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Ammonicera in Florida: Notes on the Smallest Living Gastropod in the United States and Comments on Other Species of Omalogyridae (Heterobranchia)

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ABSTRACT

The first record of a species of *Ammonicera* in Florida, with an additional record from Yucatan, Mexico, is presented and the gross morphology of the living animal is described for the first time. This smallest living snail in the United States is identified as *Ammonicera minortalis* Rolán, 1992, originally described from Cuba. Comparisons are made with closely similar species, especially *A. japonica* Habe 1972, a possibly conspecific form with known wide distribution in the Pacific Ocean. Various taxonomic problems in the genera *Ammonicera* and *Omalogyra* are addressed, and current composition of the family Omalogyridae is discussed. Lists of currently recognized omalogyrid species in the Atlantic Ocean (including the Mediterranean Sea) are presented.

Key words: Florida Keys, Gastropoda, lower Heterobranchia, *Ammonicera*, *Omalogyra*, Omalogyroidea, Atlantic Ocean, Systematics.

INTRODUCTION

The family Omalogyridae is a poorly known group of extremely small marine snails. Placed in their own superfamily Omalogyroidea, they are currently classified as members of the unresolved "lower heterobranch" gastropods (e.g., Haszprunar, 1988; Bieler, 1992; Healy, 1993). Even the most basic taxonomic and distributional information is sketchy for this group, with most faunistic studies missing or deliberately omitting the usually less-than-one-millimeter size range of the adult shells. The few studies that have concentrated on this group have brought many new species to our attention, such as the recent series of works with excellent scanning electron micrographs by Sleurs of omalogyrids in Papua New Guinea (1983) and in the Republic of Maldives (1985b), by Palazzi (1988) in the Mediterranean and Madeira, and those by Rolán in the Cape Verdes (1991) and Cuba (1992). Whether these areas are exceptional in their high species diversity of omalogyrids is doubtful, although it

is surprising that no true omalogyrids were reported in some Caribbean studies that otherwise dealt with minute species (e.g., De Jong & Coomans, 1988; Rios, 1994).

In addition to their small size, omalogyrids have anatomical features that set them apart from caenogastropods with which they were usually grouped. This led to early speculations about their systematic position. Because of their unusual radular characters, G. O. Sars (1878) placed the at the time monotypic family as the only member of his new higher taxon "Prionoglossa," giving it equal rank with other groups such as Taenioglossa and Ptenoglossa. Jeffreys (1859a) thought these animals the only surviving members of the otherwise extinct genus *Euomphalus* Sowerby, 1814. Fretter (1948) showed in a detailed anatomical study that *Omalogyra atomus* (Philippi, 1841) differs greatly from the "prosobranchs" with which it was traditionally placed. Omalogyrids have regained interest in recent years because of their presumed basal position within the heterobranchs (Haszprunar, 1988; Ponder, 1990, 1991). Their exact relationships remain uncertain; recent suggestions (Bandel, 1996; Pacaud & Le Renard, 1996) to combine the Omalogyridae with several other families in a superfamily Architectonicoidea are not supported by anatomical data (Healy, 1993; Huber, 1993).

At the nomenclatural level, certain confusion exists in the literature about the usage of genus-group names such as *Ammonicera* versus *Ammonicerina*, and about the identity and authorship of *Omalogyra*'s type species.

The discovery of an *Ammonicera* species in the Florida Keys, representing the smallest gastropod known in the United States, is here used to summarize existing data on Omalogyridae in the Atlantic Ocean and to address additional taxonomic problems.

ABBREVIATIONS USED

AMNH	American Museum of Natural History, New York, U.S.A.
BMNH	The Natural History Museum, London, United Kingdom
FMNH	Field Museum of Natural History, Chicago, U.S.A.
MLP	Museo de La Plata, Argentina
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Museo Nacional de Historia Natural, Santiago, Chile
ZMB	Zoologisches Museum, Humboldt Universität, Berlin, Germany
SEM	Scanning Electron Micrograph

RESULTS

Family **Omalogyridae** G. O. Sars, 1878: 215 [as **Homalogyridae**]

(often erroneously credited to Fischer, 1885; e.g., Abbott, 1974)

Genus *Ammonicera* Vayssi re, 1893

Ammonicera minortalis Rol n, 1992

(Figures 1–8)

Omalogyra species.—Vokes and Vokes, 1984: 168, figs. 7, 7a (SEM).

Ammonicera minortalis Rol n, 1992: 40, 42, figs. 10, 11 (teleoconch), 13, 15 (protoconch) (all SEM).

Holotype: (MNCN 15.05/6794): shell diameter 0.35 mm; type locality: north of Cuba, Baracoa; holotype from 4 m depth.

Type material studied: 3 paratypes, AMNH 226450, from type locality.

Florida material studied: 2 Florida Keys specimens collected and observed alive, one each from station FK-045 [Indian Key Fill, Mile Marker 79, Monroe County, 24 53'25"N, 80 40'28"W, Gulf side, rocks in 0.5–1 m among *Thalassia/Halodule* seagrasses, 20 September 1996] and station FK-062 [Missouri Key, Mile Marker 39.5, Monroe County, 24 40'29"N, 81 14'21"W, Gulf side of Missouri-Ohio Key bridge, subtidal rocks, 14 April 1997]. Also empty shells from sta. FK-040 [Missouri Key site as above, 12 March 1996], FMNH 279010 (1 shell); FK-057 [Missouri Key site as above, 26 September 1996], FMNH 279011 (10 shells incl. SEM material), AMNH 288137 (5 shells). All localities were fully marine and were sampled by the authors by "rock washing" (brushing and rinsing of rock surfaces).

Distribution: Now known from north and south coasts of Cuba (Rol n, 1992), the Florida Keys (this paper), and the Yucatan Peninsula (Vokes & Vokes, 1984).

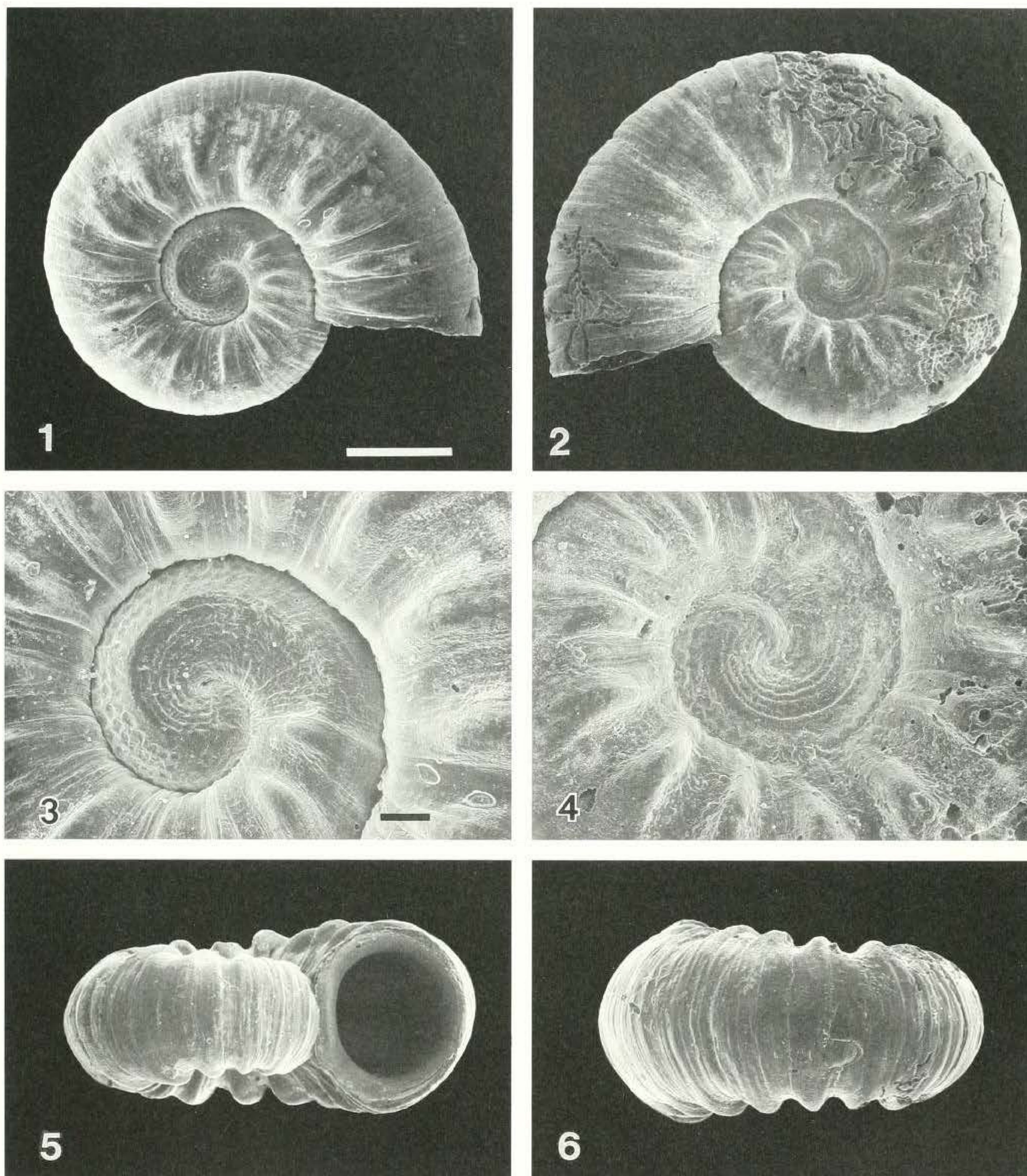
Description: Shell (Figs. 1–2) extremely minute, diameter 0.34–0.46 mm (0.2–0.4 mm, *fide* Rol n, 1992), planispiral, tightly coiled, glossy, uniformly dark brown, resembling a miniature ammonite in shape and sculp-

ture. Protoconch (Figs. 3–4) of 1.3 whorls¹ (identical in SEM but described as "3/4 whorl," by Rol n, 1992), diameter 120–135 μ m, distinctively sculptured with one major spiral cord at mid-whorl, reticulate sculpture peripheral to major cord, and 3–4 smaller spiral ridges central to major cord. No distinction of a separate larval shell ("protoconch II"), indicating the absence of a free swimming larval stage. Coiling near-planispiral, with slight initial hyperstrophy (compare Figs. 3 and 4). Teleoconch of about 1.3 rounded whorls (1–1.5 whorls *fide* Rol n, 1992), sculptured with prominent elongated axial tubercles, regularly spaced, equally sized, beginning immediately after protoconch, numbering 15–19 (13–17 *fide* Rol n, 1992) on body whorl, fading to no axial sculpture at the periphery. Tubercles and spaces between also with fine growth lines. Periphery (Fig. 6) uniformly rounded, smooth except for fine growth lines. No distinct spiral sculpture (but occasionally with extremely fine lines, see specimen in Fig. 1). Outer lip (Figs. 1–2) thin, sharp, ending in a single plane perpendicular to the plane of coiling; aperture circular; columella without folds or grooves. Head-foot (Figs. 7–8) translucent to nearly transparent. Animal gliding rapidly on short foot, with blunt, very active propodium. Shell held nearly vertically as the snail crawls. Transparent operculum on hindfoot serving as a support for the coil of the shell. Head with two finger-shaped tentacles, each held in an erect arch curving toward the midline; eyes black, near base of tentacles. Radula and internal anatomy not studied.

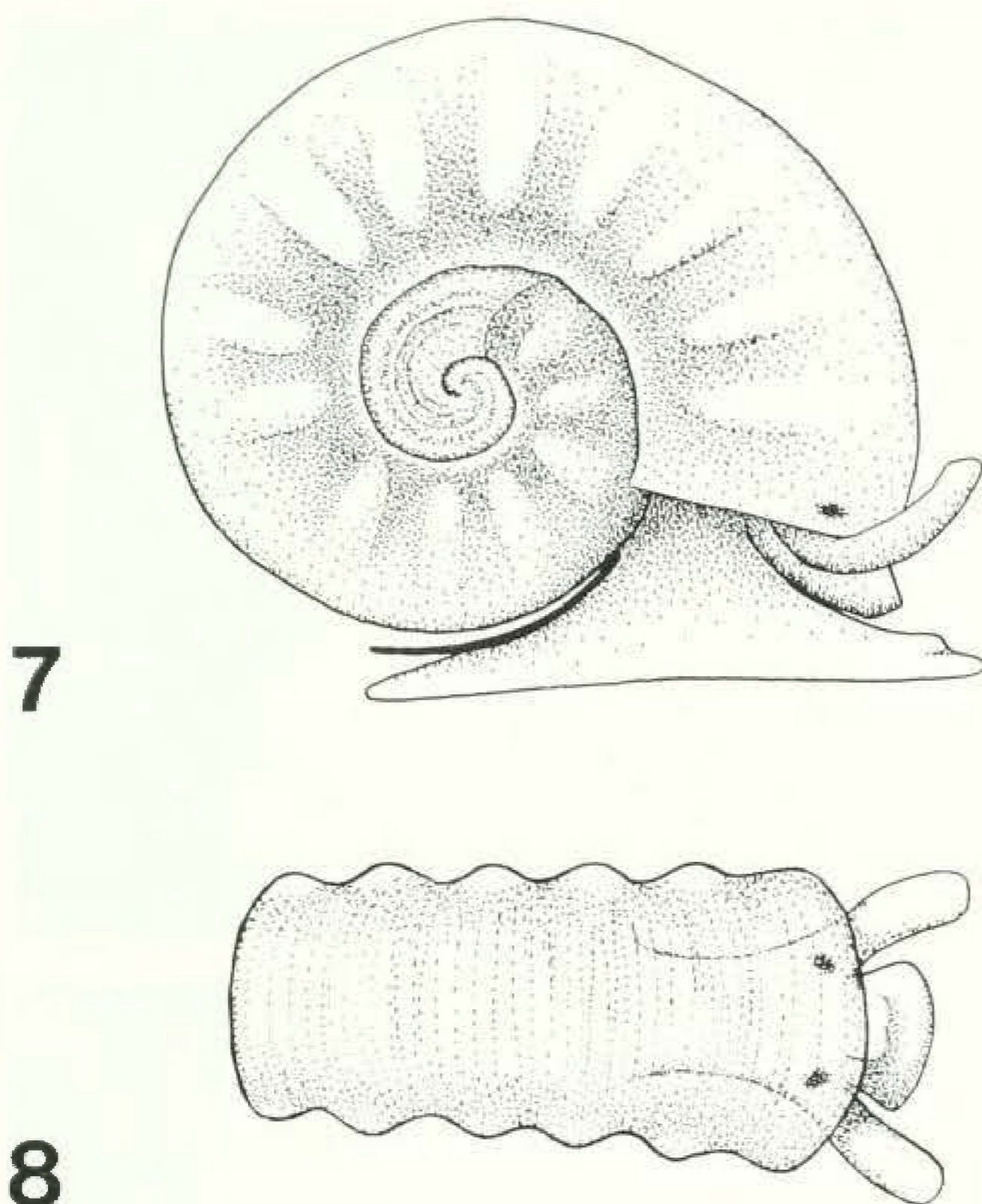
Habitat: Animals not observed *in situ*, but collected from shallow subtidal rocks covered on one or several surfaces with various polychaete worm tubes, marine algae, sponges, tunicates, and numerous other attached or free-living mollusks. Diet unknown (but see below).

Remarks: Although the diet of *Ammonicera minortalis* has not been confirmed, it is likely to feed on the variety of algal species growing in its subtidal rock habitat, based on literature records on the habitat/diet of other Omalogyridae: on *Codium* and *Zostera* (*Omalogyra atomus* [as *Euomphalus nitidissimus*]—Jeffreys, 1859a, 1859d); on *Ulva* (*O. atomus*—Fretter, 1948); on *Fucus* (*A. rota*—Nordsieck, 1972); on *Ulva* and *Enteromorpha* (*O. atomus*—Fretter & Graham, 1978; Graham, 1988); on *Fucus*, *Laminaria*, *Cladophora*, *Corallina*, *Ulva* (*Ammonicera rota*—Fretter & Graham, 1978); on *Padina* (Hawaiian *A. japonica*—Kay, 1979); piercing algal cells and sucking out the contents, and depositing egg strands on bases of *Cladophora* (*A. rota* / *A. fischeriana*—Franc, 1948; Graham, 1988); on *Halimeda* (*A. japonica* and others—Sleurs, 1985a, 1985c); on *Zostera*, *Ulva*, *Cystoseira*, and epiphytic diatoms (*O. atomus*, *A. fischeriana*—Gaglioli, 1993). Bullock *et al.*, 1990, provided the most detailed account, reporting Azorean *O. atomus* and *A. fischeriana* from a variety of algae, including

¹ Ascertained using the method of Taylor as summarized by Jablonski & Lutz (1980: 330, fig. 4)



Figures 1–6. *Ammonicera minortalis*, shells by scanning electron microscopy (four different shells, FMNH 279011). **1.** Apical view. **2.** Umbilical view. **3.** Protoconch (detail of fig. 1). **4.** Protoconch (detail of fig. 2). **5.** Apertural view. **6.** Dorsal view (from "above," as seen in crawling animal). Scale bars: Fig. 1 = 100 μm (Figs. 2, 5, 6 at same scale); Fig. 3 = 20 μm (Fig. 4 at same scale).



Figures 7–8. *Ammonicera minortalis*, sketch of living animal. Maximum shell diameter = 0.42 mm. 7. Right lateral view. 8. Dorsal view.

Enteromorpha, *Cystoseira*, *Ulva*, *Pterocladia*, *Peysonnelia*, *Halopteris*, *Asparagopsis*, as well as *Codium*. *Omalogyra atomus*, which they also found on *Gelidium* and *Sargassum*, was the dominant species on *Chondria* and the only mollusk found on *Fucus* in that study.

DISCUSSION

Species-level identification: Rolán (1992) described this species based on empty shells collected from north and south coasts of Cuba (3–20 m). A comparison with the excellent original illustrations and with paratype material at AMNH proved the identity of the Florida Keys specimens. No other known Atlantic species combines such axial teleoconch sculpture with reticulated sculpture of its protoconch. Rolán apparently was unaware of an earlier record of this form, as “*Omalogyra* species,” by Vokes and Vokes (1984) who collected it in Arrecife Alacran, about 140 km north of Progreso, Yucatan, in the Gulf of Mexico.

According to Rolán (1992: 42), only *Ammonicera japonica* Habe, 1972, described as “Japan’s smallest gastropod” from Honshu, is “superficially similar but it has very constant spiral striae.” Habe’s species (1972:115–116, figs. 1–4) was described as 0.42–0.68 mm in diameter, dark brown in color, with “about 16 annulations in the body whorl” (Habe, 1972:116). Habe did not mention or illustrate the spiral sculpture noted by Rolán.

Additional specimens were described and illustrated as *Ammonicera japonica* from Hawaii by Kay (1979:92, figs. 32A–C [SEM], as *Omalogyra*; earlier reported by Kay & Switzer, 1974:278, table 1, from Fanning Island). Kay mentioned sculpture “from 16 to 18 axial ribs on the last whorl, the ribs becoming obsolete at the periphery.” Spiral striae were not described but faint spiral sculpture is visible in one illustrated shell (Kay, 1979:fig. 32B). Sleurs’ (1985a:4–5, pl. 1, figs. 1, 6, 9 [SEM]; as *Omalogyra*) description of *A. japonica* from Papua New Guinea was very similar. He described the protoconch in detail “with reticulated sculpture at the abapical side” (his fig. 9); spiral sculpture of the 0.3 to 0.45 mm large teleoconch was not discussed, but shows very faintly in one SEM illustration (his fig. 6). Fukuda’s illustration of this species from the Ogasawara (Bonin) Islands (1994:pl. 35, fig. 697a–c; as “*Omalogyra*” *japonica*), shows no spiral sculpture. The large specimen illustrated (0.4 mm) has about 19 axial ribs.

The protoconch and teleoconch sculpture of the shells of *Ammonicera minortalis* and *A. japonica* are extremely similar according to the SEMs provided by Rolán (1992), Kay (1979), Fukuda (1994) and Sleurs (1985a), respectively, and suggest synonymy of the Caribbean and Indo-Pacific species. Faint spiral teleoconch sculpture appears to occur in some individuals of both nominal species. However, the disjunct distributional pattern makes further study necessary. No similar form has been described or recorded from the eastern Pacific (Shasky, 1989).

As also noted by Rolán (1992), *Ammonicera minortalis* is similar to the European *A. rota* (Forbes & Hanley, 1850) in its teleoconch characters (but the latter has a greater number of whorls and axial tubercles continuing over the periphery). *Ammonicera rota* has, however, a very different protoconch without reticulated sculpture (see, e.g., Rodriguez Babio & Thiriot-Quievreux, 1974: pl. 2, F–H; as *A. fischeriana*). Also similar is *A. plicata* Sleurs, 1985, from the Maldives (1985b:20 ff., figs. 2, 7, 10, 13, 14), which has a larger teleoconch (0.45 to 0.65 mm) with weaker axial ribs and a protoconch lacking the reticulate sculpture present in *A. minortalis* and *A. japonica*.

Genus-level identification: Omalogyridae currently comprises three recognized extant genera: *Ammonicera* Vayssière, 1893, *Omalogyra* Jeffreys, 1859, and *Retrotortina* Chaster, 1896. The last (with type species by monotypy: *R. fuscata* Chaster, 1896) has a sinistral teleoconch that distinguishes it from *Ammonicera* and *Omalogyra*.

Bandel (1988:9) also placed *Orbitestella* Iredale, 1917, in this family, but Ponder (1990) showed that this genus belongs in the Valvatoidea, not Omalogyroidea. Bandel (1988), who viewed omalogyrids as small-bodied members of Architectonicidae or Architectonicoidea (pp. 10, 17), attempted to introduce a new fossil genus “*Neamphitomaria*,” but did not designate a type species. Bandel (in Dockery, 1993:92) subsequently provided such a

designation (the Upper Cretaceous *Pseudomalaxis stan-toni* Sohl, 1960) and thus validated *Neamphitomaria* of that date [not as of 1988 as is frequently cited; see ICZN Art. 13(b)]. *Amphitomaria* Koken, 1897, and *Neamphitomaria* Bandel, 1993, were then placed in a new family, Amphitomariidae, by Bandel (1996), thus removing the genus again from the Omalogyridae.

The placement of the present species in the genus *Ammonicera*, rather than *Omalogyra*, is here accepted because of: (1) its protoconch sculpture with strong spiral ribs and grooves (in contrast to small tubercles in *Omalogyra*; e.g., Rolán, 1992); (2) the presence of distinct cephalic tentacles (absent in *Omalogyra*); and (3) its strong teleoconch sculpture (absent or weak in *Omalogyra*). The known radulae of *Omalogyra* and *Ammonicera* (not yet studied for *A. minorialis*) are so different between members of the two nominal genera that Sleurs (1985c:181) suggested that they might belong to different families. However, published radular data differ even within the two genera: *Omalogyra* radulae have been described as either uniserial (Jeffreys, 1859, 1867; Thiele, 1929; Sleurs, 1985c) or with a formula of 1-1-1 (G. O. Sars, 1878; Thiele, 1929; Egorova, 1991). Those of *Ammonicera* have been described with a formula of 1-1-1 (Vayssiére, 1893) or 1-1-0-1-1 (Sleurs, 1985b, c), and so definitive conclusions must await a detailed comparative study.

Unfortunately, the taxonomic history of *Ammonicera*, *Omalogyra*, and their included species is exceedingly complex and confused (see discussion below).

REMARKS ON AMMONICERA AND ITS TYPE SPECIES

Ammonicera was introduced by Vayssiére (1893:16 ff.) for *Homalogyra fischeriana* Monterosato, 1869. He provided a full anatomical description based on histology and studies of the radula. Franc (1948:142 ff.) and Sleurs (1985a:9) questioned the identity of Vayssiére's material, assuming that his work was based on misidentified "*Omalogyra rota*" Forbes and Hanley, 1850. Compared to Gaglini's descriptions and illustrations (1993:933-04, 934-03-04), Vayssiére's line drawings of the shell (1893: figs. 8-9) seem to represent typical *A. fischeriana* in color pattern and relatively fine crenulations of the periphery, although the sketched pronounced axial ribbing is more representative of the nominal species *A. rota*. Monterosato himself considered the two nominal species as varieties of one (e.g., Monterosato 1872:38; 1875:29), and many recent authors (e.g., Fretter & Graham, 1978; Backeljau *et al.*, 1984; Knudsen, 1995) have deemed them synonymous (see also Høisaeter, 1968; van Aartsen *et al.*, 1984). Gaglini (1993), on the other hand, argued convincingly for the presence of two sympatric species. Whether or not they will prove to be synonymous, they are without doubt so closely related and morphologically similar that it will not impact interpretation of the nominal genus *Ammonicera* (in contrast to Sleurs, 1985a).

In addition to Vayssiére's extensive description, pub-

lished biological information about this/these species includes description of gross anatomy (Franc, 1948), nervous system (Huber, 1993), egg capsules (Franc, 1948 [summarized by Knudsen, 1995]; Graham, 1988), and feeding (Graham, 1988).

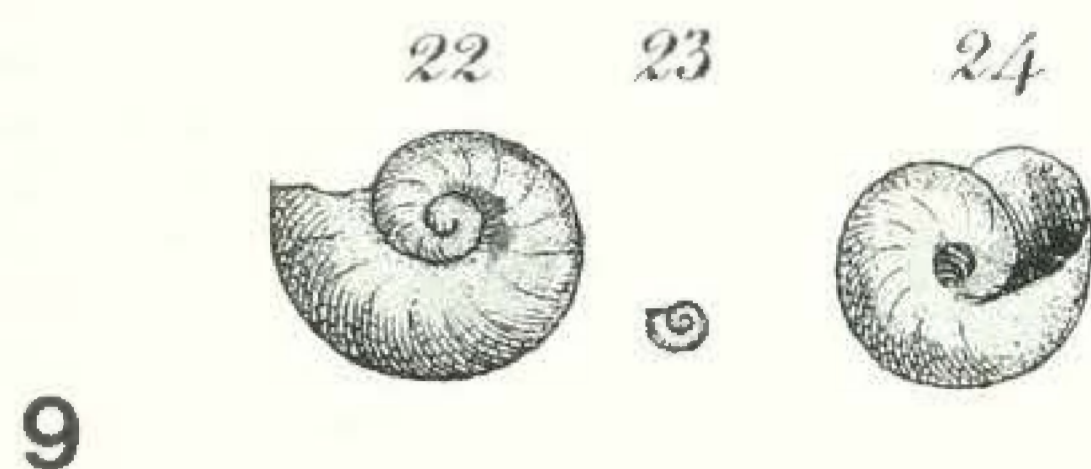
Ammonicera should not be confused with *Ammonicerina*—see synonymy of *Omalogyra* (below).

REMARKS ON OMALOGYRA AND ITS TYPE SPECIES

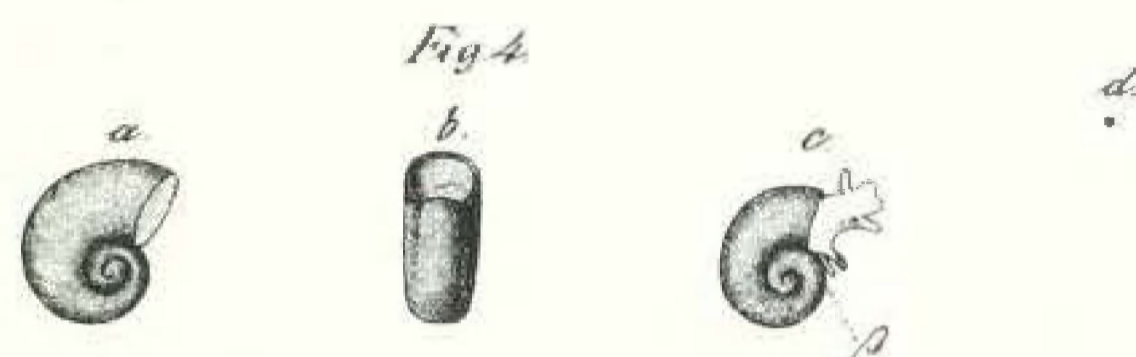
Omalogyra was introduced by Jeffreys (1859b) in the midst of an engaged discussion (with Clark, 1859) ultimately involving the identities of *Helix nitidissima* Adams, 1800, "*Skenea*" *nitidissima sensu* Forbes and Hanley, 1850, and "*Truncatella*" *atomus* Philippi, 1841. The current understanding of *Omalogyra* is based on Fretter's (1948) excellent anatomical study on British animals identified as *O. atomus*. Other published information on this species includes gross anatomy and radula (G. O. Sars, 1878), nervous system (Huber, 1993), spermatozoa (Healy, 1993), and egg capsules (Graham, 1988; Knudsen, 1995 [However, it should be noted that the accompanying SEM shell photographs, Knudsen's fig. 5, seem to be of a skeneopsid, not of *O. atomus*]). The "eggs" of *O. atomus* as described by Jeffreys (1867) and Lebour (1937) were subsequently recognized as misidentified glandular structures (Fretter, 1948).

No type material for any of these nominal taxa could be located; our following discussion thus has to concentrate on literature review: *Helix nitidissima* J. Adams, 1800, was introduced with a short description and three illustrations (here reproduced in Fig. 9). The species was accepted and cited, in various generic combinations, by subsequent authors (e.g., Weinkauff, 1868:266, as "*Spira nitidissima* Adams"). Many authors have considered *H. nitidissima* J. Adams, 1800, as synonymous with *Truncatella atomus* Philippi, 1841 (e.g., Fischer, 1857; Weinkauff, 1868; Fretter & Graham, 1978; Rolán, 1983; Graham, 1988; Poppe & Goto, 1991; Rosenberg/Malacolog, 1997). The original description by Adams (1800: 4, pl. 1, figs. 22-24) was based on the shell alone: "H.[elix] testa duobus anfractibus, subtilissime transverse striata. Obs. Corneous, pellucid, umbilicated; easily distinguished by the uncommon brilliancy of its glossiness." Original figure 23, said to be of "natural size" (1800:6) measures nearly 3 mm. The shell, much too large to be a European omalogyrid species, was subsequently recognized as "evidently the fry of *Zonites radiatulus* [J. Alder, 1830]," a land snail, by Jeffreys (1867:71). The holotype of *H. nitidissima* was not located (K. Way, BMNH, pers. comm., 1997). The interpretation as a young stage of a British land snail is here accepted; *H. nitidissima* Adams is not a senior synonym of *T. atomus*.

Much of the interpretation of "*nitidissima*" by subsequent authors was based on "*Skenea*" *nitidissima sensu* Forbes and Hanley, 1850, who used this name for a different species. Several authors erroneously credited Forbes and Hanley with the description of a new species



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Figure 9. Reproduction of original illustrations of *Helix nitidissima* J. Adams, 1800 (from Adams, 1800: pl. 1, figs. 22–24).

Figure 10. Reproduction of original illustrations of *Truncatella atomus* Philippi, 1841 (from Philippi, 1841: pl. 5, figs. 4a–d).

"*Skenea nitidissima*" (e.g., Jeffreys, 1860; Nordsieck, 1972; Nordsieck & Garcia-Talavera, 1979; Gaglini, 1993). However, Forbes and Hanley themselves (1850: 158) cited the species as "*S.[kenea] nitidissima*, Adams" with full page and figure reference to Adams' original work. It is this misidentified "*nitidissima sensu* Forbes & Hanley" that enters into the various lengthy published discussions comparing "*nitidissima*" and *Truncatella atomus*.

Philippi (1841:54, pl. 5, figs. 4a–d) described and illustrated *Truncatella atomus*, collected in Sorrento (Campania, southern Italy). He emphasized that he was able to study the animal in detail at a magnification of 60 times and placed it in *Truncatella* because of the animal's similarity to members of that genus. In 1844, he re-described the species (p. 134, pl. 24, fig. 5; again as "n. sp.") and reproduced his 1841 illustrations of *T. atomus*. Philippi's (1841) illustrations, here reproduced in Fig. 10, show a living specimen with planispiral shell (with logarithmic growth), tapering tentacles, an operculum, and a representation of actual size of about 0.5 mm. The type material has not been located in Berlin or Santiago (von Rintelen, ZMB, pers. comm., 1997; MNHN, pers. obs., 1997).

Forbes and Hanley (1850:158–160, pl. 73, figs. 7, 8) described and illustrated a British shell under the name "*S.[kenea] nitidissima*, Adams"; they did not mention the living animal. They placed Philippi's *Truncatella atomus*, with question mark, in synonymy. Jeffreys (1859a:109–111, pl. 3, figs. 15a, b, 16a–c) discussed the species, as *Euomphalus nitidissimus*, with a sketch of the animal (showing ciliated head lobes, no tentacles, and a unise-

riate radula). He reported its range as "from the Shetlands to Sicily, and probably far beyond these limits" (p. 111) based in part on the synonymy of *Truncatella atomus* of Philippi, and expressed his astonishment over Philippi's "mistake" of describing the animal so differently (i.e., with tapering tentacles).

Much of the ensuing confusion was based on (1) the treatment of Philippi's Italian "*Truncatella atomus*" specimens as members of the British "*Omalogyra nitidissima*" *sensu* Forbes and Hanley, and (2) the discrepancy between gross anatomical descriptions of these two species, i.e., with or without tapering head tentacles, respectively.

Clark (1859:410–413, text-figure), after reexamining British animals reconstituted from dried specimens, disagreed with Jeffreys and corroborated the correctness of Philippi's figure of an animal with triangular tentacles, the large eyes embedded at the center of their bases. "It appears quite clear that Mr. Jeffreys has delineated his animal with rounded lobes, or, in other words, with the tentacles retracted. . ." (p. 411). Jeffreys (1859b:498) rebutted: "What Mr. Clark supposed to be tentacula must have been the shrivelled lobes of the veil. . ." Fischer (1859:364–367) joined Clark in criticizing Jeffreys (1859c), assuming that the latter had described a larval stage with vela instead of tentacles. Jeffreys then (1860: 108–111), in rebuttal of Fischer, affirmed that his observations were based on adult specimens without tentacles. Finally, in British Conchology, Jeffreys (1867:67–71, pl. 1, fig. 5; 1869:209, pl. 70, fig. 2) again described the shell and animal in detail, reaffirming his opinion of Philippi's error, but recognized the priority of "*Homalogyra atomus*" (Philippi) over "*Skenea nitidissima*" of Forbes and Hanley. This "anatomically corrected" *Homalogyra atomus*, with "*Skenea nitidissima sensu* Forbes and Hanley in synonymy, is the *Omalogyra atomus* described in detail by Fretter (1948) and that currently forms our concept of the genus.

Unfortunately the original figures of *Truncatella atomus* Philippi, 1841, are in conflict with the descriptions of Fretter. Philippi's illustrated gross morphological details (i.e., tapering tentacles) are indicative of *Ammonicera*. Meanwhile, the sketched smooth shell appears in line with the current concept of *Omalogyra*. In the absence of type material, it is impossible to explain this discrepancy. It is possible that Philippi's material contained members of both genera and his illustration is a composite based on more than one species.

In the interest of nomenclatural stability, we base our interpretation of Philippi's *Truncatella atomus* on his illustration/description of the shell alone (excluding the anatomy in original fig. 4c), thus preserving this name for "*Skenea nitidissima sensu* Forbes and Hanley, 1850 (non Adams, 1800), and *Omalogyra atomus sensu* Jeffreys, 1859, as well as Fretter, 1948.

The taxonomic confusion has been compounded by uncertainty about the type species designation and the date of introduction of *Omalogyra*. Some authors (e.g.,

Warén, 1980:12) cited it as having been introduced by Jeffreys (1860), with type species *Truncatella atomus* Philippi, 1841, by monotypy. Others (e.g., Wenz, 1939: 647–648) gave "*O. nitidissima* (Forbes & Hanley)" as type species. The date of description is often erroneously cited as "1867" (e.g., Abbott, 1974; Castellanos, 1989a; Vaught, 1989; Rios, 1994).

The generic name "for the reception of these anomalous mollusks" was in fact proposed by Jeffreys (1859b: 498). In that paper, he referred by name to "*Euomphalus nitidissimus*" (with reference to his earlier, 1859a, article), to "*E. Rota*" and its "variety *tricarinata* of Webster." In the referenced article, he additionally stated a synonym for "*E. nitidissimus*": "I have no doubt that it is the *Truncatella atomus* of Philippi" (1859a:111). Jeffreys did not indicate a type species. Following ICZN (1985: Art. 69(i)), there are four "originally included nominal species":

Helix nitidissima J. Adams, 1800. Now considered a land snail [Jeffreys recognized the misidentification only in 1867; his (1859a, b) usage thus cannot be construed as "deliberately used in the meaning of a previous misuse" (ICZN, 1985: Art. 11(i))].

Truncatella atomus Philippi, 1841 [in synonymy].

Skenia rota Forbes and Hanley, 1850. Now considered a member of *Ammonicera*.

Skenia tricarinata Webster, 1856. Described as a potential new species; subsequently (beginning with Jeffreys in Webster, 1857) considered a variety/synonym of *S. rota*.

Jeffreys (1867:69 ff.) synonymized "*Skenia nitidissima*" *sensu* Forbes and Hanley under *Truncatella atomus*, after recognizing the true *Helix nitidissima* Adams as a land snail. He also synonymized *Skenia tricarinata* Webster under *Skenia rota*. No type species was designated. Jeffreys therein changed the generic name to *Homalogyra*, an unjustified emendation. The first authors to select a type species appear to have been Bucquoy *et al.* (1884:78) who stated "Type: *Homalogyra atomus* Philippi sp. (*Truncatella*)."

We therefore offer the following synonymies:

Omalogyra Jeffreys, 1859b:498; type species by subsequent designation of Bucquoy *et al.* (1884:78), *Truncatella atomus* Philippi, 1841.

Ammonicerina O. G. Costa, 1861: 71; type species by subsequent designation of Dall (1927b:134, as "*Ammonicerina*"), *Ammonicerina simplex* O. G. Costa, 1861. Preoccupied by *Ammonicerina* O. G. Costa, 1856 [Protista]. This taxon is usually placed in synonymy of *Ammonicera* (e.g., Palazzi & Gaglini, 1979); however, its type species by subsequent designation belongs to *Omalogyra*.

Homalogyra Jeffreys, 1867:67 (an unjustified emendation).

Note: In the description of their new genus *Transomalogyra*, Palazzi and Gaglini (1979:33) made *Ammonicerina simplex* O. G. Costa, 1861, the type species by original designation. This would make *Transomalogyra* an objective synonym of *Ammonicerina* and a subjective synonym of *Omalogyra*. However, as pointed out by

Warén (1991:74), the type species was misidentified, with Palazzi & Gaglini's illustration actually showing a shell of *Adeuomphalus ammoniformis* Seguenza, 1876. Warén (1991) thus placed *Transomalogyra* in the synonymy of *Adeuomphalus* Seguenza, 1876, as a genus *incertae sedis* in the "Archaeogastropoda."

Omalogyra atomus (Philippi, 1841)

Truncatella atomus Philippi, 1841:54, pl. 5, fig. 4a-d [excluding the sketched animal in fig. 4e].

Skenia nitidissima (Adams) *sensu* Forbes and Hanley, 1850, *et auct.* [non *Helix nitidissima* J. Adams, 1800].

Homalogyra atomus var. *vitrea* Jeffreys, 1867:69.

Homalogyra atomus var. *fasciata* Monterosato, 1877:418.

Notes on other named "varieties":

Homalogyra atomus var. *maculata* Dautzenberg and Durouchoux, 1914:27. The authorship of this name is usually credited to Monterosato, 1875 (e.g., Gaglini, 1993: 928–02). However, Monterosato's applications and some subsequent citations of the name are not available for nomenclatural purposes because they represent *nomina nuda* (Monterosato, 1875:29; 1878:88; Bucquoy *et al.*, 1884:324). The first available introduction appears to be that of Dautzenberg and Durouchoux (1914).

Ammonicerina atomus "var. *pallida* Monterosato 1884" as cited by Gaglini (1993:928–02) is likewise not available as of that date. Monterosato's usage (1884:22) of "var. *pallida*" is a *nomen nudum*, as is his *Homalogyra atomus* var. *zonata* Monterosato (1878:88), subsequently cited as "var. *ex colore* 2, *zonata* Monts." by Bucquoy *et al.* (1884:324; likewise a *nomen nudum*).

Homalogyra atomus var. *nautiliformis* De Gregorio, 1889, was recognized by Monterosato (1890:141) as a juvenile of *Capulus ungaricus* (Linnaeus, 1758). Nevertheless, the name *nautiliformis* De Gregorio, 1889, was retained by some authors to describe an *Omalogyra* morph with a much widened body whorl (e.g., Nord-sieck, 1972:148; Gaglini & Curini Galletti, 1978:210, fig. 2c). Gaglini (1993:928–02–3) introduced a new infra-specific name for this morph, *Omalogyra atomus* var. "*inflata*."

Homalogyra atomus var. *polyzona* "Brusina mss. (fide Monterosato)" in Bucquoy *et al.*, 1884:324, pl. 37, fig. 32. Earlier references to a variety "*polyzona* Brusina" by Monterosato (1872; 1875; 1878) are unavailable because they were stated in synonymy or as *nomina nuda*. Gaglini (1993:931–01, 931–02–3) showed that this is a potential synonym of *O. simplex*, not *O. atomus*.

CURRENT COMPOSITION OF OMALOGYRIDAE

Recognized western Atlantic Species: [regions of type localities in brackets]

Ammonicera albospectiosa Rolán, 1992:44, figs. 17, 19, 21 [Cuba]

- Ammonicera circumcirra* Rolán, 1992:45, figs. 23, 26, 28 [Cuba]
Ammonicera familiaris Rolán, 1992:42, 44, figs. 16, 18, 20 [Cuba]
Ammonicera lineofuscata Rolán, 1992:44–45, figs. 22, 24–25, 27 [Cuba]
Ammonicera minortalis Rolán, 1992:40, 42, figs. 10–11, 13, 15 [Cuba]
Ammonicera sculpturata Rolán, 1992:40, figs. 9, 12, 14 [Cuba]
Omalogyra atomus (Philippi, 1841:54, pl. 5, figs. 4a–d) [Mediterranean]
Omalogyra burdwoodiana (Strebel, 1908:52, pl. 6, fig. 85a–c) [Burdwood Bank, south of Falkland Islands]
Omalogyra fuscopardalis Rolán, 1992:36, 38, figs. 1, 3, 5, 7 [Cuba]
Omalogyra taludana Castellanos, 1989a:88–89, figs. 1, 2 (plus sketch of apertural aspect in 1989b:pl. 1, fig. 10) [off San Jorge Gulf, Argentina]
Omalogyra zebrina Rolán, 1992:38, figs. 2, 4, 6, 8 [Cuba]

For the western Atlantic, eleven omalogyrid species are currently recognized. Of these, eight are to date only known from Cuba (all described by Rolán, 1992). Two others, *Omalogyra burdwoodiana* (Strebel, 1908) and *O. taludana* Castellanos, 1989, are known from subantarctic waters off South America. Two omalogyrid species are now recognized from the east coast of the United States: *Ammonicera minortalis* and *O. atomus*.

Several other nominal omalogyrid species have been reported for the western Atlantic Ocean, but need to be excluded from that fauna:

"Omalogyra planorbis": A nominal species in the western Atlantic frequently cited as an omalogyrid is *Lippistes? planorbis* Dall, 1927a:131, originally described from "off Fernandina," Florida. This deep-water species was re-described in detail by Moore (1971: 114–116, fig. 1) as *Omalogyra planorbis*, and subsequently called *Omalogyra* (*Ammonicera*) *planorbis* (e.g., Abbott, 1974:81; Rios, 1994:60). This taxon was placed in *Palazzia* Warén, 1991, as an "archaeogastropod" group of uncertain affiliations, tentatively assigned to Skeneidae (Warén, 1991: 74, 76).

"Ammonicera fischeriana": Nordsieck (1972:149) referred to "*Ammonicera fischeriana* (Monterosato, 1869) = *densecostata* [sic] (Jeffreys, 1884)" in "Westindien," without further explanation. This synonymy is erroneous. The West Indian record for this Mediterranean species is based on Watson's (1886) "Challenger" material of "*densecostata*" as explained in the following.

"Omalogyra (*Ammonicera*) *densicostata*" : *Homalogyra densicostata* Jeffreys, 1884:129, pl. 10, fig. 1, was described from "Porcupine" stations (1098–2002 m) off the coast of Portugal. Additional material from a "Bulldog" cruise off Labrador (2967 m) was also included in the original description. Abbott (1974:81) reported this species as *Omalogyra* (*Ammonicera*) *densicostata* from deep water off Portugal, the Azores, and Labrador. Moore (1971:114) showed that the Labrador ("Bulldog") material in fact belongs to "*Lippistes*" *planorbis* Dall, 1927, thus removing the Labrador record for "*O.*" *densicos-*

tata. Watson (1886:677) added a "*Homalogyra densicostata* (?)" record from north of the island of Culebra, between Puerto Rico and the Virgin Islands ("Challenger" station 24, 715 m). Moore (1971:115–116) doubted both the synonymy of the Challenger material and that of the shallow-water material reported by Dautzenberg (1889:46) for the Azores, thus restricting *densicostata* again to the eastern Atlantic. The species was considered a member of the eastern Atlantic omalogyrid fauna until recently (e.g., Sabelli et al., 1990; Gaglioli, 1993). *Homalogyra densicostata* was synonymized under *Adeuomphalus ammoniformis* Seguenza, 1876, and placed as an "archaeogastropod" of uncertain affiliations, tentatively assigned to Skeneidae (Warén, 1991:74 ff.).

Recognized eastern Atlantic/Mediterranean Species: [regions of type localities in brackets]

- Ammonicera burnayi* Rolán, 1991:112, figs. 13–14 [Cape Verde Archipelago]
Ammonicera fischeriana (Monterosato, 1869:274–275, pl. 13, fig. 1) [Mediterranean]
Ammonicera lignea (Palazzi, 1988:105, figs. 8, 18) [Madeira]
Ammonicera multistriata Rolán, 1991:112, 114, figs. 15–16 [Cape Verde Archipelago]
Ammonicera nolai Rolán, 1991:110, figs. 8–9 [Cape Verde Archipelago]
Ammonicera oteroi Rolán, 1991:110, 112, figs. 10–12 [Cape Verde Archipelago]
Ammonicera robusta Rolán, 1991:114–115, figs. 17–18 [Cape Verde Archipelago]
Ammonicera rota (Forbes & Hanley, 1850:160, pl. 73, fig. 10; pl. 88, figs. 1, 2) [Ireland]
Ammonicera rotundata (Palazzi, 1988:105, figs. 10, 21, 27) [Madeira]
Ammonicera verdensis Rolán, 1991:109, figs. 6–7 [Cape Verde Archipelago]
Omalogyra atomus (Philippi, 1841:54, pl. 5, figs. 4a–d) [Mediterranean]
Omalogyra disculus Palazzi, 1988:104, figs. 1, 20 [Madeira]
Omalogyra simplex (O.G. Costa, 1861:72, pl. 11 figs. 3 a, b) [Mediterranean]
Omalogyra undosa Palazzi, 1988:104, figs. 5, 15 [Madeira]
Retrotortina fuscata Chaster, 1896:2 [Strait of Gibraltar]

In the eastern Atlantic, fifteen omalogyrid species are currently recognized, comprising ten species of *Ammonicera*, four of *Omalogyra*, as well as *Retrotortina fuscata* (for Mediterranean records see also Sabelli et al., 1990; Le Renard et al./CLEMAM, 1997). *Omalogyra atomus* is the only species known from both sides of the Atlantic; it is widely distributed, ranging from the Mediterranean, Madeira, and the Azores to Norway, Iceland, Greenland, and in New England (Abbott, 1974; Bullock, 1969, 1995; Fretter & Graham, 1978; Thorson, 1944) from Maine to Rhode Island. Egorova (1991) recognized material from Antarctic waters, previously identified and cited as *O. atomus*, as members of a morphologically extremely similar species, *O. antarctica* Egorova, 1991.

Several other nominal omalogyrid species have been described for the eastern Atlantic. Of these, *Omalogyra aperta* Sykes, 1925:192, from off Portugal, was recognized as a member of the "archaeogastropod" genus *Eu-*

daronia Cotton, 1945, by Warén (1991:80). *Homalogyra granulosa* Sykes, 1925, also from off Portugal, was placed in the "archaeogastropod" genus *Retigyra* Warén, 1989 (see Warén, 1992:168). *Homalogyra paradoxa* "Monterosato (? MS.)" of Sykes (1925:192) is a *nomen nudum*. Two other nominal species introduced by Sykes (*H. sinuosa* Sykes, 1925, and *H. (?) marshalli* Sykes, 1925) are in need of further study (see Palazzi, 1992). An additional Mediterranean species, *O. ausonia* Palazzi, 1988, was recently made the type of *Palazzia* Warén, 1991, and transferred to the "archaeogastropods," with tentative placement in the Skeneidae (Warén, 1991). Nominal species *Homalogyra ornata* Dautzenberg, 1889 (p. 46, pl. 4, fig. 9a-d), described from the Azores, is still in need of reinvestigation.

It should be noted that Palazzi (1988) used "ausonia" (Italy) and "disculus" (little disk) as nouns in apposition in the original descriptions; recent usage as "*Palazzia ausoniae*" or "*Omalogyra discula*" (e.g., Sabelli *et al.*, 1990; Giannuzzi-Savelli *et al.*, 1994; Arduini *et al.*, 1995) are incorrect subsequent spellings.

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Ammonicera in Florida: Notes on the Smallest Living Gastropod
in the United States and Comments on Other Species of
Omalogyridae (Heterobranchia)

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ABSTRACT

The first record of a species of *Ammonicera* in Florida, with an additional record from Yucatan, Mexico, is presented and the gross morphology of the living animal is described for the first time. This smallest living snail in the United States is identified as *Ammonicera minoiensis* Rolan, 1992, originally described from Cuba. Comparisons are made with closely similar species, especially *A. japonica* Habe 1972, a possibly conspecific form with known wide distribution in the Pacific Ocean. Various taxonomic problems in the genera *Ammonicera* and *Omalogyra* are addressed, and current composition of the family Omalogyridae is discussed. Lists of currently recognized omalogyrid species in the Atlantic Ocean (including the Mediterranean Sea) are presented.

Key words: Florida Keys, Gastropoda, lower Heterobranchia, *Ammonicera*, *Omalogyra*, Omalogyroidea, Atlantic Ocean. Systematics.

INTRODUCTION

The family Omalogyridae is a poorly known group of extremely small marine snails. Placed in their own superfamily Omalogyroidea, they are currently classified as members of the unresolved "lower heterobranch" gastropods (e.g., Haszpnmar, 1988; Bieler, 1992; Healy, 1993). Even the most basic taxonomic and distributional

information is sketchy for this group, with most faunistic studies missing or deliberately omitting the usually less-than-one-millimeter size range of the adult shells. The few studies that have concentrated on this group have brought many new species to our attention, such as the recent series of works with excellent scanning electron micrographs by Sleurs of omalogyrids in Papua New Guinea (1983) and in the Republic of Maldives (1985b), by Palazzi (1988) in the Mediterranean and Madeira, and those by Rolan in the Cape Verdes (1991) and Cuba (1992). Whether these areas are exceptional in their high species diversity of omalogyrids is doubtful, although it

is surprising that no true omalogyrids were reported in some Caribbean studies that otherwise dealt with minute species (e.g., De Jong & Coomans, 1988; Rios, 1994).

In addition to their small size, omalogyrids have anatomical features that set them apart from caenogastropods with which they were usually grouped. This led to early speculations about their systematic position. Because of their unusual radular characters, G. O. Sars (1878) placed the at the time monotypic family as the only member of his new higher taxon "Prionoglossa," giving it equal rank with other groups such as Taenioglossa and Ptenoglossa. Jeffreys (1859a) thought these animals the only surviving members of the otherwise extinct genus *Euomphalus* Sowerby,

1814. Fretter (1945) showed in a detailed anatomical study that *Omalogyrida* (Philippi, 1841) differs greatly from the "prosobranchs" with which it was traditionally placed. *Omalogyrids* have regained interest in recent years because of their presumed basal position within the heterobranchs (Haszprunar, 1988; Ponder, 1990, 1991). Their exact relationships remain uncertain; recent suggestions (Bandel, 1996; Pacaud & Le Renard, 1996) to combine the *Omalogyridae* with several other families in a superfamily *Architectonicoidea* are not supported by anatomical data (Healy, 1993; Huber, 1993).

At the nomenclatural level, certain confusion exists in the literature about the usage of genus-group names such as *Ammonicera* versus *Ammonicerina*, and about the identity- and authorship of *Omalogyrida*'s type species.

The discovery of an *Ammonicera* species in the Florida Keys, representing the smallest gastropod known in the United States, is here used to summarize existing data on *Omalogyridae* in the Atlantic Ocean and to address additional taxonomic problems.

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ABBREVIATIONS USED

AMNH American Museum of Natural History, New
York, U.S.A.

BMNH The Natural History Museum, Ujjidon, Unit-
ed Kingdom

FMNH Field Museum of Natural History, Chicago,
U.S.A.

MLP Museo de La Plata, Argentina

MNCN Museo Nacional de Ciencias Naturales, Ma-
drid, Spain

MNHN Museo Nacional de Historia Natural, Santiago,
Chile

ZMB Zoologisches Museum, Humboldt Universitat,
Berlin, Germany

SEM Scanning Electron Micrograph

RESULTS

Familia Omalogyridae G. O. Sars, 1875: 215 [as Homalogytidae]

(often erroneously credited to Fischer, 1885; e.g., Abbott, 1974)

Genus *Ammonicera* Vayssiere, 1893

Ammonicera inornata Rolan, 1992

(Figures 1-8)

Omalogijra species. — Vokes and Vokes, 1984: 168, figs. 7, 7a

(SEM).

Ammonicera minorialis Rolan, 1992: 40, 42, figs. 10, 11 (teleoconch), 13, 15 (protoconch) (all SEM).

Holotype: (MNCN 15.05/6794): shell diameter 0.35

mm; type locality: north of Cuba, Baracoa; holotype from 4 m depth.

Type material studied: 3 paratypes, AMNH 226450, from Kape locality.

Florida material studied: 2 Florida Keys specimens collected and observed *in situ*, one each from station FK-045 [Indian Key Fill, Mile Marker 79, Monroe County, 24°53'25"N. 80°40'28"W, Gulf side, rocks in 0.5-1 m among *Thalassia/Halodule* seagrasses, 20 September

1996] and station FK-062 [Missouri Key, Mile Marker 39.5, Monroe County, 24°40'29"N, 81°14'21"W, Gulf side of Missouri-Ohio Key bridge, subtidal rocks, 14 April 1997]. Also empty shells from sta. FK-040 [Missouri Key site as above, 12 March 1996], FMNH 279010 (1 shell); FK-057 [Missouri Key site as above, 26 September 1996], FMNH 279011 (10 shells incl. SEM material), AMNH 288137 (5 shells). All localities were fully marine and were sampled by the authors by "rock washing" (brushing and rinsing of rock surfaces).

Distribution: Now known from north and south coasts of Cuba (Rolan, 1992), the Florida Keys (this paper), and the Yucatan Peninsula (Vokes & Vokes, 1984).

Description: Shell (Figs. 1-2) extremely minute, diameter 0.34-0.46 mm (0.2-0.4 mm, fide Rolan, 1992), planispiral, tightly coiled, glossy, uniformly dark brown, resembling a miniature ammonite in shape and sculpture. Protoconch (Figs. 3^a) of 1.3 whorls (identical in SEM but described as ".3/4 whorl," by Rolan, 1992), diameter 120-135 μ m, distinctively sculptured with one major spiral cord at mid-whorl, reticulate sculpture peripheral to major cord, and .3—4 smaller spiral ridges central to major cord. No distinction of a separate larval shell ("protoconch 11"), indicating the absence of a free swimming larval stage. Coiling near-planispiral, with slight initial hyperstrophy (compare Figs. 3 and 4). Te-

leucoconch of about 1.3 rounded whorls (1-1.5 whorls fide Rolan, 1992), sculptured with prominent elongated axial tubercles, regularly spaced, equally sized, beginning immediately after protoconch, numbering 15-19 (1.3-1.7 fide Rolan, 1992) on body whorl, fading to no axial sculpture at the periphery. Tubercles and spaces between also with fine growth lines. Periphery (Fig. 6) uniformly rounded, smooth except for fine growth lines. No distinct spiral sculpture (but occasionally with extremely fine lines, see specimen in Fig. 1). Outer lip (Figs. 1-2) thin, sharp, ending in a single plane perpendicular to the plane of coiling; aperture circular; columella without folds or grooves. Head-foot (Figs. 7-8) translucent to nearly transparent. Animal gliding rapidly on short foot, with blunt, very active propodium. Shell held nearly vertically as the snail crawls. Transparent operculum on hindfoot serving as a support for the coil of the shell. Head with two finger-shaped tentacles, each held in an erect arch curving toward the midline; eyes black, near base of tentacles. Radula and internal anatomy not studied.

Habitat: Animals not observed in situ, but collected from shallow subtidal rocks covered on one or several surfaces with various polychaete worm tubes, marine diatoms, sponges, tunicates, and numerous other attached or free-living mollusks. Diet unknown (but see below).

Remarks: Although the diet of *Ammonicera minor-talis* has not been confirmed, it is likely to feed on the variety of algal species growing in its subtidal rock habitat, based on literature records on the habitat/taxa of other *Omalogyridae*: on *Codium* and *Zostera* (*Omalogyra atomis* [as *Eliomphalis nitidissima*] — Jeffreys, 1859a, 1859d); on *Ulva* (*O. atomus*—Fretter, 1948); on *Ficinia* (*A. rota* — Nordsieck, 1972); on *Ulva* and *Enteromorpha* (*O. atomis* — Fretter & Graham, 1978; Graham, 1988); on *Fucus*, *Laminaria*, *Cladophora*, *Corallina*, *Ulva* (*Ammonicera rota* — Fretter & Graham, 1978); on *Padina* (Hawaiian *A. japonica* — Kay, 1979); piercing algal cells and sucking out the contents, and depositing egg strands on bases of *Cladophora* (*A. rota* / *A. fischeriana* — Franc, 1948; Graham, 1988); on *Halimeda* (*A. japonica* and others — Sleurs, 1985a, 1985c); on *Zostera*, *Ulva*, *Codium*, and epiphytic diatoms (*O. atomis*, *A. fischeriana*—Cannon, 1993). Bullock et al., 1990, provided the most detailed account, reporting Azorean *O. atomis* and *A. fischeriana* from a variety of algae, including

' Ascertained using the method of Taylor as summarized by

[Lilonski & Liitz (1980: 50, fig. 4)

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Figures 1-6. *Ammonia minor*. shells by scanning electron microscopy (from different shells, F'MNH 279011).
1. Apical view.

2. Umbilical view. 3. Protoconch (detail of fig. 1). 4. Protoconch (detail of fig. 2). 5. Apertural view. 6. Dorsal view (from "above,"

as seen in crawling animal). Scale bars: Fig. 1 = 100 μ m (Figs. 2, 5, 6 at same scale); Fig. 3 = 20 μ m (Fig. 4 at same scale).

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Figures 7-8. *Ammonia minor*. sketch of living animal.

Maximum shell diameter = 0.42 mm, 7. Right lateral view. 8.

Dorsal view.

Enteromorpha, Cylindrocapsa, Viva, Pterocladia, Petionella, Halopteris, Asparagopsis, as well as Codium. Omalogramma atomus, which they also found on Gelidium and Sargassum, was the dominant species on Chondria and the only mollusk found on Funaria in that study.

DISCUSSION

Species-level identification: Rolan (1992) described this species based on empty shells collected from north and south coasts of Cuba (3-20 m). A comparison with the excellent original illustrations and with paratypic material at AMNH proved the identity of the Florida Keys specimens. No other known Atlantic species combines such axial teleoconch sculpture with reticulated sculpture of its protoconch. Rolan apparently was unaware of an earlier record of this form, as "*Ottialogyra* species," by Yokes and Yokes (1984) who collected it in Arrecife Alacran, about 140 km north of Progreso, Yucatan, in the Gulf of Mexico.

According to Rolan (1992: 42), only *Ammonicera japonica* Habe, 1972, described as "Japan's smallest gastropod" from Honshu, is "superficially similar but it has very constant spiral striae." Habe's species (1972:116, figs. 1-4) was described as 0.42-0.68 mm in diameter, dark brown in color, with 'about 10 annulations in the body whorl' (Habe, 1972:116). Habe did not mention or illustrate the spiral sculpture noted by Rolan.

Additional specimens were described and illustrated as *Ammonicera japonica* from Hawaii by Kay (1979:92, figs. 32A-C [SEM]), as *Omalogyra*; earlier reported by Kay & Switzer, 1974:278, table 1, from Fanning Island). Kay

mentioned sculpture "from 16 to 18 axial ribs on the last whorl, the ribs becoming obsolete at the periphery." Spiral striae were not described but faint spiral sculpture is visible in one illustrated shell (Kay, 1979:fig. 32B).

Sleurs' (1985a:4-5, pi. 1, figs. 1, 6, 9 [SEM]; as *Omalogijla*) description of *A. japonica* from Papua New Guinea was very similar. He described the protoconch in detail "with reticulated sculpture at the abapical side" (his fig. 9); spiral sculpture of the 0.3 to 0.45 mm large teleoconch was not discussed, but shows very faintly in one SEM illustration (his fig. 6). Fukuda's illustration of this species from the Ogasawara (Bonin) Islands (1994:pl. 35, fig. 697a-c; as "*Omalogijla*" *japonica*), shows no spiral sculpture. The large specimen illustrated (0.4 mm) has about 19 axial ribs.

The protoconch and teleoconch sculpture of the shells of *Ammonicera minor* and *A. japonica* are extremely similar according to the SEMs provided by Rolan (1992), Kay (1979), Fukuda (1994) and Sleurs (1985a), respectively, and suggest synonymy of the Caribbean and Indo-Pacific species. Faint spiral teleoconch sculpture appears to occur in some individuals of both nominal species. However, the disjunct distributional pattern makes further study necessary. No form has been described or recorded from the eastern Pacific (Shasky, 1989).

As also noted by Rolan (1992), *Ammonicera iniuortalis* is similar to the European *A. rota* (Forbes & Hanley, 1850) in its teleoconch characters (but the latter has a greater number of whorls and axial tubercles continuing over the periphery). *Ammonicera rota* has, however, a very different protoconch without reticulated sculpture (see, e.g., Rodriguez Babio & Thiriot-Quie\Teux, 1974: pi. 2, F-H; as *A. fischeriana*). Also similar is *A. plicata* Sleurs, 1985, from the Maldives (19S5b:20 ff, figs. 2, 7, 10, 13, 14), which has a larger teleoconch (0.45^ to 0.65 mm) with weaker axial ribs and a protoconch lacking the reticulate sculpture present in *A. minor-falis* and *A. japonica*.

Genus-level identification: Omalogyridae currently comprises three recognized extant genera: *Ammonicera* Yayssiére, 1893, *Omalogtjra* Jeffreys, 1859, and *Retro-tortina* Chaster, 1896. The last (with type species by monotypy: *R. fuscata* Chaster, 1896) has a sinistral teleoconch that distinguishes it from *Ammonicera* and *Omalogtjra*.

Bandel (1988:9) also placed *Orbitestella* Iredale, 1917, in this family, but Ponder (1990) showed that this genus belongs in the Yalvatoidea, not OmiJogy roidea. Bandel (1988), who viewed om;ilog\Tids as small-bodied members of Architectonicidae or Architectonicoidea (pp. 10, 17), attempted to introduce a new fossil genus "*Neamphitomaria*." but did not designate a type species. Ban-

del (in Dockeiy, 1993:92) subsequently provided such a

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designation (the Upper Cretaceous Psctidomalaxis stan-
toni Sohl, 1960) and thus \ahdated Ncainphitomaria of
that date [not as of 1988 as is frequently cited; see ICZN
Art. 13(b)]. Amphitomaria Koken, 1897, and Neamphi-
tomaria Bandel, 199.3, were then placed in a new family,
Amphitonariidae, by Bandel (1996), thus removing the
genus agiijn from the Omalogyridae.

The placement of the present species in the genus
Ammonicera, rather than Omalogijra, is here accepted
because of (1) its protoconch sculpture with strong spi-
ral ribs and grooves (in contrast to small tubercles in
Omalogijra; e.g., Rolan, 1992); (2) the presence of dis-
tinct cephiilic tentacles (absent in Omalogijra); and (3)
its strong teleoconch sculpture (absent or weak in Om-
alogyra). The kniovvn radulae of Omalogijra and Am-
monicera (not yet studied for A. mhwrtalis) are so dif-
ferent between members of the two nominal genera that
Sleurs (1985c: 181) suggested that they might belong to

different families. However, published radular data differ even within the two genera: *Omalogijra radulae* have been described as either uniserial (Jeffreys, 1859, 1867; Thiele, 1929; Sleurs, 1985c) or with a formula of 1-1-1 (G. O. Sars, 1878; Thiele, 1929; Egorova, 1991). Those of *Ammonicera* have been described with a formula of 1-1-1 (Vayssiere, 1893) or 1-1-0-1-1 (Sleurs, 1985b, c), and so definitive conclusions must await a detailed comparative study.

Unfortunately, the taxonomic history of *Ammonicera*, *Omalogijra*, and their included species is exceedingly complex and confused (see discussion below).

REMARKS ON *AMMOTSICERA* AND ITS TYPE SPECIES

Ammonicera was introduced by Vayssiere (1893:16 ff.) for *Homalogijra fischeriana* Monterosato, 1869. He provided a full anatomical description based on histology and studies of the radula. Franc (1948:142 ff.) and Sleurs (1985a:9) questioned the identity of Vayssiere's material, assuming that his work was based on misidentified "*Omalogijra rota*" Forbes and Hanley, 1850. Compared to Gaglioli's descriptions and illustrations (1993:933-04, 934-03-04), Vayssiere's line drawings of the shell (1893: figs. 8-9) seem to represent typical *A. fischeriana* in color pattern and relatively fine crenulations of the periph-

ery, although the sketched pronounced axial ribbing is more representative of the nominal species *A. rota*. Monterosato himself considered the two nominal species as varieties of one (e.g., Monterosato 1872:38; 1875:29), and many recent authors (e.g., Fretter & Graham, 1978; Backeljau et al., 1984; Knudsen, 1995) have deemed them synonymous (see also Hoisaeter, 1968; van Aartsen et al. 1984). Gaglini (1993), on the other hand, argued convincingly for the presence of two sympatric species. Whether or not they will prove to be synonymous, they are without doubt so closely related and morphologically similar that it will not impact interpretation of the nominal genus *Ammonicera* (in contrast to Sleurs, 1985a). In addition to Vayssiere's extensive description, pub-

lished biological information about this/these species includes description of gross anatomy (Franc, 1948), nervous system (Hulier, 1993), egg capsules (Franc, 1948 [summarized by Knudsen, 1995]; Graham, 1988), and feeding (Graham, 1988).

Ammonicera should not be confused with *Ammonicerina* — see synonymy of *Omalogyra* (below).

REMARKS ON OMALOGYRA AND ITS TYPE SPECIES

Omalogyra was introduced by Jeffreys (1859b) in the midst of an engaged discussion (with Clark, 1859) ul-

mately involving the identities of *Helix nitidissima* Adams, 1800, "*Skeneia*" *nitidissima* sensu Forbes and Hanley, 1850, and "*Tentacatella*" *atomus* Philippi, 1841. The current understanding of *Omalogijra* is based on Fretter's (1948) excellent anatomic study on British animals identified as *O. atomus*. Other published information on this species includes gross anatomy and radula (G. O. Sars, 1878), nervous system (Huber, 1993), spermatozoa (Healy, 1993), and egg capsules (Graham, 1988; Knudsen, 1995 [However, it should be noted that the accompanying SEM shell photographs, Knudsen's fig. 5, seem to be of a skeneopsid, not of *O. atomus*]). The "eggs" of

O. atomus as described by Jeffreys (1867) and Lebour (1937) were subsequently recognized as misidentified glandular structures (Fretter, 1948).

No type material for any of these nominal taxa could be located; our following discussion thus has to concentrate on literature review: *Helix nitidissima* J. Adams, 1800, was introduced with a short description and three illustrations (here reproduced in Fig. 9). The species was accepted and cited, in various generic combinations, by subsequent authors (e.g., Weinkauff, 1868:266, as "*Spira nitidissima* Adams"). Many authors have considered *H. nitidissima* J. Adams, 1800, as synonymous with *Tentacatella atomus* Philippi, 1841 (e.g., Fischer, 1857; Weinkauff, 1868; Fretter & Graham, 1978; Rolan, 1983; Gra-

ham, 1988; Poppe & Goto, 1991; Rosenberg/Malacolog,
1997). The original description by Adams (1800: 4, pi.

1, figs. 22-24) was based on the shell alone: H.[elLx]
testa duobus anfractibus, subtihsime transverse striata.
Obs. Corneous, pellucid, umbilicated; easily distin-
guished by the uncommon briUiancy of its glossiness."
Original figure 23, said to be of "natural size" (1800:6)
measures nearly 3 mm. The shell, much too large to be
a European omalogyrid species, was subsequently rec-
ognized as "evidently the fry of Zonitcs radiatuliis [J.
Alder, 1830]," a land snail, by Jeffreys (1867:71). The
holotype of H. nitidissima was not located (K. Way,
BMNH, pers. comm., 1997). The interpretation as a
young stage of a British land snail is here accepted; H.
nitidi.ssima Adams is not a senior synonym of T atomiis.

Much of the interpretation of "nitidissima " by sub-
sequent authors was based on "Skenea" nitidissima sensu
Forbes and Hanley, 1850, who used diis name for a dif-
ferent species. Several authors erroneously credited
Forbes and Hanley with the description of a new species

[Begin Page: Page 6]

/C-^ /CtJ

tB

Jug^

10

Figure 9. Reproduction of original illustrations of *Helix nitidissima*]. Adams, 1800 (from Adams, 1800: pi. 1, figs. 22-24).

Figure 10. Reproduction of original illustrations of *Tnincatella atomiis* Philippi, 1841 (from Philippi, 1841: pi. 5, figs. 4a-d).

"*Skcnca nitidissima* " {e.g., Jeffreys, 1860; Nordsieck, 1972; Nordsieck & Garcia-Talavera, 1979; Gaglini, 1993). However, Forbes and Hanley themselves (1850: 158) cited the species as "*S.lkcncal nitidissima*, Adams" with full page and figure reference to Adams' original work. It is this misidentified "*nitidissima scn.sti Forbes & Hanley* " that enters into the various lengthy published chscussions comparing "*nitidissima*" and *TntncatchHa atomus*.

Philippi (1841:54, pi. 5, figs. 4a-d) described and illustrated *Tnincatella atomtis*, collected in Sorrento (Campania, southern It;ilv). He emphasized that he was

able to study the animal in detail at a magnification of 60 times and placed it in *Tnincatella* because of the animal's similarity to members of that genus. In 1844, he re-described the species (p. 134, pi. 24, fig. 5; again as "*n. sp.*") and reproduced his 1841 illustrations of *T. atomis*. Philippi's (1841) illustrations, here reproduced in Fig. 10, show a living specimen with planispiral shell (with logarithmic growth), tapering tentacles, an operculum, and a representation of actual size of about 0.5 mm. The type material has not been located in Berlin or Santiago (von Rintelen, ZMB, pers. comm., 1997; MNHN, pers. obs., 1997).

Forbes and Hanley (1850:158-160, pi. 73, figs. 7, 8) described and illustrated a British shell under the name "*S. nitidissima*, Adams"; they did not mention the living animal. They placed *Philippis Tnincatella atomis* with question mark, in synonymy. Jeffreys (1859a: 109-111, pi. 3, figs. 15a, b, 16a-c) discussed the species, as *Euomphalus nitidissima*, with a sketch of the animal (showing ciliated head lobes, no tentacles, and a unise-

riate radula). He reported its range as 'from the Shetlands to Sicily, and probably far beyond these limits' (p. III) based in part on the synonymy of *Tnincatella atomis* of Philippi, and expressed his astonishment over Philippi's "mistake" of describing the animal so differently (i.e., with tapering tentacles).

Much of the ensuing confusion was based on (1) the treatment of Philippi's Italian "*Tnincatella atomtis*" specimens as members of the British "*Omalogt/ra nitidissima*" .sensu Forbes and Hanley, and (2) the discrepancy between gross anatomical descriptions of these two species, i.e., with or without tapering head tentacles, respectively.

Clark (1859:410¹³, text-figure), after reexamining British animals reconstituted from dried specimens, disagreed with Jeffreys and corroborated the correctness of Philippi's figure of an animal with triangular tentacles, the large eyes embedded at the center of their bases. "It appears quite clear that Mr. Jeffreys has delineated his animal with rounded lobes, or, in other words, with the tentacles retracted. . ." (p. 411). Jeffreys (1859b:498) rebutted: "What Mr. Clark supposed to be tentacula must have been the shrivelled lobes of the veil. . ." Fischer (1859:364-367) joined Clark in criticizing Jeffreys (1859c), assuming that the latter had described a larval stage with vela instead of tentacles. Jeffreys then (1860:108-111), in rebuttal of Fischer, affirmed that his observations were based on adult specimens without tentacles. Finally, in *British Conchology*, Jeffreys (1867:67-71, pi. 1, fig. 5; 1869:209, pi. 70, fig. 2) again described the shell and animal in detail, reaffirming his opinion of Philippi's error, but recognized the priority of "*Omalogt/ra atomus*" (Philippi) over "*Shenea nitidissima*" of

Forbes and Hanley. This "anatomically corrected" *Homalogi/ra atomtis*, with "Skenea" nitidissima sensu Forbes and Hanley in sMionvinv, is the *Omalogt/ra atomtis* described in detail by Fretter (1948) and that currently forms our concept of the genus.

Unfortunately the original figures of *Tnincatella atomtis* Philippi, 1841, are in conflict with the descriptions of Fretter. Philippi's illustrated gross morphological details (i.e., tapering tentacles) are indicative of *Ammonia*. Meanwhile, the sketched smooth shell appears in line with the current concept of *Omalogt/ra*. In the absence of type material, it is impossible to explain this discrepancy. It is possible that Philippi's material contained members of both genera and his illustration is a composite based on more than one species.

In the interest of nomenclatural stability, we base our interpretation of Philippi's *Tnincatella atomtis* on his illustration/description of the shell alone (excluding the anatomy in original fig. 4c), thus preserving this name for *"Skenea" nitidissima* sensu Forbes and Hanley, 1850 (non Adams, 1800), and *Omalogtjra atomus* sensu Jeffreys, 1859, as well as Fretter, 1948.

The taxonomic confusion has been compounded by uncertainty about the type species designation and the

date of introduction of *Omalogtjra*. Some authors [e.g.,

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Waren, 1980:12) cited it as having been introduced by Jeffreys (1860), with type species *TnincatcUa atoinus* Philippi, 1841, by monotypy. Others (e.g., Wenz, 1939: 647-648) gave "*O. niticliissiina* (Forbes & Hanley)" as type species. The date of description is often erroneously cited as "1867" (e.g., Abbott, 1974; Castellanos, 1989a; Vaught, 1989; Rios, 1994).

The generic name "for the reception of these anomalous *nioUusks*" was in fact proposed by Jeffreys (1859b: 498). In that paper, he referred by name to "*Eitoinphalus niti(li.ssiini.s*" (with reference to his earlier, 1859a, article), to "*E. Rota*" and its "variety *tricariiuita* of Webster." In the referenced article, he additionally stated a synonym for '*E. nitidi.'isimus*: "I have no doubt that it is the *TnincatcUa atoiuti.s* of Philippi" (1859a:III). Jeffreys did not indicate a type species. Following ICZN (1985: Art. 69(i)), there are four "originally included nominal species":

Helix nitidissima J. Adams, 1841. Now considered a land snail

[Jeffreys recognized the misidentification only in 1867; his (1859a, b) usage thus cannot be construed as "deliberately used in the meaning of a previous misuse" (ICZN, 1985; Art. II(i)).

Tinctaria atomus Philippi, 1841 [in synonymy],

Skeneia rota Forbes and Hanley, 1850. Now considered a member of *Amnicornia*.

Skeneia tricarinata Webster, 1856. Described as a potential new species; subsequently (beginning with Jeffreys in Webster, 1857) considered a variety/subspecies of *S. rota*.

Jeffreys (1867:69 ff.) synonymized "*Skeneia nitidissima*"

nitidissima Forbes and Hanley under *Tinctaria atomus*, after recognizing the true *Helix nitidissima* Adams as a

land snail. He also synonymized *Skeneia tricarinata* Webster under *Skeneia rota*. No type species was designated.

Jeffreys therein changed the generic name to *Homalogiira*, an unjustified emendation. The first authors to select a type species appear to have been Bucquoy et al.

(1884:78) who stated "*Tinctaria*: *Homalogiira atomus* Philippi sp. (*Tinctaria*)."

We therefore offer the following synonymies:

Homalogiira Jeffreys, 1859b:498; type species by subsequent designation of Bucquoy et al. (1884:78), *Tinctaria nitidissima* Philippi, 1841.

Ammonicerina O. G. Costa, 1861: 71; type species by subsequent designation of Dall (1927b: 1.34, as "*Ammonicerina*"). *Ammonicerina simplex* O. G. Costa, 1861. Preoccupied by *Ammonicerina* O. G. Costa, 1856 [Protista], This taxon is usually placed in synonymy of *Ammonicera* (e.g., Palazzi & Gaglini, 1979); however, its type species by subsequent designation belongs to *Omalogijra*.

Homalogyra Jeffreys, 1867:67 (an unjustified emendation).

Note: In the description of their new genus *Transomalogi/ra*, Palazzi and Gaglini (1979:3.3) made *Ammonicerina simplex* O. G. Costa, 1861. the type species by original designation. This would make *Transomalogijra* an objective synonym of *Ammonicerina* and a subjective synonym of *Omalogt/ra*. However, as pointed out by

Waren (1991:74), the type species was misidentified, with Palazzi & Gaglini's illustration actually showing a shell of *Adcuomphalus ammoniformis* Seguenza, 1876. Waren (1991) thus placed *Transomalogijra* in the synonymy of *Adcuomphalus* Seguenza, 1876, as a genus incertae sedis in the "Archaeogastropoda."

Omalogt/ia atomus (Philippi, 1841)

Tnincatella atonuis Philippi, 1841:54, pi. 5, fig. 4a-d [excluding

the sketched animal in fig. 4c].

Skenea nitidissima (Adams) sensu Forbes and Hanley. 1850, et

anct. [non *Helix nitidissima* J. Adams, 1800].

Homalogijra atomus var. *vitrea* Jeffreys, 1867:69.

Homalogijra atomus var. *fasciata* Monterosato, 1877:418.

Notes on other named "varieties":

Homalogipa atonis var. *maculata* Dautzenberg and Durouchoi LX, 1914:27. The authorship of this name is usually credited to Monterosato, 1875 (e.g., Gaghni, 1993: 928-02). However, Monterosato's applications and some subsequent citations of the name are not available for nomenclatural purposes because they represent nomina nuda (Monterosato, 1875:29; 1878:88; Bucquoy et al., 1884:324). The first available introduction appears to be that of Dautzenberg and Durouchoux (1914).

Ammonicerina atomus "var. *pallida* Monterosato 1884" as cited by Gaghni (1993:928-02) is likewise not available as of that date. Monterosato's usage (1884:22) of "var. *pallida*" is a nomen nudum, as is his *Homalogijra atomus* var. *zonata* Monterosato (1878:88), subsequently cited as "var. ex colore 2, *zonata* Monts." by Bucquoy et al. (1884:324; likewise a nomen nudum).

Homalogijra atomus var. *nautilionis* De Gregorio,

1889, was recognized by Monterosato (1890:141) as a juvenile of *Capuhis ungaricus* (Linnaeus, 1758). Nevertheless, the name *nautilifonnis* De Gregorio, 1889, was retained by some authors to describe an *Omalogi/ra* morph with a much widened body whorl (e.g., Nord-sieck, 1972:148; Gagghni & Curini Galletti, 1978:210, fig. 2c), GagUni (1993:928-02-3) introduced a new infraspecific name for this morph, *Omalogijra atomus* var. "*inflata*."

Homalogi/ra atomus var *poh/zona* "Brusina mss. (fide Monterosato)" in Bucquoy et al., 1884:324, pi. 37, fig. 32. Earlier references to a variety "poh/zona Brusina" by Monterosato (1872; 1875; 1878) are unavailable because they were stated in *sviiommv* or as *nomina nuda*. Gagghni' (1993:931-01, 9.31-02-3) showed that this is a potential *sviionvm* of *O. simplex*, not *O. atomus*.

CURRENT COMPOSITION OF OMALOGYRIDAE

Recognized western Atlantic Species: [regions of type localities in brackets]

Ammonicera alhospeciosa Rolan, 1992:44, figs. 17, 19, 21
[Cuba]

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Amnwnicera rirnmrirm Rolan, 1992:45, figs. 23, 26, 28

[Cuba]

Amriumicera familiaris Roldn, 1992:42, 44, figs. 16, 18, 20

[Cuba]

Aintronnicera lineofusciita Rolan. 1992:44-45, figs. 22, 24—25,

27 [Cuba]

Ammonicera minorfalis Rolan. 1992:40, 42, figs. 10-11, 13, 15

[Cuba]

Amnu>nicera sculpturata Rolan, 1992:40, figs. 9, 12, 14 [Cuba]

Omalogijra atomiis (Philippi. 1841:54, pi 5, figs. 4a-d) [Med-
iterranean]

Omalogtjra burdwoocliann (Strebel, 1905:52, pi. 6, fig. 85a-c

[Burdvwood Bank, south of Falkland Islands]

Omaloayra fiiscopardahs Rolan, 1992:36, 38, figs. 1, 3, 5, 7

[Cuba]

Onmlogtjra taludana Castellanos, 1989a:88-89, figs. 1, 2 (plus

sketch of apertural aspect in 1959b:pl. 1, fig. 10) [off San

Jorge Gulf Argentina]

Omaloajira zebrina B-olin. 1992:38. figs. 2. 4. 6. 8 [Cuba]

For the western Atlantic, eleven omalogyrid species are currently recognized. Of these, eight are to date only known from Cuba (all described by Rolan, 1992). Two others, *Omaloajira bunlwoodiana* (Streliel, 1908) and *O. taludana* Castellanos, 1959, are known from subantarctic waters off South America. Two omalogyrid species are now recognized from the east coast of the United States; *Ammonicera minorialis* and *O. afoniis*.

Several other nominal omalogyrid species have been reported for the western Atlantic Ocean, but need to be excluded from that fauna:

"*Omalogyra planorbis* . A nominal species in the western Atlantic frequently cited as an omalogyrid is *Lippistcs? planorbis* Dall, 1927a: 131, originally described from "off Fernandina," Florida. This deep-water species was re-described in detail by Moore (1971: 114-116, fig. 1) as *Omalojira planorbis*, and subsequently called *Omalojira* (*Ammonicera*) *planorbis* {e.g., Abbott, 1974:81; Rios, 1994:60}. This taxon was placed in *Palazzia* Waren, 1991, as an "archaeogastropod" group of uncertain affiliations, tentatively assigned to *Skeneidae* (Waren, 1991:

74, 76).

"*Ammonicera jischctiana*": Nortlsieck (1972:149) referred to "*Ammonicera fischeiana* (Monterosato, 1869) = *densicostata* [sic] (Jeffreys, 1884)" in "Westindien," without further explanation. This synonymy is erroneous. The West Indian record for this Mediterranean species is based on Watson's (1886) "Challenger" material of "*densicostata*" as explained in the following.

"*Omalogyra* (*Ammonicera*) *densicostata*": *Omalogyra densicostata* Jeffreys, 1884:129, pi. 10, fig. 1. was described from "Porcupine" stations (1098-2002 m) off the coast of Portugal. Additional material from a "Bulldog" cruise off Labrador (2967 m) was also included in the original description. Abbott (1974:81) reported this species as *Omalogyra* (*Ammonicera*) *densicostata* from deep water off Portugal, the Azores, and Labrador. Moore (1971:114) showed that the Labrador ("Bulldog") material in fact belongs to "*Liphiostoma planorbis* Dall, 1927," thus removing the Labrador record for "*O.*" *densicostata*.

Watson (1886:677) added a "*Omalogyra densicostata* (?)" record from north of the island of Culebra, between Puerto Rico and the Virgin Islands ("Challenger" station 24, 71.5 m). Moore (1971:115-116) doubted both the origin of the Challenger material and that of the shallow-water material reported by Dautzenberg (1889:46) for the Azores, thus restricting *densicostata*

again to the eastern Atlantic. The species was considered a member of the eastern Atlantic omalog\Tid fauna until recently (e.g., Sabelli et al., 1990; Gaglini. 199.3). Homalogifra densicostata was syiionymized imtler Adeiiomphaliis ammonifonnis Seguenza, 1876, and placed as an "archaeogastropod" of uncertain affiliations, tentatively assigned to Skeneidae (Waren, 1991:74 ff.).

Recognized eastern AtlanticAlediterranean Species: [regions of type localities in brackets]

Ammonicera biimayi Rolan. 1991:112, figs. 1.3-14 [Cape Verde Archipelago]

Ammonicera ftscheriana (Monterosato, 1869:274—275. pi. 13, fig. 1) [Mediterranean]

Ammonicern tignrn (Palazzi. 1988:105, figs. 8. 18) [Madeira]

Ammonicera midlistriata Rolan, 1991:112, 114, figs. 1.5-16 [Cape Verde Archipelago]

Ammonicera nolai Rolan. 1991:110. figs. 8-9 [Cape Verde Archipelago]

Ammonicera oteroi Rolan, 1991:110. 112, figs. 10-12 [Cape Verde Archipelago]

Ammonicern robusta Rolan, 1991:114-115. figs. 17-18 [Cape Verde Archipelago]

Ammonicera rota (Forbes & Hanley, 1850:160, pi. 73, fig. 10; pi. 88, figs. 1, 2) [Ireland]

Ammonicera rotundata (Palazzi, 1988:105, figs. 10, 21, 27) [Madeira]

Annonicera verdensis Rolan, 1991:109, figs. 6-7 [Cape Verde Archipelago]

Omalogira afomus (Philippi, 1841:54, pi. 5, figs. 4a-d) [Mediterranean]

Onuilogira discutus Palazzi, 1988:104, figs. 1, 20 [Madeira]

Omalogira simplex (O.G. Costa, 1861:72, pi. 11 figs. 3 a, b) [Mediterranean]

Omalogira undosa Palazzi, 1988:104, figs. 5, 15 [Madeira]

Retrotitiina fuscata Chaster, 1896:2 [Strait of Gibraltar]

In the eastern Atlantic, fifteen omalogyrid species are currently recognized, comprising ten species of *Ammonicera*, four of *Omalogira*, as well as *Retrotitiina fuscata* (for Mediterranean records see also Sabelli et al., 1990; Le Renard et al./CLEMAM, 1997). *Omalogira atcunus*

is the only species known from both sides of the Atlantic; it is widely distributed, ranging from the Mediterranean, Madeira, and the Azores to Norway, Iceland, Greenland, and in New England (Abbott, 1974; Bullock, 1969, 1995; Fretter & Gniliam, 1978; Thorson, 1944) from Maine to Rhode Island. Egorova (1991) recognized material from Antarctic waters, previously identified and cited as *O. atomits*, as members of a morphologically extremely similar species, *O. antarctica* Egorova, 1991.

Several other nominal omalogyrid species have been described for the eastern Atlantic. Of these, *Omalogyra apellia* Sykes, 1925:192, from off Portugal, was recognized as a member of the "archaeogastropod" genus *Eii-*

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Homalogijra Cotton, 1945, by Waren (1991:80). *Homalogijra granulosa* Svke.s, 1925, also from off Portugal, was placed in the "archaeogastropod" genus *Rctigyra* Waren, 1989 (see Waren, 1992:168). *Homalogijra paiadoxa* "Monterosato (? MS.)" of Svkes (1925:192) is a nominal. Two other nominal species introduced by Sykes

{*H. sititiosa* Sykes, 1925, and *H. (?) marshalli* Sykes, 1925) are in need of further study (see Palazzi, 1992). An additional Mediterranean species, *O. ausonia* Palazzi, 1988, was recently made the type of *Palazzia* Waren, 1991, and transferred to the "archaeogastropods," with tentative placement in the Skeneidae (Waren, 1991). Nominal species *Homalogi/ra oniata* Dautzenberg, 1889 (p. 46, pi. 4, fig. 9a-d), described from the Azores, is still in need of reinvestigation.

It should be noted that Palazzi (1988) used "*ausonia*" (Italy) and "*disculus*" (little disk) as nouns in apposition in the original descriptions; recent usage as "*Palazzia ausoniaca*" or "*Homalogi/ra discilla*" (e.g., Sabelli et al., 1990; Giannuzzi-Saveili et al. 1994; Arduini et al., 1995) are incorrect subsequent spellings.

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