

Notes on the genus *Anadema* H. and A. Adams, 1854 (Gastropoda: Colloniidae)

Notas sobre el género *Anadema* H. y A. Adams, 1854 (Gastropoda: Colloniidae)

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ABSTRACT

Shell morphology and characters of the living animal of the poorly known, Atlantic Moroccan species *Anadema macandrewii* (Mörch, 1864) are described and illustrated, based on beach collected specimens and a single live-collected specimen. The genus is monotypic and is assigned to the Colloniidae rather than Turbinidae because of the dome-shaped profile of the shell, open umbilicus, symmetrical tooth rows of the radula, lack of cephalic lappets, and the non-bicarinate juvenile shell. Within the Colloniidae, it unusual for its relatively large mature shell, juvenile shell with a keeled profile, and the lack of the secondary flap above the rachidian tooth. The species is regarded as sexually dimorphic, with the female shell having a raised periumbilical rim comparable to that of other trochoideans modified for brooding by means of an enlarged umbilical cavity.

RESUMEN

Se describe e ilustra la morfología de la concha y del animal vivo de *Anadema macandrewii* (Mörch, 1864), una especie poco conocida de la costa atlántica de Marruecos. El género es monotípico y se asigna a la familia Colloniidae, en lugar de a los Turbinidae por la forma abombada de la concha, el ombligo abierto, las filas de dientes radulares simétricas, la ausencia de lóbulos cefálicos y por su concha juvenil no bicarenada. Entre los Colloniidae, la especie es insólita por el tamaño relativamente grande de la concha adulta, el perfil de la concha juvenil con una quilla y la ausencia de un repliegue secundario sobre el diente raquídeo. Se considera que existe dimorfismo sexual en esta especie, pues la concha de la hembra tiene un reborde periumbilical elevado comparable con el de otros trocoideos modificados para incubar en una cavidad umbilical ampliada.

KEY WORDS: Trochoidea, Morocco, brooding, endemism.

PALABRAS CLAVE: Trochoidea, Marruecos, incubación, endemismo.

INTRODUCTION

The poorly known genus *Anadema* H. and A. Adams, 1854 has at times

been regarded as a trochid, a liotiid, a colloniid, and a turbinid. Here we

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review the taxonomy and update what is now known about the type and only known species of this genus.

Anadema was proposed for the combination *Omphalius* (*Anadema*) *caelata* A. Adams, 1854, an Atlantic Moroccan species then thought to be a trochid in the absence of data on a calcified operculum. The species was not to be illustrated until 19 years later but it was described in sufficient detail that its identity has never been in question. In his remarks that followed the Latin description of the species, ADAMS (1855: 39) wrote: "The character of this shell is so peculiar, on account of the internal spiral callus of the umbilicus, and the absence of characters which constitute allied forms, that I propose to consider it a subgenus of *Omphalius*, under the name of *Anadema*." The generic name *Omphalius* Philippi, 1847 now pertains to the Tegulinae, as defined by HICKMAN AND MCLEAN (1990).

Ten years after the introduction of *Anadema*, MÖRCH (1864: 46) reported that a living specimen had been collected at the type locality. Mörch stated that: "*Omphalius* (*Anadema*) *caelata* is provided with a calcareous operculum, which proves that this species may be removed to *Turbo*. As there is already a *T. caelata*, L., I propose for this species *Turbo macandrewii*." Mörch's placement of the species in *Turbo* predated most work on the genera of turbiniform gastropods, and was based on the assumption that any turbiniform species with a calcareous operculum could only be a *Turbo*. This was unfair to Arthur Adams, but the ICZN rules about secondary homonymy force us to abandon the original name and to use the replacement name. This name honors the rediscoverer Robert McAndrew, who dredged a living specimen at Mogador (now Essaouira), the type locality of the species.

The first shell figure known to us was provided still later by P. FISCHER (1873), who used the replacement name *Turbo macandrewii*; this is a drawing that has been copied by many subsequent authors. The operculum has never been

figured and the repository of the operculate specimen examined by Mörch is unknown.

PILSBRY (1888) ignored the replacement name and called it *Leptothyra caelata*, a not unreasonable choice, as it hardly resembles a species of *Turbo*. *Leptothyra* is now assigned to Colloniidae.

WENZ (1938: 340) recognized the genus *Anadema* and placed it in the turbinid subfamily Liotiinae, under a broad definition in which he also included genera with calcareous opercula related to *Homalopoma*.

KEEN (1960: 270) placed *Anadema* in the more restricted Homalopomatinae, a group with fully calcified operculum, now subsumed under the turbinid subfamily Colloniinae in the classification of HICKMAN AND MCLEAN (1990).

NORDSEICK (1968: 33) overlooked MÖRCH (1864) and placed it in Liotiinae: "Deckel spiralig und mit Kalkbesatz, nicht verdickt", apparently having assumed that it must have the opercular definition of the now understood Liotiidae, in which the operculum is multi-spiral with calcareous beads on the outer surface.

Resolution of the uncertainty is here provided by a preserved immature specimen with operculum, which was collected by the second author in 1991 at Essaouira (formerly Mogador), the type locality. We therefore take this opportunity to illustrate the species and confirm its placement.

MATERIALS

This report is based on material collected by the second author, which is now in the malacology collection of the Muséum National d'Histoire Naturelle, Paris (MNHN). The external features of the single live-collected specimen were drawn with the animal fully extended. Subsequent preservation of the specimen resulted in retraction within the shell. It was later critical-point dried for SEM examination, after which it was rehydrated for extraction of the radula for SEM analysis.

SYSTEMATICS

Superfamily TROCHOIDEA Rafinesque, 1815

HICKMAN AND MCLEAN (1990) divided the family Turbinidae into a number of subfamilies, including Liotiinae, Colloniinae, and Turbininae. However, WILLIAMS AND OZAWA (2007) have reported that their data toward a molecular phylogeny of the family Turbinidae indicates that there are two well-supported groups within the previously defined Turbinidae, which therefore precludes the placement of all of the subfamilies in the same family. In view of the ongoing reconsideration of the relationships among these groups,

we here treat the Liotiidae, Colloniidae, and Turbinidae at the family level within the superfamily Trochoidea, which simply raises the ranking in the existing classification. This has already been adopted by MCLEAN AND KIEL (2007). Additionally, and without discussion, Warén and Bouchet *in* BOUCHET AND ROCROI (2005: 245) have separated Turbinoidea and Trochoidea at the superfamily level, which also indicates that the higher classification for trochiform vetigastropods is currently unsettled.

Family COLLONIIDAE Cossmann, 1916 Subfamily COLLONIINAE Cossmann, 1916

HICKMAN AND MCLEAN (1990) provided an extensive treatment of the Colloniidae (then as Colloniinae), distinguishing them from Turbinidae (then as Turbininae) on their smaller size, non-bicarinate juvenile shell, lack of cephalic lappets, symmetrical tooth rows and inner lateral teeth that are not greatly enlarged. This is in contrast with the Turbinidae, characterized by larger size, bicarinate juvenile shell, asymmetrical tooth rows and enlarged inner lateral teeth of the radula.

MCLEAN AND KIEL (2007) distinguished two subfamilies within the Col-

loniidae, based on opercular morphology: the basal and mostly extinct Petropomatinae Cox *in* Knight *et al.*, 1960, having a calcified operculum that is conical on the inner surface, with a fully multispiral pattern, and the Colloniinae, in which the operculum is flat on the inner surface with a multispiral pattern that changes to broadly paucispiral on the final volution. There is one living genus (*Liotipoma* McLean and Kiel, 2007) of Petropomatinae, whereas there are numerous living and fossil genera of Colloniinae.

Genus *Anadema* H. and A. Adams, 1854

Anadema H. and A. Adams, 1854: 430 [as subgenus of *Omphalius* Philippi, 1847]. Type species (monotypy): *Omphalius* (*Anadema*) *caelata* A. Adams *in* H. and A. Adams, 1854 [= *Turbo macandrewii* Mörch, 1864; not *Turbo caelata* Linnaeus, 1758].

Anadema macandrewii (Mörsch, 1864) (Figs. 1-23)

Omphalius (*Anadema*) *caelata* A. Adams, *in* H. and A. Adams, 1854: 430 [as type of new subgenus]. A. Adams, 1855: 39 [more detailed description].

Turbo macandrewii Mörsch, 1864: 46 [new name for secondary homonym *Omphalius* (*Anadema*) *caelata*, not *Turbo caelata* Linnaeus, 1758].

Turbo macandrewi. Fischer, 1873: 98, pl. 29, fig. 3 [first illustration]. Pasteur-Humbert, 1962: 132 [listed].

Leptothyra coelata [sic]. Pilsbry, 1888: 255, pl. 48, fig. 38 [figure after Fischer].

Turbo (Anadema) macandrewi. Pallary, 1920: 63.

Anadema coelata [sic]. Wenz, 1938: 340, fig. 795 [figure after Fischer]. Nordesick, 1968: 33, fig. 17.00

Anadema caelata. Keen, 1960: 270 [no figure]. Trew, 1992: 19 [listing of species described by H. & A. Adams].

Material examined: BMNH, 2 syntypes, BMNH 1968183, Mogador (now Essaouira), Atlantic Morocco (height 12.3 mm, diameter 16.6 mm; height 12.1 mm, diameter 17.3 mm). MNHN, Essaouira (formerly Mogador), Atlantic Morocco (31° 31' N, 9° 47' W), 1 live-collected male specimen and several beach-worn shells, leg. Gofas, 23 September 1991. MNHN, El Jadida, Atlantic Morocco (33° 16' N, 8° 29' W), beach worn shells, leg. Gofas, 26 September, 1991. MNHN, Mohammedia (formerly Fedala), Atlantic Morocco (33° 43' N, 7° 21' W), 10 beach-worn shells, leg. Gofas, 1970-71.

Description: Because the genus is monotypic, the description that follows applies both to the genus and species.

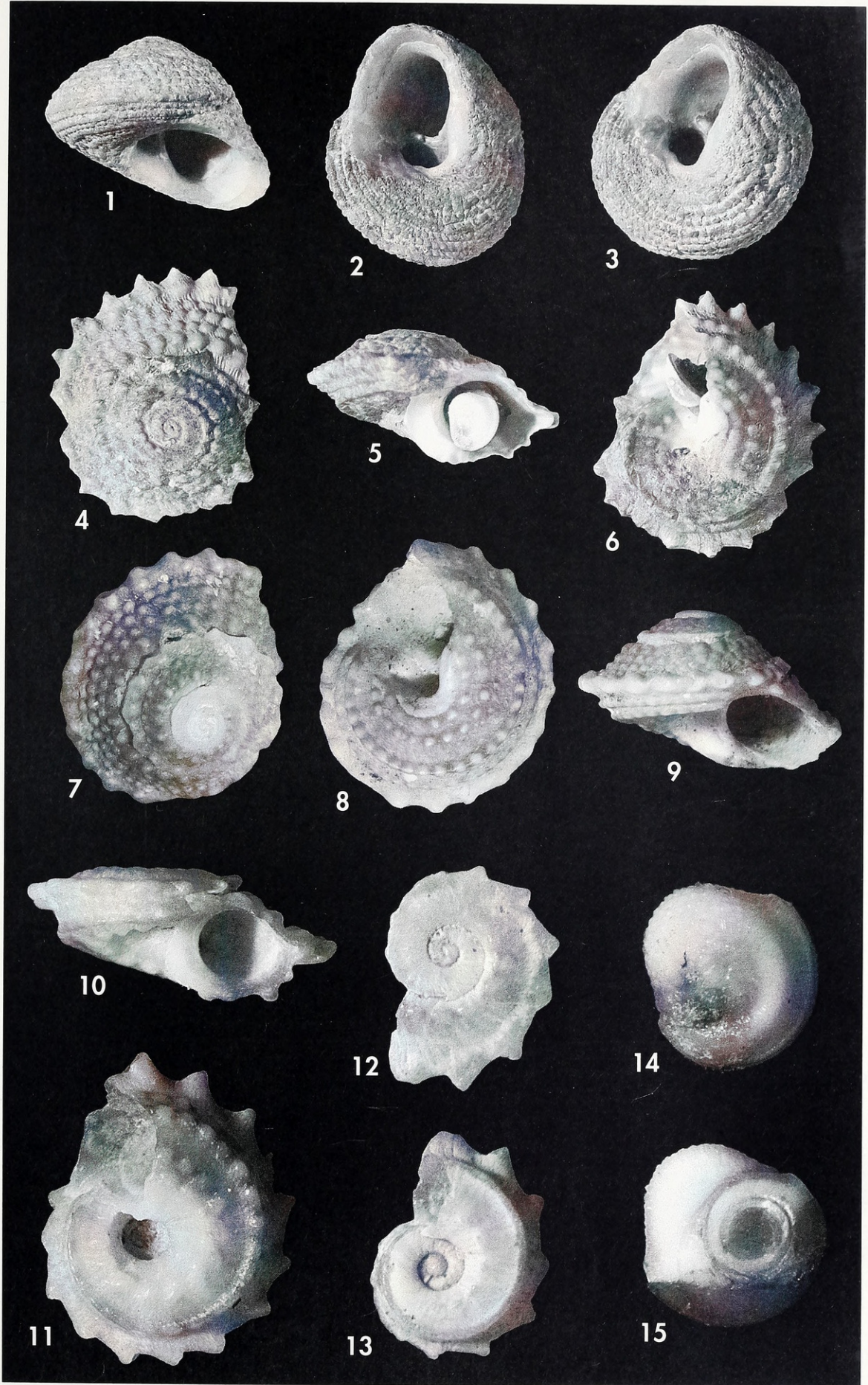
Shell composed of 5 whorls with a low spire; profile dome-shaped, broader than high, suture not impressed; whorls weakly rounded, periphery of immature shell strongly projecting, forming a keel; periphery spinose in early stages, but losing spination at maturity; mature shell with a subangulate base; axial sculpture of fine, raised lamellae; spiral sculpture of low, strongly beaded cords; cords between suture and beaded basal cord increasing from three in juvenile to 6 at maturity; base slightly convex, basal cords of comparable strength and beading to those of body whorl, increasing from three in juvenile to 8 at maturity; spiral sculpture of both body whorl and base separated by narrow interspaces; axial lamellae well

developed in interspaces but not expressed on surface of nodular beads; umbilicus open in juvenile shell, closed in male shell at basal diameter of 9 mm; remaining open in female shell; umbilicus of mature female shell bordered by raised, unbeaded peripheral cord that partially obstructs final quarter whorl and connects directly at base of aperture; aperture oblique, thickened within, descending slightly on final whorl; interior nacreous, inner wall of aperture of female shell smooth, edge with U-shaped sinus; shell colour brick-red.

Shell dimensions. Mature female shell (Figs. 1-3): height 13.0, diameter 17.1 mm; immature male shell (Figs. 4-6): height 4.9, diameter 9.1 mm; maximum dimensions possible for male shell unknown; immature female shell (Figs. 7-9), height 5.9, diameter 9.1 mm.

(Right page) Figures 1-15. *Anadema macandrewii* (Mörch, 1864). 1-3: Mature, beach-worn female shell, from Essaouira, Morocco (MNHN), 3 views, height 13.0 mm, diameter 17.1 mm; 4-6: live-collected, immature male specimen with operculum in place, same locality (MNHN), 3 views, height 4.9 mm, diameter 9.1 mm; 7-9: immature, beach-worn female shell, from Mohammedia, Morocco (MNHN), 3 views, height 5.9 mm, diameter 9.1 mm; 10, 11: juvenile beach-worn shell, from Essaouira, Morocco (MNHN), 2 views, height 2.1 mm, diameter 5.0 mm; 12, 13: juvenile shell with protoconch showing in umbilical view, from Essaouira, Morocco (MNHN), 2 views, diameter 2.7 mm; 14, 15: operculum of specimen shown in Figures 4-6 and 16, exterior and interior views, maximum diameter 2.1 mm.

(Página derecha) Figuras 1-15. *Anadema macandrewii* (Mörch, 1864). 1-3: *Concha adulta, exployada, de una hembra, de Essaouira, Marruecos* (MNHN), 3 vistas, altura 13,0 mm, diámetro 17,1 mm; 4-6: *ejemplar macho inmaduro, recolectado vivo, con el opérculo cerrando la concha; misma localidad* (MNHN), 3 vistas, altura 4,9 mm, diámetro 9,1 mm; 7-9: *concha inmadura, exployada, de una hembra, de Mohammedia, Marruecos* (MNHN), 3 vistas, altura 5,9 mm, diámetro 9,1 mm; 10, 11: *concha juvenil exployada, de Essaouira, Marruecos* (MNHN), 2 vistas, altura 2,1 mm, diámetro 5,0 mm; 12, 13: *concha juvenil con la protoconcha visible desde el ombligo, de Essaouira, Marruecos* (MNHN), 2 vistas, diámetro 2,7 mm; 14, 15: *opérculo del ejemplar representado en las Figuras 4-6 y 16, vistas exterior e interior, diámetro máximo 2,1 mm.*



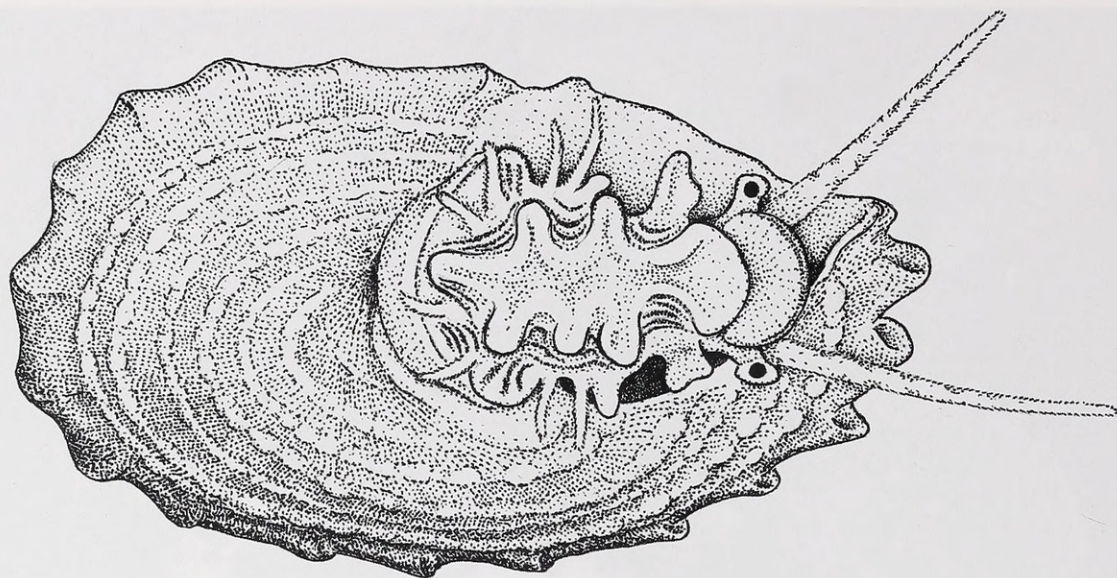


Figure 16. *Anadema macandrewii* (Mörch, 1864). Drawing of living specimen shown in Figures 4-6.
 Figura 16. *Anadema macandrewii* (Mörch, 1864). Dibujo del animal vivo, del mismo ejemplar de las Figuras 4-6.

Juvenile shell (Figs. 10-13) not with raised axial lamellae, of low profile, exposing protoconch and early whorls in basal view; profile not equally bicarinate, the upper carination spinose and more strongly projecting than lower, non-spinose carination; protoconch and first teleoconch whorl positioned slightly below level of second whorl.

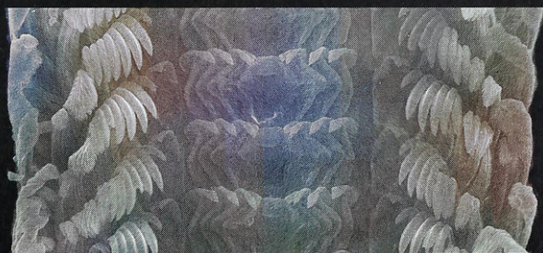
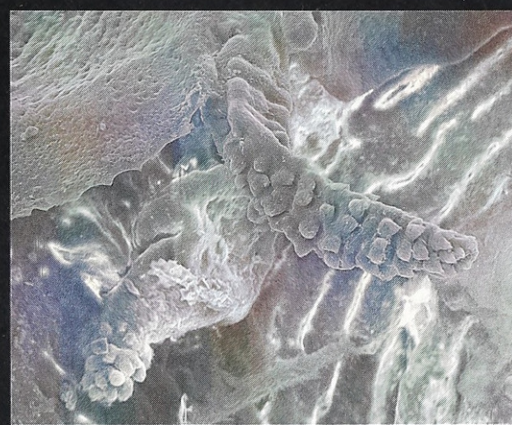
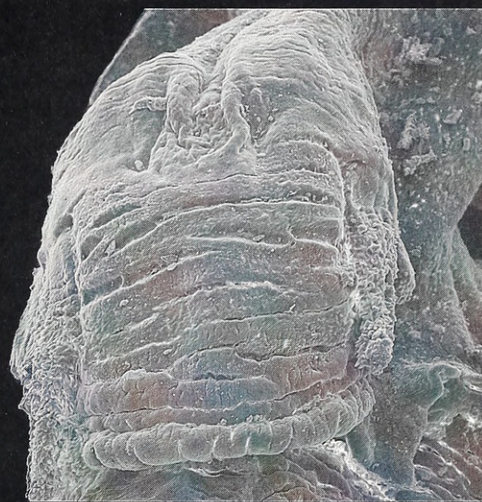
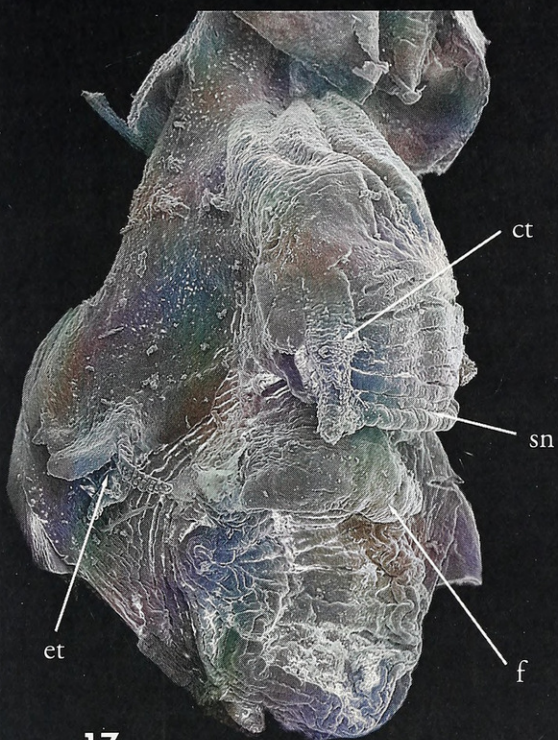
Operculum (Figs. 14-15) calcareous, thick, with a concavity at the base where the white outer surface is coloured light reddish-brown. There is a strong ridge and groove of similar width leading to

the upper part, which bears strong pustules in the region adjacent to the columella; outer edge with a narrow groove; inner surface becoming broadly paucispiral in final volution. This operculum is chipped or somehow reduced at its inner edge, to the extent that the outline is not oval; the chitinous layer of the inner surface that shows at the lower left of Figure 15 is missing at the upper left.

Head-foot (Figs. 16-19). Head proportionally large, provided anteriorly with a snout terminating in a broad,

(Right page) Figures 17-23. *Anadema macandrewii* (Mörch, 1864). 17-19. Scanning electron micrographs of critical-point dried specimen, same as shown in Figure 16. 17: general view of head-foot; 18: close-up of snout; note the absence of cephalic lappets; 19: close-up of right anterior bundle of epipodial tentacle. 20-23. Scanning electron micrographs of the radula, same specimen as Figure 16. 20: complete radula; 21: close-up of several complete rows; 22: detail of central and lateral teeth; 23: detail of marginal teeth. Abbreviations, ct: cephalic tentacle; et: epipodial tentacles; f: foot (pointing to propodium); sn: snout.

(Página derecha) Figuras 17-23. *Anadema macandrewii* (Mörch, 1864). 17-19. Micrografías electrónicas de barrido del ejemplar de la Figura 16 deshidratado por punto crítico. 17: vista general de la cabeza y del pie; 18: vista aumentada del hocico; nótese la ausencia de lóbulos cefálicos; 19: vista aumentada de un haz anterior derecho de tentáculos epipodiales. 20-23. Micrografías electrónicas de barrido de la rádula, ejemplar de la Figura 16. 20: rádula completa; 21: vista aumentada de algunas filas completas; 22: detalle de los dientes centrales y laterales; 23: detalle de los dientes marginales. Abreviaturas, ct: tentáculo cefálico; et: tentáculos epipodiales; f: pie (señalado el propodio); sn: hocico.



flattened area surrounding the mouth, laterally with two prominent, smooth bulges containing rather large, black eyes and, next to these on the anterior side, two slender, villose cephalic tentacles; cephalic lappets lacking. Neck lobes present, rather symmetrical, undivided. Foot rather small, less than half the diameter of the shell when extended; each side of the epipodium provided in its anterior part with a cluster of three tentacles, the foremost on hardly more than a rounded bulge, the next two tapering and villose, hardly one-tenth of the cephalic tentacles in size; in the posterior part with two more tentacles similar in size and shape to the latter.

Radula (Figs. 20-23) strikingly symmetrical, with broad rachidian having lateral extensions, and moderately long, tapered overhanging cusps; with four pairs of similar lateral teeth, which are elbowed like the rachidian and extend above the shaft of the next tooth; shaft of fifth lateral tooth not in close contact with shaft of fourth lateral tooth; this tooth broad on both sides, with a less prominent cusp than those of the inner lateral teeth or any of the marginal teeth; innermost pair of marginal teeth with short overhanging cusps, followed by four pairs of marginal teeth with longer cusps; outer marginal teeth with longer shafts, overhanging cusps shorter and deeply serrate on sides of the cusps.

The live-collected specimen (Figs. 4-6, 16) reported here (diameter 9.1 mm) has a nearly closed umbilicus and a generally unmodified base, with no indication of the incipient formation of the

projecting rim of mature female shells; it is therefore identified as a male specimen. There are immature beach-worn shells of about 10 mm in diameter (Figs. 7-9), which are considered to be female shells, having the beginning of a projecting rim that will form the strong periumbilical angulation of the large female shell (Fig. 2). It is evident that male shells are much less frequent among the beach-worn shells. Because the male shell with an operculum is larger than any of the comparable beach-worn shells considered to be male shells, and because the lip is immature, there is no indication from the material at hand as to the possible size reached by male shells. It may be that male shells can reach a size similar to that of female shells. If so, they would differ from female shells in having a rounded umbilical wall, rather than the projecting umbilical rim of female shells.

Both male and female shells seal the umbilicus upon attaining a half-grown diameter of about 10 mm. The female shell then proceeds to form a secondary umbilicus for the brooding cavity. The initial sealing of the umbilicus may help to protect the shell from exposure due to erosion of the apical whorls, which is also avoided in most marine gastropods by shell deposition of a plug from within.

There is variation in the peripheral spination of immature stages. The spination of the live-collected male specimen (Figs. 4-6) is stronger than that of any of the beach-worn shells of similar size, whether identified as male or female.

DISCUSSION

Knowledge of the genus *Anadema* has been slow to develop because the species *A. macandrewii* lives in the sublittoral zone on rocky bottoms exposed to strong surf, where there have apparently been few efforts at collecting by diving due to the exposure, low visibility, and extensive muddy bottoms offshore in relatively shallow water. The

single live-collected specimen reported here from the intertidal zone is an unusual record for the species.

Systematic position: There is now no doubt that *Anadema* should be assigned to the family Colloniidae, on the basis of shell and opercular characters, characters of the external anatomy, and the radula. The fine lamellar sculpture had

brought to mind a comparison with Liotiidae, but that is ruled out by the calcareous operculum.

There are many possibilities for opercular morphology in the Colloniidae, just as there are in the Turbinidae (see VERMEIJ AND WILLIAMS, 2007). There is no comparative work on the colloniid operculum, but the operculum of *Anadema* is within the range of possible expression for the family. Immature shells of the Mediterranean turbinid species *Bolma rugosa* (Linnaeus, 1767) have a resemblance to *Anadema macandrewii* in having a somewhat similar operculum and a spinose peripheral carination, but mature specimens of *Bolma* are much larger, have a higher profile and an impressed suture, a closed umbilicus and an expansive columellar callus that forms a columellar shield nearly as broad as the aperture. For a review of *Bolma*, see Beu and Ponder (1979). *Anadema macandrewii* differs from all illustrated species of *Bolma* in its low, dome-shaped profile and open umbilicus at maturity.

The keeled early juvenile shells indicate that early sculpture is not evenly bicarinate, which is a defining feature for Turbinidae, according to the restricted definition provided by Hickman and McLEAN (1990: 55) at the previously recognized subfamily level. Most colloniids have the juvenile shell with even spiral cords, but there are exceptions to that generalization. The keeled early stage brings to mind the recently described *Liotipoma* McLean and Kiel, 2007, in the basal subfamily Petropomatinae, which also has an early keel.

The lack of cephalic lappets is consistent with the assignment to Colloniidae, in which lappets are lacking (HICKMAN AND MCLEAN, 1990). This is in contrast to the Turbinidae, in which the lappets are well-developed (HICKMAN AND MCLEAN, 1990), albeit they are small in the Mediterranean *Bolma rugosa*.

The radular morphology of *Anadema* provides convincing evidence that it is colloniid rather than turbinid because the tooth rows are perfectly symmetri-

cal, and the inner marginals are not greatly enlarged. In turbinids, the asymmetrical tooth row causes the tooth alignment to be skewed, because the large inner laterals must alternate in zipper fashion when the radula is longitudinally folded (as detailed by HICKMAN AND MCLEAN, 1990).

Anadema is highly unusual within Colloniidae for its large size and its keeled early stage. With its maximum shell diameter of 17 mm, it may well be the largest known colloniid. All of the colloniid radulae illustrated by Hickman and McLEAN (1990) have a secondary flap that projects above the rachidian tooth; the radula of *Anadema* is unusual in not having the secondary flap. In addition, the morphology of the fifth lateral of *Anadema* seems also to be unusual for the family.

Larval brooding: Brooding of larvae within the umbilical cavity has been broadly reported among the Trochoidea (HICKMAN, 1992: 254). In the Trochidae it is known in *Margarites vorticiferus*, as shown by Lindberg and DOBERTEEN (1981). In Liotiidae, it has been reported for *Arene socorroensis* by SHASKY (1968) and again by HERTZ (1998), and for "*Munditia*" *subquadrata* it has been reported by BURN (1976). In the Colloniidae, it is known in the recently described genus *Liotipoma*, as reported by McLEAN AND KIEL (2007). Its occurrence in *Anadema* is therefore the second known example. In each of these cases, the umbilical rim of the female shell is raised to increase the volume of the umbilical cavity. Such a modification can be the only explanation for the strongly raised umbilical rim of what we interpret as the female shells of *Anadema macandrewii*.

The size reached by the shells of males remains to be discovered; it is possible that mature male shells are smaller than female shells. In support of that possibility, the operculum illustrated here shows the expansion of the final volution that is characteristic of a mature operculum. However, this shell is somewhat immature because the final lip is not thickened. All beach-worn

male shells in the material on hand seem to be immature. The immature male shells are represented by fewer specimens than the larger shells attributed to, for reasons unknown.

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the first author) were prepared in Photoshop by Michelle Schwengel (formerly LACM) and plate preparation for the shells was completed by Ángel Valdés (formerly LACM). Critical-point dried preparation of the live-collected specimen and the SEM views of the head-foot, as well as the SEM illustrations of the radula, were provided by Daniel L. Geiger of the Santa Barbara Museum of Natural History. We thank the reviewers for their suggestions, which led to improvements in the paper.

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