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Two new forms of *Cavolinia uncinata* (Rang, 1829) (Pteropoda, Gastropoda)

S. VAN DER SPOEL

ABSTRACT

In the species *Cavolinia uncinata* two new forms are described, one from the Atlantic and one from the Indian Ocean. The reason why the species is not subdivided into subspecies but into formae is explained.

INTRODUCTION

Cavolinia uncinata (Rang, 1829) is in every sample usually represented by rather similar specimens. Tesch (1948 : 26) is of the opinion: "Fortunately for the systematist *C. uncinata* presents, so far, no varieties....". The forma *uncinatiformis* described by Pfeffer (1880: 83) for specimens of which "Die Schale ist verhältnissmässig klein...." is usually considered to be a synonym of *C. uncinata* (cf. van der Spoel, 1967). Boas (1886) stated that the shell length of this species ranges from 6 mm to 11 mm, with an average length of 7 mm, and afterwards no mention is made of larger or smaller specimens.

Comparison of material from the Atlantic Ocean and the Indian Ocean proved that there are some small differences between specimens of *C. uncinata* from these two oceans. Material of the Pacific Ocean was not available, hence that area is not involved in this study. Some specimens collected near Bermuda¹) showed differences from specimens usually found in the Atlantic Ocean. These specimens induced me to describe a new forma of *C. uncinata*, for which the name *roperi* is proposed. The other specimens from the Atlantic agree with the original description of *C. uncinata* so that these represent the type forma *uncinata*. As the forma described by Rang (1829) and d'Orbigny (1836) differs from the specimens found in the Indian Ocean, a special forma for the latter is described, for which the name *pulsata* is proposed.

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¹) This material was collected by the Ocean Acre Project of the Smithsonian Institution supported by funds from the U.S. Navy.

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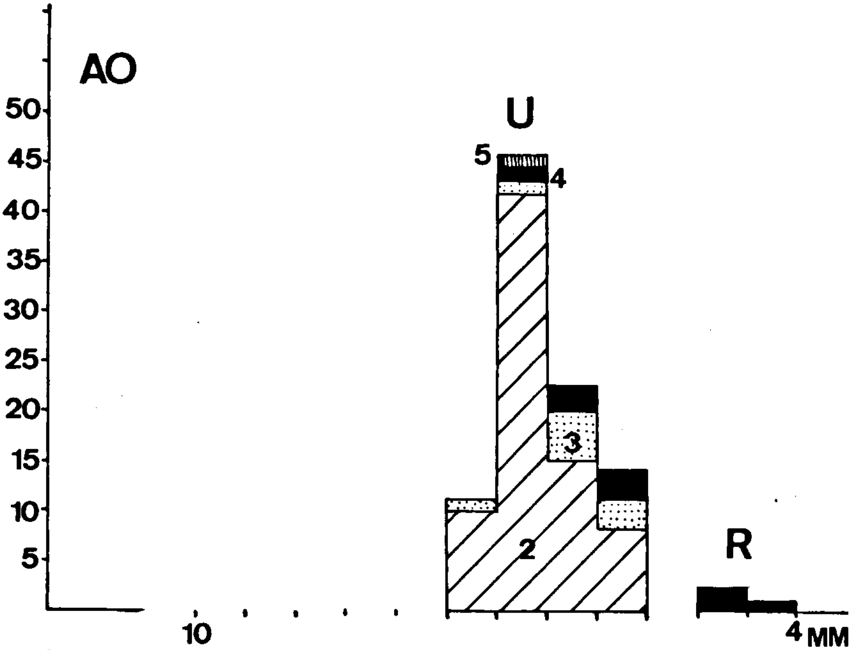
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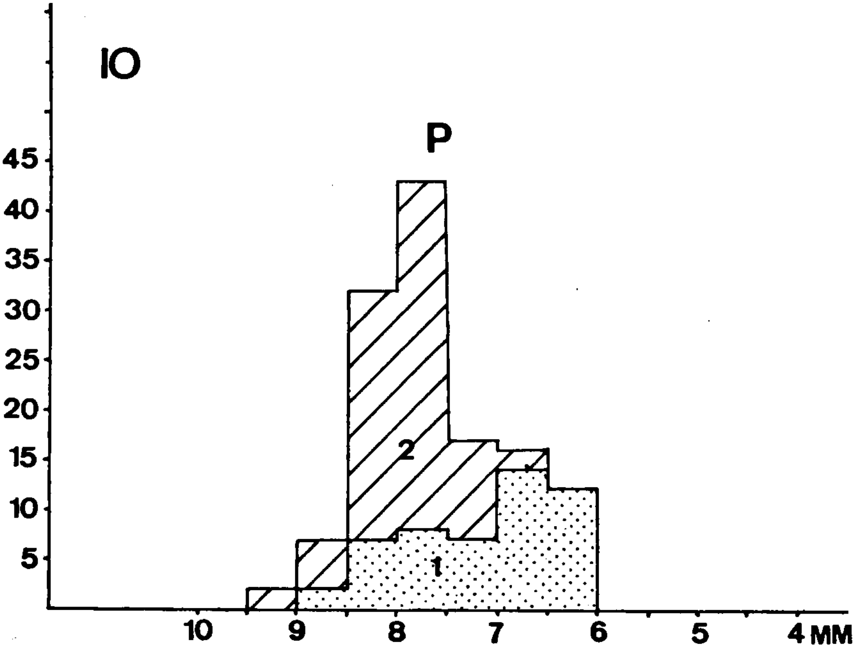
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GENERAL CONSIDERATIONS

Specimens from the Indian Ocean measure 6.0 to 9.5 mm in length, those of the Atlantic Ocean 5.5 to 7.5 mm (fig. 1). If actually two separate forms are concerned here, they overlap in size considerably (overlap is 6.0—7.5 mm), but the average lengths, 7.4 and 6.4 mm respectively, differ significantly. For some species it is known that the connection between the Indian and Atlantic Ocean is not very favourable for the transport of specimens from one ocean to the other; it is not impossible that there is a kind of boundary between the two oceans which may act as a geographical barrier. *C. longirostris* (see van der Spoel, 1967, fig. 355) and *C. globulosa* (l.c., fig. 358) show in their distributions that the corridor south of Africa acts as a barrier to their meridional distributions. The distribution of *C. uncinata* also shows a certain discontinuity (l.c., fig. 359) as the range of this species in both oceans is interrupted by the continent of Africa splitting the populations; in the Agulhas-current, however, an intermediate population seems to make the connection. Between the Atlantic and the Indian Ocean a geographical barrier for *C. uncinata* seems to exist, which is not strong enough to separate two subspecies, but in all probability is strong enough to separate formae. The specimens typical for the Atlantic are then to be considered as belonging to *C. uncinata* forma *uncinata*, those of the Indian Ocean as belonging to the forma *pulsata* n. forma.

The specimens collected by the Ocean Acre Project near Bermuda agree with those of the forma *uncinata* except for three specimens which are dark brown in colour and about 1 mm smaller than the others. The smaller ones are considered to belong to a new forma *roperi*. To give these smaller and darker individuals a higher rank than forma seems impossible, because the small number of specimens collected so far does not allow any conclusion about interbreeding or intersterility of *roperi* and *uncinata*.

THE FORMA CONCEPT

The occurrence of smaller forms is not restricted to the present species. In *Cavolinia longirostris* (cf. Tesch, unpublished), *Cavolinia gibbosa* (forma *gibbosa*), *Cavolinia inflexa* (forma *inflexa*), *Diacria trispinosa* (forma *trispinosa*) and in *Diacria quadridentata* (cf. van der Spoel, 1969) smaller forms have been described. In some other species characteristically flat forms, de-

FIG. 1. Histogram of the shell lengths of *Cavolinia uncinata* (horizontal axis) and the number of specimens (vertical axis) in the Atlantic Ocean (AO) and the Indian Ocean (IO).

U = forma *uncinata*
R = forma *roperi*
P = forma *pulsata*
1 = Dampier Exped. material
2 = Dana Exped. material
3 = Snellius Exped. material
4 = Ocean Acre Project material
5 = Lectotype of *Cavolinia uncinata* forma *uncinata*

pressed in a dorso-ventral sense, occur. These two phenomena, observed in different species, enable us to recognize groups of populations differing in one character. Such groups of populations distinguished by only one, or a few characters, can hardly be considered subspecies and the author is of the opinion that they constitute formae.

When interbreeding and thus gene flouw is absent between groups of populations, these groups can be considered species. For some planktonic animals the populations in the Atlantic Ocean and the Indo-Pacific Ocean are strictly separated by continents, which exclude interbreeding of these groups of populations, so that different species are involved. Some species exhibit no difference between the specimens from these two oceans so that it seems correct, and at least most practical, to consider them as one species indeed.

Two problems are not considered, the first concerns the influences that keep the populations of two separated areas identical in appearence, and the second concerns the difference in gene flow between formae and between subspecies. The populations in the two oceans show only small differences, because, in all probability, the selective pressure, which may be responsible for differentiation, is of the same nature in both oceans. Moreover, it is supposed that interbreeding does not take place, because the records of the populations made so far indicate a disjunction in ranges; still it is possible that future expeditions will prove that the species have uninterrupted distributions. If distribution is not interrupted, interbreeding is possible, and for this reason the concept of vicarious species can not be used for these forms.

The second problem concerns interbreeding itself. When partial barriers occur between two groups of populations permitting a limited gene flow, the groups of populations often are considered subspecies. When barriers are wanting or when they are not sufficient to prevent interbreeding and gene flow on a larger scale, one can no longer speak of subspecies. Phenotypical influences may then become responsible for the occurrence of ecophenotypic variability. When in this paper the concept "forma" is used, no kind of ecophenotypic forms are meant.

The other way in which a form can originate is by polarisation in the gene pools, which may be rather important in planktonic animals. Polarisation may occur under ecological influences of any kind and it results in the concentration of one or several genes in restricted areas of the range of the species. This phenomenon is called clinal variation by e.g. Mayr (1963). The differences between species, subspecies and formae can be explained as follows.

Each species is characterized by its gene pool. In the centre of the range the gene pool will show the greatest diversity. Subspecies are groups of populations which have gene pools differing from those of the other subspecies; the subspecies gene pool is also most complete in the centre of the range, provided the subspecies is completely isolated from the maternal species. There may exist a gene flow in the area, the contact zone, where two subspecies interbreed. In general subspecies have a rather narrow intergradation zone, in which the genotype of the one subspecies changes steeply into that of the other. A forma is a group of populations having near the contact zone with the adjacent forma a broad, and very gradual transition zone into the next forma. In the centre of the range of the forma a concentration of some special genes occurs. These genes will be absent in populations far remote, while no barrier exists between these populations and those of the other formae. This explains why formae form part of clines, as in *Limacina helicina* and *Clio pyramidata* (van der Spoel, 1967: 38, 67), and why in several species such formae differ in the same characters. The forma is thus maintained by the attraction of certain genes, the subspecies by a selective reduction of gene flow. If there is a principal difference between forma and subspecies there should be also a fixed mechanism which causes the polarisation in the gene pool of the forma, comparable with fixed mechanisms responsible for the occurrence of subspecies. When clines are concerned this mechanism is the gradual change of environmental conditions which through natural selection do concentrate genes in special parts of the range of the species. When the forms are not related to clines, concentration is also the effect of a gradual change.

When two such forms live together in the same area, at the same depth and in the same water mass, different selection can only be the result of the seasons of the year. In pteropods, and also in chaetognaths, which have a life-span of a year, and which breed only once a year, differences resulting in the distinction of forms, may occur as the result of sexual isolation. When a population breeding in spring occurs in the same geographic area as one breeding in autumn, selective pressures may alter these two populations in different ways. When there is a flux of specimens from the autumn population to the spring population and vice versa, a gene flow is maintained. When there is a greater sexual attraction between the specimens of populations of one season and the intermediate specimens, than between the specimens of different seasons, the sexual affinity between the spring and autumn population decreases gradually, which causes a type of clinal variation though no real geographic cline is found, but a climatic (seasonal) cline. In planktonic animals which show a maximal sexual activity correlated with the seasonally occurring phytoplankton bloom, a seasonal isolating mechanism is very well possible. At higher latitudes the periods of plankton bloom, two each year, are sharply delimited while in the tropics these periods are not so clearly separated. Parallel to this phenomenon the formae will be more sharply isolated at higher latitudes than in the tropics and isolation may even be absent when there is no disturbance in the sexual affinity between the two formae. The small-sized forma described in this paper probably arose through such an incipient seasonal isolation and gradual change in sexual affinity between populations. This mechanism may at last result in the loss of sexual attraction between populations of the large and the small forms, and then two species may arise. But up till now no exact data are available concerning the interbreeding and the sexual cycle of this special species so that it seems only admissable to describe a new forma.

When two forms have a different vertical distribution the clinal variation may also be found in a vertical sense and different gene pool compositions can occur then at different depths. This may also explain the occurrence of some clinal variation of formae in the same area.

Summarizing, it is clear that the subspecies concept as defined by Mayr (1963) does not completely agree with the concept "subspecies" as given in this paper. The forms which constitute a cline are considered of infrasubspecific rank. Mayr criticizes the lack of flexibility of taxonomy, when he deals with geographic speciation, as there are only two possibilities to classify a group of populations, namely as subspecies or species. The semispecies is defined by Mayr (1963) as a taxon in between subspecies and species but no taxon lower than the subspecies is indicated. The semispecies and superspecies are frequently used in taxonomy so that it seems correct to introduce the concept "forma" for groups of infrasubspecific rank. The more panmictic character of most holoplanktonic species and populations in relation to the less panmictic terrestrial and freshwater groups causes in general a smaller degree of specialization in plankton animals, which makes the concept "forma" (which in my concept is nearly identical to the term "morph") the more usefull. The forma is in this light clearly different from the geographic isolate, which, according to Mayr, has subsepecific rank while the populations, the formae, constituting a cline are lower in the speciation process.

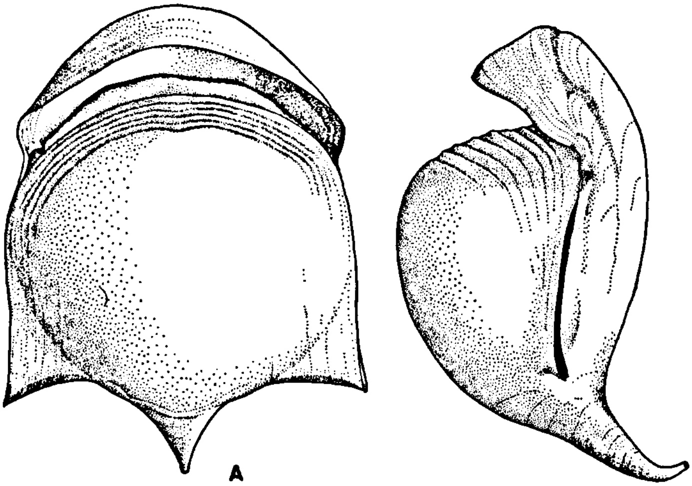


FIG. 2. The lectotype of *Cavolinia uncinata* forma *uncinata*. A, ventral view; B, dorsal view.

Cavolinia uncinata (Rang, 1829) forma **uncinata** (Rang, 1829)
Figs. 2, 3, 6 C-E, and 7 B-D

Hyalea uncinata Rang, 1829 : 114.
Hyalaea uncinata d'Orbigny, 1836 : 93 (1846) pl. 5 figs. 11—15.
Hyalea uncinatiformis Pfeffer, 1880 : 83.

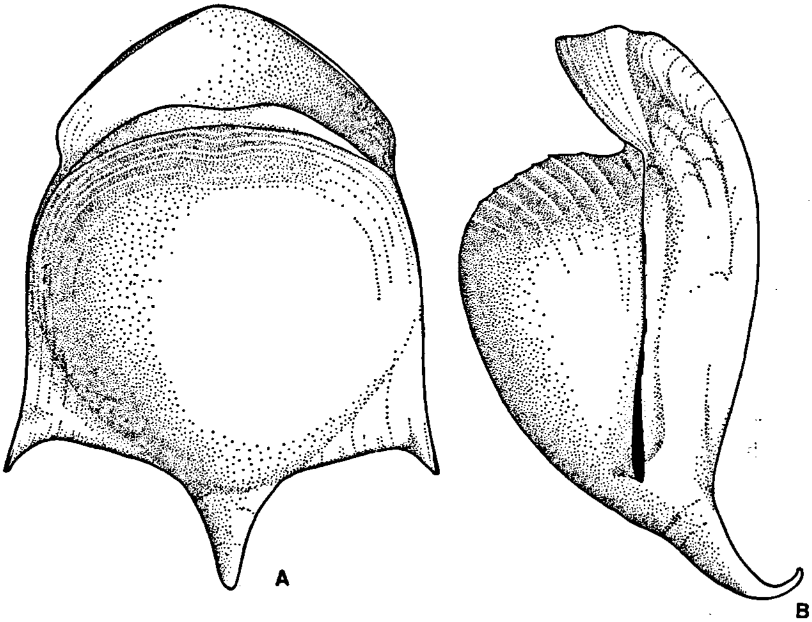


FIG. 3. *Cavolinia uncinata* forma *uncinata* collected by the Ocean Acre Project, shell length 6.05 mm; A = ventral view; B = left view.

Type locality. Atlantic Ocean.
The lectotype and the 7 paralectotypes are kept in the Muséum National d'Histoire Naturelle in Paris with the reg. indication "Collection Rang 1837".

Description. — All size data concerning the length are measured from the ventral side when the animal is lying on its dorsal side. The holotype measures 6.97 mm in length, 5.80 mm in width and 4.10 mm in thickness. The mean shell length and shell width of 89 specimens is 6.56 mm and 5.27 mm respectively. The shell surface shows faint growth-lines and a hammered structure on the ventral side. The shell is hyaline colourless except for a brown zone along the margin of the ventral lip and a brown hue on the upper part on the ventral side caused by the 10 concentric ribs. The ribs are white rimmed and imbricate in structure. In the lectotype the colour is lost, as in all specimens preserved dry for a longer period. The embryonic shell is usually broken off and an opening is left at the top of the slightly bent caudal spine; in the lectotype the embryonic shell is complete. The lateral spines bent caudally near their tips, but never as strongly as in the other two forms (fig. 6). A slight flexure of the spines in a dorsal sense is usually present. The aperture is narrow, slit-like, anterior to the closing mechanism, the median part of the aperture is a little wider but the curve of the dorsal lip usually narrows it more than in the forma *pulsata*. The aperture in the lectotype is not as narrow as usual and resembles somewhat the aperture in *pulsata*. The ventral side and the ventral lip of the aperture show a median depression. The dorsal side is colourless hyaline. The distal part of the dorsal lip is distin-

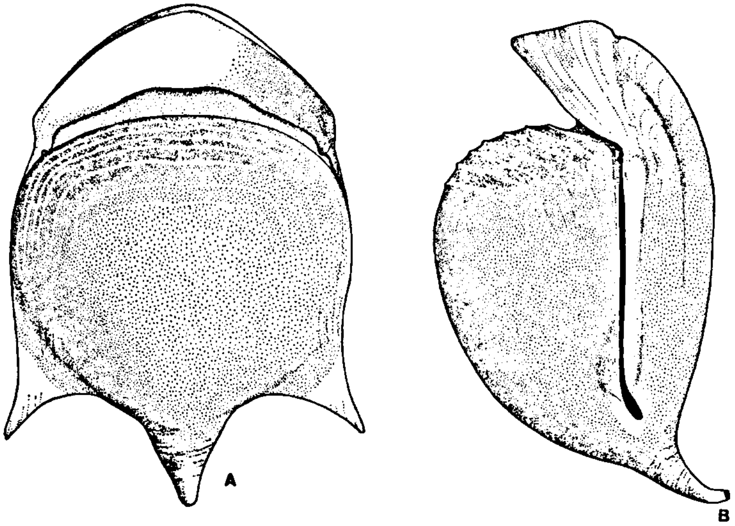


FIG. 4. The holotype of *Cavolinia uncinata* forma *pulsata*. A, ventral view; B, left view.

guished from the rest of the dorsal side by the absence of ribs. Of the dorsal ribs, numbered according to Boas (1886, fig. 9), rib 1 is strong, 2^a and 2^b are melted together, except in their upper part, 4 is strong, while rib 3 is very faintly developed. The ventral side is strongly convex, the dorsal side is rather flat, the latter is still less convex than in the forma *roperi* but more rounded than in the forma *pulsata*. The dorsal lip in ventral view is pointed but this form shows a tendency to have a rounded dorsal lip in contrast to that found in *pulsata* (fig. 7).

The description of *Hyalaea uncinata* by d'Orbigny (1836) fits completely with the characters of this form and it was clearly mentioned that the material originates from the Atlantic Ocean.

The figures given by d'Orbigny (1846b) (fig. 9) do not fit very well the present form, but they fit even less the specimens of the Indian Ocean. The colour of the figures corresponds rather well with the natural colour; the specimen figured with the soft parts in the shell is dark brown but this is the normal habitus of specimens in which the body shows through.

Cavolinia uncinata (Rang, 1829) forma **pulsata** n. forma
Figs. 4, 6A, and 7E

Hyalea uncinata Pfeffer, 1880: 82, figs. 3, 3^a, 3^b.

Type locality. Dana Expeditions Stat. 3860^{XXII}, 02°37'S 99°36' E, 20 Oct. 1929, 100 m wire, ringtrawl, S200.

The holotype is kept in the Zoological Museum in Copenhage.

This forma is named *pulsata* (= hammered) as it is the one which shows most clearly the hammered structure on the ventral side.

Description. — The holotype measures 8.14 mm in length, 5.81 mm in width and 5.08 mm in thickness. The mean shell length and shell width of 128 specimens is 7.55 mm and 5.41 mm respectively. The shell surface shows faint growth-lines and a clear hammered structure especially on the ventral side. The shell is somewhat hyaline, but a distinct brown colour covers the whole ventral side with the exception of the tips of the lateral spines and caudal spine, the ventral lip of the aperture and usually the major part of the dorsal side. The dorsal lip of the aperture, the tips of the lateral spines and the caudal spine are constantly colourless. The brown colour is most intense on the upper part of the ventral side and along the margin of the ventral aperture lip. The imbricate, concentric ribs on the ventral side, 8 in number, are white rimmed. The top of the embryonic shell is usually broken off, the caudal spine curls dorsad but never as strongly as in the other two forms. The lateral spines are evidently curved caudad with the result that the tips reach as far caudad as the middle of the caudal spine (fig. 6); a slight dorsal curving is usually present. The lateral slits of the shell aperture are narrow but the central part is broad, because the dorsal lip never bends far ventrally. The ventral side of the shell and ventral lip of the aperture show a median depression. The most distal part of the dorsal lip is not provided with ribs. These ribs do not differ much from those in the other forms. The ventral side is convex, the dorsal side is flat, but though this shell is globular it is usually less spherical than in the other forms, *roperi* being clearly the most globular one. In ventral view the dorsal lip is more or less pointed (fig. 7 E).

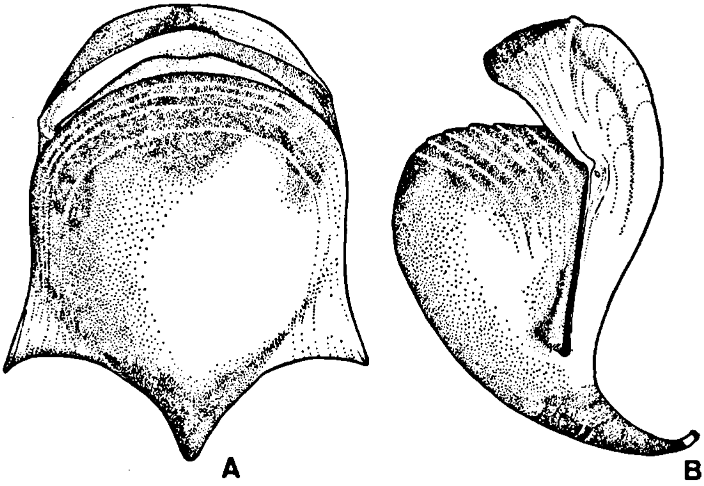


Fig. 5. The holotype of *Cavolinia uncinata* forma *roperi*. A, ventral view; B, left view.

Cavolinia uncinata (Rang, 1829) forma **roperi** n. forma

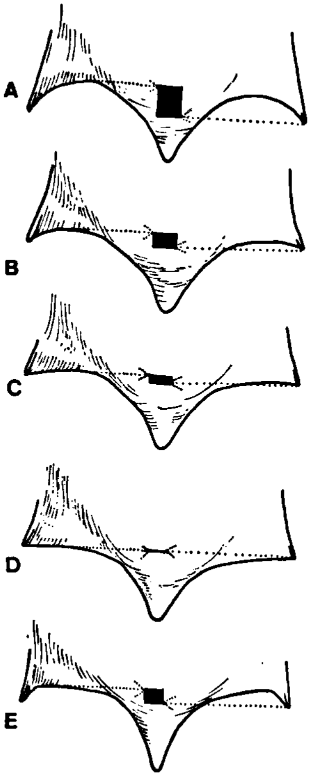
Figs. 5, 6B, and 7A

Type locality. Ocean Acre Project, Stat. 1—8 C+D, 32°16'N 64°18'W, 27 Oct. 1967, 20^{43}—22^{27} hs, 268—150 m.

The holotype is kept in the United States National Museum in Washington; Catalogue No. 576977.

This forma is named in honour of Dr. C. F. E. Roper who provided the material from the Ocean Acre Project.

Description. — The holotype measures 4.48 mm in length, 3.65 mm in width and 2.63 mm in thickness. The mean shell length and shell width of 3 specimens is 4.70 mm and 3.80 mm respectively. Shell surface with faint growth-lines and fine hammered structure, especially on the ventral side. The shell



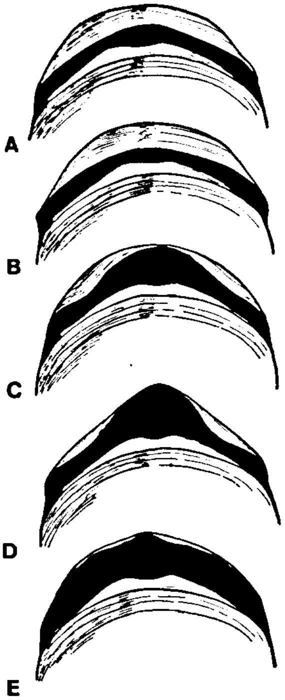


FIG. 6. Variation of the shape of the lateral spines in *Cavolinia uncinata*, the black squares give an indication for the corvature of the spines. A. forma *pulsata*; B. forma *roperi*; C, D, and E, forma *uncinata*.

FIG. 7. Variation of the shape of the dorsal aperture lip in *Cavolinia uncinata*. A. forma *roperi*; B, C, and D, forma *uncinata*; E, forma *pulsata*.

is hyaline except for the caudal spine and the adjacent part of the dorsal side, upper part of the ventral side, the base of the lateral spines and the median part of the dorsal lip. All these parts show a very intensive chestnut brown colour, especially the caudal spine. The lateral spines and the sides of the dorsal lip are colourless hyaline. The concentric imbricate ribs on the ventral side, 7 in number, are white rimmed. The top of the embryonic shell is lost and the caudal spine is more strongly curved in a dorsal direction than in the other forms. Apart from a slight dorsal flexure, the lateral spines show a curving in the caudal direction which is not as strong as in *pulsata*. The lateral slits of the shell aperture are narrow, but in this form the central part of the aperture is also slit-like by the hood shaped dorsal lip bending over the aperture. The ventral side and aperture lip show a faint depression. The hood-shaped part of the dorsal lip does not show dorsal ribs; the lower parts of the ribs are shaped like in other forms. The ventral side is convex, de dorsal side is flat, but the shell is more globular than in the other forms. The globular shape is accentuated by the strongly curved dorsal lip. In ventral view the dorsal lip is round (fig. 7).

The most characteristic features for the forma *uncinata* are the absence of

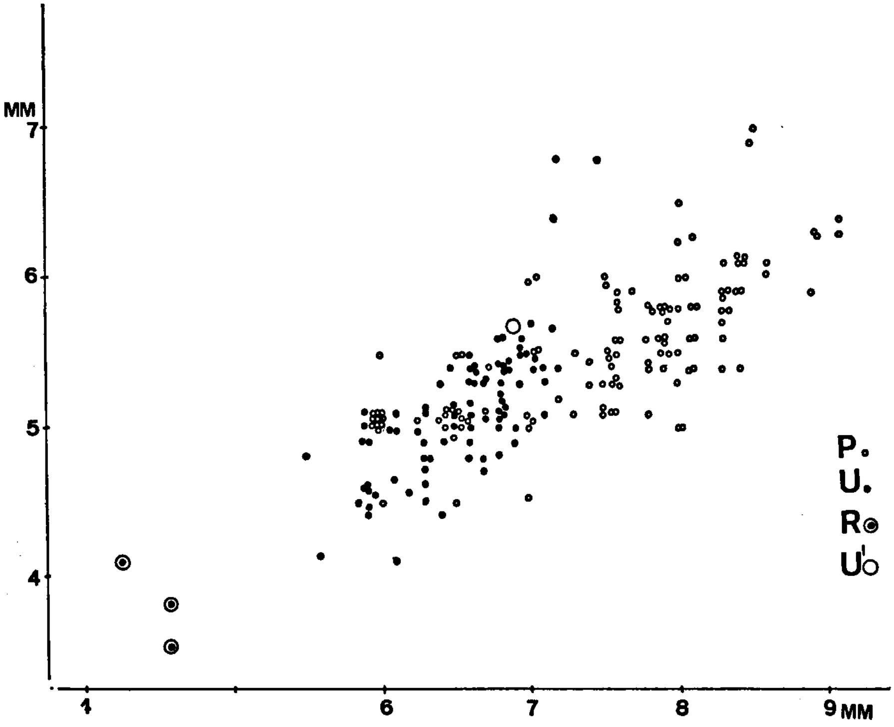


FIG. 8. Graphic representation of the relation of shell lengths (horizontal axis) and shell widths (vertical axis) in: *Cavolinia uncinata* forma *pulsata* (P), forma *uncinata* (U), and forma *roperi* (R), and the lectotype of the forma *uncinata* (U¹).

colour on the shell except on the ventral side which has a brown hue, the nearly straight laterally projecting spines, and the shape of the caudal spine.

The most characteristic features for the forma *pulsata* are the brown hue covering nearly the whole shell, the white-hyaline lateral spines which curve strongly in caudal direction, the wide shell aperture over which the dorsal lip never bends far ventrad and the short rather straight caudal spine.

The most characteristic features for the forma *roperi* are the very strongly bent dorsal aperture lip, which may seem to close the shell aperture when the shell is observed from the ventral side, the brown colour on the caudal spine and adjacent part of the dorsal side, and the strong curving of the caudal spine.

The embryonic shell, only intact in a few specimens is similar in shape in the three forms. The permanent shell passes gradually in the embryonic shell, without rings or incisions. The embryonic shell is not droplet shaped like that of *Clio* but it ends gradually, without bulging in the middle. The change of shell shape and colour pattern due to age differences is small, since growth proceeds rather quickly. From the embryonic shell a rather flat hyaline shell without any colour develops, these flat specimens are much smaller than the adult shells and devoid of clear dorsal ribs. The soft parts grow slower than the shell so that from this flat stage a specimen develops which has a normal shell but a very small body, this stage is called the minute stage (van der Spoel, 1967). The shell of the minute stage is of the same size as that of adult specimens. From the minute stage the adult stage develops, the animal becomes sexually mature and when not already finished in the minute stage, the last 0.1 mm of the dorsal lip is formed and the colour pattern gets its full intensity. It is excluded that the size differences between the three forms described before are due to age as the differences are already present when the animals are rather young; moreover, the differences between the forms are also present in the caudal spine which is the youngest part of the whole shell. For the formae *uncinata* and *roperi* it is excluded that local influences are responsible for the differences as both are collected in the same sample.

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FIG. 9. *Cavolinia uncinata* forma *uncinata* as pictured by d'Orbigny (1846), plate 5 figs. 13, 14, and 15.

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Dr. S. VAN DER SPOEL
Zoölogisch Museum der Universiteit van Amsterdam
Plantage Middenlaan 53
Amsterdam-C. — The Netherlands