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FUNCTIONAL MORPHOLOGY AND TAXONOMIC SIGNIFICANCE OF A NOVEL CUTICULAR STRUCTURE IN CRETACEOUS RANINID CRABS (DECAPODA: BRACHYURA: RANINIDAE)

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ABSTRACT—Fossil raninid crabs, *Cretacoranina punctata* (Rathbun, 1935), from the Pawpaw Formation (Upper Cretaceous) of Fort Worth, Texas, exhibit an unusual cuticular morphology. Comparison of the cuticle of extant *Raninoides louisianensis* to that of *C. punctata* reveals general similarities in endocuticular, exocuticular, and epicuticular ultrastructure; however, their gross morphology is strikingly different. The surface of the carapace of *C. punctata* appears pebbled, much like the surface of a basketball, with closely packed, hexagonal caps. In cross-section, these caps are the upper portion of fungiform structures within convoluted exocuticle. Along the anterior margin, anterolateral margins, and pterygostomial region of the carapace of *C. punctata* each cap dips slightly posteriorly, creating a series of tiny terraces. In contrast to terrace lines, questa lines, spines, and nodes that provide frictional resistance in interactions with coarse-grained sediments, the fine relief and contouring of the pebbled surface of the carapace of *C. punctata* provides frictional resistance in interactions with fine-grained sediments. *Cretacoranina dichrous*, *C. trechmanni*, *C. testacea*, and *C. schloenbachi*, as well as *Eucorystes carteri* were all found to possess variations of the exocuticular structures seen on *C. punctata*. This pebbled surface has not been recognized in any other decapod taxon, nor has its structure and function been described previously.

INTRODUCTION

DECAPOD CRUSTACEANS are frequently represented in the fossil record by their carapaces, which are composed of calcified cuticle. For many fossil decapod taxa, classification is based primarily on morphological characteristics of the carapace such as its shape and contour; the number and placement of its spines, nodes, and grooves; and the form of its orbits. The preserved cuticle itself, however, has only recently been the subject of paleontological investigation (Feldmann and Tshudy, 1987; Vega et al., 1994; Feldmann and Gaździcki, 1998). The primary purpose of this paper is to re-evaluate the description of *Cretacoranina punctata* (Rathbun, 1935) and to describe its remarkable cuticular structure which has been, at best, briefly alluded to in some previous descriptions of raninid species. Secondly, fine details of the cuticle of several raninid species are applied to re-evaluate their systematic placement. Lastly, the function of the unique structure is discussed.

STRATIGRAPHY AND GEOLOGIC SETTING

Specimens of *Cretacoranina punctata* were collected from the Pawpaw Formation in the Washita Group of the Comanche Series in northeastern Texas (Fig. 1). In Texas, the Pawpaw Formation crops out in a narrow north-south trending belt between the Brazos and Red rivers and in an east-west trending belt in Grayson County (Root, 1975).

The Pawpaw Formation is composed of 2.5 to 24 m (Slocki, 1967) of dark gray to black, laminated, calcareous shale and claystone that weathers to a dark brown (McGill, 1954, 1967). The Pawpaw Formation is bounded by the Mainstreet Limestone above, and the dense, light gray limestone ledge of the Weno Formation below (Fig. 2) (Hendricks, 1967). The formation usually forms gentle slopes, although in some areas where gullies dissect the outcrop the formation tends to recede from the face of the Weno bench below, forming a steep escarpment (McGill, 1954, 1967). The Pawpaw Formation differs from other clastic units of the Washita Group by being softer and more highly plastic (McGill, 1954, 1967).

In the vicinity of Fort Worth, the Pawpaw Formation is approximately 7 m thick. The lower 2.5 m is composed of grayish-brown, soft, slightly silty, calcareous shale with two thin beds of sandy, brownish-stained limestone (McGill, 1954, 1967). The upper 4.5 m consists of soft, calcareous, grayish-brown shale that weathers to dark brown (McGill, 1954, 1967). About 3.5 m above the base of the formation, there is a compact layer of gray claystone that has a thin coating of iron on the exposed surface (McGill, 1954, 1967). The Pawpaw Formation has been described as locally fossiliferous (Cason, 1986). Fossils include foraminiferans, brachiopods, echinoids, pelecypods, cephalopods, shark teeth, fish vertebrae (Hendricks, 1967), as well as asteroids (Blake and Reid, 1998), gastropods (Adkins, 1918), a pterosaur (Lee, 1994), a nodosaurid (Jacobs et al., 1994; Lee, 1996), and decapods (Rathbun, 1935; Hendricks, 1967; Schweitzer Hopkins et al., 1999). Specimens of *Cretacoranina punctata* were collected from a claystone layer approximately 15 cm thick in the upper part of the formation, approximately 2.75 m above the compact layer of gray claystone.

Although some of the decapods from the Pawpaw Formation are represented only by claw fragments or molts, numerous specimens exhibit excellent preservation. Schweitzer Hopkins et al. (1999) noted that the preservation of delicate features such as surface ornamentation was excellent in several decapod taxa, including four species of *Xanthosia*. Specimens of *Cretacoranina punctata* are also excellently preserved, maintaining fragile structures such as the rostrum, suborbital spines, pereiopods, and the subtle contour and surface ornamentation of the carapace. The excellent preservation of *C. punctata* permitted detailed analysis of its cuticular structure and this analysis, in turn, made it possible to consider its implications for systematic placement of the taxon.

LOCALITIES

Approximately 260 specimens of *Cretacoranina punctata* were collected by Mr. Robert Reid from several Tarrant County localities within a 15 km radius of Fort Worth, Texas (Fig. 1). Most of the specimens were collected from the ''Oak Grove'' locality; however, specimens with preserved cuticle were collected at all localities listed. The following records were taken from the locality register of Robert Reid, whose skill in collecting, documenting, and preparing specimens made this work possible.

RR3, ''Motorola.'' Approximately 460 m north of the northeast loop of I-820, 150 m east of N. Beach Street, west of Fossil Creek Blvd., Haltom City, Texas. Pawpaw Formation. Approximately 32°50′55″N, 97°18′26″W, Haltom City, Texas 15′ Quadrangle Map.

RR4, ''Browning Site.'' Approximately 1.0 km north of the NE 820 Loop and St. Louis S.W. RR., 150 m east of the Sante Fe Trail in North

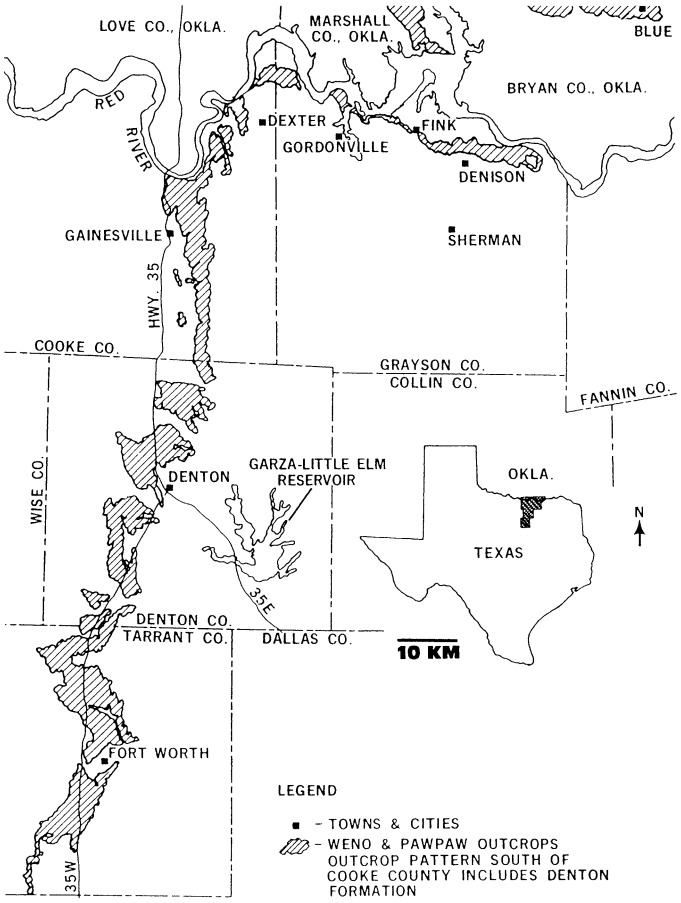

FIGURE *1*—Outcrop map of the Weno and Pawpaw formations, north-central Texas. Collecting localities for *Cretacoranina punctata* located in the Fort Worth area (modified from Root, 1975).

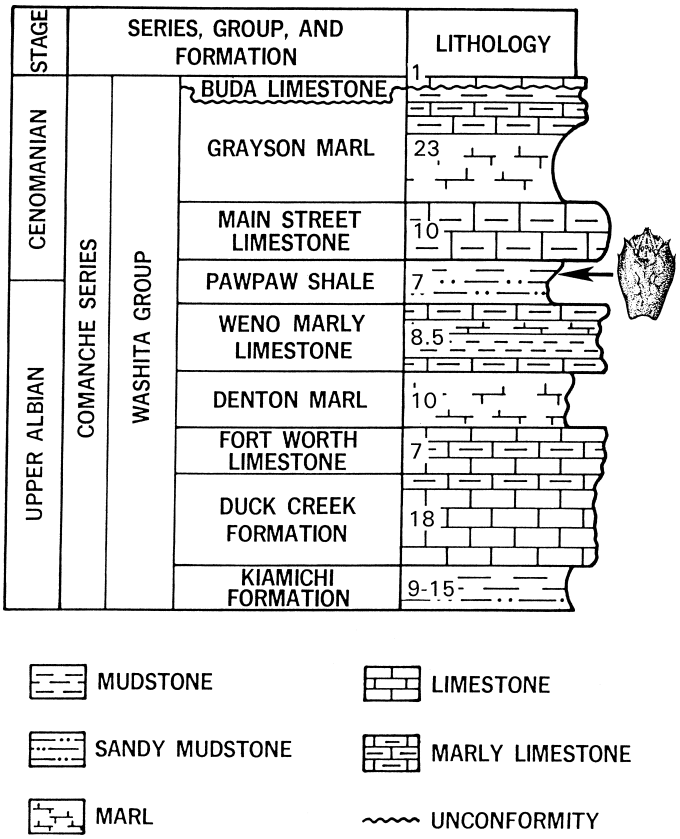

FIGURE *2*—Generalized stratigraphic column for the Comanche Series, including the Pawpaw Formation in north Texas (modified from Root, 1975). Values indicated represent formation thickness at Fort Worth, Texas, except for the Buda Limestone and Kiamichi Formation which are approximations in Tarrant County, Texas. All values indicated are rounded to the nearest meter and are from McGill (1967), except for the Buda Limestone, the Duck Creek Formation, and the Kiamichi Formation which are from Hendricks (1967). Not to scale.

Richland Hills, Texas. Pawpaw Formation. Approximately 32°50′55″N, 97°15′19″W, Haltom City, Texas 15′ Quadrangle Map.

RR6, ''Starfish Site,'' 800 m southwest of the intersection of East Berry Street and Old Mansfield Road, just east of the intersection of Ellis Ranch Trail and Annabelle Street, Fort Worth, Texas. Weno and Pawpaw formations. Approximately 32°41′58″N, 97°17′57″W, on the Fort Worth, Texas 15′ Quadrangle Map.

RR7a, ''Oak Grove.'' Approximately 100 m southwest of the Missouri Pacific RR. And 200 m north of I-20/SE I-820 Loop, along the steep escarpment of a small gully, Forth Worth, Texas. Pawpaw Formation. Approximately 32°40′24″N, 97°18′40″W, Fort Worth, Texas 15′ Quadrangle Map.

SYSTEMATIC PALEONTOLOGY

Order DECAPODA Latreille, 1802
Section PODOTREMATA Guinot, 1977
Subsection ARCHEOBRACHYURA Guinot, 1977
Family RANINIDAE De Haan, 1839
Subfamily NOTOPOCORYSTINAE Lőrenthey, 1929
Genus CRETACORANINA Mertin, 1941
CRETACORANINA PUNCTATA (Rathbun, 1935)
Figures 3, 4.1–4.6

Notopocorystes punctatus RATHBUN, 1935. RATHBUN, 1935, p. 8, pl. 12, figs. 14–16; STENZEL, 1944, p. 440.

Raninella mucronata RATHBUN, 1935. RATHBUN, 1935, p. 50, pl. 14, figs. 32, 33; FELDMANN AND MAXEY, 1980, p. 860; TUCKER, FELDMANN, HOLLAND, AND BRINSTER, 1987, p. 285; TUCKER, 1995, p. 123.

Notopocorystes parvus RATHBUN, 1935. RATHBUN, 1935, p. 48, pl. 12, figs. 11–13; STENZEL, 1944, p. 440.

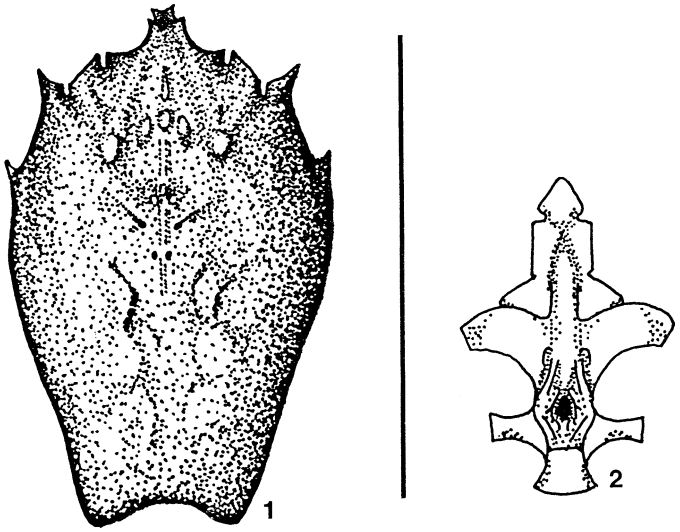

FIGURE *3*—Reconstruction of *Cretacoranina punctata*; *1*, dorsal surface; *2*, sternum. Scale bar = 1 cm.

Description.—Carapace small, obovate in outline, widest slightly anterior of midline, just posterior to anterolateral spine. Carapace weakly vaulted longitudinally, strongly vaulted transversely; maximum vault height about 60 percent maximum width, occurring at point of maximum width.

Rostrum elongate, extends beyond orbits, with two pairs of spines: first pair forming bifid termination, separated by deep V-shaped notch; second pair situated near base of rostrum, directed anterolaterally; all spines slightly curved dorsally. Rostrum downturned beginning at level of outermost spines, dorsal surface slightly sulcate, concave medially. Fronto-orbital margin wide, 50 percent of length, and 70–85 percent of maximum width; smoothly rimmed; bounded on each side by needle-like postorbital spine; spine directed anterolaterally at 35 degrees from long axis. Supraorbital margin comprised of three elements separated by two open fissures, as wide as deep; fissures weakly convergent posteriorly; innermost element concave in dorsal view and convex when viewed from anterior; second and third elements smooth; concave arc in dorsal view. Orbits directed weakly anterolaterally, ovate in anterior view, height approximately one-half width, smoothly rimmed; rim thicker laterally. Outer orbital fissure occurs at base of acute orbital spine. Sub-orbital margin with one open fissure, positioned between and below supraorbital fissures, as wide as deep, directed toward the midline and parallel to orbital spines; blunt, tabular protuberance axial to ventral fissure projected anterolaterally from axis.

Lateral margins downturned. Anterolateral margin of carapace convex in outline, bearing one short, needle-like anterolateral spine between orbital spine and maximum width of carapace. Spines directed anterolaterally, at about 35 degrees from long axis, oriented parallel to postorbital spines.

Posterolateral margin sigmoid, tapering to distinct posterolateral corner. Posterior margin concave, narrow, about one-third width of carapace.

Dorsal surface pebbled; midline slightly elevated from near rostrum through midpoint, between branchiocardiac grooves. Medial portion of cervical groove defined laterally, just anterior to midlength, terminates in pits near axis. Two pits at midlength positioned on either side of long axis, situated half way between branchiocardiac and cervical grooves. One pair of large nodes about midway between cervical groove and rostrum, directly posterior to inner, supraorbital fissures; weak prominence extends from each node onto rostrum forming lateral rim; second prominence extends from each node to tips of medial orbital teeth; carapace weakly sulcate near orbital margin between each prominence. Two triangular clusters of weakly developed nodes on epicuticle on long axis, directed anteriorly; posteriormost set closely spaced, just anterior to cervical groove; anterior-most set widely spaced, about half way between cervical groove and rostrum, positioned slightly anterior and medial to large nodes.

Pterygostomial region inflated, pebbled, region divided by deep, weakly sinuous groove; groove extends anteriorly from point of maximum width at lateral margin, toward rostrum; groove bifurcates around basal antennal article, just posterior to intersection of suborbital margin. Lateral branch of pterygostomial groove terminates at inner margin of orbit; medial branch extends into buccal cavity. Basal antennal article one-half orbital length, extends from tip of rostrum to bifurcation point of pterygostomial groove, below antennal orbit; long axis of basal antennal article at 45 degrees to long axis of carapace. Each basal antennal article ornamented with two sets of tubular spine pairs: medial pair directed anteriorly, curving slightly dorsally; lateral pair directed anterolaterally, curving slightly dorsally toward orbits.

Exopod and outer portion of endopod of third maxilliped granular; inner surface of endopod smooth. Pereiopods present, but crushed or poorly preserved.

Sternum ranging from smooth to granular. Elements 1–3 bluntly triangular, apex directed forward, constricted posteriorly between elements 3 and 4; element 4 twice as wide as elements 1–3, long, about 25 percent carapace length, with triangular projection on each side of posterior margin, apex of projection directed laterally; inner edges of triangular projections deeply grooved, groove extending adaxially onto anterior portion of element 4; grooves convergent at base of elements 1–3. Element 5 extremely wide, covering entire width of ventral surface; length 20 percent carapace length; anterior margins convex; posterior margins concave. Element 6 narrow and deeply grooved axially; pterygoid processes developed as thickened folds medial and anterior to second pereiopods, processes extending into element 5. Elements 7 and 8 obscure; deeply grooved axially. Sternal cleft absent.

Dorsal surface of carapace and pterygostomial region pebbled with small, laterally abutting, hexagonal caps. Small, infrequent setal pits located at junctions of three caps, become frequent along midline of carapace. Caps slightly convex, tangential to surface of carapace in posterior two-thirds; caps oriented at oblique angle to carapace surface in anterior one-third of dorsal surface and pterygostomial regions, each cap dipping slightly posteriorly. Caps also present on abdomen but they are more widely spaced, do not abut one another, and are weakly developed. In cross-section, the caps are the upper, thickened portion of fungiform structures arising from convolution of exocuticle.

Material examined.—University of Texas, holotype of *Notopocorystes punctatus*, UT 210; UT 284 (holotype of *Notopocorystes parvus*, junior subjective synonym of *C. punctata*); and 20 *Cretacoranina* specimens deposited at Southern Methodist University, Dallas, Texas, SMU-I 50049-68.

Occurrence.—Specimen UT 210 was collected from the Denton Clay (Upper Albian) of Tarrant County, Texas, by W. S. Adkins and W. M. and H. T. Winton (Rathbun, 1935). Specimen UT 284 was collected from the Denton Clay (Upper Albian) of Grayson County, Texas, by W.S. Adkins (Rathbun, 1935). All other specimens were collected from the Pawpaw Formation (Upper Albian to Cenomanian) of Fort Worth, Texas, by Mr. Robert Reid.

Discussion.—Rathbun (1935) originally assigned this species, collected in the Denton Clay of Texas, to *Notopocorystes* M'Coy,

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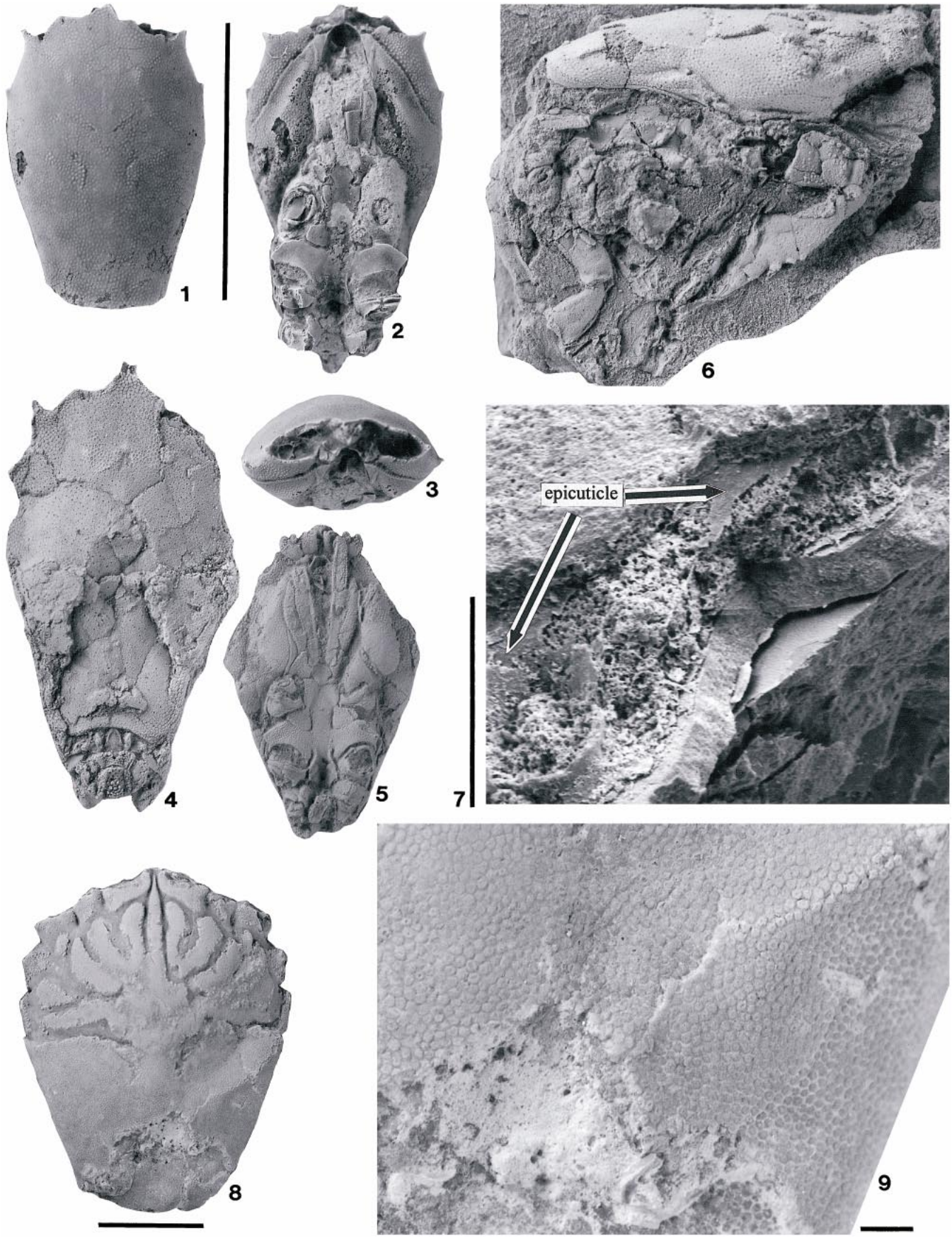
FIGURE *4—1–7, Cretacoranina punctata*; *1*, dorsal view of carapace showing surface ornamentation, SMU-I 50061; *2*, ventral view showing suborbital fissures and sternal plate, SMU-I 50061; *3*, anterior view showing orbits and antennal articles, SMU-I 50061; *4*, dorsal view showing pebbled surface and rostrum, SMU-I 50062; *5*, ventral surface showing suborbital spines and fifth maxillipeds, SMU-I 50063; *6*, lateral view showing pebbled surface, abdomen, and pereiopods, SMU-I 50064; *7*, SEM micrograph of cuticular microstructure showing the thin epicuticle surface of the fungiform structures and the fibrous cuticle within, SMU-I 50054. *8–9, Eucorystes carteri*; *8*, dorsal view showing ''strap-like'' ornamentation, B.23092; *9*, magnification of right posterolateral margin showing pebbled surface. Weathering of the surface in the lower right exposes the void spaces between fungiform structures, appearing as a widening and deepening of the recessed areas between caps, B.23092. Scale bars for figures *1-6*, and *8* = 1 cm; scale bar for figure *7* = 0.1 mm; scale bar for figure *9* = 1 mm.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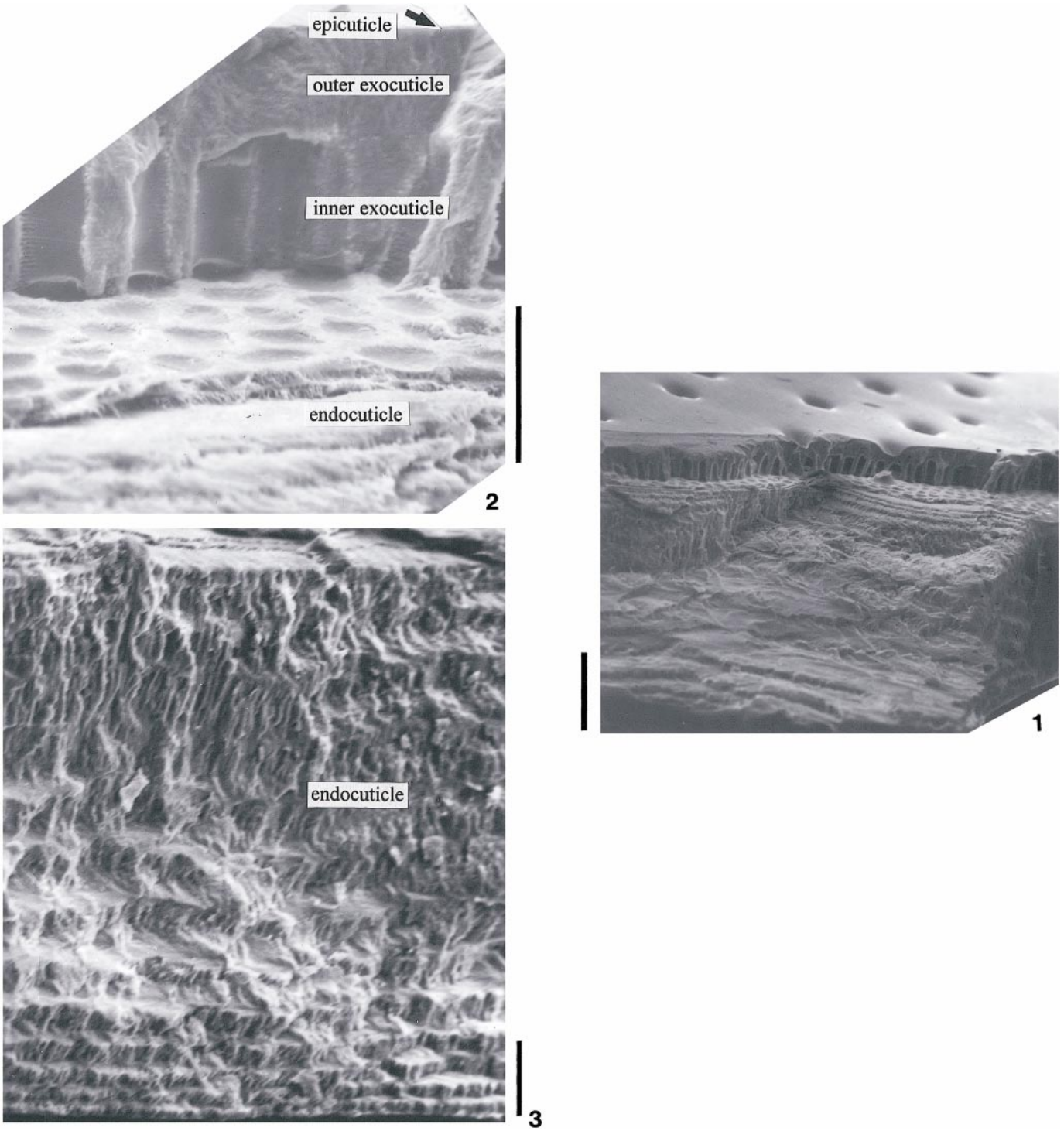

FIGURE 5—SEM micrographs of *Raninoides louisianensis* cuticle, SMU-I 50057 (Cuticle fragments from USNM 120602). *1*, Oblique view of a broken edge of the dorsal carapace showing the epicuticle with setal pits, the exocuticle with tegmental ducts, and the thick laminated endocuticle, scale bar = 100 μm; *2*, magnification of the epicuticle, exocuticle and dimpled surface of the endocuticle, scale bar = 30 μm; *3*, magnification of the edocuticular lamellae, scale bar = 30 μm.

1849. Subsequently Mertin (1941) subdivided the genus into three subspecies, based upon surface ornamentation and development of the carapace groove patterns. That classification was maintained by Wright and Collins (1972); however, Tucker (1995) argued that in order to maintain uniformity of generic descriptors throughout the family the subgenera should be elevated to generic status. We agree and, therefore, consider the species described above to be referrable to *Cretacoranina*.

Rathbun (1935) referred a second species of raninid from the Denton Clay to *Raninella*, *R. mucronata*. After close examination

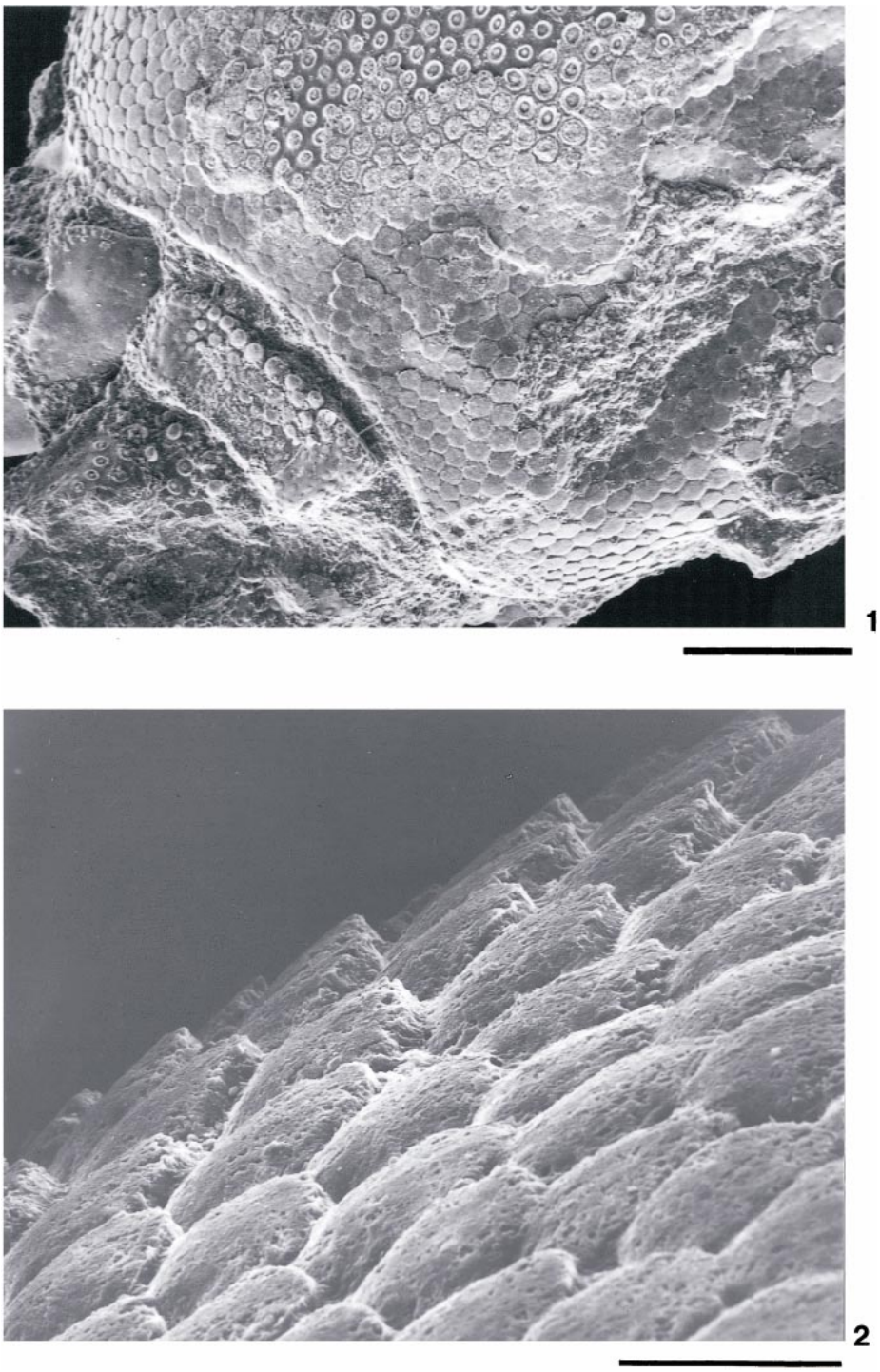

FIGURE 6—*Cretacoranina punctata. 1,* SEM view of the posterior margin of the carapace showing hexagonal plates pebbling the surface. Abrasion of the surface in the top center reveals the convoluted nature of the exocuticle and the preserved void infilling material (compare with Fig. 9.2). Weakly developed, widely spaced caps appear on the elements of the abdomen, lower left, SMU-I 50052, scale bar = 1 mm; *2,* SEM view of imbricate dorsal surface near anterolateral margin; anterior is to the upper right of the photograph, SMU-I 50053, scale bar = 100 μm.

of complete specimens collected from the Pawpaw Formation and comparison with type material, this taxon appears to be synonymous with *C. punctata*. The primary distinguishing characteristics of *Raninella* are an ovoid carapace, widest in the anterior third with converging posterolateral margins; at least one pair of anterolateral spines but typically more; a fronto-orbital region with two orbital fissures on each orbit and broad, flat supra-orbital teeth; a rostrum that is medially sulcate, but not bifid; the presence of only lateral cardiac grooves, and a sternum that narrows between the second pereiopods (Feldmann and Maxey, 1980; Tucker, 1995).

The distinguishing characteristics of *Cretacoranina* include an

oval to oblong carapace with a non-tuberculate, finely granulated to smooth surface; a distinct medial keel for almost the entire length of the carapace which may be faint to absent in some species; a lobed line that crosses the frontal area; and cervical and branchial furrows, often with just the medial portions represented; toothed anterolateral margins; a slightly produced and bifid rostrum; and strongly grooved pterygostomial region.

Cretacoranina punctata exhibits all of the characteristics of *Cretacoranina* including a bifid rostrum; a carapace bearing medial portions of the cervical and branchial grooves; and a weakly developed median keel and a line of weak lobes traversing the frontal area. The fronto-orbital margin of *C. punctata* is wide, approximately 80 percent of the maximum width of the carapace. This wide fronto-orbital margin is not typical of species within *Raninella*, but is typical of species within *Cretacoranina*. These characteristics justify the reassignment of *R. mucronata* to *Cretacoranina*.

Species within *Cretacoranina* are differentiated on the basis of shape of the anterolateral margin and the number of anterolateral spines, the presence or absence of a depressed frontal area, and the smoothness of the carapace (Tucker, 1995). The surface ornamentation of the carapace, including the lobes, the branchiocardiac and cervical grooves, the medial keel, the anterolateral and orbital spines, and the depressed frontal area are all very weakly expressed, thereby distinguishing *C. punctata* from other species within *Cretacoranina*. Also, individuals of *C. punctata* are quite small, with specimens ranging from 4 to 15 mm in length. In addition, the cuticle of *C. punctata* possesses a pebbled pavement of tightly packed, hexagonal exocuticular caps barely visible to the naked eye.

The hexagonal caps which pebble the surface of the carapace were initially thought to be unique to *Cretacoranina punctata*, but after examination of fossil specimens and descriptions of other species of Raninidae, the structure was found to be present on specimens of *C. testacea* (Rathbun, 1926); *C. dichrous* (Stenzel, 1944); *C. schloenbachi* (Schlüter, 1879); *C. trechmanni* (Withers, 1927); and *Eucorystes carteri* (McCoy, 1854). Other fossil specimens inspected and found not to possess the cuticular structures include *Carinaranina willapensis*, *C. marionae*, *Raninella eocenica*, *R. oaheensis*, *R. carlilensis*, *Eumorphocorystes naselensis*, *E. schenki*, *Notopocorystes broderipi*, *N. stokesi*, *N. normani*, *N. oxtedensis*, and *Hemioon elongatum*. This cuticular structure may be a characteristic of the genera *Cretacoranina* and *Eucorystes*, but the remainder of the species within these two genera must be carefully examined to confirm this.

THE CUTICULAR MICROSTRUCTURE OF *CRETACORANINA PUNCTATA*

The calcified cuticle of decapods comprises the hard exoskeleton of the animal and can be subdivided into four layers (Fig. 5). Although nomenclature of these layers varies from author to author, the terminology of Travis (1963), Green and Neff (1972), and Roer and Dillaman (1984) is most widely accepted and will be used in this work.

The epicuticle is ''the outermost and thinnest layer of the cuticle'' (Roer and Dillaman, 1984, p. 894). It is a thin, mineralized, bilaminar layer whose basal lamina contains mineral-filled canals normal to the surface (Hegdahl et al., 1977b).

The exocuticle lies below the epicuticle and is composed of chitin-protein fibers stacked in layers of continuously changing orientation (Green and Neff, 1972). The exocuticle can be subdivided into two intergraded regions of lamellae characterized by variations in the organization of the fibers (Green and Neff, 1972). Within the outer exocuticle, the chitin-protein fibers do not overlap, creating lamellae that appear discontinuous or amorphous. Within the inner exocuticle, the lamellae are distinct and more dense (Green and Neff, 1972). These layers appear as light and dark laminations in cross-section. The exocuticle is calcified (Travis *in* Roer and Dillaman, 1984) with mineral crystals situated between the fibers (Hegdahl et al., 1977a).

The endocuticle is ''the thickest and most heavily calcified layer of the cuticle'' (Travis *in* Roer and Dillaman, 1984, p. 894). It is composed of horizontal lamellae of chitin-protein fibers with continuously changing orientation (Green and Neff, 1972; Hegdahl et al., 1977), similar to the exocuticle. The lamellae of the endocuticle, however, have a much greater interlamellar distance (Roer and Dillaman, 1984). Thus, the lamellae of the endocuticle appear much thicker than those of the exocuticle in cross-section.

The fourth and innermost layer, rarely preserved in fossils, is a nonmineralized, membranous layer which is in contact with the hypodermis of the animal (Roer and Dillaman, 1984).

The epicuticle and exocuticle are represented in dozens of specimens of *Cretacoranina punctata*. Photographs and SEM micrographs show the surface of the carapace to be composed of a network of laterally abutting, hexagonal pebbles (Figs. 4.1–4.5, 5.1, 6.1–6.3), but upon close examination of fractured cuticle and thin sections, these pebbles are actually seen to be the upper portions, or caps, of fungiform structures within the exocuticle (Figs. 7.1, 7.2, 8.2). These fungiform structures are formed from a convolution of exocuticle. The term ''fungiform'' evolved in conversations with Dr. Francisco Vega, Instituto de Geología, UNAM, Mexico, D. F., Mexico. Because of the similarity in form to mushrooms and need to have a term to define the top plate, ''cap,'' the term seemed unusually appropriate.

The surface of the cap of each fungiform structure is either tangential, or slightly inclined, to the surface of the carapace. These caps are approximately 100 μm in diameter and 24 μm thick along the cap edge and are composed of a thick, densely calcified layer of exocuticle, termed herein the outer exocuticle. The upper surface of the cap is weakly convex and may be slightly abraded. At the edge of the cap, the thick layer of outer exocuticle becomes inverted, thus forming the lower surface of the cap. This surface is weakly convex and steepens rapidly forming a cone-like structure, or stem, which is approximately 60 μm in diameter at the base of the cap and narrows slightly toward the stem base. The densely calcified layer of outer exocuticle rapidly thins toward the stem base. At the stem base, the outer exocuticle folds acutely back to parallel the surface and continues laterally into the neighboring fungiform structure, encapsulating a void space surrounded by cuticle (Fig. 8). These spaces are presumed to have been void in life because they are bounded by the upper surface of the epicuticle (Fig. 4.7). Also, the lithology of material within the encapsulated voids is the same as that which forms the mold of the interior of the carapace (Fig. 8.1). This sediment was calcified and forms a honeycomb structure between and around each fungiform structure within the cuticle (Fig. 9.2). This laterally linked void network may

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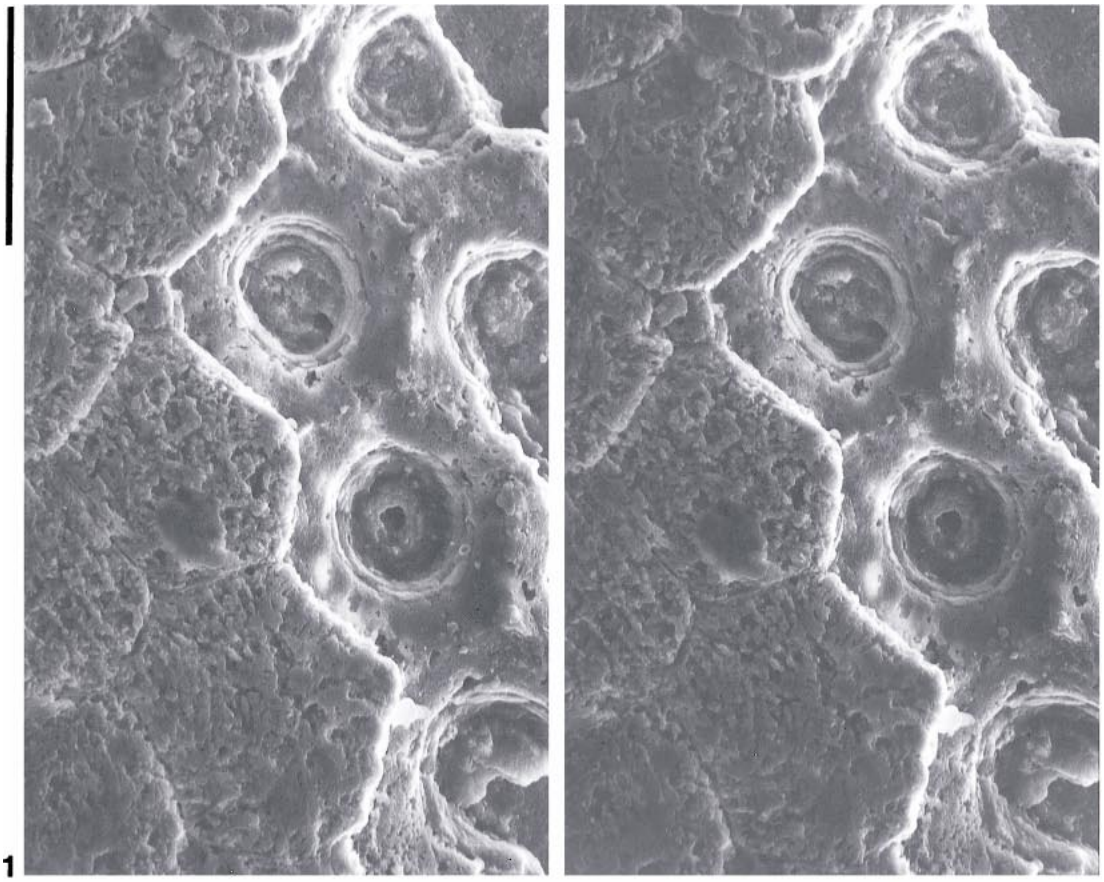
FIGURE 7—SEM micrographs of the dorsal surface of *Cretacoranina punctata*, SMU-I 50053. *1,* Stereo pair showing pebbled epicuticle and areas where fungiform caps and stems have been removed leaving empty cavities bounded by preserved void infilling material (honeycomb structure). See Figure 9.2 for an oblique view of the same structures; *2,* view showing setal pits at plate junctions. Stereo pair shown above (Fig. 7.1) is a magnification of upper right corner of Figure 6.2, SMU-I 50053. Scale bars = 100 μm.



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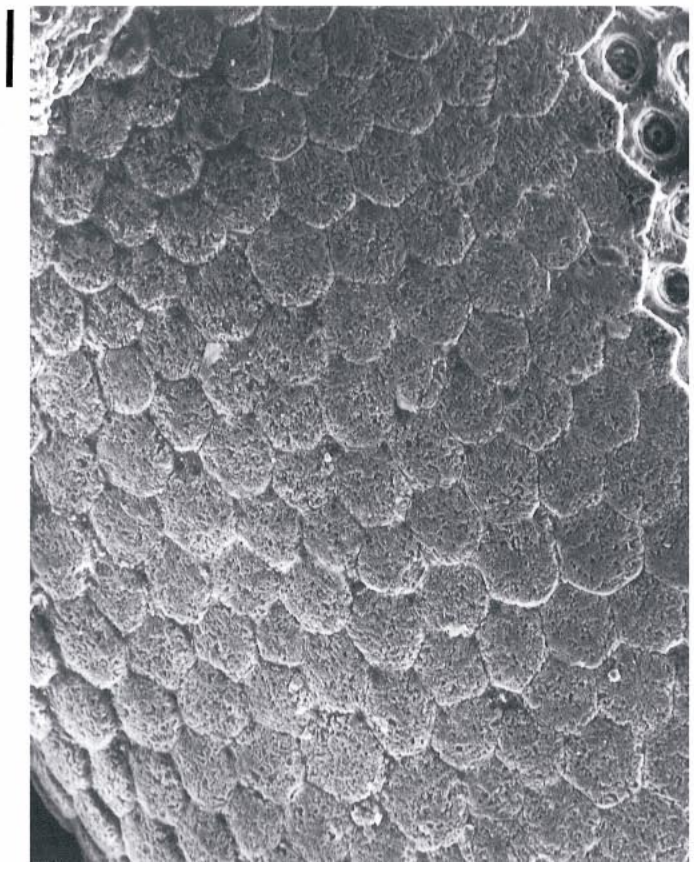

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have been exposed to the surrounding water and sediment in life, and may have functioned as pneumatic devices to press the cuticle tightly against the substratum.

Below the outer exocuticle is the finely laminated inner exocuticle. The inner exocuticle parallels the lower surface of the outer exocuticle. Lamellae within the inner exocuticle are tangential to the cuticular surface but become undulose beneath each fungiform structure (Fig. 8.1, 8.2), creating a surface of small, equally-spaced domes in dorsal view (Fig. 9.2). All specimens of *Cretacoranina punctata* are judged to be molts based upon separation of the carapace from the endoskeleton, abdomen, and legs. The molting process helps to explain the irregular base of the inner exocuticle and absence of the endocuticle (Fig. 8.1, 8.2). The thin, soft upper layer of epicuticle is also absent from the surface of *C. punctata*, possibly due to abrasion or exfoliation, but present on the lower surface of each fungiform structure (Fig. 4.7). However, the extremely thin epicuticle is present on the surface of *C. dichrous* (Fig. 9.1).

EVIDENCE OF FOSSIL PEBBLED CUTICLE WITHIN THE SUBFAMILY NOTOPOCORYSTINAE LŐRENTHEY *IN* LŐRENTHEY AND BEURLEN, 1929

Cretacoranina dichrous *(Stenzel, 1944)*.—The surface of the carapace of *Cretacoranina dichrous* has been described as smooth, ornamented with densely crowded granules which have flat, polished tops and which are separated by cracks or occasional pits (Stenzel, 1944). Photographs of *C. dichrous* show the surface of the carapace to be pebbled much like the surface of *C. punctata* (Fig. 9.1, 9.3, 9.4). SEM micrographs of *C. dichrous* reveal the characteristic fungiform structures of *C. punctata* with only subtle differences. The caps are wider than those of *C. punctata*, approximately 170 μm in diameter but similar in thickness, shape, and structure (Fig. 9.1). The epicuticle and endocuticle are preserved in addition to the exocuticle. The epicuticle consists of a thin, unilaminar layer of cuticle approximately 3 μm thick. Although exfoliated and lost in most areas, it is preserved in the recessed areas between caps (Fig. 9.1). The endocuticle, similar to the exocuticle, is composed of heavily calcified horizontal lamellae, however, the lamellae of the endocuticle are much thicker than those of the exocuticle, consistent with the pattern described by Roer and Dillaman (1984). The boundary between the exocuticle and endocuticle is obscured due to poor preservation in *C. dichrous*, but a distinct change in thickness of lamellae is evident (Fig. 9.1).

Cretacoranina trechmanni *(Withers, 1927)*.—Stenzel (1944, p. 438) also stated that in both *Cretacoranina trechmanni* and *C. dichrous*, most of the carapace is ''covered with minute, flattened granules, which are so closely set that their interspaces are mere chinks.'' The surface of the carapace of *C. trechmanni* is pebbled with hexagonal to subhexagonal, caps similar to *C. dichrous* and *C. punctata* (Fig. 10.1). The caps of *C. trechmanni*, however, are less regular in size, varying from 350 to 450 μm in diameter. Also, the setal pits at the confluences of caps on the surface of the carapace of *C. trechmanni* are much larger and more numerous than in either *C. dichrous* or *C. punctata*.

Cretacoranina testacea *(Rathbun, 1926)*.—Rathbun's description of the carapace of *Cretacoranina testacea*, noted that ''the surface is closely paved with flat, sub-hexagonal granules, which are visible to the naked eye'' (Rathbun, 1926, p. 190). Scattered punctae are also visible. All specimens of *C. testacea* examined, USNM 335986A, USNM 335986B, USNM 327238, and USNM 73121, possess the characteristic hexagonal cuticular caps. The size and shape of the caps resemble those of *C. dichrous*, however, *C. testacea* bears larger and more frequent setal pits. Also, weathering of the dorsal carapace of specimen USNM 327238 reveals an interesting pattern along the smooth, polished surface of each cap: two to three irregular, concentric rings extend from the margin to the center. These rings may indeed be relict exocuticular lamellae within each cap that were exposed as the top of the cap was worn smooth.

Cretacoranina schloenbachi *(Schlüter, 1879)*.—Although no mention was made of small, hexagonal granules on the surface of *Cretacoranina schloenbachi* by Wright and Collins (1972), the original description, in German and translated here, noted that to the naked eye the surface of the partially preserved carapace is smooth, without any noticeable sculpture, but using a hand lens, one notices small, round, tangential granules which in some places are pressed flat (Schlüter, 1879, p. 612–13). Schlüter was describing a pebbled surface similar to that of *Cretacoranina punctata*. Where the carapace of *C. schloenbachi* was broken away, only a mold of the interior of the carapace exists (Schlüter, 1879). The mold's surface is contoured with additional smaller granules somewhat farther apart from one another (Schlüter, 1879). The surface of the mold that Schlüter described probably was not the mold of the interior of the cuticle, but an area where the outer exocuticle had been exfoliated, revealing the undulose surface of the inner exocuticle, as seen in *C. punctata* (Fig. 9.2).

Eucorystes carteri *(M'Coy, 1854)*.—The surface ornamentation of *Eucorystes carteri* has been described as covered with hexagonal granules on the entire dorsal surface with slightly larger, well spaced granules along the edges of some of the raised areas, or ''straps.'' In the furrows and in the grooves between ''straps,'' the carapace is smooth with fine punctae (Wright and Collins, 1972). The dorsal surface of *E. carteri* is pebbled in the same fashion as *Cretacoranina punctata*, *C. dichrous*, and *C. trechmanni*. Cap width, regularity, and setal pit density are most similar to *C. dichrous*. No caps are observed in the recessed areas of the grooves and furrows (Fig. 4.8, 4.9). The grooves and furrows seem to be areas of the carapace where the cuticle has not been convoluted.

A RECENT ANALOG

General.—Because there are no living congenors of *Cretacoranina*, *Raninoides louisianensis* was selected as the closest extant analogue. The cuticular structure of samples of *R. louisianensis* preserved in alcohol was contrasted with the cuticular microstructure of *Cretacoranina punctata* and *C. dichrous*.

The cuticle of Raninoides louisianensis.—Three of the four basic cuticular layers can be identified: the epicuticle, the exocuticle, and the endocuticle (Fig. 5.1–5.3). The epicuticle, is a very thin, dense, apparently unilaminar layer, approximately 1 μm thick, with a smooth outer surface (Fig. 5.1, 5.2). Below the epicuticle, the exocuticle is subdivided into two layers. The outer exocuticle consists of massive, densely calcified cuticle (Fig. 5.2). The inner

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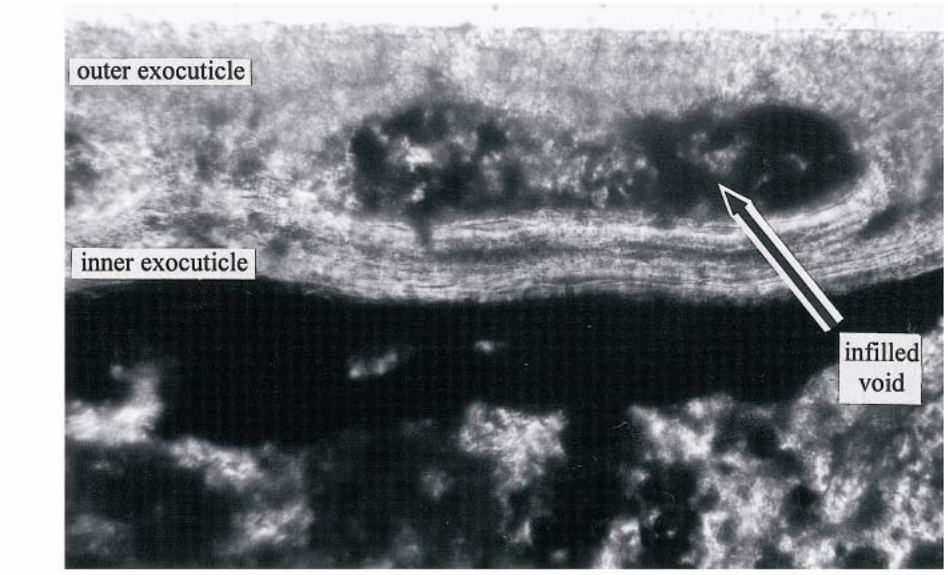
FIGURE *8*—Thin sections of cuticle of *Cretacoranina punctata*. *1*, Transverse section showing outer and inner exocuticle. The transverse section cuts across the outer edge of a cap yielding an irregular infilled void space. The similarity of lithology of material within the infilled void and that which forms the mold of the interior of the carapace (bottom of photo) can also be noted, SMU-I 50049; *2*, transverse section of cuticle showing fungiform structures with caps dipping posteriorly (left), SMU-I 50050; *3*, similar view with the outline of the convoluted outer exocuticle traced in ink; *4*, functional morphology illustration of the surface contour of the carapace, from Figure 8.2. Note that the nature of the interior of the fungiform is not well known but may be weakly calcified. Scale bar = 100 μm.


outer exocuticle
inner exocuticle
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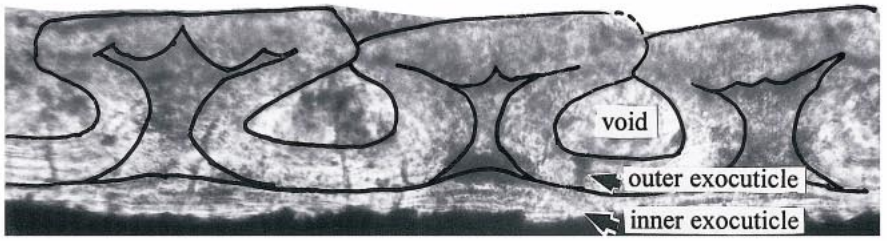
1

2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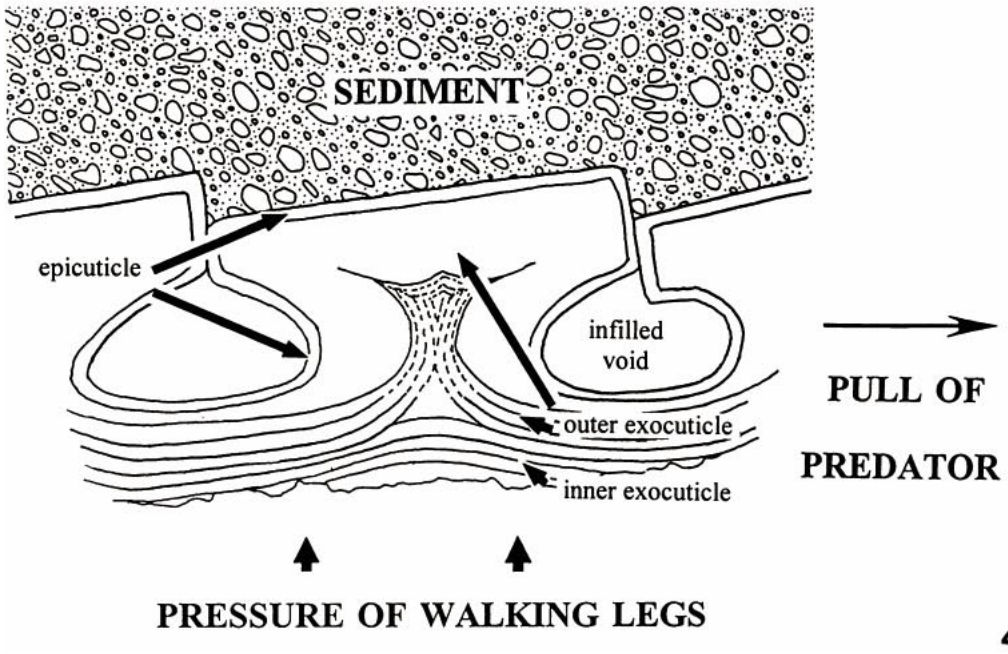
SEDIMENT
epicuticle
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PULL OF
PREDATOR
PRESSURE OF WALKING LEGS

4

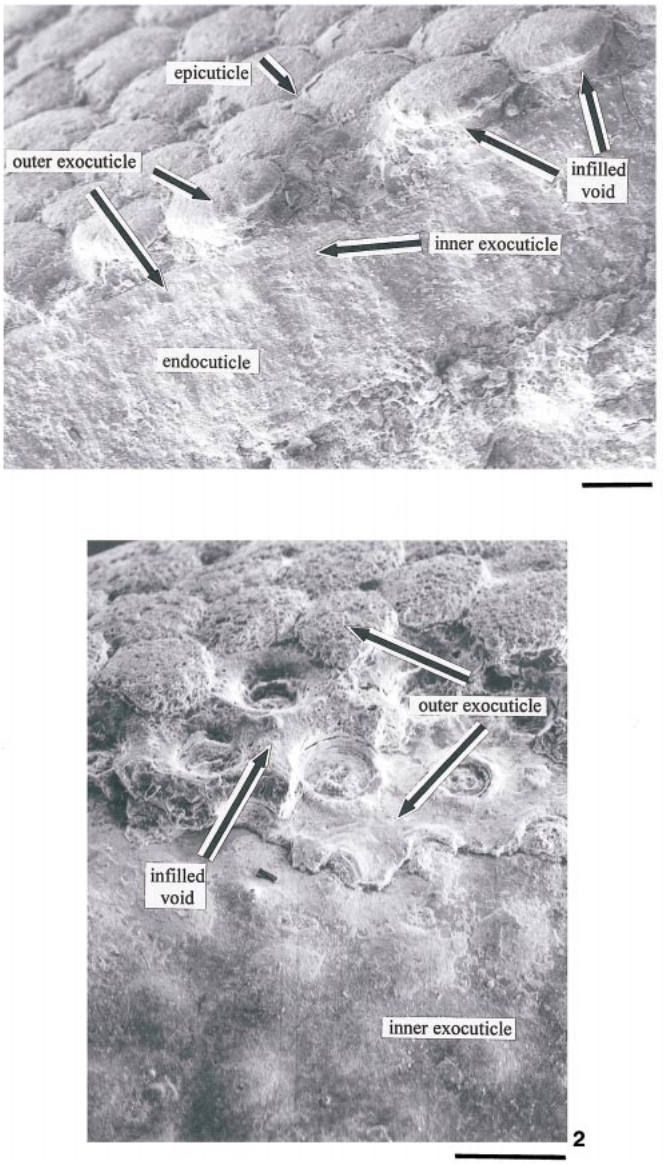

FIGURE 9—SEM micrographs of cuticular microstructure. *1, Cretacoranina dichrous*, BM(NH) In. 26011, oblique view of a broken edge of the posterior dorsal carapace showing the pebbled surface, the epicuticle preserved in recessed areas on surface, the exocuticle, and endocuticle, fragment SMU-I 50056; *2, Cretacoranina punctata*, SMU-I 50053, view of the surface of the carapace with exfoliated areas exposing preserved, laterally connected, infilled void spaces between fungiform structures and the undulose upper surface of the inner exocuticle. Conical depressions are areas where the fungiform structures have been broken away. Scale bars = 100 μm.

exocuticle features a network of tightly packed vertical tegmental ducts that terminate above depressions on the upper surface of the endocuticle (Fig. 5.2). The tegmental ducts are approximately 10 μm in diameter and are separated by 5 μm thick walls composed of finely laminated, densely calcified cuticle. The approximate thickness of the individual lamellae is 1 μm (Fig. 5.2). The exocuticle is approximately 50 μm thick.

The endocuticle is a densely calcified, multilaminar layer whose upper surface is sculpted into a network of circular depressions; the diameter of each depression is similar to the diameter of the corresponding exocuticular canal above (Fig. 5.2). The lamellae within the endocuticle are thicker than those of the exocuticle, approximately 30 μm thick, and graded in thickness, thinning to approximately 5 μm, near the upper and lower surfaces of the endocuticle (Fig. 5.3).

The membranous layer at the base of the endocuticle was not observed. Setal pits are present on the surface of the epicuticle and extend through the exocuticle to the surface of the endocuticle (Fig. 5.1).

Discussion.—The cuticular microstructure of *Raninoides louisianensis* was compared to that of *Cretacoranina punctata* and *C. dichrous*. All possess an extremely thin epicuticle and a thick, massive outer exocuticle. In specimens of *C. punctata* observed with the SEM, the epicuticle on the surface has been exfoliated. The total height of the fungiform structure within the exocuticle of *C. punctata* and *C. dichrous* is approximately equal to the thickness of the exocuticle of *R. louisianensis*. Pore canals within the inner exocuticle of *R. louisianensis* are documented features within the exocuticle of other decapods such as extant *Menippe mercenaria* and *Neopanope texana* (Roer and Dillaman, 1984), and the fossil decapod crustacean *Costacopluma mexicana* (Vega et al., 1994). However, neither *Cretacoranina punctata* nor *C. dichrous* display such structures within their exocuticle. The very thin lamellae preserved within the inner exocuticle of *C. punctata* are similar to the fine lamellae within the inner exocuticle of *R. louisianensis* (Figs. 7.1, 7.2, 10.2).

The exocuticles of *Cretacoranina dichrous*, and *Raninoides louisianensis* are both thin relative to the total thickness of cuticle. The total thickness of the exocuticle of *C. punctata* cannot be determined because the specimens are fossilized molts having the endocuticle and part of the exocuticle resorbed during molting.

The endocuticle of *Raninoides louisianensis* and *Cretacoranina dichrous* are virtually identical in microstructure. Lamellae within the endocuticle of *R. louisianensis* are distinct, thicker than the lamellae of the exocuticle and graded, thinning near the upper and lower surface of the endocuticle. Although poor preservation obscures the fine detail of the endocuticle of *C. dichrous*, the relict lamellae appear similar to those of *R. louisianensis* in thickness and grading (Fig. 9.1).

THE FUNCTIONAL MORPHOLOGY OF THE EPICUTICULAR STRUCTURES OF *CRETACORANINA PUNCTATA*

The pebbled surface of the carapace of *Cretacoranina punctata* appears to be sculptured, much like cuticular terraces. A cuticular terrace is defined as a ''ridge on the surface of the carapace with a steep face sloping more than 60 degrees and a flat face sloping less than 30 degrees'' (Schmalfuss, 1978, p. 21). The asymmetry of the terraces and the fact that the terrace is only present on the external surface of the cuticle imply that they serve a mechanical function as an adaptation to environmental factors (Schmalfuss, 1978). The primary selection pressure for the evolution of these morphological structures has been suggested to be the ecological setting of the organism (Schmalfuss, 1978).

Savazzi (1982) expanded this definition of cuticular terraces to include any cuticular structure that would increase friction with the substrate. For example, he noted that the tubercles, or granules, in *Carcinus maenas* and *Ilia nucleus* partially comply with his definition of cuticular terraces in possessing frictional asymmetry and being properly oriented in size and shape. Asymmetrical tubercles evolved from symmetrical tubercles to aid in burrowing, but still maintain their function as mechanical strengtheners (Savazzi, 1982).

The laterally abutted, hexagonal caps which pave the surface of the carapace of *Cretacoranina punctata* lie nearly flat, and generally parallel to the surface over much of the carapace (Figs. 6.1, 7.3) creating the pebbled contour of the carapace surface, much like the pebbled surface of a basketball. However, in the

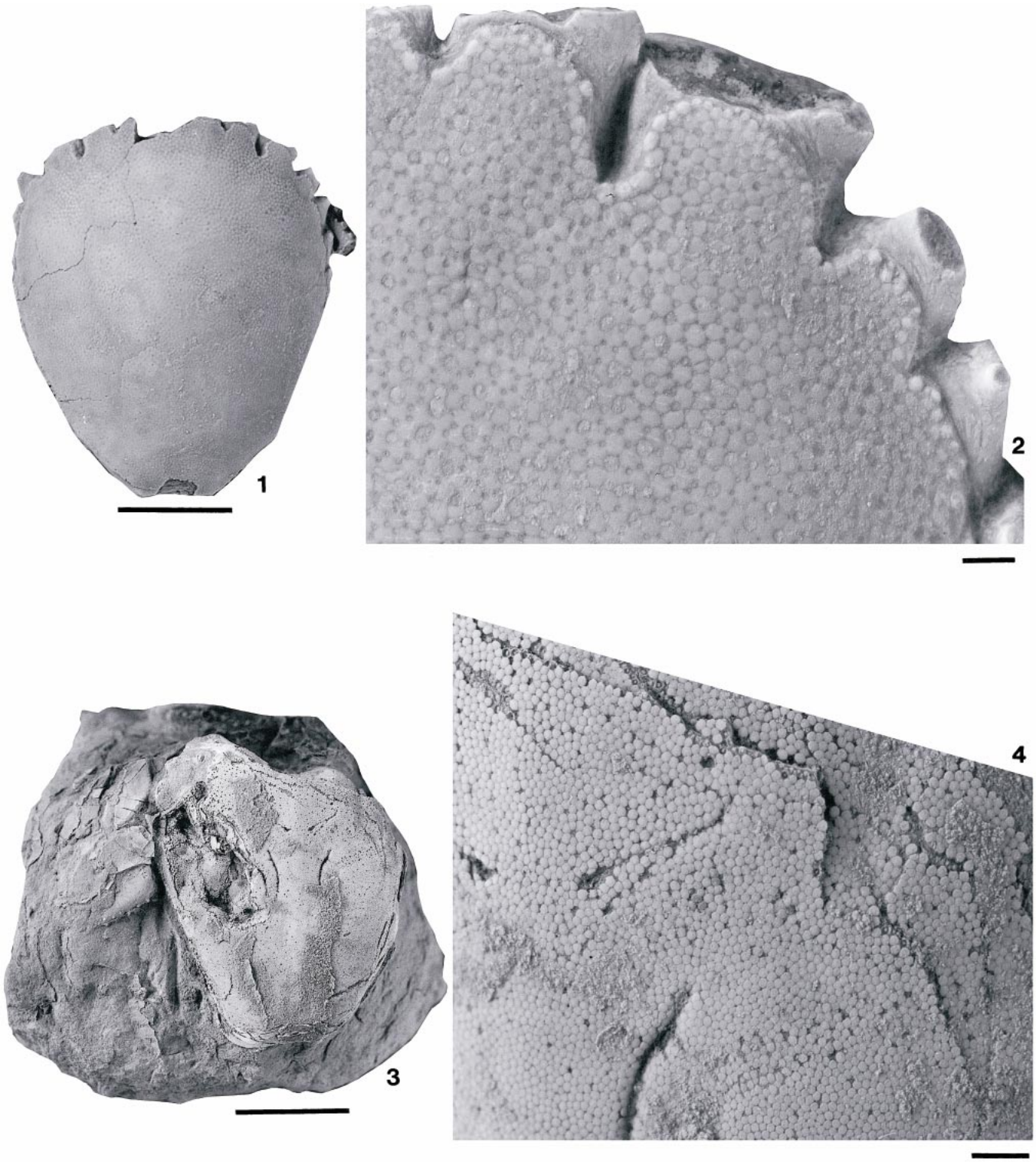

FIGURE *10—1–2, Cretacoranina trechmanni*, BM(NH) In. 26011. *1,* Dorsal view of carapace; *2,* magnification of anterolateral margin showing the pebbled surface of the carapace. *3–4, Cretacoranina dichrous*, one of two specimens in USNM #233978, U.S. National Museum of Natural History. *3,* Dorsal view of carapace; *4,* magnification of branchiocardiac region showing the pebbled surface of carapace. Scale bars = 1 cm; 1 mm in magnifications.

anterior third of the dorsal surface, and along the anterolateral margins and pterygostomial regions, each cap dips slightly toward the posterior (Fig. 6.2). The anterior edge of the cap creates a steep face, and the surface of the cap forms a flat sloping face. Although these are not technically terraces, they appear serrated in axial cross-section, as do terraces (Fig. 8.2).

In *Cretacoranina dichrous* (Fig. 9.1), the serrated edges of the caps are not observed, and the caps appear more flat-lying, as they do over much of the surface of the carapace of *Cretacoranina punctata*. The reasons are two-fold. The cuticle of *C. dichrous*, illustrated in Figure 9.1, was removed from the posterior margin of the dorsal carapace of the specimen (Fig. 9.3, 9.4). At this location on the carapace, the posterior dorsal surface, as well as on the posterolateral margins, terraces would be minimally effective when wedging within a burrow (Savazzi, 1985) and, therefore, one would not expect the caps to be dipping in these regions. Secondly, the specimen is quite large. A large, possibly adult, specimen might be more able to defend itself against, or to flee from, a predator, perhaps reducing the need for terraced structures as a defense mechanism (Savazzi, 1985). This might also explain the more frequently observed terrace-like cap structures on the relatively smaller specimens of *C. punctata*.

The range of terraced sculpture patterns within the Decapoda grades from simple tubercles to specialized burrowing terraces, and may even vary across the carapace of an individual (Savazzi, 1982). Randomly distributed tubercles may grade into terraces along the carapace, as in *Corystes cassivelaunus*; these sculptures are more subtle in taxa in which the dorsal carapace is widest in cross-section (Savazzi, 1981). *Cretacoranina punctata* also exhibits reduction in the strength of the sculpture on different areas of the carapace; this variation in sculpture is primary and cannot be attributed to wear or abrasion. This gradation is also seen in photographs of *Eucorystes carteri* (Fig. 4.8). The cuticle on the raised ''strap'' areas of the carapace of *E. carteri* is pebbled, whereas the surface of the cuticle within the deep grooves is smooth and lacks pebbled structures. Along the edges of the raised ''strap'' areas, the caps are more pronounced and asymmetrical, while on the posterior portion of the dorsal surface the cuticle has much more subdued pebbling, and the carapace lacks deep grooves.

The function of all cuticular terraces found in decapods is to provide frictional resistance with the substrate (Schmalfuss, 1978). In the case of a solid substrate, terraces serve to anchor animals such as in *Grapsus*, *Geograpsus*, and *Galathea* into rock crevices to escape specific predators (Schmalfuss, 1978). In sandy substrates, terraces function to optimize digging, as in the families Hippidae and Albuneidae, and to anchor against waves or currents scouring the sea floor (Schmalfuss, 1978).

Savazzi (1985) observed that the primary function of terraces in *Gecarcinus lateralis* and *Ocypode quadrata* is to increase the friction with the substrate when the crabs wedge themselves against the walls of their burrows, a behavior which prevents the crabs from being extracted from their burrows by predators.

The height, number per unit surface area, and shape of terraces vary greatly among decapods in any given sediment. In interaction with loose substrate, the efficiency of the terraces is determined by the number of terraces per unit surface area, the degree of serration, and the grain size of the substrate (Schmalfuss, 1978). An increase in the number of terrace sculptures per unit surface area increases frictional resistance to extraction with only a slight decrease in burrowing efficiency of the carapace (Savazzi, 1981). Also, the height of terrace structures may be smaller than the average grain size of the substrate, as in *Corystes*, or larger, as in *Lophoranina*, but may still function to aid burrowing, and provide increased friction with the substrate (Savazzi, 1982). However, there is a general correlation between grain size and terrace height in medium- and coarse-grained sediments.

It must be noted, however, that the utility of terraced structures in fine-grained sediments, silt and clay, has not been investigated in detail. If terraces were to function in fine sediments in the same fashion as in medium and coarse sediments, the terraces would have to have extremely low relief. Alternatively, a pebbled surface as in *Cretacoranina punctata*, similar to that on the surface of a basketball or a football, provides a gripping surface that is more efficient than a smooth surface when pressed against another smooth surface. Thus, it is easier for the hand to grip a basketball than it is to grip a smooth ball of equal diameter and weight. In the same fashion, the pebbled surface of *C. punctata* with its multitude of minute caps per unit area, some tangential to the surface and some inclined to it, would seemingly create a very efficient gripping surface within fine sediments. Detailed experiments may be needed to demonstrate this conclusively.

Another consideration, relative to the gripping efficiency of the pebbled surface, is that of similitude (Raup and Stanley, 1978). Specimens of *Cretacoranina punctata* tend to be very small. Because the necessary frictional force, a function of surface area, would decrease rapidly as the organisms decreased in size, which is a linear function, the relative gripping efficiency of the pebbled surface would be great in small animals and relatively less effective in larger organisms. In species characterized by larger adults, but which also possess fungiform structures and a pebbled surface, there is often an additional morphological feature that would serve to anchor the animal. In *Eucorystes carteri*, a convoluted surface and spined margin aid the pebbled surface structures in providing adhesion to the sediment. *Cretacoranina trechmanni* and *C. dichrous* also have spined anterior and anterolateral margins. At present, there is no way to test whether or not the development of anchoring mechanisms employing pebbled surfaces changes through ontogeny; growth series of the relevant taxa are not known.

CONCLUSIONS

The cuticular caps of the fungiform structures that pebble the surface of the carapace of specimens of *Cretacoranina punctata*, as well as specimens of *C. dichrous*, *C. trechmanni*, *C. testacea*, *C. schloenbachi*, and *Eucorystes carteri*, were found to be the surface manifestation of a previously undescribed cuticular structure. This structure results from convolution of the exocuticle and is a unique modification of the cuticle that creates a surface contour on the carapace similar to terrace structures described on other decapod taxa but one which is singularly adapted to gripping fine-grained sediment surfaces. The pebbled surface functions to hold the crab inside its burrow as a defense against predation and to aid in burrowing (Fig. 8.4). Furthermore, cuticular microstructure of this nature could have major implications in classification of fossil decapods.

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