

BEFORE THE VOYAGE

Prologue

This volume is devoted to the body patterns of cephalopods.

It appears almost ten years after “Cephalopod Behaviour” (1996) by Roger T. Hanlon and John B. Messenger: a landmark in cephalopod literature. *Cephalopod Behaviour* is, as far as we know, the most comprehensive account available on the behavioural biology and ecology¹ of these animals. It is «the ideal book for any biologist ... who wants an authoritative, interesting, and most of all, crystal-clear introduction to cephalopods» (Lipinski, 1999, p. 249).

In their book, Hanlon and Messenger refer to roughly 790 published contributions² on cephalopod behaviour and to a long series of personal observations and unpublished data. They have collected and organized the various sources providing a synthesis that represents our current knowledge on the behaviour of cuttlefish, squid, octopus and their relatives. In addition the «authors do not attempt to hide all the potential problems and discoveries waiting to be made, and this is one of the great strengths of the work» (Lipinski, 1999, p. 249). Thus, they solicit a renewed research effort in the study of cephalopod biology.

Like many other cephalopod students, we have been captivated by some of the “future research directions” suggested by Hanlon and Messenger.

In their review, the authors list 25 species in which they estimate the richness of the behavioural repertoire on the basis of the number of chromatic components, either already documented or based on their own observations (see Table 3.2 of Hanlon and Messenger, 1996). According to this list about 430 chromatic components have been recognized up to now, a number corresponding to an average of about 17 components³ per species, ranging from 10 of *Octopus ornatus* to 35 of *Sepia officinalis*.

Apart from a potential bias arising from the fact that not all species have received the same amount of attention, this is only a small sample of the variety that the skin of cephalopods is able to produce. In fact, 786 living species are included in the cephalopod checklist (Wood and Day – Species Database, 1998-2005) and the 25 mentioned above represent only 3% of the total. This does not necessarily mean that all species have a dynamic and rich body patterning as shown to a varying degree by the 25 protagonists.

For example, for «species [such] as the sepoid *Sepia elegans* and the octopus *Euaxoctopus pillsburyi*, we surmise that they have highly limited patterning repertoires» (Hanlon and Messenger, 1996, p. 43).

The analysis carried out by Hanlon and Messenger shows «an approximate correlation between the richness of body patterning repertoires in cephalopods and their habitats» (1996, p. 45).

1. The reader should also refer to Boyle and Rodhouse (2005) that reviews life-cycle, life-history, growth, physiological adaptations, reproductive strategies, ecology, and fisheries of cephalopods.
2. A total of 945 references is listed in the bibliography of Hanlon and Messenger (1996).
3. A “component” (*sensu* Packard and Sanders, 1971) is the basic behavioural item that constitutes the body patterns exhibited by cephalopods. Details on the terminology and hierarchical classification of body patterning are given in the following pages.

To demonstrate this point they plotted the number of chromatic components in the species studied versus increasing “habitat complexity”, where habitat complexity means physical diversity, transparency of the seawater, *etc.*

As shown in their Figure 3.9 species inhabiting tropical reefs, temperate rock reefs or seagrass habitats (mainly in the proximity of the substrate) all have rich repertoires. By contrast, nocturnal species of octopus living in the same complex habitats have more limited repertoires, similar to those of species living in murky waters or “bland” environments. In order to validate this hypothesis, a larger number of «descriptions of body patterns and their components are needed» (Hanlon and Messenger, 1996, p. 45).

Here we are not providing a description of body patterns of species not included in the aforementioned list, nor are we contributing to the study of «the neural mechanisms that bring about such sophisticated adaptive coloration» (*ibidem*, p. 185). Our aim is to provide a reference work on cephalopod body patterning, one of the most intriguing and fascinating aspects of their parallel processing capability (*sensu* Packard, 1995b). The sole purpose of our work is to assemble and summarize the “known” variety of appearances of the cephalopod’s skin, thus providing an illustrated and annotated overview that should be useful to behaviour students, including those interested in cephalopods.

In this *Catalogue* we collect, index and illustrate from published papers the overall variety of behavioural changes exhibited by Cephalopoda, the most evolved taxon among Mollusca. Such changes are chromatic, textural, postural and locomotor, which all together form the body patterns. A reference for the different behavioural items has been described for 21 species. This with the aim of constructing a homogeneous description for each item and of providing a tool for the behavioural and comparative analyses of the taxon, including taxonomy purposes (Hanlon, 1988).

The *Catalogue* is set out in index form with annotated illustrations of the various items. For the sake of homogeneity and with a few exceptions we redrew all published material here included as data set (about 180 published papers). A young artist, Vania Villani⁴, made the drawings in accordance with the principles of scientific illustration.

Before starting our voyage through the compelling richness of body patterns exhibited by the 21 cephalopod species included in this *Catalogue*, hereunder we give a brief overview of what is known about the biology of body patterning. Included are also a series of general considerations together with an outline of the rules and conventions we follow.

4. Nicola Mercurio has also drawn some illustrations. Details of authorship and/or permission for the illustrations included in this volume can be found in the Index of Plates and Figures.

What are body patterns? A brief guide

To paraphrase Wells (1978) one of the most impressive features of a living cephalopod is its skin; it changes constantly in both colour and texture.

The changes in the skin «result from the movements of the chromatophores. These structures are large pigment-containing cells distributed in the superficial layers of the skin over the whole surface of the body. By equal dilation of these cells the pigmented surface is increased and the animal consequently becomes darker in colour; on the other hand by unequal dilation in different regions a great variety of patterns may be produced» (Cowdry, 1911, pp. 5-6).

As extensively reviewed by Messenger (2001), the skin of cephalopods is a complex and sophisticated organ where the observed changes in colour and texture are brought about by a constantly regulated and refined neuromuscular mechanism. The skin acts both as barrier and as interface between the individual and its environment. It acquires in these animals a special behavioural role that serves either for concealment or expression (Packard, 1972, 1988a).

A survey of the literature shows that body patterning in coleoid cephalopods has been analyzed at different levels of organism complexity, from the subcellular and cellular, to the whole animal and finally to the social level (review in: Hanlon and Messenger 1996; Messenger, 2001). However, proximate questions have been the principal focus of the majority of studies conducted to date.

Since the pioneering works of Sangiovanni, Delle Chiaje, Sereni, and following the classic works of Cloney and Florey (1968) and Florey (1969), a great deal is now known about the functional morphology, the organization of the chromatophores in the skin, their development and neural control. None of these aspects are addressed herein (for review see: Packard, 1995a, b; Budelmann *et al.*, 1997; Messenger, 2001; Williamson and Chrachri, 2004). However, it should be borne in mind that «chromatophores are the basic elements of the complex pattern and color change abilities of the modern cephalopods» (Boyle, 1986, p. 16), and that the arrangement of chromatophores over the skin is species-specific. This, obviously, allows the identification of potential “chromatic characters” useful for species identification and diagnosis (Hanlon, 1988).

As mentioned above, body patterns represent «the result of expansion and contraction of the chromatophores, and are a display on the surface of the body of patterns in the activity of the central nervous system» (Holmes, 1940, p. 19). They are controlled by a series of brain centres organized hierarchically (for reviews see: Messenger, 2001; Williamson and Chrachri, 2004).

The surprising ability of cuttlefish, squid and octopus to change their appearance within a very limited time-frame (a few seconds; but see also Litman and Hanlon, 2004) by taking on amazing shapes and colours has been known since antiquity. Aristotle was the first to write about it in his *Historia Animalium*:

«The octopus is a stupid creature, for it will approach a man’s hand if it be lowered in the water; but it is neat and thrifty in its habits It seeks its prey by so changing its colour as to render it like the colour of the stones adjacent to it; it does so also when alarmed» (*Hist. Anim.*, IX, 622a: 2-10; here cited as Aristotle, 1910).

Likewise Charles Darwin, during his voyage around the world on the H.M.S. Beagle, jotted down the habits of some cephalopods (octopus or cuttlefish) in the Cape Verde Islands:

«These animals also escape detection by a very extraordinary, chamaleon-like power of changing their colour. They appear to vary their tints according to the nature of the ground over which they pass: when in deep water, their general shade was brownish purple, but when placed on the land, or in shallow water, this dark tint changed into one of a yellowish green. The colour, examined more carefully, was a French grey, with numerous minute spots of bright yellow: the former of these varied in intensity; the latter entirely disappeared and appeared again by turns. These changes were effected in such a manner, that clouds, varying in tint between a hyacinth red and a chestnut brown, ... were continually passing over the body. ... These clouds, or blushes as they may be called, are said to be produced by the alternate expansion and contraction of minute vesicles containing variously coloured fluids» (Darwin, 1870, p. 7)⁵.

Each cephalopod can produce dozens of body patterns, and although the total repertoire is “fixed” and species-specific, any one of these patterns – with many gradations – can be displayed according to the environment, including both the external surroundings of the organism (*e.g.* the background or the social partner) and its motivations (*e.g.* defence, aggression, or reproduction). According to Andrew Packard, they function for the purpose of crypsis and/or mimesis and evolved as defence systems against vertebrate predators (Packard, 1972). In addition, evidence is accumulating that body patterns are used in communicative systems by transferring information not only to potential predators, but also to conspecifics, especially during courtship and in agonistic contexts (Mather, 2004). Some species seem to be able to organize complex social interactions by means of these visual signals; a pattern-based language has been suggested in *Sepioteuthis sepioidea* by Moynihan and Rodaniche (1982), leading J. Mather to ask: «Do squid make a visual language on their skin?» (2001, p. 87). Thus, body patterns seem to be produced for two different reasons. The first, known since Aristotle, is for concealment from predators. During their evolution cephalopods tuned to the visual system of their predators in order to “print out” on their body surface a misleading image of their surroundings; this allowed them to survive (Packard, 1972). The second is for communication (intra- and/or inter-specific), a function that has been highly debated for its consequences in the field of ethology.

Body patterns in cephalopods: using the skin to conceal

As reviewed by Hanlon and Messenger (1996), the mimetic talent of cephalopods is extraordinary: indeed, it is unique in the animal kingdom.

They have at their disposal a variety of ways to pretend to be what they are not. Like soldiers wearing camouflage uniforms to hide from the sight of their enemies, cephalopods are able to disappear from the scene by fading away into the landscape. This is achieved by assuming the characteristic forms and shades of the background or, in the case of octopus, by collecting material (broken shells, prey remains, stones and pebbles) which stick to the suckers and help to assume the features of that particular background.

5. As a comment to Darwin’s notes, we would like to point out that, in the light of modern knowledge, this is the first description of a peculiar display exhibited by some cephalopods, now known as Passing Cloud.

Cephalopods can also pretend to be plants (e.g. *Octopus vulgaris*: Packard and Sanders, 1969, 1971), fluctuating like algae on the sea floor (e.g. *Sepia officinalis*: Hanlon and Messenger, 1988), or drifting with the current as pieces of seaweed (e.g. *Sepioteuthis sepioidea*: Moynihan and Rodaniche, 1982).

As an example, *Octopus cyanea* may assume the pattern and shape of rocks and – in a stealthy manner – use the tips of its arms to move slowly across open substrates (a pattern called Moving Rock by Hanlon *et al.*, 1999a). In addition, this species is also capable of mimicking parrotfish, particularly abundant in their local habitats. All of the above are different ways that cephalopods use to make themselves perfectly indistinguishable.

Four mechanisms of concealment are listed by Messenger (2001):

- i. General Background Resemblance (conforming to the appearance of the background in brightness, colour, pattern, and texture);
- ii. Countershading (achieving concealment by assuming a pattern where the upper parts of the body are darker than the lower, counteracting the effects of sun and shade);
- iii. Disruptive colouration (visually uncoupling a part of the body from the rest, breaking up the wholeness of the animal);
- iv. Deceptive Resemblance (resembling an inanimate object in the environment).

As pointed out by Hanlon and Messenger (1996), the capability of coleoid cephalopods to display several environmentally-cued phenotypes is an expression of their phenotypic plasticity or polyphenism.

West-Eberhard (1989) introduced the concept of “phenotypic plasticity” as a «new framework for analyzing plasticity as a potential cause of diversity in particular groups of plants and animals» (p. 250). The term “polyphenism” was, instead, coined by Mayr (1963) to indicate the «nongenetic variation of the phenotype» (p. 150); more recently, Hanlon and co-workers provided a proper definition of this term applied to cephalopod body patterning (see pages 3-4 of Hanlon *et al.*, 1999a)⁶.

According to Hanlon and co-workers, contrary to expectations a foraging octopus (*O. cyanea*) makes itself only moderately cryptic or even conspicuous (for 22-50% of the time) when it is in the open. Moreover, the rate at which the animal changes its body pattern is surprisingly high, varying from 2.6 to 4.6 times/min (Hanlon *et al.*, 1999a). In the authors’ words: «why would a foraging octopus, so seemingly vulnerable to predation, make itself only moderately cryptic or even conspicuous when it is in the open and capable of remaining highly cryptic all of the time?» (1999a, p. 18). This is possible thanks to its unique ability for rapid polyphenism that interferes with the predatory fish’s ability to form a search image (*sensu* Curio, 1976). The rarity of any phenotype might in fact counteract the habit of many predators to prey differentially upon more common phenotypes, a phenomenon of phenotypic diversity that seems to be promoted by frequency-dependent predation as occurs in other taxa (Bond and Kamil, 2002; for cephalopods see: Hanlon and Messenger, 1996; Hanlon *et al.*, 1999a).

Many examples are reviewed by Hanlon and Messenger (1996) and many are available in the literature. In the course of this volume the reader will find various examples of camouflage as it is interpreted by Cephalopoda (see for example the comparative section: Plates 101, 103-104, 107, 109-110). In these and in almost all the described circumstances, it appears clear that «cryptic body patterns of cephalopods can be regarded as mosaics that vary in size, brightness, colour, shape and texture» (Hanlon and Messenger, 1996, p. 66). The peculiarity

6. The reader should also refer to Hanlon and Messenger (1996) for the use of the term “polymorphism”.

of this mosaic aimed at resembling its surroundings is given by the fact that a cephalopod is capable of modulating its appearance (“efferent chiaroscuro”, *sensu* Packard, 1995a).

In Packard’s words: «In the differentiated environments in which the animal habitually lives, it counters discovery with a gain control that darkens the skin until its average reflectance matches the average reflectance of a mottled background» (1990, p. 30).

In achieving this goal, cuttlefish and octopus are greatly aided by reflecting elements present in their skins that allow the animal «to take on the colour as well as the tone of its surroundings» (Messenger, 1974, p. 387).

The resulting pattern «effectively deprives our retinas of the information necessary to stimulate object detectors which work on contrast of low spatial frequency. The higher spatial frequency features ... seem to achieve their effect by being indistinguishable from the kinds of details ... [typically] found in the living sea. ... The property of contrast ... is a perceptual property belonging to the visual system of the observer» (Packard, 1990, pp. 30-31).

Again, as a way of hiding themselves from view, cephalopods living in the water column become almost totally transparent (Clear or Colorless) even masking some internal organs from sight.

Apart from the available observations and consequent descriptions of the camouflaging abilities of cephalopods, little is known «about how the individual cephalopod adjusts its cryptic body pattern to match the substrate» (Hanlon and Messenger, 1996, p. 93). We have only very sparse information on the limits of the perceptual capabilities of potential predators and the possible effects of experimental impairment on concealment (Hanlon and Messenger, 1996). Of all the suggested future lines of study, the only one initiated to date is an analysis of the spatial and chromatic characteristics of the background that induce crypsis (Marshall and Messenger, 1996; Chiao and Hanlon, 2001a, b; Barbosa *et al.*, 2004; Chiao *et al.*, 2004, 2005; Litman and Hanlon, 2004).

Lastly, it should be mentioned that cryptic patterns have been considered by Moynihan and Rodaniche as anti-displays (1982), since they are not designed to transmit information, but instead to impede it. In discussing this aspect, Hanlon and Messenger pointed out that cryptic body patterns cannot be seen as forms of communication, but «as signalling false, or dishonest, information» (1996, p. 121).

Body patterns in cephalopods: using the skin to communicate

Body patterns are not exclusively utilized by cephalopods as a mechanism of concealment (review in: Moynihan and Rodaniche, 1977; Hanlon and Messenger, 1996; Messenger, 2001; Mather, 2004). In recent years greater effort has been devoted to the analysis of the role of patterns in communication.

In their review, Hanlon and Messenger (1996) summarize the visual signals that are available to cephalopods: postural, locomotor, textural, chromatic (related to changes occurring on the whole or part of the body), or others such as “pseudomorphs” (produced by inking) and photophores. This special equipment allows the animals to signal either in intra- or inter-specific contexts, such as during courtship or agonistic encounters or during prey

capture or defence. Although the adoption of non-visual channels to transmit information requires further and more detailed investigation (for review see: Budelmann, 1996; Muntz, 1999), the communication of cephalopods, and not only of shallow-water species, is largely visual and obviously relies upon the complexity and efficiency of their eyes. Recent studies have shown unexpected properties in their visual sensory modalities. In particular, a number of species produce polarization patterns in the skin that correspond, at least in some species, to specific behaviours; changes in the polarization appearance of an animal can lead to a change in the behaviour of a conspecific observing it (e.g. Shashar *et al.*, 1996, 2002). This would suggest that polarization patterns are used for visual communication in a medium that cannot be detected by polarization-insensitive animals and therefore can be adopted as a hidden or “secret” channel of intra-specific communication (Shashar *et al.*, 2002).

Hanlon and Messenger (1996) listed a number of advantages arising from the use of neurally controlled chromatophores as the main elements of body patterning in the cephalopod system of communication. The list includes: *i.* rapidity of signalling and change of signals due to direct neural control by the brain, *ii.* grading in intensity of signals, *iii.* potential for bilateral signalling (individuals can on one side repel rivals and on the other attract sexual partners), and *iv.* lack of interference of signals with other motor acts since the chromatophores are independent of the other body muscles.

Chromatic patterns provide a number of simultaneous or sequential signals that contribute to moulding the overall appearance of a communicating cephalopod, or its displays.

As defined in ethological literature, displays are often the result of ritualization (see for example, Eibl-Eibesfeldt, 1970) and appear conspicuous, stereotyped, exaggerated or otherwise specialized in order to facilitate the transmission of information (Hanlon and Messenger, 1996). In cephalopods, displays (e.g. Passing Cloud, Dymantic, Flamboyant, Lateral Display) may occur in different contexts, intra- or inter-specific, in defence or agonistic and courtship behaviours.

The adoption of more complex body patterns to communicate with conspecifics has been described in several species (*Sepia officinalis*, *Loligo plei*, *Sepioteuthis sepioidea*, *Octopus vulgaris* and *O. cyanea*, to mention a few). Because species-specificity prevents interbreeding between sympatric sibling species, body patterns that are related to courtship and reproduction can be particularly useful as valid taxonomic traits in behavioural taxonomy (Hanlon, 1988). Again, examples will be found throughout this volume (see for example the Comparative Section: Plates 105, 108, 111-112, 115-116).

That most cephalopods adopt an elaborate and refined system of intra-specific communication has two main implications for those scientists interested in their behaviour.

Firstly, since animal signals are above all tools of social behaviour, there is a general impression that, at least in some species, individual associations (for example in schooling) are more than a simple random organization (Moynihan and Rodaniche, 1982; Hanlon and Forsythe, unpublished, cited in Hanlon and Messenger, 1996; Boal and Gonzalez, 1998; Adamo and Weichelt, 1999). More in general, cephalopods do not seem to signal about their environment and there are no conspicuous alarm signals (but see: Moynihan and Rodaniche, 1982; Adamo and Weichelt, 1999). Lastly, the social organization of cephalopods is considered at most to be “weakly developed” (Hanlon and Messenger, 1996). However, data on the degree of sociality (review in Ikeda, 2004) and on the capability to recognize individuals of the same species are scanty. An exception is Boal’s (1996) work on cuttlefish (*S. officinalis*) in which social recognition is apparently lacking (Boal, 1996; but see: Boal and Marsh, 1998; Boal *et al.*, 2004).

Secondly, the discovery that some species possess a communicative system with a surprising degree of flexibility and complexity has encouraged Moynihan and co-worker to suggest

that visual signals *do* constitute a language. According to the authors, the body patterning of *S. sepioidea* shows features proper to the most elaborate repertoires of birds and primates. In addition to broadcast transmission and directional reception, rapid fading, interchangeability, specialization, arbitrariness, and discretion, Moynihan and Rodaniche (1982) suggested that the communicative system of *S. sepioidea* is endowed with the feature of semanticity. In addition, they found that the various signals differed not only in physical size but also in strength, scope, precision, and specificity of the messages encoded. Three categories of signals were identified in *S. sepioidea* and termed: *i.* signifiers (that encode a lot of information such as nouns and verbs), *ii.* modifiers (that encode less information such as adverbs and adjectives), and *iii.* positionals (that provide convenient supports or springboards for other reactions). Extending this reasoning to other cephalopods, Moynihan and Rodaniche (1982) concluded that the communicative system adopted by this taxon fulfils many of the requirements of what is usually defined as language.

A more cautious interpretation was provided by Hanlon and Messenger (1996). They argued that signalling is certainly a widespread phenomenon amongst animals and many animals, including cephalopods, spend a considerable proportion of their time signalling about the most important things in life (their signals are concerned with attack, escape, and sex, and perhaps feeding and gregariousness in some cases). Yet, however complex the communicative system may be, the messages that most animals transmit are few in number and relatively simple although this may provide the basics of a communication pipeline (Crook *et al.*, 2002).

According to Hanlon and Messenger, signalling systems in cephalopods are “closed” or “finite” since an animal has to say only a few things to bring about a successful act of reproduction, to protect its offspring or to draw attention to potential predators. By contrast, a true language is an “open” or “productive” system of communication that can transmit a virtually infinite number of messages (Hanlon and Messenger, 1996).

The question is still open and under debate (see also: Mather, 1999, 2004).

Body patterns in cephalopods: an evolutionary perspective

Cephalopods are an ancient group. They evolved from some monoplacophoran form and appeared in the earliest Franconian (upper Cambrian); *Plectronoceras*, from northeastern China, is considered the hypothetical archetype of the Cephalopoda (Teichert, 1988). During the Ordovician the group underwent an astonishing evolutionary radiation, possibly as a consequence of the new ecological niches available because of the extinction of *Anomalocaris*, a nektonic “super-predator”, at the end of the Cambrian.

With the exception of *Nautilus* spp.⁷, all living cephalopods are Coleoidea. As reviewed by Teichert (1988), the earliest record of this taxon should be dated back to Early Devonian-Permian (see also Clarke, 1988). Although we are still waiting for the appearance of the Coleoidea volume of the *Treatise on Invertebrate Paleontology*, the information available on the evolutionary history of this taxon is currently reviewed in different sources (*e.g.* Jeletzky, 1966; Clarke, 1988; Teichert, 1988). A more general review is offered by M. J. Wells (1994).

The main features of cephalopod evolution have been described by Teichert (1988). However, when the subclass of Coleoidea is analyzed, his only concern is to trace back the story of the reduction and eventual loss of an exterior shell and consequently to discuss the alternative adaptive devices that were adopted to regulate buoyancy. Color markings, together with

7. Kröger (2005) provides a review on the evolution of coiled cephalopods.

other aspects of cephalopod ethology and ecology, have been excluded from Teichert's consideration.

To the best of our knowledge, Packard is the person who must be credited with emphasizing the important role played by behaviour in the evolution of cephalopods. In a paper dating back more than 30 years, a milestone in biology and in evolutionary studies not restricted to cephalopods, Andrew Packard (1972) formulated hypotheses about the factors behind the dramatic modifications in the cephalopod *Bauplan* and on their consequences. Packard proposed that the uniqueness in morphology, physiology, behaviour and ecology of the coleoid cephalopods evolved in response to competition, including predation, from vertebrates in the Mesozoic.

In competing with vertebrates, cephalopods also reached high levels of functional convergence with them (Packard, 1972; see also: Aronson, 1991; O'Dor and Webber, 1986, 1991).

The changes in colour and texture of the skin of cephalopods are unique in the animal kingdom (Hanlon and Messenger, 1996). This uniqueness depends mainly on the fact that in cephalopods the control of these changes is provided by neural wiring found in the cephalopod "brain" (Boycott, 1952; review in: Messenger, 2001; Williamson and Chrachri, 2004). In vertebrates such changes are not so fast as they are mainly under non-neural control mechanisms. Despite such differences the two systems show remarkable functional similarity (reviews in: Packard, 1972; Demski, 1992).

Vertebrates and cephalopods both possess cells with pigments similar in spectral response; however, as mentioned above, differences exist in the neural control and in the speed. The two systems are quite different in terms of the "static morphological array". On the basis of the knowledge available, a certain degree of convergence is evident. In Teleosts, «many of the distribution patterns follow outlines related to scale position, and therefore these arrays are in many ways analogous to the skin patches in *Octopus*. In areas where the scales are not present, patterns are still observable and would seem to be more comparable to the arrays in squids» (Demski, 1992, p. 146). In terms of "motor units" the two taxa show similar properties: a single element might belong to different motor units, thus allowing it to behave coupled to or independently from other related motor units. The neural control, however, functions in opposite directions in the two groups: darkening is achieved by excitatory patterns in cephalopods, while these produce paling in teleosts. Furthermore, "chronological units" parallel in the two systems. Studies on fish «support the idea that waves of melanophore development result in distinct age classes of melanophores, which populate different embryonic, juvenile and adult patterns. In general, developmental principles similar to those in cephalopods ... seem to be involved in the process of pattern development» (Demski, 1992, p. 148). The reader should also refer to Packard (1982) for a description of the physiological-developmental units of chromatophore-age classes and of the developmental rules that allow the chromatophore system of cephalopods to establish the static morphological array and resulting colour pattern.

Finally, at the level of chromatic patterning some similarities are clear in the organization of the higher level chromatophore control. Basal and peduncle lobes connected with the chromatophore lobes in cephalopods have their equivalent in medullary areas of fish; visual centres (optic lobes and optic tectum and thalamus in cephalopods and teleosts, respectively) are also involved (Demski, 1992).

Thus «the parallels in the chromatophore control systems in the cephalopods and teleosts seem to be carried to the highest levels of organization. Similar behaviors appear to be mediated by generally comparable hierarchically organized neural systems. Chromatomotor control in cephalopods and teleosts appears to be

particularly well-suited for the analysis of convergence in neurobehavioral systems. Certainly, comparisons ... should lead to testable hypotheses concerning the organization and evolution of chromatomotor systems and perhaps of sensorimotor systems in general» (Demski, 1992, p. 153).

As reviewed by Packard (1972), the loss of a static external covering, provided by the shell, made coleoids vulnerable to sharp-toothed predators. The disappearance of the shell stimulated the capability to evolve and diversify jet propulsion (Wells and O'Dor, 1991; see also Seibel *et al.*, 2000). Moreover, this resulted in a premium: the evolution of a dynamic covering, the skin, capable of altering the animal's appearance from one moment to another and therefore of confusing predators. Coleoids came to protect «themselves by pictorial means» (Packard and Hochberg, 1977, p. 227).

The alternance of oceanic turbidity with clear water periods during geological time and the changes in perceptual abilities of coexisting animal species (Marcotte, 1999) may have provided selective pressures for modern cephalopods, allowing them to develop the "skin" as a key innovation; the correlation between the evolution of body pattern complexity with periods of turbidity oscillations should be tested (see also Johnsen, 2002).

Although Packard's scenario has been debated (Aronson, 1991) and although the timing of these events should be changed, its essence still holds good: the competition between vertebrates and cephalopods has the merit that it produced in coleoid cephalopods a number of new adaptations, body patterning included.

A neurally controlled "skin" and large brains (relative to body size) resulted in special adaptive capabilities. In the words of Hanlon and Messenger (1996), this has been achieved by special characteristics of their behavioural repertoire: «versatility and plasticity» (p. 182).

Body patterns in cephalopods: a hierarchical classification of body patterning

As stated by Packard and Sanders: «Anyone who has watched a group of small octopuses soon notices that they look individually different, and that a particular octopus can take on different appearances over a period of time. The appearance at any one moment we call the body pattern» (1971, p. 780).

A body pattern is produced by a potentially continuous change and combination of chromatic, textural, postural and locomotor components.

In the words of Packard and Sanders: «Different patterns are perceived and recognized on a 'Gestalt' basis much as we recognize faces or facial expressions independently of such things as size, orientation or the angle from which the animal is viewed. And if we ask 'How many patterns are there in the octopus?' the best, though hardly satisfactory, answer is, 'There are as many patterns as can be recognized by the classifier'» (1971, p. 780).

The classification of cephalopod body patterns is not a simple task.

It is widely recognized in the cephalopod literature and elsewhere the merit of Andrew Packard and co-workers – namely Geoffrey D. Sanders and Frederick G. Hochberg – to provide a hierarchical system (a kind of taxonomy) for the description and analysis of cephalopod body patterns (Packard and Sanders, 1971; Packard and Hochberg, 1977).

The essentials of this hierarchy are reviewed in *Cephalopod Behaviour* (see Box 3.1 of Hanlon and Messenger, 1996; see also Messenger, 2001).

In a top-down order it may be listed as follows:

body patterns,
components,
units,
elements.

According to this hierarchical system, a *body pattern* is made up by a combination of some (from one to many) components (chromatic, textural, postural, locomotor) that are on their own a by-product of units, *i.e.* morphological entities constituted by elements that, in turn, represent the morphological basics of the skin.

As quoted above, a body pattern is the appearance of the animal in a given moment.

The term *components* was coined by Packard and Sanders (1971) «in order to classify the various permutations of colour, shape, and texture observable in cephalopods» (Packard, 1995a, p. 354). This level of the hierarchy «applies to recognizably like activity occurring in different places of the skin and varying independently of other activity» (*ibidem*, p. 354).

In a “composite diagram” Packard illustrated some of the light and dark components catalogued for *S. officinalis*, *L. vulgaris* and *O. vulgaris* (Fig. 21.17 of Packard, 1995a). In the figure (for *L. vulgaris*), he also measured the «[t]ime course ... of seven such ... components in a female squid interacting with a second female» (Packard, 1995a, p. 355), and also the complementarities both in timing and spatial expression of specific components exhibited by the animals. In this way, Packard provides a down-level analysis that graphically explains many of the features of cephalopod components.

Again, Packard and colleague wrote: «Components are, by definition, the parts that go to make up the whole, and [body] patterns can be described in terms of the relative positions (arrangement) and intensity (value) of the components regularly present. A proper classification of the patterns would probably distinguish between essential and inessential components, but we are not yet in a position to do this. Components are analysable in terms of the effects of chromatophores, iridocytes, dermal and ‘skeletal’ muscle fibres and/or are supplied by movement, by the pupil, by the white surfaces of the suckers These effectors are the output elements of visual expression. Components are built from them. ... [They] are anatomically constant each presumably under the control of only a few neurones in the higher motor centres (optic lobes or ... chromatophore lobes)» (Packard and Sanders, 1971, p. 780).

A single component may be a dominant trait of a body pattern, or be the sole exhibited by an animal. For example, Frontal white spots of *O. vulgaris* are expressed as «white spots on the front of the head» (Packard and Sanders, 1971, p. 781). They may be exhibited by octopus wearing a uniform darkish appearance but may also occur in combination with a wide variety of light and dark components. At the extreme, «most components, in contributing to the whole, are perceived as part of the whole and the observer needs to perform a second operation to dissect them out» (*ibidem*, p. 781).

On the other hand, *L. vulgaris* may exhibit a uniform dark appearance; in this all the chromatophores over the skin are maximally expanded. Thus, the component All dark (Brancato and Packard, 1994) is the single one to be expressed in that given moment, producing a Deep Puce body pattern (Neill, 1971; *i.e.* All Dark).

Finally, to paraphrase Packard (1995a), components can be grouped into two categories (diffuse screens, and feature generators) on the basis of their “visual effects”. Acting as diffuse screens, components vary the ground colour and the grey level of the animal, *i.e.* by altering

its mask. As feature generators, they work on a wide range of “spatial frequencies”, *i.e.* the skin performs dots (even organized in a “centre/surround”) or bars as a result of its “visual efference”.

As mentioned before, components are not the lowest step of the hierarchy that allow a cephalopod to generate a pattern on its body. They are made up by *units*, *i.e.* groups of elements (see below) that produce components. Units correspond to special “spatial” and morphological arrangements constituting a static morphological array. In *Loligo* spp., for example, they are characterized by central large dark chromatophores surrounded by smaller lighter ones (standard discoid unit, *sensu* Hanlon, 1982); a similar arrangement is found in the cuttlefish, with some exceptions (Hanlon and Messenger, 1988). Units may also be organized in circular patches surrounded by grooves as in the octopus; this gives the skin of the animal the appearance of a «loosely woven network» (Packard and Hochberg, 1977, p. 200; see also: Froesch and Messenger, 1978; Packard, 1982, 1983).

Units have, in turn, their constituents in the *elements* (*i.e.* chromatophore organs, reflecting cells, *etc.*) that are «the basic morphological entities that produce different colours, intensities or textures of the skin» (Hanlon and Messenger, 1996, p. 31; for review see also Messenger, 2001).

It is the assemblage of this plethora of components that is the most striking feature of coleoid cephalopods: their capability of displaying “essays or compositions” (*sensu* Brancato and Packard, 1994) or, in other words, of performing the several environmentally-cued phenotypes, expression of the phenotypic plasticity or polyphenism of cephalopods.

In behavioural terms, the analysis of body patterning of cephalopods is – however – restricted to the first two levels of the hierarchy. In referring to the classification of body patterns throughout this volume we will refer to these two levels (*i.e.* body patterns and components, here referred to as *items*) and we will speak of *Packard’s hierarchical system* (or simply hierarchical system).

As a side note, a short paragraph should be dedicated to the concept of *displays* as applicable to Cephalopoda.

According to Packard and Hochberg, displays «are the visually simpler patterns They consist of a few broad bands, stripes or circles of dark contrasting with lighter skin, and it is the high contrast and rapidity with which they appear that makes them conspicuous. Such are the Black hood, the Zebra, the Dymantic and the Dark Flush (or Passing Cloud). They are seen only in the presence of other animals either of the same species, or of other species when the wearer has been observed. Included in this category are the courtship displays described by various authors In some of these patterns dark vertical components are a dominant feature» (1977, pp. 223-224).

In addition Hanlon and Messenger «define a display in cephalopods as comprising a number of signals (shown simultaneously or sequentially). Displays tend to be conspicuous, stereotyped, exaggerated or otherwise specialized expressly to facilitate the transmission of information, and they tend to be long-lasting (often tens of seconds) as opposed to signals, which are transient. Thus, we distinguish a ‘display’ from a ‘signal’ not only by a display’s complexity, but also by how long it lasts and by its greater degree of ritualization» (1996, pp. 120-121).

Body patterns in cephalopods: other definitions and methods of study

The first step, in the study of the behaviour of an animal, is to compile a catalogue of its repertoire. This, in the cephalopod context, requires the addition of a list of recognized components and body patterns exhibited by that given species. The catalogue produced (or ethogram as it is often called) is then utilized to analyse different possible combinations of components in relation to the conditions in which they take place.

It is since the '80s that cephalopod students have prepared such catalogues utilizing Packard's hierarchical system. However, the "name" of each component and/or body pattern has not been compiled on the basis of a uniform schema or following the same principles.

As a simple example, when an animal maximally expands the chromatophores over the body, the result is a uniform darkening of the skin. This has been named "Dark" (*Idiosepius pygmaeus*, *Euprymna scolopes*, *Sepioteuthis sepioidea*), "All dark" (*Sepiola affinis*, *Loligo vulgaris vulgaris*, *L. vulgaris reynaudi*, *L. (Alloteuthis) subulata*, *L. pealeii*, *L. plei*, *Octopus cyanea*) or "Uniform Dark phase" (*Octopus bimaculoides*), to mention a few. Just to give a rough estimate of the variety of names assigned, in this volume we counted a total of 128 light and 245 dark components, as recognized in the 21 species we illustrate. However, when we take into account what we call the synonyms and variations of expression provided for the same component by different authors (or even by the same author), the number rises to 188 and 419, respectively.

In order to avoid misinterpretation, Roger T. Hanlon and John B. Messenger recommend «that some convention be established in the future» (1996, p. 35).

In naming the components the authors propose to use:

stripes or *streaks* for those expressed along a longitudinal directrix;

bands or *bars*⁸ for components expressed along a transverse directrix;

lines for components expressed either on longitudinal or transverse directrices.

Despite these efforts, the naming of components and body patterns is still often muddled and misleading. In some cases, the trend is towards the assignment of new names instead of adopting the established nomenclature for similar cephalopod species. By collecting and tabulating all the names given to the components/body patterns of the 21 species we illustrate and by identifying their synonyms and variations, we hope to have contributed, with this volume, towards a standardization of the nomenclature. Bearing this in mind, we thus wish to invite other cephalopod workers to do the same in the future.

An alternative method of study is available through Internet and includes a collection of photographs (1642 images on 59 species) and video-clips of several cephalopods. These have been indexed utilizing a relational database to provide an annotated image reference of body patterning in this taxon. The database allows the construction of a query based on a term/subject and/or of a species. The result provided is a subset of images and the descriptions assigned by the authors to each one of them (Wood and Day – Image and Video Databases, 1998-2005).

Other tools have recently been developed. Our hope is that their application will spread and provide useful additions to the classical analysis of cephalopod body patterns.

Among them should be mentioned the "graphic model for skin displays" developed by Byrne and co-workers (2003). Using Adobe PhotoShop, the authors designed a multilayer model of *Sepioteuthis sepioidea* that serves to illustrate and store graphic information on displays (components and body patterns) exhibited by the animal. Computer drawings of single

8. *Rings* should be considered as equivalent to bands or bars.

components are superimposed to dorsal and/or lateral views of the Caribbean reef squid together with a background colouration (the authors consider: white, pale, yellow, gold, brown and black). For example, «Pale is shown as a pattern of small black dots on white» (Byrne *et al.*, 2003, p. 31). In the “graphic model”, each component is drawn as a single layer of the Adobe PhotoShop; in this way, a given appearance of *S. sepioidea* is the result of the stacking of multiple layers on a specific background colour. The system allows «110 layers [to be] visible by a mouse click and thus can be grouped together to construct a display [= body pattern]» (*ibidem*, p. 31). The graphic model appears as a suitable tool for analysis of intra-specific displays *sensu stricto* of *S. sepioidea* including sexual, age, geographical and population differences; it can also be used to compose camouflage patterns (Byrne *et al.*, 2003). We agree with the authors that such a system provides a more “flexible” and “interactive” system than classic photography.

It is an aid in cataloguing «the full range of displays of *S. sepioidea* and can also establish consistent terminology for the components and displays of this squid species. This tool can be easily modified or added to as changes and new patterns are observed» (Byrne *et al.*, 2003, p. 34).

We encourage the development and application of similar graphic models to other cephalopod species, as well as database-oriented graphical interfaces that may be available to cephalopod students.

As repeatedly stated, body patterning in cephalopods is dynamic: it may be subject to immediate changes, as well as to countless gradations. The properties of chromatophore organs and the fact of being coordinated by fine neural control allow components to vary in the extent of their expression from barely perceptible to fully expressed. In some studies, an analysis of the variability of the intensity of a component (or body pattern and display) has been carried out. Once again, Packard pioneered the application of image analysis to the study of chromatic patterns in cephalopods (La Gioia, 1992; see also Packard, 1995a).

Other similar applications have been designed (Fiorito, unpublished). In our view, the most interesting application of image analysis methodologies to the study of the variations in intensity of a single component (and/or body pattern) in a cephalopod is the work of Adamo and Hanlon (1996) where the authors measured the variability of the darkness (*i.e.* intensity) of a single component of the Intense Zebra Display of *S. officinalis*: Dark face.

Finally, components may appear and disappear with variable speed. Thus, on the basis of their duration, body patterns can be further categorized into *chronic* or *acute* (Packard and Sanders, 1969). As reviewed in *Cephalopod Behaviour*, chronic should be considered those worn for hours or more; they are variable and are utilized primarily for camouflage. Acute patterns are exhibited only for seconds or minutes and occur principally during intra- or inter-specific encounters (Hanlon and Messenger, 1996).

Jantzen and Havenhand (2003) developed a “three-tier system” based on component duration: *i.* short acute ≤ 10 seconds; *ii.* medium acute 11–60 seconds; *iii.* chronic > 60 seconds. The authors measured the total time and average duration of different components exhibited by *Sepioteuthis australis* in the context of its reproductive behaviour and classified them accordingly.

This approach allowed to identify a «high number of short acute component durations ... [that] indicates intense communication between reproductively active individuals and is probably important in competition for mates and in predator detection. ... The corollary of ... short acute component durations is that reproductively active individuals of *S. australis* showed few long (medium acute, or

chronic) duration components It is possible that signals are communicated by relatively brief absences of these longer duration components (rather than by their chronic presence); however, their significance has yet to be determined» (Jantzen and Havenhand, 2003, p. 301).

A quantitative approach like this may also allow to estimate the goodness and the size of the entire behavioural repertoire of a species using «a plot of the cumulative rank-order percentage-time frequencies of the behaviors» (*ibidem*, p. 301).

Likewise, Borrelli and Giuliano developed a configuration based upon The Observer (Noldus Information Technology, The Netherlands) designed to code and measure the frequencies, the simultaneity and the duration of the components exhibited by *O. vulgaris* in the context of predatory behaviour. The configuration coded for 85 items (components and body patterns) arranged into 19 behavioural and 14 modifier classes; in this way, all the items may be classified and measured allowing an unprecedented way of analysis of octopus body patterning (Giuliano, 2003; Borrelli and Giuliano, unpublished).

The above are only a few examples of how modern approaches to the study of animal behaviour may help the cephalopod community to reach a quantitative and in depth analysis of the repertoire of cuttlefish, squid, octopus, and their relatives.

A clausa

By the way of a coda, we hope to have provided a short overview of the literature dealing with how cephalopods exchange information by utilizing a special feature of their morphology: the mutable skin. In this they achieve a level of polyphenism that is utilized to establish relationships and communication between individuals at the intra-specific level (even in occasional “communities” as in solitary species such as *O. vulgaris*). Furthermore, by hiding themselves from potential predators and/or competitors (*i.e.* fish), by becoming transparent, by matching the surroundings, or by disrupting the outline of their body, cephalopods produce dishonest signals that allow them to survive. This, at least, is our interpretation of their behaviour.

In the words of Packard and Sanders: «What we do not of course know is whether the different visual expressions of the octopus, classified on the basis of our human perceptions are classified similarly by other animals» (1971, p. 780). It is possible, however, that despite the bias of our own perceptual system, our accounts are to some extent true.

In conclusion, although the literature on the biology and behaviour of cephalopods dates back to Aristotle, we have, at present, hardly begun to understand the phenomenon of body patterning in a comprehensive fashion. Throughout the history of biology, we have learned a great deal about the proximate mechanisms underlying the functioning of the chromatophores and their neural control. Instead, only a few studies have dealt with the evolutionary origin of body patterning and its role within the complex communication system adopted by many cephalopods. A comparative phylogenetic approach would help to reconstruct the evolutionary history of body patterns in cephalopods, as recently applied to vertebrates (*e.g.* Ortolani, 1999).

Why base the *Catalogue* on scientific illustrations?

In preparing this *Catalogue* we were inspired by the belief that scientific illustrations represent the visual explanation of scientific discoveries. It is widely recognized that the visual documentation of a behavioural status of an animal is of fundamental importance.

A sketch, a realistic drawing, a photograph or a video are all visual aids that either alone or in combination, primarily allow the behaviour student to document the behaviour of a subject and the context in which it occurs for future analysis or records. Such visual aids also enable the student to record his/her own observations and discoveries.

The importance of visual documentation has been stressed many times by ethologists (for example see Eibl-Eibesfeld, 1970). This may be the reason why the *Handbook of ethological methods* recommends: «Ethologists should make a photographic record of their research» (Lehner, 1996, p. 284).

It is widely recognized among cephalopod biologists: Hanlon and Messenger give it special attention in their introductory chapter where they illustrate the methodology involved in studying cephalopod behaviour (1996). Again, Roger Hanlon devotes a section of his Web page to the video documentation of underwater behavioural observations⁹. Lastly, CephBase, the dynamic relational database-driven web site dedicated to cephalopods, has a section of “Image” and “Video” searchable databases that constitute a very large repository of images of living individuals. The site also hosts a glimpse of a poster presented at the 27th International Ethological Conference (Wood and Forsythe, 2001).

In our view, it is merit of Andrew Packard to have underlined in several instances the fundamental importance of a photographic documentation of the skin of cephalopods (e.g. Packard, 1995b).

According to Packard, it is essential to «[d]ocument (by photo and video) ... the patterns of a single individual ... at various magnifications (from the whole animal, in a social or physical context, down to single groups of chromatophores). ... Photo and video supply both in parallel and sequential information» (1995b, p. 109).

However, as he points out, the two methods do not provide the same information. In fact, «photographs allow the possibility that the changes in spatial extent and in grey level of the dark components might be achieved in steps, frame-by-frame analysis of video-records fails to reveal such steps» (*ibidem*, p. 117).

This is mainly due to the time intervals between frames and «the response time and frequency of the system under observation» (*ibidem*, p. 109).

Incidentally, the photographic documentation of the skin and body patterns of *Octopus vulgaris* and *Loligo vulgaris* (just to refer to the main *corpus*) available through Andrew Packard's collection deserve special attention not only by cephalopod biologists but, more in general, by those interested in pattern recognition.

Although fully aware of these considerations, we prefer, in this *Catalogue*, to use drawings rather than photographs. In our opinion, an artistic vision, guided by the principles of scientific illustration, should provide a useful supplement to cephalopod literature and scientific photography (Cott, 1956; Blaker, 1989; Rosen, 1997; Ray, 1999; for cephalopods see: Wood and Day – Image Database, 1998-2005; Wood and Forsythe, 2001).

9. Refer to <http://www.mbl.edu/mrc/hanlon/video.html> [online; last visited, November 2005].

It is generally acknowledged that a diagram, a graph of results, a picture or a drawing of a specimen observed in the field or under a microscope, are all aids adopted by scientists. Apart from pictorial representations, known and utilized since pre-historical times, it is from Leonardo's drawing of an ornithopter that all forms of scientific illustration are based upon artistic conventions (for review see: Knight, 1977; Ford, 1992). Nevertheless, they are a child of the phenomena and of the science – from astronomy to palaeontology, up to biology and genetics – that is describing them (Laszlo, 1996; Gooding, 2004; Hildebrand, 2004).

A “scientific” drawing does not necessarily provide a realistic representation of the phenomenon itself. Even in cases where it reaches a “realistic” level of accuracy, its main purpose is to communicate information (Gooding, 2004; see also Laszlo, 1996). In this an illustration is different in principle to a photograph. Both are able to capture and convey the phenomenon, but they utilize different techniques and the message they provide is based on different perceptual cues. Photography transfers the message by variations in lights and colours, but it is a *status-quo* representation of the event in a given moment. The illustration, however, may add or delete a given detail in order to enhance the most significant components of the image, *i.e.* the phenomenon it depicts. This is a classic practice of, for example, zoological illustration either when it is oriented to depict the “classification of creatures”, their anatomy, or up to the “study of their behaviour” (Cott, 1956; Knight, 1977).

As pointed out in *Zoological Illustration*, «What the zoological artist draws will thus depend upon the end he has in view. ... In any of these directions, he may achieve what ought to be his ambition, to produce works of art which shall be aesthetically as well as zoologically valuable» (Knight, 1977, pp. 33-35).

And again, «Even if zoological illustration is less important to the working scientist than it was, partly because emphases have changed and partly because there is now a good stock of illustration done by our ancestors, it is still true that a good picture can tell us more than a page of text. We can see this from the way in which illustrations from the past have outlived their text; but one must remember that while the best pictures thus live on, there are no definitive zoological pictures. The interests and needs of each generation are very different from those of its predecessors, and hence the demands made of its zoological artists are different. We are fortunate in our own day that there is no lack of such people, producing the whole range of zoological art from sumptuous folios ... to field guides and to the diagrams in zoological textbooks and physiological works; and we are equally fortunate in having printers capable of reproducing these to a standard worthy of the great tradition of zoological art, so as to convey both pleasure and knowledge» (Knight, 1977, p. 188).

We hope to have achieved this result.

Illustrations alone – of whatever form – cannot be the single vehicle that should be utilized in explaining a phenomenon.

As reported in the *Illustrating Science* manual (Council of Biology Editors, 1988), it was Pliny the Elder who stressed the importance of the relationship and complementarities between words and pictures; a picture alone may be misleading, but verbal descriptions in absence of images may result in long and tedious lists.

An integration of text and illustration will better assist the student as to how and in what sequence he/she should view and interpret the figures. In this, maybe the first and most effective example of such integration is the *De Humani corporis fabrica*, a detailed illustration

of the human body compiled by Andreas Vesalius and appeared in the XVI century (Vesalius, 2005). In his work, Vesalius combines text and illustrations, adding a caption to single body parts, thereby producing pictures that are self-explanatory. And this is the criterion we have followed in preparing this volume.

How the *Catalogue* is organized: a short overview

Each illustration included herein is the result of cooperation between scientists and illustrators. The morphology and relative proportion of the animal, its behavioural state, the appearance and significance of a given pattern were all subject of discussion between the scientist and the illustrator in the preparation of each drawing. Photographs, *in vivo* observations and video sequences were also drawn upon by the artist.

The selection of drawings, as illustrated in this volume, is the result of a meticulous process: the combination of artistic and scientific views with the aim of preserving the artistic “perception” in many instances. The illustrations were further completed by adding pointers with names and/or comments.

In addition to the illustrations (included in the plates) this *Catalogue* also comprises two text sections. One consists in a tabularized list of items and synonyms attributed by different authors to describe a given component and/or body pattern and exhibited by a given species. These tables provide an identification tool for comparison of the naming system utilized in describing the behavioural repertoire of cephalopods. In the tables, each term is annotated with the original source – thus offering an extra tool to the student for further in depth study – and is set out following a hierarchical structure; in resembling a thesaurus of terms (*e.g.* MeSH of the National Library of Medicine, NIH, Bethesda) we follow Packard’s hierarchy for the classification of cephalopod patterns.

The other text section gives a description of all the items we illustrate, together with a series of others not herein illustrated. Each description incorporates, to the best of our knowledge, all the data and observations published, available for each species. As a result, the descriptions we supply are arranged as an anthology of parts of the original definitions utilized by authors to portray their observations.

To conclude, the catalogue is an illustrated and annotated index of the amazing variety and richness of the behavioural repertoire of most cephalopod species on which literature on body patterning is available – from cuttlefish to octopus and to squid, from temperate to tropical habitats.