No 2. — *The Starfishes of the Genus Heliaster.* By Hubert Lyman Clark.

The starfishes placed by Gray (1840) in the group to which he gave the name Heliaster are of more than usual interest because of their limited geographical distribution their exclusively littoral habitat, and the large number of rays which they have. Moreover they appear to be remarkably plastic and there has long been reason to believe that the group contains several well-marked forms, limited to very circumscribed geographical areas. As the collection of the Museum of Comparative Zoölogy contains a large number of specimens from a dozen or more different localities, it seemed worth while to make a careful study of the group, especially with reference to three questions which have been raised concerning it. (1). How many valid species of Heliaster are there, what is their relation to each other, and what is the geographical distribution of each? (2). With how many rays does Heliaster begin its post-larval life, where and how do the new rays arise, in what order, and with how much variability? (3). What is the relation of Heliaster to Asterias and other starfishes, and by what systematic arrangement can that relationship best be shown? In finding the answers to these questions, we discover some important evidence on the subject of isolation as a factor in the formation of new species.

In addition to the material in the Museum collection, I am indebted to Dr. W. K. Fisher, of Leland Stanford Junior University, for the loan of material from the Galapagos Islands, belonging to the Museum of that University, and to Dr. Richard Rathbun, of the United States National Museum, for much valuable material from the collections under his care. To both of these gentlemen I herewith extend my sincerest thanks. In all I have had, from at least 15 distinct localities, 346 specimens of Heliaster, ranging from 20 to 300 mm. in diameter.

Historical.

The following annotated bibliography gives a complete resumé of our knowledge of Heliaster and its several species, from the first published reference in 1767 down to July 1, 1906 : —

1767. **Davila, P. F.**

Catalogue systématique et raissoné des Curiosités de la Nature et de l'Art, qui composent le Cabinet de M. Davila, etc. 3 vols. **1.** Paris.

On p. 462–463 reference is made to three starfishes called "Tournesols," with 13, 37, and 38 rays, and brief descriptions are given of them; it is obvious that the two latter are Heliasters and it is fair to assume that they are *H. helianthus* (Lamarck) as that species was known in Paris, and was figured not many years later.

1791. **Bruguière, J. S.**

Tableau Encyclopédique et Méthodique, etc. Paris.

The two figures on plates 108 and 109 are fair abactinal and actinal views of a *Heliaster helianthus* (Lam.) with 29 rays.

1816. **Lamarck, J. B. P. A. de Monnet de**

Histoire Naturelle des Animaux sans Vertebres, etc. 7 vols. **2.** Paris.

On p. 558 Astérie hélianthe, *Asterias helianthus*, is given as the twentieth species of Asterias; it is said to have 30–36 rays (though reference is made to the figure of Bruguière, which has only 29) and to reach a diameter of 14–16 cm.; no locality is given.

1817. **Cuvier, G. L. C. F. D.**

Le Règne Animal, etc. 4 vols. **4.** Paris.

On p. 11, *Asterias helianthus* Lam. is listed but no information is given.

The numerous other editions and translations of Lamarck's and Cuvier's great works afford us no further information and there are no changes save that in the "Deuxieme Edition" (1840) of Lamarck the starfish is called "Astérie héliante," which is probably a misprint, and reference is made to the names *Solasterias* de Blainville and *Stellonia* Nardo, though neither is adopted; and in the German translation of Cuvier by Voigt (Das Thierreich, 1843) the species *helianthus* is listed under *Asteracanthion*, following Müller and Troschel.

1824. **Bory de Saint-Vincent.**

Tableau Encyclopédique et Méthodique, etc. Paris.

On p. 140 is the text to accompany the plates of Bruguière (1791), as follows:

Plate 108. Astérie, Asterias. 1–2. Asterias Helianthus, Lam., **2**, 558. (dessus).

Plate 109. Astérie, Asterias. 1–2. Asterias Helianthus, Lam., *loc cit.* (dessous).

1824. **Lamouroux, Bory de St. Vincent et Eud. Deslongchamps.**

Encyclopédie Méthodique. 10 vols. **2.** Paris.

On p. 119 is a direct quotation from Lamarck (1816) with the added note, "L'on ne connoît point son habitation."

1825. **Say, Thomas.**

On the species of the Linnean Genus *Asterias*, inhabiting the coast of the United States. Journ. Acad. Nat. Sci., **5**, p. 141–145. Philadelphia.

In a footnote on p. 145 is given the first published information in regard to the home of Heliaster.

"*A. Helianthus* Lam. As the native coast of this splendid species was unknown to Lamarck, I may . . . state that a fine specimen . . . was found near Guasco, . . . Chili."

1830. **Blainville, H. M. D. de.**

Zoöphytes: in Dictionnaire des Sciences Naturelles, etc. 60 vols. **60.** Strasburg et Paris.

On p. 222–223 *Solastéries* is proposed as a section of *Asterias*, admittedly artificial, for species with more than six rays, and *A. Helianthus* Lam. is named as one of them.

1834. **Blainville, H. M. D. de.**

Manuel d' Actinologie, etc. Paris.

On p. 241–242 is a repetition of the preceding suggestion, and a very poor figure of half the abactinal surface of *Helianthus* is given, plate 23, fig. 5.

1834. **Meyen, F. J. F.**

Reise um die Erde, etc. Theil **1**. Berlin.

On p. 222 *Asterias Helianthus* Lam. is said to be "besonders haüfig" on the coast at Valparaiso, and is considered the "ausgezeichnetesten" species of the genus.

1835. **Agassiz, L.**

Prodrome d'une Monographie des Radiaires ou Echinodermes. Mem. Soc. Sci. Nat., **1**, p. 168–199. Neuchâtel.

On p. 192, there is listed
"— *St. Helianthus* Ag. (Asterias Helianthus Lam.) —",
the *St.* being an abbreviation for *Stellonia* Nardo.

1840. **Müller, J. und Troschel, F. H.**

Ueber die Gattungen der Asterien, Arch. f. Naturg., Jahrgang 6, **1**, p. 318–326. Berlin.

On p. 321 *A. Helianthus* Lam. is listed as one of eight species of Asteracanthion, and on p. 324 the madreporite of the same starfish is said to be compound, a group of single plates.

1840. **Gray, John Edward.**

A Synopsis of the Genera and Species of the Class Hypostoma (Asterias, *Linnaeus*). Ann. Mag. Nat. Hist., **6**, p. 175–184. London.

On p. 179 is "Section e" of *Asterias, Heliaster*, defined thus: *Body discoidal, divided at the edge into numerous, short, tapering rays; the series of spines near the ambulacral series rather crowded, large and elongated.*

Asterias helianthus Lam. is given first, obviously as the type species, and is described as having 33 or 34 "arms," which are "about a quarter of the length of the width of the body." It is recorded from Guasco and Valparaiso, Chili. Then follow *Asterias Cumingii* with "arms 30 or 31, very short, not one-tenth as long as the diameter of the body," from "Hood's Island, on rocks at spring tide, *H. Cuming Esq.*," and *Asterias multiradiata* with "arms 22 or 24, cylindrical, elongated, tapering at the ends, one-third longer than the diameter of the body," from "Hood's Island, *H. Cuming Esq.*"

1840. Gervais, P.

Astérie, Asterias (*Actinoz*): in Dictionnaire Sciences Naturelles. Supplément. Paris.

On p. 469 *A. helianthus* Lamarck is assigned to *Stellonia* Nardo; reference is made to Gray's proposed section e (HELIASTER) of the genus *Asterias*, but curiously enough no mention is made of his proposed new species.

1842. Müller, Johannes und Troschel, Franz Hermann.

System der Asteriden. Braunschweig.

On p. 18–19 is given *Asteracanthion helianthus* nob., including *Asterias helianthus* Lamarck, *Asterias Cumingii* Gray and *Asterias multiradiata* Gray. The two latter are dismissed with the brief statement that they "do not appear to us to be different." The compound nature of the madreporite is referred to, the size is said to be "up to one foot" and the native coast is given as "Chili, Pacific Ocean."

1843. Müller, Johannes.

Über den Bau des Pentacrinus caput Medusae. Berlin.

Abschnitt 8. Ueber die Unterschiede des Baues der Crinoideen und Asteriden, p. 61–68.

On p. 64 *Asteracanthion Helianthus* Lam. is listed and on p. 67, the compound nature of the madreporite is mentioned.

1843. Müller, J. und Troschel, F. H.

Neue Beiträge zur Kenntniss der Asteriden. Arch. f. Naturg. Jahrgang 9, **1**, p. 113–131. Berlin.

On p. 128 *Asteracanthion helianthus* is listed among starfishes from the west coast of South America.

1854. Gay, Claudio.

Historia fisica y politica de Chili, etc. 26 vols. Zoölogia. **8.** Paris. Santiago.

On p. 425 is a good account of the "Estrella del Mar," *Asteracanthion helianthus*. It is said to have 28–39 rays and to occur at Valparaiso and elsewhere on the coast of Chili.

1856. Hoeven, J. Van der, translated by William Clark.
Handbook of Zoölogy. 2 vols. **1.** Cambridge (England).

On p. 148–149 *Asterias helianthus* with "rays up to 30 and more" is said to be "one of the most remarkable and most beautiful species."

1857. Carpenter, Philip P.
Report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Rept. British Ass. for 1856, p. 159–368. London.

On p. 360 it is stated that *Stylifer astericola* is known from the Galapagos parasitic in *Asterias solaris*. The starfish referred to is unquestionably a Heliaster and probably *H. cumingii* Gray, as many specimens of that species from the Galapagos are parasitized by Stylifer; the name *solaris* would be more naturally applied to this species than to *multiradiatus*, the other Galapagos Heliaster, because of its more numerous rays.

1857. Philippi, A.
Vier Neue Echinodermen des Chilenischen Meeres. Arch f. Naturg., Jahrgang 23, **1**, p. 130-134. Berlin.

On p. 134 *Asteracanthion helianthus* is listed among the starfishes of Chili.

1857. Stimpson, Wm.
On the Crustacea and Echinodermata of the Pacific Shores of North America. Boston Journ. Nat. Hist., **6**, p. 444–532, plates 18–23. Boston.

On p. 529 *Asterias helianthus* Lam. is given as occurring at "Mazatlan (Moores)." Probably *H. microbrachius* is the species intended.

1860. Lütken, Chr.
Bidrag til Kundskab om de ved Kysterne of Meilemog Syd-America levende Arter of Söstjerner. Videns. Meddel. for 1859, p. 25–96. Kjöbenhavn.

There are several references in this paper (p. 27, 31, 32, 35) to the occurrence of Heliasters on the western coast of America, but the writer considers the species in each case to be *helianthus*. In a footnote on p. 32, he indicates his doubt as to the location of Hood's Island, his disbelief in Gray's proposed species, and his final opinion that even if valid they do not enter into the West American fauna.

1860. Bronn, H. G.
Die Klassen und Ordnungen des Thier-reichs, etc. Die Klassen und Ordnungen der Strahlenthiere (Actinozoa). Leipzig und Heidelberg.

On p. 253 reference is made to the compound madreporite of *Asteracanthion helianthus*.

1860. Xantus, John.
Descriptions of Three New Species of Starfishes from Cape St. Lucas. Proc. Acad. Nat. Sci., 1860, p. 568. Philadelphia.

On p. 568 are the original descriptions of *Heliaster microbrachia* and *H. kubiniji*. The former is said to have 35 rays, the free portion equalling one-eighth of the diameter and the dorsal spines very small and numerous. The latter has 22–24 rays, the free portion rather less than one-third of the diameter, and the dorsal spines capitate; the name is said to be in honor of "my countryman, M. Kubiniji, the accomplished director of the Hungarian National Museum at Pesth." Each species is said to be 7 inches in diameter. The specimen of *microbrachia* was from Cape St. Lucas, while that of *kubiniji* was from " Cerro Blanco, Cape St. Lucas."

1862. Dujardin, F. et Hupé, H.

Histoire Naturelle des Zoophytes Échinodermes, etc. Paris.

On p. 329, 343 and 344 *Heliaster* Gray is recognized as a genus, and with *Asteracanthion* forms the first of the three tribes of Asterides. The species *Cumingii* Gray and *multiradiatus* Gray are however considered doubtful, and although the characters given by Gray are mentioned, the species are included in the synonymy of the single accepted species, *Heliaster Helianthus* Lam. (Sp.). The color of this species is said to be "variée de blanc et de noir, comme tigrinée"; the size, 20–30 cm.; the distribution, " Coast of Chili " (thus ignoring Gray's records from the Galapagos). The gastropod *Stylifer* is recorded as a parasite. No mention is made of Xantus's paper (1860) or of his proposed species.

1866. Martens, E. von.

Ueber Ostasiatische Echinodermen. Arch f. Naturg., Jahrgang 32, **1**, p. 57–88. Berlin.

On p. 60 *Heliaster* is used as a subgenus of *Echinaster* to include *solaris* Schmidel, and "Hupé und Dujardin" are quoted for authority. In this extraordinary slip of the pen are three distinct errors. (1) Hupé and Dujardin never published anything with the former as senior author. (2) Dujardin and Hupé (1862) use Heliaster as a separate genus and neither they nor any other author ever used it as a subgenus of, or allied to Echinaster. (3) Schmidel never gave the name *solaris* to any species of starfish, though in 1781 he described one, to which Schreber, twelve years later, gave that name! The starfish to which von Martens refers is obviously *Acanthaster echinites* (Ellis and Solander). — On p. 68 von Martens speaks of the peculiar madreporite of *Asterias helianthus*.

1866. Gray, John Edward

Synopsis of the Species of Starfish in the British Museum. London.

On p. 2 is what is practically a reprint of that part of p. 179, Gray 1840, which deals with Heliaster, except that *Heliaster* is now section f, instead of section e, of the genus *Asterias*.

1867 [a]. Verrill, A. E.

Notes on the Echinoderms of Panama and West Coast of America, with descriptions of new Genera and Species. Trans. Conn. Acad., **1**, p. 251–322. New Haven.

On p. 289-293 are good descriptions of *Heliaster helianthus, microbrachia, Cumingii* and *Kubiniji*, with special attention given the pedicellariae. The description of *Kubiniji*, which is considered distinct from *multiradiata* Gray, is based on a specimen "obtained at the Sandwich Islands. It probably came from Acapulco or Mazatlan." This specimen is of interest chiefly because, through a mistake of Perrier's, it is the source of all Hawaiian records.

1867 [b]. **Verrill, A. E.**

On the Geographical Distribution of the Echinoderms of the West Coast of America. Trans. Conn. Acad., **1**, p. 323–351. New Haven.

The geographical distribution of the genus *Heliaster* and of *H. Cumingii, helianthus, Kubiniji, microbrachia,* and *multiradiata,* is referred to on p. 328, 329, 331, 333-335, 344, and 348.

1868. Claus, Carl

Grundzüge der Zoologie, etc. Marburg und Leipzig.

On p. 107 *Asteracanthion helianthus* is referred to as having "30 und mehr" rays.

1869. Perrier, Edmond.

Recherches sur les Pédicellaires et les Ambulacres des Asteries et des Oursins. Ann. Sci. Nat., (5) **12**, p. 197–304, plates 17–18. Paris.

On p. 202–203 Heliaster is recognized as a good genus, but on p. 231 the writer decides it is not valid. A description of the pedicellariae of Asteracanthion and Heliaster occupies p. 202–219 and on plate 7 is a figure (16) of a forcipiform pedicellaria of *Asteracanthion helianthus.* On p. 203 it is stated: "Dans toutes les espèces appartenant aux genres *Asteracanthion* et *Heliaster* on trouve deux sortes de Pédicellaires, nous designerons . . . l'une . . . *Pédicellaires droits,* l'autre . . . *Pédicellaires croisés.*" But on p. 231 under *Heliaster helianthus,* the writer says, "Nous ne connaissons pas encore les pédicellaires droits"!

1869. Verrill, A. E.

On New and Imperfectly Known Echinoderms and Corals. Proc. Boston Soc. Nat. Hist., **12**, p. 381–396. Boston.

On p. 387 are some notes on a large specimen of *Heliaster Kubiniji* from La Paz having 23 rays.

1871 [a]. **Verrill, A. E.**

Additional Observations on Echinoderms, chiefly from the Pacific Coast of America. Trans. Conn. Acad., **1**, p. 568–593. New Haven.

On p. 578 are some further notes on *Heliaster Kubiniji* Xantus.

1871[b]. **Verrill, A. E.**

The Echinoderm Fauna of the Gulf of California and Cape St. Lucas. Trans. Conn. Acad., **1**, p. 593–596. New Haven.

This brief paper contains several references to the geographical distribution of Heliasters on the coast of Mexico.

1871. Cunningham, Robert O.

Notes on the Natural History of the Strait of Magellan and West Coast of Patagonia, etc. Edinburgh.

On p. 404 a 38-rayed specimen of *Heliaster helianthus* is referred to as a "huge" starfish taken at Pelican Rock, near Coquimbo, Chili. Unfortunately no measurements are given.

1871. Lütken, Chr.

Fortsatte kritiske og beskrivende Bidrag til Kundskab om Söstjernerne (Asteriderne). Viddens. Meddel. for 1871, p. 227–304, plates 4–5. Kjöbenhavn.

On p. 289 is an unimportant reference to "*Asterias microbrachia* Xantus," and on p. 304 the occurrence of that species and "*Heliaster Kubinjii*" at Altata, Mexico, is noted.

1872. Lütken, Chr.

Om Selvdeling hos Echinodermer og andre Straaldyr. Overs. K. Danske Vid. Sels. Forh. for 1872, p. 108–157. Kjöbenhavn.

On p. 121 is a trivial reference to Heliaster and in a footnote (2) on p. 125 et seq. is an interesting discussion of the correlation between size and number of rays in "*Asterias helianthus*," "*microbrachia*," "*Kubinjyi*," and "*Cummingii*."

1875. Perrier, Edmond.

Révision de la Collection de Stellérides du Muséum d'Histoire Naturelle de Paris. Arch. Zool. Exp., **4**, p. 265–450. Paris.

The genus *Heliaster* Gray is approved and placed in the Asteriadae (p. 285–286) and a diagnosis is given (p. 299). Later (p. 351) it is given as the fifth genus of the Asteriadae, with four species:

H. microbrachia Xantus. Acapulco.
H. kubiniji Xantus. Acapulco.
H. helianthus (Lam.). Chili.
H. canopus, sp. nov. (Mss. Valenciennes). Juan Fernandez.

The writer considers *microbrachia* the best characterized species, and describes *canopus*, which he says is 70 mm. in diameter and has only 24 rays, and may prove to be the young of *helianthus*. Perrier does not mention *multiradiatus*, but states that he could not find Gray's *cumingii* at the British Museum.

1878. Perrier, Edmond.

Étude sur la Répartition Géographique des Astérides. Nouv. Arch. Mus. d'Hist. Nat., (2) **1**, p. 1–108. Paris.

The geographical distribution of Heliaster is fully discussed in this paper on p. 8, 11, 75, 76, 98–100. By a curious slip of the pen on p. 43, Heliaster is said to be peculiar to "le côte orientale" of America, and the same slip is repeated with reference to Pycnopodia.

1878. Viguier, M.

Anatomie Comparée du Squelette des Stellérides. Arch. Zool. Exp., **7**, p. 33–250, plates 5–16. Paris.

This very important paper deals fully (p. 61, 63, 93, 99, 111–116) with the skeletal anatomy of Heliaster, and discusses its relationship with other starfishes. On plate 6 are given some structural details (figs. 4–12). The conclusion is reached that the peculiarities of Heliaster are sufficient to warrant its elevation to family rank, as the HELIASTERIDAE.

1883. Perrier, Edmond.

Mémoire sur les Étoiles de Mer, recueillies dans la Mer des Antilles et le Golfe du Mexique, etc. Also entitled: Stellérides des Dragages du "Blake." Nouv. Arch. Mus. d'His. Nat., (2) **6**, p. 127–276, plates 1–10. Paris.

The family Heliasteridae is recognized in this work, although the references to it (p. 139, 143, 153, 154) and to the type genus are unimportant.

1885. Lockington, W. N.

Echinodermata; under Lower Invertebrates, Standard Natural History. 6 vols. **1**, Asteroidea, p. 152–161. Boston.

On p. 160 the genus Heliaster (apparently under the "Asteridae") is referred to as having two species, *kubiniji* and *microbrachia*, on the west coast of North America from Panama to Cape St. Lucas.

1886. Ludwig, Hubert.

Dr. Johannes Leunis Synopsis der Thierkunde, etc. 2 vols. **2**. Hannover.

On p. 934 *Heliaster* Gray is given as a genus of Asteriadae, with "mehrere Arten," but *helianthus* (Lam.) Gray is the only one mentioned.

1887. Rathbun, Richard.

Descriptions of the species of *Heliaster* (a genus of starfishes) represented in the U. S. National Museum. Proc. U. S. Nat. Mus., **10**, p. 440–449, plates 23–26. Washington.

In this, the most important paper published dealing with the taxonomy of Heliaster, four species are clearly distinguished, fully described, and admirably figured. The writer considers *H. kubiniji* Xantus (which is spelt

Kubingii throughout the paper) as identical with *multiradiata* Gray, while *H. canopus* Perrier is not mentioned. By a curious slip of the pen, Verrill's paper of 1869 is quoted as Amer. Jour. Sci. instead of Proc. Boston Soc. Nat. Hist.

1889. Ives, J. E.

Catalogue of the Asteroidea and Ophiuroidea in the Collection of the Academy of Natural Sciences of Philadelphia. Proc. Acad. Nat. Sci., 1889, p. 169–179. Philadelphia.

On p. 170 "*H. helianthus* Lam., *microbrachia* Xantus, *multiradiata* Gray (= *Kubiiniji* Xantus)" are listed under the Asteriidae.

1889. Sladen, W. Percy.

Report on the Asteroidea collected by H. M. S. "Challenger" during the years 1873–1876. Rept. Sci. Results Voy. H. M. S. "Challenger." 32 vols. **30**, xlii, 893 pp., 118 plates. Edinburgh and London.

This magnificent monograph contains numerous references (p. xiii, xx, xxi, xxxix, xlii, 555, 556, 671, 686, 690, 701, 812, 813) to the anatomy, systematic position, and geographical distribution of Heliaster and the Heliasteridae. The author is very sceptical as to whether the genus contains more than a single species, and speaks several times of the "so-called" species.

1891. Perrier, Edmond.

Echinodermes I. Stellerides. Mission Scientifique du Cap Horn, **6.** Zoologie, p. K 1–K 198, plates 1–13. Paris.

On p. K 60, K 61, and K 67 are references to the number of rays, and formation of new rays, in Heliaster.

1892. Meissner, Maximillian.

Asteriden gesammelt von Herrn Stabsartz Dr. Sander auf der Reise S. M. S. "Prinz Adalbert." Arch. f. Naturg. Jahrgang 58, **1**, p. 183–190, plate 12. Berlin.

On p. 184 nine examples of *H. helianthus* Lam., with from 30 to 38 rays each, are recorded from Callao, Peru.

1893. Perrier, Edmond.

Traité de Zoologie. Paris.

On p. 781 and 847 are unimportant references to Heliaster.

1894. Lang, Arnold.

Lehrbuch der Vergleichenden Anatomie der Wirbellosen Thiere. — Echinodermata. p. 871–1154. Jena.

On p. 884 is this: 7. Familie. Heliasteridae. Mit zahlreichen, kurzen-armen. Heliaster.

1894. Perrier, Edmond.

Echinodermes: in Exp. Sci. du Travailleur et du Talisman, etc. 431 pp., 26 plates. Paris.

On p. 4 and 27 are unimportant references to the Heliasteridae; on p. 22 Heliaster is said to have "quarante bras et plus," but it is fair to assume that "jusqu'à" is to be understood; on p. 43 Heliasteridae is again referred to and listed as the third family of Forcipulata.

1895. Sluiter, C. Ph.

Die Asteriden-Sammlung des Museums zu Amsterdam. Bijdr. Dierk., **17**, p. 49–64. Amsterdam.

On p. 64 the family Heliasteridae is recognized and *H. helianthus* is listed from Chili.

1895. Leipoldt, Fritz.

Asteroidea der "Vettor-Pisani" Expedition (1882–1885). Zeit. f. w. Zool., **59**, p. 545–654, plates 31–32. Leipzig.

On p. 546–552 are very useful accounts of the distribution and the pedicellariae of *H. helianthus*, *cumingii*, *multiradiatus*, and *microbrachius*. Good figures of the jaws of the pedicellariae are given on plate 31, figs. 1 and 2. The peculiar coloration of specimens of *multiradiatus* from the Galapagos Islands is well described. Perrier's record of that species from the "Iles Sandwich" is very properly regarded with doubt.

1896. Plate, Ludwig H.

Zur Kenntnis der Insel Juan Fernandez. Verh. Gesellsch. Erdk. Berlin, nos. 4 und 5, p. 221–229. Berlin.

On p. 224 *H. helianthus* is reported as one of the five starfishes occurring at Juan Fernandez; some further notes are given concerning its occurrence on the South American coast.

1896. Meissner, Maximillian.

Die von Herrn Dr. L. Plate aus Chili und Feuerland heimgebrachten See-Sterne. Arch. f. Naturg. Jahrgang 62, **1**, p. 91–108. Berlin.

On p. 102 *H. helianthus* is reported from Chili as the common starfish of the coast rocks. Two young ones with 12 and 22 rays each are recorded, but, strangely enough, nothing is said as to the size of either. The writer remarks on its being unfortunate that Dr. Plate failed to bring home any specimens of Heliaster from Juan Fernandez, since he reports (1896) *H. helianthus* as being common there, while the specimens upon which Perrier based his species *canopus* (1875) came from that island, and Dr. Plate, by bringing home a series of specimens, might have settled the question as to the authenticity of that species.

1897. Harrington, N. R. and Griffin, B. B.
Notes upon the Distribution and Habits of some Puget Sound Invertebrates. Trans. N. Y. Acad., **16**, p. 152–165. New York.

On p. 156 is the following mistake: "The commonest sea-star, a gigantic species of *Heliaster*, finds shelter beneath the wharves, etc." Of course, *Pycnopodia helianthoides* is the species referred to.

1899. Ludwig, H. and Hamann, O.
Echinodermen: Asteroidea: in Dr. H. G. Bronn's Klassen und Ordnungen des Thier-reichs, etc. **2.** Leipzig.

On p. 566–568 the madreporite of Heliaster is discussed and on p. 713 the family Heliasteridae is accepted with the single genus, Heliaster, and five species, *canopus* Perrier being added to the four described by Rathbun (**1887**).

1900. Gregory, J. W.
The Stelleroidea: in Bather's Echinoderma, chap. 13, p. 237–281: in E. Ray Lankester's A Treatise on Zoölogy, Part 3. London.

On p. 258 the family Heliasteridae is accepted with two subfamilies; HELIANTHASTERINAE with the single Devonian genus, *Helianthaster* and HELIASTERINAE with the single recent genus *Heliaster*.

1900. Ritter, W. E. and Crocker, Gulielma R.
Multiplication of Rays and Bilateral Symmetry in the 20-rayed Starfish, *Pycnopodia helianthoides* (Stimpson) Proc. Wash. Acad. Sci., **2**, p. 247–274, plates 13–14. Washington.

In discussing the method of ray formation in multiradiate starfishes, there are some references (p. 249 and 263) to Heliaster, based however on assumption and not on investigation.

1902. Goette, Alexander.
Lehrbuch der Zoologie. Leipzig.

On p. 319 *Heliaster helianthus*, "mit zahlreichen Armen," is given as an example of the Cryptozonia.

1902. Kingsley, J. S.
Hertwig's Manual of Zoölogy. New York.

On p. 337 *Heliaster* is given as an example of a starfish with numerous well developed rays and "ambulacra in four rows."

1902. Clark, Hubert Lyman.
Echinodermata: in Papers from the Hopkins-Stanford Galapagos Expedition, 1898–99. Proc. Wash. Acad. Sci., **4**, 521–531. Washington.

On p. 523–524 are some notes on *H. cumingii* and *multiradiatus*.

1903. Delage, Yves et Herouard, Ed.
Traité de Zoologie Concrète. 9 vols. **3.** Les Echinodermes. Paris.

On p. 103 is this:
7 Fam.: Heliasterinae [*Heliasteridae* (Viguier); p. p. *Forcipulata* (Perrier)] — Heliaster (Gray). Bras 25 au moins. Helianthaster (Römer) (Dev.).

1906. Fisher, Walter K.
The Starfishes of the Hawaiian Islands. Bull. U. S. Fish Commission for 1903, part 3, p. 987–1130, plates 1–49. Washington.

On p. 989, 994, and 998 are brief references to *H. multiradiatus*, and on p. 1002 the family Heliasteridae is included in the Key. On p. 1104 *H. multiradiatus* is admitted to the Hawaiian fauna on the strength of Sladen's statement, but serious doubt is expressed as to the validity of the record.

As a result of the examination of this literature, our present knowledge of Heliaster may be briefly summarized as follows: Six species have been described, of which one (*kubiniji* Xantus) is commonly considered identical with another (*multiradiatus* Gray), while a third (*canopus* Perrier) is regarded as possibly the young of a fourth (*helianthus* Lamarck), and by some writers the remaining two are not considered as really distinct. The geographical limits of the genus are fairly well known, but there is still some question about the limits of the several species. The external morphology, including the pedicellariae, is very well known and the skeletal characters especially of the oral surface have been well worked out. But the internal anatomy is practically unknown, and almost nothing is recorded of the habits; absolutely nothing of the development. The amount of variability within a single species is little understood and almost nothing is known of the formation of the new rays in passing from the young stages with relatively few, to the older condition with very numerous, rays. Finally the relationship to other genera is most imperfectly understood, although there is general agreement in placing the genus apart in a family by itself.

Systematic.

We naturally turn first of all to an investigation of the number and validity of the species which Heliaster contains, and the material at hand enables us to settle all of the disputed questions in regard to this matter. In his admirable report on the Heliasters of the United States

National Museum, Rathbun (**1887**) has shown beyond question the existence of at least four well-marked species, and the present investigation confirms his conclusion. But Rathbun had no material from Juan Fernandez, and consequently does not refer to *canopus* Perrier, while he had only a few specimens from the Galapagos, and these he naturally assigns to the species named by Gray, which came from Hood's Island. The material now available, includes a fine series of adults and young from Juan Fernandez, which confirms Perrier's opinion that the species occurring at the island is quite different from *helianthus* and is entitled to recognition as a distinct species, *canopus*. The number of specimens from the Galapagos makes it possible to show that the Heliasters of that group of islands present certain characters in which they are obviously and apparently constantly different from their nearest allies on the American coast. Of course there is room for difference of opinion as to whether these characters are sufficiently tangible and constant to warrant calling the island forms separate species, but since the characters are associated with sharply distinct geographical areas (for Heliaster is littoral in the extreme) and since the island forms were long ago named by Gray, and one of the mainland near allies by Xantus, it seems better to give the other mainland ally a name, and thus recognize seven species of Heliaster. In no other way can the apparent plasticity of the genus and the results of isolation be so well brought out.

Heliaster Gray.

Asterias; section e, Heliaster Gray, 1840. Ann. Mag. Nat. Hist., **6**, p. 179.

Heliaster (used without comment as a generic name) Xantus, 1860. Proc. Acad. Nat. Sci. Phil., p. 568.

Heliaster Dujardin et Hupé, 1862. Hist. Nat. Zoöph. Echin., p. 343.

Asterias; section f, Heliaster Gray, 1866. Syn. Starf. Brit. Mus., p. 2.

Heliaster Perrier, 1875. Arch. Zoöl. Exp., 4, p. 299.

Since Perrier's diagnosis the genus Heliaster Gray has been universally recognized.

Gray's diagnosis was as follows: —

Body discoidal, divided at the edge into numerous short tapering rays; the series of spines near the ambulacral series rather crowded, large, and elongated.

To this characterization, Perrier added nothing, but Viguier (**1878**) suggested as additional features the funnel-shaped depression in which the mouth is placed, the fragmentation of the madreporite, the double interbrachial walls, and the fused condition of that interradial plate which he calls the "odontophore." Unfortunately the first and last of these characters are of doubtful value, and the

second is not true of all Heliasters. The third, although quite characteristic, is not confined to this genus. Accordingly, the following diagnosis of the genus, which represents our present knowledge, does not differ markedly from that of Gray: —

Disc large, not set off externally from the fused bases of the rays, little elevated, with reticulated abactinal skeleton, and more or less numerous spines, pedicellariae, and papulae. Rays numerous, more than 20 in normal adults, more or less united at base, so that only a relatively small part (15–70%) is free.[1] Adambulacral armature variable, usually single, sometimes double, especially near tip of ray; spines of alternate plates often of two sharply contrasted sizes, especially near base of ray. Pedicels arranged in two more or less zigzag rows, so that near middle of ray they are, as a rule, distinctly quadriserial. Forcipate and forficate pedicellariae both present, the latter often of two quite distinct sizes. Interbrachial septa double and well developed, expanding at inner (proximal) end and uniting laterally more or less extensively, to form a discobrachial wall, so that the cavity of the disc is almost completely separated from the cavities of the rays. (See plate 6, fig. 1).

This well-marked genus is easily distinguished by the number of rays alone, from all other starfishes except *Pycnopodia* and *Labidiaster*. From the former it is readily separated by the well-developed abactinal skeleton, the large disc and the fused rays. From Labidiaster it differs in the fused rays and quadriserial pedicels. The double interbrachial septa with the remarkable discobrachial wall are internal features, distinguishing Heliaster from either genus. — The distribution of Heliaster is remarkably restricted as it occurs only in very shallow water along the tropical and subtropical coasts of the eastern Pacific Ocean. I can find no record of a specimen being taken with a dredge or trawl, so that they are apparently littoral starfishes in the strictest sense of that term. They occur upon and among rocks in the neighborhood of low-water mark. The most northern point of their range, as shown by the specimens before me is San Luis Gonzales Bay, Gulf of California, in latitude 29° 15′ N., while the southern extreme on the mainland appears to be in the vicinity of Valparaiso, 33° 2′ S. lat. There are no published records of the occurrence of Heliaster, either north or south of these limits, and it is not recorded from any of the outlying islands, save Juan Fernandez, 33° 38′ S. lat., and the Galapagos, on the equator. — Nothing has been recorded of the habits of Heliaster, but preserved specimens show that the food consists very largely of small mussels, limpets, and acorn-shells (barna-

[1] In estimating the percentage of ray that is free, the length of the free portion is divided by R. (*i. e.*, the distance from centre of abactinal surface of disc to tip of ray) as it is not feasible to measure the actual length of ray. Consequently the free part is really a larger proportion of the ray itself than the percentages herein given would seem to indicate. It should also be noted that the rays are fused to a much greater extent relatively in adult than in young specimens; very young individuals often have twice as much free ray as adults of the same species.

cles). In two cases a half of a small fish was found in the stomach, but it is probable that the fish were found dead on the rocks among the mollusks and barnacles on which the Heliaster was feeding. — Parasitic gastropods (*Stylifer*) are common on specimens of Heliaster from the Galapagos Islands and occur not infrequently on specimens from the South American coast.

The following keys show the characters by which the seven species here recognized are to be distinguished. The first is wholly morphological and shows the species in what is probably their natural relationship. The second is quite artificial and takes into account the geographical distribution; it may be found useful in identifying specimens from known localities, where a large series of individuals is not available for comparison. In using these keys, it must be borne in mind that the number of rays is fewer in young individuals than in adults and that (as already mentioned) they may be free for a much greater proportion of their length. Consequently specimens under one hundred millimeters in diameter cannot always be certainly identified by means of these keys alone.

Key to the Species.

A. Rays free for 30 per cent of their length, or more.

B. Rays 30 or more, free about 35 (30–40) per cent of their length . . . . . *helianthus*

BB. Rays 28 or fewer, free for 40–70 per cent of their length.

C. Spines on abactinal surface of disc numerous, little or not at all capitate, smaller than those which form conspicuous marginal series on abactinal surface of rays; between these marginal series is a median series with a lateral series on each side; latter generally inconspicuous and made up of very small spines; marginal series converge on disc, confining median series to ray . . . . . *canopus*

CC. Spines on abactinal surface of disc comparatively few, many of them usually conspicuously capitate and larger than those of marginal series of rays; between latter are three or more not very clearly defined series of which the median is most conspicuous and continues inwardly onto the disc.

Rays free for more than half their length, 50–70 per cent; color, abactinally, pale yellowish mottled with blackish, the rays more or less distinctly banded; spines, pedicellariae, and madrepore plate, light yellowish . . . . . *multiradiatus*

Rays free usually for less than half their length, 40–55 per cent; color, abactinally, deep purplish; spines, pedicellariae, and madrepore plate, more or less deep yellow; rays sometimes indistinctly banded . *kubiniji*

AA. Rays free for less than 30 per cent of their length, rarely less than 30 in number in adults.

B. Abactinal surface covered with numerous small, often subacute, rarely capitate, spines of nearly uniform length, not arranged in radiating series except on rays, where five such series are usually more or less evident . . . . . *microbrachius*

BB. Abactinal surface with rather large, often capitate spines, arranged in more or less distinct radial series, especially on rays, where three such series are very evident.

Abactinal spines not very numerous, 15–20 per sq. cm. where thickest, more or less cylindrical, often subacute, rarely distinctly capitate; pedicellariae often wanting on actinal surface; rays often free for more than 20 per cent of their length . . . . . *cumingii*

Abactinal spines more numerous, 25–50 per sq. cm. where thickest, low, usually capitate; pedicellariae frequent on actinal surface; rays seldom free for more than 20 per cent of their length . . . . . *polybrachius*

Artificial Key to the Species.

A. Rays more than 30, rarely as few as 27 or 28.

B. Rays free for 30 per cent of their length or more; west coast of South America . . . . . *helianthus*

BB. Rays free for less than 30 per cent of their length.

C. Abactinal surface with very numerous small spines, rarely capitate; five subequal series on rays; west coast of Mexico and Central America . . . . . *microbrachius*

CC. Abactinal surface with fewer, larger, capitate spines; three series on rays.

Abactinal spines not crowded, little or not at all capitate; Galapagos Islands . . . . . *cumingii*

Abactinal spines numerous, often crowded, especially near margin of disc, usually distinctly capitate; west coast of tropical South America . . . . . *polybrachius*

AA. Rays never more than 28.

B. Abactinal surface of disc with spines smaller than the marginal series on rays; diameter of adult 80–120 mm.; Juan Ferdandez . . . . . *canopus*

BB. Abactinal surface of disc with large, often capitate spines; diameter of adult 110–180 mm.

Rays free for 40–55 per cent of their length; west coast of Mexico and Central America . . . . . *kubiniji*

Rays free for 50–70 per cent of their length; Galapagos Islands . . . . . *multiradiatus*

Heliaster helianthus (Lamarck).[1]

Plate 3, Fig. 1; Plate 7, Figs. 1-7.

Tournesol Davila, 1767.
Asterias helianthus Lamarck, 1816.
Stellonia helianthus Agassiz, 1835.
Asteracanthion Helianthus Müller and Troschel, 1842.
Heliaster helianthus Dujardin and Hupé, 1862.

Description. — Rays 30–40, averaging (51 individuals) 34.8; about 35 (29–43) per cent of ray, free. R=75–150 mm.; r=45–90 mm. Breadth of ray at base, 8–15 mm. R=7–9 br. Rays more or less flattened both actinally and abactinally, angular with nearly vertical sides, commonly tapering but often abruptly blunt-pointed, becoming more nearly terete near tip. Disc large, little or not at all elevated above base of rays; in a specimen with R=150 mm. the vertical diameter is only about 30 mm.[2] Abactinal surface covered with a stout, reticulated skeleton having rather small meshes. Skeletal plates with numerous spines of variable size, form, and arrangement. There are usually three well-marked series on each ray and these continue inward onto the disc far beyond the base of the ray; the median row is the most conspicuous and includes numerous clusters of more or less capitate spines; the lateral rows contain fewer spines, commonly arranged in a single series, which may be larger or smaller, and more or less capitate, than those in the median row. The lateral rows are nearly parallel with each other and remain separate, so that the median series is also present proximally. On the central part of the disc, the prominent and usually capitate spines do not show a serial arrangement but they are commonly grouped in more or less irregular, short lines, which form a sort of imperfect reticulation. In some specimens this network is quite distinct, the meshes being three or four millimeters in diameter and each side of a mesh consisting of a crowded single series of from three to seven spines. In other specimens no reticulation is evident, the spines being irregularly scattered, although here and there a few tend to form a crowded, linear series. Specimens sometimes occur in which no arrangement of the abactinal spines is evident even on the rays, but they appear to be scattered irregularly everywhere. Besides the conspicuous spines, smaller and more slender ones frequently occur abactinally, and pedicellariae, chiefly of the forcipate type, are more or less abundant, especially near the tips of the rays, while papulae occur everywhere. — Sides of rays with three or four longitudinal series of spines which are usually very

[1] No attempt is made to give complete synonymies of the seven species, as that would involve a virtual repetition of the bibliography already given. Only such names are listed as show some difference from the one originally given or the one herein accepted. It should be noted in passing that Gray never used Heliaster as a generic name and never published it in direct connection with any specific name; consequently it is not correct to write "*Heliaster helianthus* (Lam.) Gray" as has often been done; if two authors are to be referred to, the name should be written as Sladen gives it, "*Heliaster helianthus* (Lam.) Dujardin and Hupé."

[2] It is useless to attempt to distinguish externally the true limits of the disc, and the term is used in these descriptions to include the fused basal portion of the rays.

markedly compressed, among which are numerous pedicellariae and papulae. — Actinal surface of disc almost entirely occupied by ambulacra, adambulacral spines, pedicellariae, and papulae; interbrachial areas reduced to a minimum. — Adambulacral plates with typically a single, conspicuous, erect spine. In young specimens these may all be of equal size, but in adults, near the middle of the ray, larger and smaller spines alternate, so that every other plate has a small spine standing between the larger spines of the neighboring plates. The smaller spines are commonly almost or quite within the furrow. In some specimens the small spines are wholly wanting proximally so that only every other plate carries a spine. As a rule the spines are all of a nearly uniform size near the tip of the ray. On the distal half of the ray, some of the adambulacral plates often carry two spines, one behind the other. Beginning just proximal to the base of the ray and running outward to the tip, a series of large spines is found just outside the adambulacral series, and this is followed by one or two more, each series slightly shorter than its predecessor. These additional actinal spines differ greatly in number and size in different specimens, apparently increasing with the age of the animal. The adambulacral spines on the middle and proximal part of the ray are the largest spines of the actinal surface and may be as much as five millimeters long. Along the sides of the ambulacral furrows, among the adambulacral and other spines, are numerous pedicellariae, chiefly of the forficate type and of two quite distinct sizes (Plate **7**, figs. 2, 3); but the size and abundance of the pedicellariae vary greatly in different individuals. — At the centre of the actinal surface occurs the very large buccal membrane, thin, smooth, and conspicuous, with the mouth at the centre. The membrane in a large specimen (R=150 mm.) is 35 mm. across and the mouth is ten millimeters in diameter. Each oral (adambulacral) plate carries two or three short spines arranged side by side more or less horizontally, the innermost the longest, the others successively shorter. The actinal surface shows more or less of a tendency to become abruptly and deeply concave at the centre, so that the proximal portions of the ambulacra are almost vertical, the adambulacral spines thus lying horizontally and the oral spines vertically. This tendency is much more marked in some specimens than in others; thus, in a specimen with R=105 mm., the buccal membrane is 20 mm above the horizontal portion of the actinal surface of the rays, while in another specimen with R=150 mm. the depression is no deeper; and in a third specimen with R=48 mm., the vertical distance to the buccal membrane is only five millimeters. As no observations on the living animal have yet been recorded, it is impossible to say whether this buccal depression has any physiological importance or not. It is interesting to note however that in adult specimens where the depression is well marked, the adambulacral spines on its sides are smaller and less prominent, and the pedicels longer and more prominent, than elsewhere on the actinal surface. — Pedicels in a zigzag row on each side of each ambulacrum, scarcely crowded enough to make them quadriserial; proximally in adults and still more so in the young, they are distinctly biserial. Madreporite single; small, slightly convex and irregularly furrowed in young specimens, usually becoming broken up into a number of fragments in adults; even small specimens may show this fragmentation to some extent. — Color [1] of abactinal surface dark (gray, brown, blackish, or black), rarely more or less variegated with

[1] The color of living Heliasters has never been described; in all the descriptions here given, the colors referred to are those of alcoholic and dried specimens.

light colored blotches; spines and madreporite, yellowish or whitish; actinal surface yellowish, the pedicels darker than the spines.

Range. — San Lorenzo and Manta, Ecuador (Rathbun); Payta, Peru (M. C. Z. and U. S. N. M.); Ancon, Peru (Rathbun); Callao, Peru (Meissner); Arica and Iquique, Chili (Plate); Mejillones, Chili (M. C. Z.); Caldera, Chili (M. C. Z); Copiapo, Chili (Leipoldt); Guasco, Chili (Say); Coquimbo and Valparaiso, Chili (Plate). — How far north of the equator this species occurs we have no definite information; but there can be little question that Stimpson's (1857) record of it from Mazatlan, Mexico, is based on a specimen of *microbrachius*. It probably does not reach Panama Bay, or the many collectors who have been there would have found it, and by similar argument we may say it does not range to any great distance south of Valparaiso. It has not been taken at any of the outlying islands.[1] We are justified, therefore, in considering its range to be as follows: —

Mainland coast of western South America from northern Ecuador (about 2° N. lat.) to Valparaiso, Chili (33° 2′ S. lat.).

Remarks. — As this is the longest known and the largest species, it is probably most often seen in museums, and most frequently referred to in literature. The compound nature of the madreporite has been spoken of by many writers, but examination of a large series of specimens shows that the madreporite is not different, early in life, from that of Asterias, and not even in adults is it always broken up, for it may remain single and without peculiarities throughout life. Young specimens of *helianthus* usually have the rays much more blunt and less tapering than adults, and the three longitudinal series of spines on the abactinal side of each ray are usually very distinct. — Among the specimens sent me from the National Museum is an interesting individual (No. 21947), about 120 mm. in diameter, and having 32 rays, labelled "Loc.? Albatross, 1888." The further information is given in a list of the Heliasters sent, "Found in bottom of tank; may belong to one of above lots;" the "above lots" referred to are from the Galapagos Islands and the Gulf of California. Although too young to make identification certain, the specimen is apparently a young *helianthus*, as shown by the form and arrangement of the abactinal spines, the madreporite, and the long, free (33–40 per cent) rays. The locality of this specimen is therefore a matter of great interest, for the "Albatross" in 1888 made no shore collections between Lota, Chili (37° S. lat.), and Panama, save at the Galapagos Islands, and all of these places are well outside the known range of *helianthus*.

Material examined: —

15 specimens.	Mejillones, Chili.	M. C. Z. collection.
10 "	Payta, Peru.	" "
23 "	Caldera, Chili.	" "
2 "	"Peru."	" "
?1 specimen	Loc.?	U. S. N. M. "
51 specimens	5 localities.	

[1] Plate's (1896) reference to *helianthus* at Juan Fernandez is probably based on specimens of *canopus*.

Heliaster canopus Perrier.

Plate 3, Fig. 2; Plate 8, Fig. 7.

Heliaster canopus Valenciennes. Perrier, 1875.
Heliaster canopus (Val. MS.) Perrier. Sladen, 1889.

There is no good reason why Valenciennes' name should be associated with this species any longer, for his manuscript museum name has no standing. Perrier was the first and only describer of the species.

Description. — Rays, 20–27, averaging (27 individuals) 24; about 53 (47–60) per cent of ray free. R = 30–60 mm.; r = 15–30 mm. Breadth of ray at base, 4–7 mm. R = 7–8 br. Rays somewhat flattened, or a little arched abactinally, rather angular, with blunt and rounded tips. Disc moderately large, flat, or a little arched. Abactinal skeleton rather stout and with small meshes. Abactinal spines numerous, small, rather slender, and not at all capitate, without definite arrangement on disc, but appearing in distinct series on rays. Marginal series of ray contain largest abactinal spines; median series somewhat smaller. Between marginal and median series, a lateral series of very small spines is often present. The marginal series tend to converge as they pass on to the disc, and thus separate the median and lateral rows from the spinulation of the disc; this arrangement is usually evident, but is much more marked in some specimens than in others. — Sides of ray with two or three series of long, compressed spines. Actinal surface essentially as in *helianthus*. Pedicellariae fairly common, especially towards tip of rays abactinally, chiefly forcipate; large forficate ones rather rare and smaller than in *helianthus*. Madreporite usually simple and convex, rarely flattened and fragmented. — Color of abactinal surface deep purplish-black; spines whitish; actinal surface and madreporite yellow; pedicels brownish-yellow.

Range. — Juan Fernandez Islands (M. C. Z.).

Remarks. — This interesting little species is remarkably well characterized, and can be very readily distinguished at a glance. Perrier (**1875**) thought it possible that it was the young of *helianthus*, but the large series of specimens collected by the "Hassler" has made it possible to show that this is not the case. Young specimens of *helianthus* have more than 30 rays by the time they are 70 mm. in diameter, whereas the largest specimen of *canopus*, 120 mm. in diameter, has only 20, and there is only one specimen with as many as 27. The difference between *canopus* and a young *helianthus* in the abactinal spinulation is well shown on plate **3**. Finally, it is important to note that in the larger specimens of *canopus* the reproductive organs are fully developed, showing their sexual maturity in spite of their small size. An interesting point with reference to this species is that 17 of the specimens (or more than 60 per cent) have an even number of rays, whereas in *kubiniji* and *multiradiatus*, the two other species with relatively few rays, only 41 out of 127 (or less than 33 per cent) have an even number. Now in *helianthus* 56 per cent have an even number of rays, and it would seem as though the condition in *canopus* is further confirmation of the view that this

little species is more nearly related to *helianthus* than to the species with relatively few rays.

Material examined: — 27 specimens, Juan Fernandez, M. C. Z. collection.

Heliaster multiradiatus (Gray).

Plate 4, Fig. 1.

Asterias multiradiata Gray, 1840.
Heliaster multiradiatus Dujardin and Hupé, 1862.
Heliaster multiradiata Verrill, 1867.

Description. — Rays 21–27, averaging (10 individuals) 23.8; about 60 (50–70) per cent of ray free. R = 60–100 mm.; r = 25–47 mm. Breadth of ray at base, 6–12 mm. R = 8–10 br. Rays more or less distinctly cylindrical, sometimes slightly flattened and rather angular abactinally, especially near middle. Disc moderate, more or less distinctly and abruptly elevated at centre. Abactinal skeleton moderately stout, reticulate, with rather small meshes. Abactinal spines not very numerous, about 10–16 per sq. cm., moderately stout, high, especially on disc, and more or less cylindrical, sometimes thickened, clavate or capitate at the summit. No evident arrangement on disc, but on rays a median series, with a lateral and marginal series on each side (five series in all), can generally be clearly distinguished, though sometimes there appear to be six series, or again only four. The largest spines are on disc and at base of ray, the smallest near tip of ray; the median series is usually somewhat larger than the others. — Sides of ray with two series of compressed spines, which are usually shorter than the adjoining actinal series. Actinal surface much as in *helianthus* and the other species, but the adambulacral armature is somewhat different, for the large spines do not alternate with small ones, but are practically uniform in size, and on many of the plates a second smaller spine stands on the inner edge, thus making the armature of the furrow double. In some specimens nearly the whole series is double, while in others two spines are to be found only on scattered plates. Occasionally three spines occur on a single plate. The larger spines are about three millimeters long, quite slender, and nearly cylindrical. Outside of the adambulacral series are two rows of actinal spines, the lower of which consists of spines longer and heavier than the adambulacral, while the upper are somewhat smaller. These two series, but especially the lower, extend inward well onto the interbrachial area. Towards the tip of the ray all of the large spines become greatly reduced, so that the 15–17 series which surround the tip are of nearly uniform size, though the adambulacral and adjoining series are still distinguishably larger. Buccal depression as in *helianthus*. — Pedicels not very numerous or crowded, so that they are not truly quadriserial at any point. Pedicellariae mostly small, numerous, especially on abactinal side of rays near tip; sometimes very large forficate pedicellariae occur on the actinal surface. Madreporite rather small, usually simple and convex, very rarely showing any trace of fragmentation. — Color of abactinal surface, light gray, yellowish, or whitish, irregularly blotched with dark gray or blackish; on the rays the dark blotches appear as irregular cross-bands; spines whitish, yellowish, or brownish; actinal surface mostly light yellow or whitish, but interbrachial areas and outer side of large adambulacral spines on proximal half of rays tend to become blackish, and in most specimens there is a striking contrast between the inner and the

outer sides of the adambulacral series, and between the basal and distal halves of each adambulacral spine, on its outer side; oral spines usually dark, at least on aboral side; madreporite white or yellow.

Range. — Hood's Island (Gray); Chatham Island (U. S. N. M.); Albemarle Island (M. C. Z.); Charles Island (M. C. Z.). Confined to the Galapagos Islands. — The reported occurrence of this species in the Hawaiian Islands is to be accounted for as follows: — In 1867 Verrill described a specimen of *kubiniji*, which he said was obtained with other Panamic species from Mr. Pease at the Sandwich Islands, but probably came from Acapulco or Mazatlan, Mexico. Perrier (**1878**), ignoring or failing to understand the latter half of Verrill's statement, gives "Iles Sandwich" as one of the localities for *kubiniji*. Sladen (**1889**), accepting Rathbun's view that *kubiniji* is a synonym of *multiradiatus*, and also evidently accepting Perrier's list of localities at its face value, gives Sandwich Islands as a habitat of *multiradiatus*. On the strength of Sladen's word, Fisher (**1906**) includes *H. multiradiatus* in his list of Hawaiian starfishes, but he very properly expresses serious doubt as to any Heliaster occurring at Hawaii.

Remarks. — Verrill (**1867**) in speaking of *kubiniji* pointed out that Gray's description of *multiradiatus* did not fit specimens from Mexico, and the two species were regarded as distinct until Rathbun (**1887**) compared two specimens from Chatham Island with a large series from Mexico, and reached the conclusion that they were identical, and that *kubiniji* was therefore a synonym of *multiradiatus*. Sladen (**1889**) adopted that conclusion, and it has since been very generally accepted. In 1895 Leipoldt, referring to five specimens from Chatham Island, describes what he calls their "peculiar" coloration, his specimens agreeing well with typical *multiradiatus*, the coloring of which had never previously been described, for curiously enough neither Gray nor Rathbun make any reference to the color. Dr. Rathbun has kindly sent me, among the Heliasters from the National Museum, the two specimens from Chatham Island, on which his opinion was based. I find they agree in all essentials with the other Galapagos specimens before me, and there will be no question that to them belongs the name *multiradiatus*. After a comparison of these specimens with a very large series of *kubiniji* from Mexico I am obliged to disagree with Rathbun's conclusion that they are all one species. No one will question the close relationship between the Galapagos and Mexican forms, and it is simply a matter of personal opinion whether it is better to emphasize the relationship by uniting them under one name, or to emphasize by distinct names the differences which have arisen in completely separated geographical areas and which are obviously and reasonably constant. The latter course seems to me preferable. The differences between the two can better be discussed under *kubiniji*, and only one or two other points need to be referred to here. Both species show great diversity in the length of the different rays in a single individual, old specimens often having only two or three rays of exactly the same length. As an illustration of this fact, the following measurements (in millimeters) of the 25 rays of an excellent specimen of *multiradiatus* may be given, beginning with the ray to the left of the madrepore and going clockwise: 72, 71, 70, 69, 51, 57, 65, 68,

64, 67, 73, 68, 71, 69, 72, 40, 42, 71, 66, 44, 75, 74, 72, 45, 66. Of the 25 rays, one is 75 mm., one is 74, one is 73, three are 72, three are 71, one is 70, two are 69, two are 68, one is 67, two are 66, one is 65, one is 64, one is 57, one is 51, one is 45, one is 44, one is 42, and one is 40 mm. long. Besides this diversity in length, it is not an easy matter to say just what proportion of the ray is free, for, while of one ray 70 per cent may be free on one side and 65 on the other, another ray may be only 50 per cent free on each side. To determine the point satisfactorily four or five of the longest rays should be measured, the measurements added together and divided by four or five, as the case may be, the quotient being the average R. Then measure the free portion on each side, add, and divide by eight (or ten), the quotient being the average free portion. Dividing this by the average R gives the percentage of ray that is free. Adopting this plan for one of the best specimens of *multiradiatus*, we get these figures: —

$$83 + 83 + 82 + 76 + 80 = 404 \text{ mm.} \div 5 = 80.8 \text{ mm.} = \text{R.}$$

$$50 + 51 + 50 + 53 + 46 + 44 + 47 + 48 + 46 + 45 = 480 \text{ mm.} \div 10 = 48 \text{ mm.} = \text{free portion.}$$

$$48 \div 80.8 = .59 \therefore 59 \text{ per cent of ray is free.}$$

With the other five species of Heliaster it is not necessary to go to such trouble, as all the rays are, in normal specimens, of approximately the same length. — The specimens of *multiradiatus* from Chatham Island are notable for the large abactinal spines, which are as heavy as in most specimens of *kubiniji*. One of the specimens is further remarkable for the fact that although very large (R = 100 mm.) there are only 15 developed rays and two of these are very small; there is also a very rudimentary ray 6 mm. long, at one point on the abactinal surface. Careful examination shows that this individual was at some time badly injured, nearly bisected in fact, and has only imperfectly made up its loss.

Material examined: —

3 specimens.	Albemarle Island.	Leland Stanford Jr. Univ. collection.	
5 "	Charles "	M. C. Z.	"
2 "	Chatham "	U. S. N. M.	"
1 specimen	Albemarle "	M. C. Z.	"
11 specimens.	3 localities.		

Heliaster kubiniji Xantus.

Plate 4, Fig. 2; Plate 5, Fig. 2; Plate 6, Fig. 1: Plate 7, Figs. 8–10; Plate 8, Figs. 1–6.

Heliaster kubiniji Xantus, 1860.
Heliaster Kubiniji Verrill, 1867
Heliaster Kubinjii Lütken, 1871.
Asterias Kubinjyi Lütken, 1872.
Heliaster Kubingii Rathbun, 1887.
Heliaster Kubinijii Ives, 1889.

Description. — Rays 21–28, averaging (90 adults) 23; about 47 (40–55) per cent of ray free. R = 60–107 mm.; r = 30–60 mm. Breadth of ray at base, 6.5–15

mm. R = 6½–9½ br. Rays more or less cylindrical, sometimes slightly flattened and angular abactinally, but usually tapering more sharply than in *multiradiatus*. Disc moderate, more or less distinctly and abruptly elevated at centre. Abactinal skeleton and spines as in *multiradiatus*, but median and lateral series of spines on ray more distinct, usually with more numerous, and stouter and more capitate spines. Space between lateral and marginal series wider than between lateral and median, and usually conspicuous. Spines on disc often very stout and much thicker at top than at base, sometimes two to two and one half millimeters across, not infrequently with the broad tip distinctly concave and more or less notched in the margin. — Sides of ray and actinal surface as in *multiradiatus*, except that the spines of the series outside the adambulacral row are much stouter, and are often compressed and truncate or even clavate. The actinal aspect of the ray is thus quite as different in the two species as the abactinal. Pedicellariae, pedicels, and madreporite, as in *multiradiatus*. — Color of abactinal surface deep purplish-black; spines more or less deep yellow; pedicellariae yellowish, often so numerous as to give the distal half of the ray a nearly uniform yellow color; occasionally the rays have a banded appearance as in *multiradiatus*, but not so distinct as in that species, and seemingly due in large part to unequal distribution of the pedicellariae; actinal surface deep yellow with pedicels very dark, often blackish; adambulacral spines often blackish at base on the outer side, and those near mouth are sometimes very dark for their whole length; madreporite deep yellow.

Range. — San Luis Gonzales Bay, Lower California; Guaymas, Mexico; and San Juan, L. C. (U. S. N. M.); Margarita Bay, L. C. (Perrier); Magdalena Bay, L. C. (Ives); Puerto Balandia, La Paz and Pichilingue Bay, L. C. (U. S. N. M.); Altata, Mexico (Lutken); Mazatlan, Mexico (M. C. Z.); Cerro Blanco, Cape St. Lucas, L. C. (U. S. N. M.); Acapulco, Mexico (M. C. Z.); and Macuoha, Nicaragua (Ives). — A specimen in the National Museum labelled "Guanajuato, Mexico," was probably purchased by the collector in that inland city at a curiosity shop. Another specimen labelled "Colorado Desert" is badly worn, as though by sand, and looks as though it might have been picked up in the desert, though how it came there would be hard to decide. — There seems to be no record for this species south of Nicaragua, so that its range is apparently confined to the western coast of Central America and Mexico, between 10° and 30° N. lat.

Remarks. — This is a very easily recognized species, as the small number of rays, free for nearly half their length, the large abactinal spines and the coloration combine to distinguish it at a glance from all, except *multiradiatus*. From that species it is separated not merely by the color, which is quite distinctive, but especially by the appearance of the rays, which are less slender, less largely free, and have stouter spines. The differences are all shown in the figures given (Plate 4), where even the contrast in color is plainly indicated. Yet *kubiniji* shows great diversity even in specimens from one locality, the spines on the abactinal surface, particularly those forming the median series on the rays, varying greatly not only in actual but in relative size. There is also much variety in the relative breadth of the rays, but it must be admitted that it is only small specimens (R = less than 70 mm.) which have the rays more than 8 times as long as thick. There is

less diversity in color, for although the rays are sometimes transversely banded, *kubiniji* is always darker than *multiradiatus*, the yellow being much deeper, often becoming quite brown. Comparatively little variation in the amount of ray that is free is shown, the very great majority of specimens having half or a trifle less.

Material examined: —

42 specimens.	Acapulco, Mexico.	M. C. Z. collection.	
20 "	Mazatlan, "	"	"
5 "	Loc.?	"	"
15 "	Cape St. Lucas, L. C.	U. S. N. M.	"
16 "	Pichilingue Bay, L. C.	"	"
5 "	"Lower California."	"	"
4 "	La Paz, L. C.	"	"
3 "	Guaymas, Mexico.	"	"
2 "	San Luis Gonzales Bay.	"	"
1 specimen	"Gulf of California."	"	"
1 "	San Juan, L. C.	"	"
1 "	"Guanajuato, Mexico."	"	"
1 "	"Colorado Desert."	"	"
116 specimens.	13 localities.		

Heliaster microbrachius Xantus.

Plate 1; Plate 7, Fig. 11.

Heliaster microbrachia Xantus, 1860.
Asterias helianthus Stimpson, 1857.?
Asterias microbrachia Lütken, 1871.
Heliaster microbrachius Leipoldt, 1895.

Description. — Rays 27–44, averaging (37 individuals) 34.7; about 25 (20–30) per cent of ray free. R = 60–125 mm.; r = 45–95 mm. Breadth of ray at base 8–15 mm. R = 7–8 br. Rays more or less flattened abactinally, tapering rather sharply to a blunt point. Disc very large, somewhat elevated in well-preserved specimens, but not abruptly so. Abactinal skeleton stout, closely reticulated, with small meshes. Abactinal spines very numerous, 35–50 or even more per sq. cm., small, usually low, more or less cylindrical and without definite arrangement. In some large specimens the spines show a slight tendency to be capitate, and in many cases they are very evidently compressed. In some individuals the spines on the rays form five fairly distinct series, and these can be followed inward for a variable distance onto the disc. At the edge of the disc the marginal series of adjoining rays are sometimes very clearly separated by a bare space about 2 mm. broad, but in full-grown specimens this arrangement is not usually distinct. — Sides of ray with two series of compressed spines. Actinal surface very much as in *helianthus*, but pedicellariae are as a rule less frequent, and the reduction of the adambulacral armature reaches its extreme, for in large specimens only every other adambulacral plate bears a spine until the distal half or even third of the furrow is reached, and even at the extreme tip of the ray it is rare to find a plate with two spines. — Pedicels rather numerous, distinctly quadriserial at the middle of the ray. — Madreporite rather small, often concave, and usually fragmented. — Color of abactinal surface purplish- or grayish-black; spines deep yellow or whitish; actinal surface whitish,

yellowish, or brownish, with pedicels much darker than spines; madreporite brown.

Range. — Asuncion Island and Cape St. Lucas, L. C. (U. S. N. M.); Margarita Bay, L. C. (Perrier); Magdalena Bay, L. C. (Ives); Lequina Bay, L. C. (M. C. Z.); La Paz, L. C. (Perrier); Altata, Mexico (Lütken); Mazatlan and Acapulco, Mexico (M. C. Z.); Panama (M. C. Z.); and Pearl Island, Panama (Verrill). — Ives (1889) lists a specimen from Chili, and there is a dried specimen in the collection of the Museum of Comparative Zoölogy labelled "Chili, Hassler Expedition." The latter agrees perfectly with the numerous dried specimens from Acapulco, collected by the "Hassler," and I have no doubt it is one of the same lot, which has received an erroneous label by mistake. It is probable that the Philadelphia specimen, if it is really *microbrachius*, is to be accounted for in a similar way. — The range of this species seems to be along the coast of Central America and Mexico between the parallels 8° and 27° N. lat., thus nearly coinciding with that of *kubiniji*, but extending somewhat further south.

Remarks. — This species is so easily recognized, when adult, that its standing can scarcely be questioned, yet the young are often quite perplexing, for even when 70–80 mm. in diameter, they may have the rays quite long and slender, and free 30–35 per cent of their length. The small, slender, and numerous abactinal spines, however, make even these young ones recognizable. There are usually 35 or 36 rays, and I have seen only one specimen with more than 40, though curiously enough that one has 44. There are only two specimens before me with less than 30 rays, and of these the one with 27 is not quite full-grown, as R is less than 60 mm.

Material examined: —

32 specimens.	Acapulco, Mexico.	M. C. Z. collection.
1 specimen.	Lequina Bay, L. C.	" "
1 "	Mazatlan, Mexico.	" "
1 "	"Panama, Pacific side."	" "
1 "	"Pacific Coast of Mexico."	" "
1 "	"Chili."	" "
1 "	La Paz, L. C.	U. S. N. M. "
2 specimens.	"West Coast Central America or Mexico."	" "
40 specimens.	8 localities.	

Heliaster cumingii (Gray).

Plate 5, Fig. 1.

Asterias Cumingii Gray, 1840
Asterias solaris Carpenter, 1856.?
Heliaster Cumingii Dujardin and Hupé, 1862.
Asterias Cummingii Lütken, 1872.
Heliaster cumingi Clark, 1902.

Description. — Rays 32–40, averaging (34 adults) 35.6; about 23 (15–30) per cent of ray free. R = 55–90 mm.; r = 40–73 mm. Breadth of ray at base, 7–12 mm.

R = 7–8 br. Rays more or less flattened, both actinally and abactinally, tapering abruptly to a blunt point so that the free portion is nearly triangular; the length of the triangle is a little greater than the breadth, while the distance between the tips of any two rays about equals the breadth of a ray. Disc very large, somewhat elevated at the centre but very gradually. Abactinal skeleton very stout with small meshes. Whole abactinal surface covered more or less uniformly, but not very thickly (15–20 per sq. cm.), with nearly cylindrical, rather stout spines, one to two millimeters long. These spines are not usually capitate, but in some specimens many of them are. On the margin of the disc and bases of the rays, the spines show some tendency to arrangement in radial series with three series to a ray, but when this arrangement is most evident, the spines in each series are noticeably few and those in the lateral series are very conspicuous. — Sides of ray with one or two series of compressed spines. — Actinal surface much as in *helianthus*, but the interbrachial areas are more extensive and have numerous papulae. Adambulacral and other spines more or less variable, not essentially or constantly different from those of *helianthus*; owing to the greater fusion of rays, and consequent increase of the interbrachial areas, the series of spines outside the adambulacral extend further inward. Buccal depression and membrane as in *helianthus*. Pedicellariae very small, both forficate and forcipate present, but the latter are more abundant and are most abundant on rays abactinally. The pedicellariae are infrequent, and often seem to be entirely wanting on the actinal surface. — Pedicels in a zigzag row on each side of the ambulacrum, so crowded near middle of ray as to be quite distinctly quadriserial there. — Madreporite as in *helianthus*. — Color of abactinal surface deep bluish-black; spines (at least at tip) light brown, yellow, yellowish, or whitish; actinal surface whitish or yellowish, with pedicels darker than spines and papulae; madreporite brownish or blackish.

Range. — Hood's Island (Gray); Chatham Island (U. S. N. M); Abingdon Island (U. S. N. M.); Albemarle Island (M. C. Z.); Charles Island (M. C. Z.). — This species is confined to the Galapagos Archipelago, and apparently occurs throughout the group.

Remarks. — As the type of *cumingii* is lost, it would be impossible to decide to what form that name ought to be applied, were it not that the locality given by Gray, with his brief description, leaves no doubt that the short-rayed Heliaster of the Galapagos is the species he had before him. As Gray's description is so brief, it was very natural that Verrill (**1867**) should say of his Peruvian specimens that they "are, perhaps, the species described by Gray." When Peruvian and Galapagian specimens are laid side by side, however, the difference between them is usually very noticeable, and, as previously stated, I have felt justified in calling them by different names, for the following reasons: — (1) The differences between them are obvious and uniformly associated with locality. (2) These differences are quite constant, and connecting forms are wanting or very rare. (3) The geographical isolation of the Galapagian form is very complete, Heliaster being so exclusively littoral. (4) In no other way can the differentiation of the Galapagian Heliasters be so well emphasized. Nevertheless it is freely admitted that there is room for difference of opinion as to the wisdom of this course, for the probable existence of connecting links among Galapagian specimens would cause

some zoölogists to make use of a subspecific name, while others might not consider the differences sufficiently great and constant to warrant any attempt to distinguish the two forms by name. Although the large series of specimens before me, 101 in all, have made it possible to compare the two forms very carefully, the only apparent connecting links I have seen are from the Galapagos. None of the 53 Peruvian specimens show any intermediate characters or offer any difficulty in assigning them to the mainland form. Of the 48 Galapagian specimens, those (6) in the collection of the Leland Stanford Junior University are all unmistakably *cumingii*, and the same is true of five of those in the collection of the Museum of Comparative Zoölogy. There are two young ones, however, in the latter collection, one 44 mm. in diameter, the other about 80, which are less easily determined. The former is of course too young to show any specific characters clearly, while the larger one has the abactinal spines coarser and more nearly capitate than in most Galapagian specimens. However, as Rathbun (**1887**) has pointed out, the young quite commonly have more capitate spines than the adults. Of the 38 specimens of Heliaster, supposedly from the Galapagos Islands, sent me from the National Museum, two are evidently *multiradiatus* (as already mentioned) and 17 are typical *cumingii*, while four others are too young to show specific characters. Of the remainder, nine are evidently *cumingii*, but resemble the Peruvian species in the conspicuously capitate spines, especially along the margins of the rays. The other six specimens demand a special word for each.

1 and 2. Under No. 21947 are two specimens, one of which seems to be a young *helianthus* and has been referred to under that species. The other is similarly labelled from an unknown locality, but is much larger, 150 mm. in diameter. It is apparently *cumingii*, though the spines on the abactinal surface of the rays are decidedly capitate. It probably came from the Galapagos.

3. Under No. 15523 is a young individual, about 72 mm. in diameter, labelled "Heliaster cumingii Gray. Chatham Island, Galapagos. Dr. W. H. Jones, U. S. N." It seems to be correctly identified, but the rays are free for an unusual proportion (35 per cent) of their length, giving the specimen a peculiar appearance, somewhat like *helianthus*.

4. No. 15524 is a large specimen, about 145 mm. in diameter, labelled "Chatham Island, Galapagos," and bears a striking resemblance to *microbrachius*. It has been so well and fully described by Rathbun (**1887**) that no description need be given here. This individual represents the extreme development of the peculiar characters of *cumingii*, except that the abactinal spines are unusually numerous.

5 and 6. Under 21948 are two specimens, about 145 mm. in diameter, concerning which we have only the information that they were collected by the "Albatross" in 1888, "Loc.?" One of them is very similar to the Peruvian form, as the abactinal spines are very numerous, while the other, although similar, is more like Galapagian specimens. If these individuals are from the Galapagos Islands, they are apparently connecting links with the mainland form.

The young of *cumingii* not only have the free portion of the rays relatively longer than in the adult, but the abactinal spines are lower, stouter, and more capitate. Specimens under 75 mm. in diameter do not show the specific char-

acters clearly, and cannot always be distinguished certainly from mainland Heliasters of the same size. So far as the material at hand is concerned, the specimens from the different islands of the archipelago are quite indistinguishable, with the single interesting exception of the specimen from Abingdon Island. This individual is not adult, but has 35 rays and is unusually well preserved. The rays are remarkably slender, much as they are in some very young specimens of *microbrachius*. When compared with a specimen of the same size from Charles Island, the peculiarities of this Abingdon Island individual are well brought out.

Locality of Specimen.	R.	Free portion of ray.	Per cent free.	Breadth of ray at base.	Breadth in R.	Breadth in free portion of ray.
Charles Island	46 mm.	10 mm.	22	6 mm.	7.7 times	1.6 times
Abingdon Island	44 "	11 "	25	4 "	11 "	2.7 "

Material examined : —

6 specimens.	Albemarle Island.	Leland Stanford Jr. Univ.	Collection.
25 "	" "	U. S. N. M.	"
1 specimen.	" "	M. C. Z.	"
1 "	Abingdon "	U. S. N. M.	"
6 specimens.	Charles "	M. C. Z.	"
6 "	Chatham "	U. S. N. M.	"
?3 "	Loc.?	"	"
48 specimens	5 localities		

Heliaster polybrachius, sp. nov.

Plate 2, Fig. 2; Plate 7, Fig. 12; Plate 8, Fig. 8.

Heliaster Cumingii Verrill, 1867a, p. 291; 1867b, p. 33, line 10, 334 and 344.
Perrier, 1878, p. 11 and 99.
Leipoldt, 1895.

Description. — Rays 31–43, averaging (38 adults) 37.1; about 18 (14–23) per cent of ray, free. R = 55–90 mm.; r = 45–77 mm. Breadth of ray at base, 9–11 mm. R = 6–8 br. Rays much as in *cumingii*, but free portions stouter as a rule, with more convex sides and blunter tip. Disc as in *cumingii*, but abactinal spines much more numerous, especially on the region where disc and rays join, 25–50 per sq. cm. Marginal series of spines on rays very distinct, but not usually noticeably larger than other abactinal spines. All of the abactinal spines are commonly low, of nearly uniform height, and more or less distinctly capitate.[1] Actinal surface as in *cumingii*, but pedicellariae are commonly abundant among the adambulacral and adjoining spines. Pedicellariae all small, as in *cumingii*. Buccal depression, pedicels, and madreporite also as in *cumingii*. — Color of abac-

[1] Leipoldt (1895) refers to a specimen in which the abactinal spines were three millimeters high, but none of the specimens before me have any over two, and they are commonly about one millimeter high.

tinal surface dull greenish, blackish, or black, often variegated with yellowish blotches ; sometimes the appearance is that of a yellowish background with a few small blackish blotches ; spines and actinal surface yellowish ; pedicels and madreporite brownish.

Range. — Zorritos, Peru (Verrill) ; Payta, Peru (M. C. Z.) ; Chili (M. C. Z.). — The distribution of this species seems to be curiously limited, for while it appears to be very common at Payta, Zorritos is the only other port from which it is recorded. Aside from the specimens from Payta, there is a single poor and old specimen in the Museum of Comparative Zoölogy labelled " Chili," but nothing further is known of its origin.

Remarks. — The differences between this species and the preceding may be briefly summarized as follows : — In *polybrachius* the rays are more numerous, averaging more than 37 as against 35.6 in *cumingii*, and the free portion is shorter, stouter, and more bluntly pointed ; the abactinal spines are much more numerous (25–50 per sq. cm. where thickest), lower and more capitate, and pedicellariae are usually abundant on the actinal surface, while in *cumingii* they are often wanting ; the color of *polybrachius* is often lighter than that of *cumingii*, and the Peruvian specimens are frequently variegated abactinally with yellowish. The most obvious of these differences are well brought out in the figures given on plate **2**. Doubtless there is room for wide difference of opinion as to the significance of these differences, and whether they are important enough to entitle the Peruvian form to a separate name. There are three possible courses, any one of which we might follow : — (1) We might call the Peruvian specimens *cumingii*, and simply point out the features in which they differ from Galapagian specimens ; (2) we might call them a subspecies of *cumingii*, and make use of a trinomial name for them ; (3) we might regard them as a distinct species. I have already given (p. 52) the reasons which lead me to consider the third of these possible courses the best, but I am free to admit that *polybrachius* and *cumingii* are so closely related that were they both found on the same coast I should consider it unwise to attempt to separate them. It seems to me clear, however, that one is an offshoot of the other, and the facts already given under *cumingii* with reference to the variability of the island specimens seem to show that that species is the offshoot from *polybrachius*, as the geographical distribution of the two forms would lead us to expect. The offshoot, however, is the one which has borne a name for over sixty years, while the parent stock has remained nameless. In selecting a name for it *polybrachius* has been chosen because the average number of rays is greater than in any other species of Heliaster.

Material examined : —

51 specimens.	Payta, Peru.	M. C. Z. Collection.
1 specimen.	" Peru."	" "
1 "	" Chili."	" "
53 specimens.	3 localities.	

The Number of Rays and the Order of their Succession.

The large number of rays in Heliaster is one of the most interesting features of the genus, but owing to the scarcity of material almost nothing has been done in the way of investigating the amount of variability in this character or the order in which the successively new rays appear. In 1872, Lütken showed that there is no correlation between size and the number of the rays in Heliaster, after a certain size (about 100 mm. in diameter), which we may call that of maturity, is reached; that is to say, very small specimens have a relatively small number of rays and this number increases with increasing size, only until the animal is approximately mature, after which there may or may not be a continued addition of new rays. Having only 15 specimens (*H. helianthus*) for comparison and only one of those less than 75 mm. in diameter, Lütken did not attempt to discuss the original number or the sequence of the rays, but it is hard to understand how any one could examine his data and not see that the number of rays certainly does increase after larval life and even after the starfish is 50 mm. across. Rathbun (**1887**) in his report on Heliaster makes statements in regard to *cumingii* which indicate his belief that the rays increase in number with increasing age (see p. 441, line 8). In spite of these writers, however, Perrier, as late as 1893, states that Labidiaster is the only starfish in which additional rays develop after the larval period is passed and the adult form assumed. In 1895, Leipoldt referred to the presence of two young rays in a specimen of *H. cumingii* (=*polybrachius*), about 50 mm. in diameter, which had otherwise only 24 rays. In 1900, Ritter and Crocker showed conclusively that Pycnopodia begins its post-larval life with only six rays, and that the additional 14–18 rays are in process of appearance, normally in pairs, until well into adult life. There can no longer be any question therefore that starfishes with twenty or more rays begin their post-larval life with a much smaller number and continue to add new rays for an undetermined period. Consequently specimens of Heliaster with fewer than twenty rays are sure to be met with and if age and size are disregarded, we cannot assign on *à priori* grounds the minimum number which a starfish of this genus may show. The smallest specimen among the 346 examined measures only 20 mm. in diameter, and I can find no published record of any specimen nearly as small. It is a young individual of *kubiniji* (U. S. N. M. No. 21950) from Lower California and has 12 rays, eight well developed, three much smaller and a twelfth barely started. With it are two other specimens, 25 mm. in

diameter, with 13 and 14 rays respectively. Another specimen of the same species from Guaymas, Mexico (U. S. N. M. No. 21949) is also 25 mm. in diameter but has 15 rays. A larger one (110 mm.) from the same place (U. S. N. M. No. 21941) has only 17 rays, of which two are very small; but this specimen like the individual of *multiradiatus* referred to on p. 48, which, although 200 mm. in diameter, has only 16 rays, is almost certainly the victim of an unusual accident. A specimen of *kubiniji* 64 mm. in diameter, from Acapulco, Mexico, (M. C. Z., No. 1171), has only 18 rays. I have neither seen, nor found a record of, a specimen of any species with 19 rays. The largest specimen of *canopus*, 120 mm. in

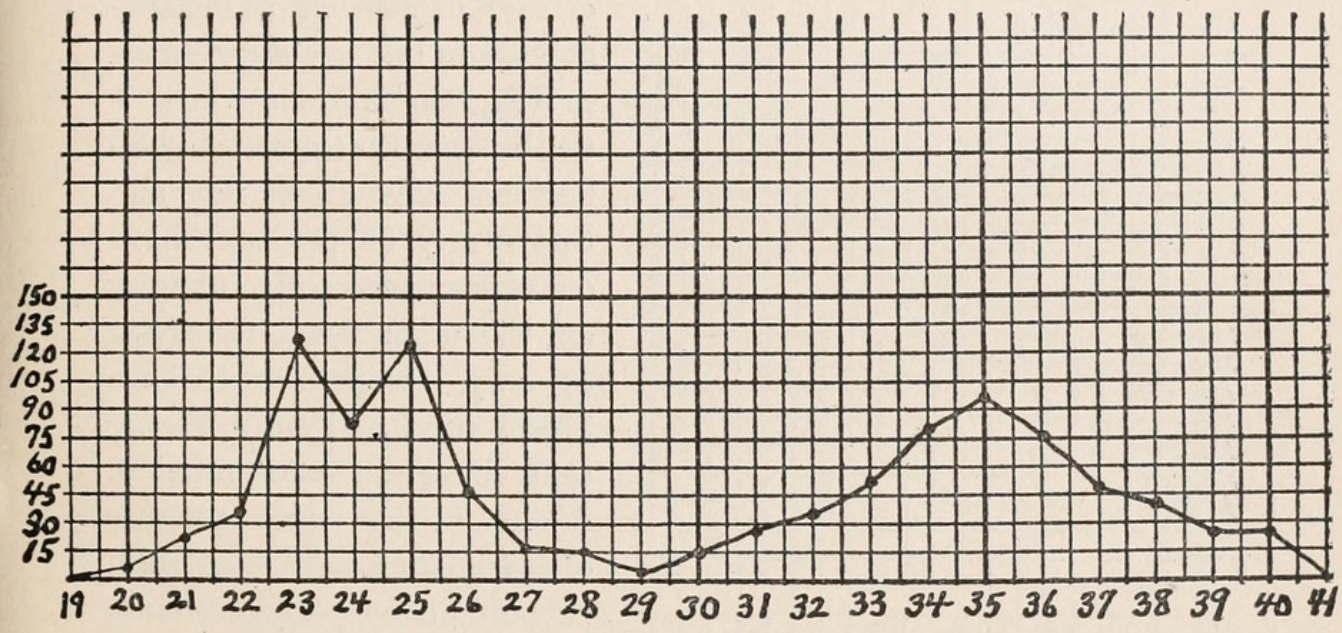

DIAGRAM 1[1].

To show the relative abundance (per thousand, regardless of species) of Heliasters with 20–40 rays. Based on 335 individuals.

diameter, and the smallest of *polybrachius*, 40 mm., have only 20 rays each. Above 20, all numbers occur up to 44, but I have seen no specimen with 41. There are eight specimens with 40 rays each (five of *polybrachius*, one of *cumingii*, one of *microbrachius*, one of *helianthus*); one *polybrachius* has 42, one *polybrachius* has 43, and one *microbrachius*, only 140 mm. in diameter, has 44. The number of specimens with from 20 to 40 rays inclusive is 335 and Diagram 1, based on this series, shows the number of individuals in a thousand having any given number of rays between 19 and 41.

A single glance at this diagram shows that there are two groups of Heliasters, one of which tends to have 23–25 rays, and the other 35, and

[1] In this and all the following diagrams: Horizontal lines show the number of individuals. Vertical lines show the number of rays.

that the two are almost completely separated from each other, since individuals with 29 rays are very rare. It is also clear that the group with fewer rays varies less from the normal number than does the other. It is worth while therefore to examine the species separately (omitting the obviously young) to bring out the difference in variability. As *cumingii* and *polybrachius* are so closely allied, they may be considered together, especially as there is no essential difference between them when tabulated separately. We will omit *multiradiatus* altogether as the number of available specimens is too few to make a reliable tabulation possible.

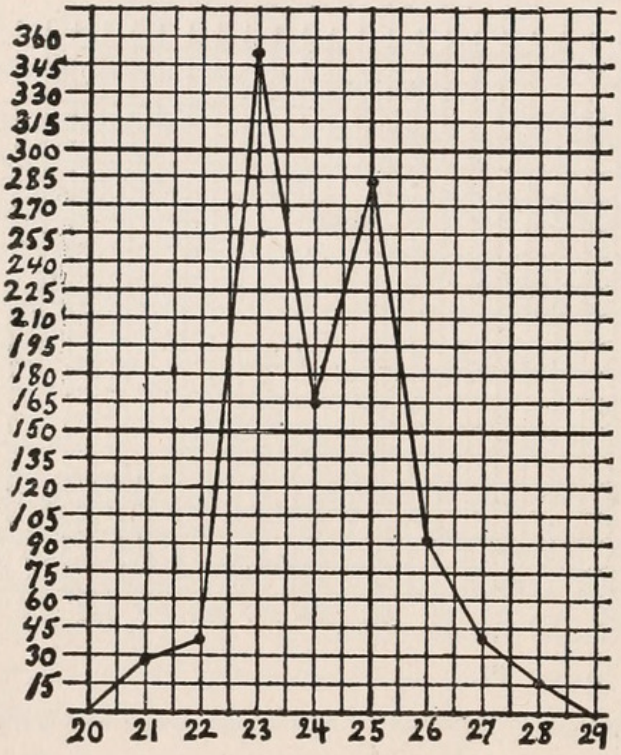

DIAGRAM 2.

To show the relative abundance per thousand, of *H. kubiniji* with 21-28 rays. Based on 110 individuals.

The diversity in the number of rays in *kubiniji* is remarkably slight and is clearly shown in Diagram 2, from which it will be seen that practically 80 per cent have 23–25 rays and that nearly 69 per cent have an odd number. In *canopus* on the other hand (Diagram 3) only 48 per cent, have 23–25 rays, and only 37 per cent have an odd number. Although the small number of specimens available for comparison undoubtedly accounts in part for these peculiarities of *canopus*, it can hardly be doubted that this species shows a much greater tendency to variability in the number of rays than does *kubiniji*. In *helianthus* (Diagram 4) the number of rays varies from 30 to 40 but 64 per cent have 34–36 rays, while only 46 per cent have an odd number. In *cumingii* and *polybrachius* (Diagram 5) the number of rays ranges from 29–40 [1] and only about 36 per cent have 34–36, while almost exactly half have an odd number. The great variability of these two short-rayed species is especially notable in view of the fact that *microbrachius*, which is also short-rayed, agrees strikingly with *helianthus*, 63 per cent of the

[1] The two specimens of *polybrachius* with 42 and 43 rays respectively are omitted from the diagram.

specimens having 34–36 rays, and only 42 per cent have an odd number.

Turning now from the amount of variability to the method of formation of new rays and the order of their appearance, we are favored by the fact that in Heliaster the stomach is provided with five pairs of conspicuous muscles attached to the ambulacral plates of five of the rays, as in Asterias, and comparison of numerous specimens of all ages leaves no doubt that these five rays are, as one would naturally suppose, the original rays of the starfish on first assuming the adult form. This arrangement is strikingly different from that shown by Pycnopodia, where Ritter and Crocker (**1900**) found that the post-larval life apparently starts with six rays. The youngest available Heliaster (*kubiniji*), 20 mm. in diameter, has 12 rays but only eight of these are at all nearly equally developed and it is fair to assume that their arrangement represents the normal condition in an 8-rayed young Heliaster. Numbering the five original rays clockwise from the madreporite, as the specimen is looked at from above, we find there is an accessory ray between rays 1 and 2, 2 and 3, 3 and 4. (Plate **8**, fig. 1). Adding now the four very young rays, in the positions where they occur, we find there are now three between 1 and 2, two between 2 and 3, two between 3 and 4, but there are still no rays between 4 and 5 or between 5 and 1 (Plate **8**, fig. 2). In another young individual (*kubiniji*) with 15 rays, we have the condition shown in fig. 3 (Plate **8**), where it may be seen that although there is now a ray between 4 and 5, 5 and 1 are still side by side. The youngest *polybrachius* has 20 rays, four of which are, however, very small; in this specimen there are three well-developed rays between 1 and 2 and also between 3 and 4, and 4 and 5, while there are only two between 2 and 3 and none between 5 and 1. On adding the four rudimentary rays, it is rather surprising to find that the conditions in the interradii 2 and 3 and 5 and 1 are not changed, but

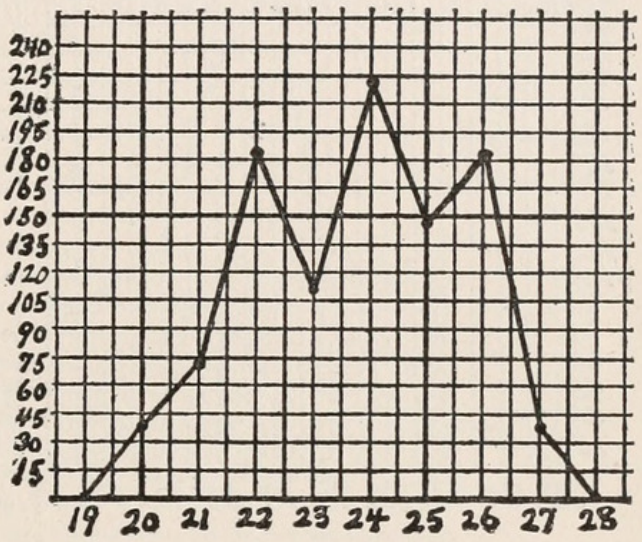

DIAGRAM 3.

To show the relative abundance per thousand, of *H. canopus* with 20–27 rays. Based on 27 individuals.

there are now five accessory rays between 4 and 5, and four in each of the interradii 1–2 and 3–4. The specimen of *canopus* with 20 rays differs only in that there are three rays in interradius 2–3, and only four in 4–5. An example of *kubiniji* with 21 rays gives the condition shown in figure 4 (Plate 8), but specimens of *canopus* with 21 rays are quite unlike this; one has six rays in 1–2, three in 2–3, four in 3–4, three in 4–5, and none in 5–1, and the other has four, three, five, four, and none, in the same order. Very similar to the latter is another *canopus* with 22 rays arranged 4, 4, 5, 4, 0. Specimens of *kubiniji* with 23 and 25 rays show the sequence given in figures 5 and 6 (Plate 8). The order 5, 5, 5, 3, 0, seems to be the normal arrangement for specimens of *kubiniji* with 23 rays, but in a specimen of *canopus*, the order is 5, 3, 5, 5, 0. With 24 rays the order in *kubiniji* is 5, 5, 5, 4, 0, while in an example of *canopus* it is 5, 3, 5, 6, 0. With 25 rays, *canopus* and *polybrachius* both agree with *kubiniji* in the symmetrical 5, 5, 5, 5, 0, and as this was found to be true of all of the six Heliasters having 25 rays, which were examined, it is fair to consider it the normal arrangement. In examples of *canopus* and *kubiniji* with 26 rays each, the additional ray occurs in interradius 1–2. In examples of the same species having 27 rays interesting conditions, undoubtedly abnormal, were found; in *canopus* (Plate 8, fig. 7) there are two rays in interradius 5–1, the only case, among 30 Heliasters examined, in which there are accessory rays in that interradius; in *kubiniji*, the stomach-muscle of 1 is missing, so that there are only four such muscles and the sequence of the rays is 9, 4, 6, 3, 0, with, of course, possible errors in the 9 and 0. After the number of rays gets beyond 26, there appears to be no uniformity in the order or position of the accessory rays, as is clearly shown by the following table: —

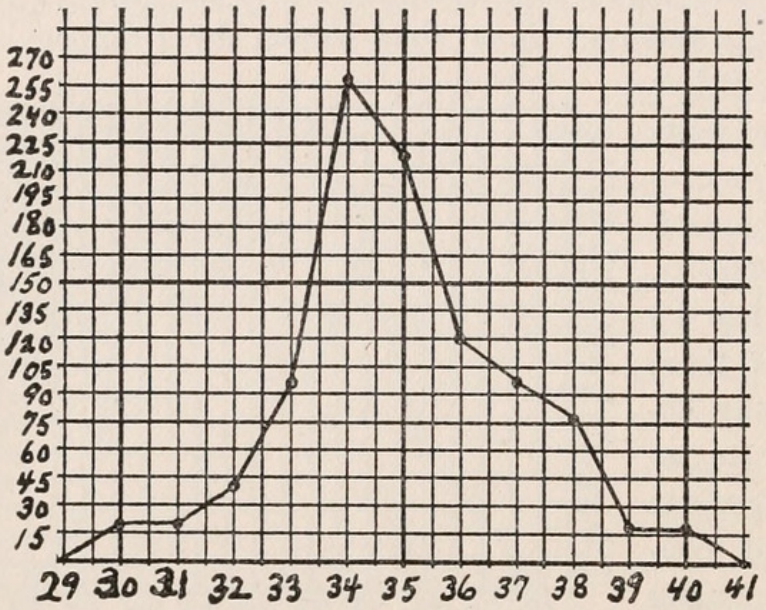

Diagram 4.

To show the relative abundance per thousand, of *H. helianthus* with 30–40 rays. Based on 50 individuals.

Species.	Number of Rays.	Sequence in the Five Interradii.
canopus	27	6, 5, 5, 4, 2. (Plate 8, Fig. 7.)
kubiniji	27	9, 4, 6, 3, 0.
polybrachius	27	5, 5, 7, 5, 0.
microbrachius	31	8, 6, 7, 5, 0.
polybrachius	31	7, 5, 8, 6, 0.
helianthus	33	8, 5, 7, 8, 0.
helianthus	34	8, 7, 7, 7, 0.
helianthus	35	8, 7, 7, 8, 0.
microbrachius	35	8, 8, 7, 7, 0.
polybrachius	35	8, 7, 8, 7, 0.
polybrachius	37	8, 7, 9, 8, 0. (Plate 8, Fig. 8.)

The first indication of a new ray in Heliaster, which can be seen without a microscope, is an internal one, simply the gradual separation of the two halves of an interbrachial wall, close to the discobrachial wall.

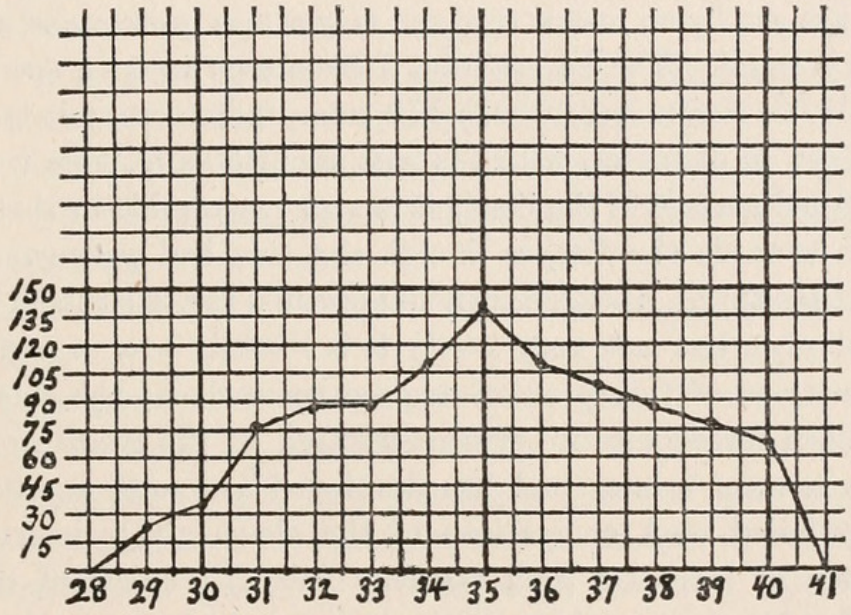

Diagram 5.

To show the relative abundance per thousand, of *H. cumingii* and *H. polybrachius* with 29–40 rays. Based on 88 individuals.

There can be little reason to doubt that the actual first step in the new ray formation is the pushing out of a bud from the outer side of the circumoral, watervascular canal, and the growth of this bud with its attendant tissues is the cause of the separation of the halves of the interbrachial wall; the bud itself becoming the radial water vessel. There is no direct evidence in support of this hypothesis, but it is reasonable, in line with the indirect evidence and open to no serious objection. After

the splitting of the interbrachial wall begins, it goes on more rapidly, if development is normal, towards the actinal surface, and the interbrachial tissues there soon separate and the pedicels of the new ray appear. The growth of the new ray forces the older rays on either side further and further apart until they are entirely separated, and the accessory ray takes its normal place between them. The growth of the new ray in length is more rapid than its increase in diameter, so that it is relatively more slender than the older rays. In many cases, owing to some obstacle, probably an unusually firm calcification of the interbrachial wall, the new ray fails to split that wall actinally and so is forced to grow upward and appear on the abactinal surface. Its subsequent growth may force the walls apart and it then settles down into its proper place and becomes a normal ray. Often, however, the interbrachial wall fails to yield and consequently the new ray is unable to develop, but remains as a rudiment on the abactinal surface, usually near the boundary between the true disc and the bases of the rays. Such rudimentary abactinal rays are by no means rare and may attain quite a size, although usually very small. The largest that I have seen is on a specimen of *cumingii* (U. S. N. M. No. 15523) 170 mm. in diameter; it is 23 mm. long and seven in diameter, with the base about 30 mm. from the centre of the abactinal surface of the disc; it is also remarkable in that the tip is turned in towards the disc, as though one side had grown very much more than the other. Usually such an abactinal ray is situated between two normal rays, but not very rarely it is directly over a normal ray. Two explanations of this position suggest themselves; the aborted ray may have been forced into its present position by the growth of one of the normal rays, or a later bud has developed a normal ray where the aborted ray failed. — A comparison of the above given description of ray formation in Heliaster with Perrier's (**1891**) account of the same process in Labidiaster reveals such similarity as to leave no doubt that the process is identical in the two genera. It may be added that Perrier's figures could be duplicated from specimens of Heliaster, were it necessary, excepting only those showing regeneration. Cases of regeneration occur in Heliaster, but are not very common. Occasionally the tip of a ray is regenerated after loss, but several specimens show broken and healed rays where no regeneration is visible. Several cases occur of apparent regeneration of a group of rays, as though a large part of one side of the Heliaster had been cut (or bitten) off and the new rays were to replace those so lost; thus in one specimen of *microbrachius*, there are 24 normal rays and 13 much smaller, obviously young rays, side by

side; and in another specimen of the same species there are 25 normal rays and ten young ones side by side.

We are now in position to answer the questions raised by Ritter and Crocker (**1900**) concerning ray multiplication in Labidiaster and to compare the process in that genus and Heliaster with what takes place in Pycnopodia. The questions may be taken up in the order in which they were asked.

(1.) *Do the new rays come in in distinct generations?* They do not, but develop entirely independently of each other. A considerable number may develop at approximately the same time, often as many as six or seven and sometimes eight or nine in *H. polybrachius*, but they show no definite relation to each other.

(2). *Do the successive rays arise at the same and definite places?* There is much evidence to show that they tend to arise in all four quadrants of the circumference of the starfish about equally, but successively rather than simultaneously. This order is by no means consistently adhered to, however.

(3). *With what number of rays does adult life begin?* In Heliaster there can be little question that the number is five. There is no evidence yet known in the case of Labidiaster.

(4). *Are the new rays disposed bilaterally?* Not as a rule; this point is discussed more fully below.

(5). *Is there a ray corresponding to ray A of Pycnopodia?* Apparently not.

The symmetry of Heliaster, referred to under question four, requires a few words of description. Perfect radial symmetry is of course out of the question, as there is only one stone-canal and madreporite, but leaving those organs and the racemose and rectal glands out of account, approximate radial symmetry is possible in Heliaster, apparently only in the 5-rayed stage; for the interradius, 5–1 rarely develops any accessory rays and never as many as the other interradii. Bilateral symmetry, however, if we except the racemose and rectal glands, is clearly shown by some individuals, but the plane of division is quite different from that which Ritter and Crocker (**1900**) show is the adult plane in Pycnopodia. For while in Pycnopodia, the madreporite lies always in the second interradius to the left of the posterior half of the line of division, in Heliaster the only possible plane of symmetry is through the madreporite. In Pycnopodia moreover the plane is determined by the position of the accessory rays and every normal individual is bilaterally symmetrical (approximately of course), while in Heliaster the accessory rays have no

definite relation to the plane and only certain, relatively few, individuals reveal the symmetry. Theoretically, of course, any Heliaster with an odd number of rays show this bilaterality but in none of those examined was it shown, except those which had at least 25 rays. In all those with just 25 rays, the plane of symmetry, with 10 accessory rays on each side, is clearly indicated. Above 25, any odd number of rays may be accompanied by bilateral symmetry but it is not commonly, for of the 11 specimens tabulated on page 61, it will be seen that only one, a *helianthus* with 35 rays, can be considered truly symmetrical.

It appears therefore that in Heliaster, the formation of new rays is fundamentally different from that in Pycnopodia. This is well brought out by a comparison of figure 1, plate **8**, with Ritter's and Crocker's (**1900**) figure 1, plate **13**. In Heliaster the first three new rays are distributed one each in the three successive interradii to the left of the one in which the madreporite lies, while in Pycnopodia all three (counting A as the first accessory ray) lie in the single interradius 1–2. It is hard to believe that the two methods have anything in common, the ray A is so conspicuous and plays such an important part in Pycnopodia. In Heliaster the first accessory ray probably (?) appears in interradius 1–2, the second in 2–3, and the third in 3–4. Then apparently, as is shown by figure 2, plate **8**, a new ray arises in 1–2, another in 2–3, another in 3–4, and then another in 1–2. Later on the process begins in interradius 4–5 and by the time 25 rays are formed, it is going on at about an equal rate in those four interradii. As we have already seen, it is only very exceptionally that the interradius 5–1 takes part in ray formation. It is not unfair to interpret the facts here brought out as showing that the formation of new rays in Heliaster follows this rule : —

The process begins in interradius 1–2, *soon after larval life ends, and goes on rapidly there until two or three accessory rays are formed, the similar activity of interradii* 2–3, 3–4, *and* 4–5 *following in order. At the time the process begins in* 4–5, *the rate of development in* 1–2 *has begun to decrease, and by the time there are* 25 *rays, each of the four interradii has formed five accessory rays, and the rate of development has greatly decreased and become approximately equal in them all. Subsequent formation of new rays follows the same general order, the twenty-sixth ray appearing in interradius* 1–2, *but after* 35 *rays are formed further development is sporadic.*

Of course it is not claimed for a moment that the above statement is a "law" governing ray formation in all Heliasters, as the material examined has been too scanty to determine how generally any such rule is

followed. But it can hardly be questioned that it indicates the usual course and is a natural deduction from the facts already given. The process is almost certainly continually modified by physiological conditions, one of which, at least, after the individual is well grown, is very possibly the amount and rate of calcification in the different interradii. Such unknown factors often cause some striking deviations from the suggested rule, as in the two cases previously mentioned, a *canopus* with 24 rays, where interradius 2–3 has only three accessory rays, while 4–5 has six, and a *polybrachius* with 20 rays, where interradius 2–3 has only two accessory rays and 4–5 has five.

If the above suggested rule is the usual course, we should expect to find that in specimens with from 21 to 30 rays, those with an odd number would predominate, but that in those with from 31–40 rays, there would be less tendency to an odd number, and the chances of odd or even would have been about equal. And such proves to be the case; for of 163 mature specimens having 21–30 rays, 98 or 60 per cent have an odd number, while of 170 specimens with 31–40 rays 86, or almost exactly half, have an even number. It is interesting in this connection to call attention to the fact mentioned on p. 45, that *canopus* has a marked tendency to an even number of rays, although they range from 20 to 27. If *canopus* is omitted, there are 89 out of 136 specimens with 21–30 rays, or 66 per cent which have an odd number. The condition in *canopus* is difficult to account for but it is apparently associated with a peculiar tendency in interradius 2–3 to fall behind in the production of new rays. In all of the six specimens examined with from 20–24 rays, that interradius has a smaller number of rays than 3–4, and in four of the six, it has the smallest number of any of the four interradii. In none of the ten specimens of *canopus* examined does interradius 2–3 have a larger number of rays than 3–4. The cause for this curious condition is obscure and we need make no attempt here to determine it, but it seems clear that it accounts for the tendency to an even number of rays in *canopus*. It may be added that there is no very obvious reason why interradius 5–1 develops no accessory rays, although it is very probable that the presence of the stone-canal and axial organ in that interradius is associated with the cause.

In the light of all the facts here brought out with reference to ray formation in Heliaster, it is, to say the least, unfortunate that Ritter and Crocker (**1900**) should have said (p. 263): — "The inconstancy and irregularity of the phenomena of new ray formation certainly finds no support in what takes place in *Pycnopodia* and, as we have shown,

the process will probably be found to be perfectly definite in *Heliaster* also."

The Relationships of Heliaster.

So obvious are the resemblances between Heliaster and Asterias, that such students of starfishes as Müller and Troschel (**1842**) and Lütken (**1872**) declined to separate them generically and even Gray (**1840** and **1866**) only proposed Heliaster as a subgenus. Dujardin and Hupé (**1862**) and Perrier (**1875**), however, considered the multiradiate forms entitled to full generic rank, but very closely related to Asterias. Viguier (**1878**), on making a careful study of the skeleton, reached the conclusion that Heliaster is not only generically different from Asterias but that it actually is entitled to rank as a family, distinct from the Asteriidae, which he called the Heliasteridae. Since the publication of his paper, Viguier's opinion has been almost uniformly adopted and the Heliasteridae has been accepted as a natural family. The examination of the large amount of material accessible to me has led me to feel that the question needs to be reopened and the evidence re-examined.

Viguier gave six characters upon which the family Heliasteridae is based and we will consider them in the order in which he presents them.

1. *The large number of rays, even more than in Pycnopodia.* This is an obvious and useful characteristic, but as Labidiaster has full as many rays as those Heliasters which have the largest number; as Pycnopodia scarcely falls short of the Heliasters which have the smallest number; and as there is as great a difference between *H. polybrachius* and *H. kubiniji*, as there is between the latter and *Coscinasterias calamaria* (Gray), it does not seem as though much stress could be laid on this point.

2. *The extended coalescence of the rays.* This is also an obvious character but it is not wholly confined to this genus for in some Asterids such as *Asterias ochracea* Brandt (Plate **6**, fig. 3) the fusion of the rays is quite as great as in some Heliasters. Thus a specimen of *A. ochracea* with R = 100 mm. has only 71 mm. free which is practically the same proportion as in some specimens of *H. multiradiatus*. Clearly this character is not altogether distinctive.

3. *The separation of the rays by very strong, true interbrachial walls.* This is probably the best character of which Viguier speaks, for such starfishes with numerous rays as Labidiaster and Pycnopodia, have no true interbrachial walls. It should be pointed out however that the

beginnings of just such walls as occur in Heliaster are to be seen in *Coscinasterias calamaria* (Gray) (Plate 6, fig. 2) and they are well developed in *Asterias ochracea* Brandt (Plate 6, fig. 3). Consequently too much importance must not be attached to this feature.

4. *The position of the mouth at the bottom of a sort of funnel.* The value of this character is an open question but there is no reason for supposing it has any great significance as a structural feature. It is nearly or quite wanting in many individuals, although the best preserved specimens show it more or less clearly. Even if it were always present in normal living individuals, it could hardly be considered of sufficient importance to be a family character.

5. *The fragmentation of the madreporite.* Although the madreporite of an adult *H. helianthus* is usually fragmented, and although the same is true of the other forms with more than 30 rays, yet in young specimens of these species and in adults of *kubiniji* and *multiradiatus* such is not the case, but the madreporite is, on the contrary, exactly as it is in Asterias, simple and convex. The condition of the madreporite cannot then be used even as a generic character.

6. *The peculiar and remarkable form of the odontophore.* In regard to this point, there is room for difference of opinion, for while no one questions the interesting fact which Viguier emphasizes that the basal interbrachial plate (or "odontophore" as he calls it) is fused in Heliaster with a larger interbrachial plate behind it, it is difficult to determine how much value such a character has from a taxonomic point of view. Sladen (1889) holds that it has little or no value and that greater differences in this plate may occur between closely allied species than between other species of quite different genera, so much depends on the number of rays and the character of the adambulacral plates. Careful comparative study of the actinal skeleton of Asterias and Heliaster leads me to believe that Sladen is quite right and that we cannot place any exceptional weight on peculiarities in this so-called "odontophore."

The characteristic features of the family Heliasteridae, then, as given by Viguier, do not seem to bear close examination, and fail to prove of sufficient constancy and distinctiveness to warrant the separation of the genus Heliaster from the Asteriidae. Before the matter is considered settled, however, there are other points to be examined which will throw some light on the subject. It is remarkable that Viguier fails to mention the conspicuous discobrachial wall of Heliaster (Plate 6, fig. 1), for there is no other feature of the anatomy which is so characteristic of the genus. It is quite possible that, with the small amount of material

at his disposal, he did not feel justified in mutilating a specimen to such an extent as to expose this wall sufficiently to make him realize its unique character. It shuts the cavity of each ray off from the cavity of the disc completely, the only communication between the two being a small foramen through which the duct of the digestive gland passes. I have found no trace of any such wall in any other starfish which I have examined, and, although further investigation may show that it is not unique, it is undoubtedly the most striking feature of the internal anatomy of Heliaster. It is easy, however, to see how such a wall might have developed, for, with the coalescence of the rays and the consequent doubling of the interbrachial walls, it would be natural that a stronger union between the rays and disc should arise by the expansion of the proximal ends of those walls. The subsequent increase and coalescence of such expansions would readily follow, thus giving a very unusual, but necessary, strength to what would otherwise be a line of weakness. — The further examination of the internal anatomy of Heliaster reveals some interesting similarities with Asterias, which have not been noted hitherto. The reproductive organs occupy the same position as in that genus, and are identical in form, so that the only difference is in the actual number of gonads, there being a pair in each ray in both genera. The form and position of the stone-canal and the axial organ are identical in the two. The racemose glands (Tiedemann's bodies) are similar in form and position, but are much more numerous in Heliaster than in Asterias, ranging from 10 to 26 in the twelve specimens of *kubiniji* and *polybrachius* examined. They do not show any regularity in position, however, or any correlation between their number and the size of the individual, or the number of rays. The digestive system of Heliaster (Plate **7**, fig. 1) is surprisingly like that of Asterias in spite of the separation of the disc cavity from the rays. The stomach is very capacious, and is obviously pushed out of the mouth in feeding, just as in Asterias, and (as already mentioned on p. 59) its five pouches are each attached by a pair of strong muscles, as in that genus, to the ambulacral plates of the basal part of a ray. These muscles pass from the stomach through the openings in the discobrachial wall (which are perhaps a trifle larger in these rays) used by the ducts of the digestive glands. This pentamerous symmetry of the stomach-muscles is most striking, and it can hardly be doubted that it reveals a close relationship to Asterias. The intestine is short, and bears the customary rectal gland, which consists, as in Asterias, of several much divided branches.

Turning now to the external features of Heliaster, we find, as is well known, that the abactinal skeleton, the papulae, the pedicellariae, and the armature of the adambulacral plates are essentially the same as in Asterias. It has commonly been stated also that the two genera are alike in the quadriserial arrangement of the pedicels. As a matter of fact, however, the real arrangement of the pedicels in Heliaster is quite different from what is found in Asterias, for while a quadriserial arrangement does occur in some species of Heliaster, it is virtually confined to the middle portion of the ray, while in other species it is hardly correct to speak of a quadriserial arrangement at all. These various conditions are shown on Plate **7** from which it will be seen that although in the middle of the ray there is a distinctly quadriserial arrangement in *microbrachius* (Fig. 11), in *kubiniji* (Fig. 9) that is scarcely the case. At the base of the ray the arrangement is unqualifiedly biserial in all the species (Fig. 10), at least for the first ten or twelve pairs of pedicels. In young individuals (Fig 12), the biserial arrangement is marked even at the middle of the ray. This condition is certainly perplexing if Heliaster is merely an Asterias with numerous rays, for if that were the case, the species with the fewest rays (*kubiniji*) ought to show most clearly the quadriserial arrangement, while a young individual with only 17 rays certainly ought to have the same arrangement well marked. As we have just seen, the reverse is the case. However, it seems probable that increase in the number of rays, in a species having four rows of pedicels, with the consequent lateral crowding, would lead to radial extension, which would result in the quadriserial arrangement gradually becoming irregularly, and finally perfectly, biserial, as we find it at the base of the rays in Heliaster. That such a result does follow an increase in the number of rays in a species with the quadriserial arrangement of the pedicels, is shown by *Coscinasterias calamaria* (Gray) (Fig. 13), where the first two or three pairs of pedicels of each ray are arranged in a single series on each side. If, however, we are to assume that the change here first indicated in Coscinasterias is continued in Heliaster to a far greater extent, we shall have to admit that it is carried to different degrees of completeness in the different species. It seems to have gone further in the species with the narrower, freer, and more cylindrical rays, where the quadriserial arrangement is nearly obliterated, than in those with broader and flatter rays, where the pedicels still appear to be in four series at the middle of the ray. Apparently, after there are 15–20 rays, the change to a biserial arrangement of the pedicels is not promoted so much by the number or degree of coalescence of the rays, as by their form and width.

From this brief summary of the more obvious anatomical features of Heliaster it is clear that the relationship with Asterias is very close, the only important differences being in the number of rays, the degree of their coalescence and the resulting modification of the actinal skeleton and arrangement of pedicels. It will of course be a matter of opinion whether these differences warrant the maintenance of the family Heliasteridae. It seems as though such a course emphasized too strongly the differences between Asterias and Heliaster and tended to conceal their much more important resemblances, and while the Heliasters might be considered a sub-family (Heliasterinae) of the Asteriidae, it would be unwise to isolate them further. If this sub-family be recognized, it is possible that the two Heliasters with relatively few, long, free rays (*multiradiatus* and *kubiniji*) could be separated generically from the others. It is difficult to do this, however, on account of the intermediate characters shown by *canopus*, which has few, rather long, and quite free rays, but whose natural relationship is obviously with *helianthus*. Should we make a second genus of these two species, leaving *cumingii*, *polybrachius*, and *microbrachius* for a third, we should doubtless have a natural grouping of the species, but the definition of these "genera" would tax the keenest specialist, and it is difficult to see any real advantage from such a division. It is, moreover, quite possible that when these starfishes are studied as living organisms (instead of as museum specimens), and from a more extensive series of localities, our idea of their interrelationships may be considerably changed.

Granting, then, that Heliaster is to be accepted as a genus of Asteriidae, we may well inquire as to its relation to other genera of that family, and we naturally turn to Pycnopodia as a probable near-ally, on account of the large number of rays. That Heliaster is allied to Pycnopodia has recently been both assumed and affirmed by Ritter and Crocker (**1900**). They make the following statement in a footnote on page 249: — "There appears to be general agreement among authorities that *Pycnopodia* and *Heliaster* are rather more closely related than are *Heliaster* and *Labidiaster*. A. Agassiz, **'77**; Perrier, **'93**; Ludwig, **'97**; Studer, **'84**; Vignier, **'78**, etc." (both in this place and on p. 270, Viguier's name is misspelled, by a common typographical substitution). As my own investigations had led me to a different conclusion, I looked up the references here given, making use of course of Ritter's and Crocker's bibliography, with the following remarkable result: —

A. Agassiz, '77.

North American Starfishes. Mem. M. C. Z., **5**, No. 1.

No mention is made of either Heliaster or Labidiaster, nor can I find the slightest hint of the writer's opinion on the position of either genus. I may add further that Mr. Agassiz assures me that he has never expressed or held any such opinion as is here ascribed to him.

Perrier, '93.

Traité de Zoologie. Première partie. Paris, 1893.

The author makes no direct reference to the question, but the position he assigns to Heliaster might not unfairly be interpreted as showing that he holds the view ascribed to him.

Ludwig, '97.

Die Seesterne des Mittelmeeres.

I have been able to find no reference whatever to any one of the three genera concerned, though I have very carefully and repeatedly examined this splendid monograph.

Studer, '84.

Abh. d. k. Akad. d. Wiss. zu Berlin, p. 1–64.

No reference whatever is made to either Heliaster or Pycnopodia.

Viguier, '78.

Arch. de Zool. exp. et gen., **7**, p. 33–250.

Although the author does not make any positive statement as to the relationship of Pycnopodia and Heliaster, it is clear from his remarks on page 116 that he does not consider them closely allied, while the statements on pages 118–119 indicate that he does consider Heliaster as intermediate between the Asteriidae and Brisingidae (to which family Labidiaster is commonly assigned), while Labidiaster, he thinks, may be intermediate between Heliaster and Brisinga.

It is clear, therefore, that the only "general agreement" which these five authors show is in avoiding the expression of any such opinion as is ascribed to them. It is very difficult to understand why Ritter and Crocker should have given these references at all, for they certainly do not support their contention, even indirectly.

On comparing specimens of the three genera concerned it will be seen that superficially they are somewhat similar, but that the more numerous rays and the larger disc ally Labidiaster and Heliaster more closely to each other than to Pycnopodia, although the stout abactinal skeleton of Heliaster separates it from both. The ambulacra in Pycnopodia are moreover very broad, and the pedicels are distinctly quadriserial almost to the actinostome, while in Heliaster the ambulacra are nar-

rower and the pedicels distinctly biserial at the base of the ray, as they are in Labidiaster throughout; the general appearance of the ambulacra in Heliaster is thus more like Labidiaster than it is like Pycnopodia. The buccal membrane and the mouth parts are essentially alike in all three genera, while the adambulacral armature shows no close similarity between either two. The pedicellariae are alike in all three, but those of Heliaster (Plate **7**, figs. 2–5), while somewhat more like those of Pycnopodia in form, are distributed more as in Labidiaster. The digestive system of the latter is more like that of Pycnopodia than it is like that of Heliaster; at least the material available to me shows no indication of the five pairs of stomach-muscles, so characteristic of Asterias and of Heliaster, in either Pycnopodia or Labidiaster, nor can I find any reference to them in the published descriptions of either genus. In the number of racemose glands, Heliaster and Labidiaster are alike, having a large number (usually more than 15, often more than 20) without definite arrangement, while Pycnopodia, according to Ritter and Crocker, has only 9 or 10, and these are definitely located. The discobrachial wall of Heliaster is wanting in both the other genera, and even their interbrachial walls are reduced to mere sheets of connective tissue with little or no calcification. Were the case to rest here we should still be somewhat in doubt as to whether Heliaster or Pycnopodia were the nearer to Labidiaster, but there could be little question that Heliaster is nearer to the latter than it is to Pycnopodia. There is, however, another and very important point to be considered, and that is the location and sequence of new rays, which, as we have already seen, is apparently alike in Heliaster and Labidiaster, and places them in striking contrast to Pycnopodia. This feature alone is sufficient to completely separate the last from the others, and Viguier's opinion that Heliaster is intermediate between Asterias and Labidiaster seems therefore to be justified by these more recently discovered facts. Whether the latter is intermediate between Heliaster and the Brisingidae is somewhat less certain. The geographical connection between Heliaster and Labidiaster is obvious, since the latter replaces the former on the southern coasts of South America, but the remainder of the Brisingidae are, for the most part, widely separated geographically from Labidiaster, and there is reason to believe that they have originated from the Asteriidae quite independently of that genus. On the whole, it looks as though Labidiaster had originated as an offshoot from Heliaster, living in colder and deeper water, while Odinia, and perhaps Brisinga, too, are probably similarly related to the genus Asterias.

The Interrelationships of the Species, and the Factors which have aided their Development.

There are few starfishes whose habitat is so exclusively littoral as that of Heliaster, and there are not many genera, containing several species, whose area of distribution is so circumscribed. For these reasons the genus offers an unusual opportunity for the study of the influence of environment and the effect of isolation. Although this study could only be properly carried on in the regions where the Heliasters live, nevertheless the examination of a large number of specimens suggests certain conclusions which are worth noting. In the first place we see there are four areas, which so far as our present knowledge goes, are distinctly separated from each other, where Heliaster occurs, namely:—West Coast of Mexico and Central America; West Coast of South America from Ecuador to Chili, inclusive; Galapagos Islands; Juan Fernandez. In each of the first three regions two species of Heliaster occur, and in the fourth, one, but there is no species common to any two of the districts. We have no means of knowing which species is nearest the ancestral form, but it seems almost certain that the species with the fewest and least united rays are the most primitive. We are equally ignorant as to the place of origin of Heliaster, but there can hardly be any question that it was somewhere along the mainland coast. If these two points are assumed, *kubiniji* must be the nearest to the original Heliaster. We can see that as there are no nearly allied species on the western tropical coasts of America to compete with it, this form might gradually spread southward, while it would not be likely to extend north of Lower California, as it would then come into competition with numerous other Asteriidæ. Whether Heliasters still occur on the coast of Colombia we do not know, but whether they do or not is of no special importance in this connection, for *kubiniji* does not range very far south of Mexico and is therefore entirely isolated at present from its South American relatives. These latter under the different environmental conditions south of the equator seem to have developed a larger number of rays and to have them more fully united, as we find in *helianthus*. By a continued (though slight) increase in the number of rays, and a marked increase in their coalescence, accompanied by the development of stouter, capitate, abactinal spines, *polybrachius* has arisen. The origin of *microbrachius* is less clear, but its affinities with *polybrachius* are so much more apparent than any with *kubiniji*, we are almost forced to believe that it represents a return northward of short-rayed Heliasters, which owing to

their obvious differences have not been in real competition with *kubiniji*, and which in the environment north of the equator, new to them, have developed the numerous, slender abactinal spines which distinguish them from their southern ally. The fact that *microbrachius* occurs at Panama and Pearl Island may be interpreted to support this hypothesis. The relationships of the island forms are obvious, for *multiradiatus* is very closely allied to *kubiniji*, *cumingii* is quite as close to *polybrachius* and *canopus* is almost certainly an offshoot from *helianthus*. — These relationships, both phylogenetic and geographical, may be indicated by such a sketch as Diagram 6, it being understood that the relative length of the lines has no significance whatever.

Because of the extremely littoral habits of Heliaster, there can be no question that the island forms have reached their present homes as larvae transported by ocean currents. Owing to the distances however and the slow rate of travel, the chance of survival is very small, and it must be seldom indeed that young Heliasters from the mainland ever reach the Galapagos or even Juan Fernandez. The latter islands seem to have been reached as yet only by the single species (*helianthus*) from the nearest mainland, which under the stress of new conditions has become changed so that it breeds earlier in life, and is consequently much smaller than its parent form, and has more delicate spines, and fewer, freer rays. The Galapagos have been reached by young *polybrachius* from South America and also by young *kubiniji* from Mexico, but if we may judge by the relative amount of change, Juan Fernandez was populated by Heliaster long before the Galapagos. At the latter islands, *cumingii* appears to be much more abundant than *multiradiatus*, so we are justified in thinking *polybrachius* was the first comer, but both are so recent, the changes are as yet slight.

Of the factors which have led to this development of diverse forms of Heliaster, one at least stands out so clearly that there can be little doubt of its importance, and that is *isolation*. Were only the mainland species known, this factor would not be so obvious, though it would be suggested by the apparent lack of Heliasters on the coast of Colombia. But when we consider the two Galapagos species, and particularly when we study *canopus*, it is hard to doubt that the complete isolation of these small groups of individuals has been of great importance in the formation of the new species. In the case of *canopus*, there has been sufficient time, so that the species is sharply distinct, while the Galapagos species seem to be as yet only imperfectly defined. It is not necessary to claim that isolation has been the only, or even the essential, factor. Indeed the

probable existence of connecting links between *cumingii* and *polybrachius* at the Galapagos makes it very unlikely that it is merely the environment and isolation which are at work there. It seems clear that natural selection has been an important agent in the case of *canopus* at any rate,

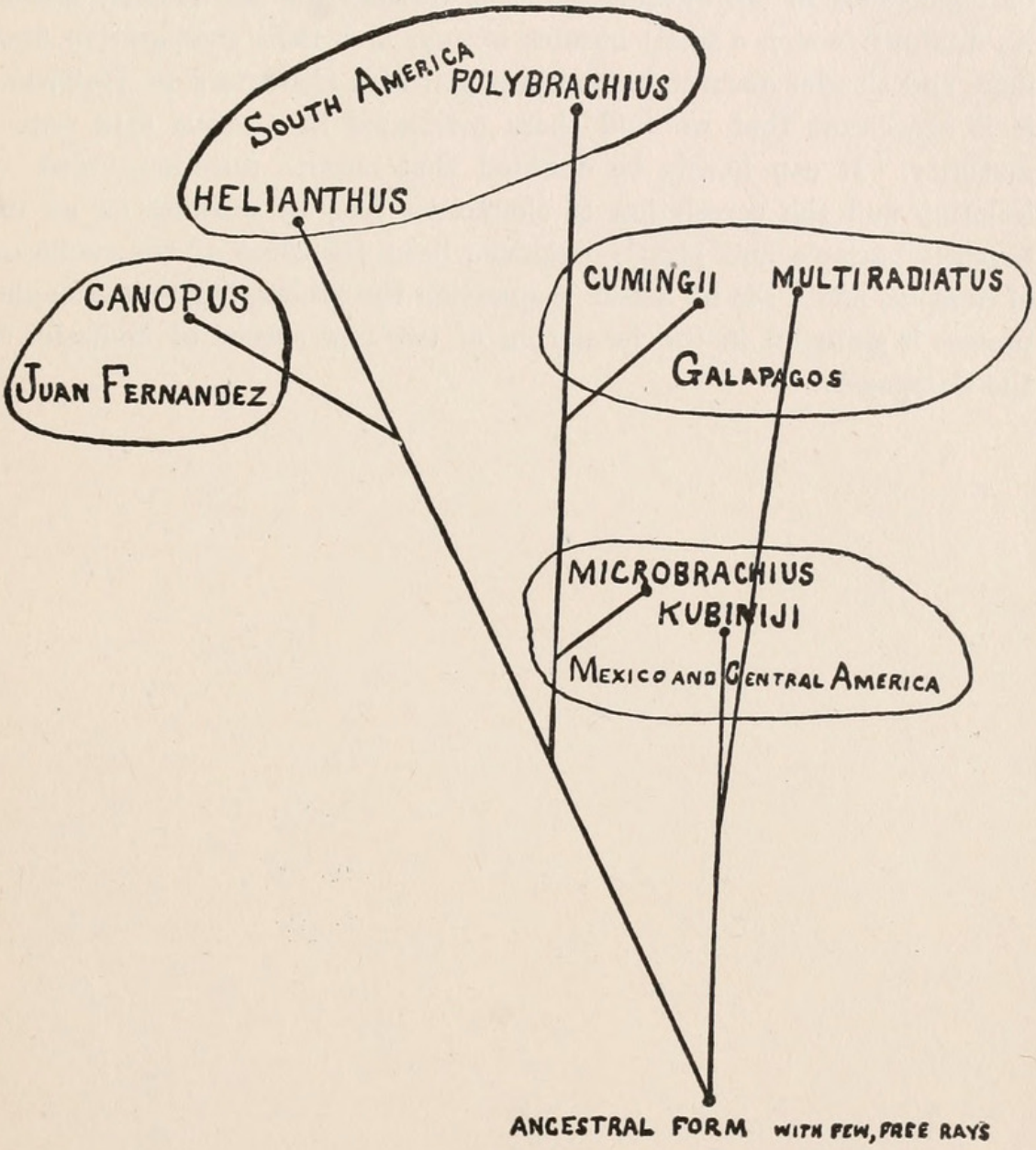

DIAGRAM 6.

To show the phylogenetic and geographical relationships of the species of Heliaster.

for while it can be claimed, if they please, by those, who are "done with meekly accepting the dictum . . . that when we understand *all* the conditions of the life of an organism, then and only then are we entitled to say of this or that character that it is not of life or death value,"[1]

[1] Kellogg, V. L., Science, Nov. 16, 1906, p. 627.

that the number of rays, the amount of their fusion, and the size and arrangement of the abactinal spines are characters of no value in the struggle for existence, there can hardly be any question that the ability to reproduce vigorous young, at an early period of life, would be a factor of importance in the establishment of Heliaster on an isolated island. As diminutive size, a small number of rays and their comparative freedom, and slender abactinal spines are youthful characters in Heliaster, it is significant that we find them correlated in *canopus* with sexual maturity. It can hardly be doubted that natural selection, aided by isolation and the correlation of characters, has, by working on an inherently variable and plastic organism, been the cause of the evolution of *canopus*, and I see no reason to question the probability that a similar process is going on in the formation of two new species of Heliaster at the Galapagos.