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OCTOPUS DOFLEINI (WÜLKER)

BULLETIN
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Octopus dofleini (Wülker)

Grace E. Pickford

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Octopus dolphini (Wülker), the Giant Octopus of the North Pacific

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by Alexander Petrunkevitch

ABSTRACT

The taxonomic status of the giant octopus of the North Pacific has been re-evaluated on the basis of published descriptions and new material from Alaska and the Pacific coast of North America; in some instances, previously described specimens have been re-examined. The results may be summarized as follows. (1) The Holotype of Octopus dobleini (Wülker) is lost, but Sasaki’s hypothesis that it was an immature male of the giant Japanese species is accepted. (2) Sasaki’s description of the Japanese species, O. dobleini, agrees in all major taxonomic characters with that of newly studied sexually mature specimens from the Puget Sound–San Juan Archipelago, Washington State. However, the specimens from Washington differ from the Japanese specimens in two minor respects; the lateral limbs of the funnel organ are shorter than the median limb, and the hectocotylized arm is almost as long as its mate of the opposite side; these differences are of subspecific significance. (3) The Holotype and Paratype of O. apollyon (Berry) from Alaska cannot be found. The Alaskan form of the giant octopus is redescribed on the basis of juvenile and immature specimens in the U.S. National Museum. The Holotype of O. gilbertianus (Berry) has been re-examined and is in essential agreement with the revised description of O. apollyon. All major characters of the Alaskan population agree with those of O. dobleini, but the Alaskan specimens are intermediate between the Japanese and Washington representatives in respect to the two subspecific characters noted above. (4) Published descriptions of specimens of the giant octopus from Siberian waters (Kondakov; Joubin)
suggest that these animals are essentially the same as those from Alaska. (5) Specimens from the Far North (Alaska and Siberia) show three minor characters that appear to separate them from both the Japanese and the American subspecies: the short first arms, the tendency toward a larger relative sucker diameter, and the distinctive groove on the rostrum of the jaw (first noted by Kondakov). The groove on the jaw is seen only in larger specimens and is thought to be an ecological character, reflecting cessation of growth during the sub-arctic winter. (6) On the basis of the foregoing statements it is proposed that three subspecies of *O. dofleini* be recognized: *O. d. dofleini* (Wülker. emend. Sasaki) from Japan, *O. d. apollyon* (Berry) from the Pacific Far North, and *O. d. martini* N. SunsP. from the Pacific coast of Washington. (7) The subspecific status of *O. dofleini* from California could not be resolved on the basis of the few poorly preserved specimens available for study. (8) *O. madokai* (Berry) from Japan may be referable to *O. d. dofleini*, but the problem requires further study. (9) The holotype of *O. hongkongensis* Hoyle is a sexually mature male of a different species. (10) Two specimens identified by Robson as *Paroctopus apollyon* are excluded from the synonymy of *O. dofleini*, but their status is not resolved.

**INTRODUCTION**

The present investigation was initiated ten years ago at the request of Dr. Arthur W. Martin, who was anxious to know the correct scientific name of the giant octopus of the Pacific, employed in his laboratory for physiological investigations. For this study, Dr. Martin provided twelve specimens, which included four mature males and a gravid female (see pp. 10 and 11). The problem proved to be frustrating and difficult. It was necessary to evaluate published descriptions of previously recorded specimens ranging from Japan via the Pacific Far North to Washington and California, and, when possible, to re-examine the original material on which these descriptions were based. No attempt has been made to re-examine small specimens, such as those described by Berry (1912), unless such re-examinations were imperative to the resolution of nomenclatural problems.

Members of what Berry (1953) has termed the "*dofleini-apollyon*" complex have been described under various names; many of the earlier descriptions are inadequate, although Verrill (1883) gave a good account of two large specimens from California. Berry (1912) described or recorded numerous specimens, from Alaska to California, but most of these were of small size, probably juveniles, and some undoubtedly belong to other species. Sasaki (1929), on the other hand, gave an excellent account of sexually mature specimens from Japan.

During this investigation it became evident that some supposed specimens of the giant octopus could be excluded from the synonymy of the "*dofleini-apollyon*" complex. These are: the type of *Octopus hongkongensis* Hoyle, which, on re-examination, has proved to be a distinct and valid species; and two specimens in the British Museum (Natural History), erroneously assigned by Robson (1929) to *Paroctopus apollyon* (Berry). A discussion of these specimens is given in Appendix B (p. 61). The material reviewed in the body
of this article includes only those specimens that can be assigned with reason­able certainty to Octopus dojleini (Wülker), or that cannot be decisively ex­cluded from *dojleini*.

There are, of course, other large or moderately large species inhabiting the areas under investigation, but these can readily be excluded on the basis of decisive taxonomic characters. The largest of these is *Octopus conispadiceus* (Sasaki), which attains a mantle length of 210 mm; it is distinguished, among other features, by the **VV** form of the funnel organ. The same condition obtains in *O. californicus* (Berry). Kondakov (1941) recorded both of these species for the Far Eastern Seas of the U.S.S.R. and separated them, rather unconvincingly, according to skin ornamentation. *Octopus tenuecirrus* (Sasaki), which reaches a mantle length of 160 mm, bears a superficial resemblance to *O. do­jleini* but is decisively separated from it by the short spermatophores and the form of the penis. Other large Pacific species, such as *O. vulgaris* Lamarck, *O. macropus* Risso [= *O. luteus* (Sasaki)], and *O. cyaneus* Gray (= *O. marmoratus* Hoyle), are well-known forms that may be dismissed without further dis­cussion. Nearly all of the Japanese species recorded by Sasaki (1929) were described on the basis of adult animals, usually males. In such instances there is no possibility that small or medium-sized species recognized by him could be immature or juvenile specimens of the giant octopus. Apart from *O. madokai* (Berry) (= *O. pustulosus* Sasaki, 1920), which is now tentatively assimilated into the synonymy of *O. dojleini* (p. 47), the few whose identification does not depend on sexually mature male characters are well defined in other ways.

Kondakov (1941) described no new species for Far the Eastern Seas of the U.S.S.R., but his article is valuable in that it enlarges our knowledge of many of the species described previously.

Since the main center of interest in the present investigation has been the identification of Dr. Martin’s specimens from the Puget Sound–San Juan area, these are treated first and have been given primary consideration. The rest of the material has been grouped geographically in an attempt to bring together known data and to evaluate the probability (i) that there is but one species of the giant octopus ranging from Japan via Siberia and Alaska to the Pacific coast of North America, and (ii) that there are racial differences in the populations that justify recognition at the subspecific level. A tentative resolution of the problem is reserved for the Discussion (p. 47), after all available data have been presented. It must be realized, however, that population studies embracing both juvenile and adult animals from critical areas are urgently needed. At the present time no such information is available, but the author believes, in view of the extensive research involved, that publica­tion of the limited material herein analyzed will facilitate the work of future investigators and lay the foundations for a final solution of the problem.

Tables I–III are distributed through the text, and, for comparative purposes, Tables IV–IX have been grouped together under Appendix A on pp. 55–60.
DEFINITION OF SYMBOLS

Measurements and indices as defined by Robson (1929) and Pickford (1945), in some instances modified or supplemented, as indicated.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ML</strong></td>
<td>Mantle length in mm (Robson).</td>
</tr>
<tr>
<td><strong>TL</strong></td>
<td>Total length in mm (Robson).</td>
</tr>
<tr>
<td><strong>MWI</strong></td>
<td>Mantle width index: mantle width ( \times 100 )/mantle length (Robson).</td>
</tr>
<tr>
<td><strong>HWI</strong></td>
<td>Head width index: head width ( \times 100 )/mantle length (Robson).</td>
</tr>
<tr>
<td><strong>ALO</strong></td>
<td>Arm length order: the sequence of arm length on the left side.</td>
</tr>
<tr>
<td><strong>MAI</strong></td>
<td>Mantle arm index: mantle length ( \times 100 )/length of longest arm (Pickford). This index is often more informative than <strong>ALI</strong>, especially in long-armed species.</td>
</tr>
<tr>
<td><strong>ALI</strong></td>
<td>Arm length index: length of longest arm ( \times 100 )/total length (Robson).</td>
</tr>
<tr>
<td><strong>ASI</strong></td>
<td>Shortest arm index: length of shortest arm ( \times 100 )/length of longest arm; the hectocotylized arm of males is excluded.</td>
</tr>
<tr>
<td><strong>WDO</strong></td>
<td>Web depth order: the sequence of web depth on the left side.</td>
</tr>
<tr>
<td><strong>WDI</strong></td>
<td>Web depth index: depth of deepest sector ( \times 100 )/length of longest arm (Robson).</td>
</tr>
<tr>
<td><strong>WSI</strong></td>
<td>Shallowest web sector index: depth of shallowest sector ( \times 100 )/depth of deepest sector. This index is more convenient than Robson’s “disparity index.”</td>
</tr>
<tr>
<td><strong>SnI</strong></td>
<td>Normal sucker diameter index: diameter of largest normal sucker ( \times 100 )/mantle length. This is Robson’s sucker diameter index (SI) modified to exclude specially enlarged suckers, for which a parallel index (SeI) is employed (Pickford).</td>
</tr>
<tr>
<td><strong>SeI</strong></td>
<td>Enlarged sucker diameter index: see under <strong>SnI</strong>.</td>
</tr>
<tr>
<td><strong>HSnI</strong></td>
<td>Head width-sucker diameter index: diameter of largest normal sucker ( \times 100 )/head width. This parameter has been employed in special circumstances (see text). A parallel index for specially enlarged suckers (HSeI) could be employed if required.</td>
</tr>
<tr>
<td><strong>FoI</strong></td>
<td>Funnel organ limb index: length of lateral limb ( \times 100 )/length of median limb.</td>
</tr>
<tr>
<td><strong>GFT</strong></td>
<td>Total number of primary gill lamellae. On previous occasions the author (G.E.P.) has followed Robson in giving the number of lamellae per demibranch (GF), but since there is frequently a single terminal lamella, the total is more convenient.</td>
</tr>
<tr>
<td><strong>HAI</strong></td>
<td>Hectocotylized arm index: length of hectocotylized arm ( \times 100 )/length of its mate on the opposite side. In dextral species, the third right arm is the denominator, in sinistral species, it is the third left; this parameter, though not hitherto expressed as an index, has been employed by several previous authors (Berry; Sasaki, et al.).</td>
</tr>
<tr>
<td><strong>MHI</strong></td>
<td>Mantle hectocotylized arm index: mantle length ( \times 100 )/length of hectocotylized arm. Used in cases where the reciprocal arm is damaged so that HAI cannot be calculated.</td>
</tr>
<tr>
<td><strong>LLI</strong></td>
<td>Ligula length index: length of ligula ( \times 100 )/length of hectocotylized arm (Robson). It is important to observe that the length of the ligula, as defined by Robson, is measured from the margin of the last sucker.</td>
</tr>
<tr>
<td><strong>CLI</strong></td>
<td>Calamus length index: length of calamus ( \times 100 )/length of ligula (Pickford).</td>
</tr>
<tr>
<td><strong>PLI</strong></td>
<td>Penis length index: length of penis + diverticulum/mantle length (Robson).</td>
</tr>
<tr>
<td><strong>PDI</strong></td>
<td>Penis diverticulum index: length of diverticulum ( \times 100 )/length of penis + diverticulum.</td>
</tr>
<tr>
<td><strong>RLI</strong></td>
<td>Rostral length index: length of rostrum of upper jaw ( \times 100 )/length of upper jaw (Robson).</td>
</tr>
<tr>
<td><strong>SpLI</strong></td>
<td>Spermatophore length index: length of spermatophore ( \times 100 )/mantle length (Pickford).</td>
</tr>
<tr>
<td><strong>OGI</strong></td>
<td>Oviducal gland index: diameter of oviducal gland ( \times 100 )/mantle length (Robson).</td>
</tr>
<tr>
<td><strong>EL</strong></td>
<td>Egg length: length of egg in millimeters, without stalk.</td>
</tr>
<tr>
<td><strong>ESI</strong></td>
<td>Egg-stalk index: length of stalk ( \times 100 )/total length of egg ( \times ) stalk.</td>
</tr>
</tbody>
</table>
Abbreviations.

BM, British Museum (Natural History), London, England.
MCZ, Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts, U.S.A.
USNM, United States National Museum, Washington, D. C., U.S.A.
YPM, Peabody Museum, Yale University, New Haven, Connecticut, U.S.A.

DESCRIPTIONS OF SPECIMENS

I. THE PACIFIC COAST OF NORTH AMERICA, EXCLUDING ALASKA

A. Washington State.

A1. New Specimens from the Puget Sound–San Juan Archipelago area.

Twelve specimens were sent to the writer at various times from the Department of Zoology, University of Washington, by Dr. Arthur W. Martin, or by his colleague, Dr. Carl Emanuel. Many of these specimens had been used in the laboratory for physiological experiments, but none had been seriously mutilated, although the preservation was not always good. The date and sometimes the locality of capture are not always known. All specimens are now in the collections of the Peabody Museum, Yale University.

Material examined:

Lot 1: Received April 1953 from A. W. Martin; taken by trawl, San Juan Archipelago; 1 mature ♂; poorly preserved in weak alcohol and later transferred to 4% formaldehyde; YPM 12800; ML 330 mm.

Lot 2: Received April 1953 from A. W. Martin; taken from dens on Lopez I., San Juan Archipelago; 1 large immature ♂, 2 immature ♀♀; preservation as in Lot 1; YPM 12801, 12802, 12803; ML 290, 158, 173 mm, respectively.

Lot 3: Received June 1953 from C. Emanuel; taken from intertidal zone of Lopez I., White Cliffs, San Juan Archipelago; 2 mature ♂♂, 1 immature ♀; preservation as in Lot 1; YPM 12804, 12805, 12806; ML 290, 275, 225 mm, respectively.

Lot 4: Received June 1953 from A. W. Martin; taken from beach near town of Lopez, San Juan Archipelago; 1 immature ♂, 1 immature ♀; moderately well preserved externally but poorly preserved internally, in 4% formaldehyde; YPM 12807, 12808; ML 215, 188 mm, respectively.

Lot 5: Received February 1954 from A. W. Martin; taken at Tacoma Narrows, 47°16.3'N, 122°13.5'W, about 15 January 1954; 1 mature ♂; moderately well preserved, in 4% formaldehyde; YPM 12809; ML 195 mm.

Lot 6: Received summer 1954 from A. W. Martin; no collection data; 1 immature ♀; preservation as in Lot 5; YPM 12810; ML 220 mm.
Lot 7: Received October 1959 from A.W. Martin; taken in the spring of 1959; 1 gravid ♀; preservation as in Lot 4; YPM 12811; ML 197 mm. [A letter from Dr. A.W. Martin dated 8 October 1959 states: “The animal was captured in the spring of 1959. About May 28 she laid several thousand small eggs in the tank in the Oceanographic Laboratory. I have not asked the embryologists if the eggs were ever fertilized but they showed no signs of development ... The female died in the tank from unknown reasons about Sept. 28.” A sample of the eggs was sent separately.]

The material from this area comprises 12 specimens, ranging in mantle length from 158 to 330 mm. The state of preservation varies greatly; some are soft and often decomposed internally, while others are hardened and therefore difficult to study.

Some interesting data on the effects of preservation on bodily proportions of a Puget Sound animal are discussed on p. 43 in connection with Japanese specimens of *O. dofleini* studied by Sasaki (1929). Standard indices and other taxonomic parameters are summarized in Appendix A, Tables iv and v (pp. 56, 57). A preliminary study of the data showed no significant differences between the sexes or between immature and mature specimens, except for those parameters in which these categories are listed separately.

There are four sexually mature males carrying spermatophores, and one gravid female. Some of the seven remaining specimens are immature, but several of large size, including two males, may be spent. The collecting dates do not permit a decision on this point: mature males were taken in April, June, and January; the gravid female that spawned in May still had ripe ovarian eggs in September when she died; the two immature or spent females were sent in April and June.

**COLOR.** Specimens are generally deep reddish brown, sometimes mottled with black streaks, patches, and reticulations; paler below.

**SKIN AND CIRRI.** The skin is wrinkled from preservation and variable in character; however, it is generally somewhat rugose or papillated dorsally, and in most of the specimens the oral face of the web is finely granulated. Dr. Martin described the character of the skin in living animals and compared it with Sasaki’s description of the skin of the Japanese giant octopus, *O. dofleini*, as follows:

As I compare Sasaki’s description of the skin with that of several of my beasts it does not impress me favorably. He is impressed with the ‘warty’ appearance and makes much of the stellate base. We agree that the skin easily slacks off to a smooth appearance but I would venture that this is a universal characteristic of this and other genera. So I would paraphrase him in this way: Surface irregularly rugose but easily slacking off into smooth condition, a state in which the animal spends much of its time in repose in the laboratory. The ridges are of various sizes, rarely pointed, often connected together into longitudinal lines. Irregularly in rows but more or less parallel to the long axis of the body, individual rugosities will often rise to an inch or more in height standing clearly above the rest of the ridges. The
skin above and just behind the eyes gives rise characteristically to a much taller pair of nearly cylindrical protrusions which come finally to a point and so resemble horns. In contrast to the foliate appearance of the other skin folds these arise from a nearly stellate base. The tissue is thickened enough at the base of these characteristic structures so that their position can be recognized even when the skin is relaxed. Near the front of the eye a second pair of conical papillae may often form which rise to about half the height of the major pair.

All preserved specimens have a conspicuous posterior cirrus above the eye, but it is flattened, more or less triangular, and frequently slightly hollowed on its lower surface so that the cirrus resembles an ear rather than a horn. In addition, there is frequently a small anterior supraocular cirrus; in one specimen (YPM 12805) the anterior cirrus is larger than the posterior one. All specimens have numerous smaller warts and papillae surrounding the eye.

Bodily Proportions. The mature males vary in mantle length from 195 to 330 mm, but the non spermatophore-bearing males are in the same size range. The gravid female is only 197 mm, but some of the immature or sexually regressed females are larger. The body is broad but the mantle width index exceeds 100 only in the gravid female distended with eggs. The head is rather narrow across the eyes; the latter do not protrude, and the neck is usually wider than the head.

Arms. The arms are moderately long and average four times the mantle length; but there is considerable variation, and the longest arm is, at the extremes, 3 to 5 times the mantle length. The arms are subequal, and the shortest arm averages 87% of the longest. In nine specimens, either a first or a second arm is the longest, but in three instances either a third (YPM 12804) or a fourth (YPM 12800, 12811) is the longest. In seven specimens either a third or a fourth arm is the shortest (excluding the third right arm of males), but in three either a first (YPM 12807, 12811) or a second (YPM 12803) is the shortest; in two specimens this parameter could not be determined on account of injury to many of the arms. Thus it is possible for individuals of this species to have an atypical arm length sequence; therefore “first arms longest” or “fourth arms shortest” cannot safely be employed as taxonomic characters. However, the most typical order of arm length on the left side, to include males, is 1 = 2 > 3 > 4 (the mean for six specimens with perfect left-arm sets).

Web. The web is moderately deep, the deepest sector being almost one quarter of the length of the longest arm. In 11 specimens the E sector is the shallowest, and in eight of these the A sector is the next shallowest. In two males (YPM 12800, 12807) the left D sector is the next shallowest, and the A sector is of intermediate depth. In two specimens (YPM 12801, 12811) the A sector is the shallowest and the E sector is the next shallowest. In the majority, however, the B, C, and D sectors are subequal, and the most typical order of web depth is B = C = D > A > E. The shallowest sector is about half as deep as the deepest.
Suckers. There are no specially enlarged suckers in either sex, but the data suggest that the suckers of males tend to be larger than those of females. There is some overlap. The gravid female has a sucker diameter index of 14.2; one of the mature males (YPM 12804) has an index of only 12.8, but the indices for the other males are higher, 15.4 to 18.8; the mean is 15.2 for the male group as compared with 13.2 for females. If sucker diameter is referred to head width rather than mantle length, the mean index for males is 38.9, for females 28.3.

Funnel. The funnel is about 35 to 40% of the mantle length; this index, which appears to be of little taxonomic importance, has been omitted from the tables. The funnel organ is not always well preserved, but in nine specimens where it is present, it is in the form of a broad-limbed W; the lateral limbs are always shorter than the median limb, usually about half as long. This was confirmed by Dr. Martin (in litt.) on a fresh specimen and provides an important taxonomic character. Frequently the junction of the lateral limbs with the median limb is broadly truncated. However, the shape of the funnel organ is variable.

Gills. The state of preservation does not justify calculations of gill length indices; in some specimens the gills are greatly stretched while in others they are strongly contracted. The total number of primary gill lamellae varies from 24 to 29; the inner demibranch usually has one less than the outer demibranch.

Jaws and Radula. The buccal mass was removed from one specimen (YPM 12800); the thin margins of the jaws were very brittle, but measurements and a drawing were possible with careful piecing together of the marginal fragments (Fig. 1, A, B). The form of the jaws does not present any features of particular interest; the rostral length index of the upper jaw is 42.4. There is no conspicuous groove on the side of the rostrum, as in larger specimens from the Far North (p. 38); however, careful inspection reveals faint parallel growth lines, some of which are more pronounced than others. The tip of the lower jaw is obtusely truncated, but not emarginated as it is in O. bimaculatus and O. bimaculoides (Pickford and McConnaughey, 1949). The radula closely resembles that figured by Sasaki (1929) for a Japanese specimen of O. dojleini; the rhachidian sequence shows an asymmetrical B4 seriation (Robson, 1929), with the lag involving one tooth; the marginals are flat rectangular plates without a tooth such as was figured by Dall (1866) for a specimen of O. punctatus (p. 21).

Hectocotylus. The third right arm of the male is hectocotylized, but it is not markedly shorter than the third left arm; it averages 93.6% of the latter in the five males in which this index could be determined. Unfortunately, the tip of the third left arm is damaged in the best-preserved male (YPM 12809); for this reason, the length of the hectocotylized arm has been calculated in relation to mantle length; the mean for this new index is 28.4.
Figure 1. Upper and lower jaws. A and B—a sexually mature male from the San Juan Archipelago, Washington State, showing extremely faint growth lines on the rostrum; USNM 12800. C and D—a large but sexually immature male from Alaska, showing the broad shallow groove on the rostrum; USNM 574595.

The ligula of mature males is long and slender; it ranges in length from 160 to 252 mm and comprises about one fifth of the arm length; in the two immature or regressed males it is shorter, 127 and 158 mm. We know nothing about possible shortening of the ligula during sexual regression, and a short ligula might be due to this circumstance rather than to immaturity. No indubitably juvenile males are represented in the Puget Sound series, hence the validity of comparison with juvenile and immature specimens of the Alaskan or Californian groups, which contain no mature representatives, is open to criticism. However, for what it is worth, a regression coefficient for the relation of length of ligula to length of hectocotylized arm has been calculated for the entire group (Fig. 2). Although it is believed that the Alaskan population is racially different (p. 49), the differences do not appear to involve this particular character. Allowing for the small number of specimens available and for wide individual variation, the calculated line provides a reasonably good fit for all specimens, although the points for the largest individuals tend to sag below the line at its upper end. The results suggest that the growth of the ligula is positively allometric with a coefficient of about 1.45 in respect to the growth of the arm. This preliminary analysis provides a framework for the evaluation of juvenile specimens that, in the past, have been taxonomically separated on account of the size of the ligula.
The calamus is short; mature males have a ligula length index of about 6.4, and the two immature males have an index that is at the upper limit for sexually mature specimens. This suggests the possibility that considerably higher calamus length indices might be anticipated for juvenile individuals, a consideration that could be applied to interpret the status of small males from other areas. With the reservations noted above in the case of the ligula length index, a regression coefficient was calculated for all specimens ranging from Alaska to California (Fig. 3). This analysis suggests a high degree of positive allometry in favor of ligula growth, with a relative growth coefficient of the order of 1.33. This does not prove that the juveniles from Alaska and California belong to the same race as the Puget Sound series, but it does show that immaturity could account for a high calamus length index, since the calculated line, common to all points, provides a satisfactory fit.

The ligula groove is usually more or less tightly closed, as described by Kondakov (1941) for O. dofleini, in contrast to O. gilbertianus, but the condition varies with the state of preservation. In the ligula of the best-preserved male (YPM 12809), the groove is ornamented with regularly arranged transverse rows of papillae; each row consists of 6 to 8 papillae, and the median four are aligned with those of adjacent rows to form four longitudinal series; the more laterally placed papillae are members of less regular, interrupted longitudinal series.
PENIS. The penis itself is short, but the diverticulum is very long; in mature specimens the diverticulum averages 80% of the total length of the penis plus diverticulum, and this index is scarcely significantly less in the immature specimens. Data for juvenile males from other regions, e.g. Alaska, suggest that this parameter is little affected by the state of maturity despite wide variations, correlated with age, in the relative length of the entire organ. The combined length of penis and diverticulum gives a standard penis length index that varies from 51 to 104.5 in mature males, but it is considerably less in immature specimens. The presence of well-preserved spermatophores appears to stretch the organ; the highest indices were found in two specimens in which this condition prevailed (YPM 12800, 12809); after removal of the spermatophores from the more flaccid specimen (YPM 12800), the penis length index decreased from 104.5 to 91.

SPERMATOPHORES. The presence of spermatophores, or remains of spermatophores, in Needham’s organ and (or) the penis plus diverticulum has been used as the criterion for sexual maturity. The number of spermatophores is low, as in the case of O. dejleini from Japan described by Sasaki (1929), but their size is enormous. Unfortunately, the state of preservation is poor at best.

YPM 12800 had two spermatophores in the penis plus diverticulum and ten in Needham’s organ; all are more or less damaged and opaque from alcohol preservation, so that the internal structure could not be studied. Of those from Needham’s organ, anterior pieces, representing the horn plus sac plus middle piece, averaged 598 mm in length, and a single sperm reservoir recovered from this organ in three pieces measured 472 mm; the total length of the spermatophore is therefore about 1,072 mm. The better preserved of the two penis spermatophores was of about the same length; the anterior piece measures 540 mm and the sperm reservoir 590 mm, totalling 1,130 mm. From this it is evident that the spermatophores are more than three times as long as the mantle length (SpLI 342).

YPM 12804 had the remains of one broken spermatophore in the penis plus diverticulum, but no measurements could be made.

YPM 12809 is well preserved in formalin, but the spermatophores are brittle and could not be removed undamaged; one was taken from the penis plus diverticulum and four from Needham’s organ.

The former was broken into several pieces, and the length could not be estimated with any degree of accuracy; however, the head and the beginning of the horn are well preserved (Fig. 4). This horn has 15 clockwise spiral turns, after which it becomes straight; the head, measured to the first turn of the spiral, is 21 mm long and about 3 mm in diameter.

One of the four broken spermatophores from Needham’s organ was pieced together. The head to the first turn of the spiral horn is 27 mm long and averages 2.5 mm in diameter. The beginning of the horn has 14 clockwise spiral turns, of which the first eight are tightly coiled and the last six opened
Figure 3. The length of the ligula relative to the length of the calamus; measurements in millimeters, log.-log plotting; the triangle at the left, below the calculated line, is for the Type of *O. gilbertianus* (Berry). Only specimens studied by the author have been employed.

out; the total length of the spiral region is about 24 mm. The distal, straight part of the horn passes uniformly into the more dilated sac region, but the internal structure is obscure and the point of junction of sac with horn could not be precisely determined. The end of the sac can be seen; the middle piece is dark brown in color. The total length of horn plus sac plus middle piece, measured by combining two fragments, is about 265 mm, of which the middle piece comprises about 55 mm; the diameter of the horn is about 3 to 4 mm and that of the middle piece 4.5 mm. The apparent length of the sperm reservoir is 460 mm but, since parts of the normally tightly coiled sperm tube are uncoiled, this measurement is probably too great. In the tightly coiled regions there are four coils per millimeter, and the total number of coils is 1,650; this gives an estimated true length of 450 mm. From the above figures, the total length of the spermatophore is about 675 mm, giving a spermatophore length index of 346, which is close to the 342 mm estimated for YPM 12800.

The remaining three spermatophores from Needham’s sac are in worse condition; two have head lengths of 32 and 28 mm, and about 9 to 10 and 11 turns of the clockwise spiral horn, respectively, but only the first 6 or 8 turns are tightly coiled. The third spermatophore shows no horn coils and is presumed to have become partially discharged through poor preservation. In two spermatophores the sac was torn away from the middle piece, into which
it fitted by a rounded end drawn out to a thin point; this is evidently the continuation of the inner tube.

YPM 12805 had fragments of two spermatophores in the penis; the head length is about 27 mm and, in the better preserved of the two, the horn has at least nine clockwise spiral turns; the horn of the other is uncoiled except for the first two turns.

**Female Organs.** Only one gravid female (YPM 12811) was studied. The distended ovary filled the greater part of the body and, when the ovarian sac was cut, ripe eggs spilled out. The total number of ovarian eggs was in the thousands, probably at least 5,000, and very likely more. The length of 14 ripe ovarian eggs varies from 5.8 to 6.3 mm, with a mean of 6.05 mm; the width is 2.5 to 3.0 mm; the stalk length of these eggs, selected for straight stalks in perfect condition, ranged from 13.8 to 17.0 mm and averaged 15.5 mm. Eggs laid naturally by this specimen (p. 11) are attached in festoons, with tangled stalks cemented together in cords; one perfect egg dissected from a festoon measures 6.0 mm, and the stalk is 13.5 mm long.

The oviducal glands of the mature female are poorly preserved, and the right one could not be studied. The left gland, shown in Fig. 5A, is soft and partly decomposed, so that the internal structure could not be investigated. The form is peculiar; the proximal and distal oviducts enter and leave the gland side by side at the hilum of what Winkler and Ashley (1954) have

![Figure 4. Anterior end of a spermatophore from the penis of YPM 12809, showing head and coiled region of horn.](image)
described as a bean-shaped gland. The diameter of the gland is about 45 mm, giving an oviducal gland index of 22.8. More details can be seen on the smaller oviducal gland of an immature female (YPM 12810; Fig. 5B), in which the index was only 8.6. Serial sections would be required to interpret the internal structure, and, at the time of writing, this has not been attempted. However, it is clear that the peculiar form of the oviducal gland is of taxonomic importance.

A2. Specimens from Washington Described as *Polypus honkongensis* (Hoyle) = *P. apollyon* Berry (1913), in part, by Berry (1912).

Three males and three females collected by the *Albatross* in the vicinity of Port Townsend, Washington, were first referred by Berry to *O. honkongensis*. Measurements for three of these were given in Berry’s table (1912: 282): a male and female from St. 4220, and a female from St. 4222. The mantle length can be estimated by using an 8% correction factor (p. 31), and corresponding indices may be calculated for several parameters.

These were small animals, with estimated mantle lengths of 41 mm for the male and 52 and 53 mm for the females. The head and mantle are broad but,
if the specimens are related to *O. dojfeini*, this could be attributed to juvenility. Arm length indices are in the range for *O. dojfeini*, and either a first or a fourth arm is the shortest.

The hectocotylized arm length index cannot be calculated for the described male, since the length of the third left arm was not given; presumably the arm was defective (see Berry, 1912: 281, table); in reference to mantle length, the index is in the normal range for the Puget Sound–San Juan specimens (MHI 30). However, an element of doubt remains; Berry’s data for two other males contained measurements for the third and third right arms (p. 281), but not for the mantle length. In these two males the hectocotylized arm is relatively short (HAI 76 and 82); this is below or at the lower limit of the range for the Puget Sound series. The ligula lengths for the three males give indices of 9.3, 10.0, and 11.3, respectively, concordant with the hypothesis that they were juveniles of the giant octopus.

Other species occur in this area, notably the two specimens that Robson (1929) erroneously identified as *O. apolyon* (p. 63). Without re-examination of the *Albatross* specimens, it is not possible to reach a decision regarding their identification.

**A3. Specimens Described as *Octopus apolyon* (Berry) by Winkler and Ashley (1954).**

Under this tentative identification, Winkler and Ashley have given an elementary account of the anatomy of the giant octopus. Their contribution, which was not intended as a taxonomic investigation, provides a most useful account of the vascular system, based on latex injections, and contains other anatomical information. Their material consisted of two poorly preserved mature specimens (♂ and ♀) and three immature females; all were from the Puget Sound–San Juan Archipelago, Skagit County. The immature females were well preserved and the method of preservation was described. The mantle lengths were not stated, and other measurements given in the text are of little taxonomic use, since the size of the animal is not known. Their fig. 1 is interesting, since it shows the caudal line at the apex of the body. The authors were unable to find any trace of the funnel organ, even in otherwise well-preserved animals. Their fig. 2 shows 13 or 14 gill filaments per demibranch, but in the text they stated that there are 12. The radula is said to resemble that figured by Robson (1929) for *O. hongkongensis* and by Sasaki (1929) for *O. dojfeini*.

The description of the female reproductive system, based on an immature animal, is interesting, since the peculiar form of the oviducal gland is described and figured for the first time (fig. 16) and is obviously of the same type as that observed in the Puget Sound series (p. 18).

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1 Note that Berry’s specimen SSB 145 is erroneously listed on p. 281 as from Port Townsend. It is actually the second specimen from Uyak Bay, Alaska, the *Cotype* of *O. apolyon*. 
The description of the male reproductive system is based on a specimen of "O. apollyon" from California (Catalina I., Allen Hancock Foundation) that is clearly not referable to the giant octopus. This possibility was recognized by the authors. Their specimen was apparently an immature animal, since no spermatophores were mentioned. The penis (fig. 18) has the form shown by Robson (1929) for a presumed specimen of O. apollyon (p. 63); there is no penis diverticulum. The ligula (fig. 19) is short and stout, with a widely open groove that shows only 13 transverse ridges.

B. California.

B1. The Type of Octopus punctatus Gabb (1862).

This specimen, apparently from San Francisco, was a comparatively small animal; Berry (1912), who reprinted Gabb's original account, stated that the specimen was lost in the San Francisco earthquake disaster and, since the name punctatus is preoccupied, it can legitimately be excluded from further consideration. However, it is one of the few previously described specimens from California, and therefore a brief review of its characters is given here (Table IV).

The color is said to have been destroyed by alcohol. The surface of the skin was "profusely marked by very minute reddish-brown, or chocolate-colored points," closely spaced on the dorsal surface. There is no mention of supraocular papillae.

The specimen measured 3.5 inches from the apex to the origin of the arms, suggesting a standard mantle length of the order of 80 mm. The head was narrow, 1.1 inches, suggesting a head width index of 33. The longest arm was about four times the length of the body (MAI ca. 25); the shortest arm was only a little shorter (ASI 95.6). The order of arm length was 2 > 1 > 4 > 3. The suckers increased progressively in size to the level of the web margin, and none was specially enlarged; the diameter of the largest sucker was 0.3 inches (7.6 mm), suggesting a sucker diameter index of the order of 9.5.

The sex was not stated.

There is nothing in the above account to preclude regarding this animal as a juvenile of the giant octopus, but there is also nothing to prove that it was such. Attention may be called to the relatively small size of the suckers (p. 28).

B2. The Radula of a Specimen Identified as Octopus punctatus Gabb (1862) by Dall (1866).

Dall figured the radula of a half-decayed specimen from San Francisco that he referred to O. punctatus. Robson (1929: 203) has commented on the cusped marginal plate, seemingly a unique feature. This supposed peculiarity must be viewed with suspicion. Robson noted that a cusped marginal was not present on a specimen that he misidentified as O. apollyon; such is not
present in the newly studied specimens from Puget Sound; Sasaki (1929) figured the radula of *O. dojleini*, and Kondakov (1941) that of *O. dojleini* and *O. gilbertianus*, but these figures do not show the marginal plate. It is possible that some Californian species may have a cusped marginal, but for the present the problem must remain unresolved.

B3. Specimens Identified as *Octopus punctatus* Gabb (1862) by Verrill (1883).

Verrill referred two large males from California to Gabb’s species and gave the first good description of the giant octopus; Verrill not only gave a table of measurements but also quoted graphic accounts of the natural color and appearance of the living animal. Both specimens have been re-examined in the present investigation.

(a) Received from “T. G. Cary, San Francisco”; 1 immature ♂; MCZ 243156 (formerly MCZ 2362); ML 182 mm.

The specimen listed by Verrill as “MCZ No. 62” could not be found in the Museum of Comparative Zoology. In reply to a letter of enquiry, Dr. Ruth D. Turner stated that their catalogue number 62 is not even a cephalopod, but that an octopus from San Francisco catalogued as number 2362, which was no longer in their collection, might be the one that had been studied by Verrill. It was then realized that a specimen bearing this number had been found in the old collections of the Peabody Museum, Yale University. The specimen has now been returned to Harvard and recatalogued as MCZ 243156. There can be no doubt that this is the animal described by Verrill and the one from which Verrill’s illustrations were prepared.

The specimen is an immature male, as shown by the small size of the testis, penis, and other secondary sexual characters. In its present condition it is flaccid, faded, apparently partially macerated internally, but well preserved externally. The specimen has been remeasured and, in view of some uncertainty as to whether Verrill’s “Length of body to eye” is to be interpreted as the standard mantle length, the parameters employed in calculating the range and mean for Californian specimens are those derived from the new measurements (Appendix A, Tables IV and V, pp. 56, 57). In 1953 the mantle length was 182 mm, whereas Verrill’s “Length of body to eye” was given as 229 mm; if the mantle length is measured from the apex to the anterior margin of the eye, the present value is 230 mm; this suggests that Verrill employed this parameter at a time when Robson’s standard mantle length had not been defined. Most of the other measurements given by Verrill are in general agreement with those given here, except for some apparent shrinkage of arm length and web depth.

When examined by S. J. Townsley in 1953, the specimen was in a very soft condition, in weak alcohol. Later it was transferred to dilute formalin,
TABLE I. COMPARISON OF SELECTED MEASUREMENTS AND CORRESPONDING INDICES FOR AN IMMATURE MALE OF "O. punctatus" (MCZ 243156) DESCRIBED BY VERRILL (1883), REMEASURED BY S. J. TOWNSLEY AFTER 80 YEARS OF STORAGE IN WEAK ALCOHOL, AND REMEASURED AGAIN BY G. E. PICKFORD NINE YEARS LATER AFTER ADDITION OF 4°/0 FORMALDEHYDE.

<table>
<thead>
<tr>
<th></th>
<th>Verrill, 1883</th>
<th>S.J.T., 1953</th>
<th>G.E.P., 1962</th>
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<tbody>
<tr>
<td></td>
<td>mm</td>
<td>Index</td>
<td>mm</td>
</tr>
<tr>
<td>Mantle length</td>
<td>229*</td>
<td></td>
<td>182</td>
</tr>
<tr>
<td>Mantle width, MWI</td>
<td>130</td>
<td>61</td>
<td>140</td>
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<tr>
<td>Head width, HWI</td>
<td>66</td>
<td>29</td>
<td>63</td>
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<tr>
<td>Longest arms, MAI, L 2</td>
<td>978</td>
<td>24</td>
<td>967</td>
</tr>
<tr>
<td>Shortest arm, ASI, R 4</td>
<td>838</td>
<td>-</td>
<td>783</td>
</tr>
<tr>
<td>Third arm:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>left</td>
<td>965</td>
<td>-</td>
<td>863</td>
</tr>
<tr>
<td>right (hectocot.)</td>
<td>737</td>
<td>76</td>
<td>700</td>
</tr>
<tr>
<td>Ligula length, LLI</td>
<td>78†</td>
<td>10.6</td>
<td>68</td>
</tr>
<tr>
<td>Calamus length, CLI</td>
<td>7†</td>
<td>9.0</td>
<td>7</td>
</tr>
<tr>
<td>Diam. largest sucker, SnI</td>
<td>18</td>
<td>7.9</td>
<td>18</td>
</tr>
</tbody>
</table>

* Verrill's "Length of body to eye" may not be the same as Robson's standard mantle length (p. 22). Indices dependent on this measurement may therefore be too low (MWI, HWI, SnI) or too high (MAI, MHI).
† Calculated from Verrill's figure (pl. 5, fig. 2) on the assumption that it is reproduced at natural size. The statement that it is at x 2 magnification is obviously in error, since the length of the ligula, measured from the last sucker, is 78 mm, and Verrill gave a length of 71 mm in his table. The difference is probably accounted for by assuming that Verrill's measurement was made from the tip of the calamus; this gives a length of 71 mm. The drawing was made by J. H. Emerton, a highly competent illustrator, and there is every reason to believe that careful attention was given to exact measurements and proportions. Since ligula length is defined by Robson (1929) as the measurement from the last sucker, the new measurement has been employed in the table. Verrill's ligula length would give a slightly lower index (LLI 9.6). The calamus length and calamus length index are also derived from Verrill's figure.

which prevented the continuation of maceration but caused some further shrinkage, especially in arm length. These changes, summarized in Table 1, are of interest in evaluating the parameters of poorly preserved museum specimens. If an animal has been well fixed originally, as in the case of Berry's type of O. gilbertianus (p. 30), the changes are usually within the limits of subjective error.

With few exceptions, the indices for this specimen (based on 1953 measurements) fall within the range for the San Juan–Puget Sound series, provided allowance is made, in the case of secondary sexual characters, for the degree of immaturity. Although there has been some shrinkage, the order of arm length is only slightly different from that reported by Verrill; on the left side the sequence is now 2 > 4 > 1 > 3 compared with Verrill's 2 > 3 > 1 > 4. The order of web is the same as Verrill's; on the left side the sequence is D > B > C >
A > E. Attention may be called to the relatively small size of the suckers (SnI 9.9) compared with those of the giant octopus from farther north. If sucker diameter is referred to head width rather than to mantle length (p. 43), the index (HSnI 28.6) reflects a similar difference since, in males from the Puget Sound area, the mean value is 38.9. The funnel organ is not preserved.

The relative length of the hectocotylized arm is less than that observed in the Puget Sound series, but this difference is not apparent when the length of the third right arm is referred to mantle length (MHI 26). The relatively undeveloped ligula, which measures only 78 mm as compared with 180 mm for the smallest mature male of the Puget Sound series (YPM 12809), accounts for a low ligula length index and, when plotted graphically (Fig. 2), the relationship is concordant with the state of immaturity. Immaturity also accounts for the relatively high calamus length index (Fig. 3).

The penis is small (PLI 19), but the diverticulum contributes 74% of the combined length of penis plus diverticulum, which is in good agreement with the index (PDI) for both immature and mature specimens from Puget Sound.

(b) From California; immature ♀ (?); USNM 33076; ML ?.

This specimen, originally described by Verrill and re-examined in the present investigation, is in miserable condition; the head and visceral mass are torn away in decomposed fragments. Presumably the specimen was already in poor condition when studied by Verrill, since he did not give mantle length or total length, although he was able to give some other measurements that are not possible now, such as web depth. In the present investigation, only the arm length, sucker diameter, and hectocotylus could be measured.

According to Verrill, the head width was 70 mm, the fourth right arm was the longest (737 mm), and the first right arm was the shortest (485 mm). Present measurements suggest some shrinkage (R4 685 mm), but the supposed shortest arm is obviously defective and must have been so at Verrill’s time, since it shows evidence that the distal third had been regenerated. The third left arm is discussed below. Under these circumstances, arm length indices cannot be calculated, and the true order of arm length is uncertain; Verrill’s sequence, for the left side, was 2 > 3 > 4 > 1; defective arm tips preclude confirmation. In respect to web depth, Verrill’s measurements suggest that the sequence was D > B = C > E > A; using his data for the length of the deepest sector and longest arm, the web depth index was 39, and the shallowest sector was 53% of the deepest. The former value is the highest recorded for any specimen of *O. doylei*, but the latter is in the normal range for this species.

The length of the hectocotylized arm, which is still in good condition, has changed very little; Verrill gave 533 mm, whereas it now measures 555 mm. The third left arm is defective and has obviously been damaged since Verrill’s day, since an estimated length of at least 60 mm is now missing at the tip; and even if this figure were added, the present length would be only about
600 mm compared with Verrill’s measurement of 673 mm. The hectocotylized arm length index, necessarily calculated from Verrill’s data, is low (HAI 79); in this respect, it is in agreement with his other specimen (MCZ 243156), which also has a low HAI. Verrill gave a ligula length of 71 mm; this may have been too low (see Table 1, fnn. †), but it now measures even less (63.5 mm), and the ligula length indices are 13.1 and 11.4, respectively. The calamus now measures 5 mm, giving a CLI of 7.9. These indices are concordant with the presumption that the specimen is an immature male of *O. dofleini*.

B4. Specimens from California Described as *Polypus hongkongensis* (Hoyle) = *P. apollyon* Berry (1913) by Berry (1911, 1912).

Berry assigned many specimens to this species. The type of *P. apollyon* was from Alaska (p. 28), and others were from Washington (p. 19), California, and Lower California. Some of the Californian specimens belong to a different species, *O. rubescens* Berry (1953); of this species, Berry stated, “It is one of the forms which were formerly confused and apparently in part illustrated under the erroneous name *hongkongensis* in my preliminary report on this fauna (see Berry, 1912: 283, and especially pl. 39, fig. 3). In size, color, integumentary sculpture, and other features it seems with better material to be amply distinct from other members of the difficult *dofleini-apollyon* group.” The figure to which Berry referred shows a specially enlarged sucker on the right dorsal arm of a young male (No. 134), which had an estimated mantle length of only 29 mm, using the 8% correction factor, a low hectocotylized arm length index (HAI 71), and a ligula length index of 7.8. Specially enlarged suckers have never been described for animals that can assuredly be assigned to *O. dofleini* and, in view of Berry’s statement, we may accept the fact that this specimen, and possibly some of his other small specimens, should be excluded from the synonymy of *O. dofleini*.

Berry also gave measurements for six other specimens: three males and three females. All were of fairly small size, the largest (No. 143, ♀) with an estimated mantle length of 76 mm. In another table, Berry (1912: 281) gave measurements for the length of the third left and third right arms of males, and for the ligula; some specimens not otherwise described are included in this table. For two males, the hectocotylized arm index is high (Nos. 151: 87, No. 158: 90); for three others it is low (No. 146: 71, No. 153: 76, No. 81: 75). These values resemble the low values for Berry’s specimen No. 134, now assigned by him to *O. rubescens*; but they are not altogether outside the range for Californian specimens of *O. dofleini*. The ligula length is also low, the LLI ranging from 2.8 (No. 151) to 8.7 (No. 81); this is indicative of extreme immaturity if the specimens are referable to *O. dofleini*. The funnel organ of No. 81 was figured by Berry (1913); it is unlike that of *O. dofleini* from the Pacific coast of North America in that the lateral limbs are as long as the
median limb of the W (cf. Sasaki's specimens from Japan). Presumably this specimen belongs to another species. The status of the remaining specimens could not be resolved without reference to the original material and would contribute little since, if any belong to *O. dofleini*, they would be juveniles.

B5. Newly Described Specimens

(a) Received 27 March 1860, from T. G. Cary; San Francisco, California; 1 immature ♀; MCZ 243157; ML ca. 195 mm.

This specimen was evidently sent to the Museum of Comparative Zoology at the same time as the male described by Verrill (MCZ 243156; p. 22); both were from San Francisco. The mantle length is about 195 mm. The specimen is soft, flaccid, and apparently stretched. Standard indices are given in Appendix A, Tables iv and v (pp. 56, 57). All indices of bodily proportions are in the expected range for *O. dofleini*.

The specimen is a faded reddish brown above; lighter below. There are sparse, low, flat papillae on the dorsal integument. Above the eyes there are two prominent supraocular cirri; the posterior one, the larger of the two, is above the posterior angle of the eye and measures about 22 mm in length.

The order of arm length on the left side is 2 > 3 > 1 > 4, with relatively short first arms. The order of web depth is typical: on the left side D > B > C > A > E. The sucker diameter index (SnI 10.5) is slightly below the limit for the Puget Sound–San Juan females. The upper jaw was dissected out and measured; the rostral length index (RLI 46) is similar to that for other specimens of *O. dofleini*. There are the usual fine parallel growth lines on the surface but no marked groove such as that observed in specimens from the Far North (p. 38).

The female reproductive organs are poorly developed, and the small diameter of the oviducal gland (OGI 6.2) reflects a high degree of immaturity.

(b) Collected from intertidal zone at Pescadero Point, Monterey County, California, by D. P. Abbott and C. H. Hand, 25 November 1947: 1 immature ♀; YPM 12812; ML 175 mm.

This specimen is fairly well preserved, but hardened by strong formalin; the head was almost severed from the body and is now completely separated from it, so that the total length is only a rough estimate. Standard parameters are given in Appendix A, Tables iv and v (pp. 56, 57). The mantle length is 175 mm, and the specimen is therefore smaller than any of the newly described males from the Puget Sound area. The arm tips are broken so that no arm length indices could be given, but estimates based on the least injured longest arm (L2) suggest that the following indices were in the normal range: MAI ca. 23, ALI ca. 73, and WDI ca. 24. Other indices are in agreement with the Puget Sound series, except for the high calamus length index (see below).
The color is a dark reddish brown mottled with black. The skin is extremely rugose, presumably from the method of preservation. There is a single earlike supraocular cirrus above each eye.

The funnel organ is poorly preserved, so that the relative length of the lateral limbs could not be determined; the median limbs are undoubtedly united, although a deep split (an artifact) reaches almost to the apex. Thus there is no possibility that this specimen might be referable to *O. californicus* (Berry), which has a VV funnel organ.

Another most important taxonomic character cannot be determined: the relative length of the hectocotylized arm. The third left arm is incomplete so that the usual index (HAI) cannot be calculated. However, if the length of the hectocotylized arm is expressed in relation to mantle length, a comparison can be made with other specimens. One might expect that this procedure would be more reliable than the usual method, but, from data given in Appendix A, Tables \( v \), \( v_{11} \), and \( r_x \), it would seem to be less sensitive.

The difference between Sasaki’s series of *O. dofleini* from Japan and the group from the San Juan–Puget Sound area is evident by either method, but, with the new index (MHI), there is an overlap that is not apparent when the standard index is employed. In the present case, in which the index HAI is unknown, the alternative index MHI yields some information, since the value (MHI 29) is almost exactly at the mean obtained for the Puget Sound series.

The high calamus length index (CLI 10.9) can presumably be attributed to immaturity, since an analysis of the relation between ligula length and calamus length (p. 15; Fig. 3) suggests marked heterogony, and this specimen falls neatly along the calculated regression line. The ligula itself is rather short (LLI 13.6), but this index is close to that for an immature specimen from the San Juan–Puget Sound series (YPM 12807; LLI 14.1); as in the case of calamus length, the regression line (Fig. 2) confirms that all of these specimens could be members of a single series.

**B6. Status of Californian Specimens**

In the preceding sections, four Californian specimens that can be assigned with a high degree of certainty to *O. dofleini* have been described or redescribed. Unfortunately, all are immature, and minor apparent differences between this small group and the larger Puget Sound–San Juan series cannot be decisively evaluated. It is possible that the Californian population represents a distinct subspecies. The first arms are short. The relative length of the hectocotylized arm is low, but on the basis of a single specimen it is not decisively lower than that of specimens from farther north; moreover, this difference is not apparent when the length of the third right arm is referred to mantle length. The low ligula length indices and the high calamus length indices are appropriate for the state of sexual immaturity. This is also true of the penis length index; but,
as might be anticipated, the relative length of the penis diverticulum is in the expected range. The only remaining character for which a distinction could be made is the relatively small size of the suckers, which are alike in both sexes and are near to or below the limit for females of the Puget Sound–San Juan series. It must be recalled that Gabb’s Type of *O. punctatus* also had relatively small suckers.

McConnaughey (1959) has stated that the mesozoan parasites of the Californian “large red octopus” are not the same as those in specimens from farther north. Unfortunately, the specimens from which McConnaughey’s smears were taken were not preserved for identification. There are other large species of octopus in California, notably *O. californicus* (Berry), which reaches a mantle length of 100 mm. Nevertheless, this information regarding possible differences in the mesozoan parasites cannot be disregarded, and the suspicion remains that we are dealing with a racially distinct population.

II. The Pacific Far North

C. Alaska

Cl. The Types of *Octopus apollyon* (Berry)

Berry (1912) tentatively referred a series of specimens, ranging in habitat from Alaska to Lower California, to *Polypus hongkongensis* (Hoyle) with the proviso that, if they proved to belong to a distinct species, the name should be *apollyon* and the Type should be a male from Uyak Bay, Alaska (SSB 142; USNM 214319). This procedure was subsequently adopted (Berry, 1913). Berry was greatly troubled by the problem of identification and, more recently, he separated one small species, *O. rubescens* Berry (1953), from this seemingly composite assemblage. Clearly any revision of his earlier descriptions must take each individual into separate account. In this section we are concerned only with specimens from Alaska. Seven such animals, or fragments of specimens, were listed, but of these only two males were described (SSB 142 and 145). The first, the Type of *O. apollyon*, was deposited in the U.S. National Museum, but it can no longer be found and is presumed lost. In respect to the second, which may be designated as the COTYPE, S. S. Berry has stated, in reply to a letter of enquiry: “I did not keep any of the paratypes of this or other Albatross species in my own collections” (in litt., 12 August 1962). Therefore the COTYPE must also be presumed lost. A re-examination of the status of the Types rests solely on Berry’s original description, assuredly accurate but unfortunately incomplete.

(a) The Type. The true mantle length, as defined by Robson (1929), must be estimated from Berry’s measurement, “Tip of body to base of dorsal arms.” An attempt was made to determine mantle length from Berry’s photograph (pl. 36, fig. 9), which is stated to be at 1/3 natural size; however, it
Pickford: Octopus dojleini (Wülker) proved to be nearly impossible to locate the true apex of the body, since the animal is shown in side view, and the ventral region of the mantle bulges beyond what appears to be the true apex. Estimates of mantle length could vary from 75 to 85 mm, depending on the supposed position of the apex, but the lower value is probably correct. Therefore it was decided to apply an 80% correction factor to Berry's measurement, as was shown to be applicable in the case of his next species, O. gilbertianus (p. 30). This gives a mantle length of 74 mm, which has been used in the calculation of the indices (Appendix A, Tables vi and vii, pp. 58, 59). All values except those pertaining to sucker diameter and to the hectocotylized arm are in the range for the Puget Sound series.

The order of arm length is the same as in the Puget Sound series: the first and second arms the longest, and the fourth the shortest. It is worth noting that, in Berry's account, on p. 282, the length of the third arm refers to the third left arm; the length of the hectocotylized arm is given by him in another table, on p. 281.

In a general statement in the text, which one is entitled to apply specifically to the Type specimen, Berry reported that the lateral sectors of the web are the deepest, extending along about one-quarter of the length of the arm (WDI ca. 25), and the E sector is the shallowest; but his table gives only the depths of the A and E sectors. The order of web depth is thus similar to that of the Puget Sound series (B = C = D > A > E), but the relative depth of the shallowest sector cannot be determined.

The suckers are said to increase in size at the level of the web margin, but Berry gave no measurements; the largest sucker shown in Berry's photograph (p. 36, fig. 1) would give an estimated diameter of 7.5 mm and a corresponding sucker diameter index of 101. This figure would be low even for females of the Puget Sound series but is in agreement with the scanty data for immature males from California, which appear to have female-type suckers; there are no such immature males in the Puget Sound series. No specially enlarged suckers seem to have been observed in the Type and none can be seen in the photograph; a Californian specimen (SSB 134) with specially enlarged suckers (pl. 39, fig. 3) has been identified by Berry (1953) as a different species (p. 25).

The funnel organ was not described and we are not entitled to assume that the funnel organ of a Californian specimen figured by Berry (1913) would have been the same as that of the Type.

The relative length of the third right arm in relation to the third left arm gives an index that is definitely below the lower limits for the Puget Sound series (HAI 79); if the length is expressed in relation to mantle length, the index is just at the upper limit, but within the range, for Puget Sound males (MHI 35). The significance of this difference, which is apparently not dependent on sexual maturity, is discussed on p. 49.
The ligula length index is low (LLI 6.8), lower than in the Type and CotYPE of *O. gilbertianus*, although the specimens are of about the same size. However, this relationship is a function of the degree of differentiation of the secondary sexual characters, and this, in turn, is a function of size, subject to a certain amount of individual variation. An allometric equation (Fig. 2) for specimens studied by the writer demonstrates this over-all relationship, and Berry’s Type of *O. apollyon*, if it were plotted on this graph, would fall close to the calculated line. The calamus length index, calculated from Berry’s figure of the ligula (pl. 39, fig. 4), is similar to that of the Type of *O. gilbertianus* but twice as great as that in the immature males from Puget Sound, which are of considerably larger size. As in the case of the ligula, the calamus length index can be interpreted in terms of immaturity; a single regression line fits the entire series of specimens studied (Fig. 3) and, if plotted, the Type of *O. apollyon* would provide no exception.

Berry did not comment on the form of the penis, and there is no evidence as to the state of sexual maturity; spermatophores were not mentioned.

(b) The CotYPE. This specimen, a little larger than the Type, had an estimated mantle length of 73 mm, using the 8°/₀ correction factor. The indices are in general agreement with those of the Type. The head is narrower and the arms are more nearly subequal. As might be anticipated in a less juvenile animal, the ligula length is greater.

C2. The TYPES of *Octopus gilbertianus* (Berry, 1912).

Berry assigned two medium-sized males from Alaska to a new species, *Polypus gilbertianus*, on the basis of a comparison with (i) the description of *O. hongkongensis* Hoyle and (ii) a series of specimens that Berry originally referred to Hoyle’s species but for which he later employed the name *apollyon* (Berry, 1913). The chief distinguishing character, employed in the Key (Berry, 1912: 271), was the relatively large size of the ligula. This seems to have been selected with total disregard for the large ligula described by Verrill (1883) for *O. punctatus* and accepted by Berry in the synonymy of *hongkongensis* (later *apollyon*).

(a) The Type (USNM 214320). This specimen, re-examined in the present investigation, is from Albatross St. 4228 in the vicinity of Naha Bay, Behm Canal, Alaska; it is a well-preserved but immature male. It had not been previously dissected. The present mantle length is 54 mm; Berry’s measurement, “Tip of body to base of dorsal arms,” is not the standard mantle length, but fortunately, the true mantle length can be estimated from Berry’s drawing (pl. 37), which is apparently correct at the stated 2/₃ reduction, since both head width and mantle width are in agreement with the expected measurements. The true mantle length, at the time his drawing was made, appears
to have been 60 mm; Berry's measurement, "Tip of body to base of dorsal arms," was 65 mm. This observation suggests that a correction factor of 8°/0 should be applied to other reported specimens for which no direct confirmation is possible.

Many measurements of the TYPE specimen after some 50 years of preservation are in almost exact agreement with those given by Berry, or with those estimated from his drawing. This is true of mantle width, head width, estimated length of third right arm (see below), length of ligula, depth of E sector of web (but not of A sector), and estimated diameter of largest sucker (pl. 37). Where there is a discrepancy, present measurements are almost always somewhat less; this is apparently true for mantle length, and it is certainly true for the length of the longest arm (R2). Such differences can well be attributed to shrinkage during long years of preservation. Indices calculated from Berry's data are given in Appendix A, Tables vi and vii (pp. 58, 59), for comparison with those observed on re-examination. In general, the agreement is good, allowing for a slight uncertainty as to the true mantle length and some differential shrinkage over the years.

The arms are more nearly subequal now than they were formerly. The longest arm (R2) now measures 215 mm, cf. Berry's length of 232 mm. The order of arm length is the same as his, 2 > 3 > 4 > 1. The order of web depth is different on the two sides: left, C > D > B; right, B = C = D. In contrast to Berry's data, the A and E web sectors are now coequally the shallowest and the right B sector is the deepest by a millimeter. Berry did not give measurements for the lateral sectors. The suckers are small but relatively larger than the estimates from Berry's drawing. As in the case of the TYPE of O. apollyon, the relatively small size of the suckers is probably associated with juvenility.

The funnel organ, not described by Berry, is well preserved and is in the form of a W, with the lateral limbs about half as long as the median limb; the limbs are broad, and the junction of lateral and median limbs is truncated basally. There are 12 gill filaments on the inner demibranch and 13 on the outer demibranch of the left gill, the last on each side being very small; the gill, measuring 14 mm in length, appears to be strongly contracted.

In regard to secondary sexual characters, the animal is obviously immature, as judged by the relatively undeveloped condition of the internal genitalia. The penis is small and weakly developed, but nevertheless it is of the form found in the San Juan–Puget Sound series and is similar to that described by Sasaki for Japanese specimens of O. dofleini. There is a relatively long blind diverticulum that constitutes about 80°/0 of the combined length of penis plus diverticulum. The low penis length index can readily be attributed to immaturity.

The relative length of the hectocotylized arm is 85°/0 of the length of the third left arm. Berry gave only one measurement for the "third arm," 168 mm, which is in close agreement with the present length of the third right arm.
(170 mm) and with the estimated length of this arm as derived from Berry's pl. 37. Unfortunately, the length of the third left arm cannot be measured with any degree of accuracy on Berry's drawing, but it is clearly longer than the third right arm. In reference to mantle length, the old and new indices are in moderately good agreement. Either method of evaluation suggests that the relative length of the hectocotylized arm is at the lower limit of the range for the San Juan–Puget Sound series, as in the Type of *O. apollyon*.

The lingula length index is low compared with that of mature specimens from farther south, but it is only a little below the indices for immature specimens; since Berry's Type is even smaller, this can readily be attributed to immaturity. The calamus length index is slightly greater than that estimated from Berry's figure (pl. 35, fig. 5), but its value is concordant with the state of immaturity. There are some 45 or 50 transverse rows of small papillae in the widely open ligula groove, the terminal ones being progressively more weakly developed. At the base, each transverse row consists of a small median papilla, on each side of which is a more prominent lateral papilla; these form three longitudinal series, but towards the middle region there is a doubling of the median papilla so that four longitudinal series are recognizable, with minor irregularities.

(b) The Cotyype. This specimen can no longer be found. Indices calculated from Berry's data, using an 8% correction factor to determine the standard mantle length, are given in Appendix A, Tables vi and vii (pp. 58, 59). The Cotyype is slightly larger than the Type, but the two specimens are otherwise in close agreement. The Cotyype may have been sexually more advanced, since the ligula length index is higher.

(c) The Status of *Octopus gilbertianus*. Taking into account the newly accumulated data, there seems to be little reason to regard *O. gilbertianus* as a distinct species. Apparent differences between the Type and Cotyype of *O. gilbertianus* and the Alaskan Types of *O. apollyon* can be readily dismissed. Berry emphasized the red color of *O. gilbertianus* and the character of the skin with its numerous small pointed papillae. Unlike the Type of *O. apollyon*, the first arms of *gilbertianus* are the shortest. Kondakov (1941) accepted this feature as a character of *gilbertianus*, but newly described specimens of the giant octopus from Alaska (see below) exhibit great variability in relative arm length although they otherwise bear a great similarity to *O. gilbertianus*. The relative length of the ligula of *O. gilbertianus*, to which Berry attached importance, is difficult to evaluate in a specimen that is so obviously immature, but it should be noted that the Types of *O. apollyon* were, on the basis of this character, even more juvenile although of similar mantle length. However, the size at which an octopus first approaches or attains sexual maturity is, in itself, a variable matter. Unexpectedly small specimens of *O. vulgaris* have been found with fully formed spermatophores (Pickford, 1945).
Not all of the differences between Berry's specimens of *gilbertianus* from Alaska and the newly described series from the San Juan–Puget Sound area can be attributed to a greater degree of immaturity. This problem is reserved for later discussion (p. 49).

C3. Newly Described Specimens from Alaska

In view of the loss of the Types of Berry's *O. apollyon* and the paucity of data on Alaskan representatives of the giant octopus, it is fortunate that the following seven well-preserved specimens collected by Dr. Waldo L. Schmitt have been available for study.

1. NW Corner of Canoe Bay, Alaska Peninsula, Alaska; 30 fms.; 19 September 1940; 2 juvenile ♀♀ and 1 juvenile ♀; USNM 574594; ML 84, 78, and 97 mm, respectively.
2. Canoe Bay, Alaska Peninsula; 22 September 1940; 2 immature ♂♂; USNM 574595; ML 190 and 210 mm.
3. King Cove, Alaska Peninsula; 15–22 fms.; 16 October 1940; 1 juvenile ♀; USNM 574596; ML 165 mm.
4. Popof Strait, just off Sand Point toward Egg Island, Alaska; 25 October 1940; 1 juvenile ♀; USNM 574597; ML 73 mm.

Two of the specimens are of large size, but unfortunately they are not fully sexually mature. However, their state of development is more advanced than that of Berry's Types of *O. apollyon* and *O. gilbertianus* and, since the three groups are clearly conspecific, this circumstance permits a more complete evaluation of the status of the Alaskan form of the giant octopus. The range and mean for the indices of bodily proportions, summarized in Appendix A, Tables VI and VII (pp. 58, 59), are compared with those of *O. apollyon* and *O. gilbertianus*; there is a good general agreement, the data for the two previously described species falling within the range for the newly described specimens. For the most part, the indices are also in agreement with those for the San Juan–Puget Sound series, but attention must be called to some differences. The general appearance, particularly of the smaller juvenile specimens, is strongly reminiscent of the Type of *O. gilbertianus*, re-examined in the present investigation (p. 30).

The color is variable: a light- or dark-reddish brown, usually with black reticulations dorsally; paler pinkish brown below. The skin is rugose in the more strongly contracted specimens but nearly smooth in others; in all specimens there are small, sparsely distributed, pointed papillae on the dorsal surface. All specimens have a single, triangular, flattened, earlike supraocular cirrus above the posterior angle of the eye.

In agreement with the Types of *O. apollyon* and in contrast to the Types of *O. gilbertianus*, the first arm is rarely the shortest, but this condition was
observed in just two specimens. However, either a first or a fourth arm is the shortest and a second or third arm usually the longest; in USNM 574594, the fourth right arm is the longest. The typical sequence of arm length, 2 > 3 > 1 > 4 on the left side, is in striking contrast to the sequence observed in the Puget Sound series, 1 = 2 > 3 > 4; undoubtedly the first arms are more often relatively short in the Alaskan population.

The E sector of the web is either the shallowest or is coequally shallowest with the A sector or, in one instance, with the left D sector; the typical order is D > C > B > A > E.

There are no specially enlarged suckers, but interest attaches to the relative diameter of the largest sucker. The mean sucker diameter index is 17.5 for males, 16.4 for females, and, although the ranges overlap, it seems that the Alaskan representatives of the species tend to have larger suckers than those from farther south. However, this difference completely disappears if sucker diameter is referred to head width rather than to mantle length; the mean index is 36.5 for males and 28.4 for females and is essentially identical with the means for the Puget Sound series (p. 13). An ultimate evaluation would have to take into account the relative significance of these two methods of expressing the size of the suckers, for in smaller animals the head is relatively broader than in adults.

The funnel organ is in the usual form of a broad W; the lateral limbs are markedly shorter than the median limb, but their relative length is rather variable, ranging from 49 to 78% of the median limb. However, the mean is in the range of the San Juan–Puget Sound series, as in the case of the TYPE of *O. gilbertianus*.

In view of Kondakov’s observations regarding the jaws of *O. gilbertianus* from Siberia (p. 38), the beak was dissected from the smaller of the two large males from Canoe Bay (USNM 574595). The rostral length index of the upper jaw is similar to that of other specimens of *O. dofleini*, but there is a wide shallow groove on the side of the rostrum, parallel to the growth lines (Fig. 1c,d). This feature, not observed on the jaw of specimens from farther south, is evidently the groove that Kondakov described as highly characteristic of large specimens of *O. gilbertianus*. There is no such groove on the beak of a juvenile female (USNM 574594) half the size of this specimen. It appears probable that this groove reflects a period of cessation of growth during the severe subarctic winter and that its presence in larger specimens from the Far North may be interpreted as an ecological rather than a genetic difference.

The length of the hectocotylized arm in relation to its mate of the opposite side tends to be less than in the Puget Sound series. However, there is a considerable degree of overlap and some indication that juveniles may have a lower index than those that are more nearly mature: the two largest males, with mantle lengths of 210 and 190 mm, have indices of 96 and 89, respec-
tively. Unfortunately, there are no comparative data for juveniles of the Puget Sound series. In terms of mantle length, the indices are correspondingly somewhat greater than those for specimens from farther south, but both methods of estimating this parameter give figures that are in agreement with those of Berry’s specimens. This is an important character since, like the funnel organ, it appears to separate the western and eastern Pacific populations of *O. dofleini*, while transitional conditions obtain in the Far North. The subject is reserved for discussion (p. 49) after presentation of data regarding the Siberian and Japanese specimens.

As might be expected, the relative length of the ligula varies with the degree of maturity; in the largest male, the index is 16.0, which is like that of similar large immature specimens from the Puget Sound area but is far below that of sexually mature individuals. The calamus length index is also in the range for immature or juvenile animals. The groove of the ligula is tightly closed in the two largest males, but more open in others. As in the *Type* of *O. gilbertianus* and in specimens of *O. dofleini* from other localities, there are transverse rows of small papillae in the ligula groove: a median and two lateral papillae basally, two median and four or more lateral papillae farther out.

The relative length of the penis plus diverticulum varies with the state of maturity; for the two large males the indices are 28 and 31; thus this index is slightly but not significantly below that observed in immature males from Puget Sound. The long diverticulum averages 74% of the combined length of penis plus diverticulum; this is highly characteristic of *O. dofleini* and is apparently independent of age.

Only juvenile females were represented in this collection, and the small size of the oviducal gland reflects this condition.

**D. Siberia**

**D1. The Specimen Identified as Octopus punctatus Gabb by Joubin (1897)**

This specimen, a large but poorly preserved male from Avatcha Bay, Kamchatka, was sent to Joubin from the former Imperial Museum in Moscow by Professor Zograff. The condition of the specimen precluded full description. It is evident from the following calculations that this was a large animal. Probably it was sexually mature, as shown below. In discussing the status of this specimen, Joubin assigned it with some reservation to *O. punctatus* Gabb but pointed out that in certain respects it was intermediate between Verrill’s specimens of *punctatus* and the *Type* of *O. hongkongensis* Hoyle. He was strongly influenced by the enormous size of the ligula, which was even larger than in Verrill’s specimens, and he noted that there was only one supraocular cirrus.
The mantle length was not given, but Joubin’s photograph (fig. 1) shows a mantle that is abnormally stretched; the magnification of the figure was not stated, but the mantle width index is low (ca. 46); the head is partially concealed by the arms so that the head width index cannot be determined. However, the diameter of the largest sucker was given by Joubin as 39 mm, and the sucker diameter index, calculated from the photograph, can be employed to estimate the mantle length, which appears to have been about 225 mm. Joubin stated that all arms were intact, except the third right, and that the arm length was 50 to 60 cm; this is probably too low. If one assumes a mantle arm index of 25, a reasonable approximation, and a mantle length of 225 mm, as calculated above, the length of the longest arm would be about 900 mm; and the total length, using an arm length index of 78, would be about 1,154 mm. Robson (1929: 201) evidently employed some similar calculation, not specified, to arrive at an estimated total length of 1,232 mm.

Joubin described the suckers in detail. As noted above, the largest sucker was 39 mm in diameter; the suckers appear to increase rather abruptly in size at the level of the web margin but, as far as one can judge, none could be classified as specially enlarged. The sucker diameter index, estimated from the photograph, is near the upper limit for males of the Puget Sound series and similar to that of specimens from Alaska.

It is unfortunate that two critical taxonomic characters are unknown: the form of the funnel organ and the standard hectocotylized arm length index. However, if the length of the hectocotylized arm is referred to the estimated mantle length, the index MHI is 40.9, which places this animal squarely in the same category as *O. dobleini* from Japan, and close to the upper limit of the Alaskan series; it is completely outside the range for the San Juan–Puget Sound series. The ligula measured 115 mm and the length of the hectocotylized arm was 550 mm; the ligula length index (LLI 20.8) is therefore similar to that of mature males of the giant octopus from other localities (U.S.A. and Japan). The calamus was evidently short, but the photograph does not show this feature with sufficient clarity for calculation of the calamus length index.

D2. Specimens Referred to *Octopus gilbertianus* (Berry) by Kondakov (1941)

Kondakov recorded a number of specimens from the Bering, Kamchatka, and Okhotsk seas that he assigned to *O. gilbertianus*. A complete translation of Kondakov’s description of this species is given in Appendix C, p. 65. Kondakov stated that 12 large octopus taken in the Okhotsk Sea were not preserved but were identified as *O. dobleini* on account of their large size and the presence of large leathery auricles above the eyes. He pointed out that the auricles are characteristic, not only for *O. dobleini* but also for *O. gilbertianus* and *O. hongkongensis*. In his opinion, *O. dobleini* is a more southern species, and the presence
of *O. hongkongensis* in this area is unlikely. The 12 large specimens from the Okhotsk Sea were therefore probably *O. gilbertianus*.

Apparently *O. hongkongensis* did not occur in Kondakov's extensive collections, but *O. dojleini* was recorded (p. 45). The differences between *gilbertianus* and *dojleini*, as recognized by Kondakov, are summarized in his Key, as follows:

- **Terminal organ of hectocotylus closed. Above each eye only one large and three small supraorbital papillae.**
  - *Octopus dojleini* (Wülker).
- **Terminal organ rather open. Above each eye only one supraorbital papilla resembling a flat rounded leathery ear.**
  - *Octopus gilbertianus* (Berry).

The form of the ligula, with closed or open groove, was described and figured in the text (figs. 39 and 34, respectively), but this problem requires further study. Infolding of the lateral walls could easily be influenced by the state of preservation and may also be a function of sexual maturity. The question of one or more supraorbital papillae is equally hard to evaluate. Some additional information may be derived from a consideration of data presented in the text.

Kondakov gave measurements for three adult females, two juvenile females, and a juvenile male. Indices and other standard parameters for these specimens are summarized in Appendix A, Tables vi and vii (pp. 58, 59). An 8% correction factor, similar to that employed for Berry's specimens (p. 31), has been used to estimate standard mantle length from Kondakov's measurement, "Length of body to base of arms." It may be observed that even the supposedly adult females were not of exceptionally large size as compared with the giant Japanese species identified as *O. dojleini* by Sasaki (1929), since the largest had a mantle length of only 180 mm. This is three times the size of Berry's Type of *O. gilbertianus* but falls in the range for newly described immature specimens from Alaska (p. 33).

Indices for mantle width and head width are highly variable; some specimens are broad like Berry's Types of *gilbertianus*, but some are narrow. The arms are rather short, as reflected in an unusually high mantle arm index, but this must be viewed with suspicion, since the standard arm length index, which depends on the stated total length rather than on the estimated mantle length, is of the same order as in the Alaskan specimens. As in the case of Berry's Types, the order of arm length is 2 > 3 > 4 > 1; but Kondakov did not give separate measurements for the left and right sides. This does not matter in the case of females, but it would be advantageous to know whether the measurement given for the third arm of the male refers to the right or left member of the pair. Web depth measurements were not given, but Kondakov stated that the web is deepest between the second and third arms (C sector) and that it extends along about one quarter of the length of the arm (ASI ca. 25).

The suckers are said to be best developed near the level of the web margin; Kondakov did not mention specially enlarged suckers, nor did he give sucker diameter.
Two important characters, neglected in earlier descriptions of specimens from the Far North, have been noted by Kondakov. (i) The form of the funnel organ was described and figured (fig. 35); the lateral limbs are about half as long as the median limb of the W (FoI 45.8). This index is in agreement with that of specimens from the Pacific coast of North America, and seemingly it separates these populations from the typical Japanese form of O. dofleini (see below). (ii) The total number of primary gill lamellae was given as 21; this is low for the giant octopus, but possibly Kondakov overlooked the small terminal ones.

Kondakov figured the radula of O. gilbertianus (fig. 36), but it does not seem to differ significantly from that of his O. dofleini (fig. 40), or from that of a specimen of O. dofleini described by Sasaki (1929: text fig. 35). Kondakov stated that the beak is powerful and that the inner edges are excavated. In large specimens there are said to be one or two grooves on the outer surface of the distal part of the dorsal jaw (fig. 37). According to Kondakov, the beak of O. gilbertianus is so characteristic that the species can be determined by this character alone. A similar groove has now been observed on the jaw of a large male from Alaska (p. 14; Fig. 1C, D). The rostral length index for the upper jaw, calculated from Kondakov's drawing (fig. 37), is 45.7, and it is therefore in the range for other specimens of O. dofleini from various localities.

As pointed out above, the length of the third right arm was not specified for the juvenile male whose measurements were tabulated; the third-arm measurement may refer to the right or left side, or to both if they were equal. The subject was not discussed by Kondakov, but, since Kondakov identified his species with O. gilbertianus and since Berry emphasized the relative shortness of the hectocotylized arm, it must be assumed that this condition also applied to Siberian animals. Kondakov stated that the ligula is large and pointed, the copulatory groove deep and transversely striated. The significance of the form of the ligula as a Key character is discussed above. The size was not given and cannot be estimated from the drawing (fig. 34), since the magnification was not stated. The relative length of the calamus, calculated from Kondakov's drawing, gives a rather high calamus length index (15.3), suggestive of immaturity, but he did not state whether it was taken from the juvenile male or from some larger specimen. The latter hypothesis seems more probable, for the juvenile male had an estimated mantle length of only 26 mm, and it is hard to believe that so small an animal would have had a well-formed hectocotylus.

On the whole, Kondakov's data appear to support the hypothesis that his O. gilbertianus is separable from Sasaki's O. dofleini, but perhaps not at the specific level. The problem is reviewed later (p. 49) following consideration of the Japanese forms.
III. The Temperate Western North Pacific

E. Japan

E1. The Type of Octopus dofleini (Wülker, 1910)

A moderately large, probably immature, male from Todohokke (Hokkaido), Japan, was described by Wülker as *Polypus dofleini*. Although the status of this species is of crucial nomenclatural importance, the type was not re-examined by either Robson (1929) or Sasaki (1929) and, unfortunately, it is no longer in existence. An evaluation must therefore depend solely on the original description. The indices, summarized in Appendix A, Tables VIII and IX (p. 60), are derived, unless otherwise indicated, from measurements given by Wülker. Mantle width, head width, and sucker diameter, employed for calculation of their respective indices, have been taken from Wülker’s excellent photograph (pl. 5, fig. 1), which is correctly stated to be at $\frac{2}{5}$ natural size, as verified by the measurement of mantle length.

The arms are of moderate length and the apparent order of arm length, excluding the hectocotylized third right arm, was $2 > 3 > 1 > 4$; however, considerations given below suggest that the length of the third left arm was underestimated and that arms 2 and 3 were subequal. The lateral sectors of the web were deepest, but they were not specified individually; the E sector was the shallowest, but the difference between the deepest and the shallowest sectors was not great (WSI 81.8). This is of particular interest, since Sasaki did not give web depths for the specimens that he assigned to Wülker’s species and since we have such data for only one other Japanese specimen.

The relative length of the hectocotylized arm in relation to its mate of the opposite side requires special consideration: the index, calculated from measurements given in the text, is high (HAI 86.5). This is outside the range for Sasaki’s series and approaches values found in the newly described specimens from Puget Sound. It may be observed from Wülker’s photograph (pl. 2, fig. 2) that the tip of the third left arm is extremely delicate, coiled, and attenuated, and it is possible that his measurement was not precise, for fear of injury to the arm tip. Anyone who has attempted to measure specimens of octopus that have been hardened by preservation will admit the difficulties entailed. On the other hand, Wülker’s photographs appear to be untouched and, as far as can be determined, reliable. As noted above, the mantle length is correct at the stated $\frac{2}{5}$ reduction. Similarly, the length of the second right arm, which can be rather accurately estimated from his fig. 1, agrees almost precisely with his published measurement, and the length of the ligula is equally accurate. On the other hand, the length of the third left arm, measured

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2 In reply to enquiries, Dr. W. Engelhardt stated (in litt., 4 July 1960) that *O. dofleini* Wülker is no longer in the collections of the Zoologische Sammlung des Bayerischen Staates in Munich and was presumably lost through bombing or vandalism during the war.
on fig. 2, is certainly greater than that stated in the text; it could not have been less than about 438 mm, whereas the stated length was 370 mm. The length of the third right arm, also measured on fig. 2, is in better agreement with the text, but possibly it is slightly longer; a minimum estimate gives 335 mm as compared with 320 mm. If the index (HAI) is calculated from measurements taken from the photograph, Appendix A, Table IX (p. 60), this index assumes a value of about 76, which is within the range for the specimens described by Sasaki. In view of the evidence presented, this interpretation seems to be reasonable. In terms of mantle length, which is independent of the third left arm, the hectocotylized arm has an index of 40.6, which again is in the range for Sasaki’s specimens.

The only other important observations concern the form of the ligula. The indices for ligula length (LLI 7.0) and calamus length (CLI 17.0) have been calculated from Wülker’s careful drawing (pl. 3, fig. 10), which is apparently at natural size; in his fig. 10 the length of the ligula, measured from the last sucker, is 23.5 mm, whereas Wülker gave a length of 20 mm; presumably his measurement was taken from the calamus rather than from the last sucker. In calculating the ligula length index given above (7.0), the revised estimate for the length of the third right arm was employed. If the ligula length index is calculated directly from Wülker’s measurements, it is a little lower (6.3). However this may be, the value for the ligula length index is low and the value for the calamus length index is high compared with Sasaki’s mature males; in view of the small size of the Type, this would be consistent with the hypothesis that it was a sexually immature male. Sasaki has stated that many of his younger specimens, in which the hectocotylus is not fully formed, agree with Wülker’s illustration in every detail.

It should be added that Wülker had two specimens, a male and a female, from Aburatsubo, that he identified, without description, as Polypus punctatus (Gabb). He pointed out that dofleini differs from punctatus in two respects: the shorter ligula and the relatively shorter arm length. Both of these differences could be due to immaturity.

E2. Specimens Identified as Polypus hongkongensis Berry = P. dofleini Sasaki (1929) by Sasaki (1920)

Under the name P. hongkongensis, assigned to Berry rather than to Hoyle, Sasaki (1920) listed a number of specimens collected by the ALBATROSS at stations ranging from the Aleutian Islands to Korea and southward to Japan. These were subsequently assimilated in the synonymy of the giant Japanese octopus (Sasaki, 1929) under the name Polypus dofleini Wülker. According to Kondakov (1941), it is probable that specimens from the more northern stations have been erroneously assigned to the typical Japanese form of O. dofleini.

Most of the specimens listed by Sasaki were unsexed juveniles; two females were noted but not described. There is a brief description of a spermatophore-
Pickford: *Octopus dojleini* (Wülker) 41

bearing male from Hyuga-nada, Japan (USNM 332992; ALBATROSS St. 4957). Sasaki considered the status of this specimen doubtful on account of: (i) its relatively small size for an adult male, (ii) the atypical character of the skin, and (iii) the limited number of suckers on the hectocotylized arm—several pairs fewer than described in what Sasaki termed the ordinary form. The last mentioned character is not one that has been taken into consideration in the present review, since it has rarely been mentioned in published descriptions.

Sasaki's specimens are in the collections of the U. S. National Museum, and a large male (USNM 332992), erroneously assumed from the catalogue number to be his mature specimen, was re-examined in the present investigation. It is an immature male, labeled *Polypus punctatus* (Gabb): ALBATROSS St. 4952, between Kagoshima and Kobe, Japan, 23 August 1906, 437 fms., Id. Madokai Sasaki. No specimen from St. 4952 was listed by Sasaki; his mature male was from St. 4957. Standard parameters for USNM 332992 are given in Appendix A, Tables VIII and IX (p. 60).

The mantle length is 98 mm and the total length 550 mm. The total length is considerably less than that reported by Sasaki for the Hyuga-nada male (71 cm) that was not found.

The head and mantle are unusually broad, but the arm length indices are in the range for *O. dojleini*, and the order of arm length does not conflict with typical sequences for this species. The same is true for the order of web depth. Two taxonomically important characters are in agreement with those of other Japanese specimens described by Sasaki (1929): the lateral limbs of the funnel organ are almost as long as the median limb, and the hectocotylized arm is markedly shorter than its mate of the opposite side (HAI 77.5).

No spermatophores are present, and the relative lengths of the ligula (LLI 12.9) and calamus (CLI 12.5) indicate that it is an immature animal, if referable to the giant octopus. The short penis diverticulum raises some doubts about this; although it is otherwise of the form found in *O. dojleini*, the diverticulum is only about as long as the penis itself. Unfortunately, at the time the specimen was examined by S. J. Townsley, the importance of the relative length of the diverticulum was not realized, and a sketch of the entire organ was not accompanied by measurements of its two parts, although the total length was recorded.

While the status of the other specimens collected by the ALBATROSS must remain undecided, there is little reason to exclude this immature male from the synonymy of the Japanese giant octopus. These animals will now be considered in detail.

E3. Specimens Described as *Polypus dojleini* Wülker by Sasaki (1929)

By far the best and, in fact, the only really complete account of the giant octopus is that given by Sasaki, who, as indicated above, identified his specimens with Wülker's species. As already pointed out, Sasaki stated that many
of his younger specimens, in which the hectocotylus is not fully formed, agree with Wülker's illustration in every detail. An evaluation of the problem supports this conclusion and, since the Type of O. dofleini is lost, it seems reasonable to accept Sasaki's well-qualified opinion. The name of the Japanese giant octopus is therefore decided: Octopus dofleini (Wülker, 1910; emend. Sasaki, 1929).

The relationship between O. dofleini and the apparently closely allied forms of the northern and eastern Pacific presents a difficult problem. Sasaki was doubtful about another Japanese species, O. hongkongensis Hoyle, and, as it proves, rightly so; it is a different species (p. 61). On the other hand, he expressed the opinion that Berry's O. apollyon was the same as his O. dofleini, but he did not discuss the status of O. gilbertianus. According to data presented in the present investigation, these two species differ from the Japanese specimens of O. dofleini in at least one decisive character: the short lateral limbs of the funnel organ. There is, therefore, good reason to agree with Kondakov (1941) that dofleini is a more southern form and, on this basis, that all northern records assigned by Sasaki and others to the punctatus-apollyon-dofleini complex are at least racially distinct.

The center of interest, in the present investigation, is the comparison of Sasaki's excellent and well-described series from Japan with the newly described material from the San Juan-Puget Sound area. The following discussion of Sasaki's specimens is oriented towards a solution of this specific problem.

Standard indices and other parameters derived from Sasaki's description and his table of measurements are summarized in Appendix A, Tables VIII and IX (p. 60). In many respects there is a good agreement between data for these specimens and for the series from the San Juan-Puget Sound area, Washington State (Appendix A, Tables IV and V, pp. 56, 57). This agreement encompasses a number of highly diagnostic taxonomic characters and includes many minor points of resemblance. Among the diagnostic characters must be noted (i) the small number of relatively enormous spermatophores, each with a few spiral coils at the oral end of the horn, (ii) the penis with an extremely long diverticulum, (iii) the size and form of the ligula, and (iv) in females, the relatively small size of the eggs for so large an animal. Other concordant characters include the very large over-all size, the large posterior supraocular cirrus, the subequal arms with a similar typical sequence (1 = 2 > 3 > 4), the order of web depth, and the absence of specially enlarged suckers.

However, certain differences must be noted. Calculations of all indices based on mantle length are beyond, or close to, the limits of the Puget Sound series. Sasaki's "Eye to end of body" would perhaps be a little different from Robson's standard mantle length, but not significantly so. More important is the fact that Sasaki's measurements were made on fresh specimens. It is possible that differential contraction resulting from preservation could cause a
shortening of the mantle length that is out of proportion to the corresponding shortening of the arms and web. Head width, on the other hand, might be little changed by preservation, since it is supported by internal cartilages. The same might be true of sucker diameter on account of the presence of a supporting ring. In an attempt to resolve this problem, an index was calculated for percentage sucker diameter in terms of head width rather than mantle length. The results are summarized in Appendix A, Tables iv, vi, and vili, under the symbol HSnI.

This treatment tells a different story from the standard sucker diameter index (SnI), which depends on mantle length and which suggests that the suckers of the Japanese specimens were relatively smaller than those of the Puget Sound series. Actually, on the basis of head width, there is no difference. Either method of calculation supports the conclusion that males tend to have relatively larger suckers than females.

Another attempt to clarify the problem was based on measurements taken from Sasaki’s photograph of a mature male from Hidaka (pl. 1, fig. 2), which had been preserved in formalin. The mantle length index is 83 and the head width index 45; both values are in the normal range for the Puget Sound specimens. Similarly, the largest sucker gives a sucker diameter index of 21.5, confirming Sasaki’s statement that this specimen had unusually large suckers; thus at least this individual is brought into the range (actually slightly above the range) for the Puget Sound series.

A rough estimate suggests that a relative mantle-length shrinkage of the order of 20% would be required to bring the indices for Sasaki’s fresh specimens into line with those of the preserved animals from Puget Sound. An experiment designed to test this hypothesis contributed further light on this problem. Dr. A. W. Martin measured a specimen from Puget Sound before and after preservation and reported results from which the corresponding indices have been calculated (Table II).

**Table II. Indices Derived from Measurements of a Specimen Before and After Preservation.**

<table>
<thead>
<tr>
<th></th>
<th>Freshly killed</th>
<th>Preserved</th>
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<tr>
<td></td>
<td>In Water</td>
<td>On Floor</td>
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<td>WDI</td>
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<tr>
<td>SnI</td>
<td>19.1</td>
<td>16.0</td>
</tr>
<tr>
<td>HSnI</td>
<td>54.8</td>
<td>48.1</td>
</tr>
</tbody>
</table>

* Measurements by A. W. Martin on a specimen at the University of Washington, June 1960.
Data for the freshly killed specimen measured in water are interesting but not relevant to the immediate problem, for Sasaki certainly measured his specimens on a flat surface in the usual manner. The comparison of parameters for the animal before and after preservation, measured on the floor, tends to support the interpretation advanced above: a differential shrinkage of mantle length with the corresponding expected changes in the indices. The mantle width index (MWI) is, for some unexplained reason, little changed; but two other indices in which mantle length is the denominator were strikingly increased after preservation: the head width index (HWI) and the normal sucker diameter index (SnI). The mantle arm index (MAI), in which mantle length is the numerator, is correspondingly decreased. As predicted, there is little change in relative sucker diameter when this measurement is expressed in terms of head width rather than mantle length. Sasaki did not give measurements of web depth, but the data included here can be interpreted to mean that preservation resulted in a greater shrinkage of arm length than of web depth. The percentage shrinkages after preservation are as follows: mantle length 42.0%, mantle width 41.0%, head width 18.5%, arm length 21.7%, sucker diameter 15.4%. The shrinkage of the mantle was thus about twice that of the head, arms, or suckers.

The observations reported above, while not decisive, appear to undermine any attempt to separate the Puget Sound series from Sasaki's specimens on the basis of differences in indices that depend on mantle length. Of those characters whose indices do not depend on mantle length, there is good agreement between Sasaki's series and the Puget Sound specimens in respect to the relative length of the shortest arm, which is almost as long as the longest, and to the size and form of the adult ligula. The hectocotylized arm of the Japanese specimens, on the other hand, is markedly shorter than its mate of the opposite side, whereas in the Puget Sound material it is almost the same length (mean HAI 70.9 cf. 93.6, respectively); there is in fact no overlap in the respective ranges for this index between the two groups. When the length of the hectocotylized arm is expressed in terms of mantle length, the difference is still apparent (mean MHI, 37.6 for Sasaki's series and 28.4 for the San Juan-Puget Sound specimens), but, by this method, the ranges for the two groups are not discontinuous. Specimens from the Pacific Far North tend to bridge the gap between the east and the west (Appendix A, Table VII, p. 59).

Apart from skin characters, which are difficult to evaluate on preserved material and which may present some differences (p. 11), the only other character by which Sasaki's animals can be separated from the Puget Sound series is in the form of the funnel organ. Sasaki stated that the median limb of the W is equal to, or only a little longer than, the lateral limbs, whereas in the Puget Sound specimens the median limb is about twice as long. Sasaki's statement is confirmed by Kondakov, who has given a figure for the funnel organ of O. dofleini; the lateral limbs are almost as long as the median limb (FoI
92.9). This is also true of a specimen of *O. dojleini* from Japan, which was re-examined in the present investigation (p. 41). In this respect the Japanese specimens differ not only from the Puget Sound series but also from those of the Pacific Far North, in which the lateral limbs of the funnel organ are short, but perhaps not as short as in the Puget Sound series. Unfortunately, the range and mean for the Japanese group is not known.

E4. Specimens Assigned to *Octopus dojleini* (Wülker) by Kondakov (1941)

Kondakov stated that *O. dojleini* is a more southern species than *O. gilbertianus* and that it is found in the Chinese markets in Vladivostok, where it is sold fresh, dried, or marinated. A complete translation of Kondakov's description of this species is given in Appendix C, p. 65. He had specimens from the Sea of Japan and from the Bay of Posseit (near Vladivostok). His description adds little to that of Sasaki (1929), but he did give an illustration of the funnel organ (fig. 38) that confirms Sasaki's statement that the lateral limbs are almost as long as the median limb. The index (FoI 93) given in Appendix A, footnote 22 (p. 55), has been calculated from Kondakov's figure. Kondakov also illustrated the ligula (fig. 39) and, in comparing it with that of *gilbertianus*, he observed that the groove is closed. The relative length of the calamus, calculated from his fig. 39, gives an index that is in good agreement with that illustrated by Sasaki (CLII 9.7). The radula (fig. 40) also resembles that figured by Sasaki, although the rhachidian seems to be rather narrower. Kondakov's evaluation of the difference between *dojleini* and *gilbertianus* is summarized in the discussion of the latter species (p. 36).

E5. *Polypus madokai* Berry (1921) Described as *P. pustulosus* by Sasaki (1920)

The TYPE of this species was first described by Sasaki under the name *Polypus pustulosus* on the basis of a single immature female taken by the ALBATROSS in the Sagami Sea (USNM 332976). Since the name *pustulosus* was preoccupied, Berry proposed the name *madokai*. Sasaki (1929), who accepted this change, supplemented the original description with a table of measurements but referred no new material to this species.

The TYPE was not re-examined in the present investigation, since Sasaki's descriptions cover all essential features. The standard indices, summarized in Appendix A, Table VIII (p. 60), conform in general to those of Wülker's TYPE of *O. dojleini*. However, a direct comparison of indices dependent on mantle length with those given by Sasaki for *O. dojleini* must be accepted with reservation, since Sasaki's measurements were made on fresh specimens (p. 42).

The head is wide, as in Wülker's specimen, but this can be related to immaturity. The arms are nearly subequal, the first being the longest, the fourth the shortest. The E sector of the web is the shallowest; the order of web depth, taking both sides into consideration (cf. Table VIII for the sequence on the left
is $B > C > D = A > E$. The suckers are relatively small ($SnI 9.4$), and this is even more apparent when the diameter of the largest sucker is referred to head width ($HSnI 12.5$). Such low indices have not been reported for any other specimens studied or reviewed in the present investigation, although some individuals (e.g. from California) are nearly as low. Specially enlarged suckers are not present.

The lateral limbs of the funnel organ are somewhat shorter than the median limb; the index, calculated from Sasaki's figure (1929: pl. 11, fig. 9), is higher than in specimens from the eastern and northern Pacific (Appendix A, Tables 1v and vi, pp. 56, 58), but possibly it is in the range for the Japanese specimens of $O. dofleini$, which is not accurately known. The index $Foi 85$ could be included in Sasaki's statement for the latter species, "the median lobe as long as, or a little longer, than the lateral." Therefore it is unlikely that $madokai$ could be separated from $O. dofleini$ on the basis of this character.

The number of gill filaments is low compared with that of $O. dofleini$; this may be a valid difference, since Sasaki himself studied specimens of both species, thus avoiding possible subjective differences in rating the smallest terminal tufts.

In comparing $madokai$ with $dofleini$, Sasaki (1929) stated that $madokai$ is distinguished by (i) its softer consistency, (ii) the broader head, (iii) the arms of unequal length, and (iv) the quite different character of the skin ornamentation. The softer consistency is hard to evaluate; the broader head could be related to immaturity; the supposed inequality of the arms can be shown, from Sasaki's own measurements, to be of little significance, the index ($ASI 86$) being in the range for his series of $O. dofleini$; and the character of the skin could be subject to the state of preservation. Re-examination of the data points up two other possible differences: the small size of the suckers and the low number of gill filaments.

E6. Specimen Assigned to Octopus madokai (Berry) by Kondakov (1941)

Kondakov recorded an adult male from the Japan Sea that he attributed to this species. His description, for the most part, follows that of Sasaki. The hectocotylus is said to be similar to that of $O. dofleini$, but the entire organ is shorter and the copulatory groove open; no measurements or figures were given. In his Key, Kondakov employed the difference in size of the warts on the skin (also described by Sasaki) as follows: "dorsal surface with little pimple-like warts and about 20 rounded regularly distributed tubercles, four of which form a rhomb on the back." Although Kondakov stated that the specimen is adult, he did not mention the presence of spermatophores. It may well have been an immature male with a partially formed ligula, in which case the comparison with mature males of $O. dofleini$ loses significance. If it is immature, it is probable that tubercles would be present, as described, in the form of a rhomb. Sasaki described this condition in juveniles of $O. dofleini$. 
E7. The Status of *Octopus madokai* (Berry)

If *O. madokai* is a valid species, it would be separable from *O. dofleini* primarily on the basis of its small suckers and the low number of gill lamellae; the character of the skin might also be distinctive. Pending a careful comparison of the Type of *O. madokai* with newly collected juvenile and immature specimens of *O. dofleini* from the Sea of Japan, as well as the capture and recognition of sexually mature specimens that could be decisively separated from the latter species, it seems probable that *O. madokai* should be incorporated into the synonymy of *O. dofleini*.

**DISCUSSION**

In the preceding sections it has been shown that specimens of the giant octopus from the Pacific coast of North America, from California to Alaska, and from Siberia agree in a majority of diagnostic characters with those ascribed by Sasaki (1929) to *Octopus dofleini* (Wülker). The Type of *O. dofleini* is no longer in existence and, after a careful review of the evidence, it seems reasonable to accept Sasaki's opinion that the giant Japanese species is correctly identified with the immature male described by Wülker. The species may be redefined as follows:

*Octopus dofleini* (Wülker, 1910; emend. Sasaki, 1929)

Abridged Synonymy:

3. *Octopus punctatus*, Gabb (1862); not *O. punctatus* Blainville (1826).

3. *Octopus punctatus*, Dall (1866); description of radula.

*Octopus punctatus*, Verrill (1883).

*Octopus punctatus*, Joubin (1817).

*Polypus dofleini*, Wülker (1910); Holotype.

*Polypus hongkongensis*, Berry (1911, 1912), in part; not *O. hongkongensis* Hoyle (1884).

*Polypus gilbertianus*, Berry (1912).

*Polypus apollyon*, Berry (1912, 1913), in part; new name for Berry's *P. hongkongensis*.

*Polypus hongkongensis*, Sasaki (1920).

3. *Polypus pustulosus*, Sasaki (1920); not *O. pustulosus* Blainville (1826).

3. *Polypus madokai*, Berry (1921); new name for *P. pustulosus*.


3. *Octopus madokai* + *O. dofleini* + *Paroctopus apollyon* (in part), Robson (1929).

3 Excluding records unaccompanied by descriptions (for which see Berry, 1912, and Robson, 1929), but including described specimens of uncertain status, indicated by a question mark.
Octopus gilbertianus + O. dojinei + O. madokai, Kondakov (1941).
Octopus apollyon, Winkler and Ashley (1954), in part; anatomy.

Described Species or Specimens Excluded from Synonymy of O. dojinei:
Octopus hongkongensis, Hoyle (1885 a, b) = O. punctatus Hoyle (1886); a valid species (p. 61).
Polypus apollyon, Fisher (1923, 1925); excluded on account of small size of brooding females, and very small size of eggs.
Paroctopus apollyon, Robson (1929) = Octopus punctatus Robson (1925); two specimens in the British Museum (p. 63).
Octopus apollyon, Winkler and Ashley (1954); the male from California (p. 21).

Definition of the Species. Octopus of large size; mantle length of mature specimens over 190 mm. Body ovoid. Color usually reddish brown with black reticulations above; paler below. Skin sparsely ornamented with small papillae; four larger papillae may form a dorsal rhomb in young animals. A conspicuous, earlike posterior supraorbital cirrus always present. Head narrow in adults, broader in juveniles. Arms of moderate length and nearly subequal. Web of moderate depth, the E sector usually shallowest and about half as deep as the deeper lateral sectors. No specially enlarged suckers in either sex; normal suckers relatively large; larger in males than in females or in juveniles of either sex. Funnel organ broad-limbed, W-shaped. Primary gill lamellae 20 to 30 per demibranch. Third right arm of male hectocotylized. Ligula of mature animals long and slender, about \( \frac{1}{3} \) length of arm. Calamus short. Ligula groove with transverse rows of close-set papillae. Spermotophores few in number and of enormous size, about three times the mantle length; oral end of spermophore horn with about 15 spiral coils. Penis with a long, blind diverticulum. Oviducal gland superficially bean-shaped, the ducts entering and leaving side by side at the hilum. Eggs 6 to 8 mm long, with moderately long stalks; attached to the substratum in festoons.

The foregoing diagnosis omits characters that are seemingly subject to geographical variation. Such characters, for three geographical groups, are summarized in Table III. Evidence relating to other specimens, discussed in the text and summarized in Appendix A, Tables IV-IX, conforms to the over-all picture that is here reflected. Thus Berry's Types and Cotypes of O. apollyon and O. gilbertianus from Alaska and Kondakov's series from Siberia are readily integrated with the newly described group from Alaska. The only outstanding problem concerns the Californian population, for which adequate information is lacking.

It is evident that there are decisive minor racial differences between the populations of the eastern and western Pacific. Japanese specimens have a relatively short hectocotylized arm, and the limbs of the funnel organ are
TABLE III. *O. dojleini.* COMPARISON OF THREE REPRESENTATIVE POPULATIONS. THE MEAN, WITH THE RANGE IN PARENTHESES, FOR RELATIVE LENGTHS OF HECTOCOTYLIZED ARM (HAI) AND LATERAL LIMBS OF FUNNEL ORGAN (Foi), AND TYPICAL ARM LENGTH ORDER (ALO).

<table>
<thead>
<tr>
<th>Group</th>
<th>HAI</th>
<th>Foi</th>
<th>ALO</th>
<th>Comments</th>
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<td>Washington (G.E.P.)...</td>
<td>94 (88-109)</td>
<td>55 (42-64)</td>
<td>1 = 2 &gt; 3 &gt; 4</td>
<td></td>
</tr>
<tr>
<td>Alaska (G.E.P.)........</td>
<td>85 (77-96)</td>
<td>62 (49-78)</td>
<td>2 = 3 &gt; 1 &gt; 4</td>
<td>Groove on jaw</td>
</tr>
<tr>
<td>Japan (Sasaki).........</td>
<td>71 (65-79)</td>
<td>subequal*</td>
<td>1 = 2 &gt; 3 &gt; 4</td>
<td></td>
</tr>
</tbody>
</table>

*Kondakov has given 93.*

subequal; the reverse is true of specimens from the State of Washington in which the hectocotylized arm is about as long as the third left arm while the lateral limbs of the funnel organ are short. These differences cannot be attributed to immaturity, since both groups comprise adult or large immature specimens; this is an important consideration in respect to the relative length of the hectocotylized arm which, in juveniles, might be misleading.

Specimens from Alaska and Siberia tend to be intermediate in respect to the two characters noted above. The lateral limbs of the funnel organ are shorter than the median limb but not usually as markedly so as in the specimens from Washington; the relative length of the hectocotylized arm is similarly intermediate. With the exception of a poorly preserved animal described by Joubin (1897), all males from the Far North are juvenile or immature, and the length of the third right arm might be expected to reflect this circumstance. One would suppose that, as in *O. bimaculatus* and *O. bimaculoides* (Pickford and McConnaughey, 1949), the hectocotylized arm would be relatively shorter in larger animals; however, the reverse actually obtains: the two large males in the Alaskan group, with mantle lengths of 210 and 190 mm, have hectocotylized arm length indices of 96 and 87, respectively, and the two smaller males have indices of 77. Small males described by Berry and by Kondakov also have low indices for this parameter.

Apart from these two characters, which appear to bridge the gap between the eastern and western populations, specimens from Alaska and Siberia present minor peculiarities of their own. Kondakov called attention to the highly distinctive groove on the rostrum of the upper jaw; this may be an ecological rather than a genetic character, but it is undoubtedly a diagnostic feature in larger specimens from subarctic waters. The number of supraorbital cirri, employed by Kondakov to separate *O. gilbertianus* from *O. dojleini,* is of doubtful significance; the large, earlike, posterior supraorbital cirrus is characteristic of the species, and the presence or absence of one or more smaller anterior cirri is sporadic, but such are generally absent in specimens from the Far North. Another character to which Kondakov has attached
importance, the form of the ligula, may be discounted, for in this case much
depends on the state of preservation; in a flaccid animal the groove is open,
in a strongly contracted specimen it is closed. Berry attached importance to
the relative length of the ligula, but this has been shown to be correlated with
the state of maturity.

The relative length of the arms may be of taxonomic significance. This is
an elusive character. There is considerable individual variation in all popula­
tions and, in a species in which the arms are nearly subequal, the exact sequence
may not be important. However, comparatively few specimens from the Far
North have a long first arm, whereas most of the specimens from farther south,
both east and west, have first arms that are longer than the third or fourth.
In the Type of *O. apollyon*, from Alaska, the arm length order is $2 > 1 > 3 > 4$,
but in the Cotype it is $2 > 3 > 1 > 4$. The latter is the most prevalent sequence
in the newly described series from Alaska. In *O. gilbertianus*, from both Alaska
and Siberia, the order is $2 > 3 > 4 > 1$. The relative shortness of the first arms
could conceivably be associated with size. Clarification of this problem would
require an analysis of juvenile, immature, and adult specimens from a single
population. Juveniles from Japan or from the San Juan–Puget Sound area
have not been described, but data available for specimens from the Far North
(Siberia and Alaska) do not appear to support the hypothesis. The Alaskan
specimens, though few in number, cover a fairly wide size-range; the largest
specimen in which the left arms are complete (USNM 574596) has a fairly
typical “northern” sequence: $2 > 3 > 4 > 1$; the smallest specimen (USNM
575597) has an atypical sequence: $2 > 1 > 3 > 4$.

Further elucidation of these problems must await the study of adequate
collections from representative geographical areas. Such an investigation would
presuppose complete familiarity with the local octopus fauna, since juveniles
cannot be as easily identified as adults. The material should be preserved and
measured under standard conditions to ensure uniformity. Preferably the
specimens should be fully relaxed under anesthesia and then fixed with the
arms extended for greater ease of measurement. The author has employed
magnesium sulfate added in progressively increasing strengths until the octopus
is immobilized, followed by preservation in $4\%$ formaldehyde. The fixing
fluid should be flushed through the funnel and into the mantle chamber with
a syringe and, in larger animals, it is essential that $40\%$ formaldehyde be
injected into the viscera.

Newer methods of study must also be employed. The probable importance
of the mesozoan parasites (p. 28) has already emerged, and the field is wide
open for serological and cytological investigations.

In the meanwhile, the taxonomer must do what he can with the available
material. After due consideration, it seems advisable to give nomenclatural
recognition to the population differences outlined above. The Japanese form
is clearly distinct and was so recognized by Kondakov (1941). The Alaskan
population more nearly resembles Kondakov’s Siberian series than it does the newly described assemblage from the State of Washington. It would be an error of judgment to place the latter group, without reservation, in the synonymy of the Alaskan form. Future studies may reverse this decision, but at present it seems desirable to designate the Washington population as a distinct subspecies. In taking this step, the author recognizes that an individual specimen cannot always be placed with certainty in the subspecies to which it belongs, owing to the overlapping of diagnostic characters; therefore, construction of a Key for identification might be misleading. With these reservations, the following formal diagnoses are proposed:

Octopus dofleini dofleini (Wülker, 1910; emend. Sasaki, 1929)

Polypus dofleini, Wülker (1910).
Polypus hongkongensis, Sasaki (1920), in part.
? Polypus pastulosus, Sasaki (1920) = P. madokai (Berry, 1921; Sasaki, 1929)
  = Octopus madokai, Kondakov (1941).
Polypus dofleini, Sasaki (1929).
Octopus dofleini, Kondakov (1941).

Hectocotylized arm relatively short, rarely exceeding 80% of the length of the third left arm. Lateral limbs of funnel organ almost as long as the median limb. Typical order of arm length I = 2 > 3 > 4.

Habitat. Temperate western Pacific (Japan and Korea); according to Kondakov (1941), Sasaki’s more northern records probably refer to O. d. apollyon, which Kondakov treated under the name O. gilbertianus.

Holotype. University Museum, Munich; believed lost or destroyed during World War II. It is not known whether any of the sexually mature specimens described by Sasaki (1929) are still in existence. Under these circumstances, and in view of a measure of uncertainty regarding Sasaki’s measurements, which were made on fresh specimens, it seems advisable to postpone designation of a Neotype until a well-preserved, spermatophore-bearing male can be described.

Octopus dofleini apollyon (Berry, 1912, 1913; emend.)

Polypus hongkongensis, Berry (1912), in part = P. apollyon Berry (1913), in part.
Polypus gilbertianus, Berry (1912).
Octopus gilbertianus, Kondakov (1941).

Hectocotylized arm of intermediate length; rarely less than 75%, or greater than 90%, of the length of the third left arm. Lateral limbs of funnel organ somewhat shorter than median limb, rarely less than 50%, or greater than 75%, of the median limb. Typical order of arm length 2 > 3 > 1 > 4.
or $2 > 3 > 4 > 1$. A conspicuous Groove on the rostrum of both upper and lower jaw in large specimens.

**Habitat.** Subarctic regions of the northern Pacific (Bering Sea, Kamchatka, Okhotsk Sea, Kurile Islands, Alaska).

**Holotype.** USNM 214319 (Alaska) cannot be found and is presumed lost. The Cotype, from the same region, is no longer in existence (fide S. S. Berry). New material, now available for study, does not include gravid females or spermatophore-bearing males, and there seems to be no object in designating a Neotype until fully mature individuals become available.

**Octopus dojleini martini,** New Subspecies

**Octopus hongkongensis,** Winkler and Ashley (1954), in part.

Hectocotylized arm about as long as the third left arm, rarely less than $90^\circ$ of the length of the latter. Lateral limbs of Funnel organ markedly shorter than the median limb, rarely exceeding $60^\circ$ of median limb. Typical order of arm length $1 = 2 > 3 > 4$.

**Habitat.** Temperate eastern Pacific (Washington, ? California).

**Holotype.** YPM 12809.

**Gynotype.** YPM 12811.

The inadequately known Californian representatives have been omitted from the synonymy or diagnosis of this subspecies.

**ACKNOWLEDGMENTS**

The writer wishes to thank Dr. Arthur W. Martin for preserved material from the Puget Sound area and for valuable observations on a living animal. Many of the measurements, especially of large specimens, were made by Dr. Sidney J. Townsley, then a graduate student in the Department of Zoology, Yale University. Specimens in the U. S. National Museum and in the Museum of Comparative Zoology at Harvard were loaned for examination through the courtesy of Dr. Harald E. Rehder and Dr. Ruth T. Turner (acting on behalf of Dr. E. R. Clench), respectively. Supplementary observations on the Type of **Octopus hongkongensis** in the British Museum (Natural History) were made by Dr. I. C. J. Galbraith; on an earlier occasion, Dr. W. J. Rees provided information concerning one of Robson's supposed specimens of **Octopus apolyon**. I am deeply indebted to Professor Alexander Petrunkevitch for the translation of Kondakov's important article on the Cephalopoda of the Far Eastern Seas of the U.S.S.R.
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ADAM, WILLIAM

BERRY, S. S.

DALL, W. H.

FISHER, W. K.

GABB, W. M.

HOYLE, W. E.

Joubin, Louis

Kondakov, N. N.

McConnaughey, B. H.

Massy, A. L.

Pickford, Grace E.

Pickford, Grace E., and B. H. McConnaughey

Robson, G. C.

Sasaki, Madokai


Verrill, A. E.


Winkler, L. R., and L. M. Ashley


Wülker, Gerhard

APPENDIX A

FOOTNOTES FOR APPENDIX A, TABLES IV–IX

1. Symbols employed in these tables are defined on p. 9. An asterisk (*) indicates that the parameter in question was determined indirectly, usually from an illustration (see text for details in each instance).
2. The male specimen was described by Verrill (1883), but the data given here are based on a new examination of that specimen (p. 22).
3. All specimens employed for calculating mean and range, unless otherwise indicated.
4. Data from Berry (SSB), Gabb (WMG), Joubin (LJ), Kondakov (NNK), Sasaki (MS), Wülker (GW), and new data by Townsley (SJT) and Pickford (GEP).
5. In both of these specimens the third left arm is defective: in the male it is certainly longer than the fourth left, and slightly shorter than the second left (probably coequal if complete), giving a presumed sequence of $1 > 2 > 3 > 4$; in the female, the third left arm is regenerating and an estimate of its original length is impossible.
6. Male YPM 12804 excluded, since both fourth arms, likely to have been the shortest, are damaged.
7. The funnel organ is not preserved in two males (YPM 12800, 12804) and in the gravid female (YPM 12811).
8. The gills of the gravid female (YPM 12811) are too damaged to study.
9. Third left arm damaged at tip so that the hectocotylized arm index cannot be calculated for YPM 12809.
10. Third left arm incomplete in YPM male.
11. Spermatophore of YPM 12800.
12. Mean and range for 14 ovarian eggs; a single egg with complete stalk, taken from egg string laid in aquarium, gave the following: EL 6.0 mm, ESI 69.
13. Using data for arms 1, 2, and 4, since Berry's measurement for the "Third arm" is apparently that of the hectocotylized third right arm (cf. discussion of type, p. 31).
14. Number of gill filaments stated by Kondakov in text.
15. Upper jaw of USNM 574595, smaller male.
16. On assumption that Berry's "Third arm" was the third right arm (p. 31).
17. Measurements on fresh specimens; owing to differential shrinkage, indices dependent on mantle length, enclosed in parentheses ( ), are not directly comparable to those of preserved specimens (p. 43).
18. Labeled as Polypus punctatus by Sasaki (p. 41).
19. Described by Sasaki (1920) under the name Polypus pustulosus, renamed by Berry (1921).
20. A third female included.
21. Sasaki stated that the E sector is the shallowest.
22. No figure or measurements; lateral limbs observed to be almost as long as median limb. Kondakov (1941) figured the funnel organ of a Japanese specimen: FoI 93.
23. Sasaki (1929) gave the range but not the mean.
24. If calculated from Wülker's photograph, the index (HAI) is only 78.
25. Measurements from Wülker's figure give a slightly lower value (MHI 38).
### TABLE IV. *Octopus dojleini*. Temperate Eastern North Pacific. Bodily Proportions.

<table>
<thead>
<tr>
<th></th>
<th>Washington</th>
<th>California</th>
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<tr>
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<td>Mean and Range 12 Specimens³ SJT and GEP</td>
<td>TYPE YPM 12812: imm. ♂</td>
</tr>
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<td>Mean and Range 3 Specimens³ SJT and GEP</td>
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<td>SJT⁴ GEP⁴</td>
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<td>ML ......</td>
<td>195 197</td>
<td>80</td>
</tr>
<tr>
<td>TL ......</td>
<td>1105 1000</td>
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<tr>
<td>MWI ......</td>
<td>87 102</td>
<td>1169 (1050-1230)</td>
</tr>
<tr>
<td>HWI ......</td>
<td>41 58</td>
<td>-</td>
</tr>
<tr>
<td>ALO ......</td>
<td>124² 41²</td>
<td>-</td>
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<td>ALI ......</td>
<td>79 81</td>
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<td>DBCAE CDBE=A B=CAE DAE</td>
<td>2143</td>
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<td>22 24</td>
<td>2314 or 2413 (MCZ ♂♀)</td>
</tr>
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<td>WSI ......</td>
<td>53 46</td>
<td>71, 87 (MCZ ♂♀)</td>
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<tr>
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<td>16.9</td>
<td>B=C=DAE</td>
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<td>14.2</td>
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<td>HSnI ♂♂ ..</td>
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<td>49 (46-50)</td>
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<td>64 -7</td>
<td>27.3</td>
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<td>GF ......</td>
<td>25 -8</td>
<td>61 (YPM ♂)</td>
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<td>RLI ......</td>
<td>-</td>
<td>-</td>
</tr>
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<td></td>
<td>42 (YPM 12800)</td>
<td>46 (MCZ ♀)</td>
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**TABLE V. Octopus dofleini. Temperate Eastern North Pacific. Sexual Characters.**

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<td>SJT and GEP</td>
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<td>SJT and GEP</td>
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<td>LLI mat.</td>
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<td>SJT and GEP</td>
</tr>
<tr>
<td>imm.</td>
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<td>SJT and GEP</td>
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<tr>
<td>CLI mat.</td>
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<td>SJT and GEP</td>
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<td>SJT and GEP</td>
</tr>
<tr>
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<td>SJT and GEP</td>
<td>SJT and GEP</td>
</tr>
<tr>
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<td>SJT and GEP</td>
</tr>
<tr>
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<td>SJT and GEP</td>
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<td>SJT and GEP</td>
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<th>Mean and Range 3 Specimens</th>
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<td>21.7 (20.0-23.8)</td>
<td>7.1, 7.6</td>
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<td>6.4 (4.8-7.5)</td>
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### Table VI: Octopus dojleini. Subarctic North Pacific. Bodily Proportions

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<th>Mean and Range</th>
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<td>WVI</td>
<td>77* (74-180)</td>
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<td>HWI</td>
<td>77* (74-180)</td>
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<tr>
<td>ALO</td>
<td>2341 (2307-2375)</td>
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<tr>
<td>MAI</td>
<td>28* (13-64)</td>
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<td>72* (25-100)</td>
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<tr>
<td>FQI</td>
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<td>GF</td>
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<td>SSB</td>
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<td>SSB</td>
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<td>USNM</td>
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### TABLE VII. *Octopus dofleini*. Subarctic North Pacific. Sexual Characters.

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<td><em>O. gilbertianus</em></td>
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<td>USNM 214320</td>
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<tr>
<td>Type</td>
<td>COTYPE</td>
<td>Type</td>
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<td>&lt;sup&gt;?&lt;/sup&gt; imm.</td>
<td>&lt;sup&gt;?&lt;/sup&gt; imm.</td>
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<tr>
<td>HAI</td>
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<td>12.1</td>
</tr>
<tr>
<td>CLI</td>
<td>14.5&lt;sup&gt;*&lt;/sup&gt;</td>
<td>12.5&lt;sup&gt;16&lt;/sup&gt;</td>
</tr>
<tr>
<td>PLI</td>
<td>-</td>
<td>23</td>
</tr>
<tr>
<td>PDI</td>
<td>-</td>
<td>80</td>
</tr>
<tr>
<td>OGI</td>
<td>...</td>
<td>...</td>
</tr>
</tbody>
</table>

<sup>1</sup> 7 Specimens

<sup>2</sup> 6 Specimens

<sup>3</sup> Mean and Range

<sup>4</sup> L1
### Table VIII. Octopus dojleini. Temperate Western North Pacific. Bodily Proportions.

<table>
<thead>
<tr>
<th>O. dojleini</th>
<th>O. dojleini</th>
<th>“O. punctatus”</th>
<th>O. madokai</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type</td>
<td>Mean and Range</td>
<td>USNM 332992</td>
<td>Type</td>
</tr>
<tr>
<td>4 adult ♂♂, 2 adult ♀♀</td>
<td>6 specimens imm. ♂</td>
<td>imm. ♀</td>
<td></td>
</tr>
<tr>
<td>MW</td>
<td>130</td>
<td>413 (360-560)</td>
<td>MS4</td>
</tr>
<tr>
<td>TL</td>
<td>570</td>
<td>2201 (1700-2700)</td>
<td>550</td>
</tr>
<tr>
<td>MWI</td>
<td>79*</td>
<td>66 (56-78)</td>
<td>97</td>
</tr>
<tr>
<td>HWI</td>
<td>55*</td>
<td>31 (27-34)</td>
<td>70</td>
</tr>
<tr>
<td>ALO</td>
<td>2134</td>
<td>1-234</td>
<td>1324</td>
</tr>
<tr>
<td>MAI</td>
<td>30</td>
<td>27 (22-31)</td>
<td>24</td>
</tr>
<tr>
<td>ALI</td>
<td>75</td>
<td>74 (66-82)</td>
<td>75</td>
</tr>
<tr>
<td>ASI</td>
<td>79</td>
<td>89 (82-92)</td>
<td>84</td>
</tr>
<tr>
<td>WDO (BCD).AE</td>
<td>-1</td>
<td>CBDEA</td>
<td>BCDAE</td>
</tr>
<tr>
<td>WDI</td>
<td>26</td>
<td>-</td>
<td>23</td>
</tr>
<tr>
<td>WSI</td>
<td>82</td>
<td>-</td>
<td>63</td>
</tr>
<tr>
<td>SnI ♂♂</td>
<td>15.4*</td>
<td>12.9 (11.5-13.9)</td>
<td>15.3</td>
</tr>
<tr>
<td>♀♀</td>
<td>...</td>
<td>(8.3, 9.0)</td>
<td>...</td>
</tr>
<tr>
<td>HSnI ♂♂</td>
<td>34.8*</td>
<td>41.3 (36.1-45.4)</td>
<td>21.7</td>
</tr>
<tr>
<td>♀♀</td>
<td>...</td>
<td>28.3 (25.0-33.1)</td>
<td>...</td>
</tr>
<tr>
<td>FoI</td>
<td>-</td>
<td>-22</td>
<td>85*</td>
</tr>
<tr>
<td>GF</td>
<td>-</td>
<td>20-30</td>
<td>25</td>
</tr>
</tbody>
</table>

### Table IX. Octopus dojleini. Temperate Western North Pacific. Sexual Characters.

<table>
<thead>
<tr>
<th>O. dojleini</th>
<th>“O. punctatus”</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type</td>
<td>Mean and Range</td>
</tr>
<tr>
<td>4 adult ♂♂, 2 adult ♀♀</td>
<td>6 specimens imm. ♂</td>
</tr>
<tr>
<td>GW4</td>
<td>MS4</td>
</tr>
<tr>
<td>HAI</td>
<td>8724</td>
</tr>
<tr>
<td>MHI</td>
<td>4125</td>
</tr>
<tr>
<td>LLI</td>
<td>7.0*</td>
</tr>
<tr>
<td>CLI</td>
<td>17.0*</td>
</tr>
<tr>
<td>PLI</td>
<td>-</td>
</tr>
<tr>
<td>PDI</td>
<td>-</td>
</tr>
<tr>
<td>SpLI</td>
<td>-</td>
</tr>
<tr>
<td>EL</td>
<td>...</td>
</tr>
</tbody>
</table>
APPENDIX B

SPECIES OR SPECIMENS EXCLUDED FROM SYNONYMY OF Octopus dojleini.

(1) Octopus hongkongensis Hoyle (1885 a, b)

In his preliminary reports, Hoyle described a moderately large male octopus, collected by the Challenger Expedition from "Ino Sima Island, Japan," under the name O. hongkongensis (Steenstrup ms.). In the final report, Hoyle (1886:100) employed the name O. punctatus Gabb, since he had seen Verrill's account of large specimens attributed to the species. Berry (1911) restored the name hongkongensis, since punctatus was preoccupied, and by this devious route hongkongensis came to be applied to both North American and Japanese specimens of the giant octopus. Berry (1912, 1913) subsequently had reservations and proposed the new name apollyon for the North American forms. This interpretation was accepted by Robson (1929). On the other hand, Sasaki (1929) employed the name O. dojleini (Wülker) for the giant Japanese species and expressed the view that Hoyle's hongkongensis, which Sasaki erroneously thought to be from China, was a distinct species. Nevertheless, the reasons for the separation of hongkongensis from the synonymy of the giant octopus were not clear, and the name, if applicable, would have priority. At the outset of the present investigation, it seemed probable that this procedure should be followed, but further study has shown otherwise.

A preliminary study of the problem, based on Hoyle's description, and supplemented by Robson (1929), who re-examined the Type (BM 84.4.24.45), yielded the following results (Table x). Some of the indices given by Robson are not in exact agreement with those calculated from Hoyle's data, but the differences are not important. Robson's redescription is complicated by the inclusion of data derived from another specimen (Leipzig), which he attributed to O. hongkongensis and which, on the basis of his own observations, should evidently be excluded. Robson also discussed specimens from the Indian Ocean that were identified by Massy (1916) as O. hongkongensis; these specimens were re-examined by Adam (1939) with dubious results. The following account refers solely to the Type specimen.

The mantle length, 90 mm, indicates that the Type was small and therefore probably immature, if referable to the giant octopus. Both head and mantle are broad; broader than in any of the Japanese specimens described by Sasaki under the name dojleini, and broader than in the giant octopus from Puget Sound. The arms are rather long and are at the upper limit of the range for the giant octopus. The order of arm length is similar to that of O. d. dojleini (1 = 2 > 3 > 4), but the shortest arm is about 77% of the longest and is therefore at the lower limit of the range for the typical subspecies. Robson stated that the web is of moderate depth (WDI 23); he gave a web depth order of B = C = D > A > E. This is in essential agreement with the order derived
from Dr. Galbraith’s measurements which gave, for the left side, the order listed in Table x. The sequence would be acceptable if this animal were referable to the giant octopus; and the relative depth of the shallowest sector is in the range for O. dofleini.

The suckers are similar in relative size to those of females of the giant octopus from Puget Sound and for either sex of the Japanese specimens (but see p. 43).

The funnel organ was described by Robson as a simple W, the median and lateral limbs being narrow and symmetrical. However, a re-examination by Dr. Galbraith clearly indicates that the lateral limbs are relatively short; his statement (in litt.) reads as follows:

The median limbs are not less than 7 mm. longer than the lateral ones. My best estimate of their lengths are 21 and 14 mm. respectively; but the corners of the organ (both the median anterior and posterior lateral bends) are diffuse and damaged, though the tips of the lateral limbs are clear, and the funnel is somewhat wrinkled.

The short lateral limbs of the funnel organ would appear to separate this species from Japanese specimens of O. dofleini.

The hectocotylized third right arm of the Type is only 66% of the length of the third left arm; thus it is relatively shorter than in Sasaki’s Japanese specimens of O. dofleini and is totally outside the range for the Puget Sound series. The ligula length is low for a mature male, if referable to the giant octopus, but it is such as might be anticipated if it were immature.

At this stage of the analysis it became imperative to confirm or disprove the hypothesis that the Type of O. hongkongensis was sexually immature. If this were established, other apparent differences between hongkongensis and dofleini might be discounted, although perhaps with reservation. The problem was resolved by Dr. I. C. J. Galbraith who, at my request, re-examined the Type specimen in the British Museum. The animal was found to be a mature male.

Dr. Galbraith described the penis, which he found to be similar to that of the specimen figured by Robson for apollyon (p. 63), although somewhat slimmer and straighter. Galbraith stated that, “The penis has been sliced open and the major part sliced again, but the part which corresponds to the long diverticulum in dofleini is clearly intact.” No such diverticulum is present.

Remains of two spermatophores were recovered from the penis, and another less severely damaged fragment was taken from Needham’s sac. These were sent to me for examination. The spermatophores from the penis proved to be so tangled as to preclude description; the spermatophore from Needham’s organ consists of a badly preserved but complete reservoir with about 35 coils of the inner tube, and a part of the remainder of the spermatophore, including the middle piece and part of the horn. The horn shows no evidence of spiral coils, nor could these be seen on a recognizable horn included in the tangled remains from the penis, but the evidence is not decisive. The total length of
the fragment from Needham’s organ is 20 mm (sperm reservoir 6 mm, the
middle piece plus part of the horn ca. 14 mm). Presumably the original length
could not have been more than twice as great, perhaps of the order of 30–40
mm, which is less than half of the mantle length. Under no circumstances
could the spermatophores have been two or three times the length of the
mantle, as in the giant octopus. This is a “short spermatophore” species.

Under these circumstances it is evident that O. hongkongensis is a valid
species, unquestionably distinct from O. dojleini as understood by Sasaki. The
name would have priority over other Japanese species described by Sasaki
(1920, 1929), but no attempt has been made to resolve this aspect of the
problem, although a preliminary inspection of the data suggests that comparison
might be made with O. tenuicirrus (Sasaki).

(2) Paroctopus apollyon (Berry), Robson (1929)

Robson’s monograph was published in the same year as that of Sasaki (1929),
and his review of the punctatus-dojleini-apollyon problem is defective for this
reason. Under the name apollyon, Robson included all older accounts of the
North American giant octopus (Gabb; Dall; Verrill; Berry) as well as numer­
ous records unaccompanied by taxonomic description. He placed O. apollyon
in the now obsolete genus Paroctopus on account of the supposedly large size
of the eggs; the evidence was inferential, based only on Tryon’s figure of
large eggs attributed to the giant octopus. We now know that North American
specimens of the giant octopus, like those from Japan, have relatively small
eggs for the size of the animal.

Robson’s review of the published descriptions was supplemented by an ex­
amination of two specimens in the British Museum: (i) a male from Vancouver
Island (BM 60.2.29.3), and (ii) a specimen from “Esquimault Harbour” that
was erroneously stated to be a female (BM 68.6.29.3). Some years ago the
present author had an opportunity to re-examine these specimens, and it was
immediately evident that they could not be ascribed to the giant octopus.
Time did not permit a complete study and, unfortunately, the presence or
absence of an ink sac was not determined. Under these circumstances it will
suffice, for the present, to make a few brief statements.

(i) The correctness of Robson’s figure of the penis of the specimen from
Vancouver Island was confirmed (1929: 203, fig. 82); the penis is curved on
itself at the base and lacks a diverticulum. Spermatophores were removed
from Needham’s organ; they are not well preserved but are certainly different
from those of the giant octopus. The length only slightly exceeds that of the
mantle, and the horn is straight except for a few rather widely open spiral
turns near the middle; beyond this there is a constriction reminiscent of that
found in the spermatophores of O. macropus (Pickford, 1945). Other param­
eters for this specimen are summarized in Table x.

(ii) The second specimen from “Esquimault Harbour” is also a male. Remains
TABLE X. SPECIES EXCLUDED FROM THE SYNONYMY OF OCTOPUS DOJELINI WILKER.

<table>
<thead>
<tr>
<th>Octopus hongkongensis Hoyle</th>
<th>Paroctopus apollyon Robson (1929)*</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>HOLOTYPE</strong> Data of**</td>
<td>BM 60.2.29.3 BM 68.6.29.11</td>
</tr>
<tr>
<td>ML .................. 90</td>
<td>Hoyle 41</td>
</tr>
<tr>
<td>TL .................. 650</td>
<td>Hoyle 170</td>
</tr>
<tr>
<td>MWI .................. 100</td>
<td>Hoyle 105</td>
</tr>
<tr>
<td>HWI .................. 72</td>
<td>Hoyle 83</td>
</tr>
<tr>
<td>ALO .................. 1&gt;2&gt;3&gt;4</td>
<td>Hoyle 2&gt;3&gt;4&gt;1</td>
</tr>
<tr>
<td>MAI .................. 17</td>
<td>Hoyle 32</td>
</tr>
<tr>
<td>ALI .................. 82</td>
<td>Hoyle 78</td>
</tr>
<tr>
<td>ASI .................. 77</td>
<td>Hoyle 89</td>
</tr>
<tr>
<td>WDO .................. D&gt;C&gt;B&gt;A&gt;E</td>
<td>Galbraith C&gt;B=D&gt;E&gt;A</td>
</tr>
<tr>
<td>WDI .................. 23</td>
<td>Robson†† 29</td>
</tr>
<tr>
<td>WSI .................. 63</td>
<td>Galbraith –</td>
</tr>
<tr>
<td>SnI .................. 12.2</td>
<td>Hoyle 13.4</td>
</tr>
<tr>
<td>Sel .................. none</td>
<td>Hoyle 17.1</td>
</tr>
<tr>
<td>FoI .................. 67</td>
<td>Galbraith –</td>
</tr>
<tr>
<td>GF .................. 20</td>
<td>Robson 22†</td>
</tr>
<tr>
<td>HAI .................. 66</td>
<td>Hoyle 95</td>
</tr>
<tr>
<td>MHI .................. 31</td>
<td>Hoyle 34</td>
</tr>
<tr>
<td>LLI .................. 10.7</td>
<td>Hoyle 9.4</td>
</tr>
<tr>
<td>CLI .................. 22.2</td>
<td>Hoyle (fig.) 16.7</td>
</tr>
<tr>
<td>PLLI .................. 12</td>
<td>Galbraith 37</td>
</tr>
<tr>
<td>SpLI .................. ≤44</td>
<td>Pickford 132</td>
</tr>
</tbody>
</table>

* Robson (1929) gave little information that could be applied specifically to these specimens. Basic parameters were studied by the writer and, in the case of the first specimen (BM 60.2.29.3), some additional information was supplied by Dr. W. R. Rees. Both specimens are sexually mature males, but the spermatophores of the second specimen were so badly preserved that study was impossible.

** Hoyle’s original description (1885a, b, 1886) was supplemented by Robson (1929); additional information has been given by Dr. I. C. J. Galbraith (in litt.), and the spermatophores were studied by the writer.

†† If Galbraith’s measurement for the deepest sector of the web (the left D sector, 128 mm) is used in conjunction with Hoyle’s length of longest arm, the index is essentially the same (WDI 24).

† On the right side, the left gill is abnormal.

of spermatophores were found in Needham’s sac, but their preservation was too poor for description. The penis may be like that of the first specimen, but minor differences were noted and further study is required; however, it is certainly not like that of O. dojelini. The sucker diameter index is very low and, since this is a mature male, the difference is meaningful. It is possible that these two specimens do not belong to the same species. If an ink sac is lacking, the small suckers would suggest comparison with Benthoctopus hokkaidensis (Berry), which is widely distributed in the North Pacific.

In an earlier paper, Robson (1925) discussed the seriation of the radula and mentioned two specimens of Octopus punctatus Gabb from the “W. Atlantic.” This reference is apparently to the two specimens that he later attributed to P. apollyon, discussed above. The recorded location must have been in error.
APPENDIX C

Translations from the Russian Text of N. N. Kondakov (1941):
Octopus gilbertianus and O. dofleini.

Octopus gilbertianus (Berry 1910)


Twelve large octopus captured in the Sea of Okhotsk (“Gagara” Stns. 223, 224, 262, 263, 266 and 267, 1932) were not fixed and have been identified at the place of capture as O. dofleini. The characters used for identification of these octopods were their size and large leathery earlets over the eyes—characters typical unfortunately not only for O. dofleini which has at present been marked as a considerably more southern form, but also for O. gilbertianus and Paroctopus gongkongensis. Exactly for this part of the Okhotsk Sea where the stations enumerated above have been taken by P. Ushakov, O. gilbertianus is noted by me from other collections, therefore it is most likely that O. gilbertianus was mistaken for O. dofleini. The finding in the Okhotsk Sea of Paroctopus gongkongensis among specimens of O. gilbertianus captured by the trawler “Gagara” is scarcely credible. The surface of the skin, wrinkly in specimens fixed in alcohol, is covered by numerous little papillae or warts which give the skin a granular structure. On the ventral side of the body the warts are smaller, on the ventral side of the arms and umbrella they are completely absent. In very young specimens the entire ventral side is free of papillae. On the entire dorsal surface of the octopod, independent of sex or age, the papillae are scattered densely and extend even into the portions of the arms free of the umbrella. By the eyes the papillae are massed, of unequal size, and much larger than the papillae which cover the body and the umbrella of the animal. Near the edge of the eye, separate papillae often merge with each other forming a rosette of radially arranged folds and tuberculate welts. Near each eye there is one soft leathery earlet of rounded shape. These earlets are clearly developed in adults, easily noticed in young specimens, while in very small ones each earlet has the appearance of a wart laterally compressed and four times larger than any other papilla near the eyes. Sharpened (thornlike)
papillae, which are characteristic of *Paroctopus gongkongensis* are absent in *O. gilbertianus*.

The funnel is short with a broad base. The funnel organ is W-shaped, its lateral lobes are wider and shorter than the medial V-shaped portion (Fig. 35).

The arms are unequal; the formula of their length: $2 > 3 > 4 > 1$. They are connected from the base up to a quarter of their length by a relatively tough umbrella, which is larger between the second and third pair of arms and least developed between the ventral arms. Relatively large suckers disposed in two rows are most developed at the distal edge of the umbrella. Each arm has from 80–100 pairs of suckers, the third right arm of the male is hectocotylized. The terminal organ is large, pointed; the copulatory groove is deep, transversely striated. The spermatophoric groove is broad and ends in a cone-shaped calamus; the latter is thickened and covered with transverse furrows (Fig. 34).

Each gill has 21 branchial lamellae.

The radula is powerfully developed; each of the middle row of teeth has, besides the usual median tooth which here is very large, from 5–6 toothlets on both sides of the tooth. The median row of teeth consists of a darker chitin; the lateral platelets are almost transparent (Fig. 36).

The beak is powerful, with one or two (in large specimens) grooves [vyrez] on the outer surface of the distal portion of the dorsal mandible; the inner edges of the beak are supplied with noticeable excavations (Fig. 37). The beak of *O. gilbertianus* is so characteristic that it permits the identification of the species by its mere presence in remains of the cephalopod.

The color of alcoholic specimens is dark red brown on the dorsal side and lighter on the ventral. For young specimens the distribution of pigment is especially characteristic in the form of a row of comparatively large chromatophores of which each is surrounded by 6 small ones in the shape of a starlet. On the dorsal surface of young specimens the pigment stars are more dense, on the ventral surface they are not as close together; on the arms they are arranged in one row, which is especially apparent on the ventral and third pair of arms in very small specimens.

**Distribution.** Alaska: Behm Canal (depth 12.5 and 40 m.); Stephen’s Passage (depth 52–39 m.)—Berry (1910, 1912). Kurile Islands; Shumagin Isl.; Kadiak [sic] Isl.—Berry. Avachinsk Bay; eastern coast of Kamchatka (as *O. punctatus* Gabb)—Dall 1895 and Joubin 1898. Aleutian Islands (as *O. dofteini* Wülker)—Sasaki 1929. Form apparently a boreal one.

*Octopus dofteini* (Wülker 1910)

A number of authors refer to it as *O. punctatus* Gadd (sic!) 1862. Localities: Japan Sea: region of Basargin, 1927, 2 very large $\varnothing$ (in museum of TIRK); Bay of Possiet, inlet of Pemzo, 1931, 1 $\varnothing$ ad. (TIRK). Occurs in the Chinese market in Vladivostock where it is sold fresh, dried, or marinated.
The animal is gigantic attaining a length of 3 m. (Sasaki 1929). The body of adults is oval, a little longer than wide, supplied on its sides with a horizontal fold and bandlike tubercles. The belly is with a clear longitudinal groove along the median line.

The surface of the skin is irregularly tuberculate. The tubercles are of different shape but usually pointed at the end, as in Paroctopus gongkongensis, and more or less stellate at the base; often connected to each other in longitudinal lines, more strongly raised on the dorsal and lateral surfaces, especially around the eyes, where they are compressed into little ribs or welts, which diverge radially from the ocular opening. Some tubercles are clearly noticeable among others, as in O. vulgaris, there are four of them and they are arranged in a regular rhomb on the dorsal side. Above each eye there are 3 or 4 cirri; one of them is of a slightly greater size and is almost semi-globular; it is situated a little behind the pupil.

The funnel is conical, widened at base. The funnel organ is comparatively large and doubtlessly wider than long; it has a W-shaped form, the cartilaginous-like band, which forms this organ, is very wide; the medial and lateral lobes of the funnel organ are of about the same length (Fig. 38). Umbrella well developed; it is widest—between the lateral arms, where it reaches 1/4 of the length of the arm.

Arms almost equal; the formula of their length: \(1 = 2 = 3 > 4\) or \(1 = 2 > 3 > 4\); they are 4 or 5 times longer than the body; their base is very stout, all arms, taken together, are clearly stouter than the body. The suckers are prominent, with enlarged edges; they are disposed on each arm in two relatively compressed rows, except at the bases of the arms, where the suckers are drawn out into one zigzag-like row. The suckers on the lateral pair of arms usually are smaller than on all others. On each arm the suckers increase in size up to the 8th or 9th pair, then to the 13th, which is the largest and lies opposite the edge of the umbrella, then become gradually smaller distally. The third right arm of the male is hectocotylized and about 1/4 shorter than the third left arm. The terminal organ occupies 1/4–1/6 of the entire arm, it is narrow, slightly blunted at the end; the copulatory groove is deep, sharply defined; the raised edges of the terminal organ, which form this groove, are high and contiguous at their edges (the hectocotylus is a closed one); the bottom of the copulatory groove is covered with numerous transverse striations. The spermatophore groove is wide, very apparent, and ends in a cone-shaped calamus (Fig. 39). On the normal portion of the hectocotylized arm 48–53 pairs of suckers. Spermatophores are proportionately tremendous, each of them sometimes reaches the length of 115 cm.

Each gill has from 30–33 branchial lamellae.

The radula is shown in Fig. 40.

The color varies, usually brownish purple in fixed specimens; the dorsal surface, as a rule, is covered with irregular dark spots, sometimes with a marbled pattern; the ventral side is usually lighter.
This species has been mentioned by many authors under different names, mostly as *O. punctatus* (nomen preoccupatum, Berry and Hoyle), as the tropical *Paroctopus gongkongensis* and, perhaps, in some cases, as *P. apollyon* (Berry (Sasaki 1929)), but sometimes was described from regions, in which the presence of *O. dojleini* is hardly credible.

It is common in northern Japan and Korea where it is brought to market in great quantities (Sasaki 1929). It has been mentioned from a series of places in Japan: Enoshima—Hoyle. Misaki;* Tadohokke (Hokkaido) Wülker. Wakkanai (Hokkaido), Shiribeshi Prov., Saporo; Hakodate; Azumoshii, Mutsu Prov.; Etchu Prov.; Awa Prov.; Akayama—Sasaki 1929. From Korea it is known from Fusun, Gensan, Dalny, Liao and locality Klokard (depth 150 feet)—Sasaki 1929. Has been described from Sakhalin (Sasaki 1929) and from the region of the Island Shimushir of the Kurile row. The last two cases, perhaps, belong to *O. gilbertianus*. Cases of finding *O. dojleini* in tropical waters seem to belong to *Paroctopus gongkongensis* which Sasaki identifies as *O. dojleini*.

* Apparently in error for Aburatsubo.
**Pickford: Octopus dobleini (Wülker)**

**ГРЭС Е. ПИКФОРД**

Вингамская Океанографическая Лаборатория

**OCTOPUS DOBLEINI** (Wülker), **ГИГАНТСКИЙ ОСЬМИНОГ СЕВЕРНОГО ТИХАГО ОКЕАНА:**

**Краткий Обзор**

Таксономическое положение Гигантского Осьминога Северного Тихого Океана переоценино на основании опубликованных описаний и изучения новаго материала из Аляски и северно-американского побережья Тихого Океана. Несколько экземпляров прежде описанных были заново обследованы. Результаты могут быть суммированы следующим образом.

(1) Голотип Octopus dobleini (Wülker) потерян но принята гипотеза Сасаки что он был неполовозрелый самец Гигантского Осьминога. (2) Описание японского вида, O. dobleini, данное Сасаки согласно со всеми главными таксономическими признаками половозрелых экземпляров из пролива "Поджет-Зундт" (Puget Sound) в Сан-Хуанском Архипелаге штата Вашингтон. Однако эти экземпляры отличаются от японских двумя менее важными признаками: их латеральная лопасть органа воронки короче медиальных, а гектокотилизированная рука почти той же длины как ее парная рука противоположной стороны. Эти отличия имеют подвидовое значение. (3) Голотип и Паратип O. apollyon (Berry) из Аляски не могут быть найдены. Форма аляскинского Гигантского Осьминога описана заново по молодым и неполовозрелым экземплярам принадлежащим Национальному Музею Соединенных Штатов: Голотип O. gilbertianus (Berry) подвергнут пересмотру и во всех важных признаках согласен с выше упомянутым новым описанием O. apollyon. Все главные признаки аляскинской популяции согласны с таковыми у O. dobleini, но два признака, выше упомянутые, у аляскинских экземпляров промежуточны между японскими и вашингтонскими. (4) Опубликованные описания экземпляров Гигантского Осьминога из Сибирских вод (Кондаков, Joubin), указывают что эти экземпляры по существу одинковы с экземплярами из Аляски. (5) Экземпляры из дальнего севера (Аляска и Сибирь) обладают тремя менее важными признаками, которые отделен из как от японских, так и от американских подвидов: более короткая руки первой пары, тенденция к более длинному диаметру присосок и предсуществие заметного прозрачного роста в росте в моменте же нереста зимы. (6) На основании выше указанных замечаний предложено установить три подвида O. dobleini: O. d. dobleini (Wülker, emend. Sasaki) из Японии, O. d. apollyon (Berry) из дальневосточного Тихого Океана, и O. d. martini N. Subsp. из Тихоокеанского побережья штата Вашингтон.
(7) Подвидовое положение O. dofleini из Калифорнии не может быть устанавлиено на основании немногочисленных, плохо сохранившихся экземпляров имеющихся для изучения. (8) O. madokai (Berry) из Японии может относиться к O. d. dofleini, но вопрос об этом нуждается в дальнейшем изучении. (9) Голотип O. hongkongensis Hoyle неполовозрелый самец особого вида. (10) Два экземпляра определенные Робсоном как Paroctopus apollyon изъяты из синонимики O. d. dofleini, но их положение остается не установленным.