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THE COLOURS OF *OPHIOCOMINA NIGRA* (ABILDGAARD)

I. COLOUR VARIATION AND ITS RELATION TO DISTRIBUTION

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Colour characters can be of importance in ophiuroid taxonomy, especially at the species level. In particular the family Ophiocomidae, in which the traditional morphological characters are notoriously variable, provides many examples of related species which are best separated by body colour or colour patterns. The usefulness of the colour characters is weakened by an incomplete knowledge of the extent of colour variation within each species and a total lack of information concerning the influence of environmental factors on coloration. In addition, there is little knowledge of the chemistry of pigmentation or of the cytology and anatomical disposition of pigments responsible for external coloration of ophiuroids generally.

These studies were undertaken in order to gather some information on the colour biology of one species of ophiocomid, *Ophiocomina nigra* (Abildgaard), in the belief that a thorough knowledge of various aspects of pigmentation of one ophiuroid species will contribute towards an evaluation of the role of colour in the functional biology of the family, at least, and may help to clarify the position of colour characters in ophiuroid systematics generally.

This present report describes the colour variations of *O. nigra*, a scheme of colour classification for the species, and the relationship between colour variation and distribution in depth. Further reports will deal with the chemistry and physiology of pigmentation.

DISTRIBUTION

Ophiocomina nigra ranges from the Azores to northern Norway, occurring abundantly around the British Isles and rarely in the Mediterranean. Throughout most of this range it is restricted to shallower regions above 50 m depth, and is generally dark-coloured. This dark, shallow-water form was described from Norwegian fjords by Abildgaard in 1789 as *Asterias nigra* (see Koehler, 1922, for synonymy). In the western part of its range, however, particularly around the British Isles and in the North Sea, the species is found in abundance down to at least 160 m (Farran, 1913). In this area the species tends to

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be larger in size, extremely variable in its coloration and is frequently brightly coloured. It was for a time considered to be a distinct species, *O. raschi* (G.O. Sars). Mortensen (1920) was able to demonstrate conclusively that there are no morphological features distinguishing *raschi* from *nigra*. He found that the small dark form typical of Norwegian fjords and shallow continental waters intergraded perfectly with the larger, deeper living form which is so variable in its coloration. Distributional data are summarized from Koehler (1924) and Mortensen (1924, 1927).

COLOUR DIFFERENCES

Investigations of pigmentation have been made on two geographically distinct populations of *O. nigra*. Animals in the vicinity of the Plymouth Laboratory were observed during the summers of 1953 and 1954, and animals near the Marine Station, Millport, were examined and collected in May 1956. Living animals were also sent from Plymouth and maintained in aquaria at Oxford.

The body colour of the specimens which I have examined ranges from black to yellow-orange in a continuous graded series. The darkest animals are black or very dark brown on the aboral surface, with the oral surface as densely coloured. Variants coloured dark brown, light brown, various shades of red-brown and fawn on the aboral surface are common. The oral surfaces of these intermediate phases are usually considerably paler than the aboral surfaces. The lightest animals have red to yellow-orange aboral surfaces, and red-orange to yellow oral surfaces. While both Millport and Plymouth populations exhibit analogous variation from very dark to very light individuals, there is a subtle difference in the tone and range of coloration between these populations.

Plymouth

The Plymouth *O. nigra* is a brilliantly coloured animal. The darkest colours are glossy black and dark brown. The light-coloured individuals are handsome shades of red and yellow-orange, while light brown and red-brown individuals form intermediates between the extremes. Within or close to Plymouth Sound, the animals are nearly uniformly dark-coloured, but as one moves south into deeper and less turbid water light colours become increasingly frequent. Light-coloured variants are particularly common on the 'Amphioxus shell-gravel' of the Eddystone grounds (45–55 m), where the colour tones of the animals tend to match those of the gravel fairly well.

Millport

The Millport population is drably coloured in contrast. The darkest individuals are very dark brown, while the lightest are dull orange-red, with various shades of red-brown connecting the extremes. All the animals, including the very darkest, have some tint of red in them. The resulting brick tones of the animals match extremely well the bottom of the Firth of Clyde and the Largs Channel in the vicinity of Millport which take on brick-red tints from the local red stone. It is curious that MacIntosh (1903) stated that there was no colour variation whatever in *O. nigra* collected in the vicinity of Millport. His material was preserved in 50% alcohol which undoubtedly extracted the carotenoids responsible for the brighter colours and thus obscured any colour variation.

The influence of substrate colour on body colour was not studied in detail through lack of time. For both populations it appeared that the colour tones of the ophiuroids tended to match the colour tones of the bottom they lived upon, and that minor differences in colour tone between the populations are correlated, at least in part, with the colour tone of the bottom on which the animals live.

COLOUR CLASSIFICATION

Since colour is a dangerously subjective quality, some standard of reference was necessary in order to ensure day-to-day uniformity of colour nomenclature or classification. Accordingly, a 'type set' of animals was selected which embraced what were considered to be the total range colour of each of the two populations.

The 'type set' of each population was arbitrarily divided into five colour classes, each class being represented by four specimens. The darkest class was designated as (1), the lightest class as (5), with classes (2), (3) and (4) in between. The capital letters P or M were prefixed to the colour-class numbers to indicate Plymouth or Millport animals, respectively.

These type sets were carefully preserved in deep-freeze in the dark and new specimens were referred to them for colour classification. Full descriptions of the colour classes of each population are as follows:

Plymouth population

P1. Black or very dark brown on aboral surface; oral surface as densely coloured as aboral.

P2. Dark brown to brown aboral surface; oral surface light brown to fawn.

P3. Light brown to reddish-brown aboral surface; oral surface fawn to red-orange; frequently with red-orange at bases of arms aborally.

P4. Red to red-orange aboral surface; oral surface red-orange to yellow-orange.

P5. Yellow-orange aboral surface; oral surface yellow-orange to yellow; bases of arms frequently red-orange.

Millport population

M1. Dark brown aboral surface; oral surface light brown with red tints; rarely some red-orange at base of arms.

M2. Dark brown with red tints on aboral surface; oral surface light brown to red-brown; frequently red-orange at base of arms.

M3. Aboral surface of disk dark red-brown; aboral surface of arms redder; oral surface dark red to orange.

M4. Disk redder than above; aboral surface of arms red; oral surface light red to orange.

M5. Aboral surface dark to light red; oral surface light red to yellow-orange.

This classification refers only to general body colour and does not take into account the various colour patterns found on the disk of many specimens of both populations.

COLOUR PATTERNS OF THE DISK

O. nigra frequently displays patterns of lighter colour on the aboral surface of the disk. The patterns are particularly obvious on the darker forms, where they appear as a fawn pattern contrasting sharply with the general black or brown body colour. Patterns are also apparent on lighter animals, appearing simply as less densely pigmented areas. The disk patterns are of two sorts: (1) a simple, more or less regular circle, and (2) a pentagonal figure, the extremities of which lie in the inter-radii and frequently reach down to the oral inter-brachial areas.

These patterns are probably truly polymorphic since intermediates between the two patterns have never been observed. There is some variability in size of the patterns, however. These patterns are probably of considerable cryptic value serving to break up the contour of the body against the gravel or rocky bottom which is the normal habitat of the animal. This cryptic effect can be seen to advantage in 'natural' aquaria provided with a rocky bottom.

THE RELATIONSHIP BETWEEN COLOUR AND DEPTH

It has been pointed out that *O. nigra* exhibits its greatest colour variation in the North Sea and around the British Isles where it also has its greatest depth distribution, whereas in shallow water along the continental coast, the animals are predominantly dark coloured. It was also observed that within the shallow water of Plymouth Sound the dark phases of *O. nigra* are found nearly exclusively. Lighter-coloured individuals become increasingly common as one moves into the deeper waters outside the Sound until, at the Eddystone trawling grounds at 75–80 m, light-coloured phases are particularly abundant. A similar situation exists at Millport where again it was observed that the incidence of light-coloured phases seems to be correlated with increasing depths. This is not to say that at greater depths the animals are exclusively light-coloured, nor that in shallower water they are exclusively dark but, rather, that the frequency of light colour phases in the two populations apparently increases with increasing depth.

This apparent relationship between depth and degree of coloration was studied at Millport in May 1956. The colour classes of *O. nigra* dredged from different depths were scored and counted, and the relationship between depth and colour tested statistically.

The sampling was carried out on the population of *O. nigra* occurring in the Largs Channel which separates the Isle of Cumbrae from the coast of northern Ayrshire. Hauls were made with an Agassiz dredge on two successive days at a total of eight stations. These stations were so arranged that two areas of the Largs Channel were sampled and in each area ophiuroids were taken from a wide variety of depths. Mud accumulates in the Firth of Clyde (of which the Largs Channel is a part) below a depth of approximately 50 m.

TABLE 1. STATIONS AT WHICH *OPHIOCOMINA NIGRA* WAS COLLECTED IN THE LARGS CHANNEL

Station	Bearings	Depth, by echo sounding (m)	Bottom
1	Hunterston Perch, SW 200 yards	20	Sandy
2	Hunterston Perch, SE 500 yards	30–32	Sandy mud
3	Hunterston Perch, SSE ½ mile	45	Sandy mud
4	Farland Point, NNW 300 yards	38	Stones and gravel
5	Farland Point, NNW 100 yards	10	Rocky
6	Keppel Pier, SW 100 yards	10	Rocky
7	Hunterston Perch, SW 100 yards	20	Sandy
8	Hunterston Perch, SE × S 200 yards	34	Sandy

This limits the depth to which *O. nigra* can penetrate in this area, since the species cannot tolerate heavy mud. No ophiuroids were encountered below 45 m, although hauls were made up to 53 m at several stations not listed.

The location, depth and nature of the bottom of the eight stations at which *O. nigra* was collected are given in Table 1.

The animals were kept alive under circulation, and colour scored against the 'type set' on two successive days in order to test for personal bias in judging colour. The scores so obtained were identical. The distribution of colour classes is shown in Table 2 which is arranged in order of increasing depth.

In order to test whether or not colour and depth were in fact related, the chi-square test was applied to the data. Because the number of individuals in each class and at each station was rather small, particularly in the samples from deeper waters, the classes were secondarily grouped, as shown in Table 3. Stations of approximately similar depth were also grouped where necessary.

With 4 degrees of freedom, a chi-square of 13·277 is significant at the 1% level of confidence. There is therefore a strong probability of a correlation between colour and bathymetric distribution, such that increasing depth is accompanied by an increase in the frequency of light-coloured individuals.

It is, of course, unlikely that depth *per se* influences colour, but that some variable or cluster of variables dependent on depth, such as light penetration, is the ultimate controlling factor. Light penetration as a factor influencing pigmentation is likely for a number of reasons. The dark pigment of these ophiuroids is a melanin and it is well known that light can be involved in the physiology of melanogenesis. Another possibility is the use of melanin as a protective light screen, as demonstrated in a variety of animals (Fox, 1953).

TABLE 2. DISTRIBUTION OF COLOUR CLASSES OF *OPHIOCOMINA NIGRA* ACCORDING TO DEPTH

		Number in colour class					
Station	Depth	1	2	3	4	5	Total per station
5	10	29	26	11	—	—	66
6	10	8	5	6	1	—	20
7	20	3	2	1	2	—	8
1	20	9	13	7	2	1	32
2	30–32	1	4	12	5	1	23
8	34	3	3	3	2	1	11
4	38	2	7	5	—	—	14
3	45	1	2	—	2	—	5
						Total collected	179

TABLE 3. RELATION BETWEEN COLOUR AND DEPTH

	Observed frequency			Frequency expected if no relation with depth		
Depth (m)	Dark (1, 2)	Light (3, 4, 5)	Total	Dark (1, 2)	Light (3, 4, 5)	Total
10	68	18	86	56·4	29·6	86
20	27	13	40	26·2	13·8	40
30–32	5	18	23	15·1	7·9	23
34	6	6	12	7·9	4·1	12
38–45	12	7	19	12·4	6·6	19
Totals	118	62	180	118·0	62·0	180

$\chi^2 = 28{\cdot}02$, D.F. $= 4$, $P < 0{\cdot}01$.

In the Oxford laboratory *O. nigra* tended to die off rather quickly in aquaria kept in bright light even though the water was cooled and circulating, and it appeared that the lighter-colour phases tended to die most quickly under these conditions. Animals in aquaria shielded from direct light lived much longer, including the light-colour phases and, under these conditions, could tolerate much warmer water than usual. This suggested the potential value of melanin pigmentation as a protective light screen to those animals living in shallow waters.

This possible function of melanin was tested at Millport, where a sample of ophiuroids of all colour classes was placed in an aquarium exposed to bright light during the day and artificially illuminated at night. A second sample was kept in a covered aquarium that was practically light-tight. Both aquaria had running sea water circulating through them. The animals used were perfect specimens, not damaged in any way by the dredge and in lively condition. After 48 hr in these aquaria, the animals were examined and those specimens which were moribund (i.e. sluggish response to tactile stimulation and other signs of impending death) were counted. The results are shown in Table 4.

TABLE 4. MORTALITY OF *OPHIOCOMINA NIGRA* KEPT IN DARK AND LIGHT AQUARIA

	Illuminated		Darkened	
Colour class	Original sample	Moribund after 48 hr.	Original sample	Moribund after 48 hr.
Dark (1, 2)	12	2	16	2†
Light (3, 4, 5)	11	8*	17	5
Totals	23	10 (43·5 %)	33	7 (21·2 %)

* Moribund *light* phases in illuminated tank, 80·0 % of total dead.

† Moribund *dark* phases in darkened tank, 28·5 % of total dead.

The results suggest that some protection from light may be beneficial to *O. nigra* since nearly twice as many die in a strongly illuminated tank. When the chi-square test is applied to these data, however, the difference is found to be significant at only about the 20 % level of confidence, and the results are therefore inconclusive. The numbers of individuals in the *light* category are too small to allow of any pronouncements as to their potential disadvantage in bright light.

The observations presented here point to at least two environmental components which may affect colour variation in *O. nigra*. First, the colour tone of the substratum in a given locality may be a factor which influences 'horizontal' or geographic colour variation in the species. Secondly, the depth at which the population lives (or, better, some factor dependent on depth) appears to be a factor influencing 'vertical' or bathymetric colour variation in the species. The remarkable colour variations noted over the whole range of the species may be accounted for by interaction of these two variable environmental components.

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SUMMARY

The ophiuroid, *Ophiocomina nigra*, is noted for its variability of colour, a phenomenon most pronounced where the species also has its greatest distribution in depth. Observations have been made on two geographically distinct populations, from the vicinities of Millport and Plymouth. The body colour of the observed animals ranges in a continuously graded series from black to orange-yellow. While both populations exhibit analogous variations, there is a distinct difference in the range and tone of coloration which each displays. It is suggested that this geographical difference is correlated in some degree with differences in colour tone of the substratum. It was observed that the incidence of light-coloured phases in each population increased with increasing depths, and some statistical evidence supports this conclusion. Thus, at least two factors, depth and substratum, may affect the distribution of colour variations in *O. nigra*.

In addition to the variations in general body colour, there are two distinct colour patterns found on the disk. These are probably truly polymorphic and may be of cryptic value.

A scheme of colour classification is described which facilitates observations in the field and in the laboratory.

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