

DISTRIBUTION AND PALEOECOLOGY OF *GLOTTIDIA INEXPECTANS*  
OLSSON, 1914 (BRACHIOPODA: LINGULIDAE)

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I. ABSTRACT

The lingulid brachiopod *Glottidia inexpectans*, previously known from the Yorktown Formation in Virginia, is here reported from the Early Pliocene beds of South Carolina and Florida. *Glottidia inexpectans* differs from intertidal to shallow subtidal Recent species in apparent habitat bathymetry. In Virginia, the associated molluscs indicate water depths of 40 to 60 meters, the fishes somewhat deeper. Associated taxa in Florida apparently lived in subtidal habitats to 20 meters.

The proclivity of *G. inexpectans* for shell degradation parallels the taphonomic destruction patterns of the more thoroughly studied Recent species. Preservation of specimens in any numbers must combine structural integrity with protection from chemical deterioration. The 155 pairs of juvenile *G. inexpectans* here reported from Carter's Grove, Zone 1, Yorktown Formation, and the smaller population reported by Olsson (1914) were preserved within closed valves of *Chesapecten jeffersonius*, a large species of scallop with thick, well-inflated valves. These two populations probably represent single spatfalls of *Glottidia* larvae which settled in gaping scallop shells partially filled with sediment. They then died of starvation or oxygen deprivation after the valves closed by relaxation of the ligament or by burial. The physical protection afforded by this micro-habitat appears essential for preservation of fragile subadult shells. Interpreting this assemblage prompted a review of the systematics, ecology, distribution, and taphonomy of *Glottidia*.

II. INTRODUCTION

The brachiopod family Lingulidae contains two Cenozoic to Recent genera. These are: *Lingula* Cuvier, 1798, with seven Recent species ranging from tropical East and West Africa to Japan, New Zealand, and Hawaii (Emig, 1982) and *Glottidia* Dall, 1870, with four or five living American species, one in the western Atlantic ranging from Chesapeake Bay to Florida, Louisiana, and the Caribbean; two species in the Baja California area, with one extending north to Monterey Bay; and one or two from Ecuador.

Paine (1963) noted numerous reports of fossil *Glottidia* from the Pacific coast of North America, beginning in the Eocene, and suggested that the genus may have originated in that area. However, Pajaud (1977) recognized the genus in the Triassic and Jurassic of Italy, and in the Cretaceous of Italy and Crimea. *Glottidia* also occurs in the Pliocene of Belgium and France (Chuang, 1964b; Pajaud, 1977). The Atlantic Coastal Plain localities documented in the present paper are Early Pliocene in age (Campbell, 1993).

III. RESULTS

*Description:* Detailed descriptions of *Glottidia inexpectans* may be found in Olsson (1914), Chuang (1964a), and Cooper (1988). It is an elongate, smooth, thin, fragile, compressed, phosphatic shell, very typical of lingulid brachiopods. *Glottidia inexpectans* shows allometric growth, embryonic shells being circular (Chuang, 1964a), juvenile specimens

developing elongate shells (figs. 1-3), and adults being proportionally broader (fig. 4). The brachial valve of *G. inexpectans* contains a single internal lamina just below the beak; the pedicle valve has two. Maximum length of *G. inexpectans* is 47 mm in Virginia (Cooper, 1988), and 56 mm in southern Florida (Florida Museum of Natural History collections, University of Florida, subsequently designated UF).

*Outcrop occurrence:* Olsson (1914) described *G. inexpectans* from fragmented specimens and one lot of over 20 five millimeter shells recovered from a paired specimen of *Chesapecten jeffersonius* found at Kingsmill, Virginia (UF loc. ZV006). The senior author discovered a second scallop shell refugium at Carter's Grove (UF loc. ZV008) containing 155 paired specimens averaging 13 mm (Table 1). Contents of the scallop pair were washed through a 0.5 mm screen to remove the fine sand matrix and all shell residue was examined. Brachiopod shells and shell fragments formed greater than 95 percent of the residue. In contrast, screened bulk samples of surrounding outcrop matrix yield mollusc shell residues with less than one percent brachiopod fragments. The *Glottidia* shells from Kingsmill and Carter's Grove were a light tan color, with an internal wash of white under the laminae. These Zone 1, Yorktown Formation (Sunken Meadow

Member of Ward and Blackwelder, 1980) shells lack anoxic indicators such as micro-pyrite crystals, uniform shell blackening, or chemical degradation. Anoxic environments blacken phosphatic shell over a span of days to weeks (Kowalewski, 1996a). Zone 2 *Glottidia* in silt-clay sediment from Rice's Pit (UF loc. ZV004) and Yadkin (UF loc. ZV007) show tan banding alternating with blackened shell. Florida specimens (UF localities listed below) are similarly blackened with tan banding.

*Associated Fauna:* Campbell (1993) documented 233 species of lower Zone 2 molluscs from Rice's Pit. The senior author (in preparation) has documented some 220 molluscan species from the Zone 1, Chama-protected beds at Kingsmill and Carter's Grove.

Fauna contained with the juvenile *Glottidia* population inside the *Chesapecten* pair include a sparse assemblage of heart urchin spines from *Echinocardium orthonotum* (Conrad, 1843 [1844]), and unpaired valves of the bivalves *Cyclocardia granulata* (Say, 1824), *Modiolus pulchellus* Olsson, 1914, and *Astarte vaginulata* Dall, 1903. Olsson (1914) reported urchin spines, *M. pulchellus*, and a valve of *Diplodonta* in association with his encased *Glottidia*.

In Florida, most carbonate shell is leached from the Bone Valley deposits (UF loc. PO002 and UF loc. PO018), leaving

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SIZE FREQUENCY OF SCALLOP-ENCASED *Glottidia inexpectans*

length (mm)	number of individuals
9	0
10	1
11	13
12	19
13	37
14	24
15	6
16	0

Brachial valves (one internal lamina) 155 specimens  
 Pedicle valves (two internal laminae) 156 specimens

Table 1: Frequency Table of maximum length for the population recovered from the scallop shell, and the proportion of brachial and pedicle valves.

Length is given for complete valves only.

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the phosphatic brachiopods and a considerable vertebrate faunule. Some localities preserve interfingering Bone Valley phosphate sand and Tamiami limestone in outcrop (Morgan, 1994). Because our specimens are from spoil, we can not rule out the possibility of a Tamiami source, but the surrounding matrix has been typical of the Bone Valley member sand, and we believe that all *Glottidia* recovered from these localities are from the Bone Valley. At the Casa de Meadows pit (UF loc. CH026), calcitic shell is preserved. Occurring with *Glottidia* are molluscs including *Dicathais handgenae* Portell and Vokes, 1992, *Ephora quadricostata* (Say, 1824), *Pterorytis umbriker* (Conrad, 1832), *Urosalpinx (Vokesinotus) lepidotus* (Dall, 1890), *Euvola raveneli* (Dall, 1898), *Euvola hemicyclius* (Ravenel, 1834), *Aequipecten muscosus* (Wood, 1828), *Argopecten* sp., *Amusium mortoni* (Ravenel, 1844), *Leptopecten leonensis* (Mansfield, 1932), *Nodipecten collierensis* (Mansfield, 1932), *Limaria caloosana* (Dall, 1898), *Ostrea sculpturata* Conrad, 1840, *Ostrea compressirostra* Say, 1824; the decapods *Calappa* sp. and a majid crab; barnacles including *Arossia glyptopoma* (Pilsbry, 1916), *Chesaconcaus tamiamiensis* (Ross, 1965), and *Tamiosoma advena* Zullo, 1992; and echinoids including *Arbacia improcera* (Conrad, 1843 [1844]) (= *A. crenulata* Kier, 1963), *Eucidaris tribuloides* (Lamarck, 1816), *Encope tamiamiensis* Mansfield, 1932, and *Echinocardium orthonotum* (Conrad, 1843 [1844]) (= *E. gothicum* (Ravenel, 1848)), (fauna from Portell and Vokes, 1992; Portell and Oyen, 1997; UF collections).

A second species of inarticulate brachiopod, *Discradisca lugubris* (Conrad, 1834) commonly occurs with *G. inexpectans* at Casa de Meadows, and at all Virginia localities. *Discradisca lugubris* is referred to *Discinisca* in most literature, but Cooper (1988) assigns it to *Discradisca*. *Discradisca lugubris* arose in the late Miocene in Virginia and survived into the Plio-Pleistocene Caloosahatchee Formation (UF collections).

*Zoogeographic and Stratigraphic Distribution of Glottidia inexpectans*: The Yorktown Formation (Pliocene) of the

Virginia and northern North Carolina Coastal Plain was divided into a lower Zone 1 and an upper Zone 2 by Mansfield (1944). Ward and Blackwelder (1980) have further divided the Yorktown into four members. A general review of the stratigraphy and its complexities can be found in Campbell (1993). Scott (1988), Morgan (1994) and Allmon *et al.* (1996) provide detail for the Florida formations from which we here report *Glottidia*.

Hertlein and Grant (1944), Chuang (1964a), Cooper (1988), and Portell and Oyen (1997) are the only published records of this species subsequent to Olsson's original 1914 report. The type lot (Paleontological Research Institution 3518, 3519, 3520, and 3521) was collected from Zone 1 beds of the Yorktown Formation (Lower Pliocene), at Kingsmill, north bank of the James River near Williamsburg, Virginia. Subsequent collecting at the type locality confirmed an abundance of fragmented *Glottidia*. This exceptional outcrop has been destroyed by development in 1996. Previously unreported Zone 1 *Glottidia* localities include the spillway of Tutter's Neck Pond just east of Williamsburg, Virginia, and the bluffs at Carter's Grove approximately 1.5 km east of Kingsmill. The scallop-encased *Glottidia* population here reported (Plate 1, UF 81774) is from Zone 1 sands at Carter's Grove.

Chuang (1964a) redescribed the species based on an adult specimen from the lower Zone 2 beds of the Yorktown Formation at the Hampton Heights Dairy Pit. Subsequently, *Glottidia* have been recovered from laterally equivalent beds at Rice's Pit, Hampton, Virginia (Cooper, 1988, USNM 551520a-i; Virginia Museum of Natural History, and USC-Spartanburg collections) and at the Chesapeake Development Co. Pit (Yadkin, City of Chesapeake: USC-Spartanburg collections).

Portell and Oyen (1997) provided the first documentation of *G. inexpectans* outside Virginia. It is also present in the Raysor Marl near Cross, South Carolina (USC-Spartanburg collections; see LOCALITY DATA below).

#### IV. INTERPRETATION

*Ecology of Recent Glottidia*: Five species of Recent *Glottidia* have been documented (Dall, 1920; Emig, 1983). *Glottidia albida* (Hinds, 1844) was originally described from Magdalena Bay, Baja California, in 14 meters of water. This species may have a commensal slipper snail (*Crepidula nivea glottidiarum* Dall, 1905) on one or both valves (Dall, 1905; 1920). Keen (1971) synonymized *Crepidula nivea* C. B. Adams, 1852, with *Crepidula striolata* Menke, 1851, but made no mention of Dall's variety or of commensalism. The presence of commensal taxa suggests that *G. albida* is a shallow burrowing species. *Glottidia albida* has been recorded as far north as Monterey Bay, California. Recorded bathymetry ranges from intertidal to 477 meters (Jones and Barnard, 1963; Plaziat *et al.*, 1978).

*Glottidia palmeri* Dall, 1871, was described from the head of the Gulf of California, with additional records from southern California (Dall, 1920). It is common in lower intertidal mud flats in northeastern Baja California (Kowalewski, 1996a; Kowalewski and Flessa, 1994). Plaziat *et al.* (1978) record a bathymetry of intertidal to one meter. Dead shells of *in situ* *G. palmeri* are found at a depth of 10 to 20 cm below the sediment surface (Kowalewski (1996a:253).

*Glottidia semen* (Broderip, 1835) is a little-known Ecuadorian species based on an unique record dredged in 31 meters (Emig, 1983; Plaziat *et al.*, 1978). It may prove synonymous with one of the better-known species.

*Glottidia audebarti* (Broderip, 1835) was collected in hard, compacted, intertidal sand at a depth of 18 cm. Its type locality is Bay of Guayaquil, western Ecuador. Davidson (1888, posthumous) united *G. audebarti* with the western Atlantic *G. pyramidata* (Stimpson, 1860), a usage continued by Olsson (1914) and Crowder (1931). Dall (1920) showed the two taxa to be distinct. He speculated that after Davidson's death, an incorrect synonymy may have been rendered by the editors. Chuang (1964a) noted that Olsson compared his new fossil species with *G. audebarti* and *G. pyramidata*. Olsson (1914) compared his species with *G. audebarti* only in the sense that the western

Atlantic *G. pyramidata* was considered a synonym. Plaziat *et al.* (1978) record a bathymetry for *G. audebarti* of intertidal to 13 meters.

*Glottidia pyramidata* (Stimpson, 1860) was described from muddy sand at low tide, Beaufort, North Carolina. Stimpson (1860) reported that Agassiz had a brachiopod specimen from the South Carolina coast. As *G. pyramidata* is the only coastal brachiopod in the area, we may assume that the Agassiz specimen is the first record from that state. Crowder (1931) gave a typical length of 27 mm and width of 10 mm, and reports specimens as "tidal, in vertical burrows, Cape Hatteras to Florida." Fox and Ruppert (1985: 44, 243, 270) reported *G. pyramidata* in mud burrows from protected beach at Debidue Island, South Carolina. They systematically sampled a set of habitats along the northern, central, and southern beaches of South Carolina, so the absence of *G. pyramidata* in two of the three areas sampled indicates patchy, disjunct distribution. Dall (1920) stated that Henderson found the species among the roots of sea grasses 2 feet below the water-sediment interface which would place them well below normal sampling efforts. However, Thayer and Steele-Petrovic (1974) used detailed observation and X-radiography to determine that the normal burrow is "U" shaped and no more than 5 cm deep. Paine (1963) suggests that the Henderson record may represent specimens buried by storm deposition. Alternatively, the Henderson report might be a lapse for "two feet of water." Recorded range is from Hampton and Fort Wool, Virginia, to southern and western Florida, Puerto Rico, and Louisiana (Cooper, 1973; Emig, 1983; Paine, 1970). Life span is about 20 months (Rudwick, 1970). In Florida, colonies of *G. pyramidata* are subject to predation by Tonguefish (*Symphurus plagiusa*) (Cooper, 1973), by Gulf Sturgeon (*Acipenser oxyrinchus desotoi*) (Mason and Clugston, 1993; UF collections), and by larger shorebirds such as Willets (*Catoptrophorus semipalmatus*) (Paine, 1962, 1963). Although sturgeon feed indiscriminately on shallow infaunal organisms (Gilbert, 1989), one sturgeon contained over 500 *G. pyramidata* (UF collections).

Paine (1962) reported up to 90 per cent infection of *G. pyramidata* by a gymno-phalline metacercaria trematode larvae, but dismissed the Willet as host of the adult trematode due to a lack of infesting organisms. The records here cited suggest that fish may possibly be host to the adult parasite. Plaziat *et al.* (1978) recorded a bathymetry for *G. pyramidata* of intertidal to 73 meters.

Paine (1963) provided a thorough analysis of the ecology of *G. pyramidata*. Spawning is coincident with spring tides which maximizes offshore transport of larvae. *Glottidia* larvae were a common component of the plankton, and after three weeks of development were swept by the tides and currents into the shallow sublittoral and littoral areas where they settled in optimal habitats, most frequently in sand stabilized by sea grass. Paine (1963) also records planktic "drift larvae" well removed from "optimal habitat" and presumably lost. More recent works document offshore populations in 40 m (Paine, 1970) and 73 m (Cooper, 1973), suggesting that *G. pyramidata* is sparingly distributed across the shelf, but as an infaunal species is rarely collected in deeper waters.

Based on these records, *Glottidia* appears to be most common in intertidal to shallow subtidal tropical and subtropical protected muddy sands where it creates straight (Kowalewski, 1996a) or "U"-shaped burrows. When feeding, the animal creates a diagnostic pattern of one large oval hole flanked by two smaller holes (Rudwick, 1970):

*Paleontology and Paleoecology of Glottidia inexpectans*: We report a range for *G. inexpectans* essentially congruent with that of the Recent *G. pyramidata*. In both species, southern Florida specimens are larger than more northern populations. *Glottidia pyramidata* grows continuously until death at about 20 months (Paine, 1963). Growth and spawning are interrupted by winter temperatures in the Carolinas and northern Florida populations, but are continuous throughout the year in the southern Florida populations (Paine, 1963). Consequently, southern populations produce larger animals (Dall,

1920). Allmon *et al.* (1996) document upwelling as a nutrient source for the rich Lower and Middle Pliocene faunas of southern Florida. This increase in nutrients should improve diet for the filter-feeding *Glottidia*, further promoting maximum growth. Consequently, size differences between the Virginia and Florida populations are ecologic rather than taxonomic, and all Pliocene lingulid populations from Virginia to Florida are interpreted as representing *G. inexpectans*.

Although the Eocene to Recent distribution of *Glottidia* in the eastern Pacific is semicontinuous (Hertlein and Grant, 1944; Paine, 1963), the distribution of fossil *Glottidia* in the Atlantic and Gulf Coastal plains is disjunct, consisting of *G. glauca* Chuang, 1964c, rare in the lower Claibornian Eocene of Texas (Chuang, 1964c); *G. inexpectans* in the Lower Pliocene, Virginia to Florida; and *G. pyramidata* in the Recent. The lack of continuum may be real, or may be an artifact of selective taphonomic destruction (Kowalewski, 1996b). Lingulids are not likely to be preserved unless catastrophically buried (Kowalewski, 1996a, 1996b). The distribution of Recent *Glottidia* (Plaziat *et al.*, 1978), and their reproductive biology (Paine, 1963) argue for shallow water, coastal habitat, an environment rarely preserved in the Oligocene, and only occasionally in the Miocene of the Atlantic Coastal Plain. However, much of the Pleistocene deposition preserved in the Carolinas and Florida is beach and intertidal to shallow subtidal habitat seemingly well suited for *Glottidia*. Alternatively, during the Pleistocene, numerous tropical and subtropical invertebrate genera retreated to Caribbean refugia. *Glottidia* are conspicuously missing in the Caribbean Cenozoic (Cooper, 1955; Harper *et al.*, 1995, 1997; Emily Vokes, 1996, pers. comm.). This lack of evidence for Caribbean refugia and lack of intervening populations, even when prime lingulid habitat and exceptional preservation occur, suggest that the species of Western Atlantic *Glottidia* may represent independent colonizing events. However, the extinction of *G. inexpectans* approximately coincides with the closing of the Isthmus of Panama, and a western Atlantic refugium

seems more parsimonious than Holocene recruiting of eastern Pacific stock across the land-bridge.

**Mortality:** The scallop-enclosed population recovered in this study averaged 13 mm (Table 1). The assemblage forms a tight cluster with normal distribution around the mean. Olsson (1914) reported a similar scallop-enclosed population averaging about 5 mm. The uniform size in the two juvenile populations strongly suggest mass mortality. In our specimens, the brachiopods were recovered from within closed valves of *Chesapecten jeffersonius*, which were partially filled with fine sand. The plane of commissure was parallel to bedding, and the scallop appeared to be in life position. This suggests that the scallop shell was slightly gaping in quiet water and partially filled with sediment. The *Glottidia* larvae settled in a single spat-fall, colonized the shell, and then died of starvation or oxygen deprivation after the scallop valves closed, either by relaxation of the ligament, or by burial of the shell. Starvation seems more likely because the shells lack anoxic indicators such as micro-pyrite crystals, shell blackening, or chemical degradation. Alternatively, artic-

ulated pairs may have washed into the shell. However, juvenile *Glottidia* shells are selectively destroyed upon reworking, and brachial valves are more subject to fragmentation than pedicle valves during transport (Kowalewski, 1996a). Also the sediment surrounding the scallop shell yielded a different faunule with abundant small disarticulated clam shells, but few brachiopods.

Paine (1963) determined that the vast majority of *Glottidia* die as larvae. Survivors preferentially populate sea grass beds, achieving a maximum density of greater than 1300 per square meter (Kowalewski, 1996a). The scallop-enclosed population of *G. inexpectans* here reported contained 156 individuals in a 15 cm diameter, circular shell. The area of containment is therefore 0.057 square meters which projects an equivalent population density of 2737 animals per square meter. This density is too great to be explainable by random drift of passive larvae. Settling *Glottidia* larvae are photonegative (Charles Thayer, 1996, pers. comm.), and those settling near a large, gaping bivalve with horizontal commissure would find the shadow attractive. Lingulids attach their pedicles to the base or wall of their

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## PLATE 1

### Figures

- 1-5. *Glottidia inexpectans* Olsson, 1914.
  1. UF 81774, length 13.9 mm, pedicle valve from *Chesapecten*-enclosed population. UF loc. ZV008.
    - 1a. External surface (note more pointed apex).
    - 1b. Internal view showing double laminae.
  2. UF 81774, length 14.4 mm, another pedicle valve from enclosed population. UF loc. ZV008.
    - 2a. External surface.
    - 2b. Internal detail.
  3. UF 81774, length 13.7 mm, brachial valve from enclosed population. UF loc. ZV008.
    - 3a. External surface (note rounder apex of valve).
    - 3b. Internal view showing single lamina.
  4. UF 11840, fragment length > 35 mm. Note predatory gastropod bore hole. UF loc. PO002.
  5. UF 11840, nearly complete pedicle valve. Length 56 mm. UF loc. PO002.
6. *Chesapecten jeffersonius* (Say, 1824). Pair containing the *Glottidia* population. Maximum width 156 mm, maximum height 142 mm, average diameter 149 mm. UF loc. ZV008.
  - 6a. Right valve UF 81775.
  - 6b. Left valve UF 81775.

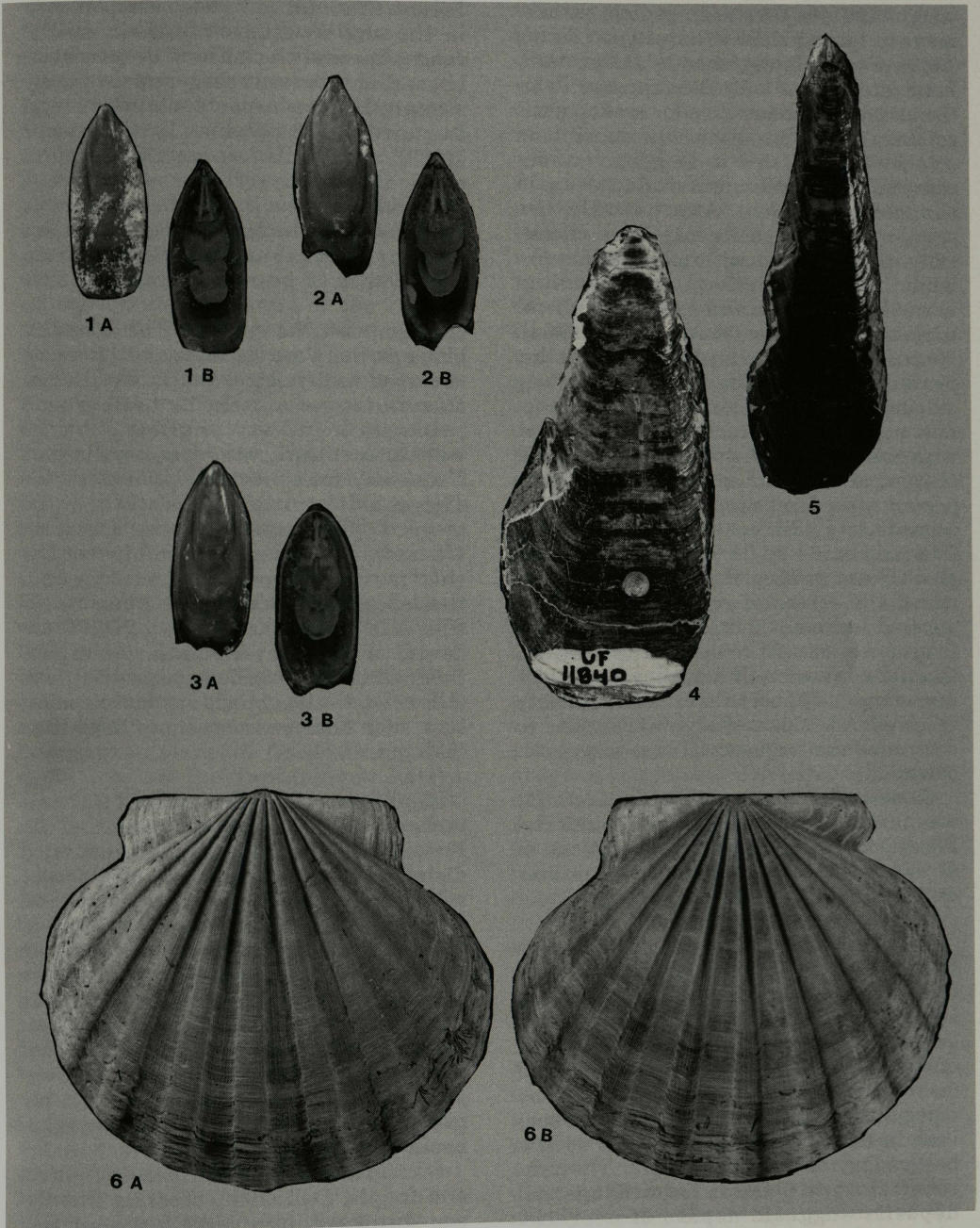


PLATE 1

mud-sediment burrows, not to a solid substrate like articulate brachiopods (Rudwick, 1970). In *Glottidia*, pedicle attachment to buried shell is fortuitous (Paine, 1963). Consequently, shadow rather than hard attachment substrate appears to be the attractant responsible for scallop shell colonization. The absence of specimens smaller than 10 mm in length may indicate high post-settling survival rates up to the mortality event. Alternatively, the smaller juvenile shells may have chemically disintegrated within their burrows while the scallop valves were open and normal circulation and sea-water chemistry were operative (Kowalewski, 1996a). We conclude that the shell-interior habitat proved initially optimal, but ultimately detrimental. Mass mortality of the juvenile population was most likely coincident with the closure of the host shell. Shell content of a second large, closed *Chesapecten* was compared with that of its immediately adjacent sediment. In both, fine sand made up 95 percent of the sediment. Scant mollusc shell fragments dominated the screened residue. The shell-encased sediment included a single beak fragment of *Glottidia*. Apparently, *Glottidia* invasion of a scallop shell was uncommon, opportunistic and probably seasonal. Additional studies are needed to determine the frequency of brachiopod colonization.

Gastropod predation of Recent *Glottidia* was first documented by Kowalewski and Flessa (1994). Rare Florida specimens of *G. inexpectans* show evidence of similar attacks (Plate 1, fig. 4).

**Paleobathymetry:** The paleobathymetry of the Zone 1 deposits at Kingsmill and Carter's Grove is equivocal. An ongoing study of the molluscan taxa has yielded over 220 species, with genera most typical of water depths of 40 to 60 meters, based on recent data from Porter (1974). The topography and distribution of Zone 1 sediments are also compatible with a bathymetry of 40 to 60 meters. The substantial otolith fauna from Kingsmill deposits suggests depths of over 100 meters (Robert Lavenberg, 1995, pers. comm.). By the measure of Recent intertidal *Glottidia* species, *G. inexpectans*

appears to have an anomalous depth distribution. It is equally possible that the Recent *Glottidia* have been sampled only in the shallowest part of their normal range. Species which live in deep burrows beyond the littoral zone remain poorly sampled. The reports of Jones and Barnard (1963), Paine (1970), Cooper (1973), and Plaziat *et al.* (1978) confirm open shelf occurrences for Recent *Glottidia*. Shallow, subtidal environments are known in the lower Zone 2 Yorktown beds at Petersburg, Virginia, but no *Glottidia* have been recovered from that area.

In contrast, the southern Florida assemblage at the Casa de Meadows pit yields two good bathymetric indicators. Recent *Dicathais* prefer rocky or hard ground substrates in very shallow subtidal waters, and *Aequipecten muscosus* is most frequently found in 10 to 40 meters. We suggest deposition in subtidal to 20 meters. Consequently, the Casa de Meadows specimens may represent the shallow water populations missing from the Virginia Pliocene. The Bone Valley sites (UF loc. PO002, UF loc. PO018) are devoid of other invertebrate species, but their vertebrates include terrestrial taxa (UF collections), which are more consistent with shallow, near-shore deposition (Morgan, 1994).

**Taphonomy:** The taphonomy of *Glottidia palmeri* was thoroughly studied by Kowalewski (1996a). He documents rapid disintegration of brachiopod shells in *in situ* burrows, found in intertidal, and supratidal environments. His study provides insights, but little data for the most commonly preserved marine habitat, the subtidal shelf environment. Kowalewski (1996, pers. comm.) states that efforts were made but the turbidity of the Gulf waters made study impossible. Consequently, *G. inexpectans* may fill this key gap in our knowledge of lingulid taphonomic pathways.

*Glottidia* valves are exceedingly thin and fragile. Dall (1920) observes that tissue shrinkage upon death and air-drying was sufficient to fracture the valves of *G. pyramidata*. Dead shells are often destroyed within their burrows by chemi-



cal degradation associated with decay (Paine, 1963; Kowalewski, 1996a). Although the shells of the Pliocene species thickened with growth, the largest specimens remained thin and fragile. Subtidal decay and transport were normally sufficient to fragment shells of all growth stages. *Glottidia inexpectans* are most common in screened and floated residue of Zone 1 fine sands. The shells are invariably broken perpendicular to the long axis, and only beak fragments or the distal quarter of the shells are typically recovered. Although care was exercised in the excavation and screening of the Zone 1 sediment, further fragmentation during the sample processing cannot be ruled out. We believe that we are observing pre-depositional fragmentation because careful search of outcrop has yielded no complete-but-broken specimens, and because the more fragile middle sections of the shell are rare or absent from the screened residue. Paired adult individuals have been found imbedded in silt-clay deposits of the lower Zone 2 beds in Virginia. *Glottidia* have been observed in Zone 2 sands only at Claremont Wharf, south bank of the James River (Warren Blow, 1996, pers. comm.). Kowalewski (1996a) found that deep burial, either by rapid sedimentation or catastrophic means was necessary to place the *Glottidia*-bearing deposit below the Taphonomic Active Zone. The Yorktown Formation in Virginia contains numerous examples of tempestite storm deposition and some "Lagerstätten" deposits in which bivalves are paired, crabs have articulated limbs, echinoids have associated spines, and shell preservation down to minute and fragile pteropod molluscs is perfect. No *Glottidia* have been recovered from these deposits. Its presence in silt-clay might reflect habitat preference, but that hypothesis is negated by its greater abundance in the fine sands of Zone 1. We conclude that subtidal taphonomic destruction of *Glottidia* shells was as rapid and effective as that documented for the intertidal and supratidal zones.

Despite rapid burial and the structural protection from the paired valves of a large, heavy *Chesapecten* shell, only 32% (100 of 311) of the exceptionally preserved

*Glottidia* valves were unbroken. Dorsal valves were more frequently broken than ventral, suggesting variable strength. Valves retained within the scallop show no chemical degradation. The pervasive valve destruction in the unsheltered sand environment accentuates the contrast with the exceptionally preserved, scallop-enclosed population. Once entombed, the *Chesapecten* shell protected the *Glottidia* valves from further taphonomic destruction.

Post-depositional taphonomy appears to be important in the preservation of *Glottidia*. In Virginia and northern North Carolina Zone 1 sediments are typically well sorted, fine sand which is highly permeable, forming a shallow aquifer. Shell carbonate is a small fraction of the bulk sediment. The flow of fresh groundwater has partially to completely leached aragonitic shell from the sediments, leaving calcitic shell, and occasional phosphatic remains, mostly bone. Along the north shore of the James River from Kingsmill to Carter's Grove, the Zone 1 beds are capped by a massive Zone 2 *Chama* reef which is greater than 80 per cent carbonate and as much as 10 meters thick. Groundwater percolating through this cap becomes less acidic, and the protected underlying Zone 1 faunas have exquisite preservation of even the most minute aragonitic species. Consequently, post-depositional chemical degradation removed both aragonitic shell and phosphatic *Glottidia* from the leached sediments. In Virginia, the destruction of *Glottidia* was complete in all stages of growth; in Florida, the juvenile specimens were selectively removed.

## V. SUMMARY AND CONCLUSIONS

*Glottidia inexpectans* Olsson, 1914, is found in Early Pliocene beds from Virginia to Florida. The species attained a larger maximum size in Florida, paralleling the pattern in the Recent *G. pyramidata*. The proclivity of *G. inexpectans* for shell degradation paralleled that of the more thoroughly studied Recent species such as *G. pyramidata* and *G. palmeri*, which typically disintegrate within a few weeks of death. Preservation of specimens in any

numbers must combine structural integrity with protection from chemical deterioration. The 155 pairs of juvenile *G. inexpectans* here reported and the smaller population reported by Olsson (1914) were preserved within paired valves of *Chesapecten jeffersonius*, a large species of scallop with thick, well-inflated valves. The added protection afforded by this microhabitat appears essential for preservation of unbroken, subadult shells in sand. Stiff silt-clay beds of lower Zone 2 Yorktown and leached silty sand deposits of southern Florida occasionally preserve broken adult *Glottidia* imbedded in matrix.

*Glottidia inexpectans* has been recovered from mid-shelf assemblages in Virginia indicative of a paleobathymetry of 40 to 60 meters. The Florida assemblage seems indicative of shallower waters, perhaps subtidal to 20 meters.

*Glottidia* species have been documented from the Atlantic Coastal Plain and Gulf Coast Eocene, Pliocene, and Recent. The stratigraphic gap between the Eocene and Pliocene *Glottidia* may be real, rather than an artifact of taphonomic megabias (Kowalewski, 1996b). However, the western Atlantic and eastern Pacific populations have been physically separated since the Middle Pliocene, necessitating an Atlantic origin for the Recent species.

The exceptional occurrence of abundant paired juvenile *Glottidia* indicates an unusual taphonomic event. *Glottidia* larvae settled in a single spat-fall, colonized a gaping scallop shell, and then died of starvation after the valves closed. Reworking is unlikely because juvenile shells are fragile, pedicle valves are more subject to breakage, and the fauna of the contained sediment differs substantially from that surrounding the scallop shell.

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ing literature. This is University of Florida Contribution to Paleontology 490.

#### VI. LOCALITY DATA

The following are collecting localities of the Invertebrate Paleontology Division, Florida Museum of Natural History, University of Florida (UF).

##### VIRGINIA

ZV004 Rice's Pit. Shell pit off Fox Hill Road, Hampton, Virginia. (Hampton Quadrangle, USGS 7.5 minute series, 37 degrees, 03 minutes, 37 seconds north, 76 degrees, 14 minutes, 33 seconds west). Lower Zone 2, Yorktown Fm.

ZV006 Kingsmill 01. North bank of James River, 100 meters east of the Marina at Kingsmill Estates, just southeast of Williamsburg, Virginia. (Hog Island Quadrangle, USGS 7.5 minute series, 37 degrees, 13 minutes, 05 seconds north, 76 degrees, 38 minutes, 45 seconds west). Zone 1, Yorktown Fm.

ZV007 Chesapeake Development pit. End of Cooke's Mill Road, between the communities of Yadkin and Deep Creek, Chesapeake, Virginia. (Norfolk South Quadrangle, USGS 7.5 minute series, 36 degrees, 45 minutes, 13 seconds north, 76 degrees, 22 minutes, 05 seconds west). Lower Zone 2, Yorktown Fm.

ZV008 Carters Grove 01. North bank of James River, Carter's Grove Plantation, 4 km southeast of Williamsburg, Virginia. (Hog Island Quadrangle, USGS 7.5 minute series, 37 degrees, 12 minutes, 35 seconds north, 76 degrees, 38 minutes, 02 seconds west). Zone 1, Yorktown Fm.

ZV009 Tutters Neck Dam 01. Spillway of Tutter's Neck Dam, Williamsburg, Virginia. (Williamsburg Quadrangle, USGS 7.5 minute series, 37 degrees, 15 minutes, 05 seconds north, 76 degrees, 41 minutes, 10 seconds west). Zone 1, Yorktown Formation.

##### SOUTH CAROLINA

ZS013 Lockheed Martin Berkeley County Quarry. Six km south of Rt. 6, on Rt. 59 between Eutaw Springs and Cross, South Carolina. (Cross Quadrangle, USGS 7.5 minute series, 35 degrees, 21 minutes, 08 seconds north, 80 degrees, 14 minutes, 04 seconds west). Raysor Marl.

## FLORIDA

- CH026 Casa de Meadows 02. Shell pit approximately 1.2 km east of Grove City, Charlotte County, Florida (NE 1/4, NE 1/4, Sec. 16, T41S, R20E; Englewood Quadrangle, USGS 7.5 minute series). Lower Tamiami Fm.
- PO002 Ft. Green #13 Dragline. Sand and phosphate pit approximately 6 km south of Bradley Junction, Polk County, Florida (NE1/4, Sec. 2, T32S, R23E; Baird Quadrangle, USGS 7.5 minute series). Bone Valley Member, Peace River Fm.
- PO018 Palmetto Mine. Sand and phosphate pit approximately 5 km northeast of Baird, Polk County, Florida (E 1/2, Sec. 9, T32S, R24E; Baird Quadrangle, USGS 7.5 minute series). Bone Valley Member, Peace River Fm.

## VII. LITERATURE CITED

- ALLMON, W. D., S. D. EMSLIE, D. S. JONES, and G. S. MORGAN, 1996, Late Neogene oceanographic change along Florida's West Coast: evidence and mechanisms: *Jour. Geology*, v. 104, p. 143-162.
- CAMPBELL, L. D., 1993, Pliocene Molluscs from the Yorktown and Chowan River Formations in Virginia: Virginia Division of Mineral Resources, Publication 127, 259 p., 43 pls.
- CHUANG, S. H., 1964a, On *Glottidia inexpectans* Olsson: *Jour. Paleont.*, v. 38, p. 153-155.
- CHUANG, S. H., 1964b, The affinity of *Lingula doumortieri* Nyst with *Glottidia*: *Jour. Paleont.*, v. 38, p. 155-157.
- CHUANG, S. H., 1964c, *Glottidia glauca* n. sp. from the Lower Claiborne of Texas: *Jour. Paleont.*, v. 38, p. 157-159.
- COOPER, G. A., 1955, New Brachiopods from Cuba: *Jour. Paleont.*, v. 29, p. 64-70.
- COOPER, G. A., 1973, Brachiopods (Recent): Marine Research Lab., Florida Dept. Nat. Resources, Memoirs of the *Hourglass* Cruises, v. 3, part 3, p. 1-14.
- COOPER, G. A., 1988, Some Tertiary Brachiopods of the East Coast of the United States: *Smithsonian Cont. Paleobiology*, v. 64, 26 p.
- CROWDER, W., 1931 (1975 reprint), Seashore life between the tides: Dover Publications, Inc., p. 209-210.
- DALL, W. H., 1870, A Revision of the Terebratulidae and Lingulidae, with remarks on and descriptions of some Recent forms: *Amer. Jour. Conch.*, v. 6, p. 154.
- DALL, W. H., 1905, Note on a variety of *Crepidula nivea* (C. B. Adams) from San Pedro, California: *Nautilus*, v. 19, no. 3, p. 26-27.
- DALL, W. H., 1920, Annotated list of the Recent Brachiopoda in the collection of the United States National Museum, with descriptions of thirty-three new forms: *U. S. Natl. Museum, Proc.*, v. 57, no. 2314, p. 261-377.
- DAVIDSON, T., 1888, A Monograph of Recent Brachiopoda: *Trans. of the Linnean Society London*, ser. 2, v. 4, parts 1-3, 248 p.
- EMIG, C. C., 1982, Taxonomie du genre *Lingula* (Brachiopodes, Inarticules): *Bull. Mus. Natn. Hist. Nat.*, v. 4 (ser. 4), p. 337-367.
- EMIG, C. C., 1983, Taxonomie du genre *Glottidia* (Brachiopodes, Inarticules): *Bull. Mus. Natn. Hist. Nat.*, v. 5 (ser. 4), p. 469-489.
- FOX, R. S., and E. E. RUPPERT, 1985, Shallow-water marine benthic macroinvertebrates of South Carolina: University of South Carolina Press, 330 p.
- GILBERT, C. R., 1989, Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic Bight) - Atlantic and shortnose sturgeons: *U. S. Fish Wildl. Serv., Biol. Rep.* 82, 28 p.
- HARPER, D. A. T., E. N. DOYLE, and S. K. DONOVAN, 1995, Palaeoecology and palaeobathymetry of Pleistocene brachiopods from the Manchiore Formation of Jamaica: *Proc. Geol. Assoc.*, v. 106, p. 219-227.
- HARPER, D. A., S. K. DONOVAN, and R. W. PORTELL, 1997, The Brachiopods *Tichosina* and *Terebratulina* from the Miocene of Jamaica: *Carib. Jour. Sci.*, v. 33, no. 1-2, p. 117-119.
- HERTLEIN, L. G., and U. S. GRANT IV, 1944, The Cenozoic Brachiopoda of Western North America: University of California, Los Angeles, Publications in mathematical and Physical Sciences, v. 3, 236 p.
- JONES, G. F., and J. L. BARNARD, 1963, The distribution and abundance of the inarticulate brachiopod *Glottidia albida* (Hinds) on the mainland shelf of Southern California: *Pacific Naturalist*, v. 4, p. 27-51.
- KEEN, A. M., 1971, Sea Shells of Tropical West America. Stanford University Press, 461 p.
- KOWALEWSKI, M., 1996a, Taphonomy of a living fossil: the lingulide Brachiopod *Glottidia palmeri* Dall from Baja California, Mexico: *Palios*, v. 11, p. 244-265.

- KOWALEWSKI, M., 1996b, Taphonomic Megabias in the fossil record of Lingulide Brachiopods, *In* P. COPPER and J. JIN (eds.), *Brachiopoda*: p. 145-150, Balkema, Rotterdam.
- KOWALEWSKI, M., and K. W. FLESSA, 1994, A predatory drill hole in *Glottidia palmeri* Dall (Brachiopoda: Lingulidae) from Recent tidal flats of northeastern Baja California, Mexico: *Jour. Paleont.*, v. 68, p. 1403-1405.
- MANSFIELD, W. C., 1944, Stratigraphy of the Miocene of Virginia and the Miocene and Pliocene of North Carolina, *In* J. A. GARDNER, *Mollusca from the Miocene and lower Pliocene of Virginia and North Carolina*: U. S. Geol. Survey Prof. Paper 199-A, p. 1-19.
- MASON, W. T., and J. P. CLUGSTON, 1993, Foods of the Gulf Sturgeon in the Suwannee River, Florida: *Trans. Amer. Fisheries Soc.*, v. 122, p. 378-385.
- MORGAN, G. S., 1994, Miocene and Pliocene marine mammal faunas from the Bone Valley Formation of Central Florida, *In* A. BERTA and P. A. DEMERA (eds.), *Contributions in marine mammal Paleontology honoring Frank C. Whitmore, Jr.*: *Proc. San Diego Soc. Nat. Hist.*, vol. 29, p. 239-268.
- OLSSON, A. A., 1914, New and interesting Neocene fossils from the Atlantic Coastal Plain: *Bulls. Amer. Paleol.*, v. 5, p. 59, pl. 5, figs. 17-21.
- PAINE, R. T., 1962, Ecological notes on a Gymnophalline Metacercaria from the Brachiopod *Glottidia pyramidata*: *Jour. Parasitology*, v. 48, no. 3, p. 509.
- PAINE, R. T., 1963, Ecology of the Brachiopod *Glottidia pyramidata*: *Ecological Mono.*, v. 33, p. 187-213.
- PAINE, R. T., 1970, The sediment occupied by Recent Lingulid Brachiopods and some paleoecological implications: *Paleogeog., Palaeoclim., Palaeoecol.*, v. 7, p. 21-31.
- PAJAUD, D., 1977, Choix et hierarchisation des caracteres taxinomiques pour la reconnaissance des Lingules post-Paléozoïques: *Geobios*, v. 10, p. 961-965.
- PLAZIAT, J. C., D. PAJAUD, C. EMIG, and J. C. GALL, 1978, Environnements et distribution bathymétrique des Lingules actuelles; conséquences pour les interprétations paléogéographiques: *Bull. Soc. Geol. France*, v. 20, p. 309-314.
- PORTELL, R. W., and C. W. OYEN, 1997, Occurrence of the regular urchin *Eucidaris tribuloides* from the Tamiami Formation (Pliocene) of Florida: *Tulane Stud. Geol. Paleont.*, v. 30, no. 2, p. 99-104.
- PORTELL, R. W., and E. H. VOKES, 1992, A new species of *Dicathais* (Gastropoda: Muricidae) from the Pliocene Tamiami Formation of southern Florida: *Tulane Stud. Geol. Paleont.*, v. 25, no. 4, p. 169-174.
- PORTER, H., 1974, *The North Carolina marine and estuarine Mollusca, an atlas of occurrence*. University of North Carolina Press, 351 p.
- RUDWICK, M. J. S., 1970, *Living and fossil Brachiopods*. Hutchinson University Library, Hutchinson and Co., Ltd., London, 199 p.
- SCOTT, T. M., 1988, The lithostratigraphy of the Hawthorn Group (Miocene) of Florida: *Florida Geol. Surv. Bull.* 59, p. 86-89.
- STIMPSON, W., 1860, *A trip to Beaufort, N. Carolina: The American Jour. Science*, v. 29 (2nd series), p. 442-445.
- THAYER, C. W., and H. M. STEELE-PETROVIC, 1974, Burrowing of the lingulid brachiopod *Glottidia pyramidata*: its ecologic and paleoecologic significance: *Lethaia*, v. 8, p. 209-221.
- WARD, L. W., and B. W. BLACKWELDER, 1980, Stratigraphic revision of Upper Miocene and Lower Pliocene beds of the Chesapeake Group, Middle Atlantic Coastal Plain: *U. S. Geol. Survey, Bull.* 1482D, 61 p., 5 pls.