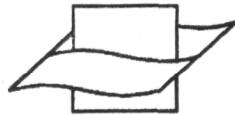


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A NEW TAXONOMIC AND ZOOGEOGRAPHIC INTERPRETATION OF THE

DIACRIA QUADRIDENTATA GROUP

(MOLLUSCA, PTEROPODA)

21695

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ABSTRACT

Re-examination of the *Diacria quadridentata* species group based upon morphology of the shell and zoogeographic data, led to a new classification comprising the recent taxa: *D. quadridentata*, *D. costata* with an equatorial and a central water form, *D. danae* with an equatorial and a central water form, *D. schmidti schmidti*, *D. erythra crassa* and the fossil taxa *D. schmidti occidentalis* and *D. erythra erythra* from surface sediments.

A method has been developed to estimate the relative age of the population, based on the development of shell and soft parts. Shell growth in the period of minute and adult stages together does not exceed 0.2 mm, and differs from species to species.

INTRODUCTION

In the polytypic species *Diacria quadridentata* six infraspecific taxa were distinguished by the second author (Van der Spoel, 1968; 1971). Some of these taxa are sympatric; in spite of this, infraspecific taxa were proposed, not excluding interbreeding.

Since then, co-occurrences of forms in var-

ious combinations have been recorded more and more often (Rampal, 1975). The absence of intergradations between most of the taxa studied over their entire range suggests that infraspecific taxa cannot be maintained in all cases. A renewed study of the morphology, growth, distribution and phylogeny has been carried out, resulting in the following more acceptable taxonomy of the group:

taxa:

- Diacria quadridentata* (MS. Lesueur) (De Blainville, 1821)
D. costata Pfeffer, 1879; central water form
D. costata Pfeffer, 1879; equatorial water form
D. danae Van der Spoel, 1968; central water form
D. danae Van der Spoel, 1968; equatorial water form
D. schmidtii schmidtii Van der Spoel, 1971
D. schmidtii occidentalis nov. subsp.
D. erythra erythra Van der Spoel

D. erythra crassa Van der Spoel, 1971

distribution:

- Indo-W. Pacific
Indo-W. Pacific
Indo-W. Pacific
bi-subtropical
circum-equatorial
East Pacific
subfossil: West Pacific
subfossil: Red Sea &
Indian Ocean
Red Sea; subfossil:
Indian Ocean

The material used in this study consists of:

Dana Expeditions Stations: (plankton samples)

681, 1194^{XI}, 1202^{IV}, 1203^V, 1214^{II}, 1241^{VII},
1269^{II}, 1279, 1322^{XXXVII}, 1334^V, 1342^{IX},
1355^{II}, 1356^{IV}, 3556^{VIII}, 3561^{IX,X}, 3567^{II},
3576^{VII}, 3579^{IV}, 3580^{IV}, 3584, 3585, 3613^{IV},
3620^{IV}, 3623^{VII}, 3718^V, 3723^V, 3730^V,
3731^{IV}, 3739^{IV}, 3768^{VI}, 3800^{IV}, 3814^{III},
3824^{VII}, 3844^{IV}, 3910^{IV}, 3914, 3915^{IV},
3918^V, 3920^{IX}, 3925^V, 3944^{IV}, 3956^V, 3962^V,
3965^{II}, 3997^V, 4003^{XI}, 4794.

United States Bureau of Fisheries collections,

Stations: (all sediment samples) 317, 5097,
5410, 5582, 5586, 5650.

Siboga Expedition Stations: (all plankton sam-

ples) 37, 59, 66, 95, 99, 136, 139, 143,
144, 165, 177^a, 185, 203, 215^a, 224, 243,
315.

Some two and a half thousand specimens were studied, about 1500 of which were measured. The accuracy was 0.03 mm, except for the protoconchae which were measured with an accuracy of 0.016 mm. The sizes measured are indicated in fig. 1. Besides, the sculpture of the shell was studied with light- and scanning electron microscope and by means of 1 mm thick slices of the dorsal lip.

The authors wish to express their thanks to Dr. J. Knudsen (Universitets Zoologisk Museum, Copenhagen) and to Dr. C.F.E. Roper (National Museum of Natural History, Washington) for kindly making available large amounts of important samples. For technical assistance the authors thank A.F. de Fluiter and for preparing the manuscript they are indebted to E. van der Zee.

GROWTH AND AGE

The three developmental stages described by Van der Spoel (1967) as occurring in the present group, viz. the juvenile, minute and adult stages, have been studied. In the juvenile stage the animal has a flattened tubular shell with a rounded or oval protoconch. The minute lives in a teloconch of nearly fullgrown dimensions with the protoconch and spine-shaped juvenile shell usually already thrown off; the soft parts are relatively small. This stage is therefore not yet full-grown. In the adult stage the soft parts as well as the shell have grown to full size. To get an impression of the aging process in the different taxa, attention has been paid to changes, especially during the development from minute into adult stages. In order to assess the relative age the following features were considered: does the animal reach the shell aperture (a); occupy the whole shell aperture (b); protrude out of the shell aperture (c); fill the entire teloconch space (d).

The more the soft parts have grown and the more of the four above mentioned characters it shows, the older the specimens will be. Growth is divided into five steps; step I is characterized by the absence of all four characters; step II by the presence of one of the four characters, etc.

To discriminate between the different stages of shell development the following four features of the shell are considered indicative: shell not transparent (e); central part of dorsal lip pigmented (f); entire dorsal lip pigmented (g); dorsal lip extended (h).

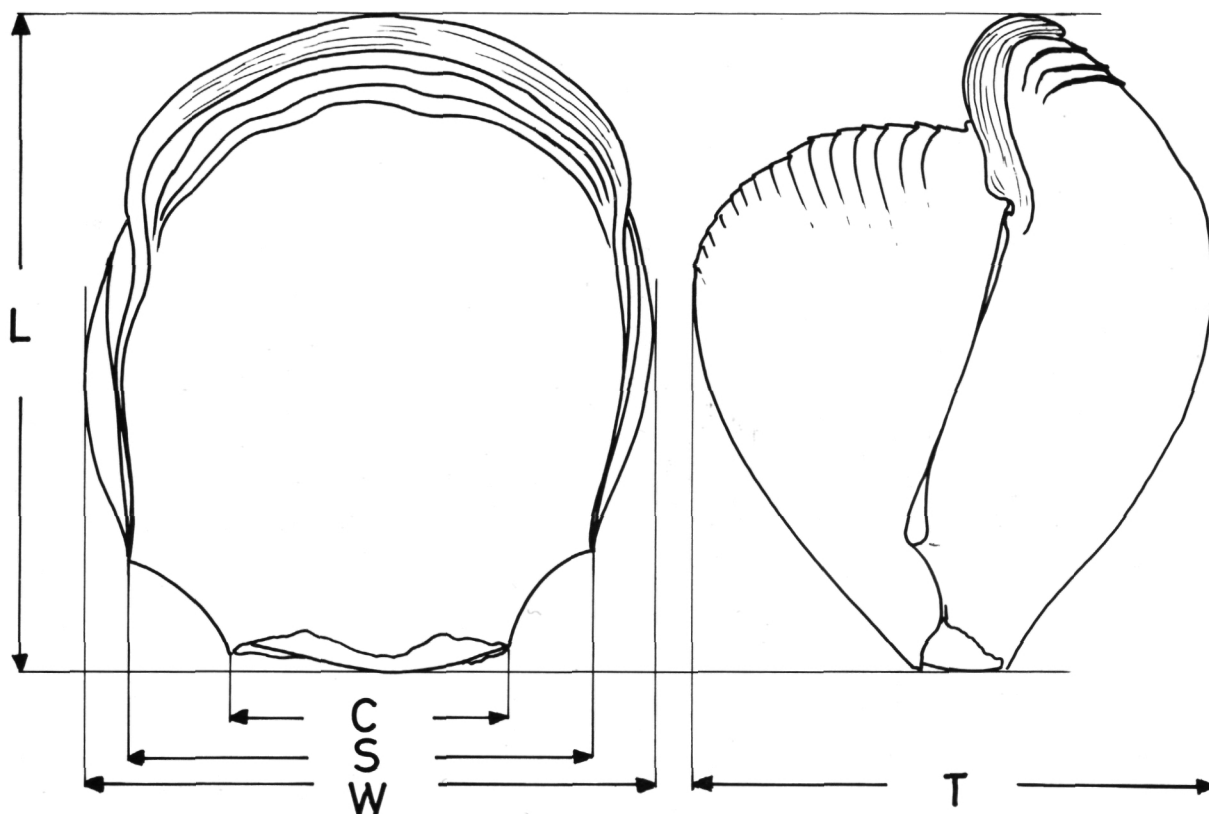


Fig. 1. Sizes measured from the shell, and growth lines counted, in dorsal and lateral view; C = width caudal spine mark, L = shell length, S = width between lateral spines, T = shell thickness, W = shell width.

Age classes are calculated in the same way for the shell as for the soft parts. Figure 2 gives the number of specimens, of four taxa, studied per age class as identified from the soft parts. The figure is subdivided (left side) into the number of specimens showing the shell characters e, f, g, h or none of these, and (right side) into the classes of shell ages found in these groups. From this figure it is clear that the occurrence of the shell characters is roughly dependent on age, though all four characters can occur in the youngest age class of the soft parts. The successive occurrence of the characters differs according to the taxa. In *Diacria quadridentata* and *D. danae* the character 'g' and in *D. costata* the character 'h' occur later in time than in the other taxa.

When identifying the two processes with the characters 'a' up to 'h' it becomes clear that shell aging is correlated with the aging of the soft parts. Development of the shell relative to that of the body goes faster in *D. costata*

and slower in *D. danae*, while *D. quadridentata* occupies an intermediate position. Though there is a correlation it is also obvious that in all four taxa the youngest stage of the soft parts can be found with the oldest stage of the shell and vice versa. From these facts it seems justified to make a better, more natural, but not finer subdivision into age classes, using the four characters of the shell and the four of the soft parts together. This results in a subdivision into nine age classes of the teloncha, growth of the juvenile being excluded by this approach.

The shell part which is entirely formed after the juvenile stage is the aperture prismatic layer (Bé et al., 1972). In a process of probably daily additions thin layers of prismatic substance are added to the rim of the aperture. In *Diacria* these thin layers are traceable by the thin lines made at the lip surface by the protruding corners of the layers as demonstrated in figure 3. Growth and growth stages of the teloncha are also marked by the

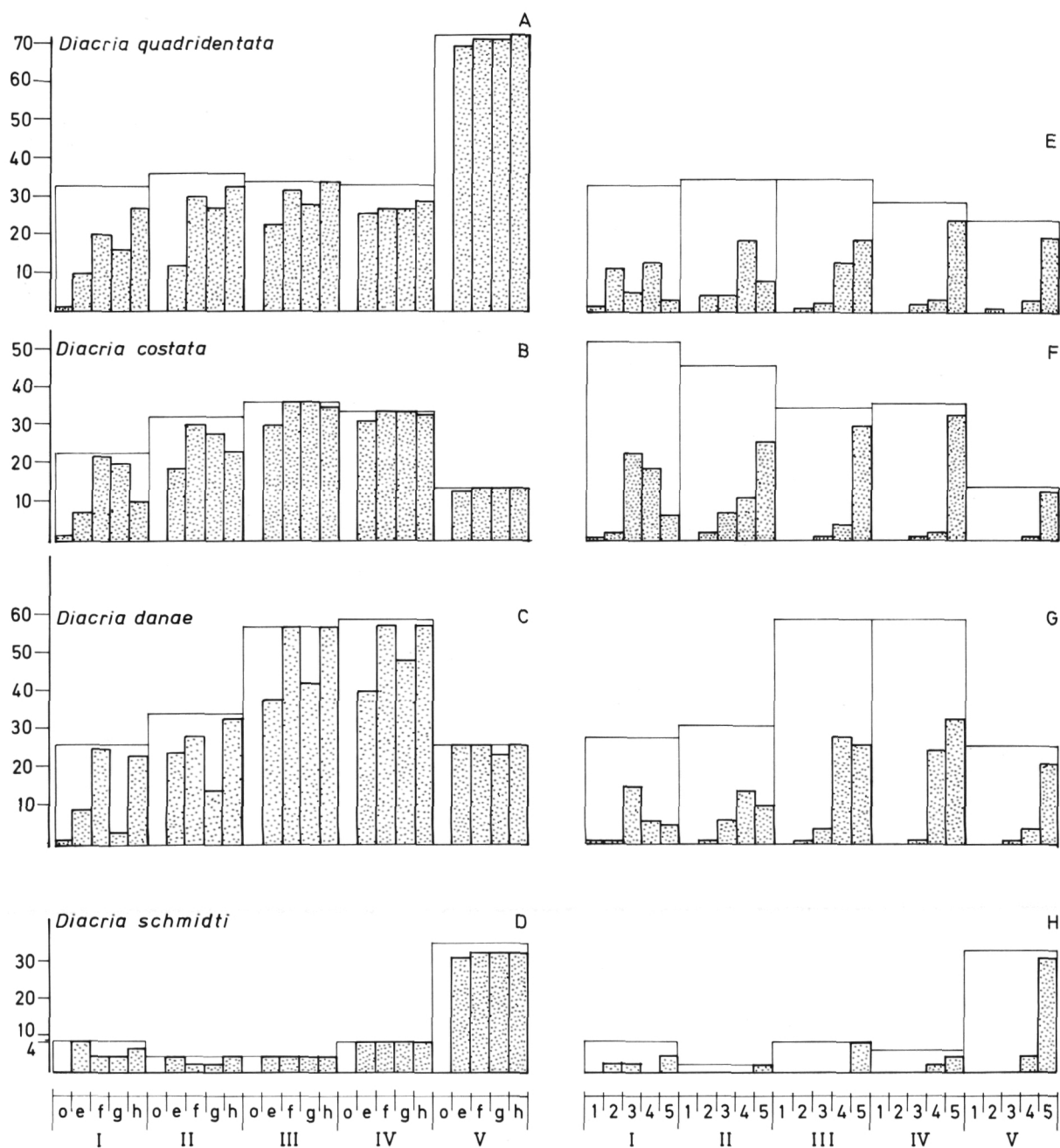


Fig. 2. Histogram for *D. quadridentata*, *D. costata*, *D. danae* and *D. schmidtii*, of the age classes of the soft parts I, II, III, IV, and V determined by the characters a, b, c and d (see text), in the diagrams A-D divided into the specimens with none, or one of the character e, f, g, or h (of the shell) and in the diagrams E-H divided into specimens with the growth stages of the shell: 1, 2, 3, 4 and 5 as determined by the characters e, f, g, h (see text).

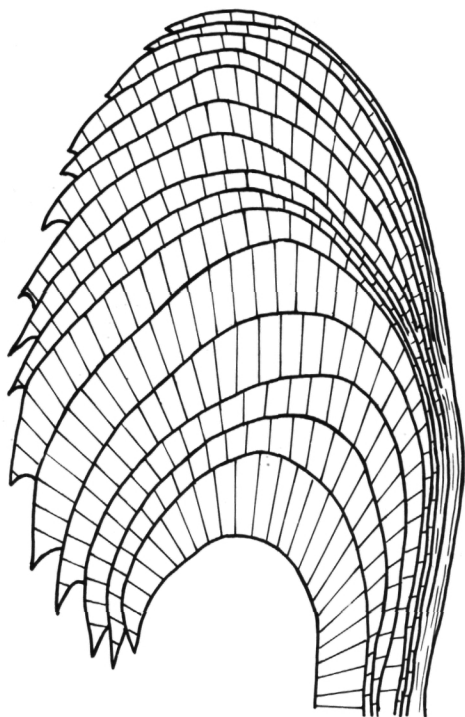


Fig. 3. Diagrammatic cross-section through the dorsal shell lip showing the (15) prismatic layers ending in the growth ridges on the dorsal lip.

number of lines on the dorsal lip surface. Figure 4 gives, for three species, the number of lines against the age class of the specimens as characterised by the eight features a-h. Aging is in this figure shown to be correlated with the increase of lines, but besides, there is the strange phenomenon that some of the youngest specimens already have lines on the dorsal lip.

The total shell length increases slightly because of growth at the aperture margin, as shown in table 1. Some large samples show that the shell length increases with the successive stages. In *Diacria danae* and *D. quadridentata* growth of the teloconcha is about 0.1 mm while it may become 0.2 mm in *Diacria costata*. The mean size in various populations differs, and as also shown in table 1, the differences in mean size do not develop during growth but the population of large adult specimens developed from large young specimens and smaller young specimens resulted in smaller adults. Size differences between populations are thus independent of teloconch growth. Populations with large specimens were almost invariably found in areas of colder water. The same phenomenon was described by Van der Spoel (1970) and Dupont

(1979) for *Clio pyramidata* Linné, 1767, and *Diacria trispinosa* (Blainville, 1821). Fertility and density of the water are factors influencing size (Van der Spoel, 1968). If density is the leading factor the question is by what mechanism a population anticipates the locally prevailing conditions, as size is already determined in a young stage or genetically. One might assume that the larger and heavier specimens in water of low density disappear from the population by sinking. When sinking has split the population into smaller and larger specimens this may introduce a barrier to reproduction between these groups which in its turn results in genetically determined populations of distinct size-classes. In this context it is important to stress that specimens from living plankton and from the sediment cannot be compared with regard to size, sediment material being usually larger. This is probably due to the greater numbers of adults in the sediment and the greater numbers of larger heavier younger teloconchae which had become too heavy for the locally prevailing water density.

Growth of the teloconch in this group is therefore slightly influenced by age and by local conditions.

In the course of the year, as far as could be concluded from stations scattered in time and place, the composition of age stages in a population does not change much. Probably a continual reproduction forms the basis of this phenomenon. Only at two places clear differences in the age composition of populations could be found. The mean age composition of a population was calculated with the formula:

$$\bar{S} = (\Sigma S)N^{-1}$$

(\bar{S} = mean age composition; ΣS = sum of all stages collected in one month, N = total number of specimens collected in that month).

In *Diacria quadridentata* near Madagascar the mean age is in December 8.82, in January 5.11 and in August 5.88.

In *Diacria costata* near India the mean age is in November 6.26, in December 3.69, in August 6.13 and in September 6.26.

In these two areas there seems to be an increased reproduction during the NE monsoon. Large numbers of *Limacina inflata* (Orbigny,

Table 1. Mean shell length, standard deviation and successive stages from different samples of three taxa of the *quadridentata* group.*D. quadridentata*

Dana Stat. 3956 ^V				Dana Stat. 3800 ^{II}			
mean length (in mm)	stand. dev.	stage	number specimens	mean length (in mm)	stand. dev.	stage	number specimens
2.41	0.098	all	61	2.64	0.126	all	33
-	-	1	0	-	-	1	0
2.30	0.055	2	6	2.54	0.077	2	4
2.39	0.101	3	3	2.60	0.069	3	3
2.42	0.094	4	12	2.68	-	4	1
2.43	0.092	5	18	2.61	0.023	5	3
2.42	0.104	6	13	2.55	0.082	6	4
2.30	0.085	7	2	2.68	0.010	7	12
2.45	0.101	8	3	2.77	0.020	8	5
2.41	0.068	9	4	2.56	-	9	1

D. costata

Dana Stat. 3824 ^{VII}				Dana Stat. 3914+3910			
mean length (in mm)	stand. dev.	stage	number specimens	mean length (in mm)	stand. dev.	stage	number specimens
2.15	0.092	all	95	2.29	0.095	all	55
-	-	1	0	2.20	-	1	1
2.08	-	2	1	-	-	2	0
2.09	0.045	3	5	2.26	0.075	3	18
2.08	0.011	4	9	2.25	0.078	4	14
2.11	0.011	5	9	2.27	0.095	5	5
2.16	0.080	6	24	-	-	6	0
2.17	0.086	7	26	2.40	-	7	1
2.18	0.085	8	15	2.38	0.096	8	9
2.23	0.079	9	6	2.31	0.104	9	7

D. danae

Dana Stat. 681				Dana Stat. 3997 ^V + 4003 ^{XI}			
mean length (in mm)	stand. dev.	stage	number specimens	mean length (in mm)	stand. dev.	stage	number specimens
1.74	0.052	all	87	1.96	0.064	all	59
-	-	1	0	1.90	0.028	1	2
-	-	2	0	1.92	0.057	2	4
1.70	0.037	3	8	1.94	0.052	3	8
1.72	0.036	4	6	1.99	0.069	4	9
1.73	0.064	5	7	1.98	0.052	5	4
1.75	0.046	6	20	2.10	0.077	6	5
1.75	0.050	7	18	1.97	0.064	7	13
1.75	0.067	8	15	1.93	0.060	8	11
1.75	0.064	9	13	1.99	0.023	9	3

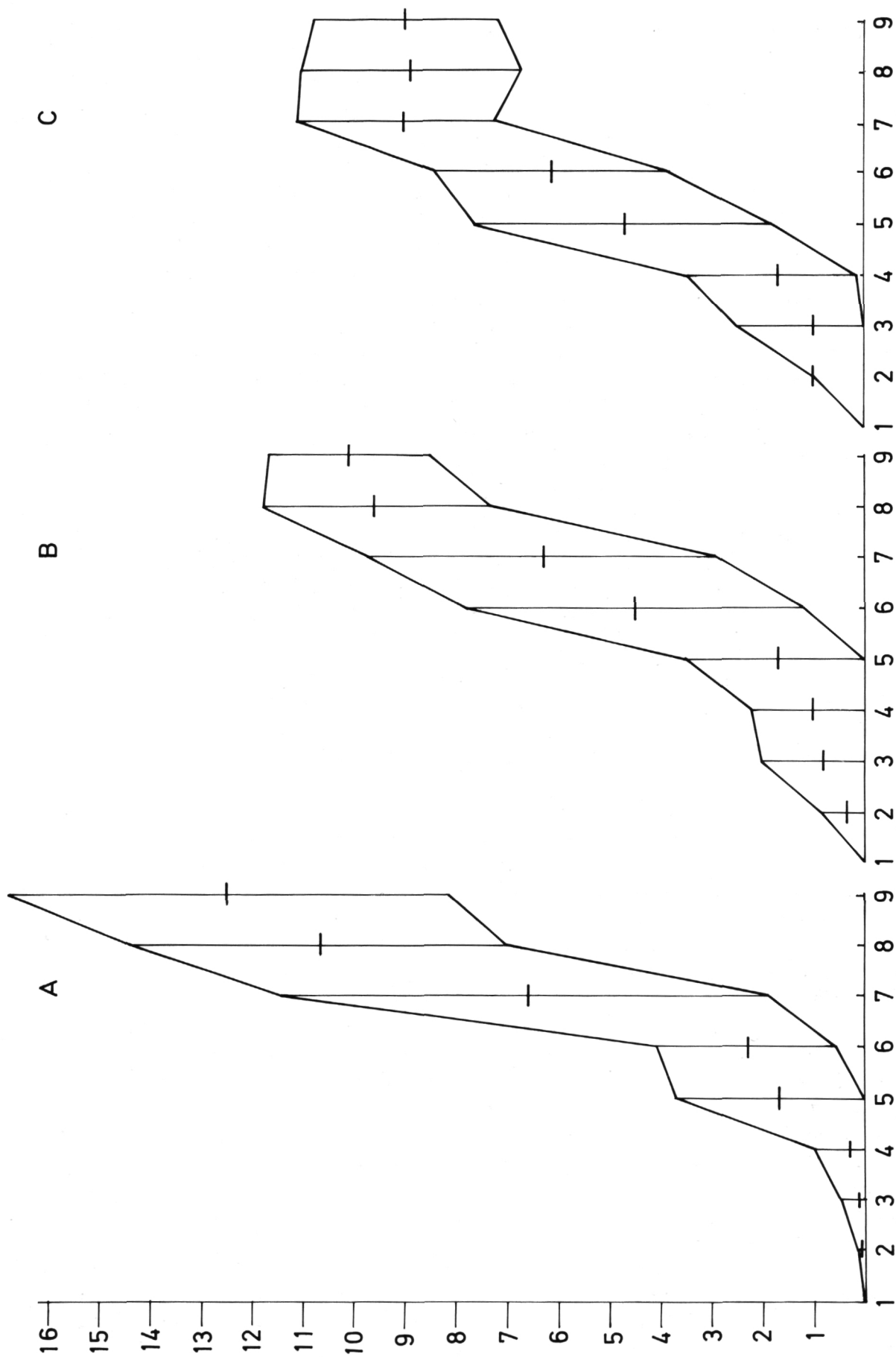


Fig. 4. Graph of the number of growth lines of the dorsal lip (mean and standard deviation) on the vertical axis, and age classes as determined by the characters a-h (see text) on the horizontal axis, for *D. costata* (A), *D. quadridentata* (B), *D. danae* (C).

1836) juveniles were found near Madagascar by Furnest (1979), also in December, and a general increase of abundance during the NE monsoon was also reported by Rao (1979).

TAXONOMY

The small within-species variation in size dependent on age and local condition, usually less than 0.4 mm within one plankton province, and the absence of intermediates between the taxa *D. quadridentata*, *D. danae*, *D. schmidtii* and *D. costata*, even when they occur in the same sample, made us consider these taxa to be valid species. *D. erythra* is considered a fifth separate species in the findings of Yaron (1977, 1978), and also a comparison of the original material with the four other species bears this out. The validity of splitting this species into two infraspecific taxa is thought at least doubtful by Yaron (1978) as the forma *crassa* Van der Spoel, 1971, proves not to be restricted to the Gulf of Elat as supposed, and as this forma also shows the imbricate dorsal ridges in numbers up to 9 as described for the forma *erythra* Van der Spoel, 1971. Frontier (1973) recorded for the Nosy Bé area the occurrence of subfossil representatives of the taxa *erythra* and *crassa* or of an intermediate as this author could not distinguish between these forms. As the original descriptions of '*erythra*' and '*crassa*' are based on sediment material it is very well possible that the smaller '*erythra*' form is a subfossil and the form '*crassa*' may be also subfossil for the Madagascar area but still lives in the Red Sea and Gulf of Elat.

Another form only known from sediment and thus probably also a subfossil is a close relative of *D. schmidtii* from the Philippine area. It can be distinguished from typical *D. schmidtii* by its slightly larger size and the higher number of imbricate dorsal striae. For this form the name '*occidentalis*' is proposed.

Size variation, probably of ecophenotypic nature, is found in *Diacria danae*, *D. costata* and *D. quadridentata* (fig. 5). *Diacria danae* is on the average larger in the Atlantic Ocean than in the Indo-Pacific Oceans. In equatorial

waters this species grows larger than in the central waters and the greatest sizes are reached at the highest latitudes. In the Atlantic Ocean an equatorial form and a central water form are easily distinguished; in the Pacific Ocean the forms show a more clinal variation and in the Indian Ocean the distinction is not clear. For *Diacria costata* an almost reverse size variation is found with a smaller equatorial form and a larger central water form. *Diacria quadridentata* shows a comparable variation but too few records are available to come to a separation into different forms.

The latitudinal variation results in length differences of max. 0.4 mm. Growth induces differences of shell length, within a population, of max. 0.2 mm. Thus, growth and ecology together may in one species induce length difference of 0.6 mm in total. The overlap in length of the species as given in table 2 is usually less than 0.6 mm which also shows their separate character.

Diacria quadridentata (MS Lesueur)
(De Blainville, 1821)

For synonymy see Van der Spoel (1976).

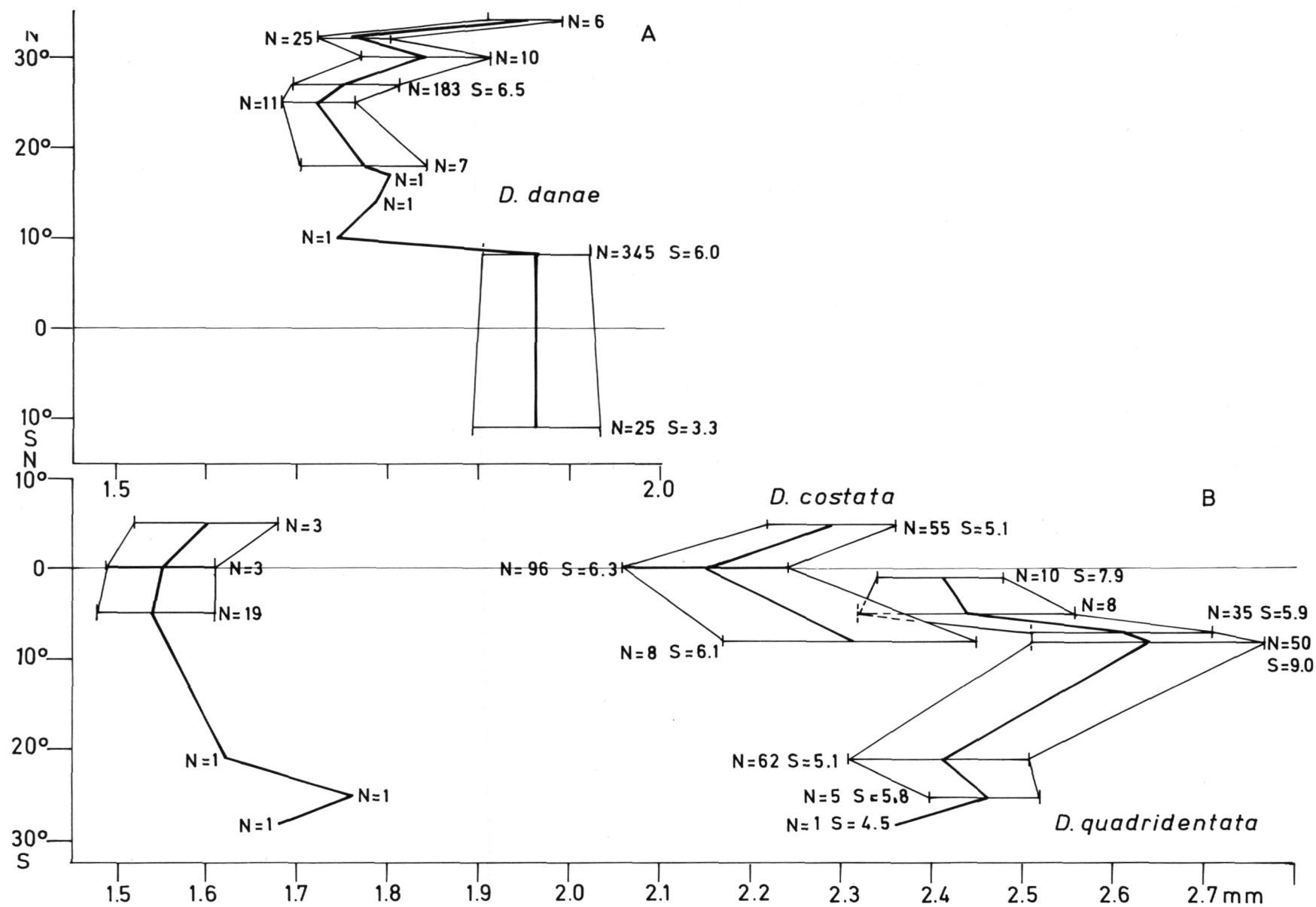
Description of teloconcha.-

The shell is rounded in shape, on the dorsal surface there are five longitudinal ribs; their continuation to the caudal spine mark is hardly visible. The ventral 'valve' of the shell is seen when looking from the dorsal side. The lateral spines are faintly curved dorsad and they point far outwards. The distance between the lateral spines approaches the maximum width of the shell. On the dorsal side about three extremely faint transversal striae are present. The imbricate transversal striae on the ventral side become more pronounced near the aperture. The ventral and dorsal lips are chestnut orange coloured in older specimens. In older specimens the dorsal lips also extend parallel to the dorsal surface. In lateral view the posterior parts of the ventral and dorsal side are, respectively, straight and slightly concave or also straight. This description is based on 284 specimens.

Table 2. Minimum and maximum sizes (in mm) and number of dorsal striae, in the *Diacria quadridentata* group.

	dorsal striae	shell length	shell width	width caudal spine mark	width between lateral spines	max. width/ width lat. spines	length/ width
<i>D. danae</i>	3	1.44-2.08	1.16-1.72	0.56-0.80	1.00-1.36	1.03-1.36	-
<i>D. costata</i>	5	1.92-2.64	1.72-2.24	0.68-0.88	1.36-1.84	1.10-1.44	-
<i>D. quadridentata</i>	3	2.04-3.00	1.84-2.48	0.76-1.08	1.56-2.12	1.00-1.22	-
<i>D. erythra</i>	6-9	2.46-4.00	2.00-3.40	0.90-1.36	-	-	1.09-1.39
'forma erythra' ¹	9	2.46-3.12	2.00-2.48	0.90-0.96	-	-	1.19-1.39
'forma crassa' ²	6	3.12-4.00	2.60-3.32	1.04-1.36	-	-	1.09-1.29
' <i>D. erythra</i> ' ³	9	3.00-4.00	2.60-3.40	-	-	-	1.14-1.33
' <i>D. erythra</i> ' ⁴	-	2.1 -4.7	1.9 -3.7	-	0.85-1.30	-	1.00-1.30
<i>D. schmidtii</i> ⁵	2-3	4.00-4.48	3.20-3.80	1.16-1.36	-	-	1.16-1.33
<i>D. schmidtii</i>	3	3.08-4.60	2.60-3.76	0.96-1.16	2.20-2.88	1.12-1.32	-
<i>D. schmidtii</i> subsp. <i>occidentalis</i>	6-14	4.20-5.04	3.20-4.16	1.04-1.64	2.80-3.52	1.05-1.33	-

¹ after v.d. Spoel, 1971; ² after v.d. Spoel, 1971; ³ after Yaron, 1978; ⁴ after Frontier, 1973; ⁵ after v.d. Spoel, 1971



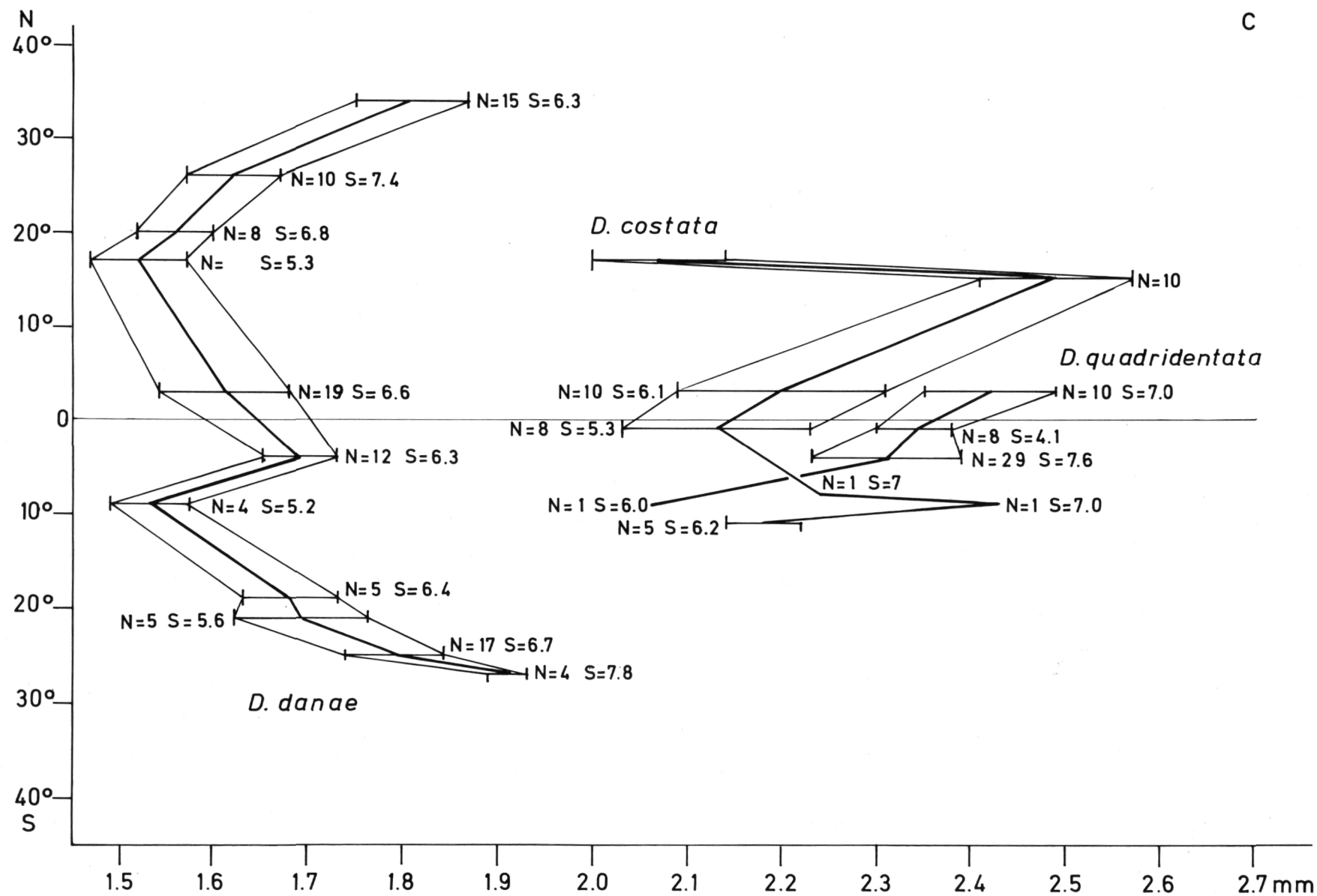


Fig. 5. Mean shell length and standard deviation (horizontal axis) against latitude (vertical axis) for *D. danae*, *D. costata*, *D. quadridentata* in the Atlantic Ocean (A), the Indian Ocean (B) and the Pacific Ocean (C); N = number of shells measured, S = mean stage.

Diacria costata (Pfeffer, 1879)

For synonymy see Van der Spoel (1976).

Formerly considered of infraspecific rank, now raised to species level.

Description of teloconcha.-

The shell is rounded in shape, on the dorsal surface five very well developed longitudinal ribs run to the caudal spine mark. In dorsal view the ventral 'valve' of the shell is visible. The lateral spines are not, or sometimes very slightly, curved caudad. The distance between the lateral spines is clearly smaller than the shell width. On the dorsal side about five well developed imbricate transversal striae are found. The transversal imbricate striae on the ventral side are pronounced. The ventral and dorsal lips of the aperture are in older specimens, and frequently also in younger ones, chestnut-orange in colour. In older specimens the dorsal lips extend far, both parallel and vertical to the dorsal surface. In lateral view the posterior parts of the ventral and dorsal sides are straight or the latter one may be slightly convex. This description is based upon 373 specimens.

Diacria costata equatorial form is found in the Indian and Pacific Oceans in equatorial waters roughly between 10°N and 5°S. This form is characterized by its small size, length is usually less than 2.25 mm.

Diacria costata central water form is found in the central waters of the Indian and Pacific Oceans, and it usually grows to more than 2.25 mm in length.

Diacria danae Van der Spoel, 1971

For synonymy see Van der Spoel (1976).

Formerly considered of infraspecific rank, now raised to species level.

Description of teloconcha.-

The shell is rounded in shape, on the dorsal surface five longitudinal ribs are very vaguely

developed and their continuation to the caudal spine mark is barely visible. In dorsal view the ventral 'valve' of the shell is visible. The lateral spines are not, or sometimes very slightly, curved caudad. The distance between the lateral spines is almost equal to the shell width. On the dorsal surface about three imbricate transversal striae are found. The transversal imbricate striae on the ventral side number ca. 4. The ventral and dorsal aperture lips are chestnut-orange coloured in older specimens. The dorsal lip is extended parallel to the dorsal surface in older specimens. In lateral view the posterior parts of the ventral and dorsal shell surfaces are straight, or the dorsal one may be slightly concave. This description is based on 467 specimens.

The protoconch I was ca. 0.27 mm long and ca. 0.16 mm wide in the single specimen found. According to Frontier (1973) these sizes are 0.22 mm and 0.145 mm resp.

Diacria danae equatorial form, in the Atlantic living between 10°N and 10°S, can easily be distinguished from the smaller, central water form by its length which exceeds 1.85 mm. At higher latitudes (34°N) also large specimens occur. This variation resembles that found in *Diacria trispinosa* by Van der Spoel (1970) and Dupont (1979). The north-south range in *D. danae* is much smaller than that in *D. trispinosa* so that there have not developed well distinguishable infraspecific groups. Misidentification of Atlantic specimens, which are sometimes referred to as *D. quadridentata* (cf. Van der Spoel, 1967) may be induced by the strong variation in the Atlantic populations. In the Indian Ocean the equatorial form is not found, only a population of large specimens, probably derived from the equatorial area is found in the Agulhas Current. In the Pacific Ocean the equatorial population is well separated from the larger high latitude populations by the central water population (cf. fig. 5).

Diacria danae central water form is very typical of the Sargasso Sea, where it does not grow larger than 1.80 mm in length. In the Pacific central waters this form is even smaller (<1.70 mm in length) which is correlated with the overall phenomenon that the Atlantic repre-

sentatives of this species are remarkably larger than the Indo-Pacific ones. Only the populations north of 20°N and south of 20°S reach sizes also found in the Atlantic (>1.70 mm).

Diacria schmidtii Van der Spoel, 1971

Formerly considered of infraspecific rank, now raised to species level. As the recent east Pacific population differs markedly from the subfossil west Pacific population a subdivision into two subspecies is proposed for this species.

Diacria schmidtii subsp. *schmidtii*

Van der Spoel, 1971

For synonymy see Van der Spoel (1976).

Description of teloconcha.-

The shell is rounded in shape, on the dorsal surface five longitudinal ribs are well developed, they run up to the caudal spine mark. In dorsal view the ventral 'valve' of the shell is visible. The lateral spines are slightly curved dorsad and do not point outwards. The distance between the lateral spines is smaller than the shell width. On the dorsal surface three thin

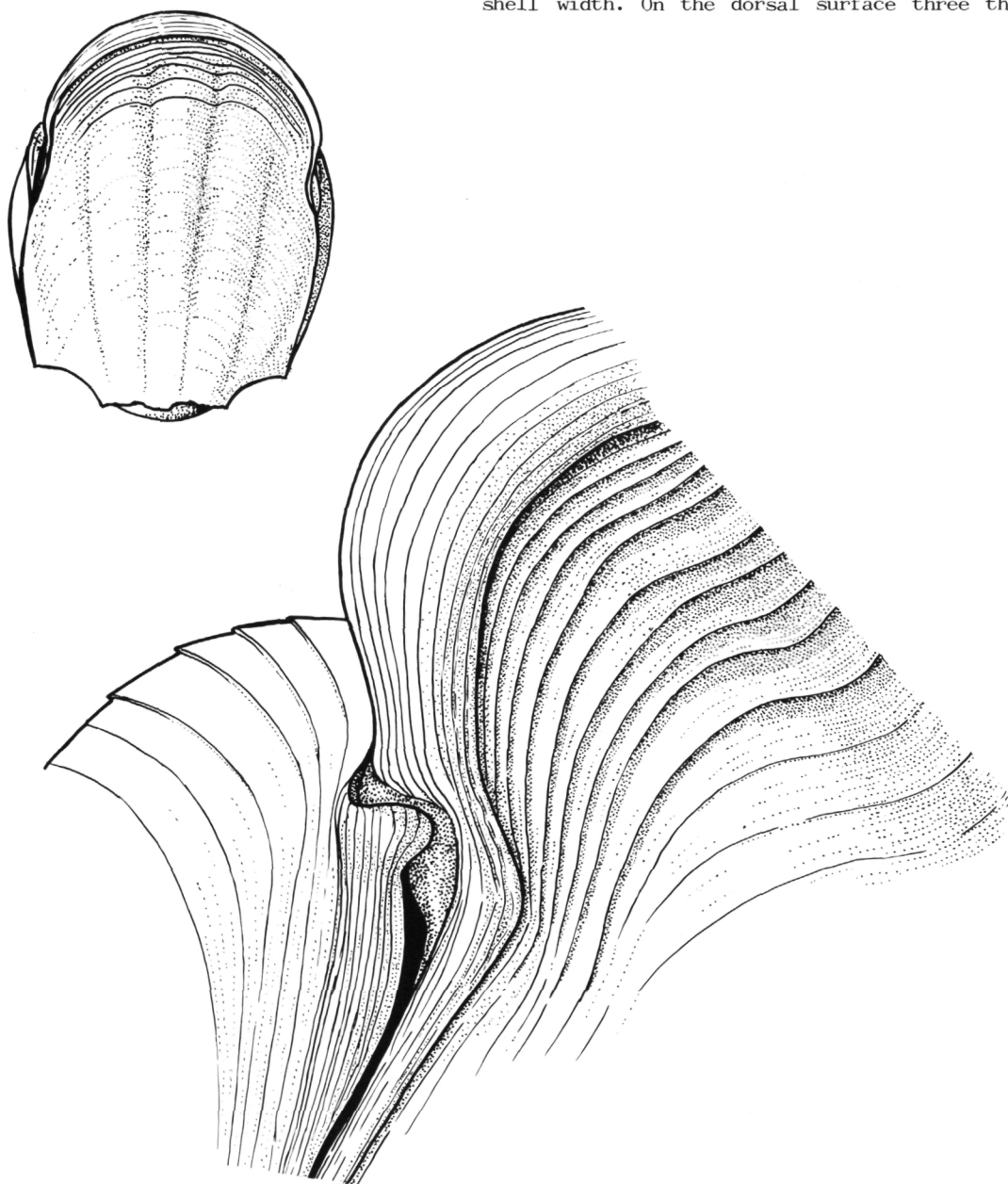


Fig. 6. *Diacria schmidtii* subsp. *occidentalis*, holotype in dorsal view, with detail of left aperture corners.

but pronounced imbricate transversal striae are found. The transversal striae on the ventral side are not imbricate but faint, though they become more pronounced near the aperture. The dorsal and ventral aperture lips are not as pigmented as in the preceding species, the whole shell, however, shows a brownish hue. In older specimens the dorsal lip is extended parallel to the dorsal shell surface, though relatively less far than in the other species. In lateral view the posterior parts of both dorsal and ventral side are straight or slightly convex. This description is based on 54 specimens.

The protoconch I was ca. 0.20 mm long and ca. 0.17 mm wide, in two specimens.

Diacria schmidtii subsp.
occidentalis nov. subspecies
(fig. 6)

Description of teloconcha.-

The shell is rounded in shape, on the dorsal surface there are five well-developed longitudinal ribs which continue to the caudal spine

mark. In dorsal view the ventral 'valve' of the shell is visible. The lateral spines are slightly curved dorsad and caudad. The distance between the lateral spines is smaller than the shell width. On the dorsal surface six up to fourteen clear imbricate transversal striae are visible. The transversal striae on the ventral side are thin but clear and more pronounced near the aperture. The sediment material did not show colour patterns. In older specimens the dorsal lip extends parallel to the dorsal surface as in the preceding species. In lateral view the posterior part of the ventral and dorsal sides are straight or slightly convex. This description is based on 20 specimens.

The holotype and 19 paratypes are preserved in the United States National Museum, USNM 289901.

The type locality is U.S.B.F. stat. 5586, 337 fms. gy. M. 44°, Borneo Sibuko Bay off Sipadan Island.

For *Diacria erythra* Van der Spoel, 1971, one is referred to the original description as no new material was studied.

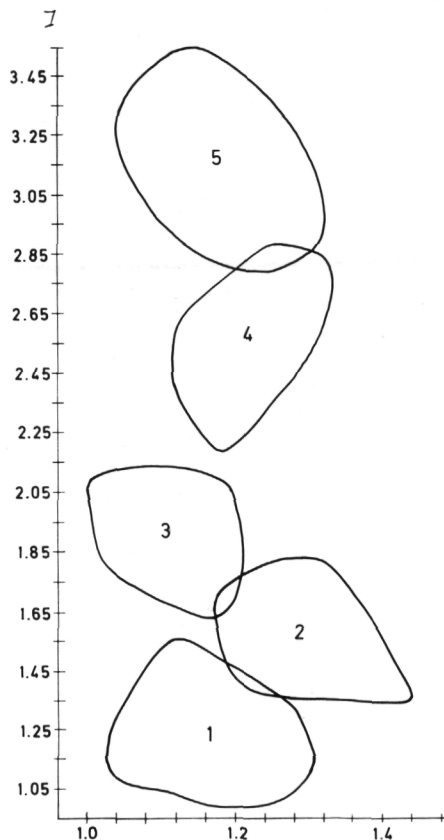


Fig. 7. Diagram of the relation between distance, between lateral spines (in mm) and the ratio shell width/distance between lateral spines. 1 = *D. danae*, 2 = *D. costata*, 3 = *D. quadridentata*, 4 = *D. schmidtii schmidtii* (East Pacific), 5 = *D. schmidtii occidentalis*.

The species which received special attention in this paper prove to be easily distinguishable by the ratio of shell width and distance between the lateral spines (fig. 7), even when there is a gradual change between the species as to their shell length, width and thickness. Only *Diacria costata* shows overlap with *D. quadridentata* and *D. danae* (fig. 7). This overlap, however, is only due to specimens from different oceans; when considering only specimens from one of the oceans there is a wide gap between each of the species. Only *D. quadridentata* from the Pacific Ocean overlaps with *D. costata* from the Indian Ocean and *D. danae* from the equatorial Atlantic overlaps with specimens from the Pacific Ocean. The overlap between subfossil West Pacific and recent East Pacific representatives of *D. schmidtii* is very small and affirms that we probably have to do with subspecies.

DISTRIBUTION

In fig. 8 the distribution of the *Diacria quadridentata* group is given. *Diacria danae* is a circumglobal warm water species living between 40°N and 40°S; *D. quadridentata* and *D. costata* are both Indo-Pacific species restricted to the latitudes between 20°N and 20°S, while *D. schmidtii* is endemic to the Pacific and *D. erythra* to the Red Sea.

D. quadridentata is found in the Indian Ocean only west of 65°E and south of Sumatra and Java in the eastern Indian Ocean. The gap between the West Indian population and that south of Indonesia is probably due to the NE monsoon as all samples studied are from this monsoon period. The absence of *D. quadridentata* in some areas is comparable with the findings by Sakthivel (1973) concerning *Limacina inflata* which also occurred only in the western Indian Ocean during the NE monsoon. To the south the distribution of *D. quadridentata* and also that of *D. danae* seems to be limited by the 20°C isotherm in August. In January the 20°C isotherm shifts to 40°S; however, none of the samples taken in this period between 30° and 40°S contained *D. quadridentata*. Samples from 30° and 25°S contained only few specimens and the denser population was only met with at

20°S. These findings make it doubtful whether real migration of *D. quadridentata* into the Atlantic by way of the Agulhas current is possible; it is more likely that the specimens reported from the Atlantic as *D. quadridentata* should be considered *D. danae*, large central water form.

The surface water of the Indian Ocean contains 4 to 5 ml O₂/l (Sverdrup et al., 1942; Rao, 1979). In the western part these surface layers gradually become subsurface layers with an also gradually decreasing O₂ content. In the eastern parts, however, there is a discontinuity between surface and subsurface layers; here, the O₂ content steeply drops to 1 ml/l. The border between these two hydrographical systems, at 65°E coincides with the area where *D. quadridentata* is replaced by *D. costata*. East of 100°E the vertical gradient of O₂ content becomes gradual again and here both species occur together: thus, besides monsoon effects, the O₂ content of the water may also have its influence. In the Indo-Malayan archipelago *D. quadridentata* occurs east of Borneo from where it continues up to 110°W in the Pacific Ocean. This species seems to be less abundant in, and sometimes absent from, equatorial water masses.

Diacria costata seems to be more abundant and frequent in equatorial waters of the Indo-Pacific. It occurs only east of the Maldives up to 130°W in the Pacific. In general, this species occurs closer to coast and islands than the other species of the group, though it does not represent a real neritic pattern of distribution. *D. costata* is slightly less stenothermal than *D. quadridentata*: it is found to be limited by the 25°C isotherm.

Diacria danae shows the 40°N-40°S distribution and, according to the rule of Fleminger & Hulsemann (1973, 1974), it should show no provincialism. Yet, the Atlantic representatives are larger than the Indo-Pacific ones and, besides, the relative distance between the lateral spines in the Indo-Pacific Oceans is greater. Besides this east-west variation in size, the north-south variation was already mentioned, with large equatorial and small central water specimens. In the Indo-Malayan archipelago west of Borneo this species is the only representative of the group.

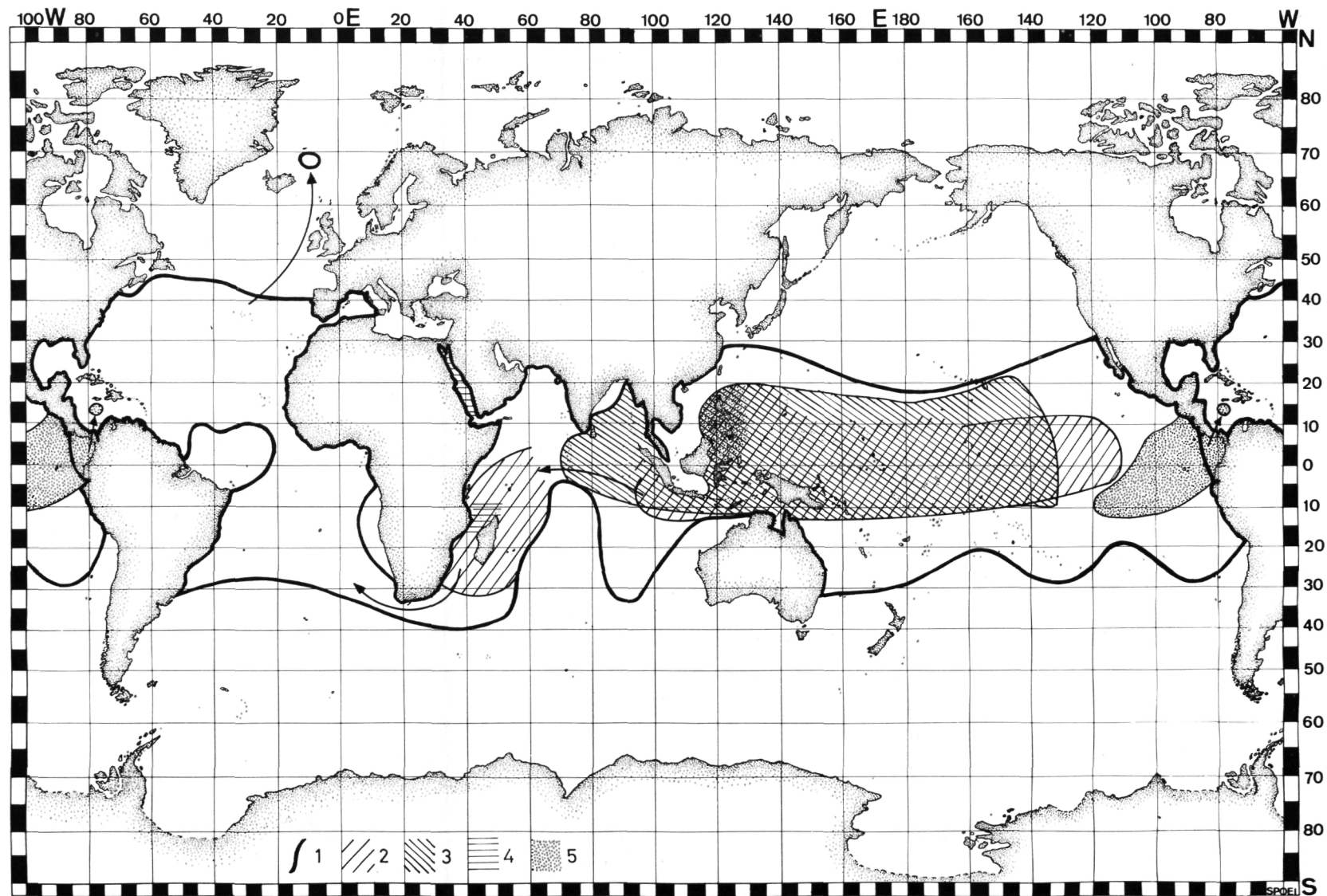


Fig. 8. Distributional map for the *D. quadridentata* group. 1 = border of *D. danae*, 2 = *D. quadridentata*, 3 = *D. costata*, 4 = *D. prythra*, 5 = *D. schmidtii*.

Diacria schmidtii is endemic to the tropical west Pacific and does not occur west of 120°W. The 9 specimens recorded from the Gulf of Mexico at Dana Stat. 1214^{II} (14°21'N; 76°50'W) are hardly to be considered migrants though the Panama Canal though other explanations are not available.

The subfossil representative of this species referred to as subspecies *occidentalis* is only known from the area north of Celebes, the NE coast of Borneo and the Philippine area.

Of *Diacria erythra* subfossils are known from the Red Sea and west Indian Ocean while the recent representative, the subspecies *crassa* is endemic to the Red Sea, though it may have occurred, in the geological past, also in the west Indian Ocean near Madagascar.

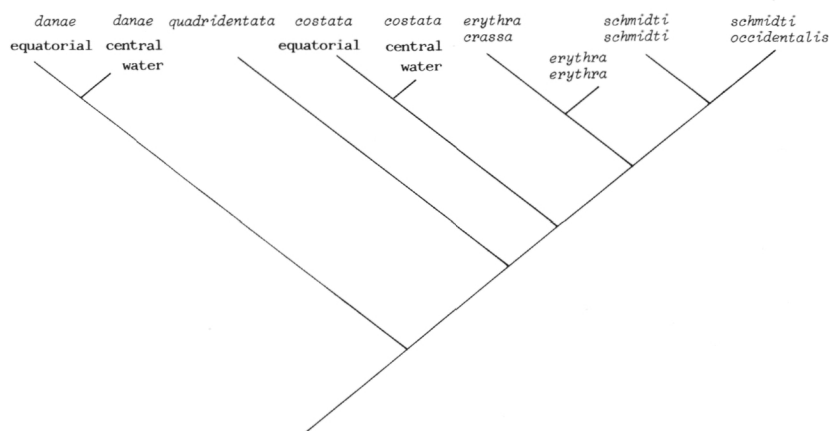
According to Herman (1971) *Diacria quadridentata* s.l. occurred in the Red Sea before the Last Glacial. Colonisation of the Red Sea took place from the Indian Ocean (Herman, 1971; Rampal, 1975). Several recolonisations took place during interglacial periods when the Red Sea population had died out during glacial ones. The Red Sea *D. erythra* population originates from the last colonisation after the glacial period. In the *quadridentata* group *D. erythra* is most closely related to *D. costata* and to *D. schmidtii*, as to conclude from shape, size and sculpture of the shell. In all probability the subfossil *D. erythra erythra* and *D. schmidtii occidentalis* as well as *D. costata* are thus at least post-glacial or late Glacial taxa. In the samples with subfossil *D. schmidtii occidentalis*, also *D. costata*, *D. danae* and *D. quadridentata* are found.

The whole speciation in the *quadridentata* group is from recent-glacial origin and can

be explained as follows. *D. danae* was isolated in the Atlantic from the other taxa in one of the first glacial periods and adapted in this ocean during the successive periods to lower temperature conditions to which the Indo-Pacific relatives were not subjected, as cooling was only that strong in the Atlantic. In warmer interglacials *D. danae*, because of its larger temperature range, could spread over all oceans. In the Indo-Pacific a division developed between an open ocean form *D. quadridentata* and a group of more coastal forms, which split into: a western group: *D. erythra* in the west Indian Ocean; a central group: *D. costata* around the Indo-Malayan archipelago; and an eastern group: *D. schmidtii* in the Pacific ocean. Of these groups the subspecies *D. erythra crassa* and *D. schmidtii schmidtii* developed only recently.

The patterns of distribution of these species fit in rather well with patterns of several species of remote groups like Copepoda and Euphausiidae. *D. quadridentata* shows roughly the same distribution as *Euphausia paragibba*; *D. costata* lives in the same area as *Euphausia pseudogibba* (Ortmann, 1893) and *Pontellina morii* Fleminger & Hulsemann, 1974, while *D. schmidtii* shows the pattern also displayed by *Pontellina sobrina* Fleminger & Hulsemann, 1974. *Pontellina plumatella* (Dana, 1849) has the circumglobal distribution also found for *D. danae*, while *Pontellina platychela* Fleminger & Hulsemann, 1971, is sympatric with the equatorial form of *D. danae* (cf. Fleminger & Hulsemann, 1974).

The hypothesis on the phylogeny based on this discussion can be summarized in the dendrogram below:



Phylogeny of the *D. quadridentata* group

SUMMARY

Growth in the *Diacria quadridentata* group was studied and it is shown that there exists a correlation between the development of the soft parts and the shell after the juvenile stage, though this correlation is far from simple. On the basis of the different developmental stages of soft parts and shell a subdivision into nine age-stages was made. The number of growth ridges on the dorsal lip of the shell proves to be correlated with age. The more ridges, the older the shell is. For the species concerned a slight length increase of the teloconcha with time is found, this increase does not exceed 0.2 mm in total.

The variation of shell length between the different populations of one species, usually not exceeding 0.4 mm, proved to be correlated to areas of occurrence. Although the variation has a more or less clinal character, the equatorial and central water populations may easily be distinguished.

The differences due to growth and environmental conditions are as a rule distinctly smaller than the size differences between the taxa of the *quadridentata* group. Intermediates between the taxa now proposed as species were not found in the large material of 2500 specimens in total. The group once considered to consist of one species with 6 formae is now considered to be composed of five species, four subspecies and 4 forms, viz.: *D. quadridentata*, *D. costata* with an equatorial and a central water form, *D. danae* with a central water and an equatorial form, *D. schmidtii* with a recent subspecies *schmidtii* and a subfossil subspecies *occidentalis*, and *D. erythra* with a recent subspecies *crassa* and a fossil subspecies *erythra*. Distribution is compared with other taxa and considered in relation to events in the geological past.

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