

Notes on the adult and young stages in *Diacria* (Gastropoda, Pteropoda)

W.L. PANHORST & S. VAN DER SPOEL

Institute of Taxonomic Zoology (Zoölogisch Museum), Amsterdam

INTRODUCTION

The adults and minute stages of the Cavoliniidae as described earlier (Van der Spoel, 1967) have been distinguished chiefly by studying their soft parts; only a few notes were made on differences in the shells of young and older specimens (Van der Spoel, 1970). A large collection of *Diacria*, made during the Ocean Acre Program¹ in the Bermuda area, made possible a more careful study of their shells. Concerning the two forms in *D. trispinosa*, the second author (Van der Spoel, 1967: 84) stated "... both formae are sometimes collected in one and the same sample. The systematic rank given to them is perhaps too low ..." and (Van der Spoel, 1970: 105) "the largest specimens", of the forma *trispinosa*, "which are as long as tropical specimens of the closely related and larger forma *major*". The differences between the two taxa are evidently small, but the forma rank is clearly too low as both are sympatric in space and time. This also implicates that we are not dealing with subspecies so that one is forced to consider both taxa separate species. That two morphs of one species are present instead of two species seems impossible as both show considerable geographic variation. Originally described as varieties (Boas, 1886) or subspecies (Tesch, 1913), and later considered formae (Van der Spoel, 1967), the two taxa now have to be considered distinct species: *Diacria trispinosa* (De Blainville, 1821) and *Diacria major* (Boas, 1886). Only a small geographic range is studied here and overlap in vertical distribution as

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found here may be absent elsewhere, but even then there is at least locally a complete overlap in occurrence.

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VERTICAL MIGRATION

In a previous paper (Van der Spoel, 1973: 132) the vertical migration of *D. trispinosa* was briefly discussed: "Migration is executed over a depth of 157 meters and 94% of the specimens crossed the average day level". These findings and the total vertical range of 0 to 500 meters were based on part of the material studied in the present paper, namely on only 118 specimens/hour catching effort, while the total material consisted of 413 specimens/hour catching effort from discrete depth samples for *D. trispinosa* and 139 specimens/hour for *D. major* (Boas, 1886). The basic statistics from table 1 (n = number, \bar{y} = mean, s = standard deviation) are shown in figure 1.

TABLE 1
Depth distribution statistics in meters

		n	\bar{y}	s
<i>D. trispinosa</i> , minute stage	day	45	199	102
	night	140	51	99
<i>D. major</i> , minute stage	day	25	65	35
	night	26	83	43
<i>D. trispinosa</i> , adult stage	day	65	129	100
	night	163	86	124
<i>D. major</i> , adult stage	day	22	173	259
	night	66	105	46

Most remarkable is the reversed diurnal migration of *D. major* during the minute stage. The vertical migration in *D. major* adults is very small. The strongest migration is found in *D. trispinosa* during its minute stage. When comparing the standard deviations it is clear that the minute and adult stages of both species live in the same water layers and this also applies when the extreme values are compared. The differences still present cannot be regarded as functional in any kind of vertical separation and isolation between the two taxa, so that sympatry is evident in a horizontal as well as a vertical sense.

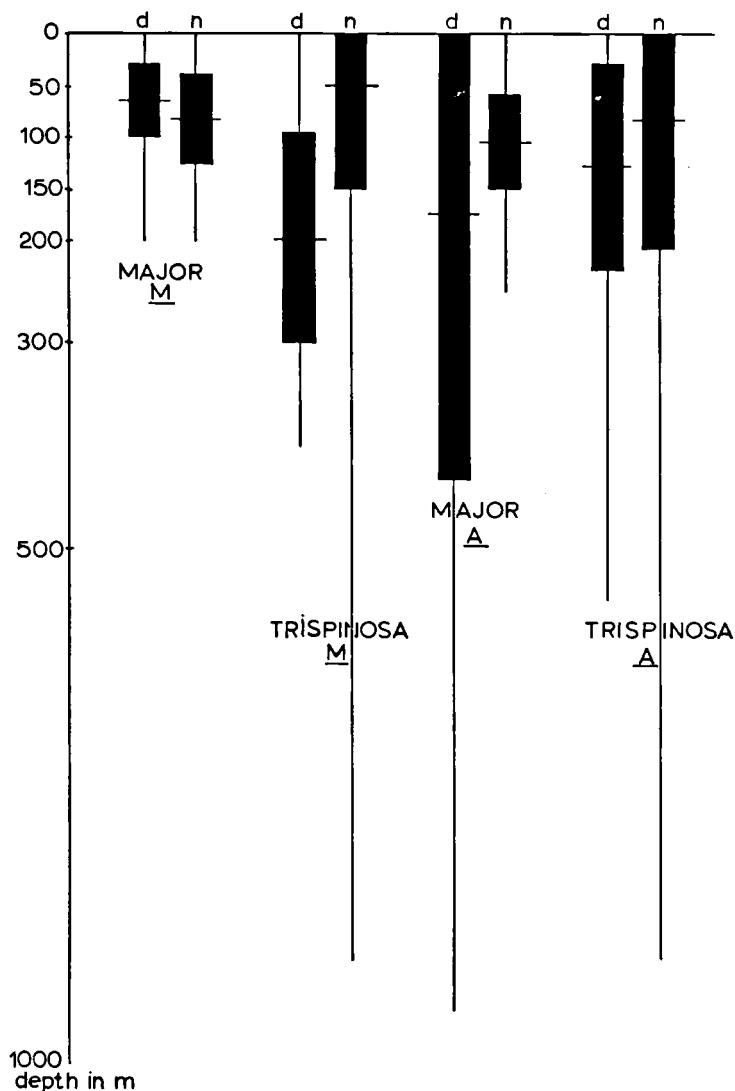


Fig. 1. Dicegram of the vertical distribution of *D. major* and *D. trispinosa* in adult (A) and minute stage (M) at day time (d) and night time (n).

SEASONAL OCCURRENCE

The seasonal occurrence in the Bermuda area is given in fig. 2. The line A gives the percentage of *D. trispinosa* in the *D. trispinosa* and *D. major* population. Both species are found throughout the year. *D. major* shows maximum relative abundance between March and August. Absolute maximum abundances are found in June and September. *D. trispinosa* also shows its absolute maxima in these two months. When the percentage of minute stages for *D. major* (fig. 2, line C) and *D. trispinosa* (fig. 2, line B) are compared it is clear that there are two maxima for both species: one in February-March and another in August. Absolute total minima for both species are found in January, July and October.

As minute stages develop from juveniles it is supposed that breeding precedes the occurrence of minute stages. As a consequence one may conclude that breeding occurs throughout the year in both species with a maximum before July. In a previous paper (Van der Spoel, 1973) the breeding cycles of *Clio pyramidata*, *Cavolinia gibbosa*, *Cuvierina uncinata* and *Diacria trispinosa* were compared. For the latter a breeding

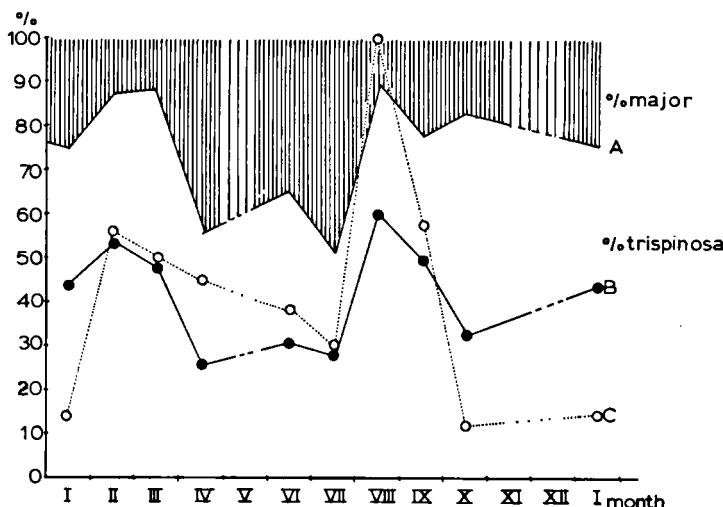


Fig. 2. Seasonal occurrence of *D. major* (hatched) and *D. trispinosa* (white) as a percentage of the sum total of both. The percentages of minute stages for *D. major* (C) and *D. trispinosa* (B) in relation to the adult stages are given as points connected with lines. Percentages along vertical axis, months along horizontal axis.

top in March-July was found which can be correlated with the top of the minutes in fig. 2. In the present studies it is not possible to determine the periods of maximum reproduction more accurately, but it seems clear that both species are not seasonally isolated.

RESULTS ON SIZE DIFFERENCES

In order to get an impression of shell development during growth all samples were subdivided into three groups: one with specimens in the adult stage, one with specimens in the minute stage, and one with specimens in a stage transitional between minute and adult stage. The stages of sexual development were checked histologically in specimens randomly selected from the various groups. Thickness and length of the shells (caudal spine excluded) are measured as indicated in fig. 3. All sizes were measured in mm with an accuracy of 0.01 mm. Shell width was not used in the present species as damage to the lateral spine occurs too frequently. To compare the size of the adult stages and the minute stages of *Diacria trispinosa* and *Diacria major* the null hypothesis (H_0): "The sizes of minute stages are systematically equal to those of adult stages", was left-sided tested with the Mann-Whitney-test. In case of the random variable W being smaller than the critical value W_1 correlated with a size $\alpha = 0.05$, " H_0 " had to be rejected in favour of the alter-

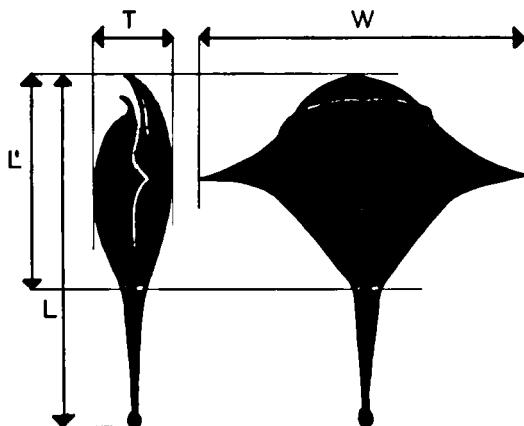


Fig. 3. Diagram of a *Diacria* shell to show measurements taken. L: shell length; L^1 : shell length caudal spine excluded; T: shell thickness; W: shell width.

native hypothesis (H_1): "The sizes of minute stages are systematically smaller than those of the adult stages". (cf. D. Wabeke & C. van Eeden: Handleiding voor de toets van Wilcoxon. Report S 176 of the "Mathe-matisch Centrum" Amsterdam). The results of this test are shown in table 2.

TABLE 2
Results from Mann-Whitney-tests; italicized groups show the smallest sizes
($\alpha = 0.05$)

Species	Parameter stages compared	W	W ₁	Rejecting H ₀ in favour of H ₁
<i>D. trispinosa</i>	thickness <i>minute</i> & adult	8373	10887.6	yes
<i>D. trispinosa</i>	thickness <i-transitional< i=""> & adult</i-transitional<>	7284	5264.2	no
<i>D. trispinosa</i>	thickness <i>minute</i> & <i>transitional</i>	3550	5518.7	yes
<i>D. major</i>	thickness <i>minute</i> & adult	1858	4345.3	yes
<i>D. major</i>	thickness <i>transitional</i> & adult	1996	2745.5	yes
<i>D. major</i>	thickness <i>minute</i> & <i>transitional</i>	1118	1230.6	yes
<i>D. trispinosa</i>	length <i>minute</i> & adult	13803	11536.8	no
<i>D. trispinosa</i>	length <i>transitional</i> & adult	7760	5196.7	no
<i>D. trispinosa</i>	length <i>minute</i> & <i>transitional</i>	6954	5905.2	no
<i>D. major</i>	length <i>minute</i> & adult	3639	4481.3	yes
<i>D. major</i>	length <i>transitional</i> & adult	2529	2770.8	yes
<i>D. major</i>	length <i>minute</i> & <i>transitional</i>	1300	1257.5	no

From these tests it can be concluded that shell thickness is smaller in minutes than in adults of *D. trispinosa* and that the transitional stage does not differ in thickness from the adults in this case. For *D. major* the same holds good, but here the transitional stage occupies an intermediate position between the minute and the adult stage with regard to its thickness. In *D. trispinosa* no difference can be shown in shell length of the compared groups; this means that during growth the only measurable increase in thickness is found in the period after the juvenile stage. In *D. major* differences in shell length (the caudal spine excluded) are found because the adults are larger than the minutes and the transitionals. The transition between minute and adult stage in *D. major* is thus less abrupt and growth continues over a longer period in this species. That the increase in thickness is more prominent than the length increase as shown in *D. trispinosa* and to a lesser degree in *D. major* is explained (Van der Spoel, 1970) by the mechanism of shell deposition at the ventral and dorsal shell aperture border. These data prove that the minute stage described for some Cavoliniidae (Van der Spoel, 1967) is not an artefact due to fixation or preservation of the material, but that it is a normal stage in the life cycle of these animals. The size frequency distribution is asymmetrical in most Cavoliniidae (Van der Spoel, 1970). The lengths of the present material are also used to

study the skewness (g_1) of the distribution with the following results:

- D. major* in minute stage shows $g_1 < 0$ and $g_2 > 0$
- D. major* in adult stage shows $g_1 < 0$ and $g_2 < 0$
- D. trispinosa* in minute stage shows $g_1 < 0$ and $g_2 < 0$
- D. trispinosa* in adult stage shows $g_1 > 0$ and $g_2 < 0$

This means that the distribution for all except for adults of *D. trispinosa* is skewed to the left and that for all but *D. major* in the minute stage platykurtosis (g_2) occurs. The skewness to the left in this species is explained as being due to the developmental phenomena related to the occurrence of minute stages in the life cycle (Van der Spoel, 1970). That the skewness in *D. trispinosa* is to the right, like the other left skewnesses, with high significance ($P < 0.001$), is difficult to explain; the more so as the minutes show the aberration to the left like the population described earlier by Van der Spoel (1970). A possible explanation is that the present material, collected over a period of more than one year consisted of more than one population. However, the modal value in the adults of *D. trispinosa* is still shifted to the left as it is also in the other group where the g_1 is smaller than 0.

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SUMMARY

The two taxa formerly considered formae of one species are separated as distinct species, *D. trispinosa* and *D. major*, as sympatric occurrence in time and space is evident. The shell size studied proves that a statistical difference exists between the shells of animals in the minute stage and animals in the adult stage, which is another indication for the fact that the minute stages are distinct and natural stages in the life cycle of the two species and in all probability also in most other Cavoliniidae.

SAMENVATTING

Het migratiegedrag, de ontwikkeling en het voorkomen in de seizoenen van *Diacria trispinosa* in het gebied rond Bermuda, waar de beide taxa "trispinosa" en "major" voorkomen, is beschreven. Aangetoond wordt dat het niet langer mogelijk is de forma-status van beide taxa te handhaven. Beide op te vatten als soorten lijkt nu de enige mogelijkheid. De twee soorten vertonen grote overeenkomsten in hun ontwikkeling, vertikale migratie en in het voorkomen in de tijd.

De schelp-grootte van dieren in het "minute-stage" bleek steeds statistisch kleiner te zijn dan de schelp-grootte van volwassen dieren. Dit is een bewijs voor de veronderstelling dat het "minute-stage" een natuurlijk stadium in de levenscyclus is en niet een abnormaliteit veroorzaakt door fixatie en preservatie.