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NEW UPPER TITHONIAN (JURASSIC) AMMONITES FROM THE CHINAMECA FORMATION IN SOUTHERN VERACRUZ, EASTERN MEXICO

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ABSTRACT—Upper Tithonian (Jurassic) ammonites occur in the Chinameca Formation at Chinameca, southern Veracruz, eastern Mexico. The fauna includes *Eopaquiericeras peraltai* n. gen. and sp. and *E. pazi* new genus and species of the family Platylenticeratidae, *Chinamecaceras maldonadoi* n. gen. and sp. of the subfamily Aspidoceratinae, *Veracruciceras ruizi* n. gen. and sp. and *V. myczynskii* n. gen. and sp. of the subfamily Simoceratinae, *Durangites zigzagcostatus* n. sp., and representatives of *Haploceras*, *Salinites*, *Kossmatia*, and *Andiceras*. *Kossmatia* is the most abundant and biostratigraphically significant ammonite in the Chinameca fauna and its age significance and distribution in Mexico is discussed. In addition, a comparison of the suture lines of *Kossmatia* and the related older genus *Lemencia* indicates that they both belong to the Tithonian subfamily Richterellinae rather than the Upper Oxfordian–Kimmeridgian families Ataxioceratidae and Lithacoceratidae. The Chinameca ammonites have affinities with taxa of the same age from central and northern Mexico, Cuba, and the southern United States.

INTRODUCTION

ONLY TWO outcrops with Upper Tithonian ammonites are known from the Gulf of Mexico coastal plain. The Chinameca Formation consists of limestone and chert in its type locality in southern Mexico. This small outcrop contains ammonites of the families Protancyloceratidae, Haploceratidae, and Perisphinctidae of Kimmeridgian to Lower Cretaceous age (Burckhardt, 1930) (Fig. 1). The second known outcrop is at Cruillas in northeastern Mexico. At this locality, argillaceous limestone and shale of the La Casita Formation contain the Upper Tithonian genera *Protancyloceras* Spath, 1924 and *Kossmatia* Uhlig, 1907 (Kellum, 1937). Both outcrops were discussed by Imlay (1980) and Cantú-Chapa (1982).

Subsurface.—In addition, there have been several subsurface stratigraphic studies of the Tithonian of the Gulf of Mexico coastal plain based on ammonites and well logs. Tithonian formations intersected by bore holes include the La Casita Formation in northeastern Mexico, the Pimienta Formation in eastern Mexico, and the Edzna Formation in southeastern Mexico. These formations lie at depths of between 400 and 4,800 m below sea level in the Gulf region (Cantú-Chapa, 1982, 1989; Cantú-Chapa and Ortuño, 2004).

Other localities.—An ammonite from the Malone Mountains in southwestern Texas which was referred to the Lower Cretaceous *Neocomites* cf. *indicus* Uhlig, 1910 by Albritton (1937) was later determined to be the Upper Tithonian species *Kossmatia varicostata* Imlay, 1943 by Cantú-Chapa (1976b) and Imlay (1980). The Artemisa Formation in the Pinar del Rio area, western Cuba, also contains a number of the same Tithonian ammonites that occur in Mexico (Imlay, 1942; Judoley and Furrazola-Bermudez, 1968; Myczynski, 1994a, 1994b, 1999a, 1999b).

The obvious affinity exhibited by Upper Tithonian ammonites from Mexico, the southern United States, and western Cuba suggests that they represent the same paleogeographic province, with similar faunal and sedimentological conditions (Imlay, 1980; Cantú-Chapa, 1989, 2001a). In addition, Tithonian ammonites are also known from east-central (Mazatepec), northeastern (Galeana), central (Mazapil, Real de Catorce, Symón), and northern (Chihuahua) Mexico (Burckhardt, 1906, 1912, 1919–1921; Imlay, 1939, 1943; Cantú-Chapa, 1967, 1968, 1976a, 1976b, 1993, 1998, 1999; Verma and Westermann, 1973; Oloriz et al., 1999).

Geological setting and location.—Ammonites described in this paper were recovered from the Chinameca Formation in the El Piedral quarry located about 5 km northeast of the village of Chinameca, in Veracruz, southern Mexico (Fig. 1). The Chinameca Formation consists of light brown, laminated, and fossiliferous limestone in beds 20–40 cm in thickness. It was originally defined by Benavides (1950) for exposures in the flanks of the Cerro Pelón Anticline, at Minatitlán, Veracruz, where it attains a thickness of 300 m. Unfortunately, the El Piedral section is in an active quarry constantly used to extract rock. The ammonite collection described herein was recovered from an area of only approximately 100 m^2. The exposure is surrounded by the Upper Oligocene Depósito Formation.

Paleontological, systematic, and biostratigraphic problems.—Recent studies of Upper Jurassic and Lower Cretaceous ammonites have emphasized classifications based on presumed sexual dimorphism, with attempts to explain their origins and centers of dispersion. Genera, subgenera, and species are divided arbitrarily into macroconchs and microconchs, depending on the relative size of the shell and the presence of lappets in complete specimens (Verma and Westermann, 1973; Donovan et al., 1981; Enay and Cecca, 1986). Such classifications are inconclusive, however, for incomplete ammonites (Cecca and Enay, 1991).

These studies have proposed ammonite classifications which employ a twofold nomenclature. For example, a form considered to be the microconch of one genus may also be considered to be the macroconch of another, such as the Upper Tithonian *Durangites–Protacanthodiscus* (Tavera-Benítez, 1985; Enay et al., 1998). Such classifications are highly subjective and arbitrary; moreover, taxonomic difficulties and inconsistencies such as those cited above have been recognized by the same paleontologists who proposed them (Verma and Westermann, 1973; Donovan et al., 1981). Consequently, they have been rejected by Ziegler (1974) and Cantú-Chapa (2001b).

The paleobiogeographic distribution, centers of dispersion, and migration routes of certain American Upper Jurassic ammonites have posed a problem to some European paleontologists. As a consequence, they have sometimes proposed unnecessary paleobiogeographic models and have considered ammonite genera originally described from America as endemic. They also show a tendency to propose single-directional migration routes from the Mediterranean Tethys to the Mexican region (Ziegler, 1971; Enay, 1980; Meléndez et al., 1998). Nevertheless, the presence of American genera has long been recognized in other continents, necessitating revision of the old concept of endemism and supporting present-day concepts of cosmopolitan paleobiogeographic distribution. Several examples will be discussed under Systematic Paleontology.

A biostratigraphic inconsistency exists between the correlated positions of the Upper Tithonian in Mexico based on microfossils and ammonites, respectively (Cantú-Chapa, 1996, 1999). Oloriz

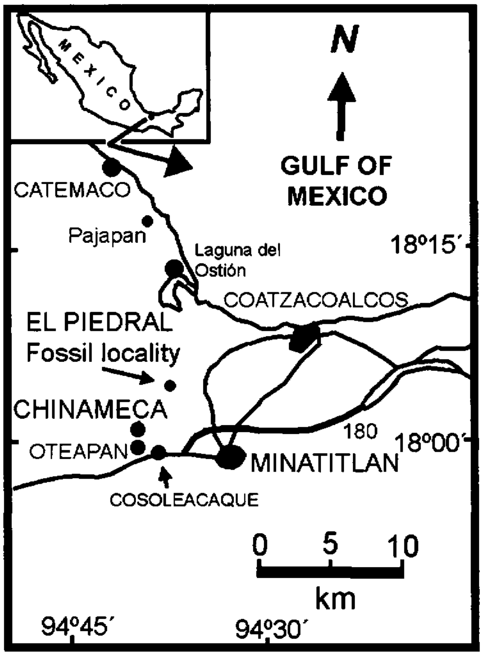

FIGURE 1—Map showing the El Piedral ammonite locality (small arrow) in the Upper Tithonian Chinameca Formation, southeastern Mexico.

et al. (1999) utilized a supposed calpionellid succession to reassign a Berriasian age to occurrences of the Upper Tithonian ammonites *Substeueroceras* Spath, 1923a, *Kossmatia*, and *Durangites* Burckhardt, 1912 from central Mexico (Burckhardt, 1930; Verma and Westermann, 1973; Imlay, 1980; Cantú-Chapa, 1999) (cf. Zeiss, 1984, 1986). However, as Adatte et al. (1996) indicated, "there are no continuous successions of calpionellid faunas during Late Tithonian time." Furthermore, they have yet to demonstrate how they characterize this substage as a chonostratigraphic unit, or to indicate which microfossils of this age are characteristic in Mexico (Stinnesbeck et al., 1993; Adatte et al., 1994).

Sudden evolutionary innovations in the berriasellid (*Substeueroceras* and *Kossmatia*), spiticeratid (*Proniceras* Burckhardt, 1919), and himalayitid (*Durangites*) ammonites clearly provide the best chronostratigraphic basis for identifying the Upper Tithonian in Mexico, Cuba, Argentina, and Iraq (A. Leanza, 1945; Imlay, 1980; Myczynski, 1989; Howarth, 1992). The ornamentation and suture lines of these genera make them reliable Upper Tithonian indices and readily separate them from Berriasian ammonite genera (Cantú-Chapa, 1999).

Age of the Chinameca ammonites.—Only ammonites were found in the El Piedra quarry at Chinameca. The fauna is dominated by representatives of *Kossmatia*, *Durangites*, *Salinites* Cantú-Chapa, 1968, and *Haploceras* Zittel, 1870. Other ammonites are described as new genera, including *Eopachiericeras*, *Chinamecaceras*, and *Veracruciceras*. The presence of *Kossmatia*, *Salinites*, and *Durangites* indicates a Late Tithonian age for the Chinameca fauna.

The pattern of the ventral ribbing and the suture lines of *Kossmatia* and *Berriasella* Uhlig, 1905, from the Upper Tithonian and Berrasian, respectively, were compared to show their differences; in the last case, they are located in S1 (Cantú-Chapa, 1999). In the present study the suture line of *Kossmatia* was also compared with genera of other Kimmeridgian–Tithonian families to demonstrate its true phylogenetic relationship with the Upper Tithonian family Berriasellidae, rather than the families Ataxioceratidae and Lithacoceratidae to which it was assigned by Donovan et al. (1981) and Zeiss (2001), respectively. There are important differences between the berriasellids and the ataxioceratids-lithacoceratids. They will be described below under the discussion of the genus *Kossmatia*.

Salinites also characterizes the Upper Tithonian; it is differentiated from the Lower Tithonian *Hildoglochiceras* Spath, 1924 from the Indo-Malgache region by its ornament and its suture line. *Durangites* is an Upper Tithonian himalayitid which has been recovered in association with *Proniceras*, and *Salinites* at several localities in Mexico and Cuba (Cantú-Chapa, 1968, 1976a; Myczynski, 1989, 1999b).

Burckhardt (1930), Verma and Westermann (1973), and Imlay (1980) showed the stratigraphic level of *Parodontoceras* Spath, 1923a, *Substeueroceras*, *Proniceras*, *Kossmatia*, *Salinites*, and *Durangites* within the Upper Tithonian of Mexico. Cantú-Chapa (1967, 1989, 1999) demonstrated that *Parodontoceras*, *Proniceras*, and *Salinites* are present in the upper argillaceous limestone and shale beds, sometime alternating with bentonite, which correspond to the top of the La Casita and Pimienta Formations and which represent to the Upper Tithonian Zone of *Parodontoceras* aff. *callistoides*. These beds differ from the overlying micritic limestone of the Taraises or Lower Tamaulipas Formations which contain *Subthurmannia* Spath, 1939 and *Spiticeras* Uhlig, 1903, and represent the Lower Berriasian Zone of *Subthurmannia mazatepense*. Both beds were cut by oil wells located along the coastal plain of the Gulf of Mexico. Each of these beds with their respective ammonite zones characterizes the Jurassic–Cretaceous boundary in eastern Mexico (Cantú-Chapa, 1967, 1989).

The same ammonite genera were found in the Upper Tithonian of Cuba (Myczynski, 1989) and in the subsurface of Louisiana (Imlay and Hermann, 1984). All of these occurrences were considered to be Upper Tithonian by Verma and Westermann (1973), Imlay (1980), Hoedemaeker (1987), and Cantú-Chapa (1989).

SYSTEMATIC PALEONTOLOGY

Morphological terminology follows Wright et al. (1996). All dimensions are given in millimeters; D = shell diameter; H = whorl height measured from umbilical seam to venter; W = whorl width; U = umbilical diameter. Described specimens are housed in the Geological Department at the Escuela Superior de Ingeniería y Arquitectura (ESIA), Instituto Politécnico Nacional (IPN), Mexico D. F. 07738, Mexico.

Order AMMONOIDEA Zittel, 1884
Suborder AMMONITINA Hyatt, 1889
Superfamily HAPLOCERATACEAE Zittel, 1884
Family HAPLOCERATIDAE Zittel, 1884
Subfamily HAPLOCERATINAE Zittel, 1884
Genus HAPLOCERAS Zittel, 1870

Type species.—*Ammonites elimatus* Oppel, 1865; by subsequent designation of Spath, 1923b.

Discussion.—The superfamily Haplocerataceae has been interpreted in accordance with concepts of sexual dimorphism by Donovan et al. (1981) and Wright et al. (1996). These authors attempted to explain phylogenetic relationships on its origin, which, according to Cecca and Enay (1991), remain uncertain.

Spath (1923b) designated *Ammonites elimatus* as the type species of *Haploceras*. Enay and Cecca (1986), however, considered that Spath's (1923b) original designation was based on a macroconch specimen of Zittel (1870). Enay and Cecca (1986) therefore proposed another type species, *A. carachtheis* Zeuschner (1846), in an attempt to characterize *Haploceras* by a microconch form (Cecca and Enay, 1991). The practice of substituting one type species for another is based on arbitrary concepts of sexual dimorphism and not on the principle of priority.

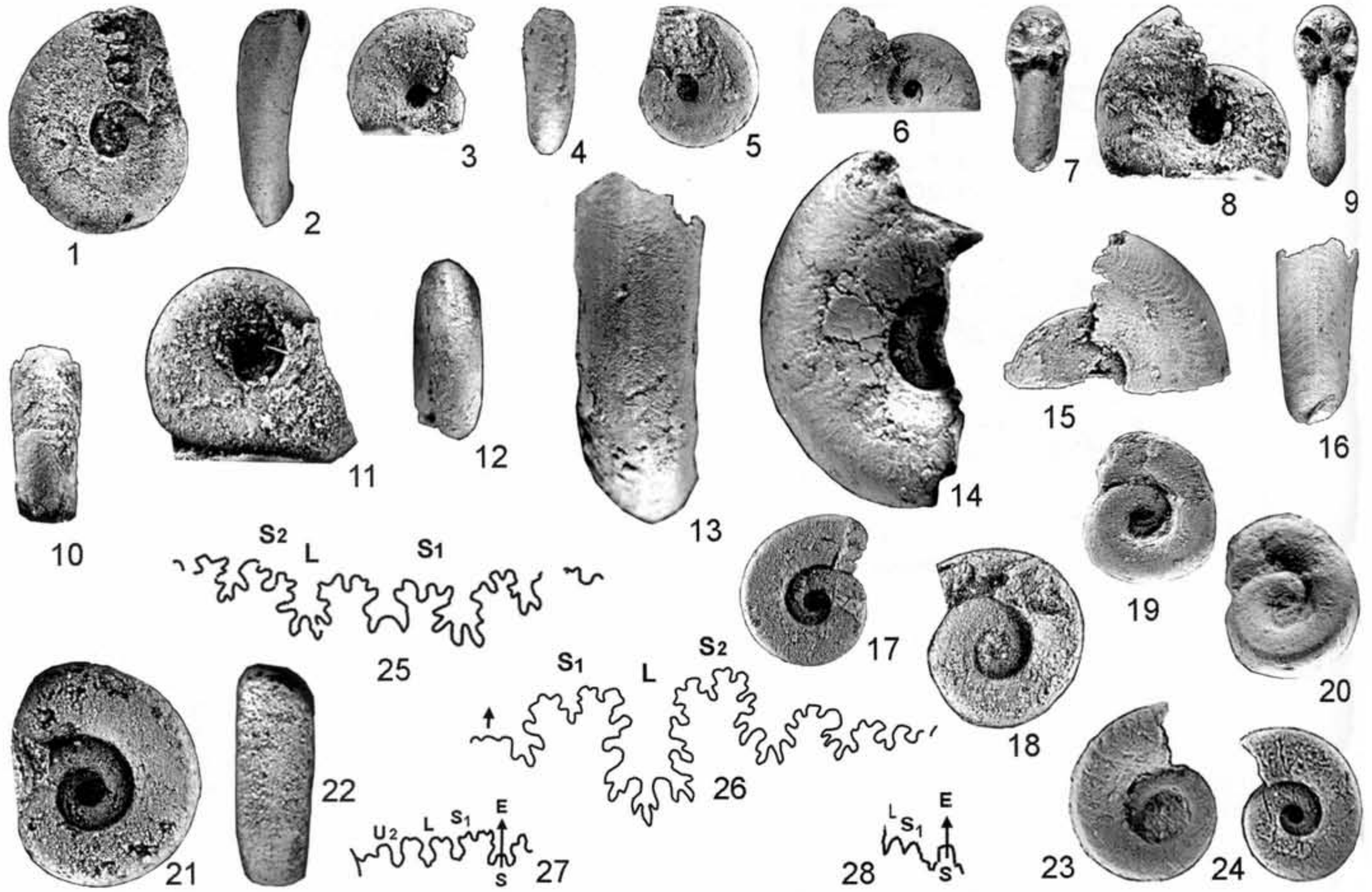

FIGURE 2—*1, 2, Glochiceras* sp., lateral and ventral views, ESIA-1065. *3–12, Haploceras* sp.; *3, 4,* lateral and ventral views, ESIA-1058; *5,* lateral view, ESIA-1059; *6, 7,* lateral and apertural views, ESIA-1060; *8–10,* lateral, apertural, and ventral views, ESIA-1061; *11, 12,* lateral and ventral views, ESIA-1062. *13–16, Salinites inflatum* (Imlay, 1939); *13, 14,* ventral and lateral views, ESIA-1066; *15, 16,* lateral and ventral views, ESIA-1067. *17, 21–24, Eopaquiericeras peraltai* n. gen. and sp.; *17,* paratype, lateral view, ESIA-1069; *21, 22,* holotype, lateral and ventral views, ESIA-1068; *23,* paratype, lateral view, ESIA-1070; *24,* paratype, lateral view, ESIA-1071. *18–20, Eopaquiericeras pazi* n. gen. and sp.; *18,* holotype, lateral view, ESIA-1072; *19, 20,* paratype, lateral and ventrolateral views, ESIA-1073. *25,* Suture line of *Salinites grossicostatum* (Imlay, 1939). *26,* Suture line of *Hildoglochiceras planum* Spath, 1928, without scale. *27,* Suture line of *Paquiericeras* (*Paquiericeras*) *paradoxum* Sayn *in* Thieuloy, 1977. *28,* Suture line of *Eopaquiericeras peraltai*, holotype, ESIA-1068. All specimens from the El Piedral locality, Chinameca, southern Veracruz. All specimens ×2, except *25, 27,* ×4; *28,* ×5; *26,* without scale. Specimens coated with ammonium chloride.

HAPLOCERAS sp.
Figure 2.3–2.12

Description.—Shell small and moderately involute with compressed to subovate whorl section; smooth and slightly convex flanks; subrounded venter; and deep umbilicus with inclined wall. Suture line not observed.

Material examined.—Five small specimens, enclosed in matrix; ornamentation lost by erosion. ESIA-1058–ESIA-1062.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—The compressed whorl section and involute coiling of these small specimens suggest affinities with *Haploceras.* They are left in open nomenclature because of their poor state of preservation. Four species of *Haploceras* are known from the Lower Tithonian (*H. transatlanticum* Burckhardt, 1906 and *H.* cf. *elimatum* Oppel, 1865) and Upper Tithonian (*H. ordonezi* Aguilera *in* Castillo and Aguilera, 1895 and *H. veracruzanum* Cantú-Chapa, 1976a) of Mexico (Aguilera *in* Castillo and Aguilera, 1895; Burckhardt, 1906; Verma and Westermann, 1973; Cantú-Chapa, 1976a). They are distinguished by their degree of involution, ornamentation, and suture.

Cantú-Chapa (1982) illustrated one specimen of *Haploceras* sp. from the Miraflores-1 well in northeastern Mexico which characterizes the condensed middle part of the Upper Tithonian La Casita Formation. Another, older specimen of *Haploceras* sp. was recovered in association with the Lower Tithonian ammonite *Mazapilites* Burckhardt, 1906 in the type section of the Taman Formation, eastern Mexico (Cantú-Chapa, 1984).

Family OPPELIIDAE Douvillé, 1890
Subfamily GLOCHICERATINAE Hyatt, 1900
Genus GLOCHICERAS Hyatt, 1900

Type species.—*Ammonites nimbatus* Oppel, 1863.

GLOCHICERAS sp.
Figure 2.1, 2.2

Description.—Shell small and moderately involute with compressed whorl section; smooth, flat flanks; subrounded venter; and deep umbilicus with vertical wall.

Material examined.—ESIA-1065.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

TABLE 1—Shell measurements (in mm) and proportions of Tithonian (Jurassic) ammonites from Chinameca, Veracruz, Mexico; central and northern Mexico; and Cuba.

Specimen	D	U	H	W	U/D	H/D	H/W
Glochiceras sp.							
ESIA-1065	15.0	3.5	6.2	3.0	0.23	0.41	—
Haploceras sp.							
ESIA-1058	11.0	2.5	6.4	4.5	0.22	0.58	—
ESIA-1059	9.7	2.0	5.3	—	0.20	0.54	—
ESIA-1060	11.3	2.1	5.0	4.2	0.18	0.44	1.19
ESIA-1061	14.1	2.9	6.7	4.8	0.20	0.47	1.39
ESIA-1062	14.7	3.0	8.3	4.8	0.20	0.56	1.73
Salinites inflatum (Imlay, 1939)							
ESIA-1066	24.4	6.0	10.0	8.2	0.24	0.41	—
ESIA-1067	15.0	3.5	6.2	3.0	0.23	0.41	—
Salinites inflatum (Imlay, 1939)							
Holotype	34.0	7.0	16.5	13.0	0.20	0.48	—
Eopaquiericeras peraltai n. gen. and sp.							
Holotype ESIA-1068	14.8	6.0	5.5	4.9	0.40	0.37	—
Paratype ESIA-1069	10.0	3.6	3.2	—	0.36	0.32	—
Paratype ESIA-1071	10.0	3.5	3.2	—	0.35	0.32	—
Paratype ESIA-1070	12.2	5.0	4.6	—	0.40	0.37	—
Eopaquiericeras pazi n. gen. and sp.							
Holotype ESIA-1072	11.7	4.0	3.4	—	0.34	0.29	—
Paratype ESIA-1073	10.4	4.0	3.9	—	0.38	0.37	—
Chinamecaceras maldonadoi n. gen. and sp.							
Holotype ESIA-1085	52.0	20.2	1.7	2.3	0.39	—	—
Schaireria neoburgensis (Verna and Westermann, 1973)							
[Mexico]	47.0	6.0	—	—	0.12	—	—
Schaireria sp. (Myczynski, 1989)							
[Cuba]	33.0	7.5	—	—	0.23	—	—
Veracruciceras ruizi n. gen. and sp.							
Holotype ESIA-1075	57.0	34.0	12.8	10.4	0.59	0.22	1.23
Corongoceras cordobai (Verma and Westermann, 1973)							
Holotype	70.0	40.0	23.0	17.0	0.57	0.33	—
Olcostephanidae gen. and sp. indet.							
ESIA-1088	7.7	2.0	3.2	4.4	0.26	0.41	—
Durangites sp. A							
ESIA-1074	30.0	9.8	5.0	—	0.32	0.17	—
Durangites sp. B							
ESIA-1087	62.3	18.3	16.0	27.4	0.29	0.25	—
Durangites zigzagcostatus n. sp.							
Holotype ESIA-1086	16.7	7.6	6.2	6.4	0.45	0.37	—
Durangites aff. *zigzagcostatus* n. sp.							
ESIA-1093	15.0	6.0	4.8	—	0.40	0.32	—
Kossmatia purisima Verma and Westermann, 1973							
Holotype	51.0	16.5	22.7	19.3	0.32	0.44	1.17
Kossmatia purisima Verma and Westermann, 1973							
ESIA-1080	28.0	11.5	14.9	10.2	0.41	0.53	1.46
ESIA-1084	31.7	12.3	11.2	—	0.38	0.35	—
Andiceras monserrati (Aguilera *in* Castillo and Aguilera, 1895) [*in* Verma and Westermann, 1973]							
	42.0	20.0	13.0	15.0	0.47	0.31	0.86
Andiceras monserrati (Aguilera *in* Castillo and Aguilera, 1895)							
ESIA-1082	20.9	7.5	8.1	—	0.36	0.39	—

Discussion.—The smooth flat flanks and absence of a midlateral furrow suggest affinities with *Glochiceras deplanatum* (Waagen, 1875) (Collignon, 1960, pl. 142, figs. 540, 542) from Madagascar. However, U/D is larger in the Chinameca specimen (0.23 vs. 0.17–0.19 in *G. deplanatum*) (Table 1).

The *Glochiceras* species described by Burckhardt (1906) and Imlay (1939) from north-central Mexico differ from the Chinameca form by their possession of a midlateral furrow, falcoidal striae, and an ovate whorl section.

Genus SALINITES Cantú-Chapa, 1968

Type species.—*Hildoglochiceras grossicostatum* Imlay, 1939; by original designation of Cantú-Chapa, 1968, p. 20.

Discussion.—Enay (1980) and Enay and Cariou (1997) questioned whether the genus *Salinites*, which was proposed by Cantú-Chapa (1968, 1976a) for glochiceratins from Mexico and Cuba, was distinct from *Hildoglochiceras* from the Indo-Malgachan region. Myczynski (1999b), however, recognized *Salinites* as distinct from *Hildoglochiceras*, based on morphological and stratigraphic studies on specimens from Cuba.

Both genera have a midlateral furrow and falcoidal ribs or striae. However, *Salinites* is involute with a keeled venter and sutural elements S1 and S2 have similar sizes; the base of S1 is narrow, and the base of S2 is larger than the top (Imlay, 1939) (Fig. 2.25). By contrast, *Hildoglochiceras* is evolute and lacks a ventral keel and sutural element S1 is lower than S2; the base of S1 is large, and the base of S2 is as large as the top (Spath, 1928) (Fig. 2.26).

Salinites and *Hildoglochiceras* differ in morphology, age, and biogeographical distribution. *Salinites* is associated with *Kossmatia*, *Proniceras*, and *Durangites* in the Upper Tithonian of Mexico and Cuba (Imlay, 1939; Cantú-Chapa, 1976a; Myczynski, 1989). *Salinites* was also reported by Imlay and Hermann (1984) from the subsurface in Louisiana, USA. *Hildoglochiceras* is apparently restricted to the Lower Tithonian of Madagascar and India (Spath, 1928; Collignon, 1960).

SALINITES INFLATUM (Imlay, 1939)
Figure 2.13–2.16

Hildoglochiceras inflatum IMLAY, 1939, p. 29, pl. 4, figs. 1–5; HILLEBRANDT, SMITH, WESTERMANN, AND CALLOMON, 1992, p. 268.
Salinites inflatum (IMLAY). CANTÚ-CHAPA, 1968, p. 20; 1976a, p. 62, pl. 2, fig. 13; MYCZYNSKI, 1999a, p. 99–100.
Hildoglochiceras (Salinites) sp. aff. *inflatum* (IMLAY). MYCZYNSKI, 1989, p. 89, pl. 14, fig. 5.

Description.—Involute shell with convex flanks; moderately wide venter with weak keel; ovate whorl section with lower midlateral furrow; falcoidal striae on outer flank.

Material examined.—Two small fragmental specimens, each comprising one-half of a whorl; ESIA-1066, ESIA-1067.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—The weak ornament of the Chinameca specimens resembles that of *Salinites inflatum* from north-central Mexico. They differ, however, in U/D (0.23–0.27 in the Chinameca specimens vs. 0.20 in the holotype *S. inflatum*) and H/D (0.41 in the Chinameca specimens vs. 0.48 in the holoype of *S. inflatum*).

Superfamily PERISPHINCTACEAE Steinmann, 1890

Discussion.—The superfamily Perisphinctaceae is represented by the families Himalayitidae and Neocomitidae in the Jurassic–Cretaceous boundary interval; they are characterized by concepts of latitudinal and climatic distribution, or presumed sexual dimorphism after Donovan et al. (1981). Wright et al. (1996) subdivided the family Neocomitidae into three subfamilies based on two different and incompatible criteria which will be discussed below.

Family PLATYLENTICERATIDAE Casey, 1973 emend.

Type genus.—*Platylenticeras* Hyatt, 1900.

Original diagnosis.—See Casey (1973).

Emended diagnosis.—Shell compressed, involute or evolute; tabulate or oxyconic venter; flanks smooth or ornamented with weak ribs, small umbilical or ventrolateral tubercles or clavi. Large, shallow S1 divided by secondary lobe with different side and position.

Discussion.—The genus *Paquiericeras* Sayn, 1901 was assigned to the family Craspeditidae, subfamily Garniericeratinae Vermeulen, 1972 by Arkell et al. (1957). Later, it was considered as a monotypic genus and placed in the family Olcostephanidae Haug, 1910, subfamily Platylenticeratinae Casey, 1973 by Casey (1973) and Thieuloy (1977). More recently, Wright et al. (1996) included *Paquiericeras* in the subfamily Platylenticeratinae, family Polyptychitidae Wedekind, 1918.

The concept of the Platylenticeratinae must be emended to include both involute (*Platylenticeras*) and evolute forms (*Paquiericeras* and *Delphinites* Sayn, 1901) simultaneously. The suture line is the principal and common morphological character in all three of these genera; it is characterized by a large and shallow S1 which is divided by a secondary lobe with a different side and position (Thieuloy, 1977) (see Fig. 2.27). This type of suture line is unknown in the Lower Cretaceous families Polyptichitidae, Olcostephanidae, and Craspeditidae where the platylenticeratins were previously included. The suture line must therefore be considered as the basic unifying morphological element; it links *Platylenticeras*, *Paquiericeras*, and *Delphinites* in a higher systematic unit which is herein designated the family Platylenticeratidae Casey, 1973.

Genus EOPAQUIERICERAS new genus

Type species.—*Eopaquiericeras peraltai* n. sp.

Included species.—*Eopaquiericeras pazi* n. sp.

Diagnosis.—Shell small, evolute, and platiconic with subquadrate whorl section and wide umbilicus; flanks smooth and subrounded, subparallel, or inclined toward umbilicus. Venter moderately wide, subrounded, or flat, ventrolateral shoulder subrounded to subangular. Suture line with shallow, angular elements; E large and divided by S; S1 large and irregularly divided; L shallow; U2 unknown.

Etymology.—The name alludes to an older Mexican form than the Valanginian genus *Paquiericeras* from France and Spain.

Discussion.—*Eopaquiericeras* has the characteristic morphology associated with the family Platylenticeratidae, including a compressed, evolute shell, subrounded to flat venter, and sutures with a large, shallow S1 which is asymmetrically divided by a superficial secondary lobe, and a shallow L (Fig. 2.28).

Eopaquiericeras is distinguished from *Haploceras*, *Neolissoceras* Spath (1923b), and *Glochiceras* by its evolute and smooth shell. *Eopaquiericeras* resembles *Paquiericeras* from France and Spain (Vermeulen, 1972; Thieuloy, 1977; Company, 1987) by its small, evolute, and compressed shell with flattened flanks, and convex or flat venter, and its similar umbilical diameter (U/D, 0.36–0.46 in *Eopaquiericeras* vs. 0.35–0.40 in *Paquiericeras*); however, it is readily distinguished from *Paquiericeras* by the absence of a ventral keel and umbilical tubercles. The suture line of *Eopaquiericeras* resembles that of *Paquiericeras* in its large and irregularly divided S1 but differs by its simple and angular elements.

In addition, a significant time interval separates *Eopaquiericeras* from *Paquiericeras*. *Eopaquiericeras* is associated with Upper Tithonian himalayitids (*Durangites*), berriasellids (*Kossmatia*), and simoceratids at Chinameca. By contrast, occurrences of *Paquiericeras* from France and Spain are referred to the Valanginian based on their association with *Bochianites* Lory, 1898; *Neocomites* Uhlig, 1905; *Olcostephanus* Neumayr, 1875; and *Saynoceras* Munier-Chalmas *in* Munier-Chalmas and de Lapparent, 1894 (Vermeulen, 1972; Thieuloy, 1977; Company, 1987; Wright et al., 1996).

EOPAQUIERICERAS PERALTAI new species
Figure 2.17, 2.21–2.24, 2.28

Diagnosis.—Shell small and evolute with subquadrate whorl section, subparallel flanks, and moderately large and subrounded venter; subrounded ventrolateral shoulders; with finely spaced striae on outer flank. S1 large and shallow, asymmetrically divided by superficial secondary lobe, L shallow.

Description.—Shell small, evolute, platiconic, and compressed with subquadrate whorl section; flanks subrounded and subparallel; venter moderately wide and subrounded; umbilical and ventrolateral shoulders subrounded; fine, spaced, and convex striae present on outer flank. Suture line with large, shallow S1, asymmetrically divided by superficial secondary lobe; L shallow.

Etymology.—Named in honor of Mr. José Antonio Peralta-Sánchez, engineer for Petróleos Mexicanos, in Agua Dulce, Veracruz, Mexico, who collected the holotype.

Types.—Holotype, ESIA-1068 (Fig. 2.21, 2.22, 2.28); paratypes, ESIA-1069 (Fig. 2.17), ESIA-1070 (Fig. 2.23), ESIA-1071 (Fig. 2.24).

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—Same as for genus, except the small specimen ESIA-1070 in Figure 2.23 has fine, incurved, and spaced striae on the outer flank.

EOPAQUIERICERAS PAZI new species
Figure 2.18–2.20

Diagnosis.—Shell small and evolute with compressed, subquadrate whorl section; flat and moderately wide venter; flat flanks inclined toward the umbilicus; and subangular ventrolateral shoulder.

Description.—Shell small and evolute with compressed, subquadrate whorl section; umbilical wall high with rounded shoulder; venter moderately wide and flat; flanks flat and inclined toward umbilicus; ventrolateral shoulders subangular. Suture line not observed.

Etymology.—Named in honor of Mr. Buenaventura Paz, engineer for Petróleos Mexicanos, in Coatzacoalcos, Veracruz, Mexico, who collected the holotype.

Types.—Holotype, ESIA-1072 (Fig. 2.18); paratype, ESIA-1073 (Fig. 2.19, 2.20).

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—*Eopaquiericeras pazi* differs from *E. peraltai* n. gen. and sp. by its flat venter, its flanks which converge toward to the umbilicus, and its subangular ventrolateral shoulder. Specimen ESIA-1073 (Fig. 2.19, 2.20) has a crushed body chamber.

Family ASPIDOCERATIDAE Zittel, 1895
Subfamily ASPIDOCERATINAE Zittel, 1895
Genus CHINAMECACERAS new genus

Type species.—*Chinamecaceras maldonadoi* n. sp.; by monotypy.

Diagnosis.—Dimorphic ornamentation; compressed whorl section varies from very narrow to subquadrate; simple, rectiradiate, and very widely spaced primary ribs arise from long umbilical tubercles projecting toward central area. Adapical half with sharp ribs and three corresponding rows of umbilical, lateral, and ventrolateral tubercles; ribs project forward crossing narrow venter at sharp angle. Adoral half with umbilical tubercles and weak ribs crossing large and subrounded venter at near right angle. Suture line aspidoceratid with shallow and simple elements.

Etymology.—After Chinameca village, southern Veracruz.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—*Aspidoceras* Zittel, 1868 and *Schaireria* Checa, 1985 are the only Kimmeridgian–Lower Tithonian aspidoceratids known from Mexico (Burckhardt, 1906, 1912; Imlay, 1939; Verma and Westermann, 1973; Checa, 1985). *Aspidoceras* has a smooth, globose shell with one or two rows of lateral tubercles, whereas *Chinamecaceras* is ornamented with ribs and tubercles in the adapical half of the shell. *Schaireria* differs from *Chinamecaceras* by its smooth and involute shell and ovate to reniforme whorl section which is compressed and very narrow to subquadrate in *Chinamecaceras*.

The Lower Tithonian genus *Pseudohimalayites* Spath, 1925 differs from *Chinamecaceras* by its depressed and subpentagonal whorl section, its very weak primary ribs, and its constant ornamentation in the final whorl corresponding to the phragmocone. In addition, *Chinamecaceras* has dimorphic ornamentation and long umbilical tubercles that project toward the central area.

CHINAMECACERAS MALDONADOI new species
Figure 3.24, 3.25, 3.28

Diagnosis.—Same as for genus.

Description.—Dimorphic shell; two distinct types of whorl section, ventral shoulder, and ornamentation are present on phragmocones. Compressed whorl section varies from narrow in adapical half to large and subrounded in adoral half. Adapical half of shell with three rows of umbilical, lateral, and ventrolateral tubercles, and six prominent and very widely spaced primary, rectiradiate ribs that project forward, crossing narrow venter at sharp angle. Adoral half with six weakened and spaced rectiradiate ribs on flanks that cross large and subrounded venter at near right angle.

Etymology.—Named in honor of Mr. Manuel Angel Maldonado-Leal, engineer for Petróleos Mexicanos, in Coatzacoalcos, Veracruz, Mexico, who collected the holotype.

Type.—Holotype, ESIA-1085 (Fig. 3.24–3.25, 3.28).

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—Verma and Westermann (1973) described a smooth and aspidoforme ammonite from the Lower Tithonian of Real de Catorce, central Mexico as *Physodoceras burkarti* (Aguilera *in* Castillo and Aguilera, 1895); it was later reinterpreted as *Schaireria neoburgensis* (Oppel, 1863) by Checa (1985). Representatives of *Schaireria neoburgensis* from Mexico (Real de Catorce) and Spain (Verma and Westermann, 1973; Checa, 1985) are readily distinguished from *Chinamecaceras maldonadoi* by their smaller U/D ratio (0.12 in *S. neoburgensis* vs. 0.39 in *C. maldonadoi*) (Verma and Westermann, 1973; Checa, 1985) (Table 1).

Schaireria occurs in the Lower Tithonian Zone of *Hybonoticeras* in Spain, whereas *C. maldonadoi* is associated with the Upper Tithonian genera *Kossmatia* and *Durangites* at Chinameca, Mexico. Oloriz et al. (1999, p. 474, fig. 7) illustrated a specimen of *Schaireria neoburgensis* from the Sierra de Catorce, central Mexico. It was recovered from the 9b bed, corresponding to the Virgatosphinctinae beds (Lower Tithonian) in the Alamitos 1 section, but in the section illustrated by these authors (ibid., fig. 2), *S. neoburgensis* is associated with the Upper Tithonian genus *Kossmatia*.

A Lower Tithonian *Schaireria* sp. was described by Myczynski (1989, p. 101, pl. 10, fig. 3) from western Cuba which differs from *C. maldonadoi* by its convex flanks, its whorl section which is wider at the umbilical shoulder, and its larger and rounded venter. In addition, the umbilicus is smaller in *Schaireria* sp. (U/D, 0.23 vs. 0.39 in *C. maldonadoi*).

Schaireria longaeva (Leanza, 1945) from the Upper Tithonian Zone of *Substeueroceras* in Argentina was placed in the Berriasian by Checa (1985) without explanation. This zone is interpreted to be Upper Tithonian in age in the Andine region (Parent, 2001). *Schaireria longaeva* has an involute and smooth shell which readily distinguishes it from the highly ornamented shell of *Chinamecaceras maldonadoi*.


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Family SIMOCERATIDAE Spath, 1924
Genus VERACRUCICERAS new genus

Type species.—*Veracruciceras ruizi* n. sp.

Included species.—*Veracruciceras myczynskii* n. sp., Upper Tithonian, Cuba (Myczynski, 1989, p. 105, pl. 11, fig. 2).

Diagnosis.—Evolute, serpenticonic, and planulate shell with subquadrate to hexagonal whorl section; simple, sharp, rectiradiate primary ribs; two rows of umbilical or lateral and ventrolateral tubercles; smooth and narrow venter. Suture line not known.

Etymology.—After Veracruz State, where Chinameca village is located and the type species was collected.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—*Corongoceras cordobai* Verma and Westermann (1973, p. 248, pl. 52, figs. 4, 5; pl. 53, figs. 2–5; pl. 54, fig. 1) from the Upper Tithonian of Real del Catorce, central Mexico, is characterized by a very evolute and planulate shell with a shallow umbilicus and widely spaced, apparently simple rectiradiate ribs bearing lateral and ventrolateral tubercles. According to Verma and Westermann (1973), "this is the only known species of *Corongoceras* with regular simple (embranches) bituberculate ribs." However, the holotype of *C. cordobai* (Verma and Westermann, 1973, pl. 5, fig. 2a) appears to show four bifurcated ribs alternating with simple ribs on the outer flank corresponding to the adoral half of the last whorl. Although it was not possible to examine the holotype of *cordobai*, which is deposited at McMaster University, it is herein retained in *Corongoceras* Spath, 1925, a genus known from Argentina, Austria, Cuba, Madagascar, Mexico, Roumania, and Spain (Krantz, 1928; Imlay, 1942; A. Leanza, 1949; Collignon, 1960; Verma and Westermann, 1973; Cantú-Chapa, 1976a; Patrulius and Avram, 1976; H. Leanza, 1980; Tavera-Benítez, 1985; Zeiss, 2001). Without giving any evidence, Oloriz et al. (1999) assigned *C. cordobai* to the Spanish genus *Simplisphinctes* Tavera-Benítez, 1985. *Simplisphinctes* has simple, retroverse, sometimes flexuose and bifurcate ribs. Percentage of U/D varies from evolute (0.58) in *C. cordobai* to relatively evolute (0.42–0.52) in *Simplisphinctes*. They represent different genera.

Evolute species with simple, rectiradial, and biturberculate ribbing must be separated from *Corongoceras*. *Veracruciceras* is herein proposed for species from Chinameca, in Veracruz State, eastern México, and from Cuba. *Veracruciceras* is assigned to the family Simoceratidae on the basis of its platiconic, evolute coiling, its simple, radial, and discrete primary ribs which are interrupted on the midventral area, and its two rows of tubercles.

VERACRUCICERAS RUIZI new species
Figure 3.3, 3.4

Diagnosis.—Same as for genus.

Description.—Shell evolute, planulate, and serpenticonic with subquadrate to hexagonal whorl section and wide, shallow umbilicus. Flanks weakly convex and venter flat and narrow. Primary ribs sharp, rectiradial, and spaced, bearing lateral external and ventrolateral tubercles. Internal whorls show lateral tubercles in contact with line of coiling.

Etymology.—Named in honor of Telésforo Ruiz, engineer for Petróleos Mexicanos, in Coatzacoalcos, Veracruz State, Mexico, who collected the holotype.

Type.—Holotype, ESIA-1075 (Fig. 3.3, 3.4).

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. *1*).

Discussion.—A specimen from the Upper Tithonian of Cuba was assigned to *Corongoceras cordobai* by Myczynski (1989, p. 105, pl. 11, fig. 2); it is evolute with simple and spaced ribbing with umbilical and ventrolateral nodes. The umbilical position of the nodes on the Cuban specimen differs from *Veracruciceras ruizi* which has lateral and ventrolateral tubercles. The Cuban specimen is herein designated the holotype of *Veracruciceras myczynskii* n. sp., which is named for Dr. R. Myczynski, in recognition of his studies on the Jurassic and Cretaceous ammonites of Cuba.

VERACRUCICERAS sp.
Figure 3.5, 3.6, 3.9

Description.—Compressed shell with flat flanks; ribs simple, rectiradiate, and separated by spaces wider than ribs; two rows of tubercles on outer flank and ventrolateral shoulder.

Material examined.—Two incomplete specimens, ESIA-1076, ESIA-1077. Both comprise only one-third of the shell.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—The evolute coiling and simple, radial ribs of these fragmentary specimens bear considerable resemblance to *Veracruciceras ruizi* n. gen. and sp. However, their poor state of preservation only warrants assignment as *Veracruciceras* sp.

Family HIMALAYITIDAE Spath, 1925
Genus DURANGITES Burckhardt, 1912 emend.

Type species.—*Durangites vulgaris* Burckhardt, 1912, by subsequent designation of Cantú-Chapa, 1968.

Diagnosis.—Shell evolute and compressed, sometimes with smooth ventral band. Ribs simple and bifurcate, all curving backwards, with or without tubercles at locus of bifurcation or at ventrolateral termination of ribs. Suture line with large and irregularly bifid S1 and S2; E large and divided by Sl; L trifid.

Discussion.—Burckhardt (1912) erected *Durangites* for himalayitids from San Pedro del Gallo, Durango, northern México, and Roman (1938) designated *D. acanthicus* Burckhardt, 1912 as its type species. Later, Cantú-Chapa (1968) described three species

←

FIGURE 3—*1, 2, Durangites* sp. A, ventral and lateral views, ESIA-1074. *3, 4, Veracruciceras ruizi* n. gen. and sp., holotype, lateral and ventral views, ESIA-1075. *5, 6, 9, Veracruciceras* sp.; *5, 9,* ventral and lateral views, ESIA-1076; *6,* lateral view, ESIA-1077. *7, 8, 12–17, 19–22, Kossmatia purisima* Verma and Westermann, 1973; *7, 8,* lateral and ventral views, ESIA-1078; *12–15,* ventral, lateral, and apertural views, ESIA-1080; both phragmocones with remains of body chamber; *16, 17,* ventral and lateral views, ESIA-1081, incomplete specimen included in a limestone concretion; *19, 20,* lateral and ventral views, ESIA-1083; *21, 22,* lateral and ventral views, ESIA-1084; last specimen somewhat crushed in the apertural part. *10, 11, Kossmatia* sp. B, ventral and lateral views, ESIA-1079; umbilical area is covered by a limestone concretion. *18, 23, Andiceras monserrati* (Aguilera *in* Castillo and Aguilera, 1895), ventral and lateral views, ESIA-1082; phragmocone included in a limestone concretion, with remains of body chamber. *24, 25, 28, Chinamecaceras maldonadoi* n. gen. and sp.; holotype, adapical and adoral ventral views; lateral view, ESIA-1085. *26, 27, Durangites zigzagcostatus* n. sp., holotype, lateral and ventral views, ESIA-1086. *30, 41, Durangites* sp. B, ventral and lateral views, ESIA-1087. *29, 32, 33, 38,* Olcostephanidae gen. and sp. indet., *29, 32,* ventral and lateral views; *33, 38,* lateral and ventral views; same specimen ESIA-1088. *34, Kossmatia* sp., ventral view, ESIA-1089. *31, Kossmatia* sp. A, lateral view, ESIA-1090. *35, 37, 40, 42, Kossmatia* aff. *purisima* Verma and Westermann, 1973; *35, 37,* lateral and ventral views, ESIA-1091; *40, 42,* lateral and ventral views, ESIA-1092. *36, 39, Durangites* aff. *zigzagcostatus* n. sp., ventral and lateral views, ESIA-1093. *43, Kossmatia* aff. *bifurcata* (Aguilera *in* Castillo and Aguilera, 1895), lateral view, ESIA-1094. All specimens from the El Piedral locality, Chinameca, southern Veracruz. All specimens ×1, except *33, 38,* ×2. Specimens coated with ammonium chloride.

of Upper Tithonian *Durangites* from Galeana, Northeast Mexico which were associated with *Proniceras* and *Salinites*. Cantú-Chapa also analyzed Burckhardt's (1912) original description of *Durangites*.

Burckhardt (1912) recognized four growth stages in *Durangites*: "micracanthus," "köllikeri," "typical," and "adult stages." Although Roman (1938, p. 323) later designated *D. acanthicus* Burckhardt (1912, p. 146, pl. 36, figs. 7, 8) as the type species of *Durangites*, this species exhibits only the "köllikeri stage," which does not represent the typical characters of the genus. Moreover, since *D. acanthicus* and *D. incertus* Burckhardt, 1912 (p. 147, pl. 36, figs. 12–14, 16, 17) do not have the "typical stage" of *Durangites*, which is characterized by its retrocostal ribs, these two species must be reassigned to *Micracanthoceras* Spath, 1925 and *Corongoceras*, respectively. For this reason, Cantú-Chapa (1968) designated *D. vulgaris* (Burckhardt, 1912, p. 149, pl. 30, figs. 1, 2) as the type species, since it has the ornamentation that characterizes Burckhardt's "typical stage."

Verma and Westermann (1973) proposed a tentative classification of the Mexican species of *Durangites* which was based on presumed dimorphism and which involved the arbitrary separation of specimens into macroconchs and microconchs on the basis of various subjective criteria. Nevertheless, they admitted that "the dimorphic relationship of the microconch is, therefore, somewhat questionable" (Verma and Westermann, 1973, p. 220).

Donovan et al. (1981) and Enay et al. (1998) also modified the systematic position of *Durangites*, interpreting it as the microconch of the macroconch *Protacanthodiscus* Spath, 1923a. This latter classification is highly subjective and is based on dimorphic concepts of ammonite classification. Moreover, it should be noted that *Protacanthodiscus* is virtually absent in Mexico.

DURANGITES ZIGZAGCOSTATUS new species
Figure 3.26, 3.27

Diagnosis.—Shell small and evolute with subcircular whorl section and moderately convex venter. Fine primary ribs bifurcate at midflank, curve weakly backwards on outer flank, and cross venter transversely in zigzag pattern.

Description.—Shell evolute with moderately convex flanks and venter; whorl section subcircular. Very fine primary ribs arise from line of coiling, becoming radial on inner flanks, and bifurcating, producing small swellings at midflank. Primary and bifurcate ribs irregularly alternate with scarce simple ribs; some simple ribs arise from umbilical shoulder, others inserted on outer flank. All ribs separated by fine interspaces and curve weakly backwards on outer flank, crossing venter transversely in zigzag pattern without weakening. Ribs number 22 in adoral one-half of last whorl.

Etymology.—The name alludes to the zigzag pattern created by the ribs as they cross the venter.

Type.—Holotype, ESIA-1086 (Fig. 3.26, 3.27).

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—This specimen resembles *Durangites heilprini* (Aguilera *in* Castillo and Aguilera, 1895) *in* Verma and Westermann (1973, p. 259, pl. 43, fig. 4) in its fine and bifurcate ribbing, but it differs by its irregularly alternating simple ribs. It is difficult to compare our Chinameca specimen with Aguilera's original types of *H. heilprini* (Aguilera *in* Castillo and Aguilera, 1895, p. 41, pl. 22, fig. 7) from Real de Catorce because of the poor quality of the original illustrations of that species.

Durangites zigzagcostatus resembles small specimens of *Durangites vulgaris* Burckhardt, 1912 (p. 150, pl. 37, figs. 32–35) in its fine and bifurcate ribbing, but differs by the absence of ventrolateral tubercles and a smooth midventral band. In addition, the secondary ribs bifurcate, forming small swellings on the flank, and small tubercles zigzag on the venter in *D. zigzagcostatus*, whereas in *D. vulgaris* the ribbing is straight across the venter.

Specimen ESIA-1093 has a crushed body chamber and is covered with matrix on one side; consequently, it is impossible to determine whether the ribs cross in a zigzag on the venter. It is provisionally included in this species as *D.* aff. *zigzagcostatus* on the basis of its fine lateral ribbing which bifurcates after a small swelling.

DURANGITES sp. A
Figure 3.1, 3.2

Description.—A middle whorl of an evolute shell with subquadrate and compressed whorl section; flanks and venter gently convex. Thick primary ribs arise at umbilical seam; these are rursiradiate on umbilical slope and curve sinuously and weakly backwards at about midflank. Some primary ribs remain simple, others bifurcate at or just above midflank. Both alternate irregularly and are separated by moderately narrow interspaces. Secondary ribs cross venter transversely and are sporadically enlarged. Umbilical area obscured by limestone concretion.

Material examined.—ESIA-1074.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—The fragmental specimen described above resembles *Durangites* n. sp. aff. *rarifurcatus* (Imlay, 1939 *in* Verma and Westermann, 1973, p. 262, pl. 55, figs. 8, 9) in its irregularly alternating bifurcate and simple ribs, but it has no lateral and ventral tubercles.

DURANGITES sp. B
Figure 3.30, 3.41

Description.—Fragmental specimen corresponding to one-half of final whorl with convex flanks and venter. Primary ribs arise at umbilical shoulder, bifurcate regularly at midflank, and are weakly retrocostal on outer flank. Ribs cross venter transversely and are weak on middle of venter. Ribs separated by interspaces narrower than primaries; number 12 in one-quarter whorl. Umbilical area obscured by limestone concretion.

Material examined.—ESIA-1087.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—This fragmental specimen resembles *Durangites* sp. indet. Cantú-Chapa (1968, p. 24, pl. 4, figs. 5, 5a, 10, 11) in its bifurcate ribs but it differs by the regular bifurcation.

Family OLCOSTEPHANIDAE Haug, 1910
OLCOSTEPHANIDAE genus and species indeterminate
Figure 3.29, 3.32, 3.33, 3.38

Description.—Shell small, semievolute, and sphaeroconic, with moderately depressed whorl section, convex flanks, and subrounded and large venter. Fine and flexuose ribs branch from umbilical tubercles; some primary ribs intercalated between tubercles from umbilical wall. All ribs cross venter normally, and are separated by interspaces as wide as ribs.

Material examined.—ESIA-1088.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—The small Chinameca specimen described above might be a juvenile. Because of the differences in their respective sizes, it could not be directly compared with the specimens described as *Proniceras* juv. sp. ind. by Burckhardt (1919–1921, p. 48–49, pl. 16) from the Upper Tithonian of central Mexico; however, its involute coiling, inflated shell, and ribbing that crosses the venter transversely distinguishes it from Burckhardt's specimens.

Since it is based on a single small specimen, this ammonite is referred only to the Olcostephanidae indet., with the anticipation that additional sampling will clarify its affinities.

Family BERRIASELLIDAE Spath, 1922

Discussion.—Donovan et al. (1981) recognized the families Himalayitidae and Neocomitidae within the Jurassic-Cretaceous boundary Perisphinctaceae, in part based on concepts of latitudinal and climatic distribution, or supposed sexual dimorphism. As previously mentioned, Wright et al. (1996) subdivided the family Neocomitidae into three subfamilies on the basis of two different and incompatible criteria: 1) position of rib branching (Berriasellinae and Neocomitinae) and 2) suture line (Endomoceratinae).

The first group (Berriasellinae and Neocomitinae) must be divided and treated as higher level categories (families); the family Berriasellidae characterizes evolute forms with subrounded venters and principal ribs which bifurcate on the outer flank. It differs from the family Neocomitidae (Salfeld, 1921) in the absence of a tabulate, grooved, or smooth venter, and by the absence of umbilical or lateral tubercles that give rise to secondary ribs.

The family Berriasellidae is herein subdivided into two subfamilies based on the attitude of the ribs in the ventral region: 1) interrupted or crossing perpendicularly in *Berriasella* and *Substeueroceras*, respectively, subfamily Berriasellinae; and 2) forming chevrons in *Lemencia* Donze and Enay, 1961 [=*Richterella* Avram, 1974], *Kossmatia*, and *Fierrites* Cantú-Chapa, 1993, subfamily Richterellinae.

Subfamily RICHTERELLINAE Sapunov, 1977 emend.

Emended diagnosis.—Moderately evolute with compressed whorl section. Primary ribs bifurcate on outer flank forming chevrons on subrounded venter, with a smooth line or crossing it without interruption. S1 subrectangular with large base, incipiently bifurcated at top; S2 narrow and elongate.

Occurrence.—Tithonian.

Discussion.—Sapunov (1977) proposed the subfamily Richterellinae to include a group of evolute ammonites with principal ribs that bifurcate on the outer flank and form chevrons on the subrounded venter. He included in this subfamily the Lower Tithonian genera *Lemencia* and *Richterella* from Europe. *Kossmatia* and allied genera from the Upper Tithonian of Mexico, Cuba, and the USA (California and Texas) were mentioned by Sapunov (1977). *Kossmatia* was misidentifed and included in different families by several authors, an error which will be commented on later.

Sapunov (1977) related Richterellinae to the tribe Sublithacoceratinae Zeiss, 1968. However, Oloriz (1978), Tavera-Benítez (1985), Cecca et al. (1989), and Cecca and Enay (1991) assigned *Richterella* to the subfamily Lithacoceratinae Zeiss, 1968, family Ataxioceratidae Buckman, 1921. Donovan et al. (1981) tentatively assigned *Richterella* to the subfamily Richterellinae, which they considered a synonym of the Lithacoceratinae. More recently, *Lemencia* and *Richterella* were assigned to the subfamily Sublithacoceratinae Zeiss, 1968, family Lithacoceratidae by Zeiss (2001).

Kossmatia, however, was assigned to the subfamily Berriasellinae in a number of studies based on American faunas (Cantú-Chapa, 1967, 1976a, 1982, 1993; Verma and Westermann, 1973; Myczynski, 1989; Oloriz et al., 1999). Moreover, the systematic position of *Kossmatia* was misinterpreted as was that of *Ammonites richteri* (Oppel *in* Zittel, 1868, p. 108, pl. 20, figs. 9, 11, 12). *Ammonites richteri* was included in *Kossmatia* (Burckhardt, 1912; Roman, 1938; Imlay, 1943; Spath, 1950; Verma and Westermann, 1973) or in *Berriasella* (Mazenot, 1939; Le Hegarat, 1973). A specimen of *A. richteri* figured by Zittel (1870, pl. 33, fig. 4) was

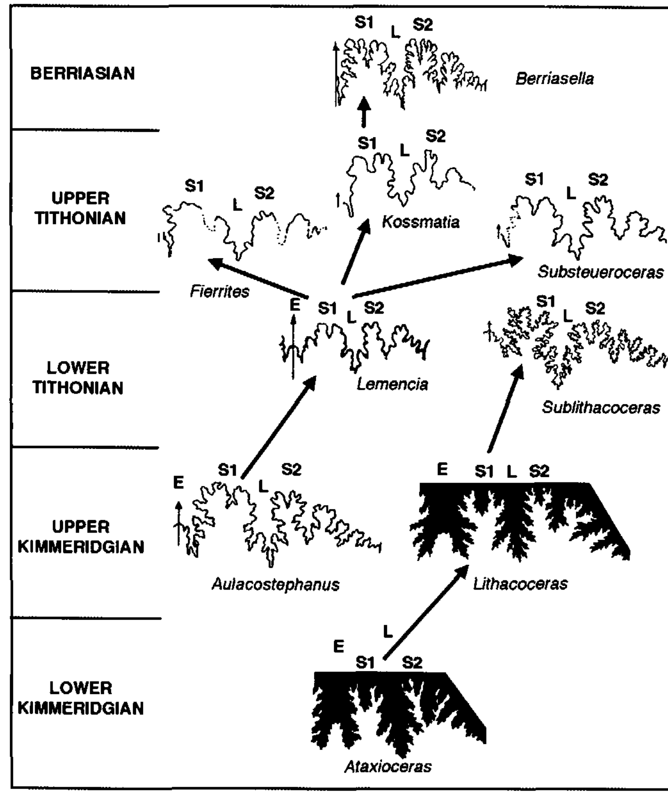

FIGURE 4—Phylogenetic sequence of suture lines of selected Lower Kimmeridgian to Berriasian Perisphinctacean genera showing differences in S1 and S2.

also assigned to *Grayiceras* Spath, 1924 by Spath (1950). *Ammonites richteri* was designated the type species of both *Lemencia* and *Richterella* [=*Richteria* Oloriz, 1978, after Cecca (1986)] from Europe. *Richterella* was considered as distinct from *Lemencia* by Oloriz (1978) and Tavera-Benítez (1985), or as a subgenus of *Lemencia* [*Lemencia* (*Richterella*)] by Zeiss (2001). *Ammonites richteri* includes forms with ribs forming chevrons on the ventral region with a smooth line (*Lemencia*), or crossing it without interruption (*Richterella*).

Both *Lemencia* and *Richterella* resemble *Kossmatia* in their ventral ribbing; it is present in *Kossmatia* when the shell is not preserved (as in *Lemencia*), or when it is preserved (as in *Richterella*) (Imlay, 1943; Cantú-Chapa, 1993). The latter case is observed in *K. zacatecana* Burckhardt, 1906, *K. interrupta* Burckhardt, 1912, *K. bifurcata* (Aguilera *in* Castillo and Aguilera, 1895), *K. purisima* Verma and Westermann, 1973, and *K. pectinata* Burckhardt, 1912, from México (Imlay, 1943; Verma and Westermann, 1973), and in *K. dilleri* (Stanton, 1896), *K. tehamaensis* Anderson, 1945, and *K. kleinsorgensis* Anderson, 1945, from California, USA (Imlay and Jones, 1970). *Lemencia*, *Richterella*, and *Kossmatia* are all moderately evolute and compressed in shape with primary ribs that bifurcate on the outer flank and form chevrons on the subrounded ventral region. However, these genera characterize different stratigraphic levels in the Tithonian (Fig. 4).

Callomon (*in* Hillebrandt et al., 1992) called attention to the great variety of names used to describe Upper Tithonian perisphinctid species with small, compressed shells and strong ventral projection (chevrons) of the secondary ribs. He mentioned *Lemencia*, *Richterella*, and *Kossmatia*, in particular, hoping to find a systematic solution. However, the suture lines of these controversial genera were never compared to determine any potentially significant differences; nor were they previously compared with the type genera of the families Ataxioceratidae and Lithacoceratidae, and with the subfamily Sublithacoceratinae to which they were variously assigned (see below).

Suture lines of *Ataxioceras* Fontannes, 1879, *Lithacoceras* Hyatt, 1900, and *Sublithacoceras* Spath, 1925 (after Geyer, 1956; and Zeiss, 1968) are herein compared with the only known suture line of *Richterella*, which was illustrated as *Berriasella richteri* (Oppel, 1865) by Mazenot (1939, pl. 21, fig. 2 bis) (Fig. 4). *Ataxioceras*, *Lithacoceras*, and *Sublithacoceras* have an S1 which is elongate and bifurcate, with a narrow base; L is deep and symmetrical. *Ataxioceras* has an S2 that is long, narrow, and trifurcate, with a narrow base. *Lithacoceras* has an S2 that is subrectangular and elongate. *Sublithacoceras* has an S2 that is large, subdivided, and jointed at U2, with "numerous pendent auxiliaries, and a very deep and symmetrical principal lobe" (Spath, 1950) (Fig. 4).

The suture lines of *Lemencia* (=*Richterella*) and *Kossmatia* differ from those of *Ataxioceras*, *Lithacoceras*, and *Sublithacoceras* by possession of an S1 which is very large at the base, and by a narrow S2. This type of suture line is also found in *Fierrites*, a related genus from the Upper Tithonian of Mexico. L1 is trifurcate in all of these genera; but it is stronger, deeper, and more symmetrical in *Lithacoceras* and *Sublithacoceras* than in *Lemencia* (=*Richterella*), *Kossmatia*, *Fierrites*, *Substeueroceras*, and *Berriasella*. *Lemencia* (=*Richterella*), *Kossmatia*, and *Fierrites* are herein grouped in the subfamily Richterellinae Sapunov, 1977 emended.

The subfamily Richterellinae must be emended based on particular characters of its suture line (S1 large at the base) and its ribbing which bifurcates on the flanks and is projected forward on the venter. As so defined, it is restricted to the Tithonian. The Richterellinae is distinguished from the families Sublithacoceratidae and Ataxioceratidae on basis of its suture line which includes an S1 with a wide base which contrasts with the narrow base of S1 in the latter two families. The Richterellinae also differs from the subfamily Berriasellinae by the attitude of the ribs which project forward on the venter in the Richterellinae but which are interrupted or cross the venter normally in the Berriasellinae.

The origin of the Richterellinae could be found in the family Aulacosphinctoidae; similarities in their suture lines, particularly in S1, link them. The type genus of the subfamily Richterellidae is *Kossmatia*. For further discussion of differences between *Kossmatia* and *Berriasella* see Cantú-Chapa (1999).

Genus Kossmatia Uhlig, 1907

Type species.—*Ammonites tenuistriatus* Gray, 1832; by subsequent designation of Roman, 1938.

Diagnosis.—Moderately evolute and subglobose to compressed; primary ribs bifurcate on outer flank, forming chevrons on subrounded venter. S1 subrectangular, with large base, and incipiently bifurcated at top; S2 narrow and elongate.

Occurrence.—*Kossmatia* is considered to be Upper Tithonian based on its association with *Proniceras*, *Salinites*, and *Substeueroceras* at a number of localities in Mexico, the USA (Texas, Louisiana), and Cuba (Burckhardt, 1906, 1912; Imlay, 1943; Verma and Westermann, 1973; Imlay and Hermann, 1984; Cantú-Chapa, 1989, 1999; Myczynski, 1989, 1999b).

Discussion.—Upper Tithonian occurrences of *Kossmatia* from Argentina, Cuba, Mexico, and the USA were reported by Burckhardt (1906, 1912), Krantz (1928), Kellum (1937), Imlay (1943, 1980), Cantú-Chapa (1967, 1976a, 1982, 1993, 1999), Imlay and Jones (1970), Verma and Westermann (1973), Hoedemaeker (1987), Myczynski (1989), and Oloriz et al. (1999). *Kossmatia* has also been recovered in the Indo-Pacific area (Sukamato and Westermann, 1992; Enay and Cariou, 1999; Fatmi and Zeiss, 1999) and Spain (Tavera-Benítez, 1985). However, reservations concerning its systematic position, age, and presence in Mexico, Cuba, and the USA (California, Texas) have been raised, as noted previously in this paper.

Hoedemaeker (1987) demonstrated that *Kossmatia* co-occurs with *Durangites* and precedes *Paradontoceras*, *Substeueroceras*, and *Proniceras* in Mexico. He also noted the absence of *Kossmatia* in the Mediterranean province, where there are many *Durangites* species which are similar to those of Mexico and the USA (California) [*Kossmatia* was subsequently discovered in the Mediterranean]. Hoedemaeker (1987) also noted that the Lower Tithonian species *Richterella richteri* (Oppel, 1865) was frequently included in *Kossmatia*.

Kossmatia is widespread in Upper Tithonian rocks throughout Mexico. Imlay (1943) described several species from the Upper Tithonian of Chihuahua, northern Mexico. Olmstead (1999) indirectly referred to these same species as the Upper Tithonian *Kossmatia* or *Richterella* from the Sierra de Chorreras, Chihuahua. *Kossmatia* has also been recovered in the subsurface, in the Lajillas-1 well, in northeastern Mexico (Cantú-Chapa, 1982) and at Malone, in southeastern Texas (Albritton, 1937; Cantú-Chapa, 1976b; Imlay, 1980).

Kossmatia exhibits a number of very distinctive morphological features which characterize the top of the Tithonian in Mexico, particularly the suture line and the ventral and lateral ribs (Cantú-Chapa, 1993, 1999). The pattern of the ribbing, which forms chevrons on the venter, and the suture line are the most important morphological elements to characterize *Kossmatia*; however, these characters are typically not mentioned in systematic discussions when *Kossmatia* is compared with the similar and recently described European genus *Lemencia* [=*Richterella*] (e.g., Donze and Enay, 1961; Avram, 1974; Oloriz, 1978; Donovan et al., 1981; Cecca, 1986; Enay and Cariou, 1997; Zeiss, 2001). Significantly, these distinguishing characters were only noted by Burckhardt (1912), Imlay (1943), Verma and Westermann (1973), and Cantú-Chapa (1993) in discussions of the Mexican species of *Kossmatia*.

The Chinameca specimens assigned to *Kossmatia* show several different types of ventral ribbing, all of which form chevrons: 1) projected at an angle, as sharp end; 2) weakening at the middle line, producing an arrow point; 3) projected and moderately linguiform without interruption; and 4) projected with interruption (see Fig. 5).

Kossmatia purisima Verma and Westermann, 1973
Figure 3.7, 3.8, 3.12–3.17, 3.19–3.22

Kossmatia purisima Verma and Westermann, 1973, p. 222, pl. 47, figs. 3–6; pl. 48, fig. 1, text-figs. 16, 21–24.

Description.—Shell small and moderately evolute with subrounded to ovate whorl section, convex flanks, subrounded venter, and inclined umbilical wall. Fine, radiating primary ribs arise from umbilical wall, regularly bifurcate at midflank, and are weakly prorsiradiate on outer flank. Ribs separated by intercostal spaces as wide as ribs. Secondary ribs project forward, forming sharp chevrons on venter in adapical one-half of shell, weakening at midline of venter in adoral one-half of shell. Typically one simple rib intercalated between four or five bifurcate ribs.

Material examined.—ESIA-1078, ESIA-1080, ESIA-1081, ESIA-1083, ESIA-1084.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian. *Kossmatia purisima* also co-occurs with *K. bifurcata* and *K. flexicostata* (Aguilera

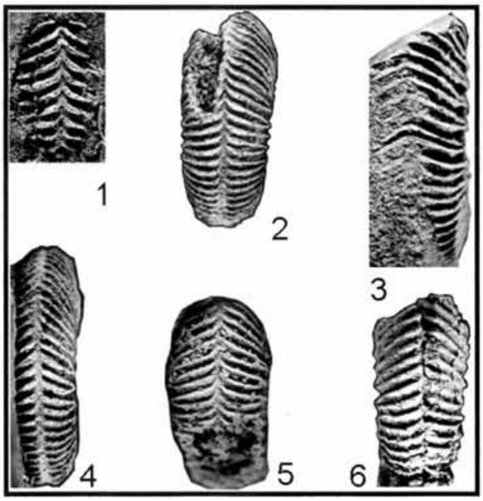

FIGURE 5—Different types of ventral ribbing in representatives of *Kossmatia* Uhlig, 1907. *1, 5,* Projected at an angle, as sharp end (chevron), ESIA-1089, ESIA-1092. *2, 6,* Weakening at the midline producing a chevron, ESIA-1080, ESIA-1078. *3,* Projected and moderately linguiform without interruption, ESIA-1079. *4,* Projected with interruption, ESIA-1084. All specimens from the El Piedral locality, Chinameca, southern Veracruz, eastern Mexico. All specimens ×1, except *5, 6,* ×2.

in Castillo and Aguilera, 1895) in the Upper Tithonian at Real de Catorce, central Mexico (Verma and Westermann, 1973).

Discussion.—The Chinameca specimens described above are very close to *Kossmatia purisima* (Verma and Westermann, 1973, p. 222, pl. 47, figs. 3–6; pl. 48, fig. 1) from Real de Catorce, central Mexico in their bifurcate ribs, but they are distinguished by their sharp ventral chevrons. The Chinameca specimens also differ by their ovate to subrounded whorl section which is larger in the internal part of the shell, in contrast to the types of *K. purisima* which have a subrectangular to subtrapezoidal whorl section. Verma and Westermann (1973) compared only the whorl sections of *K. purisima* and *K. richteri* (Oppel, 1865). Other morphological characters, including the suture line, were not mentioned.

Two other fragmental specimens from Chinameca (ESIA-1091, Fig. 3.35, 3.37; ESIA-1092, Fig. 3.40, 3.42) exhibit similar morphological characters to *K. purisima*, including the whorl section, fine, bifurcate ribs, and ventral chevrons. They are here referred to *K.* aff. *purisma*.

KOSSMATIA cf. BIFURCATA (Aguilera *in* Castillo and Aguilera, 1895)
Figure 3.43

Kossmatia bifurcata (AGUILERA). VERMA AND WESTERMANN, 1973, p. 215, pl. 40, figs. 2–4; pl. 41, figs. 1, 2.
Kossmatia cf. *bifurcata* (AGUILERA). MYCZYNSKI, 1989, p. 93, pl. 14, fig. 8.

Description.—One large, fragmental specimen corresponding to a compressed shell with flat flanks; venter poorly preserved, apparently subrounded. Primary ribs arise from umbilical shoulder, are sharp, rectiradiate, and separated by wider intercostal spaces on inner flank; ribs regularly bifurcate at midflank and curve slightly forward on outer flank and ventrolateral shoulder.

Material examined.—ESIA-1094.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—This large, fragmental specimen resembles *Kossmatia bifurcata* in its regularly bifurcate ribbing. It resembles specimens of *K. bifurcata* figured by Verma and Westermann (1973, pl. 42, fig. 1a) in the lateral bifurcation of its ribs. It is here referred to *K.* cf. *bifurcata* because of its poor preservation.

KOSSMATIA sp. A
Figure 3.31

Description.—A crushed, fragmental specimen preserving only a flattened flank of an evolute ammonite. Fine, radiating primary ribs arise from umbilical shoulder, bifurcate at midflank, and are prorsiradiate on outer flank and venter. Ribs regularly separated by intercostal spaces as wide as ribs. Rare and inconstant simple ribs intercalated between bifurcate ribs.

Material examined.—ESIA-1090.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—This fragmental and evolute specimen shows the irregular bifurcate ribbing strongly projected on the outer flanks which corresponds to *Kossmatia* sp.

KOSSMATIA sp. B
Figure 3.10, 3.11

Description.—Shell discoidal and apparently compressed, flanks on outer whorls somewhat flattened, and venter convex. Umbilical region obscured by matrix. Only fine secondary ribs visible on outer flank which are probably bifurcated from primary ribs. Ribs separated by narrower interspaces, curve on outer flank and cross ventral region forming moderate chevrons without midventral depression.

Material examined.—ESIA-1079.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—This specimen is important because it shows partly the lateral and ventral ribbing that characterize *Kossmatia*. The same type of ventral ribbing is present in *K. varicostata*.

Subfamily BERRIASELLINAE Spath, 1922
Genus ANDICERAS Krantz, 1928

Type species.—*Andiceras trigonostomum* Krantz, 1928; by subsequent designation of Arkell et al., 1957.

Discussion.—Krantz (1928) erected *Andiceras* for Tithonian forms from Argentina with evolute shells and rectiradiate ribs which bifurcate regularly on the outer flank and alternate irregularly with simple ribs. Ribs cross the ventral region perpendicularly, producing a swelling adjacent to the midline of the venter. The suture line is characterized by large, regularly bifurcated S1 and S2 elements.

ANDICERAS MONSERRATI (Aguilera *in* Castillo and Aguilera, 1895)
Figure 3.18, 3.23

Perisphinctes monserrati AGUILERA *in* CASTILLO AND AGUILERA, 1895, p. 34, pl. 22, fig. 3.
Andiceras monserrati (AGUILERA) *IN* VERMA AND WESTERMANN, 1973, p. 245, pl. 52, figs. 2, 3; pl. 53, fig. 1, text-fig. 27.

Description.—Shell evolute, with subovate whorl section, convex flanks, convex venter and moderately high umbilical wall. Primary ribs arise from umbilical wall and are rectiradiate, moderately sharp, and separated by intercostal spaces as wide as ribs. Ribs bifurcate regularly on outer flank and cross ventral region perpendicularly, forming narrow depression.

Material examined.—ESIA-1082.

Occurrence.—El Piedral, Chinameca village, southern Veracruz, Chinameca Formation, Upper Tithonian (Fig. 1).

Discussion.—This specimen is assigned to *Andiceras* based on its evolute coiling, convex venter with a slight midventral depression, and radial and bifurcate ribs that cross the venter perpendicularly. It differs from the type species, *A. trigonostomum* (Krantz, 1928, p. 37, pl. 2, fig. 1a, 1b), by its subovate whorl section and by the absence of an excavated midventral region as shown in Krantz's figure 1b. It exhibits ribbing similar to representatives of *A. monserrati* described by Verma and Westermann (1973, p. 245, pl. 52, fig. 2a, 2b) from Real de Catorce, central Mexico. These are rectiradial and bifurcate on the flanks and cross the ventral region perpendicularly; ribs are separated along the venter by a narrow discontinuous midline bounded by a slight depression. Only one specimen illustrated by Verma and Westermann (1973, pl. 53, fig. 1a, 1b) exhibits prorsiradiate ribs. U/D varies from relatively evolute (0.39) in the Chinameca specimen to evolute (0.47) in *A. monserrati* from Real de Catorce.

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