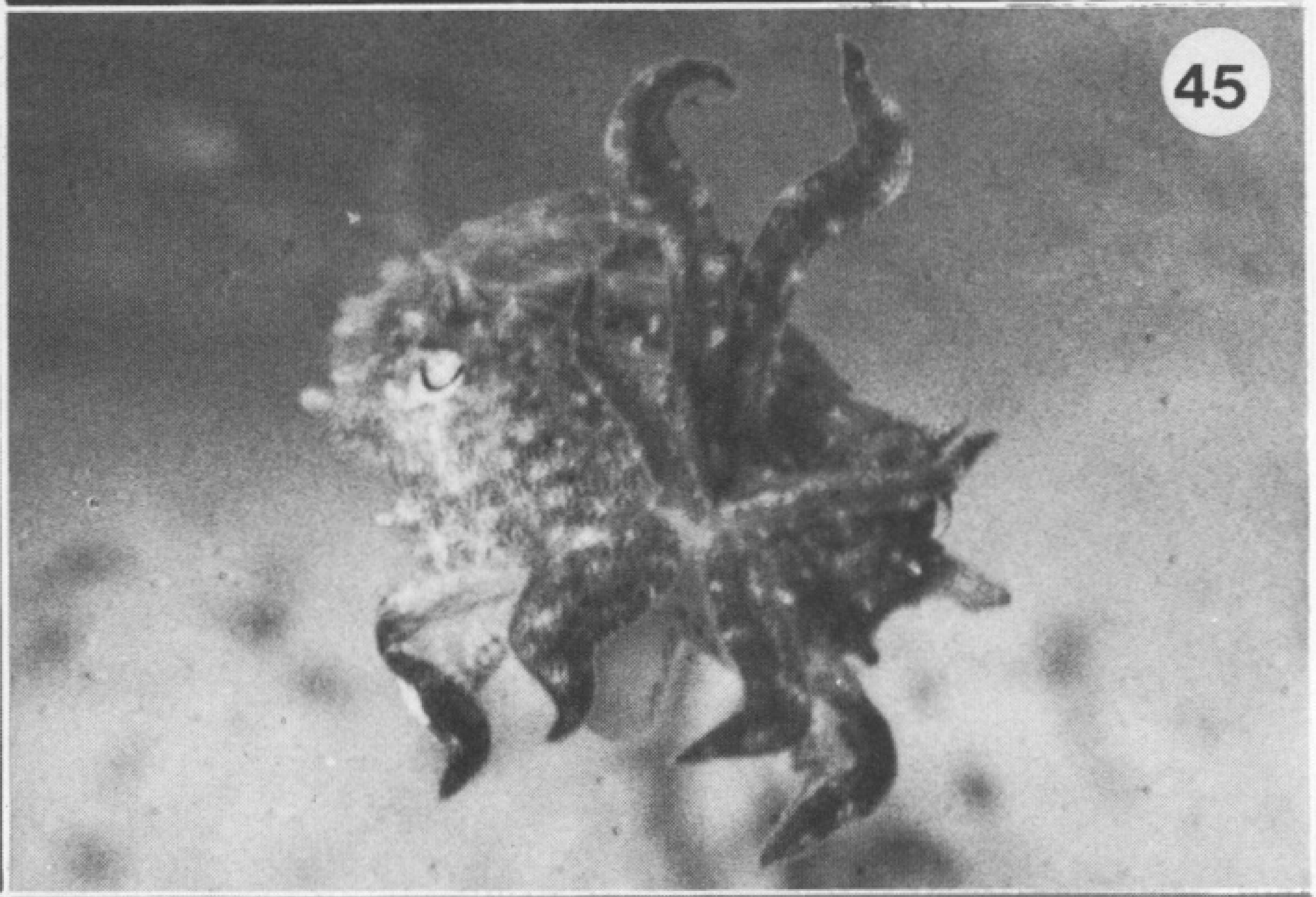
43



44



45

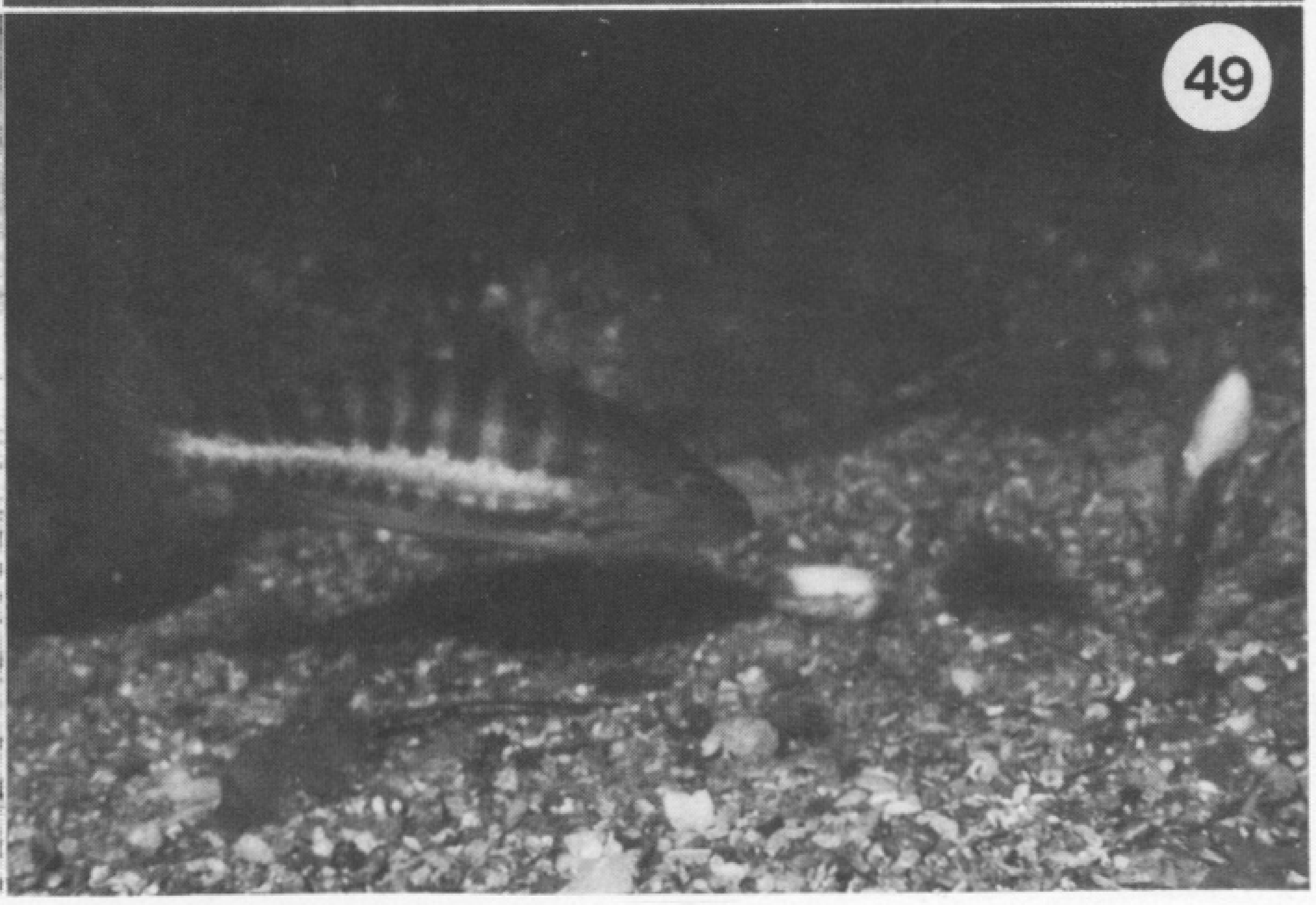


46

47

48

49

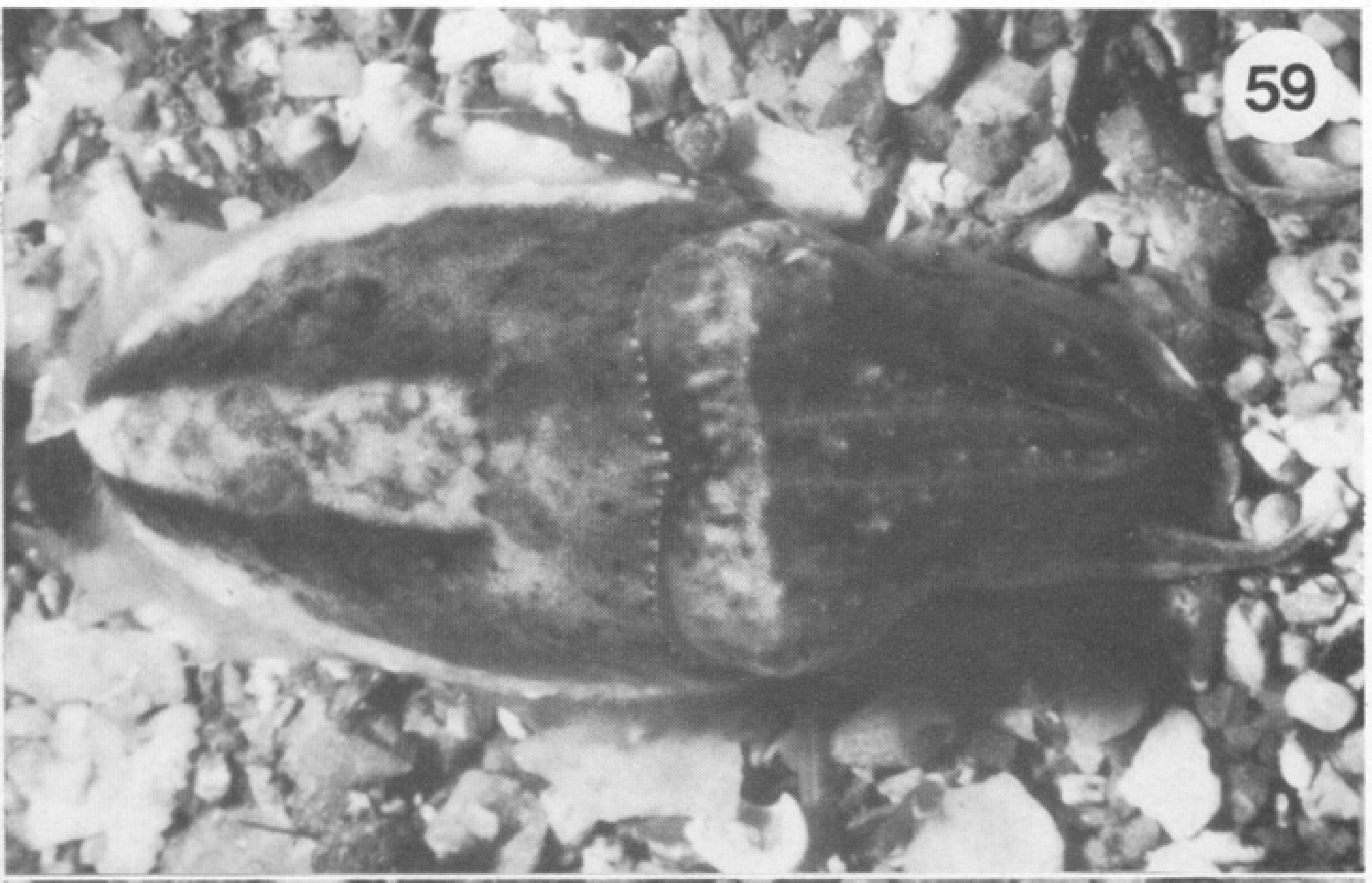


FIGURES 42–49. For description see opposite.

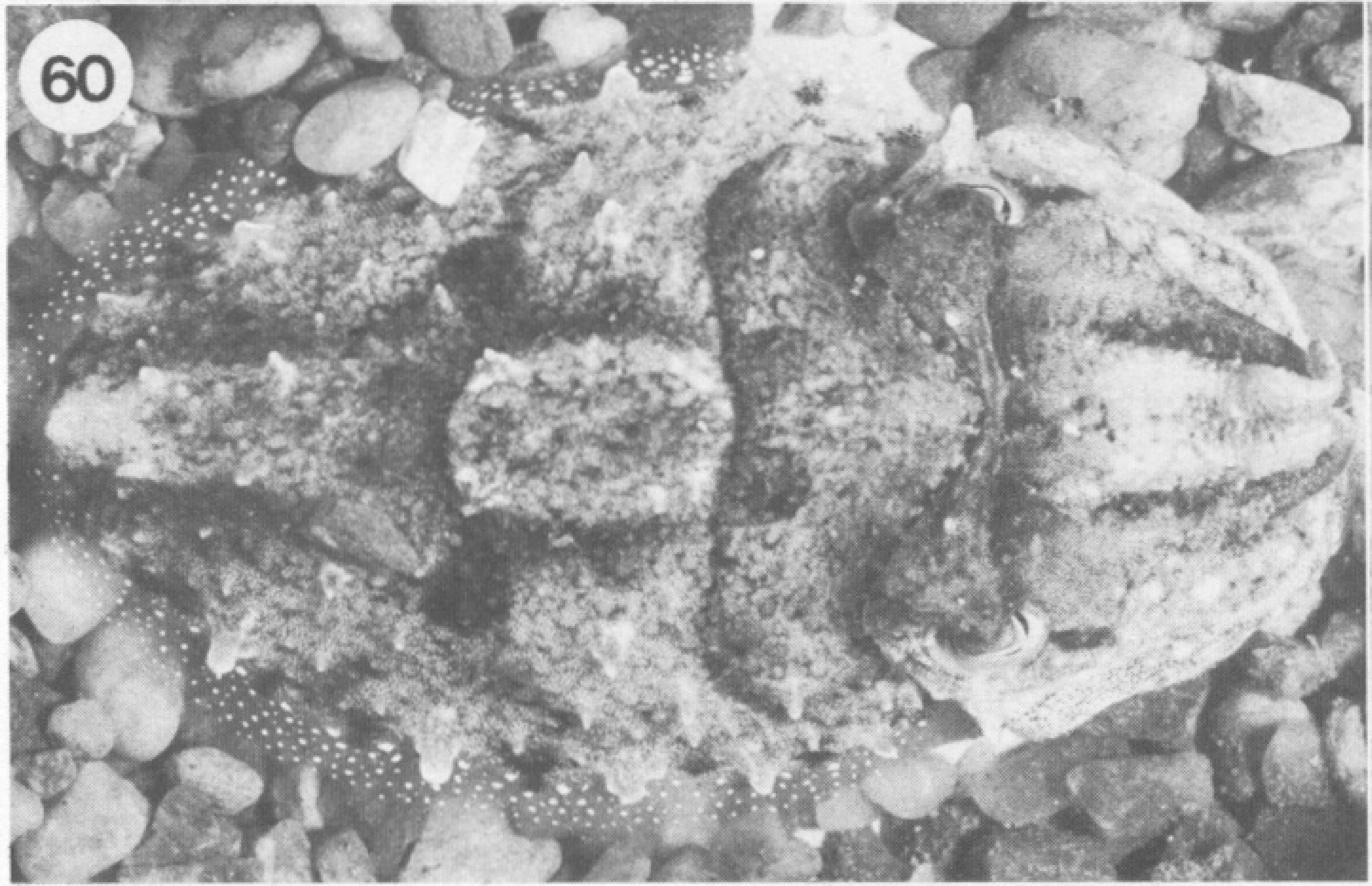
Figures 50–57. For description see p. 452.

58

59

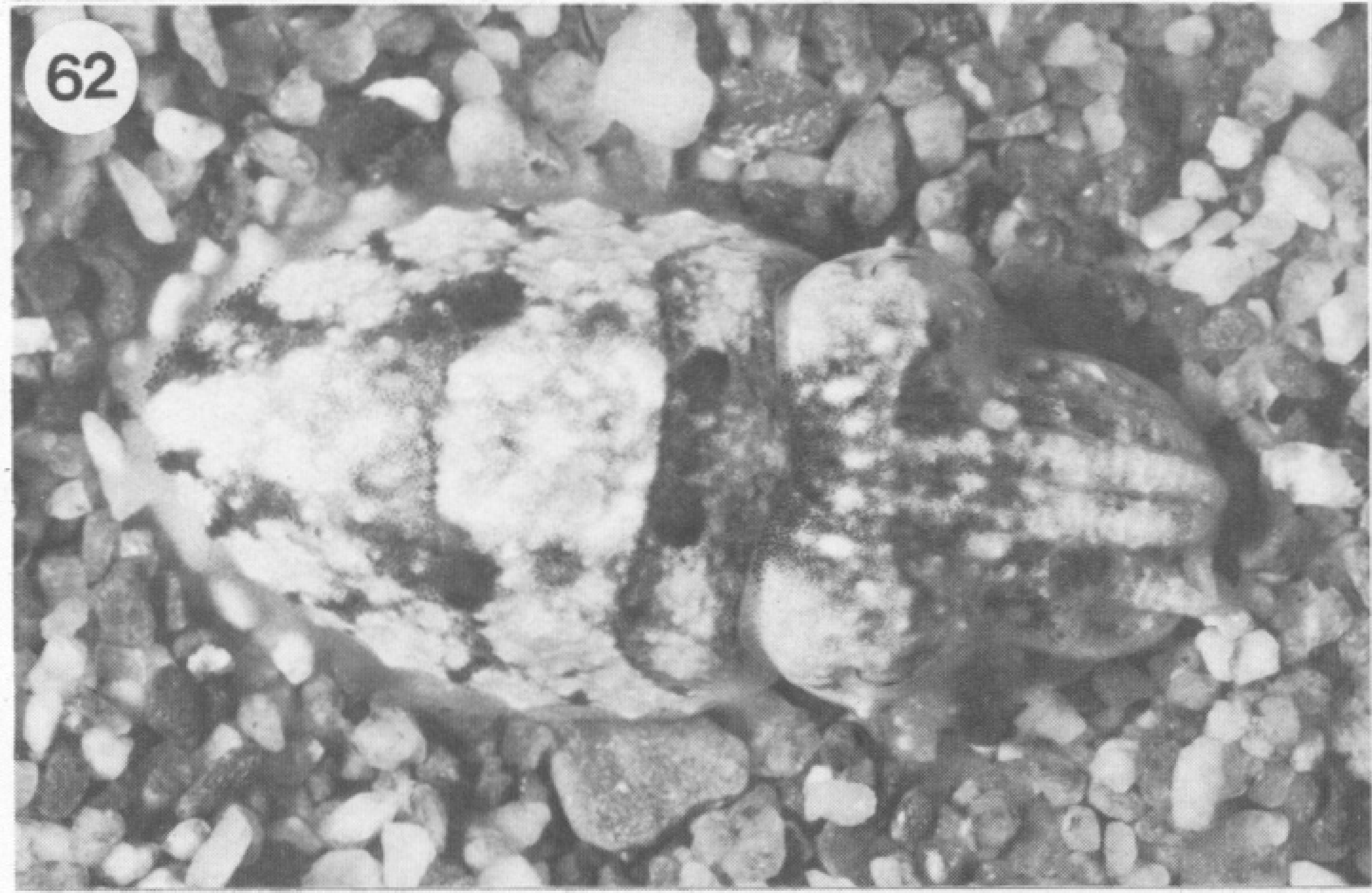


60



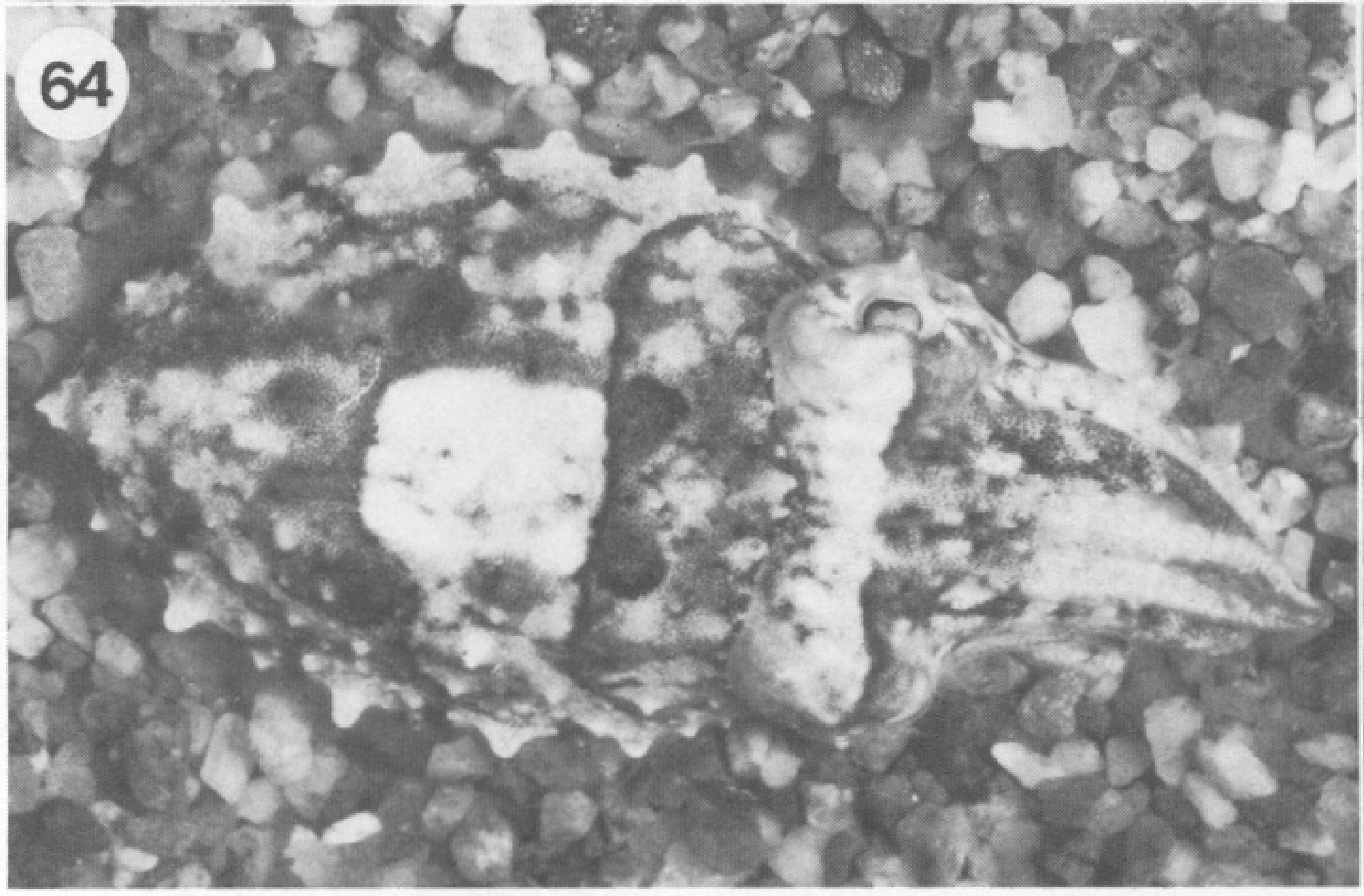
61

62

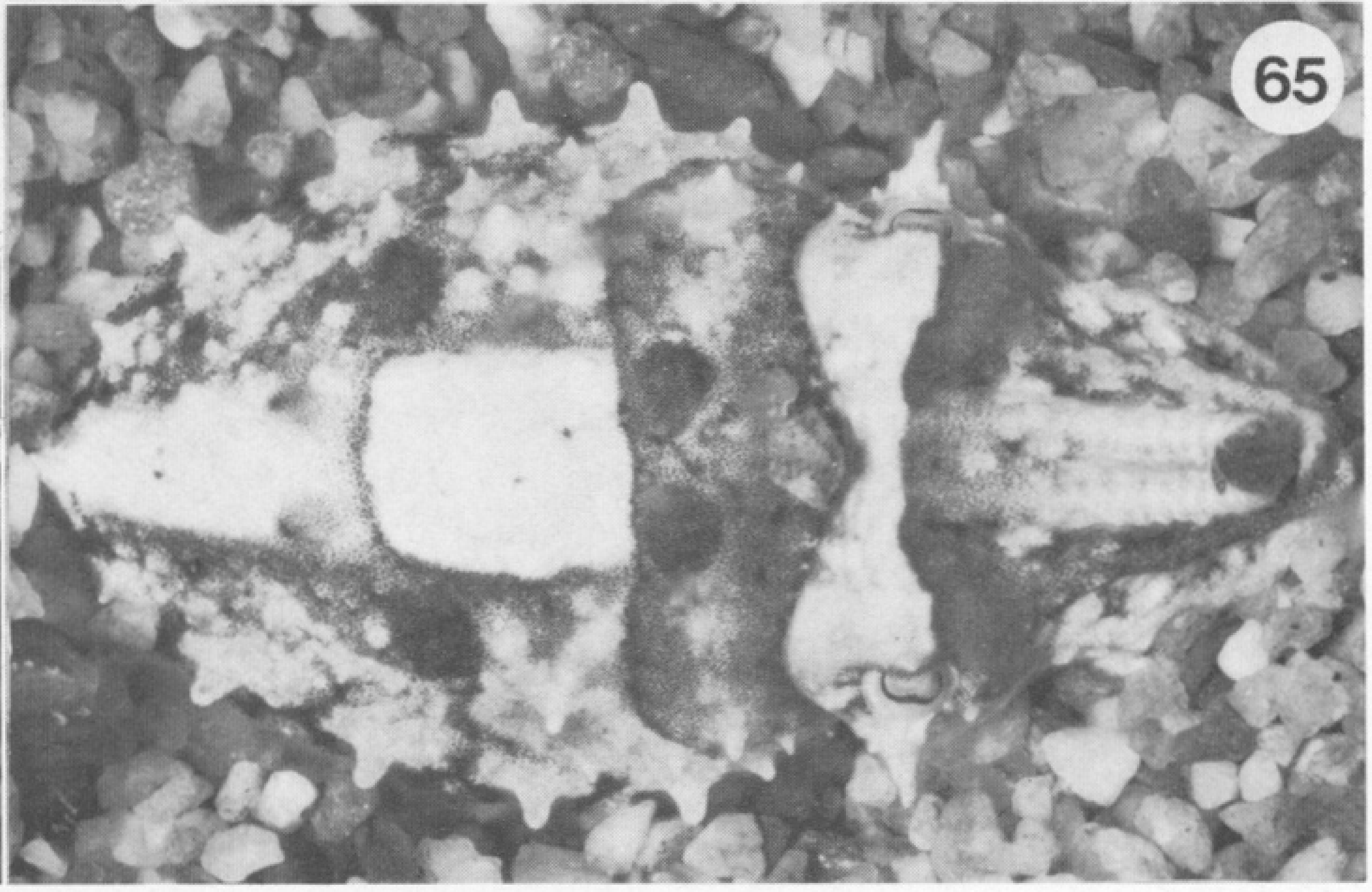


63

64

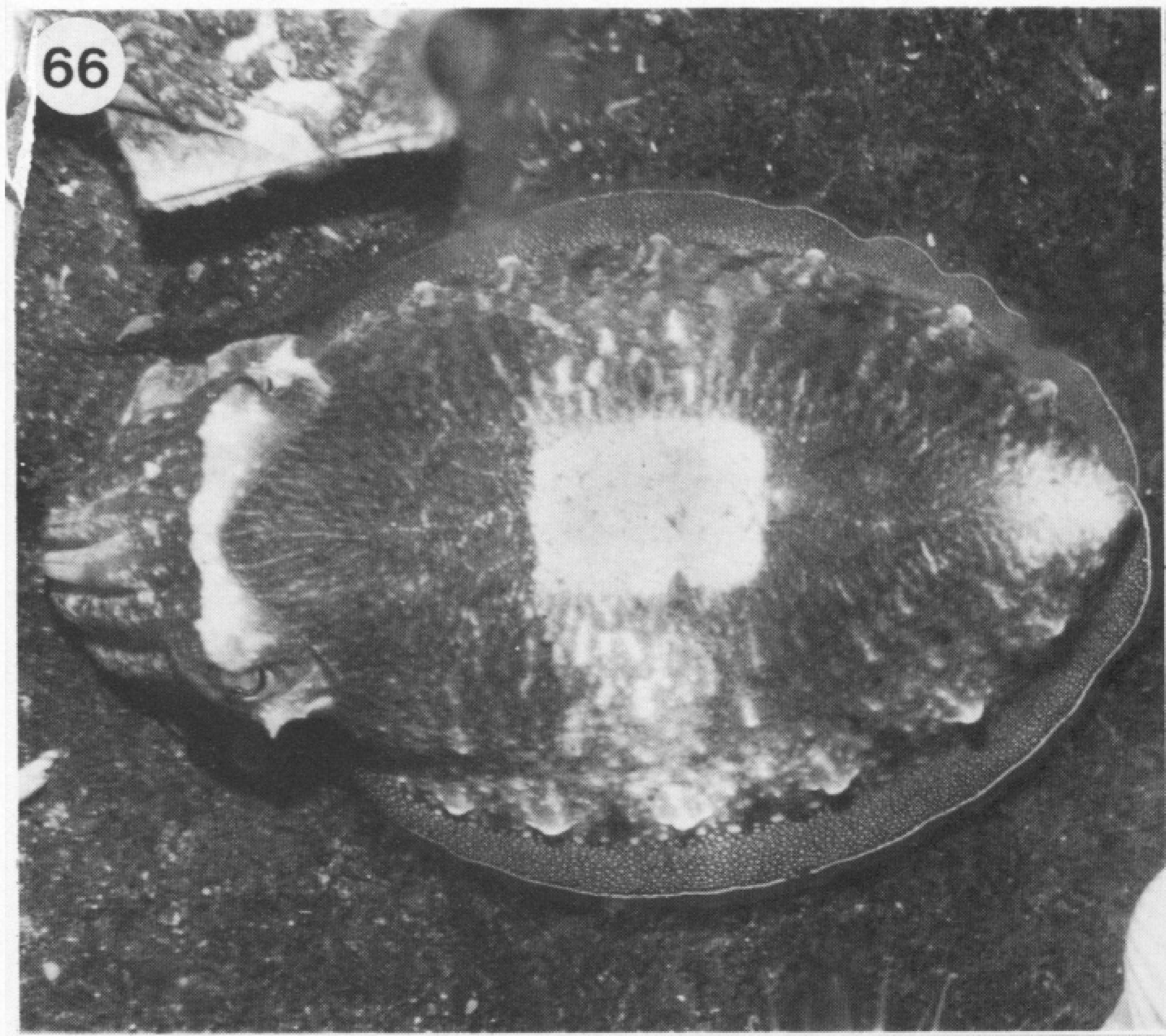


65

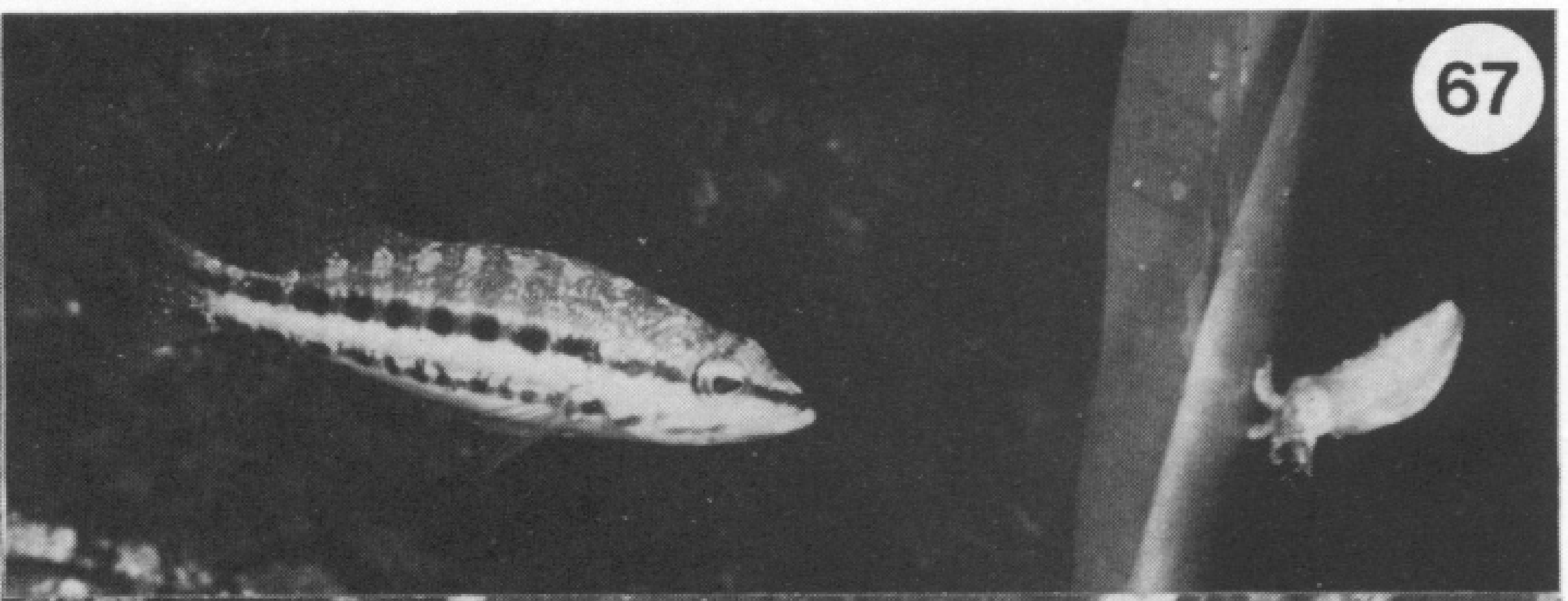


FIGURES 58–65. For description see facing plate 9.

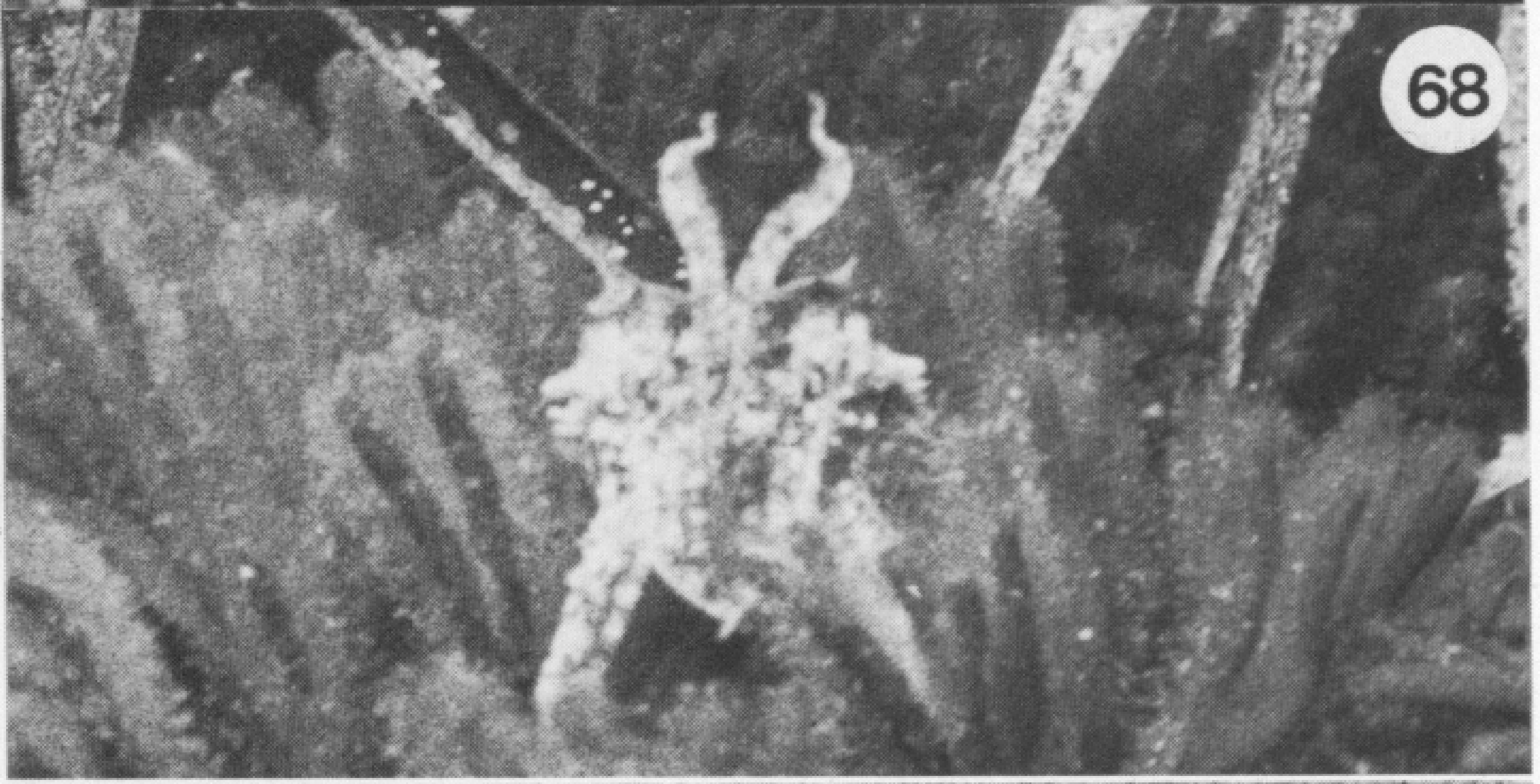
66



67

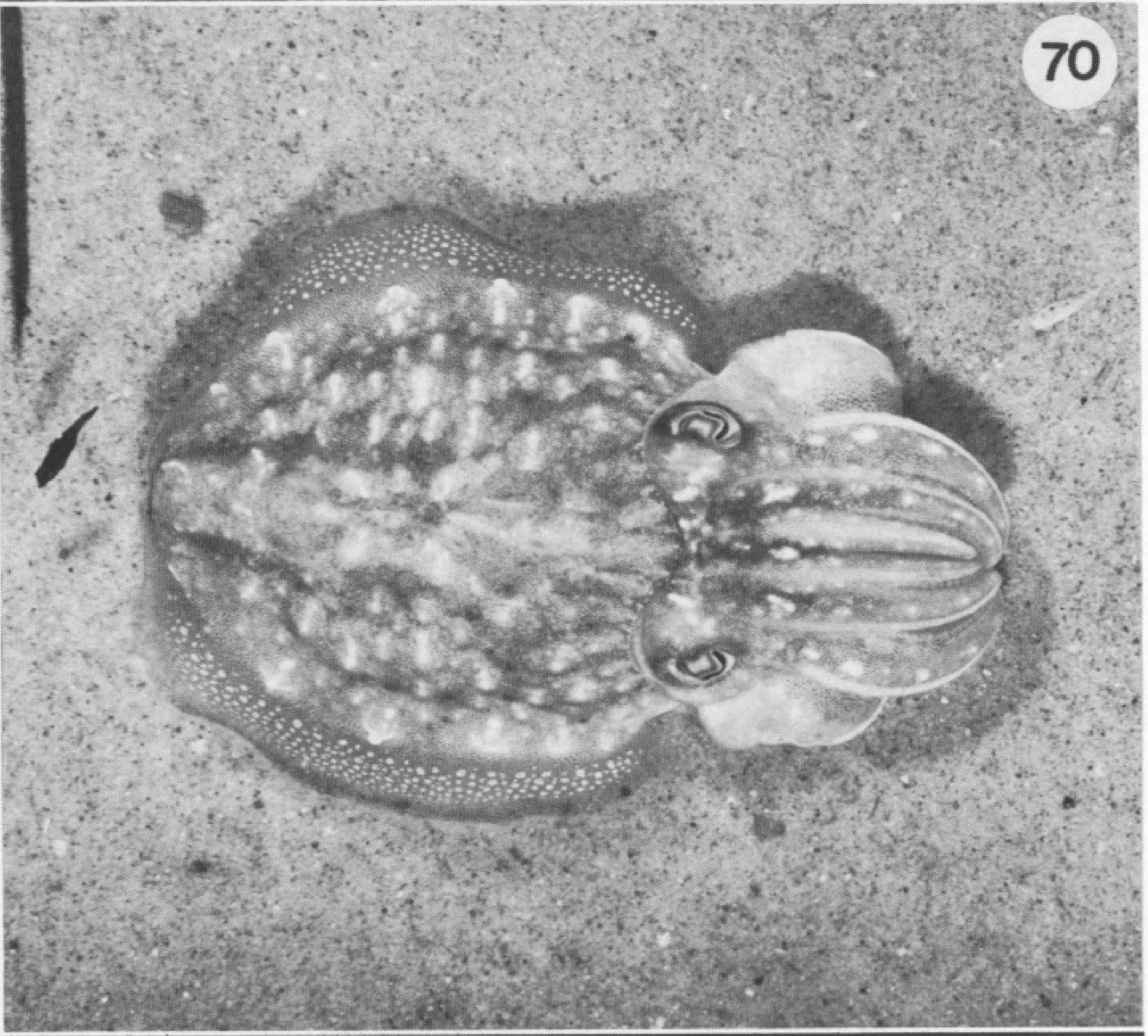


68

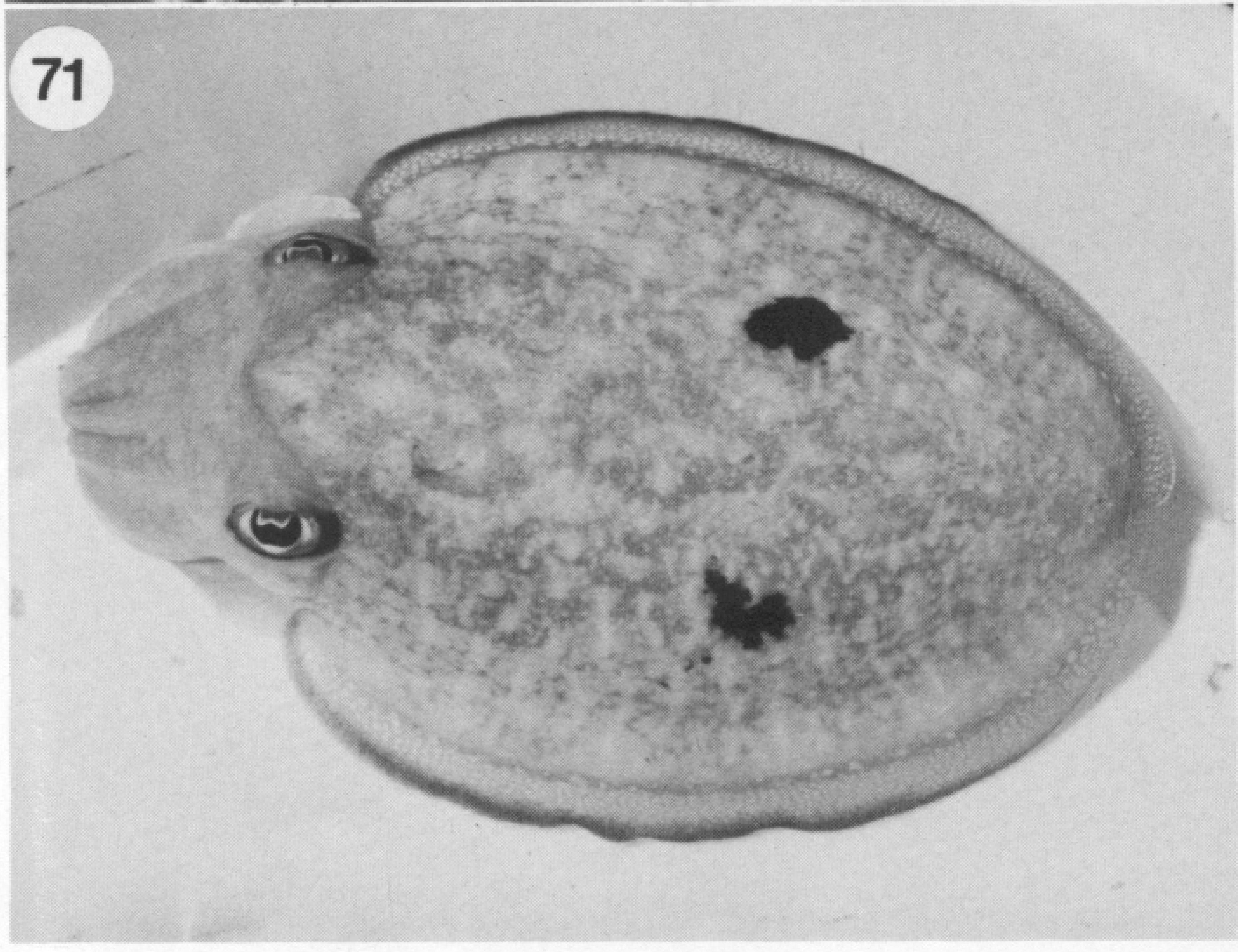


69

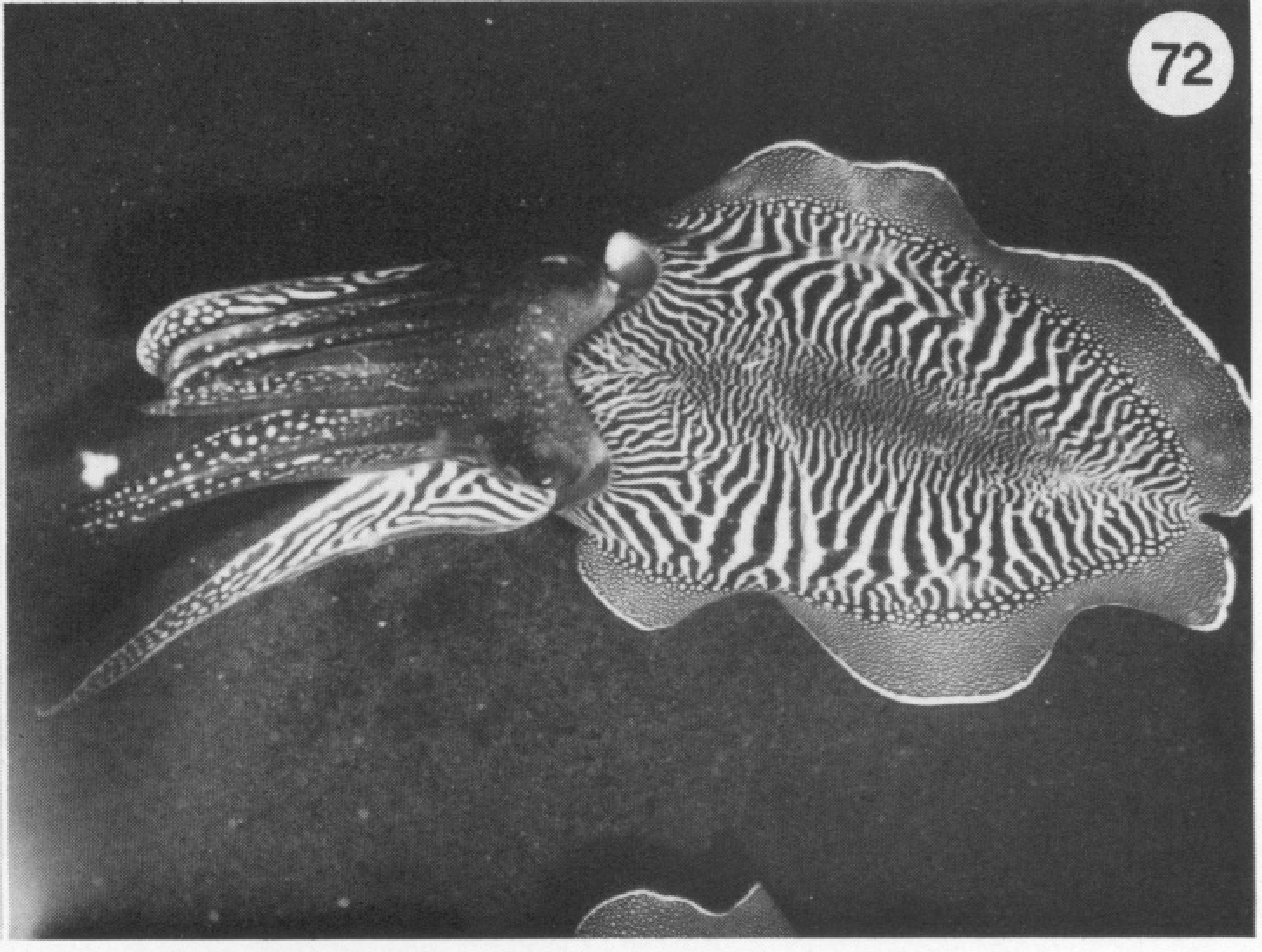
70



71



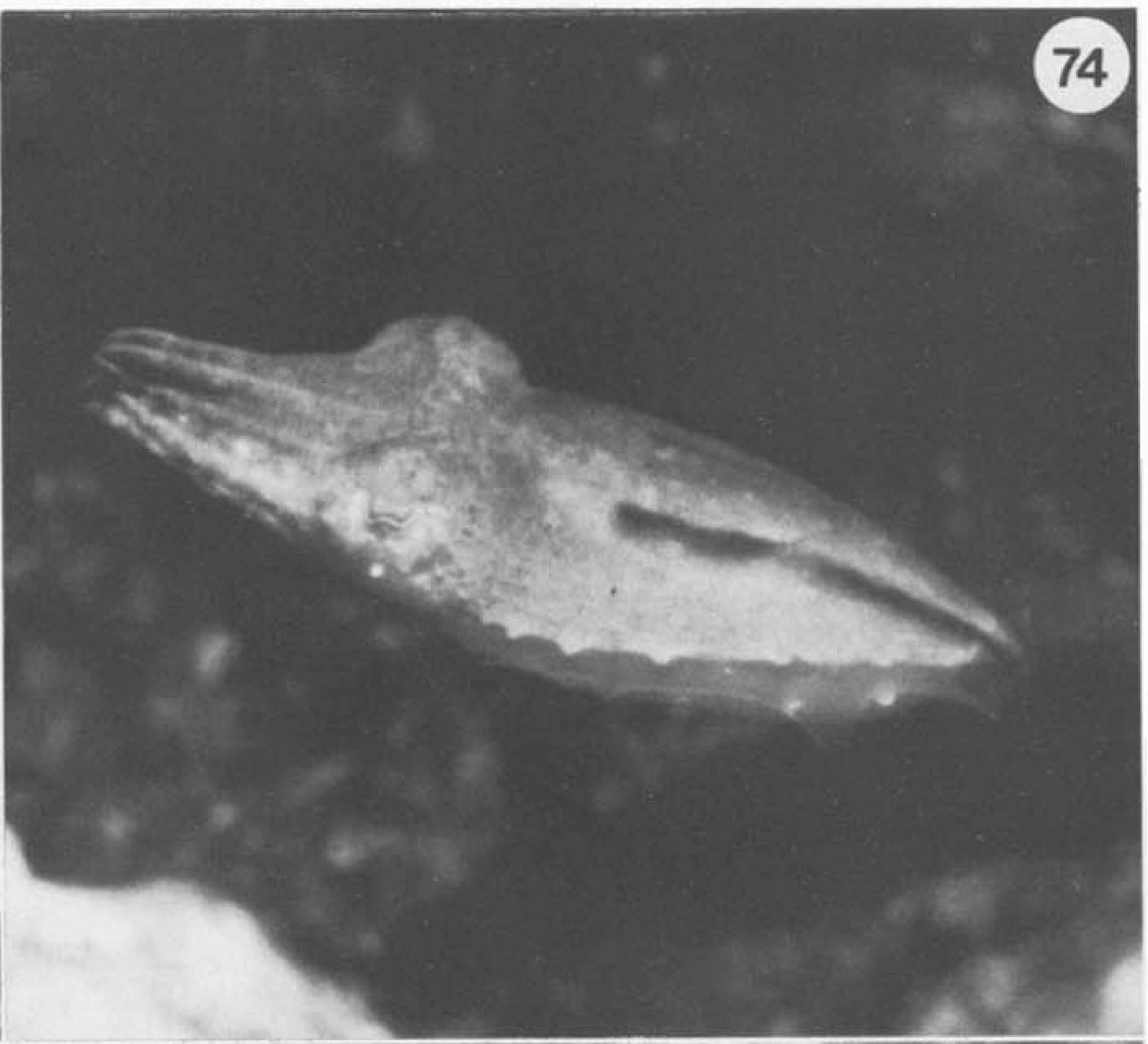
72



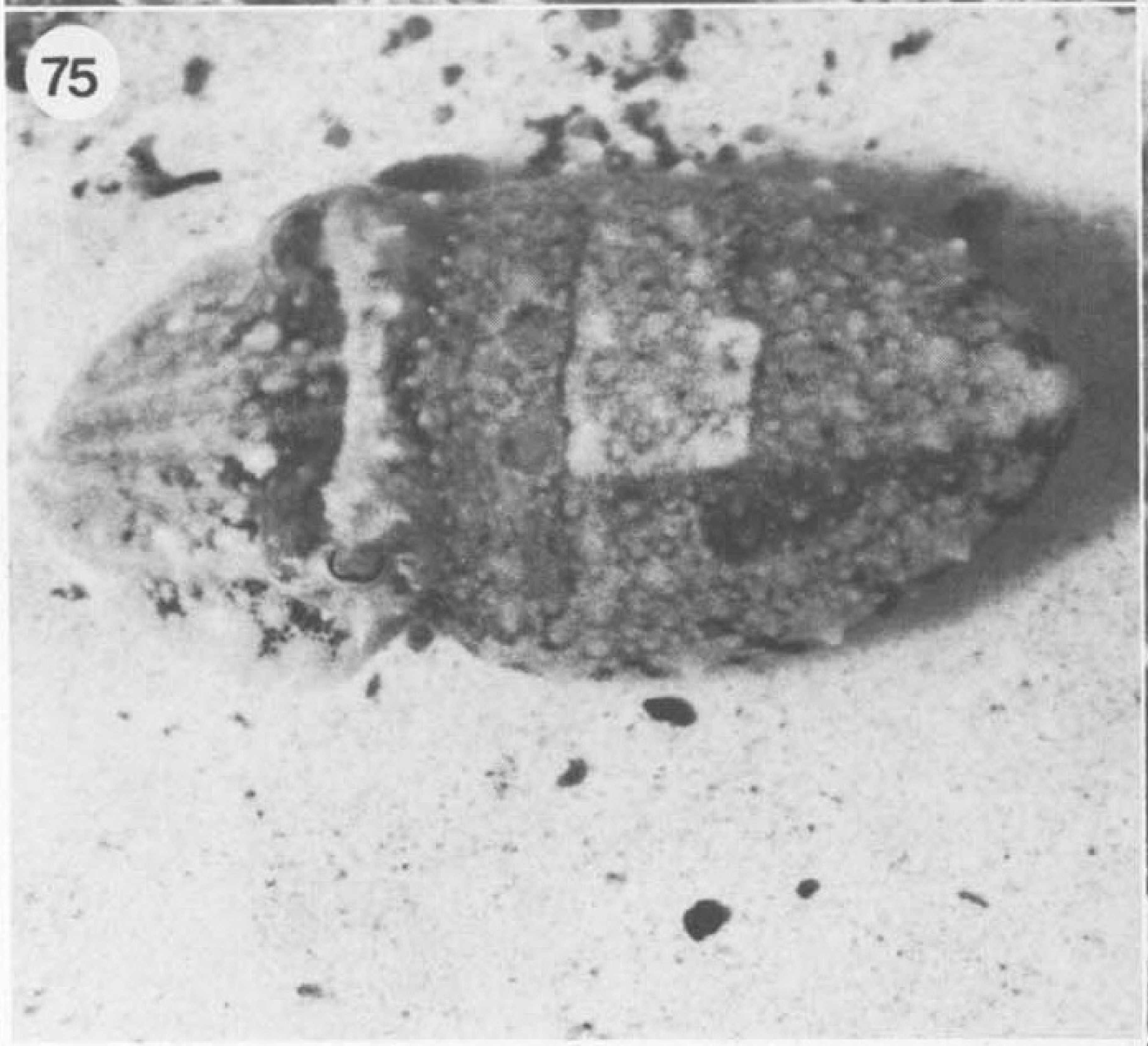
FIGURES 66–72. For description see opposite.

73

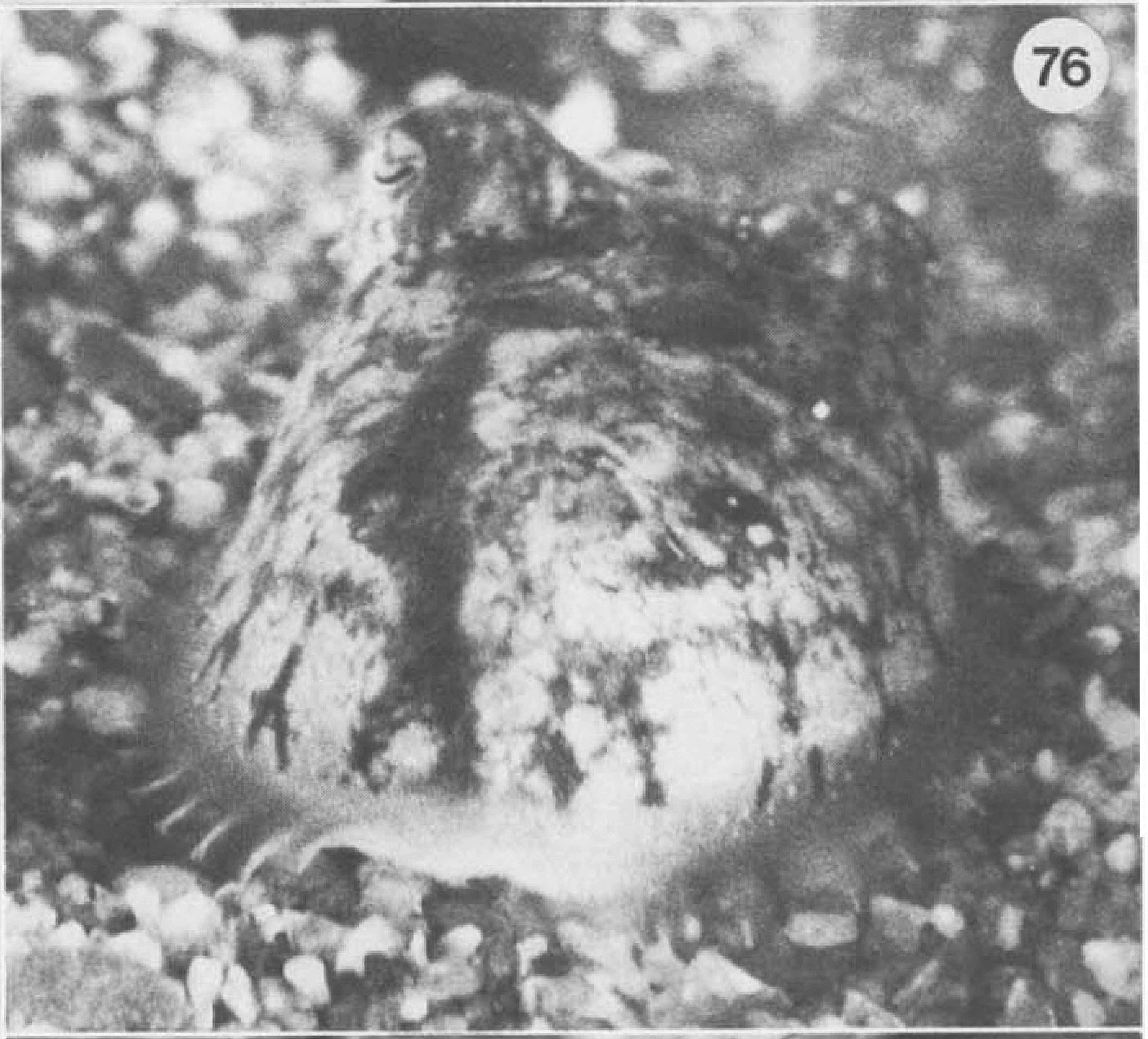
74



75

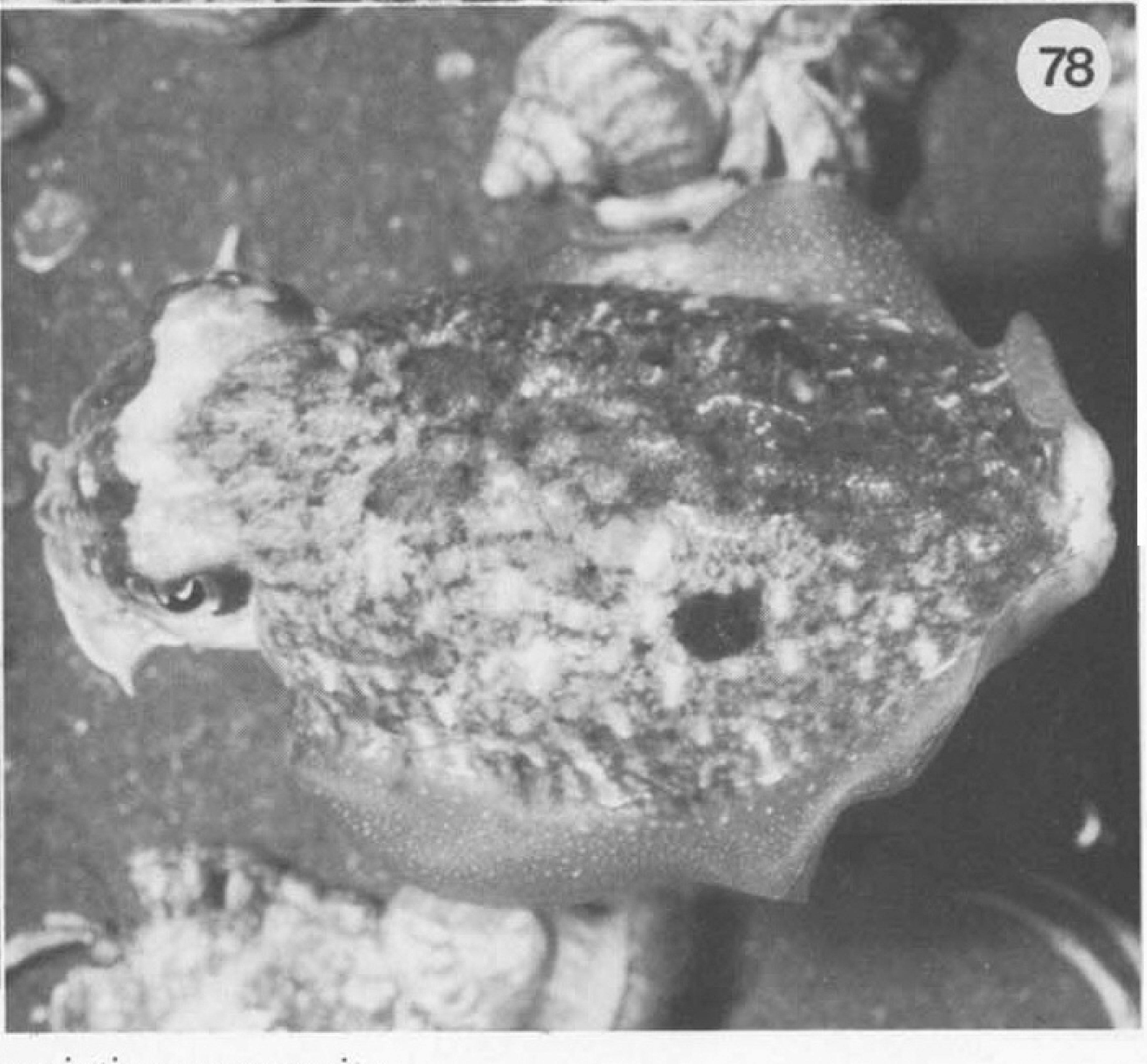


76



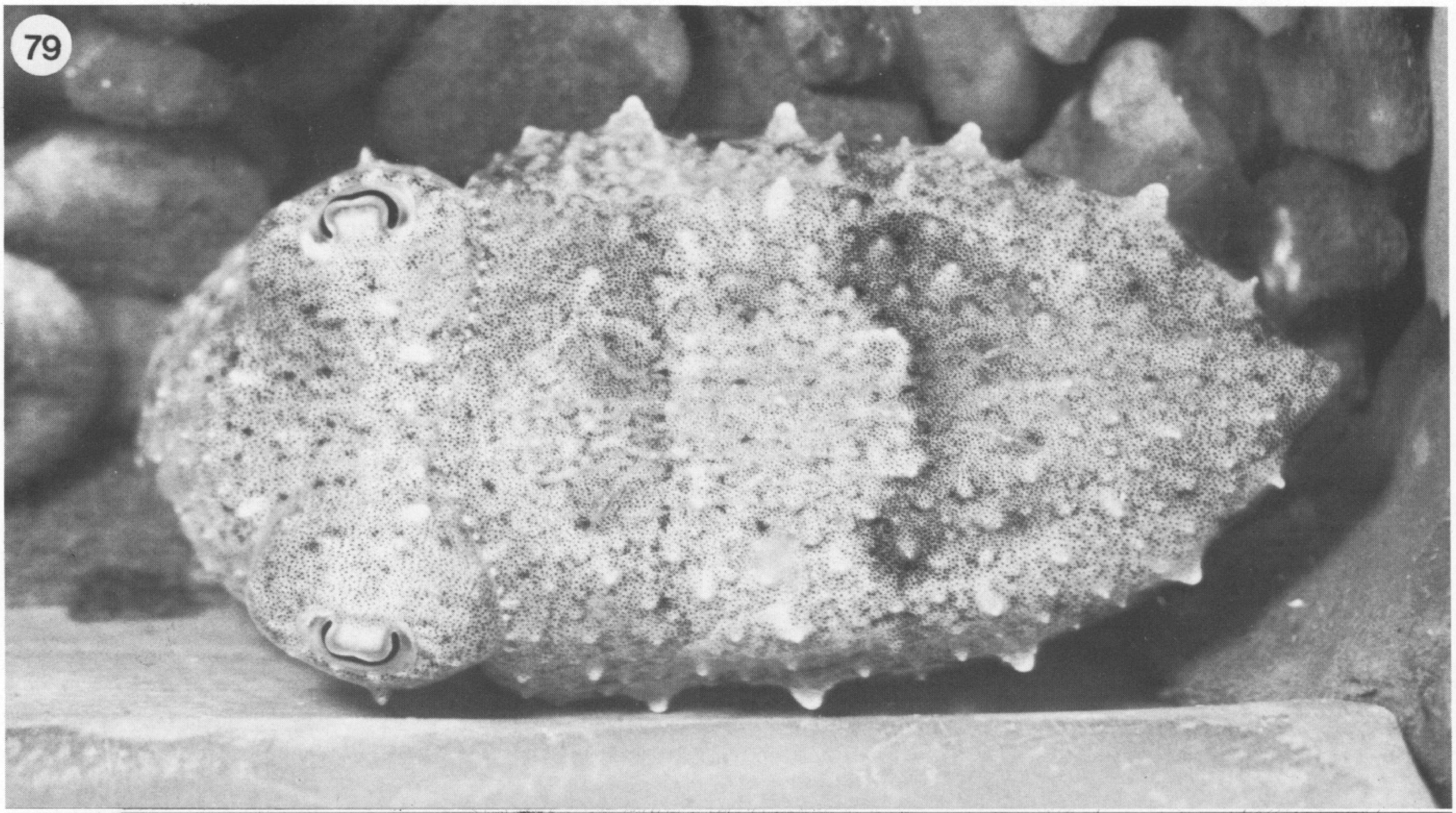
77

78

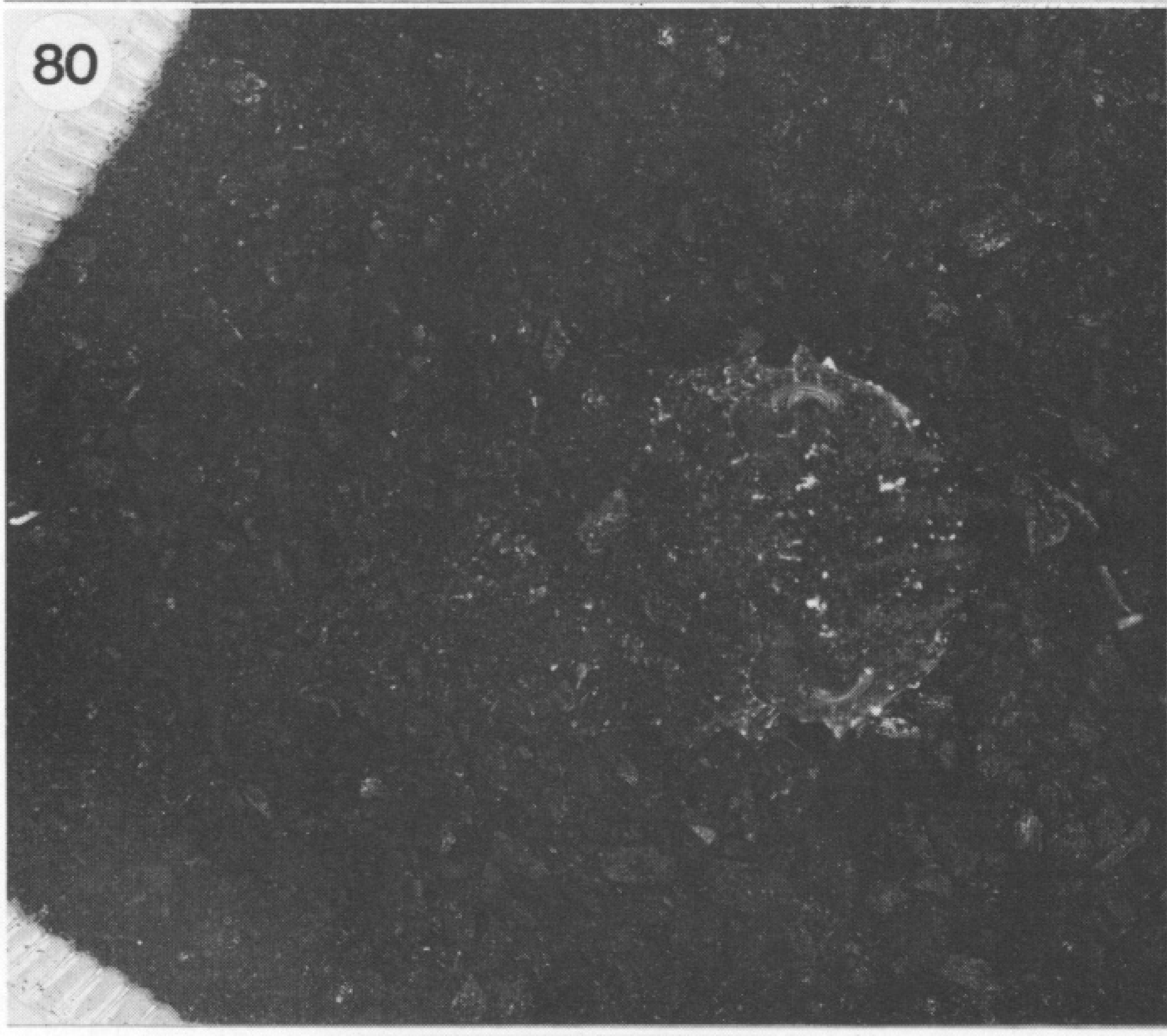


FIGURES 73–78. For description see opposite.

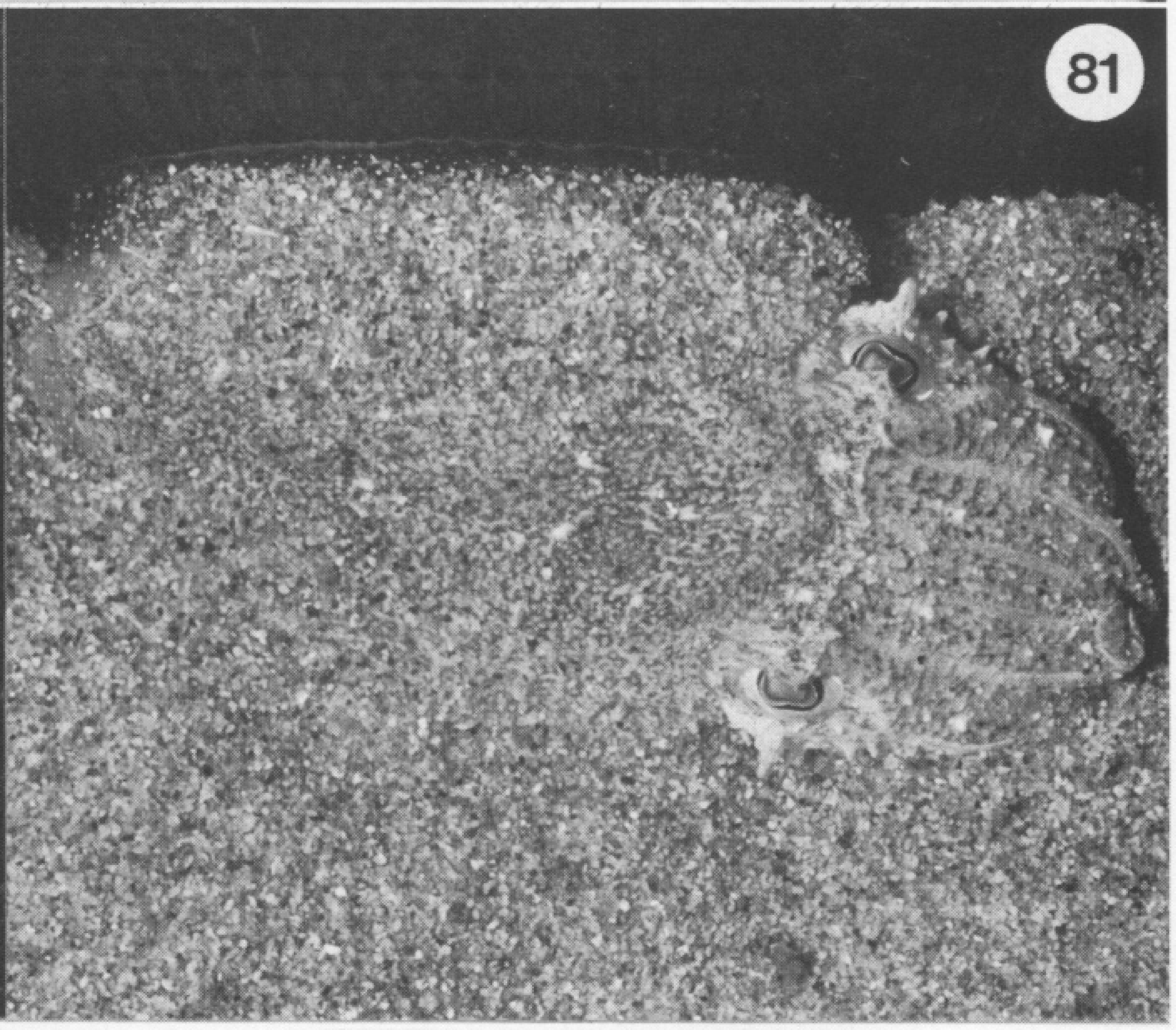
79



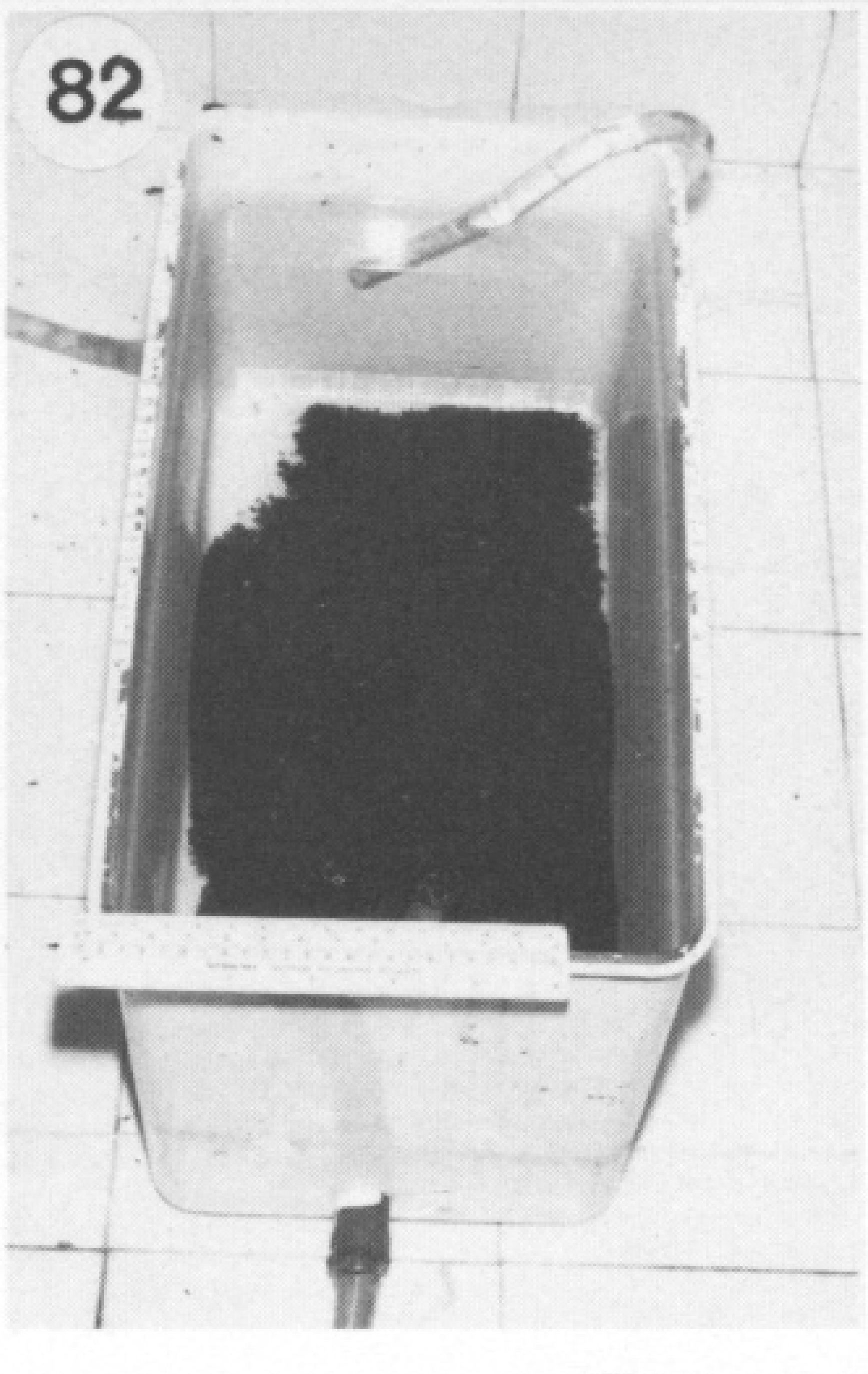
80



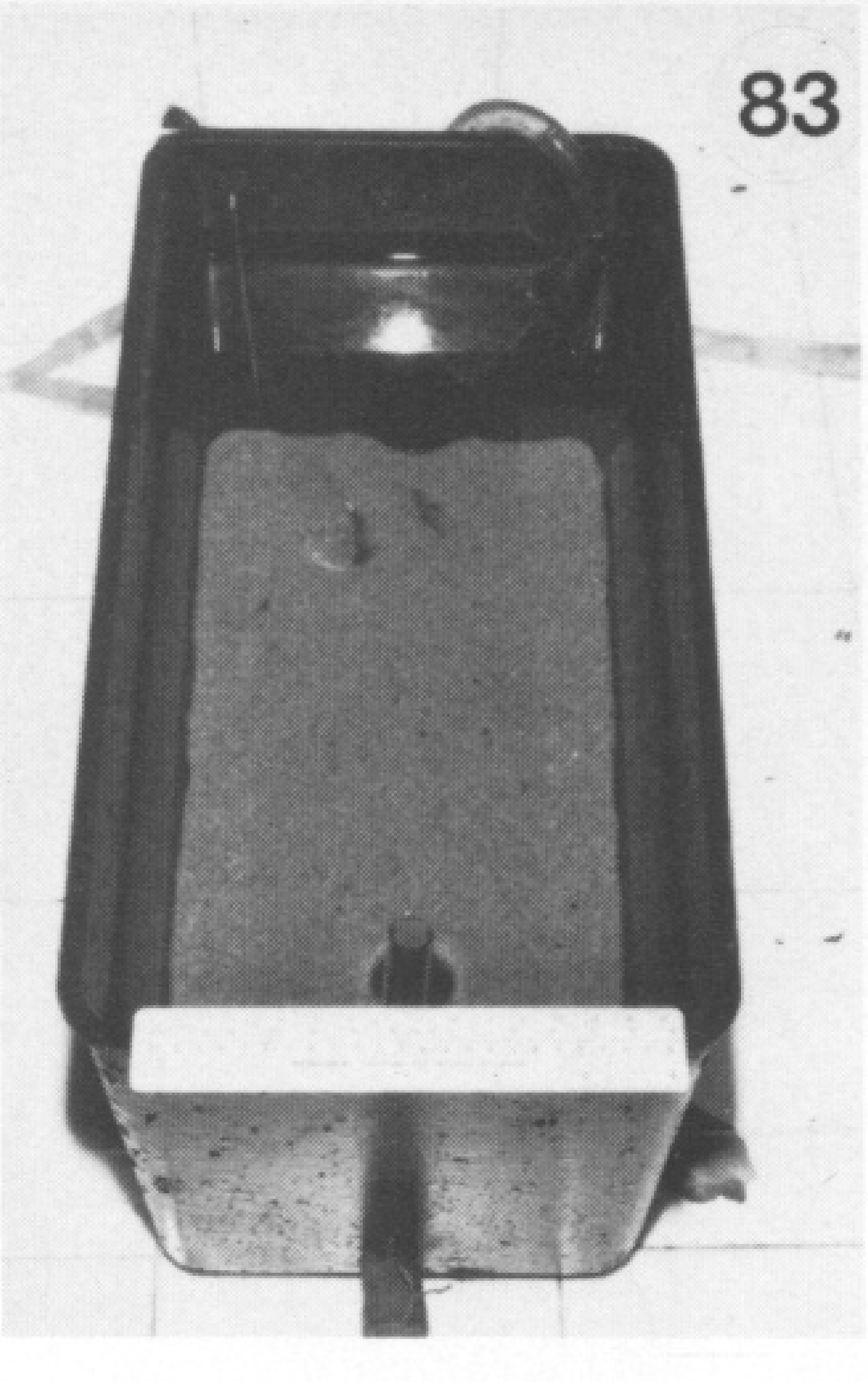
81



82

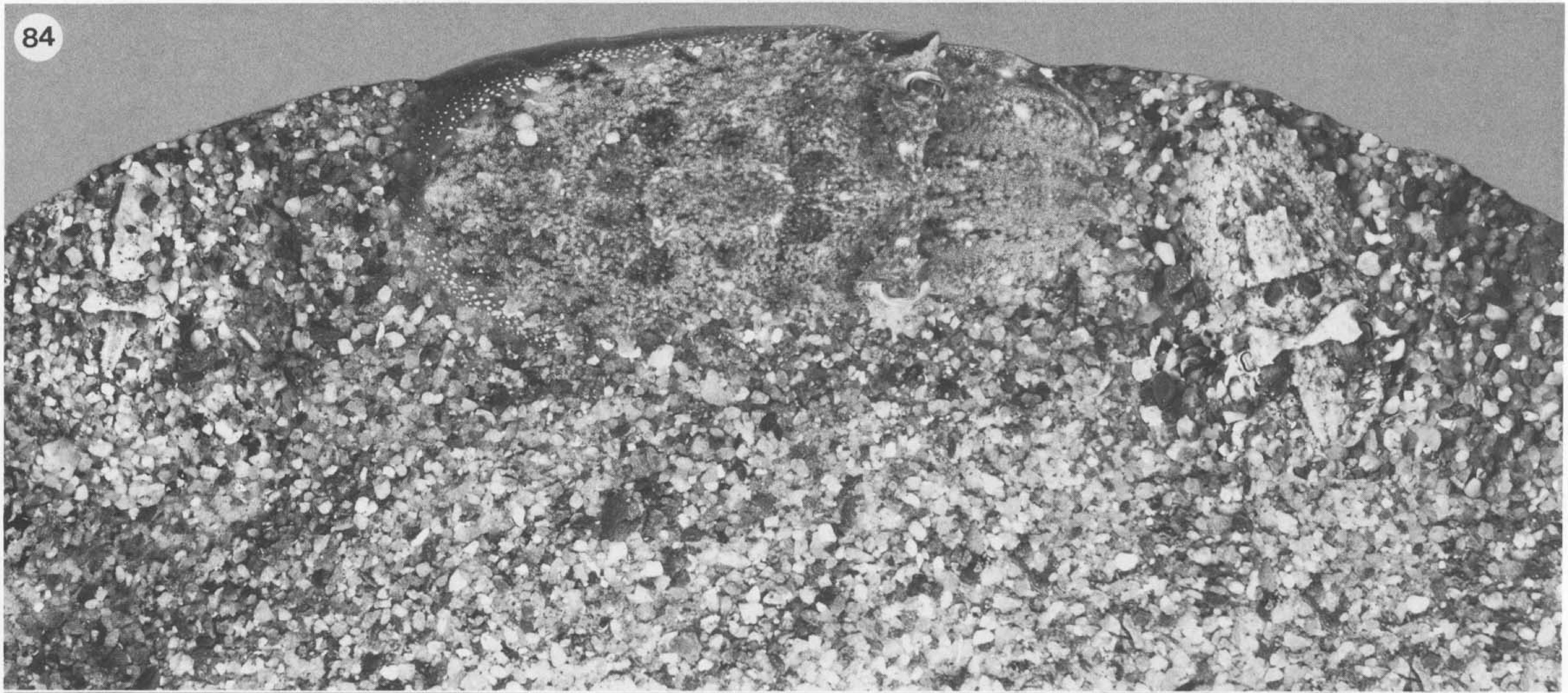


83

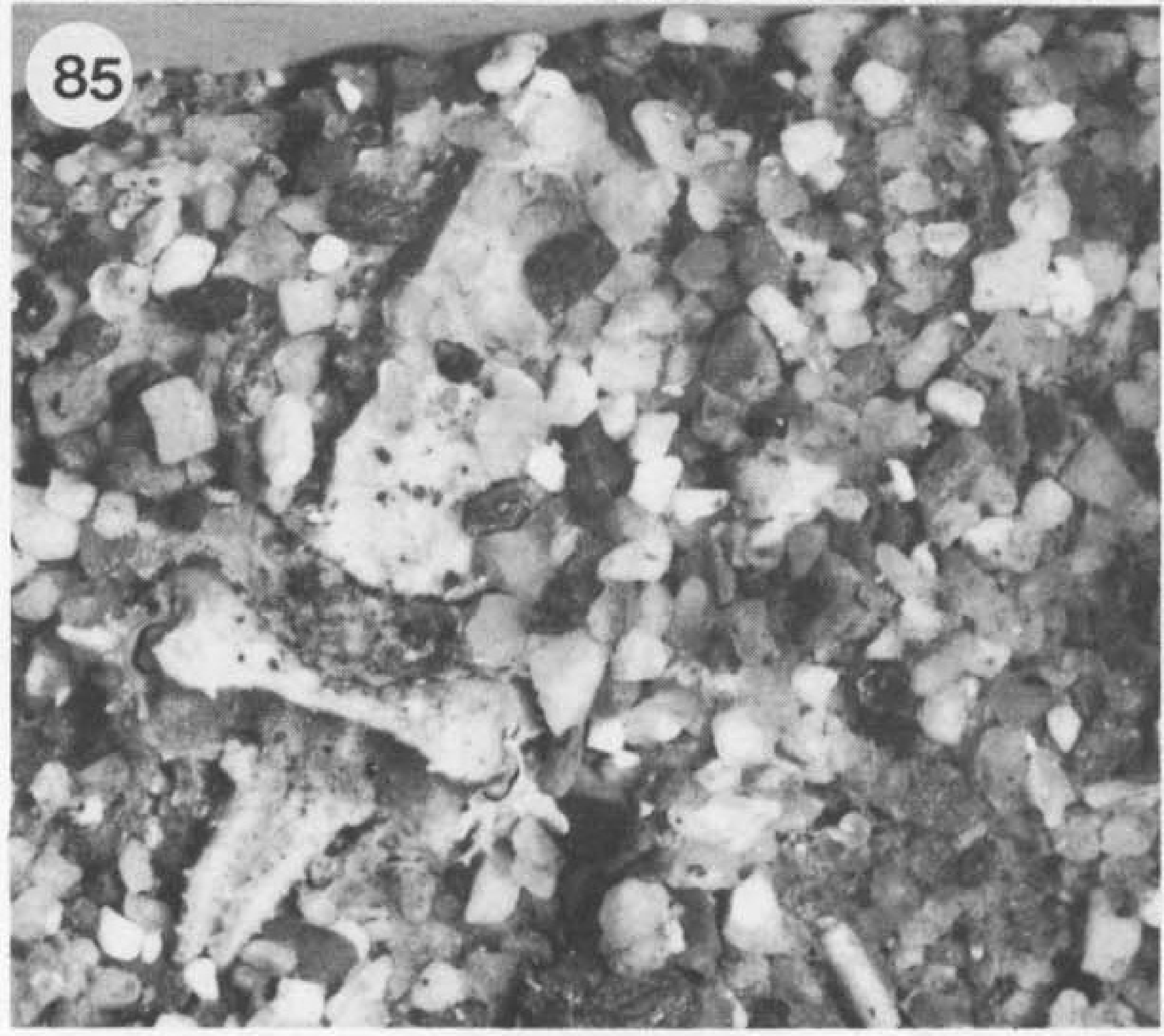


FIGURES 79–83. For description see facing plate 10.

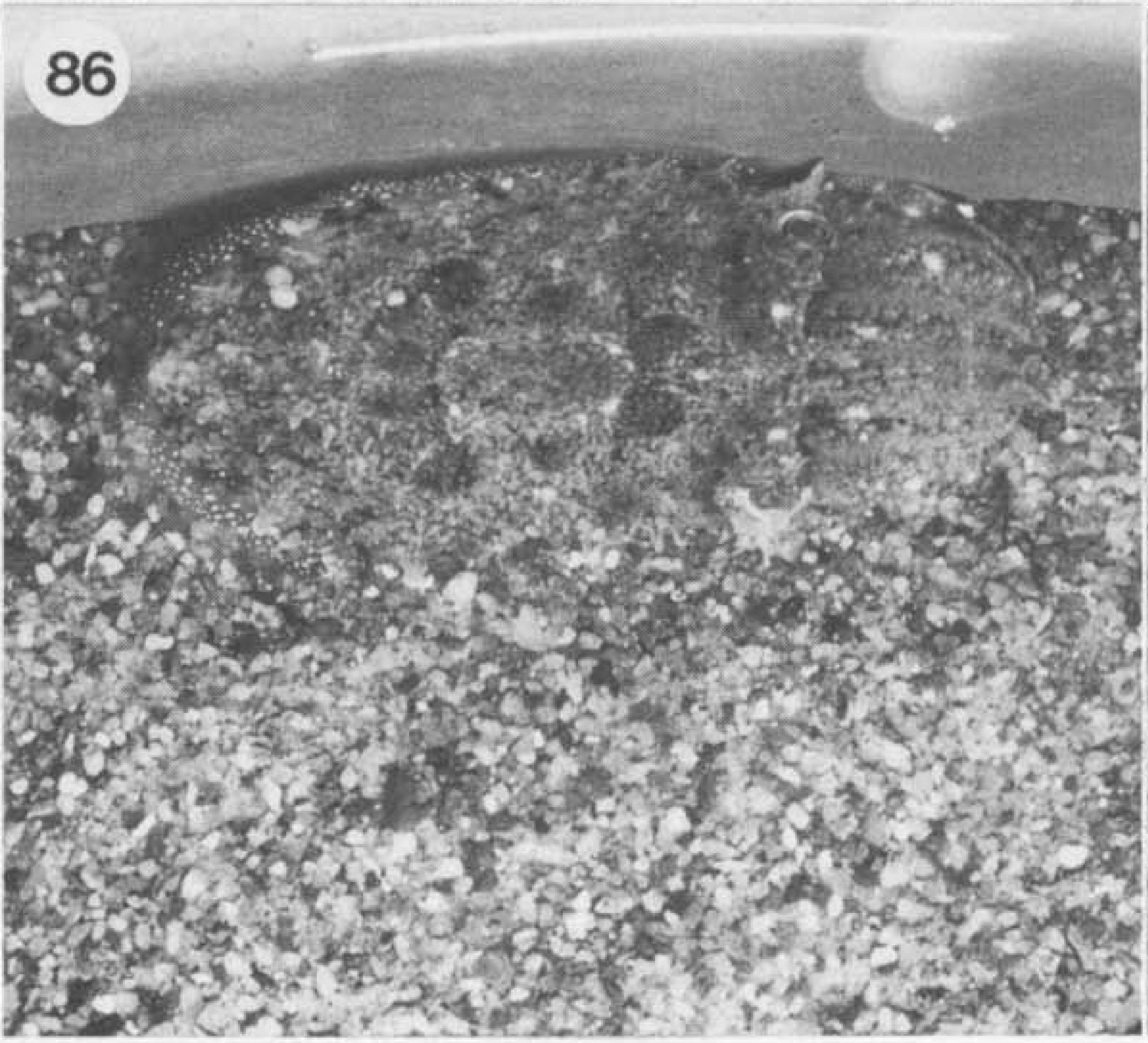
84



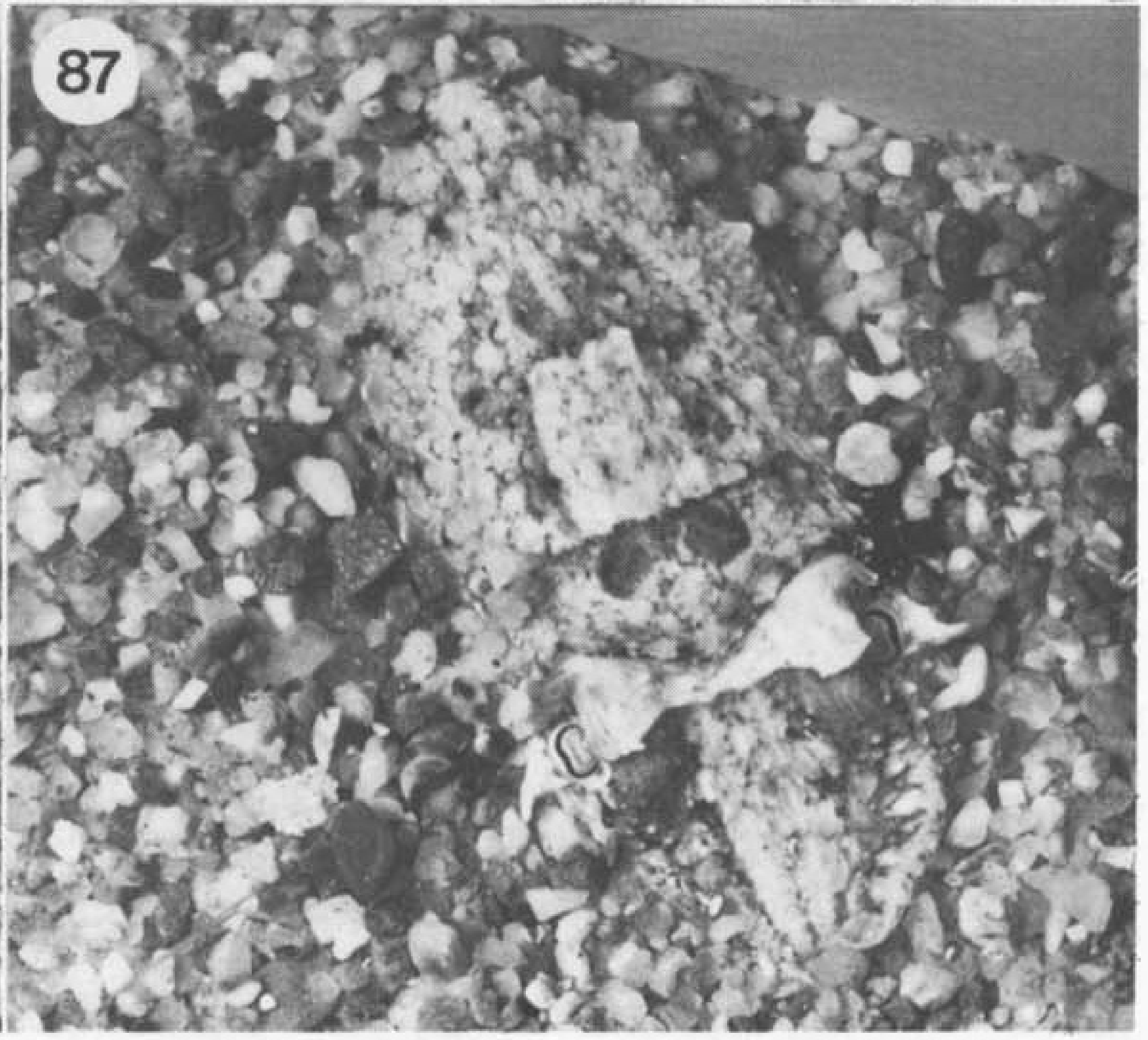
85



86



87



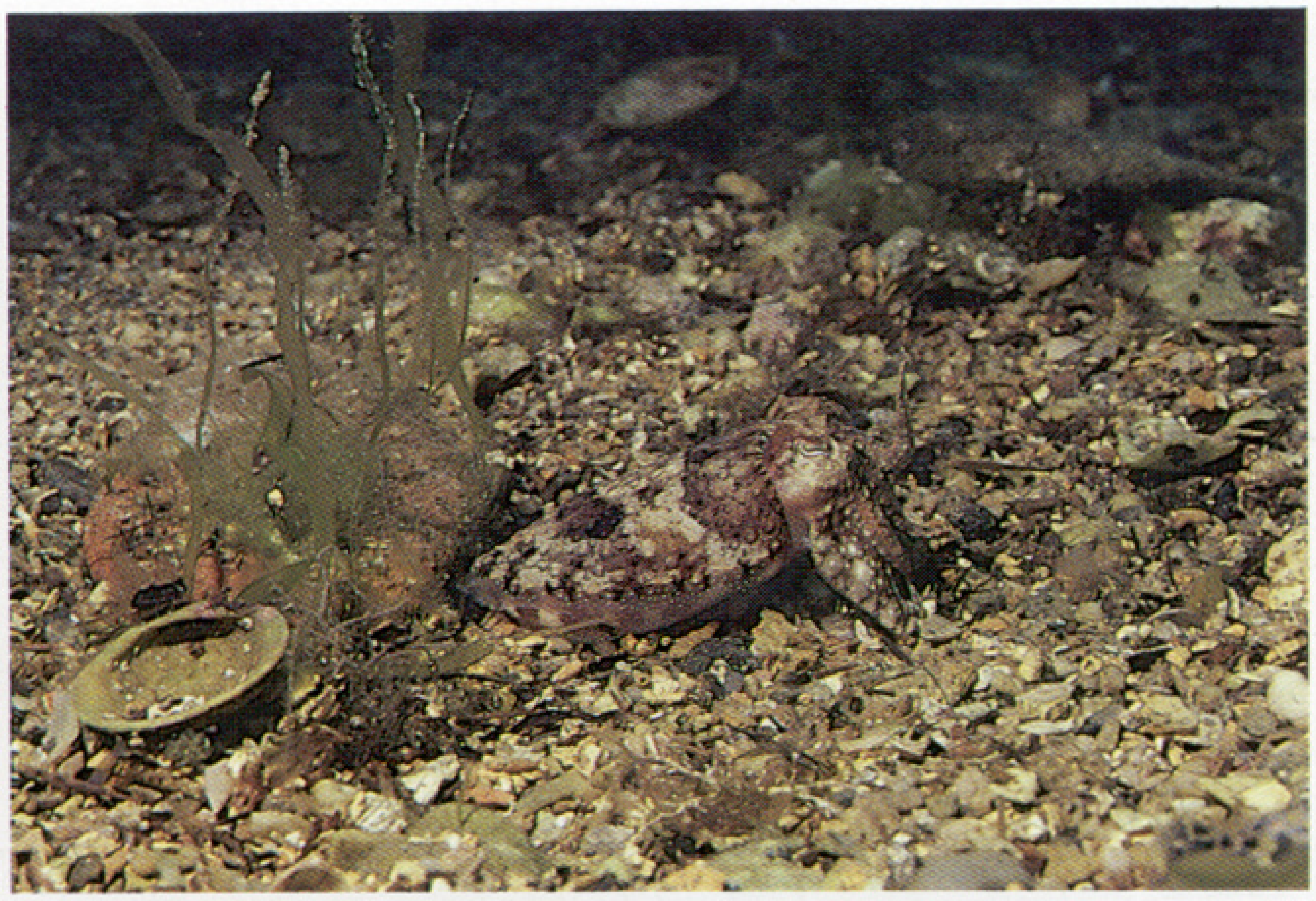
88

89

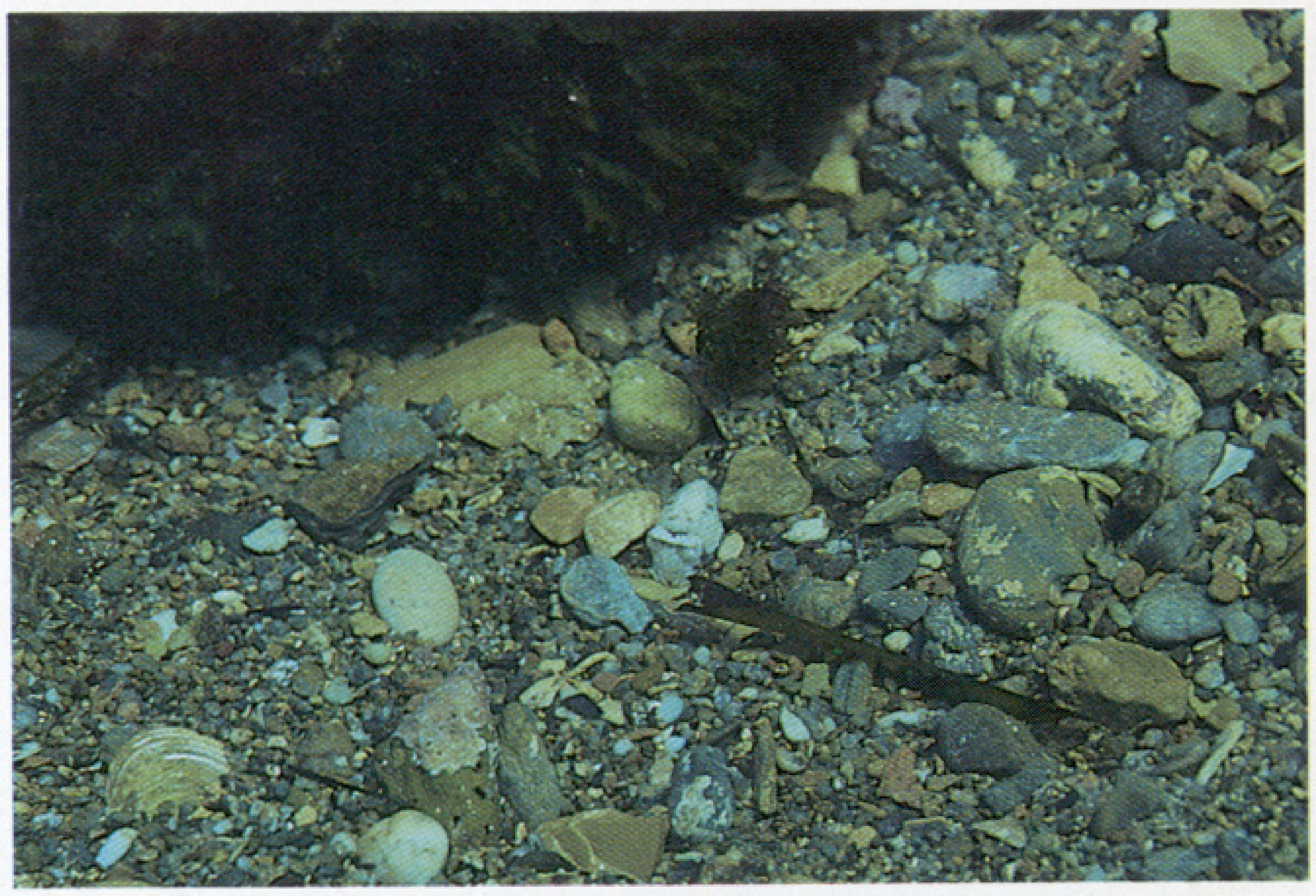
Figures 88 and 89. For description see facing plate 10.

90

91



92



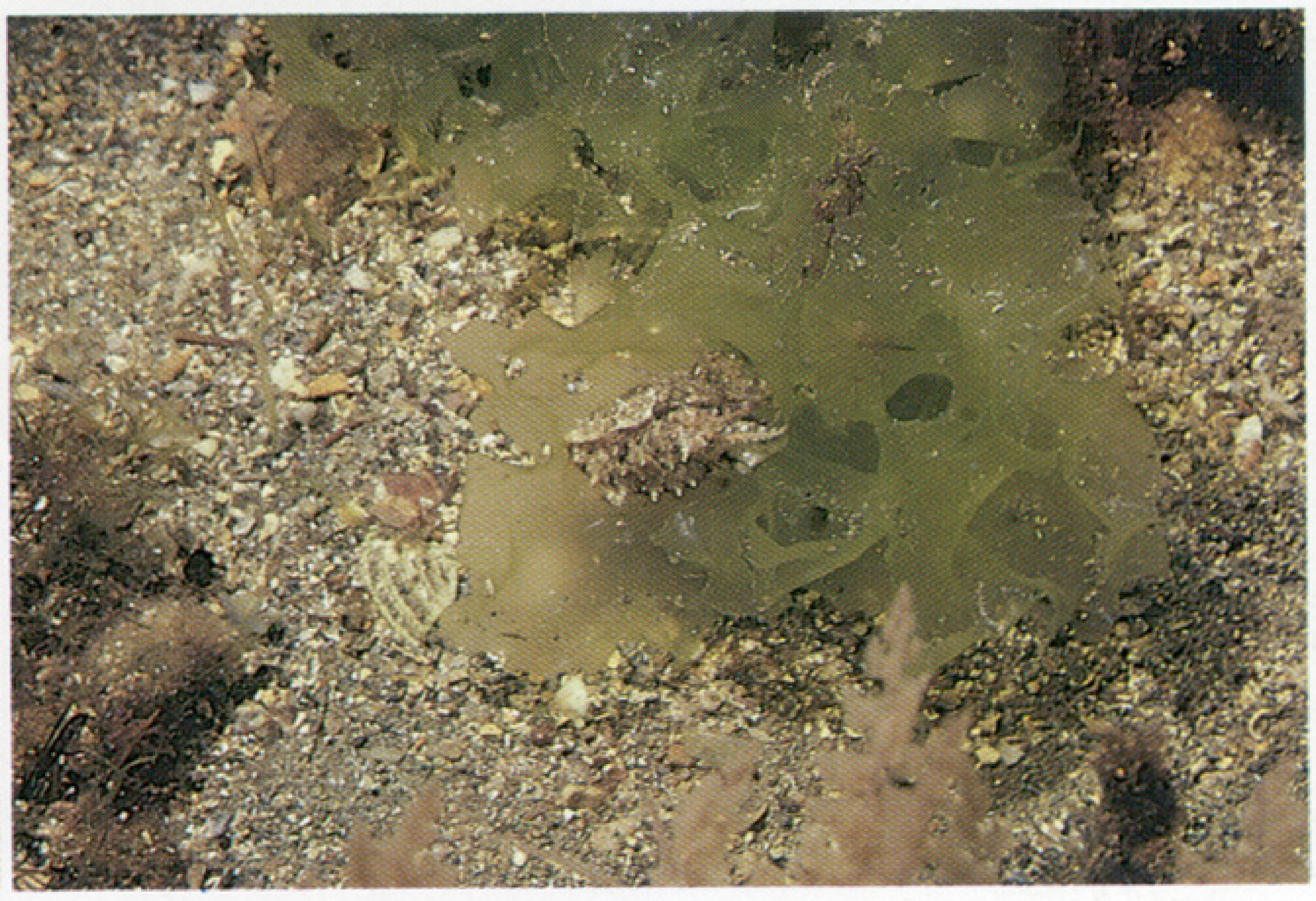
93

94

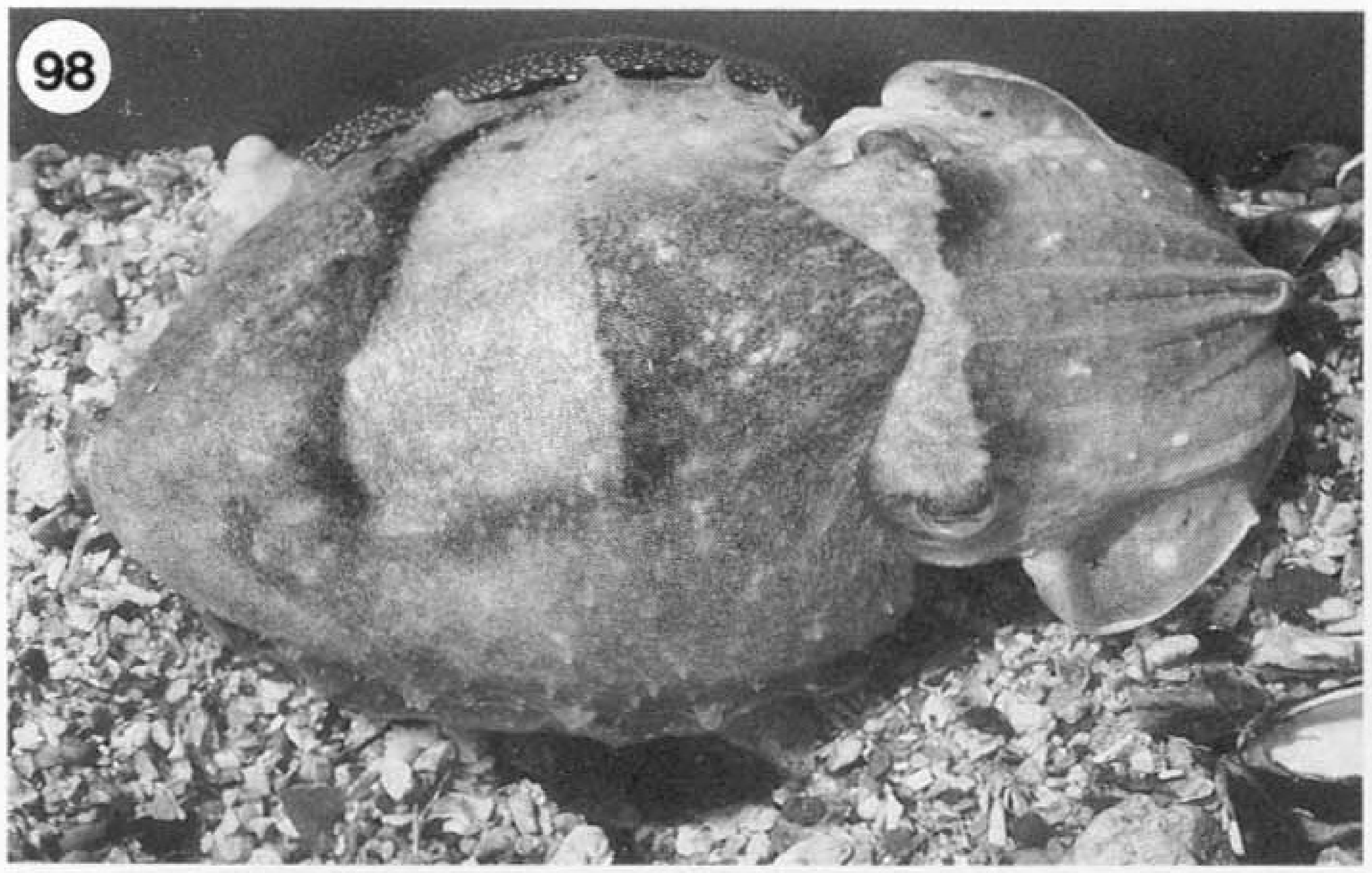
95

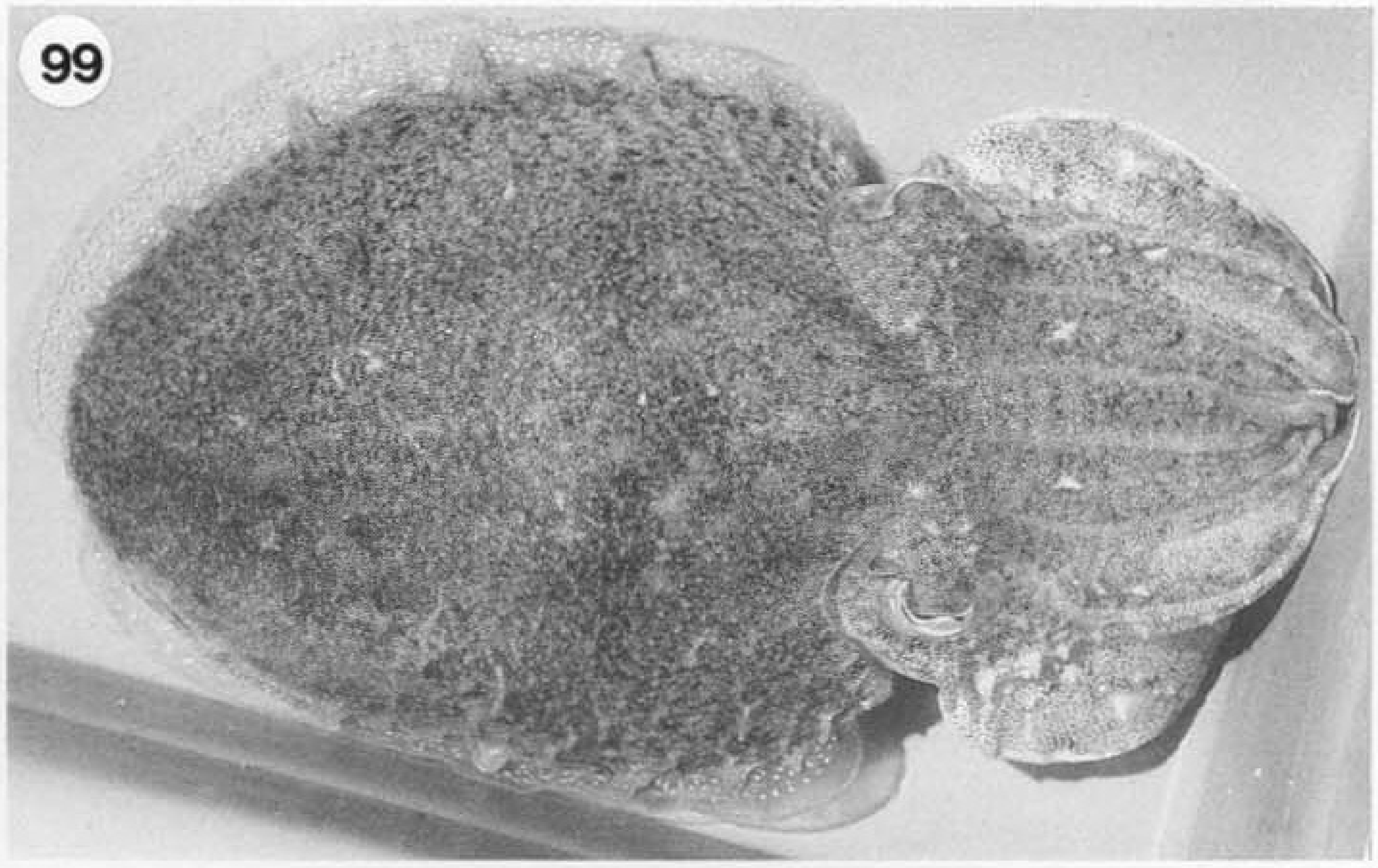
96

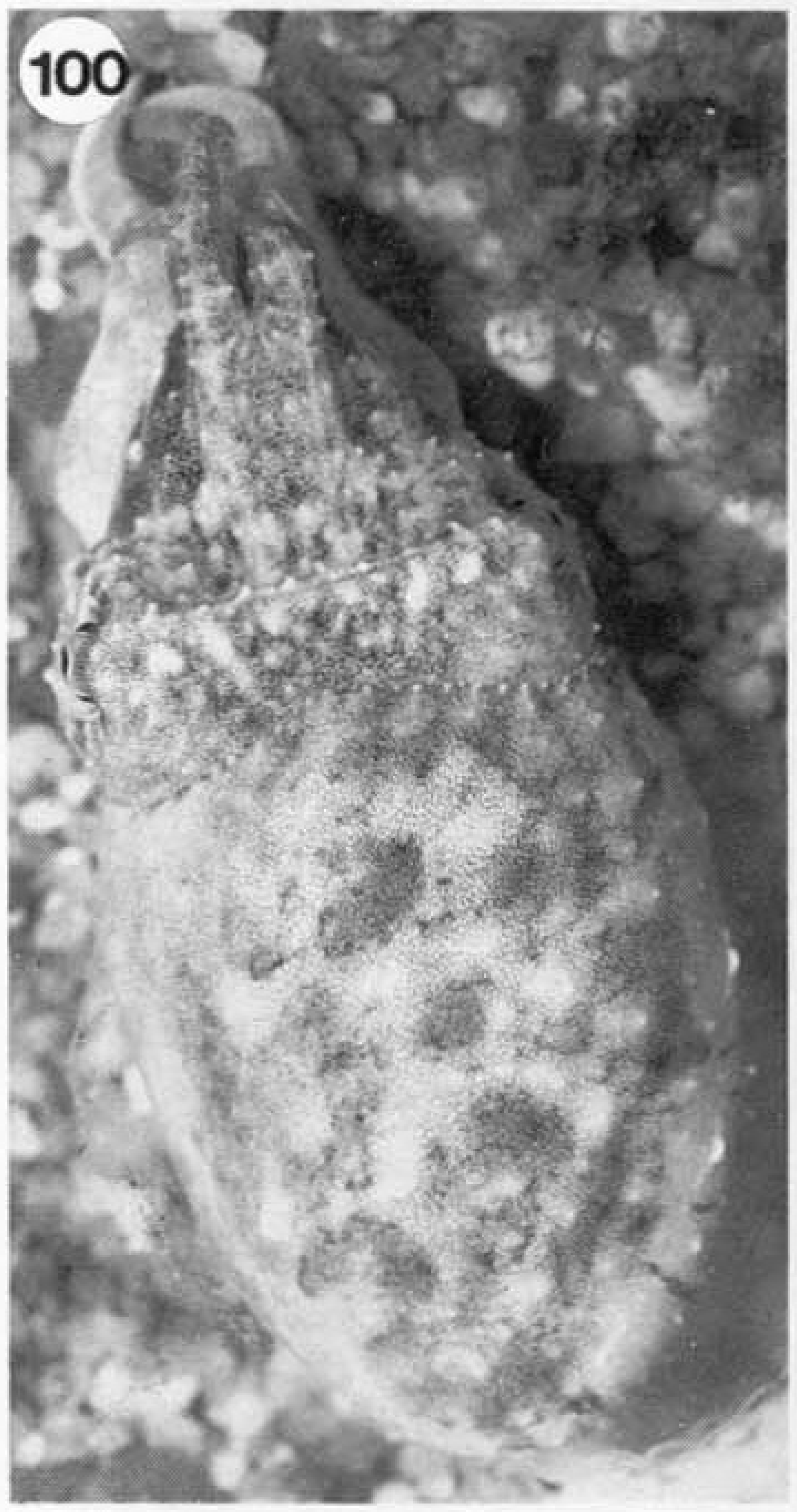
97



FIGURES 90–97. For description see facing plate 15.


98


99


100

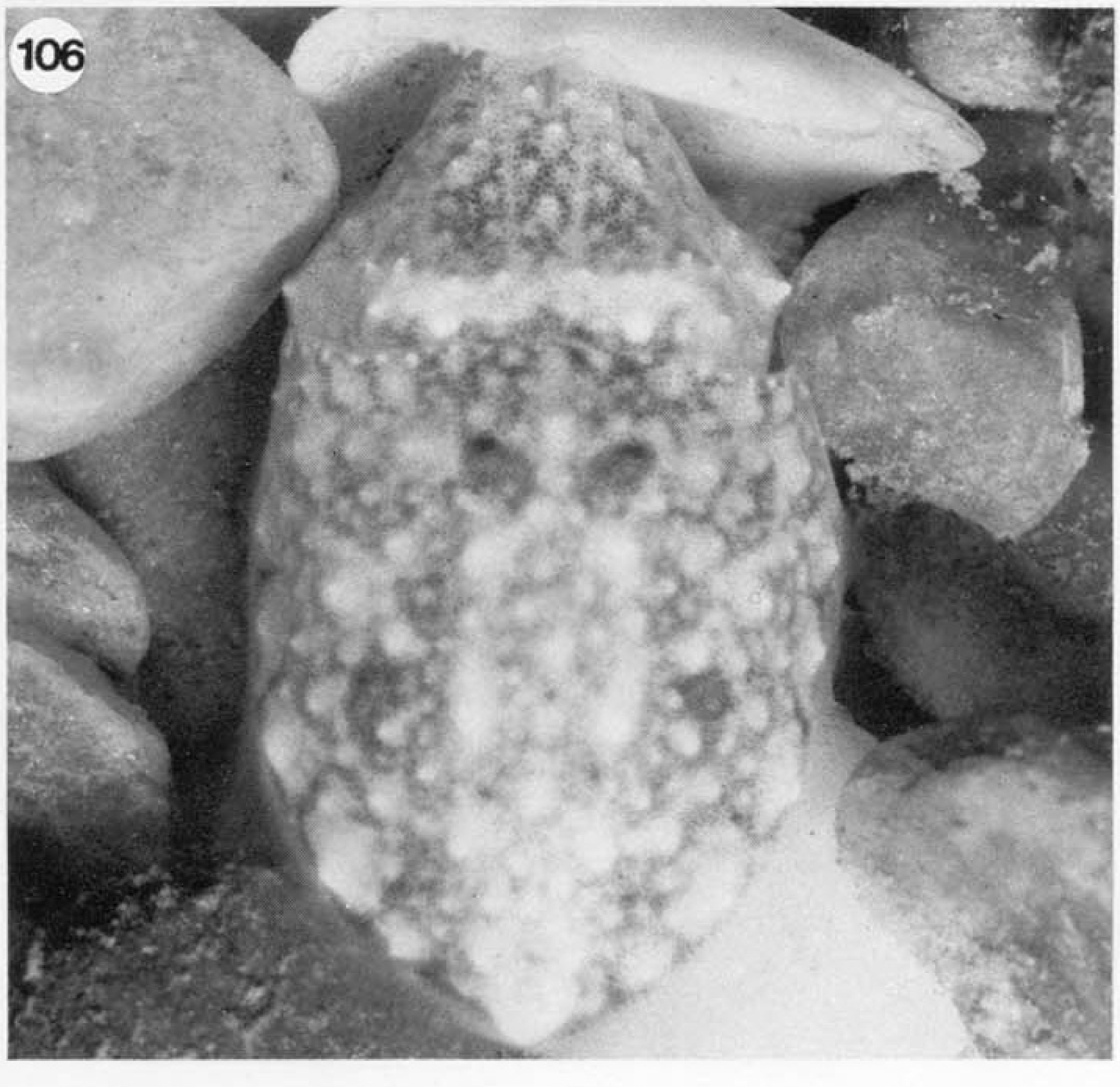

101


102


103


104


105


106

FIGURES 98–106. For description see opposite.