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ON THE TAXONOMIC AFFINITIES OF COLLISELLA EDMITCHELLI (LIPPS) (GASTROPODA: ACMAEIDAE) A LATE PLEISTOCENE LIMPET FROM SAN NICOLAS ISLAND, CALIFORNIA

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On the Taxonomic Affinities of Collisella edmitchelli (Lipps) (Gastropoda: Acmaeidae) a Late Pleistocene Limpet from San Nicolas Island, California

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Abstract.—The taxonomic affinities between the extinct acmaeid Collisella edmitchelli (Lipps, 1966) and Recent California species has been previously studied using highly variable exterior shell characters. I use shell structure, a character I believe to be more conservative than either shell or radular morphology, to determine the taxonomic and phylogenetic relationships of this species. The shell structure of C. edmitchelli is identical to that of C. scabra (Gould, 1846). This shell structure group is not known to occur in any other acmaeid species. Although closely related to C. scabra, C. edmitchelli is morphologically distinct and is retained as a valid, extinct species known only from Late Pleistocene deposits on San Nicolas Island, California.

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Collisella edmitchelli (Lipps, 1966) is an extinct acmaeid limpet from late Pleistocene deposits on San Nicolas Island, California (33°16'N, 119°30'W). It was originally described as Acmaea mitchelli Lipps, 1963, but renamed because the name was preoccupied by Acmaea striata mitchelli Oldroyd, 1933. Taxonomic affinities between C. edmitchelli and Recent California species have been questioned several times. Lipps (1963) considered C. edmitchelli to be closely related to Collisella limatula (Carpenter, 1864) based on similarity of shell sculpture, including the presence of imbricated primary and secondary ribbing. McLean (1966) considered C. edmitchelli to be only superficially similar to other California acmaeids, based on shell morphology. He compared the ribbing of C. edmitchelli to the Japanese species *Collisella dorsuosa* (Gould, 1859) and noted the similarity in width of the interior margin to that of Collisella scabra (Gould, 1846). More recently, Marincovich (1976) has used shell sculpture to synonymize C. edmitchelli with C. scabra, based on apparent intergrades between the two species in Pleistocene deposits from the southern California mainland. Lipps (1963) commented that one of the best characters for inferring acmaeid phylogenetic relationships, the radula (a structure seldom preserved in the fossil record), was not available for study. Therefore, the suggested taxonomic relationships of these authors have been based on less reliable characters of shell morphology, which in many species is environmentally controlled. In the present study, shell structure is considered to be a more conservative character in acmaeid systematics than either shell or radular morphology. Thus, taxonomic and phylogenetic relationships inferred from shell structure are thought to be most accurate.

Theim (1917) was the first to recognize differences in the shell structure of acmaeids. Bøggild (1930) further expanded this work, describing eight patelloid shell structure groups. However, the use of shell structure was not applied to



Fig. 1. Relationship of internal shell structure to interior bands or layers, also showing derivation of the schematic representation of shell structure. A-D = structural elements, M = myostracum (= muscle scar). (Modified after MacClintock, 1967.)

patellacean systematics until the work of MacClintock (1963), in which the genus *Proscutum* was reclassified based on its shell structure and muscle scar position. MacClintock (1967) later published an atlas of patelloid shell structures, in which he recognized seven acmaeid and 10 patellid shell structure groups. Because acmaeid shell structure has remained stable (or conservative) during the late Cenozoic it may be used to infer the taxonomic affinities of *C. edmitchelli* with other species.

Dr. Edward Wilson, Department of Invertebrate Paleontology, Natural History Museum of Los Angeles County (LACMIP), made available to me on loan topotypes of *C. edmitchelli* (LACMIP Locality No. 4658). In addition, I examined both the primary type material of *C. edmitchelli* and the specimens reported by Marincovich (1976) from the upper terraces of the Palos Verdes Hills.

The topotypes were examined intact, except for a single specimen which was radially sectioned and fractured by rapid alternation of heating (Bunsen burner)



Fig. 2A. Cross-sectional view of *Collisella edmitchelli* (Lipps) (LACMIP Locality No. 4658). Shaded area indicates section illustrated in Fig. 2B.

Fig. 2B. Cross-sectional view showing structural elements. Arrows indicate areas from which the inner elements have exfoliated. MF = modified foliate structure, CCL = concentric crossed-lamellar structure, and M = myostracum; DM = dorsal margin. Camera lucida drawing.

and cooling (ice water) (MacClintock, 1967:110). This technique bakes the conchioline matrix, which then induces fractures to form around the structural elements. Specimens of other species exemplifying specific shell structure groups were also prepared by this method for comparison with the *C. edmitchelli* section.

The shell of *C. edmitchelli* contains four structural elements, which are expressed as visible concentric bands on the interior shell surface. The first structural element is visible as a wide dark interior margin and as the outer surface of the shell. The second element is considerably narrower and is present between the dark margin and the myostracum (= muscle scar). The third element is the myostracum, and the fourth is the large white apical area inside of the myostracum. These visible concentric bands are also found in the shell of *C. scabra*. The relationship of the shell structural elements to the concentric bands in a generalized acmaeid with five structural elements is shown in Fig. 1.

The structural elements in the shell of *C. edmitchelli* (Fig. 2) are identical to those in the shell of *C. scabra* (Fig. 3) in structure, position, and relative thickness. The shell structure of *C. scabra* was stated to be unique among California acmaeids by MacClintock (1967). The present study shows that this shell structure is shared with *C. edmitchelli*, but remains distinctive among California acmaeids.

Discussion

Based on shell morphology, I consider the specimens of *C. edmitchelli* reported by Marincovich (1976) from Late Pleistocene of the Palos Verdes Hills to be specimens of *C. scabra*. Marincovich's report of intergrades involves specimens only of the latter species. Thus, *C. edmitchelli* remains a valid species, as yet unknown from the California mainland.



Fig. 3. Schematic representation (cf. Fig. 1) of the shell structure of *Collisella scabra* (Gould). See Fig. 2B for legend. Dorsal shell surface at top of figure. (After MacClintock, 1967.)

Both *C. scabra* and *C. edmitchelli* have primary and secondary ribbing and crenulate apertures, but the species are otherwise dissimilar in appearance. The primary ribs of *C. scabra* (Fig. 4) typically range between 10 and 20, and they are approximately twice as wide as the secondary ribs. Some of the ribs may bear nodes or spines, but they are not imbricated. The primary ribs are triangular in section and project strongly at the shell edge, producing a heavily crenulate aperture. The anterior, posterior, and lateral slopes tend to be straight giving the species an angular appearance in profile. In *C. edmitchelli* (Fig. 5) the number of primary ribs ranges between 20 and 30, although some specimens may have as few as 18. Differences in size between the primary and secondary ribs are not as distinct as in *C. scabra*, and the ribs of *C. scabra* the ribs are imbricated and projection of the ribs at the shell edge produces only a slightly crenulate aperture. The anterior, posterior, and lateral slopes are convex, giving the shell a rounded appearance in profile.

The interiors of the two species differ markedly. The shell edge of C. scabra typically has fine digitations between the projecting primary ribs. These digitations are lacking in C. edmitchelli; instead these interspaces are smooth. The apical area of C. scabra is typically overlain with a thick white callus that is streaked with irregular brown markings. Collisella edmitchelli lacks a callus and the apical area is entirely white.

Thus, *C. edmitchelli* is retained as a valid, extinct species, closely related to and sympatric with *C. scabra* on San Nicolas Island during the late Pleistocene. As pointed out by McLean (1966) the reasons for the limited geographical and geological occurence of *C. edmitchelli* are not known. Perhaps the oscillating thermal conditions of the Pleistocene coupled with the insular environment of San Nicolas Island produced this offshoot of *C. scabra*. Because *C. scabra* is a predominately warm-temperate species, species differentiation may have occurred during a cold period, so the ancestral stock of *C. edmitchelli* was a cryophilic variant of *C. scabra*. Subsequent warming may have been adverse to

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Fig. 4. *Collisella scabra* (Gould). CALIFORNIA: San Francisco County, Southeast Farallon Island. (LACM Malacology Section Catalog No. 29858.)

Fig. 5. Collisella edmitchelli (Lipps). CALIFORNIA: Ventura County, San Nicolas Island. (LACMIP Locality No. 4658.)

C. edmitchelli and favored *C. scabra* which then repopulated the former cool areas. For a short period of time *C. scabra* occurred together with *C. edmitchelli* on San Nicolas Island. Extinction of *C. edmitchelli*, possibly due to thermal mortality, may have been hastened by competition or hybridization with *C. scabra*. *Collisella edmitchelli* is not known to have populated the adjacent mainland.

Collisella edmitchelli and *Notoacmaea lepisma* (Berry, 1940) are the only acmaeids from the California Pleistocene not known in the Recent fauna.

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