

**Development of Cuvierinidae (Mollusca, Euthecosomata, Cavoliniioidea) during the Cainozoic:
a non-cladistic approach with a re-interpretation of Recent taxa**

Arie W. JANSSEN

National Museum of Natural History (Palaeontology Department), P.O. Box 9517, 2300 RA Leiden, the Netherlands; currently: 12, Triq ta'Hamrija, Xewkija VCT 110, Gozo, Malta;
ariewjanssen@waldonet.net.mt

This paper is dedicated to the memory of Dennis Curry

Numerous observations of more-or-less precisely dated occurrences of Cainozoic Cuvierinidae allow lineages to be reconstructed. The early genera *Spoelia* Janssen, 1990 and *Johnjagtia* gen. nov. (Late Oligocene/Early Miocene), the roots of which are still unknown, are included in the Cuvierinidae.

The Late Oligocene *Ireneia tenuistriata* (Semper, 1861) is the precursor of various Miocene species of *Ireneia* Janssen, 1995. The genus became extinct in the Late Miocene. The genus *Cuvierina* Boas, 1886 developed from the *Ireneia* lineage during the Early Miocene.

In Middle Miocene times *Cuvierina* s. lat. splits up into two branches, interpreted here as subgenera, viz. *C. (Cuvierina)* and *C. (Urceolaria)* subgen. nov., each with a number of species occurring from the later Miocene onward. The Recent '*C. columnella columnella* (Rang, 1827)' and '*C. columnella urceolaris* (Mörch, 1850)', as interpreted until now, are considered to represent the final stages of these lineages. Recent *Cuvierina* material from all oceans was revised, which has led to a re-interpretation of extant taxa and to the introduction of two new Recent species.

New taxa here introduced are *Cuvierina (C.) pacifica* spec. nov., *C. (Urceolaria) cancapae* spec. nov., *C. (U.) curryi* spec. nov., *Ireneia gracilis* spec. nov., *Johnjagtia* gen. nov., and *Urceolaria* subgen. nov. A neotype is designated for *C. (C.) columnella*.

Two species described from the Eocene of the United States do not fit the development model of the Cuvierinidae advocated here. For them two genera, *Praecuvierina* gen. nov. and *Texacuvierina* gen. nov. are introduced. Together they form the Praecuvierinidae fam. nov., which is considered to represent an earlier offshoot from the Creseidae.

Key words: Gastropoda, Euthecosomata, Praecuvierinidae, Cuvierinidae, lineages, Cainozoic, new species, new subgenus, new genus, new family.

INTRODUCTION

The study of fossil assemblages of so-called pteropods (Gastropoda, Heterobranchia, Euthecosomata) during the last decades has supplied interesting new data on morphology, distribution and biostratigraphy of many groups of holoplanktonic molluscs. The present paper focuses on the family Cuvierinidae. The Cuvierinidae were considered until recently to be a subfamily, Cuvierininae, in the Cavoliniidae. Janssen (2003) raised the

Cuvierininae, together with Creseinae and Clioinae, to family level.

Among extant euthecosomatous gastropods, species of the genus *Cuvierina* are well-characterised by a number of shell features, in particular the straight, cylindrical to more or less inflated shell form and the proximal aperture of reniform or rounded triangular shape. In (near-)adult shells a semispherical, more or less obliquely situated septum is formed, after which the apical shell part (larval shell) is shed.

The genus *Cuvierina* Boas, 1886, as previously interpreted, comprises but a single Recent species, which is the type species, viz. *C. columnella* (Rang, 1827) (compare Van der Spoel, 1967, 1970, 1976). In addition, quite a number of fossil species have subsequently been assigned to *Cuvierina*:

- C. astesana* (Rang, 1829) - Pliocene
- C. globosa* Collins, 1934 - Pliocene
- C. grandis* d' Alessandro & Robba, 1980 - Miocene
- C. gutta* Hodgkinson, 1992 - Eocene
- C. inflata* (Bellardi, 1873) - Pliocene
- C. jagti* Janssen, 1995 - Pliocene
- C. intermedia* (Bellardi, 1873) - Miocene/Pliocene
- C. ludbrookii* (Caprotti, 1962) - Pliocene
- C. lura* Hodgkinson, 1992 - Eocene
- C. miyazakiensis* Ujihara, 1966 - Pliocene
- C. paronai* Checchia-Rispoli, 1921 - Miocene
- C. senonica* (Blanckenhorn, 1934) - Miocene
- C. torpedo* (Marshall, 1918) - Miocene
- C. tubulata* Collins, 1934 - Pliocene

In the adult stage these are all characterised by a cylindrical or to a higher or lesser degree inflated shell, with a septum closing the apical side of the shell after the larval shell parts are shed.

The juvenile shell (see fig. 14 for an example) is regularly conical, and has an elongate protoconch with a single, near-apical swelling and a rounded tip, closely resembling certain species of the family Creseidae (especially *Styliola*, in which, however, the tip is pointed). The shed larval shell of *Cuvierina* species differs strongly from the fully grown specimens, and was, at least twice, described as a separate species (*Creseis caliciformis* Meisenheimer, 1905; *Styliola sinecosta* Wells, 1974).

Towards the aperture the adult shell becomes dorso-ventrally flattened and frequently even slightly concave on the ventral side close to the aperture, which therefore has a reniform or rounded triangular shape in adapical view, with a slightly thickened rim as a reinforcement on the inside of the apertural margin. The dorsal apertural margin is slightly higher than the ventral one. The shell surface may or may not have a micro-ornamentation, observable at a magnification of 12 ×, of numerous close-set longitudinal lines, usually more clearly developed in the lower two-thirds of the adult shell. This micro-ornament, together with the growth lines, may give the shell a beautiful reticulate pattern, especially well visible at those places where light reflects on the shell's surface. In the illustrations given here this ornament could only be drawn schematically, and in reality is much finer than seen in the drawings.

Recent *Cuvierina* populations are widely distributed in tropical and subtropical oceans (see also Van der Spoel, 1967: fig. 352). They are virtually absent, however, in the Mediterranean and the Red Sea.

Based on shell characters two formas of *Cuvierina columnella* used to be distinguished

besides the typical form, viz. *f. urceolaris* (Mörch, 1850) and *f. atlantica* Van der Spoel, 1970. Later authors considered these formas to be subspecies: *C. columnella columnella*, *C. columnella urceolaris* and *C. columnella atlantica*, although at least *C. c. urceolaris* and *C. c. columnella* were considered to be sympatric.

Below it will be demonstrated that '*C. c. columnella*' and '*C. c. urceolaris*' are distinct species, which developed along separate lineages and are therefore placed in different subgenera. Additionally, the study of many Recent *Cuvierina* samples has lead to the discrimination of no fewer than five separate species, differing in shell morphology, biometric characteristics and geographic distribution.

ABBREVIATIONS

MNHN	Muséum nationale d'Histoire naturelle, Paris, France.
RGM	National Museum of Natural History (Palaeontology Department), Leiden, the Netherlands (formerly Rijksmuseum van Geologie en Mineralogie).
RMNH	National Museum of Natural History (Malacology Department), Leiden, the Netherlands (formerly Rijksmuseum van Natuurlijke Historie).
SMF	Senckenberg Museum, Frankfurt am Main, Germany.
USNM	National Museum of Natural History, Smithsonian Institute, Washington, U.S.A.
ZMUC	Zoologisk Museum, København, Denmark.
H	shell height
St.	Station
W	shell width

All measurements are in mm.

MATERIAL AND METHODS

Apart from the many fossil samples housed in the RGM-collections as well as in several private collections, a large number of Recent samples were examined: predominantly bottom-samples from the CANCAP-expeditions, kept in the RMNH-collections, and mainly plankton-net samples, especially those from the DANA expeditions, housed in ZMUC. Some samples collected during the METEOR expeditions, housed in the SMF-collections were also available. Finally, a restricted number of samples from MNHN, Paris, was before me.

Measured parameters, indicated in fig. 28, are: shell height, shell width, aperture width, diameter of septum, position of strongest inflation.

All measurements were executed with a Wild M5 stereo binocular microscope at a magnification of 12 ×, using a 120 units micrometer ruler, in which each unit represents 0.083 mm. The units were later converted to mm. Of the said parameters only the position of strongest inflation sometimes is difficult to measure, especially in weakly inflated specimens, in which the sidelines can be almost parallel. In such cases the line perpendicular to the measuring ruler in the Wild device was very helpful. Still, the results show a wider spreading for this parameter than for all others.

Only adult, full-grown specimens were measured. In many cases remnants of the lar-

val shell are still adhering to the teleoconch, below the septum. Frequently the shell is transparent enough to measure the position of the septum, but in some cases parts of the remaining larval shell wall had to be removed.

THE FOSSIL RECORD OF CUVIERINIDAE

Early taxa

The question which fossil genera should additionally be included in the Cuvierinidae is subject of discussion. From the Eocene of northern America Hodgkinson et al. (1992) included the genera *Bucanoides* Hodgkinson, 1992, *Loxobidens* Hodgkinson, 1992, and *Tibiella* Meyer, 1884 in this family (at that time still Cuvierininae).

Loxobidens, however, exclusively known by its type species *L. aduncus* (Hodgkinson, 1992) of which only apertural fragments are known, has a certain resemblance to the creseid genus *Camptoceratops*, due to the denticles on the apertural flange (Hodgkinson et al., 1992: pl. 12, figs 1-5).

Bucanoides (with type species *B. tenuis* Hodgkinson, 1992 and two additional species), is characterised by a conical shell form, and the presence of a septum, after the juvenile shell parts are shed. This closely resembles the creseid genus *Euchilotheca*, and therefore I also exclude *Bucanoides* from the Cuvierinidae, in favour of placement in the Creseidae. In all these species the shell surface lacks longitudinal micro-ornament. The apertural flanges present in most of the species of these genera also support an assignment to the Creseidae, as such structures are not found in Cuvierinidae to date.

The type species of *Tibiella* (*T. marshi* Meyer, 1884) is characterised by the presence of a septum, similar to that seen in *Euchilotheca* and *Bucanoides*, whereas its apertural structures closely resemble those of *Thecopsella* Cossmann, 1988. Thus, *Tibiella* is included here in the Creseidae as well.

The question whether the type species of Eocene *Thecopsella* (= *T. fischeri* Cossmann, 1888) belongs in the Euthecosomata or in the Caecidae (compare Tembrock, 1965) is not problematic, as its protoconch is straight, not spirally wound, and typically creseid, unlike some species with a spiral protoconch included in this genus by Tembrock [1965: *Thecopsella lituus* (Cossmann, 1899); *T. undulata* Tembrock, 1965; *T. latdorfense* Tembrock, 1965] and R. Janssen (1978: *T. tenuiannulata* R. Janssen, 1978) that indeed belong in the Caecidae.

Cuvierina is closely related to and, as indicated by fossil occurrences, a further development of the recently introduced genus *Ireneia*, the oldest known species of which is the NW European Late Oligocene (Chattian) *I. tenuistriata* (Semper, 1861). Species of *Ireneia* resemble *Cuvierina* in shell shape, morphology of larval shell and aperture, and presence of longitudinal micro-ornamentation on the adult shell, but they differ in that the larval shell is retained, not shed.

The first genuine species of *Cuvierina* originated from the *Ireneia*-root during the Oligocene-Miocene transition. Apparently the newly developed principle of larval shell-shedding was advantageous, although necessitating drastic changes in the animal's vital functions, such as the capability to generate a closing septum and re-attachment of the columellar muscle at a higher position on the inner shell wall. Consequently, *Ireneia* became extinct during the final Miocene, whereas *Cuvierina* survives to the present day.

The development of *Cuvierina* from *Ireneia* as advocated here disregards two early taxa, introduced from the Eocene of the United States, i.e., *C. lura* Hodgkinson, 1992 (Lutetian) and *C. gutta* Hodgkinson, 1992 (Bartonian). The type material of these species

(seen September 1999) is similar to true cuvierinids. However, several differences, such as the surprisingly small dimensions and the complete absence of ornament, should be noted. As the well-documented development of *Cuvierina* from *Ireneia* started later, in the Early Miocene, the two Eocene species are here considered to represent an early, and unsuccessful, offshoot of Creseidae. In these circumstances the two taxa cannot be maintained in *Cuvierina*, and below I introduce for them new genera.

After the onset of the *Cuvierina* side-branch the genus *Ireneia* still develops several new species during the Miocene which retain the typical features of the genus, viz. *I. nieu-landia* Janssen, 1995, *I. testudinaria* (Michelotti, 1847), *I. calandrellii* (Michelotti, 1847) [inclusive of its probable synonym *I. urenuiensis* (Suter, 1917)], and *I. gracilis* spec. nov. The youngest species in this lineage is *I. marqueti* Janssen, 1995, from the Late Miocene of the North Sea Basin, characterised by the presence of transverse annulations.

In addition to *Ireneia* two other genera, occurring during the Late Oligocene and Early Miocene, are included in the Cuvierinidae. They differ from both *Ireneia* and *Cuvierina* by showing reinforcement structures in the shell. In monotypic *Spoelia* Janssen, 1995 the shell has squarish lateral carinae in the median part of the shell and a reinforced apertural margin. *S. torquayensis* Janssen, 1990 was described from the Late Oligocene of S Australia and SE France, but in the meantime it was also recognised in the Chattian 'Sternberger Gestein' in the North Sea Basin (RGM collections). Quite recently, it was also found to be present in the lowermost phosphorite-bearing level in the Maltese archipelago (Gozo, Wardija; Janssen, 2004), below the C 1 main phosphorite level, and therefore of Aquitanian age (Rehfeld & Janssen, 1995). The origin of *Spoelia* is still enigmatic; it appears unlikely that younger taxa developed from this species. The morphology of its protoconch, and the presence of micro-ornament, however, show it to be a distinct cuvierinid.

The same is true for '*Cleodora (Creseis) moulinsii* Benoist, 1873, a species as yet exclusively known from the Early Miocene (Burdigalian) of the Aquitaine Basin (France), characterised by an *Ireneia*-like shell with a distinct micro-ornament, but with a longitudinal dorso-lateral fold halfway the shell height, and a reinforced apertural margin as in *Spoelia*. It differs markedly from the other genera discussed here and below a new genus is introduced for it. The morphological characteristics indicate its systematic position to be in between *Spoelia* and *Ireneia*.

The first typical *Cuvierina* species is *C. torpedo* (Marshall, 1918), described from the Early Miocene ('Late Otaian' = Aquitanian) of New Zealand. In this species the shedding of the larval shell occurs close to the protoconch, the septum, therefore, is small and the shell retains an elongate spindle-shape with a slender basal part, strongly resembling species of *Ireneia*, inclusive of the presence of the longitudinal micro-ornament (Janssen, 1995: 55).

Although its morphology and approximate age make it likely that *C. torpedo* indeed is the first real *Cuvierina* species splitting off from the *Ireneia* root, it is difficult to interpret the New Zealand locality in terms of palaeobiogeography. The supposed ancestor species, *Ireneia tenuistriata*, is found exactly at the opposite side of the globe, viz. in the North Sea Basin. Most probably this must be explained in terms of as yet incompletely known palaeogeographical distributions.

The further development of *Ireneia* and *Cuvierina* could very well be studied in the Mediterranean Neogene, as discussed in the next section.

Cuvierinid developments in the Mediterranean area during the Miocene

In the Mediterranean area the first typical *Cuvierina* is found in the Maltese archipel-

ago. Here relatively deep-water, and therefore pteropod-rich deposits are found within the so-called Globigerina Limestone Formation (Aquitanian to Langhian), and in the Blue Clay Formation (Serravallian). In the Globigerina Limestone they occur predominantly as phosphatic internal moulds, concentrated in two main phosphorite levels (Rehfeld & Janssen, 1995), as well as in several subordinate phosphorite concentrations, or, in the uppermost part, as scattered occurrences in the sediment. In the Blue Clay Formation pteropods, and most other fossils as well, are found as limonitic internal moulds. In both cases the shells, and therefore also a possible micro-ornament of the shells, have disappeared.

In the Maltese Miocene series *Cuvierina paronai* Checchia-Rispoli, 1921 is the earliest species, found in restricted numbers in phosphorite level C 2, dated as 'Burdigalian/Langhian transition' and it continues through all pteropod bearing levels into the Blue Clay Formation, which is of Serravallian age (Kienel et al., 1995).

Cuvierina paronai was originally described, also in a phosphatised state of preservation, from strata at Gargano (Puglia, Italy) that, based on their microfauna (d'Alessandro & Robba, 1980), belong to Blow Zone N17, which according to Berggren et al. (1995) is of Late Tortonian to Messinian age. The Gargano pteropod assemblages, however, do not contain species indicating an age younger than Langhian, and thus were considered to be most probably reworked.

In *Cuvierina paronai* shedding of the larval shell occurs at a larger diameter of the shell and consequently the closing septum is considerably wider than in its supposed ancestor, *C. torpedo*. The Italian and Maltese specimens of this species are all preserved as internal moulds, but in some specimens in perfect shell preservation from the Badenian of the Central Paratethys (Zorn, 1991) it could be observed that the longitudinal micro-ornament is clearly present in this species as well. The shell form is almost cylindrical with a more conical basal part. Usually, as in most cuvierinids, the shell demonstrates a slight dorso-ventral flattening, especially towards the aperture. This species apparently is the precursor of two separate lineages, one in which the cylindrical shell-form is maintained, and another in which the shell to a higher or lesser degree is inflated.

The earliest species in the latter lineage is *C. intermedia* (Bellardi, 1873), which up to now was only known from Pliocene deposits. A quite typical specimen (B.M. Landau collection, Albufeira, Portugal; see Janssen, 1995: 41, as *C. ? intermedia*) from the Serravallian of Cacela Velha (Algarve, S. Portugal) demonstrates that *C. intermedia* already separated from the *C. paronai* root in Middle Miocene times. Also specimens from the later Miocene of S. Italy (Puglia, Salento, Lecce area) are here included in *C. intermedia*. The inflation of the shell in this species is gradual and not very strong, and there is no preapertural constriction, indicating its close relationship with *C. paronai*.

D'Alessandro & Robba (1980) also mentioned reworked occurrences of *C. paronai* in the same deposits of the Lecce area. They dated these as transitional between Blow zones N14 and N15, i.e., Late Serravallian. The pteropod assemblage from these localities contains, amongst other species, two taxa that do not occur in the Gargano area. These are both species of the genus *Cuvierina*, indicated by d'Alessandro & Robba (1980) as '*C. columnella urceolaris* (Mörch, 1850)', here considered to represent a new species (*C. curryi*, see below) and *C. grandis* d'Alessandro & Robba, 1980.

Interestingly, these two cuvierinids can be directly linked to *in situ* occurrences in the Maltese archipelago, where they are restricted to the Serravallian Blue Clay Formation. Here we find typical specimens of *C. grandis*. They resemble *C. paronai* in their cylindrical shell form, but the base of the shell generally is less conical, and they differ markedly in size, reaching a height of approximately 18 mm. They are still absent in the lower part of the Blue Clay, but relatively common in the upper part.

Next to this *C. grandis* and *C. paronai* yet another cuvierinid is present in the Blue Clay. This species differs from both *C. grandis* and *C. paronai* by its smaller and more inflated shell. They are identical with the specimens from Salento identified as *C. columnella urceolaris* by d'Alessandro & Robba.

Further cuvierinid development is demonstrated by a pteropod assemblage found in the so-called Tellaro Formation of SE Sicily. This deposit superficially resembles the Blue Clay Formation of Malta, as both consist of clayey sediments, and contain fossils in a limonitised state of preservation, with, e.g., the cephalopod *Sepia* present in both, and with many further similarities in the benthic faunas. Di Geronimo et al. (1981) dated these Sicilian clays as *Globorotalia acostaensis* Zone (= Blow Zone 17; Tortonian), but erroneously correlated them with the upper part of the Maltese Blue Clay Formation. Martini (in Janssen, 1999b: 116) analysed a nannoplankton sample from the Sicilian locality and indeed found it to belong to the NN10 zone (Middle Tortonian).

The holoplanktonic molluscan assemblage of the Sicilian Tellaro Formation includes three species of *Cuvierina* (Janssen, 1999b). The commonest in this material has a shell with a strong inflation just below mid-height and a reniform aperture, apparently a further development of the so-called '*C. columnella urceolaris*' (= *C. curryi*, described below) from Salento. The material cannot specifically be distinguished from *Cuvierina inflata* (Bellardi, 1873), described from the Early Pliocene of N. Italy. Other, less common specimens in this material still resemble *C. paronai*; they do not reach the large dimensions of *C. grandis*. A third group of specimens differs from both by the possession of an elongate, slender and cylindrical shell and by a triangular shape of the aperture.

This latter form is also known from N. Italy (Turin Hills), in a locality named Tetti Borelli, from where Pavia & Robba (1979) extensively described the holoplanktonic molluscan assemblage (revised in Janssen, 1995). The similarity between the Poggio Musenna and Tetti Borelli planktonic molluscan faunas beyond any doubt indicates that both are as good as coeval (Janssen, 1999b).

The slender *Cuvierina jagti* Janssen, 1995 found at Tetti Borelli, also present in the Poggio Musenna assemblage, appeared to have been introduced earlier as a scaphopod, i.e. *Dentalium ludbrooki* Caprotti (1962: 96, pl. 16, figs 4-6) from Early Pliocene clays of Castell'Arquato in northern Italy (Janssen, 1999a). The Tetti Borelli specimens clearly demonstrate the presence of a longitudinal micro-ornament.

From all these data it may be concluded that the ancestral species *Cuvierina paronai* developed two lineages, one characterised by a cylindrical shell and a triangular rather than reniform aperture (*Cuvierina* s. str.), and the other by an inflated shell and reniform aperture [*Cuvierina* (*Urceolaria*) subg. n., described below]. In the course of the development of *Cuvierina* s. str. a tendency to decrease the longitudinal micro-ornament is seen from the Early Pliocene onwards.

Cuvierina in the Pliocene

The trends observed in the development of Miocene cuvierinid species continue during the Pliocene. The subgenus *Urceolaria* continues until the Zanclean/Piacenzian transition with *C. intermedia* and *C. inflata*. The Recent '*Cuvierina columnella urceolaris*' apparently is the concluding form in this development, and therefore *C. urceolaris* is here considered a distinct species. This species is well-known from the Indian and Pacific oceans, and was recently also collected from strata in the Philippines, that after a first analysis are presumably Piacenzian in age (Janssen, 2000 unpublished).

Janssen (1995) synonymised *Cuvierina globosa* Collins, 1934, from the Pliocene

Agueguexquite Formation in Mexico with *C. inflata*. From the Early Pliocene of Japan (Blow zones 18-20) Ujihara (1996, figs 6.16-28) illustrated specimens from this lineage as *C. intermedia*, which because of their strongly inflated shells and preapertural constriction agree better with *C. inflata*.

The lineage containing the cylindrical species (*Cuvierina* s. str.) continues in the Mediterranean Early Pliocene with *C. ludbrooki*. This species also occurs in the Japanese Pliocene (Ujihara et al., 1990; Ujihara, 1996; as *C. cf. tubulata*) and was recently also found to occur, together with *C. intermedia*, in Pliocene deposits of the Fiji Islands (Andrew Grebneff collection).

Less slender is a common species known from the Mediterranean Zanclean and Piacenzian, *C. astesana* (Rang, 1829). In this species a reduction of the longitudinal micro-ornament is seen, and the aperture varies from reniform to triangular. The wide range of variation that could be observed in the abundant material available from French and Italian populations of *C. astesana* includes forms strongly resembling the Late Miocene-Pliocene *C. ludbrooki*, which is here considered to be its ancestral species. The Mexican species *C. tubulata* Collins, 1934 is here interpreted to be probably a synonym of *C. astesana*. Just a single, doubtful specimen of *C. astesana* is known from the North Sea Basin.

Another species, described as *C. miyazakiensis* Ujihara, 1996 (not seen), from the Pliocene of Japan (Blow zones 18-20), seems to make a perfect connection to Recent '*C. columnella*'.

Recent *Cuvierina*

Recent Cuvierinidae were extensively studied by Van der Spoel (1967, 1970, 1976). In his 1967 paper this author, as many before him, still accepted just a single species, with two formas, viz. *Cuvierina columnella* f. *columnella* (Rang, 1827) and f. *urceolaris* (Mörch, 1850). The main distinguishing characteristic was considered to be the position of the greatest shell width (close to caudal closing septum in f. *columnella* and in the middle of the shell in f. *urceolaris*). Specimens with the greatest width in between these two points were indicated intermediates.

In 1970 Van der Spoel introduced a third forma, f. *atlantica*, subdividing the f. *columnella* into a small Indo-Pacific form (*columnella*), and a larger, predominantly Atlantic form (*atlantica*). Later authors considered these formas to be subspecies, although at least f. *columnella* and f. *urceolaris* were known to be sympatric.

Since Van der Spoel (1970) explicitly introduced f. *atlantica* as an infrasubspecific taxon the name was validated as a species group name by Bé, MacClintock & Currie (1972: 58) (ICZN arts. 15.2 and 45.5.1), which authors gave an extensive description of the shell micro-architecture in '*C. columnella atlantica*'.

If we consider the development of *Cuvierina* populations during the Neogene, as described above, the conclusion is obvious that the Recent populations that used to be identified as *C. columnella* s. lat. are not monospecific. What was considered to be 'the typical form' and *C. columnella atlantica*, with hardly inflated, cylindrical shells, a lack of (at best a reduced) longitudinal micro-ornament and triangular aperture outlines are the successors of the *paronai-grandis-ludbrooki-astesana-miyazakiensis*-line, whereas the inflated *C. columnella urceolaris* with its obvious micro-ornament and reniform aperture concludes the lineage *intermedia-curryi-inflata*.

Of Recent *Cuvierina* a large number of bottom samples from the northern Atlantic Ocean, covering the Madeira, Canary and Cap Verde areas, but also from the Guyana Coast and the eastern Caribbean, was available. In this material the occurrence of *C.*

atlantica is convincingly demonstrated by its relatively large and slender shell (H min. 6.7 mm, max. 10.5 mm, mean value 8.3 mm, H/W min. 3.2, max. 3.9, mean value 3.55, $n = 190$), the virtual absence of micro-ornament, the triangular aperture and the very low position of the point of strongest inflation. It is mainly found around Madeira and the Canaries and is also present in the western Atlantic, in the Caribbean and more to the North.

A large number of samples, however, predominantly originating from the Cap Verde area, differ strongly from this *atlantica* type. Not only are the shells clearly less slender (H min. 7.6 mm, max. 9.3 mm, mean value 8.44 mm, H/W min. 2.8, max. 3.6, mean value 3.07, $n = 118$), but they also have a distinct micro-ornament, and a reniform rather than triangular aperture. These characteristics link them to the Indo-Pacific *C. urceolaris*, from which they differ by larger dimensions and a less pronounced inflation of the shell, which also is situated at a lower point. This until now unrecognised form is also present in some samples from the Guyana Coast and the Caribbean. It is described below as a new species, *Cuvierina cancapae*.

The Atlantic material from the DANA expeditions, housed in ZMUC, substantiates the existence of two taxa in this area. From this latter material *C. atlantica* appears also to be present in the S Atlantic, but I had insufficient samples available to obtain a fair idea of its distribution there. It seems that this species shows the bipolarity that is well-known in pteropods.

From the Indian and Pacific Oceans I could study many samples from the ZMUC collection. This collection includes several hundreds of alcohol samples, mainly collected alive during the DANA-expeditions and most of them (re-)identified in the 1970s by S. Van der Spoel.

Cuvierina urceolaris invariably is easily recognised in this material by its small size and distinctly inflated shell (H min. 5.1 mm, max. 6.6 mm, mean value 5.99 mm, H/W min. 2.3, max. 2.8, mean value 2.55, $n = 163$), clear micro-ornament and reniform aperture. Specimens from the Indian Ocean on average are slightly smaller (H mean value 5.49 mm, $n = 47$) than those from the Pacific (H mean value 6.19 mm, $n = 116$).

C. columnella columnella, as characterised by Van der Spoel (1972: 120, fig. 19) also is readily identified by being larger than *C. urceolaris*, more slender (H min. 6.6 mm, max. 8.9 mm, mean value 7.75 mm, H/W min. 2.9, max. 4.0, mean value 3.46, $n = 135$) and hardly inflated, with the point of maximum inflation situated rather high, and furthermore by the complete absence of micro-ornament and a triangular aperture.

Many samples, however, identified as *C. columnella* (f.) *columnella* by Van der Spoel in the ZMUC collection I had to re-identify as *C. urceolaris*, because of their inflated shells and distinct micro-ornament, as a result of which the geographic distribution of '*C. columnella*' s. str. was drastically reduced.

The quite unexpected result of this is, that 'typical' *C. columnella* sensu Van der Spoel, 1970 is exclusively found to be present in the Pacific, both N and S of the equator, with a barren zone in between. The N Pacific form (H min. 6.6 mm, max. 8.5 mm, mean value 7.59 mm, H/W min. 2.9, max. 3.5, mean value 3.23, $n = 36$) differs in measurements from the S Pacific one (H min. 7.1, max. 8.9, mean value 7.81 mm, H/W min. 3.3, max. 4.0, mean value 3.54, $n = 99$). This leads to the odd conclusion, that *C. columnella* as previously understood, does not occur in its type locality, which is 'la mer des Indes', the Indian Ocean (Rang, 1827: 323).

This 'problem', however, is rapidly solved, as apart from typical *C. urceolaris*, another as yet unrecognised form occurs, in the Indian Ocean as well as in the S Pacific, which was also identified *C. columnella* (f.) *columnella* by Van der Spoel, but differs by larger dimensions and a clear micro-ornament. Initially I considered these specimens to be identical with *C. cancapae*, but their measurements and shape of aperture resemble closely

Subgenus	species	Distribution	shape	aperture	ornament	name in Van der Spoel, 1970
<i>Cuvierina</i>	<i>atlantica</i>	N & S Atlantic	cylindrical	triangular	± absent	<i>atlantica</i> (partim)
<i>Cuvierina</i>	<i>columnella</i>	Indian, S. Pacific	cylindrical	triangular	present	<i>columnella</i> , <i>atlantica</i> (partim)
<i>Cuvierina</i>	<i>pacifica</i>	N & S Pacific	± cylindrical	triangular	absent	<i>columnella</i> (partim)
<i>Urceolaria</i>	<i>cancapae</i>	C & S Atlantic	less inflated	reniform	present	<i>atlantica</i> (partim)
<i>Urceolaria</i>	<i>urceolaris</i>	Indian, W Pacific	inflated	reniform	present	<i>urceolaris</i> , <i>columnella</i> (partim)

Table 1. Main characteristics and distribution of Recent *Cuvierina* species.

those of *C. atlantica*, from which they in fact differ predominantly by the presence of a clear micro-ornament. This form is commonly present in the southern Indian Ocean, and no doubt it is this form that was described as *C. columnella* by Rang, 1827.

Unfortunately it is impossible to check this on the type material, of which only the label survives (Van der Spoel, 1976: 191). Rang's illustration shows an extremely slender shell, with H/W-ratio = approximately 5.1, a value that exceeds by far the highest value (H/W = 4.0) found in all my measurements, and therefore I consider the drawing to be incorrect. The height of the specimen illustrated by Rang is 11 mm and that agrees perfectly with my findings (see Measurements, fig. 29).

In these circumstances I believe it necessary to designate a neotype for *C. columnella*, differing from what is currently understood under that name, and which therefore is in need of a new name. In the systematic part below I propose the name *C. pacifica* for what used to be considered 'typical' *C. columnella* from the Pacific. The neotype of *C. columnella* is designated in material from the MNHN collections, where the type of *C. columnella* Rang, 1827, used to be housed.

In summary, I conclude that no fewer than five species should be distinguished in Recent *Cuvierina*, in part different from previous interpretations of these names, and with almost completely separate geographic distributions. A summary of these is given in Table 1.

In *C. pacifica* as well as in *C. urceolaris*, to a lesser degree also in *C. columnella*, the measurements indicate that populations from different areas differ significantly in size and/or proportions; these might eventually be interpreted as geographic subspecies.

However, the main characteristics of some of these extant taxa unfortunately do not fully correspond to the overall picture as seen in the two lineages for the fossil species. The new interpretation of *C. columnella*, the type species of *Cuvierina*, indicates that the loss of longitudinal micro-ornament apparently does not occur in all Recent species of *Cuvierina* s. str., although a reduction of the micro-ornament is only found in this subgenus. Thus it is rather the cylindrical shell form and triangular aperture that characterise *Cuvierina* s. str. Still, in the N Pacific form of *C. pacifica* specimens with more or less inflated shells are also present.

C. urceolaris, the type species of *Urceolaria*, characterises the lineage with inflated shells, but *C. cancapae*, also included in that subgenus, has only a weakly inflated shell, whereas its other morphology clearly suggests *Urceolaria*.

This apparent mixture of features in the Recent populations might suggest that we are dealing with hybridisation, e.g. *cancapae* = *atlantica* × *urceolaris*, or *columnella* = *pacifica* × *urceolaris*, but this idea is by no means supported by the various distribution patterns.

Another possible explanation for these 'hybrids' might be that the genus *Cuvierina* is in the course of speciation. It must be borne in mind, that of the fossil taxa we usually have only a very poor knowledge of their horizontal distribution and therefore of their geo-

graphic variations, whereas of the Recent taxa the global distribution patterns are fairly well known.

The fact, however, that Recent *Cuvierina* populations apparently consist of more taxa than previously assumed agrees with Norris's (2000: 254) conclusion that 'biogeographic, ecological and genetic data suggest that morphological taxonomies have underestimated the number of pelagic species in a wide assortment of fish, zooplankton, and phytoplankton'.

Seen in this light extant *Cuvierina* species might offer an attractive and very promising occasion for biologists to test the results of this paper by DNA sequencing.

SYSTEMATIC PART

New fossil taxa

Class Gastropoda Cuvier, 1795
 Subclass Heterobranchia Gray, 1840
 Order Thecosomata Blainville, 1824
 Suborder Euthecosomata Meisenheimer, 1905
 Superfamily Cavolinioidea Fischer, 1883

Family **Praecuvierinidae** fam. nov.
 Genus **Praecuvierina** gen. nov.

Type species. – *Cuvierina lura* Hodgkinson, in Hodgkinson, Garvie & Bé, 1992. Holotype in USNM 360371.

Derivatio nominis. – (*L. prae* = before), as these predate genuine cuvierinids.

Diagnosis. – 'Shell small (height approximately 1 mm), barrel-shaped, highly inflated and globose, maximum diameter near mid-length. Apex truncated, blunt, closed by a septum that is adorally concave and slightly oblique to the shell axis, junction of septum and shell-wall sharp and distinct. Shell wall thin and polished, varying in thickness from about 11 to 22 μm (Hodgkinson et al., 1992: 32). Protoconch as yet unknown.

Distribution. – Exclusively known from the Eocene (Lutetian) Weches Formation, Texas, U.S.A.

Discussion. – Although strongly resembling cuvierinid species, such as *Cuvierina (Urceolaria) inflata* Bellardi, 1873 in outline and larval shell-shedding, the very small size (roughly one tenth of true cuvierinids) and the complete lack of surface ornament separate this species clearly. Furthermore, its time-stratigraphic distribution considerably predates the first development of the Cuvierinidae.

Genus **Texacuvierina** gen. nov.

Type species. – *Cuvierina gutta* Hodgkinson, in Hodgkinson, Garvie & Bé, 1992. Holotype in USNM 360369.

Derivatio nominis. – Named after the federal state of Texas, U.S.A.

Diagnosis. – 'Shell small, flask-shaped, smooth, laterally compressed, slightly constricted about one-fifth of distance from aperture, maximum diameter just slightly adoral of midlength. Apical end truncated and closed by a convex septum, aperture laterally compressed, ventral edge of aperture strongly recessed and resembles the sinus of some

other gastropods. Dorsal edge slightly recessed. Shell laterally symmetrical.' (Hodgkinson et al., 1992: 32). Protoconch still unknown.

Distribution. – Only known from the Cook Mountain Formation (Eocene, Early Bartonian) of Texas, U.S.A.

Discussion – Resembling *Cuvierina* in general shape, but reaching only approximately one fifth of its size. The (lateral ?) compression is stronger than the dorsal/ventral flattening in *Cuvierina*, and there is no trace of ornament on the shell's surface. The vertical distribution of *Texacuvierina gutta* clearly predates the first occurrence of the Cuvierinidae.

Family Cuvierinidae Gray, 1840

Genus *Cuvierina* Boas, 1886

Type species. - *Cuvieria columnella* Rang, 1827, by monotypy.

Subgenus *Urceolaria* subgen. nov. (see the section Description of Recent taxa, below)

Cuvierina (Urceolaria) curryi spec. nov. (figs 3-7)

Cuvierina columnella urceolaris (Mörch, 1850); d' Alessandro & Robba, 1981: 645, pl. 72 figs 1-4 (partim, non Mörch, includes also *C. intermedia*; excl. syn.).

Holotype. – fig. 3, leg. A.W. Janssen, 13-vi-1992 (RGM 457.567).

Type locality. – Abandoned limestone quarry at Cursi (Italy, Lecce province), approximately locality 2a of d' Alessandro & Robba (1981, fig. 1).

Stratum typicum. – 'Pietra Leccese' (level 2 in d' Alessandro & Robba, 1981, fig. 2) (Miocene, Serravallian-Tortonian).

Derivatio nominis. – This species is named after †Dennis Curry (Itchenor, U.K.), who produced several important papers on the systematics of fossil Pteropoda.

Diagnosis. – *Cuvierina* species resembling the Recent *C. urceolaris*, but differing by a more slender basal part because of larval shell-shedding at an earlier ontogenetic stage, and a consequently higher position of the maximum diameter of the shell, usually with a more accentuated swelling. Ventral side of shell more swollen than dorsal side. Dorso-ventral diameter of aperture wider than in *C. urceolaris*. Surface ornament and protoconch unknown.

Description. – Shell relatively small, height/width-ratio approximately 3.30, transverse section almost circular, dorso-ventral diameter only little less than the shell width, slightly flattened on the ventral side towards the proximal aperture. Base of shell conical with slightly concave side-lines, larval shell shed and opening closed by an oblique and convex septum, the most convex part of which lies near the dorsal side. Diameter of septum about one third of maximum shell diameter. Shell inflated, maximum diameter just below mid-height, on the ventral side the swelling is slightly more accentuated than on the dorsal one. Apertural margin thickened internally, dorsal side higher than ventral, rounded in adapical view, ventral side flattened. For further details see also d' Alessandro & Robba (1981: 645, pl. 72, figs 1-4).

Paratypes.- From the type locality (RGM 457.568, 40 specimens).

Near Melpignano (Italy, Lecce province) (Miocene, 'Upper Serravallian', Pietra Leccese), don. E. Robba (from samples published by d' Alessandro & Robba, 1981), June 1984 (RGM 458.700, 3 specimens).

Melpignano (Italy, Lecce province), active limestone quarry, locality 2a of d'Alessandro & Robba (1981, fig. 1) (Miocene, Serravallian-Tortonian, Calcareni di Andrano, 'Pietra Leccese', 1 m above base of glauconitic 'piromafo' level), leg. A.W. Janssen, 15-vi-1992 (RGM 457.841, 46 specimens, RGM 458.694-5, 2 illustrated specimens figs 4-5).

Ghasri (Malta, Gozo), southern slope of hill opposite pumping station and cemetery at UTM 308912 (Miocene, Serravallian, Blue Clay Formation, uppermost part), leg. A.W. Janssen, 8-vi-1995; RGM 397.583, 1 specimen).

Marsalforn (Malta, Gozo), coastal cliff section at NE corner of Marsalforn Bay at UTM 338925 [Miocene, Serravallian, Blue Clay Formation, middle third (= 10-15 m) of section], leg. A.W. Janssen, 3-vi-1995 (RGM 397.570, 1 specimen, illustrated fig. 7).

Marsalforn (Malta, Gozo), section on E-side of Marsalforn Bay at UTM 336925 (Miocene, Serravallian, Blue Clay Formation, lowermost exposed part above white level), leg. A.W. Janssen, 4-vi-1995 (RGM 397.602, 7 specimens).

Mgarr Harbour (Malta, Gozo), outcrop at UTM 370875 (Miocene, Serravallian, Blue Clay Formation, washed down from entire clay interval), leg. A.W. Janssen, 12-x-1995 (RGM 397.841, 6 specimens).

San Lawrenz (Malta, Gozo), hilltop exposure at UTM 269920 (Miocene, Serravallian, Blue Clay Formation), leg. A.W. Janssen, 6-9-x-1995 and 8-iii-1998 (RGM 429.045, 21 specimens; RGM 458.696, 1 specimen, illustrated fig. 6).

Zebbug (Malta, Gozo), Xwieni Bay, coastal cliff section at UTM 322932 (Miocene, Serravallian, Blue Clay Formation, base of upper brownish-green part), leg. A.W. Janssen, 5-x-1995 (RGM 429.150, 14 specimens).

Zebbug (Malta, Gozo), outcrops along road to Marsalforn, between UTM 319930 and 321932 (Miocene, Serravallian, Blue Clay Formation, lower 30 m of upper brownish-green part), leg. A.W. Janssen, 6/9-vi-1995 (RGM 397.797, 20 specimens).

Ghajn Hadid (Malta), near Mellieha, coastal cliff section at UTM 448808 (Miocene, Serravallian, Blue Clay Formation), leg. A.W. Janssen, 24-xii-1993 and 15-x-1995 (RGM 429.098, 15 specimens).

Ghar Baqrat (Malta), southern slope of Marfa Ridge, SW of Mellieha-Cirkewwa road, at UTM 412816 (Miocene, Serravallian, Blue Clay Formation, upper brownish-green part), leg. A.W. Janssen, 13-vi-1995 (RGM 397.940, 2 specimens).

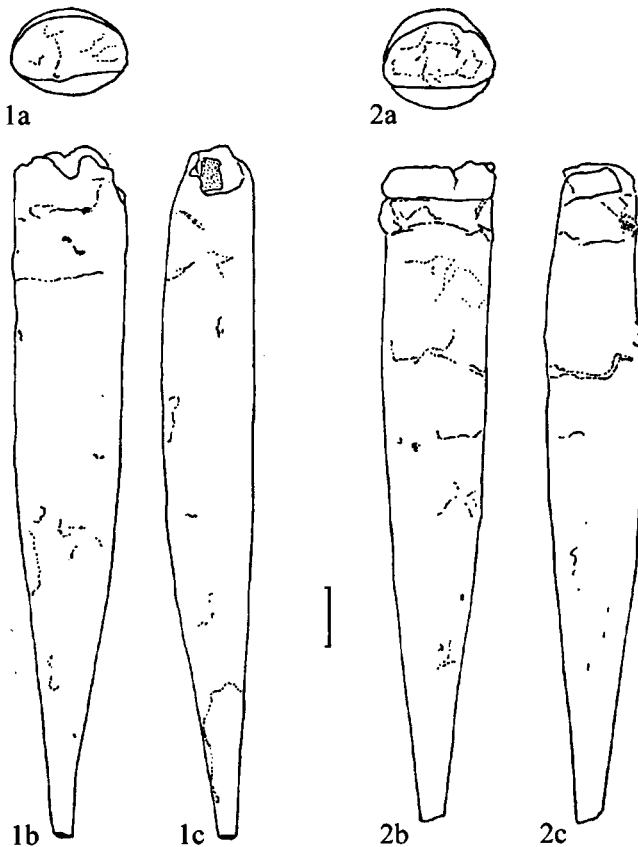
Distribution. – Miocene (Serravallian-Tortonian) of southern Italy and (Serravallian) of the Maltese Archipelago. As the Italian localities consist of reworked material the probable age of this species is just Serravallian.

Discussion. – The quite similar Recent *Cuvierina urceolaris* differs from the new species in being less slender, with a more gradual inflation and a comparatively wider septum with a diameter of approximately half the maximum shell diameter. Its basal part below the largest diameter of the shell until the septum has slightly convex sidelines instead of concave ones.

Cuvierina curryi is only known as internal phosphoritic (Italian samples) or limonitic (Maltese samples) moulds, so nothing is known about a possible surface ornamentation. Measurements on this species were not made, as in most specimens the apertural part is too much damaged, or the measurements are incorrect because of limonite expansion.

Genus *Ireneia* Janssen, 1995

Type species. – *Ireneia tenuistriata* (Semper, 1861), by original designation.



Figs 1-2. *Ireneia gracilis* spec. nov., holotype and paratype. Baldissero (Italy, Piemonte), outcrop on Str. di Valsanfra, Colli Torinesi (Miocene, Late Burdigalian, Termô-Fôrà Formation, middle part of exposed section). 1, holotype (RGM 458.697); 2, paratype (RGM 458.698). a: apertural, b: ventral, c: left lateral views. Scale bar is 1 mm.

Ireneia gracilis spec. nov. (figs 1-2)

Derivatio nominis. – *L. gracilis* adj. – slender; named after the very elongate shape of the shell.

Diagnosis. – Very slender *Ireneia* species, height/width-ratio c. 6.5, transverse section ellipsoid to circular, very slowly increasing in diameter and flattened on the ventral side close to the aperture. Ventral side slightly more convex than dorsal. Aperture reniform. Protoconch unknown.

Type locality. – Baldissero, outcrop on Str. di Valsanfra, Colli Torinesi (Italy, Piemonte).

Stratum typicum. – Termô-Fôrà Formation, middle part of exposed section (Miocene, Late Burdigalian).

Holotype. – Leg. A.W. Janssen, 19-v-1994, RGM 458.697 (fig. 1).

Description. – *Ireneia gracilis* is extremely slender. The H/W-ratio (reconstructed) approaches 6.5, which makes it the most elongate species of the genus. Most available specimens are preserved as internal clay moulds, and none of them has the apical parts preserved. Hence the morphology of the protoconch is still unknown. The transverse section of the shell is circular in its basal parts, becoming more ellipsoid adaperturally. The apical angle of the oldest preserved parts is c. 15°, at about half the shell height (ventral view) the sides become almost parallel. In a lateral view the dorsal sideline is virtually straight, whereas the ventral one is gently curved, with the maximal diameter at c. two thirds of the shell height. The shell is flattened adaperturally, resulting in a reniform shape of the aperture, which in none of the specimens, however, is completely preserved. In some specimens it can be seen that the apertural margin is internally thickened.

In one of the paratype specimens from Berzano di San Pietro some preserved shell fragments demonstrate the presence of a longitudinal micro-ornament.

Paratypes. – From the type locality (RGM 395.411, 20 more or less incomplete specimens; RGM 458.697, 1 specimen fig. 2).

Berzano di San Pietro (Italy, Asti), abandoned sandpit W of the road from Castelnuovo to Berzano, near Cascina Morra, coordinates $x = 16.800$, $y = 92.890$ (Miocene, Langhian, clay lens in coarse serpentinite conglomerate), leg. A.W. Janssen, 18-vi-1988 (RGM 397.475, 3 specimens; RGM 397.476, 2 damaged specimens).

Castelsardo (Italy, Sardinia, Sassari), coastal cliff outcrop near 2nd (wooden) staircase E of citadel (Miocene, Aquitanian-Burdigalian, greyish-brown volcano-clastic sediments), leg. A.W. Janssen, 17-x-1991 (RGM 396.380, 3 damaged specimens); coastal cliff outcrop near 3rd staircase E of citadel, same level, leg. A.W. Janssen, 16-x-1991 (RGM 397.381, 1 fragment).

Sciolze (Italy, Torino), road cut outcrop (Miocene, Burdigalian, grey marls), leg. A.W. Janssen, 19.5.1994 (RGM 396.206, 1 specimen).

Distribution. – The new species is only known from northern Italy and from Sardinia and was found in sediments of ages indicated as Aquitanian-Burdigalian, Burdigalian and Langhian. Specimens from Sardinia (Aquitanian-Burdigalian, compare Spano, 1983) and from Sciolze (Burdigalian) were found in an assemblage also containing *Vaginella depressa* Daudin, 1800 and therefore indeed are older than Late Burdigalian. The other samples were collected from sediments also yielding *V. austriaca* Kittl, 1886, meaning that they are Late Burdigalian or younger.

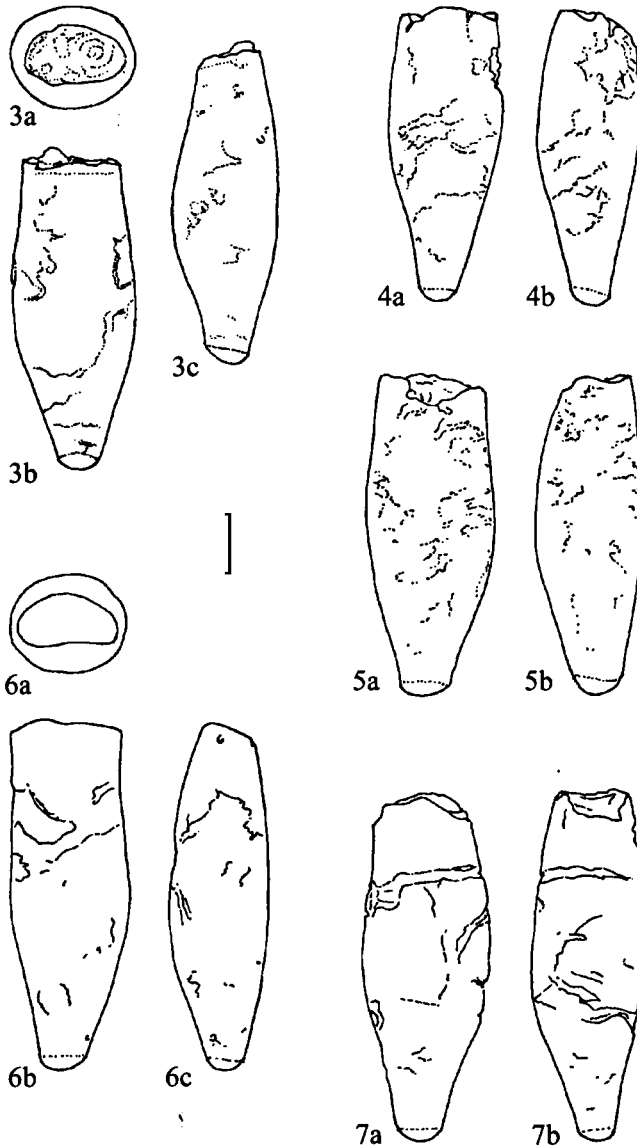
Discussion. – *Ireneia gracilis* closely resembles *I. nieulandei* A.W. Janssen, 1995, which is, however, considerably larger (twice the size of the new species) and also less slender (compare Janssen, 1995, pl. 14, fig. 4). The type specimen of *I. nieulandei* originates from Saucats (Coquillère outcrop) in the Aquitaine Basin (France) and similarly has a Burdigalian age (Falun du Pont-Pourquet). Most probably this species is the Atlantic precursor of the Mediterranean group of species including *I. gracilis*, *I. calandrellii* (Michelotti, 1847) and *I. testudinaria* (Michelotti, 1847).

Genus *Johnjagtia* gen. nov.

Type species. – *Cleodora (Creseis) moulini* Benoist, 1873.

Derivatio nominis. – This new genus is named after Dr John W.M. Jagt, of Venlo, Holland, who for many years improved the English of my papers. His suggestions, especially also with regards contents, have always been very useful and appreciated.

Diagnosis. – A genus of the Cuvierinidae, resembling *Ireneia* in general shell shape, but with a longitudinal dorso-lateral fold at about half height. Aperture rounded triangu-



Figs 3-7. *Cuvierina (Urceolaria) curryi* spec. nov., holo- and paratypes. 3, holotype, abandoned limestone quarry at Cursi (Italy, Lecce province), approximately locality 2a of d'Alessandro & Robba (1981, fig. 1); Calcareniti di Andrano, 'Pietra Leccese' (level 2 in d'Alessandro & Robba, 1981, fig. 2) (Miocene, Serravallian-Tortonian) (RGM 457.567); 4-5, Melpignano (Italy, Lecce province), active limestone quarry, locality 5 of d'Alessandro & Robba (1981, fig. 1) (Miocene, Serravallian-Tortonian, Calcareniti di Andrano, 'Pietra Leccese', 1 m above base of glauconitic 'piromafo' level) (RGM 458.694-5); 6, San Lawrenz (Malta, Gozo), hilltop exposure at UTM 269920 (Miocene, Serravallian, Blue Clay Formation) (RGM 458.696); 7, Marsalforn (Malta, Gozo), coastal cliff section at NE corner of Marsalforn Bay at UTM 338925 [Miocene, Serravallian, Blue Clay Formation, middle third (= 10-15 m) of section] (RGM 397.570). a: apertural, b: ventral, c: left lateral views. Scale bar is 1 mm.

lar, with a thickened apertural rim. Longitudinal micro-ornament distinct.

Distribution. – Miocene, Burdigalian, Aquitaine Basin, France.

Discussion. – *Johnjagtia moulinsi*, only rarely cited in literature, used to be included in the Creseidae (e.g. Peyrot, 1932: 21, as *Creseis Moulinsi*), but from new material (RGM collections) it is clear that both its surface ornament as well as the shape and reinforcements of the aperture make it a distinct cuvierinid, related to both *Ireneia* and *Spoelia*. A full redescription will be included in a forthcoming paper on pteropods from the Aquitaine Basin (Janssen, in prep.).

Description of recent taxa

Synonyms are restricted to those few references of which I could examine the material, or that could with some certainty be recognised by descriptions or illustrations. No references are included based on geographical origin.

Family Cuvierinidae Gray, 1840

Genus *Cuvierina* Boas, 1886

Type species. - *Cuvierina columnella* Rang, 1827, by monotypy.

Subgenus *Cuvierina* Boas, 1886 s.str.

Cuvierina (Cuvierina) atlantica Bé, MacClintock & Currie, 1972 (figs 8-9)

Cuvierina columnella (Rg.); Boas, 1886: 132 (partim), pl. 6 figs 95k-m (non Rang).

Cuvierina columnella (Rang, 1827) forma *atlantica* nov. forma; Van der Spoel, 1970: 120, fig. 20.*

Cuvierina columnella atlantica; Bé, MacClintock & Currie, 1972: 58ff, many illustr. (mainly of shell microstructures).

Cuvierina columnella (Rang, 1827) forma *atlantica* Van der Spoel, 1970; Van der Spoel, 1976: 49, fig. 35b (non fig. 35a = *C. pacifica*) (partim, includes also *C. cancapae*).

Cuvierina columnella (Rang, 1827); Rampal, 2002: 214 (partim, non Rang, non fig. 1Cc = *Cuvierina pacifica*).

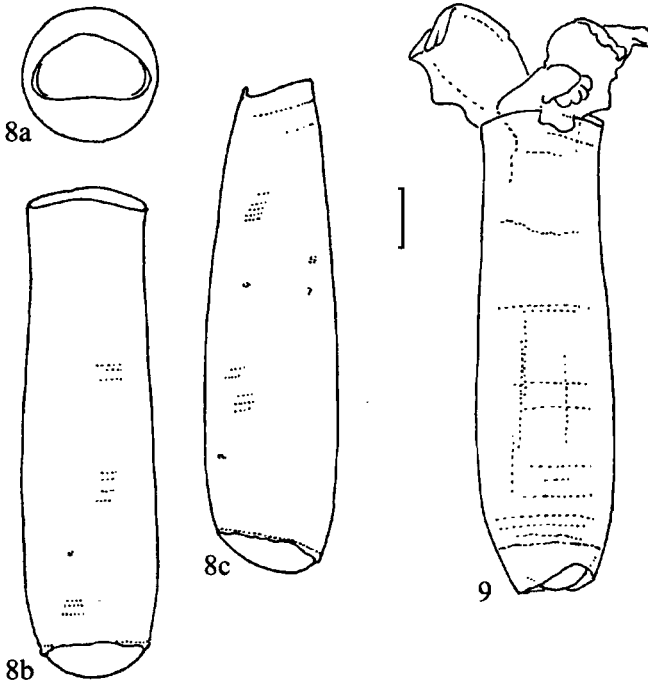
Cuvierina spoeli n. sp.; Rampal, 2002: 214 (partim, non fig. 1Cs = *Cuvierina columnella*).

Type material. – Two samples from the type locality are present in the ZMUC collections, one consisting of c. 150 specimens (here considered paratypes) and one of a single specimen. This latter sample is labeled 'holotype'.

Type locality. – Atlantic Ocean, DANA Expedition, St. 0299, 37°05'N 54°34'W, 13-vi-1911.

Diagnosis. – N and S Atlantic *Cuvierina (Cuvierina)*-species with slightly smaller dimensions than the type species and a hardly accentuated inflation at a low position (see Measurements), differing from *Cuvierina (Urceolaria)* species by the absence of distinct micro-ornament, a triangular aperture and a relatively more elongate shell.

Material examined (A = leg. Andrea; fr. = fragment[s]). – Atlantic Ocean: 43°N 35°W (ZMUC/2); 43°23'N 43°35'W, A (ZMUC/2); 42°50'N 46°10'W, A (ZMUC/2); 38°40'N 63°00'W, A 139 (ZMUC/1); 36°22'N 40°48'W, A (ZMUC/5); 35°55'N 65°45'W, A 135, A (ZMUC/3); 34°50'N, A (ZMUC/2); 34°50'N 10°50'W, A 129 (ZMUC/2); 34°16'N 42°W, A (ZMUC/2); 33°06'N 25°30'W, A (11-14) (ZMUC/4); 31°10'N 76°40'W, A 99 (ZMUC/1); 30°30'N 17°12'W, A (ZMUC/2); 29°30'N 34°30'W, A (ZMUC/1); 29°20'N 78°44'W, A (ZMUC/6);



Figs 8-9. *Cuvierina (Cuvierina) atlantica* Bé, MacClintock & Currie, 1972. 8, Tydeman Canary Islands Expedition 1977 CANCAP-II,); St. 2.078, Canary Islands, S of Fuerteventura, Punta de Jandia, 28°01'N 14°26'W, depth 790 m, van Veen grab, 30-viii-1977 (RMNH 78389); 9, Dana Expedition,); St. 1147(ii), 32°00'N 20°01'W, 20-x-1921 (ZMUC, not registered). a: apertural, b: ventral, c: left lateral views; 9: ventral view). Scale bar is 1 mm.

25°24'N 31°20'W, A (ZMUC/1); 24°70'N 34°50'W, A (ZMUC/1); 21°N 30°30'W, A (ZMUC/2); 19°30'S 02°30'W, A (ZMUC/1); 24°50'S 21°20'W, A (ZMUC/2); 30°00'S 26°00'W, A (ZMUC/1); 30°16'S 24°20'W, A (ZMUC/2); 30°30'S 22°30'W, A (ZMUC/1); 14.5°S 35.5°W, leg. Bruun (ZMUC/1); 31°N 62°W, leg. Hovgaard (ZMUC/1); 20°N 81°W, leg. Hygom VIII (ZMUC/1); 25°N 39°W, leg. Hygom XXIII (ZMUC/3); 26°N 22°W, leg. Hygom (ZMUC/1); 28°N 21°W, leg. Hygom (ZMUC/1); 34°N 34°W, leg. Hygom (ZMUC/1); 32°06'N 39°28'W, leg. Warming (ZMUC/2); 15°56'N 30°41'W, leg. Warming 31 (ZMUC/1); Off St. Augustine, Florida, U.S.A., 30°10'N 78°44'W, 435-440 fathoms, leg. Woods Hole Oceanographic Institution, Woods Hole, Mass., U.S.A. (RMNH 78456/1 fr.).

ATLANTIS EXPEDITION, leg. Woods Hole Oceanographic Institution, Woods Hole, Mass., U.S.A., St. 2.985, Santaren Channel, off N Cuba, 23°23'N 79°17'W, 250 fathoms (RMNH 78457/2 fr.); St. 2.987, Nicholas Channel, off N Cuba, 23°22'N 79°53'W, 280-300 fathoms (RMNH 78458/2); St. 3.338, Bahía de Cienfuegos, S Cuba, 21°49'30"N 80°43'W, 1075 fathoms (RMNH 78459/1 fr.); St. 3.457, Nicholas Channel, off N Cuba, 23°23'N 80°36'W, 550 fathoms (RMNH 78460/2 + 2 fr.).

DANA EXPEDITION, St. 0299, 37°05'N 54°34'W (ZMUC/c. 150, and 1, holotype); St. 0604, 35°56'N 9°05'W (ZMUC/2); St. 0628, 36°16'N 30°10'W (ZMUC/1); St. 0662, ('Texas') 24°30'N 20°31'W (ZMUC/28 + fr. of c. 10); St. 0883, 30°53'N 54°07'W (ZMUC/31 + fr.); St. 0884, 29°49'N 54°10'W (ZMUC/26 + fr.); St. 0885, 26°46'N 54°14'W (ZMUC/57); St. 1111(iii), 35°04'N 06°54'W (ZMUC/1, untypical specimen, with coarse radial ornament); St. 1121, Méditerranée occidentale, 25 m (MNHN/2 and 1, the latter is a paratype of

Cuvierina spoeli Rampal, 2002); St. 1141(xvii), Caribbean Sea, 14°38'N 61°16'W (RMNH 93493/47 alc. colln); St. 1147(ii), 32°00'N 20°01'W (ZMUC/14 + fr. of 1 more, 1 specimen illustrated, fig. 9); St. 1152(ix), 30°17'N 20°44'W (ZMUC/3); St. 1178(v), 10°24'N 54°38'W (ZMUC/2 and 10); St. 1191(viii), 17°49'N 64°54'W (ZMUC/21); St. 1192 (vii), 17°43.4'N 64°54.3'W (ZMUC/14); St. 1192 (xi), 17°43.4'N 64°54.3'W (ZMUC/30); St. 1202(v), 09°40'N 79°56'W (ZMUC/1); St. 1238(iii), 26°13'N 78°48'W (ZMUC/42, fr. of 3 more); St. 1238(iv), 26°13'N 78°48'W (ZMUC/37 + fr. of 8 more); St. 1238(v), 26°13'N 78°48'W (ZMUC/25 + fr. of 7 more); St. 1261(v), 19°04'N 65°43'W (RMNH 93497/14 alc. colln); St. 1283(v), Caribbean Sea, 14°38'N 61°16'W (RMNH 93495/26 alc. colln); St. 1283(xi), Caribbean Sea, 14°38'N 61°16'W (RMNH 93496/15 alc. colln); St. 1292(vi), 17°43'N 64°56'W (ZMUC/41); St. 1293 (v), 17°43'N 64°56'W (ZMUC/60 measured specimens, 1 specimen with shell repair, 10 damaged); St. 1294(v), 17°43'N 64°56'W (ZMUC/16 + several fr., 25 + fr. of 6 more); St. 1296(o), 17°43'N 64°56'W (ZMUC/55); St. 1296(v), 17°43'N 64°56'W (ZMUC/1 + fr. of 3 more, and 19); St. 1322(iii), 27°02'N 53°39'W (ZMUC/1 + 2 fr.); St. 1339(v), 30°00'N 64°38'W (ZMUC/25); St. 1342(ix), 34°00'N 70°01'W (ZMUC/17); St. 1345(iv), 35°07'N 72°38'W (ZMUC/181); St. 1355(iii), 31°48'N 63°38'W (ZMUC/15); St. 1356(iii), 29°56'N 59°33'W (ZMUC/38); St. 1358(xiii) 28°15'N 56°00'W (ZMUC/35); St. 1365(iv) 31°47'N 41°41'W (ZMUC/21); St. 3979(v), 27°13'S 9°10'E (ZMUC/1); St. 3988(v), 15°52'S 06°02'W (ZMUC/1 measured specimen); St. 4017, 29°13'N 14°12'W (ZMUC/8); St. 4017(x), 29°13'N 14°12'W (ZMUC/11 + fr. of 1); St. 4017(xi), 29°13'N 14°12'W (ZMUC/35); St. 4017(xi), 29°13'N 14°12'W (ZMUC/71 + fr. of 5); St. 4018(iv), 31°30'N 12°12'W (ZMUC/5); St. 4019(iv), 33°08'N 10°22'W (ZMUC/3); St. 4019(viii) 33°08'N 10°22'W (ZMUC/11 + fr., 4 + fr. of 1); St. 4019(ix), 33°08'N 10°22'W (ZMUC/28); St. 4019 (x), 33°08'N 10°22'W (ZMUC/79); St. 4193(v) 41°53'N 32°22'W (ZMUC/270); St. 4195, 41°55'N 32°22'W, 2875 m (ZMUC/4); St. 4778, 32°13'N 167°25'W, 2875 m (ZMUC/1 broken).

DIAPAR 27/087, W Guyana, 10°19'7"N 58°53'40"W (MNHN/1).

GALATHEA EXPEDITION, St. unknown, 27°53'N 25°03'W, leg. Reinhardt 208 (ZMUC/2); St. 721, 33°N 47°W, leg. Kjellerup (ZMUC/1 and 4); St. 721B, c. 36°N 43°W, leg. Kjellerup (ZMUC/2); St. 721d, c. 37°N 41°W, leg. Kjellerup (ZMUC/4); St. 'N' (ZMUC/4).

JEAN CHARCOT, 1.K.6, Atlantique marocain, 30°N (?) (MNHN/1).

JGOFS LEG-IV EXPEDITION, boxcore T90-10B, 45°21.3'N 279.1'W, 2162 m, upper 43 cms of bottom sediment, with pteropod layers throughout (RGM 458.699/2 + 12 fr.).

KOMM. F. HAVUNDERSØGELSE EXPEDITION, St. 0605, 30°50'N 16°10'W (ZMUC/5); St. 0628, 36°16'N 30°10'W (ZMUC/1).

LUYMES GUYANA SHELF EXPEDITION, 1970, St. LUY.15097, off Guyana, 6°48'N 57°31'W, 21 m (RMNH 78445/1); St. LUY.15108, off Guyana, 7°40'N 57°32'W, 63 m (RMNH 78446/27, 8 damaged); St. LUY.34056, W of Saba, 17°37'N 63°17'W, 580 m (RMNH 78447/10, 1 fr.), St. LUY.34076, SW-slope Saba Bank, 17°14'N 63°44'W, 500 m (RMNH 78448/3).

LUYMES SABA BANK EXPEDITION 1972, St. LUY.34112, S of Saba Bank, 17°06'N 63°28'W, 600-800 m (RMNH 78449/3); St. LUY.34127, N-slope Saba Bank, 17°37'N 63°32'W, 360 m (RMNH 78450/7, 2 damaged); St. LUY.34128, N-slope Saba Bank, 17°36'N 63°37'W, 350 m (RMNH 78451/10, 7 damaged); St. LUY.34129, NW-slope Saba Bank, 17°32'N 63°39'W, 290 m (RMNH 78452/5, 6 damaged); St. LUY.34135, W-slope Saba Bank, 17°25'N 63°52'W, 510 m (RMNH 78453/54); St. LUY.34149, NE of Saba Bank, 17°43'N 63°25'W, 850 m (RMNH 78454/4, 1 damaged); St. LUY.34155, N of Saba, 17°49'N 63°16'W, 980 m (RMNH 78455/39).

METEOR EXPEDITION 9c, St. 102, BG 295, Josephine Bank, 269 m, 36°44.7'N 14°14.5'W (SMF 323180/1).

METEOR EXPEDITION 19, St. unknown, Meteorbank, leg. G. Richter (SMF 323174/2).

METEOR EXPEDITION 23, St. 174, 1750 m, 35°30.6'N 08°07.3'W (SMF 323177/4); St. 116, 1659 m, 32°54.4'N 16°52.7'W, G. Richter leg. (SMF 323178/8); St. 174, 1812-1716 m, 35°30.6'N 08°07.3'W (SMF 323191/1).

METEOR EXPEDITION 36, St. 99 FD, off W Sahara, Ras al-Abiad, 21°37.6'N 18°41.5'W, leg. M. Grasshoff, 1975 (SMF 323176/9).

METEOR EXPEDITION 53, St. 169, KG 825, N of Casablanca, 34°53.5'N 07°48.9'W (SMF 323189, 6;

SMF 323190/5).

ONVERSAAGD MADEIRA-MOROCCO EXPEDITION 1976, CANCAP-I, St. 1.020, W of Deserta Grande, 32°31'N 16°32'W, 144 m (RMNH 29001/1); St. 1.021, W of Deserta Grande, 32°29'N 16°32'W, 228-240 m (RMNH 29002/5); St. 1.023, W of Deserta Grande, 32°28'N 16°36'W, 300 m (RMNH 93492/2 alc. colln); St. 1.025, SE of Madeira, 32°42'N 16°45'W, 78 m (RMNH 78379/1); St. 1.044, SE of Madeira, 32°42'N 16°42'W, 815 m; St. 1.052, SE of Madeira, 32°42'N 16°48'W, 2300 m (RMNH 93488/1 alc. colln); St. 1.062, SE of Madeira, 32°40'N 16°46'W, 680 m (RMNH 78381/1, 1 damaged); St. 1.077, SE of Madeira, 32°24'N 16°43'W, 3000-3200 m (RMNH 93489/3 alc. colln); St. 1.086, S of Madeira, 32°37'N 16°51'W, 360 m (RMNH 78382/2); St. 1.088, S of Madeira, 32°34'N 16°51'W, 1920-2060 m (RMNH 93491/1 alc. colln); St. 1.089, S of Madeira, 32°30'N 16°54'W, 2200-2370 m (RMNH 93490/1 alc. colln).

THOR EXPEDITION, St. 89, 36°28'N 08°22'W (ZMUC/3 + fr. of 2).

TYDEMAN AZORES EXPEDITION 1981, CANCAP-V, St. 5.004, Azores, NE of São Miguel, 38°06'N 24°49'W, 2400-3100 m (RMNH 78439/1); St. 5.012, Azores, S of São Miguel, 37°39'N 25°32'W, 480 m (RMNH 78440/1); St. 5.154, Azores, E of Flores; 39°22'N 30°53'W, 350 m (RMNH 93478/1 alc. colln); St. 5.176, Azores, SE of Corvo, 39°40'N 31°05'W, 142 m (RMNH 78441/3, 1 fr.); St. 5.187, Azores, E of Flores, 39°27'N 31°05'W, 500-550 m (RMNH 78442/1).

TYDEMAN CANARY ISLANDS EXPEDITION 1977 CANCAP-II, St. 2.007, S of Fuerteventura, Punta de Jandia, 27°48'N 14°24'W, 2000 m (RMNH 78383/1); St. 2.036, Morocco, W of Cape Yubi, 28°00'N 13°22'W, 540-580 m (RMNH 78384/1 damaged); St. 2.058, Morocco, W of Cape Yubi, 27°58'N 13°24'W, 500 m (RMNH 78385/1); St. 2.062, SE of Fuerteventura, Punta de Gran Tarajal, 28°07'N 13°45'W, 0-1520 m (RMNH 78386/36); St. 2.065, SE of Fuerteventura, Punta de Gran Tarajal, 28°11'N 13°57'W, 670 m (RMNH 78387/1); St. 2.067, S of Fuerteventura, Punta del Morro Jable, 27°58'N 14°12'W, 1810-1830 m (RMNH 78388/5); St. 2.078, S of Fuerteventura, Punta de Jandia, 28°01'N 14°26'W, 790 m (RMNH 78389/1 illustrated, fig. 8); St. 2.079, S of Fuerteventura, Punta de Jandia, 28°01'N 14°26'W, 870 m (RMNH 78390/1); St. 2.080, S of Fuerteventura, Punta de Jandia, 28°01'N 14°26'W, 980 m (RMNH 78391/1); St. 2.086, S of Fuerteventura, Punta de Jandia, 28°02'N 14°29'W, 450-500 m (RMNH 78392/23); St. 2.087, SE of Gran Canaria, 27°42'N 15°02'W, 2300 m (RMNH 78393/75); St. 2.100, S of Hierro, off Punta de la Restinga, 27°37'N 18°00'W, 336 m (RMNH 78394/1, 1 damaged); St. 2.101, S of Hierro, off Punta de la Restinga, 27°37'N 18°00'W, 440 m (RMNH 78395/2 damaged); St. 2.103, S of Hierro, off Punta de la Restinga, 27°37'N 17°59'W, 240 m (RMNH 78396/10, 3 damaged); St. 2.112, S of Hierro, off Punta de la Restinga, 27°13'N 18°07'W, 3750 m (RMNH 78397/1); St. 2.114, SW of Hierro, off Punta de Orquilla, 27°41'N 18°09'W, 340-480 m (RMNH 78398/18, 10 damaged); St. 2.129, SW of Hierro, off Punta de Orquilla, 27°41'N 18°10'W, 900 m (RMNH 78399/29); St. 2.131, SW of Hierro, off Punta de Orquilla; 27°40'N 18°10'W; 1200-1800 m (RMNH 93494/1 alc. colln); St. 2.154, S of Hierro, off Punta de la Restinga, 27°35'N 17°59'W, 550 m (RMNH 78400/1); St. 2.155, S of Hierro, off Punta de la Restinga, 27°35'N 17°59'W, 700 m (RMNH 78401/8); St. 2.156, S of Hierro, off Punta de la Restinga, 27°35'N 18°00'W, 1050 m (RMNH 78402/7); St. 2.157, S of Hierro, off Punta de la Restinga, 27°35'N 17°59'W, 650 m (RMNH 78403/9); St. 2.159, S of Hierro, off Punta de la Restinga, 27°36'N 17°59'W, 620 m (RMNH 78404/7); St. 2.160, S of Hierro, off Punta de la Restinga, 27°36'N 17°59'W, 550 m (RMNH 78405/61).

TYDEMAN CAPE VERDE ISLANDS EXPEDITION 1986, CANCAP-VII, St. 7.039, Cape Verde Islands, SE of Cima; 14°56'N 24°38'W, 590-610 m (RMNH 78444/1).

TYDEMAN MADEIRA-MAURITANIA EXPEDITION 1978, CANCAP-III, St. 3.007, Madeira archipelago, S of Porto Santo, 33°02'N 16°20'W, 135 m (RMNH 78406/2); St. 3.051, SE of Madeira, 32°40'N 16°40'W, 1100 m (RMNH 78407/3 damaged); St. 3.052, SE of Madeira, 32°25'N 16°54'W, 2950-3065 m (RMNH 78408/1 damaged); St. 3.059, SE of Madeira, 32°42'N 16°44'W, 108 m (RMNH 78409/1); St. 3.068, Selvagens archipelago, SW of Selvagem Grande, 30°07'N 15°53'W, 310 m (RMNH 78410/13); St. 3.071, Selvagens archipelago, SW of Selvagem Grande, 30°07'N 15°54'W, 748 m (RMNH 78411/2); St. 3.072, Selvagens archipelago, SW of Selvagem Grande, 30°06'N 15°54'W, 830 m (RMNH 78412/3); St. 3.081, Selvagens archipelago, S of Selvagem Pequena, 30°01'N 16°01'W, 91 m (RMNH 78413/1, illustrated); St. 3.083, Selvagens archipelago, S of Selvagem Pequena; 30°01'N 16°01'W, 192 m (RMNH 78414/2); St. 3.102,

Selvagens Archipelago, SW of Selvagem Grande, 30°07'N 15°53'W, 600 m (RMNH 78415/3); St. 3.107, off Western Sahara, 24°17'N 16°49'W, 1000-1100 m (RMNH 78416/7),

TYDEMAN SELVAGENS-CANARY ISL. EXPEDITION 1980, CANCAP-IV, St. 4.041, S of Lanzarote, 28°48'N 13°46'W, 120 m (RMNH 78417/2); St. 4.048, S of Lanzarote, 28°48'N 13°46'W, 215-325 m (RMNH 78418/1); St. 4.049, S of Lanzarote, 28°48'N 13°46'W, 313 m (RMNH 78419/1); St. 4.055, SE of Lanzarote, 28°45'N 13°20'W, 1209-1338 m (RMNH 78420/12); St. 4.058, SE of Lanzarote, 28°48'N 13°45'W, 509 m (RMNH 78421/1); St. 4.060, SE of Lanzarote, 28°48'N 13°45'W, 580-600 m (RMNH 78422/3); St. 4.062, SE of Lanzarote, 28°48'N 13°43'W, 820 m (RMNH 78423/6); St. 4.063, SE of Lanzarote, 28°49'N 13°42'W, 870-880 m (RMNH 78424/2); St. 4.064, SE of Lanzarote, 28°47'N 13°41'W, 1030 m (RMNH 78425/6); St. 4.069, SE of Lanzarote, 28°55'N 13°32'W, 109-116 m (RMNH 78426/2 (1 with bryozoa)); St. 4.077, SE of Lanzarote, 28°47'N 13°37'W, 1085 m (RMNH 78427/2); St. 4.080, SE of Lanzarote, 28°55'N 13°33'W, 200-220 m (RMNH 78428/1, 1 fr.); St. 4.082, SE of Lanzarote, 28°54'N 13°33'W, 450-480 m (RMNH 78429/1); St. 4.086, SE of Lanzarote, 28°54'N 13°33'W, about 785 m (RMNH 78430/11); St. 4.114, S of Palma, 28°27'N 17°51'W, about 200 m (RMNH 78727/2); St. 4.110, S of Palma, 28°27'N 17°51'W, 110-180 m (RMNH 78431/1); St. 4.112, S of Palma, 28°27'N 17°51'W, 245-141 m (RMNH 78432/6); St. 4.117, S of Palma, 28°26'N 17°51'W, 503 m (RMNH 78433/10); St. 4.139, SW of Palma, 28°39'N 17°58'W, 100 m (RMNH 78434/4, 3 fr.); St. 4.145, SW of Palma, 28°39'N 17°59'W, 160 m (RMNH 78435/8); St. 4.156, SW of Palma, 28°39'N 17°59'W, 310 m (RMNH 78436/10); St. 4.159, SW of Palma, 28°40'N 17°59'W, 400 m (RMNH 78437/7, 3 fr.); St. 4.160, SW of Palma, 28°40'N 18°00'W, 500 m (RMNH 78438/3).

Locality unknown: (ZMUC/1, 1 and 2); (ZMUC/3); (ZMUC/15); (ZMUC/3); "5°20' 41°", leg. Andrea, 25.viii.1863 (ZMUC/1).

Locality unknown: leg. & date unknown (ZMUC, 1, 1 and 2); leg. & date unknown (ZMUC, 3); leg. & date unknown (ZMUC, 15); leg. & date unknown (ZMUC, 3); "5°20' 41°", leg. Andrea, 25-viii-1863 (ZMUC, 1).

Remarks – Van der Spoel (1970: 120, fig. 20) explicitly introduced forma *atlantica* as an infrasubspecific taxon. According to ICSN arts. 15.2 and 45.5.1 (ICZN, 1999) the name was validated as a species group name by Bé, MacClintock & Currie (1972: 58). Rampal (2002: 212) rejected the name *atlantica* Van der Spoel, 1970 and introduced the name *C. spoeli* for it. This, however, is not a replacement name, as Rampal designated another specimen as holotype, from a sample originating from 21°08'S, 55°11'E (SW Indian Ocean). This sample, a paratype of which was available to me, belongs to *C. columnella*, which makes the name *C. spoeli* to a junior synonym of *C. columnella*. This paratype of *C. spoeli* is here designated neotype of *C. columnella* (see below).

Cuvierina (Cuvierina) columnella (Rang, 1827) (figs 10-13)

Cuvieria columnella Nob.; Rang, 1827: 323, pl. 45 figs 1-3 (mala).

Cuvierina columnella (Rg.); Boas 1886: p. 132 (partim), pl. 6 fig. 95n.

Cuvierina columnella (Rang, 1827) forma *columnella* (Rang, 1827). – Van der Spoel, 1970: 120 (partim, non fig. 19 = *C. pacifica*, includes *C. pacifica* and *C. urceolaris*).

Cuvierina spoeli n. sp., Rampal, 2002: 214, fig. 1Cs (partim, includes *C. atlantica*, *C. columnella* and *C. cancapae*).

Neotype. – Of the original sample studied by Rang just the label survives (Van der Spoel, 1976: 191). Considering the confusion in the interpretation of this species, as indicated above, and as is also clear from Rampal's (2002) paper, I designate a specimen from the Indian Ocean as neotype. For this purpose I select a specimen (fig. 10) from the MNHN collections, where the Rang material used to be housed. This specimen is also a paratype of *Cuvierina spoeli* Rampal, 2002.

Type locality. – Indian Ocean ('la mer des Indes', Rang, 1827: 323).

Neotype locality. – Marion Dufresne Expedition, SW Indian Ocean, coordinates 21°08'7''S 55°11'8''E, sample MD32 (from sediment sample).

Diagnosis. – Indian Ocean and Pacific large *Cuvierina* (*Cuvierina*)-species, with a barely accentuated inflation at a relatively high position (see Measurements) and clear micro-ornament, differing from *Cuvierina* (*Urceolaria*) by its triangular aperture and a relatively more elongate shell.

Material examined (fr. = fragment[s]). – Indian Ocean: 15°30'S 111°40'E, (A = leg. Andrea) O, 1870 (ZMUC/1 measured specimen); 15°35'S 109°20'E / 16°00'S 110°20'E, A, 1870 (ZMUC/2 measured specimens); 21°S 57°E, A (ZMUC/2 measured specimens); 22°S 58°E, A O, 1864 (ZMUC/9, 8 of which measured; 2 specimens transferred to RGM collection); 22°30'S 87°E, A, 1869 (ZMUC/3 measured specimens); 22°40'S 81°50'E/23°30'S 81°0' E, A, 1870 (ZMUC/3 measured specimens); 24°50'S - 103°0'E/25°50'S - 102°50'E, A, 1870 (ZMUC/4 measured specimens); 26°30'S 58°E, A L, 1864 (ZMUC/1 measured specimen); 28°10'S 97°30'E, A, 1870 (ZMUC/6 + fr. of 2, measured specimens; 2 transferred to RGM collection); 29°40'S 96°20'E, A, 1870 (ZMUC/8, 7 of which measured; 1 transferred to RGM collection); 24°30'S 70°50'E, A, 1870 (ZMUC/2); 32°40'S 55°22'E, A 84, 1861 (ZMUC/2 measured specimens).

DANA EXPEDITION, St. 3929(viii), 12°11'S 50°18'E (ZMUC/28); St. 3930, 11°55'S 49°55'E (ZMUC/1 specimen); St. 3934(iv, ix, xiv, xix), 11°24'S 50°05'E (ZMUC/2); St. 3962(v), 24°03'S 38°26'E (ZMUC/9, 6 of which measured, 1 specimen illustrated, fig. 13); St. 3965(ii), 28°18'S 33°49'E (ZMUC/1 measured specimen).

Ind. Ocean, leg. Hansen & Thalbitzer, 18.xi.1863 (ZMUC/1 measured specimen); Oc. Ind. (ZMUC/2 measured specimens); Oc. Ind., leg. Salmin, 1863 (ZMUC/3 measured specimens); Oc. Indic. (ZMUC/3, 2 of which measured); Oc. Indic. (ZMUC/3 and 3, measured specimens, one specimen illustrated, fig. 11).

Pacific Ocean: COQUILLE, Mission Nodula, 16°26'5''N 146°33'W, 01.i.1971 (MNHN/2, paratypes of *Cuvierina spoeli* Rampal, 2002).

DANA EXPEDITION, St. 3576(viii), 17°36.5'S 149°43.6'W (ZMUC/1 measured specimen); St. 3602(v), 20°00'S 174°29'E (ZMUC/29 measured specimens, one of which illustrated, fig. 12); St. 3602(v), 20°40'S 174°29'E (ZMUC/9 measured specimens); St. 3603(iv), 22°00'S 170°26'E (ZMUC/3); St. 3604(iv), 23°32'S 167°36'E (ZMUC/3 measured specimens); St. 3604(v), 23°32'S 167°36'E (ZMUC/2 + 1 fr.).

MANIHIKI PLATEAU EXPEDITION, St. U351a, 18°39.1'S 172°12.2'W, crest of Capricorn Seamount, 976-996 m, don. Dr J. Fenner, 1989 (RGM 458.692/1).

MARQUESAS, leg. Patze (ZMUC/5, 3 of which measured).

MISSION BIOGEOCAL, Nouvelle-Calédonie, CP 232, 760-790 m, 21°34'S 166°27'E (MNHN/ 2 paratypes of *Cuvierina spoeli* Rampal, 2002).

Locality unknown: (ZMUC/1 and 1).

Remarks – Specimens from the Indian Ocean reach larger dimensions than those from the S Pacific, and the diameter of the septum related to shell height is larger. The species is absent from the N Pacific.

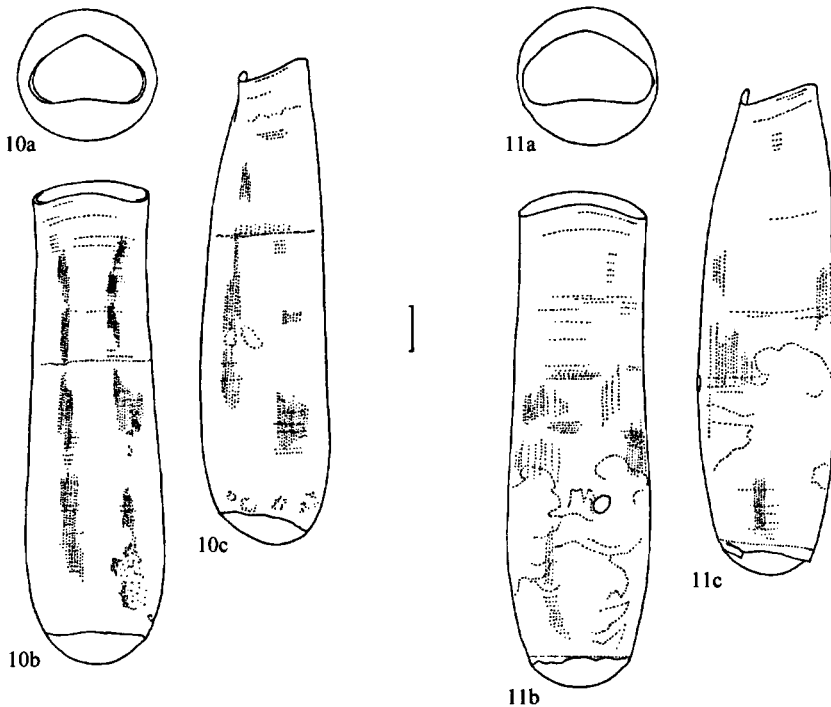
Cuvierina (*Cuvierina*) *pacifica* spec. nov. (figs 14-20)

Cuvierina columnella (Rg.); Boas, 1886: 132 (partim), pl. 6 figs 95g, h, i (non Rang).

Cuvierina columnella (Rang, 1827) forma *columnella* (Rang, 1827); Van der Spoel, 1970: 120, fig. 19 (partim, includes *C. columnella* and *C. urceolaris*) (non Rang).

Cuvierina columnella (Rang, 1827); Rampal, 2002: 214, fig. 1Cc (partim, non Rang, includes *C. atlantica*).

Holotype. – RGM 458.690, fig. 15.



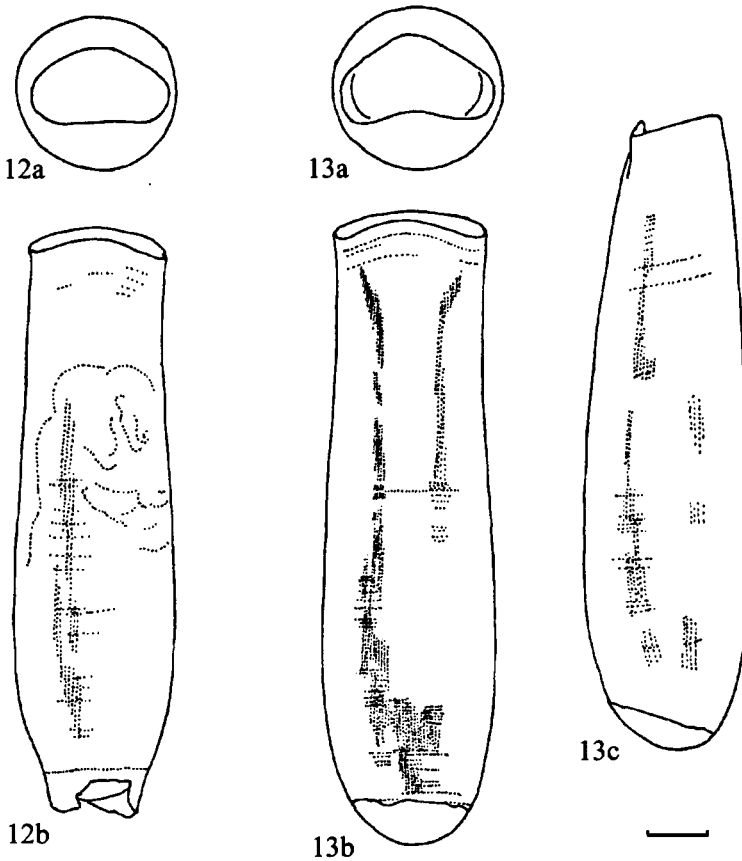
Figs 10-11. *Cuvierina (Cuvierina) columnella* (Rang, 1827), neotype and additional specimen. 10, neotype, Marion Dufresne Expedition, SW Indian Ocean, coordinates 21°08.7'S 55°11.8'E, sample MD32 (from sediment sample) (MNHN, not registered, this specimens also is a paratype of *Cuvierina spoeli* Rampal, 2002); 11, Oc. Indic., leg. & date unknown (ZMUC, not registered). a: apertural, b: ventral, c: left lateral views. Scale bar is 1 mm.

Locus typicus. – Manihiki Plateau Expedition St. U351a, 18°39.1'S 172°12.2'W, crest of Capricorn Seamount, sea depth 976-996 m, bottom sample, date unknown, don. Dr J. Fenner, 1989 (RGM 458.692, 1).

Stratum typicum. – Ocean bottom sediment (Holocene-Recent).

Diagnosis. – Exclusively Pacific *Cuvierina (Cuvierina)*-species with smaller dimensions than the type species and with a weak inflation at a distinctly higher position (see Measurements), differing from *Cuvierina (Urceolaria)* by the absence of distinct micro-ornament and a triangular aperture.

Description. – Shell moderately small, fully grown specimens between 6.6 and 8.8 mm (mean 7.56 mm, n = 154) high, height/width-ratio 2.77-3.96 (mean 3.37), N. Pacific form 2.77-3.46 (mean 3.14), S. Pacific form 3.25-3.96 (mean 3.50). Transverse section circular, dorso-ventral diameter equal to or only very slightly less than shell width. Shell dorso-ventrally slightly flattened towards the proximal aperture, especially on the ventral side. Base of shell somewhat conical with slightly convex side-lines. Position of strongest inflation of the shell at 33-45% (mean 38.9%), N. Pacific form 33-42% (mean 37%), S. Pacific form 34-45% (mean 40%) of shell height. Larval shell shed and opening closed by an



Figs 12-13. *Cuvierina (Cuvierina) columnella* (Rang, 1827), additional specimens. 12, Dana Expedition, St. 3602(v), 20°00'S 174°29'E, 22-xi-1928 (ZMUC, not registered); 13, Dana Expedition, St. 3962(v), 24°03'S 38°26'E, 14-i-1930 (ZMUC, not registered).

oblique and convex septum. Diameter of septum occupying 49-58% (mean 54.2%) of maximum shell diameter. Longitudinal micro-ornament absent. Apertural margin internally somewhat reinforced, aperture triangular in adapical view, with ventral side usually slightly concave. In ventral view the dorsal apertural margin is higher than the ventral one, both slightly produced abapically in the centre.

A sample exclusively containing *C. pacifica* [DANA 3622(i)] yielded quite a number of juvenile specimens retaining their protoconch. One of these is illustrated here in fig. 14. The specimen is regularly conical with straight sidelines. The tip is rounded and has a near-apical swelling.

Paratypes [fr. = fragment(s)]. – South Pacific Ocean: DANA Expedition St. 3576(ii), 17°36.5'S 149°43.6'W (ZMUC/1 damaged specimen); St. 3576(viii), 17°36.5'S 149°43.6'W (ZMUC/2 measured specimens); St. 3577(iii), 18°49'S 153°10'W (ZMUC/2 measured specimens); St. 3580(iii), 18°53'S 163°02.5'E

(ZMUC/1 fr.); St. 3580(iv), 18°53'S 163°2.5'E (ZMUC/1 measured specimen, fr. of one more); St. 3581(v), 17°02.5'S 166°18'W (ZMUC/24, 21 of which measured + fr. of 7 more); St. 3602(v), 20°00'S 174°29'E (ZMUC/31 measured specimens, one of which illustrated, fig. 16); St. 3603(iv), 22°00'S 170°26'E (ZMUC/2 measured specimens); St. 3604(iv), 25°32'S 167°36'E (ZMUC/1 measured specimen); St. 3604(v), 25°32'S 167°36'E (ZMUC/9 specimens, 8 of which measured + 1 fr.); St. 3611, 20°52.2'S 164°03.3'E (ZMUC/3); St. 3611(v), 20°53.2'S 164°03.3'E (ZMUC/2 measured specimens); St. 3620(ii), 24°46.5'S 170°18.5'E (ZMUC/7 measured specimens); St. 3622(i), 25°54'S 172°39.6'E (ZMUC/16, 14 of which measured + fr. of 17, c. 35 protoconchs, one of which illustrated, fig. 14, 3 protoconchs transferred to RGM 458.693; St. 3623, 27°21'S 175°11'E (ZMUC/3 measured specimens, 1 of which illustrated, fig. 17); St. 3623(iii), 27°21'S 175°11'E (ZMUC/1 measured specimen); St. 3623(vii), 27°21'S 175°11'E (ZMUC/1).

MANIHIKI PLATEAU EXPEDITION, St. U351a, 18°39.1'S 172°12.2'W, crest of Capricorn Seamount, 976-996 m, don. Dr J. Fenner, 1989 (RGM 458.691/4).

North Pacific Ocean: COQUILLE, Mission Nodula, 16°26'5"N 146°33'W (MNHN/2).

DANA EXPEDITION, St. 3718(v), 20°04'N 125°59'E (ZMUC/20 measured specimens, one of which illustrated, fig. 20, fr. of 4 or 5 more); St. 3723(v), 25°30.5'N 125°08'E (ZMUC/1 measured); St. 3729 (iii), 20°03'N 120°50'E (ZMUC/1); St. 3730(v), 16°55'N 120°02.5'E (ZMUC/1); St. 4761, 25°10'N 127°45'E (ZMUC/5 measured specimens + fr. of 7 more); St. 4773, 32°37'N 126°48'W (ZMUC/6); St. 4777, 35°59'N 129°25'W (ZMUC/13, 11 of which measured, + fr. of 5 or 6 more); St. 4778, 32°13'N 167°25'W (ZMUC/5 measured specimens); St. 4788, 32°50'N 173°10'W (ZMUC/10 measured specimens); St. 4794, 33°45'N 137°30'W (ZMUC/3, 2 of which measured, 1 specimen illustrated, fig. 18); St. 4807, 32°56'N 131°50'W (ZMUC/3, one of which illustrated, fig. 19).

FALSTRIA EXPEDITION, St. 4811, 31°50'N 130°10'W (ZMUC/1 measured specimen).

North of Philippines, 1929 (RGM 458.702/3).

Locality unknown: leg. Wessel 45 (ZMUC/4).

Remarks – The population from the North Pacific has a somewhat stronger inflation and therefore is relatively wider, with also a wider aperture and a larger diameter of the septum. In this form, that might eventually be separated taxonomically, also the maximum diameter is at a lower position (see figs 33-34).

Subgenus *Urceolaria* subgen. nov.

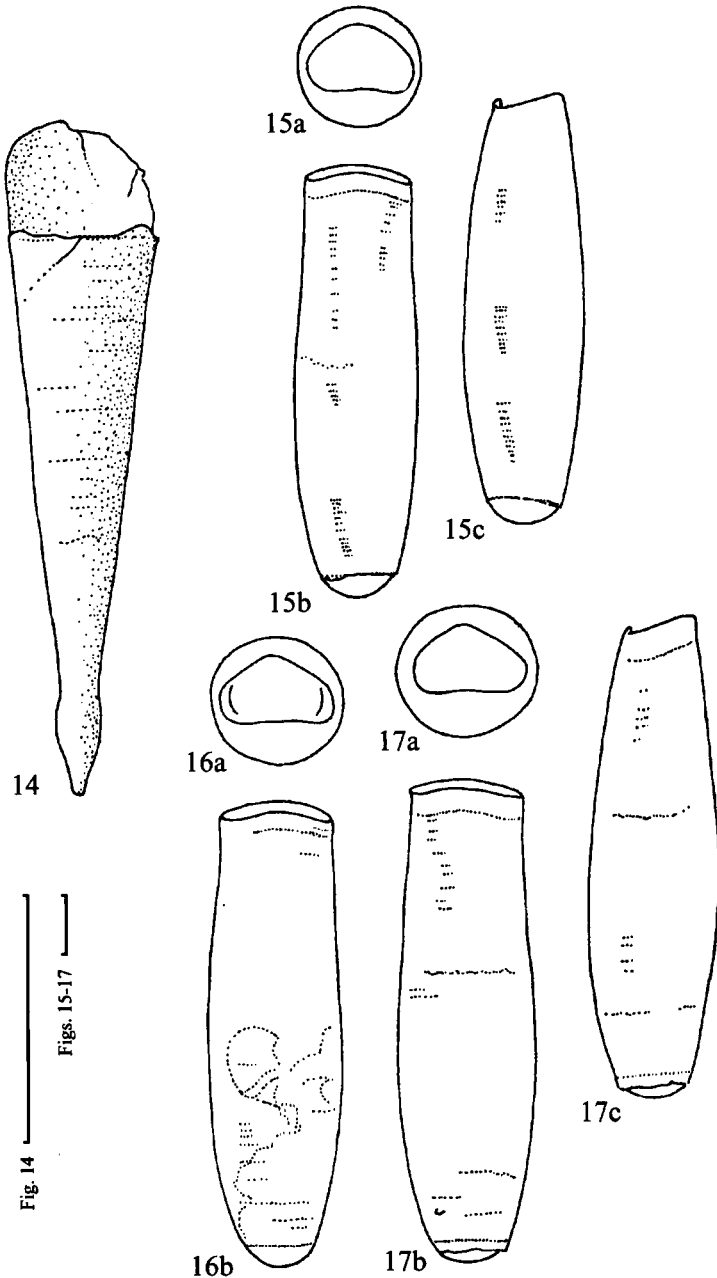
Type species. – *Cuvieria urceolaris* Mörch, 1850.

Derivatio nominis. – Subgenus name formed after the epitheton specificum of the type species.

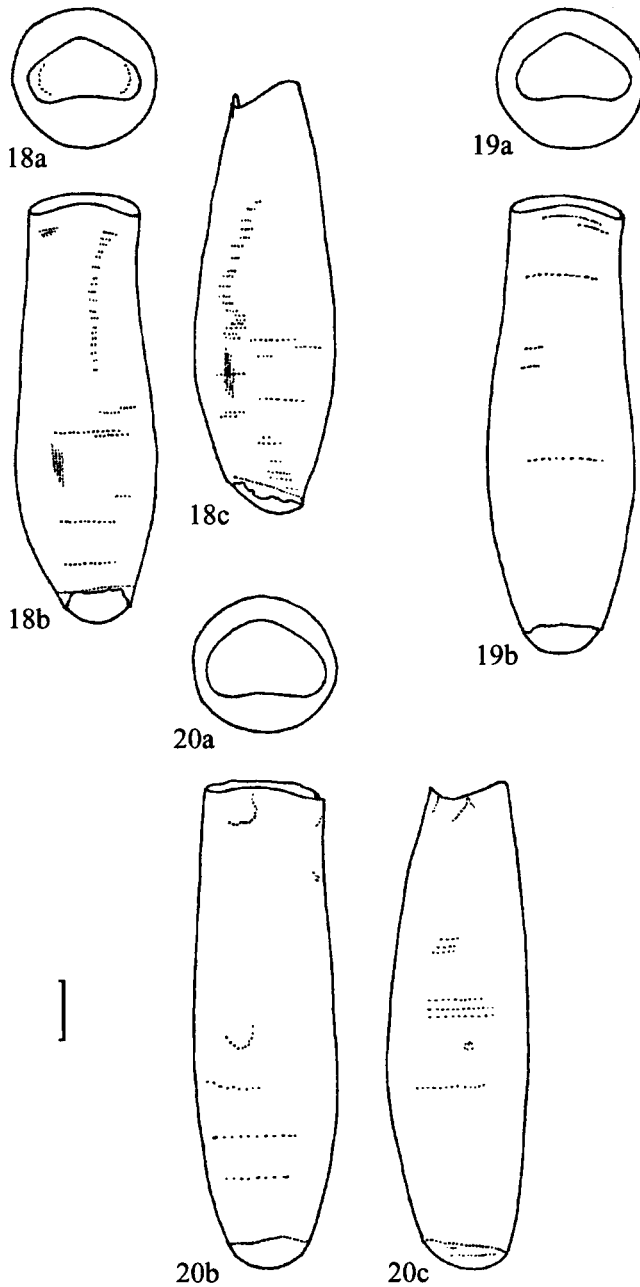
Diagnosis. – *Cuvierina* with an inflated shell form, shell surface demonstrating distinct longitudinal micro-ornament, aperture reniform rather than triangular.

Distribution. – The typical form of the type species occurs in the Recent fauna of the Indo-Pacific. A new species, *C. cancapae*, is present in the Atlantic. Fossil species included in *Urceolaria* are *C. (U.) intermedia* (Serravallian-Piacenzian: Central Mediterranean, Portugal, Japan, Fiji), *C. (U.) curryi* spec. nov. (Serravallian: Central Mediterranean) and *C. (U.) inflata* (Tortonian-Piacenzian: West and Central Mediterranean, Syria, Japan, Mexico).

Discussion. – As discussed above the inflated Recent species usually indicated as *Cuvierina columnella urceolaris* is the last stage in a lineage starting with *C. intermedia*, and continuing with the species *C. curryi* and *C. inflata* (see fig. 36).



Figs 14-17. *Cuvierina (Cuvierina) pacifica* spec. nov., holo- and paratypes, South Pacific form. 14, Dana Expedition, St. 3622(i), 25°54'S 172°39.6'E 300 mw EFD S200, 8-xii-1928 (ZMUC, not registered) (larval shell with protoconch); 15, holotype, Manihiki Plateau Expedition St. U351a, 18°39.1'S 172°12.2'W, crest of Capricorn Seamount, sea depth 976-996 m, bottom sample, date unknown, don. Dr J. Fenner, 1989 (RGM 458.690); 16, Dana Expedition, St. 3602(v), 20°00'S 174°29'E, 22-xi-1928 (ZMUC, not registered); 17, Dana Expedition, St. 3623, 27°21'S 175°11'E, 9-xii-1928 (ZMUC, not registered). a: apertural, b: ventral, c: left lateral views. Scale bar is 1 mm.



Figs 18-20. *Cuvierina (Cuvierina) pacifica* spec. nov., paratypes, North Pacific form. 18, Dana Expedition, St. 4794, 33°45'N 137°30'W, 220 mw 73 m EFD, S200, 21-viii-1933 (ZMUC, not registered); 19, Dana Expedition, St. 4807, 32°56'N 131°50'W, 12-ii-1934, Kl. 19:30 S200 (ZMUC, not registered); 20, Dana Expedition, St. 3718(v), 20°04'N 125°59'E, 25-v-1929 (ZMUC, not registered). a: apertural, b: ventral, c: left lateral views. Scale bar is 1 mm.

Cuvierina (Urceolaria) cancapae spec. nov. (figs 21-23)

? *Cuvierina columnella* (Rg.) – Boas, 1886: 132 (partim), pl. 6 figs 95o-p (non Rang).

Cuvierina spoeli n.sp., Rampal, 2002: 214 (partim, non fig. 1Cs = *Cuvierina columnella*, includes *C. atlantica* and *C. columnella*).

Holotype. – RMNH 78729, fig. 21.

Type locality. – Tydeman Cape Verde Islands Exp. 1981/1982; CANCAP-VI, St. 6.010: S of Sao Tiago, 14°53'N 23°30'W, depth 310 m, sandy mud and shell gravel, 5-vi-1981.

Stratum typicum. – Quaternary (Holocene), bottom sediment.

Derivatio nominis. – This new species is named after the so-called CANCAP-expeditions (1976-1986, Canary and Cap Verde islands) of the National Museum of Natural History, Leiden, The Netherlands.

Diagnosis. – Exclusively Atlantic *Cuvierina (Urceolaria)*-species with larger dimensions than the type species and a less accentuated inflation at a lower position (see Measurements), differing from *Cuvierina* s. str. by the presence of distinct micro-ornament, a reniform aperture and a relatively wider shell.

Description. – Shell moderately large, fully grown specimens between 7.5 and 9.3 mm (mean 8.44 mm, n = 118) high, height/width-ratio 2.77-3.58 (mean 3.07). Transverse section circular, dorso-ventral diameter equal to or only very slightly less than shell width. Shell dorso-ventrally slightly flattened towards the proximal aperture, especially on ventral side. Base of shell somewhat conical with slightly convex to slightly concave side-lines. Position of strongest inflation of shell at 21.2-35.3% (mean 30.0%) of shell height. Larval shell shed and opening closed by an oblique and convex septum, the most convex part lying near the dorsal side. Diameter of septum occupying 46-83% (mean 62%) of maximum shell diameter. Lower two thirds of shell surface covered with clear longitudinal micro-ornament. Apertural margin internally somewhat reinforced, aperture reniform in adapical view, with dorsal side rounded and ventral side flattened or even somewhat concave. In ventral view the dorsal apertural margin is higher than the ventral one, both slightly produced abapically in the centre.

Paratypes [fr. = fragment(s)]. – Atlantic Ocean: 15°19'N 24°54'W, leg. Rhrdt (ZMUC/1); 13°40'N 31°00'W, leg. Andrea (ZMUC/1); 06°N 34°(W ?), leg. Friis (ZMUC/2); 03°10'N 27°50'W, leg. Warming (ZMUC/1); 00°40'S 30°00'W, leg. Andrea (ZMUC/4, one of these transferred to RGM 459.701); 07°17'S 32°52'W, leg. E. van Benzon (ZMUC/5); 09°19'S 32°34'W, leg. Warming (ZMUC/3); 10°52'S 33°25'W (ZMUC/2); 11°44'S 35°10'W (ZMUC/1); 12°57'S 33°41'W (ZMUC/1); 17°S 22°W (ZMUC/1); 21°28'S 38°50'W (ZMUC/2); 22°44'S 36°E (should be W, presumably), leg. Andrea (ZMUC/1).

DANA EXPEDITION, St. 1161(v), 14°52'N 28°04'W (ZMUC/22, one of which illustrated, fig. 23); St. 1162, 13°35'N 30°11'W (ZMUC/5 + fr. of 2); St. 1162(iv), 13°35'N 30°11'W (ZMUC/106, 23 and 14 specimens); St. 1166(v), 10°16'N 40°41'W (ZMUC/1); St. 1168(v), 09°30'N 42°41'W (ZMUC/1); St. 1178(iii), 10°24'N 54°38'W (ZMUC/c. 185, one of which illustrated, fig. 22); St. 1178(iv), 10°24'N 54°38'W (ZMUC/26 + fr.); St. 1178(v), 10°24'N 54°38'W (ZMUC/6 and 76); St. 3997(iv), 11°00'S 07°36'W (ZMUC/3); St. 3979(v), 27°13'S, 9°10'E (ZMUC/2 ? poorly preserved); St. 4006(v), 15°31'N 18°05'W (ZMUC/1).

GALATHEA EXPEDITION, St. XI, 08°44'N c. 21°W, leg. RhdT (ZMUC/1).

INGOLF EXPEDITION, 3.5 km W of Frederiksted, 500 Fv, leg. Th. Mortensen (ZMUC/1).

LUYMES GUYANA SHELF EXPEDITION 1970, St. LUY.15052, Caribbean, off Guyana, 7°41'N 56°59'W, 96 m (RMNH 78749/2 + 8 damaged).

LUYMES SABA BANK EXPEDITION 1972, St. LUY.34076, Caribbean, SW-slope Saba Bank, 17°14'N 63°44'W, 500 m (RMNH 78750/1).

METEOR EXPEDITION 51, St. unknown, tropical Central Atlantic, leg. G. Richter, 1979 (SMF

323186/1); St. 94, tropical Central Atlantic, 0-30 m, 01°19.8'S 22°02.1'W, G. Richter leg. (SMF 323188/3 + 1 fr.); St. 94/42, tropical Central Atlantic, 30-50 m, 01°19.8'S 22°02.1'W, leg. G. Richter (SMF 323182/2 specimens, one of which with aberrant septum); St. 153, RMT 8, Hol 11, tropical Central Atlantic, 0-200 m, 02°0.0'N 22°0.0'W, leg. G. Richter (SMF 323184/1); St. 197, tropical Central Atlantic, 0-200 m, 00°0.1'N 22°0.3'W, leg. G. Richter (SMF 323185/1); St. 197, RMT 8, Hol 29, Central Atlantic, 0-1030 m, 00°0.1'N 22°0.3'W, leg. G. Richter (SMF 323179/1); St. 246 MOCNESS, tropical Central Atlantic, 30-50 m, 00°00'N 22°00'W, leg. G. Richter (SMF 323181/1); St. 246, Prof. VII, Hol 149, MC, tropical Central Atlantic, 0-250 m, 00°0.0'N 22°0.0'W, leg. G. Richter (SMF 323183/1 broken); St. 281, tropical Central Atlantic, 01°00.1'N 21°59.8'W, leg. G. Richter (SMF 323187/1 damaged); St. 281, Prof. VIII, Hol 165, MC, tropical Central Atlantic, 100-200 m, Vol. 825, 01°0.1'N 21°59.8'W, leg. G. Richter (SMF 323192/1).

SNELLIUS OCPS EXPEDITION 1966, St. F37, off Suriname, 07°24.6'N 56°22.4'W, 121 m (RMNH 78745/1 + 1 damaged).

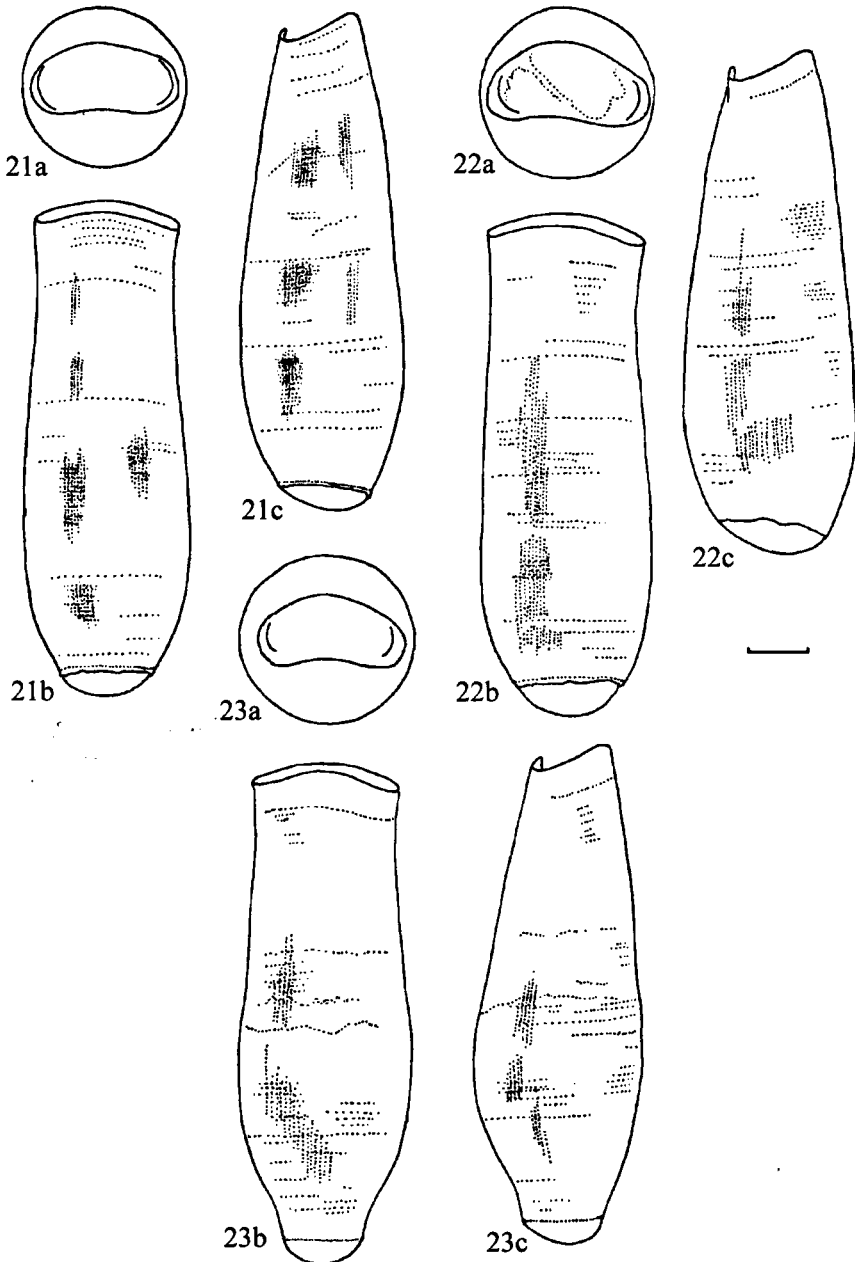
TYDEMAN CAPE VERDE ISLANDS EXPEDITION 1981/1982, CANCAP-VI, St. 6.008, Cape Verde Islands, S of Sao Tiago, 14°54'N 23°30'W, 120 m (RMNH 78739/1); St. 6.011, Cape Verde Islands, S of Sao Tiago, 14°53'N 23°30'W, 328 m (RMNH 78730/3); St. 6.012, Cape Verde Islands, S of Sao Tiago, 14°53'N 23°30'W, about 500 m (RMNH 78731/1); St. 6.013, Cape Verde Islands, S of Sao Tiago, 14°52'N 23°31'W, 710 m (RMNH 78732/3 damaged); St. 6.017, Cape Verde Islands, S of Sao Tiago, 14°53'N 23°30'W, 380 m (RMNH 78733/2); St. 6.019, Cape Verde Islands, W of Sao Tiago, 15°01'N 23°44'W, 466 m (RMNH 78734/1); St. 6.020, Cape Verde Islands, W of Sao Tiago, 15°01'N 23°44'W, 470 m (RMNH 78735/1); St. 6.025, Cape Verde Islands, bay on W coast of Sao Tiago, 15°00'N 23°44'W, 728 m (RMNH 78736/4 damaged); St. 6.040, Cape Verde Islands, W of Fogo, 14°55'N 24°31'W, 55 and 38 m (RMNH 78737/1); St. 6.044, Cape Verde Islands, W of Fogo, 14°55'N 24°32'W, 450 m (RMNH 78738/11); St. 6.052, Cape Verde Islands, W of Fogo, 14°53'N 24°31'W, 85 m (RMNH 78753/1); St. 6.062, Cape Verde Islands, SE of Boa Vista, 15°55'N 22°46'W, 82-98 m (RMNH 78740/1); St. 6.132, Cape Verde Islands, S of São Vicente, 16°46'N 25°02'W, 78-80 m (RMNH 78443/1).

TYDEMAN CAPE VERDE ISLANDS EXPEDITION 1986, CANCAP-VII, St. 7.004, Cape Verde Islands, SE of Sao Tiago, 14°54'N 23°38'W, 320 m (RMNH 78742/1 + 1 damaged); St. 7.007, Cape Verde Islands, SW of Sao Tiago, 14°54'N 23°38'W, 420 m (RMNH 78743/1 illustrated); St. 7.014, Cape Verde Islands, S of Sao Tiago, Ponta Grande da Cidade, 14°54'N 23°38'W, 450-600 m (RMNH 78744/1 + 1 fr.); St. 7.028, Cape Verde Islands, SE of Cima, 14°57'N 24°39'W, 225 m (RMNH 78746/2); St. 7.030, Cape Verde Islands, SE of Cima, 14°57'N 24°39'W, 165 m (RMNH 78747/1 damaged); St. 7.032, Cape Verde Islands, SE of Cima, 14°57'N 24°38'W, 65 m (RMNH 78748/3 damaged); St. 7.038, Cape Verde Islands, SE of Cima, 14°57'N 24°38'W, 410-460 m (RMNH 78752/1); St. 7.039, Cape Verde Islands, SE of Cima, 14°56'N 24°38'W, 590-610 m (RMNH 78741/1 + 2 damaged); St. 7.061, Cape Verde Islands, SW of Maio, Ponta Inglez/Ponta Preta, 15°07'N 23°15'W, 605 m (RMNH 78751/1 + 1 damaged).

Locality unknown: (ZMUC/1, 1, 2, 3, 3 and 4 specimens); leg. Bruun (ZMUC/1).

Discussion – The many *Cuvierina*-samples collected during the various Atlantic CANCAP expeditions could easily be split up into two species, one of which is *C. atlantica*. It is (predominantly bottom samples) found from the northern Caribbean, the Azores, Madeira and the Canary Islands, and is also present more to the North in the Atlantic.

The second type, described here as *C. cancapae*, characterised by the presence of distinct longitudinal micro-ornament, a relatively wider shell with a weak and low-situated inflation and reniform aperture, occurs predominantly near the Cap Verde Islands, but some specimens are present from the Guyana coast and from the Caribbean. The ZMUC material demonstrated its presence also more to the South Atlantic (fig. 35).



Figs 21-23. *Cuvierina (Urceolaria) cancapae* spec. nov., holo- and paratypes. 21, holotype, Tydeman Cape Verde Islands Exp. 1981/1982; CANCAP-VI, St. 6.010: S of Sao Tiago, 14°53'N 23°30'W, depth 310 m, sandy mud and shell gravel, 5-vi-1981 (RMNH 78729); 22, paratype, Dana Expedition, St. 1178(iii), 10°24'N 54°38'W, 19-xi-1921, 300 mw, S200 (ZMUC, not registered); 23, paratype, Dana Expedition, St. 1161(v), 14°52'N 28°04'W, 5-xi-1921 (ZMUC, not registered). a: apertural, b: ventral, c: left lateral views. Scale bar is 1 mm.

Cuvierina (Urceolaria) urceolaris (Mörch, 1850) (figs 24-27)

**Cuvieria urceolaris* n.; Mörch, 1850: 32, pl. 1 fig. 8.

Cuvierina columnella (Rg.); Boas, 1886: 132 (partim), pl. 6 figs 95a-f.

Cuvierina columnella (Rang, 1827) forma *columnella* (Rang, 1827); Van der Spoel, 1970: 120 (partim, non Rang).

Cuvierina columnella (Rang, 1827) forma *urceolaris* (Mörch, 1850); Van der Spoel, 1970: 120, fig. 21.

Cuvierina urceolaris (Mörch, 1850) – Rampal, 2002: 212, fig. 1Cu.

Type material. – Lectotype (Van der Spoel, 1976) and paralectotype are in the ZMUC dry collection (not studied, but see analysis of types in Van der Spoel, 1976: 191).

Type locality. – Philippine Islands.

Stratum typicum. – Recent, plankton catch.

Diagnosis. – W and N Indian Ocean and Central Pacific *Cuvierina (Urceolaria)* species of small dimensions and a distinctly accentuated inflation at a relatively high position (see Measurements), differing from *Cuvierina* s. str. by the presence of distinct micro-ornament, a reniform aperture and a relatively wider shell.

Material examined (fr. = fragment[s]). – Atlantic Ocean: METEOR EXPEDITION 19, St. unknown, Meteorbank, leg. G. Richter, 1970 (SMF 323175/2).

Indian Ocean: 06°N 74°E, leg. Hygom (ZMUC/1); 13°S 103°20'E, leg. Andrea, 1869 (ZMUC/2); 35°30'S 29°30'E, leg. Andrea 103, 1862 (ZMUC/1); central Indian Ocean (RGM 458.703/3).

DANA EXPEDITION, St. 3805, 00°31.5'S 109°37'E (ZMUC/39, 37 of which measured); St. 3814(iv), 04°38'S 99°24'E, 4960 m (ZMUC/49); St. 3824(vi), 00°08'S 97°15'E (ZMUC/2); St. 3824(vii), 00°08'S 97°15'E (ZMUC/24); St. 3824(viii), 00°08'S 97°15'E (ZMUC/12 + fr. of 3 more, 4 protoconchs); St. 3827(iv), 01°45'S 96°20'E (ZMUC/9); St. 3844(iv), 12°05'S 96°45'E (ZMUC/5 and 1); St. 3844(vii), 12°05'S 96°45'E (ZMUC/5); St. 3847(iv), 12°02'S 96°43'E (ZMUC/1); St. 3850(iii), 06°01'S 93°12'E (ZMUC/19); St. 3851(ii), 5°29'S, 93°47'E (ZMUC/24 + fr. of 4); St. 3860(vi), 02°57'S 99°36'E (ZMUC/5 and 1); St. 3860(vii), 02°57'S 99°36'E (ZMUC/3 and 1); St. 3860(xi-xv), 02°57'S 99°36'E (ZMUC/6 measured specimens); St. 3860(xxi), 02°57'S 99°36'E (ZMUC/3 + fr. of 1, and 1); St. 3860(xxii), 02°57'S 99°36'E (ZMUC/6); St. 3860(xxiii), 02°57'S 99°36'E (ZMUC/196); St. 3888(iv), 01°04'N 96°27'E (ZMUC/9); St. 3915(iv), 03°14'N 75°21'E (ZMUC/1); St. 3918(iii), 00°35'N 66°09'E (ZMUC/3); St. 3918(v), 00°35'N 66°09'E (ZMUC/39 measured specimens); St. 3919(iv), 00°07'S 63°56'E (ZMUC/20); St. 3920(v), 01°12'S 62°19'E (ZMUC/21); St. 3924(v), 05°01'S 54°46'E (ZMUC/9); St. 3925(iv), 07°13'S 52°22'E (ZMUC/25); St. 3925(v), 07°13'S 52°22'E (ZMUC/13 + fr. of 2 more); St. 3926(iii), 08°27'S 50°54'E (ZMUC/97); St. 3926(iv), 08°27'S 50°54'E (ZMUC/11); St. 3929(ii), 12°11'S 50°18'E (ZMUC/4); St. 3930, 11°55'S 49°55'E (ZMUC/10); St. 3932(ix), 11°35'S 49°45'E (ZMUC/11 + fr. of 2 or 3 more); St. 3934(iv, ix, xiv, xix), 11°24'S 50°05'E (ZMUC/50, 1 of which illustrated, fig. 26, 10 measured specimens); St. 3938(i), 09°10'S 45°17'E (ZMUC/27 + many fr.); St. 3939(iii), 08°44'S 43°54'E (ZMUC/3); St. 3948(i), 10°11'S 41°57'E (ZMUC/10, one of which illustrated, fig. 27); St. 3949(iii), 11°33'S 41°44'E (ZMUC/13, 2 of which broken); St. 3955(ii), 18°30'S 42°18'E (ZMUC/2); St. 3956(v), 21°13'S 42°26'E (W on the label !) (ZMUC/2); St. 3962(v), 24°33'S 38°26'E (ZMUC/2); St. 5953(ii), 16°12'S 42°04'E (ZMUC/1 broken specimen).

MAGGADAN, St. 233, 250-0 m, 7°47'S 51°51'E, 1967 (MNHN/1).

SHELLEY BEACH, Natal, South Africa, beach drift, leg./don. S. Tracey (RMNH 78755/2).

TYRO INDONESIAN-DUTCH SNELLIUS-II EXPEDITION, St. 4.155, off Salayer, 6°22'S 120°26'E, 233-274 m (RGM 229.529/18); St. S4.276, N of Sumbawa, Bay of Sanggar, 8°12'S 118°12'E, 750 m (RMNH 78756/1 damaged); St. S4.173, SW Salayer, NW of Pulau Bahuluang, 6°28'S 120°24'E, 300-340 m (RMNH 78760/1); St. S4.033, Tukang Besi Islands, Banda Sea, NW of Beningko, 5°52.5'S 123°58.5'E, 250-290 m (RMNH 78757/1); St. S4.112, N of Sumbawa, Bay of Sanggar, 8°19'S 118°16'E, 365 m (RMNH 78754/1 + 3 damaged); St. S4.018, Tukang Besi Islands, Banda Sea, S of Karang Kaledupa, 5°57.5'S 123°46.5'E, 465 m

(RMNH 78758/2 + 2 damaged, RMNH 78759/1 illustrated, fig. 24).

Pacific Ocean: 09°40'N 109°20'E, leg. Andrea, 1869 (ZMUC/1).

CAMPAGNE CORINDÓN, Stn. B207, 0°15'S 117°52'E, 150 m (MNHN/3).

COQUILLE, Mission Nodula, 16°26'5"N 146°33'W (MNHN/2).

DANA EXPEDITION, St. 3563(iv), 07°45.5'S 131°22'W (ZMUC/90); St. 3584, 10°51.5'S 168°40'W (ZMUC/1); St. 3584(vi), 10°51.5'S 168°40'W (ZMUC/13); St. 3585, 07°46'S 167°10'W (ZMUC/13); St. 3585(vi), 07°46'S 167°10'E (ZMUC/8, 1 of which illustrated, fig. 25); St. 3689(vii), 07°13.5'N 111°49'E (ZMUC/7); St. 3689(ix), 07°13.5'N 111°49'E (ZMUC/6); St. 3729(iii), 20°03'N 120°50'E (ZMUC/148 measured); St. 3729(v), 20°3.5'N 120°50'E (ZMUC/6); St. 3729(v), 20°3.5'N 120°50'E (ZMUC/10 + 5 juv.); St. 3730(v), 16°55'N 120°02.5'E (ZMUC/3, 1 of which with protoconch, and 7 + fr. of 6); St. 3731(i), 14°37'N 119°52'E (ZMUC/15); St. 3751(ii), 03°40.5'N 137°53'E (ZMUC/1 and 1 broken); St. 3751(iv), 03°40.5'N 137°53'E (ZMUC/28); St. 3751(v), 03°40.5'N 137°53'E (ZMUC/21); St. 3768(vi), 01°20'S 138°42'E (ZMUC/7); St. 3768(xiv), 01°20'S 138°41'E (ZMUC/3); St. 3780(ii), 16°55'N 120°02.5'E (ZMUC/8).

FALSTRIA EXPEDITION, St. 4811, 31°50'N 130°10'W (ZMUC/1).

UNKNOWN EXPEDITION, St. 690, 13°51'N 119°12'E (ZMUC/3 + 2 without shell); St. 690, 19°14'N 116°06'E (ZMUC/2); St. 690, Chinasoen (ZMUC/1); St. 690b, 12°55'N 116°26'E, leg. Ahrdt (ZMUC/6).

Mare Sinicum, 14°N 119°E (ZMUC/10 samples of 1 specimen each).

Philippine(s), leg. Cumming nr. 559, entered museum in June 1852 (ZMUC/2); leg. Cumming, 1848, nr. 192 (ZMUC/2).

Sydlig Kina Sør, leg. H. Koch, 9.iii.1872 (ZMUC/1).

Locality unknown: auction Yoldi (ZMUC/1).

Remarks – Specimens from the Pacific differ in many respects from the Indian Ocean population, as discussed in the chapter Measurements, below. These populations might be given subspecific rank, eventually.

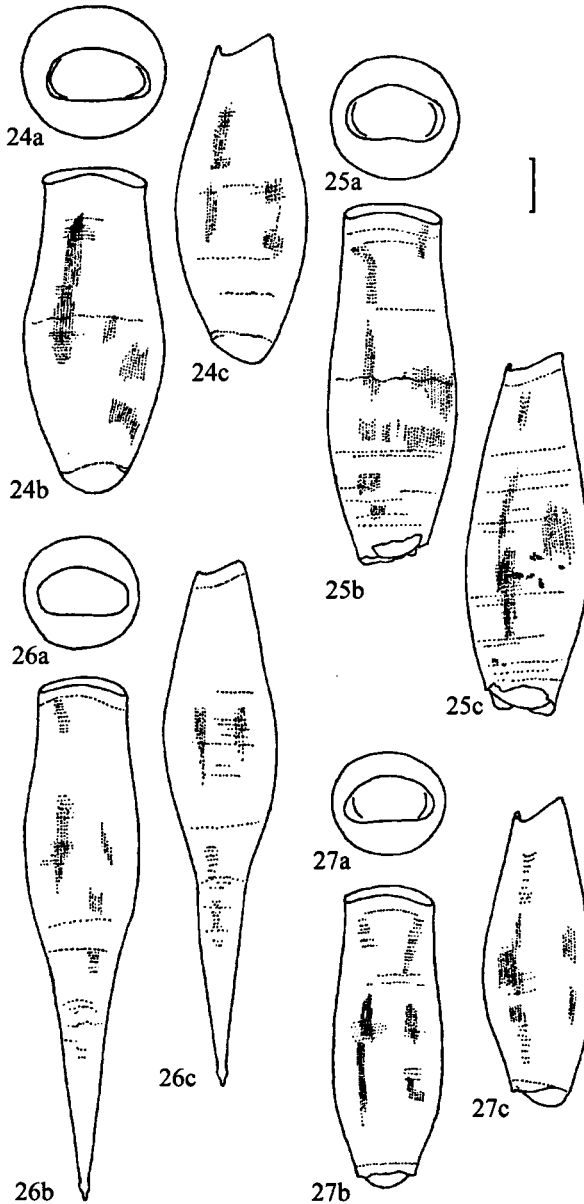
MEASUREMENTS OF RECENT TAXA

For this study 110 Recent samples totalling 735 specimens, were measured (see Table 2), the results are given in figs 29-34. Much of the Recent material studied for this paper is kept in ethanol 70%. Especially in the older samples the very fine surface ornament tends to disappear by dissolution.

In the scatter diagrams of fig. 29 and 31-33 shell width, aperture width, diameter of septum and position of strongest inflation are plotted against shell height. The height/width-ratios and the position of strongest inflation are also presented as stacked bar graphs (figs 30 and 34, respectively). In the scatter diagrams the three species of *Cuvierina* (*Cuvierina*) are given separately, the two species of *Cuvierina* (*Urceolaria*) are given in one diagram, as there is no overlap between them.

The height of the shell, and the H/W-ratio are given in fig. 29. In absolute shell height *C. columnella* is by far the largest species, and *C. urceolaris* the smallest. The three other species reach values in between. *C. atlantica* shows the widest range in height, but only little variability in H/W-ratio. In three species specimens from different geographical origin show significant differences, i.e., *C. columnella* from the Indian Ocean is larger than specimens from the Pacific, *C. pacifica* from the North Pacific is clearly wider than the population from the South Pacific (more inflated), whereas in *C. urceolaris* specimens from the Pacific are larger and wider than those from the Indian Ocean. These differences are even more clearly visible in the stacked bar graphs (fig. 30).

The width of the aperture, plotted against shell height (fig. 31) gives similar results. Again the widest range is found in *C. atlantica*. The three species showing differences according to geographical origin show this feature also for this parameter, in the case of



Figs 24-27. *Cuvierina* (*Urceolaria*) *urceolaris* (Mörch, 1850); 24-26, Pacific form; 27, Indian Ocean form. 24, 'Tyro' Indonesian-Dutch Snellius-II Expedition, St. S4.018, Indonesia, Tukang Besi Islands, Banda Sea, S of Karang Kaledupa, 05°57.5'S 123°46.5'E, fine shell gravel with forams, depth 465 m, van Veen grab, 09-ix-1984 (RMNH 78759); 25, Dana Expedition, St. 3585(vi), 07°46'S 167°10'E, 31-x-1928 (ZMUC, not registered); 26, Dana Expedition, St. 3934(iv, ix, xiv, xix), 11°24'S 50°05'E, 300 mw, 20/21-xii-1929 (ZMUC, not registered) (specimen retaining larval shell); 27, Dana Expedition, St. 3948(i), 10°11'S 41°57'E, 6-i-1930 (ZMUC, not registered). a: apertural, b: ventral, c: left lateral views. Scale bar is 1 mm.

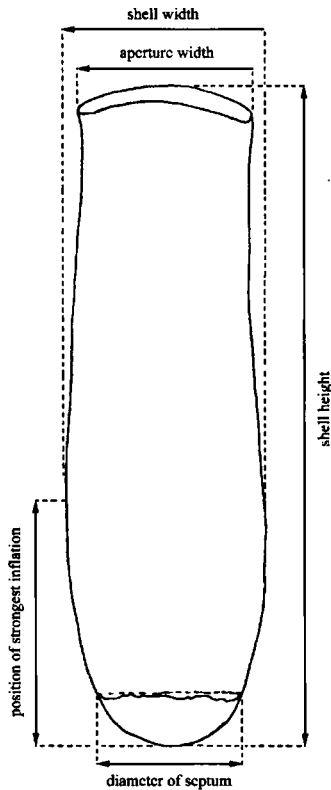


Fig. 28. Measured parameters of Recent *Cuvierina*-specimens.

C. urceolaris even without any overlap.

In fig. 32 (shell height plotted against diameter of septum) a somewhat larger variability is seen in all species, but again the species *C. columnella*, *C. pacifica* and *C. urceolaris* show differences related to geographic origin. Very striking is the width of the septum in the few available specimens of *C. atlantica* from the South Atlantic. More material from this area would be necessary to decide whether or not this is a constant feature.

Finally, shell height plotted against position of strongest inflation (fig. 33), even in spite of a relatively wide spreading because of difficult measurement, shows very similar results. The values of this parameter have been recalculated as percentages of shell height, represented as stacked bar graphs (fig. 34).

DISTRIBUTION OF RECENT *CUVIERINA* SPECIES

In fig. 35 the geographical position of *Cuvierina*-samples examined for this paper is represented. In general it can be seen that the various taxa surprisingly show well-separated distribution patterns.

Cuvierina atlantica is restricted to the Atlantic Ocean, occurring both N and S of the

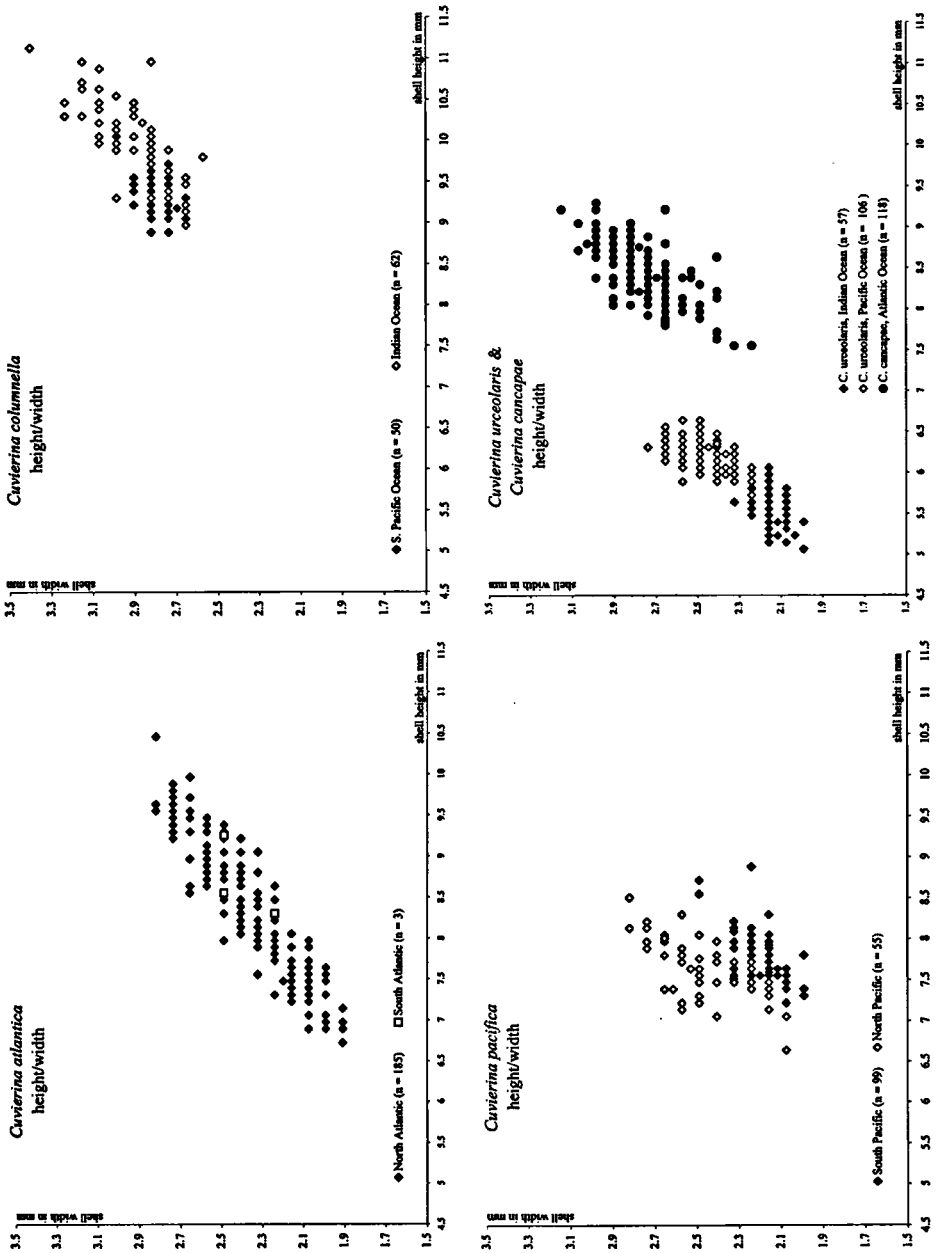
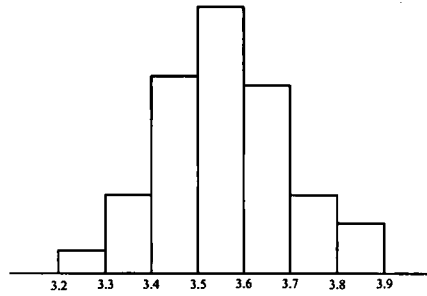


Fig. 29. Scatter diagrams of shell width plotted against shell height for the five extant *Cuvierina* species.

Height/width-ratio

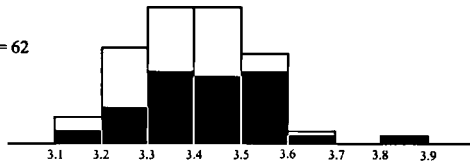
Cuvierina (Cuvierina) atlantica

□ Atlantic Ocean, n = 188
 min. 3.20
 max. 3.89
 mean 3.55
 $\sigma = 0.130$



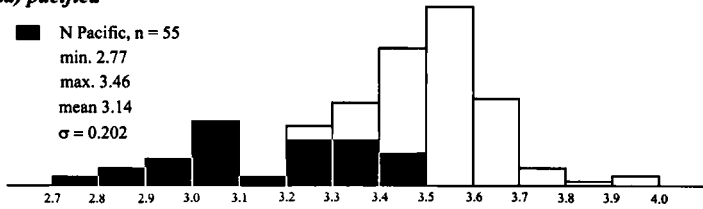
Cuvierina (Cuvierina) columnella

□ S Pacific, n = 50 ■ Indian Ocean, n = 62
 min. 3.11 min. 3.11
 max. 3.60 max. 3.88
 mean 3.35 mean 3.43
 $\sigma = 0.114$ $\sigma = 0.140$



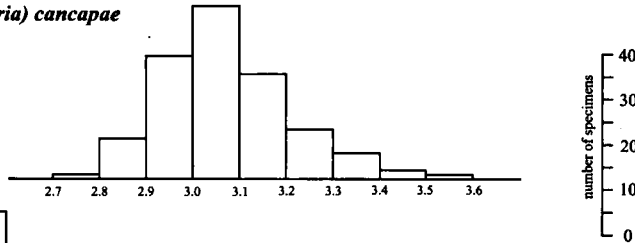
Cuvierina (Cuvierina) pacifica

□ S Pacific, n = 99 ■ N Pacific, n = 55
 min. 3.25 min. 2.77
 max. 3.96 max. 3.46
 mean 3.50 mean 3.14
 $\sigma = 0.124$ $\sigma = 0.202$



Cuvierina (Urceolaria) cancapae

□ Atlantic, n = 118
 min. 2.77
 max. 3.58
 mean 3.07
 $\sigma = 0.145$



Cuvierina (Urceolaria) urceolaris

□ Indian Ocean, n = 57 ■ Pacific Ocean, n = 106
 min. 2.38 min. 2.29
 max. 2.81 max. 2.71
 mean 2.61 mean 2.51
 $\sigma = 0.106$ $\sigma = 0.096$

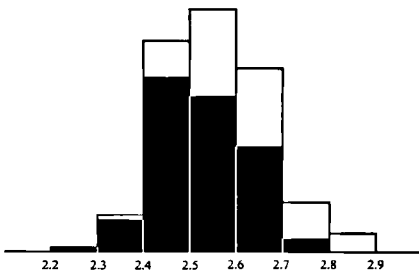


Fig. 30. Stacked bar graphs of height/width-ratio for the five extant *Cuvierina* species.

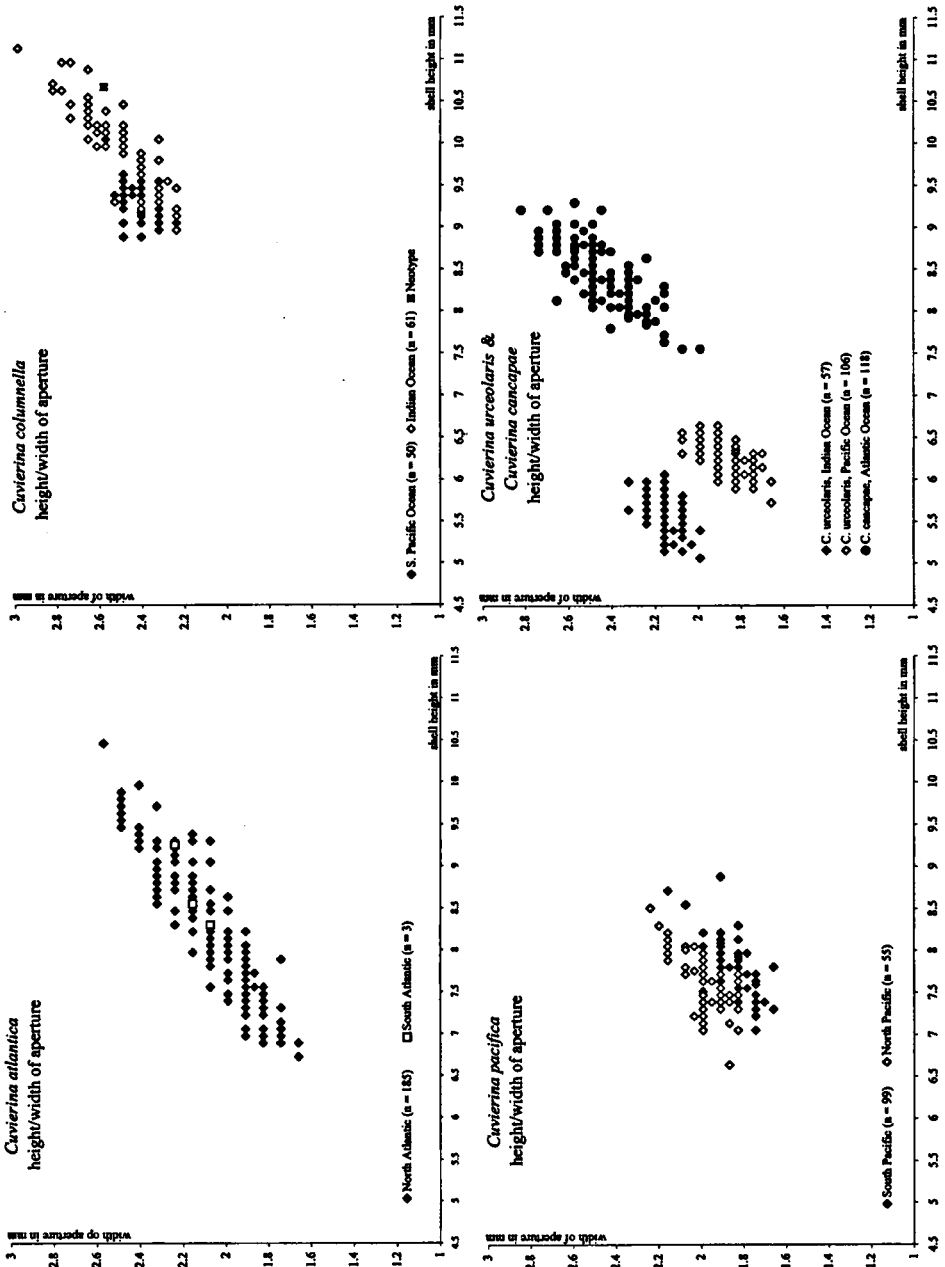


Fig. 31. Scatter diagrams of width of aperture plotted against shell height for the five extant *Cuvierina* species.

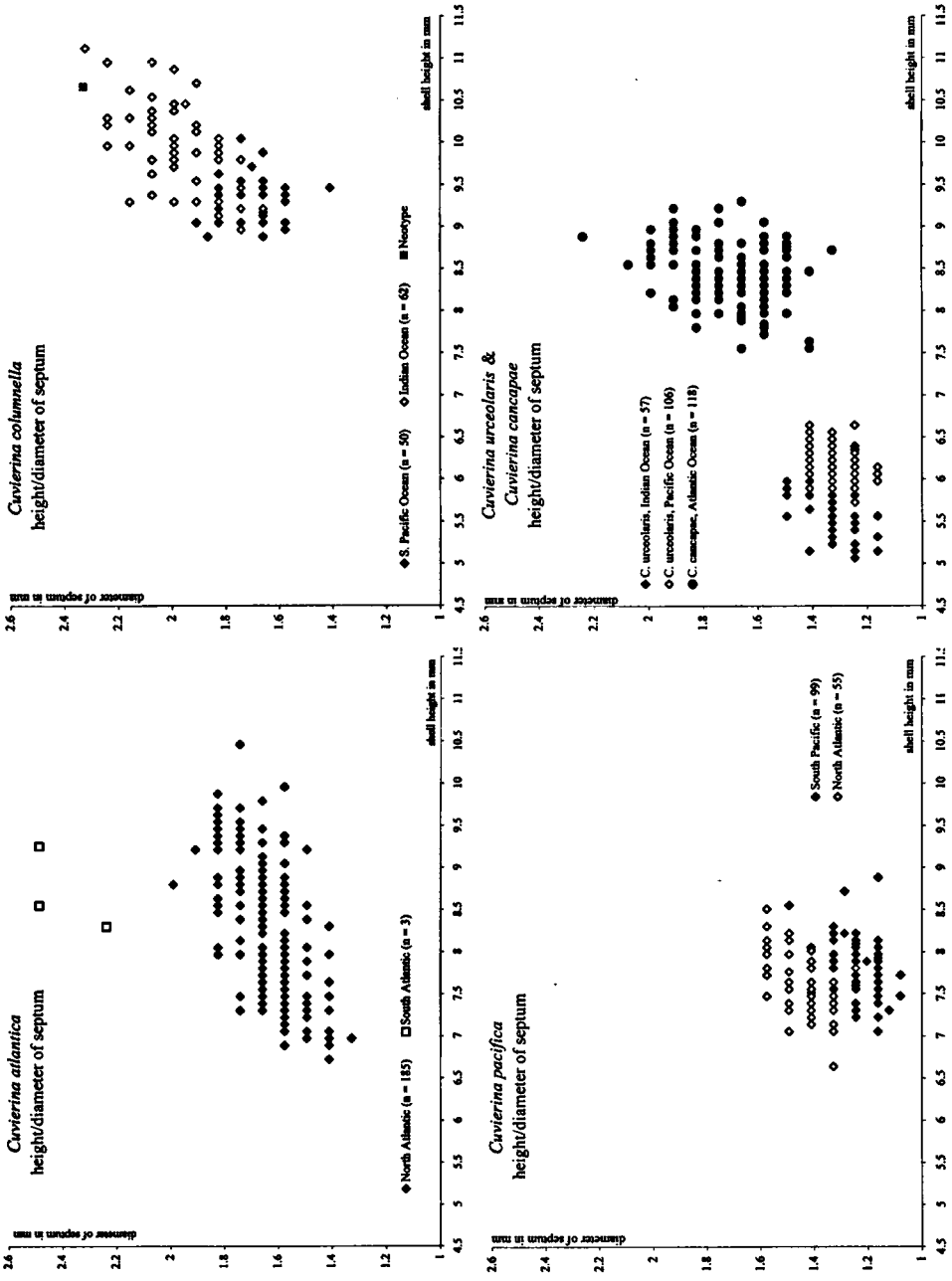


Fig. 32. Scatter diagrams of diameter of septum plotted against shell height for the five extant *Cuvierina* species.

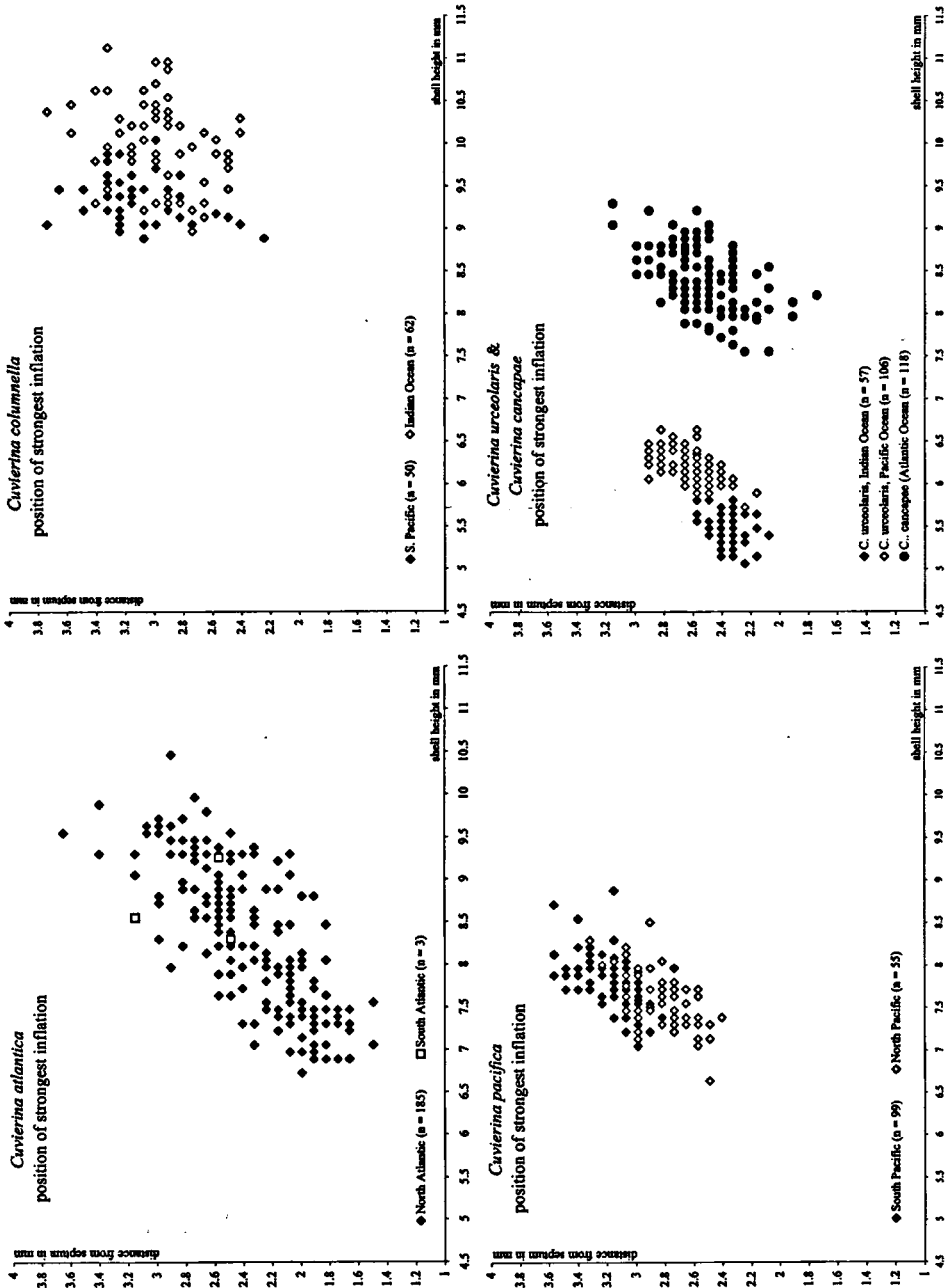


Fig. 33. Scatter diagrams of position of strongest inflation plotted against shell height for the five extant *Cuvierina* species.

**Position of strongest inflation
in percentages of shell height
from base of shell**

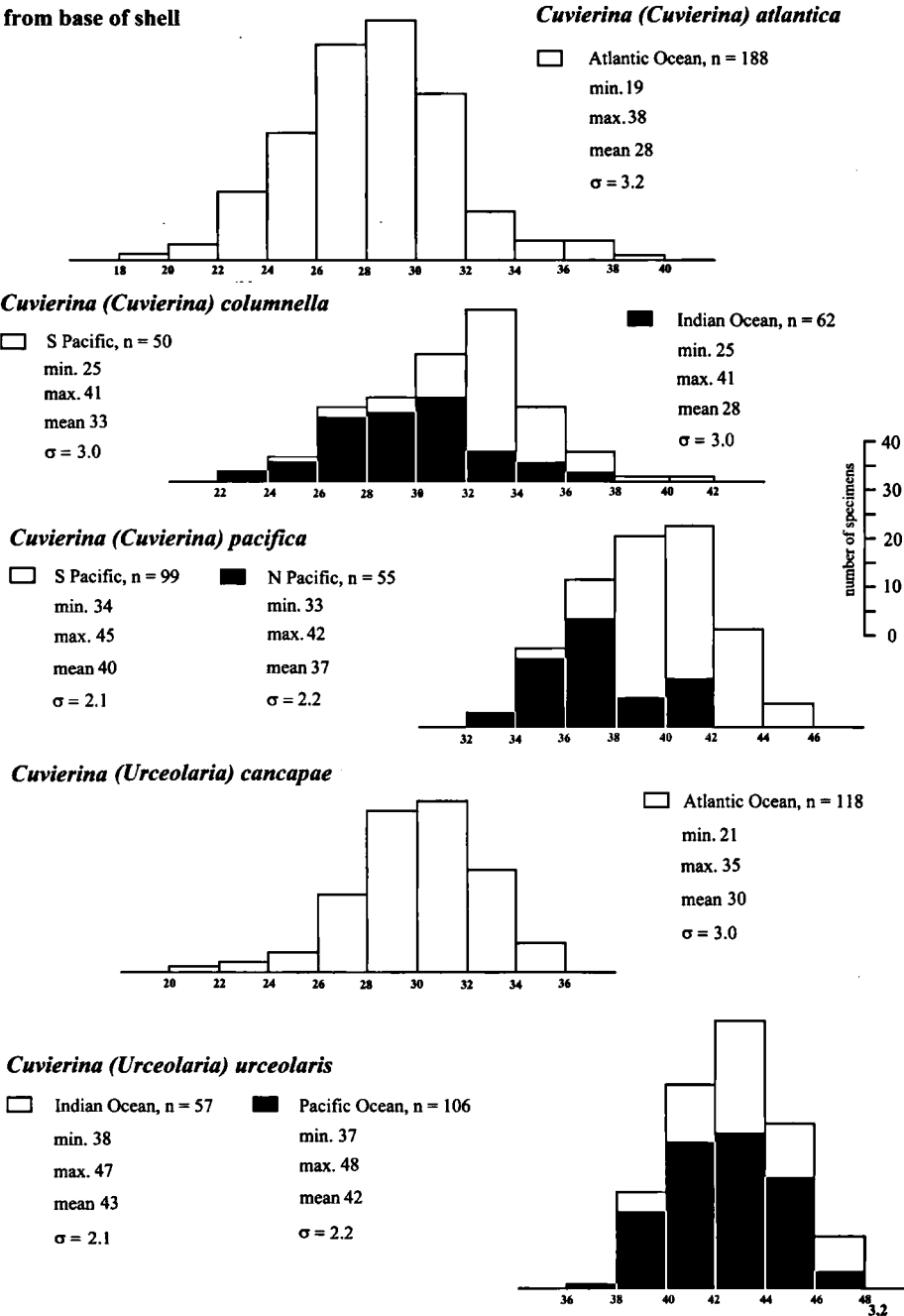


Fig. 34. Stacked bar graphs for the position of strongest inflation, in percentages of shell height, for the five extant *Cuvierina* species.

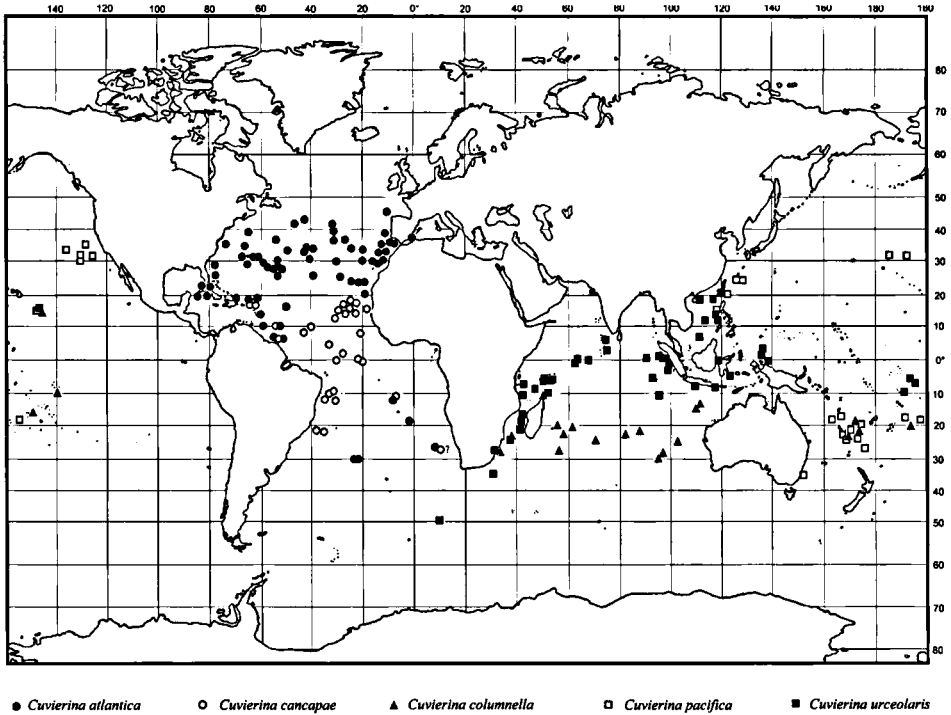


Fig. 35. Geographical distribution of Recent *Cuvierina* species, based on samples studied for the present paper only.

equator, with a 'blank' zone between approximately 5° N and 10° S. This pattern should be substantiated by more samples from the southern Atlantic.

Another species occurring in the Atlantic is *C. cancapae*, which mainly occurs in the circum-equatorial area where *C. atlantica* is absent, with some overlaps in the westernmost Atlantic, as well as in the southern Atlantic. In the available samples most specimens originate from around the Cap Verde Islands, some specimens are present from the Guyana coast and from the Caribbean (Saba Bank). More to the South *C. cancapae* is found mainly in the W Atlantic, to 23°S, just one doubtful (badly preserved) specimen was collected close to the S African coast, at 27°10'S 08°59'E.

Apparently, the *C. cancapae* specimens are transported with (or rather inhabit) the E-W running North and South Equatorial Currents. *C. atlantica* occurs mainly in the W-E running Gulfstream, as well as in the South Transitional Area (compare Van der Spoel, 1967, fig. 334), thus indicating bipolarity. Surprisingly enough the Canary Current, the southgoing branch of the Gulfstream, does not transport *C. atlantica* towards the Cap Verde's, resulting in an almost complete geographical separation of these two taxa in that area.

Cuvierina columnella is found almost exclusively between 10° S and 30° S, both in the Indian and the Pacific Oceans. In the Indian Ocean it co-occurs with *C. urceolaris* only in the Strait of Mozambique, whereas in the southern Pacific it is found together with *C. pacifica*.

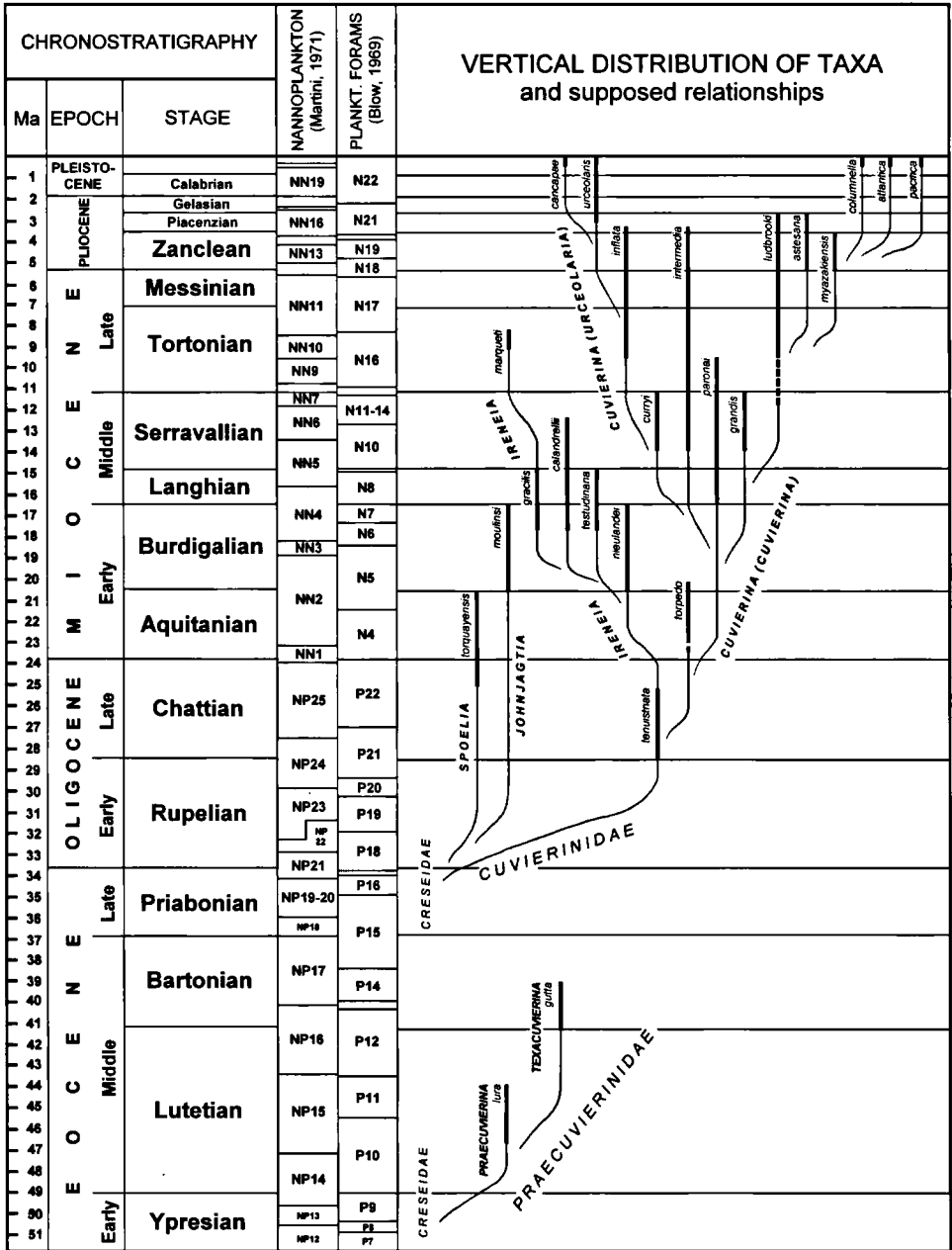


Fig. 36. Vertical distribution and supposed relationships of Cainozoic Cuvierinidae. Chrono- and biostratigraphical framework after Berggren et al. (1995).

This latter species, only found in the Pacific Ocean, again demonstrates a clear bipolarity, with the northern population living between 15 and 40° N and the southern one between 15 and 35° S, thus showing a wide distribution gap, which geographical separation must have caused the morphological differences as described above.

Cuvierina urceolaris, finally, demonstrates a rather curious distribution pattern. It is mainly found in the equatorial zone of the W Pacific, the N Indian Ocean and only more to the South along the African coast, and more northerly around the Philippines. Two specimens (SMF collection) were even collected from the Meteor Seamount, in the S Atlantic.

ACKNOWLEDGEMENTS

The author is grateful to Dr Warren C. Blow (National Museum of Natural History, Smithsonian Institution, Department of Paleobiology, Washington, U.S.A.), Dr Juliane Fenner (Hannover, Germany), Dr Edmund Gittenberger and Mr Jeroen Goud (National Museum of Natural History, Malacology Department, Leiden, The Netherlands), Dr Karl Gürs (Landesamt für Natur und Umwelt Schleswig-Holstein, Flintbek, Germany), Dr Ronald Janssen (Senckenberg Museum, Frankfurt am Main, Germany), Dr Bernard M. Landau (Albufeira, Portugal), Mr Pierre Lozouet (Muséum national d'Histoire naturelle, Paris, France), Mr Rob G. Moolenbeek (Instituut voor Systematiek en Populatiebiologie, Malacology Department, Amsterdam, the Netherlands), Dr Jeannine Rampal [Laboratoire de Biologie animale (Plancton), Université de Provence, Marseille, France], Mr Ben G. Roest (Vianen, the Netherlands), Dr Ole S. Tendal (Zoologisk Museum, Copenhagen, Denmark) and Dr Mag. Irene Zorn (Geologische Bundesanstalt, Vienna, Austria) for the loan or donation of material and/or access to collections in their care. Professor Patrick Schembri (University of Malta, Msida, Malta) kindly offered laboratory facilities.

Also I wish to thank Professor Daniel L. Geiger (Santa Barbara Museum of Natural History, University of Southern California, Los Angeles, U.S.A.), Dr Paul Jeffery (Oxford University Museum of Natural History, Oxford, U.K.), Professor Siebrecht Van der Spoel (Baarn, the Netherlands), Mr Frank P. Wesselingh (National Museum of Natural History, Palaeontology Department, Leiden, the Netherlands) and Dr Mag. Irene Zorn (Geologische Bundesanstalt, Vienna, Austria), for fruitful discussions and/or much appreciated opinions on (earlier versions of) the manuscript. Dr John W.M. Jagt (Venlo, the Netherlands) again was kind enough to improve the English.

REFERENCES

- ALESSANDRO, A. D', & E. ROBBA, 1980. Pteropodi neogenici della Puglia (Italia meridionale). – *Rivista Italiana di Paleontologia e Stratigrafia* 86(3): 605-698.
- BÉ, A.W.H., C. MACCLINTOCK & D.C. CURRIE, 1972. Helical shell structure and growth of the pteropod *Cuvierina columnella* (Rang) (Mollusca, Gastropoda). – *Biom mineralization Research Reports* 4: 47-79.
- BELLARDI, L., 1873. I molluschi dei terreni terziari del Piemonte e della Liguria, 1. Cephalopoda, Pteropoda, Heteropoda, Gastropoda (Muricidae et Tritonidae). – *Memorie della Reale Accademia di Scienze di Torino* (2)27: 1-264.
- BENOIST, E.-A., 1873. Catalogue synonymique et raisonné des testacés fossiles recueillis dans les faluns miocènes des communes de La Brède et de Saucats. – *Actes de la Société linnéenne de Bordeaux* 29: 5-78, 265-459.

- BERGGREN, W.A., D.V. KENT, C.C. SWISHER III & M.-P. AUBRY, 1995. A revised cenozoic geochronology and chronostratigraphy. *Geochronology Time Scales and Global Stratigraphic Correlation*. – SEPM Special Publication 54: 138-200.
- BLOW, W.H., 1969. Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy. – *Proceedings of the First International Conference on Planktonic Microfauna, Geneva 1967*, 1: 199-422.
- BOAS, J.E.V., 1886. *Spolia Atlantica*. Bidrag til Pteropodernes. Morfologi og Systematik samt til Kundskaben om deres geografiske Udbredelse. Videnskabernes Selskab Skrifter 6. – *Naturvidenskabelig og matematisk Afdeling* 4(1): 1-231.
- CAPROTTI, E., 1962. Altri scafopodi piacentiani di Castell'Arquato. – *Atti della Società Italiana di Scienze Naturali di Milano* 101(2): 93-101.
- GERONIMO, I. DI, M. GRASSO & H.M. PEDLEY, 1981. Palaeoenvironment and palaeogeography of Miocene marls from southeast Sicily and the Maltese islands. – *Palaeogeography, Palaeoclimatology, Palaeoecology* 34: 173-189.
- CHECCHIA-RISPOLI, G., 1921. I pteropodi del Miocene garganico. – *Bollettino del Reale Comitato Geologico d'Italia* 48(2)(1920-1921): 1-28.
- COLLINS, R.L., 1934. A monograph of the American Tertiary pteropod mollusks. – *Johns Hopkins University Studies in Geology* 11: 137-234.
- DAUDIN, [F.M.], 1800 (an 9 de la République). Nouveau genre de ver à tube calcaire, voisin des serpules et des dentales. – *Bulletin des Sciences de la Société Philomatique* (2)43: 145.
- HODGKINSON, K.A., C.L. GARVIE & A.W.H. BÉ, 1992. Eocene euthecosomatous Pteropoda (Gastropoda) of the Gulf and Eastern coasts of North America. – *Bulletins of American Paleontology* 103(341): 1-62.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE, 1999. International code of zoological nomenclature, fourth edition, adopted by the International Union of Biological Sciences: i-xxix, 1-306. The International Trust for Zoological Nomenclature, London.
- JANSSEN, A.W., 1995. Systematic revision of holoplanktonic Mollusca in the collections of the 'Dipartimento di Scienze della Terra' at Torino, Italy. – *Museo regionale di Scienze Naturali, Torino, Monografie* 17: 1-233.
- JANSSEN, A.W., 1999a. Notes on the systematics, morphology and biostratigraphy of fossil holoplanktonic Mollusca, 5. *Cuvierina jagti* Janssen, 1995, a junior synonym of *Dentalium (Gadilina) ludbrookii* Caprotti, 1962. – *Basteria* 63: 109-110.
- JANSSEN, A.W., 1999b. Notes on the systematics, morphology and biostratigraphy of fossil holoplanktonic Mollusca, 6. Biostratigraphical interpretation of an assemblage from Poggio Musenna (Sicily, Italy) in comparison to northern Italian and Maltese localities. – *Basteria* 63: 111-120.
- JANSSEN, A.W., 2000. Report on two samples of holoplanktonic Mollusca from the Pliocene of Cabarruyan Island (Philippines). Internal Report 156, National Museum of Natural History, Leiden, the Netherlands (Department of Cainozoic Mollusca): 1-8 (unpublished).
- JANSSEN, A.W., 2003. Notes on the systematics, morphology and biostratigraphy of fossil holoplanktonic Mollusca, 13. Considerations on a subdivision of Thecosomata, with the emphasis on genus group classification of Limacinidae. – *Cainozoic Research* 2(1-2) (2002): 163-170.
- JANSSEN, A.W., 2004. Fossils from the Lower Globigerina Limestone Formation at Wardija, Gozo (Miocene, Aquitanian), with a description of some new pteropod species (Mollusca, Gastropoda). – *The Central Mediterranean Naturalist* 4(1)(December 2003): 1-33.
- JANSSEN, A.W., in prep. Oligocene and Miocene pteropods from the Aquitaine area, SW France.
- JANSSEN, R., 1978. Die Scaphopoden und Gastropoden des Kasseler Meeressandes von Glimmerode (Niederrhessen). – *Geologisches Jahrbuch (A)*41: 3-195.
- KIENEL, U., U. REHFELD & S.M. BELLAS, 1995. The Miocene Blue Clay Formation of the Maltese Islands: sequence-stratigraphic and palaeoceanographic implications based on calcareous nannofossil stratigraphy. – *Berliner Geowissenschaftliche Abhandlungen* E16: 533-557.
- MARSHALL, P., 1918. The Tertiary molluscan fauna of Pakaurangi Point, Kaipara Harbour. – *Transactions*

and Proceedings of the New Zealand Institute 50: 263-278.

- MARTINI, E., 1971. Standard Tertiary and Quaternary calcareous nannoplankton zonation. In: A. FARNACCI, Proceedings 2nd Plankton Conference, Roma 1970, 2: 739-785.
- MEISENHEIMER, J., 1905. Pteropoda. – Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer 'Valdivia' 1898-1899, 9: i-vi, 1-314.
- MICHELOTTI, G., 1847. Description des fossiles des terrains miocènes de l'Italie septentrionale. – Natuurkundige Verhandelingen, Hollandsche Maatschappij der Wetenschappen, Haarlem 3(2): 1-408.
- MÖRCH, O.A.L., 1850. Catalogus conchyliorum quae reliquit C.P. Kierulf, md. dr. nunc publica auctione X Decembris MDCCCL Havniae Dividenda: i-ii, 1-33. Trieri/Hafniae.
- NORRIS, R.D., 2000. Pelagic species diversity, biogeography, and evolution. In: D.H. Erwin & S.L. Wing (eds). Deep time. Paleobiology's perspective. – *Palaeobiology* 26(4) suppl.: 236-258.
- PAVIA, G., & E. ROBBIA, 1979. La località messiniana di Borelli (Collina di Torino) e la sua fauna a pteropodi. – *Rivista Italiana di Paleontologia* 85(2): 549-572.
- PEYROT, A., 1932. Conchologie néogénique de l'Aquitaine. – Ouvrages couronnés de l'Académie des Sciences et Belles-Lettres de Bordeaux 6(2): 295-541.
- RAMPAL, J., 2002. Biodiversité et biogéographie chez les Cavoliniidae (Mollusca, Gastropoda, Opisthobranchia, Euthecosomata). Régions faunistiques marines. – *Zoosystema* 24(2): 209-258 (first published at <http://www.mnhn.fr/publication/zoosyst/z02n2som.html>).
- RANG, [P.C.A.L.], 1827. Description de deux genres nouveaux (Cuvieria et Euribia) appartenant à la classe des pteropodes. – *Annales des Sciences Naturelles* 12: 320-329 (pl. 45B is dated 1826!).
- RANG, [P.C.A.L.], 1829. Description de cinq espèces de coquilles fossiles appartenant à la classe des pteropodes. – *Annales des Sciences Naturelles* 16: 492-499.
- REHFELD, U., & A.W. JANSSEN, 1995. Development of phosphatized hardgrounds in the Miocene Globigerina Limestone of the Maltese archipelago, including a description of *Gamopleura melitensis* sp. nov. (Gastropoda, Euthecosomata). – *Facies* 33: 91-106.
- SEMPER, J.O., 1861. Beiträge zur Kenntnis der Tertiärformation, 4. Catalog einer Sammlung Petrefakten des Sternberger Gesteins. – *Archiv des Vereins der Freunde der Naturgeschichte in Mecklenburg* 15: 266-407.
- SPANO, C., 1983. I Cavoliniidae del Miocene inferiore di Castelsardo (Sardegna settentrionale). – *Rivista Italiana di Paleontologia e Stratigrafia* 89(2): 243-282.
- SPOEL, S. VAN DER, 1967. Euthecosomata, a group with remarkable developmental stages (Gastropoda, Pteropoda): 1-375. Gorinchem.
- SPOEL, S. VAN DER, 1970. Morphometric data on Cavoliniidae with notes on a new form of *Cuvierina columnella* (Rang, 1827) (Gastropoda, Pteropoda). – *Basteria* 34: 103-151.
- SPOEL, S. VAN DER, 1976. Pseudothecosomata, Gymnosomata and Heteropoda (Gastropoda): 1-484. Utrecht
- SUTER, H., 1917. Descriptions of new Tertiary Mollusca occurring in New Zealand, accompanied by a few notes on necessary changes in nomenclature, 1. – *New Zealand Geological Survey Paleontological Bulletin* 5: i-vii, 1-93.
- TEMBROCK, M.L., 1965. Zur Systematik einiger problematischer Caeciden-Gattungen (Gastropoda). – *Mitteilungen des Zentralen Geologischen Instituts* 1: 81-93.
- UJIHARA, A., 1996. Pteropods (Mollusca, Gastropoda) from the Pliocene Miyazaki Group, Miyazaki Prefecture, Japan. – *Journal of Paleontology* 70(5): 771-788.
- UJIHARA, A., H. SHIBATA & T. SAITO, 1990. Pteropods from the Sagara Group (Mio-Pliocene), Shizuoka Prefecture, Japan. – *Venus* 49(4): 306-329.
- WELLS, F.E., 1974. *Styliola sinocostata*, a new species of pteropod (Opisthobranchia: Thecosomata) from Barbados, West Indies. – *The Veliger* 16(3): 29-3296.
- ZORN, I., 1991. A systematic account of Tertiary Pteropoda (Gastropoda, Euthecosomata) from Austria. – *Contributions to Tertiary and Quaternary Geology* 28(4): 95-139.

Name	Sample	coordinates		number
<i>Cuvierina atlantica</i>				
	RMNH, CANCAP St. 1.020	32°31'N	16°32'W	1
	RMNH, CANCAP St. 1.021	32°29'N	16°32'W	4
	RMNH, CANCAP St. 1.025	32°42'N	16°45'W	1
	RMNH, CANCAP St. 1.044	32°42'N	16°42'W	5
	RMNH, CANCAP St. 1.062	32°40'N	16°46'W	1
	RMNH, CANCAP St. 2.007	27°48'N	14°24'W	1
	RMNH, CANCAP St. 2.062	28°07'N	13°45'W	23
	RMNH, CANCAP St. 2.065	28°11'N	13°57'W	1
	RMNH, CANCAP St. 2.067	27°58'N	14°12'W	4
	RMNH, CANCAP St. 2.078	28°01'N	14°26'W	1
	RMNH, CANCAP St. 2.079	28°01'N	14°26'W	1
	RMNH, CANCAP St. 2.080	28°01'N	14°26'W	1
	RMNH, CANCAP St. 2.086	28°02'N	14°29'W	20
	RMNH, CANCAP St. 2.087	27°42'N	15°02'W	26
	RMNH, CANCAP St. 5.004	38°06'N	24°49'W	1
	RMNH, CANCAP St. 5.012	37°39'N	25°32'W	1
	RMNH, CANCAP St. 5.175	39°40'N	31°05'W	2
	RMNH, CANCAP St. 5.187	39°27'N	31°05'W	1
	RMNH, LUYMES St. 15.097	06°48'N	57°31'W	1
	RMNH, LUYMES St. 15.108	07°40'N	57°32'W	20
	RMNH, LUYMES St. 34.056	17°37'N	63°17'W	4
	RMNH, LUYMES St. 34.076	17°14'N	63°44'W	3
	RMNH, LUYMES St. 34.112	17°06'N	63°28'W	2
	ZMUC, DANA 1293(v)	17°43'N	64°56'W	60
	ZMUC, DANA St. 3988(v)	15°52'S	06°02'W	1
	ZMUC, leg. Andrea, 1864	24°50'S	21°20'W	2
		total North Atlantic Ocean		185
		total South Atlantic Ocean		3
<i>Cuvierina columnella</i>				
	ZMUC, DANA St. 3576(viii)	17°36.5'S	149°43.6'W	1
	ZMUC, DANA St. 3602(v)	20°00'S	174°29'E	38
	ZMUC, DANA St. 3603(iv)	22°00'S	170°26'E	3
	ZMUC, DANA St. 3604(ii)	23°32'S	167°36'E	2
	ZMUC, DANA St. 3604(iv)	23°32'S	167°36'E	3
	ZMUC, leg. Patze, 1884	Marquesas		3
	ZMUC, DANA St. 3930	11°55'S	49°55'E	1
	ZMUC, DANA St. 3934	11°24'S	50°05'E	2
	ZMUC, DANA St. 3962(v)	24°33'S	38°26'E	6
	ZMUC, DANA St. 3965(ii)	28°18'S	33°49'E	1
	ZMUC, leg unknown	Indian Ocean		10
	ZMUC, leg. Andrea	21°S	57°E	2
	ZMUC, leg. Andrea 84, 1861	32°40'S	55°22'E	2

ZMUC, leg. Andrea L, 1864	26°30'S	58°E	1
ZMUC, leg. Andrea O, 1864	22°S	58°E	8
ZMUC, leg. Andrea, 1869	22°30'S	87°E	3
ZMUC, leg. Andrea, 1870	29°40'S	96°20'E	7
ZMUC, leg. Andrea, 1870	28°10'S	97°30'E	6
ZMUC, leg. Andrea, 1870	24°50'S	103°00'E	4
ZMUC, leg. Andrea, 1870	22°40'S	81°50'E	3
ZMUC, leg. Andrea, 1870	15°30'S	111°40'E	1
ZMUC, leg. Andrea, 1870	15°35'S	109°20'E	2
ZMUC, leg. Hansen cs, 1863	Indian Ocean		1
ZMUC, leg. Salmin, 1863	Indian Ocean		3
	total South Pacific Ocean		50
	total Indian Ocean		62

Cuvierina pacifica

ZMUC, DANA St. 3576(viii)	17°36.5'S	149°43.6'W	2
ZMUC, DANA St. 3577(iii)	18°49'S	153°10'W	2
ZMUC, DANA St. 3580(iv)	18°53'S	163°02.5'E	1
ZMUC, DANA St. 3581(v)	17°02.5'S	166°18'W	21
ZMUC, DANA St. 3602(v)	20°00'S	174°29'E	34
ZMUC, DANA St. 3603(iv)	22°00'S	170°26'E	2
ZMUC, DANA St. 3604(ii)	23°32'S	167°36'E	8
ZMUC, DANA St. 3604(iv)	23°32'S	167°36'E	1
ZMUC, DANA St. 3611(v)	20°53.2'S	164°03.3'E	2
ZMUC, DANA St. 3620(ii)	24°46.5'S	170°18.5'E	7
ZMUC, DANA St. 3622(i)	25°54'S	172°39.6'E	14
ZMUC, DANA St. 3623	27°21'S	175°11'E	3
ZMUC, DANA St. 3623(iii)	27°21'S	175°11'E	1
RMNH 78728, leg. Voorwinde	Port Stephens		1
ZMUC, DANA St. 3718(v)	20°04'N	125°59'E	19
ZMUC, DANA St. 3723(v)	25°30.5'N	125°08'E	1
ZMUC, DANA St. 3729(iii)	20°03'N	120°50'E	1
ZMUC, DANA St. 4761	25°10'N	127°45'E	5
ZMUC, DANA St. 4777	35°59'N	129°25'W	11
ZMUC, DANA St. 4778	32°13'N	167°25'W	5
ZMUC, DANA St. 4788	32°50'N	173°10'W	10
ZMUC, DANA St. 4794	33°45'N	137°30'W	2
ZMUC, FALSTRIA St. 4811	31°50'N	130°10'W	1
	total South Pacific Ocean		99
	total North Pacific Ocean		55

Cuvierina cancapae

RMNH, CANCAP St. 6.008	14°54'N	23°30'W	1
RMNH, CANCAP St. 6.010	14°53'N	23°30'W	1
RMNH, CANCAP St. 6.011	14°53'N	23°30'W	3
RMNH, CANCAP St. 6.012	14°53'N	23°30'W	2

RMNH, CANCAP St. 6.013	14°52'N	23°31'W	2
RMNH, CANCAP St. 6.017	14°53'N	23°30'W	1
RMNH, CANCAP St. 6.019	15°01'N	23°44'W	1
RMNH, CANCAP St. 6.020	15°01'N	23°44'W	1
RMNH, CANCAP St. 6.025	15°00'N	23°44'W	2
RMNH, CANCAP St. 6.040	14°55'N	24°31'W	1
RMNH, CANCAP St. 6.044	14°55'N	24°32'W	11
RMNH, CANCAP St. 6.052	14°53'N	24°31'W	1
RMNH, CANCAP St. 6.062	15°55'N	22°46'W	1
RMNH, CANCAP St. 6.132	16°46'N	25°02'W	1
RMNH, CANCAP St. 7.004	14°54'N	23°38'W	1
RMNH, CANCAP St. 7.007	14°54'N	23°38'W	1
RMNH, CANCAP St. 7.014	14°54'N	23°38'W	1
RMNH, CANCAP St. 7.028	14°57'N	24°39'W	2
RMNH, CANCAP St. 7.038	14°57'N	24°38'W	1
RMNH, CANCAP St. 7.039	14°56'N	24°38'W	1
RMNH, CANCAP St. 7.061	15°07'N	23°15'W	1
RMNH, LUYMES St 15.052	07°41'N	56°59'W	2
RMNH, LUYMES St. 34.076	17°14'N	63°44'W	1
RMNH, OCPS F37	07°24.6'N	6°22.4'W	1
ZMUC, DANA 1178(iii)	10°24'N	54°38'W	78
		total Atlantic Ocean	118

Cuvierina urceolaris

ZMUC, DANA St. 3729(iii)	20°03'N	120°50'E	61
ZMUC, DANA St. 3805	00°31.5'S	109°37'E	37
ZMUC, leg. Cuming 192		Philippines	
RMNH, TYRO St. S4.173	6°28'S	120°24'E	1
RMNH, TYRO St. S4.033	5°52.5'S	123°58.5'E	1
RMNH, TYRO St. S4.112	8°19'S	118°16'E	1
RMNH, TYRO St. S4.018	5°57.5'S	123°46.5'E	3
ZMUC, DANA St. 3860	02°57'S	99°36'E	6
ZMUC, DANA St. 3934	11°24'S	50°05'E	10
RGM, leg. Tracey		Natal	2
		total Pacific Ocean	106
		total Indian Ocean	57
		total measured	735

Table 2. Measured samples.