OCCURRENCE OF THE ATLANTIC GHOST CRAB *OCYPODE QUADRATA* FROM THE UPPER PLEISTOCENE TO HOLOCENE ANASTASIA FORMATION OF FLORIDA

Roger W. Portell, Richard L. Turner, and John L. Beerensson

(RWP, correspondence) Florida Museum of Natural History, P.O. Box 117800,
University of Florida, Gainesville, Florida 32611-7800, U.S.A. (portell@flmnh.ufl.edu);
(RLT) Department of Biological Sciences, Florida Institute of Technology,
150 West University Boulevard, Melbourne, Florida 32901-6975, U.S.A. (rturner@fit.edu);
(JLB) 8055 South Tropical Trail, Merritt Island, Florida 32952, U.S.A.

ABSTRACT

More than 500 nearly complete specimens of the Atlantic ghost crab *Ocypode quadrata* (Fabricius) were collected from the upper Pleistocene to Holocene Anastasia Formation along beaches in Brevard County, Florida. Such whole-body decapod crustaceans are rare in Quaternary deposits of the southeastern United States. The low degree of disarticulation and the posture of the crabs indicate that they died while in their burrows, probably by winterkill. Fossil *O. quadrata* were found in two conditions: those with a clearly crab-like form, bearing a loose, friable matrix of shell hash with little cementation, no visible abrasion, no calcite infilling, and no attached fossil or Recent epibionts; and those that were barely recognizable as crabs, with a thick layer of heavily cemented matrix, a highly sand-abraded (polished) surface, some voids filled with calcite-cemented grains or calcite crystals, and some with Recent epibionts in exposed cavities. The nonabraded crabs with friable matrix have been recently exhumed from a poorly consolidated part of the Anastasia Formation or from the sand dunes or upper beach escarpment by storm waves, whereas the abraded crabs have been cast upon the beach from the nearshore subtidal zone by storm waves. Deposition of the Anastasia Formation is thought to have occurred approximately 110,000 YBP. The barrier-island–sand-dune system along the central East Coast of Florida is believed to have formed within the last 7000 yr. The abraded fossil crabs could have accumulated over the past 110,000 yr, but the nonabraded specimens, if derived from the existing beach, are considerably younger.

Whole-body decapod crustaceans are rare in Neogene and Quaternary deposits of the southeastern United States and Caribbean (and elsewhere) because they possess a relatively thin exoskeleton that is easily destroyed by biologic or geologic processes (Rathbun, 1935; Bishop, 1986; Morris, 1993; Collins and Portell, 1998). Conditions occasionally permit exceptional preservation of intact specimens, although only the most heavily mineralized parts (chelae and fingers) typically are preserved.

Few published reports document Pleistocene to Holocene occurrences of crabs in Florida, and even fewer refer to the occurrence of whole-body crabs. Most recently, Portell and Schindler (1991) recorded whole-body *Menippe mercenaria* Say, 1818, from a shell bed in the upper Pleistocene Coffee Mill Hammock Formation (also known as the Coffee Mill Hammock Member of the Fort Thompson Formation) at Oldsmar in Pinellas County. Herein, we document only the second Florida Quaternary record of whole-body crabs: a collection of *Ocypode quadrata* (Fabricius, 1787) from East Coast

beaches in Brevard County (Fig. 1) based on over 500 nearly complete crabs from the upper Pleistocene to Holocene Anastasia Formation (Fig. 2). This assemblage ranks in the 96–97th percentile of North American fossil decapod collections (Bishop, 1986). Their taphonomy and diagenesis in a high-energy sand-beach environment within the realm of the Anastasia Formation of late Quaternary Florida is the subject of this work.

Earlier references to such fossils include Rathbun (1935) and Bishop (1986), who had limited material of questionable status. Rathbun (1935) questionably reported *Ocypode albicans* Bosc, 1801–1802 [= *O. quadrata* (Fabricius, 1787)] from the Pleistocene of Florida based on a single specimen from the J. J. White Collection. Based on her report, but without question or further evidence, Glaessner (1969) and Portell and Schindler (1991) both listed *Ocypode* as occurring in the Pleistocene of Florida. In December 1999, RWP examined Rathbun's specimen (USNM 371733) and found it to be nearly identical to specimens
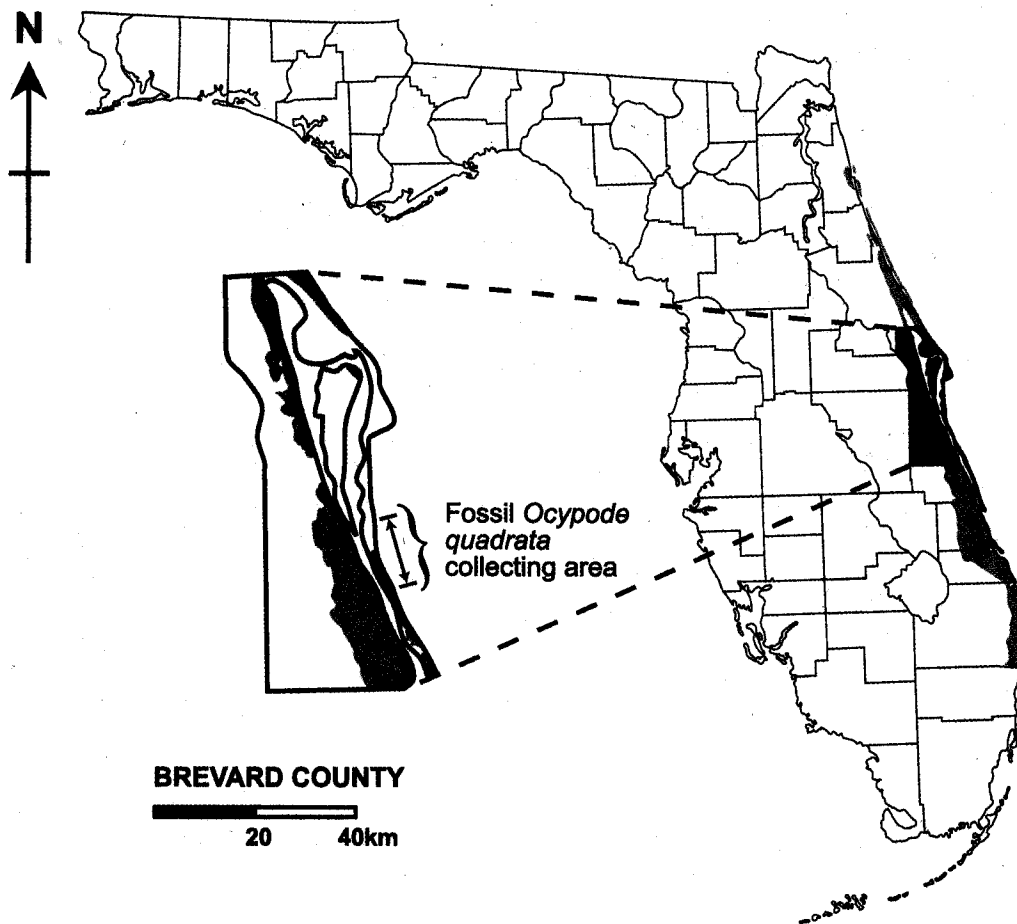
Fig. 1. Distribution of surface outcrops of the upper Pleistocene to Holocene Anastasia Formation (shaded) along the east coast of Florida. Inset: Brevard County, with collecting area indicated for fossil *Ocypode quadrata* described in this study.

discussed herein from the upper Pleistocene to Holocene Anastasia Formation of Florida. There is little doubt that Rathbun's specimen was from the same stratigraphic source. Additionally, Bishop (1986: 340), in his paper on the taphonomy of North American decapods, mentioned and figured "casts of ?stone crabs (*Menippe*?) encased in cemented coquina nodules with rough external shape of enclosed crabs" from Pleistocene? coquina at Melbourne Beach, Florida. His specimens, too, are the Anastasia Formation *O. quadrata* reported herein.

MATERIALS AND METHODS

Material Examined.—At least 508 fossil *Ocypode quadrata* out of 525 lots from four sites, upper Pleistocene to Holocene Anastasia Formation, Brevard County, Florida, in holdings of the Invertebrate Paleontology Division (IP),

Florida Museum of Natural History (FLMNH), University of Florida (UF). One specimen per lot unless otherwise noted. Site numbers refer to official designations of IP at the FLMNH. Site BR003, Melbourne Beach, about 0.8 km south of Melbourne Beach city limits along Florida State Road A1A (sec. 17, T28S, R38E; Melbourne East Quadrangle USGS 7.5′ series): UF 48138–48171, UF 48177–48179, UF 48182–48208, UF 48304–48307, UF 48405, UF 48407–48410, UF 48412–48427, UF 51090 and UF 51096 (1 broken spec. in 2 lots), UF 51091–51095, UF 51097, UF 51098, UF 51101, UF 54577–54580. Site BR008, south of Patrick Air Force Base, along beach, from near Florida State Road 404 (Pineda Causeway) south to southern part of Melbourne Beach (T26–28S, R37–38E; Tropic and Melbourne East quadrangles USGS 7.5′ series): UF 89873–89898, UF 89925–89933, UF 89934 (2 spec.), UF 89935–89947, UF 92050–92096, UF 96988–97016, UF 103049–103101, UF 103372–103402, UF 104748, UF 104750, UF 104801, UF 105162–105174, UF 108026–108041. Site 3765, Satellite Beach: UF 44507, UF 47573–47574, UF 48209–48260, UF 48262–48287, UF 48289–48300, UF 48308–48312, UF 48314–48393, UF 66851, UF 66852. Site 3777, Melbourne Beach, off Cherry
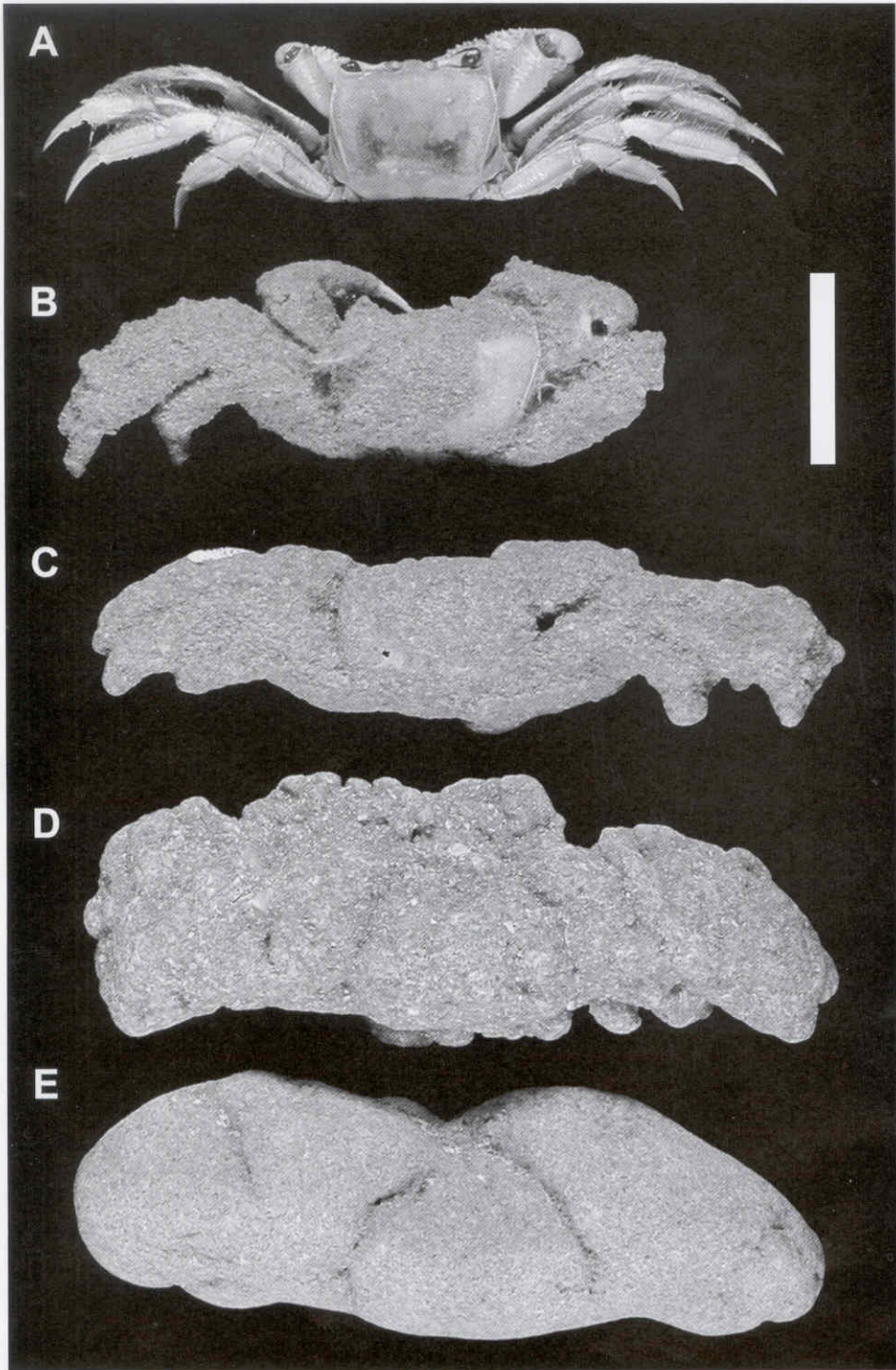
Fig. 2.   Recent and fossil *Ocypode quadrata* from Brevard County, Florida. A. Recent specimen collected from Satellite Beach (UF 2475). B. Fossil specimen with thin, friable coating of coquina. Portions of carapace and pincers exposed, right pereiopods incomplete (UF 48195). C–E. UF 47573, UF 48258, and UF 48362 (top to bottom) showing increased progression (thickening) of cemented coquina and increased abrasion by rolling. D, E nearly unrecognizable fossil crabs. Scale bar is 5 cm.

Street (Melbourne East Quadrangle USGS 7.5′ series): UF 54576.

Recent *O. quadrata*, 60 specimens in eight lots from six sites in Brevard County, Florida, in holdings of the Invertebrate Zoology Division, FLMNH, and of the National Museum of Natural History, Smithsonian Institution (USNM). Site 3766, Satellite Beach: UF 2475 (1 spec.). Seagull Park, South Patrick Shores: USNM 1001747 (12 spec.). Canova Beach Park, end of Florida State Road 518 (Eau Gallie Causeway), Melbourne: UF 1029 (13 spec.), UF 1030 (2 spec.), UF 1031 (2 spec.). Public beach, end of U.S. Highway 192, Indialantic: UF 1032 (8 spec.). Ocean Park, Melbourne Beach: USNM 1001748 (11 spec.). Coconut Point Park, south of Melbourne Beach city limits: USNM 1001746 (11 spec.).

Taxonomic identity of the fossil crabs reported herein was based on descriptions of Rathbun (1918), Williams (1984), and comparison to modern *O. quadrata*. Features included the distinctive quadrate carapace, patterns of ridges and granulation on the carapace, and morphology of the chelae. On the most heavily encrusted specimens, at least the quadrate carapace was evident, either outwardly or when sectioned.

The majority of fossil *O. quadrata* were amassed while beachcombing from Patrick Air Force Base to Melbourne Beach in Brevard County (Fig. 1) by P. Brett (1987–1992) and JLB (1993–2000). Beginning in 1994, JLB documented fossil crab finds during twice-a-week beach walks from Pineda Causeway to Eau Gallie Causeway. Monthly, he compiled abundance and wind direction data while looking for fossil *Ocypode* at low tide. During 1999–2000, JLB's notes indicate that his best-preserved specimens were found following winter storms with strong northeasterly winds, but his greatest quantities of crabs were collected during June and July of those years when winds were predominately from the south. RWP, Kevin Schindler, Phillip Whisler, and Tom McConnell collected the best-preserved material (those with loose friable matrix) in January, 1992, during and immediately following a period of extreme erosion near Spessard Holland Park, Brevard County, where nearly 5 m vertical depth of sand was eroded from the beach.

The minimum number of individuals (MNI) was determined by counting the number of specimens with more than half of the cephalothorax present, even if the dorsal carapace was missing. Handedness (major chela on the left or right) was based on the morphology of the chela in less-abraded specimens or on its comparative massiveness in well-abraded specimens. We assumed that there was equal accretion of sediment and cement and uniform abrasion of the specimens. Size of a crab was measured as the width of the carapace. On many specimens, the dorsolateral edge of the carapace was obvious due to the presence of a series of depressions in the surface detail. In addition to the fossil material, 59 live *O. quadrata* collected by net from five localities within the approximately 20-km study area were measured.

Geochemical dating to determine the exact age of the fossil *O. quadrata* was not attempted due to the their altered minerology.

Geology, Stratigraphy, and Age

The name "Anastasia formation" was applied by Sellards (1912) to "the extensive deposit of coquina rock found along the east coast" of Florida. The unit consists of interbedded quartz sands and the distinctive coquina variety limestones (Scott, 1991). Whole and fragmented mollusk shells (mostly bivalves) that commonly are abraded (waterworn) with limited amounts of quartz sand and calcite cement dominate the coquina. The sand layers are fine to medium grained, quartz dominated, with varying amounts of fossil debris. Color of the unit ranges slightly with lithology from light gray to buff to orange-brown. Fossils reported from the Anastasia include poriferans, bryozoans, mollusks, arthropods, and echinoderms, with few, if any, of the species extinct (Du Bar, 1974; Portell, unpublished data). Fossil vertebrate taxa collected include whale, tapir, horse, giant armadillo, turtles, and sharks (Portell and Beerensson, unpublished data). Most vertebrate fossils are cemented with a thick layer of coquinoid matrix.

The Anastasia Formation exhibits varied lithology both laterally and vertically due to diagenetic processes related to movements of groundwater (referred to as meteoric diagenesis; McNeill, 1983, 1985). Diagenesis in the unit is most complete in the phreatic zone (zone of groundwater saturation) and at the top of the overlying vadose zone (zone of aeration between the surface and groundwater table). In the latter zone, a caliche forms from dissolution or alteration of shells by rainwater undersaturated with calcium carbonate (McNeill, 1985), which leads to reduced permeability (i.e., water retention) and, therefore, increased cementation. In the lower vadose zone, cementation is, however, much less complete due to reduced permeability of the overlying caliche crust; and cementation usually occurs at grain contacts as calcium carbonate-saturated waters travel through the zone (McNeill, 1985). In the freshwater phreatic zone, cementation by calcite is considerable, and calcite crystals often form in available void spaces.

The areal distribution of the Anastasia Formation can be found in natural exposures scattered along the East Coast from St. Augustine to southern Palm Beach County near Boca Raton (Scott, 1991; Fig. 1). North of Boca Raton, the Anastasia forms the backbone of the Atlantic Coastal Ridge, and south of Palm Beach County it grades into the Miami Limestone of southern Florida. Some disagreement exists on the position of the western margin of the unit: Cooke (1945) estimated it to terminate within several kilometers of the Intracoastal Waterway, whereas Scott (2001) claimed it to extend as much as 32 km inland in St. Lucie and Martin counties. The Anastasia is thin throughout both its surface and subsurface distribution. Most outcrops are only 1–2 m thick, with the thickest surface exposure of 5.5 m observed in Palm Beach (Parker *et al.*, 1955: 101) and the maximum thickness of the formation measured as 37.8 m in a subsurface section in Brevard County (Du Bar, 1974). The depositional environment of the Anastasia represents a shallow nearshore marine setting, with the presence of coquina indicating deposition in a high-energy environment, such as a surf zone (Du Bar, 1974).

The Anastasia Formation is the youngest lithified marine deposit along Florida's coast (Perkins, 1977). Based on radiometric (U^{234}/Th^{230}) dating of shell and beachrock from the Cape Canaveral barrier island and lagoon complex, the principal time of deposition is thought to have occurred approximately 110,000 YBP (Osmond *et al.*, 1970). Results of amino acid racemization, used to date unaltered Anastasia Formation bivalves, also indicate the unit to be about 110,000 yr old (Mitterer, 1974). In addition, Osmond *et al.* (1970) and McNeill (1985) reported evidence of other periods of lesser accumulation attributable to the formation. McNeill (1985) noted that extensive and detailed dating would be needed before exact ages of these lesser accumulations could be made. Murphy (1973), in a study of the diagenesis of the Anastasia Formation, obtained radiocarbon dates from samples collected on Anastasia

Island that indicated an approximate age of the Anastasia in this area to be 8500–9000 YBP. Clearly, more work is needed to determine the age range of this unit, which may, as noted by Mossom (1925: 112), still be forming today.

RESULTS

Of 508 MNI, about 70 fossil *O. quadrata* had a light or incomplete coating of matrix and a limited amount of cementation of the grains. Various parts of the carapace and limbs often were exposed on these specimens. About 20 nonabraded crabs appeared to have been disturbed postmortem (scavenged?), or they might have been exuvia; a few appeared to be crushed, and others simply had misaligned or missing carapaces. Nonabraded specimens presumably had been washed recently onto the beach terrace from the dunes or from a poorly consolidated portion (i.e., lower vadose zone) of the Anastasia Formation beneath the dunes. Crabs with exposed parts and thin matrix offered the best clues to the identity of the material: they clearly are *O. quadrata* based on shape, spination, and tuberculation of the carapace and chelae (Williams, 1984) (Figs. 2B, 3). Modern epibionts never were found on nonabraded specimens.

At the other extreme, highly polished (rolled) specimens were hardly recognizable as crabs because of the high degree of cementation (coating) and the high level of abrasion, probably from having been tumbled in the surf (Fig. 2E). Even in these specimens, at least the quadrate carapace of *O. quadrata* often was evident. Rolled specimens almost always consisted of intact crabs, although the four pairs of pereiopods often were broken off; but two of the abraded specimens might have been molts or suffered postmortem disturbance. These fossil specimens most likely spent considerable time in the nearshore subtidal region. Some abraded specimens appeared to have lain undisturbed and exposed on the sea floor for a sufficiently long time to accumulate modern epibionts. These epibionts (calcareous polychaete tubes, shells of oyster spat, bryozoans) occurred both on the surface and in cavities of the broken cephalothorax, chela, or oral field (Fig. 4). One museum lot (UF 89934) consists of two crabs strongly fused together.

The primary area of disarticulation was in the oral field, with the loss of mouthparts. Only the mandibles were found in the void of the cephalothorax of one specimen (UF 97012; Fig. 5B). Typically, the face of the crabs consisted of a hole leading into the cavity of the cephalothorax, which rarely was completely filled with sediment, coquina, or crystals of calcite (Fig. 5A). It was difficult to determine whether eyestalks were present except in a few animals. Otherwise, most crabs appeared to be in a relaxed normal position (i.e., chelae fully adducted; pereiopods parallel, extended laterally but arcing downward with the dactyls pointing as if standing on the substratum; also see Bishop, 1986). Posture of the animals and their low degree of disarticulation indicate that they died while buried in burrows. No specimens were found in association with fossilized burrows; but ten specimens (both nonabraded and abraded) had large lithified Anastasia plates extending from their carapaces (see Fig. 2D), which probably served as depositional nuclei (Bishop, 1986).

Carapace sizes of both modern and fossil crabs were not normally distributed, and mean widths (31.7 and 41.9 mm, respectively) and ranges were quite different (Fig. 6). The largest specimen in our small sample of modern crabs was 42.4 mm and approximated the mean for the sample of fossil crabs; the sample probably was biased toward capture of larger crabs on the beach. Measurements of carapace width in fossil specimens were overestimated due to the accretion of matrix. Estimates of accretion were made from some broken specimens for which the carapace widths with and without the matrix could be measured (e.g., UF 48179: 43.2 mm vs. 39.9 mm; accretion of 1.7 mm of matrix), but accretion was small compared to the difference in mean sizes of fossil and Recent crabs from Brevard County. Measurements of the cut edges of the carapace in horizontally sliced fossil specimens were underestimates because the pleura slope medially below the dorsolateral edge, where the carapace is widest.

Of 508 MNI, handedness was discernible in 395 (78%). The ratio of right-handed to left-handed fossil crabs (1:1.16) was equal (χ^2; $P > 0.05$). The handedness ratio also was equal in 59 Recent specimens, in males as well as in females. Only seven fossil specimens could be sexed based on exposed parts of the abdomen; all had a light coating of loose matrix, and among these were three males [UF 48197, UF 48201 (Fig. 5A), UF 48412] and four females [UF 48160, UF 48165 (Fig. 3C), UF 48186, UF 48200]. An eighth specimen (UF 89880), strongly waterworn and with a thick coating of matrix, was likely a female.
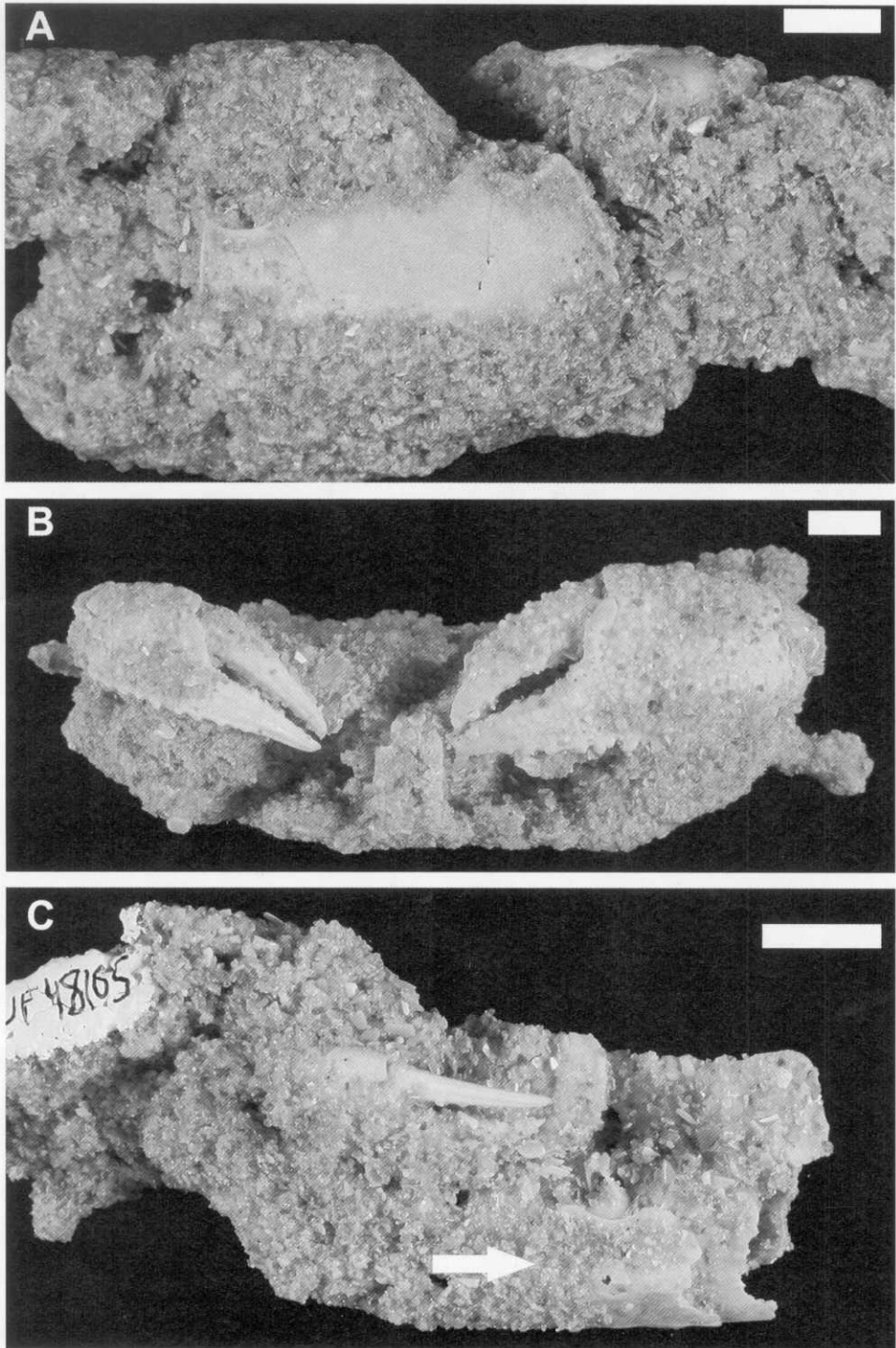
Fig. 3.   Fossil *Ocypode quadrata*. A. UF 48179 with frontal area of dorsal carapace exposed. B. UF 48305 with chelipeds partially exposed. C. UF 48165 with wide abdomen (female) (see arrow) and portions of right propodus and dactylus exposed. All exhibit a light coating of matrix with limited cementation of adhering shell and sand. Scale bars are 1 cm.
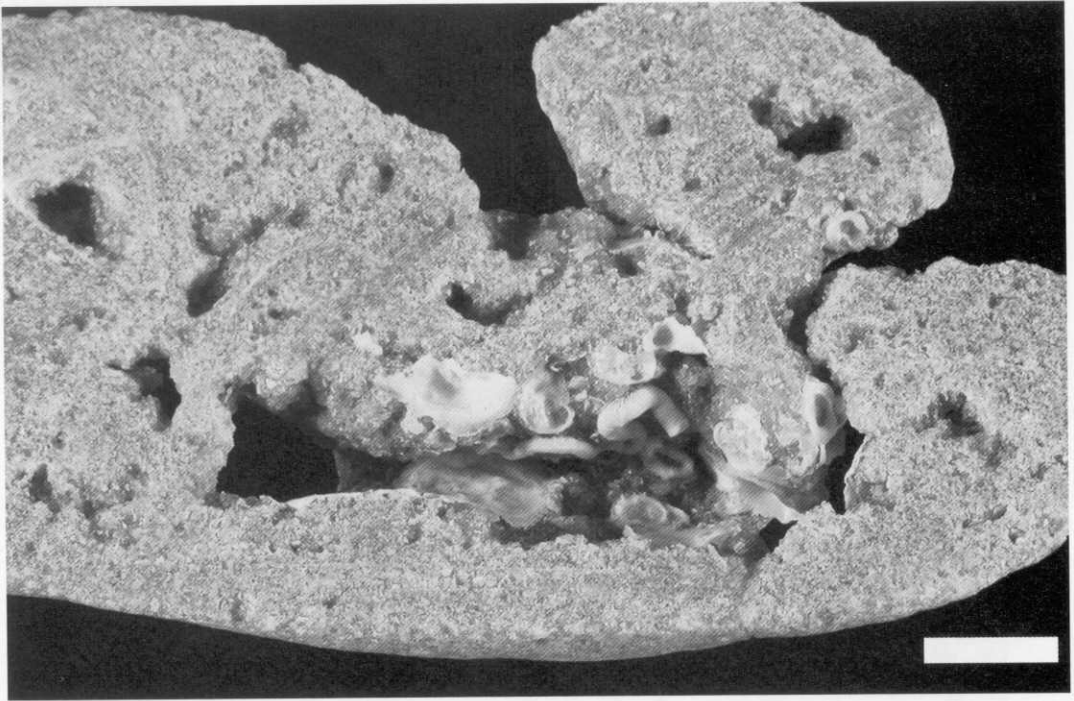
Fig. 4. Abraded fossil *Ocypode quadrata* (UF 103100) sectioned horizontally to expose modern epibionts (calcareous polychaete tubes and shells of oyster spat) inside cephalothorax. Scale bar is 1 cm.

DISCUSSION

Ocypode quadrata inhabits high-energy sand beaches from Rhode Island, U.S.A., to Brazil (Williams, 1984). The common name "Atlantic ghost crab" (Williams *et al.*, 1989) derives from its grayish white or pale yellow color (Williams, 1984) and, perhaps, from its fleeting image before beachcombers (Phillips, 1940). A second common name, "sand crab," refers to its habitat: it lives on the beach terrace as an adult, only occasionally entering the surf either for escape from terrestrial predators or to release hatching larvae. On land, the crabs are fleet-footed (thus, *Ocypode*: ωκυσ "swift", ποδοσ "of foot"), probably aided by their light body construction; their ability to attain speeds up to 2 ms^{-1} (Loraam, 1990) gives rise to a third common name of "racing crab." Their speed undoubtedly helps in avoidance of terrestrial and aerial predators as well as in navigating the wash of waves sandpiper-style during foraging bouts for their main prey, mole crabs and coquina clams (Wolcott, 1978). The gills are moistened from sand in the wash zone of the intertidal beach terrace or in their burrows by capillary action of setae on the ambulatory limbs

(Wolcott, 1976). Burrows extend to 1.2 m depth and occur from the upper intertidal (newly recruited juveniles) to as far as 400 m inland (Williams, 1984). Aside from adaptations of adult crabs to terrestrial life and their relative independence from the sea, *O. quadrata* rarely enter the surf, where a different host of predators awaits them in the subtidal zone and where survivability is limited (Williams, 1984). Although Koepcke and Koepcke (1952) placed the ghost crab *Ocypode gaudichaudii* Milne Edwards and Lucas, 1843, centrally in their Peruvian sand-beach food web, *O. quadrata* is the only permanent macrofaunal element of the exposed (upper) beach and foreslope of the dune along Atlantic shores, a testimony to its adaptation to a harsh environment. The ghost crab is heterochelous in both sexes (Williams, 1984), and handedness seems not to be fixed generally or by sex, despite Phillips's (1940) claim of right-handedness of this species. The life span of *O. quadrata* is about 3 yr (Haley, 1972).

Despite the wide geographic range of Recent *O. quadrata*, fossil ghost crabs—called "stoned crabs," "beach crabs," and "coquina crabs" by local collectors (e.g., Katz, 1995; Katz and Mikkelsen, 2000)—are found only where
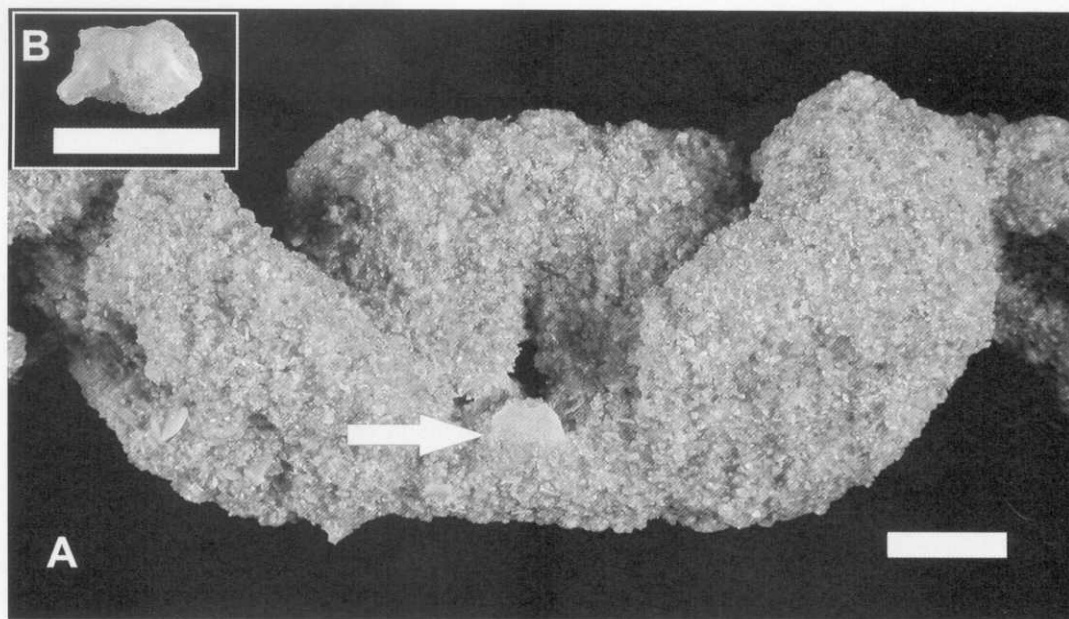
Fig. 5. Fossil *Ocypode quadrata*. A. UF 48201 in which mouthparts have fallen away, exposing the cavity leading to the hollow cephalothorax. Note narrow abdomen (male) (see arrow) of UF 48201. Scale bars are 1 cm. B. Mandibles removed from UF 97012.

terraces and loose coquina rock of the Anastasia Formation are alternately exposed and covered by shifting sands. Fossilization of the crabs might depend, therefore, on conditions that favor formation of coquina rock. Furthermore, the fossils are restricted to an approximately 20-km stretch of Atlantic Ocean beach in Brevard County (Fig. 1). This restriction indicates that exhumation of fossil crabs depends on local shoreline processes that prevail today.

We propose the following scenario to explain the stratinomy, taphonomy, and diagenesis of fossil *O. quadrata*. It is most unlikely that the crabs described here died on the beach or in the nearshore subtidal zone because of the prevalence of terrestrial, aerial, and marine scavengers. Moreover, *O. quadrata* does not have a robust or heavily calcified body and would disarticulate quickly in the surf. The relaxed normal posture (i.e., "Normal Position" of Bishop, 1986) indicates that most of the fossil ghost crabs died in their burrows, possibly during severe winter freezes (i.e., well below the 6–8°C lethal thermal limit; see Wolcott, 1988: 60), and body posture was maintained by gradual infilling with sediments. Because of the limited disarticulation of the fossils (primarily loss of mouthparts but possibly also eyestalks and antennae), the crabs must have remained

undisturbed by bioturbators (e.g., ghost crabs, sea turtles, raccoons) and beach erosion for a long time (Plotnick, 1986; Plotnick *et al.*, 1988). Those that happened to lie in a freshwater lens or area of groundwater discharge (McLachlan *et al.*, 1992) in loose coquina shell hash of low organic content might have experienced conditions of anoxia and calcium-rich pore water that would have retarded bacterial decay (particularly by marine sulfate reducers) and dissolution of minerals from the skeleton (Plotnick, 1986; Allison, 1988; Plotnick *et al.*, 1988). These conditions would also have favored early concretion formation (Plotnick, 1986) or rapid formation of a layer of calcium soaps with subsequent mineralization (Berner, 1968; Allison, 1988) and adherence of a cemented coquinoid matrix. Through this process, the crabs might have acted as nucleation sites for coquina rock (Bishop, 1986; Turner, 1989), although conditions that produced the Anastasia Formation might have lacked the biogenic influence.

The greater mean size of fossil *O. quadrata* cannot be attributed to accretion of coquina matrix alone. Fossilization might favor more deeply burrowing adults (Williams, 1984), or conditions for fossilization might prevail at times of the year when juveniles comprise
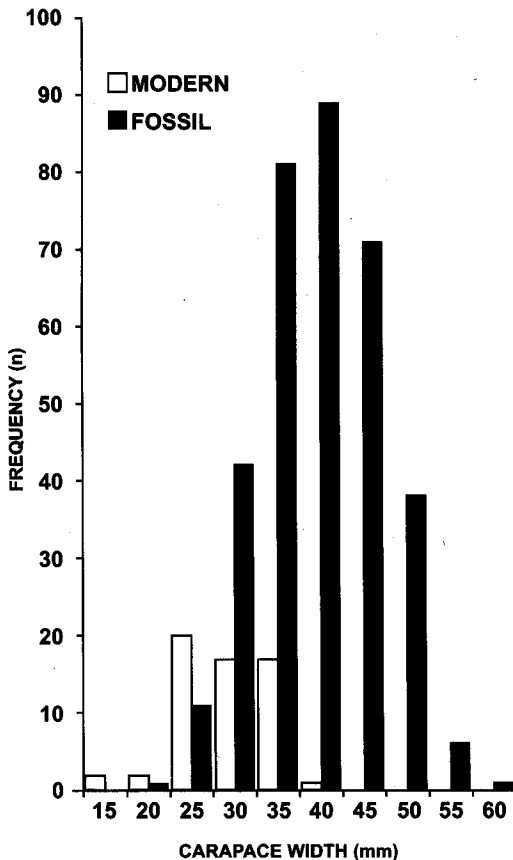
Fig. 6.   Size distributions of modern ($n = 59$) and fossil ($n = 340$) *Ocypode quadrata* from Brevard County, Florida, beaches. Individuals were grouped into 5-mm size classes based on carapace width.

a smaller component of the population (Negreiros-Fransozo *et al.*, 2002). Younger crabs burrow nearer the surf (Williams, 1984), a location that is physically more rigorous and devoid of groundwater; and their smaller corpses with a thinner cuticle might not develop a sufficiently anaerobic microenvironment (Allison, 1988) or thick enough concretion (Plotnick, 1986). In addition to the possible sampling biases of fossilization, small fossils might be more easily overlooked owing to small size or to more rapid abrasion and breakage. Of course, it is possible that the mean and range of sizes of *O. quadrata* were much greater in the past, as they presently vary geographically (Haley, 1969; Negreiros-Fransozo *et al.*, 2002). For example, Haley (1969) recorded the maximal carapace width in a Texas population to be 53.5 mm, a size much larger than those in our Recent sample from Brevard County; but Haley's

specimen is exceeded in size by only 2.6% of our measurable fossil specimens and only 1.5% if our values are adjusted for accretion of matrix based upon specimen UF 48179.

Fossil *O. quadrata* were found in a range of conditions: at one extreme, those with a clearly crab-like form, bearing a loose friable matrix of shell hash with little cementation, no calcite infilling, and no attached fossil or Recent epibionts; and at the other extreme, those that were barely recognizable as crabs, with a heavily polished surface, thick layer of matrix with heavy cementation, some voids filled with calcite-cemented grains, and some with Recent epibionts in exposed cavities. We suspect that fossil crabs found on beaches in Brevard County derive from several sources. The non-abraded crabs with friable matrix have recently been eroded from a poorly consolidated portion of the Anastasia Formation, most likely the lower vadose zone where a lower degree of cementation occurs because of reduced permeability of the overlying caliche crust, or possibly washed from the dunes or upper beach escarpment by storm waves. Upon transport to the subtidal zone, these poorly lithified fossils are unlikely to survive abrasion (Bishop, 1986). Abraded crabs have been cast upon the beach from the nearshore subtidal zone by storm waves. Many of these specimens contain calcite crystal growths on the hollow interior surfaces of the cephalothorax and cavities of the broken chelae. These crystals along with the heavy cementation indicate that fossilization likely occurred in the phreatic zone. The presence of epibionts on some specimens indicates subsequent exposure in the marine subtidal zone. The population of abraded fossil crabs might have accumulated over the past 110,000 yr (the generally accepted age of the Anastasia Formation) but especially in the last 18,000 yr of more rapid sea-level rise during recession of the continental shoreline (Milliman and Emery, 1968). The nonabraded fossils, possibly derived from the dunes or upper beach escarpment, might be as young as a few thousand years.

The barrier-island–sand-dune system along the central East Coast of Florida is believed to have formed within the last 7,000 yr as the rate of sea-level rise slowed (Parkinson, 1995). Studies by Mayhew (2000) indicate that in Brevard County (just south of our fossil *O. quadrata* collecting localities), seaward shoreline advance (progradation) has continued over the last 7000 yr, primarily because of abundant

sediment supply provided by Cape Canaveral. But, farther south in Brevard County, continued transgression occurred until about 1,500 YPB owing to insufficient sediment supply, and the area became susceptible to overwash by storm surge and formation of tidal inlets (Mayhew, 2000). It is not, therefore, surprising that crab fossils are found only from Satellite Beach to south Melbourne Beach and not farther south where conditions probably were not stable enough for *Ocypode* fossils to form.

Although fossil crabs have probably been exposed by erosion of dunes slowly during the Holocene marine transgression, the large numbers found in recent decades by beachcombers in the study area might be due to erosion enhanced by acceleration of sea level rise over the last 150 yr (Brooks, 1972) or by construction of the inlet at Port Canaveral in 1951–1954. Prior to inlet construction, the 40-km stretch of beach between the towns of Cape Canaveral and Melbourne Beach was stable to accretional, gaining 108,000–156,000 yd^3yr^{-1}; but the same shoreline has lost 207,000–318,000 yd^3 yr^{-1} since construction (Bodge, 1994). Bodge (1994) reported also that the dune line has been receding faster than the shoreline at mean high water. Recent (2002) beach renourishment projects in our study area may limit future discoveries of fossil *O. quadrata* for some time.

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