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THE *OCTOPUS BIMACULATUS* PROBLEM: A STUDY IN SIBLING SPECIES

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ABSTRACT

The Two-spotted Octopus population of southern California consists of two sympatric, sibling species. *O. bimaculatus* Verrill lays minute eggs (1.8–4.0 mm. long) with long stalks, attached in festoons. *O. bimaculoides* n. sp. lays large eggs (9.5–17.5 mm. long) with relatively shorter stalks, attached in small clusters. *O. bimaculatus* is larger, the arms are relatively longer, the suckers relatively larger, the penis relatively longer and the hectocotylized arm relatively shorter than in *O. bimaculoides.* Other features are essentially alike (jaws, radula, hectocotylus, spermatophores, ocellus, gills, and arrangement of cirri). The juvenile population appears homogeneous, but both species are probably represented in the collection; differentiation of the two species is effected at puberty. In *O. bimaculoides*, puberty is accompanied only by certain changes in the allometric growth rate, as of arm-length from isometry to negative allometry. In *O. bimaculatus* there is a "break" affecting all relationships in which mantle-length is taken as the independent variable; subsequent to the "break" the allometric growth coefficients are the same as in *O. bimaculoides.* The parts of the arm-crown behave as a unit, and growth relationships of arm-width, sucker-diameter and length of hectocotylized arm, in respect to arm-length, are identical in the two species. Secondary differences arise as a result of non-isometric growth rates; thus the length of the hectocotylized arm is negatively allometric and therefore the smaller species, *O. bimaculoides*, has a relatively longer hectocotylized arm. Suckers of juvenile animals are isometric in respect to arm-length; at puberty the specially enlarged suckers on the second and third arms of males continue to grow at the larval rate, whereas the relative growth rate of normal suckers shows an abrupt change to negative allometry. The two species are sympatric but inhabit ecologically different niches: *O. bimaculatus* lives in deeper water, on rocky bottoms, *O. bimaculoides* in shallower water, frequently where rocks rest on a soft bottom. Males of *O. bimaculatus* will not copulate with females of *O. bimaculoides*, and vice versa. *O. bimaculatus* is parasitized by the mesozoan *Dicyemennea abelis* McConn., *O. bimaculoides* by *D. californica* McConn. *D. granularis* McConn. infects both species. Three juvenile specimens infected by *D. abelis* are tentatively referred to *O. bimaculatus.* Large egg-size may be correlated with the elimination of a planktonic larval stage in the species that inhabits shallower tidal water. Both species are recorded from localities between Los Angeles and Ensenada south of the Mexican border; their wider distribution is not known. Verrill's supposed records of *O. bimaculatus* from San Salvador and Panama are erroneous; the specimens belong to an as yet unidentified species. Naef's genus *Paroctopus* cannot be sustained because of the close similarity of the sibling species, which differ primarily in respect to the supposed generic character, egg-size.

INTRODUCTION

During the course of an investigation of the mesozoan parasites of the Cephalopoda of southern California, it was observed by one of us (B. H. M.) that among the La Jolla population of the common Two-spotted Octopus, which has long gone under the name of *Octopus bimaculatus* Verrill, there were some that laid large eggs, 10 mm. or more in length, and others that laid very small ones, only 2–4 mm. in length. The senior author was consulted in regard to the taxonomic situation, and a series of 58 animals, representing both "varieties" and all ages, was sent for examination. The results of a co-operative investigation have brought to light the existence of a cryptic or sibling species which is so similar to the true *O. bimaculatus*, except in respect to egg-size, as to have gone unrecognized until the present time. The taxonomic sections (Parts I and II) have been contributed by the senior author, while data on the ecology, mating behavior and parasite distribution (Part III) have been assembled by the junior author. Much still remains to be studied, especially in the biological field and in respect to the growth of juvenile specimens; moreover, nothing is known as regards the wider distribution of either species, which are sympatric in the regions so far investigated. Since neither author is now working on the coast of southern California, it is to be hoped that other investigators will be stimulated to a further examination of the problem.

PART I. TAXONOMY

The subject matter of this section is restricted to the formal taxonomic description of the species; a comparative study is reserved for Part II.

1. *Octopus bimaculatus* VERRILL, 1883

Specimens studied[1]

(1) B. H. M. No. L-78 (S. C. C. No. 27); gravid female, mantle-length c. 80 mm., 981 g.; Point Loma, Calif., II. 4. 1946, killed VI. 10. 1947.

(2) B. H. M. No. L-74 (S. C. C. No. 23); gravid female, mantle-length c. 66 mm., 987 g.; Scripps Pier, La Jolla, Calif., I. 9. 1947, killed VI. 10. 1947.

(3) B. H. M. No. L-77 (S. C. C. No. 12); gravid female, mantle-length c. 84 mm., 1055 g.; Scripps Pier, La Jolla, Calif., X. 9. 1946, killed VI. 10. 1947.

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[1] Initials are as follows: B. H. M. = Bayard H. McConnaughey; G. E. M. = G. E. MacGinitie; H. S. = Horace W. Stunkard; S. C. C. = Sheldon C. Crane.

Unless otherwise stated, the mantle-length is that of the preserved animal, the weight is always that of the fresh specimen before dissection and preservation.

Numbers assigned in this and the following lists do not correspond to the numbers in the senior author's register, in which the two species are confused.

(4) B. H. M. No. L-69 (S. C. C. No. 29); gravid female, mantle-length c. 84 mm., 620 g.,; Scripps Pier, La Jolla, Calif., IV. 28. 1947, died V. 11. 1947 by escaping from tank.

(5) San Clemente I., Calif., B. W. Walker and C. Hubbs coll., I. 4. 1947; sexually immature female, mantle-length 56 mm.

(6) B. H. M. No. L-127 (S. C. C. No. 44); gravid female, mantle-length 98 mm., 848 g.; Devil's Slide, La Jolla, Calif., XII. 26. 1947, preserved IV. 22. 1948; laid eggs in aquarium.

(7) B. H. M. No. L-128 (S. C. C. No. 45); gravid female, mantle-length c. 97 mm., 903 g.; Scripps Point, La Jolla, Calif., II. 20. 1948, killed IV. 22. 1948.

(8) B. H. M. No. L-124 (H. S. No. C); gravid female, mantle-length c. 120 mm., 739 g.; Devil's Slide, La Jolla, Calif., III. 4. 1948, died III. 26. 1948 due to failure of aeration.

(9) S. C. C. No. 48; sexually immature female, mantle-length 63 mm.; Scripps Point, La Jolla, Calif., II. 20. 1948, died II. 25. 1948.

(10) B. H. M. No. L-130 (S. C. C. No. 47); gravid female, mantle-length 78 mm., 422 g.; Scripps Point, La Jolla, Calif., II. 20. 1948, killed IV. 22. 1948.

(11) B. H. M. No. L-114 (S. C. C. No. 37); sexually immature female, mantle-length 61 mm., 504 g.; Scripps Pier, La Jolla, Calif., X. 10. 1947, killed II. 24. 1948.

(12) B. H. M. No. L-129 (S. C. C. No. 46); sexually immature female, mantle-length 68 mm., 364 g.; Scripps Point, La Jolla, Calif., II. 20. 1948, killed IV. 22. 1948.

(13) B. H. M. No. L-79; sexually immature female, mantle-length 35 mm., 39 g.; Devil's Slide, La Jolla, Calif., VI. 22. 1947.

(14) B. H. M. no number; sexually immature female, mantle-length 42 mm.; Devil's Slide, La Jolla, Calif., V. 29. 1948.

(15) Peabody Museum, Yale Univ., No. 10269; sexually immature female, mantle-length 53 mm.; San Diego, Calif., Dr. Edw. Palmer, 1875.

12.GP17712 (16) Peabody Museum, Yale Univ., COTYPE; mature male, mantle-length 75 mm.; San Diego, Calif., D. S. Jordan; purch. Yale Univ., May 1894.

(17) B. H. M. No. L-76 (S. C. C. No. 28); mature male, mantle-length 83 mm., 638 g.; La Jolla Cove, Calif., II. 23. 1947, killed VI. 10. 1947.

(18) B. H. M. No. L-16 (S. C. C. No. 13); mature male, mantle-length c. 100 mm., 817 g.; La Jolla, Calif., X. 19. 1946, died X. 29. 1946.

(19) B. H. M. No. L-75 (S. C. C. No. 24); mature male, mantle-length c. 90 mm., 804 g.; Scripps Pier, La Jolla, Calif., I. 13. 1947, killed VI. 10. 1947.

(20) B. H. M. No. L-81; mature male, mantle-length 48 mm., 126 g.; Devil's Slide, La Jolla, Calif., VI. 22. 1947, died VII. 9. 1947 by escaping from tank.

(21) B. H. M. No. L-118 (S. C. C. No. 43); mature male, mantle-length 72 mm. (77 mm. when fresh), 552 g.; Scripps Pier, La Jolla, Calif., X. 17. 1947, killed II. 24. 1948.

(22) B. H. M. No. L-113 (S. C. C. No. 36); mature male, mantle-length 59 mm., 329 g.; Scripps Pier, La Jolla, Calif., X. 1. 1947, killed II. 24. 1948.

(23) B. H. M. No. L-116 (S. C. C. No. 41); mature male, too damaged to measure, mantle-length 55 mm. when fresh, 229 g.; Scripps Point, La Jolla, Calif., X. 14. 1947, killed II. 24. 1948.

(24) B. H. M. No. L-131 (S. C. C. No. 49); mature male, too damaged to measure, mantle-length 57 mm. when fresh, 265 g.; Scripps Point, La Jolla, Calif., II. 20. 1948, killed IV. 22. 1948.

(25) B. H. M. No. L-115 (S. C. C. No. 40); mature male, mantle-length 55 mm., 263 g.; Scripps Point, La Jolla, Calif., X. 14. 1947, killed II. 24. 1948.

(26) B. H. M. No. L-117 (S. C. C. No. 42); mature male, mantle-length 54 mm. (same when fresh), 204 g.; Scripps Point, La Jolla, Calif., X. 14. 1947, killed II. 24. 1948.

Clutches of eggs (unaccompanied by specimens)

(1) B. H. M.; small eggs "recently laid in our aquarium," preserved VI. 10. 1947; La Jolla, Calif. Two festoons, c. 45 and 25 mm. long with c. 120 and 50 eggs respectively; many of the eggs appear dead (empty) or unfertilized.

(2) B. H. M.; small eggs "laid by one of the octopuses on exhibit in the public aquarium, date unknown. Collected early in July when it appeared the female was eating them." Five broken festoons of which three are abnormal in appearance, with slender, narrow eggs. La Jolla, Calif., VII. 1947.

(3) G. E. M.; bunch of small eggs with advanced embryos, species not known; Anaheim Slough, Calif., VI. 1933. Two festoons attached to the same base, 40 and 55 mm. long and estimated to contain c. 200 and c. 300 eggs respectively.

O. bimaculatus was rather fully described by the earlier investigators (Verrill, 1883; Berry, 1911, 1912) and their accounts have been analyzed and synthesized by Robson (1929). However, in view of the discovery of the sibling species, it has become necessary to re-examine the original descriptions in order to determine whether one or both were included.

a) *Verrill's Specimens.* Verrill's original description is based on two mature males (COTYPES), an immature female, and a series of small specimens that do not belong to this species. His discussion shows that he was well aware of the variations in skin character, development of cirri, and coloration, that may result from different effects of preservation. The internal anatomy is not described, nor are the jaws, radula, penis and spermatophores. The larger of the two males is in the U. S. National Museum and has not been re-examined in the present investigation; the smaller male and the young female are in the collections of the Peabody Museum of Yale University and have been subjected to a careful re-examination. The small specimens, collected by Bradley from San Salvador and Panama, are also in the Peabody Museum, but it is practically certain that none of them belong to the *Octopus bimaculatus* complex. The ocellus is now so badly faded that it often cannot be seen and, although it appears to have a pale center, this may well be the result of fading. One of the largest of the series is a small male, 19 mm. mantle-length, that is sexually mature and has a relatively long ligula; the existence of this as yet undescribed small ocellate species has been noted in a previous publication (Pickford, 1945: 747) and the subject is reserved for a later contribution.

On the other hand, there can be no doubt that Verrill's three larger animals belong to the long-armed, small-egg species, to which the name *O. bimaculatus* is therefore correctly applied. In evaluating the material, the following points may be noted. (1) In the male and female examined, the ocellus has an inner ring, overlooked by Verrill, which has evidently become more conspicuous with time due to the fading of the surrounding dark areas. The specimens themselves are now almost completely pallid. (2) The ligula of the hectocotylus has a calamus, clearly shown in Verrill's figure, which *may* have been taken from the Peabody Museum COTYPE; however, the calamus is situated slightly beyond the middle, not one-third from the base, and hence both Verrill's figure (Pl. V, fig. 1a) and Robson's transcription of it (1929: Fig. 13*b*) are erroneous. (3) Verrill's figure (Pl. VI) of the oral face of the web was certainly taken from the Peabody Museum COTYPE. (4) All measurements are now a little different, and in general smaller, than those given by Verrill; evidently the specimens have shrunk through long preservation in alcohol. The original arm-length indices cannot be calculated, because Verrill did not give total length; however, his "length of body" is probably equivalent to mantle-length, since, for the previous species in his article (*"Octopus punctatus* Gabb"), he explicitly states that it is "Length of body to eye." On this assumption the mantle-length index of the U. S. N. M. COTYPE was originally 12.7, that of the Peabody Museum COTYPE 23.3. The latter figure is more typical of the *bimaculatus* arm-length (average mantle-arm index, 23) than the present value of 27.3, which is rather high. Evidently both COTYPES belong to the long-armed species.

Present measurements of the Peabody Museum male are as follows: mantle-length, 75 mm.; total length, 345 mm.; mantle-width, 56 mm.; head-width, 41 mm. First left arm, 257 mm.; second left, 250 mm.; third left, 275 mm.; fourth left and first right arms, regenerating tip; second right, 275 mm.; hectocotylized third right, 250 mm.; fourth right, 275 mm. Sector A of web, 49 mm.; left B, 55 mm.; left C, 63 mm.; left D, 58 mm.; right B, 62 mm.; right C, 77 mm.; right D, 60 mm.; E sector, 51 mm. Greatest arm-width, 17.5 mm. Diameter of largest normal sucker, 12 mm.; diameter of largest special sucker, 20 mm. Length of ligula, 2.9 mm.; length of calamus, 1.8 mm. Penis-length, 17 mm.

The immature female need not be described in detail. She has a mantle-length of 53 mm. and a mantle-arm index of 24.7. The ovary contains minute ova.

The spermatophores of the Peabody Museum COTYPE, which proved to be very interesting, are moderately well preserved. They are of two sorts, long-headed and short-headed, but the latter are in the great majority. Measurements and indices of two typical spermatophores of each type are given in Table III. Thirty-nine out of 43

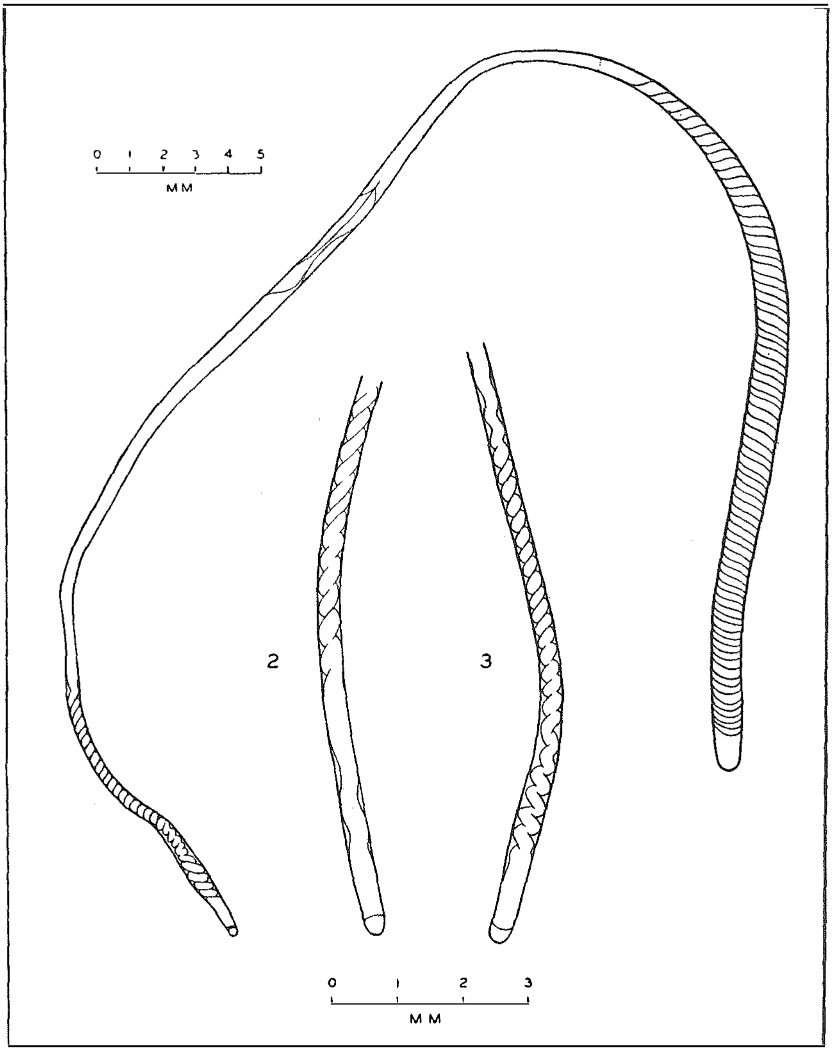

Figure **1**. *Octopus bimaculatus* Verrill, Cotype. Complete spermatophore, short-headed type; the state of preservation did not permit details of sac and middle piece. **2**. Head of a long-headed spermatophore from Cotype. **3**. Head of a short-headed spermatophore, showing reversal of spiral, from Cotype.

spermatophores examined had short heads. The short head, about 1.4 mm. in length, is correlated with (1) a swelling of various size at the beginning of the spiral (Figs. 1 and 3), probably an artifact of preservation, and (2) a very tightly coiled and short spiral. Furthermore, the first four or five turns of the spiral are always sinistral, the remainder dextral. The length of the head in the four long-headed spermatophores varies from 3.1–5.8 mm.; the spiral is less tightly coiled at the beginning and there is no swelling. The direction of the spiral is dextral throughout. In other words, the first four or five sinistral turns are lacking in the long-headed spermatophores, and the corresponding region is either straight or marked by an exceedingly wide open turn of the spiral (Fig. 2) which, even when present, is dextral. It might reasonably be argued that the condition in the long-headed spermatophores is abnormal and results from partial uncoiling or deterioration, a very common situation in preserved material. However, if a certain number of turns of the spiral had become uncoiled one would expect that the total number would be correspondingly less. The range and *mean* for eleven short-headed spermatophores is 25–*27.8*–33; the range and *mean* for the four long-headed spermatophores is 28–*30.3*–33. From this we must conclude that the long-headed spermatophores tend to have more rather than fewer turns of the spiral, contrary to what would be expected if the condition were the result of uncoiling. This fact, taken in conjunction with the absence of a proximal region of sinistral coiling, indicates quite clearly that two sorts of spermatophores are present. The bearing of this on the more general problem of spermatophore variations in the sibling species is reserved for subsequent treatment.

b) *Berry's Specimens.* These are described in two papers by Berry (1911 and 1912), but they have not been re-examined in the present investigation. However, certain conclusions may be drawn from the published data. In his first paper Berry states that *O. bimaculatus* is the common octopus of the coast of southern California and that it is easily recognized by the "exceeding minuteness" of the ligula and by the ocellus which he quite correctly notes is not unicolored throughout but which shows "a narrow, well-defined, bluish ring enclosing a blackish center and surrounded by a wider outer border of similar hue." In his second paper Berry figures the ligula (1912: Pl. XXXV, Fig. 2); the calamus is clearly shown though hidden in a rather deep groove formed by the marginal cheeks which were evidently strongly contracted. Apparently Robson did not notice the calamus; he does not show it in his copy of Berry's figure (Robson, 1929: Fig. 13*a*), and in a footnote he states that it is absent. Berry also notes the presence of 3–5 transverse grooves, present in all specimens.

The jaws are figured in side view, but no description and no measurements are given. From the figure (1912: Pl. XXXIX, Fig. 5) the rostral-length index for the upper jaw is estimated to be 30.3. One cannot see whether the beak of the lower jaw is pointed or emarginate, but it looks rounded in profile and was probably truncate or emarginate.

Berry describes the arrangement of the cirri very fully and his account is in good agreement with Verrill's observations and our own. He notes that they are more prominent in young specimens. The ocellus is again described as having a bluish ring.

Measurements are given for five specimens, two females, two males and a juvenile. Unfortunately mantle-length is not given in the usual form and his measurement "Tip of body to base of dorsal arms" cannot be interpreted in terms of mantle-length. However, the arm-length index may be calculated from the total length, as follows: females, 87, 80; males, 72, 67; immature, 71. It is quite obvious that the two females belong to the long-armed species; on the other hand, the two males are probably *bimaculoides*, and this is quite in accordance with their smaller absolute size (total length, 178 and 225 mm. respectively). The status of the young animal is uncertain.

The following localities are given by Berry: White's Point, San Pedro, La Jolla and San Diego. It is reasonably certain that he did not confuse this species-complex with Verrill's small ocellate species from San Salvador and Panama because of his careful attention to the minute ligula.

c) *Additional Observations.* The range and *mean* for all the more important characteristics of this species are summarized in Table VIII and discussed in connection with the detailed comparison of *O. bimaculatus* and *O. bimaculoides* (Part II). In this section attention will be paid only to certain characters not treated in the comparative discussion. The jaws and radulae of three specimens were examined, an adult female (No. 1), an adult male (No. 17), and an immature female (No. 14). The jaw-lengths are 22.0, 19.0 and 8.6 mm.; the rostral-length indices are 36.4, 38.4, and 44.2. The form of the jaws is quite similar to that of *bimaculoides* (*q.v.*); in particular, the beak of the lower jaw is similarly emarginate. In the adult female the emargination is actually nicked, the injury evidently being due to biting some hard object. The radula is also quite similar to that of *bimaculoides;* the rhachidian has an asymmetrical seriation, predominantly B 6 or 7 in the two adults, B 5 or 6 in the young animal. The only previous description of the radula of this species is that of Stuart (1941) who presented her observations in the form of a tabular comparison with that of *O. cyanea* Gray and a newly described species, *O. roosevelti.* She states that she examined a number of specimens of *bimaculatus* in the collection of the Allan Hancock Foundation, but her observations suggest that the description must have been based upon a study of the old, worn part of the radula. It is otherwise difficult to account for the extraordinary difference between her account and the present observations. The rhachidian is said to have a low main cusp and a broad base which is nearly twice the height of the main cusp, and occasionally a tooth in the series is said to have a minute cusp on the outer edge. The absence of ectocones is a most unusual feature in the Octopodinae and in any case should have been viewed with suspicion. It is certainly not the typical conditions in *bimaculatus.* Stuart also states that she observed a minor cusp on the second lateral; this was not found on specimens studied in the present investigation.

Ovarian eggs in a fully ripe condition, ready to be spawned, were obtained from four animals. In addition there are two clutches of eggs that were certainly laid by this species, but neither contains advanced embryos. A third clutch is listed but is not definitely known to belong to *bimaculatus.* The eggs are quite small, ranging from 2.1–3.8 mm. in *mean* length (Table I). Egg-length is not apparently a function of the size of the animal (Table II), but the data are inadequate. On the other hand, egg-width is definitely a function of egg-length; longer eggs are relatively more slender, as shown by the egg-width index also listed in Table II. The length of the egg-stalk is extremely variable (Figs. 6 and 7), even in eggs from the same animal, since it ranges from half to twice the length of the egg itself; the *mean* length varies from 1.9–4.6 mm. and really short stalked eggs are the exception rather than the rule. The length of the stalk is reflected in the manner in which the eggs are attached, woven together in long festoons as in *O. vulgaris* Lam. They are not at-

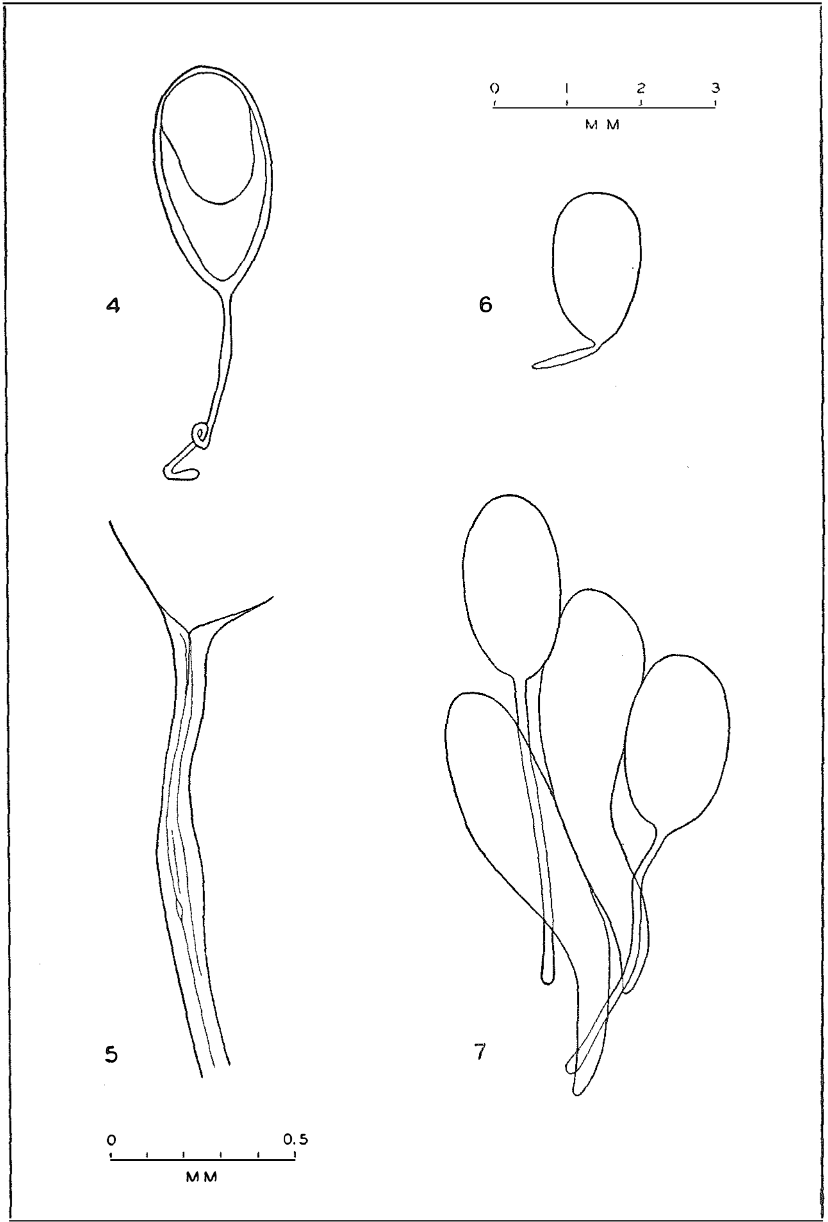

Figure 4. *Octopus bimaculatus* Verrill. Isolated egg from Clutch No. (1), early developmental stage with yolk mass. Stalk is unusual, showing swelling near junction with egg. **5.** Details of swelling on stalk. **6.** Ripe ovarian egg from specimen No. (3), showing an unusually short stalk and also a constriction at the junction of stalk with egg capsule which was present in some eggs of this specimen. **7.** Group of four ovarian eggs from specimen No. (7); two ripe and two unripe; note change in shape.

TABLE I. *Octopus bimaculatus* VERRILL. MEASUREMENTS OF EGGS, INCLUDING OVARIAN EGGS WHICH APPEARED TO BE FULLY RIPE; ONLY THE TWO CLUTCHES KNOWN TO HAVE BEEN LAID BY FEMALES OF THIS SPECIES HAVE BEEN STUDIED. FIGURES REPRESENT MINIMUM AND MAXIMUM RANGE AND MEAN (ITALICS).

Specimen No.	*Material*	*E. L.**	*E. W. I.**	*E. S.**
(1)	Ripe ovarian eggs; 10 measured, all with stalks	2.4–*2.6*–2.8	43–*47*–50	1.7–*3.7*–5.5
(3)	Ripe ovarian eggs; 10 measured, all with stalks	1.8–*2.1*–2.3	48–*55*–67	1.0–*1.9*–2.6
(4)	Ripe ovarian eggs; 10 measured, all with stalks	3.5–*3.8*–4.0	35–*36*–40	3.7–*4.6*–5.2
(7)	Ripe ovarian eggs; 9 measured, all with stalks	2.4–*2.5*–2.7	49–*51*–49	2.3–*3.4*–4.1
Clutch (1)	10 eggs measured, only 4 with perfect stalks; early stage	2.7–*3.0*–3.1	45–*48*–52	2.7–*3.5*–4.2
Clutch (2)	10 eggs from normal festoons, none with stalks; early stage or unfertilized	2.5–*2.6*–2.9	45–*52*–57	—
Clutch (2)	10 eggs from abnormal festoon, one with stalk; unfertilized or unripe (?)	2.5–*3.1*–3.8	28–*38*–49	3.4

* E. L. = Egg-length, excluding stalk, in mm.
E. W. I. = Egg-width index: Egg-width x 100/Egg-length.
E. S. = Stalk-length in mm.

TABLE II. *Octopus bimaculatus* VERRILL. COMPARISON OF MANTLE-LENGTH, EGG-LENGTH AND EGG-WIDTH INDEX. DATA FROM TABLE I; MEAN VALUES FOR E. L. AND E. W. I.

Spec. No.	*M. L.*	*E. L.*	*E. W. I.*
(1)	80	2.6	47
(2)	66	2.1	55
(6)	98	3.8	36
(7)	97	2.5	51

tached singly, as in *O. joubini* Robson of the Gulf Coast, nor even in small clusters as in *O. bimaculoides*. In one case there was a small dilation along the course of the egg-stalk, proximal to the egg (Figs. 4 and 5), similar to the little "float" described by Robson (1932) from the eggs of an unidentified species of *Octopus* from Florida. This condition is quite unusual.

Characteristics of the spermatophores of eleven specimens are given in Table III. It will be seen that there is great variation. It was only in the COTYPE that two different types were encountered; other specimens show greater uniformity. But some have short heads and others have long heads; some have only dextral or, in one case, only sinistral coiling of the spiral; others show alternation. The fundamental pattern is always the same and similar to that of *bimaculoides.*

TABLE III. *Octopus bimaculatus* VERRILL. SPERMATOPHORE CHARACTERISTICS. HORN-LENGTH OMITTED ON ACCOUNT OF VARIATION DUE TO PARTIAL UNCOILING. UNLESS OTHERWISE INDICATED, ONLY ONE SPERMATOPHORE HAS BEEN MEASURED.

Spec. No.	*Sp.L.*	*Sp.L.I.*	*Sp.R.I.*	*Sac I.*	*D.Ej.I.*	*Hd.I.*	*Ho.Coils*	*Spiral*
(16)*	53.0	71	55	33	0.78	11.0	30	D
COTYPE	53.5	71	51	33	0.69	8.8	30	D
	53.0	71	42	25	0.70	2.6	27	4–5S,D
	53.5	71	43	24	0.79	2.6	c 27	4–5S,D
(17)	45.0	54	29	38	0.56	3.3–4.2	29–*30*–34†	4S,D
(18)	34.0	34	31	59	0.78	1.4–1.7	30–*36*–40†	D
(19)‡	47.0	52	28	38	0.64	3.9	30	D
	45.0	50	29	39	0.66	3.7	31	D
(20)	21.0	44	34	48	0.81	8.1	? 17	S
	21.5	44	35	40	0.86	6.2	c 20	S
(21)	42.0	58	36	49	0.64	3.3	26, 30, 31	D
(22)	38.0	64	37	37	0.53	4.0	35–36	alt. S,D
(23)	c 35.0	(64)	34	47	0.57	4.9	31–35	D
(24)	37.0	65	32	46	0.51	6.5	25–27	D
(25)	36.0	65	31	47	0.56	5.8	33	D
(26)	36.0	67	36	50	0.56	3.9	34–35	S, D

Definitions of these measurements and indices are given by Pickford (1945, 1946).
Sp.L. = Spermatophore-length
Sp.L.I. = Spermatophore-length index
Sp.R.I. = Sperm-reservoir index
Sac I. = Sac-length index
D.Ej.I. = Index of the diameter of the ejaculatory region
Hd.I. = Head-length index
Ho.Coils = Number of turns of spiral
Spiral: D = dextral, S = sinistral

*See text for further data and discussion of differences between the long- and short-headed spermatophores of this specimen.
† Range and mean for five spermatophores.
‡ Three others have 30, 31 and 31 horn coils.

2. *Octopus bimaculoides* N. SP.

Specimens studied[2]

(1) B. H. M. No. L-149 (H. S. No. L); gravid female, mantle-length 65 mm., 218 g.; Point Loma, Calif., given to H. S. VI. 14. 1948, died VIII. 23. 1948.

(2) B. H. M. no number; Devil's Slide, La Jolla, Calif., V. 29. 1948; brooding female taken with eggs under rock, mantle-length 39 mm. HOLOTYPE.

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[2] See Footnote 1.

(3) B. H. M. No. L-123 (H. S. No. B); nearly-gravid female, mantle-length 60 mm., 172 g.; Devil's Slide, La Jolla, Calif., III. 4. 1948, killed III. 12. 1948.

(4) B. H. M. No. L-125 (H. S. No. D); gravid female, mantle-length c. 67 mm., 135 g.; Devil's Slide, La Jolla, Calif., III. 20. 1948, died IV. 10. 1948 due to failure of aeration.

(5) B. H. M. no number; gravid female, mantle-length 60 mm.; Devil's Slide, La Jolla, Calif., about first week VI. 1947, died VIII. 6. 1947, very flaccid.

(6) B. H. M. No. L-72; gravid female, mantle-length not measureable owing to damaged condition, 55 g.; Devil's Slide, La Jolla, Calif., III. 15. 1947, killed V. 31. 1947; in two pieces.

(7) B. H. M. no number; mature male, mantle-length 60 mm.; Devil's Slide, La Jolla, Calif., VIII. 6. 1948, preserved VIII. 16. 1948.

(8) B. H. M. no number; mature male, mantle-length 52 mm.; Devil's Slide, La Jolla, Calif., VIII. 6. 1948, preserved VIII. 16. 1948.

(9) B. H. M. no number; mature male, mantle-length 43 mm.; Devil's Slide, La Jolla, Calif., V. 29. 1948, preserved VI. 23. 1948. ANDROTYPE.

(10) B. H. M. No. L-134A; mature male, mantle-length 39 mm.; Devil's Slide, La Jolla, Calif., III. 20. 1948, died VI. 23. 1948; tapeworm pleurocercoids in mantle chamber.

(11) B. H. M. No. L-71; mature male, mantle-length 50 mm., 85 g.; Devil's Slide, La Jolla, Calif., V. 23. 1947, died V. 28. 1947 by escaping from tank.

(12) B. H. M. No. L-132 (H. S. No. G); immature female, mantle-length 38 mm., 49 g.; Devil's Slide, La Jolla, Calif., III. 20. 1948, died IV. 25. 1948. By an oversight this specimen was not included in the calculations of indices and regression coefficients.

Clutches of eggs (unaccompanied by specimens)

(1) B. H. M.; large eggs, Devil's Slide, La Jolla, Calif., VI. 10. 1947; one cluster of eight eggs, four of which are broken or empty; early stage of development.

(2) G. E. M.; large eggs, Corona del Mar, Calif., no date; one bunch of 35 eggs and two separate eggs of same clutch; half-grown embryos; alcohol.

(3) G. E. M.; large eggs, Corona del Mar, Calif., no date; three clusters with 3, 9, and 15 eggs respectively; one egg dissected free with complete stalk; early stage of development; alcohol.

(4) G. E. M.; large eggs, Corona del Mar, Calif., no date; one cluster of 16 eggs and 3 separate eggs of same clutch, advanced embryos with yellow yolk sacs; alcohol.

(5) G. E. M.; large eggs, Corona del Mar, Calif., no date; one cluster of 24 eggs and 5 separate eggs of same clutch; advanced embryos with brown yolk sacs, near hatching; alcohol. Newly hatched embryos probably belong to this or to the previous clutch (all were together in one jar).

(6) G. E. M.; large eggs, Corona del Mar, Calif.; collected I. 24. 1948, preserved V. 7. 1948 after 15 weeks of incubation; three clusters, of which two had 8 and one had 12 eggs (two removed), and a number of loose eggs with broken stalks; eggs contain advanced embryos; sea water formalin.

Description of HOLOTYPE. The specimen here designated as the HOLOTYPE, NO. 2, is a sexually mature female that was taken with a clutch of eggs under a rock at Devil's Slide, La Jolla by one of us (B. H. M.) on May 29, 1948. The general color, after preservation in sea water formalin, is dark grey above and paler brownish grey below as well as on the oral face of the web. The ocellus, very dark grey, is 4–5 mm. in diameter but of a slightly irregular shape (Fig. 21); it encloses a slightly depressed and rather inconspicuous dark inner ring, about 3 mm. in diameter, and is surrounded by a poorly defined paler area. The center is dark grey. The surface of the skin is finely granular all over, even on the oral face of the web, but it is somewhat more coarsely so on the dorsal surface of head and mantle. The most conspicuous cirri are arranged as follows. (1) A prominent pair of supraocular cirri situated above the hind angle of the eye; (2) three median dorsal mantle cirri disposed as follows: one just behind the neck region that may be designated as the nuchal, one close to the apex of the body, and one intermediate in position; (3) two pairs of dorsolateral mantle cirri alternating in position with the medians. The anterior pair of laterals form a diamond-shaped pattern with the nuchal and intermediate median; the posterior pair form a similar figure with the intermediate and apical median.

Standard measurements of this specimen are as follows: mantle-length, 39 mm.; total length, 150 mm.; mantle-width, 29.5 mm.; head-width, 23 mm. First left arm, 95 mm.; second left, 106 mm.; third left, 117 mm.; fourth left, 100 mm.; first right, regenerating; second right, 114 mm.; third right, 118 mm.; fourth right, 105 mm. Sector A of web, 19.5 mm.; left B, 24.5 mm.; left C, 28 mm.; left D, 20.5 mm.; right B, 24 mm.; right C, 30 mm.; right D, 24.5 mm.; E sector, 16 mm. Greatest arm-width, 10 mm. There are no specially enlarged suckers in the HOLOTYPE nor in any of the females studied; the diameter of the largest sucker, which appears to be somewhat contracted, is 4.5 mm.

The funnel is 15 mm. long (funnel index 38.5); the free projecting part is 10 mm. The funnel organ is W-shaped, with the lateral limbs slightly shorter than the median; the median limbs are closely approximated, separated only by a line which almost divides them apically into the V V form of the organ. Previous investigators have often attached considerable taxonomic importance to the form of the octopodan funnel organ, but in the experience of the senior author it is a difficult and unreliable character, often rubbed or weakly developed and hard to study.

The gills are 10 mm. in length; there are eight primary lamellae in each demibranch which, with the small terminal lamella, makes a total of 17. A pair of anal appendages is present. The ink sac is largely embedded in the substance of the liver; a part of its ventral wall comes to the surface and is exposed under the liver capsule.

The jaws are shown in Figs. 10 and 11. The upper jaw is 8.5 mm. long, the rostrum 2.9 mm. (rostral-length index 34.1). The beak of the lower jaw is rather peculiar in that it is emarginate rather than pointed at its apex. A similar condition is seen in the ANDROTYPE, and in *O. bimaculatus* (q. v.). Published figures of octopodan jaws almost invariably show the mandibles in side view, and therefore we are unable to say whether the condition observed here occurs in other species not studied at first hand. In those species with which the senior author is familiar the beak of the lower jaw is pointed, like that of the upper. A part of the radula is shown in Fig. 8; the lateral teeth call for no special comment; the rhachidian is asymmetrical (type B of Robson), the seriation is such that every sixth, seventh or eighth tooth repeats itself as illustrated in the figure.

The ovary is almost completely spawned out, although one ripe egg is still lodged in the ovisac. The young developing ova of the

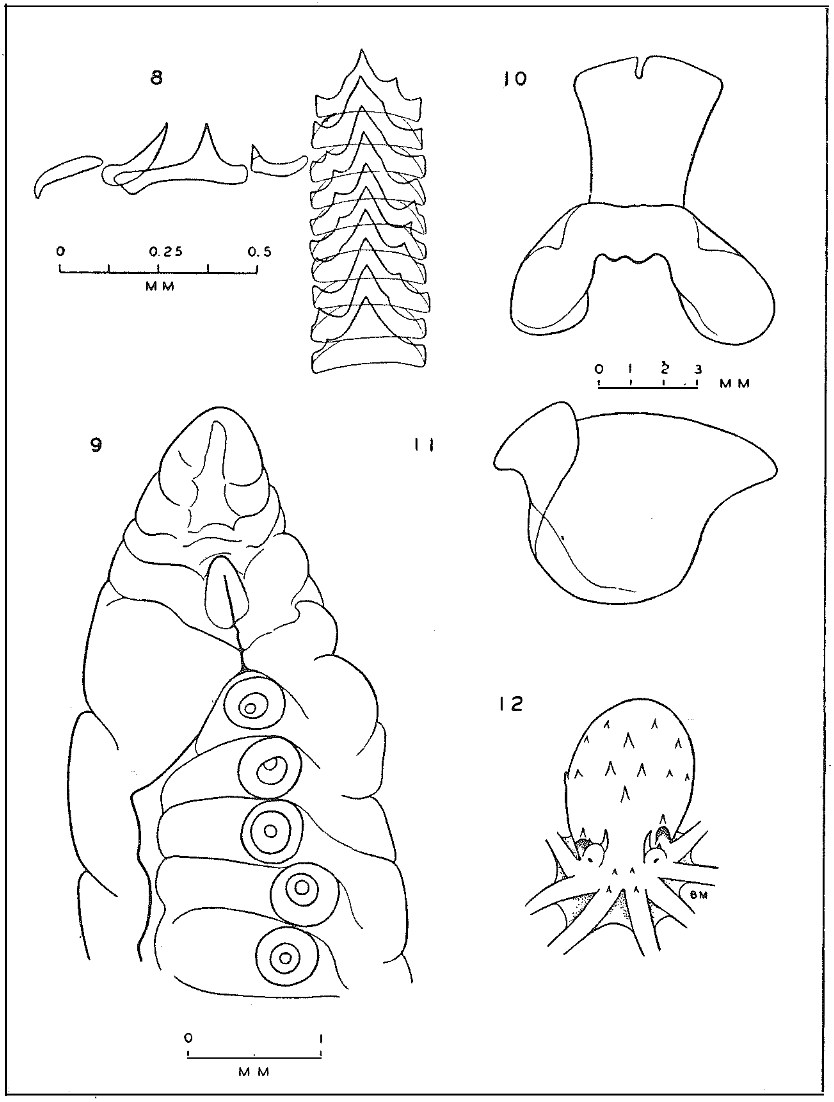

Figure 8. *Octopus bimaculoides* n. sp. Part of radula of HOLOTYPE showing seriation of rhachidian. **9.** Distal end of hectocotylized arm of ANDROTYPE showing ligula; the distal extremity is slightly curved towards the observer. **10.** Lower jaw of HOLOTYPE in face view showing emargination of beak. **11.** Upper jaw of same, in side view. **12.** Sketch of a juvenile specimen, No. (5), made while alive to show arrangement of principal cirri. The apical cirrus is not shown.

next generation, although very small and slender, are recognizably those of a large-egg species, since ova of *bimaculatus* at a corresponding stage are much more minute. The recently spawned eggs that were taken with this female consist of 15 small clusters containing a total of about 154 eggs; the largest cluster contains 19. A small cluster is illustrated (Fig. 19). The stalks are tightly woven and cemented together, so that they cannot be separated, but they are probably about 10 mm. long. The average length of an egg is 10.4 mm. (Table IV); the average width is 34.2% of the length. The ovum shows no recognizable stage of development.

The oviducal gland has a diameter of 4 mm. Its structure has been studied in serial sections. Unfortunately the state of preservation is not good and therefore the following account will be restricted to a brief outline of the microanatomy, without histological detail. Neither the structure nor the function of the oviducal gland of the Octopoda has been adequately investigated, but it is probable that it is a receptaculum seminis (see Robson, 1929: 137–138). This view is strongly supported by the present investigation. The oviducal gland of *O. bimaculoides* is situated, as in other species of *Octopus,* along the course of the oviduct and near to its place of origin from the ovarian sac. In external appearance it is a rounded, glandular swelling. When bisected transversely, or studied in serial sections (Figs. 15 and 16), it is seen to consist of a central duct with a thick muscular wall that is surrounded by about 20 lateral chambers, separated from each other by septa. External to these chambers there is a heavy glandular wall that is penetrated by irregularly shaped channels at regular intervals corresponding to the chambers; these are the lumina of the glandular ducts. The section illustrated in Fig. 15 passed somewhat obliquely in such a way as to show the glandular part more fully developed on one side; on the other side the cavities of the chambers are enlarged as they approach their blind ental ends, while the glandular zone is reduced. Another section (Fig. 16) passes diagonally through the junction of the ectal oviduct with the oviducal gland; the chambers arise radially by narrow openings into the lumen of the oviduct. The glandular ducts of the peripheral zone communicate with the oviducal chambers in this region. The chambers themselves appear to contain spermatozoa and, in some cases, remains of spermatophores. Thus spermatophores introduced into the oviduct find their way into the radial, backwardly projecting chambers which

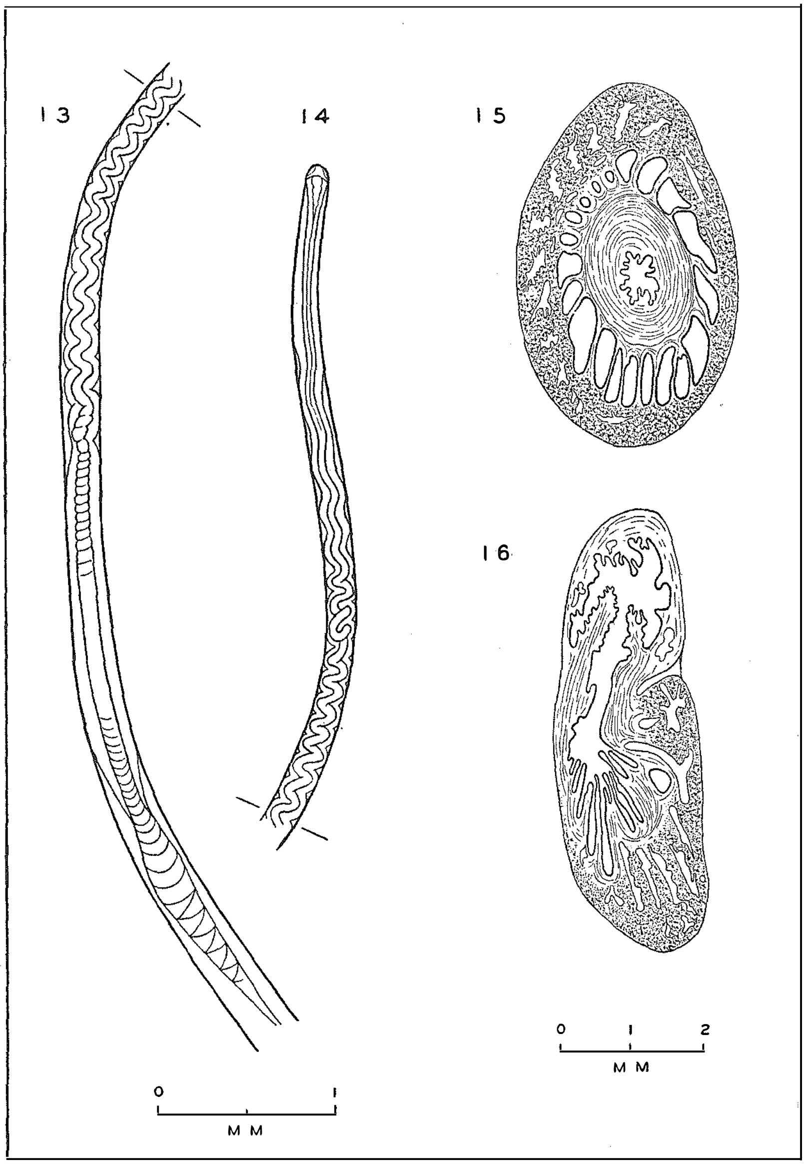

Figure **13.** *Octopus bimaculoides* n. sp. Part of a spermatophore of Androtype, showing distal end of horn and its continuation into the sac. **14.** Head and proximal part of horn of same spermatophore. **15.** Left oviducal gland of Holotype; slightly oblique transverse section showing central canal surrounded by circular muscle, radially arranged chambers, and glandular peripheral zone (stippled) with lumina of ducts. **16.** Sagittal section of same at junction of ental oviduct (above) with oviducal gland (below), showing openings of radial chambers into central canal. Ducts from the peripheral glandular zone communicate with the radial chambers in this region.

function as seminal receptacles. Presumably the eggs are fertilized as they pass the oviducal gland into the ectal oviduct.

Description of the ANDROTYPE. The ANDROTYPE (specimen No. 9) is a male taken at the same time and in the same locality as the HOLOTYPE. It is similar in general appearance and color; the cirri are similarly arranged and very prominent. Standard measurements are as follows: mantle-length, 43 mm.; total-length, 155 mm.; mantle-width, 31 mm.; head-width, 27 mm. First left arm, regenerating; second left, 110 mm.; third left, 125 mm.; fourth left, 100 mm.; first right, 101 mm.; second right, 117 mm.; hectocotylized third right, 105 mm.; fourth right, 110 mm. Sector A of web, 23 mm.; left B, 27 mm.; left C, 29 mm.; left D, 34 mm.; right B, 29 mm.; right C, 34 mm.; right D, 31 mm.; E sector, 23 mm. Greatest arm-width, 9 mm. The largest normal suckers have a diameter of 5 mm., but specially enlarged suckers at the level of the web margin are present as follows: on the second arms, two each, one belonging to the anterior series while the other is an adjacent member of the posterior series; on the third arms, one each, belonging to the posterior series. The diameter of the largest special sucker is 6 mm.

The ocellus is similar to that of the female but slightly larger, 7 mm. in diameter; however, the inner ring is of the same size. The funnel is 15 mm. long (funnel-length index 34.9), the free part 9.5 mm. The gill is similar to that of the female, 10 mm. long with eight primary lamellae in each demibranch. The upper jaw is 8.4 mm. long, the rostrum 3.2 mm. (index 38.1). The radula is similar to that of the female, with a B5, 6 or 7 seriation of the rhachidian.

The penis has the form shown in Fig. 20 with a small ovoid diverticulum. It is 4.5 mm. long. The ligula of the hectocotylus is minute, like that of *O. vulgaris* Lam.; it is 2.1 mm. in length and represents only 2% of the length of the hectocotylized arm. The spout of the calamus is 0.85 mm. from the margin of the last sucker and is thus situated almost half way along the length of the ligula (calamus-length index 40.5). Beyond the calamus there is a widely open, vaguely margined groove with a few faint transverse ridges (Fig. 9).

Characteristics of a typical spermatophore are given in Table VI. They are about 22 mm. long and the sperm reservoir constitutes about 41% of the total length. The head is rather long, 8.2% of the spermatophore-length, and coiling of the horn begins very gradually. The

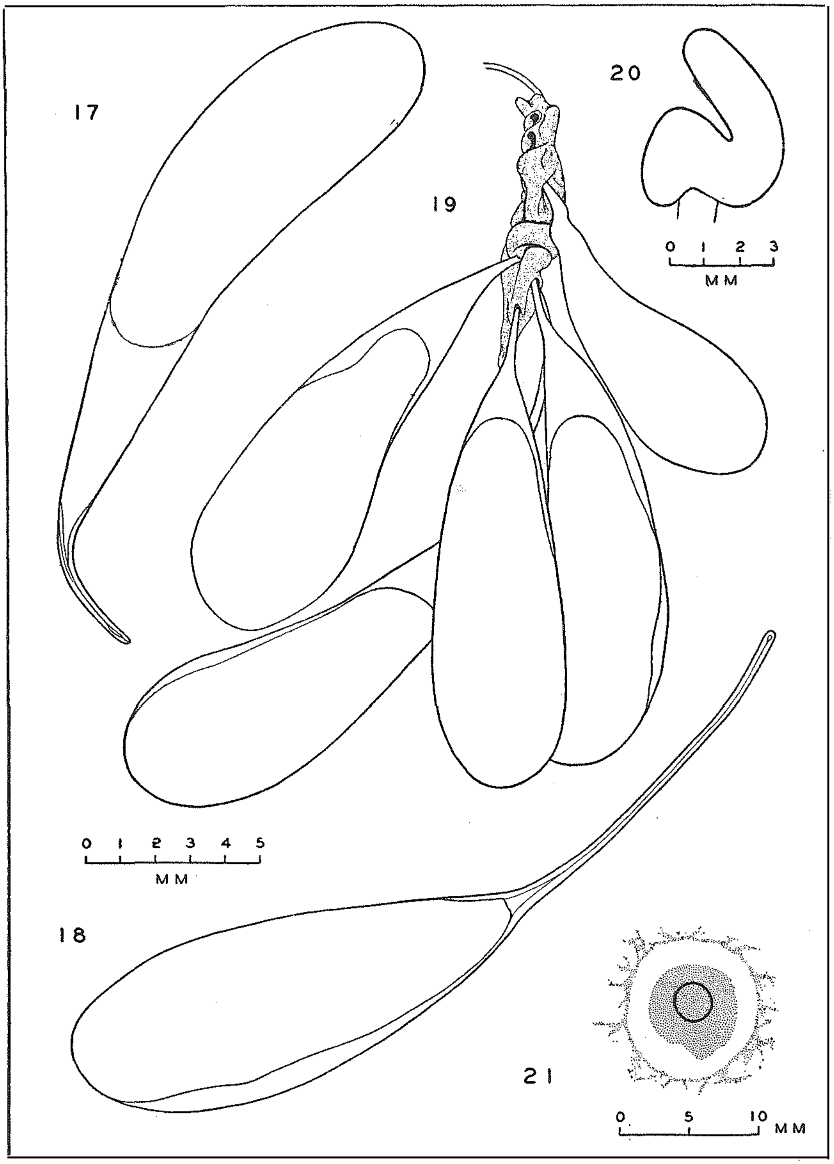

Figure **17**. *Octopus bimaculoides* n. sp. Ripe ovarian egg from specimen No. (1), an example of an egg with an unusually short stalk. **18**. Another ripe ovarian egg from same specimen, showing a long stalk. **19**. Small cluster of eggs laid by HOLOTYPE, showing manner in which the stalks are cemented together. **20**. Penis of ANDROTYPE. **21**. Left ocellus of HOLOTYPE.

first few turns of the spiral are anticlockwise, but the direction of coiling then becomes dextral (Fig. 14); towards the sac there is again a reversal and the last few turns are sinistral (Fig. 13). The sac region is about one-third the length of the spermatophore; the sac is distended distally, as shown in Fig. 13, but the state of preservation does not permit a more detailed description. The maximum breadth of the ejaculatory region, across the spiralled part of the horn, is 0.18 mm.

Other Specimens. The range and *mean* for all the more important taxonomic measurements are given in Table VII and are fully discussed in comparison with *O. bimaculatus* in Part II. However, certain additional features, not so treated, will be discussed here.

The ocellus is essentially similar in all specimens of this species and of *O. bimaculatus.* Most frequently the inner circle has a bluish tinge, as described by Berry (1911, 1912). Apparent differences between specimens may be traced to the following causes: (1) Failure to recognize the presence of the inner circle when the whole ocellus is very dark; (2) fading through long preservation, which may leave only the inner circle visible, as in the COTYPE of *bimaculatus,* so that the ocellus appears to have a pale center; (3) variations in the degree of development of the outermost pale area, which is often absent.

The surface appearance of the skin may be very different in different specimens, due to different states of preservation. When fully relaxed it is quite smooth or shows only minute conical papillae, each often in the center of a pale polygonal area. This condition is seen, for example, on the head of specimen No. 1. However, no importance can be attached to these variations. The arrangement of the cirri is essentially the same in all specimens, but they may be more or less conspicuous. In fully relaxed animals none may be visible, but during life they are raised and lowered rather vigorously, as observed by one of us (B. H. M., Fig. 12). Some of the smaller cirri observed in living animals are scarcely noticeable in the preserved condition.

The color is usually more reddish than in the HOLOTYPE and ANDROTYPE, and there is frequently a black reticulation, especially at the bases of the arms. Since the chromatophores are under nervous control it is evident that variations must occur in the preserved specimens, depending on whether anaesthetics were used and of what sort.

By far the most important character of the species is the size of the eggs, which require some further description; the data are summarized in Table IV. Ripe ovarian eggs were obtained from three gravid females. In addition, six clutches in various stages of development have been available for study, and it is almost certain that these were laid by females of *bimaculoides*, since there is no evidence that any other species lays such large eggs in the region under investigation. The *mean* length of ovarian eggs varies from 10.4–14.2 mm., the extreme limits being 9.5–16.0 mm. Thus there is absolutely no overlap between this species and *bimaculatus*, in which the largest egg yet discovered is only 4.0 mm. The width of the eggs is approximately one-third of the length; thus the eggs are relatively more slender than in *bimaculatus*. The three specimens studied offer no support for the thesis that smaller animals lay smaller eggs (Table V). The stalk is variable in length, but on the average it is about half as long as the egg itself, whereas in *bimaculatus* it tends to be of the same length. This difference is reflected in the small egg clusters, which usually consist of about ten eggs. The maximum observed was 35, and they are never found in long festoons, as in *bimaculatus*.

Eggs containing early developmental stages are of about the same size as the ovarian eggs (*mean* length 11.3–12.2 mm.), while those containing advanced embryos are definitely larger (*mean* length 15.7–16.8 mm.; extreme limits 13.5–17.5 mm.) although the relative width is about the same. The increase in size of the eggs during development was noted by Mrs. G. E. MacGinitie who writes as follows concerning clutch number (6): "The eggs, attached to a 'two-man rock,' and the mother were brought into the laboratory on January 24, 1948. They appeared to have been freshly laid . . . As you will see by the label, the eggs were incubated for 15 weeks, and, judging from former observations, they would not have hatched for two or three weeks more. Unfortunately, the water stopped during the night, and both the mother and the embryos died before morning. Although the egg cases were somewhat larger than when they were first laid, the preservative caused them to enlarge considerably more." (Personal communication.)

Newly hatched larvae are associated with Clutch No. 5; they have a mantle-length of 6 mm., but no ocellus is visible. However, in a slightly more advanced larva of 9 mm. mantle-length the ocellus is already well developed.

TABLE IV. *Octopus bimaculoides* n. sp. Measurements of Eggs (See Table I). All Clutches of Large Eggs Are Included, Even When They Are Not Certainly Known to Have Been Laid by Females of This Species.

Specimen No.	*Material*	*E.L.*	*E.W.I.*	*E.S.*
(1)	Ripe ovarian eggs; 12 measured, all with stalks.	10.5–*14.2*–16.0	22–*30*–43	3.3–*5.9*–10.0
(2)	Clutch taken with Holotype, early stage; 10 measured, none freed with stalk.	9.5–*10.4*–11.5	30–*34*–39	——
(4)	Ripe ovarian eggs; 5 measured, all with stalks.	11.0–*11.5*–12.1	29–*32*–33	6.5–*7.3*–8.0
Clutch (1)	Early stage; 4 undamaged eggs, stalks not freed.	11.0–*11.3*–11.5	35–*36*–36	——
Clutch (2)	Young embryos; 6 eggs measured, one with stalk.	11.5–*12.2*–12.5	29–*32*–35	8.0
Clutch (3)	Early stage; 10 eggs measured, one with stalk.	10.5–*11.5*–13.0	25–*34*–38	7.0
Clutch (4)	Advanced embryos; 10 eggs measured, 2 with stalks.	16.0–*16.8*–17.5	30–*31*–33	8.5–*8.5*–8.5
Clutch (5)	Advanced embryos; 10 eggs measured, one with stalk.	15.8–*16.4*–17.4	31–*34*–38	9.0
Clutch (6)	Advanced embryos; 9 eggs measured, 2 with atalks.	13.5–*15.7*–17.0	35–*38*–43	7.0–*8.0*–9.0

TABLE V. *Octopus bimaculoides* n. sp.: Comparison of Mantle-length, Egg-length and Egg-width Index; See Table II.

Spec. No.	*M.L.*	*E.L.*	*E.W.I.*
(1)	65	14.2	30
(2) Holotype.	39	10.4	34
(4)	67	11.5	32

TABLE VI. *Octopus bimaculoides* n. sp. Spermatophore Characteristics (See Table III).

Spec. No.	*Sp.L.*	*Sp.L.I.*	*Sp.R.I.*	*Sac I.*	*D.Ej.I.*	*Hd.I.*	*Ho.Coils*	*Spiral*
(7).	33.0	55	46	26	0.97	8.2	23–25	D
(8).	33.0	64	41	32	0.76	8.2	23–24	alt.D,S
(9) Androtype. .	22.0	51	41	34	0.82	8.2	24,26,27	alt.D,S
(10).	24.0	62	46	29	0.83	7.1	26–27	D

Spermatophores were obtained from three other males, in addition to the Androtype. They are all essentially alike with rather long heads, but experience with *O. bimaculatus* (*q. v.*) suggests that this feature must be viewed with extreme caution. The horn may show a change in direction of coiling of the spiral or it may be purely dextral.

3. JUVENILE SPECIMENS

Specimens studied[3]

(1) B. H. M. No. L-51; female, mantle-length 43.5 mm., 57 g.; Devil's Slide, La Jolla, Calif., II. 3. 1947.

(2) B. H. M. No. L-48; female, mantle-length 29 mm., 29 g.; Point Loma, Calif., II. 2. 1947, C. Hubbs coll.

(3) B. H. M. No. L-33; female, mantle-length 31 mm., 27 g.; Devil's Slide, La Jolla, Calif., I. 6. 1947, R. Rickey coll.

(4) B. H. M. No. L-49; male, mantle-length 30.5 mm., 25 g.; near Point Loma, Calif., II. 3. 1947, C. Hubbs coll.

(5) B. H. M. No. L-135; female, mantle-length 27.0 mm., 15.5 g.; Devil's Slide, La Jolla, Calif., V. 29. 1948.

(6) B. H. M. No. L-80; female, mantle-length 31 mm., 21 g.; Devil's Slide, La Jolla, Calif., VI. 22. 1947, killed VI. 27. 1947.

(7) B. H. M. No. L-27; male, mantle-length 34 mm.; Devil's Slide, La Jolla, Calif., XII. 8. 1946.

(8) B. H. M. No. L-140; male, mantle-length 24 mm., 11 g.; Devil's Slide, La Jolla, Calif., VI. 12. 1948.

(9) B. H. M. No. L-133; male, mantle-length 28 mm., 12 g.; Devil's Slide, La Jolla, Calif., III. 20. 1948, died V. 17. 1948.

(10) B. H. M. No. L-136; male, mantle-length 20 mm., 7 g.; Devil's Slide, La Jolla, Calif., V. 29. 1948.

(11) B. H. M. No. L-50; male, mantle-length 24 mm., 6 g.; Devil's Slide, La Jolla, Calif., II. 3. 1947.

(12) B. H. M. No. L-52; sex uncertain, mantle-length c. 19.5 mm., 7 g.; Devil's Slide, La Jolla, Calif., II. 3. 1947.

(13) B. H. M. No. L-102; male, mantle-length 16 mm., 4 g.; Bird Rock, La Jolla, Calif., X. 29. 1947.

(14) B. H. M. No. L-134; male, mantle-length 17 mm., 3 g.; Devil's Slide, La Jolla, Calif., III. 20. 1948, died V. 17. 1948.

(15) B. H. M. No. L-12; male, mantle-length 18 mm., 2.5 g.; Lower Calif., about 25 mi. below Tiawana, on rocky beach flats, X. 23. 1947.

(16) B. H. M. No. L-13; sex uncertain, mantle-length 19 mm., 2.4 g.; same as previous.

(17) B. H. M. No. L-10; sex uncertain, mantle-length 14 mm., 1.6 g.; same as previous.

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[3] See Footnote 1.

(18) B. H. M. No. S-2; sex uncertain, mantle-length 13 mm.; Bird Rock, La Jolla, Calif., VIII. 1946. Coll. by Steinhart Aquarium, died San Francisco, given to B. H. M. VIII. 8. 1948, one day after death, overnight in refrigerator.

(19) B. H. M. No. S-3; sex uncertain, mantle-length 13 mm.; same as previous.

(20) B. H. M. No. S-8; sex uncertain, mantle-length 11 mm.; same as previous.

(21) B. H. M. No. L-56; sex uncertain, mantle-length 10.5 mm., 0.7 g.; Devil's Slide, La Jolla, Calif., II. 3. 1947.

(22) B. H. M. No. L-15; sex uncertain, mantle-length 13.5 mm., 0.8 g.; Lower Calif., as for specimen (15).

The specimens listed above are unmistakably young of the *bimaculatus-bimaculoides* complex, but they cannot be identified with certainty as to species. The problem is discussed at the end of Part II.

PART II. AN ANALYTICAL COMPARISON OF THE SPECIES

1. SURVEY OF THE CHARACTERS

In Table VII the mantle-length, indices of bodily proportions, and number of primary gill lamellae are summarized in a manner that permits ready comparison between the sexes and between the two species. Each characteristic is represented by the mean value, in *italics*, and by the lower and upper limits, since extreme values are of practical importance to the taxonomer. The 16 characters listed will now be discussed individually, together with certain other features not susceptible to a numerical tabulation of this type. Standard deviations are calculated for small numbers.

Mantle-length (1). Females are, on the average, 8.2 (*bimaculatus*)–8.4% (*bimaculoides*) larger than males. Females of the new species are markedly smaller than females of *bimaculatus*, averaging 58.2 ± 11.1 mm. as compared with 88.4 ± 16.9 mm. In fact, in the limited series of adult females under investigation there is scarcely any overlap in respect to mantle-length between the two species. There is no possibility that the two groups are sampled from a population that is homogeneous ($s_d = 2.65$, $t = 11.40$). On the other hand, there is some overlap in size between the largest mature males of *bimaculoides* and the smallest mature males of *bimaculatus*. The average mantle-length of the new species is considerably less, 48.8 ± 7.3 mm., as

TABLE VII. COMPARISON OF *Octopus bimaculatus* VERRILL (A) AND *O. bimaculoides* N. SP. (B); MANTLE-LENGTH, NUMBER OF PRIMARY GILL LAMELLAE AND INDICES OF BODILY PROPORTIONS. RANGE AND *Mean.*

	*Character**	*Species*	*Females*	*Males*	*Total*	*Number*	
						♀♀	♂♂
1.	M. L. (adults)	A	66–*88*–120	48–*68*–100	66–*77*–120	8	11
		B	39–*58*–67	39–*49*–60	39–*54*–67	5	5
2.	M. W. I.	A	70–*79*–90	67–*77*–93	70–*78*–93	10	4
		B	74–*76*–78	54–*66*–72	54–*70*–78	3	5
3.	H. W. I.	A	44–*54*–67	38–*55*–60	38–*54*–67	15	11
		B	39–*47*–59	50–*54*–58	39–*50*–59	5	5
4.	A. L. I.	A	72–*85*–95	78–*84*–88	72–*85*–95	14	9
		B	74–*77*–79	76–*79*–82	74–*78*–82	6	5
5.	M. A. I.						
	(all)	A	14–*23*–37	17–*22*–27	14–*23*–37	14	11
	(adults)	A	14–*22*–29	17–*22*–27	14–*22*–29	7	11
		B	32–*33*–35	29–*34*–39	29–*34*–39	5	5
6.	Ah. A. I.	A	—	63–*75*–91	—		10
		B	—	80–*84*–90	—		5
7.	A. W. I.	A	17–*24*–32	19–*25*–28	17–*25*–28	15	11
		B	13–*19*–26	18–*22*–29	13–*21*–29	5	5
8.	W. D. I.	A	15–*21*–31	14–*20*–28	14–*20*–31	14	11
		B	18–*23*–29	20–*25*–28	18–*23*–29	6	5
9.	Wh. W. I.	A	75–*94*–100	65–*84*–100	—	15	11
		B	82–*88*–100	70–*84*–96	—	6	5
10.	Sn. D. I.	A	9–*13*–18	13–*16*–19	9–*14*–19	15	11
		B	7–*10*–13	9–*11*–14	7–*10*–14	5	5
11.	Se. D. I.	A	—	16–*19*–26	—		10
		B	—	10–*13*–15	—		5
12.	G. L.	A	7–*8.4*–10	7–*8.3*–9	7–*8.4*–10	15	11
		B	7–*8.3*–10	7–*8.1*–9	7–*8.2*–10	6	5
13.	O. D. I.	A	8–*16*–20	—	—	8	gravid
		B	9.*12*–17	—	—	3	gravid
14.	L. L. I.	A	—	1.2–*2.0*–2.8	—		10
		B	—	1.4–*1.9*–2.3	—		5
15.	C. L. I.	A	—	40–*50*–63	—		10
		B	—	39–*44*–50	—		5
16.	P. L. I.	A	—	14–*19*–23	—		10
		B	—	11–*14*–22	—		5

*A. L. I. = Arm-length index; length of longest arm × 100/total length.
Ah. A. I. = Hectocotylized arm-length index; length of hectocotylized arm × 100/length of longest arm.
A. W. I. = Arm-width index; width of widest arm × 100/mantle-length.
C. L. I. = Calamus-length index; length of calamus × 100/ligula-length.
G. L. = Number of primary gill lamellae per demibranch.
H. W. I. = Head-width index; width of head × 100/Mantle-length.
L. L. I. = Ligula-length index; ligula-length × 100/length of hectocotylized arm.
M. A. I. = Mantle-arm index; mantle-length × 100/length of longest arm.

compared with 68.0 ± 17.1 mm., and the difference between the means is significant at the 5% level ($s_d = 7.06$, $t = 2.72$). This makes it reasonably certain that males, like females, are sampled from a mixed population that is bimodal in respect to mantle-length.

Mantle-width (2). The body of an octopus, unsupported internally by a rigid gladius, is subject to great changes of shape. In addition to this flexibility, which makes the mantle-width index of preserved specimens highly variable and of no great taxonomic significance, many of the specimens under investigation have been slit open in order that the kidneys might be examined for Mesozoa. This operation adds greatly to the unreliability of the mantle-width measurement. Many specimens could not be measured at all, and it is doubtful whether any importance can be attached to the small differences that appear in the tabulation. The situation does not call for a statistical treatment of the data, but it may be noted that in general the mantle-width is about three-quarters of the mantle-length in both species.

Head-width (3). The head-width indices do not show any significant differences between the species; head-width is approximately half the mantle-length. A further treatment of head-width is reserved for more detailed analysis in Part II (2 and 3).

Length of Longest Arm (4 and 5). There are no differences in respect to arm-length between the sexes, but the arms of *bimaculatus* are relatively much longer than those of *bimaculoides*, approximately 85% of the total length as against 78%. This is expressed in terms of Robson's standard arm-length index, which compares the length of the longest arm with the total length of the animal. In relatively long-armed species, such as those discussed in this paper, the mantle-arm index which compares arm-length with mantle-length is better

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M. L. = Mantle-length.
M. W. I. = Mantle-width index; mantle-width × 100/mantle-length.
O. D. I. = Oviducal gland index; diameter of oviducal gland × 100/mantle-length.
P. L. I. = Penis-length index; penis-length × 100/mantle-length.
Se. D. I. = Special sucker-diameter index; diameter of largest special sucker × 100/mantle-length.
Sn. D. I. = Normal sucker-diameter index; diameter of largest normal sucker × 100/mantle-length.
W. D. I. = Web-depth index; depth of deepest web-sector × 100/length of longest arm.
Wh. W. I. = Hectocotylized web-sector index; depth of sector right D × 100/depth of deepest web-sector.

suited to the data (Pickford, 1945). Since there are no differences between the sexes, the mantle-arm indices of the two species may be compared on the totals for both sexes.

The average mantle-arm index of *bimaculoides* is markedly larger than that of *bimaculatus,* in accordance with the relatively shorter arms of the former species, 33.6 ± 2.75 as compared with 22.5 ± 4.53. The ranges scarcely show any overlap; one sexually immature *bimaculatus* (No. 14) has an index of 36.5 and one adult (No. 8) has an index of 28.6; one *bimaculoides* (No. 11) has an index of 29.4. The difference between the means is highly significant, precluding any possibility that the combined population from which the samples were drawn was homogeneous in respect to relative arm-length ($s_d = 1.54$, $t = 7.2$).

Order of Arm-length. The most frequent order of arm-length is arrived at through a summation of arm-length for all perfect half sets (left or right sides), the sum for the first, second, third and fourth arms being expressed as a percentage of the total for all four arms. It would have been preferable to use complete arm sets, but there are so few specimens with eight undamaged arms that this is impossible. The results are shown in Table VIII. In females of *bimaculatus* there is evidently no difference in the order of arm-length on the left and right sides, and therefore the data may be combined. Probably this would also be evident for *bimaculoides* if a sufficiently large number of perfect half sets had been available for study, and no importance can be attached to the apparent slight difference of order on the two sides. Therefore they may be taken together for females of this species as well. Males will be considered separately.

In comparing the females of the two species, it is evident that a third arm is usually longest in *bimaculatus* while the second and third arms tend to be coequally long in *bimaculoides.* A statistical analysis has not been pursued, since the numbers are small and the difference is of little taxonomic importance. The characteristic arm-length order for females of *bimaculatus* is $3 > 2 > 4 > 1$, while for *bimaculoides* it is $3 = 2 > 4 > 1$.

The hectocotylized right side of males requires special treatment, but it might be supposed that the unmodified left side would be similar to that of females. The evidence on this point is not clear, and the limited number of perfect male left half sets precludes an

TABLE VIII. COMPARISON OF *Octopus bimaculatus* VERRILL (A) AND *O. bimaculoides* N. SP. (B); ORDER OF ARM-LENGTH EXPRESSED AS PERCENT OF TOTAL ARM-LENGTH IN PERFECT HALF SETS

Sex	*Side*	*Species*	*No. half sets*	*Number of arm, % length* *1*	*2*	*3*	*4*
♀	L	A	7	22.5	25.4	27.2	24.8
♀	R	A	6	22.3	25.8	27.0	24.9
♀	L + R	A	13	22.4	25.6	27.1	24.9
♀	L	B	3	21.8	26.2	27.1	25.0
♀	R	B	2	22.4	28.0	25.9	23.6
♀	L + R	B	5	22.0	27.0	26.6	24.4
♂	L	A	5	23.5	26.3	25.7	24.5
♂	L	B	1	22.7	24.5	27.8	25.0
♂	R	A	7	24.9	27.7	21.3	26.1
♂	R	B	5	23.7	27.0	24.2	25.1

adequate analysis. However, in *bimaculatus* there is some indication that the second and third arms tend to be coequally long on the left side, thus differing from the female. No conclusions can be drawn from the single perfect left half set of a male *bimaculoides.*

Length of Hectocotylized Arm (6). In males of *bimaculatus* the hectocotylized third right arm is normally the shortest of its side, the second the longest and the fourth almost as long as the second. Therefore the typical order is represented by the formula $2 > 4 > 1 > 3$. In *bimaculoides* the second right is also the longest, but the hectocotylized arm tends to be relatively slightly longer than in *bimaculatus* and is of the same length, or possibly slightly longer, than the first. The typical order is thus $2 > 4 > 3 = 1$. The significance of this difference between the species may be tested by the use of an hectocotylized arm-length index (Table VII). In *bimaculatus* the hectocotylized arm is 75% of the longest arm, the mean value of the index being 75.2 ± 8.5. In *bimaculoides* the hectocotylized arm is relatively longer, 84.4 ± 3.5%. The ranges for the two species overlap, but the difference between the means is significant at the 5% level ($s_d = 3.96$, $t = 2.32$).

Position of Longest and Shortest Arm. The treatment outlined previously gives an estimate of the most frequent order of arm-length, but it is the actual, rather than the most probable position of the longest and shortest arm that is of practical taxonomic importance on account of the frequent occurrence of atypical arrangements.

One of the third arms of *bimaculatus* is longest in about four-fifths of the females (Table IX), while in *bimaculoides* there is apparently an equal chance that one of the second arms will be longest. No cases in which either a first or a fourth arm was longest were observed in females of either species. The first arms are almost always the shortest; rarely a fourth may be coequally short or shorter.

Data for the unmodified left side of males present no special features. In *bimaculatus* there is the same tendency that was observed in the study of arm-length order, viz., the longest arm is as often in position two as in position three. The single left half set of a male *bimaculoides* has the third arm longest.

In respect to the hectocotylized right side, the second arm is usually the longest, as might be expected from the arm-order, but in both species one finds an occasional specimen in which the fourth arm is longest. The position of the shortest arm also conforms with evidence from the order of arm-length. The hectocotylized arm is usually the shortest in *bimaculatus*, the first arm more usually so in *bimaculoides* in which arms one and three are approximately coequal on a percentage rating. One *bimaculoides* has the fourth arm shortest.

TABLE IX. COMPARISON OF *Octopus bimaculatus* VERRILL (A) AND *O. bimaculoides* N. SP. (B); POSITION OF LONGEST AND SHORTEST ARMS IN PERFECT HALF SETS.

Sex	*Side*	*Category*	*Species*	*Number of Arm**			
				1	*2*	*3*	*4*
♀	L + R	Longest	A	—	2.5	10.5	—
			B	—	2.5	2.5	—
♀	L + R	Shortest	A	11.5	—	—	1.5
			B	4.0	—	—	1.0
♂	L	Longest	A	—	3	2	—
			B	—	—	1	—
♂	L	Shortest	A	4	—	1	—
			B	1	—	—	—
♂	R	Longest	A	—	6	—	1
			B	—	4	—	1
♂	R	Shortest	A	1	—	6	—
			B	3	—	1	1

* Numbers entered in these columns indicate the number of specimens in which the longest or shortest arm occurs in the position indicated. When two arms are coequally long or coequally short, each is rated at 0.5.

Arm-width (7). There can be no doubt that the arms of *bimaculatus* tend to be a little stouter than those of *bimaculoides*, although the extreme values of the arm-width indices practically coincide in the two species. The difference between the means is significant at the 5% level ($s_d = 1.55$, $t = 2.70$). In *bimaculatus* the arm-width averages about one-quarter of the mantle-length, 24.0 ± 3.56, while in *bimaculoides* it is only one-fifth, 20.5 ± 4.9.

In *bimaculatus* there is no difference in arm-width between the sexes, and the apparent difference in *bimaculoides* is not statistically significant.

Deepest Web Sector (8). There is no difference between the sexes, but the indices suggest that the web of *bimaculoides* tends to be relatively deeper than that of *bimaculatus,* 23.4 ± 3.75 as compared with 20.4 ± 4.07; the difference is not statistically significant ($s_d = 1.76$, $t = 1.70$). In both species the web is of moderate depth, as in *O. vulgaris* Lam.

Order of Web-depth. The order of web-depth is studied by methods similar to those used for the study of arm-length, except that all web sectors are usually perfectly preserved; therefore it is not necessary to restrict the analysis to perfect half sets. The typical arrangement is shown by percentage depths for each of the eight sectors (Table X). In the female of *bimaculatus,* sector A is the shallowest while sectors C and D are the deepest and of approximately coequal depth. The E sector is not quite as shallow as the A sector and is of approximately the same depth as the B sectors. Left and right sides are essentially alike. The relations are expressed by the formula $C = D > B = E > A$

The percentage web-depths of females of *bimaculoides* are essentially the same as in *bimaculatus,* and the typical formula is similar: $C = D > B > E > A$. The E sector is definitely shallower than the B sector.

TABLE X. COMPARISON OF *O. bimaculatus* VERRILL (A) AND *O. bimaculoides* N. SP. (B); ORDER OF WEB-DEPTH EXPRESSED AS PERCENT OF TOTAL WEB-DEPTH.

Sex	*Species*	*No.*	*Web Sector*							
			A	*LB*	*RB*	*LC*	*RC*	*LD*	*RD*	*E*
♀	A	15	10.1	11.5	11.7	13.9	14.0	13.6	14.0	11.1
	B	6	9.2	12.3	11.7	14.4	14.1	14.6	13.6	10.1
♂	A	10	10.6	12.1	12.6	14.0	14.4	13.3	12.3	10.6
	B	5	10.4	13.0	12.4	14.0	13.5	14.0	12.2	10.4

The Hectocotylized Web Sector (9). The web-depth of *bimaculatus* males is similar to that of females, except in respect to the D and E sectors which are relatively shallower. Thus the E sector is coequally shallow with the A sector, the C sectors markedly deeper than the D sectors. The difference is most striking in respect to the D sector of the hectocotylized right side. This is the sector from which springs the spermatophore groove that runs outwards along the side of the hectocotylized arm. It is only 12.3% of the total web-depth as compared with 14% in females. The significance of the difference was tested by means of an hectocotylized web-sector index (Table VII). In females the right D sector represents 94.2 ± 6.7% of the depth of the deepest sector; in males it is only 84.7 ± 12.6%. In spite of great variability, the difference between the means is statistically significant at the 5% level ($s_d = 3.86$, $t = 2.46$). The typical web-depth formula for males of this species is $\mathrm{C} > \mathrm{LD} > \mathrm{RD} = \mathrm{B} > \mathrm{E} = \mathrm{A}$.

Males of *bimaculoides* differ from females in exactly the same way that males of *bimaculatus* differ from females of that species. The A and E sectors are coequally shallow, and the hectocotylized right D sector comprises only 12.2% of the total, as compared with 13.6% in females. The index for this sector is 88.2 ± 6.8 in females and 84.1 ± 4.2 in males. The difference is not statistically significant on account of the small number of specimens and high degree of variability, but there can be little doubt that the same tendency occurs in both species.

TABLE XI. Comparison of *O. bimaculatus* Verrill (A) and *O. bimaculoides* n. sp. (B); Position of Deepest and Shallowest Sectors of Web.

Sex	*Category*	*Species*	*Web Sector**				
			A	*B*	*C*	*D*	*E*
♀	Deepest	A	—	—	8.0	7.0	—
		B	—	—	2.0	4.0	—
♀	Shallowest	A	11.3	0.3	—	—	3.3
		B	3.5	—	—	—	2.0
♂	Deepest	A	—	0.5	7.5	3.0	—
		B	—	—	3.5	1.5	—
♂	Shallowest	A	5.5	—	—	1.0	3.5
		B	2.5	—	—	—	2.5

* Numbers entered in these columns indicate the number of specimens in which the deepest or shallowest sector occurs in the position indicated. When two sectors are coequally deep or coequally shallow, each is rated at 0.5; when three are coequal each is rated at 0.3. Left and right sides are taken together.

Position of Deepest and Shallowest Sector. In both species either a C or a D sector is deepest, or the C and D sectors may be coequally deep (Table XI). The situation has not been examined statistically, but apparently in females there is an equal chance that a C or a D sector will be the deepest, while in males the C sector is more frequently favored. There is one male of *bimaculatus* (No. 19) in which the right B and C sectors are coequally deepest.

The A sector is more frequently the shallowest in both species, but the A and E sectors may be coequally shallow, with the E sector quite frequently the shallowest. This tendency is more marked in males in accordance with evidence from the order of web-depth. One female of *bimaculatus* (No. 1) has a left B sector that shares the shallowest position with the A and E sectors, so that each is rated at one-third. One male of *bimaculatus* (No. 19) has a quite unusual arrangement, the two D sectors being coequally shallowest.

Sucker-diameter (10 and 11). In both species the largest suckers are on the second and third arms, at about the level of the web margin. Females have no specially enlarged suckers, but these are usually present in adult males of both *bimaculatus* and *bimaculoides*. They were lacking, however, in one male *bimaculatus* (No. 25). When present, they occur on the second and (or) third arms at the level of the web margin; the maximum number on any one arm is two, one anterior and one posterior; the maximum number in any one specimen is therefore eight, two on each affected arm. More usually there is only one special sucker on an arm, and not all of the four possible arms are affected. The variability is great and no attempt has been made to determine the most probable arrangement, since the numbers of male specimens are so few.

Robson (1929) used the sucker-diameter index without any very serious attempt to distinguish between normal and specially enlarged suckers, although he was well aware of the complications contingent on this situation. The senior author has proposed the use of two separate indices, one for normal and one for specially enlarged suckers, SnD I and SeD I respectively (Pickford, 1945). In many species the distinction is an easy one, but in others, like the two species under investigation, there is a strong tendency for the suckers immediately adjacent to the specially enlarged suckers to be slightly larger than normal. Thus the normal sucker-diameter index is slightly higher in males than in females. Consequently, in making a comparison between the two species it is preferable to consider the sexes separately and to take only the largest suckers in each sex. The normal sucker-diameter index for females is less in *bimaculoides* than in *bimaculatus*, 10.2 ± 2.4 as compared with 13.2 ± 2.5. The difference between the means is significant at the 5% level, in spite of some overlap in the ranges ($s_d = 1.24$, $t = 2.43$). A similar situation exists in respect to the specially enlarged suckers of males. The enlarged sucker-diameter index for *bimaculoides* is markedly lower than that of *bimaculatus*, 12.8 ± 1.9 as against 19.3 ± 3.9, excluding from the calculation the one male in which no suckers were specially enlarged. The range for the two species shows no actual overlap in the series studied, but variability is high and some overlapping must almost certainly occur in nature. The difference between the means is significant at the 5% level ($s_d = 2.08$, $t = 2.65$). In regard to the male without enlarged suckers, it is of interest that the normal sucker-diameter index (18.2) is near to the upper limit, even for males, and quite at the upper limit for females.

Gill Lamellae (12). There is no difference between the sexes or between the species. Usually one finds eight or nine primary lamellae in each demibranch, making a total of 17 to 19, including the terminal. The extreme limits are seven and ten respectively per demibranch.

Diameter of Oviducal Gland (13). The oviducal gland is relatively small in immature females as well as in adults that are not about to spawn. For this reason only gravid females containing ripe or nearly ripe ova are included in the calculations. This procedure greatly reduces the numbers available for study, which is unfortunate, but there appears to be no difference between the species. The mean values of the indices are 16.1 ± 4.0 in *bimaculatus* and 11.7 ± 4.5 in *bimaculoides*, for eight and three specimens respectively. The difference is not statistically significant.

The structure of the gland is apparently similar in the two species. A female *bimaculatus* shows about 20 radial chambers when the gland is bisected transversely, just as in the HOLOTYPE of *bimaculoides* (Fig. 15).

Ligula (14 and 15). The hectocotylus is similar in the two species and closely resembles that of *O. vulgaris* Lam. The ligula is minute, approximately 2% of the length of the hectocotylized arm. The spout of the calamus opens about halfway between the margin of the last sucker and the tip of the arm; a slight difference between the means for the two species is not statistically significant.

The length of the hectocotylized arm is treated under the heading "Order of Arm-Length." It is relatively longer in *bimaculoides* than in *bimaculatus*.

Penis-length (16). The penis has the same form in the two species, but it appears to be relatively longer in *bimaculatus*, with an index of 19.0 ± 2.4 as compared with 13.9 ± 4.5 in *bimaculoides*. The difference between the means is highly significant ($s_d = 1.76, t = 2.91$). This is unexpected, because the calculations for *bimaculoides* include one animal in which the penis is quite abnormally extended, apparently due to irritation caused by the presence of two tapeworm pleurocercoids that were found in the mantle-chamber.

Spermatophores. The spermatophores have been fully described already under the detailed accounts of the two species in Part I. It is disappointing to find that they are essentially alike, but this is not surprising in view of the extremely close relationship that evidently exists. The situation might well have been otherwise; for example, the two Florida species that lay large eggs and that differ from each other primarily in relative arm-length, have characteristically different spermatophores (Pickford, 1945). In order to facilitate a comparison, the measurable characteristics are summarized in Table XII. The relative length of the spermatophores, in terms of mantle-length, is the same; furthermore little importance can be attached to small apparent differences in the number of coils of the horn, in the relative length of the reservoir and sac, and in the relative diameter. The variations are most likely due to the rather small number of male *bimaculoides* that were available for study. Although a real difference appears to exist in the relative length of the head, some specimens of *bimaculatus* have long heads, and in the COTYPE both long- and short-headed spermatophores occur in the same specimen. Therefore this character must be discounted.

2. THE INTERPRETATION OF SIGNIFICANT DIFFERENCES BETWEEN THE INDICES

When the indices are alike, one might assume that growth is isometric and that the arithmetic and geometric constants of the growth equations are alike in the two species. But when the variation is considerable and the numbers of specimens limited, as in the present instance, it is dangerous to draw any such simple conclusion. As an example we may consider the head-width index which is apparently not significantly different in *bimaculatus* and *bimaculoides*. If the simplest interpretation were true, that growth relations of head and

TABLE XII. *Octopus bimaculatus* VERRILL (A) AND *O. bimaculoides* N. SP. (B); COMPARISON OF THE SPERMATOPHORES. DATA FROM TABLES III AND VI. FIGURES REPRESENT THE RANGE AND *Mean;* IN CALCULATING THE MEAN, AN AVERAGE VALUE WAS TAKEN WHEN THERE WERE SEVERAL SPERMATOPHORES FROM THE SAME ANIMAL.

Species	*Sp.L.I.*	*Ho.Coils*	*Sp.R.I.*	*Sac I.*	*D.Ej.I.*	*Hd.I.*
A	34–*58*–71	17–*30*–40	27–*34*–55	24–*44*–50	.51–*.64*–.86	1.4–*4.6*–11.0
B	51–*58*–64	23–*25*–27	41–*44*–46	26–*30*–34	.76–*.85*–.97	7.1–*7.9*– 8.2

mantle are the same in the two species, then a single equation should provide an approximate fit for the entire series. This equation is shown graphically (Fig. 22, line 2). It will be seen immediately that the points for *bimaculatus* tend to lie above the line while the points for *bimaculoides* tend to lie below it. Moreover, growth is not isometric but rather strongly negatively allometric ($k = 0.698$). This would mean that specimens of the smaller species (*bimaculoides*) should have relatively wider heads, which is not the case. Evidently one equation cannot be applied, and separate calculations must be made for the two species. The growth coefficients remain negatively allometric, 0.613 for *bimaculatus* and 0.440 for *bimaculoides*, and are not significantly different from each other; the low value for *bimaculoides* must be due to chance because of the small number of specimens and high degree of variability. The two lines (Fig. 22, lines 3 and 4) should really be regarded as parallel, but within each species, on account of the negative value of k, it is true that smaller specimens tend to have relatively larger heads. This is entirely in accordance with our limited knowledge of other species. In *O. vulgaris* Lam., for example, the head-width index of young specimens is higher than that of adults (Pickford, 1945). The difference between *bimaculatus* and *bimaculoides* must be traced to a difference in the geometric constant. The growth relationships of juvenile specimens also has a bearing on the problem, but this subject is reserved for further discussion in Part II (4).

A similar treatment could be applied to other measurements whose indices appear to be alike in the two species, but the data do not justify detailed analysis. Attention will therefore be concentrated on those indices which can be shown to be statistically different and which might be used for specific diagnosis.

When the indices are different it is important to realize that several interpretations are possible. (1) The growth coefficients may be different, with or without differences in the arithmetic and geometric constants. (2) The growth coefficients may be alike, but the initial relations, represented by the geometric constant of the allometric growth equation, may be different, so that the two lines are parallel. As a special case we may designate the condition in which growth is isometric. (3) Growth relations may be the same and may be expressed by an identical equation, but the slope of the line may not be isometric. In this case a group of specimens of small size will be

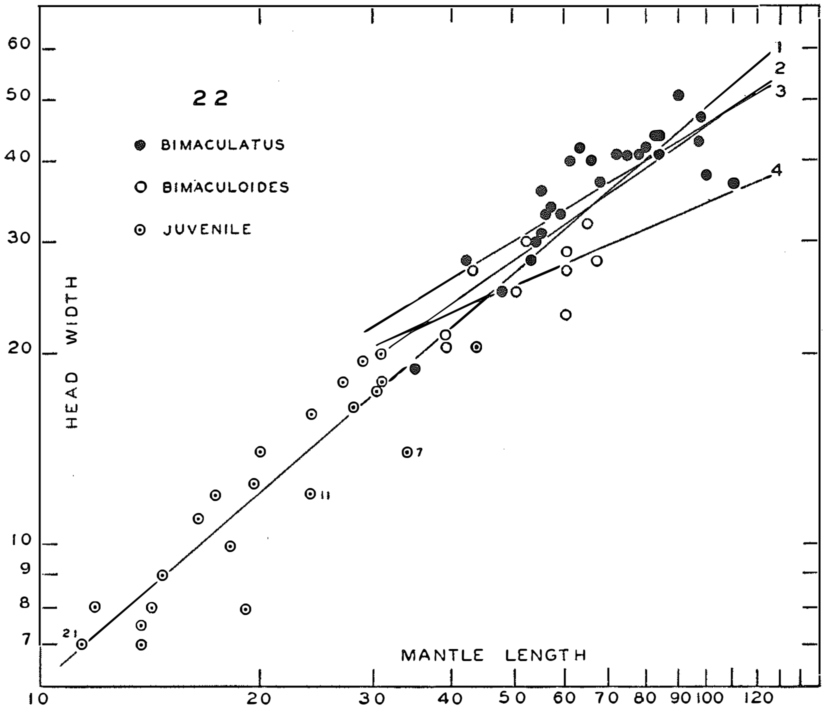

Figure 22. Relationship between head-width and mantle-length in *Octopus bimaculatus* Verrill, *O. bimaculoides* n. sp., and juvenile specimens of the *bimaculatus-bimaculoides* complex. The number (N), correlation coefficient (r), and the geometric and exponential constants (b and k) in the theoretical equation, $Y = bX^k$, are as follows:

	N	r	b	k
1. All specimens...........................	58	0.967	0.923	0.861
2. *O. bimaculatus* + *bimaculoides*............	36	0.821	1.842	0.698
3. *O. bimaculatus*..........................	26	0.817	2.740	0.613
4. *O. bimaculoides*.........................	10	0.652	4.596	0.440
The equation for juvenile specimens only is almost identical with that for the whole series and the line has been omitted.....................	22	0.916	0.933	0.851

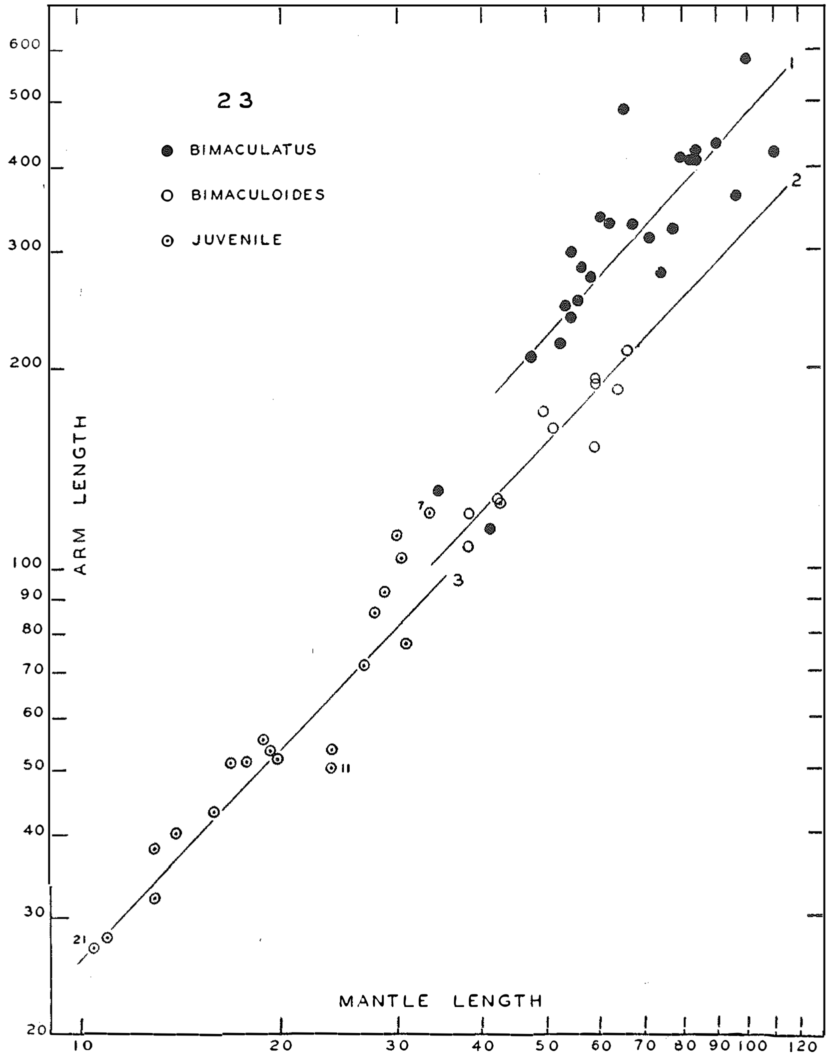

Figure 23. Relationship between arm-length and mantle-length in *Octopus bimaculatus* Verrill, *O. bimaculoides* n. sp., and juvenile specimens of the *bimaculatus-bimaculoides* complex. Constants in the theoretical equations (see Fig. 22) are as follows:

	N	*r*	*b*	*k*
1. *O. bimaculatus*	25	0.864	2.504	1.141
2. *O. bimaculoides*	10	0.937	2.490	1.046
3. Juveniles, AL under 100 mm	18	0.938	2.385	1.033

characterized by a different index from larger ones; if the coefficient is greater than one the index will be smaller and if it is less than one the index will be larger. The first two interpretations can only mean that we are dealing with dissimilar groups in which growth relations are different. The third interpretation can apply equally well to large and small members of the same species. It is proposed to analyze apparent differences between our two species in the light of these considerations.

The most striking difference between *bimaculatus* and *bimaculoides*, apart from the fundamental difference in egg size, is provided by relative arm-length. The difference between the mean values of the indices is highly significant, and in adult animals there is scarcely any overlapping of the extremes. Calculations (Fig. 23) show that arm-growth in respect to mantle-length is probably isometric in both species. The coefficients, 1.141 and 1.046 respectively, are not significantly different from each other, and neither is significantly different from one. The rather high value for *bimaculatus* is entirely due to the inclusion of two rather immature females of mantle-length 35 and 42 mm. (Nos. 13 and 14); the points for these two animals fall in line with those for juvenile specimens and *bimaculoides*. A much clearer picture is obtained if these two specimens are excluded from the calculation; the constants then become $N = 23$, $r = 0.801$, $b = 7.199$, $k = 0.898$. This treatment has the effect of reducing the slope of the line so that it becomes virtually isometric, as it evidently should be; at the same time it greatly increases the value of the geometric constant which, in the initial calculation, appeared fictitiously to be the same as for *bimaculoides*. The proper interpretation for the growth relations of arm-length in adults is the same as for head-width; that is, the two lines run parallel and are separated by a constant geometric difference which is apparently established at puberty. This point will be discussed further in connection with juvenile specimens.

The analysis of relative sucker-diameter is also illuminating. For purposes of calculation, the normal sucker-diameter of both males and females has been taken together in order to increase the numbers available for analysis. This neglects the tendency, discussed previously, for the normal suckers of males to be slightly larger than those of females; but the procedure is justified, since the sexes are about equally represented in both species. When normal sucker-diameter is plotted against mantle-length, the two species give parallel

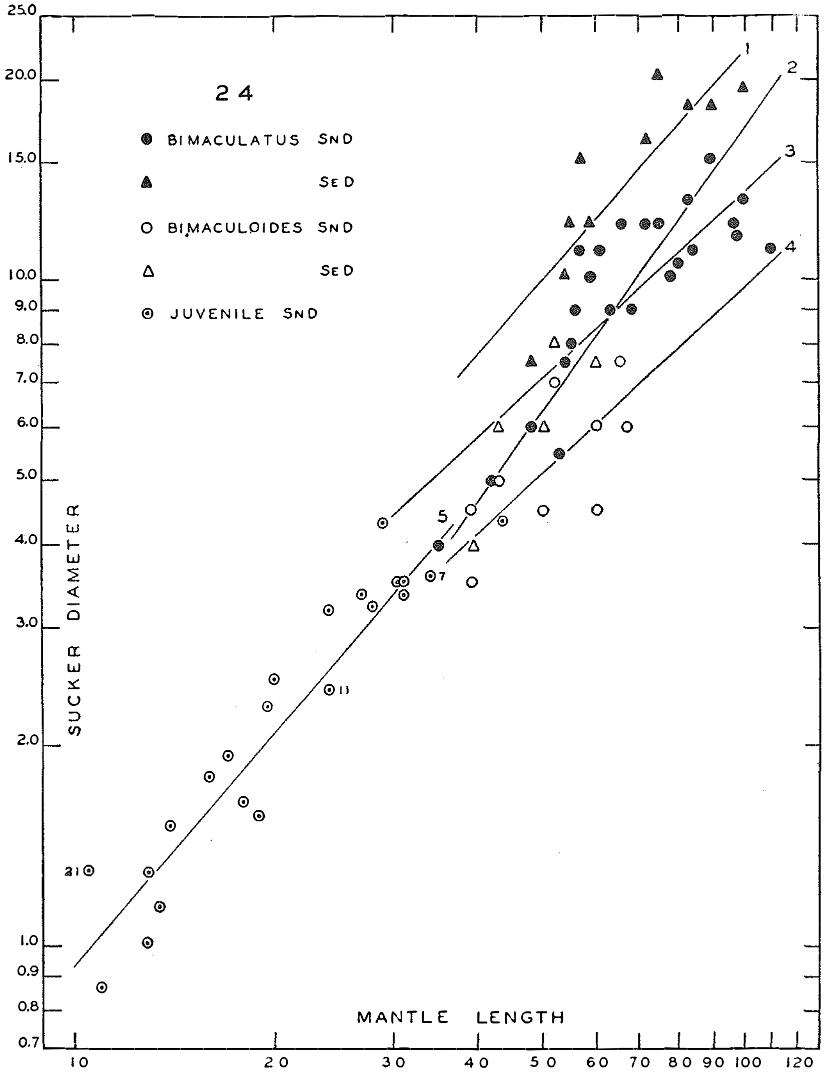

Figure 24. Relationship between normal (SnD) and special enlarged (SeD) sucker-diameter in respect to mantle-length in *Octopus bimaculatus* Verrill, *O. bimaculoides* n. sp., and juvenile specimens of the *bimaculatus-bimaculoides* complex. Constants in the theoretical equations (see Fig. 22) are as follows:

	N	*r*	*b*	*k*
1. *O. bimaculatus*, SeD	10	0.872	0.123	1.126
2. *O. bimaculoides*, SeD	5	0.780	0.0285	1.385
3. *O. bimaculatus*, SnD	26	0.815	0.217	0.897
4. *O. bimaculoides*, SnD	10	0.704	0.163	0.886
5. Juveniles	22	0.950	0.0633	1.174

curves (Fig. 24, lines 3, 4); the growth coefficients are alike, 0.897 and 0.886, and neither is significantly different from one. Growth is isometric and, as in the case of arm-length, we are dealing with two distinct populations separated by a constant geometric ratio of sucker-diameter in respect to mantle-length. On the other hand, when sucker-diameter is related to arm-length instead of to mantle-length, the two species may be treated as one; a single line (Fig. 25, line 2), with a

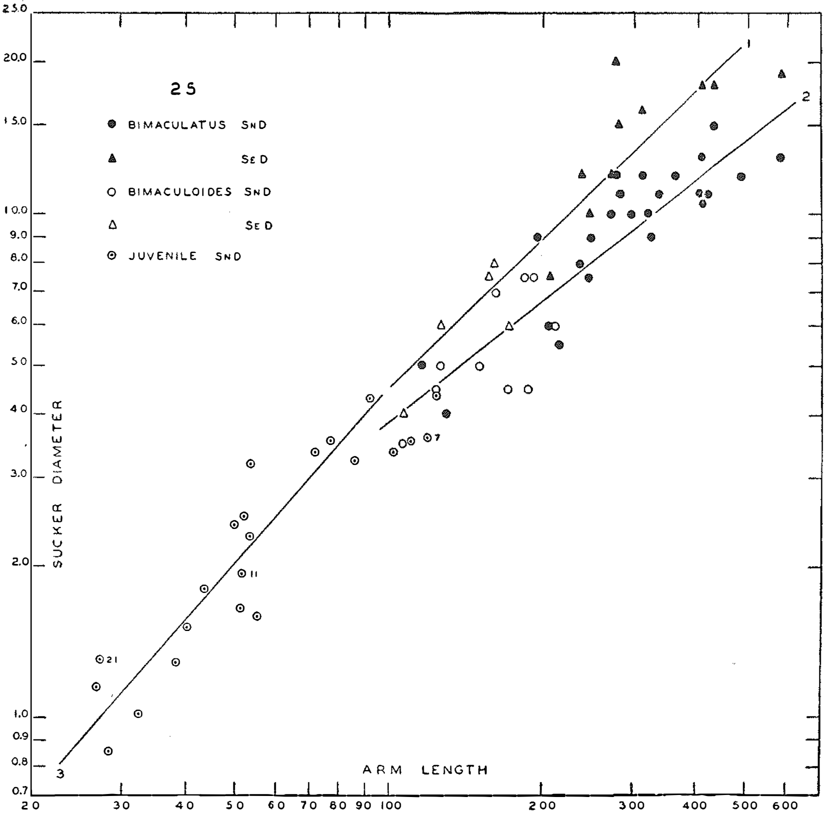

Figure 25. Relationship between normal (SnD) and specially enlarged (SeD) sucker-diameter in respect to arm-length in the *Octopus bimaculatus-O. bimaculoides* complex. Constants in the theoretical equations (see Fig. 22) are as follows:

	N	*r*	*b*	*k*
1. *O. bimaculatus* + *bimaculoides*, SeD	15	0.918	0.0505	0.979
2. *O. bimaculatus* + *bimaculoides*, SnD	36	0.915	0.0980	0.798
3. Juveniles, under 100 mm AL	18	0.911	0.0233	1.145

moderate degree of negative allometry, provides a reasonably good fit for the entire series of points ($k = 0.789, r = 0.915$). The value of the growth coefficient is significantly less than one ($s_{dk} = 0.0598$, $t = 3.371$).

The growth relationships of the specially enlarged suckers of males may be treated in a similar manner. When plotted against mantle-length (Fig. 24, lines 1 and 2), the two species must obviously be considered separately, but the numbers are undesirably small for statistical treatment. However, when plotted against arm-length (Fig. 25, line 1) the two species may be taken together, in which case the points fall smoothly about a single line. The corresponding equation indicates that the enlarged suckers are growing isometrically in respect to

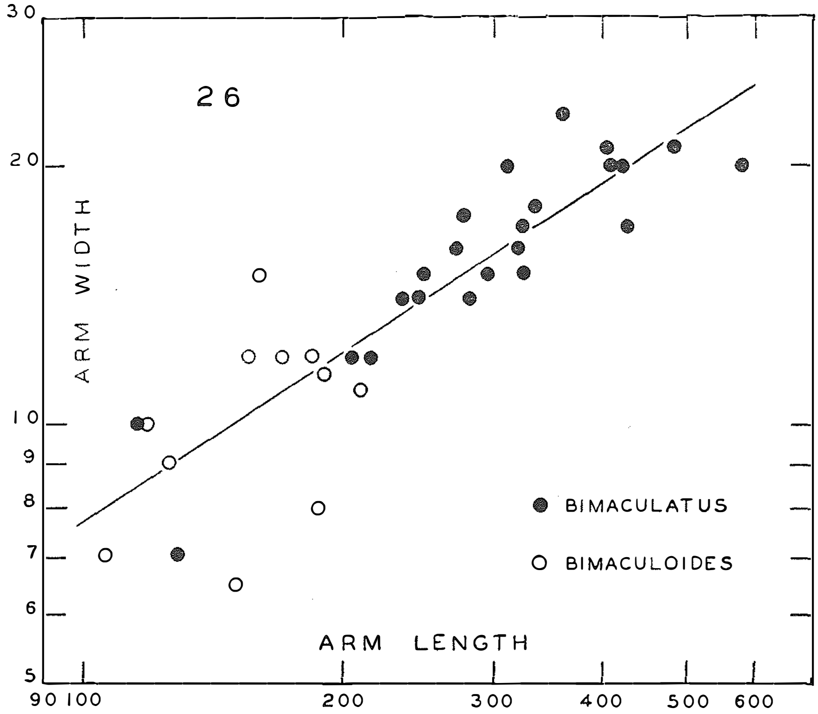

Figure 26. Relationship between arm-width and arm-length in the *O. bimaculatus-bimaculoides* complex. Constants in the theoretical equation (see Fig. 22) are as follows:

	N	*r*	*b*	*k*
O. bimaculatus + *O. bimaculoides*................	36	0.882	0.361	0.663

arm-length, the value of the growth coefficient being 0.979. Furthermore, this line is virtually a continuation of the line representing sucker-growth in juvenile specimens, which will be discussed subsequently. The results suggest some kind of an inhibition in the growth of normal suckers which takes place at puberty. The special suckers of males are established, not by an onset of positive allometry, as might have been anticipated, but by a simple continuation of the larval growth-rate which, in their case, is not subject to this inhibition.

Arm-width (Fig. 26) is also a simple allometric function of arm-length and, as in the case of the suckers, the two species can apparently be treated as one. The growth coefficient is negative, 0.663. Thus, in respect to arm-length, the arms of larger animals are relatively less stout, although they appear stouter when compared with mantle-length by means of indices. The difference between the mean arm-width indices undoubtedly resides in differences in the geometric constant similar to those obtaining in the case of head-width, arm-length, and sucker-diameter when these are plotted against mantle-length. The character is taxonomically unimportant and has not been studied further.

The hectocotylized arm appears, from the study of indices, to be relatively shorter in larger animals (*bimaculatus*). Analysis of the data (Fig. 27) provides a spectacular example of the operation of a strongly nonisometric growth coefficient in the creation of significantly different indices in animals of different size. The two species may be taken together and the points fall with remarkable fidelity about the theoretical line, yet, since growth relationships are negatively allometric, the hectocotylized arm of the smaller species is relatively longer than that of the larger.

The only other character that appeared worthy of further analysis is that of penis-length (Fig. 28). Unfortunately the numbers are too few and the variation is too great for an adequate treatment. One male *bimaculoides* has an abnormally elongated penis, due to irritation from the presence of pleurocercoid parasites in the mantle-chamber; the other four provide points that fall well below the theoretical line for *bimaculatus*. In the latter species, growth appears to be negatively allometric, $k = 0.654$. It may be anticipated that an adequate series of both species would provide two parallel lines differing primarily in respect to the geometric constant.

From the foregoing paragraphs it will be seen that the sucker-diameter, arm-width and length of hectocotylized arm, when treated as functions of arm-length, encompass both species. Differences between the two groups are due only to the slope of the allometric line. Thus the smaller species has relatively larger normal suckers, stouter arms and a longer hectocotylized arm, in respect to arm-length. On the other hand, the index of arm-length in respect to mantle-length, and therefore of its dependent variables when similarly treated, reflects a significant difference between the two species. Head-width and penis-length also belong in this category. Differences in bodily proportions between the adult populations of the two

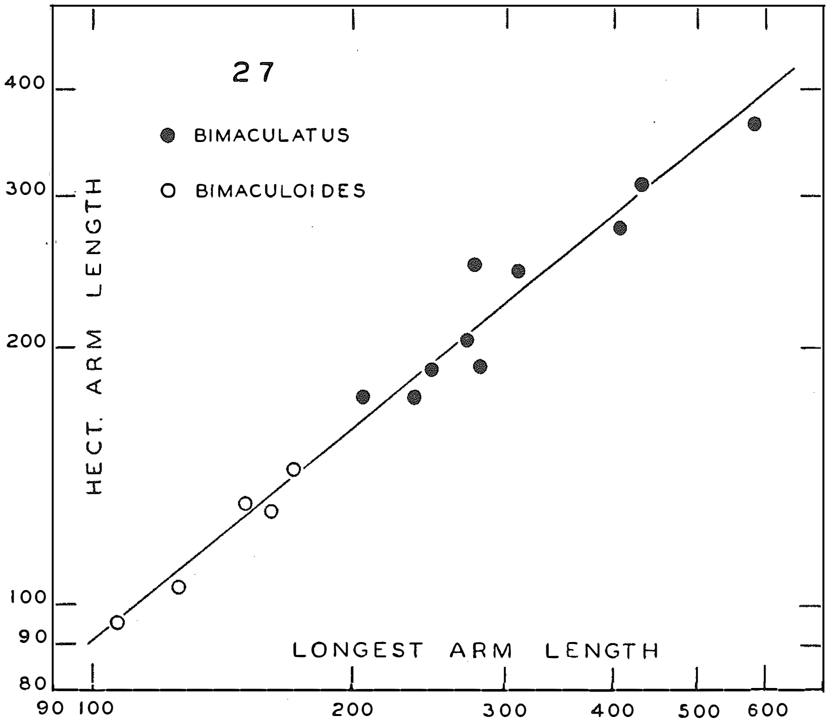

Figure 27. Relationship between length of hectocotylized arm and longest arm-length in the *O. bimaculatus-bimaculoides* complex. Constants in the theoretical equation (see Fig. 22) are as follows:

	N	*r*	*b*	*k*
O. bimaculatus + *O. bimaculoides*.................	15	0.985	0.208	0.821

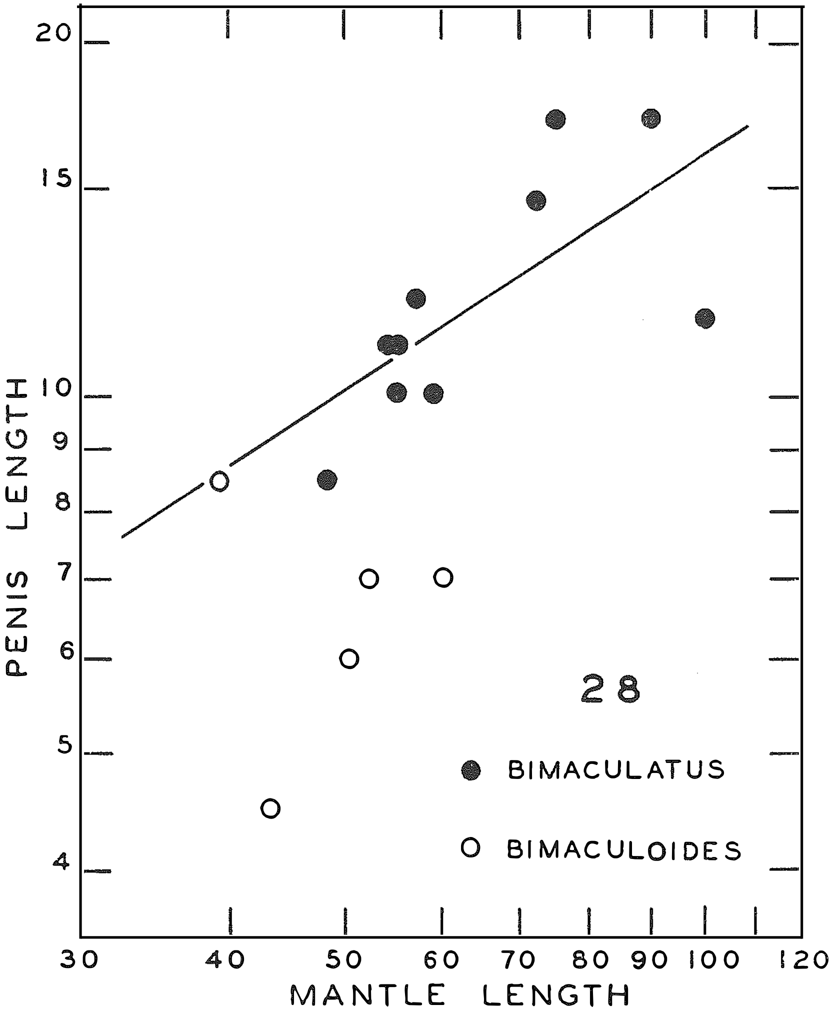

Figure 28. Relationship between penis-length and mantle-length in *O. bimaculatus* Verrill and *O. bimaculoides* n. sp. Constants in the theoretical equation (see Fig. 22), calculated only for *O. bimaculatus*, are as follows:

	N	*r*	*b*	*k*
O. bimaculatus..................................	10	0.687	0.782	0.654

species are not due to differences in the rate of allometric growth, but can all be traced to differences in the geometric ratio which are apparently established at the time of puberty. This point will be examined under a separate heading in connection with the juvenile population.

3. The Problems of Identification of Adult Specimens

Adult, and near adult females can be identified with complete certainty from the condition of the ovary. In the entire series studied, no intermediates have been encountered; either the eggs are large and less numerous or small and very numerous. Identification from external characters is less certain, as is that of males. External characters that may be used for the identification of females are four in number; of these, the two most satisfactory are absolute mantle-length and relative length of longest arm. Sucker-diameter and arm-width are merely functions of the latter and, although the means are significantly different, the range of the indices shows considerable overlap between the two species.

In the series studied there are four females of *bimaculatus* whose mantle-arm indices are as great, or nearly as great, as those of *bimaculoides*. Two of these are gravid females, Nos. 7 and 8, with mantle-arm indices of 26.9 and 28.6 respectively. No. 8 also has the more slender arms (AWI = 16.7) and smaller suckers (SnD = 9.2) characteristic of *bimaculoides*. Both specimens had been thoroughly dissected for Mesozoa before the measurements were made; therefore the mantle-lengths could only be estimated and are probably too large on account of stretching (No. 7: ML = 97 mm.; No. 8: ML = 120 mm.). If the true mantle-length were somewhat less, the mantle-arm index would be smaller and the sucker diameter and arm-width indices larger, bringing both specimens more fully in line with typical *bimaculatus*.

On the other hand, mantle-length is not in doubt in the case of two small and immature but identifiable females of *bimaculatus*. Specimen No. 13, with a mantle-length of 35 mm., could not have been identified correctly without an examination of the ovary. The mantle-arm index is high, 36.5, while the arm-width index, 19.0, and the sucker-diameter index, 11.9, are low. The mantle-arm index in particular is quite outside the range for adults of *bimaculatus*. Specimen No. 14, with a mantle-length of 42 mm., though less extreme, could not be certainly identified without an examination of the ovary: mantle-arm index, 27.3; arm-width index, 20.0; sucker-diameter index, 11.4.

In males there is no absolute criterion, such as is provided by the ovary of females; moreover, the absolute size difference between mature males of the two species is less clear cut than in the case of mature females. The four characters used for external identification of females may be supplemented by two more, the relative length of the hectocotylized arm and penis-length. Neither of these provides an absolute criterion for identification, but since both are independent of arm-length, the cumulative effect is helpful. In the limited series studied there is no overlap in the values of the arm-length indices of males and, as with females, arm-length certainly provides the most reliable external character for species identification. One male of *bimaculatus*, the COTYPE (No. 16), has arms that are shorter and more slender than normal (mantle-arm index 27.3, arm-width index 23.3), but in all other respects this animal is quite typical and there can be no doubt as to the fact that it is a male of the small-egg species. One male of *bimaculoides* (No. 11), with a mantle-length of 50 mm., has arms of intermediate proportions (mantle-arm index 29.5), although in other respects it is typical of the new species.

Evidently there are specimens of both species whose correct identification presents real taxonomic difficulty, and it is essential that great caution should be used.

4. THE PROBLEM OF JUVENILE SPECIMENS

In the present state of our knowledge the identification of juvenile specimens of the *bimaculatus-bimaculoides* complex is not possible. The series of 22 specimens is listed at the end of Part I; they were not studied as exhaustively as the adults, since measurements of the most important characters, mantle-length, head-width, arm-length, and sucker-diameter, showed that the assemblage could not be divided into two species-groups. No doubt a careful histological investigation of the condition of the developing ovary would make it possible to identify juvenile females, but this was not attempted, since it would constitute a major project and would require the study of properly fixed material. In the present state of our knowledge it seems very doubtful whether juvenile males could be identified at all.

Two interpretations of the situation must be considered. (1) The juvenile series may, by chance, consist almost exclusively of one or the other of the two species. (2) The divergence in bodily proportions does not commence until puberty, so that juvenile specimens are alike. These two hypotheses will be examined further.

A study of the best diagnostic character, relative arm-length, appears to indicate that the juvenile group is composed almost exclusively of the young of *bimaculoides*. The curve for juveniles (Fig. 23, line 3) is almost a direct continuation of that for the adults of *bimaculoides;* the values of the growth coefficient are essentially the same, and the small difference in the geometric constant is negligible. If *bimaculatus* is present, its mantle-arm relationships at arm-lengths of less than 100 mm. must be the same as those of *bimaculoides*. This interpretation is probably the correct one. It is supported by the condition of the two smallest identifiable but immature females of *bimaculatus* (Nos. 13 and 14) whose relative arm-lengths fall more nearly about the line for *bimaculoides*.

Sucker-diameter is also of unexpected interest. When sucker-diameter is plotted against mantle-length, the line for juvenile specimens (Fig. 24, line 5) appears to be most nearly a continuation of the line for the specially enlarged suckers of *bimaculoides*. It must be admitted that this is only a general impression; since there are only five males of *bimaculoides*, a statistical treatment can only show that it is not impossible that the two lines are identical. A much larger series would be necessary to prove that this is actually the case. However, since a study of adult specimens has indicated that the two species may be treated as one when sucker-diameter is referred to arm-length instead of to mantle-length, it has been possible to pursue the analysis a little further in this direction, which permits the use of a larger series of specimens. The line for juveniles (Fig. 25, line 3) can probably be interpreted as a continuation of the line for the relative growth of the specially enlarged suckers of males. The values of the growth coefficient are not significantly different from each other, and neither is significantly different from unity ($s_{dk} = 0.554$, for SnD juv. and SeD males; $t = 0.0296$); similarly, it is doubtful whether any importance should be attached to the difference in the b constant. On the other hand, the growth coefficient for the normal suckers of adults is significantly negatively allometric and under no circumstances can the relationships be regarded as a continuation of the line for normal suckers of juveniles. The normal suckers of juveniles are growing isometrically in respect to arm-length, like the enlarged suckers of males; they are not growing more slowly like the normal suckers of adults. This finding supports the hypothesis that normal sucker growth is inhibited after puberty. Finally, returning to the relationship between sucker-diameter and mantle-length, the same situation exists as in respect to arm-length. Either the juvenile group is composed almost exclusively of *bimaculoides*, or else the relatively larger sucker-diameter of *bimaculatus* is established by a rather rapid change in the geometric constant at the time of puberty. The latter interpretation seems probable.

The head-width of juvenile specimens has also been examined. The theoretical line for young animals has not been plotted since it is almost the same as one that was calculated for the entire population (Fig. 22, line 1); the value of k is not significantly different from unity ($s_{dk} = 0.266$, $t = 0.567$). The continuation of the line is such that the adults of *bimaculatus* tend to lie above it while the adults of *bimaculoides* tend to lie below. Interpretation is therefore complicated by a change in the relations of head and mantle when the animals approach sexual maturity, perhaps due to an enlargement of the reproductive organs since, in both species, the head-width becomes relatively smaller. At most it can be said that the data are concordant with a provisional hypothesis that the juvenile group is composed chiefly of *bimaculoides* and that a change in the head-mantle relationship takes place at a mantle-length of about 45 mm., where the lines for juvenile and adult specimens cross. Nevertheless, some of the young animals are probably *bimaculatus*, and the change in growth relations of head and mantle for this species may take place at a somewhat larger size and is probably accompanied by a "break." This point is difficult to prove on the available data, but it is clearly indicated by the following considerations. The theoretical line for the adults of *bimaculoides* crosses the line for juvenile animals in just about the place where it would be expected if the change in the growth coefficient were concomitant with the onset of puberty. On the other hand, the theoretical line for the adults of *bimaculatus* crosses the line for juveniles, which is not plotted in Fig. 22, but lies slightly below and divergent from line 1 (all specimens), at a mantle-length of about 100 mm., that is to say, long after the onset of puberty, which is at about 50 mm. The inference is that puberty is accompanied in this species not only by a change in the relative growth coefficient but also by a rapid change resulting in the establishment of a new initial ratio.

Collateral evidence that two species are involved in the juvenile group may be derived from a study of the mesozoan parasites. Three juvenile specimens were infested with a species that is characteristic of *bimaculatus* (see Part III); the rest, as far as studied, harbored the form that is peculiar to *bimaculoides.* Thus at least three juvenile individuals may be tentatively assigned to *bimaculatus;* they are Nos. 7, 11 and 21. The points for these specimens are marked with their respective numbers on the graphs, and it can be seen by inspection that they fall conformably among the points for the entire juvenile population.

Evidently the data do not permit one to conclude that the young of *bimaculatus* are morphologically distinguishable from those of *bimaculoides.*

PART III. BIOLOGY

1. Distribution and Ecology

Both *Octopus bimaculatus* and *O. bimaculoides* are quite abundant along the coast of southern and lower California. The geographical ranges of the two species coincide as determined thus far, but unfortunately neither the northern nor southern limits of either are known.

As a rule *O. bimaculatus* is found in the lower part of the intertidal area in the so-called *Laminaria* zone, where the larger seaweeds begin, or in deeper channels extending up into rocky areas. It also ranges on out into deeper water for an undetermined distance. Specimens are frequently taken from the end of the Scripps pier in about 20 feet of water; sometimes they are taken in lobster traps at somewhat greater depths.

On the other hand, *O. bimaculoides* is found higher in the intertidal area above the *Laminaria* zone, in areas uncovered by medium and very low tides. It is most abundant in rocky tidal flats where large numbers of loose boulders provide suitable hiding places, but it is also found in shallow bays and mud flat areas, under stones or boards or in holes in the mud. It has been termed the "mud flat octopus" by MacGinitie. To our knowledge it has not been taken in deeper water, such as from the end of the Scripps pier or in lobster traps.

Thus it appears that while the populations of the two species enjoy the same geographical distribution so far as has been determined, they are nevertheless separated to some extent by differences in ecological preferences, though these differences are not so great as to preclude some overlapping.

2. Reproduction and Mating Behavior

The breeding season of both species extends through the spring months from the latter part of March to the early part of July. During this time the females are found to contain large numbers of eggs in the ovary so that the body becomes fuller and more turgid than at other times. Females kept in captivity in separate tanks also develop mature ovaries at the appropriate season, laying the eggs and brooding them even though they are unfertilized. The eggs are laid at night and are fastened in clusters by means of a greenish adhesive substance plastered on the sides of the aquarium. Under natural conditions the festoons of eggs are fastened to the under side of rocks.

Occasionally there appears to be an inability to lay the eggs, at least in the case of captive females. The body of the octopus continues to become more swollen and turgid until it is markedly abnormal, and finally the octopus dies. When such a female is dissected, the space around the ovary is found to contain a considerable amount of serous fluid, and the eggs appear to be partially disintegrated. This has happened to individuals of both species in our aquaria.

The mating and egg-brooding habits of aquarium specimens of *O. bimaculatus* have been described by Fox (1938), and our observations agree in all respects with those reported in that paper. Mating takes place readily with little or no preliminary courtship. The two octopuses maintain a distance of about a foot or more apart. The male extends his third right arm and touches the female gently, promptly withdrawing it if she shows any signs of objection. Soon he inserts it her mantle cavity. The two octopuses remain motionless in this position for periods of an hour or more if undisturbed. Copulation occurs repeatedly during the breeding season.

Observations on the mating behavior of *O. bimaculoides* are much more limited. The following account is based largely on experiments involving one female (No. 2) which was taken May 29, 1948 brooding a clutch of eggs. The fact that she had already laid eggs may be responsible for her negative attitude towards the overtures of the males.

When she was put in a large aquarium with two male specimens no actual contacts were observed, although the males appeared to become quite excited. They swam rapidly around the tank, sometimes bumping against the female and then swimming away in haste. Sometimes they approached her swimming forewards, with the umbrella spread wide open and with cirri raised. Often they would assume a mottled coloration with blotches of yellowish and black over the body. The female remained partly hidden behind a small stone and raised her forearms defensively if the males came too near, whereupon they would immediately withdraw or cautiously extend an arm out toward her from the extreme distance which they could reach. When males were placed by themselves in the large tank they did not display this excited attitude towards each other.

In one case when a male was placed in a smaller glass aquarium with the female he promptly showed great interest, and after a few seconds of preliminary feeling about by both animals he grappled with her. They wrestled for several minutes. In the tangle of 16 squirming arms it became impossible to tell which was which, or whether or not copulation actually had taken place. This same performance was repeated in a later trial. However, no such wrestling was observed in the case of *O. bimaculatus*, nor when only males of *bimaculoides* were placed together in the small aquarium.

It is uncertain whether this wrestling represented mating or simply fighting. Further uncertainty was introduced because one small octopus (*O. bimaculatus* No. 14), which the junior author had included among the males which had displayed this interest towards the female *bimaculoides*, proved upon dissection to be a small female of *O. bimaculatus*. It is possible that two of the small octopuses became interchanged during preservation and packing.

When the female *bimaculoides* was placed with a male *bimaculatus*, neither of them showed any interest whatsoever in each other. The same was true when the male *bimaculoides* and female *bimaculatus* were placed together.

In summary it seems possible that the courtship and mating behavior of the two species may be characteristically different, although this conclusion is based on observations of the behavior of only a few specimens, one of which may have been diagnosed incorrectly at the time. The complete lack of interest shown by males of each species toward females of the other species, especially at a time when they had invariably displayed prompt interest in females of their own sort, indicates that there is a real difference between the two species. It seems unlikely that cross mating takes place even where the two species occur in the same area, as at Devil's Slide, La Jolla, California.

3. SPECIFICITY OF THE MESOZOAN PARASITES

In order to determine whether these two species of octopus harbored the same or different species of dicyemid mesozoans, the junior author's slide collection of Mesozoa was re-examined, since most of the collection had simply been listed previously as taken from *O. bimaculatus* (McConnaughey, 1941, 1949*a* and *b*). After the determination of the Mesozoa had been made they were matched with the data on the cephalopods from which they had been taken. The findings are summarized in Table XIII, where the host specimens for each species of mesozoan are listed. For convenience in analysis the male, female, and unsexed specimens are listed separately, and in the case of females with developed eggs in the ovary the type of egg present is indicated.

It will be seen by inspection that all of the egg-bearing females containing *Dicyemennea abelis* were of the small-egg type, *O. bimaculatus*, while all of those containing *D. californica* were of the large-egg type, *O. bimaculoides*. Furthermore, it will be noted that the data for the remaining females and for the males are consistent with the conclusion that *D. abelis* is characteristically a parasite of *O. bimaculatus* while *D. californica* is restricted to *O. bimaculoides*. The mature octopuses containing *D. abelis* are consistently larger (heavier) as a group than those infected with *D. californica*, with little overlap occurring between the extremes of the two groups.

Dicyemennea granularis apparently may infect either species, and *Dicyema sullivani* has been found too few times to warrant a definite statement with regard to its host limitations. In all instances to date (3) it has been found in *O. bimaculoides* in company with *D. californica*.

Regarding the juvenile specimens, it seems likely that an analysis of their mesozoan parasites may prove to be the most reliable, if not the only definite, guide to their determination. Since the octopus population along the coast of southern California appears to be 100% infected with Mesozoa, and since the infection is acquired at a very early age, all the specimens ordinarily found along the coast are infected. Therefore the analysis of the parasites could be a regularly available and useful diagnostic method.

TABLE XIII. DICYEMID PARASITES OF *Octopus bimaculatus* VERRILL (A) AND *O. bimaculoides* N. SP. (B). HOST NUMBERS ARE THOSE IN THE CEPHALOPOD REGISTER OF THE JUNIOR AUTHOR RATHER THAN THOSE ASSIGNED IN THE PRESENT PAPER, BECAUSE THE LIST INCLUDES A NUMBER OF SPECIMENS WHICH WERE DESTROYED DURING DISSECTION, OR WHICH, FOR OTHER REASONS, WERE NOT SUBMITTED FOR IDENTIFICATION.

Females				*Males*			*Sex undetermined*		
No.	*Wt. (g)*	*Egg type∅*	*Species**	*No.*	*Wt. (g)*	*Species**	*No.*	*Wt. (g)*	*Species**
(a) Parasitized by *Dicyemennea abelis* McConnaughey.									
L–21	444	—	—	L–9	240	—	L–19	140	—
L–24	398	—	—	L–16	817	A	L–20	1	—
L–37	1679	—	—	L–22	401	—	L–28	4	—
L–66	614	—	—	L–27	—	C	L–36	0.8	—
L–68	2011	S	—	L–50	6	C	L–39	1	—
L–69	620	S	A	L–67	259	—	L–56	79	C
L–73	843	S	—	L–75	804	A	L–61	2	—
L–74	987	S	A	L–76	638	A	L–62	1	—
L–77	1055	S	A	L–81	126	A	L–63	3	—
L–79	39	S	A	L–113	329	A	107	—	—
L–107	151	—	—	L–115	263	A	110	—	—
L–112	398	—	—	L–116	229	A	111	—	—
L–114	504	S	A	L–117	204	A	113	—	—
L–124	793	S	A	L–118	552	A			
L–127	848	S	A	L–131	266	A	Ball group†	—	—
L–128	903	S	A						
L–129	364	S	A						
L–130	422	S	A						
L–138	823	S	—						
(b) Parasitized by *Dicyemennea californica* McConnaughey.									
L–29	23	—	—	L–12	2.5	C	L–10	1.6	C
L–33	27	—	C	L–23	286	—	L–13	2.4	C
L–46	45	—	—	L–38	33	—	L–14	—	—
L–48	29	—	C	L–45	22	—	L–15	0.8	C
L–51	57	—	C	L–47	73	—	L–25	1.0	—
L–54	4	—	—	L–49	25	C	L–34	1.2	—
L–59	345	L	—	L–58	32	—	L–35	1.0	—
L–65	84	L	—	L–71	85	B	L–41	2.0	—
L–80	21	—	C	L–102	4	C	L–42	2.5	—
L–122	59	—	—	L–133	12	C	L–43	0.8	—
L–123	172	L	B	L–134	3	C	L–44	1.0	—
L–125	135	L	B	L–136	7	C	L–52	7.0	C
L–132	49	L	B	L–140	11	C	L–55	6.2	—
L–135	15.5	—	C	L–145	—	—	L–57	15.0	—
L–149	184	L	B	101	—	—	L–64	—	—
				103	—	—	L–100	1.5	—
(c) Parasitized by *Dicyemennea granularis* McConnaughey.									
L–8	185	—	—	L–38	33	—	102	—	—
L–70	695	S	—	L–47	73	—			
L–72	55	L	B	L–53	670	—			
L–77	1055	S	A						
L–78	981	S	A						
L–124	793	S	A						
L–127	848	S	A						
L–138	823	S	—						
L–141	575	S	—						
L–149	184	L	B						
(d) Parasitized by *Dicyema sullivani* McConnaughey.‡									
L–65	84	L	—	L–58	32	—	L–14	—	—

DISCUSSION

1. The Status of the Genus *Paroctopus*

The generic name *Paroctopus* was proposed by Naef (1923) for *Octopus digueti* Perrier and Rochebrune, a species from Lower California that lays large eggs very different in size from those of any of the species of *Octopus* with which Naef was familiar. Robson (1929) accepted the new genus with reservations. Doubtful of the importance of egg-size as a systematic criterion, Robson attempted to amplify the diagnosis of the genus; the possession of a relatively long hectocotylus (7–20% of the arm-length), the (usually) short arms and squat body were added to the generic definition. Several other Pacific species were included by Robson on the basis of large egg-size and associated characters. At a later data the senior author (Pickford, 1945) assigned two Caribbean species with large eggs and a relatively long hectocotylus to the genus *Paroctopus*. However, one of these (*Octopus briareus* Robson) has long arms; moreover, the possession of a relatively long hectocotylus is not confined to species that lay large eggs. Furthermore, grave doubts were entertained as to exactly what absolute or relative egg-size should be considered to constitute a "large egg," and an attempt was made to set up an index of relative egg-length in respect to mantle-length (Pickford, 1946).

The situation now discovered in the sibling species of *O. bimaculatus* throws new but not altogether unexpected light on the problem. The two species under investigation are so closely alike, except in respect to egg-size, that they might easily have been considered as subspecies were it not for the fact that they are sympatric. This similarity is fundamental, not superficial. Furthermore, the hectocotylus is minute, as it is in *Octopus vulgaris* Lamarck, and although it is true that the species that lays small eggs has relatively longer arms, the over-all similarity between the two is so great that a generic separation on this basis is excluded. The genus *Paroctopus* cannot be sustained, even at the subgeneric level.

[ø] Egg type: S = small, L = large.

[*] Species: A = *O. bimaculatus*, B = *O. bimaculoides*, and C = juvenile specimens examined in present investigation that are not identifiable. A dash (—) in this column indicates that the specimens were not preserved for identification.

[†] Ball group: Five slides made by Kritchevsky, 1932, from "Octopus bimaculatus" obtained from fishermen.

[‡] All three of these octopuses also contained *D. californica*.

2. THE STATUS OF *O. bimaculatus* AND *O. bimaculoides* AS SIBLING SPECIES

When the problem first came to our attention, two possibilities were considered: (1) That the "large-egg form" was, in fact, a sibling species, and (2) that the "large-egg form" might be a phase of the "small-egg form"; for example, females in their first year of spawning might lay fewer and larger eggs. This hypothesis, which was suggested by the observation that "large-egg" females are of smaller bodily size and more closely resemble juvenile specimens in bodily proportions, must be rejected. In the entire series no females were discovered that contained, or had spawned, eggs of intermediate size. The young ova developing in the ovary of the HOLOTYPE of *bimaculoides*, which had recently spawned large eggs, are clearly of the large-egg type; no metamorphosis towards a "small-egg" stage is indicated. Furthermore, the "large-egg form" is not only somewhat smaller but differs from the true *bimaculatus* in relative arm-length and in other bodily proportions in a statistically significant manner; it appears to inhabit a somewhat different ecological environment, females are associated with similar small sized males, and neither sex appears to mate with the opposite sex of the larger species. Finally, the "large-egg form" harbors a different mesozoan parasite, not found in the true *bimaculatus*. There can be no doubt that we are dealing with a sibling species and that the first hypothesis is correct.

The modern concept of sibling species is largely due to Mayr (1942, 1947, 1948), who first proposed a suitable English term for the phenomenon. The concept of sympatric sibling species requires (1) that they should not habitually interbreed, i. e., that there should be an effective method of sexual isolation preventing genic interchange between the two populations, and (2) that the two species should inhabit ecologically different habitats. Without such environmental preferences the species would be brought into direct competition, so that one or other would be eliminated by natural selection. Our two species fulfill both these requirements, since they appear to be sexually isolated and ecologically segregated from each other.

In regard to the origin of such sympatric siblings, Mayr is of the opinion that geographical isolation is in all cases a necessary prerequisite for the evolution of subspecifically and specifically different populations, in accordance with the well known concepts of Wright. Mayr goes even further than this and postulates that subspeciation and speciation in geographically isolated populations is necessarily accompanied not only by morphological and physiological differentiation but also by ecological differentiation in favor of divergent environmental requirements. The latter hypothesis may be disputed, but certainly it is clear that ecological differentiation is a necessary preliminary to interdigitation leading to the co-occurrence of two related but noncompeting species in the same geographical area. Otherwise, a breakdown of the geographic barrier would lead to the disappearance of one of the competing species, either through natural selection, or, in the absence of effective sexual isolation, through hybridization and swamping accompanied by natural selection of the best adapted combinations.

It is unfortunate that the wider distribution of the members of the *bimaculatus-bimaculoides* complex is not known. All records of both species are confined to some 120 miles of coastline between Los Angeles and Ensenada, just south of the Mexican border. We are able to exclude Verrill's supposed record of this species from San Salvador and Panama, since the specimens, now in the collection of the Peabody Museum, belong to a small ocellate species with a relatively long hectocotylus, quite distinct from the *bimaculatus* complex. However, neither the northern nor the southern limits of either of our species are known, and we are unable to say whether one or the other of them may be predominantly a more southern form. The concept of geographical isolation as a prerequisite to speciation would lead one to suppose that this must be the case, and certainly the evidence is not such as to permit proof of the much debated question of sympatric speciation.

3. The Significance of Large Egg-size

The possession of large eggs must have far reaching ecological significance but, in the present case, the interpretation is not clear. The work of Thorson (1946 and earlier references therein; 1948) on other groups of marine invertebrates has brought to light the fact that yolky eggs, viviparity, and similar devices that eliminate the necessity for a planktonic, feeding larval stage are associated with conditions of life in the high arctic and antarctic and in the deep waters of the ocean. However, most species of the former genus *Paroctopus* are tropical or subtropical forms, so that the adaptation, in this instance, must be associated with other causes than the lack of adequate nutrition during planktonic larval life. A more intensive study of the ecology and breeding habits of the two species is necessary. *O. bimaculoides*, called the "mud flat octopus" by G. E. MacGinitie (in litt.), is apparently an inshore species; *O. bimaculatus* favors deeper water and rocky bottoms. Possibly the conditions on the tidal flats operate in favor of a large-sized larva that can assume a benthonic mode of life from the time of its emergence and hence does not need to pass through a transitory planktonic phase. A planktonic larva is not known to exist in the case of *bimaculatus*, but it may be assumed to occur by analogy with the larval stages of the better known small-egg species of *Octopus*.

4. The Morphological Differentiation of the Siblings

Analysis of the allometric growth relations was restricted to selected characters of taxonomic importance. Nevertheless, the findings brought to light an interesting and unexpected situation. It appears that the morphological divergence of the two species does not become apparent until puberty, and that it resides primarily in a set of "breaks" in the growth relationships of the larger species, *bimaculatus*.

The juvenile population is apparently homogeneous; nevertheless, there is reason to suspect that both species are represented. Three juvenile animals were hosts to a mesozoan parasite that is found otherwise only in *bimaculatus*, while most of the others are known to have harbored the characteristic parasite of *bimaculoides*. Furthermore, two of the sexually immature but identifiable females of *bimaculatus* belong to the juvenile population in regard to their bodily proportions. The evidence, although indirect, is thus fairly conclusive, and, in the absence of further information, we must assume that the juveniles of *bimaculatus* are superficially indistinguishable, or nearly indistinguishable, from those of *bimaculoides*.

The *bimaculoides* group, which becomes recognizable at puberty, appears on the graphs either as a direct continuation of the juvenile group, e. g., arm-length in respect to mantle-length, or shows an abrupt change in the allometric growth rate, e. g., relative head-width in respect to mantle-length, which changes from isometry to negative allometry. On the other hand, the *bimaculatus* group shows the characteristic "break" referred to above; thus the relative arm-length increases quite suddenly, although subsequent growth is isometric in respect to mantle-length, as before. The theoretical line runs parallel to the juvenile + *bimaculoides* line but at a higher level. Similarly, the changed growth rate of the head, which becomes negatively allometric in respect to mantle-length as in *bimaculoides,* is apparently accompanied by a "break," so that the new relationship is established at a higher, but parallel, level.

It is not surprising that changes in bodily proportions should become manifest at puberty. Changes similar to those noted above, which affect almost every measurable part of the body, accompany the metamorphosis of the four-finned larva of *Vampyroteuthis infernalis* Chun into the two-finned adult animal (Pickford, 1949). The transformation of a juvenile into an adult *Octopus* is less spectacular than the metamorphosis of this archaic bathypelagic species, but it cannot be doubted that processes of a similar nature are at work. The point of interest is that it is these changes, which accompany the onset of puberty, that lead to the morphological differentiation of the species. Moreover, *bimaculoides* is more larval in character; it becomes sexually mature with a minimum disturbance of the bodily proportions, although changed growth rates appear in respect to certain characters. On the other hand, in *bimaculatus* the onset of puberty is accompanied by a "break" that reflects radical changes in the bodily proportions. The differentiation of the two species is effected primarily by this "break" rather than by differences in the rates of allometric growth.

The differentiation noted above rests on a changed relation of the part studied in respect to mantle-length; it becomes evident whenever mantle-length is treated as the independent variable in the relative growth equation. The absolute mantle-length of *bimaculatus* is of course greater, but its relative length is less in respect to head-width, arm-length, sucker-diameter, and probably also in respect to many other characters. On the other hand, the components of the arm-crown behave as a unit. If the allometric growth rates are taken into account, the arm-crown of *bimaculatus* can be treated as a larger replica of the arm-crown of *bimaculoides,* and the two species can be lumped together, since a single theoretical line provides the best fit for the entire series of adult animals. This relationship exists when the following characters are plotted against the length of the longest arm: arm-width, length of hectocotylized arm, and diameter of normal and of specially enlarged suckers.

The apparent differences in bodily proportions between the two species may be traced to two quite different causes, viz., real differences that are established by the "break" at puberty and fictitious differences that result from nonisometric growth of component parts of the arm-crown. The relative length of the hectocotylized arm, which is significantly greater in *bimaculoides*, provides a striking example of the operation of nonisometric growth in the creation of a difference that depends entirely on the smaller average size of the animals. The difference is a real one only in so far as it is the resultant of a real difference, the smaller bodily size.

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SUMMARY

1. The Two-spotted Octopus population of the southern California Coast consists of two sympatric, sibling species that have been confused hitherto under the name *Octopus bimaculatus* Verrill. One of the siblings, the true *bimaculatus*, lays minute eggs (1.8–4.0 mm. in length), usually with rather long stalks, that are attached in festoons similar to those of *O. vulgaris* Lam. The other, for which the name *O. bimaculoides* n. sp. is proposed, lays large eggs (9.5–17.5 mm. in length), usually with relatively shorter stalks, that are attached in small clusters.

2. *O. bimaculatus* and *O. bimaculoides* are closely and fundamentally alike. The form of the jaws, radula, hectocotylus, spermatophores,

ocellus, gills, arrangement of dorsal cirri, and many other features, are essentially similar.

3. *O. bimaculatus* is a larger animal (av. mantle-length of females 88 mm., of males 68 mm.), the arms are relatively longer (av. mantle-arm index 23) and both the normal and specially enlarged suckers are relatively larger (av. normal sucker-diameter index 14; av. enlarged sucker-diameter index 19). The penis is relatively longer (av. penis-length index 19), but the hectocotylized arm is relatively shorter (av. hect. arm-length index 75).

4. *O. bimaculoides* is smaller (av. mantle-length of females 58 mm., of males 49 mm.), the arms are relatively shorter (av. mantle-arm index 34) and the suckers are relatively smaller (av. normal sucker-diameter index 10; av. enlarged sucker-diameter index 13). The penis is relatively shorter (av. penis-length index 14), but the hectocotylized arm is relatively longer (av. hect. arm-length index 84).

5. The juvenile population appears to be morphologically homogeneous; nevertheless both species are probably represented. The differentiation of the two species is effected at puberty. The transformation of juveniles into adults of *bimaculoides* is accomplished with a minimum disturbance of bodily proportions, although some relationships reflect an abrupt change in the allometric growth coefficient. Thus the relative arm-length remains unchanged while relative head-width changes from isometry to negative allometry in respect to mantle-length. The transformation of *bimaculatus*, on the other hand, is accompanied by a characteristic "break" in the growth relationships, although the adult growth relations of this species do not differ from those of *bimaculoides* in respect to the growth coefficient.

6. The "break" that accompanies puberty in *bimaculatus* affects all relationships in which mantle-length is taken as the independent variable. The true differentiation of the species is effected by this "break."

7. The parts of the arm-crown behave as a unit, and the growth relationships of its component parts, e. g., arm-width, sucker-diameter, length of hectocotylized arm, are identical in the two species which, for this purpose, may be taken together. Secondary differences between the species arise as a result of nonisometric growth of components of the arm-crown; thus the length of the hectocotylized arm in respect to longest arm-length is negatively allometric, and therefore

the smaller species, *bimaculoides,* has a relatively longer hectocotylized arm.

8. The suckers of juvenile animals are growing isometrically in respect to arm-length. At puberty the specially enlarged suckers of males continue to grow at the larval rate, whereas the relative growth rate of normal suckers shows an abrupt change to negative allometry. The change in the growth coefficient appears to indicate that there is an inhibition which affects all except the specially enlarged suckers of males.

9. Although the two species are sympatric they inhabit ecologically different environmental niches, and therefore, in accordance with the theory of Mayr, they are not brought into direct competition with each other. *O. bimaculatus* lives in deeper water and on rocky bottoms; *O. bimaculoides* has been called by G. E. MacGinitie the "mud flat octopus"; it occurs in shallower water, sometimes in rocky areas but usually where the rocks rest on a soft or sandy substratum.

10. Males of *bimaculatus* will not copulate with females of *bimaculoides,* and vice versa. The second postulate in the concept of sympatric sibling species, sexual isolation, is therefore fulfilled.

11. *O. bimaculatus* is parasitized by the mesozoan, *Dicyemennea abelis* McConn.; *O. bimaculoides* is parasitized by *D. californica* McConn. A third species of mesozoan, *D. granularis* McConn., occurs in both *bimaculatus* and *bimaculoides.* Most of the juvenile animals were infected with *D. californica* and therefore they may be attributed to *bimaculoides;* however, three morphologically indistinguishable specimens were infected by *D. abelis.* This is regarded as indirect evidence that both species are present in the juvenile population.

12. Large egg-size may be correlated with the elimination of a planktonic larval stage in the species that inhabits tidal mud flats.

13. Both species are known only from the coast of southern California, between Los Angeles and Ensenada just south of the Mexican border. The wider distribution is not known. Possibly one of them may be a more southern species, in accordance with the generally accepted hypothesis that speciation can take place only in geographically isolated populations and that intermingling is a secondary phenomenon. Verrill's supposed records of *O. bimaculatus* from San Salvador and Panama are erroneous; his specimens belong to a quite different and as yet undescribed species.

14. The genus *Paroctopus* Naef cannot be sustained, either at the generic or at the subgeneric level, because of the extremely close similarity of the sibling species which differ from each other primarily in respect to the supposed generic character, large egg-size.

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