

ART. XL.—Revision of the Genera of Starfishes of the Subfamily Asterininæ; by A. E. VERRILL.

THERE is, perhaps, no family of starfishes that is so much in need of revision as the Asterinidæ. Even in recent standard works very erroneous statements are made as to the morphology of the group* and the characteristic structures of the genera and subfamilies,† while very diverse species are still included in the old genus *Asterina*. In this brief article I propose to give a summary of the classification of those Asterininæ more nearly allied to *Asterina* proper, and in part usually referred to that genus, but it is not possible to classify all the numerous species at this time. The group is well represented in all the warmer seas, but no species is found on our Atlantic coast‡ north of Florida, except the large and very aberrant species, *Tremaster mirabilis* Ver., often made the type of a separate subfamily. It is from the northern fishing banks. Only one is found on the Pacific coast north of southern California, viz., *Patiria miniata* (Br.).

Subfamily ASTERININÆ.

Asterinidæ (pars) GRAY, Ann. and Mag. N. Hist., vi, p. 228, 1840; Synopsis, p. 15, 1866. Perrier, Revis. Stell., iv, p. 291, 1875; v, p. 209, 1876. Viguier, Squellette des Stell., Arch. Zool. Exper., vii, p. 205, pl. xiv, figs. 1-13, 1878 (structure). Sladen, Voy. Challenger, xxx, p. 374, 1889. Perrier, Expl. Trav. et Talism., pp. 141, 163, 1894. Fisher, op. cit., 1911, p. 253 (table of genera).

Body usually rather flat, often thin, sometimes stellate with long rounded rays; usually with five or six short rays, rarely eight. Margins usually thin and formed mainly by the infero-marginals; marginal plates small, usually scarcely larger than the adjacent dorsals, usually with a comb or cluster of spinules. Dorsal plates usually flat and more or less imbricated, sometimes not imbricated; generally covered with minute spinules, often in tufts or combs; sometimes covered with a soft, naked, or granular dermis. Under side flat; actinal plates angular,

* Thus Gregory, 1900, in Lancaster's Treatise on Zoology, p. 238, erroneously states that the madreporic plate is on the ventral side in *Asterina*, and on page 250 gives as family characters, the absence of pedicellariæ; imbricated plates; and other characters of only generic value.

† Sladen, Voy. Challenger, 1889, p. 374, and Fisher (Asteroidea of N. Pacific, 1911, p. 253), are both in error in stating that the papulæ are generally distributed, and that the dorsal plates do not have descending processes or pillars in Asterininæ, while these characters exist in Anseropodinae. In fact, the papulæ are always definitely localized, and many typical Asterininæ (e. g. *Patiria*) have strong vertical pillars.

‡ The small specimen formerly described by me, from off the coast of Maine, as *Asterina pymæa*, proves to be the young of a *Porania*.

flatish, imbricated or closely united, usually covered with small combs or tufts of spinules, sometimes with only one; these plates form regular oblique rows. Adambulacral spines simple, divergent; in two sets; the furrow-spines form small, usually webbed combs of two to eight. Those on the outer surface are in groups or fans, or like the interactinals. Pedicellariæ usually lacking; when present they are two-bladed, erect, forciform.

The papular pores are dorsal and form several rows on the median and lateral parts of the rays, and sometimes on adjacent parts of the disk, but are absent from the more or less

FIG. 1.

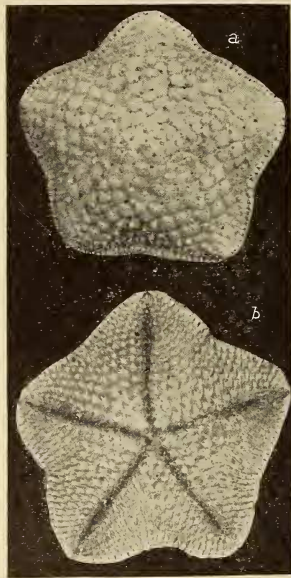


FIG. 1. *Asterinides folium* (Ltk.); a, dorsal side; b, ventral side, natural size.

large interradial areas, where the plates assume a different shape and are more closely united.

There is generally no single dorsal median, radial row of plates; its place is taken by two to four or more alternating rows; the larger of these plates have a papular pore under the proximal edge. These larger plates usually show only one of the edges and part of one side; seen from the inside they appear much larger, often four-lobed, and obliquely imbricated. The dorsal plates of the outer interradial areas, in many species, have conical or pillar-like processes extending downward and meeting similar uprising processes from the

outer interactinal plates, as stalactites meet stalagmites*; or they may not join directly, but be united by an intermediate ossicle. In some genera they are differently joined. In typical *Asterina*, and doubtless in many other genera, if not in all, the genital pores are on the ventral side, in a pair, just outside the jaw plates, but they are seldom visible in preserved specimens. The madreporic plate is usually rather large and placed close to the central area of the disk; sometimes there are two or more, rarely five. The rays vary from five to eight, and some species are probably autotomous. The genus *Tremaster* Ver. is remarkable for having an oblong perforation passing entirely through the disk in each interradian area, and for having only one or two furrow-spines.

The following table shows the classification, now proposed, for the principal generic groups:

Table of Genera and Subgenera of Asterininæ.

I. Interradian areas of the disk not perforated.

- A. Adambulacral spines form a separate comb or combs within the furrow edge, and another group on outer surface; ventral plates and interspaces not covered by a granulated dermis.
- B. Principal dorsal plates are all imbricated.
- C. Margins of disk and rays thin, subacute; rays depressed; usually short.
- D. Interactinal or ventral plates in regular oblique rows, each with a fan-shaped group of two to eight small spines, usually webbed.
- E. Dorsal plates of papular areas nearly all of one kind, the exposed part usually roundish, elliptical, cordate, or shield-shaped, wholly or partly spinulose. Genus *Asterina*, in a wider sense.
 - a. Two-bladed pedicellariæ occur on the dorsal plates and intervening dermis.

Asterina (restr.) Nardo. Type, *A. minuta* Nardo = *A. gibbosa* (Pen.) = *verruculata* (Retz.) = *A. pulchella* Per. Europe.

aa. No pedicellariæ present.

Asterinides Ver., genus nov. Type, *A. folium* (Itk.). W. Indies; see fig. 1, Bermuda; Florida.

EE. Dorsal plates of papular areas of two or more diverse kinds, the larger proximally arched or lunate, and notched for passage of papulæ; between these are groups of small ovate or pyriform ossicles inserted endwise, mostly bearing small roundish clusters of spinules. Internal vertical pillars present in interradian areas.

α. No pedicellariæ found.

* This feature has been regarded hitherto as peculiar to Anseropodinae, but it occurs also in several genera of Asterininæ, perhaps in all with thin stiff margins.

Patiria Gray, 1840 (monotypic). Type, *P. coccinea* Gray. Cape Good Hope ; E. Africa (not *Patiria* Per. nor of Sladen).

b. Ventral plates have a large solitary spine, or sometimes two. Dorsal plates nearly as in *Patiria*, but with fewer small ossicles.

Patiriella Ver., gen. nov. Type, *P. regularis* Ver. New Zealand ; Australia, etc.

bb. Ventral plates have a fascicle of slender spines.

Asterinopsis Ver., gen. nov. Type, *A. penicillaris* (Lam.). Red Sea ; E. Indies ; Japan ; Australia. *A. pilosa* (Per.), off Dominica I. ; *A. lymani* (Per.), off Barbados.

xx. Two-bladed pedicellariæ on dorsal plates.

Enoplopatiria Ver., nov. Type, *E. marginata* (Hupé) = *A. stellifera* (Mob.) = *A. braziliensis* Ltk. = *A. minuta* (M. & Tr., non L.). Brazil ; W. Indies ; Canary Is. ; W. Africa.

CC. Margin of disk and rays not thin ; rays elongated and rounded ; dorsal plates imbricated and spinulated.

c. Adambulacral plates have two or more fan-like rows of superimposed webbed spines on the furrow margin, and an outer group of many spinules. Ventral plates covered with numerous small spinules ; principal dorsal plates imbricated, lunate, finely spinulated, with a small one proximal to papular pore.

Nepanthia Gray. Type, *N. maculata* Gray. E. Indies. Includes, also, *N. brevis* Per. E. Indies, etc.

cc. Adambulacral plates with a single inner comb and an outer fan of spines. Ventral plates with a central roundish cluster of many spines. Dorsal plates nearly as in *Patiria* ; with many interposed small ossicles.

Callopatiria Ver., gen. nov. Type, *C. bellula* Sladen, as *Patiria*. Cape Good Hope. *C. obtusa* (Gray, non Ver.). Panama.

BB. Principal dorsal plates are not all imbricated.

F. Rays elongated and rounded.

d. Principal dorsal plates contiguous ; notably enlarged, rounded or elliptical, with a central group of spinules and marginal series of pedicellariæ. Ventral plates with a fan of several spines.

Allopatiria Ver., gen. nov. Type, *A. ocellifera* (Gray), as *Patiria*. Australia.

dd. Principal dorsal plates not greatly enlarged, roundish, separated by small, roundish ossicles around papulæ ; all spinulated. Ventral plates crowdedly spinulated.

Parasterina Fisher. Type, *P. crassa* (Gray), as *Patiria*. Australia. *P. obesa* Clark. Chili; Peru.

FF. Rays not elongated and rounded.

G. Dorsal plates of papular areas roundish, separated by naked skin, having papular pores. Ventral plates with one or two simple spines.

Disasterina Per. Type, *D. abnormalis* Per. New Caledonia; also, *D. ceylonica* Dod. Ceylon.

GG. Dorsal plates of rays thin, contiguous, not overlapping, linear or narrow, transversely elongated, often bent, with many small interpolated ossicles, all covered with even granules. Internally the plates are supported on an alveolar structure. Ventral plates thin, each with a cluster of webbed spines, those adcentral having about four to six in an irregular group; admarginal ones with about three small ones in a comb. Adambulacral furrow spines in convex webbed fans of four or five.

Desmopatiria Ver., gen. nov. Type, *D. flexilis*, nov. Chili?

AA. Adambulacral spines form a continuous webbed series, the individual combs of three to five being united together; no spinules on outer surface. Dorsal and ventral plates and interstices covered with a finely granulated dermis, which also forms the web between the minute spines, in a fan, on the ventral plates. No dorsal spinules. Papular pores form six or more rows. Internal dorso-ventral columns are present near margins. Form depressed pentagonal, with thin margins. A few small ossicles between dorsal plates, usually one.

Stegnaster Sladen. Type, *S. wesseli* Per. Florida; Bahamas; W. Indies; Colon. *S. inflatus* Hutton. New Zealand.

II. Interradial areas of disk perforated vertically. Form large, pentagonal, with the thick disk arched upward and the margins thin; concave beneath. Dorsal plates strong, convex, imbricated, larger papulary ones with spinules on the edge; others with granules. Papular areas radial, petaloid, with numerous papulae. Ventral plates with one or two flat spines; outer surface of adambulacrals with two; inner margin usually with one spine.

Tremaster Ver. Type, *T. mirabilis* V. Newfoundland Banks.

ASTERINA Nardo (restricted).

Asterina NARDO, Oken's Isis, p. 716, 1834. Gray (*pars*), Ann. and Mag. Nat. Hist., vi, p. 286, 1840; Synopsis, p. 16, 1866. Perrier, Revis. Stell., Arch. Zool. Exper. et Gen., v, p. 214, 1876. A. Agassiz, North American Starfishes, p. 106, pl. xiv, 1877 (structure). Viguiet, op. cit., vii, p. 207, pl. xiv, figs. 8-13, 1878 (structure). Sladen (*pars*). Voy. Challenger, xxx, p. 388, 1889. Fisher (*pars*), op. cit., 1911b, p. 254. *Asteriscus* (*pars*) MÜLLER and TROSCHEL, 1840, p. 104; Syst. Aster., p. 39, 1842.

The type of this genus is undoubtedly the common Mediterranean species, *A. gibbosa* (Pen.) = *minuta* Nardo. The genus, as here restricted, has the larger dorsal plates closely imbricated, convex, relatively large and wide, notched on the proximal side; when seen from the inside they are rather rhombic or quadrate and only slightly lobed. There is often a single small, rounded ossicle between them, but no large clusters. The dorsal interradial plates near the margin have stout, conical, descending processes internally. The dorsal radial plates usually have one or two rows of spinules on the edge, and also bear pedicellariæ about as large as the spinules. There may be as many as twelve rows of papulæ. The genital pores are on the ventral side, in pairs, near the jaws. The restricted genus includes, among others, the following:

A. trochiscus (M. & Tr.). E. Indies.

Asterinides Ver., nov.

Includes, besides the type, the following and several others:

A. burtoni (Gray) = *A. cepheus* (M. & Tr.). S. Africa to Red Sea; Ceylon; E. Indies; Philippines; New Guinea, etc.

A. vega (Per.). Has six to eight rays. Red Sea; Mauritius.

A. minuta (Linn., ex Gray), non M. and Tr. Antilles. Perhaps = *A. folium*.

A. modesta Ver. Panama; Pearl Is.

Patiria Gray, 1840. Type, *P. coccinea* Gray.

This genus includes, among others, the following, besides the type:

P. miniata (Br.). California to Alaska.

P. chilensis (Ltk.). Païta, Peru, to Chili.

P. gayi (Per.). Chili.

P. granulosa Per. Hawaiian Is.

P. pectinifera (M. & Tr.) Japan.

P. granifera (Gray). Cape Good Hope.

P. novæzelandiæ (Per.). New Zealand.

Patiria miniata (Br.) Verrill.

Asterias miniata BRANDT, Prodrömus, p. 68, 1835.

Patiria miniata VERRILL, Trans. Conn. Acad., i, pp. 234, 236, 1867 (distribution).

Asterina miniata SLADEN, op. cit., p. 774, 1889. Verrill, American Naturalist, xliii, p. 547, fig. 2 (six-rayed), September, 1909. Fisher, Aster. N. Pacific, p. 254, pl. Lvi, figs. 6, 8; pl. Lxi, figs. 1-4; pl. Lxii, figs. 1, 2, 1911.

This large and variously colored species is common at low-tide and in shallow water from California to southern Alaska.

Though normally five-rayed, six-rayed and seven-rayed examples often occur. It is a typical *Patiria*, closely allied to the type. It has been well described and illustrated recently by Professor Fisher. The following remarks are intended chiefly to illustrate the generic characters.

The larger plates of the papular areas, when the spinules are removed, have the admedian edge prominent, lunate, concave beneath, for the papular pores, and having, on the convex upper side, a raised lunate ridge or crest, which carries the spinules. The small interpolated ossicles form clusters, often of ten to fifteen or more, and on the central area of the disk, often of twenty or more. They are mostly ovate or pyriform with the smaller end inserted into the dermis-like pegs. They do not show on the interior surface. Near the end of the ray, beyond the papulæ, the plates are small, roundish or pelecoidal, with an evenly convex surface. When well preserved or living the plates are covered by a rather thick canaliculated dermis.

The papulæ form ten to twelve radial rows, or even more in large specimens, and extend over the inner part of the inter-radial areas and center of the disk.

Seen from the inside, the larger radial plates of papular areas are stout, mostly four-lobed, with the two rounded abmedian lobes underlapping two adjacent plates; and the two admedian lobes overlapping the lobes of two plates, with a large papular pore between the lobes. The plates that form the two median rows are obliquely placed, long-ovate, curved, not lobed internally, but with the smaller ends crossed over the median line.

Beyond the papular areas, in the interradian areas, the dorsal plates have a descending conical process, becoming longer on the plates nearer the margin, and united to the ventral plates by a similar process from the latter, or by an interpolated ossicle.

Patiriella Ver., nov. Type, *P. regularis* Ver.

The type has two furrow-spines, sometimes three adorally, and one on the outer surface; these are rather large, tapered, acute, not webbed; spines of the ventral plates are similar, usually solitary. The ventral plates form numerous oblique rows, about fifteen in the longer rows; adoral ones are large and thick, the exposed part three-lobed or shield-shaped, sometimes four-lobed; innermost odd one larger, bilobed, or subcordate; distal ones lancet-shaped; jaw-plates large and thick, angular, prominent; comb of spines about five on each side, stout, blunt.

The larger dorsal radial plates are prominent, arched or lunate, strongly concave and notched beneath, for exit of papulæ; on the summit there is a single or double curved row of

small spinules. A few small, rounded ossicles, with similar spinules, are interpolated, usually one or two to a papular pore, but none in the interradial areas, beyond the papular region, where the plates become rounded or shield-shaped and bear a small cluster of spinules.

The inferomarginal plates are small and irregularly placed, smaller and less prominent than the upper ones. Papular pores form about twelve rows.

To this genus, besides the type, belong the following species :

P. exigua (Lam.) = *A. pentagonus* (M. & Tr.) ; = *A. kraussii* (Gray). Cape Good Hope ; East Indies.

P. calcar (Lam.). Australia.

P. fimbriata (Per.). Bourbon I. ; Magellan Str.

P. squamata (Per.). Senegal.

P. calcarata (Per.). Chili.

P. pusilla (Per.). Chili.

P. gunnii (Gray). New Zealand ; Australia.

Desmopatiria Ver., gen. nov.

This very peculiar starfish, of which the principal generic characters are given in the table, p. 481, is remarkable for the peculiar alveolar structure underlying the plates, above and below, and in the interradial areas extending from the dorsal to the ventral plates, as tubes. It is possible that in life they contained calcareous deposits that have been dissolved by the acidity of weak alcohol, for the ventral spinules appear corroded in many places.

Aside from this structure the dorsal skeleton is peculiar in having very numerous linear plates, with smaller, roundish, closely granulated flat plates, not overlapping nor imbricated ; and in the irregular clusters of webbed spines on the ventral plates.

The dry specimen has the disk swollen and distorted and the rays strongly curved upward, showing unusual flexibility in life.

Desmopatiria flexilis Ver., sp. nov.

Form stellate, with five short, broad rays. Disk swollen, in the central and radial areas ; margins thin, with small marginal plates, about the size of adjacent dorsals and closely granulated in the same way ; the lower ones are the more prominent. Radii, 17^{mm} and 26^{mm} ; ratio, 1:1.53 ; elevation in middle of disk, 15^{mm} when dry.

The larger dorsal plates of the wide radial areas are narrow, transversely elongated, often in transverse series, partly nearly straight, but often bent, closely crowded together but not overlapping, and with narrow grooves between them. Between these

are many much smaller ones, of varying form and size, mostly rounded or elliptical. All the dorsal plates are entirely and evenly covered with crowded, minute granules, or granule-like blunt spinules. The plates in the interradial areas become more regular, polygonal or roundish, closely compacted, thin, and rest on the summits of polygonal tubes, having a honeycomb-like appearance, in miniature, when the plates are removed. On the radial and central areas, and also on the ventral side, there is a short tube or cell under each plate, limited below by the underlying thin membrane, producing an alveolate structure.

Papulæ are small and stand singly, in several ill-defined radial rows.

The adambulacral spines form a strongly webbed fan of three or four unequal spines on each plate, and an outer rounded cluster of four or five rather stout spinules, webbed together. The ventral plates, toward the center, have an irregular group of three to six webbed spines; toward the margin these become more regular and finally form transverse combs of about three on each plate. Jaw-spines form a regular rounded comb of about six on each side, webbed together.

Locality uncertain; received in a lot containing Chilean starfishes, such as *Heliaster helianthus*, and *Meyenaster** *gelatinosus* (Meyen) Ver., but without a label. (Mus. of Yale Univ.; one, dry.)

* *Meyenaster* is proposed as a new genus, with this species as the type. It is monacanthid; has one interradial row of plates, and a reticulated dorsal skeleton, with numerous papular areas and one or three rows of stout spines. The type is six-rayed; another species is five-rayed.