

GEOGRAPHICAL VARIATION IN *CAVOLINIA TRIDENTATA* (MOLLUSCA, PTEROPODA)

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ABSTRACT

A redescription is given for five formae of *Cavolinia tridentata* and four formae new to science are described. The distribution of the species is given and the zoogeography of the formae is discussed.

INTRODUCTION

Studying cavoliniid pteropods it seemed necessary to change existing views on the variation in *Cavolinia tridentata* (MS. Forskål) (Niebuhr, 1775).

Forskål (spelling: Forsskål according to Wolff (1968)) is usually considered the author of this taxon. In my opinion this is incorrect since Petrus Forskål, according to Wolff (1968), wrote only a manuscript consisting of 1800 loose leaflets which had been sent back from the Danish Expedition to "Arabia Felix" (1761—1767). Wolff (1968) supposed that Niebuhr is not the actual author either but only the editor, while another expert, probably Johan Zoëga, made the manuscript ready for publication.

Reference to original author and year of publication is not only of administrative value but also an indication of the expert responsible for the descriptions as finally published; therefore it is proposed to maintain the citation mentioned above. Niebuhr was the only man to survive the expedition, who took responsibility for the material, the notes, the manuscripts, and for the final publication of this and other works by Forskål. Since it is unknown who made the selection from the 1800 leaflets for the manuscript and which changes, if any, were made in editing, it seems not correct to consider Forskål the only scientist responsible for the final descriptions.

The majority of the material used in this study was collected by the United States National Museum at Washington D.C. in the Atlantic Ocean and Mediterranean ¹⁾ and in the Indo-Pacific Oceans ²⁾. Additional material was available from the Zoological Museum at Copenhagen and the Institute of Taxonomic Zoology at Amsterdam, collected by the Dana Expeditions and the Siboga Ex-

pedition respectively.

At the time five forms of *C. tridentata* are described, viz.: forma *tridentata* (MS. Forskål) (Niebuhr, 1775) from the Mediterranean, forma *kraussi* Tesch, 1913 from the Southern Atlantic and Southern Indian Ocean, forma *occidentalis* (Dall, 1908) from the North Pacific, forma *platea* Tesch, 1948 from the Malayan waters and the forma *affinis* (d'Orbigny, 1836) from the East Pacific Ocean. The forma *bermudensis* from the Western Atlantic, the forma *dakarensis* from the Northeastern Atlantic, the forma *atlantica* from the Southern Atlantic and the forma *danae* from the Indian Ocean are described as new to science in the present paper. Moreover, it proved to be justified to propose the new name *teschi* for the forma first named *platea*.

ACKNOWLEDGEMENTS

The author wishes to acknowledge the kind aid of Dr. C. F. E. Roper from the United States National Museum, Washington D.C. who collected also part of the material, and of Dr. J. Knudsen from the Zoological Museum at Copenhagen who made the Dana collections available. Thanks are also due to Dr. H. Janus from the Staatliches Museum für Naturkunde at Stuttgart, Dr. A. Zilch from the Forschungs-Institut Senckenberg at Frankfurt, Mrs. A. H. Testud from the Muséum d'Histoire Naturelle at Paris, and to Mr. L. A. van der Laan who made the photographs.

ZOOGEOGRAPHY

In fig. 1 the distribution of *C. tridentata* is given together with the eleven faunal centres (indicated

¹⁾ This material was collected by the Ocean Acre Program of the U.S.N.M. supported by funds from the U.S. Navy.

²⁾ Study of this material in the collections of the U.S.N.M. was made possible by funds of the U.S. National Science Foundation.

by roman numerals) which will be discussed below. From this map it is clear that *C. tridentata* is a species of warm and transitional waters, absent in cold waters and rare in halostaze centres. Though cosmopolitan in its distribution, discontinuity is obvious. The absence of the species south of the Australian continent seems due to insufficient sam-

pling rather than to real absence, since the southern populations from the Indian and Pacific Oceans resemble each other very closely. Gene-flow between the two southern populations seems to exist and is not interrupted by a real gap in distribution.

The isolated population in the North Atlantic is

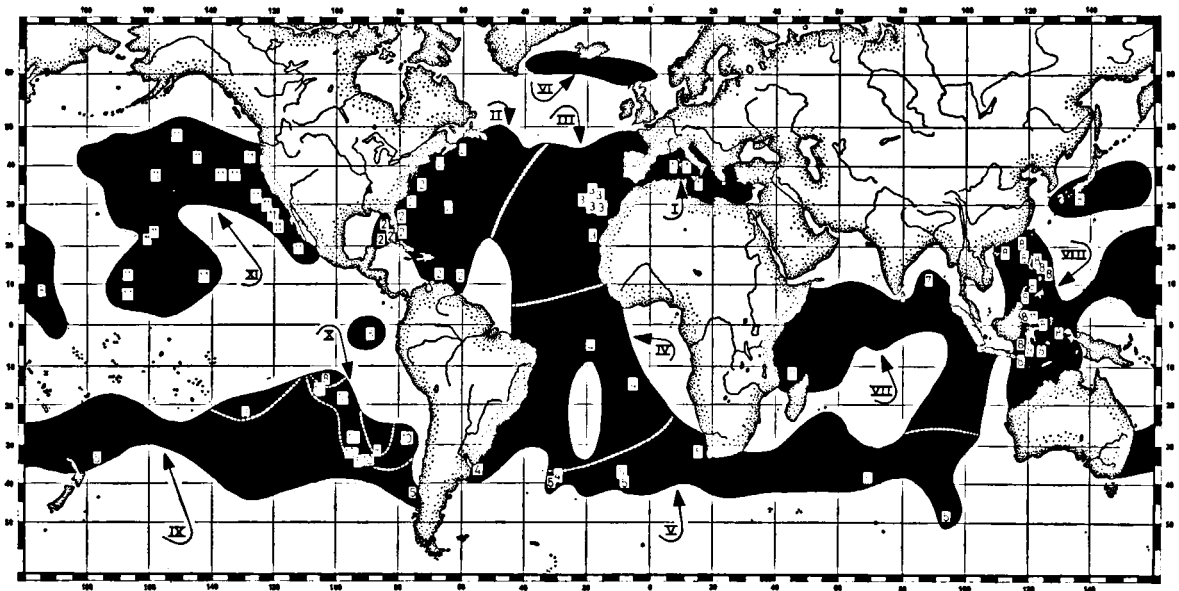


Fig. 1. Distributional map for *Cavolinia tridentata* with the eleven faunal centres indicated by roman numerals. The numerals in squares indicate the localities from which material is studied and refer to the numbers of the centres (cf. list page 103). The numerals indicate the forma *tridentata* (1), *bermudensis* (2), *dakarensis* (3), *atlantica* (4), *kraussi* (5), *danae* (7), *teschi* (8), *affinis* (10) and *occidentalis* (11).

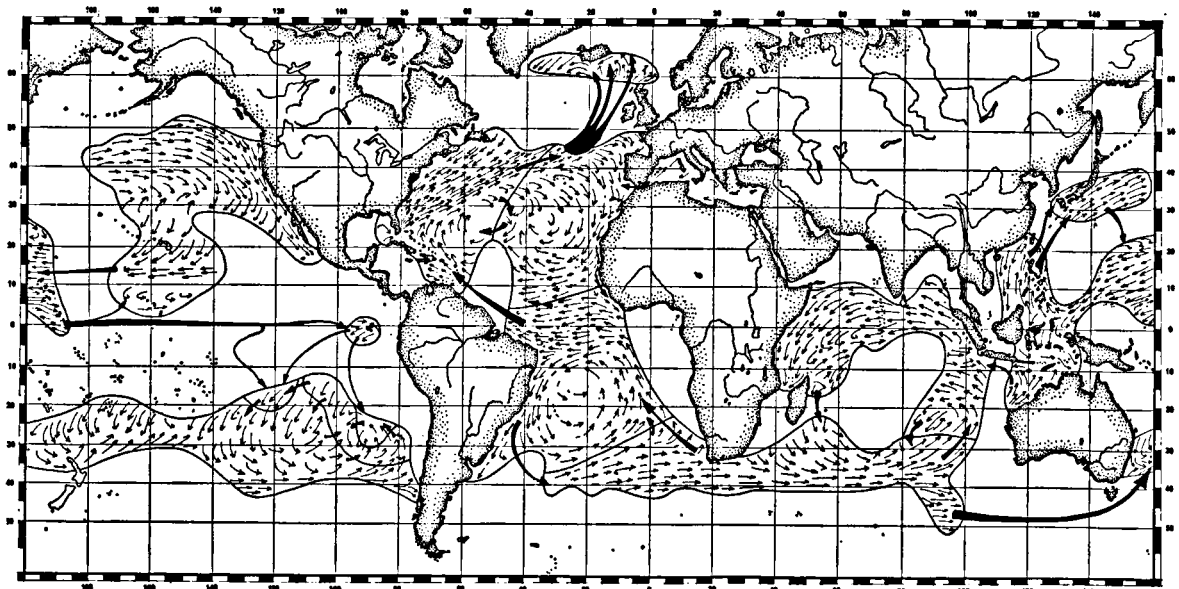


Fig. 2. Distributional map for *Cavolinia tridentata* (cf. fig. 1) with the water movements in the distributional areas and, thick arrows, the transport of specimens and genes in between the different centres.

in all probability an instable population developing from time to time by migration of animals from the central Atlantic. Schiemenz (1906) described an uninterrupted distribution of the species from 60°N to the equator. In my opinion, however, self-supporting isolated faunal elements are not to be expected in the faunal centres VI and IX.

The populations around the southern islands of Japan and around the Galapagos Islands take an isolated position. Still they are not considered as separate faunal elements. The populations south of Japan are in all probability related to, or descending from the faunal centre VIII while the same is assumed for the populations around the Galapagos Islands. Specimens studied from both areas do not differ in characters from those investigated from the faunal centre VIII.

Truly different, self-supporting and rather isolated faunal elements are found in the centres I, II, III (with VI), IV, V (with IX), VII, VIII, X and XI. These faunal centres are considered hydrographically determined areas where special planktonic faunas occur and where the existing species have developed special formae, as representative elements of these faunas. Between the centres, areas are found where the formae interbreed and merge gradually into each other.

Concerning the Northern and Eastern Pacific, McGowan (unpubl.) stated: "The indications are, from the SIO-POFI data that *C. tridentata* var. *affinis* is the commonest form present in the Eastern North Pacific. However, it seems possible that these varieties are merely growth stages since there is a regular size increase and gradation of form from one (var. *platea*) to the other (var. *affinis* and var. *kraussi*) and populations of var. *kraussi* did occur in areas where var. *affinis* were caught at neighbouring stations".

McGowan (unpubl.) was correct when considering the var. *platea* a mere growth stage. Tesch (unpubl.; 1948) described this variety from Malayan, Indian and Pacific waters but it occurs also in the Atlantic; and it is the growth stage of this species which I (van der Spoel, 1967; 1970) called the minute stage (fig. 5k). It should be mentioned that McGowan did not distinguish between the formae *occidentalis* and *affinis*. From the area of centre IX, Dana material and material of the collections of Dall were studied, which proved the forma *kraussi* to occur in this centre. The forma *affinis* is a typical element of the centre X overlapping partly the centre IX. This area in the South East Pacific is rather complicated as repre-

sentatives of the centre VIII are also met here. Probably with the Equatorial Counter Current and the northern parts of the West Wind Drift, transport of populations towards this area is possible (fig. 2).

Material from the Albatross Expeditions and the original material described by Dall (1908; 1921) proved that the forma *occidentalis* occurs in the faunal centre XI. This forma is not mentioned by McGowan (unpubl.), in all probability he considered this forma synonymous with the forma *affinis*. Tesch (1904) did not mention the forma *occidentalis* either, which seems logical as only the forma *teschi* (see below) is found in the Indo-Malayan waters. But the forma *affinis* is given by Tesch (1904) as occurring in the Indo-Malayan Archipelago. The specimen considered by Tesch to belong to the forma *affinis* and collected at Siboga station 116 is reexamined and it proved to resemble most the forma *occidentalis*. The occurrence of this forma at 00°58.5'N 122°42.5'E (Siboga sta. 116) is exceptional, probably due to transport through the Pacific by Equatorial Currents.

In the present study the formae *occidentalis* and *affinis* are both considered valid. The forma *affinis* as described by d'Orbigny (1836) and discussed by Boas (1886) consists of the two formae mentioned. The most typical difference between *affinis* and *occidentalis* is not the curvature of the caudal spine as described and pictured by Boas (1886), but it is formed by the greater average size and the less perfect round shape of the ventral surface in *affinis*. The original description by d'Orbigny is based on a specimen with the embryonic shell intact, and it is only this embryonic shell which strongly bends dorsad, which is normal for both the formae *occidentalis* and *affinis*.

The populations of Indo-Malayan waters are clearly separated from the other Pacific populations. Microevolution in the Pacific has not led to subspecies formation as the mixture of populations by currents is still too intensive, but the differences between the Indo-Pacific formae are greater than those between the Atlantic formae.

Representatives of the Atlantic and Indian Ocean have incorrectly been considered always to be identical to the Mediterranean form. The populations from the southern oceans, found in the centres V and IX, consist of the forma *kraussi*, and are usually considered as such; but the populations of the Indian Ocean and North Atlantic Ocean differ also strongly in shape and size from the Mediterranean ones, which was usually not recog-

nized. The first who recognized differences between Atlantic and Indian Ocean populations was Fryer (1869). The zoogeography and description of the three species which are recognized by Fryer are, however, too vague to be reproduced here. In the synonymy to the formae the names used by Fryer (loc.cit.) are given where possible. The Mediterranean populations show special characters, which is explained by the isolated character of this ocean basin. Less easily explained are the differences between the faunal elements of the centres II, III and IV. These centres are not at all isolated. The centre IV may coincide with the South Atlantic halostaze limited in the north by the Equatorial Current and in the south by the Tropic Front. Probably different ecological selective pressures are responsible for the differences between the populations in the areas II and III. An indication for clinal variation is not found in the North Atlantic; therefore the ecological or climatological influences could not be traced.

The special characters of the forma living in centre VII can be explained by the relatively isolated position of this warm water centre separated by land from the other warm water areas. The only contact with other representatives of the present species of this faunal element is formed by the forma *kraussi* from transitional waters.

TAXONOMY

The total number of different formae which may be recognized in *C. tridentata* is nine, viz.:

- Cavolinia tridentata* forma *tridentata*
from faunal centre I
- Cavolinia tridentata* forma *bermudensis*
from faunal centre II
- Cavolinia tridentata* forma *dakarensis*
from faunal centre III (and VI)
- Cavolinia tridentata* forma *atlantica*
from faunal centre IV
- Cavolinia tridentata* forma *kraussi*
from faunal centre V (and IX)
- Cavolinia tridentata* forma *danae*
from faunal centre VII
- Cavolinia tridentata* forma *teschi*
from faunal centre VIII
- Cavolinia tridentata* forma *affinis*
from faunal centre X
- Cavolinia tridentata* forma *occidentalis*
from faunal centre XI

The description of these infra-subspecific taxa

does not make it easier to identify specimens but more accurate studies on the biology can be executed with this more accurate subdivision of taxa. For the forma concept one is referred to van der Spoel (1971).

In this paper the name *teschi* is proposed for the Indo-Malayan populations replacing the name *platea*, though the growth stage mentioned by Tesch (unpubl.; 1948) is undoubtedly a young stage of the forma living there. The name given by Tesch is to be considered a nomen nudum as it is not accompanied by a description in the 1948 publication.

Affinis and *kraussi* are treated in the present paper as formae though they do sometimes occur sympatrical as stated also by McGowan (unpubl.). But when they actually occur sympatrically they show interbreeding as indicated by the high number of intermediates. In some samples I found two formae together without their intermediates but these samples are always from open net hauls from greater depth.

Most of the faunal centres and their populations need a more detailed study than is possible at this moment but a few remarks can be made already. The "typical" *C. tridentata* form is considered restricted to the Mediterranean; *Cavolinia tridentata* was originally described from material collected in the Mediterranean. The forma *kraussi* shows not only interbreeding with the forma *affinis* in the Pacific as mentioned, but also with the forma *atlantica* in the Atlantic and with the forma *danae* in the Indian Ocean. Populations in the Caribbean Sea near 10°N show strong influences of the forma *atlantica*. Consequently strong interbreeding among the formae *bermudensis* and *atlantica* is to be expected, which may be explained by a transport by Equatorial Currents of the latter forma. The forma *dakarensis* may show in the periphery of its range a gradual changeover into the formae *atlantica* and *bermudensis*. A clear interbreeding between the formae *tridentata* and *dakarensis* is not expected at the moment because a changeover between the two could not be demonstrated. The contact between the faunal centres V and IX and their populations is already mentioned.

The forma *occidentalis* from the faunal centre XI shows a clear affinity to the forma *affinis* from faunal centre X. From a morphological point of view one should be inclined to consider the forma *occidentalis* as a forma of *Cavolinia uncinata* (Rang, 1829), an idea already given by Tesch (1904). The formae *affinis* and *teschi* however, constitute

clear intermediate forms to the other representatives of *C. tridentata*.

The forma *teschi* penetrates the East Pacific north of 25°S and interbreeds there with the forma *affinis* and *kraussi* which gives the *teschi* populations east of 180°W another appearance than those from the Indo-Malayan waters but there is no reason to distinguish between eastern and western *teschi* populations as a boundary between the two is absolutely absent. Closely related to *teschi* is the forma *danae* from the Indian Ocean, though frequent interbreeding is not to be expected as the distribution is discontinuous. Contact of the forma *danae* with the forma *atlantica* south of the African continent is at least restricted as the forma *kraussi* has its northern limit north to the Cape of Good Hope.

From the above mentioned relations one can conclude that there are two clearly separate formae *kraussi* and *tridentata*, an Atlantic group of three

formae viz.: *atlantica*, *bermudensis* and *dakarensis*, an Indian Ocean group of two formae viz.: *danae* and *teschi* of which *teschi* is also found in the Pacific and an endemic Pacific group composed of *affinis* and *occidentalis*.

Size differences between the formae are not of discriminating value. The formae *bermudensis*, *teschi*, *danae* and *kraussi* are of an average size, the forma *dakarensis* is the largest forma while the formae *tridentata*, *atlantica*, *occidentalis* and *affinis* constitute a group of smaller types (fig. 3). Clinal variation in size, however, is not concerned. In fig. 2 the distribution of the formae is given with possible movements of specimens in between the centres indicated by thick arrows. Water current patterns in the area of distribution are given with thin arrows. From this map it is clear that exchange of specimens, and as a consequence of genes, may exist between all the faunal centres. This explains the great resemblance between the formae and the identity within populations.

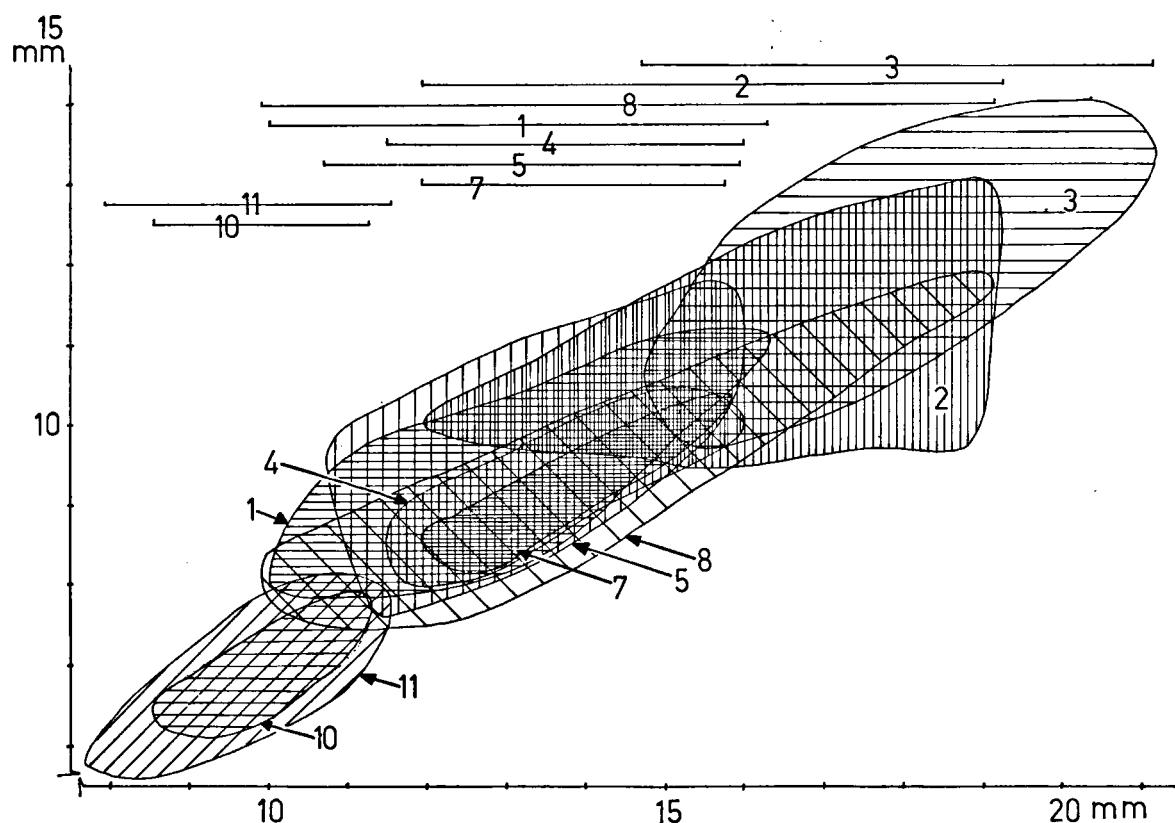


Fig. 3. Length-width relation for *Cavolinia tridentata* forma *tridentata* (1), forma *bermudensis* (2), forma *dakarensis* (3), forma *atlantica* (4), forma *kraussi* (5), forma *danae* (6), forma *teschi* (7), forma *affinis* (8), forma *occidentalis* (9) and forma *occidentalis* (11) in mm.

DESCRIPTION OF THE FORMAE OF *CAVOLINIA TRIDENTATA*

In the respective lists of material the localities are given only for measured or figured specimens, while in fig. 1 all identified material is represented by a square. Abbreviations used in the lists below are U.S.N.M. for United States National Museum at Washington D.C., Z.M.U.C. for the Zoological Museum at Copenhagen and Z.M.A. for the Institute of Taxonomic Zoology at Amsterdam, while Med. stands for the Mediterranean cruises executed in 1971 by the U.S.N.M.

Cavolinia tridentata forma *tridentata*

(MS. Forskål) (Niebuhr, 1775).

Figs. 4a;6c.

Synonymy

Monoculus telemus Linnaeus, 1758: 635; *Anomia tridentata* (MS. Forskål) Niebuhr, 1775: 124, 1776: pl. 40, figs. B, b1, b2; *Cavolinia natans* Abildgaard, 1791: 175; *Cavolinia tridentata* (part) Philippi, 1853: 290; *Hyalaea tridentata* (part) Fryer, 1869: 266; *Cavolinia tridentata* forma *tridentata* (part) van der Spoel, 1967: 94, fig. 89.

Material

40°32'N 12°28'E (Med. 3—20 M, U.S.N.M.) (fig. 4a); 40°23'N 12°43'E (Med. 3—24 M, U.S.N.M.); 40°26'N 12°33'E (Med. 3—18 P, U.S.N.M.); 40°27'N 12°52'E (Med. 3—3 B, U.S.N.M.); Napels (coll. Schepman, Z.M.A.); Messina (Z.M.A.).

Description

The shell of hyaline or opaque nature is triangular in ventral view, showing a relatively flat, dorsal surface with moderately developed dorsal ribs. The dorsal lip is separated from the dorsal surface by a prominent arch-shaped rib between the aperture closing mechanisms. The dorsal lip is rounded and sometimes even pointed, so that the aperture is triangular in shape. Lateral sides show no keels. The lateral spines are directed slightly caudad. The shell margin between caudal and lateral spines is regularly concave. The ventral surface is vaulted. The structures on the shell consist of clearly developed transversal ribs and faint growth lines. The shell shows a chestnut brown colour over its entire surface. The shell length varies between 10.0 and 18.0 mm, its width varies between 7.5 and 11.5 mm, the averages are 11.2 and 8.5 mm respectively.

Range

This form is endemic for the Mediterranean (centre I). Type locality: The type material could not be traced. The species, and this forma is originally described from the Mediterranean.

Cavolinia tridentata forma *bermudensis* n. forma. Figs. 4d;6a.

Synonymy

This forma is usually named *C. tridentata* in previous works or considered to belong to the typical subspecies or forma as it has never been recognized as a separate forma.

Material

Off Sambo Reef, Fla. (U.S.N.M. 357035); Albatross sta. 2385 (U.S.N.M. 614075); off Pelican Isl., Barbados (U.S.N.M. 502290); Barbados (U.S.N.M. 199037); off Havana, Cuba (U.S.N.M. 199041); several stations off Bermuda made during the Ocean Acre Program (U.S. N.M.); George Banks (U.S.N.M. 52104); Gulf of Mexico (U.S.N.M. 223656); 27°20'N 51°54'W (Dana sta. 1325 III, Z.M.U.C.).

Description

The hyaline or opaque shell shows a slightly vaulted dorsal surface, with moderately or even poorly developed ribs. The dorsal lip is separated from the dorsal surface by a well developed arch-shaped rib. In ventral view the lateral margins of upper lip and shell-body form a smooth regular line without clear incisions near the base of the dorsal lip. The upper aperture lip is rounded. The lateral sides show no keels and the lateral spines do not project caudad. The caudal spine is straight, while the shell margins between the caudal and lateral spines are composed of a concave and a straight section. The ventral side is moderately vaulted. The aperture has a triangular shape. The shell structure consists of tiny transversal ribs and nearly invisible growth lines. The whole shell is yellowish-brown in colour. The shell length varies between 12.0 and 19.5 mm, while the width varies between 9.5 and 13.5 mm, the averages are 15.8 and 10.2 mm respectively.

Range

The forma occurs in the North West Atlantic (centre II). Type locality: Off Martha's Vineyard, U.S. Fish. Com. sta. 876. The holotype (U.S.N.M. 38334) (fig. 4d) is kept dry in the United States National Museum, together with four (U.S.N.M. 703761, 703762, 703763, 703764) paratypes, one paratype is kept in the Institute of Taxonomic Zoology at Amsterdam.

Cavolinia tridentata forma *dakarensis* n. forma. Figs. 4b;6b.

Synonymy

This forma is usually referred to as *Cavolinia tridentata* in previous works. *Hyalaea tridentata* (part) Fryer, 1869: 266, fig. 1.

Material

Atlantic (U.S.N.M. 127281); 29°13'N 14°42'W (Dana sta. 4017 XI, Z.M.U.C.); 28°09'N 15°19'W (Dana sta. 4014 IV, Z.M.U.C.); 34°15'N 16°52'W (Dana sta. 1141 IV, XVI, XX, Z.M.U.C.); 31°30'N 12°12'W (Dana sta. 4018 II, Z.M.U.C.); 30°17'N 20°44'W (Dana sta. 1152 V, Z.M.U.C.).

Description

The usually hyaline or sometimes opaque shell shows a rather flat dorsal surface with moderately developed ribs. The dorsal lip is separated from the dorsal side by a moderately or poorly developed arch-shaped rib between the closing mechanisms. The lateral sides have no lateral keels, and the margin of upper lip and shell-body forms an irregular line by the incisions at the base of the lip. This dorsal lip is truncated so that a more or less straight upper border of about 4 mm length is found. The aperture is irregular, triangular in shape. The caudal spine is straight and relatively long. The lateral spines curve caudad. The margin of the shell between the caudal and lateral spines shows a concave and a straight part. The ventral side is moderately vaulted. The structure on the shell consists of faint growth lines and a very faint transversal striation. The yellowish-brown hue over the shell is less intense on the dorsal lip and along the lateral sides. The shell length varies between 14.5 and 21.5 mm, the width varies between 9.5 and 14.5 mm, the averages are 16.9 and 11.4 mm respectively.

Range

This forma occurs in the Northeastern Atlantic (centres II and VI). Type locality: 32°55'N 21°51'W, Dana sta. 1148 VII. The holotype and 10 paratypes (fig. 4b) are kept in alcohol in the Zoological Museum at Copenhagen; 2 paratypes are preserved in the Institute of Taxonomic Zoology at Amsterdam.

Cavolinia tridentata form atlantica n. forma.

Figs. 4c; 6i.

Synonymy

This forma is usually named *C. tridentata* in previous works.

Material

South Atlantic (U.S.N.M. 127289); 5°S 20°W (U.S.N.M. 169292); 40°S 30°35'W (Walter Herwig Exped. 1971 sta. 371 II, U.S.N.M.).

Description

The hyaline or less frequently opaque shell shows a moderately vaulted dorsal surface. The central

rib on the dorsal side is well developed, the lateral ribs are much less developed. A well developed arch-shaped rib is found at the base of the dorsal lip. The lateral sides are not provided with keels. The lateral spine points are directed slightly caudad, the caudal spine is short and straight. The shell margin between caudal and lateral spines is concave with a more or less straight horizontal section. The ventral side is moderately vaulted. The aperture is triangular in shape. The dorsal aperture lip is rounded or it may be provided with a small additional part with a short straight section of about 3 mm length. The growth lines on the shell are faint and the transversal striation on the shell is poorly developed. A light-brown hue covers nearly the whole shell. The shell length varies between 11.5 and 16.0 mm, the width varies between 8.0 and 10.5 mm, with averages of 15.2 and 9.9 mm respectively.

Range

This forma occurs in the Southern Atlantic between 5°N and 40°S (centre IV). Type locality: St. Helena, coll. Turton. The holotype (U.S.N.M. 123920) (fig. 4c) and one paratype (U.S.N.M. 703765) is kept dry in the United States National Museum, one paratype is kept dry in the Institute of Taxonomic Zoology at Amsterdam.

Cavolinia tridentata forma kraussi Tesch, 1913.

Figs. 4e; 6f.

Synonymy

Hyalaea truncata (non Lesueur, 1821) Krauss, 1848: 34, pl. 2, fig. 12; *Hyalaea teniobranchia* (part) Fryer, 1869: 266, fig. 2; *Cavolinia tridentata kraussi* Tesch, 1913: 51; *Cavolinia tridentata forma kraussi* van der Spoel, 1967: 97, fig. 94; *Cavolinia tridentata* var. *kraussi* McGowan, unpubl.: 129.

Material

40°00'S 30°35'W; 39°53'S 21°33'W; 40°35'S 09°57'W; 40°34'S 09°50'W; 40°03'S 07°30'W; 40°02'S 07°28'W; 40°01'S 07°25'W; 38°06'S 01°12'E; 34°25'S 14°47'E; 24°22'S 00°29'E, Walter Herwig Exped. 1971, sta. 371 II, 380 III, 399 II, 402 I, 402 II (fig. 4e), 402 III, 409 I, 419 I and 439 I respectively (U.S.N.M.); 33°36'S 179°10'W (Dana sta. 3629 I, Z.M.U.C.); West of Tristan da Cunha (Z.M.A.).

Description

The hyaline or opaque shell shows a slightly vaulted dorsal surface with three well developed longitudinal ribs and two less prominent ribs along the lateral sides. The dorsal aperture lip is separated from the dorsal side by a prominent arch-shaped rib between the closing mechanisms. The aperture lip is strongly truncated, usually even

showing two anterior projections. The lateral sides are provided with strong side keels composed by thin "wings" of the ventral and the dorsal shell surface. The lateral spine points are directed caudad. The caudal spine is straight. The shell margin between the caudal and lateral spines is irregularly concave. The ventral side is strongly vaulted. The shell aperture is trapezoid in shape. The structure on the shell consists of growth lines and transversal ribs on the ventral side which are very variable, sometimes they are coarse, sometimes faint. The colour of the shell consists of a brown to dark-brown or purple pattern over the ventral and dorsal side. The dorsal aperture lip is always lighter in colour and the lateral keels are whitish. The shell length varies between 10.5 and 16.0 mm, the width varies between 8.0 and 10.5 mm, with averages of 13.3 and 10.2 mm respectively.

Range

This forma occurs in the Subantarctic waters of Atlantic, Indian and Pacific Oceans (centre V and IX). Type locality: Vals Bay (South Africa). The type material, formerly kept in the Staatliches Museum für Naturkunde at Stuttgart, has been lost (Dr. Janus in lit.).

Cavolinia tridentata forma *danae* n. forma.

Figs. 5f, 6e.

Synonymy

This forma is usually named *C. tridentata* in previous works and Tesch (1948) probably used var. *platea* for part of this taxon. *Hyalaea affinis* (non d'Orbigny, 1836, non Sowerby, 1878) (part) Fryer, 1869: 266.

Material

Gulf of Bengal (U.S.N.M. 12726); Indian Ocean (U.S.N.M. 127290; this sample shows some characters of the next forma).

Description

The shell is hyaline or opaque with a rather flat dorsal surface, provided by nearly invisible longitudinal ribs. The dorsal lip is separated from the dorsal side by a very flat but distinct arch-shaped rib. The lateral sides have no keels, the lateral spine tops are directed caudad. The dorsal aperture lip is truncated giving rise to a straight upper margin of about 4 mm. The relatively long caudal spine is straight and the shell margin between caudal and lateral spines is concave. The ventral side is moderately vaulted. The growth lines and transversal ribs on the ventral surface are not distinct. The aperture is trapezoid. The colour pattern consists of a yellowish-brown irregularly distribut-

ed over the shell. Shell length varies between 12.0 and 16.0 mm and width varies between 8.0 and 10.5 mm, with averages of 14.8 and 9.5 mm respectively.

Range

This forma is endemic in the Indian Ocean north of 25°S (centre VII). Type locality: 14°16'S 41°48'E, Dana Exped., sta. 3951 IV. The holotype (fig. 5f) is kept in alcohol in the Zoological Museum at Copenhagen, two paratypes are preserved in alcohol in the Institute of Taxonomic Zoology at Amsterdam.

Cavolinia tridentata forma *teschi* n. forma.

Figs. 5g, j, k; 6d.

Synonymy

Hyalaea affinis (non d'Orbigny, 1836, non Sowerby, 1878) (part) Fryer, 1869: 262, 266, pl. 21, fig. 3; *Cavolinia tridentata platea* (part) Tesch, 1948: 25, fig. 21 E—F; *Cavolinia tridentata* forma *platea* (part) van der Spoel, 1967: 96, fig. 93; *Cavolinia tridentata* var. *platea* (part) McGowan, unpubl.: 129.

Material

Ally Isl. Ujae Atoll (U.S.N.M. 607392); 7°24'S 118°15.2'E (fig. 5j); 52.9°S 119°56.7'E; 0°34.6'N 119°8.5'E; 5°43.5'N 119°40'E; 6°11'N 120°37.5'E; 2°40'S 128°37.5'E; 5°39'S 122°12'E; 6°24'S 124°39'E; Banda, Siboga sta. 45, 52, 88, 95, 100, 178, 208, 221 and 240 respectively (Z.M.A.); 3°40'30"N 137°53'E (Dana sta. 3751 III, Z.M.U.C.) (fig. 5k).

Description

The hyaline or opaque shell shows a rather flat dorsal surface with slightly developed longitudinal ribs. The dorsal aperture lip is separated by a moderately developed rib forming an arch between the closing mechanisms of the aperture. This dorsal aperture lip is rounded, only in some of the older specimens provided by a small additional part giving rise to a truncated part with a straight margin of only about 3 mm. The lateral sides have no keels, the lateral spine points are directed caudad. The caudal spine is straight and the shell margin between this spine and the lateral spines is concave. The ventral side is moderately vaulted. The wide shell aperture has a lunar shape. Growth lines are very faintly developed and the transversal striae on the ventral side are very thin, nowhere disturbing the smooth character of the shell. The colour pattern consists of a yellowish-brown hue over the shell, the central parts of ventral and dorsal side are usually lighter than the remaining shell parts. The shell length varies between 10.0 and 19.0 mm, the width varies between 7.5 and



Fig. 4. Photographs of shells of *Cavolinia tridentata* (magnification $\times 3$ approx.); in the upper row dorsal views in the middle row ventral views and in the lower row lateral views of the formae *tridentata* (a), *dakarensis* (b), *atlantica* (c), *bermudensis* (d), and *kraussi* (e).

12.0 mm, with averages of 13.7 and 8.9 mm respectively.

Range

This forma is found in the Indo-Malayan waters, Equatorial and Tropical Pacific (centre VIII). Type locality: 5°40.7'S 120°45.5'E (Siboga sta. 211). The holotype (fig. 5g) and three paratypes are kept dry in the Institute of Taxonomic Zoology at Amsterdam.

Tesch (1948) did not publish a description, and as he did never indicate type material the name "*platea*" is in fact a nomen nudum. As a nomen nudum is not available according to the code the name *teschi* is proposed for this forma new to science in honour to the late Dr. J. J. Tesch.

To show the development of the shell during its growth a photograph (fig. 5k) of a young shell, with an animal in minute stage (cf. van der Spoel, 1967) and a photograph (fig. 5j) of a more developed but still not yet fullgrown specimen is given. It was a growth stage like given in fig. 5k on which Tesch (unpubl.; 1948) based the variety "*platea*".

Cavolinia tridentata forma *affinis*

(d'Orbigny, 1836).

Figs. 5i; 6h.

Synonymy

Hyalaea affinis (non Sowerby, 1878, non Fryer, 1869) (part) d'Orbigny, 1836: 91 (1846), pl. 5, figs. 6–10; *Hyalaea tridentata* var. *affinis* (part) Boas, 1886: 116, 212, fig. 100; *Cavolinia tridentata* var. *affinis* (part)

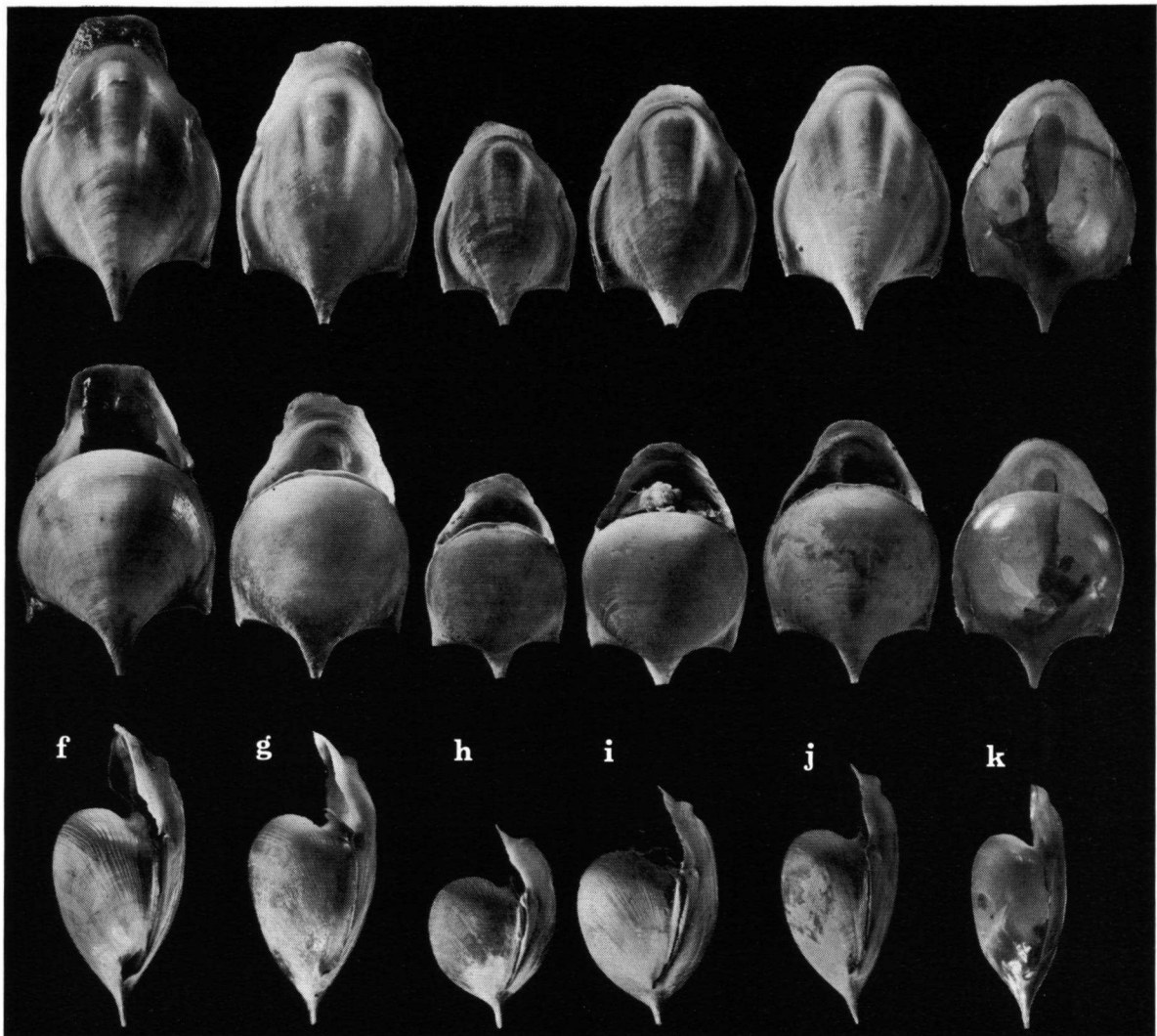


Fig. 5. Photographs of shells of *Cavolinia tridentata* (magnification $\times 3$ approx.); in the upper row dorsal views, in the middle row ventral views and in the lower row lateral views of the formae *danae* (f), *teschi* (g), *occidentalis* (h), *affinis* (i), early adult stage of *teschi* (j), and the minute stage of *teschi* (k).

Tesch, 1904: 39, pl. 2, fig. 32; McGowan, unpubl., 129; *Cavolinia tridentata affinis* (part) Tesch, 1913: 51, Tesch 1948: 25, fig. 21 C—D; *Cavolinia tridentata* forma *affinis* van der Spoel, 1967: 96.

Material

19°37.7'S 108°27.7'W (U.S.N.M. 670196) (fig. 5i).

Description

The shell is small in relation to the other formae, though the average size seems still higher than in the forma *occidentalis*. The caudal spine is curved dorsad in some specimens, but usually the spine is straight and projecting a little caudad, so that its axis makes an angle with the shell axis. This oblique position is typical for all the Indo-Pacific

formae though it occurs always to a lesser extent than in the forma *occidentalis*. The usually opaque shell shows a slightly vaulted dorsal surface with normally developed longitudinal ribs. The dorsal aperture lip is rounded and the lateral sides show no keels. The lateral spine points are not or only slightly directed caudad. The arch-shaped rib at the base of the dorsal aperture lip is not as strong as in most other formae. The shell margin between the caudal and lateral spines is concave. The aperture has a lunar shape. The ventral aperture lip is relatively small while the ventral side is strongly vaulted. This side is, however, not circle round in profile view like in the next forma as the greatest shell thickness is found anterior to the middle.

Growth lines and shell structures are very faint. The number of transversal striae on the ventral side is very high. The shell colour consists of a light purple brown hue over the whole shell. The shell length varies between 8.5 and 11.5 mm, the width varies between 6.0 and 8.0 mm; too few specimens were available to give averages.

Range

This forma occurs in the Southeastern Pacific (centre X). Type locality: South Pacific between 30° and 34°S and between 80° and 92°E (Paris-longitude). The two syntypes are kept dry in the Museum of Natural History at Paris, the adult specimen (11.4 mm length, 7.2 mm width) is indicated as lectotype, the young specimen (11.2 mm length, 6.8 mm width) is indicated as paralectotype.

The two specimens forming the type material are in all probability less "typical" for this forma as they are representing intermediate specimens.

Cavolinia tridentata forma *occidentalis* Dall, 1908. Figs. 5h; 6g.

Synonymy

Hyalaea affinis (non Sowerby, 1878, non Fryer, 1869) (part) d'Orbigny, 1836: 91; *Cavolinia tridentata* var. *affinis* (part) Tesch, 1904: 39, pl. 2, fig. 32; McGowan, unpubl.: 129; *Cavolinia occidentalis* Dall, 1908: 223, pl. 12, fig. 1; Dall, 1921: 59; *Cavolinia tridentata affinis* (part) Tesch, 1913: 51; Tesch, 1948: 25, fig. 21 C-D; *Cavolinia tridentata* forma *tridentata* (part) van der Spoel, 1967: 94.

Material

Taka Islet, Marshall Isls. (U.S.N.M. 615457); 40°11'N 125°9'W (U.S.N.M. 253050); S. coast of Oahu; Hawaii Isls. (U.S.N.M. 334809) (fig. 5h); 00°58.5'N 122°42.5'E (Siboga Exped. sta. 116, Z.M.A.).

Description

The shell is very small in relation to those of the other formae of this species. In general appearance the specimens resemble *Cavolinia uncinata*, though the caudal spine is completely straight. The opaque shell shows a relatively strongly vaulted dorsal surface with three moderately developed central ribs and two faintly developed lateral ribs. The dorsal aperture lip is separated from the dorsal surface by a prominent arch-shaped rib. The dorsal lip is rounded and the lateral sides show no keels. The lateral spine tops are not or only slightly directed caudad. The shell margin between the caudal spine and lateral spines is composed of a more or less straight section and a concave

part. The ventral aperture lip is very small in comparison with the other forms. The ventral side is strongly vaulted, in profile view it is perfectly circle round. The aperture has a triangular lunar shape. The sculpture on the shell consists of growth lines and up to 20 transversal ribs on the lateral side. The shell shows only a light brown or yellowish hue colour pattern, the upper lip and lateral sides are lighter. The shell length varies between 7.5 and 11.5 mm, the width between 5.5 and 8.5 mm, with averages of 10.3 and 6.6 mm respectively.

Range

This forma occurs in the North East Pacific (centre XI). Type locality: 38°4'N 137°W, coll. Dall. The holotype (U.S.N.M. 110591) and four paratypes (U.S.N.M. 110590) are kept dry in the United States National Museum at Washington D.C.

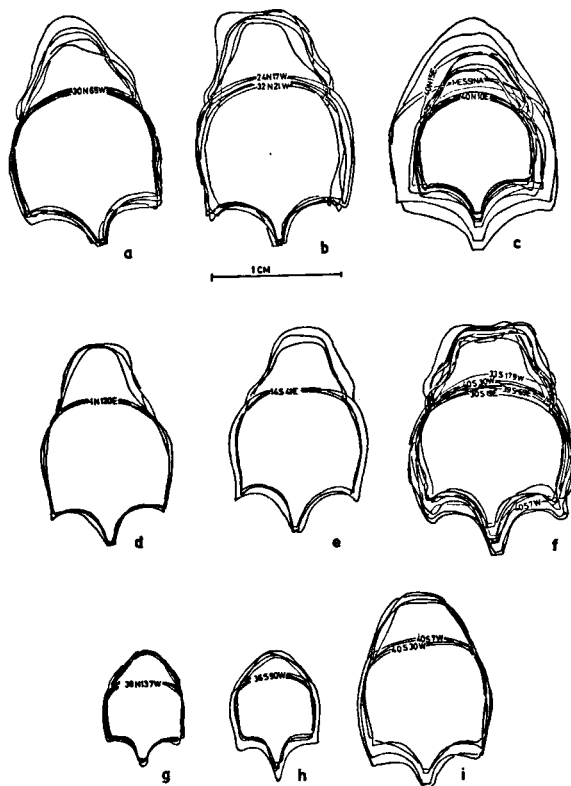


Fig. 6. Outlines of shells of *Cavolinia tridentata* in ventral view made with the camera lucida of the formae *bermudensis* (a), *dakarensis* (b), *tridentata* (c), *teschi* (d), *danae* (e), *kraussi* (f), *occidentalis* (g), *affinis* (h), and *atlantica* (i).

KEY TO THE FORMAE OF *CAVOLINIA TRIDENTATA*

The great resemblance between the formae makes it necessary to give a key for their identification. In fig. 6 the outlines of the different forms seen from the ventral side are given for comparison when using the key. During growth the shell shows two remarkable changes. In older specimens the shell is thicker than in the younger minute stages so that the shell thickness is variable. Secondly, the upper aperture lip continues growing for a long period. Very young specimens show always a rounded aperture lip, while in older specimens an additional part is formed which tends to be more blunt. Shell thickness is not used in the key. In point 3 of the key the aperture lip is given as discriminating character and it should be mentioned that older specimens show sometimes a small blunt addition to the lip though it is considered "rounded" in the key. In the formae *kraussi*, *dakarensis* and *danae*, however, a large blunt, or straight aperture part is found in all specimens, whereas the other formae show only a small, blunt aperture part of maximal 3 mm in some of the older specimens.

- 1 a) Shell triangular in ventral view, dorsal aperture lip rounded forma *tridentata*
b) Shell not triangular or without rounded aperture lip 2
- 2 a) Shell with keels along the lateral sides forma *kraussi*
b) Shell without keels along the lateral sides 3
- 3 a) Dorsal aperture lip rounded 4
b) Dorsal aperture lip with straight anterior margin or with two points 8
- 4 a) Shell longer than 13.5 mm 5
b) Shell length less than 13.5 mm 7
- 5 a) Lateral spine points not directed caudad forma *bermudensis*
b) Lateral spine points directed usually caudad 6
- 6 a) Caudal spine length 1/3 of the distance between the lateral spine tops, the outline of lateral sides and

dorsal aperture lip is not continuous forma *teschi*

- b) Caudal spine length 1/4 of the distance between the lateral spine tops, the outline of lateral sides and dorsal aperture lip is continuous without interruption forma *atlantica*
- 7 a) Ventral side in lateral view perfectly circle round, caudal spine straight forma *occidentalis*
b) Ventral side in lateral view not circle round but bulging more in cranial direction, caudal spine directed or bended caudad forma *affinis*
- 8 (Lateral spine not curved caudad, or lateral keels present see 4)
a) Lateral spine curved caudad, shell larger than 16.5 mm forma *dakarensis*
b) Lateral spine curved caudad, shell smaller than 16.5 mm forma *danae*

SUMMARY

The geographical variation in *Cavolinia tridentata* is discussed, and nine formae of the species are described. The material described originally from the Mediterranean belongs to the endemic forma *tridentata*. The forma *bermudensis* from the Western Atlantic between 5° and 50°N, the forma *dakarensis* from the Eastern Atlantic between 5° and 65°N, and the forma *atlantica* from the Southern Atlantic are described as formae new to science. In the southern oceans south of about 30°S the forma *kraussi* is found. In the Northeastern Pacific the forma *occidentalis* is found and in the Southeastern Pacific the forma *affinis* is present. The three latter formae were already known but a general picture of their distribution is for the first time given in this paper. For the Indian Ocean and Indo-Malayan and Central Pacific waters two formae new to science are described. In the Indian Ocean the forma *danae* is found and in the Indo-Malayan waters a population of the forma *teschi* is found which penetrates into the Central Pacific.

The more or less intensive interbreeding between the formae is discussed.

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