

A catalog of the chromatic, postural, and locomotor behaviors of the pharaoh cuttlefish (*Sepia pharaonis*) from Okinawa Island, Japan

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Abstract Coleoid cephalopods such as cuttlefishes, squids, and octopods are able to produce a diverse array of visual expressions that are used for mimesis and inter- and intraspecific communication. They achieve this by intricately combining several neurally controlled behaviors, which include chromatic, textural, postural, and locomotor components. To understand this diverse range of body patterns, it is necessary to develop an accurate and extensive catalog of them, which can then be used as a tool for future behavioral monitoring and quantitative analyses, as well as for the identification of morphologically identical sub-species. In this study, a catalog of the chromatic, postural, and locomotor behaviors was produced for the pharaoh cuttlefish (*Sepia pharaonis*) from coastal waters of Okinawa Island, Japan. Data were collected from aquacultured animals using egg masses sampled from around the island and hatched in aquaria during 2010, 2011, 2012, and 2014. In total, 53 chromatic, four supplementary chromatic conditions, three textural, 11 postural, and nine locomotor components were identified and described in detail. Many of the described components are similar to previously described body patterns of *Sepia officinalis*. However, there are notable differences between the two species, which may indicate that they use body patterns in different ways for cryptic behavior and inter- and intraspecific communication.

Keywords Body patterns · Cephalopods · Cuttlefish · Catalog · *Sepia pharaonis*

Introduction

In many animal species, body color and/or texture play an important role in predator/prey interactions, such as crypsis (Endler 1978) and disruption (Cott 1940). Most animals have fixed or slightly changeable appearances (Cott 1940). However, coleoid cephalopods such as cuttlefishes, squids, and octopods are not only able to change their body color and texture rapidly, but also to exhibit a variety of visually complex appearances. These appearances comprise a combination of chromatic, textural, postural, and locomotor components for both camouflage and communication. The total appearance of the animal is defined specifically as its body pattern while components are the individual parts that make up the body pattern (Packard 1972; Packard and Hochberg 1977; Moynihan 1985; Hanlon and Messenger 1988, 1996).

The chromatic component of the body pattern is changed by neuromuscular control of the size of many pigment-filled organs called chromatophores (Messenger 2001). A chromatophore is connected to a set of radial muscles that contract and relax to change its effective surface area (Hanlon 1982). In addition, two types of light-reflective cells—iridophores and leucophores contribute to the overall color palette of the animal. Iridophores selectively reflect light producing iridescent blue, green, and pink colors, and are also neurally controlled (Messenger 2001; Wardill et al. 2012). Leucophores also reflect light, creating high-contrast white appearance (Messenger 2001). Octopods and cuttlefishes are also able to alter the physical texture of their skin from smooth to three-dimensional by using dermal muscles to produce erectile

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papillae (Holmes 1940; Packard and Hochberg 1977). The postural component is changed by altering the positional orientation of the flexible, muscular arms, tentacles, mantle, head, and fins (Packard and Sanders 1971). Finally, the locomotor component involves the movement of the entire body of the individual (Roper and Hochberg 1988). Each of these components can appear for seconds (acute) or for hours (chronic) and can be displayed in a wide variety of combinations to create the overall appearance of the animal (Packard and Hochberg 1977; Hanlon and Messenger 1996). Therefore, each component of the body pattern of a species needs to be cataloged and described to allow quantitative analysis of its behaviors and for species identification.

More than 100 species of cuttlefishes have been described to date (Jereb and Roper 2005), of which one species—the benthic, shallow-water common cuttlefish (*Sepia officinalis*)—is the most extensively studied for its body pattern. These studies have shown that *S. officinalis* can create a wide range of body patterns allowing it to either blend into its visually rich and complex natural habitat or to stand out startlingly, with 87 components (42 chromatic, eight textural, 13 postural, and 24 locomotor) identified and described to date (Holmes 1940; Boycott 1958; Neill 1971; Hanlon and Messenger 1988). Although recent study suggests that cuttlefishes are able to detect colors by chromatic aberration (Stubbs and Stubbs 2016), they possess one visual pigment and are color blind (Marshall and Messenger 1996; Mäthger et al. 2006). Hence, their visual behavior has been directly correlated with multiple visual cues, such as the scale of a light object, the edge detection, the relative tonal differences between the foreground and background, and the two- and three-dimensional visual depths. Visual information is gathered by highly developed eyes, processed by a hierarchically organized set of lobes in their brain, and then converted into an appropriate pattern as a motor output (Muntz and Johnson 1978; Messenger 2001; Zylinski et al. 2009).

In addition to *S. officinalis*, over 20 extensive body pattern catalogs have been produced for other cephalopod species including the flamboyant cuttlefish, *Metasepia pfefferi* (Thomas and MacDonald 2016; Roper and Hochberg 1988); slender inshore squid, *Doryteuthis plei* (Postuma and Gasalla 2015); longfinned inshore squid, *Doryteuthis pealeii* (Hanlon et al. 1999); Large Pacific striped octopus (Caldwell et al. 2015); Humboldt squid, *Dosidicus gigas* (Trueblood et al. 2015); northern shortfin squid, *Illex illecebrosus* (Harrop et al. 2014); deep sea squid, *Octopoteuthis deletron* (Bush et al. 2009); Cape Hope squid, *Loligo reynaudii* (Hanlon et al. 1994); and common octopus, *Octopus vulgaris* (Packard and Sanders 1971) (reviewed by Borrelli et al. 2006; Hanlon and Messenger 1996). Many of these reports were produced through extensive analysis of photographic and video data recorded from both in situ and in the laboratory. More recently, an automated signal classification system

has been used as a less subjective and repeatable cataloging approach (Thomas and MacDonald 2016).

The pharaoh cuttlefish, *Sepia pharaonis* (Ehrenberg 1831), lives in tropical coastal waters in the Indo-Pacific region from 35°N to 30°S and 30°E to 140°E down to 100 m depth (Norman and Reid 2000; Nabhitabhata and Nilaphat 1999). This species is divided into three sub-types depending on the body pattern and geographical distribution: Type I in the Arabian Gulf, western Indian Ocean, and Red Sea; Type II from Japan to the Gulf of Thailand, the Philippines, and northern Australia; and Type III from the Andaman Sea to the Maldives. These three types differ in size, growth rate and in color patterns of mating animals. Type I and Type II males have zebra stripes on their third arms, while Type III males have spots on their third arms (Norman 2000). Previous studies on the body patterns of this species have particularly focused on camouflage and its visual cues. These studies have found that *S. pharaonis*'s disruptive coloration is affected largely by area rather than the shape or aspect ratio of a light colored object on a substrate (Chiao and Hanlon 2001) and that visual orientation of substrate pattern has little effect on its body pattern selection (Shohet et al. 2006). However, aside from 34 chromatic components assumed based on *S. officinalis* (Shohet et al. 2007), there has been no extensive catalog of their body pattern diversity that includes chromatic, textural, postural, and locomotor components. Hence, the aim of this study was to document the range of body pattern components exhibited by *S. pharaonis*. We hope that these findings will provide a useful foundation for the identification of *Sepia* species and sub-species and for future quantitative behavioral analyses.

Materials and methods

Egg cases of Type II *S. pharaonis* were collected from the Sunabe beach area (depth ranging from 10 to 12 m, water temperature ranging from 23 °C to 25 °C) in Okinawa Island on April of 2010, 2011, and 2012. Egg cases were immediately transported to the laboratory of the Department of Chemistry, Biology, and Marine Sciences at the University of the Ryukyus, where they were reared and cultured in three 20 L (300 mm diameter x 170 mm depth) cylindrical, acrylic, closed-system tanks (Multi-hydense®, Aqua Co., Ltd Japan). All tanks were filled with artificial seawater (Tetra Marine Salt Pro, Tetra Japan Inc., Japan), and 2 L of seawater was exchanged in each tank every few days. In addition, fresh water was added to the tanks as required to compensate for evaporation. The water quality (temperature, salinity, pH, and concentration of ammonia, nitrite, and nitrate) was monitored regularly using an electric pH/temperature meter, a salinity meter, and a commercial-grade water testing kit (Test Lab, Red Sea) to maintain the following levels:

temperature = 24.5–25.5 °C; pH = 7.8–8.2; and salinity = 33–35 psu. If the pH dropped below 7.7, a pH/al adjuster (LIVEsea Buffer pH/al, Delphis Japan) was added to the tanks. Lighting was provided by fluorescent light tubes, which were set on a 12 h light/12 h dark cycle.

In total, 75 animals (35 [102–118 days old] in 2010, 22 [81–99 days old] in 2011, eight [105–116 days old] in 2012, and 10 [117–118 days old] in 2014) were used without determining each animal's sex. The animals were separated into three 50 L (400 mm diameter x 360 mm depth) cylindrical acrylic tanks in 2010 and three rectangular polypropylene containers in 2011 and 2012 (540 mm length x 380 mm width x 200 mm height, plastic box 06, Shinwa Japan, in 2011; and 600 mm length x 430 mm width x 380 mm height, plastic box 09, Shinwa, in 2012). The cylindrical acrylic tanks are light gray at the base and polypropylene containers are semi-transparent white at the base. All tanks had black cloth on all four sides to reduce visual stress. The animals were fed frozen Japanese anchovy (*Engraulis japonicus*), Sakura shrimp (*Sergia lucens*), and/or black tiger prawns (*Penaeus monodon*) twice per day. For the observation, each animal was individually taken out of the holding tank, transported to the observation apparatus in a semi-opaque plastic container, and then returned to the holding tank in the same manner after the session. All animals were shared with lab-mates.

During the observation sessions, the animals were placed in ADA Cube Garden frameless glass tanks (450 mm x 270 mm x 300 mm, Aqua Design Amano Co., Niigata, Japan) with and without crushed coral sand substrate. The observations were conducted six times per animal between morning and evening feedings. Animals were allowed 5 min to acclimate to the tank and recorded for 10 min unless the animal showed clear signs of stress (inking, dashing, and smashing into the tank wall). Videos and still images were recorded using a Canon 5D Mark II Digital SLR camera with a Canon EF 50 mm 1:2.5 Compact Macro Lens, a Canon EF 24–105 mm 1:4 L IS USM Zoom Lens, and a Canon EF 50 mm 1:1.2 L USM Lens (Canon USA Inc., NY, USA). The camera was mounted on a tripod with a horizontal extension arm and suspended 300–600 mm above the water surface. Still images were approximately 5616 x 3744 pixels, while videos were recorded in full high-definition (HD) (1080p) at 30 frames/s (1920 x 1080 pixels). EOS Utility (version 2.13.0) was used to remotely capture both videos and photographs to reduce disturbance to the animals. The ambient light was provided by a fluorescent tube suspended 2.5 m above the tank, and the animals were sheltered from any direct light. Still frame photographs and videos of the underside of each animal were obtained by placing a mirror beneath the tank at a 45° angle and then placing a camera in front of the mirror.

In total, 325 HD videos (duration ranging from 42 s to 15 min) and 9799 still images of the animals were obtained.

These were then filtered to select only acute (lasting more than a few seconds to several minutes; sensu Hanlon and Messenger 1996: Box 3.1) total body pattern expressions and to remove any repetitive images without noticeable changes, which resulted in 784 still images being extracted from the set for detailed analysis. *Sepia officinalis* chromatic components have been organized into light and dark components, reflecting the expansion and contraction of the chromatophores (Hanlon and Messenger 1988). In this study, we employed a graphic image construction method that is used by the graphic design industry. Both Adobe Illustrator (v. CS6; Adobe, San Jose, CA, USA) and Adobe Photoshop (v. CS6; Adobe, San Jose, CA, USA) were used manually to break down digital photography into separate visual layers. Illustrator is vector-based graphics software that allows graphic elements to be organized as layers rather than pixel based organization. All of the components can be stored as individual layers that can be easily combined (Fig. 1) like puzzle pieces to create an overall body pattern appearance of any given image. Furthermore, the catalog can be edited and updated by others using the same software. This method provides flexibility as a visual catalog of components that track body patterns and behavior with better accuracy and may contribute to the greater database of cephalopod body pattern and behavior when combined with database of other species.

Results

The body pattern components observed and documented comprised 53 chromatic components, 11 postural components, nine locomotor components, three textural, and four supplementary chromatic conditions (Table 1). Detail descriptions of the components are as follows.

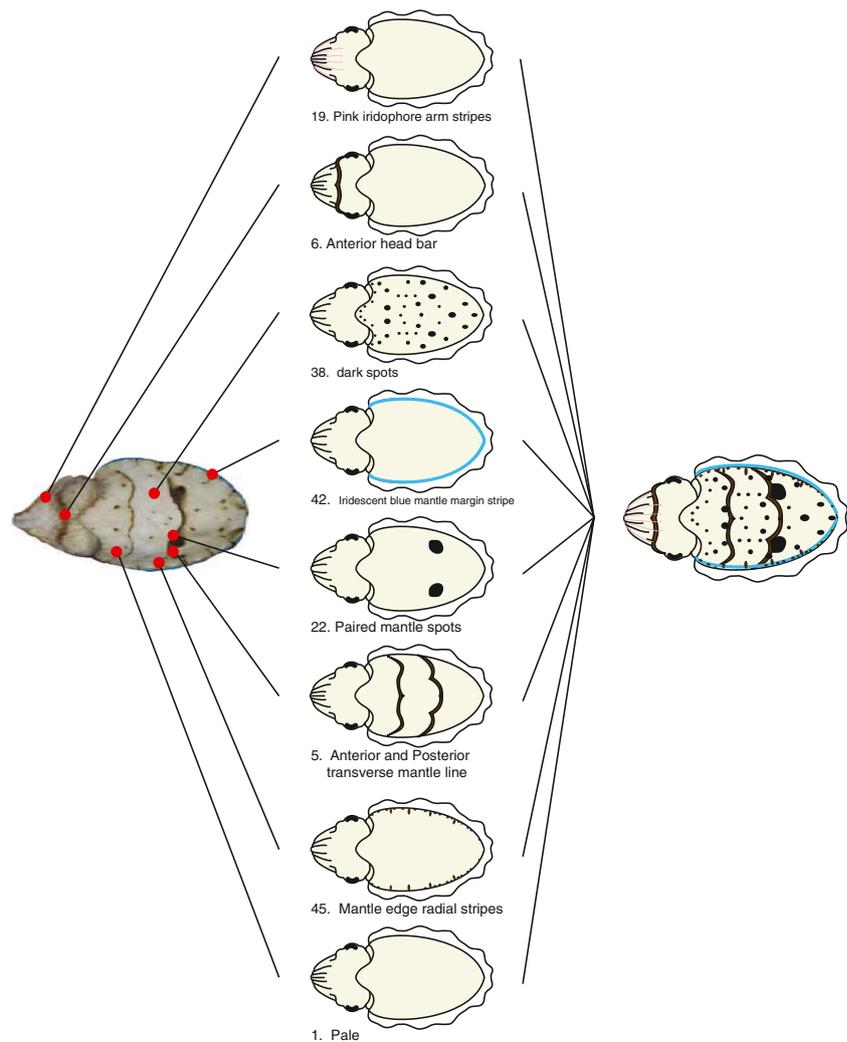
Chromatic components

Uniform (1–4, Fig. 2a) – Four uniform colors were identified:

1. Pale (observed number (n) = 471)
2. Yellow (n = 230)
3. Dark brown (n = 70)
4. Dark red (n = 13)

Colors ranging from pale (1) to yellow (2) were often observed often (701/784 cases, or 90% of the total images analyzed). By contrast, dark brown (3) was only recorded in only 70 cases (8%) and mainly in smaller animals with a mantle length <5 cm. Base colors form the chromatic foundation, to which other components are added to produce the complete body pattern. White (#1) was the most basic color and is very similar to the pale mantle category of Boal et al. (2004). It has

Fig. 1 An example of reconstruction of a body pattern using chromatic components in this study



been shown that animals appear to be white as a result of chromatophore contraction making the leucophore layer visible (Messenger 2001). By contrast, animals appear dark brown when there is maximum expansion of the chromatophores and yellow coloration falls between these two extremes. We also observed *S. pharaonis* turning reddish purple (4) in 13 cases, usually following heavy inking and jetting behavior.

Head and arm (5–21, Fig. 2a) – A total of 17 head and arm chromatic components were identified:

5. Anterior head bar ($n = 69$) (Packard and Sanders 1971; Hanlon and Messenger 1988). A dark or light line that crosses the anterior part of the head and the base of the arms. It also lies at the boundary of the dark arm.

6. Arm bar ($n = 22$). A dark line at the anterior of the head bar that is visible half way between the anterior head bar (6) and the tips of the arms.

7. Posterior head bar with stripe ($n = 69$) (Hanlon and Messenger 1988). A dark brown band that is located along the edge of the posterior region of the head. The band extends

the pattern into the center axes of the head with finer horizontal lines branching out to the posterior head margin.

8. Red posterior head bar with stripe ($n = 107$) (Hanlon and Messenger 1988). A reddish band that is located along the edge of the posterior region of the head that is similar to Posterior head bar stripe.

9. White landmark head spots ($n = 80$). A total of 4–6 prominent white spots between the anterior and posterior head bars.

10. White head bar ($n = 173$) (Holmes 1940; Hanlon and Messenger 1988). An almost transparent white band that connects the dorsal-most part of each eye. This was most commonly observed when the animals were using very few chromatic components. However, when it appeared in combination with a darker anterior mantle bar (12), dark arms (13), and a posterior mantle bar (14), it created a striking tonal contrast.

11. Dark arms ($n = 73$) (Hanlon and Messenger 1988). Expressed as darkening arms (I, II, and III), which create a triangular form, the boundary of which starts at the anterior head bar (6).

Table 1 The ethogram of body pattern components for *Sepia pharaonis*. (n) is the number of times each component was observed on video

	n=
Chromatic components:	
White	(471)
Yellow	(230)
Dark brown	(70)
Dark red	(13)
Anterior head bar	(69)
Arm bar	(22)
Posterior head bar	(69)
Red posterior head bar	(107)
White landmark head spots	(80)
White head bar	(173)
Dark arms	(73)
Dark eye patch	(122)
Eye ring	(32)
Anterior eyespots	(23)
Dark arm stripes	(13)
Pink iridophore arm stripes	(73)
Red arms I	(10)
Brown arms I	(12)
Extended head crown	(51)
Head crown	(19)
Head spot	(13)
Anterior and Posterior transverse mantle line	(404)
Anterior mantle bar	(78)
Fragmented anterior mantle bar	(127)
Anterior mantle crown	(19)
Posterior mantle bar	(43)
Fragmented posterior mantle bar	(127)
Posterior mantle crown	(46)
Central dark mantle shield	(13)
Posterior mantle spot	(13)
Joined paired mantle spots	(97)
Fragmented paired mantle spots	(19)
Paired mantle spots	(161)
White square	(20)
Dark Square	(35)
Mantle shield	(101)
Black dots	(620)
White dots	(568)
Fragmented dark mantle	(51)
Paired central mantle spots	(22)
Triangular Wedges	(60)
Median Mantle Stripe	(18)
Wide mantle edge radial bands	(30)
Iridescent blue lateral stripe	(62)
White lateral margin stripe	(43)
Dark red lateral margin stripe	(48)
Mantle edge radial stripes	(479)

Table 1 (continued)

White major lateral papillae	(316)
Pale Ventral mantle	(26)
Lateroventral patches	(26)
Unilateral lateroventral patch	(37)
Iridescent ventral mantle	(25)
Inverse lateroventral patches	(6)
Dark ventral mantle	(2)
(Supplementary chromatic condition)	
Symmetrical lateral divider	(46)
Symmetrical lateral divider (ventral)	(15)
Full asymmetrical shift	(6)
Partial asymmetrical shift	(17)
Textural components:	
Smooth skin	(234)
Coarse skin	(338)
Papillate skin	(77)
Postural components:	
Bipod	(5)
Extended first arms	(16)
Flattened body	(96)
Extended and curled fourth arms	(40)
Fully extended arms	(27)
Streamlined extension	(23)
Diamatic flare	(62)
Deimatic frontal flare	(3)
Bipod headstand	(2)
Crustaceans like aggressive mimicry	(12)
Sitting	(548)
Locomotor components:	
Frontal lift	(38)
Sideway roll	(34)
Deimatic vertical lift and roll	(7)
Escape (jetting)	(8)
Bottom suction	(24)
Hovering	(465)
Inking	(15)
Sand digging	(173)
Swimming	(553)

Compare Fig. 2, 3, 4, 5, 6, 7 and 8

12. Dark eye patches ($n = 122$). Dark brown to black patches on the dorsal side of the eyes. These patches can be connected by eye-lines (Neill 1971) to create dark, circular shapes surrounding the eyes. They can also appear independently from the dark patches on the ventral side.

13. Eye rings ($n = 32$) (Packard and Sanders 1971; Hanlon and Messenger 1988). Dark semicircular bands that follow the lower perimeters of the eyes and often appear with dilated pupils, creating complete circles and giving the impression of larger eyes.

14. Anterior eye spots ($n = 23$). A pair of dark spots located between the anterior perimeter of the eyes and the anterior head bar (#6), creating an impression of frontally elongated pupils.

15. Dark arm stripes ($n = 13$) (Hanlon and Messenger 1988). Darker longitudinal lines that appear on all arms, which, in combination with the lighter lines of the iridophores on the outer edges of the arms, create high-contrast stripes.

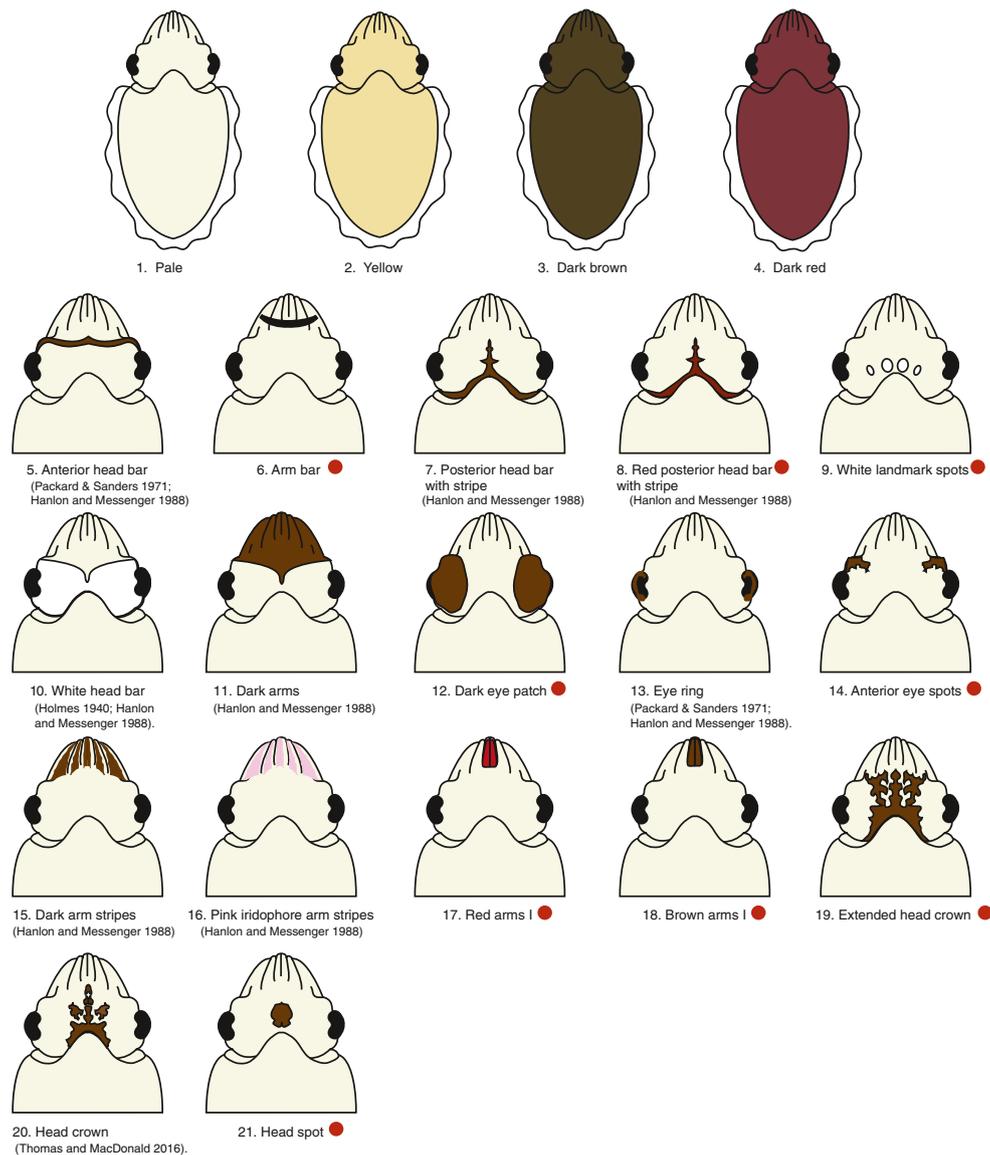


Fig. 2 a, b, c, and d Diagrammatic representations of chromatic components of body patterning in the cuttlefish *Sepia pharaonis*. Red dots in the figure indicate that component is newly described

16. Pink iridophore arm stripes ($n = 73$) (Hanlon and Messenger 1988). Thin, pink iridophore lines that begin at the anterior of the head and extend to the tip of each arm. These lines run along the center of arms I and II, and along the outer edge of arms III and IV. Although the lines most often appear as an iridescent pink color, they can also have iridescent green and light blue hues at times. The line on arm IV most often appears white.

17. Red arms I ($n = 10$). Expressed through the color of arm I changing to red. This component was observed during two behavioral circumstances a) during a confrontation with another member of the same species, where arm I was extended straight toward the opponent with the bright red color concentrated at the tip of the arm and b) while the individual was

completely submerged under the sand, with only arm I extending through the surface.

18. Brown arms I ($n = 12$). A thin, triangular-shaped area that is created by the darkening of arm I from its posterior base to the tip. This component symmetrically divides the arm in two.

19. Extended head crown ($n = 51$). A crown-shaped area that is created by three jagged and scalloped stripes extending out from the posterior head bar (7) towards the arms.

20. Head crown ($n = 19$) (Thomas and MacDonald 2016). A crown-shaped area that is created by three jagged stripes extending out from the posterior head bar (7) towards the arms. It is a compact version of the extended head crown (19) described above with smaller area coverage.

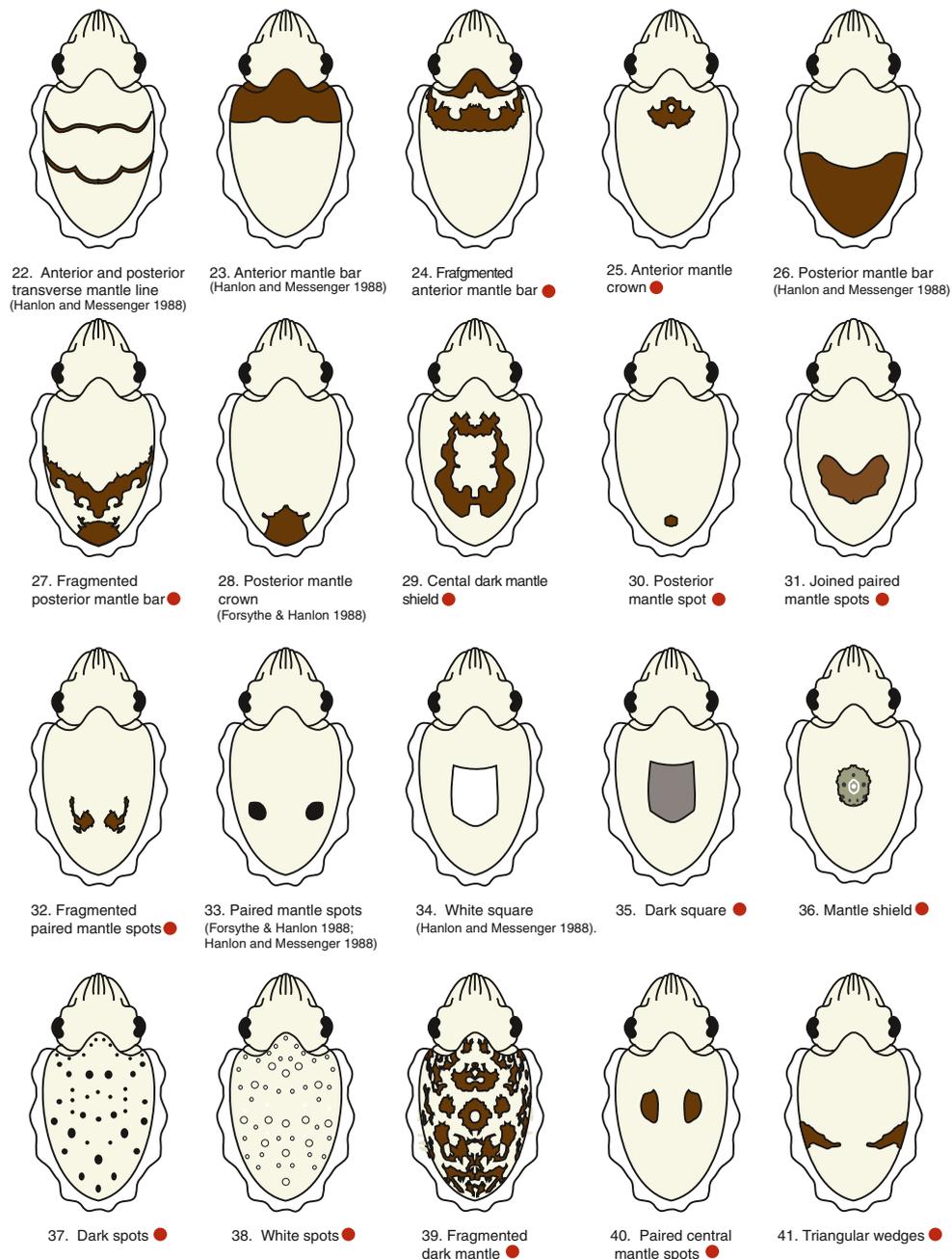


Fig. 2 continued.

21. Head spot ($n = 13$). A dark circular spot located at the central axis of the head between the posterior head bar and the arms (7).

Dorsal mantle (22–47, Fig. 2b and c)– A total of 28 dorsal mantle chromatic components were identified:

22. Anterior and posterior transverse mantle lines ($n = 404$) (Hanlon and Messenger 1988). Thin and dark scalloped lines that cross the entire mantle width at 1:1:1.5 division ratios between the anterior and posterior mantle margins. These lines are perhaps the most important chromatic components for *S. pharaonis*, defining the visual boundaries for many other

components. In some instances, these lines appeared to be thicker than usual.

23. Anterior mantle bar ($n = 78$) (Hanlon and Messenger 1988). A dark banded area that is situated in the anterior quarter of the mantle between the mantle margin and the anterior transverse mantle line (22).

24. Fragmented anterior mantle bar ($n = 127$). This component has the same attributes as anterior mantle bar (23) component described above, while not fully completing the component. It has a more jagged and flame-like design that emphasizes Anterior transverse mantle lines (22), as well as the

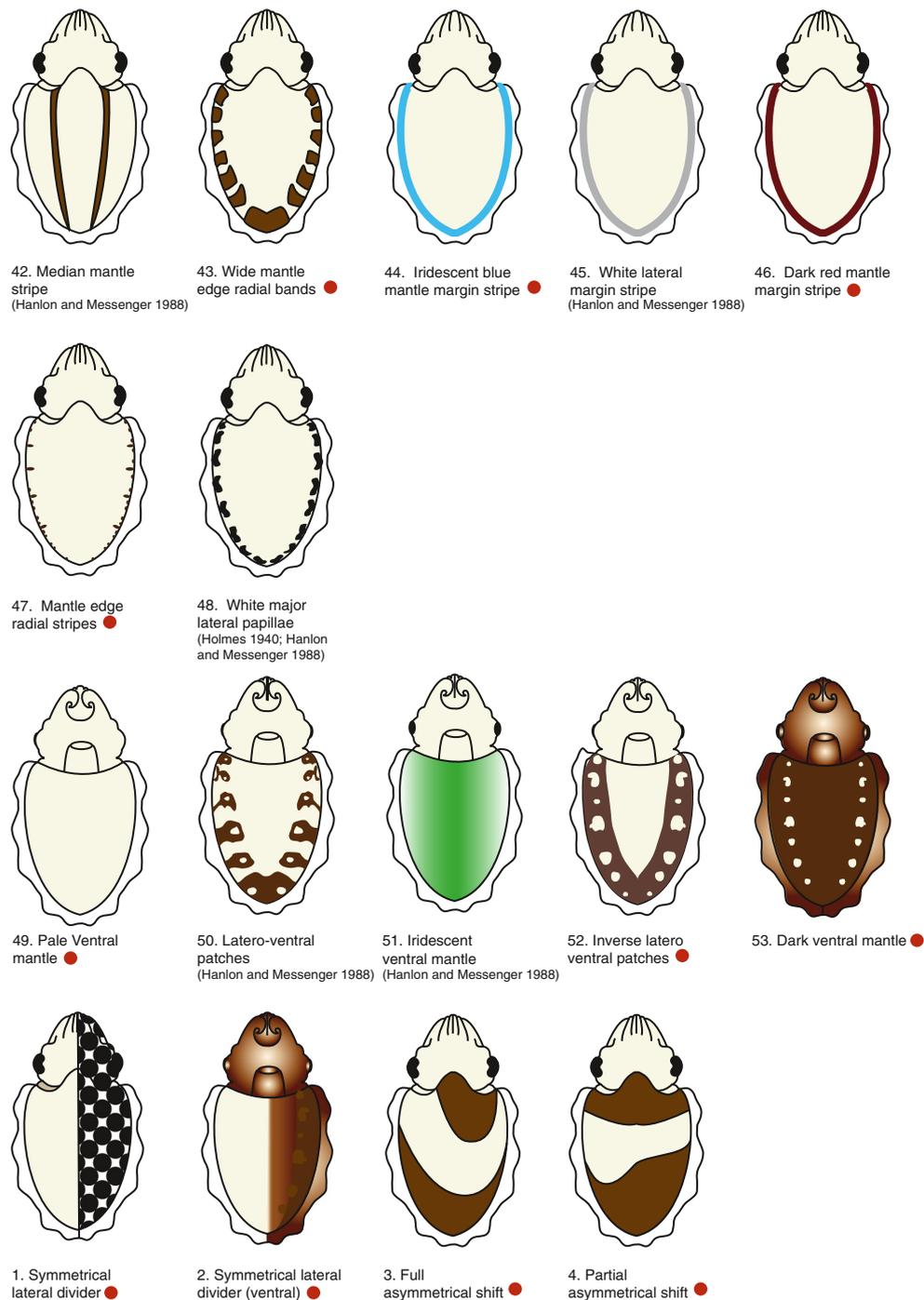


Fig. 2 continued.

anterior mantle margins. In many occasions, it appeared together with the fragmented posterior mantle bar (27) creating disruptive body pattern.

25. Anterior mantle crown ($n = 19$) A crown shaped area situated along the central axis of the mantle, bordering the anterior transverse mantle lines (22). It often appears together with the fragmented paired mantle spots (32) and the head crown (20).

26. Posterior mantle bar ($n = 43$) (Hanlon and Messenger 1988). A dark banded area that is situated in the posterior third of the mantle between the posterior mantle edge and the posterior transverse mantle line (5). There are many variants that give the impression of this component, such as a thickened posterior transverse mantle line (22), paired mantle spots (33), and triangular wedges (41). This area can also be broken up into a combination of a fragmented

posterior mantle bar (27) and joined paired mantle spots (31).

27. Fragmented posterior mantle bar ($n = 127$). This component has the same attributes as posterior mantle bar (26) component described above, while not fully completing the component. It has a more jagged and flame-like design that emphasizes posterior transverse mantle lines (22), as well as the posterior mantle margins.

28. Posterior mantle crown ($n = 46$) (Forsythe and Hanlon 1988). A dark, trapezoid-shaped area at the central posterior margin of the mantle. The top of the shape reaches the halfway point between the posterior transverse mantle lines (22) and the posterior mantle edge.

29. Central dark mantle shield ($n = 13$). On the mantle, a negative shield-like shape is created by connecting paired central mantle spots (40), paired mantle spots (33), and the upper central region of the posterior mantle bar (26).

30. Posterior mantle spot ($n = 13$). A single small circular shape located near the center of the posterior mantle bar (26.)

31. Joined paired mantle spots ($n = 94$). A butterfly-shaped dark area that is created by connecting paired mantle spots toward the center of the mantle.

32. Fragmented paired mantle spots ($n = 19$). A pair of spots located at the joined paired mantle spots (31) with two larger spots at the posterior of the mantle with thinner stripes extending towards the center of mantle.

33. Paired mantle spots ($n = 209$) (Forsythe and Hanlon 1988; Hanlon and Messenger 1988). A pair of very dark spots that appear posterior to the posterior transverse mantle line (22). These spots are also known as eye spots and are associated with a deimatic pattern (Hanlon and Messenger 1988), which is an interspecific signal that is induced by and directed toward a potential predator (Moynihan 1975). In *S. pharaonis*, we detected only one pair of spots, which were either round or rectangular in shape. The spots can appear as pair or as single spot on either right or left side of the mantle.

34. White square ($n = 23$) (Hanlon and Messenger 1988). A white, square-shaped area at the center of the mantle between the anterior and posterior transverse mantle lines (22). This component can also appear asymmetrical at times when the posterior edge of the white square is unevenly stretched down. This does not seem to be created by chromatophore arrangement, but rather to be brought about by stretching the skin downward towards the posterior mantle margin.

35. Dark square ($n = 35$). A brownish, dark, square-shaped area at the center of the mantle between the anterior and posterior transverse mantle lines (22). Unlike the white square (34), this square has edges undefined by contrast color.

36. Mantle shield ($n = 101$). Dark and light dots that appear in the same area as the white square at the center of the mantle between the anterior and posterior transverse mantle lines (22). This complex arrangement of both light and dark chromatic components creates a radial and symmetrical design. In

some instances, a central white dot is a very large and dominant compositional element of this component.

37. Black dots ($n = 620$) & 38. White dots ($n = 568$). Small dark brown to black or white dots, respectively, that are homogeneously distributed across the entire dorsal mantle, head, and arm area. The combination of black and white dots produces a visual transition from a uniform body pattern to one that is stippled or mottled by regulating the overall tonal and two-dimensional textural expression of the animal. Subtle differences in color and the contraction/expansion of the chromatophores create a diverse range of tones within the mottled body pattern from light mottle to dark mottle (Holmes 1940; Hanlon and Messenger 1988).

39. Fragmented dark mantle ($n = 51$). Larger, high-contrast patches that are evenly and symmetrically distributed on the mantle, giving an overall appearance that is similar to damask ornamental design (Ward 1817). Each patch appears between the anterior and posterior transverse mantle lines (22). The patches along the mantle margin are created by the aggregation of dark chromatophores into long scalloped patterns. This is the most visually complex combination of chromatic features.

40. Paired central mantle spots ($n = 22$). Two half-dome-shaped components that appear between the anterior and posterior transverse mantle lines (22). The domes touch the lateral margins of the white square.

41. Triangular wedges ($n = 66$). Two V-shaped patterns located on the posterior transverse line (22) toward the posterior mantle edge. Laterally, these border the mantle boundary at the base of the fins. The posterior side of the shape tends to fade toward the posterior mantle margin. This component can appear on either the right- or left-hand side of the posterior transverse line toward the posterior mantle edge.

42. Median mantle stripe ($n = 18$) (Hanlon and Messenger 1988). A pair of distinctive dark lines that run along the full length of the mantle from the posterior end to the anterior margin.

43. Wide mantle edge radial bands ($n = 30$). Fourteen dark and robust rectangular blocks (seven each on the right and left sides), which form a wide radial band around the mantle edge. At the posterior mantle edge, the last two dark patches merge to form a larger block. This component is very similar to its ventral counterpart lateroventral patches (51) (Hanlon and Messenger 1988).

44. Iridescent blue lateral stripe ($n = 62$). A bright blue iridescent stripe that runs longitudinally along the entire mantle margin at the base of the fins that outline the mantle. This stripe is often visible with other components, contributing to the deimatic pattern.

45. White lateral margin stripe ($n = 43$) (Hanlon and Messenger 1988). A white stripe that runs longitudinally along the entire mantle margin at the base of the fins that outline the mantle. It appears at the same place as the iridescent blue

lateral stripe described above and the dark red lateral stripe described below.

46. Dark red lateral margin stripe ($n = 48$). A dark red stripe that runs longitudinally along the entire mantle margin at the base of the fins that outline the mantle. It appears at the same place as the iridescent blue and white lateral margin stripes described above.

47. Mantle edge radial stripes ($n = 479$). Short to long dark lines that extend from the lateral margin toward the center of the mantle, running longitudinally along the entire mantle perimeter. The position of these radial lines seems to correspond with the mantle margin scalloping the major lateral papillae and the lateroventral patches (51) (Hanlon and Messenger 1988).

48. White major lateral papillae line ($n = 316$) (Holmes 1940; Hanlon and Messenger 1988). Six to eight white lines created as a result of papillae contraction located along the mantle margin by the base of the fins. When papillae contracted, they have a white line-like appearance as a result of the iridophores (Hanlon and Messenger 1988).

Ventral mantle (49–53, Fig. 2c) – 5 ventral mantle chromatic components were identified:

49. Pale ventral mantle ($n = 26$). Similar to the Pale mantle of Boal et al. (2004), which has been described as a base color component that is produced by contracting the chromatophores to create a pale, white appearance.

50. Lateroventral patches ($n = 63$) (Hanlon and Messenger 1988). Six patches that are located on each side of the ventral mantle directly below the base of the fins along the lateral mantle margin. Each patch has a small circular opening that contracts and expands according to the darker portion of the patch. Lateroventral patches can only appear on either side of the ventral mantle.

51. Iridescent ventral mantle ($n = 25$) (Hanlon and Messenger 1988). A green, smooth, iridescent area distributed equally on the ventral surface of the mantle and on the edge of arm IV, and can be seen from the side or underneath.

52. Inverse lateroventral patches ($n = 6$). The light and dark areas of the lateroventral patches are inverted, creating a much larger dark area. The tonal contrast is reduced by increasing the surface area of the darker lateral band around the ventral mantle margin while leaving six to seven smaller white circles on both sides.

53. Dark ventral mantle ($n = 2$). This component is produced by homogeneously expanding the darker chromatophores on the ventral mantle, creating a solid and continuously dark appearance. Some of the small white circles along the edge of the ventral mantle are the only areas that remain slightly lighter in tone.

Supplementary chromatic condition (1–4, Fig. 2c) – The following four chromatic conditions were identified. These are not independent components; however, they supplement other

chromatic components in describing the total body pattern expression of the animal.

1. Symmetrical lateral divider ($n = 46$). A chromatic condition where two complete body patterns coexist on two sides of the animal, divided by the central axis. This condition seems to be more

apparent when fewer chromatic components are present, i.e., paired mantle spots, triangular wedges, pale mantle, anterior and posterior transverse mantle lines, and black and white dots.

2. Symmetrical lateral divider (ventral) ($n = 15$). A chromatic condition where half of the ventral mantle becomes darker with the expansion of the chromatophores. Although it is not a conventional understanding of countershading where the ventral surface is lighter than the dorsal of an animal, this chromatic condition has been previously described as an example of the countershading reflex of cuttlefish (Ferguson et al. 1994). The dark and light sides are divided along the central axis of the ventral mantle. In some instances, the lateroventral patches are slightly visible.

3. Full asymmetrical shift ($n = 6$). A condition where the anterior and posterior transverse mantle lines (22) are warped asymmetrically toward the anterior mantle edge. This condition does not appear to be created by the arrangement of the chromatophores but rather is brought about by uneven contracting of the skin which distorts body pattern.

4. Partial asymmetrical shift ($n = 17$). This mechanism appears to be similar to the Full asymmetrical shift (3) except that only the posterior transverse mantle line is shifted by unevenly stretching the skin toward the posterior mantle edge, without affecting the anterior side.

Textural components

Three textural components (54–56 Fig. 3) were identified:

54. Smooth skin ($n = 234$) (Packard and Hochberg 1977; Hanlon and Messenger 1988). A smooth texture with a total absence of any textural projections.

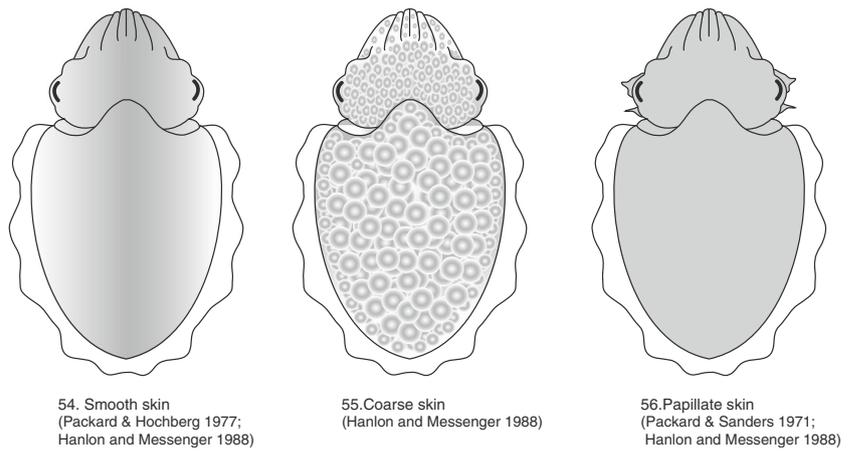
55. Coarse skin ($n = 338$) (Hanlon and Messenger 1988). A homogenous distribution of small projections on the surface of the skin, creating a more matte overall impression.

56. Papillate skin ($n = 77$) (Packard and Sanders 1971; Hanlon and Messenger 1988). A highly textured skin created by papillae (Holmes 1940) that protrude three-dimensionally away from the mantle surface. The papillae are most obviously observed along the mantle margin at the base of the fins. The papillae found on the mantle margin are flattened (Hanlon and Hixon 1980) and triangular shaped when viewed from above and the dorsal mantle papillae (Hanlon and Hixon 1980) are often cone shaped.

Postural components

Sixteen postural components (57–67 Fig. 4): were identified:

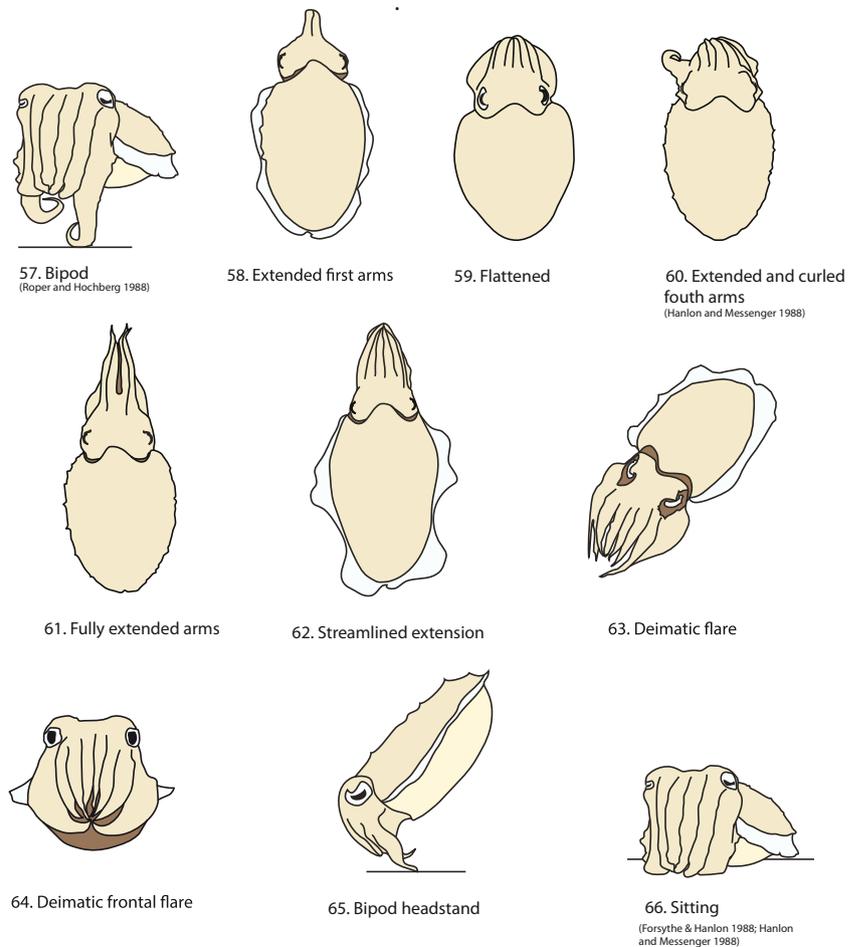
Fig. 3 Diagrammatic representations of textural components of body patterning in the cuttlefish *Sepia pharaonis*



57. Bipod ($n = 5$) (Roper and Hochberg 1988). Arms IV are lowered to touch the substrate while the mantle is hovering parallel to the substrate. Arms I, II, and III can be either spread or together.

58. Extended first arms ($n = 16$). Arms I are extended out very much like the raised arms component only opening up into a V-shape. All of the other arms are tucked closer to the head, making Arms I an isolated forward protrusion.

Fig. 4 Diagrammatic representation of postural components of body patterning in the cuttlefish *Sepia pharaonis*



59. Flattened body ($n = 96$) (Hanlon and Messenger 1988). The entire body is widened to reduce its thickness of the animal. This change in the entire shape of the animal forces the eyes to move from a lateral and frontal position to a more upward position.

60. Extended and curled fourth arms ($n = 40$) (Hanlon and Messenger 1988). One Arm IV is extended outward to the side of the head, often curled up at the tip. This component was expressed in many juveniles and may be a premature form of the interspecific interactions that are described by Hanlon and Messenger (1988).

61. Fully extended arms ($n = 27$). All arms are fully extended forward into an elongate triangular shape. In some instances, the arms appeared to be stretched forward as water extruded from the funnel, making a wave-like movement.

62. Streamlined extension ($n = 23$). While swimming, the animal's body transforms into a hydrodynamic shape. All of the arms are extended forward and together, and the mantle is slightly flattened and elongated.

63. Deimatic flare ($n = 62$). A flattening of the body combined with various other chromatic components such as eye spots, an iridescent mantle stripe, an eye patch, and a yellowish skin tone in response to a potential threat. The animal's head and arm regions are also flattened and widened with exaggerated Arms IV. The pink iridophore stripes are also very prominent.

64. Deimatic frontal flare ($n = 3$). While the animal hovers, Arms IV flare outward to make the animal look bigger. Simultaneously, chromatic components such as dilated pupils with dark eye rings and pink iridophore lines are expressed. In some instances, the animal also quickly reverses the chromatic expression from a Weak deimatic combination (56) to High-contrast frontal striping (59). This component was most often expressed during intraspecific interactions.

65. Bipod headstand ($n = 2$). A variation of Bipod (68), Arms IV are extended and touch the substrate. Using the contact points between the tips of the arms and the substrate as pivot points, the entire body is suspended in the water column at a sharp angle. This component was observed only twice in very small animals that exhibited a very dark chromatic component combination. Thus, it may be a type of masquerade, although this requires further investigation in the future.

66. Sitting ($n = 548$) (Forsythe and Hanlon 1988; Hanlon and Messenger 1988). The animal rests on the substrate without burying itself. In many occasions, anterior mantle of the animal is held up so that the funnel is out of the sediment.

67. Crustacean-like aggressive mimicry ($n = 12$). (Fig. 5) The physical configuration of the arms is very similar to the Flamboyant (Hanlon and Messenger 1988; Okamoto et al. submitted) and bipod (57) displays described previously. However, the posture described here is more similar to actively moving crustaceans rather than passively floating pieces of algae. Arms I are raised vertically with high-contrast stripes that

range in color from red to dark brown. Arms II and III are extended forward with a similar dark stripe pattern. These arms are all bent in a way that resembles crustacean leg joints. Arms IV are spread out and positioned on the sides of the head, much like the pincers of a crab and/or lobster. The mantle is flattened down and almost invisible from the direct frontal view. The bases of Arms IV at the edge of the anterior head bar have distinctive and pulsating dark patches on both sides, similar to a passing cloud. This component was observed specifically during predation, with active side and frontal movement.

Locomotor components

Nine locomotor components (68–76 Fig. 4) were identified:

68. Frontal lift ($n = 38$). The animal raises its head as it moves backward, showing its iridescent ventral mantle.

69. Sideways roll ($n = 34$). The animal hovers sideways as it rotates on its central axis to expose its ventral mantle, particularly the lateroventral patches. This movement was frequently observed when multiple animals were in close proximity to each other.

70. Bottom suction ($n = 24$) (Hanlon and Messenger 1988). Juvenile animals sit on a smooth surface by creating a pocket of space between the external perimeter of their arms and the ventral mantle, which produces a suction cup, allowing them to adhere to the substrate.

71. Deimatic vertical lift and roll ($n = 7$) The animal lifts its head up, body almost perpendicular to the substrate while displaying distinctive deimatic chromatic components in both the mantle and head/arm regions in response to an alarming stimulus from above. Upon lifting its body, the animal swims sideways in a circular motion while maintaining its distance from the potential threat. This component combined with the chromatic expression makes the animal resemble a much larger fish-like animal when seen from the front.

72. Hovering ($n = 465$) (Hanlon and Messenger 1988). The animal maintains a steady position in the water column by using a combination of fin movements, water jetting from the funnel, and the buoyancy of the cuttlebone. It can also rotate its orientation without changing its location.

73. Escape/jetting ($n = 8$) (Hanlon and Messenger 1988). The animal jets water from its funnel to rapidly move backward to avoid predation. The body posture is streamlined, with the arms kept together in a central symmetrical line to create the maximum hydrodynamic position. This component may also occur in combination with various types of inking and a change in color to dark red.

74. Inking ($n = 15$) (Hanlon and Messenger 1988). This is expressed in two forms: pseudomorph where dense ink with a higher mucus content that holds the shape of the ink together in salt water and a less dense puff of ink.

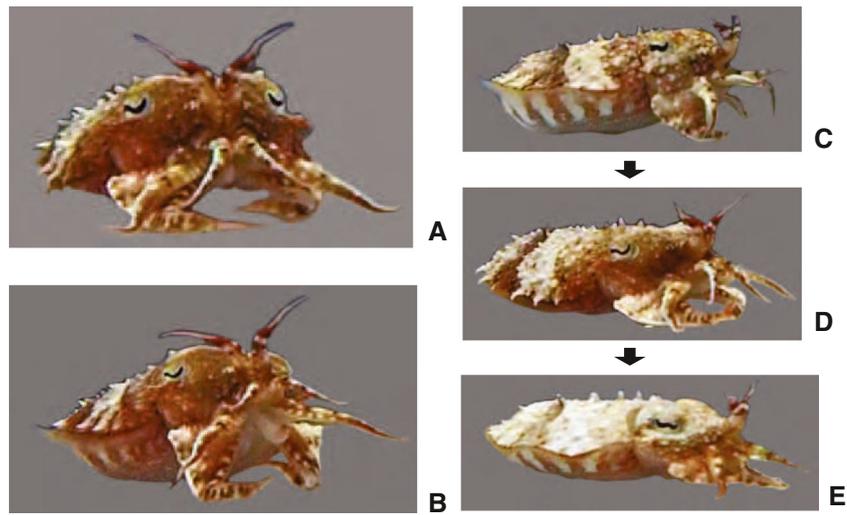


Fig. 5 Diagrammatic representation of postural components of body patterning in the cuttlefish *Sepia pharaonis* in crustacean like aggressive mimicry. **a)** frontal view **b)** 3/4 view, **c)** side view with

thicker mantle profile, **d)** mantle flattening during forward movement, **e)** fully flattened streamlined profile is expressed after fully engaged in hunting

Fig. 6 Diagrammatic representation of postural components of body patterning in the cuttlefish *Sepia pharaonis* during sand-digging behavior

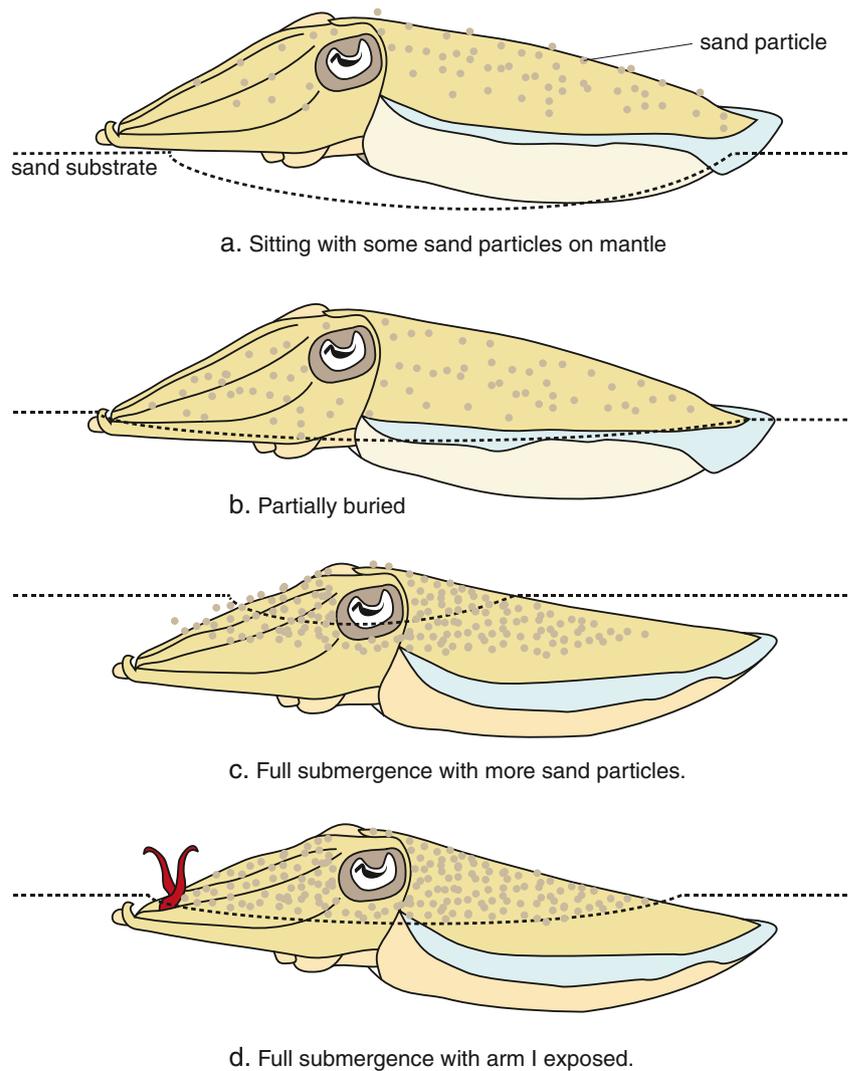
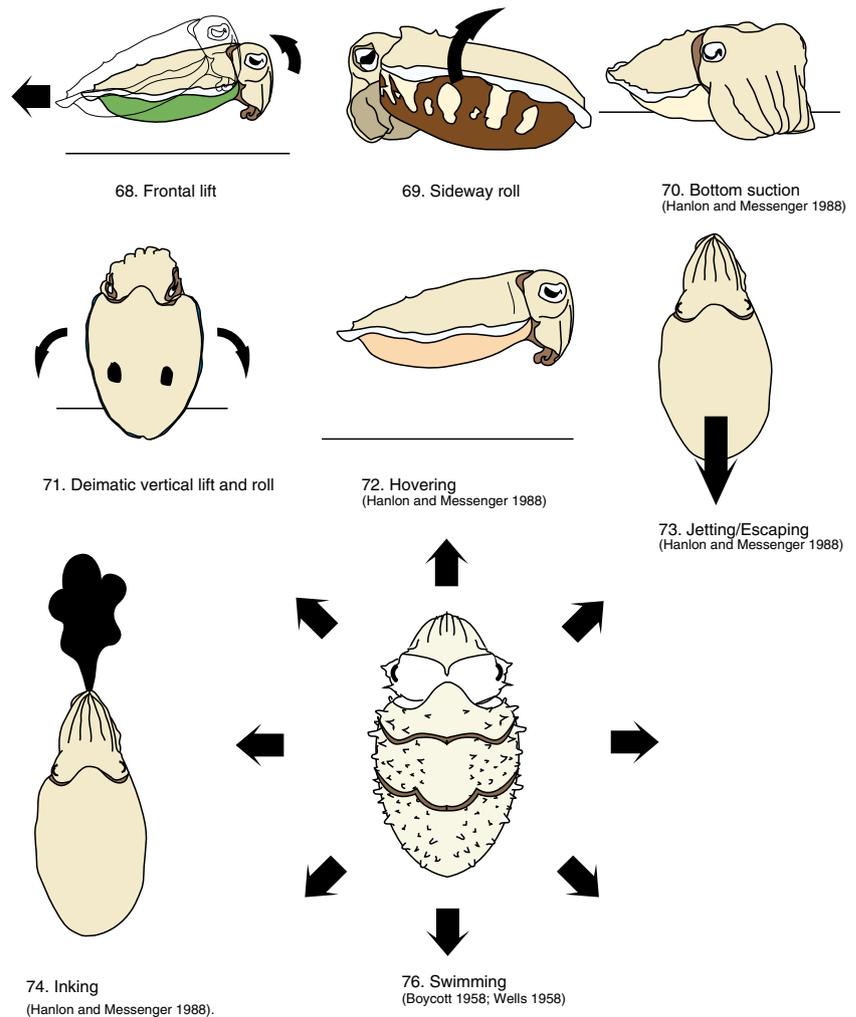


Fig. 7 Diagrammatic representation of locomotor components of body patterning in the cuttlefish *Sepia pharaonis*



75. Sand digging ($n = 173$). (Fig. 6) (Mather 1986; Poirier et al. 2004; Packard and Sanders 1971; Hanlon and Messenger 1988). The animal digs into the sand to bury itself under the substrate. Mather (1986) described this process as three different motor patterns. Sand digging can result in a sitting, partially buried, or fully buried animal. We have observed four different manifestations of this behavior: a) sitting with some sand on its mantle - most of its body is visible from above with some sand particles on its mantle; b) partially buried – much of the mantle is lower than the average substrate height with flattened body (3); c) full submergence with more sand – most of the animal is buried under the substrate and much of its mantle is covered with sand particles; d) full submergence with first arm exposed – posture is the same as c) with its first arm protruding out of the sand. In many cases, the arm pair is red (Figs. 7, 8 and 9).

76. Swimming ($n = 553$) (Boycott 1958; Wells 1958). The animal swims around in the water column and is able to move forward, backward, or to either side without any rapid jetting movement.

Discussion

Sepia pharaonis expressed a remarkable diversity of body patterns, which included 53 chromatic components, 11 postural components, and nine locomotor components and three textural components, which together provide this species with a wide range of behavioral expressions. This diversity is made possible by this species' well-developed central nervous system (Boycott 1961), neurally controlled chromatophore and iridophore organs, and flexible, soft-tissue arm design that lacks a skeletal structure. The number of body-pattern components that was observed in *S. pharaonis* (76) is comparable to the number that has been observed in other shallow water to coastal species: 87 in *Sepia officinalis* (Hanlon and Messenger 1988), 42 in *Sepia papuensis* (Hanlon and Messenger 1996), 39 in *Idiospius pigmaeus* (Moynihan 1985; Hanlon and Messenger 1996), 48 in *Loligo reynaudii* (Hanlon et al. 1994, 2002), and 58 in *Sepioteuthis sepiodea* (Moynihan and Rodaniche 1982) (Table 2). Upon comparison among the species, it appears that benthic *Sepia* species show larger

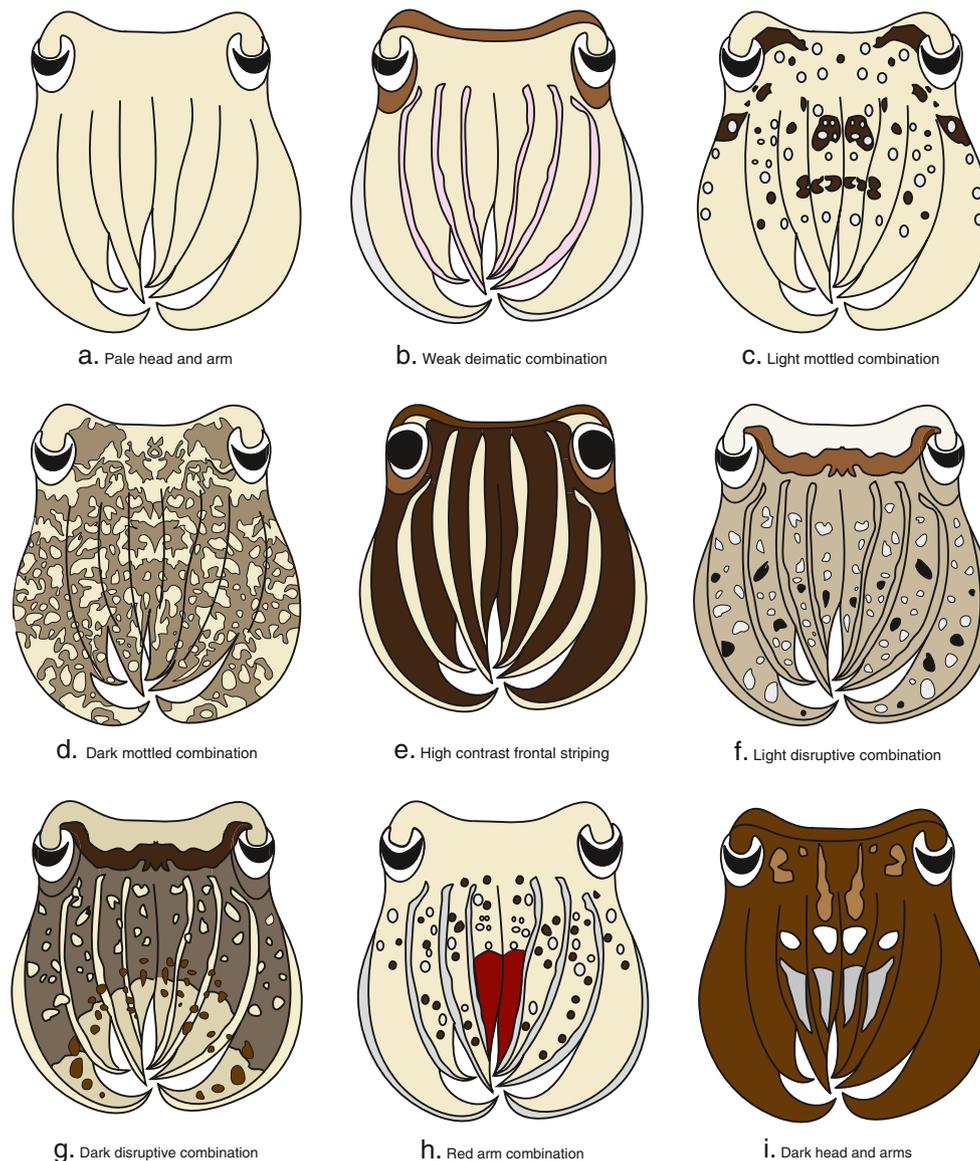
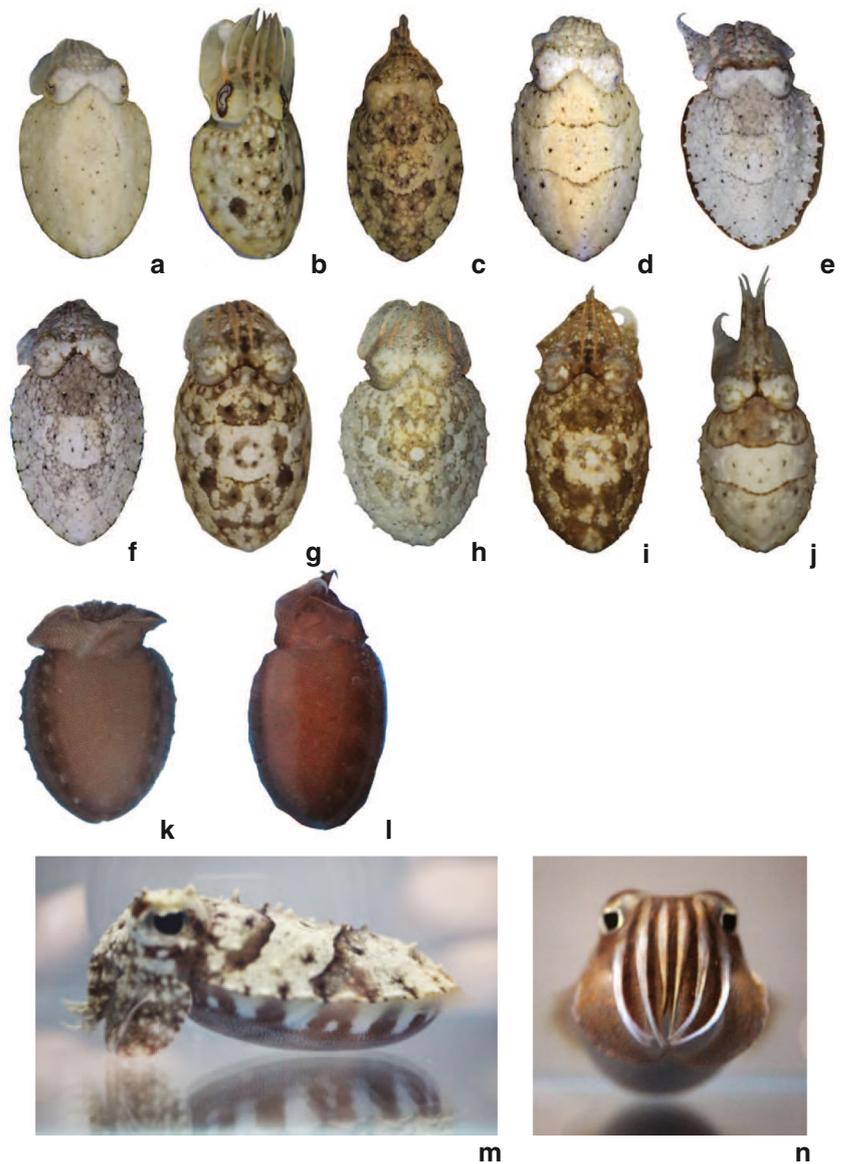


Fig. 8 *Head and arms chromatic combinations*- The head and arm chromatic components are slightly more difficult to observe due to variation in the postural components. However, if the animal stretches itself horizontally, parallel to the substrate surface, its thickness is reduced, and the entire body, head, and arms can be visible simultaneously, allowing easier component detection. **a**) Pale head and arm - The entire head and arm region remains homogeneously pale due to the contraction of the chromatophores. **b**) Weak deimatic combination - Combines the dark posterior head bar (7) and lower eye ring (13) (Hanlon and Messenger 1988) components and also includes white stripes that accent the outer edge of each arm. These three visual elements give a slightly deimatic appearance. **c**) Light mottled combination & **d**) Dark mottled combination. Small dark brown/black (37) and white dots (38) homogeneously and symmetrically distributed across the entire head and arm regions, creating a diverse tonal difference between dark and light mottled appearances. **e**) High-contrast frontal striping A combination of the posterior head bar (7), lower eye ring (13), and dark arms (15) (Hanlon and Messenger 1988), giving a reddish brown to dark brown impression. This is also characterized by a set of large, dilated pupils, and distinctive stripes (16) (the polarization region described by Hanlon and

Messenger 1988) in the middle of each arm, creating extremely high-contrast stripes that are laterally distributed evenly across the entire frontal area. **f**) Light disruptive combination & **g**) Dark disruptive combination - Consists of a white head bar (10), anterior head bar (5), and dark arms (15) and may also include dark dots (37) and white dots (38). The distinctively contrasting tones divide the head into two regions, giving it a disruptive (Hanlon and Messenger 1988, 1996) quality. The dark disruptive combination has the same components as the light disruptive combination only with more highly contrasting tones. The anterior regions of Arms I, II, and III beyond the arm bar may also have a lighter tone, which divides the head and arm regions into three distinctive areas. **h**) Red arm combination - A component that includes red Arm I (17) expression. In some instances, the animal is fully submerged in sand, making it impossible to determine the exact combination of chromatic components for any body part except Arm I. **i**) Dark head and arms - A uniformly dark coloration across the entire head and arms area, with four sets of smaller light patches on Arms I and II, and three sets of lighter brown patches between the anterior (5) and posterior head bar (7). This component appeared with other equally dark components, creating a very dark, rock-like expression. This component was observed in smaller juveniles

Fig. 9 Sample photographs of body patterning in the cuttlefish *Sepia pharaonis*. Each photograph listed contains specified components in numbers corresponding to the other charts. **a)** 1, 9, 10, 37, and 47 and 41; **b)** 1, 13, 16, 20, 33, 37, 38, and 47; **c)** 2, 6, 11, 14, 24, 27, 33, 36, 37, 38, and 47; **d)** 1, 10, 22, and 47; **e)** 1, 7, 11, 16, 37, and 47; **f)** 2, 16, 19, 28, 29, and 36; **g)** 1, 10, 13, 16, 36, 37, 38, and 39; **h)** 3, 16, 19, 24, 27, 29, and 36; **i)** 1, 7, 10, 16, 22, 23, and 37; **j)** 1, 19, 8, 5, 37, 13, and 12; **k)** 52; **l)** 2; **m)** 1, 11, 13, 24, 27, 37, 47, and 53; **n)** 3, 15, and 16



body pattern repertoires than more pelagic species. This may be due to more complex visual environments caused by wide varieties of substrates with which *Sepia* needs to blend. Since comparative data have been collected in situ and may be limited to specific behavioral conditions such as mating behavior, this remains speculative. The function and effect of each individual and/or collective body pattern expression remain undetermined. However, they may function in interspecific interactions, such as hunting prey and avoiding predator detection, and intraspecific interactions, such as mating, agonistic behavior, and species identification. These attributes help increase fitness of the species.

Prior to the present study, the most extensive cephalopod ethogram had been developed for *S. officinalis* (Hanlon and Messenger 1988), which has been the basis of our understanding of the behavioral ecology of the genus *Sepia*, particularly

in terms of the chromatic components. Some of the components described in the present study have been previously described in *S. officinalis*, while others are unique to *S. pharaonis*. In total, 53% of the dorsal mantle chromatic components, 14% of the ventral mantle chromatic components, 56% of the postural components, 100% of the textural components, and 66% of the locomotor components have been observed in both species. By contrast, the following components were observed by Hanlon and Messenger (1988) in *S. officinalis*, but not in the present study: white posterior triangle, white landmark spots, white neck spots, white fin spots, white fin line, paired mantle spots, dark fin line, tri-radial marking, white square papillae, wrinkled first arms, flanged fin, and raised head. Although these two species are not morphologically similar and do not share the same habitat, *S. officinalis*, of the 107 described *Sepia* species, has

Table 2 Comparison of body pattern component among coleoid cephalopods

	Body pattern component					Distribution	Reference
	Chromatic	Textual	Postural	Locomotor	Habitat		
<i>Sepia pharaonis</i>	63	3	13	8	Benthic	Indo Pacific	This study
<i>Sepia officinalis</i>	42	8	13	24	Benthic	Mediterranean	1)–6)
<i>Sepia papuensis</i>	14	12	9	7	Benthic	Indo Pacific	8)
<i>Idiospius pignaeus</i>	17	14	4	4	Benthic	Indo Pacific	9)
<i>Sepioteuthis sepioidea</i>	33	0	13	12	Pelagic	Caribbean	3), 10)–12)
<i>Euprymna scolopes</i>	14	0	7	8	Benthic	Hawai'i	13)–14)
<i>Loligo reynaudii</i>	35	0	4	9	Pelagic	South Africa	15)–16)
<i>Doryteuthis pealeii</i>	32	0	9	12	Pelagic	N. America to S. America	17)
<i>Doryteuthis plei</i>	22	0	13	11	Pelagic	Caribbean to S. America	19)–20)
<i>Lolliguncula brevis</i>	12	0	1	3	Pelagic	N. America to S. America	21)

1) Holmes 1940, 2) Boycott 1958, 3) Hanlon and Messenger 1988, 4) Boal et al. 2004, 5) Adamo and Hanlon 1996, 6) Neill 1971, 7) Mather 1986(b), 8) Roper and Hochberg 1988, 9) Moynihan 1983b, 10) Moynihan and Rodaniche 1982, 11) Boycott 1965, 12) Byrne et al. 2003, 13) Moynihan 1983a, 14) Anderson and Mather 1996, 15) Hanlon et al. 1994, 16) Hanlon et al. 2002, 16) Hanlon et al. 1999, 17) Hanlon et al. 1983, 18) Hanlon 1978, 19) Hanlon 1982, 20) DiMarco and Hanlon 1997, 21) Dubas et al. 1986

the most extensive ethogram. Thus, comparison between these two species provides us with unique visual cues for species identification and may also provide us with a better understanding of the differences and similarities in the behavioral strategies of *Sepia* spp.

In this study, we included chromatic components produced by the iridophores that are green, pink, and blue. In *Sepia officinalis*, visual polarization sensitivity appears to play a role in hunting behavior. Cuttlefish use their polarization sensitive vision to cut through the silvery reflection that helps many finfish species evade their predators (Shashar et al. 1998, 2002), improving their ability to detect prey items in the water column against the lighter water surface. In addition, there is evidence that some cephalopods also use the polarized reflective components produced by the iridophores for intraspecific communication (Shashar et al. 1996; Land and Nilsson 2012; Boal et al. 2004; Mäthger et al. 2006). The polarized light that is produced by cephalopods is not detectable by predators such as sharks and marine mammals, as these are not thought to have polarization sensitive vision. Therefore, cephalopods are able to have a discreet communication channel using visual signaling. More recent studies have demonstrated that such reflective organs are also neurally controlled, indicating that they play an active role in cephalopod body patterns (Wardill et al. 2012) during intra- and interspecific interactions. The components produced by iridophores in *S. pharaonis* may also be important for such interaction.

Three forms of *S. pharaonis* have been recognized: *S. pharaonis* I in the Western Indian Ocean (Red Sea and Arabian Gulf); *S. pharaonis* II from Japan to the Gulf of Thailand and northern Australia; and *S. pharaonis* III in the

Indian Ocean to Andaman Sea (Norman 2000). However, morphological and genetic studies suggest that it is a species complex (Reid et al. 2005), and a more recent phylogenetic study (Anderson et al. 2010) has divided this complex into five clades: western Indian Ocean, northeastern Australia, Persian Gulf/Arabian Sea, western Pacific, and central Indian Ocean clade. That study also suggested that *Sepia ramani* Neethiselvan 2001 is part of this complex (Anderson et al. 2010). These studies clearly indicate the complexity and diversity of this species and demonstrate that more extensive morphological and phylogenetic studies are still required, as well as more comprehensive study of body patterning. However, we hope that this catalog of type II *S. pharaonis* will complement such studies and help with species identification once extensive ethograms have been produced for the other 5–6 morphological/taxonomic groups. Such data are required to further understand the species' distribution and population size, as well as its life cycle and reproductive rate. *Sepia pharaonis* makes up a large percentage of the cuttlefishes that are harvested in the Indian Ocean and southeast Asia region, and so improved species identification will also play an important role in future stock assessments and protection from overfishing.

We believe that this catalog of the chromatic, postural, and locomotor behaviors provides a comprehensive list of the body patterns produced by type II *S. pharaonis*, at least in captivity, which will not only help with species identification, but can also be used as a tool for analytical and quantifiable behavioral studies. Most existing ethograms of cephalopods have been produced from direct observations in their natural habitats. Such natural habitat observations are an effective method for producing ethograms, as there are significant and

abundant external stimuli to trigger behavioral responses in the animals. In addition, *S. pharaonis* reared in an enriched environment exhibited significantly better growth rates and memorization abilities (Dickel et al. 2000; Yasumuro and Ikeda 2016), indicating that the environment in which this species lives alters its physiological condition and behavior. Therefore, animals that are in their natural habitat should be equipped with more complete behavioral repertoires. However, the natural habitat observation method also brings challenges due to the difficulties in making underwater observations, which results in limited access to the animal's behavior, e.g., during the mating season. *Sepia pharaonis* has been reported to live at a depth of 100 m, which requires a remotely operated underwater vehicle (ROV) and other similar devices to observe it in its natural habitat. Therefore, during this study, we observed the body pattern components of *S. pharaonis* in an artificial environment, which resulted in a comparable number of components being recorded as for other shallow coastal species. There are three possible explanations for this similarity: 1. Animals are also able to produce a rich variety of behavioral patterns in an artificial environment; 2. In situ observations that are made under selective conditions, such as during mating, can produce a much larger number of behavioral patterns than other conditions combined; and 3. There is a large overlap in the behavioral patterns recorded in situ and under laboratory conditions. Regardless of which of these is the case, our ethogram should provide a solid foundation and catalog of *S. pharaonis* body patterns that can be built on in the future.

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