

Visual Tactics and Evolutionary Strategies

(Taktik der visuellen Erkennung und evolutionäre Strategien)

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With 4 Text Figures

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Abstract: The paper gives examples of behavioural interactions (called here *survival events*) between coleoids and their predators (and prey) in support of the theme that mechanisms of visual perception have played a directing role — as agents of selection — in their coevolution through the pattern-generating and pattern-recognising systems of the participants. The triple response of coleoids to disturbance is described. *Octopus* camouflage (part of the response) is analysed in terms of counter measures that enable octopuses to escape detection and to manipulate the attention of their vertebrate predators. These visual tactics are discussed in relation to the evolutionary forces acting on ectocochlia in the Mesozoic.

Zusammenfassung: Es werden Beispiele gegeben von Verhaltens-Interaktionen (hier "Überlebens-Ereignisse" genannt) zwischen Coleoiden und ihren Feinden (bzw. Beute). Sie dienen zur Stütze der These, daß Mechanismen der visuellen Erkennung durch Systeme der Muster-Bildung und Muster-Erkennung eine maßgebliche Rolle als Selektionsfaktor bei der Coevolution der Beteiligten gespielt haben. Die dreifache Antwort der Coleoiden auf Störungen (Verbergen, Überraschen, Ablenkungsmanöver) wird behandelt. Die Tarnung von *Octopus* (als Teil der Antwort) wird im Sinne von Gegenmaßnahmen beschrieben, die *Octopus* in die Lage versetzen, der Entdeckung zu entgehen und die Aufmerksamkeit ihrer Wirbeltier-Räuber abzulenken. Diese Taktik der visuellen Erkennung wird hinsichtlich der evolutionären Kräfte diskutiert, die auf die Ectocochlia im Mesozoikum einwirken.

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Professor Seilacher has been asking us in this symposium "what are the major extinction events?" He is mindful perhaps that it is only too easy to slip into the habit of referring to the evidence leading to an end-point in the fossil record as if the end-point itself were the extinction "event", confusing effects with causes and so failing to ask the right questions. In this essay, I would like to turn his question round and ask: *what are the major survival events* in the history of cephalopods?

Since last writing on this subject at any length (Packard 1972), I have been exploring the colour pattern and colour change systems of coleoids, especially of the octopus (see Packard & Hochberg 1977 also Packard & Sanders 1969 and 1971). The research has provided remarkable and often quite unexpected confirmation of my view that the main events determining the evolution of coleoids — and particularly the modal changes between them and their ectocochlian ancestors — took place in *behaviour space*. On this view, vertebrate vision was the main selective force

operating on cephalopods during the late Palaeozoic radiations of reptiles and fish into the sea.

To put this in the context of general evolutionary theory, let me say that I have little time for explanations of progressive evolution that rely on cataclysmic events such as the end-Cretaceous impact of a large meteorite, or a rapid and drastic change in climate. However good the evidence for such events having occurred at intervals since the early Palaeozoic, they are *not sufficient* to explain why more advanced forms should become dominant in the wake of the event, *unless* some other ingredient is present that actively promotes the emergence of higher forms. That causal ingredient has to be sought not in the earth sciences but in the life sciences. Hence my use of the term “behaviour space”. I decided that it was not by chance that the modal changes undergone by cephalopods and vertebrates during the evolution of their modern representatives — loss of external hard parts, differentiation of jaws and pharynx¹ and/or appendages that can manipulate the environment, adoption of active exploratory modes of life, proportionately larger brains and sense organs than possessed by their ancestors, etc. — are the same modal changes in the phylogenetically quite separate groups, and concluded a) that modern cephalopods and higher vertebrates had co-evolved, b) that the main agency for this coevolution has been behavioural interactions between the two groups centred around food. I envisaged a scenario of predator-prey relationships in which vertebrates — initially reptiles and fish, latterly mammals and birds — competed with cephalopods for common resources forcing possessors of a primitive pinhole-type eye (still seen in *Nautilus*) to evolve a single chamber lens-eye and more elaborate brain able to match in performance the eye and brain of vertebrates. I saw no other way of explaining the extraordinary functional correspondence between the two visual systems, coleoid and vertebrate, starkly illustrated by the simple fact that a squid will shoal with a fish or by the performance of *Octopus* in the kinds of visual discrimination experiments usually conducted by experimental psychologists on vertebrates (see Young 1961). Not only does vision, of remarkably similar design and performance, stand out as a major theme in the psychological evolution of the two groups, but it seemed to me that the selection pressures for that psychological evolution had operated, in a feed-forward manner, largely *through* vision.

In surveying here some of the evidence that confirmed this point of view, I would like readers to bear in mind that the forces being talked about must — if they are to have any meaning at all — have applied way back in geological time and *mutatis mutandis* have acted on Mesozoic ammonites and belemnites as on Cenozoic octopuses and squids. Vision research has advanced greatly in the last twenty years, both in the neurophysiology of visual coding in animals and, to a lesser extent, in the field known as “ecological optics” (Gibson 1979), which explores visual properties of the environment that are of significance to animals. Although not formalised until Gibson, the principles of ecological optics — i.e. that visual systems are processors of information in the optical array emanating from the environment — have long

¹“The arms [of coleoids] are the operational equivalent of the pharynx and jaws of fish” (Packard 1972: 261).

been assumed by biologists and must potentially have been valid in Mesozoic as in present-day seas. I shall present evidence that some of the mechanisms for exploiting the information content more fully had been evolved by vertebrates well before the Mesozoic.

The advances in our understanding of visual perception raise new questions about such fossil characters as ornamentation. By the same token, the evident importance of eyes and of chromatophores in the lives of present-day cephalopods should act as a spur to palaeontologists to look for fossil evidence of these. I am reluctant to believe that there never existed conditions of fossilisation able to preserve some trace of the hard δ -cristallin core of the underwater spherical lens or traces of chromatophore pigments. Chromatophore pigments are known to contain concentrations of nickel (Froesch & Packard 1979). Might analysis of belemnites reveal punctate accumulations of this element?

Vertebrate vision

The following properties of visual perception with known neurophysiological basis are used by vertebrates to process the image received by the retina:

a) *simultaneous contrast* perception: a property by which the illumination of a surface is always perceived in relation to an adjacent surface and signalled, already at the level of the retina, as a ratio rather than as an absolute value.

b) *opponent processing* by retinal ganglion cells whose receptive fields are maximally excited only when the periphery and centre of the fields (usually circular or oval) receive stimuli of opposite sign.

c) orientated bar detectors and spatial frequency-tuned channels.

d) relative movement detectors.

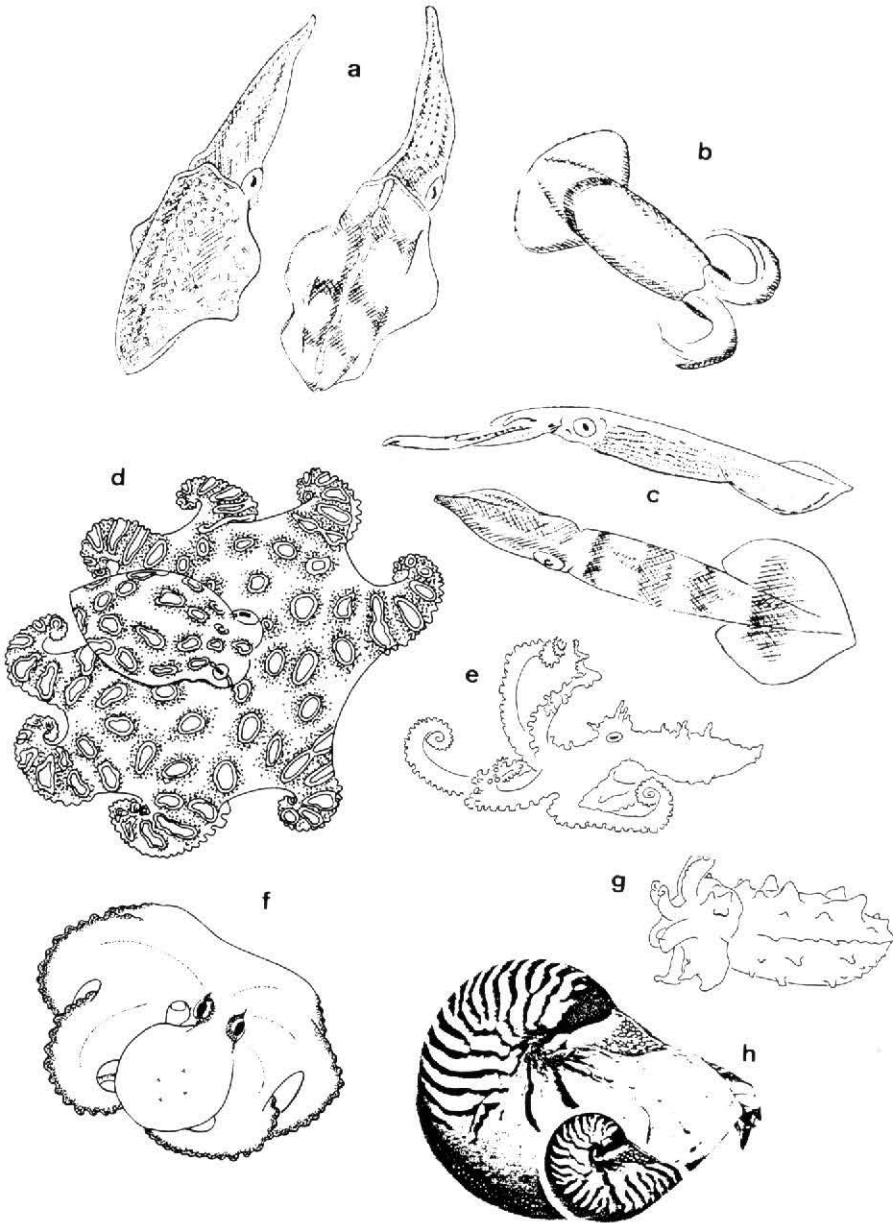
e) foveal versus ambient processing.

They make up parts of the pattern recognising system (PRS) of vertebrates. (N.B. There are several modern texts on the psychology and physiology of vision to which the reader can turn for partial summaries of the above, e.g., Bruce & Green 1985).

Survival events

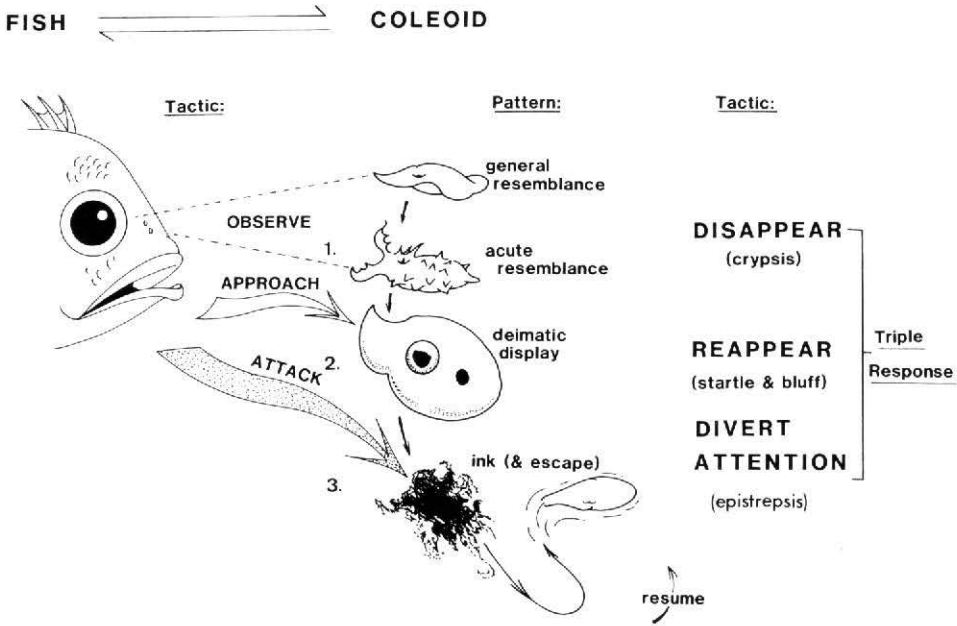
Response of coleoids to disturbance. The soft integument of coleoids with its remarkable colour change capabilities is used in two different kinds of behaviours: a) for warning and signalling (Text Fig. 1 and the various figures in Moynihan & Rodaniche 1977 and Moynihan 1985), b) for camouflage (Text Fig. 3). Both of them are directed towards other animals either of their own or other species.

Sepia and *Octopus*, although far apart systematically, both show the same sequence of responses — called here the “triple response” — to disturbance by an intruder or potential predator (Text Fig. 2) that must often be repeated in nature and be of primary importance in the survival of individuals. When the intruder is first noticed they adopt a camouflage pattern of *acute resemblance* which is maintained until the intruder either goes away or approaches to within touching distance,



Text Fig. 1. "Ornament" and "sculpture" in living coleoids.

The squids a - *Sepioteuthis sepioidea*; b - *Lolliguncula panamensis*; c - *Loligo plei*, octopuses; d - *Hapalochlaena lunulata*; e and f - *Octopus vulgaris* and a cuttlefish; g - *Metasepia tullbergi* compared with h -adult and juvenile *Nautilus belauensis*, illustrating the emphasis on dark/light and light/dark contrast and on stereo features ("sculpture") created by papillae and "flamboyant" postures (e and g). (a and b from Moynihan & Rodaniche 1982, c from Hanlon 1982, d after a photograph by C. Bryce, W. Australian Museum, e and g from Packard & Hochberg 1977, h from Saunders 1981).



Text Fig. 2. Survival event No. 1. (Coleoid survives, fish goes hungry). Sequence of reciprocal visual tactics between a coleoid and a vertebrate predator that takes the form of a *triple response* to the disturbance caused by the intrusion of a fish predator into the scene.

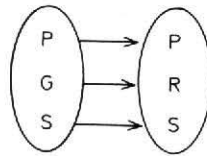
whereupon they suddenly switch on the *deimatic display*² which may cause the intruder to back away, but if instead it attacks or persists in approaching, the cuttlefish or octopus physically *escapes* from the scene by jetting backwards and simultaneously *emitting ink* with the result that the predator, usually strikes at the blob of ink rather than at the prey. The whole sequence often occupies no more than a few seconds, nevertheless the outcome of these few seconds may be of critical importance to the survival of the cephalopod and, if successful, is a true *survival event*.

I do not know whether teuthids with their considerably less elaborate chromatophore system exhibit all of the behaviours of the triple response. Moynihan & Rodaniche (1982) do not list camouflage amongst the extensive repertoire of colour and body patterns found in *Sepioteuthis sepioidea*, the Caribbean reef squid, one of the most differentiated of the group. Squids do, however, exhibit the deimatic display, and of course belemnites possessed ink and presumably also the inking response. The point to bear in mind is that the triple response achieves its effect through an elaborate sequence of subterfuge: a series of "lies" each employing a

²This is the same as the "dymantic" display of most authors on cephalopods. The name *deimatic* is preferred for reasons of priority (see Hanlon & Messenger, unpublished, also McFarland 1981).

different tactic — 1) hiding, 2) bluff, 3) diversion of attention — directed very specifically at the visual perceptions of the intruder. The communication aspect of these and other patterns has recently been explored as a subject in its own right by Moynihan 1985. For our purposes, it is sufficient to notice that each phase of the triple response is tuned to a different aspect of the pattern recognising system (PRS) of the predator; each involves surprise (i.e. interferes with the expectations of the observer) especially the rapid and startling change from the first to the second phase of the response.

Camouflage. The photographs in Text Fig. 3 give an idea of just how sophisticated the camouflage patterns can be in an *Octopus* inhabiting shallow water. Very similar patterns are produced by the cuttlefish *Sepia*. I have indicated alongside the photographs some of the ways in which specific components of the patterns achieve their camouflage effects. To follow the reasoning, the reader must enter the perceptual world of the observer. In fifteen years spent analysing these patterns, I have not found a single property of the chromatophore and body-patterning system that is not in some way directly reflected in properties of the vertebrate visual system (known either from neurophysiological or from psychophysical experiments). It is truly a looking-glass world in which the pattern generating system (PGS) of the cephalopod reveals itself to be directly plugged into the pattern recognising system (PRS) of vertebrates at many points:



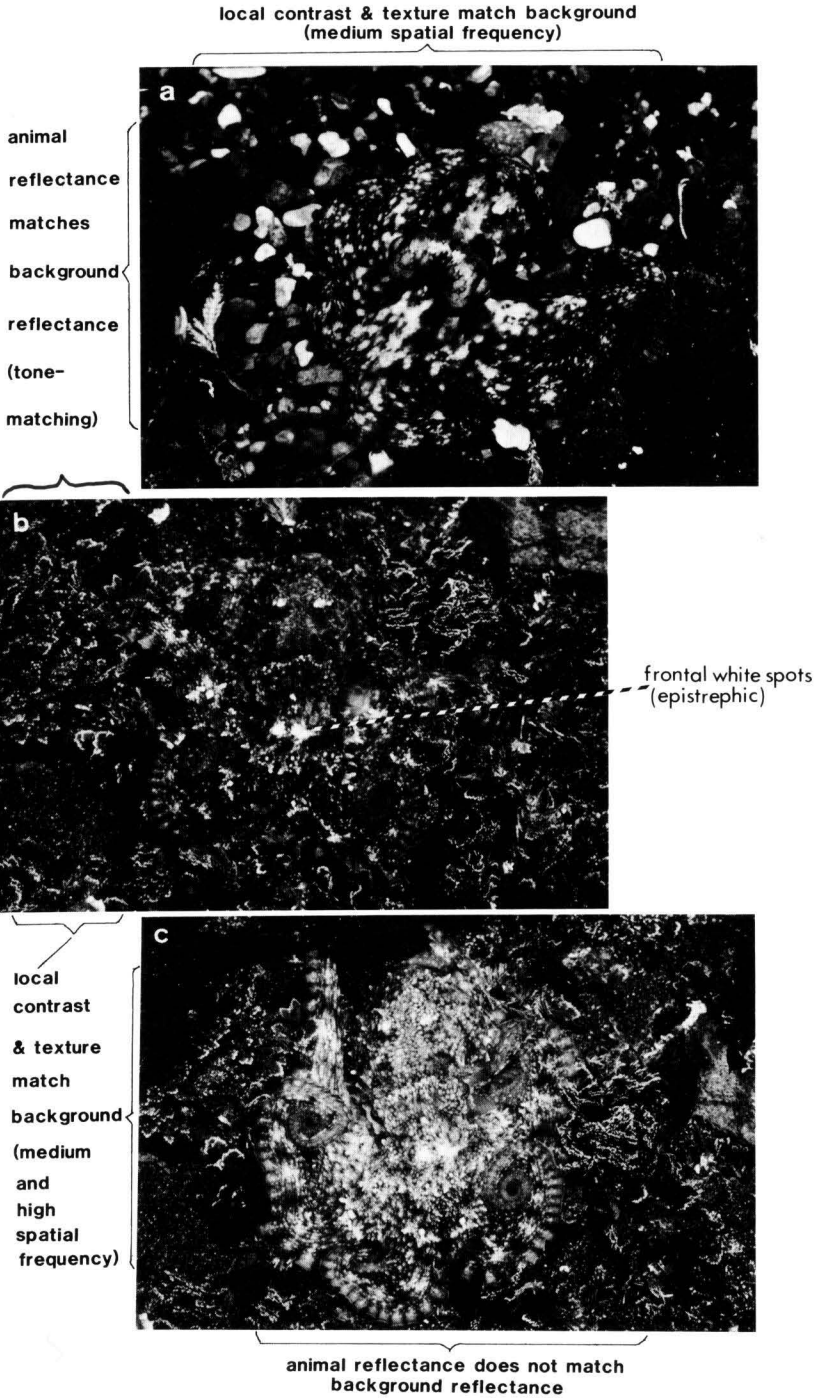
I give four examples of these properties, all of them illustrated in the photographs of Text Fig. 3.

1) *Overall tone-matching* (see Froesch & Messenger 1978, for details). As seen in Text Fig. 3c, the octopus was at first paler than its background — i.e. it reflected, on average, more light than the average reflectance of the background. A few moments later (Text Fig. 3b) the average level of reflectance was adjusted to equal that of the background.

This was achieved without changing the basic pattern (a complex mottle comprising many dark/light, colour and textural components) but by changing their degree of expression: i.e. by an amplitude control mechanism that increases the expansion of dark components already active through increase in nerve firing rate. This alters the grey level, and the effect on the visual system of the observer is to abolish contrast between animal and background denying to low spatial-frequency detectors information that a distinct object exists.

Text Fig. 3. Camouflaged Juvenile Octopus (*Octopus vulgaris*).

a - on a coarse sandy background, b and c on a fine sandy background containing coralline algal encrustations.



2) *Feature matching*. The upper octopus (Text Fig. 3a) has a smoother skin and wears a coarser mottle characterized by repeating dark/light and light/dark features, both round and orthogonally orientated, of medium size range (medium spatial frequency) and high contrast with abrupt transformations between dark and light. The details of the mottle match in size range, shape and degree of contrast the natural background of multi-colored gravel with its rounded outlines and sharp discontinuities between neighbouring elements.

The octopus in the lower photograph (Text Fig. 3c) also employs dark/light and light/dark features and the same repeating arm bars, etc. as in the upper photograph, but the mottle includes, throughout the skin, units of a smaller order of size (higher spatial frequency) close to the spatial frequency of the sand and branchlets of coralline algae that make up the natural background. The effect on the visual system of the observer is to feed medium- and high-frequency detectors in the eye with information indistinguishable from background information. Notice that many of the details of the mottle have a centre/surround organisation (usually light centres with dark surrounds).

3) *Stereo-genesis*. While the skin of the octopus in the upper photograph is smooth apart from a few large lateral papillae, in the lower photographs it is raised into papillae of different sizes and suckers along the exposed edges of the arms protrude mimicking the 3-dimensional structure of the background of coralline algae, etc. As with the dark/light features mentioned above, these stereo-effects can be enhanced by increasing the firing rate of nerves to the skin (increasing the height of the papillae) and by raising and twisting the arms (see Text Fig. 1e and g) when, for instance, the background includes sargassum weed. They are presumably tuned to stereo- (i.e. retinal disparity) detectors in the visual systems of binocular animals (mammals, birds and many reef-living teleosts). Like the dark/light features, they achieve their camouflage effect by generating information consistent with (and ? indistinguishable from) background information.

4) *Epistrepis*. The paired *white spots* at the front of the head of the camouflaged octopus visible in all three photographs are sometimes the only features visible in the conditions of low illumination that exist underwater when the rest of the octopus is tone-matched (see above) with the surroundings. Their shape varies from one octopus to another: sometimes they are elongated, sometimes they are fused into a dumbbell shape. They are not recognisable as an octopus to the uninformed observer (any more than the headlights of a car are recognisable as a car), nevertheless, when switched on, they capture the attention of the observer as irresistibly as do the headlights of an oncoming car on a dark night when one should be attending to the road. I call this process "epistrepis" from the Greek $\epsilon\pi\iota\sigma\tau\epsilon\rho\epsilon\psi\iota\varsigma$ and any stimulus which draws attention to itself "epistreptic" and any such response to that stimulus "epistrepic". The spots achieve their effect in much the same way as the ink ejected in the triple response: by drawing attention to itself it diverts attention from parts of the visual scene that would reveal the cephalopod lurking. When played on the attention mechanisms of creatures like ourselves or reef-living teleosts searching with well-developed retinal foveae, epistrepis lands the image of the white spots at the centre of the fovea. When I first described the function of the frontal white spots (Packard & Sanders 1971), I referred to them as a foveal trap. The spots are under

independent nervous control and can be switched momentarily on and off; no doubt this serves to sustain or to switch off the interest of the observer.

Mechanisms of Attention

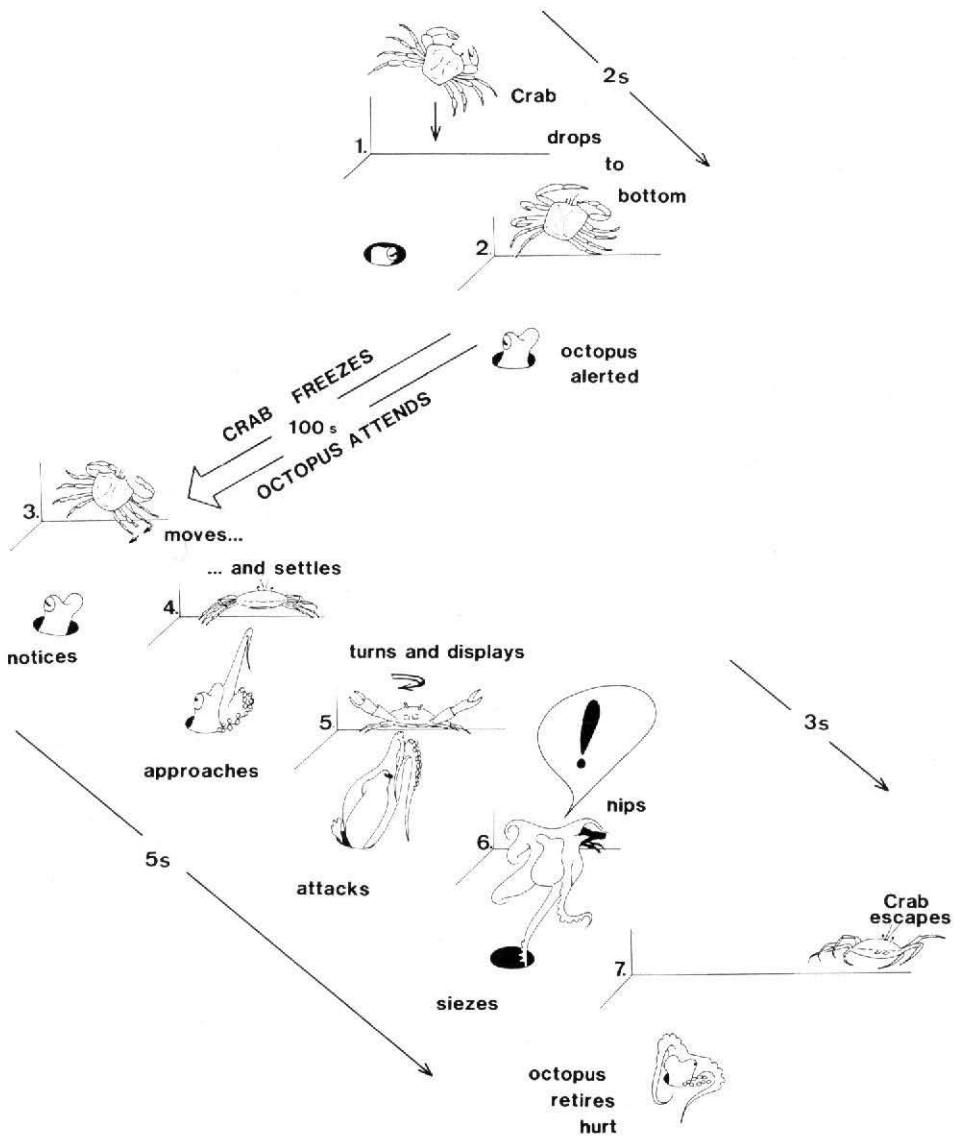
It would be very difficult to arrive at an understanding of the function of the frontal white spots of an octopus if we had only anatomical evidence to go on: that is, from details of their shape and location in the skin or from trying to recreate them in preserved specimens. Yet the behavioural evidence suggests that these white spots may be crucial to the survival of an octopus during the kind of brief but dramatic encounter in which the octopus may be eaten — or avoid being eaten — by a predator.

It might be argued that epistresis and the other tricks employed by coleoids to disrupt the pattern-recognition abilities of predators are modern phenomena or that evidence for the existence of such coevolutionary adaptations in fossil coleoids and ectocochlia is inaccessible to palaeontologists. But there are three lines of evidence against this; the first is the wide range of common denominators in visual processing amongst the different classes of vertebrates (and many invertebrates) long separated phylogenetically; second, the identical defensive adaptations that have been evolved by the three main orders of living cephalopods to combat these visual processes (I have mentioned here the close similarities in the acute camouflage mottles of *Octopus* and *Sepia* and drawn attention elsewhere (Packard 1972, Packard & Hochberg 1977) to homologies in warning displays (see also Moynihan & Rodaniche 1977). Third, there is the direct palaeontological evidence from cranial endocasts showing the nerve foramina that images were captured by the eyes of fossil vertebrates.

Anyone with a classical training in comparative anatomy who has dissected the orbit of a dogfish (elasmobranch) has seen the six extraocular muscles that attach to the eyeball and that they are innervated by no less than three of the ten cranial nerves. The arrangement is stable from jawed fish onwards. This evolutionary emphasis on oculomotor assignments to the cranial nerves, testifies to their having a very important function. That function, well studied at the physiological level, is to provide the eyes with their own locomotory system that stabilizes them in the visual field and renders them independent from movements of the rest of the body. In vertebrates possessing a retinal fovea capable of resolving fine detail (i.e. of high acuity) the three oculomotor nerves have the added function of generating eye movements for capturing and retaining in the fovea the images of objects of interest that are first picked up by the ambient retina. Ambient and foveal retinae thus play cooperative and complementary roles: ambient retina with its wide field but poor definition, foveal retina with its narrow field but high resolution.

The oculomotor movements that execute these complementary roles are an essential part of the *attention mechanism* and are generated in the brainstem which is fed by higher parts of the brain. The mechanism has become greatly refined in higher vertebrates — particularly the visual fixation and scanning processes employing saccadic eye movements that allow a target to be positioned and held on the fovea to within a few minutes of arc. In such animals, foveal and ambient vision (Trevorthen 1968) have differentiated as two systems nested in one. Whatever the details of the later refinements, however, the fact that the nerve centres for eye movements are located in parts of the brain that are very old — in the middle and posterior brainstem close to the midline — suggests that the mechanism too is very old.

Some squids (e.g. *Benthoteuthis*) have a highly developed anatomical fovea (Glockauer 1915). *Sepia* (Muntz 1977) has a zone of longer receptors both anteriorly and posteriorly on the equator of the retina, recalling the double fovea of some fish, one for binocular vision the other for monocular vision. *Octopus* (Young 1962) has no obvious anatomical fovea but the receptors are longer and slightly more crowded along the retinal equator than elsewhere. Nevertheless, octopuses exhibit sustained visual attention.



Text Fig. 4. Survival event No. 2. (Crab survives, octopus goes hungry). Reciprocal tactics adopted by small octopus (*Octopus vulgaris*) and crab (*Carcinus maenas*) emphasising the role played by freezing of movement, sustained visual attention and other coevolved behaviours. Note the brevity of the absolute time durations (in seconds, large arrows).

My last example of a survival event (Text Fig. 4) comes not from cephalopod/vertebrate interactions, but from cephalopod/arthropod behaviour space and illustrates how closely tuned are the specific components of defensive behaviour to the visual pattern-recognising mechanisms of the cephalopod predator. The example

also illustrates the important role that learning plays in these visual tactics. The main sub-events are shown in Text Fig. 4. A crab (*Carcinus maenas*) dropped into a tank in which a small octopus (*Octopus vulgaris*) had a hole. On reaching the bottom, the crab remained absolutely still for more than a minute, but its fall had alerted the octopus which steadily fixated the crab until the crab eventually moved one of its legs to settle on the bottom, at which point the octopus reached towards the crab to launch an attack, the crab responded by rapidly turning to face its adversary with open claws outstretched. The octopus completed its attack covering the crab with its web and was nipped on one arm, whereupon the octopus withdrew to its hole and the crab escaped into a dark corner of the tank where it remained motionless with the octopus looking on.

Several specific adaptations are involved in this interchange: 1) the alerting response to a moving stimulus recognised as a crab. (Recognition of the crab "Gestalt" by some cephalopods seems to be innate) but the stimulus must *move* if it is to act as a releasing stimulus for an attack (Young 1956, Boulet 1958, 1964, Maldonado 1964); 2) the crab freezing to counteract 1): (the "freezing" response as an adaptation to avoid detection is widely distributed in the animal kingdom (Cott 1940)); 3) the sustained visual attention — or psychological "set" — of the octopus over many seconds: (this holds the crab in the visual field and its address in memory processes even in the absence of the specific releasers (movement of the stimulus) for an attack); 4) the crab turning to face the predator has the effect of simultaneously exposing its defensive weapons and avoiding exposure of the vulnerable posterior surface of the body at the junction between carapace and abdomen. (When capturing crabs of similar size to themselves, small *Octopus vulgaris* always manoeuvre the crab so that their mouth can be applied to this part of its body to poison the prey); 5) the shape and power of the crab's claws which are adapted to give a sustained nip, not a cutting action, that maximally stimulates pain fibres but does not necessarily damage the skin; (I can personally testify that the pain is quite excruciating, even from a small crab, but never produces any lasting damage); 6) the pain felt by the octopus and the well known ability of pain to modify the original behaviour first on a short-term basis — causing retreat — and subsequently as a long-term memory that inhibits further attacks on crabs. (N. B. Most of the visual learning (discrimination) experiments carried out on *Octopus vulgaris* at Naples are of the associative learning type in which electric shock is employed as punishment for attacks on those shapes that the experimenter has designated as the negative shape, while attacks on positive shapes are rewarded with food. With this trial-and-error method octopuses learn quickly and reliably. Ross (1971) has pointed to the possible effects that such learning abilities have had on arrangements in the natural world; he found that the distribution of hermit crabs carrying stinging anemones as commensals corresponds to the distribution of octopuses).

For a summary of some of these behaviours including the ethology of octopuses in visual training experiments see Young 1961, Wells 1978 and Packard 1963.

Discussion

The title of this section of the symposium is "Major Evolutionary Strategies". I have provided instances of a category of events operating in behaviour space, that determine whether an organism survives or is extinguished. Like other categories of selection, the events act upon individuals; but they also act *through the agency* of individuals, usually on a 1:1 basis. Such selection of and by behaviours is very different from the selection to which an organism's biochemistry and physiology are directly exposed by conditions in the physical environment as conventionally conceived. Moreover, as it acts through the agency of the higher behaviours of the participants in predator/prey interactions, particularly through the processes involved in visual perception, the selection can be said to be, in the broad sense, psychological and to be progressive in the sense that it selects for similar and/or counter be-

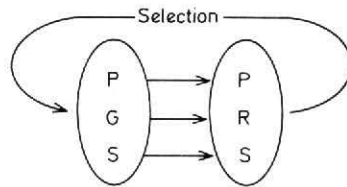
havioural adaptations in the object organism perceived. Where visual attention is involved, attention itself becomes the selecting agency.

Precious evidence of discrete survival events of the kind illustrated in this paper — each occupying a few seconds, but with consequences for a lifetime and preserved for ever in the fossil record — is provided by Bond's detailed analysis in this symposium giving the incidence of sublethal injury to the shells of ammonoids. They indicate the likely levels of predation amongst ancient cephalopods and the efficacy of the external shell as a protective structure able to repair itself. Presumably the predators were mainly reptiles and also other cephalopods. It is reasonable to assume that cephalopods have always been good to eat and that the overall risk of predation has remained much the same throughout time. When the incidence of sublethal injury is plotted against shell-thickness factors for the different ammonoid species a non-random distribution is obtained which Bond interprets as indicating that the ability to *survive* injury (i.e. not to succumb to injury) increases with shell thickness: an interpretation tellingly supported by the high incidence of repaired injuries in the thick-shelled modern *Nautilus*. It suggests that in ectocochlian lines in which the shell became thinner, and in coleoid lines where the shell became internal and lost its protective function, there would have been high selection pressure for the evolution of dynamic means to protect the vital soft parts of the animal including appropriate behaviour strategies and tactics for avoiding physical contact with predators. Presumably the attacks made on the shells studied by Bond were visually directed. The best tactic for avoiding contact is to avoid being seen.

Behind this reasoning lies an important assumption about the difference between the two sensory modalities vision and touch (see Gregory 1967). In principle, an animal that protects itself within a hard external shell needs little or no advance notice of an attack. Its solid shell is its defence; and if it is already drawn into its shell it does not necessarily even need to see its attacker. But if it has no external shell and uses dynamic means to avoid being seen — for instance switching on camouflage at the appropriate moment, as in the triple response to disturbance — it needs to see the predator (ideally, before the predator sees it) and to hold the information that the predator is present for as long as the risk of an attack lasts. We have just seen that a similar consideration obtains in the visually mediated predator/prey interaction between an octopus and a crab. Selection for shell reduction must have been coupled — through camouflage — to selection for eyes, brains and perceptual processes (including the necessary memory processes that could bridge the time gap between what is seen and what is eaten). At the cellular level, for instance, this would have meant selection simultaneously for processes as disparate as those controlling secretion by the shell epithelium, development and differentiation of nerve cells, and morphogenesis of chromatophores (or their ancestral analogues). In such an evolutionary scenario a major extinction event would occur when this coupling was strained or broken. Shell reduction followed a different course in the orthocone ancestors of the coleoids from that seen in many spiral-shelled ammonoid and ammonite lines whose shell remained external. One evolutionary strategy may have permitted the necessary coupling between adaptations affecting the shell and adaptations affecting behaviour, while the other did not. It would be interesting to know if there were lines of ammonites with transparent shells (postlarval as well as larval) that would have allowed dynamic colour change to have been visible through the shell. In many coleoids the first chromatophores that can be seen very clearly in transparent larval and juvenile forms are deep inside the body, for instance overlying the visceral mass, and not in the integument.

It is sometimes argued (for instance Ward 1983) that the great variability in ammonite ornamentation speaks for its having little evolutionary significance, and Dzik (1981) uses a similar argument when describing the great variability of aperture patterns within populations of early cephalopods. But in visual matters, high variability may be a positive advantage. The camouflage patterns of *Octopus vulgaris*

are highly individual (see, for instance, the mantle white spots illustrated in Packard & Hochberg 1977) presumably for the same reason that Batesian mimics are usually polymorphic. A predator — especially one that learns by experience — is less likely to recognise an edible prey if the prey image varies widely or continuously than if the image is a standard one (see Curio 1976). If the pattern-generating system (PGS) of the coleoid skin is to defeat the pattern recognising system (PRS) of the vertebrate eye, variation in the information — or “misinformation” — must be continuously generated and be continuously subject to the selection process, i.e.:



The main colouration on the shell of the living ectocochlian, *Nautilus*, consists of disruptive markings (Text Fig. 1h) of the kind seen in scombrids and other pelagic blue fish in a dorso-ventral arrangement that is basically one of counter-shading in the adult. It has been looked at from the camouflage point of view (both in the adult and the juvenile) by Cowen et al. (1973). These authors then looked at the ornamentation of ammonites which many have considered to have a defensive role (see Moore 1957 and Ward 1981). Applying the reasoning adopted with *Nautilus*, they conclude that “ammonite ‘ornament’ can satisfactorily be interpreted as shell sculpture providing camouflage. Camouflage patterns deal with light and shade. In the photic zone, raised and depressed structures on a shell could generate light and shade patterns which would in large part be functionally equivalent to permanent pigment”.

Curiously they also argue that the heavily sculptured microconchs of sexually dimorphic genera such as *Cadoceras* would not have been countershaded (and were therefore probably benthonic) simply because they were ribbed throughout the conch. Shadows depend on the pattern of illumination under water. There are many conditions in which the dorsal surface may be illuminated by downwelling light which has a strong directional component and so is able to cast local shadows, while the ventral surface is illuminated by diffuse (multidirectional) light in which ventral ribbing would cast no extra shade.

This then is a plea for palaeontologists to enter still more deeply into the ecological optics of Mesozoic seas. The task may not be as daunting as might at first seem. In this essay I have stressed the basic unity of vertebrate vision. Most of the characters that palaeontologists recognise or puzzle over in their specimens are characters that he or she sees and some of them may be the same characters that reptiles, or that conspecifics, adopted to recognize — or be confused by! — these creatures when they were alive.

However, anyone wishing to follow up this line of thought and practise visual tactics on their specimens should be advised to view them under water.

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