BULLETIN
ZOÖLOGISCH MUSEUM

UNIVERSITEIT VAN AMSTERDAM

Vol. 16 No. 11 1998

# VARIATION IN THE *DIACRIA TRISPINOSA* GROUP, NEW INTERPRETATION OF COLOUR PATTERNS AND DESCRIPTION OF *D. RUBECULA* N. SP. (PTEROPODA)

**B. Bontes & S. van der Spoel**

Key words: biogeography, speciation, pteropods, colour patterns.

## ABSTRACT

The development of the initial stages of the colour pattern on the ventral shell side in the eight taxa of the *Diacria trispinosa* group is studied. A new species: *D. rubecula,* is split off from *D. maculata* on the basis of the discriminating value of these initial colour patterns. The relation of the taxa in the group is discussed and their distributions are compared.

## INTRODUCTION

During a detailed study of the development of colour patterns in specimens of the *D. trispinosa* group collected by the 101A project in 1980 and 1981 in the N. E. Atlantic (van der Spoel, 1981; Van der Spoel & Meerding, 1983) the first author made clear that each taxon of the group shows its distinct colour pattern in young specimens that may become far less distinctive in older specimens.

The distribution of *Diacria maculata* Bleeker & van der Spoel, 1988, as published with the original description of the species, is problematic as this species seems to be found discontinuously in western boundary currents of the Pacific and Atlantic Oceans. Moreover, among *D. trispinosa* (De Blainville, 1821) forma *atlantica* Dupont, 1979 from the N. E. Atlantic Ocean deviating colour patterns resembling *D. maculata,* caused identification problems.

The results of a detailed study of the 'initial colour patterns' is given in this paper. The discriminating value of these pattern in young specimens is used to get a better insight in the taxonomy and distribution of the taxa within the *D. trispinosa* group, in particular *D. maculata.* This species proves to have a wider distribution in the Pacific and to be absent in the Atlantic where another taxon is found for which a new description is given below.

## MATERIAL AND METHODS

For this study material from the 1980 and 1981 cruises in the N. E. Atlantic of the 101A project between approximately 25°N-55°N and along 30°W (van der Spoel, 1981; Van der Spoel & Meerding, 1983) is used. Dana Expedition samples from the Pacific Ocean (Tesch, 1948) are used to study the Pacific populations of *D. maculata.* Samples are selected from which a growth series of the teleoconch and its colour pattern could be composed. For each series it is noticed where the first colour patches occur and how the colour spreads over the shell surface. Only the ventral shell surface is considered for the mere reason that the dorsal side is less informative by its more vague and homogeneous pattern. The material used is given in Table I.

## RESULTS

The genus *Diacria* shows a rather complicated ontogeny. From the egg a larva hatches with a nearly globular protoconch I. During the first days of life a dorso-laterally compressed tubular protoconch II develops, still inhabited by a veliger larva. On top of this 'tube' the colourless teleoconch grows in a period of about a week. The larva metamorphosis into the adult stage and it shifts over into the

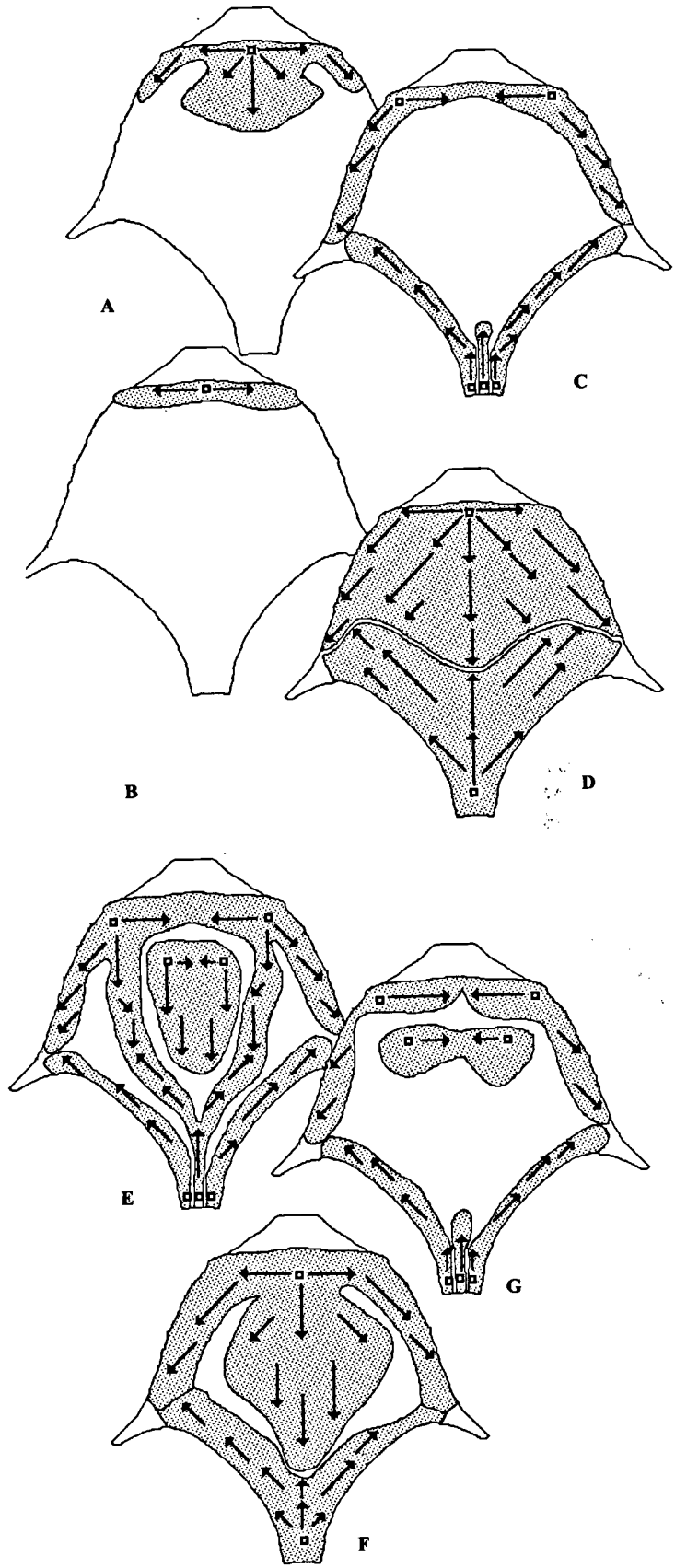


Fig. 1. Colour patterns in the *D. trispinosa* group: A= *D. rampali*, B= *D. major*, C= *D. trispinosa*, D= *D. atlantica* 'dark form', E= *D. rubecula*, F= *D. atlantica*, G= *D. maculata*. The crosses indicate the colour spots from which the pattern develops.

Table I. List of material used in this study. The positions and dates given are the averages for each station. The taxa given are only the dominant taxa for the station concerned.

| Station | Position | Date | Dominating taxon |
|---|---|---|---|
| | | 101A project | |
| 9 | 52°38'N 019°11'W | 12-4-1980 | atlantica |
| 13 | 49°00'N 029°30'W | 17-4-1980 | rubecula |
| 14 | 45°10'N 029°50'W | 18-4-1980 | atlantica |
| 16 | 41°40'N 034°55'W | 20-4-1980 | rubecula |
| 17 | 41°00'N 035°50'W | 21-4-1980 | trispinosa & rubecula |
| 18 | 39°50'N 036°00'W | 22-4-1980 | rubecula |
| 38 | 50°50'N 029°45'W | 6-10-1981 | atlantica |
| 39 | 47°45'N 030°25'W | 5-10-1981 | atlantica |
| 40 | 45°30'N 030°00'W | 2-10-1981 | atlantica |
| 42 | 41°44'N 034°25'W | 30-9-1981 | atlantica & rubecula |
| 43 | 41°10'N 035°43'W | 29-9-1981 | atlantica |
| 45 | 37°08'N 034°55'W | 27-9-1981 | rubecula |
| 47 | 35°07'N 031°10'W | 24-9-1981 | rubecula |
| 49 | 31°45'N 029°35'W | 22-9-1981 | rubecula |
| 54 | 26°10'N 024°30'W | 16-9-1981 | trispinosa |
| 55 | 27°00'N 020°15'W | 15-9-1981 | trispinosa & rubecula |
| | | Dana Expeditions | |
| 3561 | 04°20'S 116°46'W | 24-09-1928 | rampali |
| 3604 | 23°32'S 167°36'E | 24-11-1928 | maculata & trispinosa |
| 3620 | 24°45'S 170°18'E | 07-12-1928 | maculata |
| 3623 | 27°21'S 175°11'E | 09-12-1928 | trispinosa |
| 3629 | 33°36'S 179°10'W | 16-12-1928 | maculata |
| 3653 | 30°30'S 165°53'E | 26-01-1929 | maculata |
| 3768 | 01°20'S 138°42'E | 25-07-1929 | rampali |
| 3981 | 19°16'S 001°48'W | 19-02-1930 | rubecula |
| 4807 | 32°56'N 131°50'W | 12-02-1934 | maculata |

teleoconch after which a closing membrane is formed between proto- and teleoconch and the whole protoconch is shed off (van der Spoel, 1967). The colour of the teleoconch starts to develop as one or a few small colour spots. First these initial spots are very light brown \ reddish in colour, later on they spread out and in the older places the pattern become darker so that by the time the adult stage is reached a typical dark pattern is found. Ageing of the shell may result in further spreading of the colour so that its typical shape becomes masked.

In *D. major* (Fig. 1B) the most simple pattern is found with one initial colour spot centrally under the ventral aperture lip, which expands only slightly laterally.

In *D. rampali* (Fig. 1A) also a simple pattern is found. One initial colour spot centrally under the ventral aperture border spreads laterally along the aperture borders and slightly posterior in the middle.

In *D. atlantica* (Fig. 1F) two initial colour spots are found viz.: the one also found in *D. rampali,* centrally under the aperture, and one centrally on the posterior shell spine in the vicinity of the closing membrane. Expansion of the pattern from these two centres finally results in a nearly complete coverage of the ventral side. Expansion of the central posterior initial spot towards the lateral sides starts abruptly so that in the first stage three posterior spots seem to be present. Only two narrow uncoloured moon-shaped areas are left.

In *D. atlantica* 'dark form' (Fig. 1D) the colour pattern starts to develop from the same two spots as in *D. atlantica* but the expansion from the posterior spot is more prominent and results in a complete coverage of the ventral side with pigment.

In *D. trispinosa* (Fig. 1C), and the two following species, the pattern of initial colour spots becomes more complicated by a splitting of each centrally located spot into two lateral spots. In *D. trispinosa* laterally two spots are found under the aperture rime and two spots on the posterior shell spine. Usually, but not in all specimens, also an initial central spot is present on the posterior spine. From the four lateral spots colour spreads along the shell margins without invading the central parts of the ventral surface. The central posterior spot expands only very slightly to form a small 'flame' on the shell on the lowest part of the ventral side.

*D. rubecula* (Fig. 1E) shows two more initial spots than *D. trispinosa* does. On the anterior half of the ventral side at the left and the right of the middle spots form the origin of the dark pattern in the middle of the ventral side. The four laterally positioned spots expand like in *D. trispinosa*, along the shell margins, but the two lateral initial spots under the aperture rime give also a 'flame' downwards on the more central parts. The central posterior spot expands

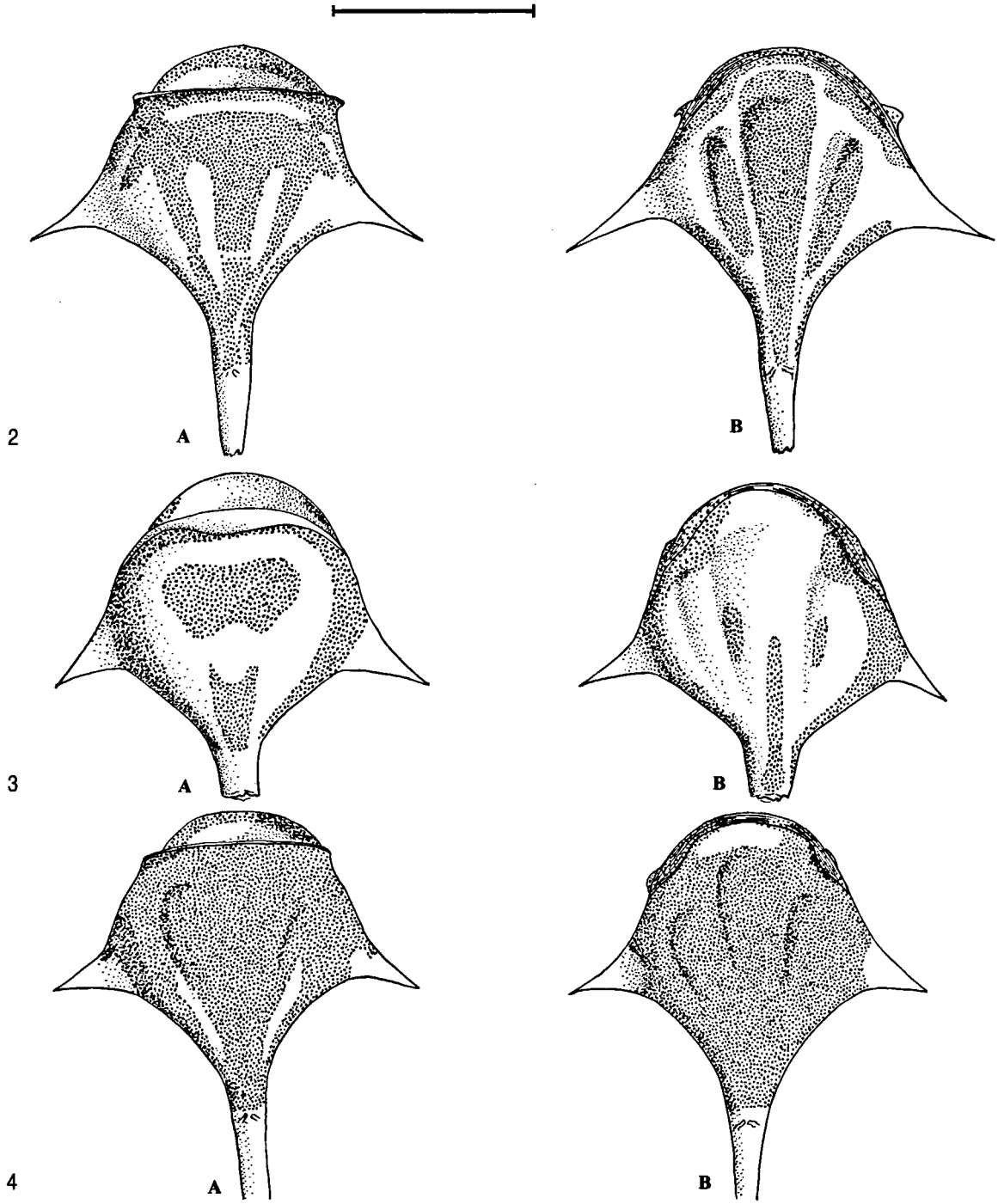


Fig. 2. Holotype of *D. rubecula* in ventral (a) and dorsal (b) view.

Fig. 3. Specimen of *D. maculata* in ventral (a) and dorsal (b) view, from 32°56'N 131°50'W, thick dots colour pattern, thin dots shadow, scale as in fig. 4.

Fig. 4. Specimen of *D. atlantica* in ventral (a) and dorsal (b) view, from 39°21'N 21°51'W, thick dots colour pattern, thin dots shadow, scale 5 mm.

bifurcating anteriorly. The left and right spot on the anterior half of the shell surface expand mainly in posterior direction.

*D. maculata* (Fig. 1G) shows the same seven spots as *rubecula* does but the two on the anterior shell part are positioned more to the left and the right side. The five initial spots also found in *trispinosa* expand exactly as they do in *trispinosa*. The left and right anterior spots do not spread posteriorly but only to the centre of the ventral shell surface, thus in a transversal direction. The most typical difference with *D. atlantica* is the opening in the colour pattern between the central part and the band along the lip rime.

Sympatric occurrence is determined in several samples for *trispinosa* and *major, rampali* and *major, rampali* and *trispinosa, trispinosa* and *rubecula, atlantica* and *rubecula, trispinosa* and *maculata*.

## DESCRIPTIVE PART

The descriptions below are all based on plankton samples thus on specimens collected alive, which was not the case in the original description of *D. maculata*.

The isolated *D. maculata*-like Atlantic populations are considered to form a species new to science for which the name *D. rubecula* is proposed.

### ***D. rubecula*** n. sp.
(Fig. 2)

#### Type material
Holotype ZMA 398011, adult specimen; 44 paratypes ZMA 398012, full grown shells with different developmental stages of colour pattern, all material is preserved in the Zoological Museum of the University of Amsterdam.

#### Type locality
Project 101A, Stat. 13-haul 1, 48°58.9'N 30°01.3'W, 16 April 1980. Depth 40-100 m, temperature at depth 10. 9°C.

#### Etymology
The red thorax of the Robin, *Erithacus rubecula*, resembles the ventral side of this species.

#### Description
The caudal spine is usually broken off below the closing septum. The lateral spines are straight and sharp, slightly directed caudally. The dorsal side shows three moderately developed ribs. The central rib is most elevated in the caudal part, the lateral ones in the middle. The lateral sides between lateral spines and closing septum are slightly curved, crossing under an angle of 100° to 120°. Growth lines are present on both sides. The colour pattern on the dorsal side consists of a small band along the lateral shell margins; separate patches of colour are found on the median and lateral dorsal rib and on the upper lip. The upper lip is curved strongly dorsally. The ribs on the ventral side are very indistinct. The ventral aperture lip curves prominently ventrally. For the colour on the ventral side see above. In the holotype the pattern on the ventral side coming from anterior and posterior along the lateral sides has not yet fused. Sizes in the holotype are: shell width 10.3 mm, shell length 8.7 mm, length above caudal septum 4.0 mm, distance between closing septum and lateral spines 6.2 mm, distance between lateral spine and centre of upper lip 7.1 mm, width of shell aperture 4. 3 mm, height of shell aperture 1.0 mm, width closing septum 0.9 mm.

#### Distribution
Atlantic Ocean.

### ***D. maculata*** Bleeker & van der Spoel, 1988
(Fig. 3)

#### Description
(after Bleeker & van der Spoel, 1988)
The caudal spine is usually broken off below the closing septum. The lateral spines are straight and sharp, directed clearly caudally resembling the position in *D. major*. The dorsal side shows three moderately developed ribs. The central rib is most elevated in the caudal part, the lateral ones in the middle. The lateral sides between lateral spines and closing septum are straight, crossing under an angle of 109°. Growth lines are evident on both sides. The colour pattern on the dorsal side consists of a continuous band along upper and lateral shell margins, on the centre of the dorsal lip a colourless area splits the left and right side bands; a separate patch of colour is found on the caudal half of the median dorsal rib and sometimes on the lateral ribs. The upper lip is curved only slightly dorsally. The ribs on the ventral side are very indistinct. The ventral aperture lip curves strongly ventrally but less abruptly as in *rubecula*. For the colour on the ventral side see above. Sizes in the holotype are: shell width 8.8 mm, shell length 7.36 mm, above caudal septum 3.2 mm, distance between closing septum and lateral spines 4.80 mm. distance between lateral spine and centre of upper lip 5.68 mm, width of shell aperture 3.20 mm, height of shell aperture 0.72 mm, width closing septum 1. 0 mm

#### Distribution
Pacific Ocean.

### ***D. atlantica*** Dupont, 1979
(Fig. 4)

#### Description
(after Dupont, 1979) and paratypes ZMA 379002
The caudal spine is usually broken off below the closing septum. The lateral spines are straight and sharp, directed caudally. The dorsal side shows three equally, and moderately developed ribs. The central rib is most elevated in the central part like the lateral are. The lateral sides between lateral spines and closing septum are nearly straight, crossing under an angle of about 110°. Growth lines are evident on both sides. The colour pattern on the dorsal side fuse to cover the whole dorsal side except for a small area centrally on the dorsal lip and except for the spine points. The upper lip is curved dorsally. The ribs on the

ventral side are distinct. The ventral aperture lip curves only slightly ventrally. For the colour on the ventral side see above.

Sizes in the holotype are: shell width 10.52 mm, shell length 8.9 mm, length between aperture and caudal septum 4.6 mm, distance between closing septum and lateral spines 6.15 mm, distance between lateral spine and centre of upper lip 6.92 mm, width of shell aperture 4.22 mm, height of shell aperture 0. 93 mm, width closing septum 0.8-09 mm.

**Distribution**
Atlantic Ocean north of about 40°N.

***D. atlantica*** Dupont, 1979 ***'dark*** form' Hilgersom & van der Spoel, 1987

**Description**
The shell shape and size are the same in the specimens from the more northern populations, though the average shell size in the upwelling samples is slightly smaller. The colour pattern on the ventral side is described above. The colour pattern on the dorsal side is so far expanded that the whole dorsal side except for the lateral spine points is occupied.

**Distribution**
Upwelling area off N. W. Africa.

A comparison of shell size for the group is given in Table II.

## DISCUSSION

The fact that *D. maculata* in the Atlantic ocean shows an ontogeny of the colour pattern different from that in the Pacific ocean and the larger average size of the specimens, proves that at least different populations are concerned. The consistent differences make us propose the new species for the Atlantic populations.

Another consequence of the colour pattern differences

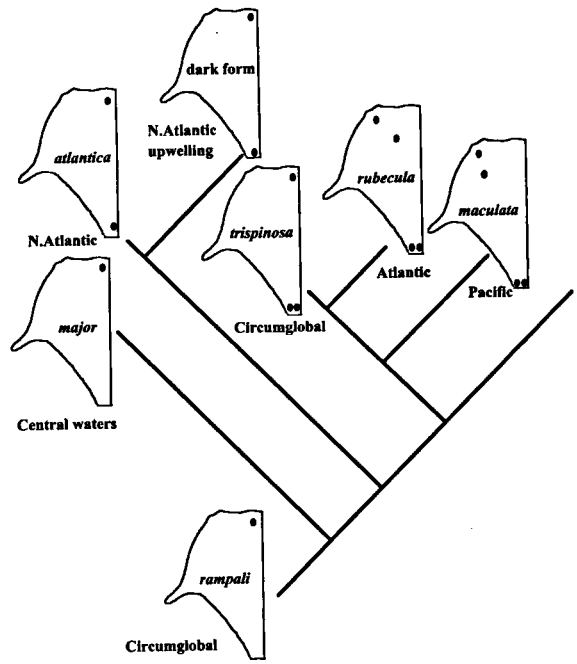


Fig. 5. Relations of the colour patterns on the ventral side with the geographic occurrence presented as a cladogram, thick dots colour pattern, thin dots shadow, scale as in fig. 4.

is that the relation of *D. trispinosa* and *D. t. atlantica* has to be reconsidered, so *atlantica* is raised to species level as it shows another initial colour pattern than *D. trispinosa* and as it occurs sympatric with its relatives.

Having made these taxonomic changes it is possible to recognise in the *D. trispinosa* group a line of increasing complexity of the initial colour patterns (Fig. 5). *D. rampali* with only one colour spot seems to be the most simple representative with a circumglobal distribution. *D. major* from the Central Water masses resembles in colour strongly *D. rampali.* The robust shell shape of *D. major,* however, contrasts markedly with all members of the group and especially with the elegant shell of *D. rampali.* Probably a rather

Table II. Morphometric data (minimum-maximum, in mm) based on the present material and literature data.

| Species | | Shell width | Shell length | Aperture height | Angle of lateral sides |
|---|---|---|---|---|---|
| rubecula | 5) | 6.7 - 10.8 | 8.0 - 9.7 | 0.6 - 1.0 | 100 - 120 |
| maculata | 4 & 5) | 5.5 - 9.0 | 5.0 - 8.0 | 0.5 - 0.9 | 100 - 120 |
| atlantica | 1 & 5) | 6.5 - 12.0 | 6.0 - 9.5 | 0.4 - 0.9 | 110 - 120 |
| 'dark form' | 2 & 5) | 7.0 - 10.0 | 6.0 - 8.0 | 0.5 - 0.9 | 100 - 110 |
| trispinosa | 1 & 4) | 5.5 - 9.0 | 5.0 - 6.8 | 0.5 - 0.9 | 80 - 90 |
| rampali | 1 & 4) | 5.5 - 7.8 | 5.4 - 6.8 | 0.5 - 0.8 | 80 - 90 |
| major | 1 & 4) | 6.5 - 11.0 | 7.2 - 9.4 | 0.5 - 1.0 | 100 - 110 |
| piccola | 4) | 2.0 - 2.4 | 2.5 - 2.8 | 0.24 | 65 - 80 |

1) after Dupont, 1979
2) after Hilgersom & van der Spoel, 1988
3) after van der Spoel, 1982
4) after Bleeker & van der Spoel, 1988
5) present study

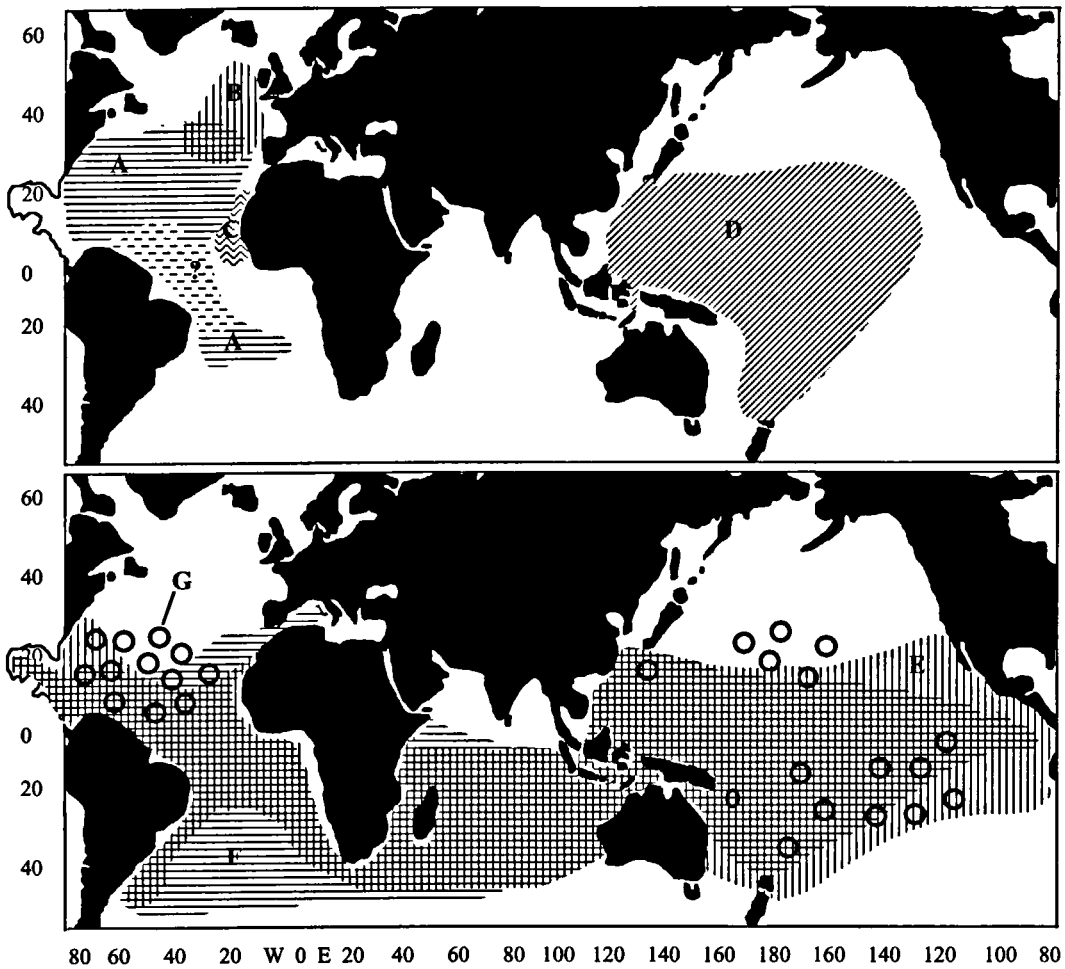


Fig. 6. Distributions in the *D. trispinosa* group. A= *D. rubecula* (black), B= *D. atlantica* (hatched), C= *D. atlantica* 'dark form' (black), D= *D. maculata.* (black), E= *D. trispinosa* (black), F= *D. rampali* (hatched), G= *D. major* (ovals).

old separation between these two taxa is concerned; the Central Water masses are the oldest water masses known (van der Spoel et al, 1990; van der Spoel, 1991) and *D. major* is the only member of the group developing such special characters.

In *D. atlantica* a second initial spot indicates further development in this endemic N. Atlantic taxon. The deviating upwelling population 'dark form' belongs to this same line and can only represent a recent Post Glacial development (cf. Badcock, 1981).

*D. trispinosa* shows in the Atlantic and Indian Ocean a more narrow N-S range than *D. rampali* does. For the Pacific Ocean this difference seems to be reversed but for this ocean less reliable data are available; not enough material is at our disposal and most information comes from literature (van der Spoel & Heyman, 1983). Accurate studies have to conform it, but possibly *D. rampali* shows a 40°N-40°S range and *D. trispinosa* a 30°N-30°S range, which indicate an old split of the two taxa. *D. trispinosa* with a doubling of the colour spots may be derived for *D. rampali* and it is than ancestral to the Pacific *D. maculata* with two extra initial spots and the Atlantic *D. rubecula* with two extra initial spots. Since the two extra spots in the latter two species are not identical neither in position nor expansion, a closer relation of the two species than the one proposed here with *D. trispinosa* is not expected.

The proposals made for the taxonomic changes in the *D. trispinosa* group result in a taxonomy as given below:

*D. major* (Boas, 1886)
*D. rampali* Dupont, 1979
*D. atlantica* Dupont, 1979 (raised to species level)
*D. atlantica* Dupont, 1979 'dark form' Hilgersom & van der Spoel, 1987
*D. trispinosa* (De Blainville, 1821)
*D. maculata* Bleeker & van der Spoel, 1988 (restricted to the Pacific)
*D. rubecula* n. sp. (was considered the Atlantic '*maculata*' population)
*D. piccola* Bleeker & van der Spoel, 1988 (not considered here due to lack of new material)

The zoogeography of the *D. trispinosa* group (Fig. 6) is congruent with the patterns of many other open ocean species. Two circumglobal species, probably with a 40°N-40°S range and a 30°N-30°S range and a Central water species, an Atlantic and a Pacific species and speciation in the N. Atlantic Ocean.

The finding of taxonomic useful characters in minor differences like de scribed for example in *Diacavolinia* (Van der Spoel et al., 1993) and here above for *Diacria* show that probably large numbers of so-called cryptic oceanic species can still be discovered in the pelagic. As the same trend is seen in micronekton species like *Cyclothone* (Miya & Nishida, 1997) it may turn out that biodiversity in the open ocean is many times larger than assumed up till now.

## REFERENCES


Badcock, J. , 1981. The significance of meristic variation in Benthosema glaciale (Pisces, Myctophidei) and the species distribution off north west Africa. Deep-Sea Res., 28A(12): 1477-1491.

Bleeker, J. & S. van der Spoel, 1988. D. piccola and D. maculata: two new pteropod species from the Atlantic and Pacific Oceans. Proc. Biol. Soc. Washington , 101 (1): 60-66.

Hilgersom, P. C. J. & S. van der Spoel, 1987, East-west variation in Diacria off Northwestern Africa. Malacological Review, 20: 97-104.

Miya, M. & M. Nishida, 1997. Speciation in the open ocean. Nature 389(6653): 803-804.

van der Spoel, S. , 1967. Euthecosomata, a group with remarkable developmental stages (Gastropoda, Pteropoda). J. Noorduyn & Zn, Gorinchem, 375 pp.

van der Spoel, S. , 1981. List of discrete depth samples and open net hauls of the Amsterdam Mid North Atlantic Plankton Expedition 1980 (project 101A). Bull . zool . Mus. Univ. Amst., 8 (1):1-10.

van der Spoel, S., 1991. Hydromedusan distribution patterns. Hydrobiologia, 216/217: 489-496.

van der Spoel, S. , J. Bleeker & H. Kobayasi, 1993). From Cavolinia longirostris to twenty-four Diacavolinia taxa, with a phylogenetic discussion (Mollusca, Gastropoda). Bijdr. Dierk., 62(3): 127-166.

van der Spoel, S. & R. P. Heyman, 1983. A comparative atlas of zooplankton. Biological patterns in the oceans. Bunge, Utrecht, Springer Verl. , Berlin: 1-186.

Van der Spoel, S & A. G. H. A. Meerding, 1983. List of discrete depth samples and open net hauls of the Amsterdam Mid North Atlantic Plankton Expedition 1981 (project 101A). Bull. zool. Mus. Univ. Amst., 9 (9): 77-91.

Van der Spoel, S., A. C. Pierrot-Bults & P.H. Schalk, 1990. Probably Mesozoic vicariance in the biogeography of Euphausiacea. Bijdr. Dierk., 60(3/4): 155-162. Tesch, J. J. , 1948. The thecosomatous pteropods, 2. The Indo-Pacific. Dana Report, 30: 1-45.



B. Bontes
S. van der Spoel
Zoological Museum,
P.O. Box 94766,
1090 GT Amsterdam
The Netherlands



Received: 1 September 1998
Distributed: 18 December 1998



This periodical is irregularly published by the Zoological Museum and the Institute for Systematics and Population Biology, both of the University of Amsterdam.
Requests for exchange or subscription (NLG 120.- per volume) should be addressed to the Library of the Faculty of Biology, University of Amsterdam, Plantage Middenlaan 45, 1018 DC Amsterdam, the Netherlands.
This periodical may be quoted in abbreviation as Bull. zool. Mus. Univ. Amsterdam.
ISSN 0165-9464