Revision of the ostracode genus *Fossocytheridea* Swain and Brown 1964: Mesozoic ancestral root for the modern eurytopic *Cyprideis* Jones

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ABSTRACT: The ostracode genus *Fossocytheridea* Swain and Brown 1964 is emended herein. A summary of the diagnostic characters include: (1) a median sulcus, (2) a tripartite antimerodont hinge with distinct heart-shaped terminal elements, (3) distinct sexual dimorphism; (4) a narrow inner margin that has 20-28 straight radial pore canals, and (5) variability in the external carapace (pore shape, pore density, and patterns of reticulation) that bears close resemblance to *Cyprideis*. Two new species are described from southwest Utah (U.S.A): *Fossocytheridea mosbyense* sp. nov. and *Fossocytheridea kirklandi* sp. nov. and 21 taxa previously assigned to *Fabanella*, *Sarlatina, Ovocytheridea*, *Dolocytheridea*, *Antibythocypris,* and *Cytheridea* are assigned to the emended genus. *Fossocytheridea* resembles *Cyprideis* with respect to both shell morphology and ecology since it occurs in association with euryhaline biota in coal-bearing strata. Expansion of marginal marine environments during the highest sea level of the Mesozoic saw *Fossocytheridea* successfully migrate and dominate restricted coastal environments. Since this expansion, the prominent characters of *Fossocytheridea* have been preserved in descendent genera belonging to the tribe Cyprideidini Kollmann 1960 that are preserved to this day in *Cyprideis*.

INTRODUCTION

Cyprideis Jones 1857 is arguably one of the most widely used ostracodes for paleoecologic applications within modern restricted, marginal marine settings. Yet, *Cyprideis* is only known to extend back to the latest Oligocene-earliest Miocene (*Cyprideis traisensis* Malz and Triebel 1970) and van den Bold's (1976) detailed account of taxa from Neogene marginal environments in the Caribbean region confirms this. What is apparently lacking are ancient brackish species assigned to *Cyprideis* in pre-Neogene times. Instead, most early Cenozoic Cytherideidae have been assigned to the *Cytheridea* lineage *sensu* Stephenson (1936), Howe and Chambers (1935), and Howe (1971) (e.g., *Clithrocytheridea* Stephenson 1936, *Haplocytheridea* Stephenson 1936, *Ouachitaia* Howe 1971, *Cocoaia* Howe 1971). For example, Howe (1971) described and discussed Paleogene Cytherideidae species from the American Gulf Coast that exhibit phenotypic characters common to *Cyprideis* such as noding, punctation, and dimorphism; these Cytherideidae taxa may be related to the Cyprideidini tribal lineage.

In this paper, we provide a revision of the brackish water genus *Fossocytheridea* Swain and Brown 1964 that is widely distributed in Aptian to Maastrichtian marginal marine facies located in North and South America, North Africa, southern Europe, and China. We provide descriptions of 2 new species from Utah, and propose that several species previously assigned to *Fabanella* Martin 1961, *Sarlatina* Babinot and Colin 1976, *Ovocytheridea* Grékoff 1968, *Asciocythere* Swain 1952, *Dolocytheridea* Triebel 1938, *Antibythocypris* Jennings 1936, *Clithrocytheridea* Stephenson 1936, and *Cytheridea* Bosquet 1852 be included in *Fossocytheridea*. Further, we argue that the phenotypic features observed in all acknowledged species of *Fossocytheridea* provide an affirmative test for the hypothesis first proposed by Babinot and Colin (1976), that Mesozoic representatives of sulcate Cytherideinae belong to the Tribe Cyprideidini Kollmann 1960 and, therefore, represent the ancestors of the eurytopic genus *Cyprideis*. Given the potential to make uniformitarian comparisons between ancestor and descendant, the recognition and paleoecological application of *Fossocytheridea* will help researchers to evaluate high frequency environmental changes in Mesozoic marginal marine deposits along the perimeter of the Tethys Ocean.

GEOLOGIC INTERVAL AND LOCALITIES

Ostracoda are well known for the Cenomanian-Turonian boundary interval (~93-94 Ma) (Jarvis et al. 1988; Babinot and Airaud 1990; Johnson 1996, 1998). During this time, species turnover rates were high (80-90%) and few new originations occurred during the Turonian (Whatley 1988; Babinot and Airaud 1990; Babinot and Colin 1992). The Cenomanian-Turonian boundary interval was the most active of the Mesozoic where 19 of 71 genera went extinct (Whatley 1988, 1990). Generic endemism is well-known among marine ostracode taxa at this

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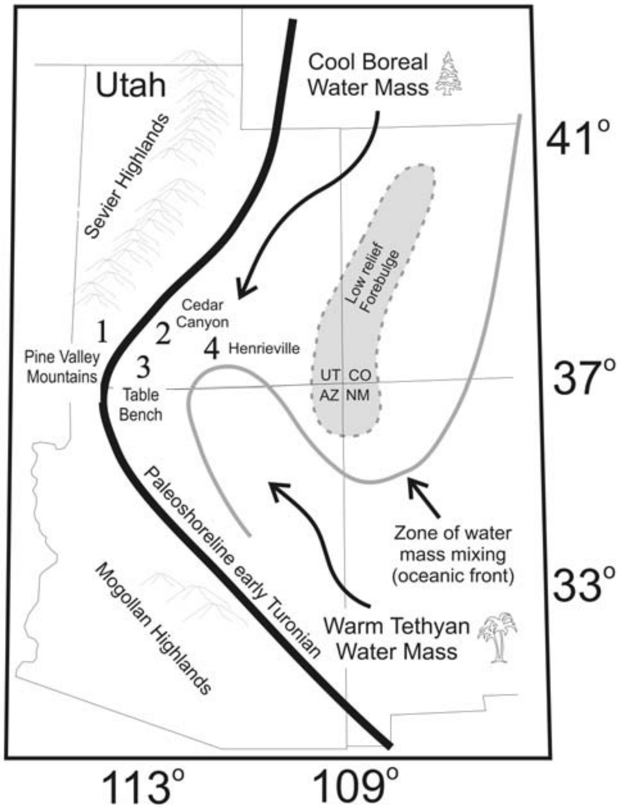


TEXT-FIGURE 1
Paleogeographic map of the Western Interior Seaway for the Cenomanian-Turonian boundary interval. Note the approximate position of the paleoshoreline during peak flooding of the Greenhorn Cycle. Localities from west to east include: (1) Pine Valley Mountains comprising an oligohaline fauna; (2) Table Bench comprising an oligo-mesohaline fauna; (3) Cedar Canyon comprising an oligo-mesohaline fauna; and (4) Henrieville comprising a meso-normal marine fauna (Tibert and Leckie, in press). Leckie et al (1998) interpreted the southwestern region of the Colorado plateau as an area ocean water mass mixing westward within the foredeep of the basin.

time and 6 faunal provinces compartmentalize the Tethyan realm (Babinot and Colin 1992).

Marine ostracodes from the Western Interior Basin (WIB) and the Atlantic and Gulf Coastal Plains of North America are described in publications by Alexander (1929; 1933), Brouwers and Hazel (1978), and Puckett (1994). Hazel (1969) acknowledged *Cythereis eaglefordensis* Alexander 1929 as a latest Cenomanian indicator for the WIB. Swain and Brown (1972) and Swain (1982) documented nonmarine and brackish ostracodes (including *Fossocytheridea*) from North Carolina and Florida. With the exception of Lankford (in Peterson et al. 1953) and Peck (1951), there are few references to Cenomanian-Turonian ostracodes from coal measures in Utah. The recovery of previously undescribed ostracodes and foraminifera from marginal marine coal-bearing strata in southwest Utah (Tibert et al. 2003) prompted this revision of the genus *Fossocytheridea.*

The new species of *Fossocytheridea* described herein were recovered from the upper Cenomanian-middle Turonian Cretaceous stages that comprise the transgressive Dakota and regressive Straight Cliffs formations (text-figs. 1, 2) from southwest Utah. The regional stratigraphic relationships can be found in Elder et al. (1994), Eaton et al. (2001), Tibert et al. (2003), and Tibert and Leckie (in press). Ostracoda were recovered from the molluscan biozones of Kauffman et al. (1993) that include the *Metoicoceras mosbyense*, *Sciponoceras gracile*, *Neocardioceras juddii*, *Watinoceras coloradoense*, and *Prionocyclus hyatti* zones (text-fig. 2). Most ostracode-bearing beds occur within coal zones associated with gastropods *Admetopsis* spp. and *Craginia* spp., bivalves *Crassostrea* and *Carycorbula*, and charophytes.

In the broadest context, these strata record coastal deposition of the Greenhorn transgressive-regressive cycle that mark the highest sea level of the Mesozoic (Kauffman 1977; Hancock and Kauffman 1979; Haq et al. 1988) where the westernmost reaches of the WIB recorded the effects of marine influence preserved in a brackish water fauna (Eaton et al. 1997; Eaton et al. 1999; Tibert et al. 2003; Tibert and Leckie, in press). The Greenhorn marine cycle has received much detailed study. For example, Leckie (1985) documented significant turnover of planktonic foraminifera through the Cenomanian-Turonian boundary interval, a pattern replicated by the molluscan fauna (Elder 1987, 1991). Coincident with the stepped extinction of the biota is a positive d^{13}C excursion (Pratt et al. 1993) that has been linked to global oceanic anoxia during the latest Cenomanian (Arthur et al. 1987; Schlanger et al. 1987; Jarvis et al. 1988; Elder 1991; Johnson 1996). Overall, the WIB recorded global oceanographic changes in addition to tectonic, eustatic, and local climatic signals (for review see Leckie et al. 1998).

CLASSIFICATION OF THE CYPRIDEIDINI

Standard classification systems for the ostracode subfamily Cytherideinae (Benson et al. 1961; Morkhoven 1962) do not acknowledge the necessary tribes to accommodate phylogenetic histories for the Mesozoic brackish Cytherideinae. Therefore, for the remainder of this discussion, we follow the systematic classification scheme of Kollmann (1960), subsequently followed by Puri (1974) and Hartmann and Puri (1974), where the ostracode subfamily Cytherideinae includes the following 3 tribes: Haplocytherideini Kollman 1960 (e.g., *Haplocytheridea*); Cytherideini Kollman 1960 (e.g., *Cytheridea*); and Cyprideidini Kollman 1960 (e.g., *Cyprideis*). All taxa illustrated herein belong to the tribe Cyprideidini that are related to either the latest Jurassic ostracode *Fabanella* (Babinot and Colin 1976; Colin 1983; Colin and Carbonel 1990; Colin et al. 1990) or the lower Jurassic *Phraterfabanella* Whatley and Boomer (in Boomer et al. 2001). We contend that the characters derived from *Fabanella* are still expressed in numerous species of *Cyprideis* known for their environmental cued polymorphism or plasticity within brackish ecosystems worldwide. Text-figure 3 illustrates the ostracode characters referred to in this manuscript.

Modern Cyprideis

According to the type description of *Cyprideis* Jones 1857 and the emended diagnosis of Whatley et al. (1998), the diagnostic features for the modern genus include a Cytherideidae central muscle field (*sensu* Stephenson 1936), a generally smooth to punctate carapace where reticulation and noding are common, a transverse sulcus (oblique or straight), an entomodont hinge (quadrapartite) where all elements are crenulate, and distinct dimorphism where brood swelling is evident in female carapaces. Puri's (1974) normal pore classification scheme assigns

Cyprideis to the tribe Cyprideidini because of its Type C sieve pore. We consider the median sulcus, sexual dimorphism, hingement, and variable patterns of reticulation of the carapace diagnostic characters that set *Cyprideis* apart from most other Cytherideinae. An important aspect of this group of ostracodes is the observed variability in carapace noding, pore morphology (size, shape, and distribution), and the degree of ornamentation, aspects of phenotypic expression that are apparently linked to environmental parameters during the ostracodes life cycle (e.g. salinity, temperature, ionic composition of the water). Landmark papers on this topic include Van Harten (1974), Sandberg and Plusquellec (1974), van den Bold (1976), Rosenfeld and Vesper (1977), and Schweitzer and Lohmann (1990) to name a few.

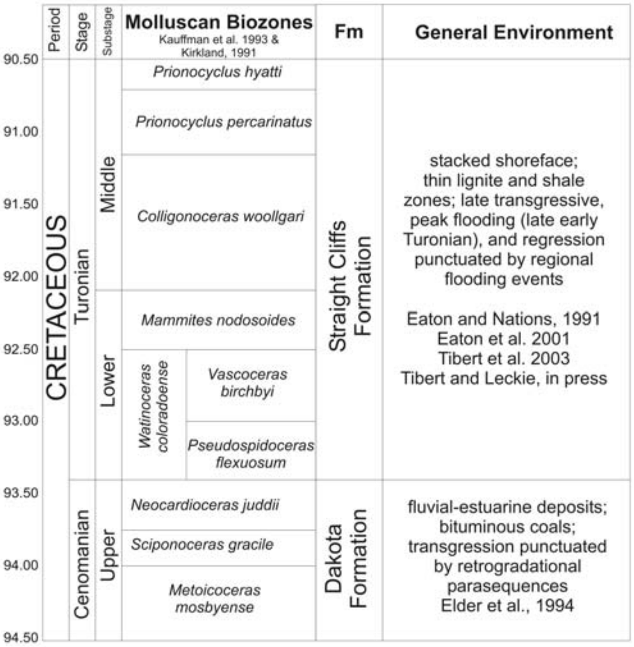
Mesozoic Genera

The family Cytherideidae were prominent ostracodes during the Cretaceous. Few Mesozoic taxa belonging to the Cytherideidae have been described with sulcation. This section provides a brief description and discussion of the Mesozoic representatives of the tribe Cyprideidini Kollmann 1960 where sulcation and dimorphism (in addition to the cytherid muscle scars and hingement) are prominent diagnostic features.

Fabanella

The early Jurassic-early Cretaceous genus *Fabanella* Martin 1961 is considered the root of the Cyprideidini phylogeny that includes the *Neocyprideis-Miocyprideis* and *Sarlatina-Cyprideis* lineages (Colin and Carbonel 1990; Colin et al. 1990). Boomer et al. (2001) recently illustrated *Phraterfabanella* Whatley and Boomer from Lower Jurassic strata in northern Italy which further extends the range of the lineage. Babinot and Colin (1976) and Colin (1983) outlined the diagnostic characters that warrant placement of *Fabanella* within the Cyprideidini: (1) a Cytherideidae adductor muscle scar field, (2) an antimerodont hinge (tripartite), (3) a narrow anterior vestibule, and (4) distinct sexual dimorphism. *Fabanella* differs from the descendant *Cyprideis* because of its generally sub-quadrate shape where the dorsal and ventral margins are sub-parallel, its few radial pore canals, and distinct ocular swelling (eyespot: see *Fabanella tumidosa* Swain and Brown 1972, plate 7, figs. 6, 7a). What is striking about *Fabanella* is the pronounced dimorphism expressed as swollen posteriors of the females (brood pouches) and rare noding (Colin et al. 1990). *Fabanella tumidosa* from the Aptian U.S. Atlantic Coastal Plain yields pore structures that are Type C (sieve plate with central pore) (Swain and Brown 1972, plate 7, fig. 9c). The paleoenvironmental association for *Fabanella* is marginal marine that includes the S-Phase marine bands of the Purbeck-Wealden facies where it has been documented as a prominent ostracode (Kilenyi and Allen 1968; Horne 1995).

Following our examination of material provided by Swain, we acknowledge that *Quadrashuleridea* Swain and Anderson 1993 from the Lower Cretaceous Gulf Coast (Cottonwood Valley Group) may also represent a potential ancestor for the Cyprideinini lineage given the general oval shape and median sulcation of the specimens. However, the poor preservation of the material leaves uncertainty regarding the nature of hingement and the specimens apparently demonstrate simple Type A pores (no sieve plates); therefore, *Quadraschuleridea* while certainly related, seems an unlikely candidate for the ancestral root.



TEXT-FIGURE 2
Generalized stratigraphy of the Cenomanian-Turonian boundary interval for the Western Interior Seaway. Molluscan biozones are widely recognized across the basin. The duration for each zone approximate 100-300 kyr (Obradovich 1993; Kauffman et al. 1993).

Fossocytheridea

Swain and Brown (1964) erected *Fossocytheridea* to encompass a new species of Cretaceous ostracode (middle Cenomanian) that very much resembles *Ovocytheridea* in lateral outline. The presence of a median sulcus and the antimerodont hingement, however, prompted the following comment:

> "The new genus is similar in general shape to *Ovocytheridea* Grékoff and *Dolocytheridea* Triebel, but differs from both in having an antero-median sulcus, and in details of hingement. *Fossocytheridea* closely resembles *Cyprideis* Jones in shape and hingement, pronounced dimorphism, and that genus also may be weakly sulcate; the sulcus in *Cyprideis*, however, is more medially located and generally broader and shallower than in *Fossocytheridea*."

Swain and Brown (1964) described the new genus *Fossocytheridea* with *Fossocytheridea lenoirensis* as the type species. They proposed a left female valve as the holotype. This appears problematic because the female right valve was illustrated (Swain and Brown 1964: plate 1, figure 11d). Puckett (1994, p. 1329) discussed the uncertain status of the holotype and questioned the validity of the genus. The mix-up is apparently a technical error easily corrected by establishing that the right female valve (Swain and Brown 1964: plate 1, figure 11d) is indeed the holotype (Kempf, pers. comm. 2001). Nonetheless, *Fossocytheridea* has been formally recognized (Swain and Brown 1964, 1972) and remains the first described genus of Cretaceous ostracoda to encompass those taxa with both distinct dimorphism and sulcation, in addition to other prominent features described below.

Sarlatina

Babinot and Colin (1976) provided detailed taxonomic descriptions of Cenomanian ostracodes with sulcation, antimerodont crenulated hinge elements, and distinct dimorphism, features that initiated the suggestion that the new genus *Sarlatina* may represent the ancestral root for the lineage leading to *Cyprideis*. Colin et al. (1996) noted that *Fossocytheridea* was a closely related genus. Babinot and Colin (1976) summarized the following prominent features for *Sarlatina*: (1) a vertical sulcus; (2) a strongly crenulated antimerodont hinge where the anterior element is elongate and the terminal hinge teeth are secondarily incised dorsally which give them an overall heart-shape; (3) numerous straight or sinuous radial pore canals (60 in total and 25-28 anterially); and (4) distinct sexual dimorphism.

Andreu (1978) provided the first comparison between *Sarlatina* and *Fossocytheridea* in his unpublished doctoral thesis. He considered the deep sulcus and the relatively wide radial pore canals of *Fossocytheridea* a sharp contrast from those observed for *Sarlatina*. Also according to Andreu (1978), *Sarlatina* could be distinguished from *Fossocytheridea* by the irregular shape of the normal pores. Andreu further classified the normal pores of *Sarlatina* and *Fossocytheridea* as Type B (sieve plate without a central pore) and Type D (a sieve plate and a separate single pore) following Puri (1974). Babinot and Colin (1976), however, illustrated normal pores of *Sarlatina* with either circular and/or oblong shapes and depressed inner sieve plates that clearly have central pores (Type C Pore *sensu* Puri 1974).

Comparative Material and Paleogeographic Distribution

The primary objective of this paper is to demonstrate that the taxa assigned to *Fossocytheridea* Swain and Brown and its junior synonym *Sarlatina* Babinot and Colin comprise the ancestral lineage of the modern genus *Cyprideis*. Two new species of *Fossocytheridea* are described from southwest Utah and *Cytheridea posterovata* Lankford (in Peterson et al. 1953) is redescribed. Species from localities outside the Cretaceous WIB are also illustrated here, including *Fossocytheridea lenoirensis* Swain and Brown provided by Swain, *Sarlatina merlensis* (type-species of *Sarlatina*) and two species assigned to *Dolocytheridea* (*Parastenbergella*) provided by Andreu. To further expand our revision of *Fossocytheridea*, remarks are provided for published material from Aptian to Maastrichtian age localities that include (Table 1; text-fig. 4): France, Portugal, Spain, Morocco, West Africa (Mali, Senegal), China, the U.S. Atlantic Coastal Plain (North Carolina), the Gulf of Mexico Coastal Plain (Alabama), and South America (Argentina, Bolivia). Figure 4 shows the distribution of *Fossocytheridea* for the mid- Cretaceous (Aptian-Turonian) and the Late Cretaceous (Coniacian-Maastrichtian). All taxa assigned to *Fossocytheridea* occupied warm temperate to tropical marginal marine environments of the Tethyan Seaway that encircled the globe during Cretaceous times.

SYSTEMATICS

We follow the classification system of Hartmann and Puri (1974). All descriptions for new taxa will include detailed diagnoses. For those taxa previously illustrated in the literature, we provide remarks and their corresponding primary reference. Text-figure 3 illustrates the applied morphologic terminology used herein. Holotypes and paratypes of the proposed new species are located at the Smithsonian National Museum of Natural History (USNM) at Washington D.C., USA. The curatorial numbers are included both in the taxonomy and their corresponding plate captions.

Subclass OSTRACODA Latreille 1806
Order PODOCOPIDA Muller 1894
Suborder PODOCOPINA Sars 1866
Superfamily CYTHERACEA Baird 1850
Family CYTHERIDEIDAE Sars 1925
Subfamily CYTHERIDEINAE Sars 1925
Tribe CYPRIDEIDINI Kollmann 1960

Genus ***Fossocytheridea*** Swain and Brown 1964
Type-species: *Fossocytheridea lenoirensis* Swain and Brown 1964

Emended diagnosis: See original detailed description provided by Swain and Brown (1964, 1972). Based on their original description we propose the following diagnostic characters for identification of Fossocytheridea:

1) an antimerodont hinge where all elements are crenulate and the anterior teeth maintain a distinct heart-shape;

2) a subovate shape where most taxa display a slight cardinal angle at the anterior hinge element;

3) approximately 25-28 straight or slightly sinuous marginal pore canals along the anterior inner margin;

4) a relatively narrow inner lamella with a vestibule present along the anterior-ventral margin;

5) an anterior-dorsal sulcus that may be vertical or obliquely inclined towards the anterio-ventral margin and an ocular swelling may be present;

6) type C normal sieve pores; and

7) variable patterns of reticulation.

Remarks: Specimens of Fossocytheridea may be smooth or reticulate. Pore shape and shell distribution density also show considerable variability. Swain and Brown (1964) illustrate noded juveniles and well-developed reticulation in some specimens.

Occurrence: Taxa have been described from the WIB through Tethyan marginal facies of southern Europe, northern Africa, South America, and eastward into China (low temperate to tropical settings).

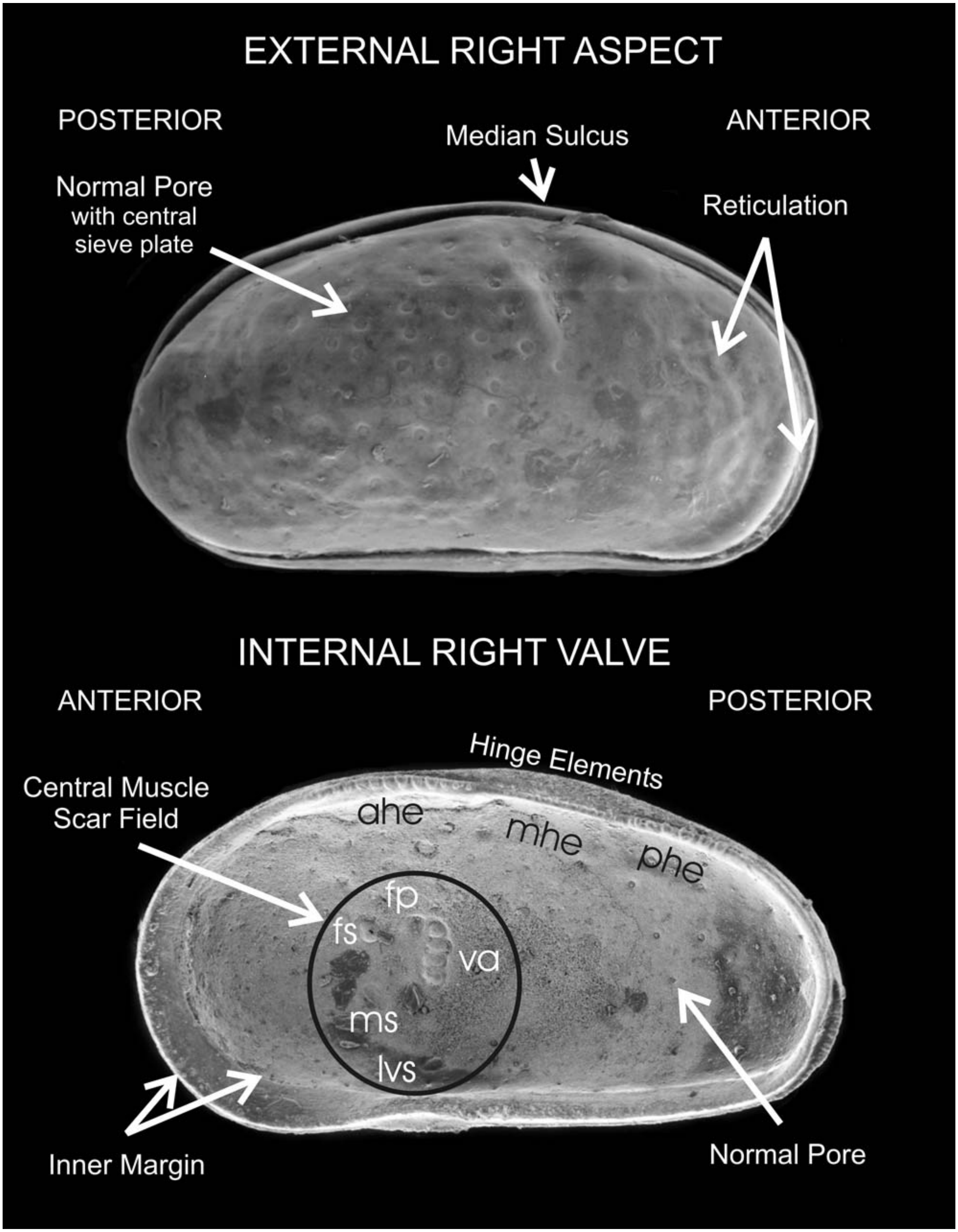
Geologic Range: Aptian to Maastrichtian

Paleoecology: Brackish water deposits in lignite coal zones associated with charophytes and gastropods such as *Admetopsis* and *Craginia*. Also observed in oyster reef deposits (Puckett 1994).

Synonymy: Listed below are species we assign to *Fossocytheridea*. The taxa are listed with original reference, location, and age and when appropriate additional remarks.

Antibythocypris dimorphicus Puckett 1994, Santonian of Alabama, U.S.A.

Asciocythere lusitanica Damotte et al. 1988, Aptian of Portugal. Cabral (1995) considered *Dolocytheridea* ? sp. 251 Damotte et al. (1988) as males of *Asciocythere lusitanica* and assigned the species to *Clithrocytheridea*. She also considered *Asciocythere algarvensis* Damotte et al. (1990)



TEXT-FIGURE 3
Ostracode morphological terminology applied within this paper. The prominent characteristics that warrant placement of *Fossocytheridea* within the Cyprideidini Kollmann 1960 include: median sulcation; type C sieve type pores; coarse reticulation; standard cytherid muscle scar field of 4 vertical adductors; an antimerodont hinge; and distinct dimorphism. For the central muscle scar field we note the following abbreviations: va = vertical array; fp = fulcral point; fs = frontal scar; ms = mandibular scar; lvs = lower ventral scar. For the hinge elements: ahe = anterior hinge element; mhe = median hinge element; phe = posterior hinge element.

TABLE 1
List of *Fossocytheridea* and their geographic occurrences. We have grouped the synonyms into geographic regions. The age and localities are presented following the originally assigned designation and the corresponding author(s). Text-figure 4 shows the localities plotted on the paleogeographic maps for both 94 and 69 Ma.

EUROPE

SW France: *Sarlatina merlensis* BABINOT and COLIN 1976, Cenomanian
Spain: *Sarlatina merlensis* BABINOT and COLIN 1976, Cenomanian
    Ovocytheridea hispanica BREMAN 1976, Turonian
Portugal: *Sarlatina merlensis* BABINOT and COLIN 1976, Cenomanian
    Dolocytheridea? sp. 251 DAMOTTE *et al.* 1988, Aptian
    Asciocythere lusitanica DAMOTTE *et al.* 1988, Aptian

ASIA
SE former Soviet Union: *S. leguminoformis* (ANDREEV), Lower Senonian
China (Tarim Basin): *Neocyprideis ? leguminoformis* ANDREEV 1971, Turonian
    Sarlatina longielliptica YANG *et al.* 1995, Santonian-Campanian
    Sarlatina yigeziyanensis YANG *et al.* 1995, Santonian-Campanian
    Sarlatina sp. 1 YANG *et al.* 1995, Santonian- ?
    Sarlatina sp. 2 YANG *et al.* 1995, Coniacian ?

AFRICA

Algeria: *Sarlatina* sp. Cenomanian (possibly *merlensis*)= *Fabanella* sp. GREKOFF
    Clithrocytheridea? rhoundjaiensis BASSOULLET and DAMOTTE 1969, Cenomanian-Turonian
Offshore Libya: *Sarlatina merlensis* BABINOT and COLIN 1976, Cenomanian
Niger: possibly *S. merlensis* BABINOT and COLIN 1976, Cenomanian
    Sarlatina maliensis COLIN *et al.* 1996, Santonian-Campanian
Morocco: *Dolocytheridea* sp. 3 ANDREU 1991, Cenomanian
    Dolocytheridea (*Parasternbergella*) sp. 6 ANDREU 1991, Cenomanian Turonian
Senegal-Gambia: *Bronsteiniana africana* APOSTOLESCU 1963, Cenomanian-Turonian
Mali: *Sarlatina maliensis* COLIN *et al.* 1996, Campanian-Maastrichtian

SOUTH AMERICA

Argentina: *Ovocytheridea*? *rionegrensis* MUSACCHIO 1973, Cenomanian
Bolivia: ?*Ovocytheridea* sp. MUSACCHIO 1990 (in Rodrigo & Branisa), Cenomanian

NORTH AMERICA

North Carolina: *Fossocytheridea lenoirensis* SWAIN and BROWN 1964, Albian?-early Cenomanian
Florida: *Fossocytheridea* sp. SWAIN, 1982, late Albian-early Cenomanian
Utah-Wyoming: *Fossocytheridea mosbyense* sp. nov., late Cenomanian
    Fossocytheridea kirlkandi sp. nov.., latest Cenomanian
    Fossocytheridea posterovata LANKFORD 1953: Turonian
Alabama (Gulf Coast): *Antibythocypris dimorphicus* PUCKETT 1994, Santonian

and *Dolocytheridea vendaensis* Damotte et al. (1990) as synonyms of *Asciocythere lusitanica.*

Bronsteiniana? *africana* Apostolescu 1961, Cenomanian-Turonian of Gambia, West Africa. Tentatively assigned to *Sarlatina* by Colin et al. (1996) (inner characters unknown).

Clithrocytheridea? *rhoundjaiensis* Bassoullet and Damotte 1969, Cenomanian and Turonian of Algeria.

Dolocytheridea (Parasternbergella) transatlasica Andreu 1996, Cenomanian-Santonian of Morocco (= *Dolocytheridea* (*Parasternbergella*) sp. 6 Andreu (Andreu 1991).

Dolocytheridea sp. 3 Andreu 1991, Cenomanian of Morocco. Morsi and Bauer (2001) report this taxon from the Cenomanian Sinai peninsuls Egypt.

Fabanella? OUM 2318 Grékoff 1968, Cenomanian of Algeria, Libya, Eastern Niger (Babinot et al. 1996). Possibly *Sarlatina merlensis* (Babinot and Colin 1976).

Fabanella? sp. A van den Bold 1964, late Cenomanian-early Turonian of Egypt. Shahin (1991) assigned this taxon to *Neocyprideis vandenboldi* Gerry and Rosenfeld (1973).

Fossocytheridea sp. Swain 1982, early Cenomanian of Florida.

Neocyprideis? *leguminoformis* Andreev 1971, lower Senonian of southern Russia. Turonian of the Tarim Basin (Tang et al. 1989; Yang et al. 1995). Tentatively attributed to

Sarlatina by Babinot and Colin (1976). Attributed to *Sarlatina* by Yang et al. (1995).

Neocyprideis boukharyi Morsi and Bauer 2001, Cenomanian of Sinai peninsula Egypt.

Ovocytheridea? *rionegrensis* Musacchio 1973, Upper Cretaceous of Argentina. Tentatively assigned to *Sarlatina* by Colin et al. (1996).

?*Ovocytheridea* sp. Musacchio in Rodrigo and Branisa 1990, Cenomanian of Bolivia. Recently attributed to *Sarlatina* by Simeoni and Musacchio (1998).

Ovocytheridea hispanica Breman 1976, Turonian of central Spain.

Sarlatina babinoti Morsi and Bauer 2001, Cenomanian of Sinai peninsula Egypt.

Sarlatina longielliptica Yang et al. 1995, Santonian-Campanian (Middle Dongpa Formation) of the Tarim Basin, China.

Sarlatina maliensis Colin et al. 1996, Campanian-Maastrichtian of Mali and western Niger (Carbonnel and Monciardini 1995; Colin et al. 1996). Santonian-Campanian of eastern Niger (Colin et al. 1990).

Sarlatina merlensis Babinot and Colin 1976, Cenomanian of southwest France, Portugal and Spain (Babinot and Colin 1976; Andreu 1978; Babinot et al. 1978; Colin 1983; Babinot et al. 1991).

Sarlatina sp. 1 Yang et al. 1995, Santonian-Campanian (Lower Yigezia Formation), Tarim Basin, China (Yang et al. 1995).

Sarlatina sp. 2 Yang et al. 1995, Coniacian? Wuytake Formation., Tarim Basin, China (Yang et al. 1995).

Sarlatina yigeziyanensis Yang et al. 1995, Santonian-Campanian (Middle Yigezia Formation), Tarim Basin, China (Tang et al. 1989; Yang et al. 1995).

Sarlatina sp. P1 Viviers et al. 2000, Santonian-Lower Campanian of Potiguar Basin, Brazil.

Sarlatina c.f. *merlensis* Babinot and Colin 1976, early Turonian of Sinai Egypt (Bassiouni 2002).

Sarlatina faizabadensis (authors unknown) in Andreev et al. (1999), Cenomanian of central Asia.

Sarlatina mandelstami (authors unknown) in Andreev et al. (1999), Cenomanian of central Asia.

Sarlatina c.f. *merlensis* BABINOT and COLIN, in Bassiouni (2002), early Turonian of Sinai, Egypt.

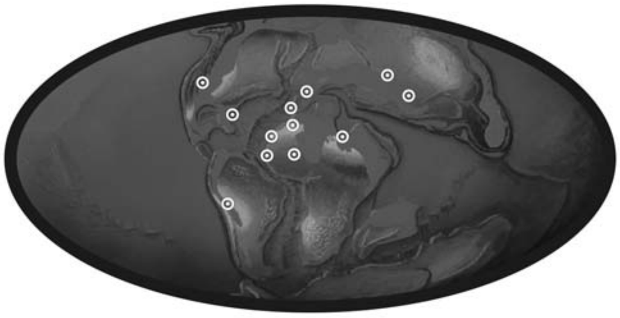
Fossocytheridea lenoirensis Swain and Brown 1964
Plate 1, A-C

Fossocytheridea lenoirensis SWAIN and BROWN 1964, p. 20, pl. 1, 11a-h, pl. 2, figs. 1a-j.

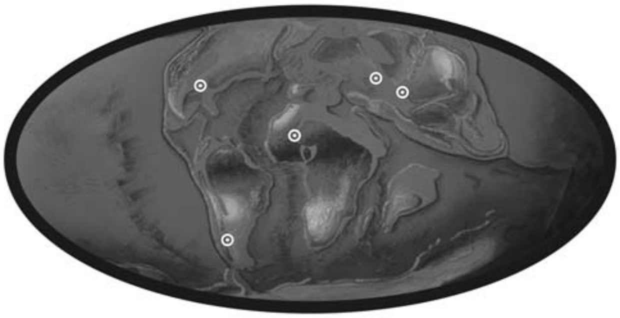
Fossocytheridea lenoirensis Swain and Brown, in SWAIN and BROWN 1972, p. 25, pl. 6, figs. 1-3.

Remarks: A detailed description of this species is provided by Swain and Brown (1964; 1972). *Fossocytheridea lenoirensis* differs from the other species of this genus because it possesses an acute posterior margin and a rather deep sulcus. The angularity of the juveniles is apparently preserved in all species to the extent that we find it nearly impossible to distinguish between instars of the taxa that comprise the genus (text-fig. 9). The sulcus often maintains an arcuate shape lying directly below the anterior hinge element. *Fossocytheridea lenoirensis* closely resembles *Fossocytheridea kirklandi* sp. nov., which can be distinguished by its shorter length and flattened anterior margin, especially noticeable in dorsal view.

Occurrence: The type specimens were recovered from the 723-826 foot position of the Dupont Water Well, Lenoir County, North Carolina. These strata are assigned to Unit F of the Atlantic Coastal Plain in North Carolina (Swain and Brown 1972).



“Middle” Cretaceous 94 Ma



Late Cretaceous 69 Ma

TEXT-FIGURE 4
Paleogeographic distribution of taxa assigned to *Fossocytheridea* Swain and Brown 1964. We use paleogoegraphic reconstructions from Scotese (1997) and include the middle Cretaceous and latest Cretaceous times to present the occurrences reported in the literature. Table 1 provides the list of taxa and their corresponding localities that are marked on the figure as white circles.

Material: Eight specimens. Albian-early Cenomanian. Auger-hole from Halifax County, North Carolina, USA.

Dimensions: All measurements are in microns.

Specimen	Length	Height	Width
Female	836	507.3	
Female	769.5	551	418
Male	780.9	463.6	
Juvenile	571.9	361	

Geologic Range: Albian-early Cenomanian.

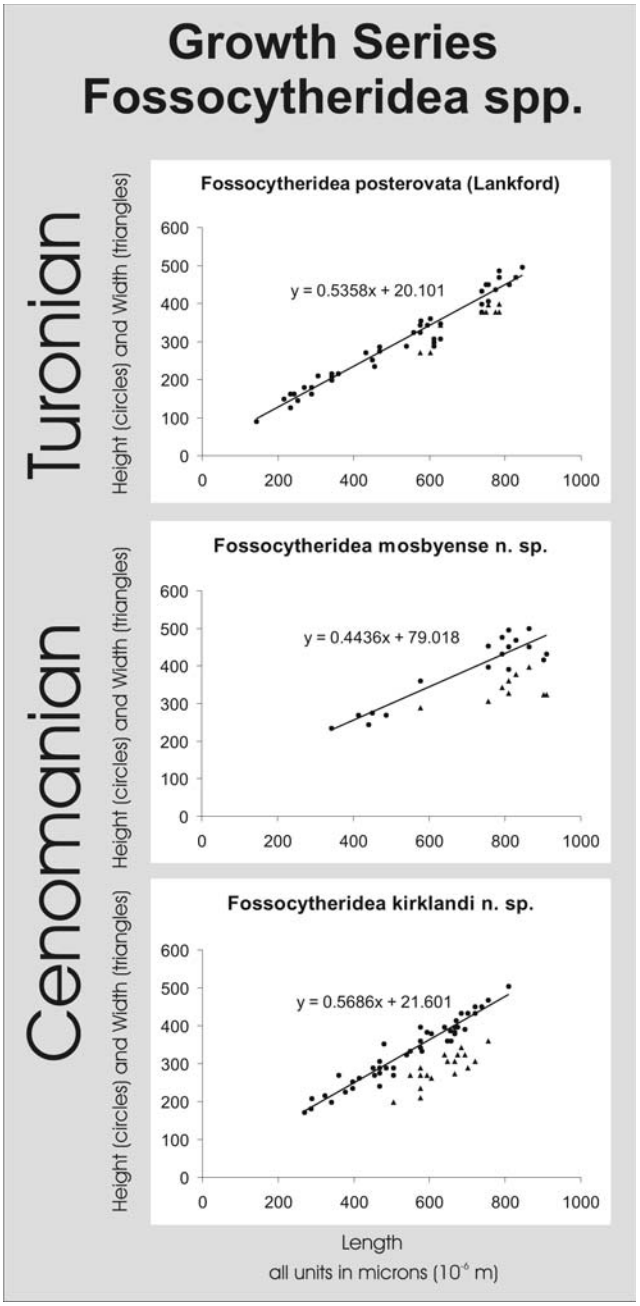
Paleoecology: Lagoonal or brackish water deposits.

Fossocytheridea merlensis (Babinot and Colin 1976)
Plate 1, D-G

Fabanella? sp., OERTLI 1963, pl. 78, fig. 2e, pl. 89, figs. 1-2.

Sarlatina merlensis BABINOT and COLIN 1976, p. 164, pl. 2, figs. 8-17, pl. 3, figs. 1-12; COLIN 1983, pl. 10, 18, figs. 1-3, pl. 10, 20, figs. 1-3; COLIN et al. 1990, p. 94, pl. 3, figs. 1-4.

Remarks: A detailed description of this species is provided by Babinot and Colin (1976) and Colin (1976). This species



TEXT-FIGURE 5
Length-to-height and length-to-width growth plots for *Fossocytheridea* spp. from southwest Utah.

closely resembles *Fossocytheridea posterovata* Lankford (in Peterson et al. 1953) because of the generally smooth carapace, slightly angular posterior-dorsal slope, narrow inner lamella, and 26 marginal pore canals. The shorter length and angularity of the females and the laterally compressed posterior seen in dorsal view distinguishes *F. merlensis* from *F. posterovata*. *Fossocytheridea lenoirensis* differs from *F. merlensis* in displaying a deeper and more-oblique sulcus that is located below the anterior hinge element.

Occurrence: The type specimens were recovered from a borehole at Merle, village of Berbiguieres, Dordogne, southwest France. Cenomanian localities include southwest France, Portugal, Spain, and North Africa.

Material: Six specimens, mostly articulated carapaces. Cenomanian Moyen, Gare de Cacem, Portugal.

Dimensions: All measurements are in microns.

Specimen	Length	Height	Width
Female	902.5	608	
Female	893	456	
Female	856.9	532	361
Female	855	513	
Male	894.9	461.7	380
Male	855	494	
Male	807.5	476.9	

Geologic Range: Cenomanian.

Paleoecology: Mono or oligospecific associations in brackish water deposits.

Fossocytheridea mosbyense sp. nov.
Plate 1, H-L

Name: Named after the encompassing *Metoicoceras mosbyense* ammonite biozone.

Holotype: Plate 1, H — right external aspect adult carapace, USNM 520360.

Paratypes: Plate 1, I — right external aspect male carapace, USNM 520362; J — details of hinge of left internal valve, USNM 522945; K — left external aspect adult carapace, USNM 520361; and L — details of adductor muscle scar field right internal valve, USNM 522946.

Material: Cenomanian. Kaiparowits Plateau, Utah. Fifty seven specimens, mostly articulated adults and a few disarticulated carapaces.

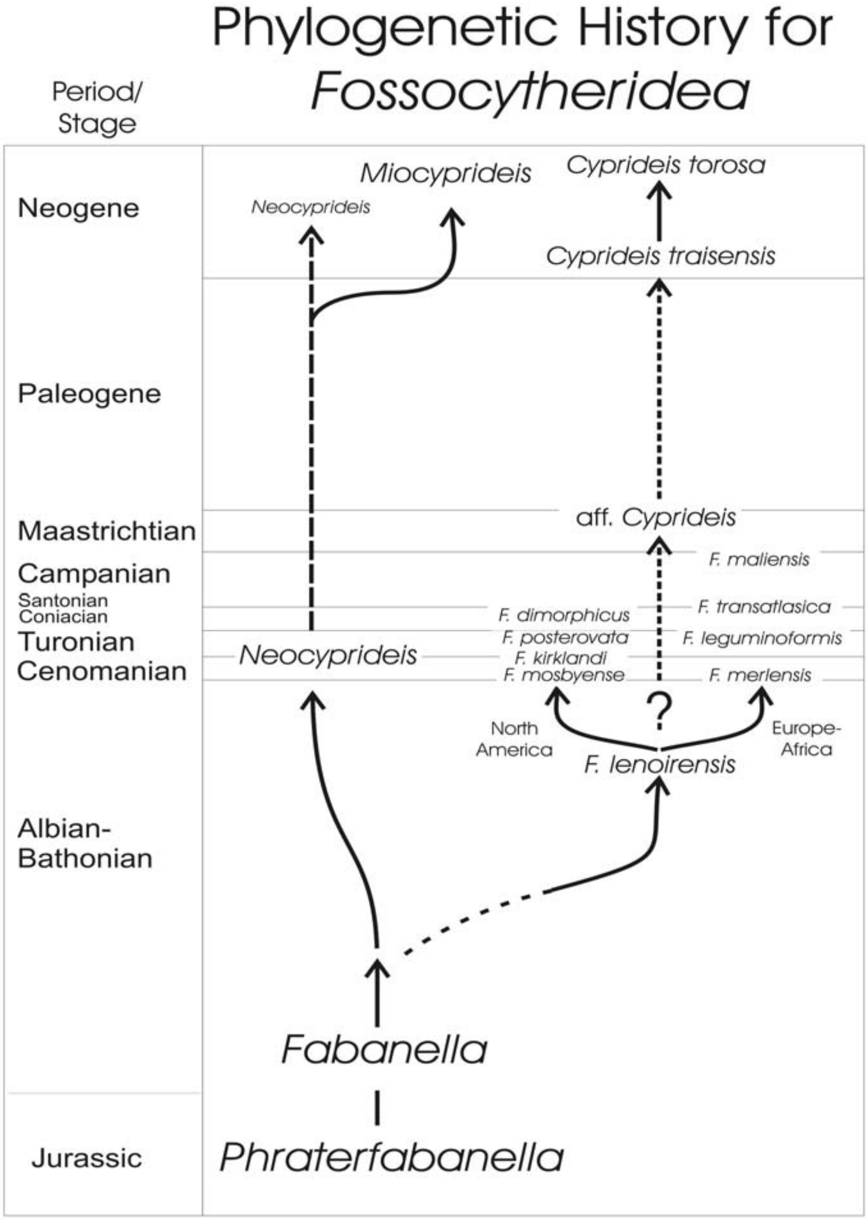
Type Locality: East of the town of Henryville Utah on Route 12 at the entrance to Grand Staircase National Monument (Locality 4, Fig. 1).

Type Level: Upper member of the Dakota Formation assigned to the *Metoicoceras mosbyense* ammonite biozone of Kauffman et al. (1993).

Diagnosis: Medium sized. Smooth, evenly swollen, and thinly calcified carapace. Elongate subovate males and females that display a high length to height ratio (text-fig. 5). Narrow inner margin.

Description: This species of *Fossocytheridea* demonstrates a sub-angular shape marked by a posterio-dorsal slope. The left valve overlaps the right only slightly around the entire free margin. The normal pore density is low and reticulation has not been observed for this species. The shallow sulcus is observed in the anterior cardinal area. The inner lamella is fairly narrow and there is a faint antero-ventral vestibule.

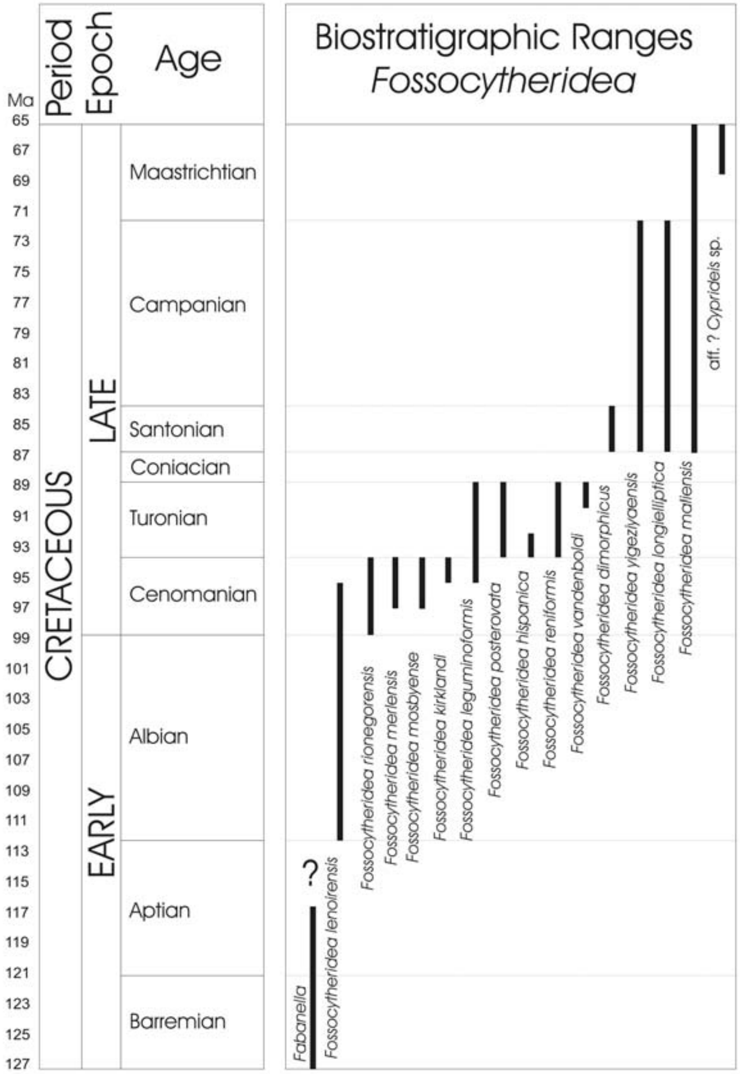
Hingement: Antimerodont. The tooth sockets of the right valve display the distinct heart-shape although the relief is subtle.



TEXT-FIGURE 6
Schematic summarizing the phylogenetic history of the Cyprideidini hinge. Note that *Fossocytheridea* shows marked speciation at the time of the Cenomanian-Turonian boundary interval world-wide.

Muscle Scars: The central muscle scars comprise a sub-vertical array of four adductors. A fulcral point is visible anterior and between the first and second adductor. Parallel with the fulcral point is a pear-shaped frontal scar. Directly below the frontal scar is an oblique mandibular scar that lies below the vertical array. At the base of the inner margin lies a single ovate ventral (or second mandibular) scar in alignment with the vertical array.

Remarks: This species most closely resembles *Fossocytheridea posterovata* and *Fossocytheridea merlensis.* However, the relief of the hinge characters are less pronounced than *Fossocytheridea mosbyense.* Sexual dimorphism is more pronounced in this species; both male and female specimens display a median width greater than the other species of the genus. The rather subtle sulcus located in the position of the anterior cardinal angle makes this taxon distinguishable from *Fossocytheridea kirklandi* and *Fossocytheridea lenoirensis.* Also, *Fossocytheridea kirklandi* can be distinguished from *Fossocytheridea mosbyense* by its greater height at the position of the anterior hinge element. The slight overlap of the thinly calcified

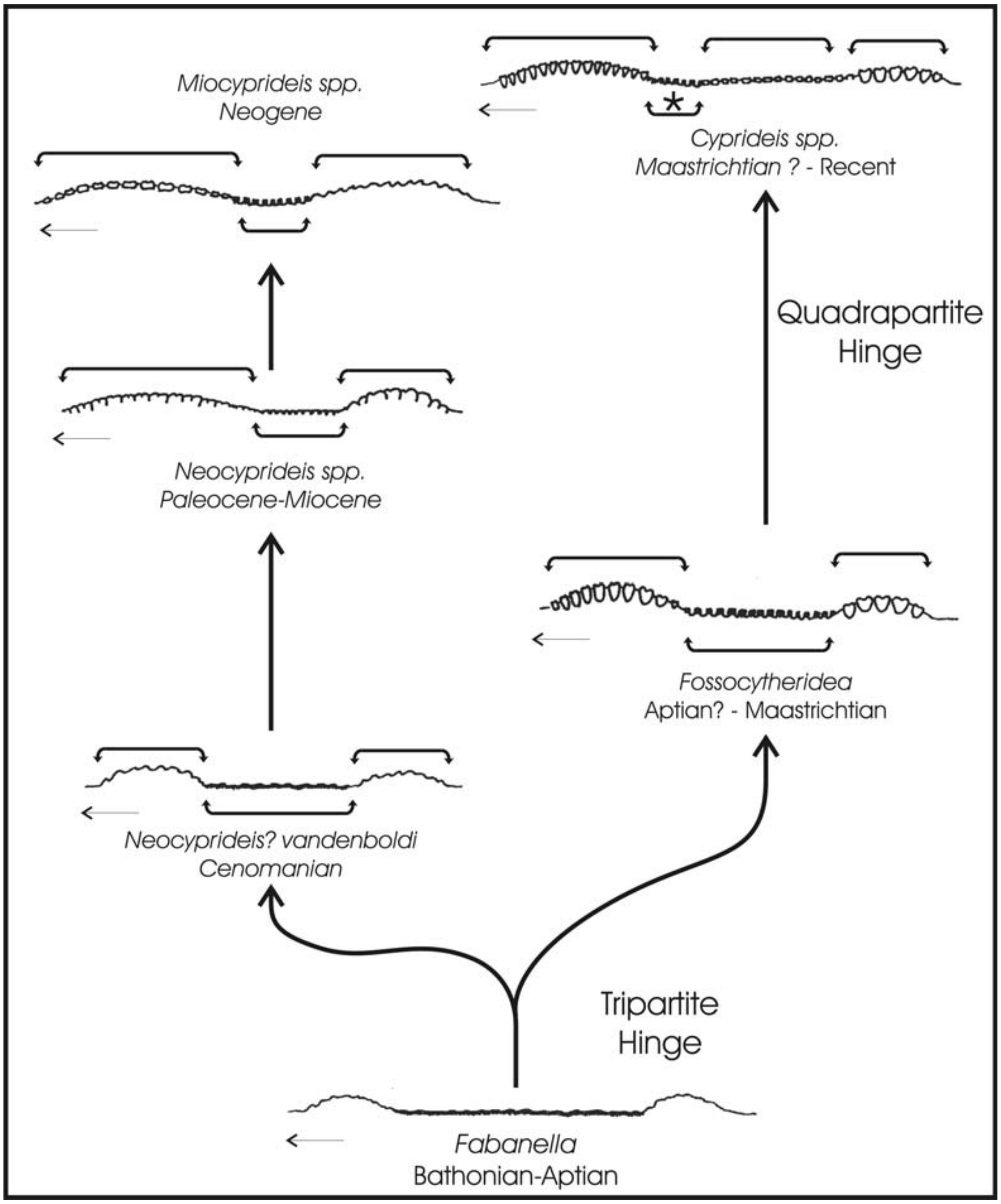


TEXT-FIGURE 7
Biostratigraphic ranges for *Fossocytheridea* plotted in order of their first occurrence. Note that the Cenomanian-Turonian boundary interval shows relative "high diversity" for the genus. It may be that the global perturbations (anoxia and greenhouse conditions), recorded at this time of extremely high sea level, created highly unstable offshore conditions that favored successful experimentation and ultimate survival of this eurytopic lineage within the refuge of marginal water bodies. The 100-300 kyr duration of the biozones allowed enough time for the microspeciation process to be preserved as short lived, distinct taxa in southwest Utah.

valves, the thin inner margin, the faint vestibule, and the absence of anterior compression sets this taxon apart from all other taxa described herein.

Dimensions: All measurements are in microns. A growth series is shown in text-figure 5.

Specimen	Length	Height	Width
Female	864	500	396
Female	864	450	
Female	828	468	378
Female	810	496	360
Female	810	450	328
Female	810	390	360
Female	792	477	342
Female	792	432	
Female	756	453	
Female	756	396	306
Male	909	432	324
Male	902	417	324
Juvenile	576	360	
Juvenile	450	274	288
Juvenile	441	243	
Juvenile	414	270	



TEXT-FIGURE 8
The two primary phylogenetic lineages traced to *Phraterfabanella* and *Fabanella* (modified from Babinot and Colin 1976). The *Cyprideis* lineage is characterized by a relatively broad medial hinge element. The primary distinction between *Cyprideis* and *Fossocytheridea* is the fourth element located behind the anterior element (arrow indicates anterior).

Juvenile	342	234

Geologic Range: Upper Cenomanian (*Metoicoceras mosbyense* ammonite zone).

Paleoecology: Associated with abraded valves of *Darwinula*, *Hourcqia*, *Paracypris*, and numerous agglutinated foraminifera probably representing estuarine conditions.

Fossocytheridea kirklandi Tibert, Colin, Leckie and Babinot, **n. sp.**
Plate 1, M-S

Name: After paleontologist James Ian Kirkland in recognition of his help to travel to and collect the samples in southwest Utah.

Holotype: Plate 1, M — right external aspect adult carapace, USNM 520365.

Paratypes: Plate 1, N — right external aspect adult carapace, USNM 520363; O — left external aspect juvenile carapace, USNM 520364; P — dorsal aspect adult carapace, USNM 522947; Q — right external aspect adult carapace, USNM 522948; R — right external aspect juvenile carapace, USNM

522949; and S — internal aspect right valve illustrating inner lamella and muscle scar field, USNM 522950.

Material: Cenomanian. Markagunt Plateau and Pine Valley Mountains, Utah. Hundreds of specimens, mostly articulated adults and a few disarticulated carapaces. Often they are crushed laterally.

Type Locality: Southwest of Cedar City, Utah, at Browse, in the Pine Valley Mountains (Locality 1, Fig. 1).

Type Level: Beds yielding this species are confined to the coal-bearing units that comprise the upper member of the Dakota Formation and Iron Springs Formation equivalent (Tibert et al. 2003). Strata are assigned to the uppermost Cenomanian *Sciponoceras gracile* and *Neocardioceras juddii* ammonite biozones of Kauffman et al. (1993). The designated holotype USNM 520365 was recovered from Browse, in the Pine Valley Mountains (Locality 1). Numerous specimens were recovered east of the town of Cedar City, Utah at mile markers 6-9 on Route 12 (Locality 2, Maple Canyon and Coal Creek: Eaton et al. 2001; Tibert et al. 2003). Specimens were also recovered at Table Bench north of Zion National Park (Locality 3, Fig. 1) (Tibert et al. 2003).

Diagnosis: Medium sized. Normal pores densely distributed on the reticulate, heavily calcified carapace. Deep sulcus located in front of the anterior hinge element. Narrow inner margin. Females display a low length to height ratio (Fig. 5).

Description: This species of *Fossocytheridea* displays an ovate to sub-quadrate shape where the greatest height occurs posterior of the deep, oblique sulcus. An oblique ridge occurs above the sulcus and this may represent an ocular swelling. The anterior margin is compressed laterally. The left valve overlaps the right along the entire free margin. The pore density is high and reticulation is common, especially evident in the anterior and posterior ventral areas. The sulcus is deep and occurs just in front of the anterior hinge element. The inner lamella is fairly narrow and there is slight vestibule present along the anterior ventral margin.

Hingement: Antimerodont. The tooth elements of the right valve display the distinct heart-shape and the relief is subtle.

Muscle Scars: The scar arrangements are much the same as *Fossocytheridea mosbyense* described above.

Remarks: Males are rarely observed. *Fossocytheridea kirklandi* has a greater height at the position of the anterior hinge element and the lateral compression seen in dorsal view makes this species easily identifiable. The juveniles are angular and not distinguishable from instars of other species of the genus (plate 1, figs. O, R; text-fig. 9). This species most closely resembles *Fossocytheridea lenoirensis* to the extent that specimen USNM 522948 (Plate 1Q) from Browse in the Pine Valley Mountains may be considered transitional to that species. At the stratigraphic position below the Cenomanian-Turonian boundary at Maple Canyon, Utah, specimens of *Fossocytheridea kirklandi* resemble *Fossocytheridea posterovata*. Consequently, *Fossocytheridea kirklandi* represents an intermediate form between Albian-early Cenomanian *Fossocytheridea lenoirensis* and the earliest Turonian *Fossocytheridea posterovata*. *Fabanella tumidosa* from the Aptian Atlantic Coastal Plain has an ocular swelling oblique to the sulcus (Swain and Brown 1972, plate 7, figures 5-9) reminiscent of *Fossocytheridea kirklandi*. The oblong and oblique pore shapes observed behind the sulcus, in the central area of the carapace, resemble those observed on *Cyprideis salebrosa* van den Bold (1963) from the Hudson River, New York (plate 3).

Dimensions: All measurements are in microns. A growth series is shown in text-figure 5.

Specimen	Length	Height	Width
Female	738	450	
Female	720	450	
Female	693	390	324
Female	675	396	324
Female	670	414	
Female	666	383	
Female	666	378	306
Female	655	387	
Female	639	396	324
Female	480	351	
Female	270	171	
Male	657	360	
Male	540	324	
Juvenile	576	360	288
Juvenile	576	342	234
Juvenile	576	342	210
Juvenile	504	270	198

Geologic Range: Upper Cenomanian (*Sciponoceras gracile – Neocardioceras juddii* ammonite zones).

Paleoecology: Associated with abraded adult valves of *Darwinula, Paracypris, Candona, Virgatocypris, Rosacythere, Clithrocytheridea*?, *Cythereis eaglefordensis, Cytheropteron eximium*, and *Phodoeucythere* (Tibert et al. 2003). The association of both marine and nonmarine taxa suggests a eurytopic ecological tolerance for the taxon. The abundance of well preserved adult carapaces and juvenile valves indicate this taxon was autochtonous. The observed monospecific ostracode assemblage associated with well-preserved nonmarine gastropods and charophytes, at the westernmost proximal estuarine localities in the Pine Valley Mountains, Utah, suggests either hypo or hypersaline tolerances (Tibert et al. 2003). The reticulation and oblong pores (Plate 3) support the hypothesis that this taxon lived in an environment where wide ranging salinity and/or chemical variability punctuated an isolated marginal marine ecosystem.

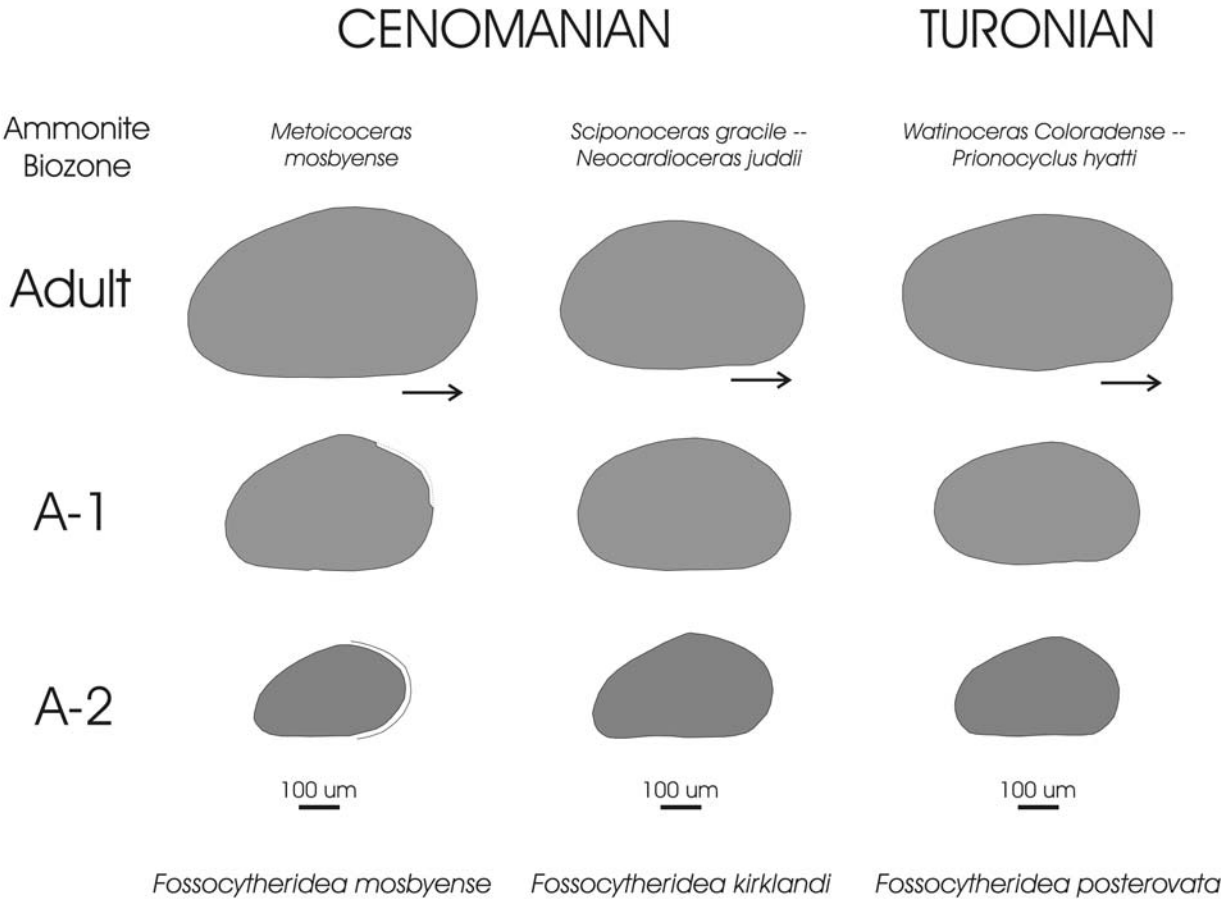
Fossocytheridea posterovata (Lankford in Peterson et al. 1953)
Plate 2, figures A, B, C, D, E, G

Cytheridea posterovata LANKFORD in Peterson et al. 1953, pl. 15, fig. 3a-c.
Cytheridea trisulcata LANKFORD in Peterson et al. 1953, pl. 15, fig. 5a-c.
Cytheridea posterovata var. *alta* LANKFORD in Peterson et al. 1953, pl. 15, fig. 4a-c.

Paratype: Plate 2, A — left external aspect adult carapace, USNM 522951.

Material: Cenomanian. Paunsagunt Plateau and Kaiparowits Plateau, Utah. Thousands of specimens that comprise mostly articulated adults and a few disarticulated carapaces.

Emended Diagnosis: Medium to large sized. Generally ovate and cylindrical. Posterior swelling observed in dorsal view; width-to-height values similar (text-fig. 5). Sulcus with low relief located behind the anterior hinge element (median). Narrow



TEXT-FIGURE 9
Line tracings of *Fossocytheridea* from SEM images that were scanned at the same scale (×100) to facilitate size comparisons between taxa. Juveniles have acuminate posteriors and the patterns of reticulation are subtle. The 3 species of *Fossocytheridea* from southwest Utah have juvenile instars that are indistinguishable.

inner margin; anterio-ventral region distinctly thickened with well-developed vestibule.

Description: Lankford (in Peterson et al. 1953) provided the original diagnosis and we emphasize additional and prominent features here. This species of *Fossocytheridea* demonstrates an ovate and elongate shape where the greatest height occurs posterior of a vertical sulcus. The anterior margin is slightly compressed laterally. The left valve overlaps the right along the entire free margin. The pore density is low in most specimens and reticulation is commonly observed at the ventral margin in some specimens. The sulcus is shallow and occurs behind the anterior hinge element. The inner lamella is relatively broad and there is vestibule present along the anterior ventral margin.

Hingement: Antimerodont. The tooth sockets of the right valve display the distinct heart-shape and the relief is subtle. Although the hinge is clearly tripartite, some specimens reveal a very subtle indentation of the crenulations directly behind the anterior hinge element (pseudoentomodont).

Muscle Scars: The scar arrangements are much the same as Fossocytheridea mosbyense described above except that the frontal scar is more arcuate in shape and the fulcral point is parallel with first scar of the vertical array.

Remarks: This species closely resembles both *Fossocytheridea mosbyense* and *Fossocytheridea merlensis.* The muscle scars of *F. posterovata* are strikingly similar to *Cyprideis torosa paraobesa* Decima 1964. They differ from older *Fossocytheridea* spp. because: (1) the fulcral point is parallel with the uppermost vertical array and (2) the frontal scar is arcuate and not pear-shaped. Lankford (in Peterson et al. 1953) described three species of *Cytheridea* where the distinction between them includes differences in general shape and patterns of reticulation within the central sulcus field. We interpret the shorter taxon *Cytheridea posterovata* var. *alta* Lankford as females and the more elongate *Cytheridea trisulcata* Lankford as males. *Cytheridea posterovata* Lankord is the recommended lectotype for the species.

Occurrence: The type locality is on Highway 189 adjacent to Echo Reservoir near Coalville, Summit County in northeastern Utah. All 3 species of *Fossocytheridea* occur at this locality (Lankford in Peterson et al. 1953). *Fossocytheridea posterovata* has been observed in southwest Utah at Cedar Canyon, the Pine Valley Mountains, and near the town of Tropic on the easternmost side of Paunsagunt Plateau (Tibert et al. 2003). The ages range from the lower to middle Turonian (*Pseudospidoceras flexuosum* to *Prionocyclus hyatti* ammonite biozone).

Dimensions: All measurements are in microns. Growth series are shown in text-figure 5.

Specimen	Length	Height	Width
Female	846	495	
Female	828	468	
Female	810	450	
Female	783	486	378
Female	783	468	399
Female	774	436	378
Female	756	450	396
Female	738	432	378
Male	756	405	
Male	749	450	378
Male	738	378	

PLATE 1

All scale bars equal 100μm unless otherwise indicated.

Fossocytheridea lenoirensis Swain and Brown 1964. Cenomanian — Halifax County, North Carolina.

A right external aspect articulated adult

B internal view left valve disarticulated adult

C enlargement of the normal pores in the median area of A to illustrate the Type C (sieve plate and central pore).

Fossocytheridea merlensis (Babinot and Colin 1976). Cenomanian – Gare de Caçem, Portugal.

D right lateral aspect of articulated adult valve

E dorsal view adult articulated carapace

F internal view of anterior hinge element of disarticulated valve

G interior view of a posterior hinge element of a disarticulated valve.

Fossocytheridea mosbyense sp. nov. Cenomanian – Kaiparowits Plateau, Utah.

H right external aspect of articulated adult carapace (Holotype USNM 520360)

I right external aspect of male articulated carapace (Paratype USNM 520362)

J internal view of hinge of a disarticulated left valve (Paratype USNM 522945)

K left external aspect of adult carapace (Paratype USNM 520361)

L internal view of adductor muscle scar field and its corresponding line tracing of a disarticulated valve fragment (Paratype USNM 522946).

Fossocytheridea kirklandi sp. nov. Cenomanian – Markagunt Plateau and Pine Valley Mountains, Utah.

M right external aspect of articulated adult carapace (Holotype USNM 520365)

N right external aspect of adult articulated carapace that demonstrates oblique sulcation and patterns of enhanced reticulation (Paratype USNM 520363)

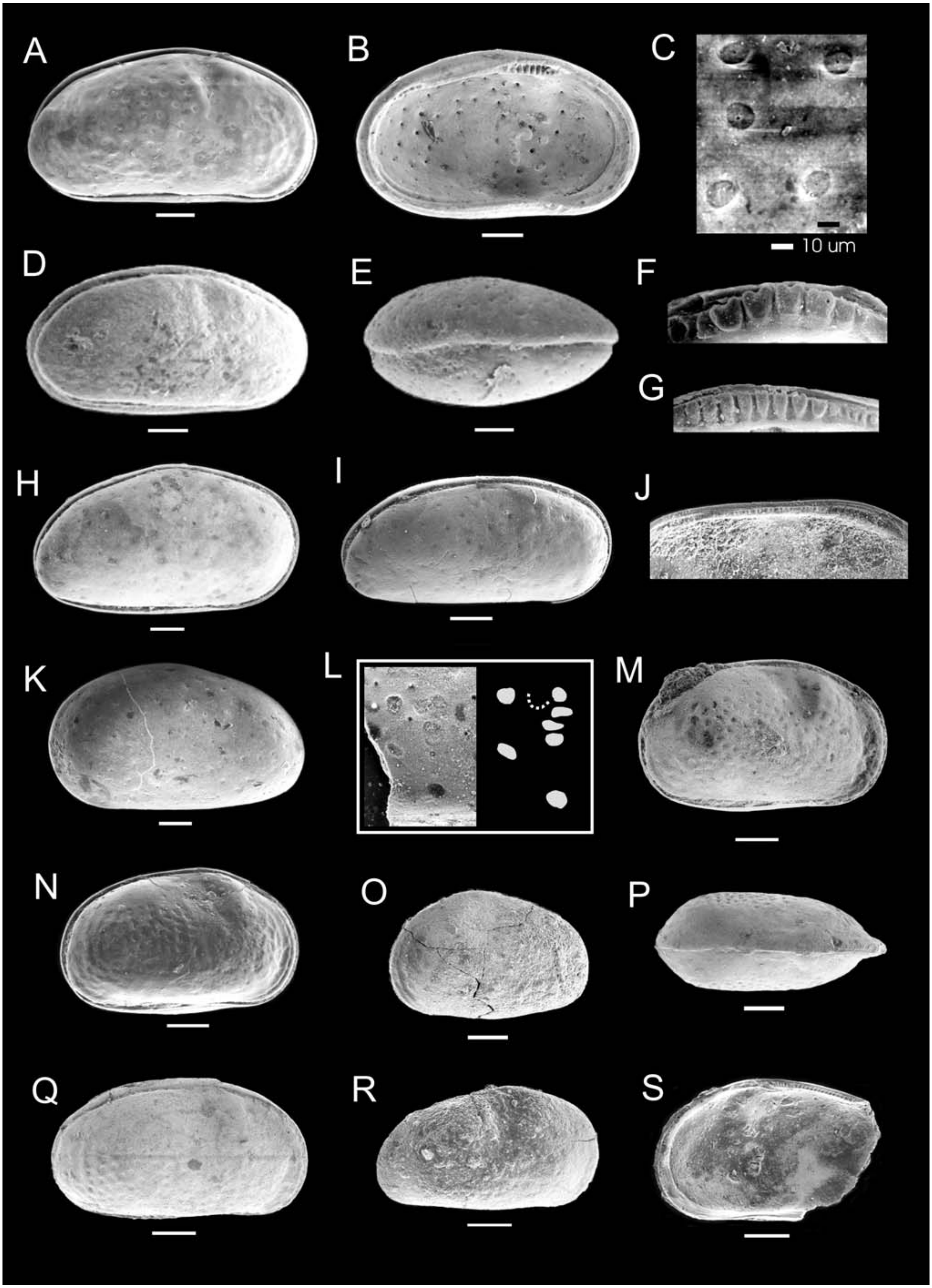
O left external aspect of juvenile disarticulated valve (Paratype USNM 520364)

P dorsal view of articulated adult valve that illustrates the lateral compression (Paratype USNM 522947)

Q right external aspect of articulated adult (Paratype USNM 522948)

R right external aspect of disarticulated juvenile valve (Paratype USNM 522949),

S internal view of adductor muscle scar field and hinge of right disarticulated valve (Paratype USNM 522950).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Juvenile	603	360	270
Juvenile	468	285	
Juvenile	455	234	
Juvenile	360	216	

Geologic Range: Early to middle Turonian (*Pseudospidoceras flexuosum – Prionocyclus hyatti* ammonite biozones).

Paleoecology: Associated with *Looneyella* spp., *Cytheromorpha* spp., and a rich assemblage of estuarine agglutinated foraminifera (Tibert and Leckie, in press). Charophytes and nonmarine ostracodes rarely occur with *F. posterovata* that we attribute to meso-to-normal marine conditions. Numerous species of marine ornate gastropods and bivalves also characterize the fauna.

Fossocytheridea dimorphicus (Puckett 1994)

Antibythocypris sp. A PUCKETT 1994, figs. 78, 7.11, 7.13, 7.14.
?*Fossocytheridea*? n. sp. GOHN, et al. 1992, p. 7-9, pl. 1, fig. 14.
Antibythocypris dimorphicus PUCKETT 1994, p. 1327-1328, figs. 4.7, 4.8, 6.1, 6.2. – PUCKETT 1996, p. 62-63, pl. 2, figs. 9-11, 13, 15.

Remarks: Gohn et al. (1992) proposed that this new species from the Gulf region of the United States be assigned to *Fossocytheridea*. Puckett (1994), however, suggested that the genus *Fossocytheridea* might be invalid because of confusion regarding the holotype elected by Swain and Brown (1964) for *Fossocytheridea lenoirensis*. As a result, Puckett (1994) placed this newly described species in the genus *Antibythocypris* Jennings and commented that the new species maintains a different lateral outline than all other taxa within that genus. We feel that the acuminate posterior, the distinct dimorphism, the numerous thin radial pores, the antimerodont hinge, and the sieve type normal pores warrant placement in the genus *Fossocytheridea* as originally suggested by Gohn et al. (1992). This taxon occurs in an Upper Santonian (Eutaw Formation) oyster reef association in Alabama.

Fossocytheridea maliensis (Colin et al. 1996)

Neocyprideis aff. *N. mississippiensis* HOWE and LAURENCICH in Carbonel and Monciardini 1995, p. 59-60, pl. 6, figs. 9-12.
Sarlatina maliensis COLIN et al. 1996, p. 216, pl. 1, figs. 1-5.

Remarks: Colin et al. (1996) described this species from west Africa and assigned it to *Sarlatina*. The heart-shaped antimerodont hinge elements, the external shape, sulcation, and dimorphism clearly justify placement within *Fossocytheridea*. Specimens occur in Campanian-Maastrichtian nonmarine and brackish beds in Mali, west Africa.

Fossocytheridea transatlasica (Andreu 1991)
Plate 2, figures F, H, J, K, N

Dolocytheridea (*Parasternbergella*) sp. 6 ANDREU 1991, pl. 16, figs. 5-12, pl. 17, figs. 1-4.
Dolocytheridea (*Parasternbergella*) *transatlasica* ANDREU 1996

Material: Cenomanian, North Africa. Dozens of specimens.

PLATE 2

All scale bars equal 100µm unless otherwise indicated.

Fossocytheridea posterovata (Lankford 1953). Turonian – Markagunt Plateau, Pausagunt Plateau, and Kaiparowits Plateau Utah.

A left external aspect of adult carapace that illustrates a faint anterior reticulation (Paratype USNM 522951)

B dorsal view of articulated adult carapace showing shallow sulcation and swollen posterior

C interal view of adductor muscle scar field and corresponding line tracing of a disarticulated right valve

D internal view of the hinge area of a disarticulated left valve

E, G right external aspects of two articulated adult valves.

Fossocytheridea transatlasica (Andreu 1996). Cenomanian – North Africa.

F internal view of disarticulated right valve

H left external aspect of disarticulated valve

J right external aspect of articulated adult carapace

K right external aspect of disarticulated adult valve showing a shallow sulcus

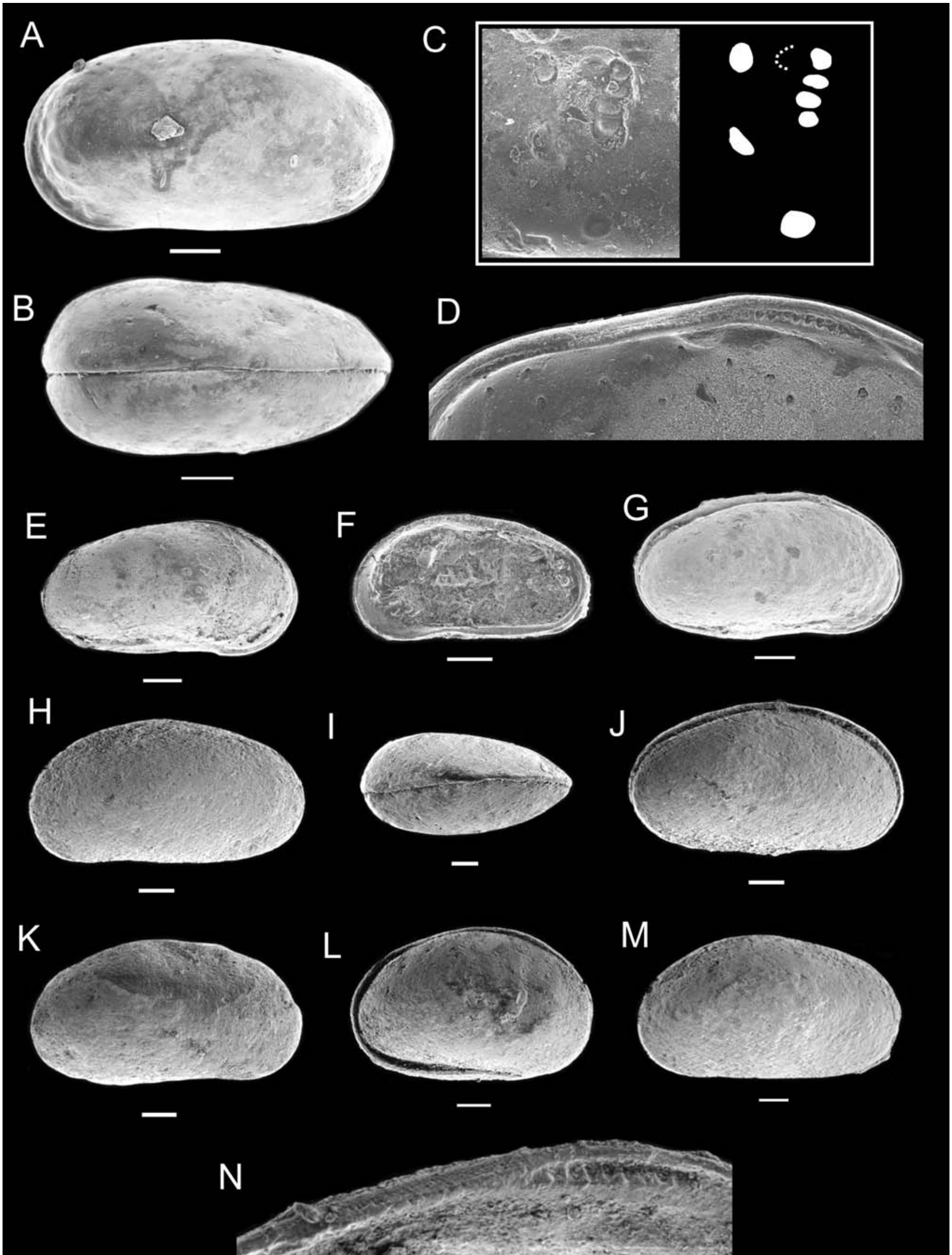
N internal view of hinge area of disarticulated left valve showing dentition of heart-shape terminal elements.

Fossocytheridea sp. 3 (Andreu 1991). Cenomanian – North Africa.

I dorsal view of adult articulated carapace (female)

L right external aspect of articulated adult carapace (female)

M left lateral aspect of disarticulated left valve (male).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Remarks: A species of *Fossocytheridea* as identified by the antimerodont hinge with heart-shaped elements and the median sulcus. The specimens maintain a somewhat triangular outline where the anterior and posterior margins are gently sloped. The dorsum is incised at the position of the hinge observed in dorsal view. Dimorphism is pronounced. This species differs from other species of *Fossocytheridea* because of the fewer (18-20) and thicker marginal pore canals, the acute anterior, and the weakly incised dorsum. This species occurs in Cenomanian-Santonian marginal marine facies in Morocco.

Fossocytheridea sp. 3 (Andreu 1991)
Plate 2, figures I, L, M

Dolocytheridea sp. 3 ANDREU 1991, pl. 15, figs. 12-16.

Material: Cenomanian, North Africa. Dozens of abraded specimens.

Remarks: A species of *Fossocytheridea* from the Cenomanian of Africa that resembles very much *F. merlensis* in lateral outline. The internal features are poorly preserved and require further study. This species occurs in marginal marine facies from Portugal in rocks of Cenomanian age and may be synonymous with *F. merlensis* given the close proximity of two localities.

Tribe Cyprideidini — Halobionts From Mesozoic To Recent

Swain and Brown (1964) highlighted the resemblance between *Fossocytheridea* and *Cyprideis*. Babinot and Colin (1976) advanced this hypothesis further and provided a phylogenetic history for the Cyprideidini lineage (text-fig. 6). Colin and Carbonel (1990) and Colin et al. (1990) discussed the origin of the Cyprideidini and showed that the hingement, dimorphism, and sulcation of *Sarlatina* made it a likely ancestor to the modern *Cyprideis*. What was apparently missing for *Sarlatina* were the observed noding, oblong pore shapes, and general patterns of reticulation seen in *Cyprideis*. This discussion outlines the morphologic features of *Fossocytheridea* (both external and internal) that include the patterns of reticulation, porosity, and noding that confirm the earlier suggestion that Mesozoic Cytherideinae are in fact ancestral to *Cyprideis*. Lastly, we briefly discuss the unique Tethyan global setting and the role that the environment played to advance the rapid speciation of Fossocytheridea during Cenomanian-Turonian times (text-figs. 6, 7, 8).

Internal Features — Muscle Scars and Hingement

Babinot and Colin (1976) and Colin and Carbonel (1990) attribute the origin of the Cyprideinini to *Fabanella* and this genus is a potential descendant of *Phraterfabanella* (Boomer et al. (2001). We recognize 2 lineages based on hinge development: *Neocyprideis* and *Cyprideis* (text-fig. 8). The *Neocyprideis* lineage is characterized by a relatively short median hinge element that has persisted since the Campanian (e.g., *Neocyprideis coudouxensis* Babinot 1975 and *Neocyprideis murciencis* Damotte and Fourcade 1971) and a modern representative, *Tanganyikacythere* Ducasse and Carbonel 1993 can be found in African lakes. The *Cyprideis* lineage is characterized by a relatively long median hinge element. The fundamental differences between *Fossocytheridea* and *Cyprideis* is that the former exhibits antimerodont dentition (tripartite) and this represents a contrast to the entomodont dentition (quadrapartite) of the latter (text-fig. 8).

All species exhibit tripartite hinges, but *Fossocytheridea merlensis* shows a peculiar change in tooth relief and vertical orientation immediately posterior of the anterior hinge element which can be considered pseudoentomodont (Plate 2, D). Because *Cyprideis* is apparently restricted to the Neogene (van den Bold 1976), the origin of the quadrapartite entomodont hinge in the lineage remains undetermined. Liebau (1971; aff. ? *Cyprideis*) potentially reports the oldest occurrence of a entomodont hinge from Maastrichtian brackish strata in the southern Pyrenees. Plate 4 illustrates the similarities between specimens of *Fossocytheridea posterovata* and *Cyprideis australiensis*. The general shape and muscle fields are obvious, however, the heart-shaped hinge elements should be regarded as a diagnostic character of the Cyprideidini lineage.

With respect to the central muscle scar field, *Cyprideis* and *Fossocytheridea* both exhibit a standard vertical array, a fulcral point, frontal scars, and a lower ventral scar that apparently have changed little from Mesozoic to Recent times (Plate 4). Identification of a median sulcus and carapace reticulation in Mesozoic-Cenozoic Cytherideidae should prompt future researchers to closely examine the internal shell features, especially in the areas of hingement. For example, Howe (1971) describes torose Cytherideidae including taxa assigned to *Ouachitaia*, *Cocoaia*, *Vetustucytheridea* which pending further study may include species of the Cyprideidini (see plate 1, Howe 1971).

External Features — Reticulation and Pore Morphology

Evident from taxonomic descriptions herein, are patterns of shell reticulation and pore characteristics that existed for

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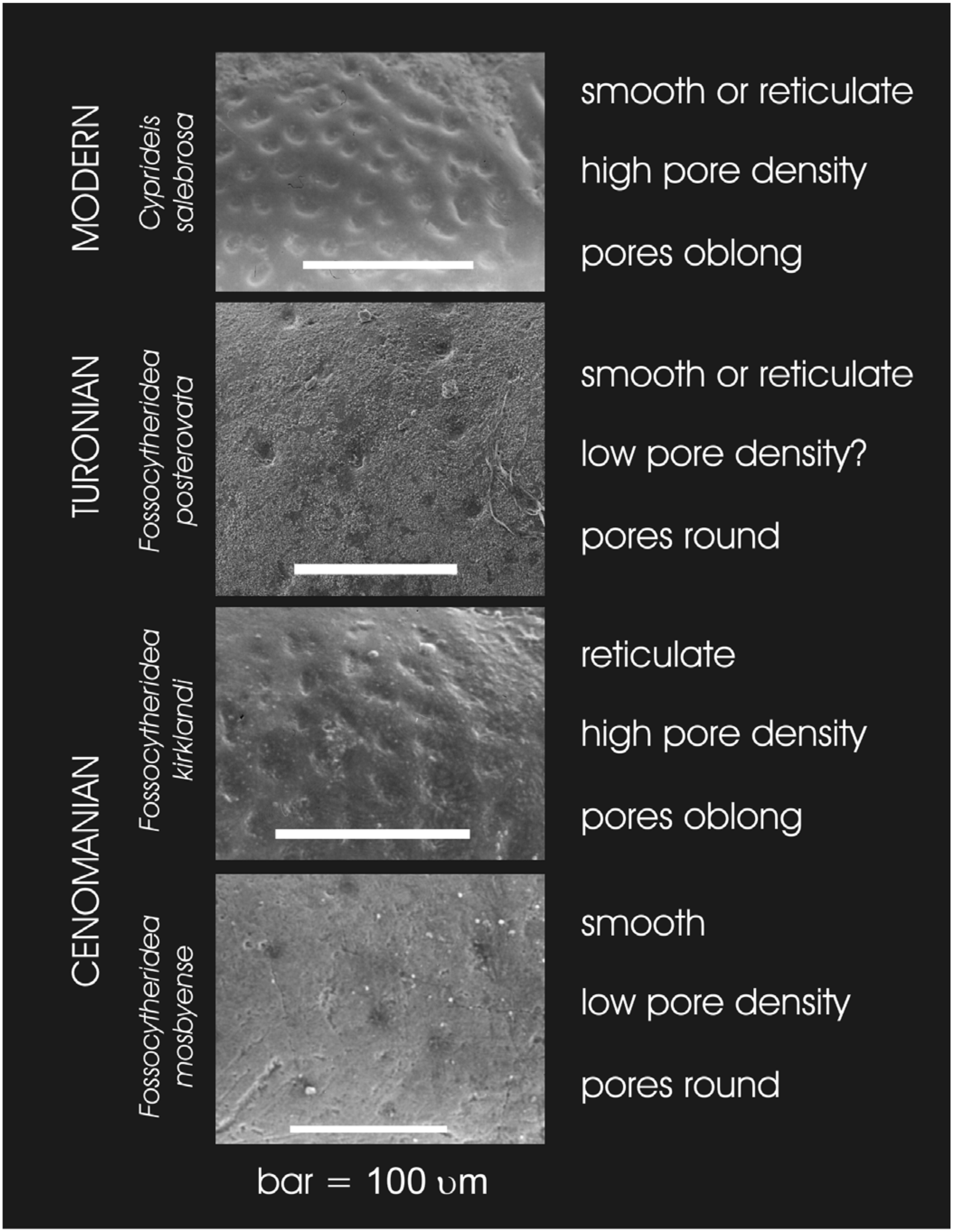
PLATE 3

All scale bars equal 100µm unless otherwise indicated.

Composite plate showing the pore shape, distribution density, and general reticulation of the 3 species of *Fossocytheridea* from southwest Utah compared with a specimen of *Cyprideis salebrosa* obtained from the high marsh along the Hudson River, New York (USA). Note that *Fossocytheridea kirklandi* sp. nov. has a pattern similar to *Cyprideis salebrosa*; both represent low salinity brackish conditions as indicated by associated nonmarine biota (chara and viviparid gastropods). *Fossocytheridea mosbyense* and *Fosssocytheridea posterovta* contrast *Fossocytheridea kirklandi* in that they posses low pore densities, circular shapes, and smooth carapaces; they both occur in association with rich estuarine foraminiferal populations and marine invertebrates (Tibert and Leckie, in press).


MODERN
Cyprideis salebrosa
smooth or reticulate
high pore density
pores oblong
TURONIAN
Fossocytheridea posterovata
smooth or reticulate
low pore density?
pores round
CENOMANIAN
Fossocytheridea kirklandi
reticulate
high pore density
pores oblong
Fossocytheridea mosbyense
smooth
low pore density
pores round
bar = 100 υm

Fossocytheridea from the Albian through to Maastrichtian times. Detailed examination of the external carapace shows that the ancestral Cyprideidini had an antimerodont hinge and their external surfaces were characterized by circular normal pores that contained a depressed sieve plate with a central or subcentral smaller pore (Plate 1C, Plate 3). This pore type satisfies Puri s (1974) Type C Pore classification of the Cyprideidini.

With respect to pore shape and distribution density, both *Fossocytheridea mosbyense* and *Fossocytheridea posterovata* maintain a generally smooth carapace, small circular pores, and low pore density (Plate 3). In contrast, *Fossocytheridea mosbyense* bears a striking resemblance to *Cyprideis* with respect to the irregular oblong pores located posterior of the oblique median sulcus (Plate 3). Further, *Fossocytheridea mosbyense* and *Fossocytheridea posterovata* exhibit reticulation patterns along the anterio-ventral margin (Plate 3). We propose that the pore shape, pore distribution, and patterns of carapace reticulation, that vary within the genus of *Fossocytheridea*, probably record changing environmental conditions during carapace growth. This is supported by our observation that increased reticulation and pore irregularity occur at the westernmost position of the shoreline in restricted facies (Locality 1) associated with a low salinity fauna (see next section). Similar morphologic expressions have been observed for *Cyprideis* where the shape and distribution density of the pores vary with changing salinity and ion composition of the water (Rosenfeld and Vesper 1977).

Fossocytheridea lenoirensis and *Fossocytheridea kirklandi* both show evidence for sulcus depth and obliquity variations. Colin and Danielopol (1980) and Carbonel et al. (1988) point out that the sulcus amplitude in all tribal genera (*Fossocytheridea*, *Sarlatina*, and *Cyprideis*) may relate to termination of the calcification process at different developmental stages. We feel that the differences between pore shape and depth and orientation of the sulcus may have recorded variable environmental conditions during development, and this has also been documented in Quaternary populations of *Cyprideis* (Schweitzer and Lohmann 1990; Whatley et al. 1998).

Ecology and Carapace Morphology

Locality 4 (text-fig. 1) marks the most distal brackish water deposits of the Cenomanian-Turonian in southwest Utah. Within these estuarine facies (Tibert et al. 2003), specimens of *Fossocytheridea mosbyense* occur in carbonaceous units overlain by calcareous mudstones that contain planktonic foraminifera and marine ostracodes that include *Cythereis eaglefordensis, Cytheropteron eximium*, and *Clithrocytheridea* (?). In general, specimens of *Fossocytheridea mosbyense* are smooth and they occur with rich agglutinated foraminiferal populations dominated by *Trochammina*, *Ammobaculites*, and *Miliammina* that indicate estuarine conditions (Tibert et al. 2003); marine ostracodes are uncommon at western localities (Localities 2, 3) where *Cythereis eaglefordensis* and *Clithrocytheridea*? comprise only a few disarticulated valves. Our most proximal locality is positioned in the vicinity of the Pine Valley Mountains (Locality 1). These strata were deposited at the foot of the ancient Sevier Mountains and mark the most landward position of the Cenomanian-Turonian shoreline (text-fig. 1). Brown, calcareous, organic-rich mudstones enclose specimens of *Fossocytheridea kirklandi* noted for their enhanced patterns of reticulation and intense sulcation (pl. 1, figs. M, P, Q). At this locality, monospecific populations of *Fossocytheridea kirklandi* occur with charophytes, nonmarine gastropods, and the bivalve *Unio* (Kirkland pers. comm. 2000). The total absence of foraminifera testifies to low salinity conditions far removed from direct marine influence.

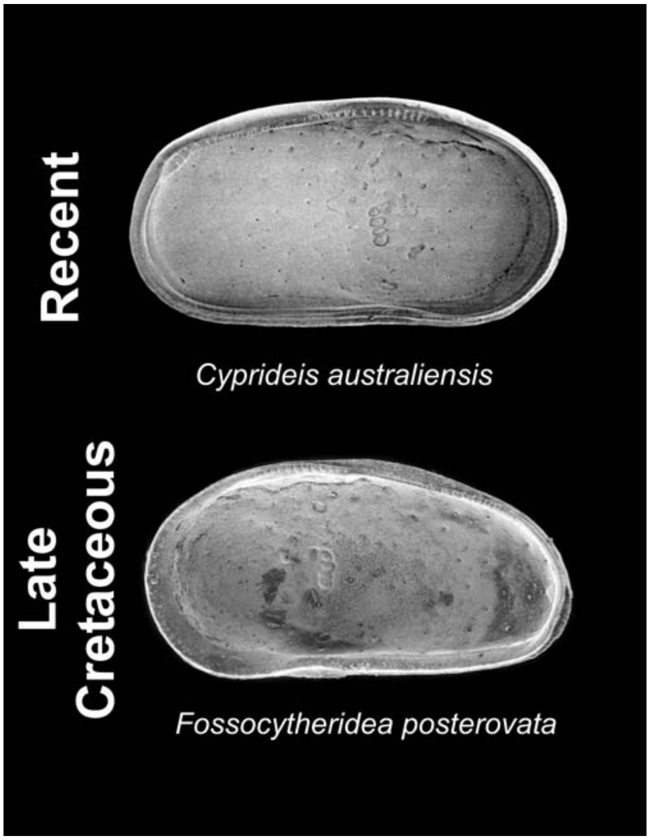


PLATE 4

Fossocytheridea posterovata (right valve, Turonian — Markagunt Plateau, Utah) compared with *Cyprideis australiensis* (internal view of left valve; image modified from DeDeckker et al. 1988, cover inset). Note the similarity in the lateral outline and the dentition.

Rosenfeld and Vesper (1977) demonstrated that both pore distribution density and shape irregularity in *Cyprideis* increase when salinity ranges from optimal; either hyposaline or hypersaline. Noding of the carapace is most prominent in extremely low salinity settings (Van Harten 1975; Gliozzi and Mazzini 1998) and *Fossocytheridea lenoirensis* records this phenomenon along the latest Albian Atlantic Coastal Plain (Swain and Brown 1964). Numerous chemical studies (Mg/Ca and Sr/Ca) of the ostracode carapace suggest that the ionic concentration (especially Mg and Sr) of the water and not simply water salinity influences the observed patterns of carapace reticulation (De Deckker 1981; Carbonel 1988; Carbonel et al. 1988; De Deckker et al. 1988; De Deckker and Forester 1988). Peypouquet et al. (1988) show that there is a relationship between patterns of reticulation and the amount of detrital organic matter that can greatly effect the carbonate equilibrium at the water/sediment interface which may have some bearing on whether or not a carapace aggrades (e.g., increased reticulation) or degrades (e.g., thinly calcified). What is most striking for *Fossocytheridea*, is that the low salinity faunal associations that include nonmarine Cyridacea, *Darwinula* spp., brackish Cytherideidae (e.g. *Clithrocytheridea*), charophytes, the brackish gastropods *Admetopsis* and *Craginia*, and the brackish bivalves *Carycorbula* and *Fulpia* (Tibert et al. 2003). Assemblages from Florida (Swain 1982) and western Europe (Babinot and Colin 1976; Colin 1983; Colin and Carbonel 1990; Colin et al. 1990; Colin et al. 1996) also yield similar low salinity biotic associations where ostracode populations are dominated by *Fossocytheridea*. Given these observations, it is likely that carbonate availability in a low salinity setting contributed to the observed phenotypic variability of *Fossocytheridea*.

Ontogeny and Development

Schweitzer and Lohmann (1990) illustrated delayed development and accelerated maturity for modern species of *Cyprideis* and they suggested that ontogeny contributes to the microspeciation process in marginal marine environments. Similar ontogenetic trends in the fossil record are not uncommon (Reyment 1988). An interesting feature observed for *Fossocytheridea* from southwest Utah, is that we cannot distinguish between the early instars for most taxa (A-9 A-2) (text-fig. 9). Given that the descendant adults resemble late instar and adult ancestors (referred to as paedomorphosis), ontogeny may have factored significant during speciation of the late Cretaceous *Fossocytheridea*.

Overall, it may be that the brood rearing capacity of the Cyprideidini lineage contributed to its success; this mechanism has been inferred for many sulcate genera of Cytherideidae that occur in the restricted fauna of the Upper Jurassic-Lower Cretaceous Purbeck-Wealden facies (Horne 1995). The fundamental characters and opportunistic strategies that typify most eurytopic taxa (e.g. brood rearing, phenotypic plasticity) were expressed in *Fossocytheridea* during the late Mesozoic and this ultimately contributed to the success of the Cyprideidini.

Global Setting and Evolutionary Considerations

Stepped speciation patterns characterize the lineage of *Fossocytheridea* across the Cenomanian/Turonian boundary interval (text-fig. 7). This same speciation pattern is recorded in the normal marine mollusks that occur in coeval marine facies of the Tropic Shale (Elder 1987, 1991) and for the brackish molluscan associations that co-occur with *Fossocytheridea* on Markagunt Plateau (Locality 2; see fig. 4 in Eaton et al. 2001). *Fossocytheridea mosbyense* sp. nov. is restricted to the upper Cenomanian *Metoicoceras mosbyense* ammonite zone, *Fossocytheridea kirklandi* sp. nov. is restricted to the uppermost Cenomanian *Sciponoceras gracile* and *Neocardioceras juddii* ammonite zones, and *Fossocytheridea posterovata* is confined to the Turonian (Tibert and Leckie, in press). We have not identified any of these species together within a single sample. As mentioned above, the uppermost beds of a given ammonite biozone contain end member specimens which we believe are intermediate forms between taxa; where *Fossocytheridea kirklandi* is intermediate between *Fossocytheridea mosbyense* and *Fossocytheridea posterovata*. The nearly continuous temporal record within this stratigraphic succession supports this observation. Apparently, *Fossocytheridea* experienced heightened and fairly rapid turnover across the Cenomanian-Turonian boundary interval spanning several hundreds of thousand years (text-figs. 2, 7); these ages are approximated using the ammonite biozones calibrated to radiometrically dated volcanic ash beds (Kauffman et al. 1993; Obradovich 1993).

What are the mechanisms responsible for the speciation of *Fossocytheridea* during the middle Cretaceous? The Cenomanian-Turonian was a time when heightened global sea level contributed to an expansion of marginal marine habitats world-wide (Hancock and Kauffman 1979; Haq et al. 1988). Also at this time, oxygen depletion characterized the ocean basins (Jarvis et al. 1988; Whatley 1991; Johnson 1996) and this event has been identified in the Western Interior Basin (Elder 1991; Leckie et al. 1991, 1998; Pratt et al. 1993; West et al. 1998). Whatley (1988) and Babinot and Airaud (1990) report significant species level turnover at the Cenomanian-Turonian boundary (~80-90%); yet, few genera and families went extinct. It is certainly no surprise, therefore, that the potential ancestor to *Cyprideis* saw enhanced rates of speciation at this time. We ascertain that *Fossocytheridea*, with the capacity to brood rear and to adjust its external morphology to adverse and persistent environmental change, reveals a record of selective preservation of the very characters that have contributed to the success of the Cyprideidini lineage.

In terms of dispersal mechanisms, the late Cretaceous was characterized by a global Tethyan circulation pattern, a situation ideal for latitudinal migration within tropical to warm temperate zones. The paleographic distribution of *Fossocytheridea* illustrates that the expansion and migration occurred largely within and adjacent to the Tethys Ocean (text-fig. 4). Indeed, Babinot and Colin (1992) report similar paleogeographical distribution patterns for shallow and deep-water ostracode faunas. The Cyprideidini as a whole, are well-equipped to endure harsh environments and their patterns of rapid speciation are exemplified in the more than 15 species associated with a *Neocyprideis* faunas in Lake Tanganyika and the *Cyprideis* faunas of the Miocene-Pliocene Paratethys (Bassiouni 1979). Whatley et al. (1998) also document rapid speciation during the Miocene in the Upper Amazon Basin which is an isolated body of saline water. We believe that it is the evolutionary and environmentally cued expressions (Peypouquet et al. 1988) of Cyprideidini ostracodes that aided their survival during both active (e.g., *via* animals) and passive transport (e.g. *via* storm surges) within marginal marine settings, which is a process described for modern *Cyprideis* (Sandberg and Plusquellec 1974). The success of the Cyprideidini since the Cenomanian-Turonian and their dominance in modern marginal habitats is a strong testament for this hypothesis.

CONCLUSIONS

The genus *Fossocytheridea* encompasses all Mesozoic taxa that possess traditional Cytherideidae muscle fields, sulcation, and variable external morphologies that include species previously assigned to *Sarlatina* which is therefore considered as a junior synonym of *Fossocytheridea*. Twenty-three species that range in age from Albian to Maastrichtian are attributed to the emended genus *Fossocytheridea*. These include taxa previously assigned to *Ovocytheridea*, *Clithrocytheridea*, *Asciocythere*, *Antibythocypris*, and *Dolocytheridea*. Two new species are described from southwest Utah: *Fossocytheridea mosbyense* and *Fossocytheridea kirklandi*. The genus *Fossocytheridea* is considered the ancestor to the modern eurytopic ostracode *Cyprideis* based on the following aspects of their occurrence:

1) Internal characters: Cytherideidae central muscle field and a crenulate antimerodont hingement;

2) External carapace morphology: median straight to oblique sulcus, Type C normal pores that show variable patterns of surface density and general shape, and variable antero-lateral reticulation (including rare noding);

3) Association with marginal and/or restricted marine deposits and low salintiy biota that include nonmarine charophytes, gastropods, and mollusks, agglutinated foraminiferal assemblages, and other brackish invertebrate taxa;

4) Pronounced dimorphism and potential brood rearing capacities that promoted survival during significant oceanographic perturbations during the middle Cretaceous; and

5) Paleogeographic distribution along the marginal marine habitats of the Late Cretaceous circum-Tethys.

Paleoenvironmental conditions influenced both distribution and speciation patterns in *Fossocytheridea* during late Cretaceous times. It is our hope that closer examination of both Mesozoic and Cenozoic sulcate Cytherideidae will ultimately result in more taxa being assigned to the Cyprideidini.

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