

**Table 1** Effects of biotic and abiotic elicitors on accumulation, synthesis, and degradation of glyceollin in soybean cotyledons

Elicitor	Elicitor concentration	Accumulation ( $\mu\text{g}$ )	Glyceollin synthesis (% of control) (3,400–4,200 c.p.m.)*	Degradation (% of control) (220–245 $\mu\text{g}$ )*
H <sub>2</sub> O (control)	—	<20	100	100
<i>Effective abiotic elicitors</i>				
HgCl <sub>2</sub>	1.5 mM	972 ± 202	110 ± 34	28 ± 8
CdCl <sub>2</sub>	1.0 mM	932 ± 219	138	48
AgNO <sub>3</sub>	3.3 mM	1,280 ± 274	202 ± 56	19 ± 10
CuSO <sub>4</sub>	10.0 mM	472 ± 125	35	17
K <sub>2</sub> Cr <sub>2</sub> O <sub>7</sub>	3.3 mM	495 ± 194	42	29
Triton X-100	5.0 mg ml <sup>-1</sup>	1,391 ± 320	105 ± 10	28 ± 6
Nonidet P-40	5.0 mg ml <sup>-1</sup>	1,205 ± 295	98 ± 5	25
<i>Ineffective abiotic elicitors</i>				
HgCl <sub>2</sub>	0.1 mM	<20	119	92
	10.0 mM	<20	6	11
CdCl <sub>2</sub>	0.1 mM	<50	105	97
	10.0 mM	<100	9	28
CoCl <sub>2</sub> †	10.0 mM	<100	28	55
CrCl <sub>3</sub> †	10.0 mM	<20	18	48
CsCl†	10.0 mM	<30	139	97
SnCl <sub>4</sub> †	10.0 mM	<20	113	104
<i>Effective biotic elicitors</i>				
Fungal extracellular metabolite	5.0 $\mu\text{g ml}^{-1}$	1,352 ± 281	691 ± 181	102 ± 2
	20.0 $\mu\text{g ml}^{-1}$	1,605 ± 309	831 ± 274	103 ± 5
Fungal cell wall	50.0 $\mu\text{g ml}^{-1}$	1,295 ± 382	756 ± 126	97 ± 5
	250.0 $\mu\text{g ml}^{-1}$	1,895 ± 225	856 ± 205	101 ± 4
Fungal cytoplasmic supernatant	100.0 $\mu\text{g ml}^{-1}$	1,025 ± 125	721	95
	500.0 $\mu\text{g ml}^{-1}$	1,434 ± 194	777	93
<i>Ineffective biotic elicitors</i>				
Fungal culture medium control†	5.0 $\mu\text{g ml}^{-1}$	<20	132	97
Soybean cell wall†	200.0 $\mu\text{g ml}^{-1}$	<20	115	105
Soybean cytoplasmic supernatant†	200.0 $\mu\text{g ml}^{-1}$	<20	142	98

Amounts of glyceollin accumulated and degraded were measured at 24 and 8 h, respectively, and rates of synthesis at 18 h after incubation of cotyledons with elicitors, as described in Fig. 1. For preparation of fungal extracellular metabolite, *Phytophthora megasperma* var. *sojae* was cultured as described in Fig. 1. After fungal mycelium was removed by filtration, the culture fluids were lyophilised, dissolved in 10 mM Tris-HCl (pH 7.2), and passed through a column of Sephadex G-50 equilibrated with the same buffer. Fractions eluted in the column void volume were used. Fungal cytoplasmic supernatant was prepared by centrifuging a mycelial homogenate of the same fungus in 10 mM Tris-HCl (pH 7.2) at 80,000 g for 30 min and by dialysing the resulting supernatant against the same buffer. Fungal culture medium control was the fraction corresponding to the fungal extracellular metabolite fraction but the medium was not inoculated with the fungus. Soybean cell wall and cytoplasmic supernatant were prepared using the same methods described for preparation from the fungus. Means and standard errors are indicated where 3 to 5 replicate experiments were run, and other values are means of two replicate experiments.

\* Actual values of incorporation of <sup>14</sup>C-phenylalanine into glyceollin (c.p.m.) or of amounts of glyceollin degraded ( $\mu\text{g}$ ) in the control cotyledons.

† Abiotic chemicals or biotic substances which did not induce glyceollin accumulation at all concentrations tested (0.033–20 mM for abiotic chemicals and 5–1,000  $\mu\text{g ml}^{-1}$  for biotic substances). Concentrations of effective abiotic elicitors were those approximately optimum in inducing glyceollin accumulation. Concentrations of all biotic substances were based on glucose equivalents measured by anthrone assay.

tinguished from the specific response associated with disease resistance, as it seems that the fungal metabolites operate differently from the abiotic elicitors.

The results presented here suggest that it may be possible to discover a new type of plant protectant, protecting against infection not through intrinsic antibiotic activity, but through an effect on plant-pathogen interaction resulting in higher accumulation of phytoalexins.

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## The blind octopus, *Cirrothauma*

THE rare deep-sea octopod *Cirrothauma murrayi* Chun 1910 was first described from a single specimen caught during the Michael Sars Expedition of 1910 (ref. 1). Until now it has been caught only four more times<sup>2</sup>. We describe here three specimens of this species that were recently caught during biological cruises of RRS Discovery (Fig. 1). All of these animals, including the Discovery ones, have been caught at depths of more than 1,500 m, except one that was dip-netted through the ice of the Arctic Ocean<sup>3</sup>.

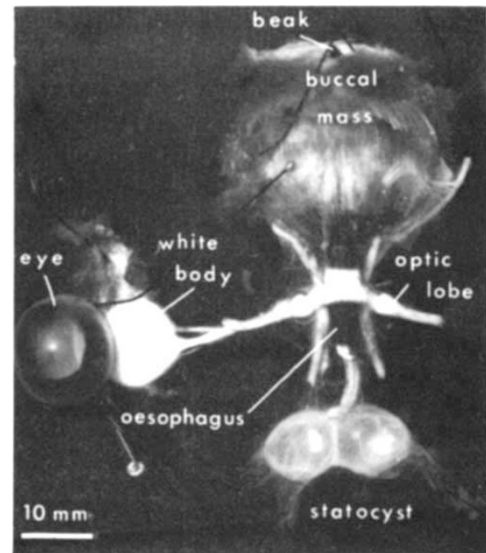
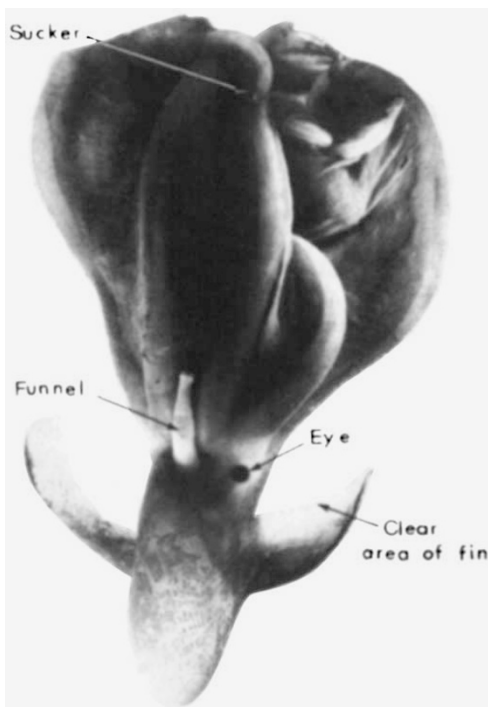
*Cirrothauma* belongs to a poorly known family, the Cirroteuthidae, which have cirri along the arms, a pair of fins, a deep interbrachial web and no radula<sup>1</sup>. *Cirrothauma* is reddish-brown semi-transparent and gelatinous in consistency (Fig. 1). Photographs of other cirroteuthids taken with deep-sea cameras have shown them swimming close to the bottom and looking like medusae, with head down and arms and web widely extended<sup>4,5</sup>. In other photographs they are swimming backwards with a more typical cephalopod posture<sup>5</sup>.

The eyes are remarkable, being simple open cups, with no trace of lens, iris or ciliary body (Fig. 2). The cup is closed by a transparent continuation of the sclera and covered by a thin gelatinous layer less than 1 mm thick. The eyes were only 3 mm in diameter in Chun's animal, the mantle length being 40 mm. Our specimens are larger (155 mm (A), 130 mm (B) and 220 mm (C) mantle length) with an oval pupil 9 mm × 12 mm in the smallest (Fig. 2). The retinae are better developed than is implied from Chun's description<sup>1</sup> (Fig. 3a). However, the rhabdomes are not regularly packed as they are in *Octopus*, and there is no limiting membrane covering their outer ends, which therefore turn and taper irregularly. In one of the Discovery specimens part of the retina was folded, to make a series of chambers, lined by separate, single rhabdomes, looking, as Chun put it, "like little flames"<sup>1</sup> (Fig. 3b). The retina of specimen B therefore seems to be in a degenerating condition similar to that of some deep-sea fishes<sup>6</sup>.

The optic nerves are very long and pass through a large mass of tissue, the 'white body', to a minute optic lobe (Fig. 2). The structure of this is very simple, it lacks the peripheral layers of small cells that are characteristic of cephalopods with good vision. The vertical lobe and other parts of the visual memory system, so well-developed in *Octopus vulgaris*<sup>7</sup>, are reduced. It is difficult to understand what use may be made by the animal of a photoreceptor system such as this, with neither lens nor pin-hole aperture. That the animal has some use for photoreceptors is shown by the fact that the epistellar bodies, photosensitive vesicles near the stellate ganglion, are especially large in *Cirrothauma*.

There are large sac-like statocysts, suspended by muscles at some distance from the brain. As in other octopods there are inner and outer sacs separated by a perilymph (Fig. 4). The maculae are long oval patches with small circular statoliths not covering the whole area. There are no maculae neglectae. The

**Fig. 1** *Cirrothauma murrayi* Chun 1910 photographed on board RRS Discovery while still just alive. The posterior end of the mantle is translucent and parts of the fins are transparent. Marks from the nets can be seen on the skin. One eye is visible at the side of the long, slender funnel. The arms are united by the web along most of their length. The stalked 'suckers' lie towards the tips of the arms. Specimen B caught at 3,000–3,500 m, mantle length 130 mm, funnel length 61 mm.

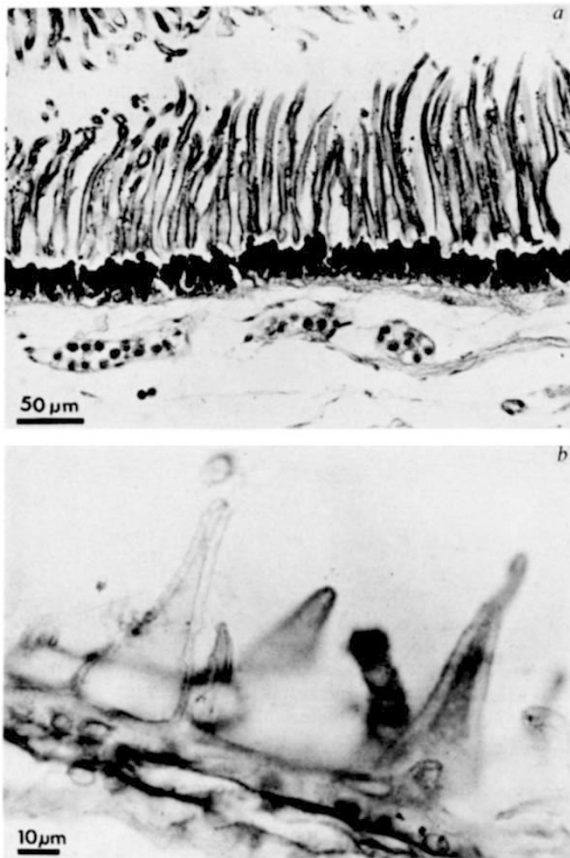


**Fig. 2** The central nervous system, one eye, the statocysts and the buccal mass after dissection. The black rostral tip of the lower beak projects beyond the lips. The oesophagus is heavily pigmented and can be seen just behind the brain. Specimen B.

crista runs round the circumference of the sac, constricting it somewhat by a waist to form lateral and medial parts. There is a single anticrista, as in other octopods. The large volume of endolymph is presumably related to the need for the crista to detect slow angular rotations. This condition resembles that found in *Vampyroteuthis*, but the latter has several anticristae, as in decapods<sup>8</sup>.

The cirri are characteristic of the Cirroteuthidae and are absent from all other cephalopods with the exception of *Vampyroteuthis*. *Cirrothauma* has a longitudinal row of cirri on either side of the single row of suckers. Though not shown in Fig. 1, they can probably extend to a considerable length and are presumably tactile organs. They were stretched outwards and away from the arms in the cirroteuthids photographed in the sea<sup>5</sup>. Sections of the Discovery specimens show that the tactile centres of the brain are well-developed, unlike the visual system, and perhaps the cirri provide the main source of information about the surrounding conditions and for the detection of food. There are 38 suckers along each arm of our specimen of 155 mm mantle length (A) and 36 on the Chun (or 'type') specimen<sup>1</sup>. Chun recognised two distinct sets of suckers, one being unique amongst cephalopods<sup>1</sup>. He described the latter as 'tiny suckers situated on long, plump, spindle-shaped gelatinous stalks . . . 4–5 mm long in the middle of the arms and gradually become shorter towards the tips and proximally'. He suggested that they had lost their function as there was no opening. That they are suckers, even though they do not have an orifice, is shown in histological sections by the presence of a cuticle very similar to that found covering the infundibular surface of the suckers of *Octopus vulgaris* and other octopods<sup>9</sup>. In view of the presence of this sucker cuticle, it seems unlikely that Chun's<sup>1</sup> reserved interpretation that there were 'certain similarities with luminous organs' can now be upheld. Dr P. J. Herring (Institute of Oceanic Sciences) has also looked at the sections for us and can find no trace of light organs. The second type of sucker does have an opening and these suckers lie near the mouth, being the first six in both Chun's animal and in specimen A. The opening of the sucker is restricted and does not lead to a suction chamber such as is usually found in octopods<sup>9</sup>. There is a very shallow cup with radial muscles and a typical cuticle which, like that in other octopods, can be shed as a disk<sup>9</sup>.

The buccal mass is large as is the rostrum of the lower beak, which projects beyond the lips (Fig. 2). As in other cirroteuthids the radula is absent<sup>1,10</sup>, in its place there is a fleshy tongue-like

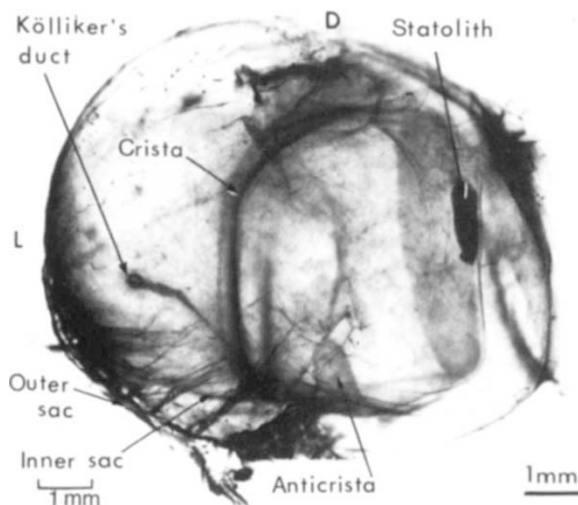


**Fig. 3** a, Section of the retina of specimen C. b, Isolated rhabdoms from a sac formed by folding of the retina of specimen B.

structure attached ventrally along most of its length. At the front of this 'tongue' there is a large papilla, perhaps the salivary papilla.

The funnel is extremely long and slender<sup>1</sup>, being 47, 61 and 185 mm in animals A, B and C, respectively (Fig. 1). The mantle opening is small and closely surrounds the base of the funnel. The function of this long funnel is not known but it could be important in directing fine jets of water during delicate manoeuvring movements while swimming upside down in the

**Fig. 4** Left statocyst from specimen A seen from in front. The statolith is displaced and seen edge on near to the macula. D, dorsal; L, lateral.



medusoid form. Perhaps its jets of water are used to stir up the sediment on the seabed to expose small prey, or possibly to bury the eggs in soft sediment.

The cirroteuthids differ from all other octopods and resemble decapods in the presence of fins (Fig. 1). These, like the cirri, recall the condition in *Vampyroteuthis*<sup>11</sup>. It seems probable that these deep-sea animals still retain characteristics common to both octopods and decapods. In this connection it is interesting that *Cirrothauma* and another cirroteuthid of which we also have sections, both have a system of giant nerve fibres<sup>11</sup>, which are usually only associated with decapods<sup>12</sup>. We hope that further study of the Discovery specimens may help to settle several problems of structure, function and mode of life of these curious animals.

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## Spike frequency adaptation in amphibian sensory fibres is probably due to slow K channels

SPIKE frequency adaptation (SFA)—a decrease in firing frequency during the action of a maintained stimulus—is a mechanism for the input-output transformation of a signal and it is common at many levels of the animal kingdom. The occurrence of SFA in amphibian sensory nerves<sup>1-4</sup> offers an opportunity to explain the phenomenon at the membrane level in terms of the Hodgkin-Huxley (HH) theory<sup>5</sup>. Here we show that SFA in amphibian nerve is probably due to a current through slow K channels, and we suggest that these channels must also be responsible for different cases of SFA in nerve cells of various types.

The HH model for the node<sup>1,6</sup> gives, for constant current steps, rhythmic firing but not SFA<sup>1,7</sup>. Further mechanisms with relatively long time constants are obviously needed to account for SFA. As SFA lasts only from several ms to a few tens of ms it is evident that slow Na (ref. 8) and fast K (ref. 9) inactivations, with time constants of several hundred ms and even 1 s, cannot be a source for SFA. Electrogenic pumping is also excluded (for refs and discussion see ref. 10). K<sup>+</sup> accumulation near the node<sup>11</sup> can be expected, by analogy with squid axon<sup>12</sup>, not only to fail to cause SFA but also to give inappropriate changes of successive overshoot and undershoot amplitudes in a train, decreases rather than increases. Therefore, we consider that the necessary mechanism involves the currents flowing through slow K channels. The addition of slow K channels with the properties we have measured gives calculated SFA with most of the properties measured by others. Also, there are indications of slow K channels in amphibia in which SFA is usually observed, *Xenopus*