

A revision of selected Lower Cretaceous American caprinoid rudists: implications for phylogeny and biostratigraphy

SIMON F. MITCHELL

Department of Geography and Geology, The University of the West Indies, Mona, Kingston 7, Jamaica
(email: barrettia2000@yahoo.co.uk)

ABSTRACT. A revision of the Caprinuloideidae Damestoy is undertaken investigating the myocardial arrangements, the presence or absence of an external ligamental groove, and the distribution of pallial canals in order to arrive at a phylogenetically sound method of classification of the family. The Caprinuloideidae are placed in the Caprinoidea d'Orbigny under the suborder Radiolitidina Skelton, together with three other families: the Caprinidae d'Orbigny, the Ichthyosarcolitidae Douvillé and the Antillocaprinidae Mac Gillavry. The Caprinuloideidae is here subdivided into three subfamilies: the Amphitriscolinae subfam. nov., the Caprinuloideinae Damestoy, and the Youngicaprininae subfam. nov. The Amphitriscolinae subfam. nov. are characterized by a thin ventral wall adjacent to the body cavity that lacks pallial canals, the Caprinuloideinae, by a thickened ventral wall with pallial canals, and the Youngicaprininae subfam. nov. by a modified myocardial arrangement with a tooth-like anterior myophore and a ribbed posterior myophore. Two new genera are described; *Neokimbleia* gen. nov. and *Youngicaprina* gen. nov.; and three new species: *Neokimbleia acutus* gen. et sp. nov., *Youngicaprina sangabrielii* gen. et sp. nov. and *Y. gloria* gen. et sp. nov.

Key words: Rudist bivalves, Cretaceous, Albian, Caprinuloideidae, *Youngicaprina*, *Neokimbleia*.

1. INTRODUCTION

Lower Cretaceous caprinoid (formerly caprinid) rudists are important biostratigraphic indicators for the carbonate platforms of the New World (e.g., Palmer, 1928; Mac Gillavry, 1937; Coogan, 1973, 1977; Alencáster, 1999; Alencáster and Aguilar-Pérez 1996, Alencáster and Pantoja Alor, 1996a, b, c, 1998; Pantoja-Alor et al., 2004; Chartrousse and Masse, 2004; Scott, 2002; Scott and Filkorn, 2007). Their taxonomy has been developed during the last 100 years, or so, largely in a piecemeal fashion. In this study a revision of the group is undertaken with the intention of determining which characters are important for establishing genera and in refining their phylogeny. An additional objective of this paper is to provide a framework into which specimens can be placed to refine their biostratigraphic value.

The systematics of the caprinuloideid rudists are currently based largely on the distribution and form of the pallial canals, particularly which elements (teeth and myophores), if any, of the myocardial system are invaded by pallial canals (Palmer, 1928; Coogan, 1973, 1977). Less attention has been paid to the form of the myocardial arrangement, which, rather than pallial canals, would seem to represent a better way of classifying the group.

A particular problem also exists with the genus

Texicaprina. Coogan (1973) erected this genus and nominated *Sabinia vivari* Palmer, 1928, as its type species. The type material of *Sabinia vivari* is strongly recrystallized and the form of the teeth and myophores cannot be distinguished. Much of Coogan's (1973) description is based on *Sabinia kugleri* (Bouwman, 1937) from Trinidad, and most of these features cannot be seen in *S. vivari*. Because the type material of *Sabinia vivari* is too poorly preserved to fix the characteristics of a genus, we need to look to the *Code for Zoological Nomenclature* to address this problem.

In this study, nearly all the type and figured specimens of Albian caprinuloideids available in museum collections around the world have been re-examined and photographed, together with studies of abundant additional material in the Smithsonian Institute and the Texas Memorial Museum. The following is a list of institutions from which material has been studied together with their designation: The American Museum of Natural History (AMNH); California Academy of Sciences, San Francisco, California (CAS); Museum of Paleontology, Institute of Geology, Universidad Nacional Autónoma de México, Ciudad Universitaria, México (IGM); Naturhistorisches Museum Basel (NHB); The Natural History Museum, London (BMNH); The National Natural History Museum, Havana, Cuba (NNHMC); Naturalis, Leiden, The Netherlands

(NL); Smithsonian National Museum of Natural History, Washington D.C. (SNMNH); Texas Memorial Museum, University of Texas at Austin, Texas (TMM); Geological Museum, University of Puerto Rico, Mayaguez (UPRGM); and The University of the West Indies Geological Museum, Kingston, Jamaica (UWIGM).

2. SYSTEMATIC PALAEONTOLOGY

In this paper new genera and species are described, and where necessary new descriptions of previously published species are given. In order to understand the distribution of taxa both geographically and stratigraphically, synonym lists together with discussions are given for some other taxa. The classification adopted here broadly follows Skelton (2011, 2013 [this volume]) and Carter et al. (2011).

Order Hippuritida Newell, 1965

Suborder Radiolitidina Skelton, 2013

Discussion. Two suborders are recognized by Skelton (2013 [this volume]) in the Hippuritida, the Radiolitidina Skelton, 2013, for those forms attached by the right valve, and the Requiiniidina Skelton, 2013, for those forms attached by the left valve. The Radiolitidina is divided into two superfamilies, the Caprinoidea d'Orbigny, 1847, which includes four families (see below), and the Radiolitoidea d'Orbigny, 1847, which includes all other families in the Radiolitidina.

Superfamily Caprinoidea d'Orbigny, 1847

Diagnosis. Trace of ligamentary invagination marked by an external groove in primitive forms, but lost in several later derived forms. The posterior myophore of the left valve is rooted on the posterior valve wall and separated from the body cavity by a large endomyophoral cavity formed by a lamina extending from the anterior tooth to the postero-ventral margin. Primitive forms have the anterior tooth much larger than the posterior tooth, but this is lost in some more derived forms.

Discussion. Four families are recognized in the Caprinoidea d'Orbigny: the Caprinidae d'Orbigny, 1847 (Hauterivian to Albian), the Caprinuloideidae Damestoy, 1971 (Hauterivian to Cenomanian), the Ichthyosarcolitidae Douvillé, 1887 (Albian to Cenomanian), and the Antilocaprinidae Mac Gillavry, 1937 (Santonian to Maastrichtian). Only the Caprinuloideidae are discussed here, for further details see Mitchell

(2013 [this volume]) for the Ichthyosarcolitidae and Mitchell (in press) for the Antilocaprinidae.

Family Caprinuloideidae Damestoy, 1971

Diagnosis. An external groove marking the trace of ligamentary invagination is present as a primitive character but is secondarily lost in some more advanced genera. The posterior myophore of the left valve is a plate which projects into the endomyophoral cavity in the right valve and faces outwards towards the posterior wall of the right valve; the endomyophoral cavity of the right valve is separated from the body cavity by a septum. Pallial canals are developed in both valves of all but the earliest forms.

Discussion. The family is distinguished from the Caprinidae by the orientation of the posterior myophore (Chartrousse, 1998a). In the Caprinidae, the posterior myophore of the right valve is a projecting vertical plate separated from the posterior valve wall by a narrow ectomyophoral cavity and rotated into the left valve where it faces outward onto the inner face of the posterior myophore of the left valve. In contrast, in the Caprinuloideidae, it is the posterior myophore of the left valve that is rotated into the right valve to face outwards onto the posterior shell wall. Three subfamilies are recognized in the Caprinuloideidae here, the Amphitriscoelinae subfam. nov., the Caprinuloideinae Damestoy 1971, and the Youngicaprininae subfam. nov.

Members of the Amphitriscoelinae subfam. nov. are characterized by a thin ventral shell wall in which pallial canals are not developed, pallial canals are only developed in 'gutters' between the myophores and the shell margin. The Caprinuloideinae Damestoy 1971 are characterized by a thickened ventral shell wall in which pallial canals are developed around most or all of the circumference including the ventral shell wall. Both these families have plate-like myophores, whereas in the Youngicaprininae subfam. nov. the anterior myophore is modified, enwrapping the anterior tooth, whereas the posterior myophore becomes tooth-like.

Subfamily Amphitriscoelinae subfam. nov.

Diagnosis. A subfamily in which the ventral wall of the shell adjacent to the body cavity is not thickened and this part of the shell does not contain pallial canals. Pallial canals are therefore either absent (in primitive forms) or occur on the anterior or posterior sides of the shell where the

gutters between the myophores and the shell margin are subdivided to produce pallial canals. The posterior and anterior myophores of the left valve are wall-like and connected to the posterior and anterior teeth respectively.

Discussion. The subfamily Amphitriscoelinae subfam. nov. include five genera: *Retha* Felix, 1891, Hauterivian to Early Aptian (Skelton and Masse, 1998; Brown and Mitchell, 2010; Mitchell and Green, 2011); *Amphitriscoelus* Harris and Hodson, 1922, Late Barremian to Early Aptian (Pantoja-Alor et al., 2004; Skelton and Masse, 1998; Brown and Mitchell, 2010; Mitchell and Green, 2011); *Pantojaloria* Alencáster, 1996 (in Alencáster and Pantoja-Alor 1996b), Late Barremian to Early Aptian (Alencáster and Pantoja-Alor 1996b; Pantoja-Alor et al., 2004); *Conchemipora* Chartrousse and Masse, 1998, Early Aptian (Chartrousse and Masse, 1998); and *Oedomyophorus* Skelton, 2004, Early Aptian. The first three are recorded from the Caribbean-Central American region (Felix, 1891; Harris and Hodson, 1922; Skelton and Masse, 1998; Pantoja-Alor et al., 2004; Mitchell and Brown, 2010; Mitchell and Green, 2011); the fourth is recorded from the Pacific (Chartrousse and Masse, 1998); and the fifth is from Saudi Arabia (Skelton, 2004).

Subfamily Caprinuloideinae Damestoy, 1971

Diagnosis. A subfamily in which the ventral wall of the shell between the body cavity and the shell margin is thickened and contains one or more rows of pallial canals. The posterior and anterior myophores of the left valve are wall-like and connected to the posterior and anterior teeth respectively.

Discussion. The Caprinuloideinae Damestoy, 1971, includes a large number of genera: *Huetamia* Alencáster and Pantoja-Alor, 1998 (Early Aptian); *Coalcomana* Harris and Hodson, 1922 (Early Albian); *Planocaprina* Palmer, 1928 (Early Albian); *Caprinuloidea* Palmer, 1928 (Early to Late Albian); *Mexicaprina* Coogan, 1973 (Late Albian); *Kimbleia* Coogan (Late Albian); and *Neokimbleia* gen. nov. (Late Albian). The myocardial arrangement in *Muellerreidia* Alencáster, 1998, is essentially identical to that of *Mexicaprina* Coogan, 1973, and therefore *Muellerreidia boesei* Alencáster, 1998, which has a short right valve, is placed in *Mexicaprina* here.

Huetamia is seen here as the route of all the Caprinuloideinae. Chatrousse (1998b, p. 118)

noted that in some of the pyriform canals in this genus, a transverse septum divided off an inner rounded canal from the outer canal. The same feature is also seen in some specimens of *Coalcomana*, and numerous canals are seen in other taxa (*Caprinuloidea*, *Mexicaprina*, *Kimbleia*, etc.).

Genus *Caprinuloidea* Palmer, 1928

Type species. *Caprinuloidea perfecta* Palmer, 1928, from Soyatlan de Adentro (?Early Albian), state of Jalisco, Mexico.

Diagnosis. A genus of Caprinuloideinae characterized by an external ligamental groove that is connected by a fissure to an inner crescentric or hook-shaped ligament, two or more rows of pallial canals within the shell wall, and wall-like anterior and posterior myophore plates in the left valve, the former fitting onto a ledge and the latter into a cavity in the right valve.

Discussion. *Huetamia*, *Coalcomana* and *Caprinuloidea* form an evolutionary plexus beginning in the Early Aptian and ending in the Late Albian. It would appear that there is a gradation between these forms in relation to the distribution of pallial canals, beginning with an incomplete circuit of simple canals (with occasional rounded canals) in *Huetamia*, canals which are subdivided in *Coalcomana* leading to first a few and later many rows of polygonal canals (earlier *Caprinuloidea*) and finally the invasion of canals into other elements of the myocardial structure (later *Caprinuloidea*). Although the names are somewhat artificial (although transitional forms between *Coalcomana* and *Caprinuloidea* have not been seen), they are valuable in biostratigraphic studies because forms having a single row (albeit having occasional rounded canals) of complex pallial canals (*Coalcomana*) are limited to the Early Albian; and for this reason the generic names are retained here.

The holotype of *Caprinuloidea perfecta* Palmer is a large bivalved specimen (but see Chartrousse, 1998b, and below under type specimen) that was apparently disarticulated to show the apertural surfaces of the left and right valves, although the myophores of the left valve are partly damaged. The diagnoses of the genus as given by Palmer (1928) and Coogan (1977), refer to an external row of pyriform canals and an internal row or rows of polygonal canals; they do not mention the presence of canals in the central tooth or the myophoral

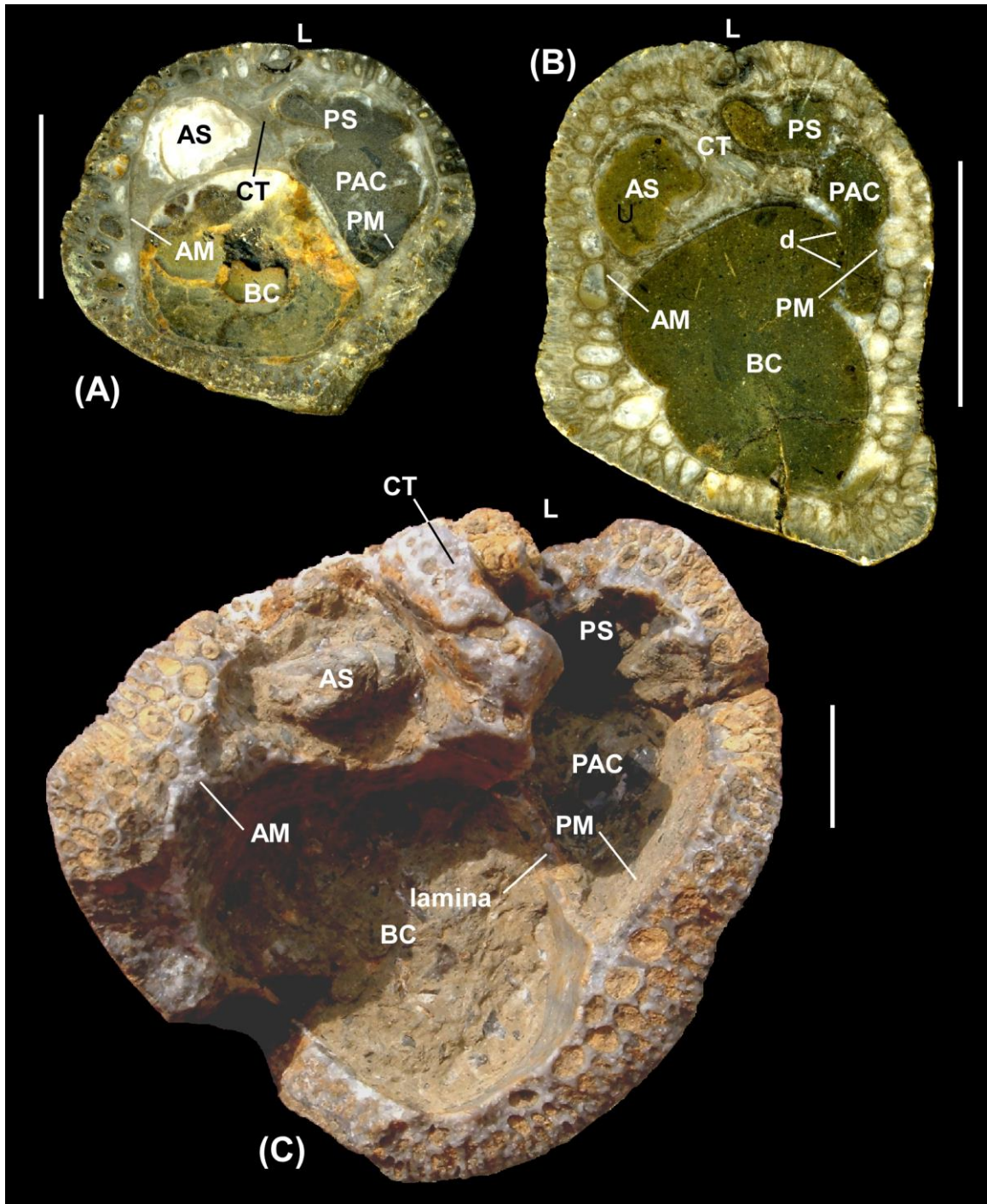


Figure 1. A, *Caprinuloidea septata* Palmer 1928, holotype (CAS.66651-11, Palmer's no. 2171), Right Valve cut below the commissure, adapical view, note the lack of pallial canals invading the Central Tooth. B-C, *Caprinuloidea perfecta* Palmer 1928. B, holotype of *Caprinuloidea perfecta gracilis* Palmer 1928 (CAS.66651-10, Palmer's no. 2169), Right Valve cut just below the commissure, adapical view, note central tooth with small pallial canals and a few pallial canals invading the Anterior Myophore region. C. *Caprinuloidea perfecta*, holotype (CAS.2168), right valve, apertural view, note pallial canals in the central tooth. All specimens from Soyatlan de Adentro, state of Jalisco, Mexico. AS, anterior socket; PS, posterior socket; CT, central tooth; AM, anterior myophore attachment area; PM, posterior myophore attachment area; L, ligament; PAC, endomyophoral cavity; BC, body cavity; d, damaged areas. Scale bar is 20 mm long.

areas which are clearly visible in the type specimens of *Caprinuloidea perfecta* (Figure 1C) and less distinctly in *Caprinuloidea perfecta gracilis* Palmer (Figure 1B). Coogan's (1973, 1977) diagnosis of *Texicaprina* relies on the invasion of pallial canals into the teeth and myophores (since other characters he mentions are not visible in the type specimens of the type species of his genus), something that is already apparent in the right valves of the type specimens of *C. perfecta* and *C. perfecta gracilis* (see also Chartrousse, 1998b, p. 137, figs. 38, 39).

From an examination of type specimens of the various species assigned to *Caprinuloidea* as well as an analysis of a large numbers of specimens preserved in the Smithsonian Institution and the Texas Memorial Museum, specimens of *Caprinuloidea* can be divided into three main groups: (1) those in which the central tooth is completely solid, as in the holotypes of *Caprinuloidea septata* Palmer and *C. multitubifera* Palmer; (2) those specimens in which the central tooth is invaded by small to normal sized pallial canals as in the holotypes of *Caprinuloidea perfecta* and *C. perfecta gracilis*; and (3) those forms in which large canals invade the myocardial areas as in *Caprinuloidea romeri* sp. nov. The type specimens of *Caprinuloidea septata*, *C. multitubifera* and *C. perfecta* come from Soyatlan de Adentro (Palmer, 1928) where they occur with *Coalcomana ramosa*, yet outcrops here (written commun., Peter Skelton 2013) consist of roadside exposures and the stratigraphic relationship of these forms cannot be determined. Elsewhere (e.g., the Seaford Limestone of Jamaica), *Caprinuloidea multitubifera* and *C. perfecta* and *Coalcomana ramosa* occur together (Brown and Mitchell, 2011; Mitchell and Green, 2011) although this does not appear to be the case in Texas (Scott, 2002). Whether forms of *Caprinuloidea* that lack pallial canals in the central tooth (*C. septata*) occur at a lower level than those that have them (*C. perfecta*) is not known. Yet, the progressive invasion of pallial canals into the central tooth of the right valve, the myocardial areas of the right valve, and the myophores of the left valve, as described here, could represent a progressive sequence that might allow the erection of chronospecies for high-resolution biostratigraphy. This is further strengthened by the case that the holotype of *C. perfecta* already has canals invading the central tooth. In this paper, four species of *Caprinuloidea* are recognized and discussed below.

***Caprinuloidea septata* Palmer, 1928.**

Figure 1A

- ? 1898 *Sphaerucaprina Felixi* n. sp.: G. Boehm, p. 329, fig. 6 (LV).
- ? 1898 *Sphaerucaprina Lenki* n. sp.: G. Boehm, p. 330, fig. 7.
- v. 1928 *Caprinuloidea septata*: Palmer, p. 62, pl. 9, fig. 4, pl. 10, fig. 3, pl. 11, fig. 1.
- ? 1977 *Caprinuloidea felixi* (Boehm); Coogan, pl. 13, fig. 7 (LV from Boehm 1898, fig. 6)
- ? 1977 *Caprinuloidea lenki* (Boehm); Coogan, pl. 13, fig. 2. (LV from Boehm 1898, fig. 7)

Type specimen. Holotype (CAS.66651-11, Palmer No. 2171) from Soyatlan de Adentro, State of Jalisco, Mexico.

Discussion. The name *Caprinuloidea septata* Palmer is used here for forms in which the central tooth and myophore areas of the right valve are composed of compact shell material and lack pallial canals and in which both the anterior and posterior myophores are represented by narrow wall-like plates. Whereas right valves can be easily assigned to this species, left valves do not show sufficiently diagnostic characters that allow distinction between *C. perfecta* and *C. septata*. Boehm (1898) figured several left valves under the names *Sphaerucaprina Lenki* Boehm and *S. Felixi* Boehm that might belong to this species. Since these species are based on left valves, they cannot be unambiguously placed in current species concepts.

Distribution. *Caprinuloidea septata* has only been described from the ?Early Albian of Soyatlan de Adentro, State of Jalisco, Mexico (Palmer, 1928), but might be found where the details of the Right Valve can be seen.

***Caprinuloidea perfecta* Palmer, 1928.**

Figure 1B-C

- v. 1928 *Caprinuloidea perfecta*: Palmer, p. 59-60, fig. 6., pl. 8, fig. 8, pl. 9, figs. 1-2.
- v. 1928 *Caprinuloidea perfecta gracilis*: Palmer, p. 60-61, pl. 9, fig. 3, pl. 10, fig. 1.
- ?. 1936 *Caprinuloidea perfecta* Palmer; Thiadens, p. 1134-1138, fig. 4.6.
- ? 1977 *Caprinuloidea septata* Palmer; Coogan, pl. 13, fig. 3.
- 1977 *Caprinuloidea perfecta* Palmer; Coogan, pl. 12, fig. 2a-c (holotype).
- ? 1991 *Caprinuloidea perfecta* Palmer; Scott and Gonzalez-Leon, p. 62, figs. 7C-F.
- 2002 *Caprinuloidea perfecta gracilis* Palmer; Scott, fig. 3.3 (from Palmer, 1928).
- ?. 2011 *Caprinuloidea perfecta* Palmer; Mitchell and Green, fig. 5D.

Type specimen. Palmer nominated as Holotype (CAS.66651-10, Palmer No. 2168) a bivalve specimen from Soyatlan de Adentro, State of Jalisco, Mexico. Chartrousse (1998b) noted that there were differences in the sizes of the CT, CTS and that the anterior socket of the RV contains a fragment of the anterior tooth, whereas in the left valve the anterior tooth is complete. He concluded that the two valves came from different individuals and nominated the RV as Lectotype and the LV as Paralectotype. This is formally accepted here.

Discussion. The name *Caprinuloidea perfecta* is used here for specimens of *Caprinuloidea* with small pallial canals in the central tooth, and also locally in the myophoral areas of some right valves. The holotype (which is a very large specimen) has somewhat larger pallial canals, but since it occurs with the other specimens, all material is placed in the same species. Specimens assigned to *C. perfecta gracilis* by Palmer (1928) only differ by being smaller and narrower than *C. perfecta*, and are also included in *C. perfecta* here.

Geographical and Stratigraphical Range. *Caprinuloidea perfecta* has been widely reported from New World localities including: Soyatlan de Adentro, State of Jalisco, Mexico (Palmer, 1928); the Río Hatillo Limestone of the Dominican Republic (Myczyński and Iturralde-Vinent, 2005); the Seafield Limestone of Jamaica (Chubb, 1971; Mitchell and Green, 2011); the Barranquitas Limestone of Puerto Rico (Skelton, 1996); and from limestones in Southern Santa Clara Province in Cuba (Thiadens, 1936). All of these forms are tentatively placed in the species *C. perfecta*, although the details of the right valve have not been reported in many instances. Specimens reported as *C. perfecta* from the Edwards Limestone in Texas are here placed in the species *C. romeri* sp. nov. because their pallial canals are regularly developed and some pallial canals invade the myophores.

***Caprinuloidea multitubifera* Palmer, 1928.
Figure 2A-C**

- v. 1928 *Caprinuloidea multitubifera*: Palmer, p. 61-62, pl. 10, fig. 2.
- v. 1977 *Caprinuloidea multitubifera* Palmer; Coogan, pl. 13, fig. 8 (holotype after Palmer, 1928, pl. 10, fig. 2).
- . 1996 *Caprinuloidea multitubifera* Palmer; Rojas et al., pl. 2, figs. 2-3.

Type specimen. Holotype (CAS.66651-06, Palmer

No. 2170) from Soyatlan de Adentro, State of Jalisco, Mexico.

Discussion. Specimens assigned to *Caprinuloidea multitubifera* have broad posterior myophores, as well as having a greater number of smaller pallial canals than other species of *Caprinuloidea*. The pallial canals also have very thick walls which contrasts with the other species of *Caprinuloidea*.

Geographical and Stratigraphical Range. *Caprinuloidea multitubifera* occurs in the ?Lower Albian of Soyatlan de Adentro, State of Jalisco, Mexico (Palmer, 1928). Specimens have also been seen in the Lower Albian Seafield Limestone of Jamaica which are attributed to this species here.

***Caprinuloidea romeri* sp. nov.
Figures 3A-E, 4A-D**

- ? 1888 *Ichthyosarcolithes anguis* n. sp.: Roemer, p. 9-10, pl. II (XXXII), fig. 2a-d.
- 1900 *Caprinula anguis* Roemer; H. Douvillé, p. 220, fig 16-17.
- 1969 *Caprinuloidea* sp.: Perkins, p. N762, fig. E232.
- 1973 *Caprinuloidea gracilis* Palmer; Coogan, p. 61, pl. 5, fig. 2 (poorly preserved).
- ? 1973 *Caprinuloidea multitubifera* Palmer; Coogan, p. 61, pl. 5, fig. 3 (this RV has many more Canals in the Shell layer than usual, and the CT is poorly preserved).
- ? 1977 *Caprinuloidea perfecta* Palmer; Coogan, pl. 12, fig. 4 (RV Canals in AM area, possibly not in CT)
- 1977 *Caprinuloidea anguis* (Roemer); Coogan, pl. 12, figs 3a (questionably referred to this species), fig 3b (reproduction of Roemer 1888, fig. 2a), fig. 3c (reproduction of Douvillé 1900, fig. 16); pl. 13, fig. 1.
- 1977 *Caprinuloidea gracilis* Palmer; Coogan, pl. 13, fig. 5-6.
- 1977 *Caprinuloidea* sp.: Coogan, pl. 13, fig. 9
- .? 1977 *Texicaprina vivari* Palmer; Coogan, pl. 14, figs. 3-4.
- .? 1977 *Texicaprina* sp.: Coogan, pl. 15, figs. 4-5.
- 2002 "*Ichthyosarcolithes*" *anguis* Roemer, 1888; Scott, p. 420-421.
- . 2007 *Caprinuloidea perfecta* Palmer; Molineux, Scott, Ketcham, and Maisano, p. 3-5, figs. 1-4.
- v. 2010 *Caprinuloidea perfecta*; Scott and Weaver, fig. 8D.

Diagnosis. A species of *Caprinuloidea* with a long straight or twisted right valve and a shorter partially coiled left valve with an external ligamental groove, in which pallial canals invade the central tooth and myocardinal areas of the right valve; pallial canals partially invade the posterior

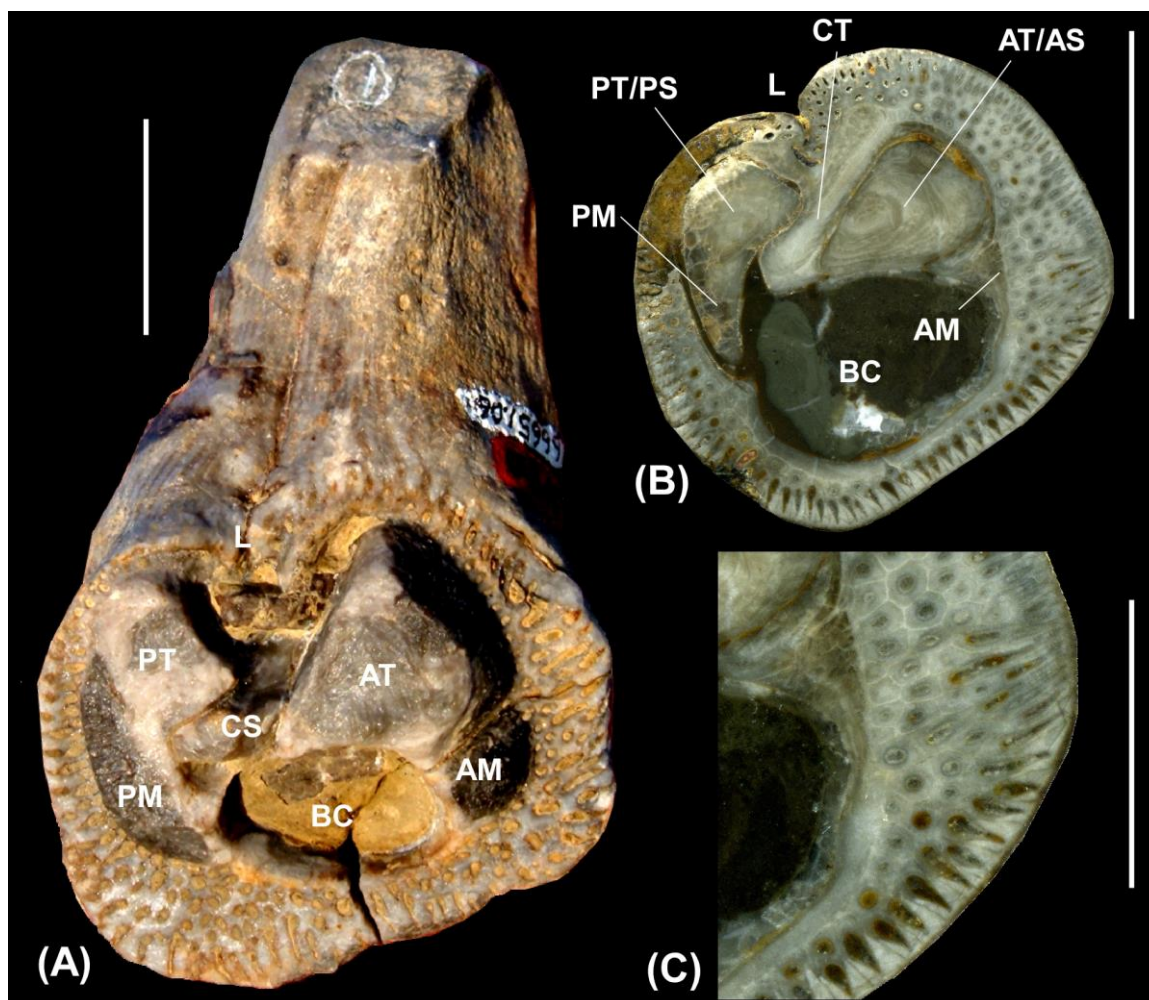


Figure 2. A-C, *Caprinuloidea multitubifera* Palmer 1928. A, holotype (CAS.66651-06, Palmer's no. 2170), Left Valve, apertural view; note the long narrow cavity for the central tooth; scale bar is 20 mm. B-C, Right Valve (TMM.UT-50694) cut below commissure with dentition elements from the left valve preserved in place (posterior and anterior myophores still partially encased in matrix); B (scale bar = 20 mm) shows the narrow central tooth, and the broad posterior myophore filling most of the posterior accessory cavity (although the lamina separating the posterior accessory cavity and body cavity is not preserved); C (scale bar = 10 mm) shows the construction of the pallial canals, with a central narrow wall and a thick layer of shell material around each canal; differential thickening gives rise to pyriform marginal canals. Both specimens from Soyatlan de Adentro, State of Jalisco, Mexico. Scale bar 20 mm. AT, anterior tooth; AS, anterior socket; PT, posterior tooth; PS, posterior socket; CT, central tooth; CS, central socket; AM, anterior myophore; PM, posterior myophore; L, ligament; BC, body cavity.

myophore and anterior myophore in the left valve; there is a marginal row of more-or-less uniform pallial canals with their long axes orientated radially; and the shell wall contains three to six rows of pallial canals inclusive of the marginal row.

Type material. Holotype (TMM.UT.10932) and Paratypes (TMM.UT-10930.1, 11268, 33867, 10922), Edwards Limestone, Austin, Texas.

Material. This species is common in the Edwards Limestone of Texas, and ranges from small

specimens to gigantic specimens.

Description. Right valve generally elongate and may be straight to somewhat irregularly twisted, cylindro-conical to cylindrical; grows communally as elevators and possibly isolated as a recumbent. The right valve has a well defined external ligamental groove, extending along the length of the valve; the ligamental groove is connected by a fissure, lined with a thin layer of outer shell layer to the hook-shaped infolded ligament. Transverse sections are circular to subquadrate to pear-shaped with a narrow rounded elongate ventral margin,

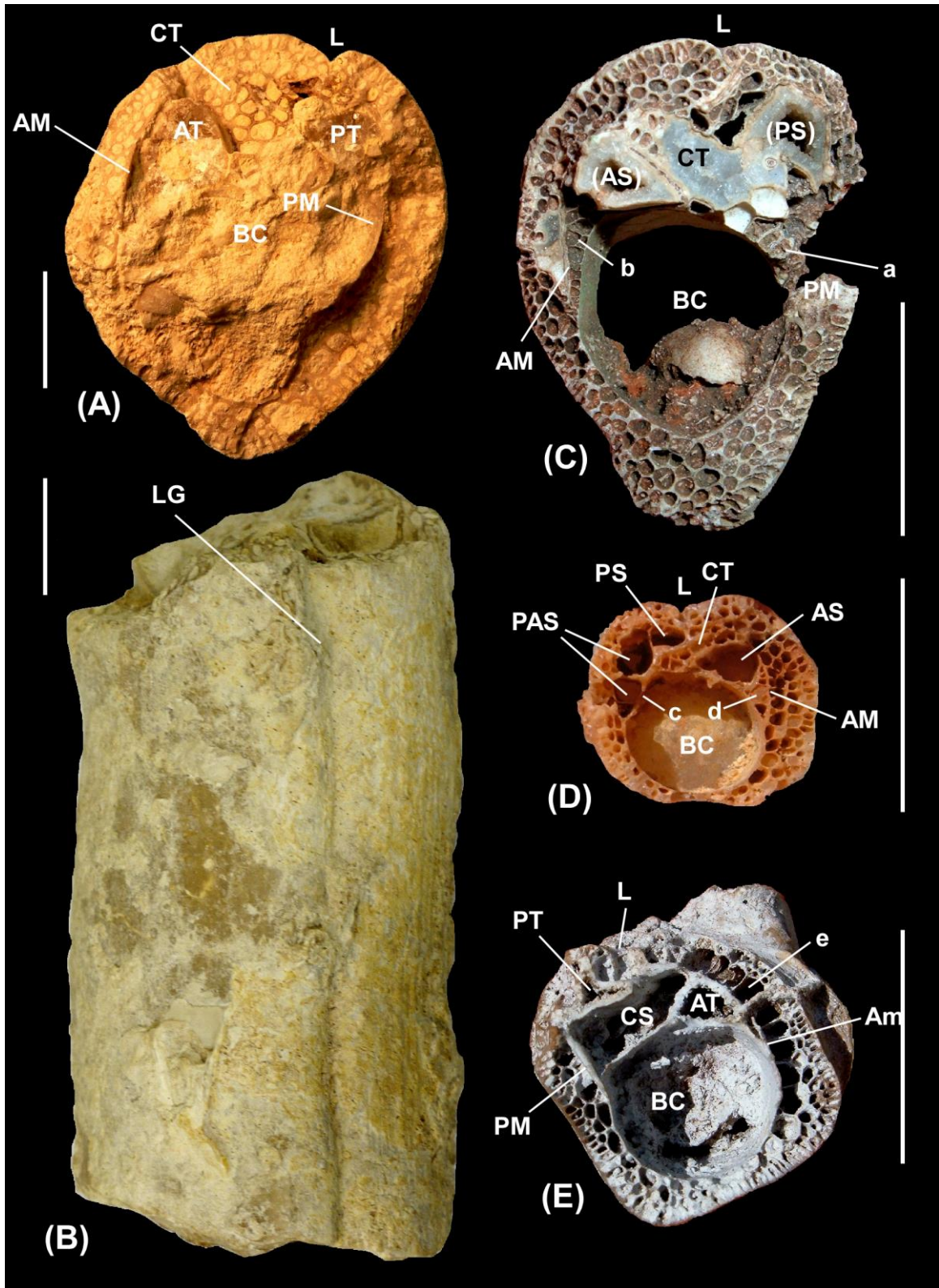


Figure 3. *Caprinuloidea romeri* sp. nov. All specimens from the Edwards Limestone of Texas. A-B, Right Valve (SI.USNM.221518), Whitney Dam: A, commissure view, with myocardial elements of the LV in place: note the narrow wall like form of the PM and AM and the CT filled with pallial canals; B, view of dorsal flank showing ligamental groove. C, Right valve (TMM.UT-10930.1), San Gabriel River, Roy Gunn's Ranch, Texas, commissural

and the anterior margin generally flattened. The central tooth is broadly rectangular, orientated at a low angle (about 45 degrees) to a line joining the posterior and anterior tooth sockets. The sockets for the teeth are deep, the posterior tooth socket connected, via a constriction, to the posterior myophore cavity. There is an embayment for the projecting (rotated) anterior myophore of the left valve. The anterior myophore of the left valve is a vertical wall that starts on the anterior margin of the anterior tooth socket and is orientated towards the wall of the body chamber. The anterior tooth socket is separated from the body cavity by a septum that stops at the same level as the ledge for the anterior myophore. The cavity for the posterior myophore is separated from the body cavity by a septum, which in small forms is composed of compact shell material but in larger forms has a single row of pallial canals. The ligament is invaginated with the invagination marked by an external groove connected to the interior hook-shaped ligament. The body cavity is broadly rounded, and the lower part is filled with concave tabulae. The margin of the shell is composed of rather uniform, radially elongated, elliptical rather than pyriform canals; some pyriform canals may be present but either the inner or outer ends may be narrower. The remainder of the shell is composed of uniformly sized canals up to 1.5 mm in diameter. The marginal pallial canals lack tabulae, whereas the interior pallial canals have 'concave towards the aperture' tabulae spaced at irregular (1 to 8 mm) intervals. The central tooth is filled with normal pallial canals identical to the remainder of the shell wall. The anterior tooth socket contains concave tabulae; the details of the fill of the posterior tooth socket have not been seen.

The left valve is coiled, forming up to three-quarters of a revolution. In cross section it ranges from circular to pear-shaped with the ventral margin narrower and elongated. The anterior surface is generally gently flattened. A prominent ligamental groove extends around the anterior-dorsal margin and is folded in to form a small hook. The anterior tooth is generally triangular in

cross-sectional shape; the posterior tooth is elongated antero-posteriorly, and narrows both towards the posterior and the anterior. The anterior myophore is wall-like and extends along the wall of the body cavity from the anterior tooth. The posterior myophore skirts around the posterior margin of the LV endomyomorphical cavity and only extends a little way beyond the ventral end of the septum separating the endomyophoral cavity from the body cavity. The marginal row of pallial canals is weakly to moderately radially elongate, they are not pyriform. The remainder of the shell structure is filled with pallial canals; in many individuals the two accessory cavities on the outside of the myophores are filled with a row of larger pallial canals (up to two times the size of the 'normal' pallial canals), but in some forms the pallial canals are of more uniform size throughout the shell. The body cavity is regularly elliptical; the presence or absence of tabulae in the body cavity or the central tooth socket has not been confirmed.

Stratigraphic distribution. The material preserved in the Texas Memorial Museum comes from a variety of locations in the Edwards Limestone of Texas. These include: South San Gabriel River, Roy Gunn's Ranch, Texas (this locality now lies under Lake Georgetown); and Witney Dam, Texas.

Discussion. The material described and figured as *Ichthyosarcolithes anguis* by Roemer (1888), which he collected from two miles above the mouth of Barton Creek, Austin, Travis Co., Texas, from somewhere in the Edwards Limestone (Scott, 2002, p. 421), appears to be heterogeneous. Roemer's specimens in his plate II (XXXII), figs. 2a-d, have external ligamental grooves and could be referred to *Caprinuloidea romeri* sp. nov.; in contrast, the specimens in his plate I (XXXI), figs. 7a-b, lack external ligamental grooves and would appear to represent *Youngicaprina sangabrieli* gen. et sp. nov. Both species are common in the Edwards Limestone of Texas, but the figures given by Roemer (1888) are too stylistic to determine the true affinity of these specimens. Furthermore, the

[Figure 3 continued] view, containing teeth from left valve, note the CT filled with pallial canals, pallial canals in the ledge below for the AM (b) and a row of pallial canals in the lamina dividing the damaged posterior accessory cavity from the BC; the sockets are filled by the broken teeth of the LV which are lined by chert suggesting that they were originally solid. D, Right Valve (TMM.UT-11268), abumbonal view, note sockets for teeth without apparent tabulae, area of AM filled with pallial canals (d), PAC divided into three by septa (as in *Mexicaprina*), and the elongate pallial canal filled CT (unlike in *Mexicaprina*). E, Left valve (TMM.UT-10922), commissural view, showing myocardial elements; the PT and AT are broken off and lined by crystals suggesting they were solid, the PM is wall like, the AM, is triangular with a single pallial canal, and the ectomyophoral cavity is filled with large pallial canals (e). Scale bar 20 mm. AT, anterior tooth; AS, anterior socket; PT, posterior tooth; PS, posterior socket; CT, central tooth; CS, central socket; AM, anterior myophore; PM, posterior myophore; L, ligament; BC, body cavity.

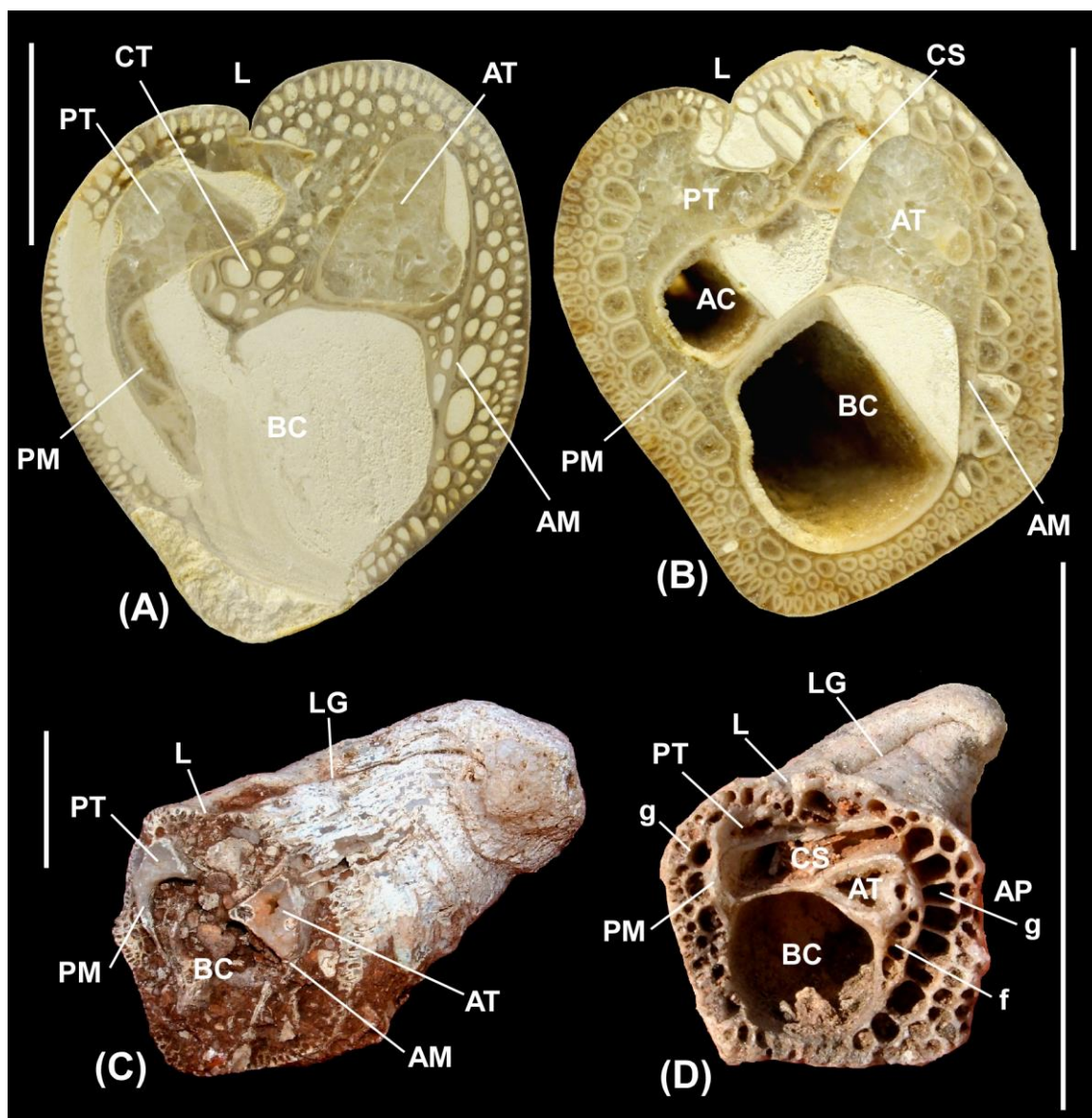


Figure 4. *Caprinuloidea romeri* sp. nov. All specimens from the Edwards Limestone of Texas. A-B, Bivalve (SLUSNM.PAL.534223), Whitney Dam: A, transverse section of Right Valve, abumbonal view, showing teeth and myophores; B, transverse section of Left Valve, abumbonal view showing teeth and myophores. C, Left Valve (TMM.UT-33867) showing the well developed external ligamental groove and myocardial elements; the PM is wall like and attached to the PT. D, Left Valve (TMM.UT-10932), commissural view, showing myocardial elements; the PT and AT are broken off and lined by crystals suggesting they were solid, the PM is wall like, the AM, is triangular with a row of pallial canals (f), and the ectomyophoral cavities are filled with large pallial canals (g). Scale bar 20 mm. AT, anterior tooth; AS, anterior socket; PT, posterior tooth; PS, posterior socket; CT, central tooth; CS, central socket; AM, anterior myophore; PM, posterior myophore; L, ligament; BC, body cavity.

repository of the actual specimens is not known and they may be lost (Scott, 2002, p. 421). Coogan (1977) suggested that the specimens figured as *Caprinula anguis* Roemer by H. Douvillé (1990) were the same specimens as Roemer's (1888) plate I (XXXI), figs. 7a-b. Yet H. Douvillé's illustrations show a distinct external ligamental groove and represent *Caprinuloidea*

romeri sp. nov., whereas this groove is not shown in Roemer's illustrations which are tentatively referable to *Youngicaprina sangabrieli* gen. et sp. nov. Coogan's (1977) assertion that these are the same specimens is, however, incorrect; H. Douvillé's illustrations were based on photographs of material collected from the Fredericksburg Group by R. T. Hill (Scott, 2002, p. 421). In

consequence the illustrations of *Ichthyosarcolites anguis* as given by Roemer (1888) are probably heterogeneous, are highly stylistic, and the original specimens appear to be lost; I follow Scott (2002) in avoiding this name in palaeontological and biostratigraphical studies.

Caprinuloidea romeri sp. nov. and *Youngicaprina* gen. nov. occur in the same units and have been confused in the past. *Caprinuloidea romeri* is distinguished from *Youngicaprina* as follows: marginal canals are radially elliptical rather than pyriform as in *Youngicaprina*; an external ligamental groove is present in *Caprinuloidea romeri* sp. nov. and absent in *Youngicaprina* gen. nov.; the angle between the long axis of the central tooth and the centre points of the anterior and posterior teeth is small in *Caprinuloidea romeri* sp. nov. and large in *Youngicaprina* gen. nov.; the posterior and anterior myophores are wall-like in *Caprinuloidea romeri* sp. nov.; and the posterior myophore (PM) forms a sharp angle around the endomyophoral cavity in *Caprinuloidea romeri* sp. nov. rather than forming a broad arc in *Youngicaprina* gen. nov.

Genus *Mexicaprina* Coogan, 1973

Figure 5A-B

Type Species. *Mexicaprina cornuta* Coogan, 1973.

Description. See Coogan (1973, 1977) and Scott (2002).

Genus *Kimbleia* Coogan, 1973

Figure 5C-E

Type species. *Kimbleia capacis* Coogan, 1973

Description. See Coogan (1973, 1977) and Scott (2002).

Discussion. The recognition of two species based on differences in the size of the pallial canals is not considered sufficiently diagnostic to separate *Kimbleia albrittoni* (Perkins, 1960) from *Kimbleia capacis*, and *K. capacis* is placed in synonymy with *K. albrittoni* herein (see Scott, 2002, p. 415).

Genus *Neokimbleia* gen. nov.

Figure 6A-E

Type species. *Neokimbleia acutus* gen. et sp. nov. from the El Abra Formation (Upper Upper Alban), El Madroño, state of Querétaro, central Mexico.

Diagnosis. An inequivalve caprinuloideid with an elongate straight right valve and a shorter coiled left valve. The anterior tooth is large (and may be bifid) and the posterior tooth is smaller and has a prominent posterior ridge making it 'arrow'-shaped. The anterior myophore of the left valve is connected to the anterior tooth. The posterior myophore of the left valve is blade-like, strongly elongated and fits into an elongate cavity in the right valve; the endomyophoral cavity and the socket for the anterior tooth are separated by a long septum. There is no external ligamental groove; the ligament being represented by a pear-shaped cavity completely isolated from the exterior of the shell.

Discussion. *Neokimbleia* gen. et sp. nov. shows many characters which align it with *Kimbleia*; the distribution of the teeth and sockets, and the transverse cross-section of the shell. It differs by the nature of its ligament: in *Kimbleia*, the ligament is represented by an obvious external groove; whereas in *Neokimbleia*, the ligament is represented by a pear-shaped cavity and is not connected to an external ligamental groove. *Neokimbleia* gen. nov. can be seen as an evolutionary development from *Kimbleia* in which the external ligamental groove has been lost.

Neokimbleia acutus sp. nov.

Figure 6A

- v. 1936 *Sabinia* sp.; Thiadens, p. 1140-1141, fig. 5(1).
- ? 1978 *Kimbleia*? sp.: Coogan, pl. 17, fig. 2.
- v. 1998 *Kimbleia albrittoni* (Perkins, 1960) pars; Alencáster and Oviedo-García, p. 175-177, fig. 8.2, fig. 9.5-6.

Diagnosis. A species of *Neokimbleia* with a bifid AT and a triangular flange on the ventral shell margin.

Type material. Holotype: Transverse section of a right valve (IGM.4586), El Abra Formation, El Madroño, state of Querétaro, central Mexico

Description. No articulated specimens are known. Cross sections are flattened in an anterior-posterior direction, have a rounded dorsal margin and an acutely pointed ventral margin. Only myocardial details of the right valve are known. There is no external ligamental groove, and the ligament is represented by a rounded pit enclosed in the shell structure. The socket for the anterior tooth is broadly rounded, has two cavities separated by pallial canals recalling the bifid socket seen in *Immanitas* Palmer and some *Mexicaprina*. The

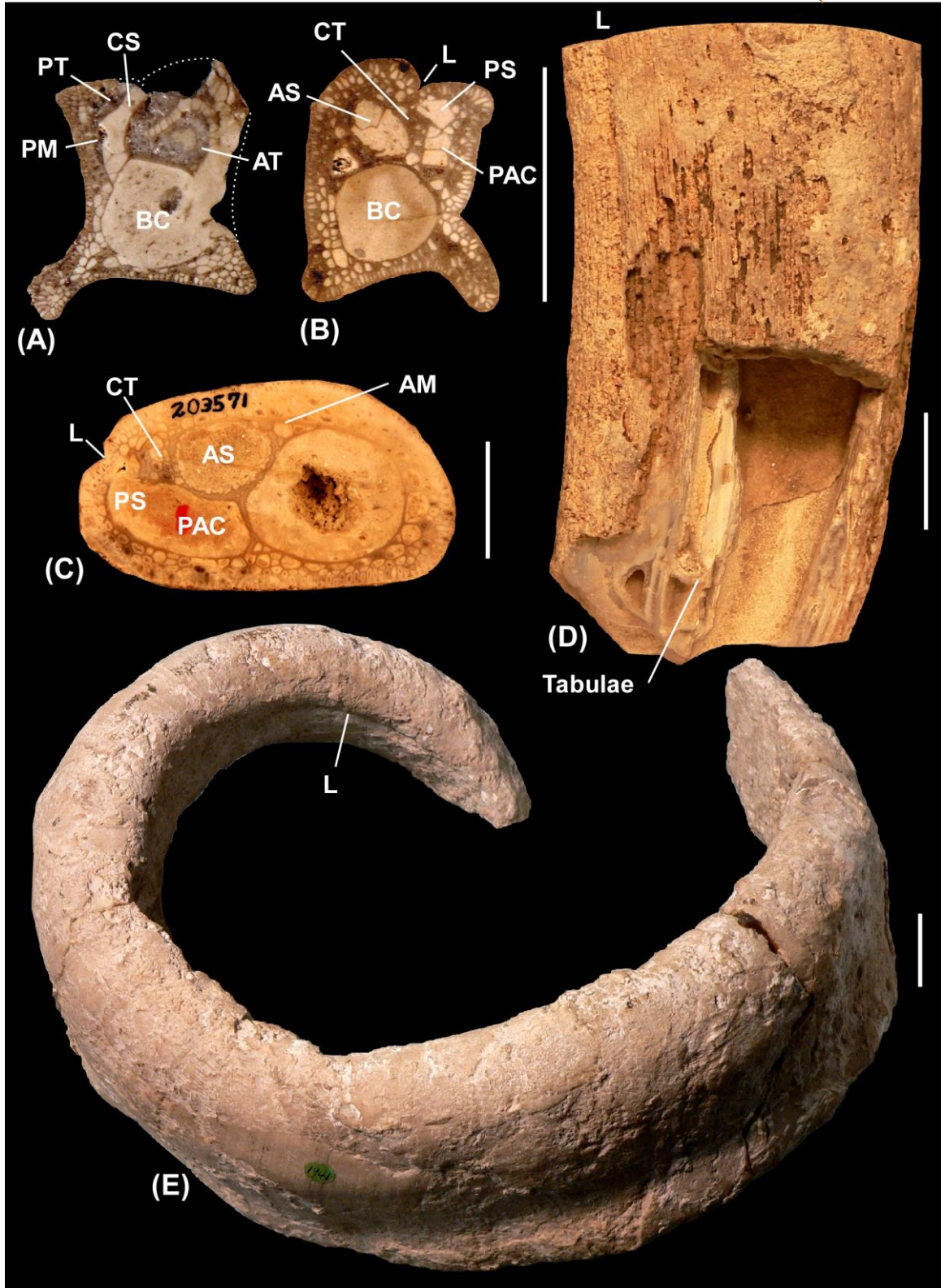


Figure 5. A-B, *Mexicaprina coruuta* Coogan 1973. El Abra Limestone, Sierra de El Abra, San Luis Potosi, Mexico. A, left valve (IGM.2585), transverse cross section, adapical view, showing myocardinal features. B, Right valve (IGM.2584) transverse cross section, adapical view, showing myocardinal features. C-D, *Kimbleia albrittoni* (Perkins 1960). Segovia Formation, Lopez Ranch, Kimble County, Texas. C, Right valve (UT.203571), abumbonal view,

ledge for the attachment of the anterior myophore is clearly developed extending from the anterior margin of the anterior tooth socket to the margin of the body cavity. The socket for the posterior tooth is joined to the posterior endomyophoral cavity with the posterior margin of the accessory cavity strongly curved. The shell is filled with regular-sized small pallial canals with diameters of 1 to 2.5 mm; the marginal canals are radially elongated, and the inner rounded canals are arranged in from 2 to 4 rows. The central tooth is filled with similar canals as the rest of the shell, and extends towards the anterior from a position near the midpoint of the cavity formed by the posterior tooth socket and the posterior accessory cavity. The posterior accessory cavity is separated from the anterior tooth socket and the body cavity by a 1-mm wide septum that lacks pallial canals, a similar septum separates the anterior tooth socket from the body cavity.

Discussion. *Neokimbleia acutus* gen. et sp. nov. is distinguished from species of *Kimbleia* by the lack of an external ligamental groove, and the positioning of the rounded ligament of the right valve within the pallial-canal bearing shell structure. The pallial canals of *N. acutus* gen. et sp. nov. are smaller than those of *Kimbleia capacis* Coogan and *K. albrittoni* (Perkins); but in *N. acutus* the anterior tooth is bifid whereas in *K. capacis* and *K. albrittoni* it is rounded.

Distribution. *Neokimbleia acutus* gen. et sp. nov. occurs in the latest Albian El Abra Formation, El Madroño, state of Querétaro, central Mexico. A specimen from Cuba figured by Thiadens (1936) as *Sabinia* sp. also seems to belong to this species.

***Neokimbleia planata* (Conrad, 1855)**

Figure 6B-E

- v. 1855 *Caprina occidentalis*: Conrad, p. 268.
- v. 1855 *Caprina planata*: Conrad, p. 268.
- v. 1857 *Caprina occidentalis*: Conrad, p. 147, pl. 2, figs. 1a-c.
- v. 1857 *Caprina planata*: Conrad, p. 147, pl. 2, figs. 2a-b.
- v. 2002 “*Caprina*” *occidentalis* (Conrad, 1855); Scott, p. 419-420, figs. 9.1-2, fig. 10.1.
- v. 2002 “*Caprina*” *planata* (Conrad, 1855); Scott, p. 420, figs. 9.3-4, fig. 10.2.

Diagnosis. A species of *Neokimbleia* with a single, non-bifid anterior tooth, the shell flattened in an antero-posteriorly direction, with the shell smoothly rounded, without flanges.

Type specimen. The holotype is preserved in the Smithsonian Institute (SNNHM.USNM-9891) and was collected from Oak Creek near Puercos, Texas. Scott (2002; pers. commun. 2013) considers the most likely locality was at Live Oak Creek on the Pecos River near present-day Fort Lancaster, from a level in the Fort Lancaster Formation of the Washita Group rather than from the Fort Terrett Formation of the Fredericksburg Group.

Description. A large species of *Neokimbleia* gen. nov. with strongly curved left and right valves. The valves are strongly flattened in an anterior-posterior direction and regularly rounded. The dorsal-ventral diameter of the shell is about 2 to 3 times the anterior-posterior diameter of the shell.

The right valve is elongate and gently curved. The body cavity is rounded and filled with tabulae. There is no external ligamental groove, and the ligament is represented by an enclosed cavity between the posterior tooth socket and the central tooth that is completely embedded within the pallial-canal-bearing shell material. The socket for the anterior tooth is gently rounded and separated from the body cavity by a septum that lacks pallial canals. The socket for the posterior tooth is connected to the posterior endomyophoral cavity, with the tooth socket delineated by a slight constriction. A marginal row of radially elongated pallial canals is present around the extremity of the shell, and the interior of the shell is filled with pallial canals; in some specimens the pallial canals are predominately small forms (diameters of 1 to 3 mm) whereas in other specimens the inner row of pallial canals adjacent to the posterior accessory cavity are larger (up to 5 or 6 mm across) and elongated in a dorsal-ventral direction. The central tooth is filled with pallial canals, and extends from a distance of about two-thirds of the way from the posterior end of the cavity for the posterior tooth/posterior myophore anteriorly towards the anterior side of the shell; the central tooth is large and anterior-posteriorly elongated, and is

[Figure 5 continued] transverse cross section (orientated with anterior side at top), note the well-developed external ligamental groove and the short CT with the AS and the PAC separated by a lamina. D, Right valve (SI.USNM.203566), anterior aspect, note the well-developed external ligamental groove. E, *Kimbleia* sp. (SI.USNM.547501 [CS2; #1941]), articulated specimen, posterior dorsal view, showing external ligamental groove. Scale bar 20 mm. AT, anterior tooth; AS, anterior socket; PT, posterior tooth; PS, posterior socket; CT, central tooth; CS, central socket; AM, anterior myophore; PM, posterior myophore; L, ligament; BC, body cavity.

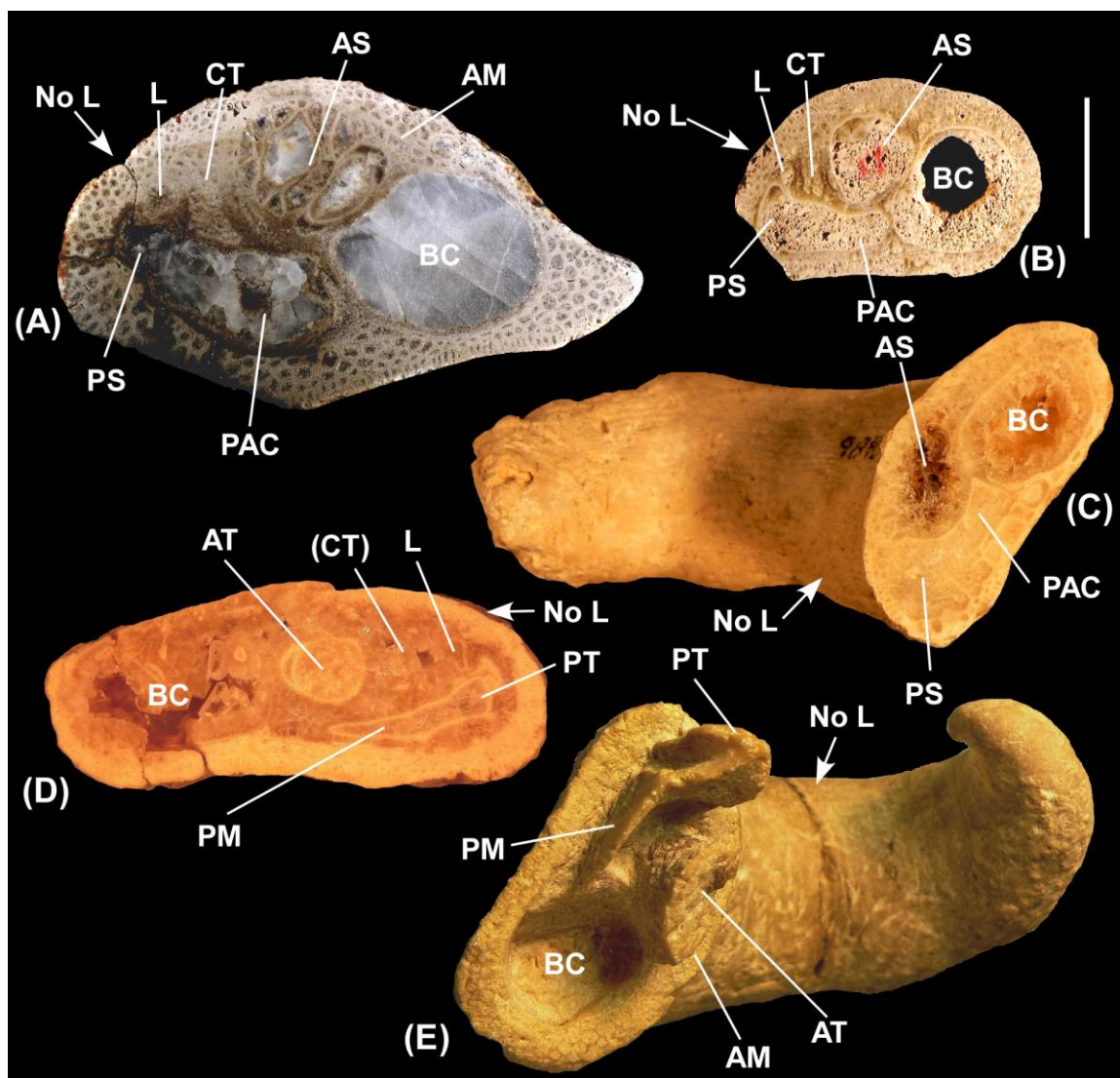


Figure 6. A, *Neokimbleia acutus* sp. nov. Right valve (Holotype, IGM.4586), transverse cross section, abapical view, note the lack of an external ligament groove (there is a crack, but this passes across pallial canals) and myocardinal arrangements, El Madroño, state of Querétaro, central México. B-E, *Neokimbleia planata* (Conrad, 1855). B, Right valve (IGM.2575, figured by Googan, 1973, pl. 2, fig. 1 as *Kimbleia albrittoni*), note lack of external ligamentary groove, internal ligamentary cavity, but otherwise a dentition similar to *Kimbleia*; El Abra Formation, Mexico. C, Holotype of *Caprina occidentalis* Conrad 1855 (SI.USNM.9840) Left Valve (with part of Right Valve?), adapical cross-section, collected from near the mouth of the Percos river, Texas. D, Holotype of *Caprina planata* Conrad, 1855 (SI.USNM.9891), adapical slice through RV close to commissure containing the myocardinal structure of the left valve, collected at Oak creek, near Puercos, Texas. E, Left Valve (SI.USNM.547500 [CS1]), showing myocardinal arrangement and lacking an external ligamentary groove. Nb., transverse sections orientated with anterior side at top. Scale bar 20 mm. AT, anterior tooth; AS, anterior socket; PT, posterior tooth; PS, posterior socket; CT, central tooth; CS, central socket; AM, anterior myophore; PM, posterior myophore; L, ligament; BC, body cavity.

almost arrow shaped. The posterior myophore is surrounded by compact shell material. The left valve is shorter than the right valve and more strongly coiled (Figure 6E). There is no external ligamentary groove. The posterior myophore is attached to the centre of the posterior tooth and forms a wall like feature which initially extends in a posterior-ventral direction, before

making an angle and extending parallel to the posterior margin of the shell; the myophore gradually decreases in height from the posterior tooth, and also gradually decreases in width. The anterior tooth is relatively large and rounded, and is poorly separated from the anterior myophore. The central socket is a slot between the anterior tooth and the posterior tooth.

Discussion. Scott (2002) regarded Conrad's (1855) species *Caprina occidentalis* and *Caprina planata* as indeterminate and suggested that the names should be applied only to the type specimens and should not be maintained in biostratigraphic or taxonomic studies. In contrast, I recognize that Conrad's *Caprina planata* shows sufficiently distinctive features (the forms of the posterior tooth and posterior myophore, the shape of the anterior tooth, the enclosed pear-shaped ligament cavity) that allows it to be placed in the genus *Neokimbleia* gen. nov. *Neokimbleia planata* differs from *Neokimbleia acutus* sp. nov. by having a rounded, rather than bifid anterior tooth, the absence of a large triangular flange on the ventral margin; and the distribution and number of flanges is considered a specific character in separating caprinuloid rudists (Mitchell and Gunter, 2006).

The three specimens of *Neokimbleia planata* shown on **Figure 6** include a range of different-sized pallial canals. These range from small canals, similar to those seen in *Kimbleia capacis*, to an inner row of large elongated canals, similar to those seen in *K. albrittoni*. The presence of such variations in pallial canal size in two different genera, which are likely to be ancestor and descendant, suggests that the size of pallial canals is of little specific importance and that *Kimbleia capacis* Coogan, 1973, should be placed in the synonymy of *Kimbleia albrittoni* (Perkins, 1960).

Subfamily Youngicaprininae subfam. nov.

Diagnosis. Caprinuloideidae in which the anterior myophore of the LV is modified to form a low platform, with or without blades or tubercles, that wraps around the anterior side of the anterior tooth; and a posterior myophore which becomes tooth-like and is separated from the posterior tooth.

Discussion. This group has a distinctly different myocardial arrangement to the Amphitriscoelinae and the Caprinuloideinae, and may show a transition towards the Antilocaprinidae Mac Gillavry, 1937, but transitional forms have not been found. The Antilocaprinidae are differentiated because the endomyophoral cavity between the posterior tooth and the body cavity that is characteristic of the Caprinuloideidae has been lost and the posterior tooth is directly adjacent to the body cavity.

Three genera are included within the Youngicaprininae: *Texicaprina* Coogan, 1973,

Middle to Upper Albian; *Youngicaprina* gen. nov., Middle to Upper Albian; and *Jalpania* Alencáster and Aguilar-Pérez, 1996. The Upper Albian *Immanitas* Palmer, 1928, may also belong here (see Aguilar Pérez, 2008, fig. 58).

Genus *Texicaprina* Coogan 1973

(=*Guzzyella* Alencáster 1998)

Type species. *Sabinia kugleri* Bouwman, 1937, from Point-a-Pierre, Trinidad (see discussion below).

Diagnosis. A genus of Youngicaprininae subfam. nov. with an external ligamental groove, a 'tooth-like' posterior myophore that is separated from the posterior tooth by a gutter filled with pallial canals, and a low anterior myophore that wraps around the anterior tooth.

Discussion. Coogan (1973, p. 59) erected the genus *Texicaprina*, nominating *Sabinia vivari* Palmer, 1928, as type species, and then stated that "*The illustrations of Texicaprina vivari (Palmer) ... do not show adequately the characters which make this species a Texicaprina*" and that "*Examination of Palmer's types at the California Academy of Science shows that they are badly recrystallized internally, but otherwise appear to be the same species as found in the Edwards Limestone in central Texas.*" Coogan (1973) based many of the features in describing his genus *Texicaprina* on *Sabinia kugleri* Bouwman, 1937, from Trinidad, which is preserved as specimens free from matrix where the teeth, sockets and myophores had been illustrated, and not on *Sabinia vivari* from Mexico (Coogan in an unpublished report, dated 1960, for Humble Oil and Refining Company, suggested the manuscript name *Texicaprina* citing *Sabinia kugleri* as the type species; see also Alencaster and Oviedo-García, 1998, p. 176).

Since *Texicaprina* has been used in biostratigraphic studies it is desirable to stabilize this name rather than abandon it and a proposal is being sent to the *Bulletin of Zoological Nomenclature*, to use Plenary Powers to place *Texicaprina* and *Sabinia kugleri* Bouwman, 1937, on the approved list of names in zoology, to place *vivari* in the combination *Sabinia vivari* Palmer, 1928, on the list of invalid names in Zoology, and to select *Sabinia kugleri* Bouwman, 1937, as the type species of *Texicaprina* Coogan, 1973 (note that Chartrousse, 1998b, also suggested a similar solution in his unpublished doctoral thesis).

Coogan (1973) included forms in *Texicaprina*

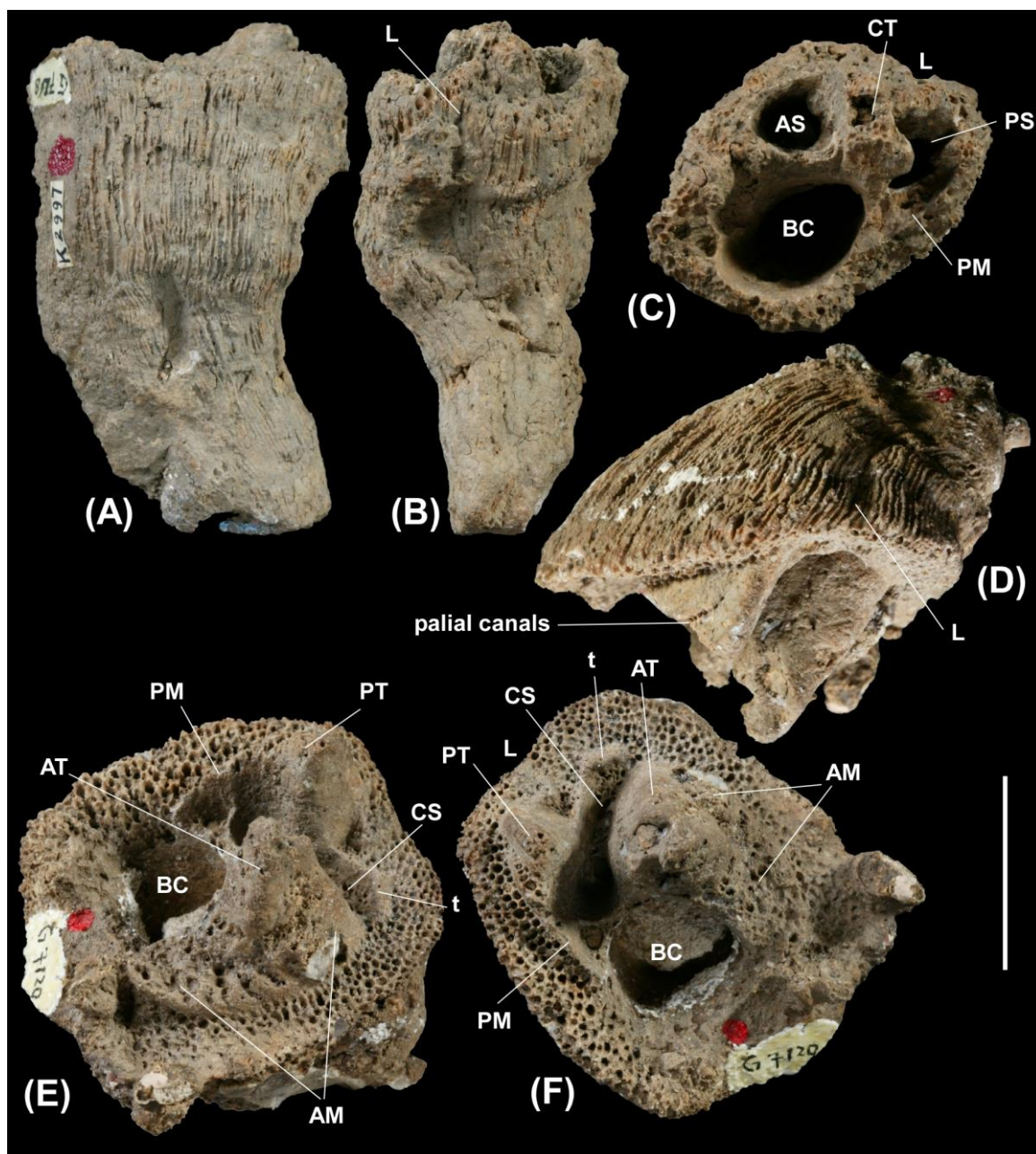


Figure 7. *Texicaprina kugleri* (Bouwman 1937). Erratic block, Point-A-Pierre, Trinidad. A-C, Right valve, syntype (BM.K2997); A, posterior flank of Right Valve; B dorsal aspect of Right Valve showing ligamental groove; C, apertural aspect of Right valve, note 'w'-shaped posterior socket weakly separated from the endomyporal cavity by a septum, Central Tooth partially dissolved. D-F, Left Valve, nominated lectotype herein (BM.G7120); D, postero-dorsal flank of Left Valve showing ligamental groove; E, Left Valve, oblique view of apertural surface showing the form of the anterior myophore which is composed of solid radiating blades and intervening canal-bearing furrows and wraps around the anterior side of the large anterior tooth; F, apertural view of Right Valve, the posterior myophore is separated from the posterior tooth by a pallial-canal bearing trough. Scale bar 20 mm. AT, anterior tooth; AS, anterior socket; PT, posterior tooth; PS, posterior socket; CT, central tooth; CS, central socket; AM, anterior myophore; PM, posterior myophore; L, ligament; BC, body cavity; t, tubercle.

which had pallial canals invading the teeth and myophores. I consider that the form of the myocardial arrangement is more important for generic placement than the distribution of pallial

canals, and, as with *Caprinuloidea*, regard the invasion of pallial canals into different elements of the myocardial structure to be a specific character.

I place *Caprinuloidea bisulcata* Palmer, 1928, in the genus *Texicaprina* on the basis of the morphology of the anterior myophore, and consequently *Texicaprina bisulcata* Palmer, 1928, becomes a senior homonym of the type species of the genus *Guzzella*, *G. bisulcata* Alencáster, 1998, which I also place in *Texicaprina*. Here, I consider that *Guzzella acuminata* Alencáster, 1998, falls within the population of *Guzzella bisulcata* Alencáster, 1998, and use this name as the valid name for the species of *Texicaprina* from El Madroño, state of Querétaro, central Mexico.

Alencáster (1998) distinguished *Guzzella* from *Texicaprina* based on the fact that *Guzzella* had a wrinkled rather than ribbed anterior myophore, and the fact that “*Texicaprina* is totally perforated” with pallial canals. Alencáster (1998) based her interpretation of *Texicaprina* on specimens from El Madroño which she attributed to *Texicaprina kugleri* (Bouwman), but which lack an external ligamental groove and are here referred to the genus *Youngicaprina* gen. nov. *Sabinia kugleri* Bouwman has an external ligamental groove, a slightly tooth-like posterior myophore, and a low anterior myophore that envelops the anterior tooth and has distinct ribs separated by pallial canal filled furrows. It seems likely that the ribbed morphology of the anterior myophore is directly related to the invasion of pallial canals, and would be absent in species which lack pallial canals in the anterior myophore. Given the progressive invasion of pallial canals into different elements of the myocardial structure already described in *Caprinuloidea*, it seems unwise to place species in different genera based on the distribution of pallial canals.

***Texicaprina kugleri* (Bouwman, 1937)**

Figure 7A-F

- v. 1937 *Sabinia kugleri* (n. sp.): Bouwman, p. 450-453, figs. 1-10.
- v. 1977 *Texicaprina kugleri* (Bouwman); Coogan, pl. 14, figs. 2a-b.
- non v. 1998 *Texicaprina kugleri* (Bouwman); Alencáster and Oviedo-García, p. 167-171, fig. 3, fig. 4.1-4.10, fig. 5.1-5.7 (= *Youngicaprina gloria* sp. nov.)
- non v. 1998 *Texicaprina vivari* (Palmer); Alencáster and Oviedo-García, p. 171, fig. 5.8-5.9 (but fig. 5.7-5.8 in the text in error) (= *Youngicaprina gloria* sp. nov.)
- . 2002 *Texicaprina vivari* (Palmer); Scott, p. 416, fig. 7.6.

Diagnosis. A species of *Texicaprina* with a weakly tooth-like elongate, posterior myophore

separated from the posterior tooth by a gutter filled with pallial canals, and an anterior myophore that envelops the anterior-side of anterior tooth and is ribbed with the ribs composed of compact shell material and the furrows filled with pallial canals.

Type Series. Bouwman (1937) illustrated two specimens under the name *Sabinia kugleri* which are the syntypes and are preserved in the Natural History Museum at Basel, Switzerland. The left valve illustrated by Bouwman, 1937, fig. 1 and figs. 8-9 (NHMB.G7220) is nominated here as lectotype. The material came from erratic boulders at Pointe-a-Pierre, Trinidad, so that the age cannot be directly assessed. Judging solely on the morphology it is most likely of late Albian age.

Description. No articulated specimens are known, so the relative size of the valves cannot be determined. The right valve is moderately short and conical to cyclindroconical; preserved right valves appear longer than left valves (and so were probably longer). The ligament is represented by an infold into the shell and a gentle hook, and is marked on the exterior by a prominent external ligamental groove. The material has been somewhat eroded, and the external ligamental groove has been opened up in this process. The central tooth is represented by a broad ridge at an angle of about 105° to a line joining the centres of the posterior and anterior tooth sockets. The anterior tooth socket is relatively large and rounded; the posterior tooth socket is ‘w’-shaped. The endomyophoral cavity is deep and separated from the posterior tooth socket by a lamina. The anterior myophore fits partly into an embayment of the shell wall. Pallial canals are present filling the wall of the shell, and there are between 3 and 6 rows of canals. The marginal pallial canals are poorly preserved, so that their form cannot be determined. Pallial canals invade the central tooth (which has a cavity possibly due to dissolution), and the ledge area for the anterior myophore.

The left valve is relatively short and gently coiled; it has a well developed external ligamental groove that is folded into the shell as a hook. The central socket is narrow at the dorsal end and gently expands towards the posterior-ventral end. A low wall runs along the posterior margin of the central socket and terminates in a tubercle. The anterior tooth is larger than the posterior tooth and is triangular in shape, the posterior tooth is an elongate blade that is separated from the posterior tooth by a weak gutter. The anterior myophore envelops the anterior tooth on the anterior side and

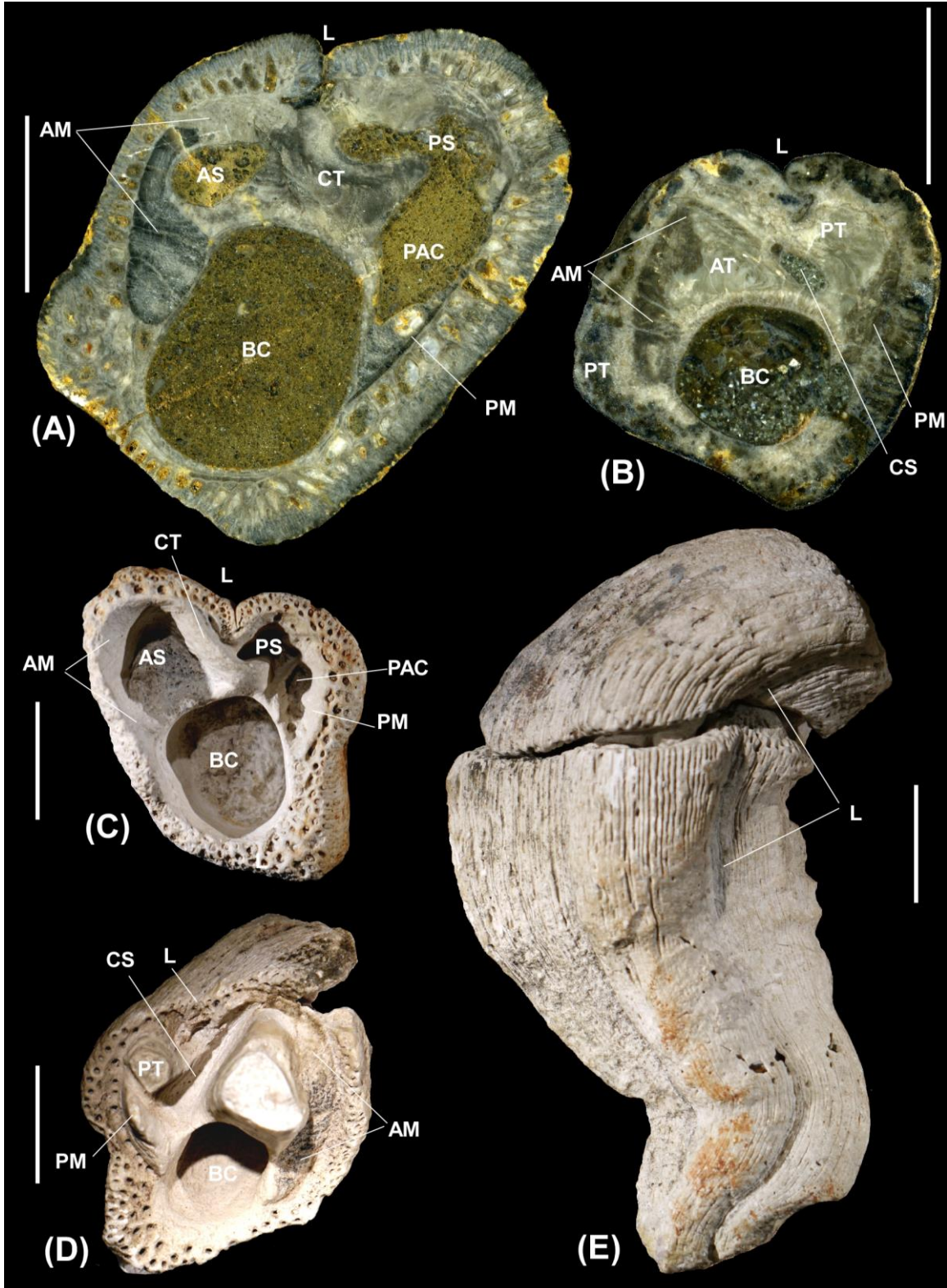


Figure 8. A-B, *Texicaprina bisulcata* (Palmer 1928). A, holotype (CAS.), transverse section of right valve, adapical view, note thickened anterior myophore that wraps around the cavity for the anterior tooth; the posterior myophore is as in *Caprinuloidea*. B, transverse section of a left valve (TMM.UT.50626), abapical view, note thickened anterior myophore that wraps around the anterior tooth. C-E, *Texicaprina acuminata* (Alencáster 1998), holotype (IGM.4590) of *Guzyella bisulcata* Alencáster 1998: C, Right Valve, D, Left Valve, E, Bivalve.

extends ventrally a little way along the body cavity. It is a low platform with ribs that are orthogonal to the body cavity/anterior tooth, and are separated by furrows. The shell is filled with numerous pallial canals which number six or seven rows. The teeth appear to be largely compact shell structure, a few small holes are present which appear to be either borings or dissolution features, rather than pallial canals. The gutter between the posterior myophore and the posterior tooth has one or two rows of pallial canals. The furrows on the anterior myophore are filled with pallial canals whereas the ribs are formed of compact shell structure. The low wall on the posterior side of the central socket and the tubercle are formed of compact shell structure. The fill of the socket for the central tooth has pallial canals at least at its dorsal end.

Discussion. Coogan (1973, 1977) placed *Sabinia kugleri* in his new genus *Texicaprina* and seems to have based his description of the genus on this species, rather than his nominated type species *Sabinia vivari*.

Scott (2002, fig. 7.6) illustrated a specimen of a right valve from the Pecos River at Painted Canyon as *Texicaprina vivari* (Palmer). This specimen shows an external ligamental groove, the anterior socket with the tip of the anterior tooth in place and an irregularly defined area (anterior myophore socket) that extends from the body cavity and enwraps the anterior side of the anterior tooth; and what appear to be separated sockets for the posterior tooth and posterior myophore. This specimen I tentatively place in *T. kugleri*, because the central tooth appears to be invaded by pallial canals, although there is some apparent recrystallization.

***Texicaprina bisulcata* (Palmer, 1928)**

Figure 8A-B

- v. 1928 *Caprinuloidea bisulcata*: Palmer, p. 64, pl. 12, figs. 1-2.
- v. non 1998 *Guzzyella bisulcata* new species: Alencáster, p. 93-96, figs. 2.1-2.8, 3.1-3.10.

Diagnosis. A species of *Texicaprina* that has a broad anterior myophore that wraps around the anterior margin of the anterior tooth, and a triangular posterior myophore, and a furrow on its posterior flank.

Types. Holotype (CAS.66651.05, Palmer No. 2174) Soyatlan de Adentro, State of Jalisco, Mexico.

Material. Texas Memorial Museum (TMM.UT-50626), Soyatlan de Adentro, state of Jalisco, Mexico.

Description. A large species of *Texicaprina*. The right valve is broadly pentagonal in transverse cross-section with a strong external ligamental groove infolded into the shell as a hook, and an additional groove on the anterior flank. The posterior tooth socket is separated from the endomyophoral cavity by a constriction. The central tooth appears arc shaped but is only partially distinguishable from the compact shell material forming the septa and other shell areas adjacent to the tooth. The endomyophoral cavity extends ventrally along the posterior side of the body cavity such that the posterior myophore would extend along about half the length of the body cavity. The anterior and posterior tooth sockets are about the same length, but the anterior socket is wider than the posterior socket. The anterior myophore is represented by a broad area that extends ventrally along half the body cavity and also wraps around the anterior side of the anterior tooth. The fill of the tooth sockets and posterior myophore cavity has not been seen. The pallial canals are represented by a marginal band of relatively narrow canals with their narrow ends directed towards the exterior and intercalated in about three orders in the marginal band. A series of rounded canals extend on the interior side of the pyriform canals around virtually the whole shell's circumference, although sometimes the pyriform canals from the marginal band separate adjacent rounded canals of the interior circuit. Occasional additional rounded canals may be present between the pyriform canals and the rounded canals. The antero-ventral area of the shell may contain a few extra canals in the thickened area on the ventral side of the anterior myophore. No pallial canals invade the central tooth or the myocardial areas. The anterior myophoral area and the ventral-most portion of the posterior myocardial area are represented by compact shell material.

The left valve is broadly quadrangular in shape with a weak groove on the anterior flank. The external ligamental groove is very well developed with a prominent ligamental hook which is adjacent to the posterior tooth. The central tooth socket is well developed and orientated at an angle of about 60 degrees to the line joining the centres of the teeth. The anterior tooth is represented by compact shell material and extends ventrally into the broad anterior myophore which is also composed of compact shell material. The posterior

tooth extends ventrally into a triangular posterior myophore which is truncated at its ventral end by an endolithic boring, such that its ventral-most morphology cannot be ascertained. The pallial canals are largely filled with calcite and are not very distinct; where best preserved on the posterior side of the shell, they consist of a marginal band of narrow pyriform canals with their narrow ends pointing outwards and an inner zone of rounded canals.

Discussion. The extension of the anterior myophore around the anterior side of the anterior tooth and the triangular posterior myophore, which appears to be, at least slightly, differentiated from the posterior tooth would place this species in the genus *Texicaprina*. *Texicaprina bisulcata* is distinguished from *Caprinuloidea* by its broad anterior myophore that wraps around the anterior margin of the anterior tooth. It differs from *Texicaprina acuminata* (Alencáster) described below by the form of the pallial canals, which are elongate and in one or two rows in *T. bisulcata* and small and rounded and in up to eight rows in *T. acuminata*.

Stratigraphic and Geographical Distribution. This is a relatively rare species at Soyatlan de Adentro, state of Jalisco, Mexico. The *Coalcomana-Caprinuloidea* association is generally attributed to the Lower Albian (Scott, 2002; Scott and Filkhorn 2007), and it would appear that the most primitive forms of *Texicaprina* first appear in the ?Lower Albian.

***Texicaprina acuminata* (Alencáster, 1998)**

Figure 8C-E

- non v. 1928 *Caprinuloidea bisulcata*: Palmer, p. 64, pl. 12, figs. 1-2.
- v. 1998 *Guzzyella bisulcata* new species: Alencáster, p. 93-96, figs. 2.1-2.8, 3.1-3.10.
- v. 1998 *Guzzyella acuminata* new species: Alencáster, p. 96-98, figs. 4, 5.1-5.6.
- ?. 1998 *Guzzyella* sp. 1: Alencáster, p. 98, figs. 6, 7.1-7.9.
- ?. 1998 *Guzzyella* sp. 2: Alencáster, p. 98-99, figs. 8.1-8.4.
- ? 1998a *Caprinuloidea* sp.; Chartrousse, fig. 5.1-4.
- v. 2002 *Guzzyella bisulcata* Alencáster; Scott, fig. 3.8.

Discussion. Here, the name *Texicaprina acuminata* (Alencáster, 1998) is used as a replacement for the preoccupied name *Texicaprina bisulcata* (Alencáster, 1998), which is preoccupied because *Caprinuloidea bisulcata*

Palmer, 1928, is transferred here to *Texicaprina* and therefore becomes a secondary senior homonym of *Texicaprina bisulcata* (Alencáster, 1998).

Diagnosis. A species of *Texicaprina* with a prominent tooth-like posterior myophore, a wrinkled anterior myophore and pallial canals in the wall structure but not in the myocardial (teeth, myophores) elements.

Type Series. Holotype (IGM-4590), Paratypes (IGM-4591 to IGM-4593, IGM-4614 to IGM-4621); all from the mid-late Albian of El Madroño, state of Querétaro, central Mexico.

Description. See Alencáster (1998).

Stratigraphic and Geographic distribution. The species has only been recorded in the late Albian of El Madroño, state of Querétaro, central Mexico (Alencáster, 1998).

Discussion. Alencáster (1998) placed two named species and two further forms under open nomenclature within the genus *Guzzyella*. All these forms have essentially the same myocardial arrangement and the same distribution of pallial canals and I recognize only a single species here which is assigned to *Texicaprina* on the basis of its myocardial arrangement. *Texicaprina acuminata* combines essentially primitive features (the lack of pallial canals in the myocardial elements) and advanced features (a tooth-like posterior myophore separated from the posterior tooth by a deep gutter.

Genus *Youngicaprina* gen. nov.

Type species. *Youngicaprina gloria* sp. nov. from the mid-late Albian of El Madroño, state of Querétaro, central Mexico.

Origin of name. From Keith Young for his work on the Cretaceous of the North American region, particularly his stratigraphic work on the ammonites of the Texas region as well as his stratigraphic studies on rudist bivalves of Texas and Mexico (Young, 1985).

Diagnosis. A genus of Youngicaprininae with a straight to arcuate curved to spiral-shaped Right Valve and a gentle prosogyally coiled left valve; the ligament is internal and crescent-shaped in the right valve, and represented by a pit in the left valve; there is no external ligamental groove. The right valve inner shell, including the central tooth,

is filled with pallial canals, except the sockets for the teeth and the body cavity which are filled with tabulae. The anterior tooth is larger than the posterior tooth, both teeth are solid, or contain a few rudimentary irregular pallial canals in the Left Valve. The posterior myophore of the left valve is tooth-like and solid; it fits into a socket in the right valve. The anterior myophore of the left valve is composed of four to ten compact ribs separated by furrows filled with lines of pallial canals; it fits into a cavity and embayment in the right valve.

Discussion. *Youngicaprina* gen. nov. shows an advanced myocardial arrangement and has lost the external ligamental groove; in many ways *Youngicaprina* gen. nov. is very similar to the genus *Texicaprina* but differs in its lack of the external ligamental groove. Specimens of *Youngicaprina* have formerly been assigned to *Caprinuloidea* (Scott and Weaver, 2010, fig. 3A-B), *Kimbleia* (Coogan, 1973, 1977; Alencáster and Oviedo-García, 1998) or to *Texicaprina* (Alencáster and Oviedo-García, 1998).

***Youngicaprina gloria* sp. nov.**

Figure 9A-H

- v. 1998 *Texicaprina kugleri* (Bouwman, 1937); Alencáster and Oviedo-García, p. 167-171, fig. 3 (1-2), fig. 4 (1-10).
- ?. 1998 *Texicaprina vivari* (Palmer, 1928); Alencáster and Oviedo-García, p. 171, fig. 5.8-5.9 (but fig. 5.7-5.8 in the text in error).

Diagnosis. A species of *Youngicaprina* with a short weakly coiled left valve, with eight or nine blades in the anterior myophore of the left valve that extend around the antero-dorsal margin of the anterior tooth.

Types. Holotype (IGM.7639), Paratypes (IGM.7637, IGM.7638 and IGM.7643); all from the mid-late Albian of El Madroño, state of Querétaro, central Mexico.

Description. Bivalved specimens are not known, so the relative sizes of the left and right valves are unknown. The Right Valve is conical to cylindrical, and relatively short. Transverse cross sections are broadly triangular with rounded angles. The central tooth is moderately broad and filled with numerous small pallial canals. The posterior tooth socket is deep and forms an angle of about 60 to 70 degrees to the cardinal line (line connecting the centres of the posterior and anterior teeth). A slight restriction separates the

posterior tooth socket from the posterior myophore cavity. The endomyophoral cavity is separated from the body cavity by a septum which is solid without pallial canals. The anterior tooth socket is elongated dorso-ventrally. The cavity for the anterior myophore is separated from the anterior tooth socket by a septum containing pallial canals. The anterior myophore cavity is triangular in form and subdivided into three or four sectors by two or three low septa, it extends into and embayment adjacent to the anterior side of the anterior tooth. The ligament is represented by a crescent shaped structure which is concave to the dorsal margin; the ligament is completely embedded within the shell structure and there is no external ligamental groove. No complete body cavity has been seen. The nature of the fill of the body cavity and tooth sockets is not known. Pallial canals have a uniform size throughout the shell, and have a size of less than 0.5 mm; the marginal layer of pallial canals is poorly preserved. Pallial canals invade the entire shell structure including the tooth and most of the septa, pallial canals are also visible filling the myophore sockets. Pallial canals have tabulae spaced at distances of 1.5 to 3.5 mm.

The left valve has a transverse cross-section which is triangular with rounded corners. Coiling is slightly asymmetrical. There is no external ligament groove; the dorsal side of the posterior tooth having a depression corresponding to the ligament in the right valve. The posterior tooth is elongated antero-posteriorly, and is concave on the dorsal side. The anterior tooth is much larger than the posterior tooth and is quadrangular to broadly rounded. The central tooth socket is narrow between the teeth and expands a little posteriorly between the posterior tooth and the body cavity, its bottom contains antero-posteriorly arranged ribs, with the most dorsally positioned rib rising to form a tubercle on dorsal side of the central socket. The posterior myophore is represented by a triangular projection that is separated from the posterior tooth by a zone of pallial canals. The posterior myophore extends a little beyond the septum separating the central socket from the body cavity. The anterior myophore forms an arc that extends from the dorsal extremity of the anterior tooth, around the antero-dorsal margin of the tooth and for a short distance around the margin of the body cavity. It consists of eight or nine projecting blades that are separated by recessing areas with pallial canals; the blades are arranged orthogonal to the antero-dorsal margin of the anterior tooth but become broadly orthogonal to the body cavity at the antero-ventral margin of the anterior myophore.

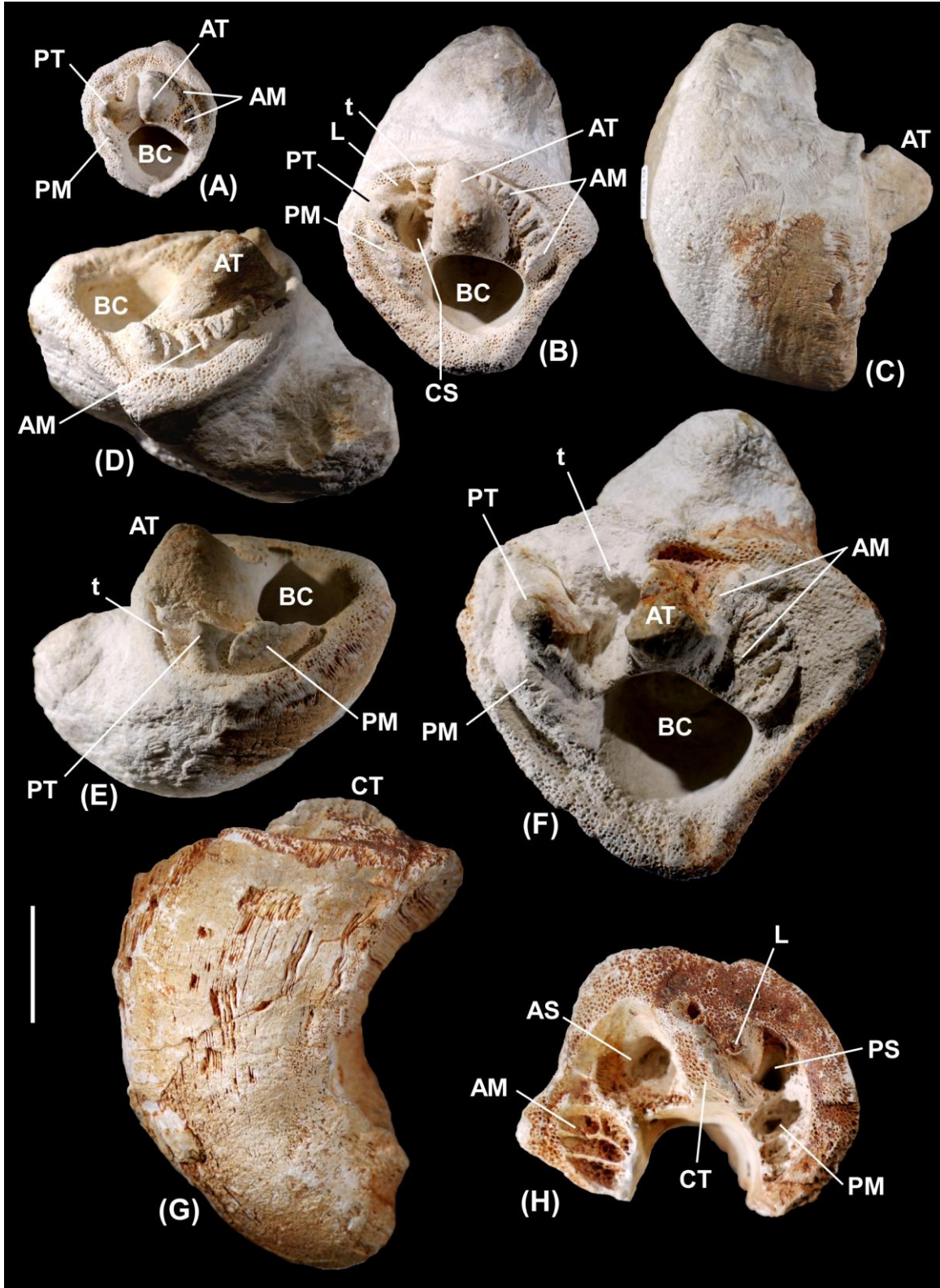


Figure 9. A-H. *Youngicaprina gloria* sp. nov. A, Left valve (IGM.7637), showing myocardial arrangement. B-E, left valve (holotype, IGM.7639): B, apertural view showing myocardial elements, note the pit for the ligament and the tubercle; C, posterior flank; D, oblique view of aperture from anterior side showing details of the anterior myophore; E, oblique view of aperture from posterior showing details of posterior myophore. F, left valve (IGM.7638) showing

The blades get progressively longer and higher passing from the dorsal margin of the anterior myophore to the antero-ventral end of the anterior myophore. The canals in the marginal row of pallial canals in the right valve are slightly radially elongated. The canals fill the inner shell structure, but do not invade the two teeth, the posterior myophore, the blades of the anterior myophore, or the ribs and tubercle of the central socket. The body cavity is broadly rounded, but its fill is unknown.

Discussion. *Youngicaprina gloria* sp. nov. is distinguished from *Y. sangabrieli* sp. nov. by: its less strongly coiled left valve; its triangular cross-section; the triangular form of the posterior myophore separated from the posterior tooth by a zone of pallial canals; the concave margin of the posterior tooth; and the extension of the anterior myophore, with its greater number of blades, around the antero-dorsal side of the anterior tooth.

***Youngicaprina sangabrieli* gen. et sp. nov.**
Figures 10, 11A-F

- ?pars 1888 *Ichthyosaroclitus anguis* n. sp.: Roemer, p. 9-10, pl. I (XXXI), fig. 7a-b (Collected from two miles above the mouth of Barton Creek Austin, Travis Co., Texas, from somewhere in the Edwards Limestone: Scott, 2002, p. 421)
- v. 1973 *Kimbleia* sp.; Coogan, p. 58 (two LVs only), pl. 1, fig. 3, pl 2, figs 5a-b.
- v. 1977 *Kimbleia* sp.; Coogan, pl. 16, figs. 2a-b.
- v. 1998 *Kimbleia albrittoni* (Perkins, 1960) pars; Alencáster and Oviedo-García, p. 175-177, fig. 8 (1), fig. 9 (1-2).
- v. 2010 *Caprinuloidea perfecta*; Scott and Weaver, fig. 3A-B, fig 5A, fig. 6C, fig. 7.

Diagnosis. A species of *Youngicaprina* with a strongly coiled left valve, and with four or five ribs on the anterior myophore of the left valve that are arranged orthogonally to the anterior surface of the anterior tooth, large pallial canals in 5 to 7 rows.

Types. Holotype (TMM.UT-36135.5); Paratypes (TMM.UT-36135.1-4, BEG.2523.1, UT.3388, UT.33871); all from the Edwards Limestone (Middle Albian) of South San Gabriel River, Roy Gunn's Ranch, Texas (the locality now lies under Lake Georgetown).

Description. The right valve is conical to cylindrical, relatively short to relatively long, straight. Transverse cross sections are quadrate with an expanded, narrow ventral margin. The posterior tooth is narrow and expands laterally towards its ventral end. The posterior tooth socket is deep and elongated in an anterior-posterior direction; it forms an angle of about 60 to 70 degrees to the cardinal line. A slight restriction separates the posterior tooth socket from the endomyophoral cavity. The endomyophoral cavity is separated from the body cavity by a septum which is solid in small specimens but has a row of pallial canals in larger specimens. The anterior tooth socket is elongated dorso-ventrally. The anterior myophore cavity is separated from the anterior tooth socket by a low septum. The anterior myophore cavity is triangular in form and subdivided into three or four sectors by two or three low septa. The ligament is represented by a solid area that is concave to the dorsal margin; the ligament is completely embedded within the shell structure and there is no external ligamental groove. The body cavity is broadly elliptical and carries tabulae that are convex in an adapical direction. The anterior tooth socket also carries conical tabulae; the fill of the posterior tooth socket is not known. Pallial canals have a uniform size throughout the shell, they range from 0.5 to 1.5 mm in diameter; a marginal layer of elongated pyriform canals with their narrow end directed outwards encircles the entire shell; they lack tabulae. Pallial canals invade the entire shell structure including the central tooth and in larger specimens also the septa. Pallial canals have tabulae spaced at distances of 1.5 to 3.5 mm.

The left valve is coiled forming up to half a revolution. It is much smaller than the right valve. The left valve has a transverse cross-section which is pear-shaped with the ventral side expanded to form a rounded angle, and the anterior aspect strongly flattened. Coiling is slightly asymmetrical. There is no external ligament groove, and no enclosed ligament has been seen. The posterior tooth is elongated antero-posteriorly, and is essentially a little flattened on the dorsal side. The anterior tooth is elongated dorso-ventrally. The central tooth socket is narrow between the teeth and expands postero-ventrally between the posterior tooth and the body cavity. The posterior myophore is represented by a broad

[Figure 9 continued] myocardial elements. G-H, Right valve (IGM.7643): G, posterior flank; H, apertural view showing myocardial elements, note the crescent-shaped ligament embedded in the interior of the shell. Scale bar 20 mm. AT, anterior tooth; AS, anterior socket; PT, posterior tooth; PS, posterior socket; CT, central tooth; CS, central socket; AM, anterior myophore; PM, posterior myophore; L, ligament; BC, body cavity; t, tubercle.



Figure 10. *Youngicaprina sangabrieli* sp. nov. Right valve, (SI.USNM.547502), Edwards Limestone, Whitney Dam.

arc that extends from the posterior tooth past the septum separating the central tooth socket from the body cavity and a short distance around the body cavity. The anterior myophore is a triangular area formed by four or five dorso-ventral blades; the blades are arranged parallel to the anterior margin of the anterior tooth, with adjacent blades

separated by a row of pallial canals. The pallial canals are the same as in the right valve; there is a distinct marginal row of radially elongated pallial canals; canals fill the remainder of the shell wall, other than as described above for the myocardial elements. The body cavity is broadly elliptical, and its upper part is filled with simple concave tabulae.

Discussion. The type material comes from Texas and is more robust than *Y. Gloria* gen. et sp. nov. Alencáster and Oviedo-García (1998, fig. 9.1-2) figured a large weathered left valve under the name *Kimbleia albrittoni* (Perkins), but this specimen has large pallial canals and a typical *Youngicaprina*-like anterior myophore; for these reasons, it is here placed in *Y. sangabrieli* gen. et sp. nov. Two right valves were found associated with *Kimbleia* in the Segovia Formation at Lopez Ranch, Kimble County, Texas (Coogan, 1973, 1977; Plate 6F) and were tentatively assigned to *Kimbleia* sp. by Coogan (1973, 1977). These specimens, although coarsely silicified, show all the characteristics of *Youngicaprina* and are here attributed to *Y. sangabreili* gen. et sp. nov.

Stratigraphic and Geographic Distribution (Figure 12)

During the Hauterivian-early Barremian, *Retha tulae* was inhabiting the carbonate platforms of the Americas (Jamaica, ?Mexico) and gave rise to the first evolutionary explosion of the Amphitriscoelinae. The division of the gutters between the myophores and shell margin gave rise to pallial canals, and several distinct lineages developed; *Amphitriscoelus* and *Pantojalaria* in the Americas and *Conchemipora* in the Pacific (Harris and Hodson, 1922; Alencáster, 1996; Chartrousse and Masse, 1998; Skelton and Masse, 1998; Pantoja-Alor et al., 2004; Mitchell and Brown, 2010). This diversification was wiped out with the collapse of carbonate platforms in the Early Aptian (Skelton and Gili, 2011).

By the Early Aptian, *Huetamia* the first representative of the Caprinuloideinae had appeared, and with the re-establishment of extensive carbonate platforms in the Early Albian of the Americas, a major diversification of the Caprinuloideina occurred. The Early Albian saw the appearance of *Coalcomana*, *Planocaprina* and *Caprinuloidea*, the first two disappearing by the end of the Early Albian, and the latter ranging into the early Late Albian. Further diversification occurred in the Late Albian with the appearance of *Mexicaprina*, *Kimbleia* and *Neokimbleia*, with *Neokimbleia* evolving from *Kimbleia* by the loss of the external ligamental groove.

The Early Albian also saw the first representatives of the Youngicaprinae, which have a distinctive myocardial arrangement. Primitive *Texicaprina* appear in the Lower Albian and are joined by *Youngicaprina* in the Middle Albian and *Jalpania* in the upper Upper Albian. *Immanitas*, which is also found in the upper Upper Albian, may also belong here.

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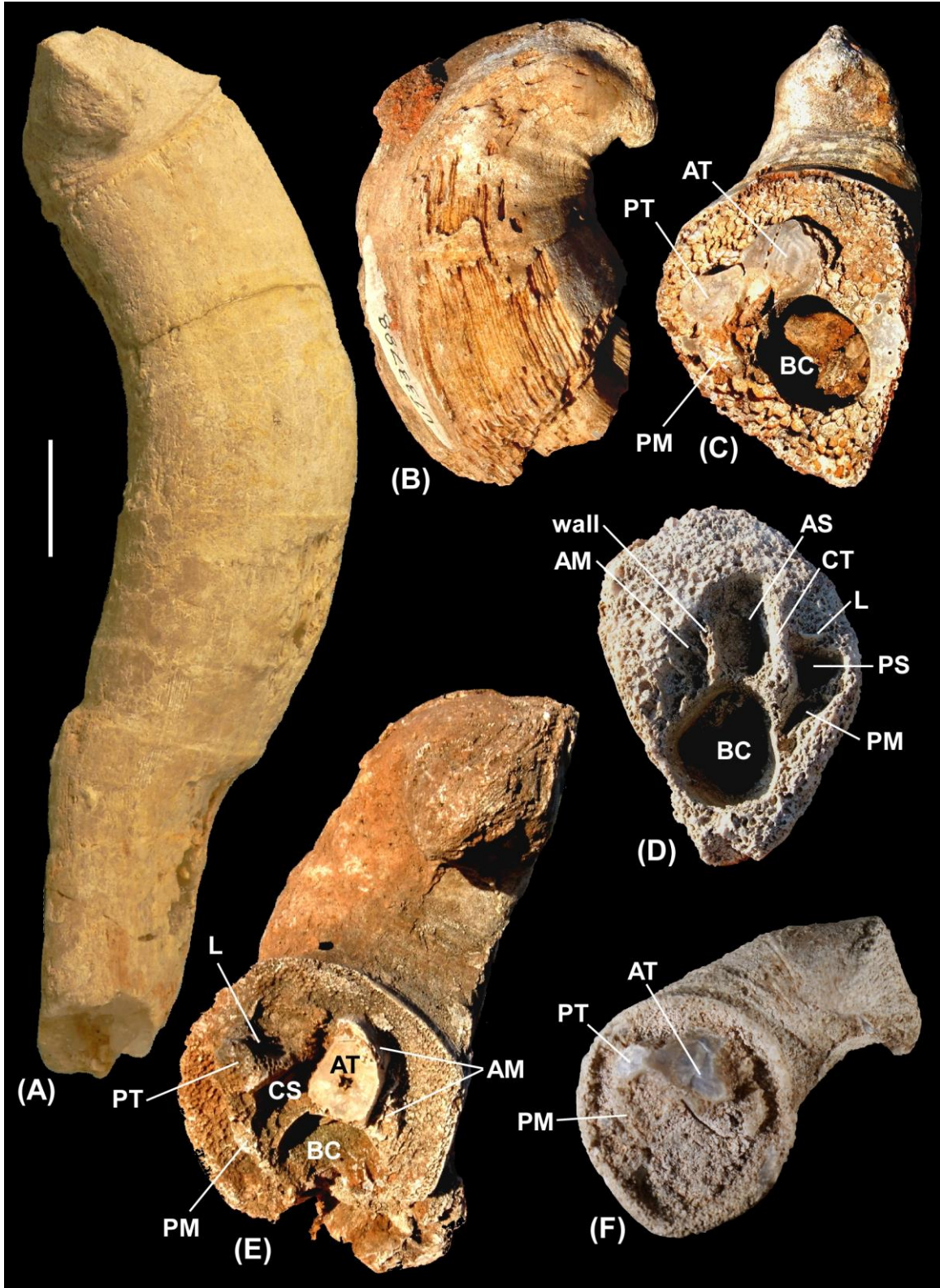


Figure 11. A-F, *Youngicaprina sangabrieli* sp. nov. A, bivalve specimen (SIUSNM.547503 [CS3]), Edwards Limestone, Whitney Dam. B-C, Left valve (Paratype, TMM.UT-33788), San Gabriel River, Roy Gunn's Ranch, Texas, showing large pallial canals and silicified myocardial arrangement. D, Right valve (Paratype, TMM.UT-33871), San Gabriel River, Roy Gunn's Ranch, Texas, showing enclosed ligament and sockets for myophores separated from

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[Figure 11 continued] sockets for teeth. E, Left Valve (Holotype, TMM.UT-36135.5) San Gabriel River, Roy Gunn's Ranch, Texas, showing myocardinal structure. F, Left valve (IGM.2574), Segovia Formation at Lopez Ranch, Kimble County, Texas, coarsely crystallized but showing features typical of this species. Note that all specimens lack any indication of an external ligamental groove. Scale bar 20 mm. AT, anterior tooth; AS, anterior socket; PT, posterior tooth; PS, posterior socket; CT, central tooth; CS, central socket; AM, anterior myophore; PM, posterior myophore; L, ligament; BC, body cavity; t, tubercle.

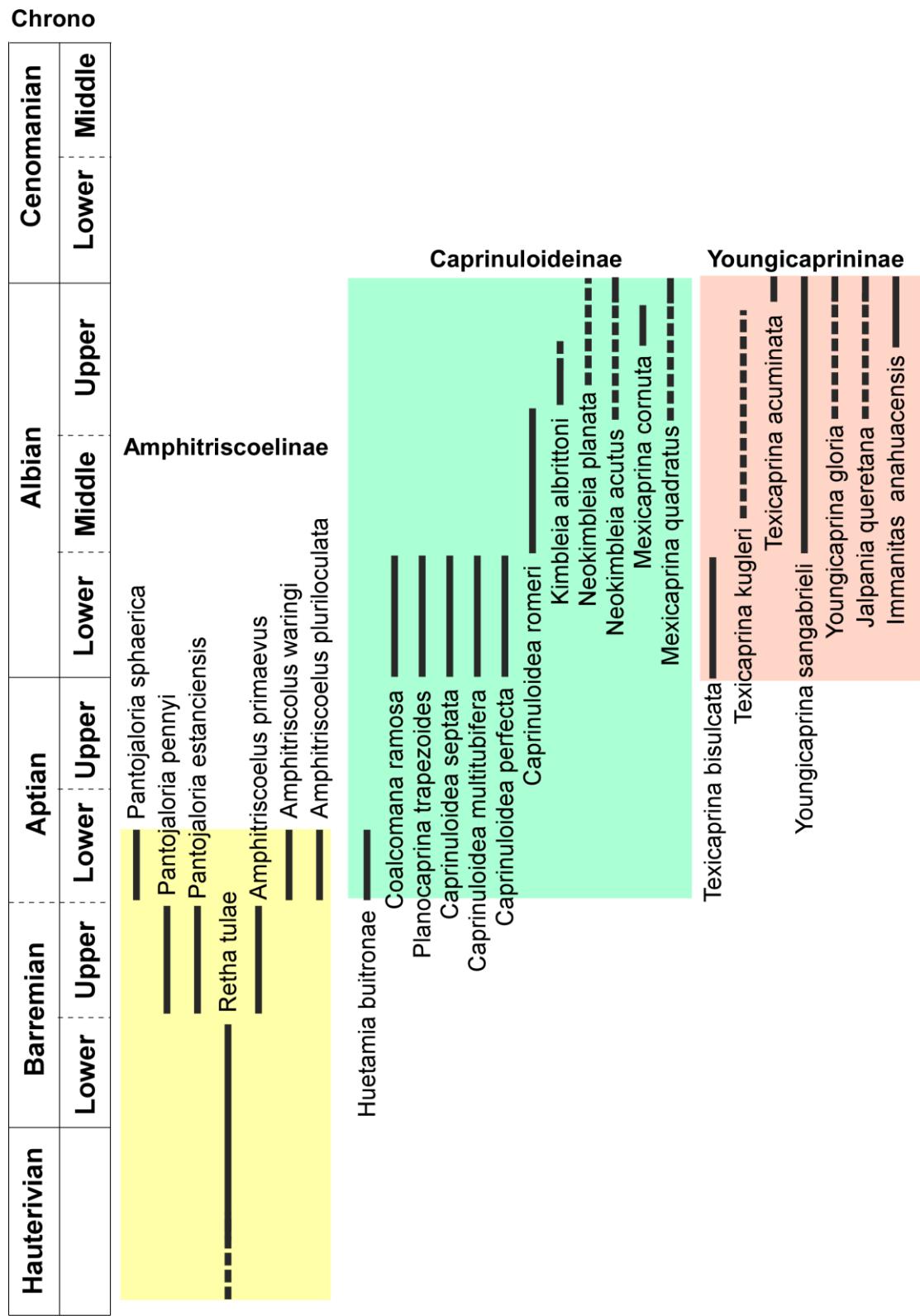


Figure 13. Evolution and biostratigraphic distribution of the Caprinuloideidae for the Lower Cretaceous of the Americas.

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