

SEX-REVERSAL AND VIVIPARITY IN *OPHIOLEPIS*  
*KIERI*, N. SP., WITH NOTES ON VIVIPAROUS  
BRITTLESTARS FROM THE CARIBBEAN  
(ECHINODERMATA: OPHIUROIDEA)

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*Abstract.*—A new species, *Ophiolepis kieri*, appears to be more closely allied to *Ophiolepis impressa* than to its other Caribbean congeners *Ophiolepis elegans* and *Ophiolepis paucispina*. Three sympatric species *Ophiolepis kieri*, *Ophiolepis paucispina*, and *Ophiomyxa flaccida* brood their young, bringing the number of known viviparous, tropical shallow-water ophiuroid species to seven. *Ophiolepis kieri* probably broods sequentially, but *O. paucispina* carries more than one clutch simultaneously. *Ophiomyxa flaccida* is a gonochore, *O. paucispina* is a simultaneous hermaphrodite, and *O. kieri* is a protandric hermaphrodite. A speculative sequence is presented for the rapid evolution of small *Ophiolepis* species through paedomorphosis, facilitated by preadaptations for viviparity and selection for hermaphroditism.

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The 57 species of viviparous ophiuroids that have been described are predominantly coldwater or deepwater forms (Bernasconi, 1965; Madsen, 1967; Mortensen, 1936; Murakami, 1941). Livebearers from shallow, tropical waters are so rare that Mortensen (1933) remarked on the novelty of the only examples: *Amphiura stimpsoni* Lütken, Caribbean; *Cryptopelta granulifera* H. L. Clark, Mascarene Islands and Northern Australia; *Ophioconis vivipara* Mortensen, Northwest Africa; and *Ophionereis vivipara* Mortensen, Mozambique and Mascarene Islands.

Three additional species of tropical viviparous ophiuroids collected from the Caribbean coast of Panama are discussed below. Two of them have widespread distributions: *Ophiomyxa flaccida* (Say) ranges from Bermuda to Brazil and *Ophiolepis paucispina* (Say) from Bermuda to Brazil and West Africa (H. L. Clark, 1919; Madsen, 1970). The third species, described in this paper as *Ophiolepis kieri*, has been collected only at Portobelo, Panama (9°33'30"N, 79°40'45"W). It is the fourth *Ophiolepis* reported from the Western Atlantic and is sympatric with *Ophiolepis impressa* Lütken and *Ophiolepis paucispina* (Say).

Dissections that demonstrated brooding in these species also revealed several different types of sexuality. Specimens of *O. flaccida* proved to be gonochoristic, like most ophiuroids, and specimens of *O. paucispina* were

simultaneous hermaphrodites as are a majority of the viviparous brittlestars. However, the protandric hermaphroditism found in *O. kieri* was an exceptional discovery.

Although protandry had previously been reported in ophiuroids, the progressive stages of sex-reversal involving small males, hermaphrodites of intermediate size, and large females were documented convincingly for only one species, *Amphiura stepanovii* Tscherniawsky (Fedotov, 1926). Therefore, the process of sexual transformation in *O. kieri* is described in detail below, and other notable aspects of the species are discussed.

*Ophiolepis kieri*, new species

Fig. 1

*Etymology*.—Named for Porter M. Kier, an echinodermologist of outstanding stature, to honor his retirement as Director of the National Museum of Natural History.

*Material examined*.—Holotype (USNM E18177) and 18 paratypes (USNM E18175) collected 2 September 1977, Iron Castle Point, Portobelo, Panama, on sand under rocks, less than 2 meters depth, by the author. Ten paratypes (USNM E18176) collected 15 October 1975, Iron Castle Point, Portobelo, Panama, under rocks, less than 4 meters depth, by the author.

*Description of holotype*.—Disc diameter 4.7 mm; longest arm 11.9 mm, all arms broken before tips. Disc circular, slight indentations at bases of arms; dorsal side convex; ventral side flat. Arms gradually tapering. Major disc scales with lateral and distal edges thickened; bordered but usually not completely surrounded by small scales. Primary plates forming distinct rosette; central and radial plates larger than any dorsal scales but radial shields. Radial plates ovoid; middle of long distal edge straight.

Interradial field of disc with 3 columns of major scales; 3 scales in middle column larger than scales in lateral columns. Proximal scale in middle column as long as wide, central scale longer than wide, peripheral scale wider than long. Radial field of disc with: 3 major scales distal to each radial plate; elongate scale between radial shields; supplementary radial shields linked by small scale, paired supplementary radial shields and connecting scales forming crescentic shape. Surface of some radial shields minutely wrinkled.

Each jaw bearing pointed apical papilla plus 5 pairs lateral papillae. Proximal pair robust, pyramidal; next pair smaller, flat, rhomboidal, proximal edge sometimes drawn to point; succeeding pair similar but lacking acute point; next pair much larger, shaped like quarter-circle, radial edge curved; last pair long, triangular, attached to adoral shield, tip extending beneath penultimate pair.

Oral shield slightly longer than wide; proximal angle acute, margins concave; lateral margins nearly parallel; distal margin deeply convex. Madre-

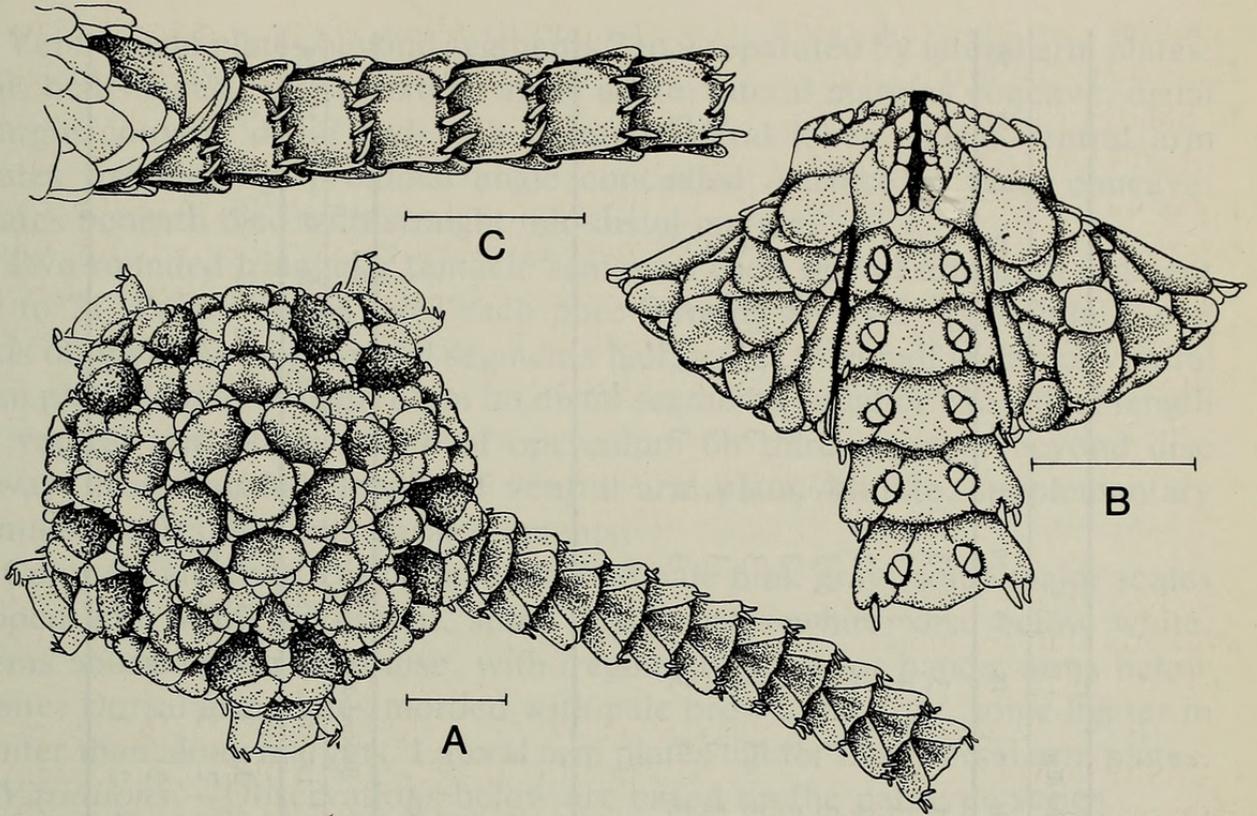


Fig. 1. *Ophiolepis kieri*, holotype. **A**, Dorsal view of disc and of arm; **B**, Ventral view of two jaws with contiguous arm and interradiar fields of disc; **C**, Lateral view of basal arm segments and part of adjoining disc. Scale lines equal 1 mm.

porite resembling oral shield, larger; with small depression near center. Adoral shield widest distally; radial edge straight, adradial edge indented at point of contact with oral shield; surface of shield inflated.

Genital slit extending nearly to edge of disc; bordered by long genital plate, 2 smaller scales proximad. Ventral interbrachial field with fewer than 25 scales.

Dorsal arm plates triangular; basal plates with concave lateral edges, distal edge with straight medial margin; remaining dorsal arm plates with straight lateral edges, distal edge with small blunt median projection. First 10 to 11 dorsal arm plates overlapping, remaining dorsal arm plates separated by lateral arm plates.

Supplementary dorsal arm plates present only on first 7 to 10 arm segments; miniscule, all except first pair smaller than arm spine.

Lateral arm plates flaring in dorsal view; trapezoidal, widening distally in lateral aspect.

Arm spines generally aligned with arm, not erect; tips of spines attenuate, middle thick. Ventralmost spine longest until segment 13 to 19, then same size as dorsal spines. Spines equal or less than length of ventral arm plate; spines on third segment beyond disc characteristically shorter than ventral arm plate. Spines often lacking on first lateral arm plate; increasing in number to 3 per lateral arm plate, then decreasing to 2 as indicated in Table 1.



Ventral arm plates beyond segments 7 to 9 separated by lateral arm plates; flat, bell-shaped, with proximal angle acute, lateral margins concave, distal margin convex, distal end with pointed lateral lobes. Basal ventral arm plates overlapping, proximal angle concealed, surface of plate concave. Plates beneath disc with straight mid-distal margin.

Two rounded triangular tentacle scales on each side of arm until segment 20 to 21. Paired scales over each pore forming an oval operculum. Long axis of opercula on proximal segments half or less than half length of ventral arm plate; length of operculum on distal segments equal or exceeding length of ventral arm plate; length of operculum on third segment beyond disc always less than half length of ventral arm plate. Minute, supplementary tentacle scales on some basal segments.

Color (in alcohol): Disc above mottled pale pink-gray, some major scales tipped with white or brown, some small scales white; disc below white. Arms above lighter than disc, with irregular blotches or bands; arms below white. Dorsal arm plates mottled with pale brown and gray, some lighter in center than along margins. Lateral arm plates lighter than dorsal arm plates.

*Variations.*—Observations below are based on the paratype series.

Dimensions: For specimens 1.9 to 5.5 mm disc diameter  $y = 3.41x - 3.37$ , where  $y$  = arm length and  $x$  = disc diameter ( $n = 27$ ,  $r = 0.95$ ).

Disc scalation: The prominence and shape of the primary (central and radial) plates is consistent throughout a size series from 1.9 to 5.5 mm d.d. The number of ventral interbrachial scales varies directly with size, a specimen 5.5 mm d.d. having but a few more scales than the holotype. Specimens 2.6 mm d.d. and less have a reduced number of small scales and lack scales between the supplementary radial shields. Specimens less than 2.0 mm d.d. have the radial shields in direct contact and their major scales are reduced in number.

Arm plates: With decreasing body size there is less overlapping both of adjacent dorsal arm plates and of adjacent ventral arm plates. In the smallest specimens, dorsal and ventral arm plates are both separated by the lateral arm plates for nearly the full length of the arm. The first arm segment with the dorsal arm plate surrounded by lateral arm plates is, in a specimen: 3.4 mm d.d., at segment 4 beyond the disc; 3.2 mm d.d., segment 3; 2.6 mm d.d., segment 2; 1.9 mm d.d., segment 1. The first arm segment with the ventral arm plate surrounded by lateral arm plates is, in a specimen: 3.7 mm d.d., at segment 6; 3.4 mm d.d., segment 4; 3.2 mm d.d., segment 4; 2.6 mm d.d., segment 3; 1.9 mm d.d., segment 2. The distal edge of the ventral arm plate is rounded rather than pointed in small specimens. Concavity of the surface of the ventral arm plates is not pronounced in small specimens, but is still perceptible in an ophiuroid 1.9 mm d.d.

The number of arm segments beneath the disc varies directly with body size: 3 segments are covered in specimens 4.1 mm d.d. or larger, and 2 segments are covered in specimens 3.6 mm d.d. or smaller.

Arm spines: The absence of spines on the first lateral arm plates is most pronounced in larger specimens, indicating that some spines are resorbed as individuals mature. Specimens at least 3.4 mm d.d. average fewer than 5 first lateral arm plates carrying spines, and for specimens less than 3.2 mm d.d. an average of fewer than 7 first lateral arm plates bear spines. For specimens of different sizes, the number of arm spines along one side of a typical, unbroken arm varies as indicated in Table 2.

Tentacle scales: Scales over the tentacle pores are paired. Distally the radial scale of the pair becomes increasingly smaller than the abradial scale and disappears near the arm tip. Smaller specimens have fewer segments with paired tentacle scales. The first segment with only one scale over each pore is, for a specimen: 5.5 mm d.d., segment 26; 4.1 mm d.d., segment 20; 3.7 mm d.d., segment 18; 3.4 mm d.d., segment 14; 3.2 mm d.d., segment 13; 2.6 mm d.d., segment 8; 1.9 mm d.d., segment 6.

Color (in alcohol): Specimens less than 3.2 mm d.d. are pale beige; those less than 2.9 mm d.d. are entirely white.

*Relationships.*—*Ophiolepis kieri* differs dramatically from congeners such as *O. elegans* Lütken and *O. paucispina* (Say) which, even as juveniles, have a row of small scales of uniform size surrounding the major disc scales and have large supplementary dorsal arm plates on most arm segments. *Ophiolepis kieri*, with incomplete, irregular rows of small disc scales and with supplementary dorsal arm plates of reduced size and number is more closely allied to *Ophiolepis impressa* Lütken and *Ophiolepis pacifica* Lütken.

The latter species are relatively large, exceeding the size of the biggest (6.4 mm d.d.) *O. kieri*. However, there is a striking similarity in the ontogeny of disc scales of the three species, the disc armament of *O. kieri* resembling that of young *O. pacifica* and *O. impressa*. *Ophiolepis kieri* may be distinguished from small *O. pacifica* and *O. impressa* as follows: *O. kieri* has 3 rather than 4 or more arm spines on the basal arm segments; 3 rather than 4 or more major scales in the central scale column of the dorsal inter-radial field; primary radial plates that form a ring, and are larger than other dorsal scales except the radial shields. Specimens of *O. impressa* also differ from *O. kieri* because their dorsal arm plates are in contact for over half the length of the arm, their first lateral arm plates each bear 2 spines, and the length of their tentacle-scale pairs is generally greater than half the length of the ventral arm plate.

*Ecology.*—*Ophiolepis kieri* has been collected only at Portobelo, Panama, in the lee of Iron Castle Point. The species inhabits a shallow, sheltered sublittoral zone where numerous allochthonous boulders and cobbles pave a substratum of fine sand. The rocks bear encrusting calcareous algae, porifera, bryozoa, and *Millepora*. *Ophiolepis kieri* is found only up to 3 m. At

that depth, the rocky habitat abuts a steep reef slope supporting large corals and sponges. The reef ends at 20 m on a calcareous mud bottom. Salinities at Iron Castle Point ranged from 32 to 37‰ but it is likely that the very heavy rains in this locality create temporary, steep salinity and temperature gradients in shallow water.

Under the rocks at the type-locality there were dense populations of ophiuroids including, in order of abundance: *Ophiocoma echinata*, *Ophiocoma wendti*, *Ophiothrix angulata*, *Ophioderma rubicundum*, *Ophiocoma pumila*, *Ophioderma appressum*, as well as rarer species of ophiuroids and conspicuous macroinvertebrates such as brachyura, actinaria, and polychaeta.

Specimens of *Ophiolepis kieri* were found only beneath cobbles firmly lodged in fine, dark sand. Under any particular rock they were either found in numbers or were absent, but they were never found under rocks sheltering macroinvertebrates other than their congeners, *O. impressa* and *O. paucispina*. *Ophiolepis kieri* was more numerous than *O. paucispina*. In a series of collections at Portobelo, the ratio of the two species was 103:30.

When their rock shelters were dislodged, the three sympatric *Ophiolepis* species "froze" rather than moving to escape, and their variegated, dusky coloration camouflaged their location. Labrid fish feed on ophiuroids at Portobelo, but the protected microhabitat and behavior of *O. kieri* probably reduce predation mortality. The same factors also minimize the physical disturbance of these lilliputian forms by large active organisms.

#### Notes on viviparous Caribbean Ophiuroids

*Ophiolepis kieri*.—Male, female, and hermaphrodite specimens differed in body size (Fig. 2). Males ranged from 1.9 to 5.0 mm d.d. ( $\bar{x}$  = 3.6 mm). They had a single, white testis near each genital slit. The testes contained spermatozoa with tails at least 10 times the length of the spherical spermatozoan head.

The transitional, hermaphroditic individuals were intermediate in size between males and females (3.8 to 5.1 mm d.d.,  $\bar{x}$  = 4.5 mm). Their gonads were pure testes, pure ovaries, or ovotestes. Hermaphroditic individuals might function as males, but not as females. Their ovaries and ovotestes contained small, incompletely yolked oocytes and they did not brood embryos. Although some ovaries may form *de novo* in the hermaphrodites, it is obvious that testes transform to ovotestes, and the ovotestes become ovaries.

Females were 4.5 to 6.4 mm d.d. ( $\bar{x}$  = 5.0 mm) and had 1–2 ovaries with grayish-violet oocytes, at each genital slit. The yolky, opaque oocytes reached a maximum diameter of 0.35 mm. The maximum number of fully

developed oocytes in an individual was 32, and the maximum number of embryos was 39 ( $n = 13$ ). The embryos in a female were generally all at the same stage of development; usually either early stages, small stars with terminal arm plates, or juveniles with 1 to 2 arm segments.

Brooding females, and males with active spermatozoa, were collected in January, February, March, April, June, August, and December, indicating there might be a long breeding season and recruitment period. Newly hatched young were rarely encountered. The size-frequency curve (Fig. 2) shows the distribution of males to be skewed toward the larger sized individuals, a scarcity of transitional hermaphroditic forms, and a restricted, unimodal distribution for females.

The size-frequency curve suggests delayed sex-reversal of the males. Assuming the population is in equilibrium and that size-specific mortality of males is not significant, there appears to be infrequent, but rapid, transformation from males to females.

It is possible that protandry is labile and that sexual transformation is retarded in the presence of mature females. However, the pronounced segregation by size of males and females may indicate that sex-reversal is genetically predetermined rather than environmentally controlled. Whatever the cause, the bottleneck to growth or sex-reversal contributes to maintenance of a population dominated by males. The sex ratio is 2.4:1 (hypothesis that the ratio is 1:1 is rejected:  $\chi^2$ ,  $P < 0.005$ ). Such a proportion would tend to ensure that females would be fertilized.

*Ophiolepis paucispina*.—Nearly all individuals from Portobelo were simultaneous hermaphrodites. Those from 3.2 to 5.4 mm d.d. had functional testes, and ovaries with large oocytes. There was no tendency for the larger individuals to have a greater number of ovaries (and fewer testes) and thus no indication of protandry (hypothesis that the Kendall coefficient of rank correlation equals zero not rejected,  $P > 0.99$ ). Only 3 of the 30 *O. paucispina* dissected were males, and these were large (6.2 mm d.d.) as well as small (4.0 mm d.d.) individuals.

There was generally one gonad to each genital slit, and the testes and ovaries were ordered in an irregular sequence around the disc. However, series of consecutive genital slits with only male or female gonads sometimes formed statistically significant "runs." There was a "functional sex-ratio" favoring females since 170 ovaries, but only 80 testes and 2 ovotestes were counted in 30 individuals.

The largest oocytes were 0.35 mm in diameter, opaque and pink. The maximum number of fully developed oocytes found in an individual was 16, and the maximum number of embryos was 41 ( $n = 11$ ). Specimens brooding young were collected in March, April, June, and December and individuals often contained embryos at different stages of development. Broods consisted of yolky embryos in early developmental stages or juve-

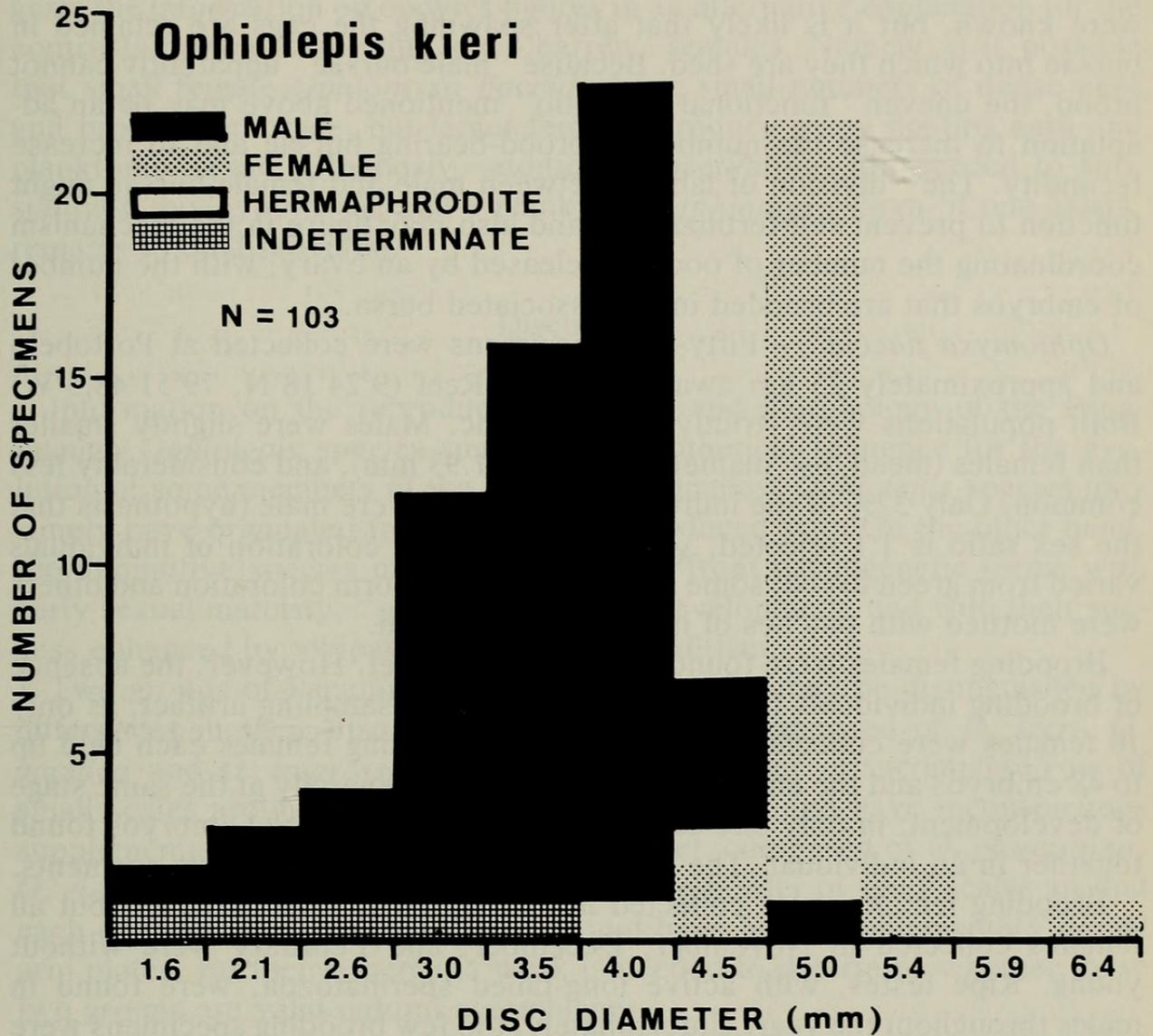


Fig. 2. Size-frequency histogram for the population of *Ophiolepis kieri* sampled at Portobelo, Panama, showing the transformation during maturation through male, hermaphrodite and female phases. Indeterminate individuals lacked gonads with recognizable gametes.

niles with 2 to 3 arm segments. White testes with active spermatozoa were found both in brooding individuals and those not brooding embryos.

Although *O. kieri* and *O. paucispina* brood approximately equal numbers of embryos, individuals of the latter species produce a smaller "clutch" of eggs and brood embryos of different ages within the same bursa. This suggests that *O. kieri* is a sequential brooder but *O. paucispina* simultaneously broods embryos from more than one clutch of eggs.

Viviparous ophiuroids such as *Axiognathus squamata*, which have ovaries and testes associated with every bursa, may bear embryos simultaneously in all their bursae (personal observation). In contrast, in *O. paucispina* all of the bursae next to testes were empty, while 59% of the bursae associated with ovaries contained embryos. It would be easier to interpret this phenomenon if the position of the gonoduct in relation to the bursa

were known, but it is likely that after spawning the eggs are retained in bursae into which they are shed. Because "male bursae" apparently cannot brood, the uneven "functional sex ratio" mentioned above may be an adaptation to increase the number of brood-bearing bursae and to increase fecundity. The "division of labor" between male and female bursae might function to prevent self-fertilization, and also may figure in the mechanism coordinating the number of oocytes released by an ovary, with the number of embryos that are brooded in the associated bursa.

*Ophiomyxa flaccida*.—Fifty-two specimens were collected at Portobelo and approximately 25 km away at Galeta Reef (9°24'18"N, 79°51'48.5"W) Both populations were strictly gonochoristic. Males were slightly smaller than females (mean disc diameters 1.72 vs. 1.93 mm), and considerably less common. Only 32% of the individuals examined were male (hypothesis that the sex ratio is 1:1 rejected,  $\chi^2$ ,  $P < 0.005$ ). The coloration of individuals varied from green to red; some specimens had uniform coloration and others were mottled with patches of intense pigmentation.

Brooding females were found only at Galeta Reef. However, the absence of brooding individuals from Portobelo may be a sampling artifact, as only 10 females were collected at that site. The brooding females each held up to 48 embryos and the embryos in a female were generally at the same stage of development; in only one case were early and advanced embryos found together in an individual. The largest embryos had up to 6 arm segments.

Brooding females were collected in March, May, June and July, but all females collected in November, December, and February were without young. Ripe testes, with active long-tailed spermatozoa, were found in males throughout the year. Unfortunately, too few brooding specimens were found to detect reproductive periodicity.

Egg counts and measurements, though taken only for a few specimens, suggest important differences between brooding females and those without young. The largest oocytes were roughly the same diameter in brooding females (0.75 mm,  $n = 2$  specimens) and females lacking embryos (0.70 to 0.88 mm,  $n = 3$  specimens). In brooders, as well as females without young, the immature oocytes were translucent pinkish-gray and the yolky oocytes were opaque green. However, ripe oocytes teased from the gonads of non-brooding females were buoyant but those from brooding females were heavier than seawater. Furthermore, brooding females (1.76 and 1.82 cm d.d.) carried approximately 260 and 200 ripe oocytes respectively, while a non-brooding individual (1.95 cm d.d.) had approximately 915 oocytes.

Changes in yolk composition of oocytes before shedding and lowered oocyte counts due to spawning, could account for the variability of the oocytes noted above. However, a significant difference between the mean disc diameter of brooding females (1.52 cm,  $n = 7$ ) and of those without broods (2.05 cm,  $n = 24$ ) (Wilcoxon two-sample test,  $0.02 > P > 0.01$ ), sug-

gests the information on oocytes figures in an alternative explanation for the contrasts between brooding and "barren" females. Namely, it is possible that small female *Ophiomyxa flaccida* have small numbers of dense eggs and brooded embryos, but larger females produce many floating eggs and planktonic larvae. Obviously, additional observations are needed to substantiate this hypothesis, and a planktonic *Ophiomyxa* larva, if one exists, remains to be discovered.

### Discussion

Information on the reproductive biology and morphology of the Panamanian *Ophiolepis* species suggests a hypothetical sequence for the evolution of some members of the genus. The smallest *Ophiolepis* species may simply have originated from selection for reduced size. On the other hand, the diminutive species might have evolved from paedogenetic forms with early sexual maturity, "juvenile" somatic development; and with their success enhanced by viviparity and hermaphroditism.

Two groups of Panamanian *Ophiolepis* species may be distinguished by differences in their disc scalation. One set is composed of *O. kieri*, *O. pacifica* and *O. impressa*, which have an irregular or incomplete row of small scales around the major dorsal disc scales, and have inconspicuous supplementary dorsal arm plates. Another set, composed of *O. paucispina*, *O. elegans*, and *O. variegata* have a uniform border of small scales around each of the major dorsal disc scales, and have large supplementary dorsal arm plates. Further systematic work is needed to determine whether these two groups are valid natural assemblages.

While certain specialized features, such as the arrangement of the oral papillae, exhibit the same degree of complexity in the small and large representatives of both species sets, there are other features, such as disc scalation that are simplified in the smaller species in both groups. The pattern of disc scalation increases in complexity during ontogeny, as well as according to size within a series of allied species. For example, the scale pattern of a small form such as *O. kieri* approximates that of juveniles of larger species such as *O. impressa* and *O. pacifica*.

The co-occurrence of simplified somatic growth and sexual maturity at a small size in the diminutive *Ophiolepis* species, *O. kieri* and *O. paucispina*, suggests that they evolved by paedogenesis (progenesis, *sensu* Gould, 1977). If this were so and a tendency to produce yolky eggs of moderate size were fixed in the genotype of the small species, their potential fecundity, limited by the room for oocytes in the disc, would have been considerably lower than that of their larger congeners. In this situation, the disadvantages of low fecundity would have been mitigated by an adaptation such as brooding, that enhanced the survival of young.

There is a tendency for both large and small *Ophiolepis* species to produce yolky eggs of moderate size and modified embryos or larvae. *Ophiolepis kieri* and *O. paucispina* have yolky eggs and are viviparous, while *O. elegans* and *O. cincta* have yolky eggs, lecithotrophic larvae, and abbreviated development (Mortensen, 1938; Stancyk, 1973). It is likely that a Caribbean species, *Ophiolepis impressa*, and its Eastern Pacific congener, *Ophiolepis pacifica*, also have abbreviated development. Females of both species do not brood, but have dark brown, opaque yolky oocytes 0.2 mm in diameter (personal observation). Eggs of that size typically undergo abbreviated development (Hendler, 1975). The yolky eggs and abbreviated development characteristic of the genus could be preadaptations for viviparity.

Consequently, in the genus *Ophiolepis*, paedogenesis coupled with preadaptations such as yolky eggs, modified development, and genital bursae (brood sacs), in concert with selective pressure for brooding because of low fecundity, may have contributed to rapid evolution of small size and viviparity. The chief evidence for paedogenesis, the juvenile (not simply miniature) appearance of the small species, does not exclude the alternative possibility of gradual selection for small body size. However, evidence for the speculative sequence of events above might be found through further study of the reproduction, ontogeny, and phylogenetic relationships of the genus *Ophiolepis*, and by inference from similar trends for paedogenesis associated with abbreviated development and viviparity in other genera.

The significance of hermaphroditism in viviparous species of *Ophiolepis*, in fact the reason that all hermaphroditic ophiuroids are viviparous, is as yet unexplained (Hendler, 1975). The most appropriate hypotheses are the "density model" which suggests that hermaphroditism increases the likelihood for sedentary organisms to encounter a mate, and the "resource allocation model" which suggests that hermaphroditism increases the efficiency of apportioning energy between male and female functions (Smith, 1978). Either of these hypotheses helps explain the adaptive importance of hermaphroditism in these relatively small, rare brooding brittlestars.

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