Patterns of Diversity and Extinction in Transmarian Muricacean, Buccinacean, and Conacean Gastropods

Edward J. Petuch
Department of Geology
Florida Atlantic University
Boca Raton, FL 33431, USA

ABSTRACT

An analysis of patterns of species-richness in ten muricacean, buccinacean, and conacean families found in the Maryland Miocene formations has uncovered a previously-undetected Serravallian Stage extinction event that decimated the fauna of the Calvertian Subprovince of the Transmarian Province. Prior to the extinction event, the molluscan fauna of the Langhian Stage (Calvert Formation) contained many tropical elements (here referred to as "caloosagenic taxa") that were derivatives of the Miocene Caloosahatchian Province. At the Langhian-Serravallian boundary and the initiation of Choptank deposition, most of the earlier caloosagenic taxa suffered a regional extinction. Breakdown of local ecosystems, probably due to a cooling marine climate, increased toward the end of Choptank time, culminating in the extinction of prominent endemic thaidid and turrid genera. During the latest Serravallian Stage and the beginning of Tortonian time (St. Mary's Formation), the marine climate returned to Langhian conditions and there was an accompanying return to pre-Choptank levels of diversity. The post-Choptank molluscan assemblages differed, however, in containing new caloosagenic taxa, such as *Conus*, and had an extremely reduced thaidid fauna. Several biogeographically important new taxa are also proposed and these include three new genera, *Patuxentrophon* n.gen. (Muricidae: Trophoninae), *Calverturris* n. gen. (Turridae: Mangeliinae), and *Transmariaturris* n.gen. (Turridae: Mangeliinae), and six new species, *Ecphorosycon lindajoyceae* n.sp. (Thaididae: Ecphorinae), *Buccinofusus patuxentensis* n.sp. (Fasciolariidae), *Busycotypus choptankensis* n.sp., *Turrifulgur marylandicus* n.sp., and *Turrifulgur prunicola* n.sp. (all Melongenidae: Busyconinae), and *Calverturris schmidti* (Turridae: Mangeliinae).

Key words: Extinction, Maryland, Miocene, Transmarian Province.

INTRODUCTION

As a biogeographical entity, the Transmarian Molluscan Province of the northern and central Atlantic Coastal Plain has been relatively unstudied. This early Neogene paratropical province, whose fauna evolved in the Oligocene and became extinct during the Messinian Miocene, has recently been shown to contain numerous endemic gastropod taxa (Petuch, 1988a,b,c). Primary among these are a plethora of distinctive genera in the superfamilies Muricacea, Buccinacea, and Conacea, many of which are indicators of the provincial boundaries.

At its height, the Transmarian province extended from the present-day Cape Fear, North Carolina area northward to at least Nova Scotia (figure 46), and encompassed three distinct subprovinces; the southern Pungoian Subprovince, the central Calvertian Subprovince, and the northern Sankatian Subprovince (Petuch, 1988b). The Pungoian Subprovince was centered on the Miocene Albemarle Embayment of North Carolina, while the Calvertian Subprovince had its focus on the diverse biotopes of the Salisbury Embayment of Chesapeake Bay, southern New Jersey, Delaware, Maryland, and northern Virginia. Since the best-preserved and most accessible Transmarian faunas are located along the Patuxent River, the St. Mary's River and the western shore of Chesapeake Bay in Maryland, and since these were the principal faunas used in my provincial analysis, I will deal only with Calvertian taxa in this paper.

In Maryland, the Calvertian Transmarian molluscan fauna is contained within several extremely fossiliferous members of three classic Miocene formations and a possible new formation, the Calvert (contemporaneous with the well-known Kirkwood Formation of New Jersey) (Langhian Stage), the Choptank (early Serravallian Stage), the Little Cove Point Unit (late Serravallian Stage) (the status of this unit is still in debate among authorities; I here follow the nomenclature of Ward and Blackwelder, 1980:D4), and the St. Mary's (latest Servallian–early Tortonian Stages). Within these formations, a molluscan extinction event, interspersed between two periods of speciation and diversity augmentation, can be recognized within the stratigraphic record and these give insight into possible middle Miocene catastrophic climatic fluctuations along the eastern coast of North America. In this paper, I also hope to shed some light on the higher order diversity patterns of the Transmarian muricacean, buccinacean, and conacean gastropod families. Several important new taxa are also described here in order to fill some nomenclatural gaps in the Calvertian fossil record. These include three new genera, *Patuxentrophon* (Muricidae: Trophoninae), *Calverturris* (Turridae), and *Transmariaturris* (Turridae), and new species of *Ec-*

phorosycon (Thaididae: Ecphorinae), *Buccinofusus* (Fasciolariidae), *Busycotypus* (Melongenidae: Busyconinae), *Turrifulgur* (Melongenidae: Busyconinae), and *Calverturris* (Turridae). The three superfamilies studied, which include ten families and forty-one genera (listed here in Appendix 1), are excellent indicators of ecosystem collapse during times of extreme climatological stress.

THE TRANSMARIAN GASTROPOD FAUNA

As demonstrated in my earlier work (Petuch, 1988b:11), the Transmarian molluscan fauna represents one of the strangest mixtures of gastropods that can be found anywhere in the fossil record. Unlike any known Recent malacofauna, the Transmarian assemblages contain sympatric suites of both boreal, high arctic gastropod genera such as *Boreotrophon* (Muricidae), *Admete* (Cancellariidae), *Oenopota* (Turridae), and *Euspira* (Naticidae), and eutropical genera such as *Conus* (*Leptoconus*) (Conidae), *Strioterebrum* (Terebridae), *Laevityphis* (Muricidae), and *Cymatosyrinx* (Turridae). These arctic and tropical elements coexisted with a large compliment of endemic Transmarian genera. Although the Transmarian Province contained taxa from several tropical families, the fauna lacked most of the classic eutropical index groups, such as the Strombidae, Turbinellidae, Cypraeidae, Ovulidae, Cerithiidae, Potamididae, and Lyriinae (Volutidae) (Petuch, 1988b). Based on the absence of these eutropical elements, the Transmarian province can only be considered to have been a paratropical faunal region.

As determined by Gibson (1967), using foraminiferal assemblages, the marine climate of the Transmarian Province ranged from cool-temperate to temperate, with only a small seasonal fluctuation in water temperature. This climatic stability allowed the evolution of a physiologically stenothermal temperate molluscan fauna, with the endemic genera being unable to live in both the colder boreal conditions to the north and in the warmer tropical conditions of the Miocene Caloosahatchian Province to the south (Petuch, 1988b) (figure 46). The Transmarian arctic and tropical elements represent physiologically eurythermal "invaders" from the Miocene Boreal and Caloosahatchian Provinces. These opportunistic species appear to have evolved physiological tolerations for the warmer (for the boreal taxa) or colder (for the tropical taxa) water conditions of the Transmarian region, and evolved their own endemic Transmarian temperate species complexes.

Transmarian faunal elements that were derived from the tropical Miocene Caloosahatchian Province are here referred to as "caloosagenic". The caloosagenic influence varied through time in the Calvertian Subprovince, with some stages, such as the early Tortonian, containing many tropical taxa and other stages, such as the early Serravallian, containing fewer taxa. Some caloosagens were present only during the Langhian Stage and disappeared from Maryland during the Serravallian Stage, being found subsequently in the fossil beds of Virginia and Florida. Primary examples of these early Calvertian caloosagens include *Phyllonotus* (*P. millvillensis* (Richards and Harbison, 1942)), *Murexiella* (*M. shilohensis* (Heilprin, 1887)), *Oliva* (*O. harrisi* Martin, 1904), *Amaea* (*A. reticulata* Martin, 1904 and *A. prunicola* Martin, 1904), *Niso* (*N. lineata* (Conrad, 1841)), *Ficus* (*F. harrisi* (Martin, 1904)), and *Architectonica* (*A. trilineatum* (Conrad, 1841)). Other caloosagens make their first appearance in the Calvertian Subprovince at the very end of Salisbury deposition, in the late Serravallian and early Tortonian Stages. Some of these late Calvertian caloosagenic taxa include the previously-mentioned conid genus *Conus* (*Leptoconus* species complex) and the volutacean genus *Mitra* (*M. mariana* Martin, 1904). Still other caloosagenic groups, such as the busyconine genera *Busycotypus* and *Turrifulgur*, the volutid *Volutifusus*, and the turritellid *Torcula*, existed within the Calvertian area throughout the Langhian, Serravallian, and Tortonian Stages.

Transmarian faunal elements that were derived from the arctic Boreal Province are here referred to as "boreogens". As in the case of the caloosagens, the boreogenic influence also fluctuated through time, being more prevalent in some molluscan assemblages than in others. Unlike the caloosagens, however, very few boreogens were present in the Calvertian Subprovince during the Langhian stage. Of these, only a single genus (the naticid *Euspira*) is known to have ranged throughout the entire Maryland Miocene. The Tortonian Stage, on the other hand, saw the appearance of many new boreogenic taxa that previously had not existed within the Salisbury Embayment. Examples of these later boreal "invaders" include the previously-mentioned genera *Admete* and *Oenopota*.

DYNAMICS OF TRANSMARIAN DIVERSITY

By recognizing that three separate groups of faunal elements coexisted within the Transmarian Province, the caloosagens, the boreogens, and the Transmarian endemics, it is now possible to undertake a fine-resolution analysis of the diversity patterns of Calvertian Transmarian muricacean, buccinacean, and conacean gastropods. These are discussed in the following sections. A listing of all known Calvertian species in these three superfamilies is given in Appendix 2.

Muricacean diversity patterns: Although comprising two families and fourteen genera, the Transmarian muricacean taxa were not distributed equally over time. Only two muricid genera, *Laevityphis* and *Chesatrophon* (figure 32), and one thaidid genus, *Ecphora* s.s., are temporally distributed throughout the Langhian, Serravallian, and Tortonian Stages. During Langhian time, in the Calvert and Kirkwood (New Jersey) Formations, only two other muricid groups, the caloosagens *Murexiella*, and *Phyllonotus*, are present. The Langhian ecphorine thaidids, on the other hand, underwent a large species radiation, evolving at least four species of *Ecphora* s.s., at least five species of *Trisecphora* (figure 38), two species of *Ecphorosycon*, and two species of *Chesathais* (figure 34) (Petuch, 1989). (*Note:* The genus *Chesathais*, although possibly arising from a Caloosahatchian stem species (*C. biconicus*), was represented in Maryland by the *C. ecclesiasticus* species complex and can be considered to be an endemic Transmarian radiation.) The large ecphorines apparently dominated the Langhian molluscan assemblages, as their shells are abundant in most units of the Calvert Formation. The small Calvert muricids of the genera *Laevityphis*, *Chesatrophon*, *Murexiella*, and *Patuxentrophon* (figures 1, 2), however, are rare in most assemblages and appear to have occupied the ecological "fringe" areas.

During Serravallian time, the Maryland *Murexiella* species disappeared, (and presumably the New Jersey Kirkwood *Phyllonotus* species), while the caloosagen *Urosalpinx* first made an appearance. This ubiquitous Caloosahatchian ocenebrine taxon survived to become an abundant component of the late Serravallian-Tortonian assemblages of the St. Mary's Formation, and is also extant in the Recent. Also appearing in the early Serravallian was the small muricid *Stephanosalpinx* (figure 31). This distinctive muricacean disappeared by the late Serravallian and is confined to the Choptank Formation.

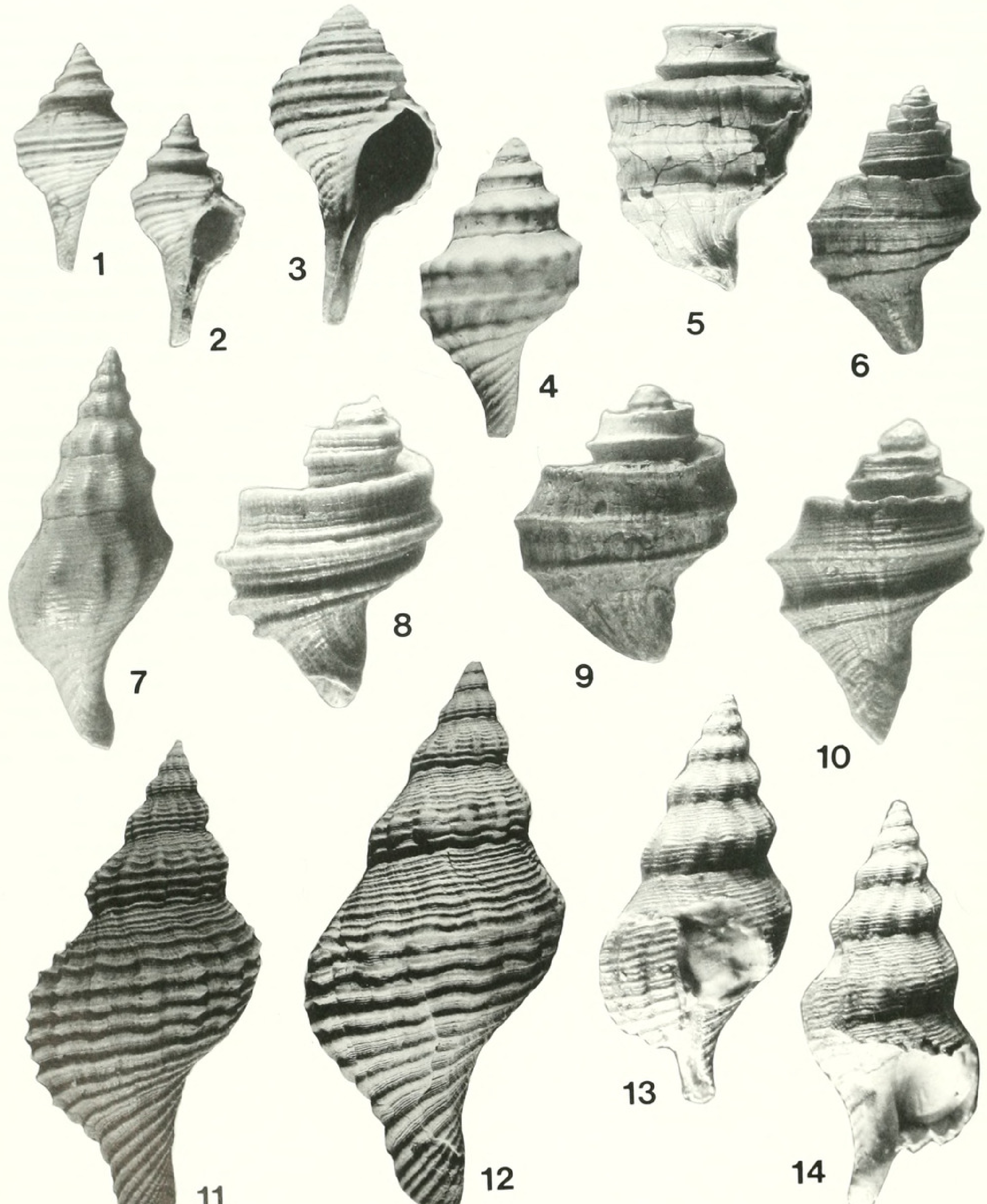
As during the Langhian, the predominant muricacean radiation during the early and middle Serravallian time was a complex of ecphorine thaidids. During this time, the genus *Ecphora* s.s. was abundantly represented by at least four species and four stratigraphic subspecies. The subgenus *Trisecphora*, although not as species-rich as during Langhian time, was also abundantly represented by two species and at least one stratigraphic subspecies. Likewise, the morphologically-conservative genus *Chesathais* was also present in the Choptank Formation, in this case as a species and two stratigraphic subspecies. Although the primitive genus *Ecphorosycon* was originally thought to have become extinct at the end of Langhian time (Petuch, 1989:43), the recent discovery of a rare Choptank species (*E. lindajoyceae* n.sp., described here) demonstrates that the genus survived into earliest Serravallian time and was part of the rich Choptank ecphorine fauna.

Although ecphorine species diversity declined at the end of Choptank time, muricid diversity increased dramatically at the beginning of Little Cove Point-St. Mary's time (late Serravallian–Tortonian). The abundant presence of the trophonine genera *Chesatrophon* (figure 32), *Boreotrophon*, (figure 29, 30) *Scalaspira* (figure 4), *Lirosoma* (figure 3), and the ocenebrine genera *Urosalpinx* and *Mariasalpinx* (figure 33), particularly underscore this shift toward muricid dominance. This predominance is emphasized even further by the fact that only a single species of *Ecphora* occurs sympatrically with the rich trophonine and ocenebrine faunas found within the various members of the St. Mary's Formation. Although only a single *Ecphora* species is found within any bed of the St. Mary's Formation, these species are much larger than any ancestral species from the Calvert and Choptank Formations, and are, in fact, the largest muricaceans found in the entire Maryland Miocene (*Ecphora gardnerae* Wilson, 1987 often exceeds lengths of 110 mm). This gigantism gave the post-Choptank ecphorine survivors an ecological advantage over their more numerous, but much smaller, muricid cousins—allowing them to utilize large prey items, such as adult specimens of the bivalves *Mercenaria* and *Dosinia*, which were inaccessible to the contemporaneous muricids (Petuch, 1989: 15). Interestingly enough, of all the late Transmarian endemic muricid genera, only *Scalaspira*, *Lirosoma*, and *Boreotrophon* (Transmarian complex) survived into the early Pliocene (Zanclian Stage). The last species of these groups, *S. strumosa* (Conrad, 1832), *L. sulcosa* (Conrad, 1830), and *B. tetricus* (Conrad, 1832), respectively, can be found in the Yorktown Formation.

Buccinacean diversity patterns: Comprising five families and twelve genera, the Transmarian buccinacean gastropods, unlike the muricaceans, were more equitably distributed over time. Eight of the twelve genera are found in all three Maryland Miocene formations and are represented by continuous species lineages. Only during St. Mary's time do additional genera appear, and these include the Transmarian endemics *Mariafusus* (figure 39), *Pseudaptyxis* (figure 35), and *Bulliopsis*. No boreogenic buccinacean taxa are known from the Pungoian, Calvertian, or Sankatian Subprovinces.

Of the five Transmarian buccinacean families, only the Fasciolariidae showed any appreciable augmentation through time. During Calvert and Choptank time, the family Fasciolariidae was represented by only a single genus, *Buccinofusus* (with two of the species shown here in figures 7, 13, 14). By Little Cove Point-St. Mary's time, however, the number of fasciolariid genera had jumped to three, with the Transmarian endemics *Mariafusus* and *Pseudaptyxis* possibly representing offshoots that now coexisted with their *Buccinofusus* ancestral stock (Petuch, 1988b). The primitive genus *Buccinofusus*, in particular, underwent rapid evolution, producing three species in the Calvert Formation and one species, each, in the Choptank and St. Mary's Formation and Little Cove Point Unit. Unlike the other Transmarian buccinacean families, all the Transmarian fasciolariid genera were endemic to the province, with most taxa being confined to the Salisbury Embayment of the Calvertian Subprovince.

As the complete opposite of the Fasciolariidae, the families Buccinidae and Columbellidae were represented in the Transmarian Province only by caloosagenic genera. The species within these tropically-derived groups, however, represented endemic Transmarian species radiations that paralleled those of their congeners to the south. The genera *Celatoconus*, *Ptychosalpinx*, and *Solenosteira* were all common and prominent components of the Calvert, Choptank, and St. Mary's faunas. In the case of *Ptychosalpinx*, the genus had radiated into an endemic Transmarian species complex with at least



Figures 1–14. Muricid, thaidid, and fasciolariid gastropods from the Transmarian Province. **1, 2.** *Patuxentrophon patuxentensis* (Martin, 1904), dorsal and ventral views of 18 mm specimen, Zone 17, Choptank Formation, Drum Cliff, St. Mary's County, Maryland. **3.** *Lirosoma mariana* Petuch, 1988, holotype, length 27 mm, St. Mary's Formation, St. Mary's River, Maryland. **4.** *Scalaspira harasewychi* Petuch, 1988, holotype, length 13 mm, St. Mary's Formation, St. Mary's River, Maryland. **5.** *Ecphorosycon lindajoyceae* new species, holotype, length 55 mm (incomplete), Zone 16, Choptank Formation, Sandgates, St. Mary's County, Maryland, UF 21466. **6.** *Ecphorosycon pamlico* (Wilson, 1987), 68 mm specimen from Zone 10, Calvert Formation, Plum Point,

two sympatric species during St. Mary's time. The Columbellidae, which normally exhibits a high degree of species-richness in eutropical areas, was represented in the paratropical Transmarian Province by only a single genus, *Mitrella*. Although common in all the Maryland Miocene exposures, *Mitrella* never underwent any species radiation and was represented by only two sympatric species in the Calvert Formation and one species, each, in the Choptank and St. Mary's Formations and in the Little Cove Point Unit.

Considering that the overwhelming majority of Transmarian biotopes, as in the Recent Carolinian Province, were composed of soft-bottom sand or mud areas, the family Nassariidae could be expected to be present in the Calvertian region as a large species radiation. Although comprising only two genera, the caloosagenic *Ilyanassa* and the endemic *Bulliopsis*, the Nassariidae dominated many facies of the Calvert and St. Mary's Formations and were the predominant group of small buccinaceans in the Transmarian Province. *Ilyanassa* is present in all Maryland Miocene formations as a series of species swarms, with at least two species in the Calvert Formation, four in the Choptank, and at least three in the St. Mary's. This species-richness is comparable to that seen in the Pliocene, in such formations as the Duplin and Yorktown. The endemic Transmarian genus *Bulliopsis*, on the other hand, is restricted to the Calvertian Subprovince and appears only at the end of Salisbury deposition during Little Cove Point and St. Mary's time.

The most extensive macrobuccinacean radiation within the Transmarian Province is seen in the busyconine melongenids. These large and abundant predatory gastropods were represented in the Calvertian Subprovince by species swarms in three genera; *Busycotypus* (examples shown here in figures 15–20), *Sycopsis* (figures 36, 37), and *Turrifulgur* (examples shown here in figures 21–23, 26, 27). These groups are present in all the Maryland Miocene formations and exhibit only gradual morphological shifts through time. *Sycopsis*, the least commonly encountered busyconine, was present in the Transmarian Province as only a single species per formation. The caloosagenic genera *Turrifulgur* and *Busycotypus*, on the other hand, were often present as sympatric species pairs, and in some cases, such as *Busycotypus* during St. Mary's time, was present as a complex of four species. The species radiations of both of these genera will be discussed in greater detail under the description of new *Busycotypus* and *Turrifulgur* species in the systematic section at the end of this paper.

Conacean diversity patterns: Of the three Transmarian conacean families, only two, the Turridae and the Terebridae, are temporally distributed throughout the Maryland Miocene and are found in all three formations. The third family, the Conidae, is only known from the St. Mary's Formation and makes its appearance in the Calvertian Subprovince only at the end of Salisbury deposition. Although an abundant and diverse family in the Miocene Caloosahatchian Province, the Conidae was represented in the Transmarian Province by only a single subgenus of *Conus*. This group, *Leptoconus* (figures 40, 41), had evolved into a complex of three endemic sympatric species, *C. diluvianus* Green, 1830, *C. sanctaemariae* Petuch, 1988, and *C. asheri* Petuch, 1989, by the end of St. Mary's time.

The Terebridae, although a common component of all Transmarian molluscan assemblages, was present as only two genera, the caloosagenic *Strioterebrum* and the endemic genus *Laevihastula*. The absence of core tropical terebrids such as *Myurella*, *Hastula*, and *Paraterebra*, which are all found in the Miocene Caloosahatchian and Gatunian Provinces to the south, points to the marginal paratropical nature of the Transmarian Province, and the Calvertian Subprovince in particular. *Strioterebrum* shows an interesting bimodal evolutionary pattern, with two spurts of speciation, one during Calvert time and one at the end of Salisbury deposition, during St. Mary's time. The decline in *Strioterebrum* species-richness during Choptank time may be linked to lower water temperatures during the early Serravallian stage. Unlike *Strioterebrum*, *Laevihastula* is absent in the Calvert Formation but underwent a large species radiation during St. Mary's time, evolving at least four sympatric species.

The third Transmarian conacean family, the Turridae, is present in the Calvertian Subprovince as four subfamilies, twelve genera, and over thirty-five species, making it the single largest toxoglossate radiation in the Maryland Miocene. Of the twelve turrid genera, nine were endemic to the Transmarian Province, two were caloosagenic, and one was boreogenic. The most species-rich subfamily in the Calvertian Subprovince, the Clavinae, comprised three genera; the Transmarian endemics *Chesaclava* (figure 42) and *Sedilopsis*, and the caloosagen *Cymatosyrinx*. The largest number of species of these genera, particularly *Cymatosyrinx*, is found in the St. Mary's Formation, and this species-richness probably reflects a response to the warmer marine climate during the early Tortonian.

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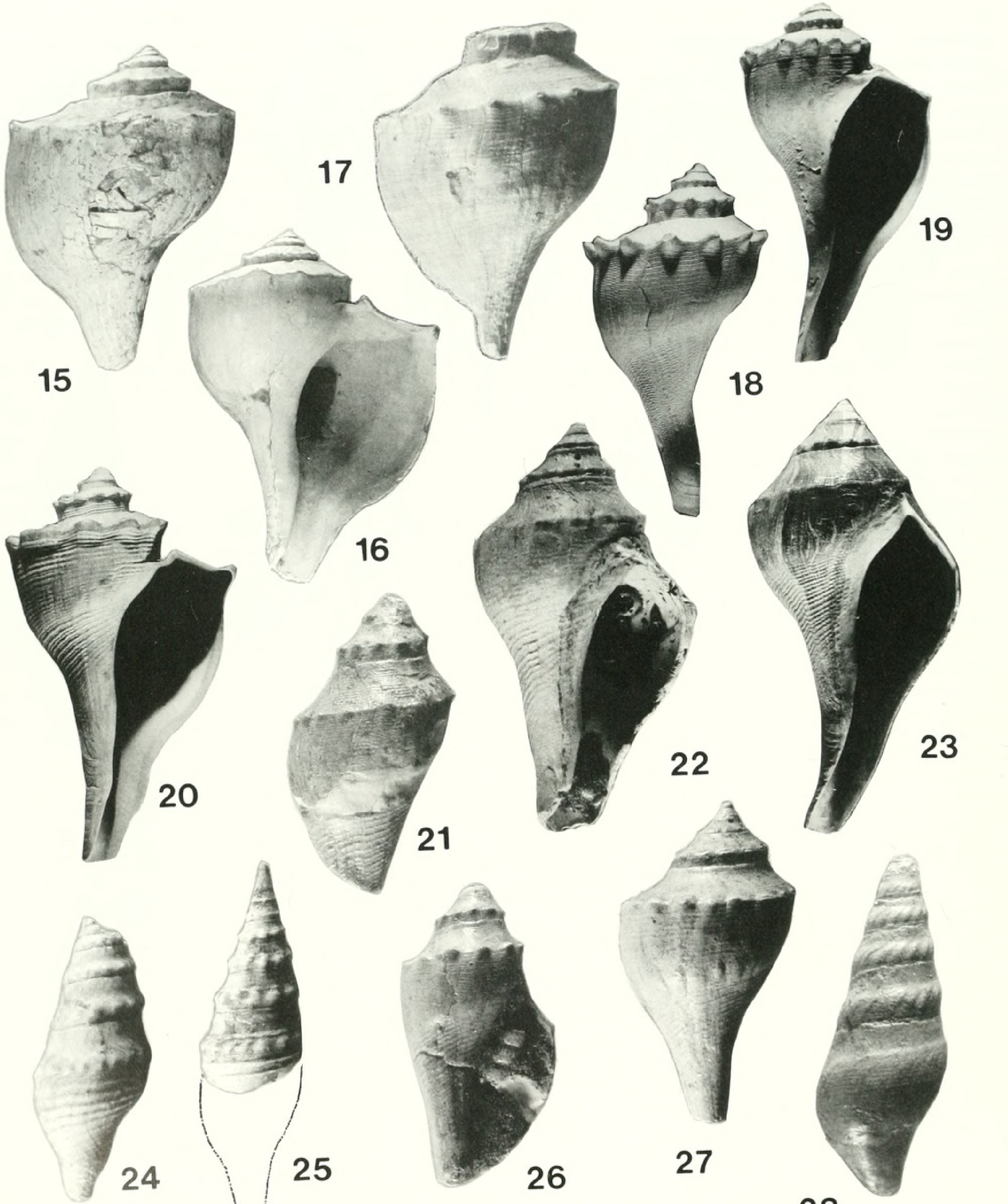
Calvert County, Maryland. **7.** *Buccinofusus devexus* (Conrad, 1843), 60 mm specimen from Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland. **8.** *Ecphorosycon kalyx* (Petuch, 1988), 23 mm specimen from Zone 12, Calvert Formation, Scientist's Cliffs, Calvert County, Maryland. **9.** *Ecphorosycon lindajoyceae* new species, reconstructed paratype, length 69 mm, Zone 16, Choptank Formation, Sandgates, St. Mary's County, Maryland. **10.** *Ecphorosycon pamlico* (Wilson, 1987), juvenile specimen, length 32 mm, Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland. **11.** *Buccinofusus parilis* (Conrad, 1832), 106 mm specimen from St. Mary's Formation, St. Mary's River, Maryland. **12.** *Buccinofusus chesapeakensis* Petuch, 1988, holotype, length 93 mm, Little Cove Point Unit, Little Cove Point, Calvert County, Maryland. **13, 14.** *Buccinofusus patuxentensis* new species, dorsal and ventral views of holotype, length 76 mm, Zone 17, Choptank Formation, Drum Cliff, St. Mary's County, Maryland, UF 21499.



Figures 15–28. Busyconine melongenid and turrid gastropods from the Transmarian Province. **15, 16.** *Busycotypus choptankensis* new species, dorsal and ventral views of holotype, length 192 mm, Zone 19, Choptank Formation, Drum Cliff, St. Mary's County, Maryland, UF 23798. **17.** *Busycotypus calvertensis* Petuch, 1988, dorsal view of holotype, 44 mm (incomplete), Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland. **18.** *Busycotypus chesapeakensis* Petuch, 1988, dorsal view of holotype, length 83 mm, Little Cove Point Unit, Little Cove Point, Calvert County, Maryland. **19.** *Busycotypus coronatum* (Conrad, 1840), dorsal view of 59 mm specimen, St. Mary's Formation, St. Mary's River, Maryland. **20.** *Busycotypus rugosum* (Conrad, 1843), ventral view of 64 mm specimen, St. Mary's Formation, St. Mary's River. **21, 26.** *Turrifulgur marylandicus* new species, dorsal and ventral

In the Maryland Miocene, the subfamily Mangeliinae was represented by the most number of genera, with the Transmarian endemics *Calverturris*, *Mariadrillia*, and *Transmariaturris*, the caloosagen *Glyphostoma*, and the boreogen *Oenopota*. Unlike the Clavinae, the mangeliine turrids were not equally distributed through time, but were divided into two groups: one that was confined to the Calvert and Choptank Formations and the other that appeared only during St. Mary's time. The former group contains *Calverturris* (figures 24, 25), *Transmariaturris* (figure 28), and *Glyphostoma*, all of which disappeared during the mid-Serravallian. The latter group contains only *Mariadrillia*, which is common in the St. Mary's Formation.

The subfamily Turriculinae contained the largest-known Calvertian turrid species radiation, that of the endemic genus *Mariaturricula* (figure 45). This group of large, fusiform conaceans had evolved over seven species during the Maryland Miocene, and these were probably the primary predators on large infaunal polychaetes. The last-known species, *Mariaturricula biscatenaria* (Conrad, 1834), may have competed with the caloosagenic *Leptoconus* species complex of the St. Mary's Formation. Another endemic Transmarian turriculine group, *Chesasyrinx* (figure 43), is rare in the Calvert and Choptank Formations but is abundant in the St. Mary's Formation, where it evolved into at least two sympatric species. This surge of *Chesasyrinx* evolution may have been in response to the warmer marine climate during St. Mary's time. Coinciding with the early Tortonian speciation acme of *Chesasyrinx* is the appearance of a new turrid group, *Nodisurculina* (figure 44), which is restricted to the St. Mary's Formation.

The subfamily Turrinae, which is characterized by large species radiations and complexes of genera in most Neogene tropical provinces, was poorly represented in the Transmarian Province. Only a single genus, *Hemipleurotoma*, was present, but was equally distributed throughout the entire Maryland Miocene and is found in all three formations. This endemic Transmarian genus is morphologically very conservative, with all known species closely resembling each other. Throughout its temporal range, *Hemipleurotoma* probably occupied the ecological "fringe" area, having had to compete with the extensive vermivorous radiations of the subfamilies Clavinae, Mangeliinae, and Turriculinae. Underscoring this possible competitive exclusion is the fact that only a single *Hemipleurotoma* species is found in each formation, as opposed to the contemporaneous sympatric species swarms of such successful vermivores as *Sediliopsis*, *Cymatosyrinx*, and *Mariaturricula*.

DYNAMICS OF TRANSMARIAN EXTINCTION

Based on both the presence and absence, through time, of caloosagenic and endemic taxa in the Calvertian area, an early Serravallian extinction event can be delineated within the temporal sequence of the Maryland Miocene. This extinction interval began at the initiation of Choptank deposition, at the boundary of Planktonic Foraminifer Zones N10–N11 and N12 (Gibson, 1983:38), and reached a peak at the end of Choptank deposition, at the boundary of Planktonic Foraminifer Zones N12 and N13. During this time, which ranges from 13 million years B.P. to approximately 12.3 million years B.P. (Gibson, 1983: fig. 2), several dominant gastropod groups disappeared from the Transmarian ecosystems, resulting in post-Choptank molluscan assemblages that differed in appearance from those of Langhian age.

Since eutropical caloosagenic taxa such as *Glyphostoma*, *Oliva*, *Niso*, *Ficus*, and *Architectonica* disappeared at the end of Calvert time, but boreogenic taxa such as *Oenopota* and *Euspira* persisted throughout Choptank time, it can be assumed that a climatic cooling event was the primary culprit in the extinction of the dominant Langhian Transmarian gastropod taxa. As pointed out by Stanley (1986), a "refrigeration" event, such as the Serravallian cooling episode, is most probably the cause of both regional and mass extinctions of neritic faunas throughout the Phanerozoic. Since many of the typical Transmarian endemic genera, such as *Chesatrophon*, *Buccinofusus*, *Sycopsis*, *Chesaclava*, and *Mariaturricula*, survived the Serravallian extinction and are present in the subsequent St. Mary's Formation, the Choptank-aged refrigeration event was not as severe as that of the mass extinction episode during the late Tortonian and Messinian Stages (the "Transmarian Extinction" of Petuch, 1988b:12). During that late Miocene time, over 95% of the Transmarian gastropod species lineages disappeared. The Serravallian extinction episode, then, may have been a precursor to the catastrophic Transmarian Extinction of two million years later. The reduction of muricacean, buccinacean, and conacean species-richness during Choptank time is shown, graphically, in figure 47.

Although not totally devastating to Transmarian gastropod assemblages, the Serravallian extinction was apparently severe enough to cause the extinction of tem-

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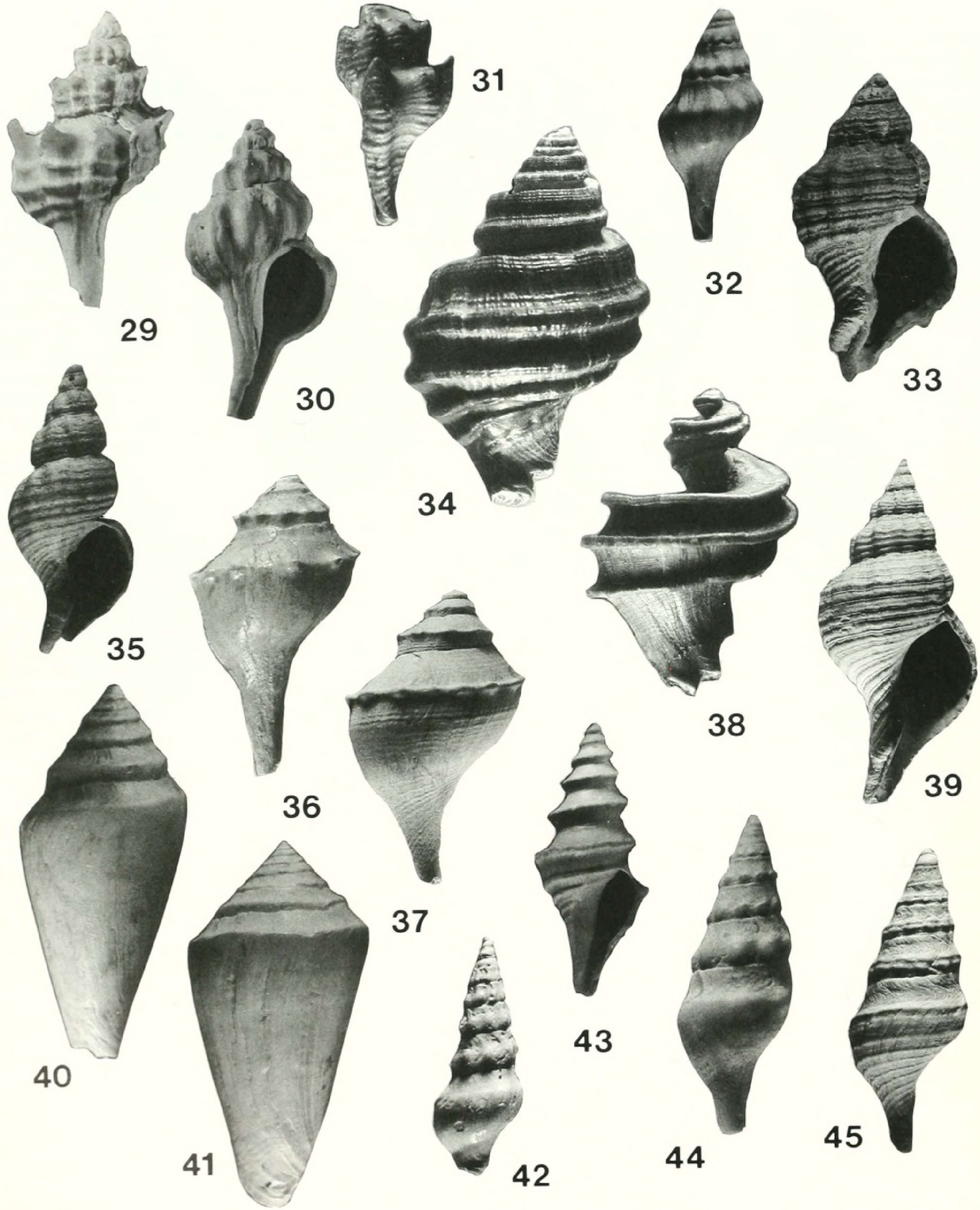
views of holotype, length (incomplete) 60 mm, Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland, UF 21467. **22.** *Turrifulgur turriculus* Petuch, 1988, holotype, length 32 mm, St. Mary's Formation, St. Mary's River. **23.** *Turrifulgur fusiforme* (Conrad, 1840), 69 mm specimen, St. Mary's Formation, St. Mary's River. **24.** *Calverturris bellacrenata* (Conrad, 1841), 28 mm specimen, Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland. **25.** *Calverturris schmidti* new species, dorsal view of incomplete holotype (outline reconstructed), length 23 mm, Zone 17, Choptank Formation at Drum Cliff, St. Mary's County, Maryland, UF 21500. **27.** *Turrifulgur prunicola* new species, dorsal view of holotype, length 35 mm, Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland, UF 21468. **28.** *Transmariaturris calvertensis* (Martin, 1904), dorsal view of 40 mm specimen, Zone 10, Calvert Formation, Plum Point, Calvert County, Maryland.



Figures 29–45. Representative species of endemic Transmarian gastropod genera and endemic species complexes. **29.** *Boreotrophon lindae* Petuch, 1988, length 13 mm, St. Mary's Formation (*Boreotrophon* Fischer, 1884, Transmarian species complex). **30.** *Boreotrophon harasewychi* Petuch, 1988, length 16 mm, St. Mary's Formation (*Boreotrophon* Fischer, 1884, Transmarian species complex). **31.** *Stephanosalpinx candelabra* Petuch, 1988, length 18 mm, Choptank Formation, lateral view showing small labial tooth (*Stephanosalpinx* Petuch, 1988). **32.** *Chesatrophon chesapeakeanus* (Martin, 1904), length 11 mm, St. Mary's Formation (*Chesatrophon* Petuch, 1988). **33.** *Mariasalpinx emilyae* Petuch, 1988, length 28 mm, St. Mary's Formation (*Mariasalpinx* Petuch,

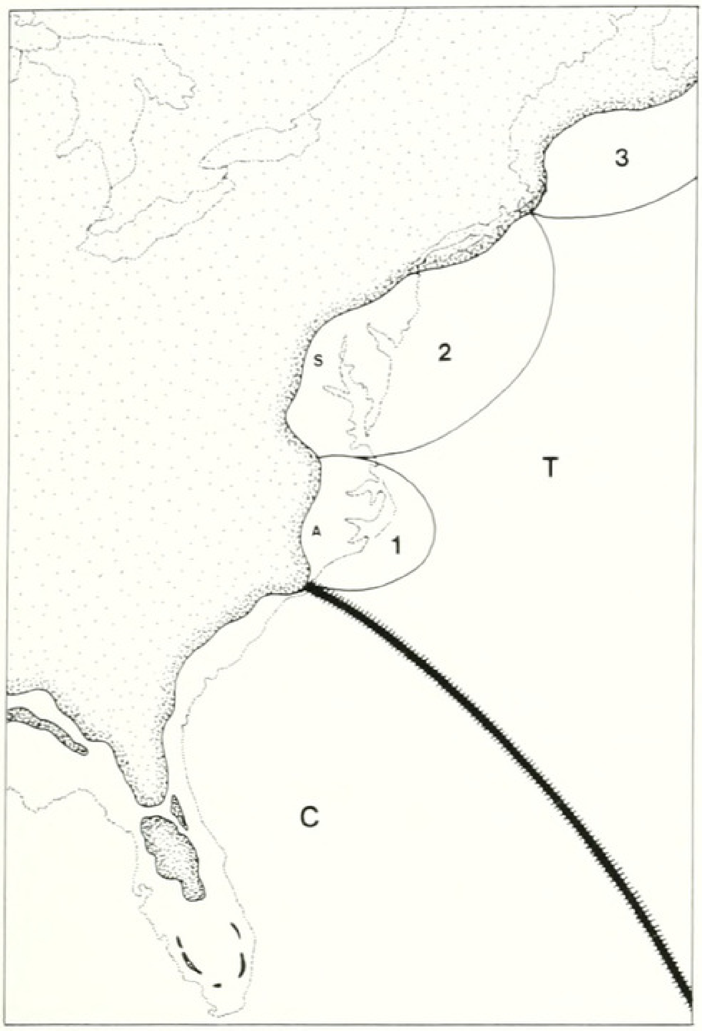


Figure 46. Miocene eastern North America, showing continental configuration (stippled area) and molluscan faunal provinces, superimposed upon the outline of Recent North America (dotted line). C = Miocene Caloosahatchian Molluscan Province; T = Transmarian Province, with its three subprovinces, the Pungoian (1), the Calvertian (2), and the Sankatian (3); thick fence-line represents the boundary between the Transmarian and Miocene Caloosahatchian Provinces; S = Salisbury Embayment; A = Albemarle Embayment.

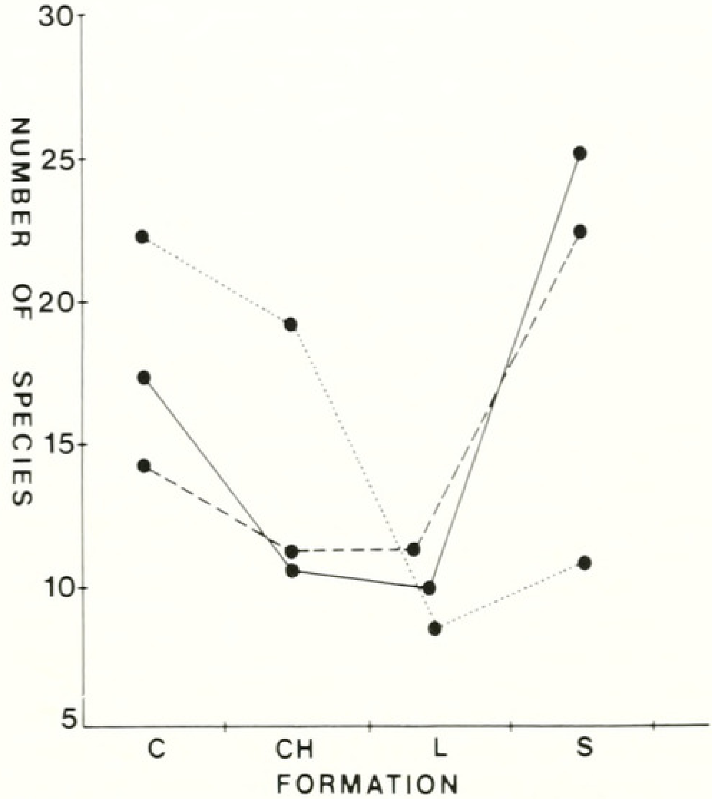


Figure 47. Species-richness of Calvertian Transmarian muricacean, buccinacean, and conacean gastropods during the middle Miocene, showing drop in diversity during Choptank-Little Cover Point time. *Dotted line* = number of known muricaceans; *dashed line* = number of known buccinaceans; *solid line* = number of known conaceans. Calvertian formations include the Calvert (C), Choptank (CH), Little Cove Point Unit (L), and St. Mary's (S). Numbers of species per superfamily are taken from the data listed in Appendix 2.

perature-sensitive organisms such as the Transmarian *Nautilus* species (Martin, 1904:130), the Transmarian archeocetian whales of the genera *Priscodelphinus* Cope, 1868, *Ixacanthus* Cope, 1890, *Cetophis* Cope, 1868, and *Delphinodon* Leidy, 1869, and the porpoise genus *Orycterocetus* Cope, 1867 (Case, 1904). These last mentioned cetacean genera disappeared abruptly at the end of Calvert deposition, contemporaneously with the disappearance of the caloosagenic gastropod genera *Glyphostoma*, *Niso*, *Oliva*, and *Ficus*. Besides the endemic cetaeans, a large fauna of other Transmarian vertebrates died out at the Langhian-Serravallian boundary. Included are the giant endemic stingray *Raja dux* Cope, 1867, the *Myliobatus gigas* Cope, 1867—*M. pachydon* Cope, 1867 complex of rays, the giant carchariid sharks *Carcharias collata* Case, 1904, *C. laevissimus* (Cope, 1867), *C. mag-*

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1988). **34.** *Chesathais lindae* Petuch, 1988, length 50 mm, Choptank Formation (*Chesathais* Petuch, 1988). **35.** *Pseudaptyxis sanctaemariae* Petuch, 1988, length 26 mm, St. Mary's Formation (*Pseudaptyxis* Petuch, 1988). **36.** *Sycopsis lindae* Petuch, 1988, length 65 mm, Choptank Formation (*Sycopsis* Conrad, 1867). **37.** *Sycopsis tuberculatum* (Conrad, 1840), length 52 mm, St. Mary's Formation (*Sycopsis* Conrad, 1867). **38.** *Ecphora* (*Trisecphora*) *eccentrica* Petuch, 1989, length 58 mm, Calvert Formation (*Trisecphora* Petuch, 1988, subgenus of *Ecphora* Conrad, 1843). **39.** *Mariafusus marylandicus* (Martin, 1904), length 60 mm, St. Mary's Formation (*Mariafusus* Petuch, 1988). **40.** *Conus* (*Leptoconus*) *asheri* Petuch, 1988, length 42 mm, St. Mary's Formation (*Leptoconus* Swainson, 1840, subgenus of *Conus* Linnaeus, 1758, Transmarian species complex). **41.** *Conus* (*Leptoconnus*) *diluvianus* Green, 1830, length 63 mm, St. Mary's Formation (*Leptoconus* Swainson, 1840, subgenus of *Conus* Linnaeus, 1758, Transmarian species complex). **42.** *Chesaclava quarlesi* Petuch, 1988, length 14 mm, St. Mary's Formation (*Chesaclava* Petuch, 1988). **43.** *Chesasyrinx rotifera* (Conrad, 1830), length 24 mm, St. Mary's Formation (Conrad, 1862), length 14 mm, St. Mary's Formation (*Nodisurculina* Petuch, 1988). **45.** *Mariaturricula biscatenaria* (Conrad, 1834), length 35 mm, St. Mary's Formation (*Mariaturricula* Petuch, 1988).

na (Cope, 1867), and *C. incidens* Case, 1904, and the giant manatee *Trichechus giganteus* (DeKay, 1842) (Case, 1904). It seems noteworthy that the Calvert-Choptank molluscan extinction correlates with the impressive mammalian and elasmobranch extinctions, indicating that there was a province-wide catastrophic event that affected many animal groups.

After the initial Langhian-Serravallian boundary refrigeration event, there was a gradual and further climatic deterioration during Choptank time. This gradualistic pattern is demonstrated by the sequential extinction of several taxa. Victims of the initial Langhian-Serravallian boundary event were the caloosagenic, eutropical muricid genera *Murexiella* and *Phyllonotus*, which disappeared at the end of Calvert-Kirkwood time. These thermophilic genera, which are widespread in the Recent eutropical Caribbean Province (Petuch, 1987), would have been particularly sensitive to lowered water temperature. Another caloosagenic muricid genus, *Laevityphis*, was extremely rare in the Choptank Formation, possibly indicating a sensitivity to cooler temperatures and a marginal survival ability. Likewise, the ecphorine thaidid subgenus *Trisecphora*, which had previously undergone a large species radiation in the Calvert Formation, was present during Serravallian time only as a single species per stratigraphic unit. This drop in *Trisecphora* species richness may also have been in response to lower water temperatures.

Of particular interest is the thaidid genus *Ecphorosycon*, which appeared to have its center of speciation in the warmer southern Pungoian Subprovince (Petuch, 1989). This distinctive Transmarian endemic survived into the very beginning of Choptank deposition (Zone 16) as a single Calvertian species, but became extinct before the deposition of the upper bed of the Drum Cliff Member (Zone 17). This ephemeral existence of the thermophilic genus *Ecphorosycon* also points to a cooling event during earliest Serravallian time. The possibly more cool-tolerant genus *Ecphora* s.s., however, proliferated into several species complexes during Choptank time and this accounts for the lag in muricacean extinction seen in figure 47. Climatic conditions apparently deteriorated so greatly by the end of Serravallian time, however, that even less thermophilic genera such as *Ecphora* s.s., *Chesathais*, and *Trisecphora* declined in species richness. At the end of Choptank deposition, the latter two thaidid genera and all but one complex of *Ecphora* s.s. became extinct, underscoring the ecological impact of the cooling event. In the overlying Little Cove Point Unit (late Serravallian Stage), only one, or possibly two, species of *Ecphora* s.s. are known to exist; a feeble "ghost" of the large Calvert and Choptank ecphorine radiations.

The turrid genera *Calverturris* and *Transmariaturris* and the trophonine genus *Patuxentrophon* also disappeared during late Choptank time, along with *Ecphorosycon*, *Chesathais* and *Trisecphora*. The simultaneous loss of these stenothermal temperate endemics could only have been produced by a refrigeration catastrophe. Interestingly enough, the large Calvertian trophonine radiation, which appears in the subprovince only at the end of the Serravallian refrigeration event, may have been a left-over of a boreal invasion during the coldest time, at the Choptank-Little Cove Point Unit boundary. This strong post-Choptank boreogenic influence, which includes *Boreotrophon* and *Scalaspira*, may have represented physiological adaptations to warmer water conditions during Little Cove Point-St. Mary's time.

SYSTEMATICS

The type material of the following new species is deposited in the invertebrate paleontology collection of the Florida Museum of Natural History, University of Florida, Gainesville, Florida, and bears UF numbers.

Order Caenogastropoda
Superfamily Muricacea
Family Thaididae
Subfamily Ecphorinae Petuch, 1988
Genus *Ecphorosycon* Petuch, 1988

Ecphorosycon lindajoyceae new species
(figures 5, 9)

Material examined: HOLOTYPE—length 55 mm (incomplete), in basal bed (Zone 16) of Choptank Formation, along waterline of Patuxent River at Sandgates, St. Mary's County, Maryland, UF21466; PARATYPE—length 69 mm (reconstructed with plasticine clay), same locality as holotype, collection of author.

Description: Shell inflated, with globose body whorl and distinctly pyriform outline; spire protracted, scalariform; shoulder sloping; subsutural area flattened, producing stepped spire whorls; body whorl ornamented with 3 rounded, thin, low, adherent cords; cord along shoulder of body whorl projecting upward (posteriorward), becoming progressively more bladelike on earlier whorls; entire body whorl, spire whorls, and siphonal canal sculptured with spiral threads; spiral threads give entire shell silky texture; spire whorls ornamented with 2 thin cords, with cord along shoulder being bladelike in form; siphonal canal proportionally short and broad for genus; umbilicus wide, flaring, well developed.

Etymology: Named for my wife, Linda Joyce Petuch, who assisted me with my collecting along the St. Mary's River and Chesapeake Bay.

Discussion: Previously (Petuch, 1989:43) I had stated that the genus *Ecphorosycon* had become extinct at the end of Langhian time, in the upper beds of the Calvert Formation. The discovery of an *Ecphorosycon* species in the lowest bed of the Choptank Formation (Zone 16), however, demonstrates that the genus survived into early Serravallian time. Within Zone 16, the last surviving *Ecphorosycon*, *E. lindajoyceae*, is rare, with only a few fragmentary specimens having ever been collected. The new species has never, to my knowledge, been collected in the upper Choptank beds (Zones 17, 18, and 19), whose faunas have been relatively well-studied. The absence of this large and distinctive ecphorine from Zone 17 indicates that *Ecphorosycon* became extinct in earliest Serravallian time, making it an excellent index fossil for Zone 16.

Ecphorosycon lindajoyceae is most similar to *E. pamlico* (Wilson, 1987) from Zone 10 of the Plum Point Member of the Calvert Formation and from the Bonnerton Member of the Pungo River Formation of North Carolina. The new species differs from *E. pamlico* (figure 6, 10) in being a much wider, much more inflated shell with a wider, stumpier, less elongated siphonal canal. The spire of *E. pamlico* is higher and much more protracted than the spire of *E. lindajoyceae*, which is distinctly lower and depressed. The spiral threads on the spire, body whorl, and siphonal canal of the new species are also much finer than those of the coarsely-sculptured *E. pamlico*. The new species is also quite different from *E. kalyx* (Petuch, 1988) from Zones 12 and 14 of the Plum Point Member of the Calvert Formation (figure 8), and differs in being a much more inflated, globose shell, in having reduced, less developed cords, and in having a sculpture pattern of fine spiral threads.

The preservation of shells within Zone 16 is poor, with almost every specimen being collected in a fragmentary state. The paratype of *E. lindajoyceae* (figure 9) was actually flattened by the pressure of sedimentary compaction and was collected, piecemeal, as a handful of fragments. These were later reassembled over a template of plasticine clay. The holotype is the best, most complete, specimen found to date. Although fragmentary, the holotype exhibits enough salient characteristics to allow for easy separation from the older *E. pamlico* and *E. kalyx*. At the type locality, Sandgates on the Patuxent River in Zone 16 of the Choptank Formation, *Ecphorosycon lindajoyceae* co-occurs with a large ecphorine fauna, including *Ecphora* (*Ecphora*) *meganae sandgatesensis* Petuch, 1989, *E.* (*Ecphora*) *rikeri harasewychi* Petuch, 1989, *E.* (*Ecphora*) *choptankensis vokesi* Petuch, 1989, *Ecphora* (*Trisecphora*) *smithae* Petuch, 1988, and *Chesathais lindae donaldasheri* Petuch, 1989.

Family Muricidae
Subfamily Trophoninae Cossmann, 1903

Genus *Patuxentrophon* new genus

Diagnosis: Shell vase-shaped, with sharply angled, carinated shoulder and high, distinctly scalariform spire; body whorl wide and inflated, tapering rapidly anteriorly into siphonal canal; siphonal canal long, slender, straight, equal in length to body whorl; body whorl ornamented with 10 large, rounded cords; smaller, secondary cords often present between larger, primary cords; shoulder cord largest; spire whorls ornamented with 5 cords; siphonal canal ornamented with 15–20 large, rounded cords; aperture oval.

Type species: *Chrysodomus patuxentensis* Martin, 1904, Choptank Formation, Serravallian Miocene of Maryland (figures 1, 2).

Other species in *Patuxentrophon*: *Patuxentrophon* unnamed species, Zone 10 of the Plum Point Member of the Calvert Formation.

Etymology: A combination of "Patuxent", for the Patuxent River of Maryland, and the muricid genus *Trophon*.

Discussion: Martin (1904:184) referred this small muricid group to the archaic neptuniid genus *Chrysodomus* Swainson, 1852, primarily on the basis of a similarity in ribbed sculpture patterns. *Patuxentrophon*, however, differs from neptuniids in being a much tinier shell with a proportionally much longer and much better developed siphonal canal. The new genus is distinctly trophonine, having the same general size, siphonal canal development, and spiral sculpture pattern as living *Boreotrophon* species such as the Oregonian *B. disparilis* (Dall, 1891) and living *Trophonopsis* species such as the Alaskan *T. kamchatkanus* (Dall, 1902). *Patuxentrophon* also shares many characteristics with the late Serravallian, Tortonian, and Messinian trophonine genera *Lirosoma* Conrad, 1862 (figure 3), and *Scalaspira* Conrad, 1862 (figure 4), having the sculpture of the former and the shape of the latter. It is possible that the Langhian–early Serravallian *Patuxentrophon* represents the stem-stock from which the later Miocene *Lirosoma* and *Scalaspira* evolved.

Superfamily Buccinacea
Family Fasciolariidae
Subfamily Fasciolariinae Gray, 1853
Genus *Buccinofusus* Conrad, 1868

Buccinofusus patuxentensis new species
(figures 13, 14)

Material examined: HOLOTYPE—Length 77 mm, from Zone 17, Drum Cliff Member of Choptank Formation, at Drum Cliff, Jones Wharf, St. Mary's County, Maryland, Patuxent River, UF 21499; PARATYPE—length 54 mm, same locality as holotype, collection of author.

Description: Shell elongately fusiform, with very elevated, protracted spire; subsutural area sloping, shoulder rounded; shoulder and middle section of body whorl ornamented with 10–12 low, axially-arranged riblike knobs; spire whorls with 8–12 riblike knobs bordering suture; entire shell, in turn, sculptured with extremely numerous fine spiral cords and threads; cords finest along subsutural area, becoming coarser on midbody, and coarsest on siphonal canal; siphonal canal well developed, short in proportion to length of spire.

Etymology: Named for the Patuxent River, which borders the type locality.

Discussion: *Buccinofusus patuxentensis* occupies the evolutionary midpoint between the primitive *B. devexus* (Conrad, 1843) of the Calvert Formation (figure 7) and the more advanced *B. chesapeakensis* Petuch, 1988 of the Little Cove Point Unit (figure 12) and *B. parilis*

(Conrad, 1832) of the St. Mary's Formation (figure 11). Morphologically, *B. patuxentensis* resembles the slender and proportionally higher-spired *B. devexus* in shape, but shares the coarser spiral sculpture of *B. chesapeakensis*. Of the known *Buccinofusus* species, *B. patuxentensis* is closest to the Little Cove Point *B. chesapeakensis*, but differs in having finer and more numerous spiral cords on the body whorl and spire, and in having stronger and more numerous knobs on the spire whorls.

Through time, from the Langhian to the Tortonian, the genus *Buccinofusus* underwent parallel shifts in two morphological characters; shell length-width ratio and degree of sculpture coarseness. The oldest species, *B. devexus*, is the most slender and is only faintly sculpted with fine spiral threads. The Choptank *B. patuxentensis* retains the slender shape of *B. devexus* but presages the heavier sculptural pattern of the later forms. The Little Cove Point *B. chesapeakensis* retains the sloping shoulder and fine sculpturing on the subsutural area, as seen in the earlier species, but has the inflated body whorl and coarse, widely-spaced cords around the midbody and siphonal canal that typify the advanced forms. This characteristic Transmarian lineage culminates in the St. Mary's *B. parilis*, which has the most inflated body whorl, lowest spire, and uniformly coarse sculpture over the entire shell.

Family Melongenidae
Subfamily Busyconinae Finlay and Marwick, 1937
Genus *Busycotypus* Wenz, 1943

Busycotypus choptankensis new species
(figures 15, 16)

Material examined: HOLOTYPE—Length 192 mm (incomplete), in Zone 19 of Choptank Formation, at Drum Cliff, Jones Wharf, St. Mary's County, Maryland, along Patuxent River, UF 21498.

Description: Shell vase-shaped, very inflated, with ovately-cylindrical body whorl; shoulder very broad, wider than length of body whorl; shoulder sharply angled, carinated, ornamented with 16–20 low, undulating knobs per whorl; spire low, stepped; sutural area with wide, deep, flat-bottomed sulcus, producing widely canaliculate spire whorls; periphery of sutural sulcus bordered with large, rounded, undulating cord; body whorl ornamented with longitudinal growth lines, devoid of spiral sculpture; spire whorls ornamented with 6–8 faint spiral threads; siphonal canal broad, ornamented with 10–12 low, nearly obsolete spiral cords; aperture extremely wide, open, flaring, with smooth, unornamented interior; parietal area glazed.

Etymology: Named for the Choptank Formation, for which this new species is an index fossil.

Discussion: As in the case of *Buccinofusus patuxentensis*, *Busycotypus choptankensis* fills in a gap in the evolutionary record of the Maryland Miocene *Busycotypus* lineage. The new species is closest to *B. chesapeakensis* Petuch, 1988 (figure 18) of the younger Little Cove Point Unit, especially in being a smooth, unornamented shell with low, undulating shoulder coronations. The Choptank ancestor differs from its Little Cove Point descendant, however, in being a much more inflated shell, by being proportionally thinner and more fragile, and in having less developed, lower coronations on the shoulder and spire whorls. Of the two related St. Mary's species, *B. coronatum* (Conrad, 1840) (figure 19) and *B. rugosum* (Conrad, 1843) (figure 20), *B. choptankensis* is most similar to the latter, but differs in having lower, less developed coronations and in lacking the heavy spiral corded sculpture that characterizes *B. rugosum*. From the small, ancestral *B. calvertensis* Petuch, 1988 (figure 17), *B. choptankensis* differs in being a smooth, unsculptured shell with a much better developed, wider canaliculate suture.

Through time, the Transmarian coronated *Busycotypus* species exhibited three morphological trends; becoming proportionally less inflated, developing wider and deeper sutural sulci, and developing larger and more prominent shoulder and spire coronations. The primitive *B. calvertensis* is a very wide, inflated shell with small coronations and a tiny, almost nonexistent sutural canal. *Busycotypus choptankensis* retains the inflated shell shape of the ancestral *B. calvertensis*, but has large, well defined shoulder coronations, and has a very well developed, wide sutural canal. The next youngest in the sequence, *B. chesapeakensis*, has a wide sutural canal like *B. choptankensis* but has even larger, better defined shoulder coronations. Unlike the primitive species *B. calvertensis* and *B. choptankensis*, however, *B. chesapeakensis* has the slender, more attenuated body form of the advanced species. The two St. Mary's species, *B. coronatum* and *B. rugosum*, both appear to have evolved from the Little Cove Point *B. chesapeakensis*, and share the same attenuated body form. *Busycotypus coronatum* retains the smooth, unsculptured body whorl of *B. choptankensis* and *B. chesapeakensis*, but has the largest, most pronounced shoulder coronations of the whole complex. The contemporaneous and sympatric *B. rugosum*, on the other hand, has a heavily sculptured, corded body whorl and large, rounded, knoblike shoulder coronations. The noncoronated *Busycotypus* species from the St. Mary's Formation, *B. asheri* Petuch, 1988, and *B. alveatum* (Conrad, 1863), appear to belong to a separate species complex and are not closely related to the coronated forms.

Genus *Turrifulgur* Petuch, 1988

Turrifulgur marylandicus new species
(figures 21, 26)

Material examined: HOLOTYPE—Length (incomplete) 60 mm, in Zone 10, Plum Point Member of Calvert Formation, at Plum Point, Calvert County, Maryland, UF21467.

Description: Shell elongated, cylindrical in form, with high, protracted spire; shoulder sharply angled, low on body whorl, below wide, very sloping subsutural area; shoulder ornamented with 12 evenly-spaced, small, sharply-pointed knobs; spire whorl ornamented with 12 knobs per whorl; siphonal canal (missing on holotype) elongated and slender (extrapolated from holotype); body whorl sculptured with numerous fine spiral threads, which become nearly obsolete around mid-body; sloping subsutural area sculptured with 12 large spiral threads; siphonal canal sculptured with numerous large, evenly-spaced spiral cords; aperture proportionally narrow.

Etymology: Named for the State of Maryland.

Discussion: The elongate, high-spired *Turrifulgur marylandicus* stands out as unique among the known Transmarian *Turrifulgur* species. The extremely attenuated body form is reminiscent of *T. atraktoides* (Gardner, 1944) from the late Burdigalian Oak Grove Formation of northern Florida, and the Langhian *T. marylandicus* appears to belong to the same species complex. The new Maryland busyconine, however, differs from the older Oak Grove species in being an even more-elongated shell with a more drawn-out body whorl, in having a more protracted, scalariform spire, and in having a much more sloping shoulder and subsutural area. *Turrifulgur marylandicus* also has fewer knobs per whorl on the spire than does its more finely-ornamented Caloosahatchian relative.

This new protracted Transmarian *Turrifulgur* is sympatric with *T. prunicola* n.sp. (described in the next section) at Plum Point. *Turrifulgur marylandicus* differs from this congener in being a larger, more elongated shell with a much higher spire. The presence of two sympatric species of *Turrifulgur* in the Calvert Formation reflects a similar pattern seen in the early Langhian Shoal River Formation of northern Florida, where two species, *T. aldrichi* (Gardner, 1944) and *T. dasum* (Gardner, 1944), also co-occur.

Turrifulgur prunicola new species
(figure 27)

Material examined: HOLOTYPE—Length 35 mm, in Zone 10, Plum Point Member of Calvert Formation, at Plum Point Calvert County, Maryland, UF21468.

Description: Shell vase-shaped, fusiform, with sharply-angled shoulder; spire slightly stepped, comparatively low and flattened for genus; subsutural area only slightly flattened, subplanar; shoulder of body whorl ornamented with 14 small, low, evenly-spaced knobs; spire whorls ornamented with 14 small knobs per whorl; body whorl pinching-in abruptly to base of siphonal canal; siphonal canal slender, narrow; body whorl, siphonal canal, spire whorls and subsutural area sculptured with numerous very fine spiral threads, giving shell silky appearance; aperture oval.

Etymology: Named for Plum Point, Calvert County, Maryland, the type locality.

Discussion: Although sympatric with *Turrifulgur marylandicus* in Zone 10, *T. prunicola* belongs to a separate species lineage. The narrow *T. marylandicus* appears to be a member of the *T. atraktoides* (Gardner, 1944)–*T. dasum* (Gardner, 1944) species complex, while *T. prunicola* probably belongs to the *T. aldrichi* (Gardner, 1944) species complex. Both Calvert species are caloosagenic offshoots of these contemporaneous complexes. Although the *T. prunicola* lineage survived until the Tortonian Stage (as *T. fusiforme* (Conrad, 1840) and *T. turriculus* Petuch, 1988), the *T. marylandicus* lineage died off during the Langhian Stage, and is not found in the upper beds of the Calvert Formation nor in the Choptank Formation.

Turrifulgur prunicola is closest in general shell morphology to *T. turriculus* Petuch, 1988 (figure 22) from the Windmill Point Member of the St. Mary's Formation. The new species differs from its St. Mary's descendant in having a much lower spire, in having fewer and smaller knobs on the shoulder and spire whorls, and in having finer and more delicate spiral threaded sculpture. *Turrifulgur prunicola* is also similar to *T. fusiforme* (Conrad, 1840) (figure 23) from Zone 24 of the St. Mary's Formation, but differs in being a smaller shell with a more sharply angled shoulder and proportionally lower spire.

Superfamily Conacea
Family Turridae
Subfamily Mangeliinae Fischer, 1887

Genus *Calverturris* new genus

Diagnosis: Shells elongately fusiform, with high, protracted spires and extended, slender siphonal canals; shoulders subcarinated, ornamented with nodulose cord below greatly sloping subsutural area; nodulose cord borders suture on spire whorls; body whorls ornamented with 6–8 large, evenly-spaced spiral cords; fine spiral threads present between cords of some species; siphonal canals ornamented with numerous spiral threads; anal notch shallow, with greatest indentation corresponding to nodulose shoulder cord; protoconchs proportionally small, rounded, domelike, composed of one and one-half whorls; apertures narrow.

Type species: *Pleurotoma bellacrenata* Conrad, 1841, Calvert Formation, Langhian Miocene of Maryland (figure 24).

Other species in *Calverturris*: *Calverturris schmidti* n.sp., Choptank Formation, Serravallian Miocene of Maryland, described here.

Etymology: A composite of "*Calvert*", for the Calvert Cliffs of Maryland, and "*turris*", "tower".

Discussion: This small group of Transmarian turrids is one of the most morphologically-distinctive of the known Chesapeake Miocene conacean gastropods. The prominent nodulose carina around the shoulders of *Calverturris* species, along with the large, evenly-spaced cords on the body whorls, sets this genus aside from all other Transmarian mangeliine taxa. In general body form and sculpture pattern, *Calverturris* is closest to *Sediliopsis* Petuch, 1988, but differs in having larger and more inflated shells and in having the characteristic nodulose shoulder carina.

As *Calverturris* is only known from the Calvert and Choptank Formations, the genus appears to have become extinct during mid-Serravallian time.

Calverturris schmidti new species
(figure 25)

Material examined: HOLOTYPE—Length (fragmentary) 23 mm, in Zone 17, Drum Cliff Member of Choptank Formation, at Drum Cliff, Jones Wharf, St. Mary's County, Maryland, along Patuxent River, UF 21500.

Description: Shell shape and form as outlined in genus description; shoulder carina with evenly-spaced, large nodules; single large cord present on sloping subsutural area, just posterior to nodulose carina; body whorl ornamented with 67 large spiral cords (extrapolated from fragmentary holotype); fine threads present between large spiral cords.

Etymology: Named for Mr. Robert Schmidt of Calvert County, Maryland, who collected the holotype at Jones Wharf.

Discussion: The Choptank *Calverturris schmidti* is similar to the Calvert *C. bellacrenata*, the type of the genus, but differs in having larger and less numerous shoulder knobs and in having fine spiral threads between the large cords on the body whorl. The steeply-sloping subsutural area of *C. bellacrenata* is also smooth and devoid of spiral sculpture, while that of *C. schmidti* is sculptured with a single large cord and several faint spiral threads.

While *Calverturris bellacrenata* is a common species in Zone 10 at Plum Point, *C. schmidti* is a much rarer shell, with only a few fragmentary specimens having ever been collected along the Patuxent River. Apparently, the genus was already dying out by Choptank time.

Genus *Transmariaturris* new genus

Diagnosis: Shells elongately terebriform, with rounded shoulders and greatly protracted, elevated spires; siphonal canals proportionally short, stubby; subsutural area of all species slightly depressed, producing faintly indented sutural band; last whorls with smooth, unornamented shoulders; spire whorls of some species ornamented with rows of low, riblike knobs along suture margin; spire whorls of some species smooth, unornamented; body and spire whorls sculptured with only very faint, delicate spiral thread, giving shells silky texture; siphonal canals ornamented with 10–12 thin spiral cords; apertures proportionally small, oval; protoconchs unknown; anal notch shallow, with indentation corresponding to depressed subsutural band.

Type species: *Pleurotoma* (*Hemipleurotoma*) *calvertensis* Martin, 1904, Calvert Formation, Langhian Miocene of Maryland (figure 28).

Other species in *Transmariaturris*: "*Pleurotoma* (*Hemipleurotoma*)" *choptankensis* Martin, 1904, Choptank Formation, Serravallian Miocene of Maryland.

Etymology: A combination of "*Transmaria*", for the Transmarian Province, and "*turris*".

Discussion: Based on general shell shape, I had originally placed this compact group of elongated, terebriform turrids in the clavine genus *Chesaclava* Petuch, 1988 (Petuch, 1988:35). Further study, however has shown that these two groups of turrids differ in a number of ways and actually belong in separate subfamilies. *Transmariaturris*, although convergent on the protracted spire form of *Chesaclava*, differs from that genus in having larger, more inflated shells with proportionally larger body whorls, by having longer and better developed siphonal canals, in having more indented anal notches that produce solenozones, and in having spriral sculpturing. The small, smooth *Chesaclava* species closely resemble miniature *Cymatosyrinx* Dall, 1889 species and develop a varix-like adult lip and stromboid notch. These two characters are not seen in *Transmariaturris*.

Although the diagnostic protoconchs were missing on all *Transmariaturris* specimens examined, I have placed this new genus in the subfamily Mangeliinae, primarily on its similarity to the genus *Calverturris*. Both genera are of the same general shape and size, and share the same type of anal notch and outer lip structure. *Transmariaturris* differs from *Calverturris*, however, in lacking the large, prominent spiral cords on the body whorl and also in lacking the distinctive nodulose shoulder carina. The subsutural area of *Calverturris* is planar, while that of *Transmariaturris* is slightly depressed.

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Appendix 1. Muricacean, Buccinacean, and Conacean Higher Taxa from the Calvertian Subprovince of the Transmarian Province. T = Transmarian endemic genus, C = Caloosagenic genus, B = Boreogenic genus.

	T	C	B
Superfamily Muricacea			
Family Muricidae			
Subfamily Muricinae da Costa, 1776			
Phyllonotus Swainson, 1833		*	
Subfamily Muricopsinae Radwin and D'Attilio, 1971			
Murexiella Clench and Farfante, 1945		*	
Subfamily Ocenebrinae Gray, 1847			
Mariasalpinx Petuch, 1988	*		
Sephanosalpinx Petuch, 1988	*		
Urosalpinx Stimpson, 1865		*	
Subfamily Trophoninae Cossmann, 1903			
Boreotrophon Fischer, 1884			*
Chesatrophon Petuch, 1988	*		
Lirosoma Conrad, 1862	*		
Patuxentrophon Petuch, 1992	*		
Scalaspira Conrad, 1862	*		
Subfamily Typhinae Cossmann, 1903			
Laevityphis Cossmann, 1903		*	
Family Thaididae			
Subfamily Ecphorinae Petuch, 1988			
Chesathais Petuch, 1988		*	
Ecphora Conrad, 1843		*	
Ecphorosycon Petuch, 1988	*		
Trisecphora Petuch, 1988	*		
Superfamily Buccinacea			
Family Fasciolariidae			

Appendix 1. Continued.

	T	C	B
Subfamily Fasciolariinae Gray, 1853			
Buccinofusus Conrad, 1868	*		
Mariafusus Petuch, 1988	*		
Subfamily Fusininae Swainson, 1840			
Pseudaptyxis Petuch, 1988	*		
Family Melongenidae			
Subfamily Busyconinae Finlay and Marwick 1937			
Busycotypus Wenz, 1943		*	
Sycopsis Conrad, 1867	*		
Turrifulgur Petuch, 1988		*	
Family Buccinidae			
Celatoconus Conrad, 1862		*	
Ptychosalpinx Gill, 1867		*	
Solenosteira Dall, 1890		*	
Family Nassariidae			
Bulliopsis Conrad, 1862	*		
Ilyanassa Stimpson, 1865		*	
Family Columbellidae			
Mitrella Risso, 1826		*	
Superfamily Conacea			
Family Conidae			
Leptoconus Swainson, 1840		*	
Family Terebridae			
Laevihastula Petuch, 1988	*		
Strioterebrum Sacco, 1891		*	
Family Turridae			
Subfamily Clavinae Powell, 1942			
Chesaclava Petuch, 1988	*		
Cymatosyrinx Dall, 1889		*	
Sediliopsis Petuch, 1988	*		
Subfamily Mangeliinae Fischer, 1887			
Calverturris Petuch, 1992 T	*		
Glyphostoma Gabb, 1872		*	
Oenopota Mörch, 1852			*
Mariadrillia Petuch, 1988	*		
Transmariaturris Petuch, 1992	*		
Subfamily Turriculinae Powell, 1942			
Chesasyrinx Petuch, 1988	*		
Mariaturricula Petuch, 1988	*		
Nodisurculina Petuch, 1988	*		
Subfamily Turrinae Swainson, 1840			
Hemipleurotoma Cossman, 1903	*		

Appendix 2. Muricacean, Buccinacean, and Conacean Species from the Calvertian Subprovince of the Transmarian Province. C = Calvert Formation, Ch = Choptank Formation, L = Little Cove Point Unit, S = St. Mary's Formation.

	C	CH	L	S
Muricidae				
Muricinae				
[1]*Phyllonotus millvillensis* (Richards and Harbison, 1942)	*			
Muricopsinae				
Murexiella shilohensis (Heilprin, 1887)	*			
Ocenebrinae				
Mariasalpinx emilyae Petuch, 1988				*
Mariasalpinx new species			*	
Stephanosalpinx candelabra Petuch, 1988		*		
Urosalpinx rusticus (Conrad, 1830)			*	*
Trophoninae				
Boreotrophon harasewychi Petuch, 1988				*
Boreotrophon laevis (Martin, 1904)			*	*
Boreotrophon lindae Petuch, 1988				*
Chesatrophon chesapeakeanus (Martin, 1904)			*	*
Chesatrophon new species a.	*			
Chesatrophon new species b.		*		
Lirosoma mariana Petuch, 1988				*
Patuxentrophon patuxentensis (Martin, 1904)		*		
Patuxentrophon new species	*			
Scalaspira harasewychi Petuch, 1988				*
Scalaspira vokesae Petuch, 1988			*	
Typinae				
Laevityphis acuticosta (Conrad, 1830)			*	*
Laevityphis new species a.	*			
Laevityphis new species b.		*		
Thaididae				
Ecphorinae				
Chesathais ecclesiasticus (Dall, 1915)	*			
Chesathais lindae lindae Petuch, 1988		*		
Chesathais lindae donaldasheri Petuch, 1989		*		
Chesathais lindae drumcliffensis Petuch, 1989		*		
Chesathais whitfieldi Petuch, 1989	*			
Ecphora asheri Petuch, 1988			*	
Ecphora calvertensis Petuch, 1988	*			
Ecphora calvertensis subspecies	*			
Ecphora chesapeakensis Petuch, 1992	*			
Ecphora choptankensis choptankensis Petuch, 1988		*		
Ecphora choptankensis delicata Petuch, 1989		*		
Ecphora choptankensis vokesi Petuch, 1989		*		
Ecphora gardnerae gardnerae Wilson, 1987				*
Ecphora gardnerae angusticostata Petuch, 1989				*
Ecphora germonae Ward and Gilinsky, 1988			*	
Ecphora meganae meganae Ward and Gilinsky, 1988		*		
Ecphora meganae sandgatesensis Petuch, 1989		*		
Ecphora rikeri rikeri Petuch, 1988		*		
Ecphora rikeri harasewychi Petuch, 1988		*		
Ecphora turneri Petuch, 1992	*			
Ecphora wardi Petuch, 1989	*			
Ecphora wardi subspecies	*			
Ecphora williamsi Ward and Gilinsky, 1988		*		
Ecphora (*Trisecphora*) *eccentrica* Petuch, 1988	*			
Ecphora (*Trisecphora*) *martini* Petuch, 1988	*			
Ecphora (*Trisecphora*) *patuxentia patuxentia* Petuch, 1988		*		
Ecphora (*Trisecphora*) *patuxentia shattucki* Petuch, 1989		*		
Ecphora (*Trisecphora*) *prunicola* Petuch, 1988	*			
Ecphora (*Trisecphora*) *scientistensis* Petuch, 1992	*			
Ecphora (*Trisecphora*) *schmidti* Petuch, 1989	*			
Ecphora (*Trisecphora*) *smithae* Petuch, 1988		*		
Ecphora (*Trisecphora*) *smithae* subspecies	*			

Appendix 2. Continued.

	C	CH	L	S
Ecphora (Trisecphora) tricostata Martin, 1904	*			
Ecphorosycon kalyx (Petuch, 1988)	*			
Ecphorosycon lindajoyceae Petuch, 1992		*		
Ecphorosycon pamlico (Wilson, 1987)	*			
Ecphorosycon new species	*			
Fasciolariidae				
Buccinofusus (?) *calvertanus* (Martin, 1904)	*			
Buccinofusus chesapeakensis Petuch, 1988			*	
Buccinofusus devexus (Conrad, 1843)	*			
Buccinofusus migrans (Conrad, 1843)	*			
Buccinofusus parilis (Conrad, 1832)				*
Buccinofusus patuxentensis Petuch, 1992		*		
Mariafusus marylandicus (Martin, 1904)				*
Pseudaptyxis sanctaemariae Petuch, 1988				*
Melongenidae				
Busyconinae				
Busycotypus alveatum (Conrad, 1863)				*
Busycotypus asheri Petuch, 1988				*
Busycotypus calvertensis Petuch, 1988	*			
Busycotypus chesapeakensis Petuch, 1988			*	
Busycotypus choptankensis Petuch, 1992		*		
Busycotypus coronatum (Conrad, 1840)				*
Busycotypus rugosum (Conrad, 1843)				*
Sycopsis lindae Petuch, 1988		*		
Sycopsis tuberculatum (Conrad, 1840)				*
Syncopsis new species a.	*			
Sycopsis new species b.			*	
Turrifulgur fusiforme (Conrad, 1840)				*
Turrifulgur marylandicus Petuch, 1992	*			
Turrifulgur prunicola Petuch, 1992	*			
Turrifulgur turriculus Petuch, 1988				*
Turrifulgur new species a.		*		
Turrifulgur new species b.			*	
Buccinidae				
Celatoconus asheri Petuch, 1988			*	*
Celatoconus protractus (Conrad, 1843)	*			
Ptychosalpinx lienosa (Conrad, 1843)	*			
Ptychosalpinx lindae Petuch, 1988				*
Ptychosalpinx pustulosus Petuch, 1988				*
Ptychosalpinx new species		*		
Ptychosalpinx new species		*		
Solenosteira cumberlandiana (Gabb, 1860)			*	*
Solenosteira new species	*	*	*	
Nassariidae				
Bulliopsis integra (Conrad, 1842)			*	*
Bulliopsis marylandica (Conrad, 1862)			*	
Bulliopsis ovata (Conrad, 1862)				*
Bulliopsis quadrata (Conrad, 1830)				*
Bulliopsis subcylindrica (Conrad, 1862)				*
Ilyanassa calvertensis (Martin, 1904)	*			
Ilyanassa elongata (Whitfield, 1894)		*		
Ilyanassa greensboroensis (Martin, 1904)		*		
Ilyanassa gubernatoria (Martin, 1904)	*			
Ilyanassa marylandica (Martin, 1904)			*	*
Ilyanassa peralta (Conrad, 1868)			*	*
Ilyanassa peraltoides (Martin, 1904)		*		
Ilyanassa trivittatoides (Whitfield, 1894)		*		
Ilyanassa new species				*
Columbellidae				
Mitrella calvertensis (Martin, 1904)	*			
Mitrella communis (Conrad, 1862)				*

Appendix 2. Continued.

	C	CH	L	S
Mitrella new species a.	*			
Mitrella new species b.		*		
Mitrella new species c.			*	
Conidae				
Conus (*Leptoconus*) *asheri* Petuch, 1988				*
Conus (*Leptoconus*) *diluvianus* Green, 1830				*
Conus (*Leptoconus*) *sanctaemariae* Petuch, 1988				*
Terebridae				
Laevihastula inornata (Whitfield, 1894)			*	*
Laevihastula marylandica Petuch, 1988				*
Laevihastula patuxentia (Martin, 1904)		*		
Laevihastula simplex (Conrad, 1830)			*	*
Laevihastula sublirata (Conrad, 1863)			*	*
Strioterebrum calvertensis (Martin, 1904)	*			
Strioterebrum curvilineata (Whitfield, 1894)	*			
Strioterebrum curvilirata (Conrad, 1843)				*
Strioterebrum dalli (Martin, 1904)		*		
Strioterebrum sincera (Dall, 1895)			*	*
Strioterebrum whitfieldi (Martin, 1904)	*			
Turridae				
Clavinae				
Chesaclava dissimilis (Conrad, 1830)				*
Chesaclava pseudeburnea (Whitfield, 1894)	*			
Chesaclava quarlesi Petuch, 1988				*
Chesaclava whitfieldi (Martin, 1904)	*			
Chesaclava new species	*	*		
Cymatosyrinx limatula (Conrad, 1830)			*	*
Cymatosyrinx mariana Petuch, 1988				*
Cymatosyrinx pyramidalis (Martin, 1904)				*
Cymatosyrinx new species a.	*			
Cymatosyrinx new species b.		*		
Sediliopsis angulata (Martin, 1904)				*
Sediliopsis calvertensis (Martin, 1904)	*			
Sediliopsis distans (Conrad, 1862)				*
Sediliopsis gracilis (Conrad, 1830)				*
Sediliopsis incilifera (Conrad, 1830)			*	
Sediliopsis patuxentia (Martin, 1904)		*		
Mangeliinae				
Calverturris bellacrenata (Conrad, 1841)	*			
Calverturris schmidti Petuch, 1992		*		
Glyphostoma obtusa (Martin, 1904)	*			
Oenopota cornelliana (Martin, 1904)	*			
Oenopota marylandica (Petuch, 1988)				*
Oenopota parva (Conrad, 1830)			*	*
Mariadrillia parvoidea (Martin, 1904)				*
Transmariaturris calvertensis (Martin, 1904)	*			
Transmariaturris choptankensis (Martin, 1904)		*		
Turriculinae				
Chesasyrinx mariana (Martin, 1904)				*
Chesasyrinx rotifera (Conrad, 1830)				*
Chesasyrinx new species	*	*		
Mariaturricula marylandica (Conrad, 1834)				*
Mariaturricula biscatenaria (Conrad, 1841)	*			
Mariaturricula rugata (Conrad, 1862)		*		
Mariaturricula new species a.	*			
Mariaturricula new species b.	*			
Mariaturricula new species c.		*		
Mariaturricula new species d.			*	
Nodisurculina engonata (Conrad, 1862)				*
Turrinae				
Hemipleurotoma communis (Conrad, 1830)			*	*

Appendix 2. Continued.

	C	CH	L	S
Hemipleurotoma protocommunis (Martin, 1904)	*			
Hemipleurotoma new species		*		

[1] Known from the Calvert-equivalent Kirkwood Formation of New Jersey; possibly occurring in the Calvert Formation.