MAUREEN E. DOWNEY

Zorocallida, New Order,
and Doraster constellatus,
New Genus and Species,
with Notes on the
Zoroasteridae
(Echinodermata: Asteroidea)

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# SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY

NUMBER 64

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Zorocallida, New Order, and Doraster constellatus, New Genus and Species, with Notes on the Zoroasteridae (Echinodermata: Asteroidea)

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# **ABSTRACT**

Downey, Maureen E. Zorocallida, New Order, and Doraster constellatus, New Genus and Species, with Notes on the Zoroasteridae (Echinodermata: Asteroidea). Smithsonian Contributions to Zoology, 64: 1-18. 1970.—During a study of the Asteroidea of the Caribbean and Gulf of Mexico, a new genus of the family Zoroasteridae was discovered. A general survey of the family revealed apparent relationships with the fossil Calliasterellidae and prompted the conclusion that both of these families were incorrectly placed in the order Forcipulatida. A new order, the Zorocallida, is therefore erected for the Zoroasteridae and Calliasterellidae. The new genus, Doraster, is described, with the type-species D. constellatus. Several other observations on the classification of the Zoroasteridae are made, including the synonymizing of three species of Zoroaster found in the Atlantic.

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As every asteroid systematist realizes, the order Forcipulatida has been a catchall for starfishes which could not conveniently be placed in other orders. An artificial group, of obviously polyphyletic origin, the forcipulates should be accorded more attention than they have received from systematists concerned with the present unsatisfactory classification of the Asteroidea. Tortonese's (1958) new order, Euclasteroidea, erected to accommodate those manifest misfits, the Brisingidae, was a decided advance toward the reorganization of the Forcipulatida. It is hoped that the removal of the Zoroasteridae and Calliasterellidae from this order, proposed in this paper, will further elucidate the definition of the forcipulates. The Zoroasteridae are the only living family heretofore referred to this order which do not have crossed pedicellariae; whose skeleton does not form a reticulate network; and in which the mouth plates are deeply sunken in the actinostome. More important, they are also the only ones with superambulacral plates—a very unlikely character for a supposedly advanced group like the Forcipulatida. Their removal leaves only the Heliasteridae and the very large polyphyletic family Asteriidae (and probably some of the fossil Uractinina) in the forcipulates. With Euclasterida and Zorocallida removed, the way should be clear for a resorting and reassessment

Maureen E. Downey, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. of the Asteriidae and a better understanding of their relationships.

The Forcipulatida have been defined as follows:

Pedicellariae of basal piece and two valves, either straight or crossed.

Skeleton reticulate, forming a network of rectangular or very irregular meshes.

Podia in two or four rows, always with a suckered disc; with simple ampullae.

Papulae on all surfaces.

Paxillae never present.

Spines and tubercles not occurring in groups or bundles.

Madreporite always on aboral surface.

Median carina frequently present.

No conspicuous marginals.

Aboral ossicles usually arranged in regular rows.

Adambulacral plates generally short and crowded.

Mouth plates frequently inconspicuous and sunken in actinostome; with ambulacral plates prominent except in Brisingidae.

Generally stellate, with small disc and long tapering arms; arms five to many.

Most of the statements in the above definition, drawn from a number of sources (Fisher, 1911, 1928; Hyman, 1955; Spencer and Wright, 1966), are either qualified in some way, or totally untrue for some asteroids heretofore included in the order. Table 1 shows the more simple and straightforward definitions which result

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TARTE 1 -	Comparison of	f major characteristics of	f Euclasterida	Zorocallida	and Forcipulatida
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Characteristic	Euclasterida	Zorocallida	Forcipulatida		
Pedicellariae	Always crossed.	Always straight.	Straight or crossed.		
Skeleton	Weakly developed, not reticulate, of thin plates or transverse arches widely separated.	Very regular longitudinal and transverse rows of imbricating plates.	Reticulate, more or less open meshwork.		
Podia	In two rows, with large suckered disc; ampullae simple.	In four rows, becoming two distally; with large suckered disc proximally, pointed distally; ampullae bilobed.	In two or four rows, with large or small suckered disc; ampullae simple.		
Papulae	Wanting or confined to aboral disc and arm bases.	None below inferomarginals.	On all surfaces.		
Paxillae	Never present.	Present only in certain fossil forms.	Never present.		
Spines and tubercles	Singly, never in groups of bundles.	Same.	Same.		
Median carina	Never present.	Always present.	Sometimes present.		
Marginals	Never present.	Present and well-defined.	If present, inconspicuous, mostly irregular.		
Aboral ossicles	In irregular transverse arches.	In regular longitudinal and transverse rows.	Mostly irregular.		
Adambulacral plates	Not compressed.	Compressed.	Compressed.		
Mouth plates	Expanded, neither ambs nor adambs predominant; not sunken in actinostome.	Adambs project into sunken actinostome.	Ambs predominant; sometimes, sunken in actinostome.		
Arms	Always more than five.	Never more than five.	Five to many.		

from separating the Euclasterida and Zorocallida from the remaining Forcipulatida.

# ZOROCALLIDA, new order

Diagnosis.—Disc more or less domed, with a definite arrangement of enlarged primary plates; median carina on arms, with all arm plates in rather compact and imbricating longitudinal and transverse series; mouth-frame deeply sunken in actinostome; alternating carinate and noncarinate adambulacral plates; at least some tubefeet large and conical, with tiny suckered disc.

Contents.—Families Zoroasteridae (recent) and Calliasterellidae (fossil).

Discussion.—A new order, the Zorocallida, is here proposed to accommodate the Paleozoic-Mesozoic family Calliasterellidae and the recent family Zoroasteridae. This new order suggests a common root with the Forcipulatida and certain of the Valvatida. Like the forcipulates, the Zorocallida have pedicellariae consisting of a basal piece and two valves. They have both

the quadriserial and biserial tubefoot arrangement, while the forcipulates may have either arrangement. In both orders, the adambulacral plates are compressed, and spines and tubercles occur singly, never in groups or bundles. A median carina, always present in the Zorocallida, is present also in some Forcipulatida. The Zorocallida share with many of the Valvatida the orderly arrangement of primary disc plates, compact longitudinal and transverse series of arm plates, similar mouth-frame, and the presence of superambulacral plates. It seems possible to theorize that the Zorocallida are more ancient than the Valvatida and Forcipulatida, with which they share certain basic characters, and perhaps they may provide a clue to the descent of the valvate and forcipulate starfishes from a common origin.

The strong resemblance between the Zoroasteridae and the Middle Devonian-Upper Cretaceous family Calliasterellidae was noted by C. Wyville Thomson (1873), the author of the first species described in the Zoroasteridae. In his decription of Zoroaster fulgens, he called attention to the affinities of this species

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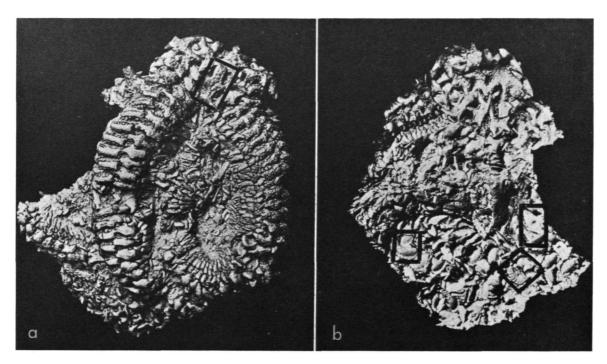


FIGURE 1.—a, Calliasterella mira (Trautschold). Note the so-called "odontophore" displaced toward the right, and the space to the left of it. b, Calliasterella mira. Note the paired carinate and noncarinate adambulacral plates. (From Schondorf, 1910.)

with Arthraster dixoni Forbes, an Upper Cretaceous starfish from the lower chalk of Balcome pit near Amberley, Sussex. Examination of Doraster, the new genus described herein, confirms beyond a doubt that these two families are indeed very closely related; Doraster corresponds almost plate for plate with Calliasterella mira (Trautschold) in dorsal aspect (the only one exposed with plates in situ), as far as can be determined from photographs published by Schondorf in 1909 (Figures 1a, b, 2a), and from a plaster cast of part of the type, obtained through the courtesy of Dr. A. N. Soloviev of the Paleontological Institute in Moscow. I hestitate to place these two asteroids in the same subordinate taxon, however, especially as Schondorf's careful and detailed study does not agree in certain details from my own observations of his photographs and of Doraster. For example, Schondorf's reconstruction of the mouth-frame of C. mira is mostly imaginary, as the mouth is not fully exposed in the material he worked with. In fact, Schondorf himself, in his discussion of the mouth-frame of C. mira, implies that his reconstruction is based on Viguier's (1878) figure of the mouth-frame of Asterias glacialis (=Marthasterias glacialis), an assumption he justifies by certain similarities between the ambulacral plates of C. mira and the ambulacral pieces of the mouth-frame figured by Viguier.

The alternating carinate and noncarinate adambulacral plates and the large conical tubefeet with small suckered discs are characteristics unknown in the fossil Calliasterellidae, but their presence can be inferred from a reexamination of Schondorf's photographs of C. mira. Scattered in the matrix of the specimen are numerous, mostly dissociated, plates. Among them Schondorf quite correctly identified several large carinate plates as adambulacrals, but he failed to notice that, in nearly every case, a smaller noncarinate plate lay next to them (Figure 1b). In view of the condition of this character in the Zoroasteridae, I believe these smaller noncarinate plates are also adambulacrals which alternate with the larger carinate adambulacrals, just as in the recent Zoroasteridae. Given these simi-

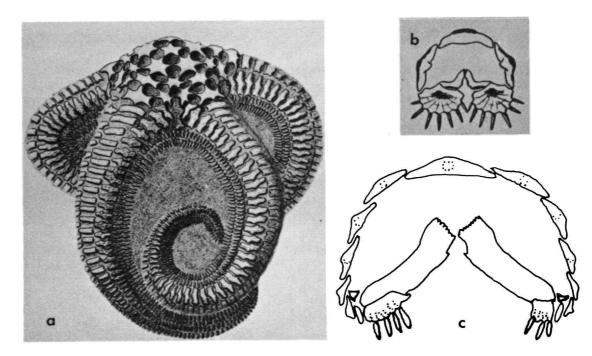


FIGURE 2.—a, Schondorf's reconstruction of Calliasterella mira. b. Schondorf's reconstruction of cross section of arm of Calliasterella mira; compare with c, cross section of arm of Doraster constellatus.

larities, it is only reasonable to suppose that the tubefeet were also similar (although it is unlikely that we shall ever know with certainty), especially in view of the postulated relationship with the Valvatida.

As my experience with fossil asteroids is limited, it would be best not to get deeply involved in a discussion of the similarities between other Calliasterellidae and Zoroasteridae, but a few further comments on the striking resemblance between Calliasterella mira and Doraster seem called for. Schondorf's reconstruction of C. mira shows a single, centrally located interradial plate at the edge of the disc (Figure 2a), which he calls an odontophore; however, careful examination of his photographs shows this plate is actually displaced to the right of the interradial center (Figure 1a), and there is a hiatus between it and the next plate to the left, thus indicating the possibility that there were originally a pair of plates in this position, as is the case with Doraster. I also question Schondorf's interpretation of what he calls "spines" below the adradial plates on the sides of the arms; his description of them sounds more like small actinolateral plates, and again, the photographs (Figure 1a) help to support this view. Thus the reconstruction of the cross section of the arm (Figure 2b) by Schondorf is probably incorrect.

Incidentally, the species described by Kesling and Strimple (1966) as Calliasterella americana, while superficially resembling C. mira, seems a much more "primitive" animal; the so-called adambulacral plates are completely different, and there are definitely no small plates between the "adradials" and the "adambulacrals." Also, the type and placement of the spines is completely different.

# Characters of the Recent Zoroasteridae

Enlarged disc plates, in a definite arrangement of primary radials, interradials, central, and perhaps additional plates, is a very important character in this family, as in the order. So are carinal plates along the

mid-arm and longitudinal and transverse series of arm plates, in most cases decreasing in number of longi-rows from proximal to distal.

Alternate carinate and noncarinate adambulacral plates are present in all recent Zoroasteridae, if we eliminate the very doubtful genus *Prognaster*. (See page 14.)

Superambulacral plates are present in all members of this family, although they are present only proximally in most genera, and in Zoroaster are much reduced.

Large, duck-billed pedicellariae are a distinctive feature of many of the recent Zoroasteridae. No other family has these huge curved pedicellariae, with one valve longer and broad-topped. They have a decidedly bird-headed look, more like avicularia than pedicellariae. They are very large and numerous in *Doraster*, slightly smaller and less curved in *Zoroaster*, shorter and heavier in *Myxoderma*, like *Doraster* in *Cnemid*-

aster (the genus perhaps nearest to Doraster in many ways), blunter and more equal-valved in Bythiolophus, and frequently absent in Mammaster. Small straight pedicellariae are numerous in all these genera. There are no pedicellariae in Pholidaster, and they are unknown in Prognaster (if, indeed, Prognaster exists).

Tubefeet, changing from straight with a large suckered disc within the peristomial cavity to stout and conical with a very small suckered disc, in four rows proximally, becoming two rows distally, are another prominent characteristic shared by all living Zoroasteridae.

All the members of this family are regularly fiverayed, with long slender, tapering arms, and a relatively small disc.

The bathymetric range of the family is from 100 to 2000 fathoms, and they extend from about 50° N to about 40° S, with the greatest number of species occurring in the tropical Indo-Pacific.

# Key to the family ZOROASTERIDAE

(Modified from H. L. Clark, 1920)

A.	Disc plates conspicuously enlarged, more or less convex, bare, or at least not covered with
	spinules; disc and upper part of arms skin-covered.

BB. Disc plates decidedly swollen, more round than stellate.

AA. Disc plates plane, or, if convex, closely covered with spinules; no covering of skin on dorsal surface.

BB. Carinals not surrounded by series of skin-covered squamules; both small straight and large duck-billed pedicellariae present.

C. First superambulacral plate modified to form a conspicuous buttress connecting first two ambulacrals with body wall.

D. Adradials present; superomarginals not over lapping carinals

Myxoderma
DD. Adradials absent; superomarginals strongly overlapping carinals

Bythiolophu

# Doraster, new genus

With the characters of the type-species, D. constellatus, new species.

ETYMOLOGY.—Greek, dora=skin, hide, and aster=star, (m.); specific name: Latin, con-stellatus=with stars, starry (m.).

## Doraster constellatus, new species

FIGURES 3-11

DESCRIPTION.—The plates of the disc dorsum are large, flat, stellate, smooth, skin-covered. The central plate usually bears a stubby tubercle and a similar

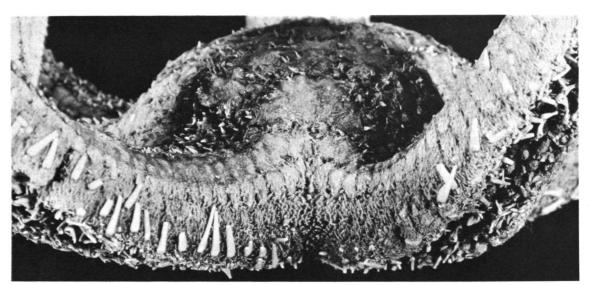


FIGURE 3.—Doraster constellatus, side view (interradius). Note fused interradial adradials. Holotype (USNM E11352).

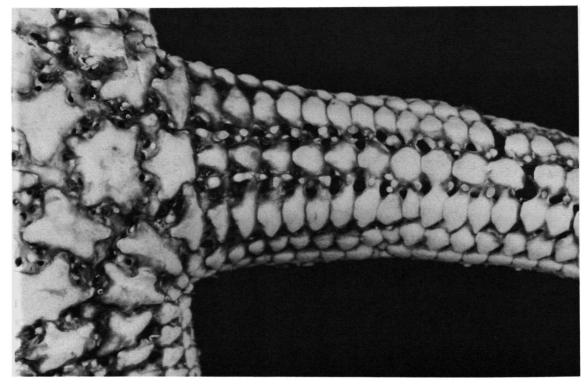


FIGURE 4.—Doraster constellatus (specimen cleared with chlorox). Small supplementary platelets visible between carinal and adradial plates. Paratype (USNM E11353).

Table 2.—Measurements of specimens of Doraster constellatus

Specimen	Preservation	Major radius R(mm)	Minor radius r(mm)	Height of disc (mm)	Height of arm at third carina (mm)	Number of interradial actinolateral rows	Number of terminal actinolateral rows	Number of carinals
Oregon 3583	dry	80	12	9	6	5	2*	52*
Alaminos 21/ 68-A-13	dry	121	15	10	9	4–5	1	73
Oregon 382 A	dry	122	12	12	7	3	*	69
В	dry	*	14	14	11	3	*	*
C	dry	105	11	11	9	3	0	80
D	dry	*	11	11	8	3	*	*
E	dry	95	13	12	8	3	0	60
F	dry	110	12	11	8	3	0	81
Oregon II 10602	dry	183	23	23	14	5	0	99
Albatross 2376 A	dry	66	9	11	7	2	0	50
В	dry	119	11	20	10	3	0	73
C	dry	109	16	16	10	3	0	60
D	dry	118	16	20	15	3	1	72
Oregon 2780 A	dry	239	38	31	20	4	0	100
В	dry	*	18	13	11	4	0	*
Albatross 2376 A	alc	180	17	22	14	3	0	+
В	alc	134	21	22	11	4	0	+
C	alc	110	13	14	9	3	0	+
D	alc	87	12	14	7	+	+	+
Albatross 2377 A	alc	134	18	17	11	+	+	+
В	aic	136	17	21	16	+	+	+
Albatross 2396	alc	57	9	7	5	2	0	+
Albatross 2376 A	alc	66	9	11.5	6	+	+	+
В	alc	46	8	7	5	+	+	+
Albatross?	alc	102	15	18	10	3	0	+

<sup>\*</sup>All arms broken or regenerating.

tubercle sometimes occurs on other primary disc plates. The anus, surrounded by small spinelets, is located in one of the angles of the central plate. Surrounding the centrodorsum are 5 primary interradial plates, and between and underneath them are 5 radial plates on which the 5 pointed lobes of the centrodorsum rest; just outside and partly overlaying the primary interradials are 5 large primary radials; a pair of interradial plates, entirely concealed by skin and the overlapping primary radials, lie between and beneath the primary radials and 4 enlarged imbricating (in large specimens, fused) adradials (Figure 3) which occupy the interradial angle. Small pedicellariae and tiny granuliform platelets (Figure 4) occur between the plates of the disc. The madreporite is slightly smaller than the disc plates, raised, covered with irregular channels, and located between a primary interradial and the enlarged interradial adradials; it actually rests on a pair of concealed interradials. The first carinal is enlarged, about the same size as the interradial adradials.

The interradial gonads are in grape-like clusters, short, hardly extending into the arm; they are attached interadially 1 on either side of the enlarged 1st superambulacral plates.

The jaw (Figures 5, 6) is one solid piece (made up of 2 pairs of adambulacral plates), projecting into the peristome. Behind it are 4 pairs of adambulacrals joined across the interradius by a tooth-and-socket arrangement strongly reminiscent of the way the ambulacral plates are joined at the top of the ambulacral groove. Internally, the front of the jaw is flaired like the carinate adambulacral plates and bears, on each side, 3 subequal spines completely covered with tiny straight

<sup>+</sup>Skin-covering obscures plates.

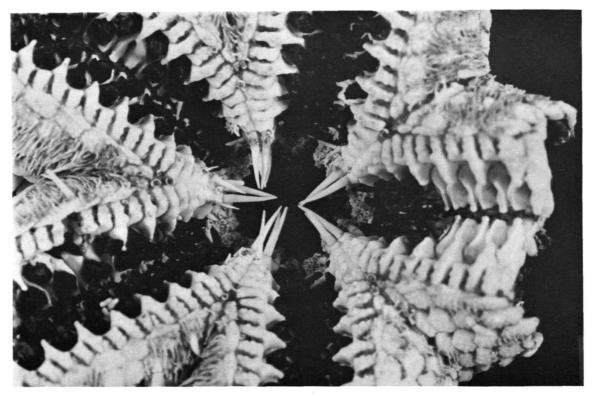


FIGURE 5.-Doraster constellatus, oral view from outside. Paratype (USNM E11353).

pedicellariae, which thus form a wreath around the peristome. External to these 3 pairs of oral spines is a single pair of long sharp spines. The next 2 pairs of adambulacral plates behind the jaw bear each a single pair of long sharp spines, and the 2 pairs behind them bear 4 to 6 similar spines. The 7th and 8th pairs of interradial adambulacrals are separated by a large duck-billed pedicellaria. The first 2 pairs of ambulacral plates are also strongly fused and greatly swollen. The ambulacrals curve sharply upward under the disc and thus support the disc in a domed position. The 2 fused pairs are buttressed against the body wall by a solid ridge formed of the first 2 (enlarged) superambulacral plates. A pore for the oral tubefoot occurs in the angle between the fused ambulacrals and the buttressing superambulacrals. Superambulacral plates of two kinds occur, alternately, but do not continue to the end of the arm; rather, they diminish in size and eventually disappear. A straight, triangular superambulacral plate alternates with a thin, flaired superambulacral plate which terminates in a broad flat disc resting on the ambulacral plates. They gradually become similar, small, and granuliform, and do not continue much beyond the middle of the arm. The tubefeet are in 4 rows proximally, 2 rows distally. Around the mouth, they are straight and conspicuously annulated and terminate in a large suckered disc, but beyond the confines of the disc, they are stout and conical and taper to a tiny disc, indicating that the original, more "primitive" condition in this order was with a large suckered disc, while the pointed tubefoot is a functional adaption.

On the arms, the carinal plates and 2 rows of plates on either side (adradials and superomarginals) are covered with skin, devoid of spines or spinules, but may have small pedicellariae, especially proximally. The carinals may have a central, non-spine-bearing tubercle. Adradial plates overlap carinals and superomarginals.

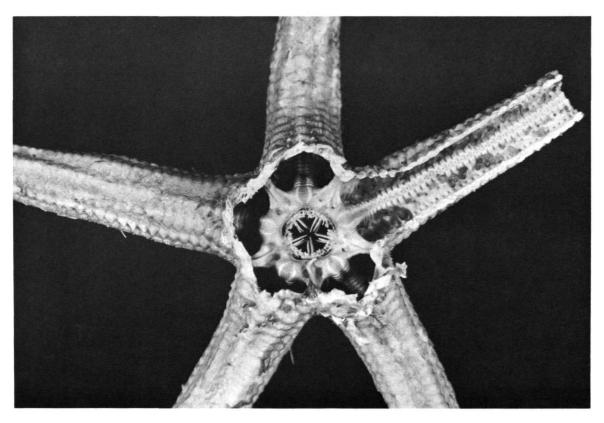


FIGURE 6.—Doraster constellatus, oral view from within disc. This specimen shows also the skin covering the dorsal surface of the arms, and the wreath of small pedicellariae around the mouth. Paratype (USNM 10742).

Carinals and adradials about equal in size, somewhat cruciform, wider than long; superomarginals slightly smaller, lobed or, in large specimens, somewhat triangular, tapering toward actinal surface. On large specimens, an irregular row of tiny granuliform platelets (Figure 4) occurs between the carinals and the adradials; a few also occur sporadically on the disc. Proximally, there are 5 rows of plates between the superomarginals and the adambulacrals covered with small sacculate spinules; the row adjoining the superomarginals is the inferomarginal row. About halfway out on the arm, one row of plates between the inferomarginals and the adambulacrals drops out, then further out, another, until at the end of the arm only the carinals, adradials (by this time very small), superomarginals, and inferomarginals remain. The row of plates adjoining the adambulacrals is very narrow, longer than broad, and only the edge of the plate may be visible. Most of the actinolaterals carry a long, flattened, appressed spine, directed upward and attached to a prominent tubercle. All of these arm plates are in regular longitudinal and transverse rows; however, the latter do not correspond to the adambulacrals. Papulae occur singly or in groups of up to 5 between the plates; none occur below the inferomarginals. The terminal ocular plates are cordiform, covering the arm tip, with 3 or more coarse terminal spines.

Adambulacral plates are of two alternating sorts, carinate and noncarinate (Figure 7); the carinate adambulacrals project strongly into the ambulacral groove and bear 4 movable spines on a transverse row of tubercles. The spines are stout and rounded at the

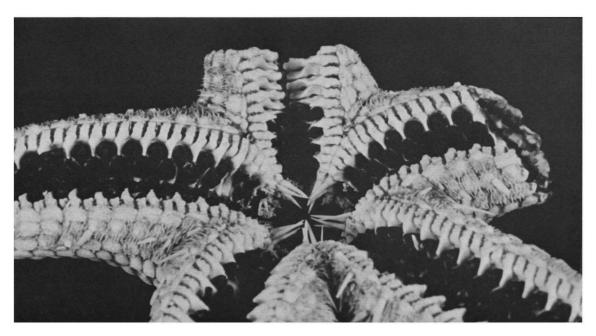


Figure 7.—Doraster constellatus, cleaned specimen, showing the carinate and noncarinate adambulacral plates. Paratype (USNM E11353).

FIGURE 8.—Doraster constellatus, showing the large duck-billed pedicellariae typical of the Zoroasteridae. Holotype (USNM E11352).



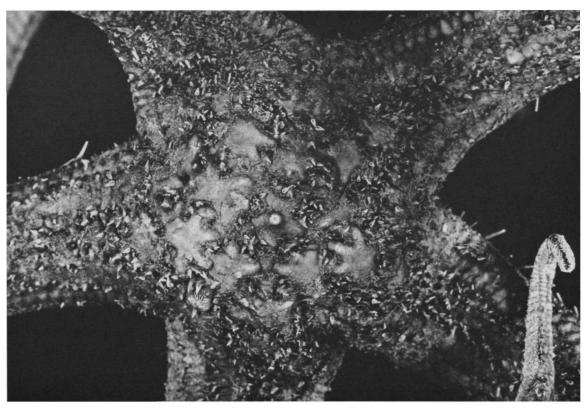
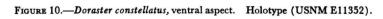
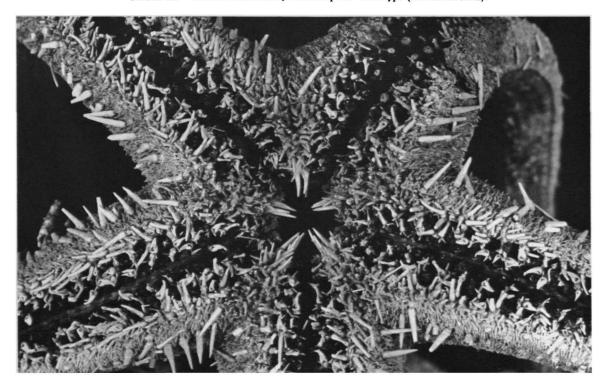


FIGURE 9.—Doraster constellatus, dorsal aspect. Holotype (USNM E11352).





point of attachment, tapering rapidly to a point; they may be curved. The 1st or 2nd spine usually bears a large duckbilled pedicellaria (Figure 8), and there are numerous small straight pedicellariae. The noncarinate adambulacrals bear 3 to 5 small spinelets on their outer surface and do not project into the furrow; they may also bear small straight pedicellariae.

Size RANGE.—R=42 mm to 220 mm; r=7 mm to 32 mm. Average R/r=10/1. R=major radius, from center of disc to tip of arm. r=minor radius, from center of disk to interbrachial margin.

MATERIAL EXAMINED.—Oregon station 3583, 09° 16'N, 81°37'W, 280 fms., May 1962, 1 specimen; Oregon station 382, 29°11.5'N, 88°07.5'W, 190-210 fms., June 1951, 6 specimens; Oregon station 2780, 11° 36'N, 62°52'W, 215-230 fms., April 1960, 2 specimens; Alaminos station 21/68-A-13, 27°37.5'N, 95°20'W, 350 fms., November 1968, 1 specimen; Oregon II station 10602, 07°46'N, 54°35'W, 299 fms., May 1969, 1 specimen; Albatross station 2376, 29°03'N, 88°16'W, 324 fms., February 1885, 8 specimens; Albatross station 2377, 29°07'N, 88°08'W, 210 fms., February 1885, 4 specimens; Albatross station 2396, 28°34'N, 86°48'W, 335 fms., March 1885, 1 specimen; Albatross station unknown, winter cruise 1885, 1 specimen.

LOCATION OF TYPE-MATERIAL.—Holotype (USNM E11352) and 22 paratypes in United States National Museum; 1 paratype in British Museum; 1 paratype in Museum of Comparative Zoology at Harvard.

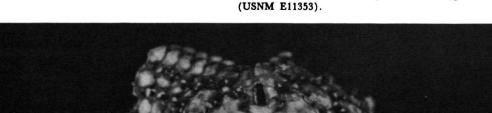
## Mammaster sigsbeei (Perrier, 1880)

In view of the fact that some specimens of Doraster constellatus have previously been misidentified as Mammaster sigsbeei (Perrier), it may be helpful to include here a brief redescription of M. sigsbeei.

DESCRIPTION.—The arrangement of plates on the disc is definite and unmistakable: a centrodorsal plate, next, 5 interradial plates, then 5 larger radial plates. In each interradial arc are 2 large somewhat crowdedlooking plates, and over the base of each arm are 3 large tumid plates. All these plates are raised, tumid, round, somewhat bare (although they may have small spinelets around the edge). The madreporite is small and inserted between the 2 interradial arc plates and the interradial primary plate.

The jaws bear 3 transverse rows of 2, 2, and 3 to 4 long acute spines, and inside the mouth, not visible without dissection, are 2 more pairs, the central pair short and blunt, and the outer pair curved away from the jaws like cow's horns, both pairs covered with small pedicellariae. Both small and large straight pedicellariae are present in the ambulacral groove and on the dorsal surface, especially on the disc.

The number of rows of tubefeet diminishes from 4 to 2 about half to three quarters of the way down the arm. Only the carinal plates and 1 row of plates on each side extend all the way to the end of the arm. The terminal plate is as broad as long, with an indentation



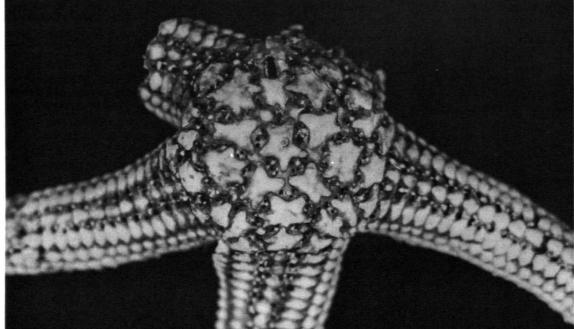


FIGURE 11.—Doraster constellatus, dorsal aspect of cleaned specimen. Paratype

on the proximal dorsal side. The carinals are overlapped on each side by the plates of the next adjoining row. These 3 rows of plates are comparatively bare, with only a few spinules on the distal edges of the plates, and are probably covered by a thin skin. The next row of plates is covered with tiny spinules, is overlapped by the adradials, and in turn overlaps the similar row of plates below it. Both of these rows diminish and disappear before reaching the end of the arm, the lower row first, then the upper. Next come 2 rows of narrow elongate plates which disappear distally before the rows above. Each of the plates in these 4 spinose rows bears 1 larger spine on a turbercle. The adambulacral plates are alternately carinate and noncarinate, with every other one projecting strongly into the furrow and bearing 4 stout movable spines in a transverse row. These spines are frequently curved and the 1st or 2nd often bears 1 or 2 large pedicellariae. The adambulacral plates between do not project into the furrow, and have no furrow spines, but bear 2 to 4 somewhat flattened spines distally side by side in pairs. The difference between the alternating adambulacrals becomes less distinct distally.

JUVENILE.—A specimen from Combat station 450 has R=9mm. The centrodorsal plate is by far the largest plate and bears a blunt tubercle. There are only 2 rows of plates on the arms beyond the carinals proximally and only 1 row distally. There is no appreciable alteration of the adambulacral plates. There are only 2 rows of tubefeet the whole length of the arm. The primary plates of the disc, except for the centrodorsal plate, are not appreciably raised and tumid. There are no pedicellariae.

MATERIAL EXAMINED.—MCZ 876, cotype, 1 dry, off St. Kitts, 208 fms., Blake collection; MCZ Ex. 877, cotype, 1 dry, 28°42'N, 88°40'W, 321 fms., Blake collection; MCZ 4048, 8 dry, Cuba, Old Bahama Channel off Punta Alegra, 195-230 fms., Atlantis stations 2981B, 2982B, 2982C, March 1938; MCZ 4049, 7 dry, west end of Old Bahama Channel, 235-260 fms., Atlantis stations 2983, 2983A, March 1938; MCZ 4053, 1 dry, Cuba, off Puerto Tanama, 295 fms., Atlantis station 3371, April 1938; MCZ 4054, 4 dry, Cuba, Old Bahama Channel off west end of Cayo Romano, 245-255 fms., Atlantis stations 3387, 3388, April 1939; MCZ 4057, 3 dry, Cuba, off Bahia de Matanzas, 285 fms., Atlantis station 3483, May 1939; MCZ 4050, 4 dry, south end of Santoren Channel, southeast of Cay Sal Bank, 250 fms., Atlantis station 2985; MCZ 4051, 3 dry, Nicholas Channel south of Cay Sal Bank, 280–300 fms., Atlantis station 2987, March 1938; MCZ 4056, 1 dry, Nicholas Channel south of Cay Sal Bank, 325 fms., Atlantis station 3443, May 1939; MCZ 4055, 13 dry, Cuba, off Caibarien, 245–265 fms., Atlantis stations 3431, 3434, 3435, 3436, 3437, 3438, April 1939; MCZ 4052, 1 dry, Cuba, off Bahia Matanzas, 170–255 fms., Atlantis station 3000, March 1938; MCZ 880, cotypes, 2 wet, same as MCZ 876; USNM E3967, 1 dry, Smithsonian-Johnson expedition station 23, 18°32′N, 66°21′W, 260 fms., 1933; Combat station 450, 10 dry, 23°59′N, 79°43′W, 350 fms., July 1957; Oregon, 5 dry, no station, Florida Keys, 200 fms.; Oregon station 2775, 1 dry, 11°35′N, 62°37′W, 220–230 fms., April 1960.

# The Genera and Species of Zoroasteridae

The characters of the other genera of Zoroasteridae are firmly established by the original authors and by H. L. Clark (1920) and W. K. Fisher (1919a, b). I see no need to redescribe any of them here. A list, however, of the genera and species and their known distribution follows.

GENERA AND SPECIES

Zoroaster Thomson, 1873 fulgens Thomson, 1873

actinocles Fisher, 1919 adami Koehler, 1909 alfredi Alcock, 1893

angulatus Alcock, 1893 barathri Alcock, 1893 carinatus Alcock, 1893 carinatus philippinensis Fisher, 1916 evermanni Fisher, 1905

evermanni mordax Fisher, 1919 gilesii Alcock, 1893 hirsutus Ludwig, 1905 (ejuv.) macracanthus Clark, 1916 magnificus Ludwig, 1905 microporus Fisher, 1916 ophiactis Fisher, 1916 ophiurus Fisher, 1905 orientalis Hayashi, 1950 perarmatus Clark, 1920 planus Alcock, 1893 DISTRIBUTION

North Atlantic, 120–1600 fms.
Aleutians, 1217 fms.
Bay of Bengal, 569 fms.
Bay of Bengal, 1300–1380 fms.
Indian Ocean, 597–705 fms.
Bay of Bengal, 1520 fms.
Andaman Sea, 130–250 fms.
Borneo, 415 fms.

Southern California, 216-510 fms. Washington to California, 275-815 fms. Andaman Sea, 400-500 fms. Acapulco, Mexico, 1878 fms. Eastern Tropical Pacific, 780-1320 fms. Australia, 250-450 fms. Gulf of Panama, 1671 fms. Moluccas, 700 fms. Celebes, 834 fms. California, 1059 fms. Japan, 105-475 fms. Peru, 536 fms. Laccadive Sea, 1200 fms.

#### GENERA AND SPECIES

spinulosus Fisher, 1906 tenuis Sladen, 1889 (?juv.) Bythiolophus Fisher, 1916 acanthinus Fisher, 1916 Cnemidaster Sladen, 1889 wyvillei Sladen, 1889 nudus Ludwig, 1905 squameus Alcock, 1893 zea Alcock, 1893 Doraster, new genus constellatus, new species

Mammaster Perrier, 1894 sigsbeei (Perrier, 1880) Myxoderma Fisher, 1905 sacculatus Fisher, 1905

platyacanthus Clark, 1913
platyacanthus rhomaleum
Fisher, 1919
Pholidaster Sladen, 1889
squamatus Sladen, 1889
distinctus Fisher, 1919
Prognaster Perrier, 1891
(genus doubtful)
grimaldii Perrier, 1891
(? see page 14)

#### DISTRIBUTION

Hawaii, 328-558 fms. New Guinea, 1070 fms.

Celebes, 559 fms.

Philippines, 761–1089 fms. Gulf of California, 998 fms. Laccadive Sea, 1043 fms. Indian Ocean, 597–1200 fms.

Caribbean, Gulf of Mexico, 190-350 fms.

Caribbean, 200-450 fms.

West coast of North America, 284-916 fms. Lower California, 284 fms. Oregon to California, 223-550 fms.

Philippines, 100 fms. Banda Sea, 140 fms.

Azores, 1568 fms.

## The Atlantic Species of Zoroaster

In the course of this study, I examined critically the Atlantic species of the genus *Zoroaster*. Unfortunately, the types of many species from other parts of the world were not available to me, and a complete revision of the genus was neither possible nor, at this point, particularly necessary. It is appropriate, however, to include here my conclusions regarding the species found in the Atlantic.

The characters used to distinguish the species of Zoroaster are, on the whole, unsatisfactory. Degree of development of the adradial plates is more a function of growth than a firm taxonomic character; presence of a central spine on certain plates is untrustworthy, because of the weakness of attachment (presence or absence of a tubercle is not necessarily indicative of presence or absence of a spine) and also because this, too, may be a function of growth. Large duck-billed pedicellariae are lacking in Pholidaster and sometimes in Mammaster, but their number and placement are variable within the species of Zoroaster. The armature of the actinolateral plates apparently is also variable within a species.

As with most asteroids, the number of furrow spines is a dependable character. Armature of the disc plates, degree of ensacculate spinulation, and tumidity of disc plates are mostly useable but less dependable specific characters. The ratio of minor to major radius may prove useful and if so, I would be inclined to separate Perrier's longicaudus from the rest of the Atlantic Zoroasters. Long slender arms also characterize ackleyi and seem to set it apart from trispinosus, fulgens, and diomedeae; however, gradations between ackleyi and these last three "species" lead one inevitably to the conclusion that R/r is an environment-dependent factor. Size and placement of papular pores should, perhaps, be given more attention, but are probably a function of R/r.

The synonymizing of diomedeae, ackleyi, and trispinosus (and possibly longicaudus) with fulgens has the unfortunate effect of rendering H.L. Clark's (1920) key to the species of Zoroaster practically useless. With the types, however, of many of the species he listed unavailable to me for study and comparison, I feel it would be unwise to attempt a revised key here. As this is mostly a deep water family, I am sure that further synonymizing among the Zoroasteridae, particularly in the genus Zoroaster, is inevitable with further study on a worldwide basis.

H.L. Clark (1920) indicates that Prognaster longicauda Perrier is a Zoroaster; in this he is quite correct. It is probably Zoroaster fulgens. Neither Clark nor myself, however, had an opportunity to examine Prognaster grimaldi Perrier, the type species of the genus. P. grimaldi is known only from the type specimen (Azores, 1568 fms.), and I suspect, as did Clark, that it, too, is a Zoroaster, probably fulgens. The only character on which Prognaster is separated from Zoroaster is that the former has all adambulacral plates alike, the latter has the usual zoroasterid alternate carinate and noncarinate adambulacrals. Adambulacral plates alike would be a very important and unusual character in this family, but I doubt that it really exists in Perrier's specimen. Perrier's figures in his Monaco report (1896) show an unusually wide area between the carinate adambulacrals and the figures look, in every respect, like Zoroaster fulgens; Perrier, however, states that he did not observe two kinds of adambulacral plates. As he had only one specimen, he was probably reluctant to dissect it sufficiently to determine this character.

## Zoroaster fulgens Thomson, 1873

Zoroaster ackleyi Perrier, 1883. Zoroaster diomedeae Verrill, 1884. Zoroaster trispinosus Koehler, 1895. Zoroaster bispinosus Koehler, 1909.

Description.—A 5-lobed centrodorsum, 8 primary radials (in overlapping pairs) and 5 large interradials, plus five large first carinals, make up the disc dorsum. The anus is between the centrodorsum and 2 primary radials, which are single rather than being paired like the other 6. The anal pore is surrounded by small flattened spines. Small pedicellariae may be scattered over the disc. The madreporite is small, flat, channeled, and located just distal to a primary interradial.

Each carinal plate on the arms has 2 lobes on each side and overlaps the carinal plate proximal to it. Transversely, the carinals overlap the adradials and the superomarginals overlap both the adradials and the inferomarginals. Below the inferomarginals are 6-2 rows of actinolateral plates (6 near the disc, becoming 2 by the end of the arm). Each actinolateral plate bears a long, slender, appressed spine, directed upward, and mounted on a horseshoe-shaped tubercle, plus numerous small sacculate spinelets. The inferomarginals are similarly armed. The superomarginals and carinals frequently (but not always) bear a stout erect central spine or tubercle, and these plates, as well as the adradials, are covered with small spinelets. The carinals are broader than long proximally and longer than broad distally.

The superambulacral plates are very small and do not extend beyond about the middle of the arm. The tubefeet are in 4 rows proximally, becoming 2 rows less than half way out on the arm. They are stout, conical, terminating in a small suckered disc (except for those actually within the peristomial cavity, which have large suckered discs), and the ampullae are double. The adambulacral plates are alternately carinate and noncarinate; the carinate adambulacrals bear 5 spines, 2 long slender furrow spines with many small straight pedicellariae (a large duck-billed pedicellaria may replace the many small ones) and 3 outer spines which are similar to the 3 small spines of the noncarinate adambulacrals; these small spines do not bear pedicellariae.

The jaw, of 4 fused adambulacral plates, bears 2 short stout oral spines on each side in a row along the

oral edge of the jaw, covered with small straight pedicellariae, and behind them are 2 pairs of long acute spines.

Discussion.—Careful examination of the three socalled species of Atlantic Zoroasters reveals that they belong to one rather variable species. H. L. Clark (1920) reviewed the Zoroasteridae very thoroughly and gave keys to the genera and species. He stated, quite correctly, that Zoroaster trispinosus Koehler is a synonym of Z. fulgens; Z. bispinosus Koehler is a lapsis calami for Z. trispinosus. The other species names which he listed from the Atlantic as having once been considered species of Zoroaster have been put into other genera in the family (Z. sigsbeei=Mammaster sigsbeei; Z. longicauda=Prognaster longicauda). P. longicauda, however, is definitely a Zoroaster and must be returned to that genus. Without more material, it is not possible to decide if this is a distinct species of Zoroaster or another synonym of Z. fulgens.

The types of Zoroaster fulgens could not be located; however, a specimen from Wyville Thomson's own collection, identified by him and now in the British Museum (Faroe Channel, 500 fms.) has been examined, as have the types of Z. ackleyi and Z. diomedeae. In addition, several hundred nontype specimens of the three so-called species have been examined and compared. Presence, absence, or degree of development of the superomarginal spines, and relative width of the carinal plates are the sole characters on which the Atlantic Zoroasters have been separated. These characters, vague and unsatisfactory to begin with, prove extremely variable throughout the range of the genus in Atlantic waters. As the oldest name, Zoroaster fulgens has priority, and Z. ackleyi and Z. diomedeae are junior synonyms.

On the whole, Zoroaster fulgens from the northern part of its range tends to be more spinous and more robust; also, it is generally found below 1000 fathoms. In the southern part of its range, it is more compact of skeleton, less spinous, and the arms, because of the more compact skeleton, seem to be more slender; it is found in waters as shallow as 200 fathoms.

MATERIAL EXAMINED.—USNM 9066, Albatross station 2052, 39°40'N, 69°21'W, 1098 fms., August 1883, 7 specimens (syntypes of Zoroaster diomedeae); USNM 26258, Albatross station 2043, 39°49'N, 68°-28'W, 1467 fms., July 1883, 1 specimen (syntype of Z. diomedeae); USNM 14050, Albatross station 2043, see above, 6 specimens (syntypes of Z. diomedeae);

USNM 14049, Albatross station 2095, 39°29'N, 70°-58'W, 1342 fms., September 1883, 40 specimens (syntypes of Z. diomedeae); USNM 14048, Albatross station 2035, 39°26'N, 70°02'W, 1362 fms., July 1883, 73 specimens (syntypes of Z. diomedeae); USNM 9017, Albatross station 2035, see above, 7 specimens (syntypes of Z. diomedeae); USNM 9019, Albatross station 2051, 39°41'N, 69°20'W, 1106 fms., August 1883, 5 specimens (syntypes of Z. diomedeae); USNM 9223, Albatross station 2084, 40°16'N, 67°05'W, 1290 fms., September 1883, 1 specimen (syntype of Z. diomedeae); USNM E4944, Dry Tortugas, Florida, collected by P. Bartsch, 13 specimens; USNM 14274, Albatross station 2077, 41°09'N, 66°02'W, 1255 fms., September 1883, 1 specimen; USNM 14275, Albatross station 2084, see above, 2 specimens; USNM 7864, Albatross station 2208, 39°33'N, 71°16'W, 1178 fms., July 1884, 1 specimen; USNM 11265, Martha's Vinyard, Massachusetts, 1390 fms., 2 specimens; USNM 14830, Albatross station 2684, 39°35'N, 70°54'W, 1106 fms., July 1886, 1 specimen; USNM 12041, Albatross station 2571, 40°09'N, 67°09'W, 1356 fms., September 1885, 11 specimens; USNM 11263, Albatross station 2562, 39°15'N, 71°25'W, 1434 fms., August 1885, 54 specimens; USNM 11265, Albatross station 2564, 39°22'N, 71°23'W, 1390 fms., August 1885, 80 specimens; USNM 11262, Albatross station unknown, 1885, 10 specimens; USNM 15544, Albatross station 2732, 37°27'N, 73°33'W, 1152 fms., October 1886, 6 specimens; USNM 17999, Albatross station 2196, 39°35'N, 69°44'W, 1230 fms., August 1884, 1 specimen; all of the above specimens were identified by A. E. Verrill as Zoroaster diomedeae.

USNM E5696, South of Dry Tortugas, Florida, collected by W. Schmitt, August 1932, 1 specimen; USNM 18507, Albatross station 2655, 27°22'N, 78°-07'W, 338 fms., May 1886, 5 specimens; USNM 10422, Albatross station 2394, 28°38'N, 87°02'W, 420 fms., March 1885, 2 specimens; USNM 18450, Albatross station 2396, 28°34'N, 86°48'W, 335 fms., March 1885, 2 specimens; USNM 18504, Albatross station 2659, 28°32'N, 78°42'W, 509 fms., May 1886, 1 specimen; USNM 18505, Albatross station 2380, 28°-02'N, 87°43'W, 1430 fms., March 1885, 1 specimen; USNM 18506, Albatross station 2381, 28°05'N, 87°-56'W, 1330 fms., March 1885, 1 specimen; USNM 38243, Fish Hawk station 7281, 24°13'N, 81°58'W, 304 fms., February 1902, 1 specimen; Alaminos station 3C/68-A-7, 27°42'N, 87°44'W, 1500 fms., July

1968, 1 specimen; Oregon station 1537, 24°29'N, 83°27'W, 212 fms., June 1956, 2 specimens; Oregon station 2574, 26°34'N, 89°53'W, 1450 fms., July 1959, 4 specimens; Oregon station 3561, 16°35'N, 80°04'W, 400 fms., May 1962, 1 specimen; Oregon station 3560, 16°35'N, 80°10'W, 315 fms., May 1962, 2 specimens; Oregon station 5929, 15°39'N, 61°10'W, 335 fms., March 1966, 5 specimens; Oregon station 4413, 11°-53'N, 69°25'W, 350 fms., October 1963, 3 specimens; Oregon station 2571, 26°30'N, 90°31'W, 1300 fms., July 1969, 1 specimen; Oregon station 2202, 28°58'N, 88°11'W, 625 fms., June 1958, 2 specimens; Oregon station 2779, 11°35'N, 62°59'W, 260 fms., April 1960, 1 specimen; Oregon station 2824, 29°75'N, 88°04'W, 365 fms., July 1960, 2 specimens; Oregon station 2652, 18°18'N, 67°18'W, 300 fms., October 1959, 10 specimens; Oregon station 1538, 24°29'N, 83°32'W, 200 fms., June 1956, 6 specimens; Oregon station 382, 29°11'N, 88°07'W, 200 fms., June 1951, 6 specimens; Oregon station 2650, 18°16'N, 67°17'W, 250 fms., October 1959, 5 specimens; all of the above specimens were identified by various people as Zoroaster ackleyi.

British Museum (Natural History) 1949–2–14–29, Faroe Channel, 500 fms., 1 specimen, collected by Wyville Thomson; USNM 33308, west coast of Ireland, gift of Department of Agriculture, Ireland, 2 specimens; USNM 7865, Albatross station 2206, 39°35′N, 71°24′W, 1043 fms., August 1884, 1 specimen; USNM 31265, Fish Hawk station unknown, San Juan, Puerto Rico, 1 specimen; USNM 31266, same as 31265, 1 specimen; Alaminos station 1/68–A–13, 25°42′N, 96°04′W, 480 fms., November 1968, 2 specimens; Alaminos station 10B/68–A–3, 25°12′N, 96°21′W, 550 fms., March 1968, 2 specimens; Oregon station 3654, 29°08′N, 88°00′W, 400 fms., July 1962, 6 specimens; Oregon II station 10619, 07°51′N, 54°23′W, 425 fms., May 1969, 1 specimen.

MCZ 873, Santa Cruz, 248 fms., Blake collection, 4 specimens (syntypes of Z. ackleyi); MCZ 4045, Cuba, off Bahia de Matanzas, 145–255 fms., Atlantis stations 2999, 3000, March 1938, 19 specimens; MCZ 4047, Cuba, off Bahia de Matanzas, 175–285 fms., Atlantis stations 3465, 3467, 3478, 3479, 3480, 3482, 3483, May 1939, 23 specimens; MCZ 4041, Cuba, Old Bahama Channel, 105–260 fms., Atlantis stations 2980A, 2982B, 2982C, March 1938, 5 specimens; MCZ 4044, Cuba, Nicholas Channel off Bahia de Santa Clara, 475–580 fms., Atlantis stations 2991A, 2992A, 2993, March 1938, 3 specimens; MCZ 874, off Yucatan, 600 fms.,

Blake collection, 1 specimen; MCZ 3046, South Tortugas, 240 fms., 5 specimens; MCZ 4046, Cuba, off Caibarien, 260 fms., Atlantis station 3437, May 1939, 2 specimens; MCZ 4040, Cuba, off Punta Lucrecia, 1015 fms., Atlantis station 2975, March 1938, 1 specimen; MCZ 4042, Cuba, west end of Old Bahama Channel off north coast, 235–260 fms., Atlantis station 2983A, March 1938, 2 specimens; MCZ 4043, Nicholas Channel, south of Cay Sal Bank, 280–300 fms., Atlantis station 2987, March 1938, 1 specimen; MCZ 879, Santa Cruz, same as 873, 3 specimens (syntypes of Z. ackleyi); MCZ 4075, same as 4047, 6 specimens; all of the above were identified as Zoroaster ackleyi.

MCZ 3719, off Nantucket, 40°05'N, 67°52'W, 1325 fms., Atlantis station unknown, 1939, 37 specimens; MCZ 3744, 40°06'N, 68°06'W, Atlantis, July 1939, 1160–1100 fms., 8 specimens; MCZ 872, Albatross station 2043, Gulf Stream, 4 specimens; MCZ 878, south of Nova Scotia, Challenger collection, 1 specimen; MCZ 949, 38°96'N, 73°10'W, 1186 fms., Blake collection, 2 specimens; all of the above specimens were identified as Zoroaster diomedeae. MCZ 2730, northwest of Azores, 1000 fms., 1903, 2 specimens, identified as Zoroaster trispinosus.

MCZ 1856, North Atlantic, Thor collection, 1906, 1 specimen. I also examined MCZ 875, Eastern Atlantic, Talisman collection, 1 specimen, which was identified by Perrier (1894) as Prognaster longicauda; as H. L. Clark suggests, it is definitely a Zoroaster, but because of the disportionately small disc and long slender arms, I hesitate to synonymize it with Z. fulgens.

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