THE OCCURRENCE OF THE GENUS HETERONARDOA (ASTEROIDEA: OPHIDIASTERIDAE) IN THE INDIAN OCEAN, WITH THE DESCRIPTION OF A NEW SPECIES

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ABSTRACT

The distribution of the genus *Heteronardoa* Hayashi (1973a) is described. Nardoa carinata and N. squamulosa Koehler (1910) and Narcissia mohamedi Macan (1938) are considered conspecific and are referred to *Heteronardoa*. H. carinata has priority. H. sagamina Hayashi (1973a) is considered conspecific with H. carinata. A new species of *Heteronardoa* is described.

INTRODUCTION

The genus Heteronardoa was described by Hayashi (1973a), with the genotype H. sagamina Hayashi, from Sagami Bay, Japan. He considered the genus to be intermediate between Certonardoa H.L. Clark, 1921 and Narcissia Gray, 1841 in having groups of papulae restricted to the abactinal surface, the partial regularity of the abactinal plates and the presence of pedicellariae. Recently, 16 specimens from the Smithsonian Institution (U.S.N.M.) collections, including 14 specimens collected from the western parts of the Indian Ocean during the International Indian Ocean Expedition (I.I.O.E.) and 2 specimens from the Philippine Islands which had been identified by Fisher (1919) as Nardoa squamulosa Koehler, and 18 specimens from the Western Australian Museum collections, including 6 collected from off north-western Australia and 12 from off the Aru Islands in Indonesia, were examined. 14 of the U.S.N.M. specimens (including the 2 identified by Fisher) and 17 of the Western Australian Museum (W.A.M.) specimens are identified as Nardoa carinata Koehler, which is here transferred to the genus Heteronardoa. The other 3 specimens are described and considered to represent a new, nominal species of Heteronardoa. Also in this paper, Nardoa squamulosa Koehler, Narcissia mohamedi Macan and H. sagamina Hayashi

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are considered synonyms of *H. carinata* (Koehler). The extended distribution of *Heteronardoa* is described.

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Heteronardoa carinata (Koehler) (Figs 1-9.)

Nardoa carinata Koehler, 1910, p. 165, pl. XV fig. 6, pl. XVI figs 10-11.

N. squamulosa Koehler, 1910, p. 168, pl. I fig. 8, pl. XV figs 7-8; Fisher, 1919, p. 383, pl. 105 fig. 5, pl. 111 figs 7-8;

Certonardoa carinata, H.L. Clark, 1921, p. 56; A.M. Clark, 1967, p. 186.

C. squamulosa, H.L. Clark, 1921, pp. 56-57.

Narcissia mohamedi Macan, 1938, p. 408, pl. I figs 2 & 10.

Heteronardoa sagamina Hayashi, 1973a, p. 6; 1973b, p. 65, fig. 8, pl. 9 figs 4-5.

Material examined

One specimen, Mariel King Memorial Expedition (hereafter indicated by M.K.M.E.), stn AW I/5, west of Wasir I., western Wokam, Aru, 15.vi.70, Lat. 5° 30'S, Long. 134°12'E, 55-58m; 1 specimen, M.K.M.E., stn AW IV/7, off west end of Udjir I., Wokam, Aru, 16.vi.70, Lat. 5° 37'S, 134°10'E, 78-86m; 8 specimens, M.K.M.E., stn AM II/3, 8 mls south-west of Tg Ratoe, Maikoor, Aru, 18.vi.70, Lat. 6°7'S, Long. 133°57'E, 55-64m; 1 specimen, as above, stn AM II/4-6, 45m; 1 specimen, as above, stn AM II/8-11, 60-64m; 3 specimens, H.M.A.S. 'Diamantina', cruise 4, stn 187, west of Point Quobba, Western Australia, 24.vii.64, Lat. 24°20'S, Long. 112°46'E, 117m, W.A.M. Nos 1759-74, 1760-74(2), A.M. No. J9192(1); 2 specimens, R.W. Geroge, 50 mls north-east off Adele Island, northwestern Australia, Lat. 15°31', Long. 123°09'E, 20.x.62, 91.4m, W.A.M. Nos 1758-74, 1763-74; 2 specimens, Philippine Islands (Albatross Expedition), U.S.N.M. Nos 40835, 40549 (these two specimens identified by Fisher (1919) as Nardoa squamulosa); 2 specimens 'Anton Bruun', cruise 9, stn 444, 16.xii.64, Lat. 9°36'N, Long. 51°01'E, 78-82m, U.S.N.M. No. E13779 (1). A.M. No. J9190 (1): 2 specimens, 'Anton Bruun', cruise 9, stn 445, 16.xii.64, Lat. 9°41'N, Long. $51^{\circ}03'E$, 60-70m, U.S.N.M. No. E13780 (1), A.M. No. J9189 (1); 4 specimens, 'Anton Bruun', cruise 9, stn 447, 16.xii.64, Lat. 10°00'N, Long. $51^{\circ}15'E$, 59-61m, U.S.N.M. No. E13781 (3), A.M. No. J9187 (1); 4 specimens, 'Anton Bruun', cruise 9, stn 449, 16.xii.64, Lat. 10°03'N, Long. $51^{\circ}15'E$, 31-39m, U.S.N.M. No. E13782 (3), A.M. No. J9191 (1).

Diagnosis

R/r 4 to 8.2; arms tapering to a narrow tip; abactinal surface with a carinal and up to 6 lateral rows of plates, dependant on arm length; carinal and first abactinal-lateral rows of plates extend (distally irregularly) to the arm tip; carinal plates transversely rectangular, larger than the abactinal-lateral plates, at least proximally on the arms; superomarginal and inferomarginal plates aligned along the arm; actinal-intermediate plates in 2-4 rows; adambulacral plates with 4-6 (usually 5-6) furrow spines, 4-5 subambulacral spines and 4-5 enlarged granules; surface with rounded to polygonal granules, those towards the centre of the plates and those around the papulae similar in size but larger than the granules towards the edge of and between the plates; papulae in groups, single only in juveniles, confined abactinally above the superomarginal plates; pedicellariae sometimes present.

Remarks

Koehler (1910) described this species from the Andaman Islands on the largest of seven small specimens (R/r= 40mm/10mm= 4). His smallest specimen had R=9mm. He described a second species (N. squamulosa) on a single specimen, from the same area, which was smaller than the holotype of carinata (R/r=37-38mm/7mm=c.5.5). Macan (1938) based his description of Narcissia mohamedi on the larger of 2 specimens (R/r= 95mm/14mm= 6.8), which had been collected in the Gulf of Aden. The second specimen (R/r = 39mm/6mm= 6.5) was collected from the Maldives. Fisher (1919) recorded 2 specimens of N. squamulosa from the Philippine Islands. H.L. Clark (1921) considered carinata and squamulosa to be congeneric with Certonardoa semiregularis, the type-species of a new genus which he described. A.M. Clark (1967) recorded a pedicellariae-bearing specimen of similar size to the holotype of Certonardoa carinata, from Galle, Sri Lanka. Hayashi (1973a) described a new species, Heteronardoa sagamina, for his monotypic genus Heteronardoa, after examining 7 specimens (R/r= 54mm-90mm/10mm-18mm = 4.7-5.8) from Sagami Bay, Japan. He nominated a specimen with R/r= 68mm/13mm= 5.2 as the holotype on which the description was mainly based.

Table 1

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	No. Specs recorded	R:r mm	R/r	No. rows abactlat. plates	Most frequent no. furrow spines	Maximum No. papulae/ area	Presence/Absence pedicellariae
Nardoa carinata Andaman İslands (From Koehler, 1910)	7	40.0:10.0 37.0: 7.0 28.0: 5.0 18.0: 4.0 10.0-18.0	4.0 5.3 5.6 4.5 -	3 - 2 1	6 - - - -	c.6	-
N. squamulosa Cape Negrais, Burma (From Keohler, 1910)	1	37.0-38.0: 7.0	c.5.5	3	Ġ	c.5-6	-
'Anton Bruun' stations 449	. 4	23.0: 4.5 49.0: 7.0 56.0: 7.5 65.0: 8.0	5.2 7.0 7.5 8.2	2 3 4 (+) 4	4-5 5 5-6 5-6	3-4 4-5 4-6 5-6	
447	4	38.0: 6.0 40.0: 6.5 60.0: 8.0 61.0: 8.0	6.3 6.1 7.5 7.5	3 · 3 4 4	5 6 5 5	3 3 4-5 5 (occas. 6)	- - -
445 .	2	56.0: 8.5 74.0: 9.0	6.6 8.2	4 5	6 5-6 (rarely 7)	4-6	-
444	2	58.0: 7.5 60.0: 8.0	7.7 7.5	3 4	5-6 6	3-4 3-4	-
M.K.M.E. stations AW IV - 7	. 1	40.0: 6.0	6.6	2	5	3	+
AW 1/5	1	16.3: 3.5	4.8	1	5	1 (occas. 2)	•
AM II/8-11	1 .	22.0: 3.0	7.3	1	5	1-2	+

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88

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Table 1 continued

AM II/4-6	1	15.0: 5.0	5.0	1	4	1	-
AM II/3	8	28.0: 4.5	6.2	2	5	1 (occas. 2)	+
		20.5: 2.5	8.2	1	4	1	-
		20.5: 3.5	5.8	1	5	1 (occas. 2)	-
		16.0: 2.7	6.0	1	5	1	+
		15.5: 2.5	6.2	1	5	1	+
		15.5: 2.5	6.2	1	5	1	+
		15.5: 2.5	6.2	1	5	1	-
		14.5: 2.5	5.8	1	4	1	-
'Diamantina' station				·····		1	
187	3	25.0: 4.0	6.2	1	5	1 1	_
		17.5: 3.2	5.3	1	6	1	
		17.5: 4.0	4.4	1	5	1	-
N.E. Adele Id.	2	17.5: 3.5	5.2	1	5-6	1	-
(R.W. George)		45.5: 6.0	7.6	2 (3)	6	3 (occas. 4)	-
N. squamulosa Philippines	2	24.5: 4.5	5.5	2	5	1 (occas. 2)	-
(identified by Fisher 1919)		42.0: 7.0	6.0	2	6	2-3 (occas. 4)	-
Narcissia mohamedi		1	1				
A. Gulf of Aden	2	A. 95.0:14.0	6.8	6	5	4-5	
B. Maldives		B. 39.0: 6.0	6.5	3	4-6	2-3	-
(From Macan, 1938)						2-0	-
Certonardoa carinata							
Galle, Ceylon	1	42.0: - 7	6.0	2(3)	5-6	3.5	
(From A.M. Clark, 1967)						0-0	
Heteronardoa sagamina	7	54.0-90.0:	4.7-5.8	3-4	4-6	3-4	
Sagami Bay, Japan	(incl	10.0-18.0			**		Ť
(From Hayashi, 1973)	holotype)						
	Holotype	68.0:13.0	5.2	4	5-6	3.4	
		1		-		1°-1	Ŧ



Figs 1-3: Heteronardoa carinata (Koehler). Abactinal view, M.K.M.E. specimen Stn AM II/3, R= 15.5 mm; 20.5 mm; 28.0 mm respectively.



Fig. 4: Heteronardoa carinata. Abactinal view, 'Diamantina' specimen, Stn 187 (W.A.M. No. 1759-74). R= 25.0 mm.

Fig. 5: Heteronardoa carinata (Koehler). Abactinal view, N.E. Adele Is. specimen (W.A.M. No. 1763-74). R= 45.5 mm.

The specimens examined here fall between Nardoa carinata and Narcissia mohamedi in size (see Table 1) and show such changes in development, with increase in size, that it would seem illogical to consider that the larger N. mohamedi and the smaller N. carinata are not conspecific. Table 1 records the R/r measurements, number of abactinal-lateral rows of plates, number of furrow spines per adambulacral plate, number of papulae per papular area and the presence or absence of pedicellariae for each of the specimens

examined together with the holotype and other specimens of N. carinata and N. squamulosa (taken from Koehler, 1910), N. mohamedi [examined in the British Museum (Natural History)] and H. sagamina (from Hayashi, 1973b). The influence of arm length on the development of abactinal-lateral plates and in the number of furrow spines can be clearly seen, Figs 1-9. The R/r ratio generally increases markedly in the middle of the size range, during which time the disc does not increase in diameter at the same proportional rate. By the time the species has reached the largest size recorded (i.e. for N. mohamedi) arm lengthening has either slowed downed or stopped while increase in disc diameter reduces the R/r ratio from over 8 to under 7 (or 6 in the Japanese specimens). This would tend to indicate that the animal has a distinctive growth pattern, through an arm lengthening phase and then a maturation phase. The extent of regularity of the abactinal plates along the arm and the number of furrow spines per adambulacral plate is variable to such a degree that N. carinata, N. squamulosa, Narcissia mohamedi and H. sagamina cannot justifiably be separated on these characters. Neither do I believe that the somewhat stouter-armed form of sagamina is sufficient grounds for considering it specifically distinct from the other species. From the examination of the smaller specimens of this collection, I believe that Koehler (1910) was mistaken in the number of papulae he recorded (c.6) per papular area in both carinata and squamulosa (see table 1), but I can agree with his opinion (1910: 170) that squamulosa would probably prove to be only a variety of carinata when more material was available for study. Neither Koehler nor Macan described the presence of pedicellariae on their specimens. Nor were there any pedicellariae to be found on the 'Anton Bruun' specimens or those from north-western Australia. I can confirm A.M. Clark's (1967) record of alveolar pedicellariae on a small specimen of H. carinata (as Certonardoa) from Sri Lanka. The specimen, with R= 42mm, compares in size with Koehler's holotype and differs only in its possession of pedicellariae. Also, 6 of the 12 specimens collected from the vicinity of Aru Island have pedicellariae of the type figured by Hayashi (1973b, fig. 8b). These 6 specimens have R= 15.5-40.0mm. A similar situation occurs in Certonardoa semiregularis, as Hayashi has indicated and which the present author can confirm, and in Narcissia canariensis, according to Sladen (1889). The occurrence of pedicellariae, as a species, character, in some (if not most) ophidiasterids is therefore very unreliable. Clark (1921) considered the presence of pedicellariae might represent a juvenile character, though the spasmodic nature of the occurrence within single populations and the occurrence of pedicellariae on specimens ranging in size from R= 15.5 mm-90mm, could possibly indicate a genetic factor. Either suggestion needs further investigation. Hayashi (1973b) records the life colour of H. sagamina as 'capucine buff, papular areas scarlet and arm tips morrocco-red'. A colour transparency of the largest specimen from off Adele Island, north-western Australia, shows it to be cream coloured with a ring of radial and interradial disc plates orange. Within that ring the plates are blotched orange/cream. Along the abactinal



Fig. 6: Heteronardoa carinata (Koehler). Abactinal view, I.I.O.E. specimen, Str. 449 (A.M. No. J9191). R= 23.0 mm.



Fig. 7: Heteronardoa carinata (Koehler). Lateral arm, I.I.O.E. specimen. Stu 447 (U.S.N.M. No. E13781). R= 38.8 mm.

side of the arms some of the plates are orange or blotched orange and these form 4 or 5 irregular but recognisable transverse bands. In its dry state the specimen is uniformly off-white.



Fig. 8: Heteronardoa carinata (Koehler). Lateral arm, I.I.O.E. specimen, Stn 447 (A.M. No. J9187). R= 60.0 mm.



Fig. 9: Heteronardoa carinata (Koehler). Lateral arm, I.I.O.E. specimen, Stn 445 (U.S.N.M. No. E13780). R= 74.0 mm.

Heteronardoa diamantinae sp. nov. (Figs 10-15.)

Nardoa semiregularis, Fisher, 1919, p. 383, pl. 105 fig. 3 (non Scytaster semiregularis Muller and Troschel).

Material examined: Holotype

H.M.A.S. 'Diamantina', stn 17, off Point Cloates, north-western Australia, 31.i.64, Lat. 22°59.7'S, Long. 113°25.5'E, 128m, W.A.M. No. 1762-74; 2 paratypes, 'Anton Bruun', cruise 8, stn 403E, 9.x.64, Lat. 19°09'S, Long. 36°55'E (Mozambique Channel), 88m, U.S.N.M. No. E13783(1), A.M. J9188(1).

Diagnosis

R/r= 6-7; 4 or 5 arms which taper to a narrow tip; abactinal surface with a carinal and 3-4 lateral rows of plates; no abactinal-lateral plates extend beyond 2/3 length of the arms; carinal plates squarish, similar in size to abactinal-lateral plates; superomarginal and inferomarginal plates similar, aligned along the arm; actinal-intermediate plates in 3-4 rows; adambulacral plates with 5-8 (usually 7) short furrow spines, 5-7 subambulacral spines and a second row of 5-6 slightly enlarged granules; surface with rounded to polygonal granules, those towards the centre of the plates and those around the papulae similar in size but larger than the granules towards the edge of and between the plates; papulae in groups, confined abactinally above the superomarginal plates; pedicellariae present or absent.

Description

The description is based on the holotype, followed by comments on each of the paratypes.

The holotype has 5 arms which are flat actinally, arched abactinally and taper to a narrow tip. R = 41.3 mm, r = 6.3 mm, R/r = 6.5 (one arm R = 32 mm shows regeneration from a severence), Figs 10 & 12.

The abactinal disc plates are rounded and vary in size to a maximum of about 1.5 mm diameter. Five plates surround the anus. A ring of radial and interradial plates is evident. Along the abactinal side of the arms is a carinal row and, basally, 3 (with 2 small plates in each angle of adjacent arms indicating the 4th) lateral rows of plates each side, Fig. 11. The basal carinal plates are about 1.5 mm square, and of similar size to the adjacent lateral plates. The plates diminish gradually in size along the length of the arms. The carinal and first lateral rows of plates extend regularly along the arm to about the 10th superomarginal, only the carinal plates extend to the tip of the arms. The second lateral rows of plates do not extend beyond the 6th superomarginal plate along the arms; the third to about the 4th superomarginal and the 4th does not extend beyond the 1st superomarginal. There are 28-30 superomarginal and inferomarginal plates of similar dimensions which are aligned along the arms. There are 2 rows of actinal-intermediate



Fig. 10: Heteronardoa diamantinae n. sp. Holotype. Abactinal view (W.A.M. No. 1762-74). R=41.3 mm.



Fig. 11: Heteronardoa diamantinae n. sp. Holotype. Actinal view (W.A.M. No. 1762-74). R=41.3 mm.

plates, with the indication of a 3rd as 2 plates in the angle between 2 adjacent arms. The innermost row of about 31 plates extends to the 20th inferomarginal and the second row of about 4 plates to the 2nd inferomarginal.



Fig. 12: Heteronardoa diamantinae n. sp. Holotype. Lateral view (W.A.M. No. 1762-74). R=41.3 mm.





Fig. 13: Heteronardoa diamantinae n. sp. Paratype. Abactinal view, I.I.O.E. specimen, Stn 403E (U.S.N.M. No. E13783). R-57.0 mm.



Fig. 14: *Heteronardoa diamantinae* n. sp. Paratype. Adambulacral furrow, I.I.O.E. specimen, Stn 403E (U.S.N.M. No. E13783). R=57.0 mm.

The 48 adambulacral plates bear 6, proximally, increasing to 7 or 8 short, blunt furrow spines on the 8th to 20th plates, thereafter the number of spines decreases. The first and last 1 or 2 spines are shortest and are flattened, spatulate, the remaining spines are subequal and square in cross-section. These are backed by a row of 5-7 truncate subambulacral spines and, at least proximally, a row of 5-7 slightly enlarged granules. The mouth plate has 9 furrow spines backed by 5 stout spines and a second row of 4-5 enlarged granules, the rest of the plate being covered by about 8 or 9 coarse granules.

Papulae occur only between the abactinal plates and are not found either between the superomarginals and inferomarginals or actinally. The papulae are in groups of 3, reducing to 2 and 1 distally and laterally. There are no papulae between the plates of the distal one fourth or one fifth of the arms. There are no pedicellariae.

The plates, where they are not rubbed bare, are covered with close granulation, but this does not obscure the limits of the plates. The granules towards the centre of the plates and those around the papulae are similar in size but larger than those towards the edge of and between the plates. The actinal granules are similar in size to the larger abactinal granules. The colour of the dry specimen is dusky-pink, the colour in life is not recorded.



Fig. 15: Heteronardoa diamantinae n. sp. Paratype. Abactinal view, I.I.O.E. specimen, Stn 403E (A.M. No. J9188). R= 36-42.0 mm.

The larger paratype has 5 arms with R/r- 57mm/9mm= 6.3, Fig. 13. The disc plates reach about 2 mm maximum diameter and only 3 plates surround the anus. There are 4 (one arm 5) abactinal-lateral rows of plates and the basal carinal plates are about 1.75 mm square. The carinal and first lateral rows of plates extend regularly to the 30th superomarginal; the second lateral row extends to about the 25th superomarginal; the third row to the 16-18th superomarginal; the fourth row to the 8-10th superomarginal and the fifth, where present, to the 3rd superomarginal. There are 42 superomarginals and inferomarginals and 3 rows of actinal intermediate plates, with a 4th row indicated by 2 plates in the angle between 2 adjacent arms. The innermost actinal intermediate row comprises 48 plates extending to the 30th inferomarginal; the 2nd row of 7-8 plates to the 5th inferomarginal and the 3rd row of 4 plates to the 2nd-3rd inferomarginal.

The adambulacral armature is similar to the holotype except that 7-8 furrow spines occur from the 10th-35th plates, Fig. 14. The mouth plate has 10-11 furrow spines backed by 6 large, stout spines and a second row of 4-5 enlarged granules, the rest of the plate being covered by 10 coarse granules. The papulae occur in groups of up to 5. There are no pedicellariae. The granulation is as in the holotype. The colour, in alcohol, is a very light pink; colour in life not recorded. The 2nd paratype has only 4 arms measuring R=36 mm-42mm, with r= 6mm; R/r= 6-7, Fig. 15. There are 3 rows of abactinal-lateral plates (though there is evidence of a 4th row on one side of one arm). The ring of radial plates is not distinct on the disc. There are 34 superomarginal and inferomarginal plates (R= 42 mm). There are 3 rows of actinal intermediate plates. There are 5-7 furrow spines but in this specimen 7 spines occur from as early as the 5th adambulacral plate. The mouth plate is as in the holotype. The papulae occur in groups of up to 4. There are no pedicellariae. The granulation and colour is the same as for the larger paratype.

The specimen identified by Fisher (1919) as Nardoa semiregularis has been re-examined by Miss M.E. Downey (Smithsonian Institution, U.S.A.), who informs the author that the specimen is grey-brown in colour; has usually 6 furrow spines; the granules over the papular areas seem infinitesimally smaller than those on the plates; no papulae occur intermarginally or actinally and that there are a few very tiny ophidiasterid (sugar-tong) pedicellariae on a few of the proximal superomarginals.

Similarly there are pedicellariae on the smaller specimens of H. carinata (see table 1). The apparent lack of difference between the granules on the plates and papular areas is surprising but with all factors considered, from both Fisher's description and plate and Miss Downey's re-examination, there seems little doubt that Fisher's specimen represents the species H. diamantinae. With R= 29 mm this is the smallest specimen of diamantinae so far recorded.

Remarks

Heteronardoa diamantinae is clearly quite closely related to *H. carinata* but can be readily distinguished from that species by the fact that the abactinal-lateral plates do not extend to the tips of the arms, the similarity in size of the carinal and abactinal-lateral plates, the squarish carinal, the higher number of furrow spines and the colour.

Discussion

The genus *Heteronardoa* was established by Hayashi for a Japanese species of ophidiasterid, *H. sagamina*. It is considered (see table 1), however, that the Indian Ocean species *Nardoa carinata* Koehler, *N. squamulosa* Koehler and *Narcissia mohamedi* Macan are not only congeneric with *H. sagamina* but conspecific with it. *Heteronardoa carinata* (Koehler) has priority. Despite this synonymy, it is also apparent that a second, but new, species of Heteronardoa, H. diamantinae, occurs in the Indian Ocean and Philippine Islands.

In his description of the genus 2 characters should have been given more emphasis by Hayashi. These are the lack of papulae not only actinally but also intermarginally, and the similarity in size of the granules in the central area of the abactinal plates with those around the papulae and the smaller size of the granules towards the outer margins of and between the abactinal plates. Papulae are found between the marginal rows of *Certonardoa* and *Narcissia* and the granulation is even. The presence or absence of pedicellariae is obviously variable in all three genera (Sladen, 1889; Hayashi, 1973b; Table 1).

H. carinata is geographically widely distributed, occurring from the Gulf of Aden, Arabian Sea, Maldives, Andaman Islands, off north-western Australia, Aru Islands, the Philippine Islands and Japan. *H. diamantinae* is, at present, known only from three localities as far apart as the Mozambique Channel, the North-West Cape of Australia and the Philippine Islands. This compares with *Certonardoa* which is restricted to Japan and Indonesia and *Narcissia* from the tropical Atlantic and the Gulf of California (Hayashi, 1973b). The species of *Heteronardoa* occur in depths of between 30-230m, though more generally between 60-100m, which is deeper than *Certonardoa* but probably the same depth as *Narcissia*.

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