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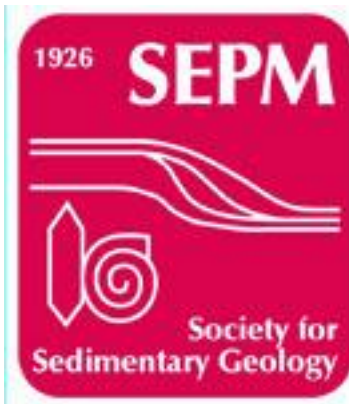


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TRACEMAKING ACTIVITIES OF CRABS AND THEIR ENVIRONMENTAL SIGNIFICANCE: THE ICHNOGENUS *PSILONICHNUS*¹

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ABSTRACT—Modern crabs are common inhabitants of shallow subtidal, intertidal, and supratidal environments, and many crabs are capable of producing traces that can be preserved in the rock record. The first crabs, Early Jurassic in age, probably were not fossorial. By Cretaceous time, however, diverse endobenthic lineages were established. Many representatives of these lineages undoubtedly produced domiciles that are preserved in shallow marine to quasimarine sediments and that should be useful in characterizing the depositional environment of the sediments. Nonetheless, most such dwelling structures have been studied little and remain essentially unnamed.

The ichnogenus *Psilonichnus* Fürsich is amenable to the taxonomic concept of several forms of crab burrows; presently recognized ichnospecies include *P. tubiformis* Fürsich and *P. epsilon* (n. ichnosp.). Future work may reveal the need for further ichnospecific differentiation. The occurrence of *Psilonichnus epsilon* and related burrow forms should prove to be a useful criterion for the identification of marine-margin facies in the rock record.

Certain crabs also produce domiciles referable to *Thalassinoides*, *Gyrolithes*, and *Skolithos*, and possibly *Macanopsis* and *Spongiomorpha*. Except for *Skolithos*, such structures traditionally have been attributed to shrimp, lobsters, or stomatopods. Ethologic and taxonomic re-evaluation of these burrow forms is needed.

INTRODUCTION

SEVERAL ichnogenera have been established for trace fossils of presumed crustacean origin: *Ardelia* Chamberlain and Baer (1973), *Chagriniichnites* Feldmann et al. (1978), *Gyrolithes* Saporta (1884), *Macanopsis* Macsotay (1967), *Ophiomorpha* Lundgren (1891), *Pholeus* Fiege (1944), *Spongiomorpha* Saporta (1887), and *Thalassinoides* Ehrenberg (1944). Most of these burrows have been ascribed to the activities of shrimp, lobsters, or stomatopods (Pemberton, Frey, and Walker, personal observ.). Fossil burrows such as those excavated by modern crabs, although well-documented locally (Richards, 1975; Jenkins, 1975), have rarely received formal ichnogenus and ichnospecies names.

With taxonomic emendation, the ichnogenus *Psilonichnus* Fürsich (1981) is amenable to many crab trace fossils and, hence, is the major subject of our report. Presently recognized ichnospecies include *P. tubiformis* Fürsich (1981) and *P. epsilon* n. ichnosp., described herein. We also present brief

reviews of related ichnogenera, modern burrowing crabs, and the known fossil record of crab or crab-like burrows.

In terms of species diversity and adaptive radiations among crustaceans (26,000 species), the crabs (4,500 species) are approached in importance only by copepods (4,500 species), isopods (4,000 species), amphipods (3,600 species), and non-crab decapods collectively (4,000 species) (Warner, 1977). Thus, crab body fossils and crab burrows surely must be more common in the rock record than the present literature indicates.

In addition to their preserved domiciles, crabs may be represented in the ichnologic record by various bioturbate textures imparted to host sediments (Edwards and Frey, 1977, p. 228-230; Katz, 1980); they also may be responsible for appreciable bioerosion of sediments (Letzsch and Frey, 1980a, p. 208-210). Crabs thus have considerable importance as geologic agents.

NATURAL HISTORY OF CRABS

Decapods are represented by about 8,500 species, of which more than half are crabs.

¹ Contribution number 498, University of Georgia Marine Institute, Sapelo Island.

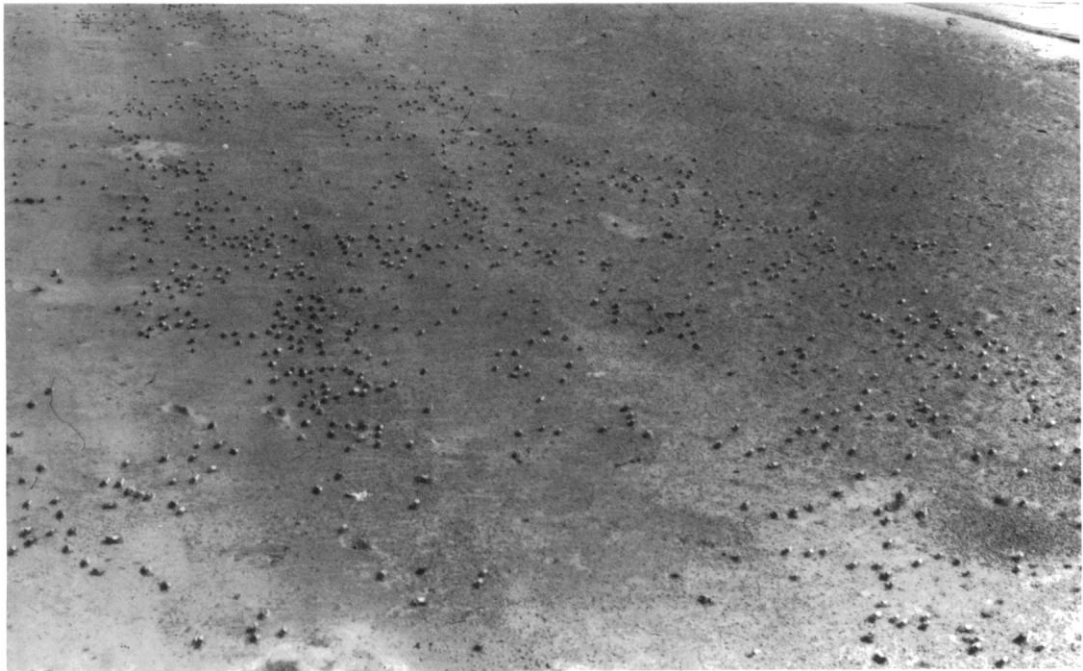


FIGURE 1—Dense population of the sand fiddler crab, *Uca pugilator*, feeding on an estuarine beach. Blackbeard Creek, Sapelo Island, Georgia.

Not only are crabs among the most successful of all decapods, more is known about their biology than of any other single group of crustaceans (Kaestner, 1970; Warner, 1977; Barnes, 1980). Members of the genus *Uca*, prodigious burrowers, perhaps have been studied most intensively (Crane, 1975).

Crabs are divided into two major taxonomic groups: the Anomura—hermit crabs and their kin, and the Brachyura—or true crabs. Here, we are concerned mainly with brachyurans. They range in size from the tiny male oyster crab *Pinnotheres ostreum* and sand dollar crab *Dissodactylus mellitae*, only 2 to 4 mm in width, to the giant Australian xanthid crab *Pseudocarcinus gigas*, which may have a carapace width of 43 cm, a chela of about the same length, and a body weight of about 14 kg (Warner, 1977). Some brachyurans, such as the soldier crab *Mictyris* (Schmitt, 1965) and the fiddler crab *Uca* (Figure 1), may be extremely abundant locally. Many species leave conspicuous records of their forays (Figure 2).

Adaptations.—Brachyurans exhibit a broad spectrum of habitat adaptations (Williams,

1965), and appear in terrestrial environments as well as in marine, brackish, and fresh waters. Most crabs that inhabit brackish or fresh waters must return to salt waters to breed, e.g., *Rhithropanopeus*; strictly fresh-water crabs include the Potamidae and their allies, or “river crabs” (Chace and Hobbs, 1969; Barnes, 1980). All land crabs occupy burrows or conceal themselves beneath protective cover, e.g., *Cardisoma* (Herreid, 1963; Henning, 1975); members of the genus *Gecarcinus* (e.g., Bliss et al., 1978) are best adapted for terrestrial life (Kaestner, 1970, p. 356). Terrestrial crabs may obtain respiratory water by burrowing down to the water table. The same is true of the so-called amphibious crabs such as *Uca* (Frey and Mayou, 1971).

In addition to the various habitat adaptations mentioned above, as well as formal taxonomic ranks, brachyurans may be divided into five general, nonexclusive categories of life styles (Warner, 1977, p. 68–84). Each category is characterized by a particular behavioral pattern and, in some cases, by specific morphological adaptations:

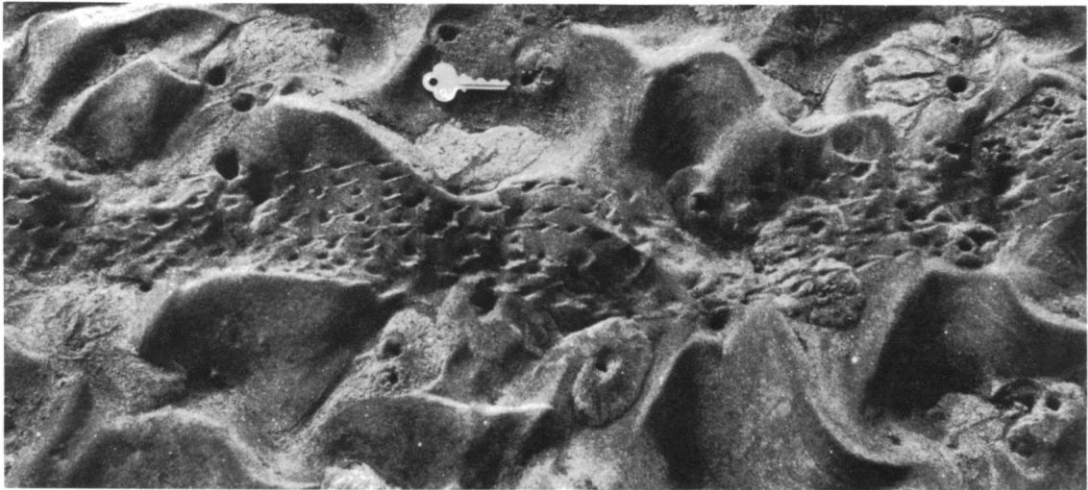


FIGURE 2—Trackway of the shore crab *Pachygrapsus crassipes* crossing a ripple-marked sand flat. Associated burrows made by the ghost shrimp *Callinassa californiensis*. Lagoon near Torrey Pines, California. (Photo courtesy of J. E. Warme.)

1) Locomotion by means of walking, running, or climbing. Some species progress very slowly, whereas individuals of *Ocypode*, the fastest of all running crabs, may attain speeds up to 1.6 m/sec (Barnes, 1980). Many species in this category also burrow.

2) Swimming, especially among the Portunidae. Posterior appendages typically are flattened to function as oars, e.g., *Callinectes*. Many such crabs are adept at intercepting prey animals in the water column; yet the crabs may seek temporary refuge, or may conceal themselves from their prey, by burrowing shallowly into the substrate.

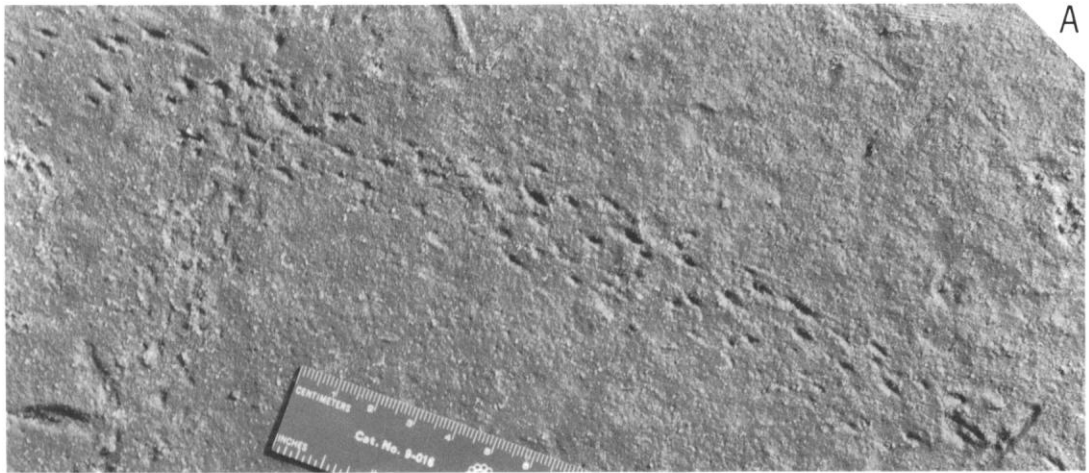
3) Burrowing, discussed below.

4) Incorporation of camouflage or inconspicuousness as a major adaptive feature. Cryptic coloration (*Daldorfia*), tufted hairs (*Pilumnus*), and encrustations by sessile epibionts (*Pisa*) are typical means of concealment. The ghost crab *Ocypode* is a master at blending into its beach-sand background.

5) Adaptation to commensal, symbiotic, or parasitic relationships with other species. Members of the Pinnotheridae are well-known associates of diverse shelled or burrowing organisms (Warner, 1977, p. 81–84), and the anemone-hermit crab association is equally well documented (Ross, 1974). On the other hand, diverse invertebrates and some fish may be common commensals inside crab burrows (Powell and Gunter, 1968).

Locomotion, burrowing, and feeding activities of benthic crabs are most apt to leave an ichnologic record. Locomotion typically results in a trackway representing a single excursion (Figures 2, 3A); in some instances, however, the path is used repeatedly. Feeding traces are especially common on substrate surfaces exploited by amphibious crabs such as *Uca* (Figures 3B–C, 4A); similar surficial traces—and dwelling structures—are produced by the sand-bubbler crab *Scopimera* (Schmitt, 1965, figs. 53, 54). Underlying sediment laminae may be disrupted, on a small scale, where penetrated by tips of the dactyli (Schäfer, 1972, fig. 140; Frey, 1973, fig. 5). Such “undertracks” have some potential for preservation in the rock record (cf. Goldring and Seilacher, 1971).

Among burrowing crabs, two distinct behavioral patterns are discernible: back-burrowers and side-burrowers (Warner, 1977, p. 75–78). Back-burrowers tilt the body backward and dig with the walking legs. Loosened sediment becomes a semifluid; the crab, utilizing various morphologic adaptations, ordinarily works itself downward until only the eyes or antennae remain visible (Savazzi, 1982). In the portunid crab *Macropipus* (Kaestner, 1970, p. 346), the flattened fifth pereopods are pushed horizontally into the sediment while the chelipeds are forced forward, thereby moving the body backward into



the substrate; the buried crab then nestles its chelipeds along the anterior curvature of its carapace, enclosing a sediment-free space filled with respiratory water. The teeth of the anterior margin of the carapace extend over the water chamber to the chelae, straining out detrital sand. The soldier crab *Mictyris* (Schmitt, 1965, p. 135, fig. 55) buries itself extremely rapidly; its actions produce a corkscrew spiral because it digs with the legs of one side of its body while rotating its position in the substrate by means of the legs on the other side.

Back-burrowers thus are temporarily embedded within the substrate. Resting traces so created would appear in the rock record as a pocket-like disruption of sediment laminae (Schäfer, 1972, figs. 226, 227), although these structures remain poorly documented in current geologic literature (cf. Hannibal and Feldmann, 1983).

Side-burrowing, on the other hand, results in the construction of a regular domicile (Figure 5), which may provide shelter for extended periods of time. Various heterogeneities in habitat may influence the selection of an actual burrow site. Juvenile through adult burrows of the ghost crab *Ocypode* are typically zoned according to beach slope and tide levels (Frey and Mayou, 1971). In salt marshes, variations in the density of grass root mats may influence the density and distribution of burrows of the fiddler crab *Uca* (Ringold, 1979). Territoriality also may be involved; among freshwater crabs of the Pseudothelphusidae, which burrow in rocky streams, the most favorable sites are preempted by the larger, more dominant individuals (A. E. Smalley, 1983, personal commun.).

Side-burrowers employ their legs, the dactyli of which may be slightly flattened dorsoventrally, to excavate sediment. Usually, only the legs on one side of the body are engaged. Excavated sediment may be formed into a spherical pellet, carried out of the bur-

row, and deposited near or scattered around the aperture (Figures 3C, 4B) (Chakrabarti, 1972); this sediment reworking may alter the grain-size distribution of particles (Chakrabarti, 1980). In some species, the pelleted sediment may be used to construct a chimney that effectively extends the burrow aperture vertically (*Uca*) or horizontally (*Sesarma*) (Basan and Frey, 1977). Most side-burrowers are terrestrial or amphibious, yet a few sublittoral crabs—such as *Goneplax*—construct their burrows underwater (Rice and Chapman, 1971).

Although the structures excavated by side-burrowers generally serve as protective domiciles, more specific functions may be discerned. For example, males of some species of the ghost crab *Ocypode* dig spiraled burrows thought to be used in copulation (Hughes, 1973). Similarly, the location and quality of burrow construction is intimately related to reproductive patterns in the fiddler crab *Uca pugilator* (Christy, 1983).

Side-burrowers are the chief subject of our report, because their traces are more likely to be represented in the rock record. Several examples of their burrow construction are cited in Table 1, and their fossil counterparts are discussed subsequently.

Geologic history.—The most primitive crabs, the Dromiacea, first appeared in the Early Jurassic (Warner, 1977, p. 164–172, tables 4, 5, figs. 41A, 43). They probably stemmed from the Glypheoidea, a macruran lineage related to the spiny lobsters (Pemberton, Frey, and Walker, personal observ.). Early dromiaceans lack the characteristic brachyuran morphology, however, and are not likely to have constructed distinct, readily preservable dwelling structures. Families of modern crabs containing fossorial members seem to have become well established by Cretaceous time, and their burrows should be correspondingly prominent in post-Jurassic rocks. Some possibly occur

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FIGURE 3—Crawling and grazing traces of the sand fiddler crab, *Uca pugilator*. Washover sands within a salt marsh, St. Catherines Island, Georgia. *A*, crossing trackways, with distinctive dactylus imprints. Bird track at lower left corner. *B*, *C*, grazing traces, those in *C* superimposed on raindrop imprints. Cheliped scrapings in the substrate surface reflect deposit-feeding activities (Miller, 1961); individual scrapes are sharper in moist sediment (*C*) than in wet sediment (*B*). Small sediment pellets (3–4 mm) discarded during feeding; large pellets (>10 mm) discarded during burrow excavation.

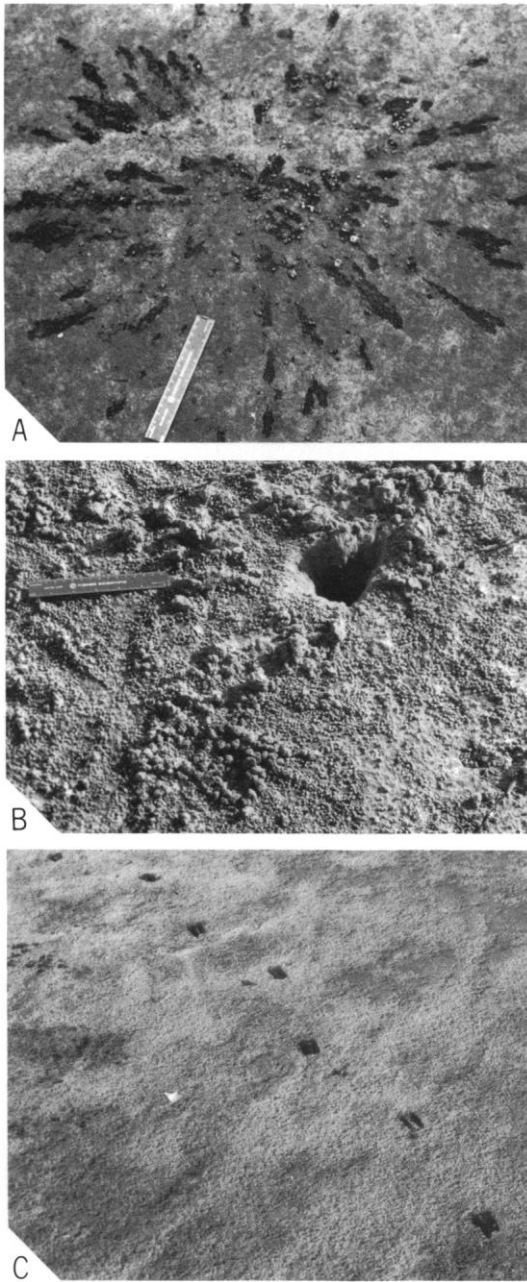


FIGURE 4—Surficial lebensspuren made by ocypodid crabs. Locality as in Figure 3. *A*, radially disposed grazing traces of the fiddler crab *Uca pugilator*, wet sediment. *B*, entrance to large burrow of the ghost crab *Ocypode quadrata* surrounded by profuse sediment pellets discarded by *Uca pugilator*, dry sediment. *C*, a similar surface crossed by the white-tailed deer *Odocoileus virginianus*.

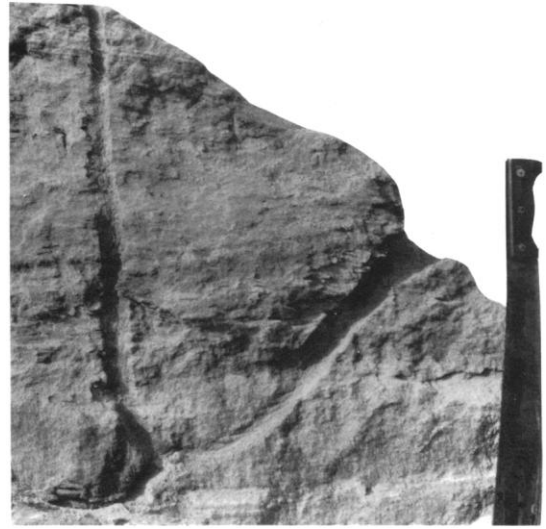


FIGURE 5—Domicile of the ghost crab *Ocypode quadrata* exposed by storm-wave erosion of a sand dune. Cabretta Island, Georgia. Length and configuration of burrow arms controlled partly by topography of substrate surface (cf. Frey and Mayou, 1971). Only uppermost part of basal shaft (below bifurcation) is exposed. Cheliped sculptings common locally within burrow.

in Upper Jurassic rocks (Fürsich, 1974, fig. 7).

MODERN AND ANCIENT CRAB BURROWS

Modern benthic crabs and their burrows are abundant in numerous sedimentary environments, from terrestrial clastics to shoaling marine carbonates. Representative brachyuran families (Table 1) include: 1) portunids—swimming crabs, 2) xanthids—mud crabs, 3) goneplacids—xanthid-like, bottom-dwelling crabs, 4) ocypodids—amphibious crabs, 5) grapsids—crabs of diverse habits and habitats, and 6) gecarcinids—land crabs. Certain anomuran sand crabs, such as *Albunea* (Farrow, 1971, fig. 10), also may construct distinctive burrows; most, however, produce only bioturbate textures in the sediment (Frey and Howard, 1972, p. 173, fig. 2).

Fossorial members of the above groups, as a whole, are most characteristic of high-intertidal to supratidal environments. Terrestrial burrowing crabs also are significant locally (Bliss et al., 1978). Of the latter, *Cardisoma* (Table 1) is perhaps best known

ichnologically. Other species of land crabs generally remain poorly studied from this standpoint. Freshwater crabs (e.g., Chace and Hobbs, 1969) are comparatively rare, and none is known to be an extensive burrower. However, the habit is widespread among members of the Pseudothelphusidae (A. E. Smalley, 1983, personal commun.); their typical environment is small streams, where they burrow under and between rocks. The saber crab *Platychirograpsus typicus*, in contrast, burrows into the clay banks of rivers (Marchand, 1946, p. 94).

Fossil burrows attributed to crabs have been reported from the Upper Cretaceous of British Columbia (Richards, 1975), the Miocene or Pliocene of Japan (Nomura and Hatai, 1936), the ?Miocene of Taiwan (Hayasaka, 1935), the Miocene of Poland (Radwański, 1977a, 1977b), the Miocene and Pliocene of Australia (Jenkins, 1975), the Pleistocene of the southeastern United States (Frey and Mayou, 1971; Curran and Frey, 1977) and the Bahamas (Figure 6), and possibly the Oligocene of Egypt (Bown, 1982, p. 281). Subfossil crab burrows also occur in relict Holocene salt-marsh deposits of Georgia (Frey and Basan, 1981; Pemberton and Frey, personal observ.) and South Carolina (personal observ.).

Evidence for crabs as the tracemaker is circumstantial in most ancient settings; the strongest conclusions obviously are drawn when the fossil burrows closely resemble modern crab burrows. Nevertheless, body remains were found in association with the burrows reported by Richards (1975), Jenkins (1975), and Frey and Basan (1981). They also were observed in the relict Holocene burrows from South Carolina, mentioned above. Individuals of many species of crustaceans ordinarily desert their burrows before death (Schäfer, 1972), probably accounting for the dearth of body parts preserved inside burrows. Whether the same is true for most crabs is not known, however.

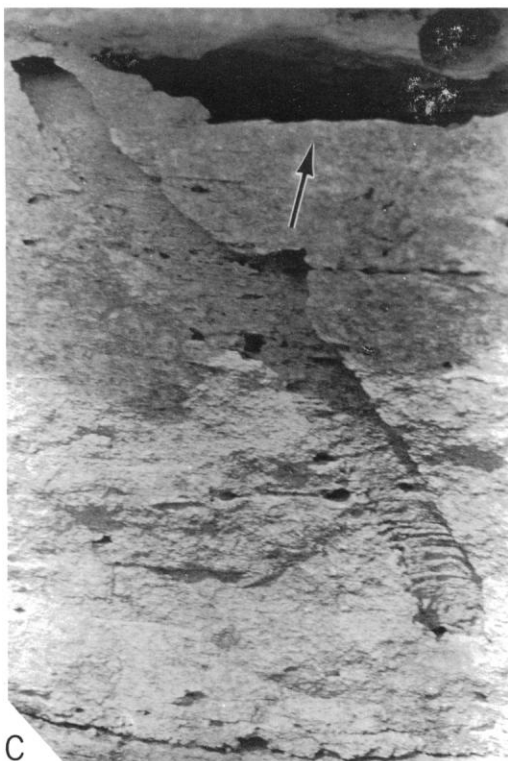
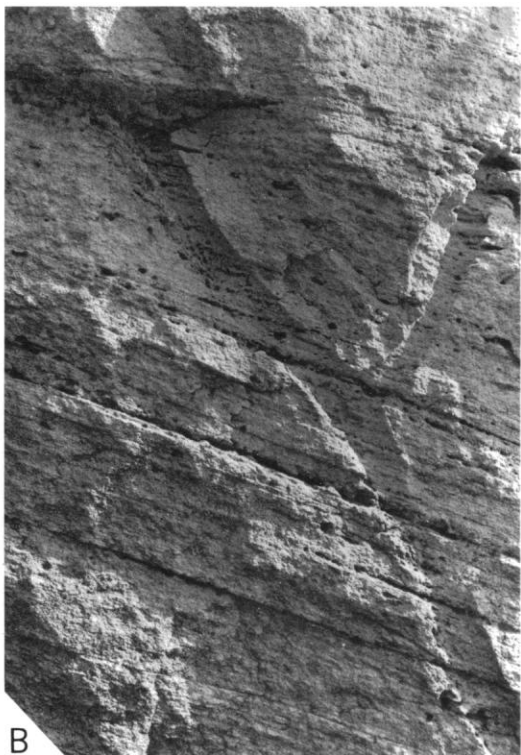
Aside from the obvious limitations of circumstantial evidence, certain fossil burrows resembling modern crab burrows are older than the oldest known, unequivocally endobenthic crab remains. "Crustacean burrows" (Fürsich, 1974, fig. 7) from the Upper Jurassic of England are possible examples.

TABLE 1—Selected examples of studies on modern crab burrows. (The albuneids are anomuran crabs; all others are brachyurans.)

ALBUNEIDAE	
	<i>Albunea</i> (Farrow, 1971).
PORTUNIDAE	
	<i>Ovalipes</i> (Caine, 1974).
XANTHIDAE	
	<i>Menippe</i> (Powell and Gunter, 1968).
	<i>Panopeus</i> (Basan and Frey, 1977; Pemberton and Frey, personal observ.).
	<i>Eurytium</i> (Basan and Frey, 1977).
GONEPLACIDAE	
	<i>Goneplax</i> (Rice and Chapman, 1971).
OCYPODIDAE	
	<i>Uca</i> (Frey and Howard, 1969; Frey, 1970; Frey and Mayou, 1971; Farrow, 1971; Braithwaite and Talbot, 1972; Allen and Curran, 1974; Basan and Frey, 1977; Garrett, 1977; Ferreira, 1980).
	<i>Ocypode</i> (Hayasaka, 1935; Utashiro and Horii, 1965; Frey and Mayou, 1971; Farrow, 1971; Braithwaite and Talbot, 1972; Hill and Hunter, 1973, 1976; Allen and Curran, 1974; Ferreira, 1980; Chakrabarti, 1981).
	<i>Macrophthalmus</i> (Farrow, 1971; Braithwaite and Talbot, 1972).
	<i>Ilyoplax</i> (Hayasaka, 1935).
GRAPSIDAE	
	<i>Sesarma</i> (Braithwaite and Talbot, 1972; Allen and Curran, 1974; Basan and Frey, 1977; Garrett, 1977).
	<i>Pachygrapsus</i> (Warme, 1971).
GECARCINIDAE	
	<i>Cardisoma</i> (Shinn, 1968; Braithwaite and Talbot, 1972).

Because prominent crab burrows generally are most abundant in intertidal, supratidal, and terrestrial environments—facies having relatively low potential for preservation—fossil crab burrows are inherently less abundant in the rock record than other crustacean burrows made in low intertidal and subtidal environments (e.g., Frey, Howard, and Pryor, 1978; Dworschak, 1983). Even where the appropriate facies are preserved, the crab burrows may be truncated by scour horizons (Radwański, 1977a, fig. 1) or otherwise modified or poorly preserved, as by concretionary overgrowth; diagenetic mineralization may impart thick "burrow linings" where none existed during the lifetime of the crab (Frey and Basan, 1981, Pl. 5, figs. 22–23).

In general, therefore, crab burrows are less abundant, less well preserved, and less readily identifiable in the rock record than such structures as *Ophiomorpha* (Frey, Howard, and Pryor, 1978). However, where ancient crab burrows are preserved, they may have



considerable significance in the interpretation of associated depositional environments (Frey and Mayou, 1971), and they warrant formal trace fossil names.

Finally, interpretations of many such fossil burrows are hampered by the relatively small amount of information available for numerous kinds of modern crab burrows. For example, in the Pleistocene of North Carolina we observed large concretionary burrow systems (Curran and Frey, 1977, Pl. 5d) possibly made by the stone crab *Menippe mercenaria*; yet a paucity of information on modern burrows of *M. mercenaria* (Powell and Gunter, 1968, p. 286–287) precludes rigorous uniformitarian comparison. Comparable burrows have been cast, by means of polyester resin, in Georgia estuarine environments (Figure 7). No other local decapods (Williams, 1965) or stomatopods (Manning, 1969) are of a size consistent with this tracemaker; however, even though individuals of the crab were seen in close proximity, none was observed within the large burrows sampled. Additional work on burrows of *M. mercenaria* from the Georgia coast therefore is being undertaken (Walker and Frey, in progress).

TAXONOMY OF BRACHYURAN AND OTHER CRUSTACEAN BURROWS

The ichnogenus *Pylonichnus*, as emended herein, is well suited for the accommodation of certain kinds of fossil crab burrows. Yet, somewhat similar burrows are constructed by various shrimp or shrimp-like animals (Dworschak, 1983)—as well as by some crayfish (Hobbs, 1981)—and certain crab burrows are referable to ichnogenera other than *Pylonichnus* (Table 2). For example, body fossils of the crabs *Ommatocarcinus* (Jenkins, 1975) and *Longusorbis* (Richards, 1975) are associated with *Thalassinoides*. The same is true of burrow systems excavated by the modern crab *Panopeus herbsti* in coherent muds (Letzsch and Frey, 1980a, fig. 5; Pemberton and Frey, personal observ.); similar

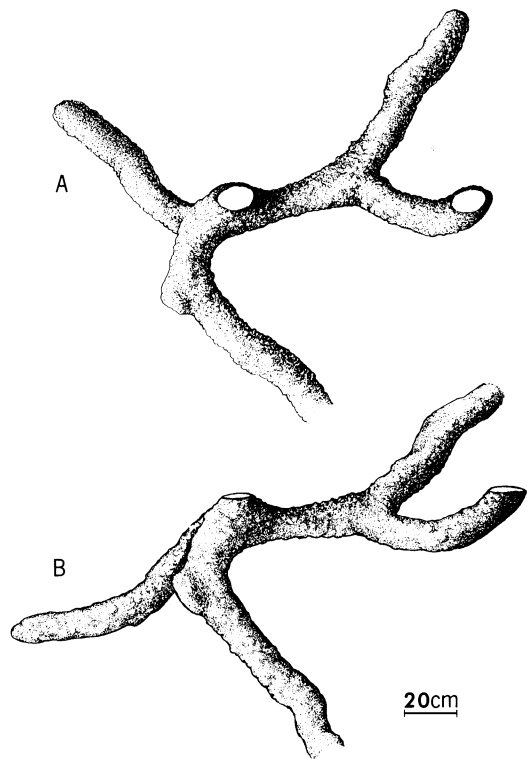


FIGURE 7—Polyester cast of probable stone crab burrow, *Menippe mercenaria*. Muddy sand of tidal stream point bar within a salt marsh, between Sapelo and Blackbeard islands, Georgia. Cheliped sculptings common on burrow walls. A, steep oblique view. B, shallow oblique view (cf. Powell and Gunter, 1968). (Sketches by G. Maddock.)

fossil burrows were reported by Nomura and Hatai (1936), but no body remains of crabs were observed.

Similarly, individuals of the same species of crab may construct burrows referable to different ichnospecies or even different ichnogenera. Juveniles of the modern ghost crab *Ocyropode quadrata* (Frey and Mayou, 1971, Pl. 2, fig. 3) sometimes excavate simple vertical shafts in foreshore sediments that, in

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FIGURE 6—*Pylonichnus upsilon* in its type area. Pleistocene calcarenites, San Salvador Island, Bahamas. A, inclined Y-shaped burrow; right arm slightly smaller in diameter (2.5–3 cm) than left arm (4–4.5 cm); length is 1.2 m. B, enlargement of bifurcation in A. C, upper part of bifurcated burrow, 2.5–3 cm in diameter; position of right arm, behind plane of rock exposure, indicated by arrow. D, segment of apparently unbranched shaft, ca. 5 cm in diameter and 1.35 m in length.

TABLE 2—Ichnogenera most likely to include crabs as tracemakers. *Pholeus* is omitted because of the uncertainty of its taxonomic status.

A—Taxonomic Key	
<i>Unbranched burrows:</i>	
1. Predominantly vertical; essentially uniform in diameter	<i>Skolithos</i>
2. Erect, arcuate; with basal chamber	<i>Macanopsis</i>
<i>Sparsely branched burrows:</i>	
1. Erect spirals	<i>Gyrolithes</i>
2. Externally striated components of variable orientation	<i>Spongeliomorpha</i>
3. J-, Y-, or U-shaped, erect components	<i>Psilonichnus</i>
<i>Well-integrated burrow systems</i> <i>Thalassinoides</i>	
B—Diagnoses	
<i>Skolithos</i> —Cylindrical to subcylindrical, straight to gently curved, distinctly walled, vertical to steeply inclined burrows (Alpert, 1974).	
<i>Macanopsis</i> —Slightly to highly curved J-shaped burrows terminating in a basal chamber; upper part of burrow essentially vertical (Macsoy, 1967).	
<i>Gyrolithes</i> —Rarely branched, spiraled burrows; helix essentially vertical, consisting of dextral, sinistral, or reversing coils (Bromley and Frey, 1974).	
<i>Spongeliomorpha</i> —Sparsely developed burrow systems; components vertical to horizontal, characterized by sets of longitudinal or oblique, fine, elongate striations on exterior of burrow casts (Fürsich, Kennedy, and Palmer, 1981).	
<i>Psilonichnus</i> —Predominantly vertical J-, Y-, or U-shaped structures of variable diameter; lateral branches, if present, form singular or bifurcated culs-de-sac and tend to emanate from vertical shafts (this report).	
<i>Thalassinoides</i> —Three-dimensional burrow systems consisting predominantly of smooth-walled, essentially cylindrical components of variable diameter; branches Y- to T-shaped, enlarged at points of bifurcation (Howard and Frey, 1984).	

the fossil record, could only be designated as *Skolithos*; adults of the same crab produce structures typically referable to *Psilonichnus upsilon*. In modern salt marshes of Georgia, the fiddler crab *Uca pugnax* may construct *Skolithos*-like shafts where population density is low (Basan and Frey, 1977, Pl. 4f) or integrated burrow systems referable to *Thalassinoides paradoxicus* where population densities are high (Frey, Basan, and Scott, 1973, fig. 1D; Letsch and Frey, 1980b, fig. 2B). Even more problematical, taxonomically, is the occasional interpenetration of burrows of *Uca pugnax*, *Sesarma reticulatum*, and *Eurytium limosum* in these marshes (Basan and Frey, 1977, Pl. 4a, c). Somewhat comparable ethologies and burrow morphologies probably are to be expected in the fossil record.

The degree to which spiraled burrowing patterns exhibited by certain modern crabs (Schmitt, 1965, p. 135, fig. 55; Farrow, 1971, p. 465, fig. 7) may approach typical specimens of the fossil burrow *Gyrolithes* (Table 2) remains to be seen. Ratios of coil height to coil diameter are very different; yet, the mere presence of a distinct helix satisfies the chief taxonomic criterion (Bromley and Frey, 1974, p. 320–321). Similarly, some forms of the striated burrow *Spongeliomorpha*—which is fully intergradational with *Thalassinoides*—need ethologic reevaluation from the viewpoint of brachyuran tracemakers; the same is true of *Macanopsis*.

Thalassinoides systems produced by crabs (Richards, 1975, p. 1856) are more apt to exhibit cheliped sculptings along burrow walls than those excavated by shrimp (Figure 8), lobsters (Pemberton, Frey, and Walker, personal observ.), or stomatopods. We speculate that *Spongeliomorpha* specimens excavated by crabs would bear much shorter, more stumpy or bulbous sculptings than those produced by shrimp or shrimp-like animals (Häntzschel, 1975, fig. 67.2a–b; Fürsich, Kennedy, and Palmer, 1981, Pl. 3, figs. 3–6). Furthermore, swollen bifurcations and nodal enlargements along burrow components, seen in various specimens of *Thalassinoides*, *Spongeliomorpha*, and *Gyrolithes* (Kennedy, 1967; Bromley and Frey, 1974; Fürsich, Kennedy, and Palmer, 1981), are more characteristic of shrimp or shrimp-like animals than of crabs. Local burrow enlargements, called “turn arounds,” are necessary for reversals in direction of movement by animals having a circumference similar to the diameter of the burrow; but these swellings are of no advantage in the bidirectional movements of crabs.

Among *Thalassinoides* systems attributable to crabs, those reported by Jenkins (1975) seem to be most typical of the ichnogenus in terms of overall burrow configuration. Those reported by Nomura and Hatai (1936) and Richards (1975) are less typical in that they seem to consist of vertical or inclined shafts stemming from a horizontal basal tunnel; however, comparable configurations have been observed in *Thalassinoides* systems attributable to shrimp (Figure 8).

As presently defined, the main distinction between unbranched, J-shaped burrows of

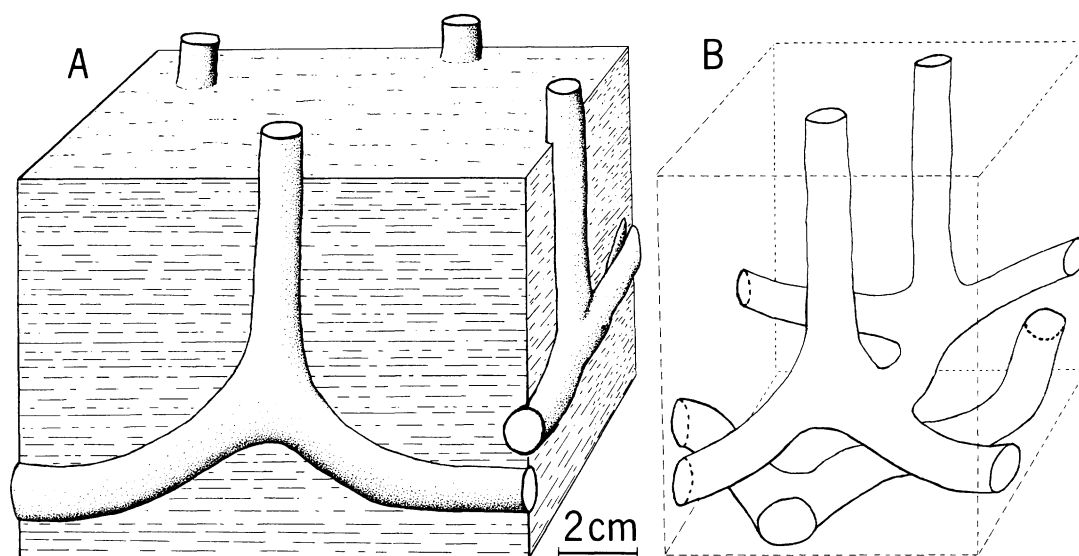


FIGURE 8—Reconstruction of smooth-walled burrows referable to *Thalassinoides paradoxicus*. Impure limestones at transitional contact between Clinchfield Sandstone and overlying Ocala Limestone (Eocene), near Perry, Georgia. Associated cheliped fragments, some inside burrows, indicate that *Callianassa* sp. was the tracemaker. *A*, unusual burrow systems in which horizontal bifurcations are comparatively rare; burrow fills more resistant to outcrop weathering than host stratum. *B*, burrow systems in which horizontal and vertical bifurcations are almost equally prominent; the structures therefore are somewhat more typical of *T. paradoxicus*.

modern crabs (Figure 9) (see Frey and Howard, 1969, Pl. 3, fig. 4) and the fossil burrow *Macanopsis* (Table 2) is the presence of a prominent basal chamber or cell in the latter. Although slight enlargements have been observed at the base of certain crab burrows, we know of none that closely duplicate *Macanopsis*.

Thus, the majority of fossil and recent crab burrows observed to date exhibit a characteristic, definitive range of morphologic variations amenable to ichnological taxonomy. Certain intergradations present taxonomic problems and require subjective judgments; but these problems, conceptually, are no different from those of any other trace fossil group (Pemberton and Frey, 1982).

Most fossil crab burrows with which we are familiar, other than the exceptions outlined above, fall within a distinctive but heretofore unnamed trace fossil group. For this group we propose the name *Psilonichnus upsilon*. *P. upsilon* corresponds rather closely to modern burrows of the ghost crab *Ocypode* and certain other members of the Ocypodidae. As additional information accumulates

on fossil burrows attributable to crabs, further differentiation of the ichnogenus *Psilonichnus* may prove necessary.

SYSTEMATIC ICHNOLOGY

Ichnogenus PSILONICHNUS Fürsich, 1981

- Sandstone casts or rods HAYASAKA, 1935, p. 99–100, Pl. 1, fig. 5, Pl. 2, fig. 2.
- Fossil burrows STEPHENSON, 1965, p. 850–851, fig. 1.
- Burrows of *Callianassa* sp. RADWAŃSKI, 1969, p. 93, fig. 33.3.
- Callianassid burrows RADWAŃSKI, 1970, p. 386–388, fig. 4a, Pl. 6, figs. a–c.
- Ghost crab burrows FREY AND MAYOU, 1971, p. 67–68, Pl. 4, fig. 3a–b.
- ?Crustacean burrows FÜR SICH, 1974, p. 10–11, fig. 7a–c.
- J-shaped burrows CURRAN AND FREY, 1977, p. 158–159, Pl. 5, fig. e; BELT, FREY, AND WELCH, 1983, p. 250–252.
- Burrows attributable to ghost crabs RADWAŃSKI, 1977a, p. 219–221, fig. 1a, Pl. 2, figs. 1–2a, b, Pl. 3, figs. 1–4; RADWAŃSKI, 1977b, p. 233–235, Pl. 3, fig. b1–4.
- Psilonichnus* FÜR SICH, 1981, p. 157.
- ?Ichnofossil type 4 BOWN, 1982, p. 280–281, fig. 11F.



FIGURE 9—J-shaped burrows of the ghost crab *Ocypode quadrata*. Polyester casts; lower backshore, Sapelo Island, Georgia. Ghost crab burrows in uppermost foreshore are simple, inclined shafts; in upper backshore and dunes, burrows typically are branched (cf. Frey and Mayou, 1971).

Emended diagnosis.—Predominantly vertical, cylindrical, unlined burrows ranging from irregular shafts to crudely J-, Y-, or U-shaped structures; lateral branches, not necessarily the same diameter as parent trunks, may be present and tend to form singular or bifurcated culs-de-sac.

Discussion.—Burrows are preserved as endichnia and are interpreted as dwelling structures of fossil decapod crustaceans, including brachyuran crabs. Diameters of most specimens fall within the 1 to 10 cm range, depending partly on the identity and ontogenetic stage of the tracemaker; lengths may be as much as 1.5 to 2 m, although many specimens are considerably shorter.

More or less similar ichnogenera include *Pholeus* (Fiege, 1944, p. 401–404, 415–416, 426, figs. a, 1; Häntzschel, 1975, p. W93, fig. 59.1), which consists of two or more vertical or inclined shafts stemming from a horizontal basal tunnel, and *Macanopsis* (Macsothy, 1967, p. 32, figs. 44, 46, 60; Häntzschel, 1975,

p. W79, fig. 51.1), which consists of an unbranched, slightly to highly curved J-shaped burrow terminating in a basal, subhemispherical chamber; the upper part of the burrow is vertical, and the lower part becomes increasingly oblique with depth; in rare cases the basal chamber is horizontal.

Pholeus remains poorly known; the ichnogenus was established on the basis of specimens found in a museum, and has yet to be described in detail from a field locality. It may well prove to be a form of *Thalassinoides* (cf. Figure 8). *Macanopsis*, on the other hand, may be more closely related to *Skolithos*, even though partially overlapping the morphology of simple J-shaped specimens of *Psilonichnus* (cf. Figure 9). As presently defined, the chief distinguishing feature of *Macanopsis* is the basal chamber; however, that trait may prove to be most significant as a taxonomic character within the overall group of unbranched, shaft-like burrows typified by *Skolithos* (the ichnogenus *Skolithos* and related forms are presently undergoing extensive monographic reevaluation; Pemberton and Frey, in preparation).

PSILONICHNUS TUBIFORMIS Fürsich, 1981

Psilonichnus tubiformis FÜRSTICH, 1981, p. 157–158, Pl. 1, figs. 1–2, Pl. 4, fig. 5.

Diagnosis.—*Psilonichnians* consisting typically of upper, Y- or U-shaped components, grading downward to predominantly vertical, straight to slightly curved or twisted shafts bearing irregularly spaced, horizontal or oblique dead-end branches, some of which bifurcate.

Discussion.—The ichnospecies is distinguished primarily on the basis of the lower, vertical shafts and irregular lateral branches. *P. epsilon* n. ichnosp. consists mainly of inclined shafts bearing relatively few, or no, branches; where present, the branches either comprise, or tend to be congruent with, the overall Y-shaped configuration of the burrows (cf. Frey and Mayou, 1971, Pl. 2, fig. 4; Chakrabarti, 1981, text-figs. 11–12).

In its type area, *P. tubiformis* occurs in marginal marine to terrestrial deposits, possibly a low-lying coastal plain inundated subsequently by marine waters (Fürsich, 1981, p. 158). We speculate that these burrows may have been excavated by a thalassinidean

decapod somewhat like *Upogebia* (cf. Dworschak, 1983) in a low-energy, brackish water setting. Alternatively, the burrows may have been excavated by shrimp or shrimp-like animals in an extremely shallow, possibly intertidal environment near the shoreline (Fürsich, 1981, p. 165).

PSILONICHNUS UPSILON n. ichnosp.

Figure 6A–D

- Burrows of *Callianassa* sp. RADWAŃSKI, 1969, p. 93, fig. 33.3.
 Callianassid burrows RADWAŃSKI, 1970, p. 386–388, fig. 4a, Pl. 6, figs. a–c.
 Ghost crab burrows FREY AND MAYOU, 1971, p. 67–68, Pl. 4, fig. 3a–b.
 J-shaped burrows CURRAN AND FREY, 1977, p. 158–159, Pl. 5, fig. e; BELT, FREY, AND WELCH, 1983, p. 250–252.
 Burrows attributable to ghost crabs RADWAŃSKI, 1977a, p. 219–221, fig. 1a, Pl. 2, figs. 1–2a, b, Pl. 3, figs. 1–4; RADWAŃSKI, 1977b, p. 233–235, Pl. 3, fig. b1–4.
 Y-shaped crab burrows CURRAN, 1984, p. 312–321. Fig. 4A.

Diagnosis. — Ppsilonichnians consisting typically of gently inclined, sparsely branched to unbranched, J- or Y-shaped burrows; inclined shafts straight to slightly arcuate; branches slightly to markedly curved, not horizontal.

Origin of name. — Derived from the Greek *ypsilon*, meaning bare, mere, or simple Y; refers to the typically Y-shaped burrow form.

Repository. — Type specimens, from the Pleistocene of San Salvador Island, Bahamas, have been placed in the Paleontological Collections of the Department of Geology, University of Georgia. Specimen numbers: holotype, TF-Q-001; paratype, TF-Q-002.

Description of specimens in the type area. — Unbranched to Y-shaped, unlined burrows; shafts, steeply inclined to bedding, typically 2.5 to 4.5 cm in diameter and up to 1.2 m or more in length. Where branched, the angle of bifurcation is 65° to 80°; typically, one branch is slightly smaller in diameter than the other. Openings of branches at the ancient substrate surface are somewhat enlarged. Terminus of burrows not preserved; therefore, measured shaft lengths are less than the original lengths.

Occurrence and geologic setting. — Well-preserved specimens of *P. epsilon* occur rarely in medium- to fine-grained, planar cross-

bedded Pleistocene calcarenites exposed on sea cliffs along the northeast (Atlantic-facing) coast of San Salvador Island, Bahamas. Based on physical sedimentary characteristics, associated fossils, and stratigraphic position, the deposits are interpreted to have accumulated in an uppermost foreshore to backshore environment. Fine-grained eolian calcarenites immediately overlie the beds bearing *P. epsilon*. Further information on the geologic setting of San Salvador is given by Curran (1984).

Segments of *P. epsilon* shafts may be rather common at this locality; holes of the proper diameter can be located easily in the friable calcarenites of the sea-cliff exposures. However, these beds also contain rhizocretions. The hard calcrete cores of large-diameter rhizocretion shafts frequently break out of the rock, leaving unlined, relatively straight shafts that can be difficult to distinguish from segments of *P. epsilon*. The Y-shaped branching pattern thus is the key to positive identification of *P. epsilon*; but the juncture in many cases is not preserved. We therefore recommend a conservative approach to the identification of *P. epsilon* specimens here; after further study and increased familiarity with various preservations of the form, however, it may yet prove to be a common trace fossil.

Comparison with modern analogs. — Burrows of the ghost crab *Ocypode quadrata* are common on the narrow, upper foreshore and backshore zones of the carbonate-sand beaches of San Salvador Island. These burrows are unlined; most have diameters of 1 to 3 cm; and many have two entrances that join below in a Y-shaped pattern. However, single-entry burrows are far more common on these beaches than are double-entry forms.

Specimens of *P. epsilon* preserved in adjacent Pleistocene beds are comparable with the modern burrows of *Ocypode quadrata* and undoubtedly were formed by that animal. Diameters of Pleistocene shafts are somewhat larger than typical shafts of modern burrows on San Salvador Island, but they are within the range of diameters reported for *O. quadrata* burrows along the Georgia coast (Frey and Mayou, 1971, table 1). Thus, specimens of *P. epsilon* here have a direct modern analog in the burrows of *Ocypode quadrata*—excavated by a tracemaker of narrow environmental preference and well-known habits

(Frey and Mayou, 1971; Allen and Curran, 1974; Hill and Hunter, 1973, 1976)—and can be used as a reliable indicator of ancient upper foreshore and backshore environments, as represented by rocks on San Salvador Island and in other, similar settings.

Other occurrences.—The friable, poorly consolidated Pleistocene backshore sediments of Georgia and northeastern Florida are easily scraped or excavated; serial sections of these deposits reveal *P. epsilon* morphologies that are virtually identical with burrows of the modern ghost crab *Ocypode quadrata* (Frey and Mayou, 1971, Pls. 2–3), including the common association with amphipod cryptobioturbation (Pl. 4, fig. 3a). North Carolina specimens of *P. epsilon* (Curran and Frey, 1977, Pl. 5e) are less well preserved but are clearly the same as the Georgia-Florida forms.

In the Miocene of Poland, upper parts of burrows have been removed by erosion (Radwański, 1977a, p. 221, fig. 1); the remainder of the structure is quite like equivalent components of *P. epsilon* mentioned above. Burrows described by Hayasaka (1935, Pl. 1, fig. 5, Pl. 2, fig. 2) and Stephenson (1965, fig. 1) probably can be ascribed to *P. epsilon*, although additional evaluation is required.

ENVIRONMENTAL SIGNIFICANCE

Ancient depositional environments in which populations of *Psilonichnus epsilon* might abound constitute a mixture of marginal-marine and quasimarine facies. Typical modern environments include the uppermost foreshore and backshore of beaches, dunes, washover fans, and supratidal flats. Marine conditions characterize the backshore during spring and storm tides, and also characterize washover fans and supratidal flats during storm surges. In contrast, maritime eolian conditions characterize dunes, the backshore during neap tides, and washover fans and supratidal flats during non-storm periods. Relatively few invertebrate trace-makers are tolerant of such stressful conditions (Dörjes and Hertweck, 1975); among marine or quasimarine species, only the amphibious crabs have succeeded in exploiting this highly variable coastal zone.

In the rock record, vertical sequences and associated physical sedimentary structures also are important in ichnological and en-

vironmental reconstructions. For example, the somewhat aberrant specimens of *Thalassinoides paradoxicus* mentioned previously (Figure 8) occur in clayey, somewhat fissile limestone; these beds are underlain by relatively clean sandstones characterized by vertical shafts of *Ophiomorpha nodosa* and are overlain by limestones characterized by horizontal tunnels of *Thalassinoides suevicus* (Frey and Seilacher, 1980, fig. 4). The *T. paradoxicus* animal thus seems to have exploited a peculiar environment transitional between the nearshore sands and offshore carbonates. For similar reasons, *Psilonichnus epsilon* might occur in facies other than the shoreline sequence mentioned above; one possibility is point-bar deposits within the seaward part of an estuarine sequence (Frey and Howard, 1980; Howard and Frey, 1980a).

Similarly, during beach progradation, long shafts of *P. epsilon* (e.g., Figure 6D), although originating at a substrate surface in the backshore, might penetrate well into underlying foreshore deposits replete with *Ophiomorpha nodosa*. In such instances, the spatial range of the two ichnospecies (cf. Frey and Mayou, 1971, fig. 3) would overlap both laterally and vertically. Somewhat comparable trace fossil overprintings have been observed in related settings (Howard and Scott, 1983, p. 178–182). Deep penetrations of this sort possibly also account for the difficulty experienced by Radwański (1977a, p. 222–224) in interpreting the occurrence of *P. epsilon* shafts in marly sands containing scour horizons, whether part of a shoreline, embayment, or estuarine sequence.

Nevertheless, Pleistocene shoreline sequences of Georgia and northeastern Florida (Howard and Scott, 1983) are virtually identical with their Holocene counterparts (Howard and Frey, 1980b): well-laminated foreshore deposits characterized by vertical *Ophiomorpha nodosa* are overlain by cross-laminated backshore deposits characterized by *Psilonichnus epsilon*. The only exceptions are local isolated lenses of cross-laminated sand containing *P. epsilon* that seem to represent the backshore- or dune-like part of nearshore bars or small spits; but these features, occupied by *Ocypode quadrata*, also are known from the modern coast.

Finally, unlike most other marine or marginal-marine facies, these deposits may con-

tain a mixture of invertebrate and vertebrate lebensspuren (Figures 3A, 4C) (Howard and Frey, 1980b). Presence of bird and tetrapod tracks is unequivocal evidence for the proximity of a terrestrial environment, and their overlap with *Pylonichnus upsilon* is equally strong evidence for a high-intertidal or supratidal environment.

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