

New species of lower Tithonian macroconchiate *Hybonoticer* from Mexico and the co-occurrence of *Mazapilites* and *Hybonoticer* in the Mexico-Caribbean area

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Abstract.—The ammonite *Hybonoticer* *authariformis* new species [M] is erected from the lower Tithonian of Mexico, adding a new example of endemism for the genus *Hybonoticer* in records from epicontinental areas. The newly described species is the first evidence of unequivocal lowermost Tithonian macroconchiate hybonoticeratines reported from the Mexico-Caribbean area. Precise biostratigraphic control based on bed-by-bed sampling is first reported for the combined record of macroconchiate *Hybonoticer* Breistroffer, 1947 with *Mazapilites* Burckhardt, 1919 in Mexico, indicating an early but not earliest Tithonian age. A preliminary revision of the type material of species assigned to the genus *Mazapilites* points to an inconclusive understanding of both intraspecies diversity and the real meaning of the nominal species formulated by Burckhardt, thus revealing defective knowledge about precise biostratigraphy at both the genus and species levels. Published hybonoticeratines and mazapilitines from Mexico and Cuba are revisited to update precise interpretation of their systematics, biostratigraphy, and correlation potential, and to investigate their combined occurrence. Previous information about Cuban hybonoticeratines and mazapilitines is too limited to be conclusively interpreted; their combined record cannot be demonstrated in Cuba. Special relevance is given to a potential occurrence of *Mazapilites* in uppermost Kimmeridgian horizons in Cuba. The obtained results update the biostratigraphic meaning and systematic interpretation of the investigated ammonites, and signal topics for future research of interest in their paleobiological and paleobiogeographic interpretation.

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Introduction

Approaching a precise identification of the Kimmeridgian-Tithonian boundary in Mexico based on ammonite biostratigraphy has been a difficult task due to the occurrence of widespread endemism, unfavorable facies, and/or the scarcity of precise, bed-by-bed sampling programs (Villaseñor et al., 2000, 2012, and references therein). Mexican ammonites traditionally related to the Kimmeridgian-Tithonian boundary were first interpreted as *Waagenia* Neumayr, 1878 and later as *Hybonoticer*. Their occurrence was variably related to those belonging to genus *Mazapilites* Burckhardt (1919 in 1919–1921). No precise biostratigraphy has been reported for these two genera since pioneer works, after more than one hundred years of research, and only three publications have approached fine biostratigraphy, phenotypic response to paleoenvironmental forcing, and paleobiogeographic dynamics for *Hybonoticer* based on bed-by-bed sampling (Olóriz et al., 1993, 2000; Olóriz and Villaseñor, 1999). Updated data and interpretations about these two genera will improve the potential for correlation involving the Kimmeridgian-Tithonian boundary, which is one of the topics receiving special attention by the

International Subcommission on Jurassic Stratigraphy. Moreover, they will provide support for future research focused on species-level definitions and intraspecies structure, as well as on paleobiogeographic interpretations in Mexican-Caribbean areas. Given the long history of contributions including data about Mexican records of *Hybonoticer* and *Mazapilites*, a revision of relevant, previous works is obligatory.

Ammonites currently included in the genera *Mazapilites* and *Hybonoticer* have been known in Mexico since the first quarter of the past century. Among the types housed in the Colección Paleontológica Nacional, María del Carmen Perrilliat (Instituto de Geología, UNAM, Mexico City), there are six specimens and fragments of *Waagenia* (= *Hybonoticer*) belonging to Burckhardt's collections that have been revised and reillustrated; a seventh type specimen is lost. Also housed there, and analyzed, is a plaster cast of the type of *Waagenia parrasensis* Imlay, 1939. Three plaster casts of *Hybonoticer* sp. gr. *H. beckeri* (Neumayr, 1873) studied by Zell et al. (2014), housed in the Colección del Museo del Desierto (Saltillo, Coahuila) were also analyzed. All of these records refer to macroconchiate specimens of the genus *Hybonoticer*. Also found in the Colección Paleontológica Nacional, María del

Carmen Perrilliat, and re-examined are 18 specimens and fragments of *Mazapilites* from the Burckhardt (1906, 1919–1921) collections, two *Mazapilites* from the Peña-Muñoz (1964) collection, one from the Verma and Westermann (1973) collection, and one from the authors' collection (Olóriz et al., 1999); the syntypes of *Pulchellia mexicana* Aguilera in Del Castillo and Aguilera, 1895 (= *Mazapilites mexicanus*) are lost, but a plastotype from the Smithsonian Institution's National Museum of Natural History was available for analysis. An additional specimen of *Mazapilites* was analyzed from the Villaseñor et al. (2005) collection, which is housed at the Estación Regional del Noreste del Instituto de Geología, UNAM (Hermosillo, Sonora).

Based on new material collected bed-by-bed and the analysis of existing material and references in the literature, the aims of the present research are: (1) to provide the first conclusive evidence of lower Tithonian macroconchiate *Hybonoticeras* from Mexico, with identification of a new species, and evaluation of its value for precise biostratigraphy and intercontinental correlation; (2) to provide a preliminary re-evaluation of the genus *Mazapilites* based on the analysis of type material to explore its precise biostratigraphic meaning and present status at the species level; (3) to revise reported occurrences of *Hybonoticeras* and *Mazapilites* in the Mexico-Caribbean area, approaching an updated interpretation at the species level; (4) to report new material collected bed-by-bed that makes it possible to illustrate for the first time the co-occurrence of *Hybonoticeras* and *Mazapilites* in Mexico; and (5) to revisit previous reports of co-occurrences of these two genera from the Mexico-Caribbean area.

Geographic range, stratigraphy, and general paleoenvironmental setting

The present geographic distribution of *Hybonoticeras* records covers a wide area across north-central Mexico (i.e., north-central San Luis Potosí, northern Zacatecas, eastern Durango, and southern Coahuila) and northeastern Mexico (i.e., eastern Chihuahua, southeastern Nuevo León, and southeastern and northeastern Tamaulipas). The geographic distribution of *Mazapilites* is larger, including northwestern and southeastern Mexico. Both genera also occur in western Cuba (Fig. 1.1). The paleobiogeographic ranges of *H. hybonotum* Oppel, 1863 and closely related species, as well as of members of the genus *Mazapilites*, are shown in Figure 2.1.

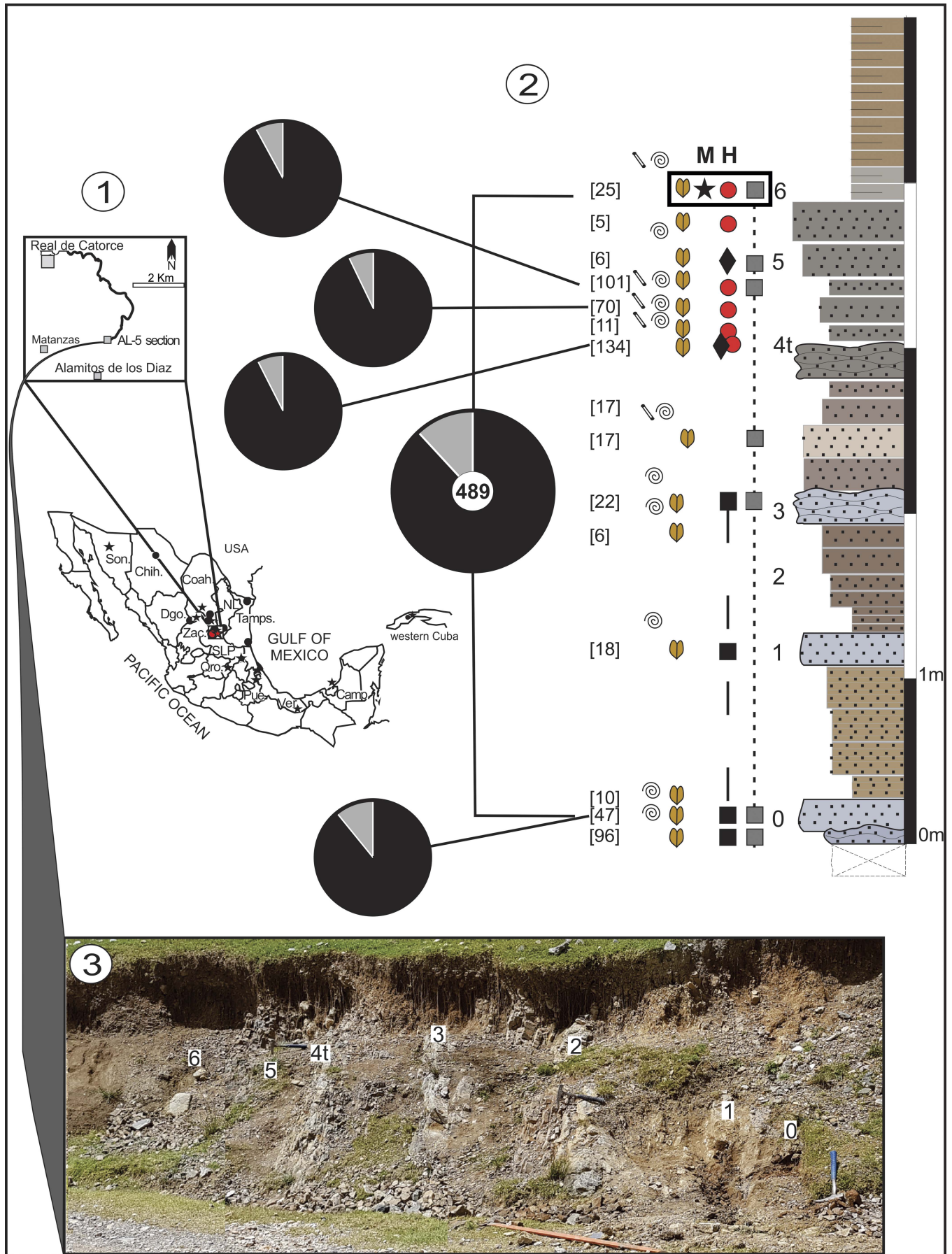
The revised material was retrieved from the La Caja and La Casita formations, which include the Kimmeridgian to the lowermost Berriasian epicontinental, distal-to-proximal mixed carbonate-siliciclastic deposits in north-central and northern Mexico, respectively (Olóriz et al., 2003), and from the Cucurpe Formation, representing Late Jurassic proximal, mainly siliciclastic deposition under volcanic influence from intra-arc to backarc contexts in northwestern Mexico (Mauel et al., 2005,

2011). Other reports of *Mazapilites* without illustrations have been published from the following formations: La Casita Formation (see above); Las Trancas Formation (carbonate and siliciclastic deposition in basinal to shallow nearshore and estuarine environments, under the influence of backarc vulcanism in the Mesa Central Basin and southern areas of the eastern Sierra Madre; Kimmeridgian–Valanginian?; López-Ramos, 1985; PEMEX, 1988; López-Palomino and Piña-Arce, 2007); Tamán Formation (organic matter-rich, mixed carbonate-fine, siliciclastic deposition on a wide-shelf system across eastern Mexico; upper Kimmeridgian–lower Tithonian, Cantú-Chapa, 1971, 1984; Tamán or Tamán-like deposition is assumed for a proximal fringe offshore, at least in the Tampico-Tuxpan area); Pimienta Formation (mainly silty to muddy-limy and organic-rich deposition on a wide, irregular shelf under volcanic influence across eastern Mexico; uppermost Kimmeridgian–Tithonian, Cantú-Chapa, 1971; lower but not lowermost Tithonian to upper Tithonian, Cantú-Chapa, 1984; Tithonian–Valanginian?, López-Palomino and Piña-Arce, 2007; Pimienta or Pimienta-like to more shaley deposition is postulated for a proximal fringe offshore, at least in the Tampico-Tuxpan area); Chinameca Formation (organic matter-rich carbonates and fine clastics, shelf deposits, across southeastern Mexico, on land and offshore; Kimmeridgian to Lower Cretaceous, Burckhardt, 1930, Cantú-Chapa, 2006; Kimmeridgian–Barremian, Sáenz-Pita and López-Palomino, 2011; Oxfordian pars. to Hauterivian in Sierra de Chiapas, Tehuantepec Isthmus, Quezada-Muñetón and Ferrusquia-Villafranca, 2013); and Edzna Formation (basinal, organic-rich carbonate and fine-clastic deposition recorded from subsurface at the Campeche region, on land and offshore; Tithonian, Cantú-Chapa and Ortuño-Maldonado, 2003).

The revised material from Cuba was mainly retrieved by Myczyński (1989, 1999), and partially re-interpreted by Pszczółkowski and Myczyński (2003, 2010) from western Cuba, with indication of limited data of *Mazapilites*, but no *Hybonoticeras*, from the Camajuaní Belt in central Cuba (Pszczółkowski and Myczyński, 2003). Fossiliferous horizons of reference in western Cuba were reported from: (1) well-stratified gray-black limestones, with occasional fine clayey intercalations from the El Americano Member of the Guasasa Formation in Sierra de Los Órganos, which represents Tithonian to early Berriasian outer-shelf-to-upper-slope deposition; and (2) well-bedded and commonly laminated black mudstones to wackestones, with occasional intercalations of shales and siltstones, and laminated shales and marls upward, from the La Zarza Member of the Artemisa Formation in Sierra del Rosario, which are interpreted as outer ramp deposits deepening throughout younger Tithonian times. Thus, analogous paleoenvironmental conditions during the same time interval can be interpreted for both areas (Cobiella-Reguera and Olóriz, 2009, and references therein).

Precise citations of authors and publications involved in the particular cases analyzed are given throughout the text.

Figure 1. Geographic location, lithologic log, and outcrop view: (1) geographic distribution of *Hybonoticeras* (dots) and *Mazapilites* (stars) in Mexico and western Cuba; inset shows new records in San Luis Potosí State; (2) lithologic log of section AL-5 (levels 0–6) with records of ammonites (spirals), genus *Hybonoticeras* (*H.*, large filled circles), *H. authariformis* n. sp. [M] (diamonds), genus *Mazapilites* (M, stars), haploceratines (black squares), perisphinctines (gray squares), bivalves (bilobate symbols), and serpulids (cylinders); faunal spectra (pie diagrams) shown for the complete section and characteristic beds, with numbers in brackets indicating the total fauna for each bed, and black and gray colors for benthics and ammonites, respectively; rectangle indicates the precise horizon of the combined record of *Hybonoticeras* and *Mazapilites*; (3) outcrop view of the studied section AL-5 located near Alamitos de los Díaz, known in the geological literature as Rancho Los Alamitos, 23°39'1.6"N, 100°50'54.7"W. Mexican states: Camp. = Campeche Shelf; Chih. = Chihuahua; Coah. = Coahuila; Dgo. = Durango; NL = Nuevo León; Pue. = Puebla; Qro. = Queretaro; SLP = San Luis Potosí; Son. = Sonora; Tamps. = Tamaulipas; Ver. = Veracruz; Zac. = Zacatecas.



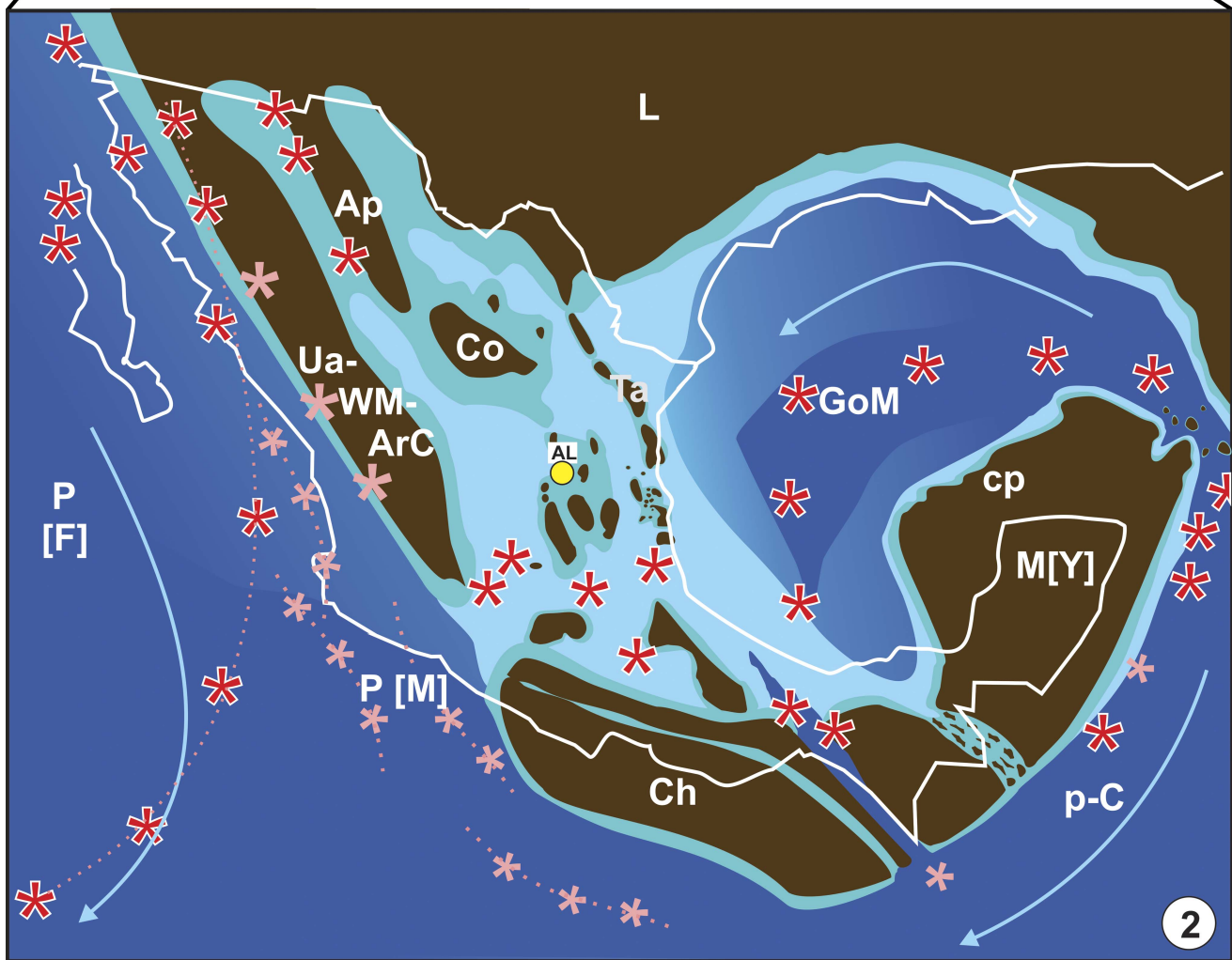
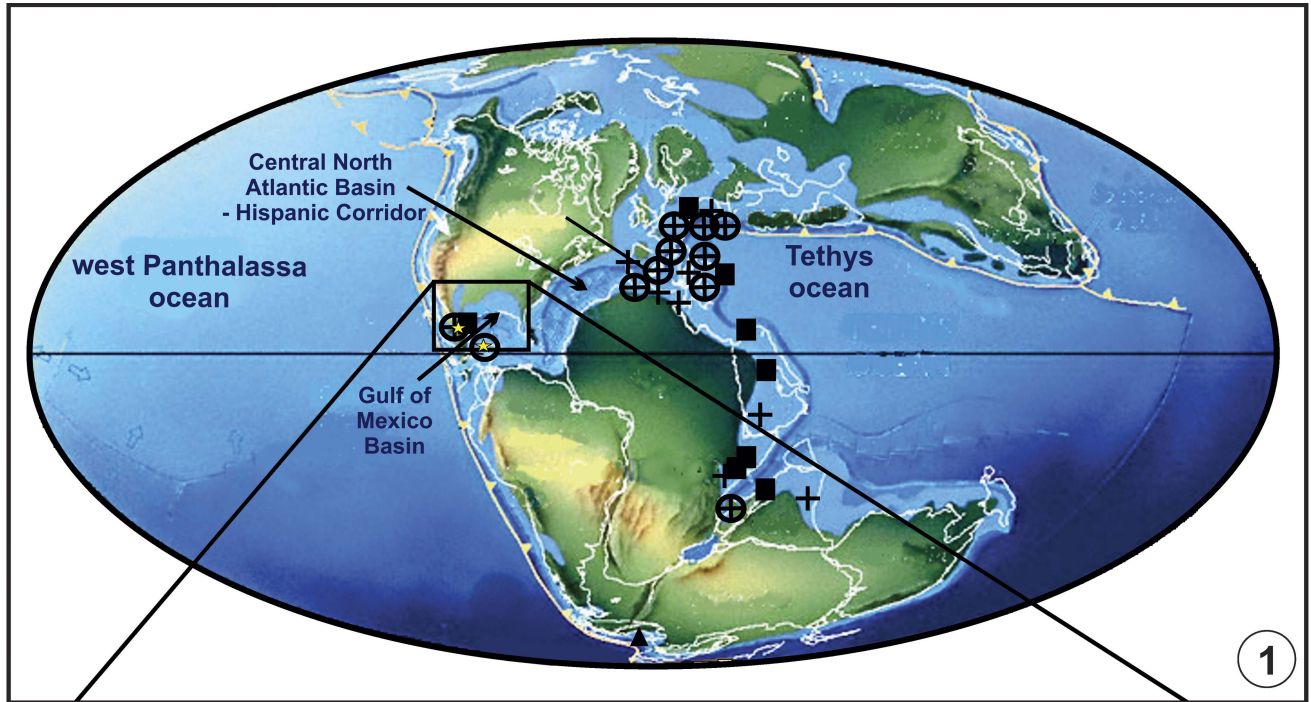


Table 1. Bibliographic database used in support of the synthetic interpretation of paleogeography and major marine water masses shown in Figure 2.

Selected Topics	Bibliography
Emergenced lands in Mexican areas, and seafloor topography in the eastern Gulf of Mexico gateway and the neighboring proto-Caribbean	Viniegra (1971, 1981); Enos (1983); López-Ramos (1985); Salvador (1987, 1991); Sedlock et al. (1993); Iturralde-Vinent (1994); Goldhamer (1999); Marton and Buffler (1999); Eguiluz de Antuñano et al. (2000); Eguiluz de Antuñano (2001); Magoon et al. (2001); Pineda-Acevedo (2001); Gaumet and Letouzey (2002); Cantú-Chapa (2003); García-Díaz (2004); Buchy et al. (2006); Padilla y Sánchez (2007); Cobiella-Reguera and Olóriz (2009); Buchy (2010); Stern and Dickinson (2010); Mauel et al. (2011); Muñoz-Cisneros et al. (2013)
Seaways, surface currents, and major transgressions	Carfantan (1983); Peterson (1983); Quezada-Muñetón (1983); Scott (1984); Blair (1987, 1988); Delgado-Argote (1989); Rosaz (1989); Tardy et al. (1989); Dercourt et al. (1993); Ricou (1996); Marton and Buffler (1999); Dickinson and Lawton (2001a); Meneses-Rocha (2001); Ford and Golonka (2003); Olóriz et al. (2003); Rogers (2003); Rueda-Gaxiola (2003); García-Díaz (2004); Ángeles-Moreno (2006); Giunta et al. (2006); Challinor and Hikuroa (2007); Fillon (2007); Golonka (2007); Mann (2007); Mann et al. (2007); Cobiella-Reguera and Olóriz (2009)
Western Mexico, including alternative interpretations of a potential correlation of the Chortís Block with southeastern Mexican terranes, and the location of volcanic-arc complexes and the Mezcalera Plate	Carfantan (1983); Gordon (1993); Freyrier et al. (1996); Viland et al. (1996); Mills (1998); Dickinson and Lawton (2001a); Pindell and Kennan (2001); Rogers (2003); García-Díaz (2004); Bird et al. (2005); Busby et al. (2005); Ángeles-Moreno (2006); Bird and Burke (2006); Giunta et al. (2006); Ferrari et al. (2007); Mann (2007); Mann et al. (2007); Rogers et al. (2007); Torres de León et al. (2007); Silva-Romo (2008); Martini et al. (2011, 2012); Mauel et al. (2011); Boschman et al. (2014)
Western front of the oceanic crust domain related to the western Gulf of Mexico transform fault zone, identified by diverse names, or unnamed, and the southeastern margin of Yucatán	Campa et al. (1974); Castro-Mora et al. (1975); Ibrahim et al. (1981); Quezada-Muñetón (1983); Scott (1984); López-Ramos (1985); López-Infanzón (1986); Todd et al. (1988); Alzaga-Ruiz and Pano-Arciniega (1989); Delgado-Argote (1989); Sosson (1989); Tardy et al. (1989); Byerly (1991); Delgado-Argote et al. (1992); Sedlock et al. (1993); Iturralde-Vinent (1994); Freyrier et al. (1996); Ricou (1996); Goldhamer (1999); Eguiluz de Antuñano et al. (2000); Lapiere et al. (2000); Dickinson and Lawton (2001b); Goldhamer and Johnson (2001); Lawton et al. (2001); Pindell and Kennan (2001); Prost and Aranda (2001); Ford and Golonka (2003); Olóriz et al. (2003); Rogers (2003); Rueda-Gaxiola (2003); Bird et al. (2005); Busby et al. (2005); Mauel et al. (2005, 2011); Ángeles-Moreno (2006); Buchy et al. (2006); Giunta et al. (2006); Lewis et al. (2006); Centeno-García et al. (2007); Fillon (2007); Golonka (2007); James (2007); Ortega-Gutiérrez et al. (2007); Padilla y Sánchez (2007); Talavera-Mendoza et al. (2007); Silva-Romo (2008); Cobiella-Reguera and Olóriz (2009); Mickus et al. (2009); Pérez-Gutiérrez et al. (2009); Buchy (2010); Stern and Dickinson (2010); Martini et al. (2011, 2012); Mauel et al. (2011); Vega-Granillo et al. (2011); Boschman et al. (2014); Christeson et al. (2014); Lawton and Molina-Garza (2014)
Areas under the influence of magmatic activity related to intra-plate and plate boundary dynamics (including seepage, effusive-extrusive flows, and volcanoclastics)	Moore and Castillo (1974); Rosencrantz (1990); Sedlock et al. (1993); Marton and Buffler (1999); Dickinson and Lawton (2001a); Prost and Aranda (2001); Bird et al. (2005); Ángeles-Moreno (2006); Bird and Burke (2006); Fillon (2007); Mickus et al. (2009); Stern and Dickinson (2010); Martini et al. (2011, 2012); Lawton and Molina-Garza (2014)
Tectonic phases or pulses, with reference to Nevadan Orogeny times, including Gulf of Mexico evolution	Carfantan (1983); Peterson (1983); Scott (1984); Blair (1988); Radelli and Calmus (1988); Delgado-Argote (1989); Rosaz (1989); Tardy et al. (1989); Palafox et al. (1992); Sedlock et al. (1993); Hacker et al. (1995); Viland et al. (1996); Mills (1998); Meneses-Rocha (2001); Ford and Golonka (2003); Olóriz et al. (2003); Rogers (2003); García-Díaz (2004); Bird et al. (2005); Busby et al. (2005); Ángeles-Moreno (2006); Bird and Burke (2006); Giunta et al. (2006); Centeno-García et al. (2007); Fillon (2007); Golonka (2007); Rogers et al. (2007); Torres de León et al. (2007); Cobiella-Reguera and Olóriz (2009); Mauel et al. (2011); Vega-Granillo et al. (2011); Boschman et al. (2014); Christeson et al. (2014)

A general paleoenvironmental context can be approached taking into account climatic conditions for Mexican areas and their surroundings during Tithonian times. These have been interpreted within global contexts, including paleogeography (Fig. 2.2; Table 1), according to weather-sensitive fossils and rocks, and considering the highest sea-level phase during the Jurassic and its potential forcing (e.g., Scott, 1984; Ross et al., 1992; Weissert and Mohr, 1996; Rees et al., 2000, 2004; Ford and Golonka, 2003; Ziegler et al., 2003; García-Díaz, 2004; Busby et al., 2005; Sellwood and Valdes, 2006; Holz,

2015). According to these authors, relevant features of the paleoenvironmental context were: (1) paleolatitude ranges of 0–20°N and 0–30°N, but smaller ranges were also proposed (10°N to slightly more than 22°N), favoring development of reefs and shallow carbonates in the surroundings of the Gulf of Mexico (GoM) Basin and evaporites between 15°N and 22°N in the area; (2) surface temperature ranging 20–36°C, with a winter to summer mean temperature difference of ~8°C; (3) low to moderate relief modeled for southwestern and northwestern Mexico; (4) generally low precipitation, with a regionally

Figure 2. Paleogeographic maps: (1) global paleogeography for 152 Ma (earliest Tithonian; Gradstein et al., 2012) adapted from Scotese (2001); for improved resolution of the Antarctic regions, see Golonka (2007, figs. 25, 28); black symbols indicate records of macroconchiate *Hybonoticeras hybonotum* (plus signs); closely related, inconclusively known forms with scarce, local records (squares); microconchs belonging to the group of *H. mundulum*, which first appear in uppermost Kimmeridgian horizons (circles); poorly known records of early Tithonian *Hybonoticeras* microconchs (triangle); and *Mazapilites* (stars); updated to complement citations in the Systematic paleontology chapter; (2) synthesized paleogeography for the Mexican mainland and GoM during Tithonian times, based on the publications cited in Table 1 and interpretations by the authors; areas under influence of magmatic activity related to intraplate and plate boundary dynamics, seepage, effusive-extrusive flows, and volcanoclastics included (asterisks); note the combined representation of alternative locations of eastern Panthalassa volcanic arcs forcing subduction-accretion complexes in western Mexico (i.e., Guerrero-arc terrane complexes in distal and proximal settings), and assumed maximal extension of the ‘Nevadan Orogeny building’ (UaWMArC) at the expense of the subducting Mezcalera Plate and diminishing Arperos Ocean; major marine environments shown in increasing tone darkness seaward from coastal inner shelf areas for increasing depth of slightly deeper to moderate deep waters from mid-to-outer shelves, and then deeper, oceanic waters related to oceanic crust domains with assumed horst-graben seafloor topography and restricted deep-water circulation, at least for the GoM and the proto-Caribbean seaway; emerged lands (blackish). AL = Alamitos, 5 sections; Ap = Aldama platform; Ch = Chortís Block, only central and eastern Chortís terranes; Co = Coahuila Island/Peninsula; cp = Campeche platform; GoM = Gulf of Mexico; L = Laurentia; M[Y] = Maya Block, Yucatán; P[F] = Panthalassa Ocean and Farallon Plate; P[M] = Panthalassa Ocean and Mezcalera Plate; p-C = proto-Caribbean seaway; Ta = Tamaulipas archipelago; UaWMArC = Uplifted-Active-West-Mexico-Magmatic-Arc-Complexes. See text for further explanation.

distinct precipitation/evaporation rate—net precipitation westward and net evaporation eastward—with aridity being higher southward; (5) however, in terms of Walter biomes, northern Mexico has been considered subtropical to dry whereas southern Mexico would be tropical to subtropical-humid; (6) global climate models indicating upwelling influence from the western coast to eastern Panthalassa Ocean; (7) major oceanic anoxic event (OAE) and organic-rich deposition across the GoM; and (8) northward drifting of 10–15° during the Tithonian. The possibility of an end to the monsoonal climate pattern, which dominated during Jurassic times, has been also considered to occur at the end of the Jurassic (Weissert and Mohr, 1996).

To complement the general paleoenvironmental context expounded, it should be remembered that the Tithonian was a time interval involved in plate-boundary reorganization, in the area and worldwide (Ford and Golonka, 2003). Punctuated activity occurred in the Mexican convergent-transpressive margins, as well as northward in Cordilleran terranes, whereas progressive spreading with the rotation of Yucatán affected the GoM during Tithonian times (Delgado-Argote, 1989; Goldhamer, 1999; Bird and Burke, 2006; Stern and Dickinson, 2010; LaMaskin, 2012).

Some additional comments address the marine waters in the Mexican-GoM region. On the whole, the paleogeographic scenario for marine upper-layer waters (i.e., those inhabited by ammonites in Mexican areas during Tithonian times) was related to epicontinental seas across Mexican blocks accreted to southwestern Laurentia as part of the North American Plate. There, the scenario was of irregular, more or less restricted shelves with adjacent, more depressed, basinal areas. Local, constrained, and ephemeral epicontinental connections with proto-Caribbean water masses occurred southward (Fig. 2.2). A rather tortuous circulation of marine upper layers is envisaged across Mexican epicontinental shelves, where emerged lands occurred (Fig. 2.2). Forcing of sea surface currents by easterlies, distorted by local, irregular upwellings, would be expected, and fertilization of water masses was common during Tithonian times. Without evidence of discharges of major fluvial systems affecting these epicontinental shelves, fertilization would be rather forced through frequent volcanic activity and secondarily by winds. In contrast, fluvial influence was higher northward, in the extensional-to-transensional system of the Border Rift and in the northern rim of the GoM. The influence of volcanism was common and related to: (1) volcanic-arc activity westward, at the western Mexico margin, (2) transensional rifting with volcanic activity north-northwestward, (3) progressing oceanization during the opening of GoM to the east, with southward displacement of the Maya Block, and (4) associated progressing oceanic seaways connecting the Hispanic Corridor with the easternmost Panthalassa Ocean southward (Fig. 2.2). Deeper, epioceanic-oceanic water masses were located west-, east- and southward of the Mexican mainland. Deep-water conditions (currents, oxygenation, etc.) are envisaged as those corresponding to intricate rift and magmatic-arc related systems submitted during Tithonian times to limited spreading phases and block tectonics, or to transpression (and accretion), respectively—i.e., restricted ocean circulation and resulting low oxygen content, together with additional effects of common submarine volcanism and seepage. The combination of restricted marine currents, low oxygenation of bottom waters, and fertilization by volcanic activity in rifted, arc-related, and foredeep basins

resulted in common deposition of organic-rich, gray-to-black sediments (calcareous shales and argillaceous-to-silty carbonates). Variation in deposition depths, clay content, and oxygenation determined differences among Tithonian source rocks, but these Tithonian sediments gave rise to the main Jurassic hydrocarbon source rocks in Mexico, the GoM, and Cuba (Viniestra, 1981; Peterson, 1983; Santamaría-Orozco et al., 1995; Rodríguez-Viera et al., 1998; Ángeles-Aquino and Cantú-Chapa, 2001; Cole et al., 2001; Eguiluz de Antuñano, 2001; Guzmán-Vega et al., 2001; Magoon et al., 2001; Mancini et al., 2001; Prost and Aranda, 2001; Williams-Rojas and Hurley, 2001; Gaumet and Letouzey, 2002; Cantú-Chapa and Ortuño-Maldonado, 2003; Moretti, et al., 2003; Santamaría-Orozco and Horsfield, 2003; Padilla y Sánchez, 2007; Schenk, 2010; Muñoz-Cisneros et al., 2013). Paleogeographic interpretations of western areas related to active plate margins facing the Panthalassa Ocean are still inconclusive and controversial. These areas were submitted to the influence of subduction-accretion complexes—see Figure 2.2 and Table 1 for a draft and references, combining alternative interpretations about the location and eastward displacement of the Guerrero magmatic-volcanic-sedimentary-arc complex and others.

The studied section

The AL-5 section studied at the Sierra de Catorce, San Luis Potosí (23°39'1.6"N, 100°50'54.7"W; Fig. 1.2, 1.3), is 5 m thick and made of sandy to silty, grayish phosphoritic, and more or less calcareous horizons. The former is less common but more resistant to erosion. A brownish surface color results from weathering. Bedding is well defined, with strata showing flattish lower and upper surfaces, especially in silty phosphoritic horizons. Less common sandy phosphoritic horizons have more or less irregular top surfaces and local concretionary features, and seem to be the end members of upward thickening sedimentary packages. Bed thickness throughout the first 4 m (levels 0–5) shows values of 15–20 cm (46%), 10 to < 15 cm (29%), and < 10 cm (17%), without counting shaly interbeds. Microfacies in phosphoritic horizons indicate a coarse-silt-to-fine-sand matrix, with less common medium-sand and scattered coarse-sand grains. The latter are commonly phosphatized and brownish under transmitted, plane-polarized light, thus indicating collophane. The uppermost 1 m of the studied section is composed of < 10 cm thick, silty-to-very-fine-sandy horizons.

Within the paleoenvironmental and paleogeographic context provided earlier, and to consider a depositional context for the studied section AL-5, the following site effects must be considered: (1) location at a mid-range of latitude for Mexico mainland areas during the early Tithonian (i.e., ~22–23°N); (2) under east-northeast dominant winds (easterlies) forcing westward transport of surface waters with net offshore displacement in coastal waters; and (3) constituting a raised bottom (Olóriz et al., 1999). Hence, and in accordance with the paleoenvironmental and paleogeographic context, the AL-5 site was under warm-water masses with rather restricted circulation, and received upwelling events of variable intensity during the time corresponding to the studied interval. At first, upwelling influence could be expected from the west but, given the assumed paleogeography (Fig. 2.2), marine events geologically propagated from east or west would be forcing factors rather than prevalent winds. Restriction of

wide-ranging phosphoritic deposits to particular stratigraphic intervals across north-central Mexico, without identifiable cyclicity, strengthens this interpretation. In such a context, and at a mid-shelf position, phosphoritic sediments in the AL-5 site were deposited as higher-energy inflows barging into relatively restricted water masses. The latter would be warmer than mean surface temperature ($> 30^{\circ}\text{C}$; see above) and with an at least dysoxic lower water column and seabed. This context resulted in increased nutrients according to the abundance of low diversified benthics (overwhelmingly abundant bivalves, and persistent, rather isolate serpulids and planolites-maker burrowers), and moderate, short-time oxygenation of lower waters and seabed (particulate organic-rich sediments) during episodes of relatively higher-than-background energy.

In accordance with the paleoenvironmental scenario presented, the ecostratigraphic interpretation of section AL-5 (Fig. 1.2, 1.3, levels 0–6) is attempted by analysis of 489 fossil remains of which 88.14% are benthics (mainly bivalves) and 11.86% are ammonites (Ammonitina, incomplete specimens and fragments). Excluded from the analysis were data obtained from the basal horizon underlying level 0 because of taphonomic condensation, i.e., biostratigraphic mixing and top surface of stratigraphic discontinuity with the studied overlying section, which most probably represents a hiatal contact. Paleodepth interpretations are controversial whether sedimentologically or paleoecologically approached. However, it is now accepted that Ammonitina inhabited upper marine waters, and estimates of preferred depths of particular groups exist, as do considerations of their relative abundances with respect to benthics and related depths in terms of dozens of meters (Ziegler, 1967; Gygi, 1986, 1999; Olóriz et al., 1988, 1996, 2002, 2006; Westermann, 1996; Westermann and Tsujita, 1999; Lewy, 2002; Olóriz and Villaseñor, 2010, and references therein). Whatever the case, we are still far from precise concerning inhabited habitat depths by distinct Ammonitina within marine upper-water masses. On this basis, and considering these limitations, figures from levels 0–6 in the AL-5 section (Fig. 1.2), showing an overabundance of bivalves and secondary records of ammonites without evidence of colonization by epizoa, indicate shallow waters ($\sim 30\text{ m}$ or less). Similar assemblages of macroinvertebrates were reported by Olóriz et al. (1993) from interpreted *Hybonoticeras hybonotum* Biozone horizons in Durango, Mexico, and by Olóriz (1992) who provided a general picture of Mexican shelves with rather shallow depths and irregular, unstable sea bottoms forcing relative abundance in macroinvertebrate assemblages with ammonites. Short term postmortem transportation and subsequent common reworking (i.e., without biostratigraphic incidence) is suggested for the ammonites analyzed (see below). In addition, the record of benthics—mainly epifaunal and infaunal bivalves (e.g., Paralleodontidae Dall, 1898, Pteriidae Gray, 1847, Ostreidae Rafinesque, 1815, Astartidae d'Orbigny, 1844, Lucinidae Fleming, 1828, and Pleuromyidae Dall, 1900)—shows a moderate number of articulated specimens and less fragmentation than that seen in ammonites. The total abundance of bivalves reveals a slight decrease from level 0 to level 3, and a later sixfold recovery to level 4t, which shows the highest concentration of specimens (epi- and endofauna mixed in the same stratigraphic horizon). All of this agrees with increasing life

conditions for benthics and limited reworking under persistent but fluctuating upwelling conditions in shallow waters.

Materials and methods

Bed-by-bed sampling was conducted in the outcrop corresponding to the AL-5 section from the Sierra de Catorce, San Luis Potosí, Mexico (Fig. 1.3). It provided a total of 587 specimens and fragments (IGM 10190–10749), including 86% benthics (mainly bivalves, IGM 10225–10641; under study) and 14% ammonites (Ammonitina, see Systematic paleontology). The new ammonite material of *Hybonoticeras* and *Mazapilites* is 2% of the total material obtained.

Material for thin sections was selected from hand samples under stratigraphic control. All materials described and/or mentioned in The studied section and Systematic paleontology chapters are housed in the Colección Paleontológica Nacional, Museo María del Carmen Perrilliat of the Instituto de Geología, UNAM (Mexico City, Mexico). Usual procedures for preparation and study of ammonites and petrographic samples were applied, as well as those for stratigraphic and ecostratigraphic analyses in the section investigated.

A careful analysis was made of descriptions and stratigraphic interpretations in publications appearing in the early twentieth century to date. This revision is presented as selected comments of the cases of interest, with precise reproduction of original texts (relevant sentences) when appropriate. This treatment is followed by a precise, direct analysis of available types, and then by the updated interpretation of all information considered. The research conducted under these terms, comprising a careful analysis of all citations of hybonoticeratin and mazapilitin ammonites reported from Mexico and Cuba, aims to support their revision and updated interpretation.

Repositories and institutional abbreviations.—The studied types correspond to the preserved specimens, illustrated or not, belonging to old and modern collections housed in the following institutions: CPC, Colección del Museo del Desierto, Saltillo, Coahuila, Mexico; ERNO, Estación Regional del Noroeste Collection, Sonora, Mexico; IGM, Colección Paleontológica Nacional, Museo María del Carmen Perrilliat, Instituto de Geología, UNAM, Mexico City; MÁFI, Magyar Állami Földtani Intézet, Budapest, Hungary; McM-J, McMaster University, Hamilton, Canada (some specimens of which are housed in the museum at the Institute of Geology, Mexico City); SNSB-BSPG, Bayerische Staatssammlung für Palaontologie und Historische Geologie, Munich, Germany; UM, University of Michigan, Ann Arbor, Michigan, USA; UNAM, Universidad Nacional Autónoma de México, Mexico City; USNM PAL, National Museum of Natural History (United States National Museum), Smithsonian Institution, Washington, DC, USA.

Abbreviations of morphological terms.—Those used in morphological descriptions are: CI = costal or ribbing index, indicating the number of external, peripheral, secondary ribs per 10 primary ribs; Dm = shell diameter; ET/2 = number of external tubercles per half whorl; H = whorl height; H/Dm = whorl height to shell diameter ratio; H/W = whorl height to whorl width ratio; IT/2 = number of internal tubercles per half whorl; M = macroconch;

m = microconch; U = umbilicus; U/Dm = umbilicus to shell diameter ratio; UR/2 = number of umbilical ribs per half whorl; W = whorl width.

Systematic paleontology

Class Cephalopoda Leach, 1817

Order Ammonoidea Zittel, 1884

Suborder Ammonitina Hyatt, 1889

Superfamily Perisphinctoidea Steinmann in Steinmann and Döderlein, 1890

Family Aspidoceratidae Zittel, 1895

Subfamily Hybonoticeratinae Olóriz, 1978

Remarks.—The use of a family group name for hybonoticeratin ammonites shows rather unstable treatment and needs formal stabilization. The hybonoticeratines, or ‘hybonoten’ of classic authors (e.g., Neumayr, 1873, p. 190; 1878, p. [70]34), are a morphologically well defined but inconclusively known ammonite grouping. As reported by Olóriz (1978, p. 333–335), these ammonites have been interpreted in different, imprecise evolutionary relationships within aspidoceratines, which were mainly, but not exclusively, referred to as the family Aspidoceratidae in a variable sense by diverse authors (e.g., Zittel, 1884; Salfeld, 1919; Roman, 1938; Arkell in Arkell et al., 1957; Barthel, 1959; Berckhemer and Hölder, 1959; Ziegler, 1959; Christ, 1960). Moreover, hybonoticeratin ammonites have been considered to be more or less closely related to simoceratines (e.g., Spath, 1924, 1925, 1930, 1931; Arkell in Arkell et al., 1957 with hybonoticeratines in the subfamily Simoceratinae Spath, 1924 within Aspidoceratidae; Schindewolf, 1925, 1966), placed with aspidoceratines (e.g., in Aspidoceratinae by Schindewolf, 1925; Trauth, 1927; Arkell in Arkell et al., 1957, see above), or related to an unclear, alternative origin in Simoceratinae or Aspidoceratinae but included in Simoceratinae (e.g., Spath, 1931). Subsequent proposals suggested inconclusive evolutionary relationships within the stem Perisphinctidae Steinmann in Steinmann and Döderlein, 1890, the latter being interpreted in a broad sense to include aspidoceratin and euaspidoceratin ammonites (Olóriz, 1978; Callomon, 1981).

Interpretations of hybonoticeratines since the middle of the past century entail common references at the family level (e.g., Aspidoceratidae by Barthel, 1959 and Berckhemer and Hölder, 1959; Ziegler, 1959; Schweigert et al., 2012 with *Hybonoticeratas* belonging to aspidoceratids without mention of a formal taxonomic level of reference). References at the subfamily level and strictly focused on hybonoticeratines have been common since the 1970s (e.g., Hybonoticeratinae, recte Hybonoticeratinae, proposed as new subfamily by Olóriz, 1978), whereas reference to Simoceratinae was maintained by Sapunov (1979), Krishna (1983), and Verma and Westermann (1984); in turn, Pathak (1993) linked hybonoticeratin ammonites to the family Simoceratidae. Hybonoticeratinae was again proposed by Callomon (1981) without reference or comments on the previous proposal

made by Olóriz (1978). Reference to the subfamily Hybonoticeratinae has been common since the 1980s but involving different proposals: (1) Hybonoticeratinae Olóriz, 1978 (by Rossi, 1984; Olóriz et al., 1993, 2000; Olóriz and Villaseñor, 1999; Fatmi and Zeiss, 1999; Myczyński, 1999; Zell et al., 2014); (2) Hybonoticeratinae Neumayr, 1878 (by Sarti, 1984; Vigh, 1984), most probably by re-interpretation of the footnote no. 1 by Neumayr (1878, p. 70[34]); (3) Hybonoticeratinae Callomon, 1981 (by Schlamp, 1991; Pathak, 1993; Schlegelmich, 1994; Schweigert, 1998); (4) Hybonoticeratinae without reference to an author (by Krishna and Pathak, 1993); and (5) Hybonoticeratinae Callomon, 1981 (by Sarti, 1993; Howarth, 1998; Enay, 2009, who modified the composition interpreted by Callomon to a quasi-identical coincidence with the one made by Olóriz, 1978).

Olóriz (1978, p. 332–335) erected the subfamily name Hybonoticeratinae (sic) with precise indication of morphological features (ICZN, 1999, art. 13.1.1, recommendation 13A), genera and species composition (ICZN, 1999, art. 11.7.1.2), and a revision of previous treatments of the alluded ‘hybonoten’ ammonites. Without an explicit statement of intention (ICZN, 1999, art. 33.2.1), and based on the valid genus-level name *Hybonoticeratas* (ICZN, 1999, arts. 11.7.1.1, 13.2, 29.1), the correct spelling for the subfamily name is Hybonoticeratinae (ICZN, 1999, arts. 11.7.1.1, 29.3), as later prevailed and valid per se, as well as according to ICZN (1999) article 32.2.1. Hence, the original spelling Hybonoticeratinae by Olóriz (1978, excepting p. 659 where Hybonoticeratinae was correctly used) can be considered an incorrect original spelling (ICZN, 1999, arts. 32.5, 32.5.1, and the example following the latter) to be formally corrected (ICZN, 1999, arts. 32.5.3, 32.5.3.3). Olóriz et al. (1993 and subsequent works by this author and collaborators, as well as by other authors; see above) used the correct spelling Hybonoticeratinae in the same sense as that proposed by Olóriz (1978). These citations therefore represent the proper use of correct original spellings (ICZN, 1999, arts. 24.2.3, 24.2.4), taking into account the proper citation of the name Hybonoticeratinae by Olóriz (1978, p. 659). In addition, the proposal made by Callomon (1981) coincided with that previously made by Olóriz (1978) in the family group name selected (Hybonoticeratinae), but not in the precise evolutionary meaning of lineage relationships with older, Oxfordian taxa proposed by Callomon (1981). These comments are presented as a justified emendation according to ICZN (1999) articles 19.2, 32.2.2, 32.5, 33.2.2, and 50.4.

Genus *Hybonoticeratas* Breistroffer, 1947

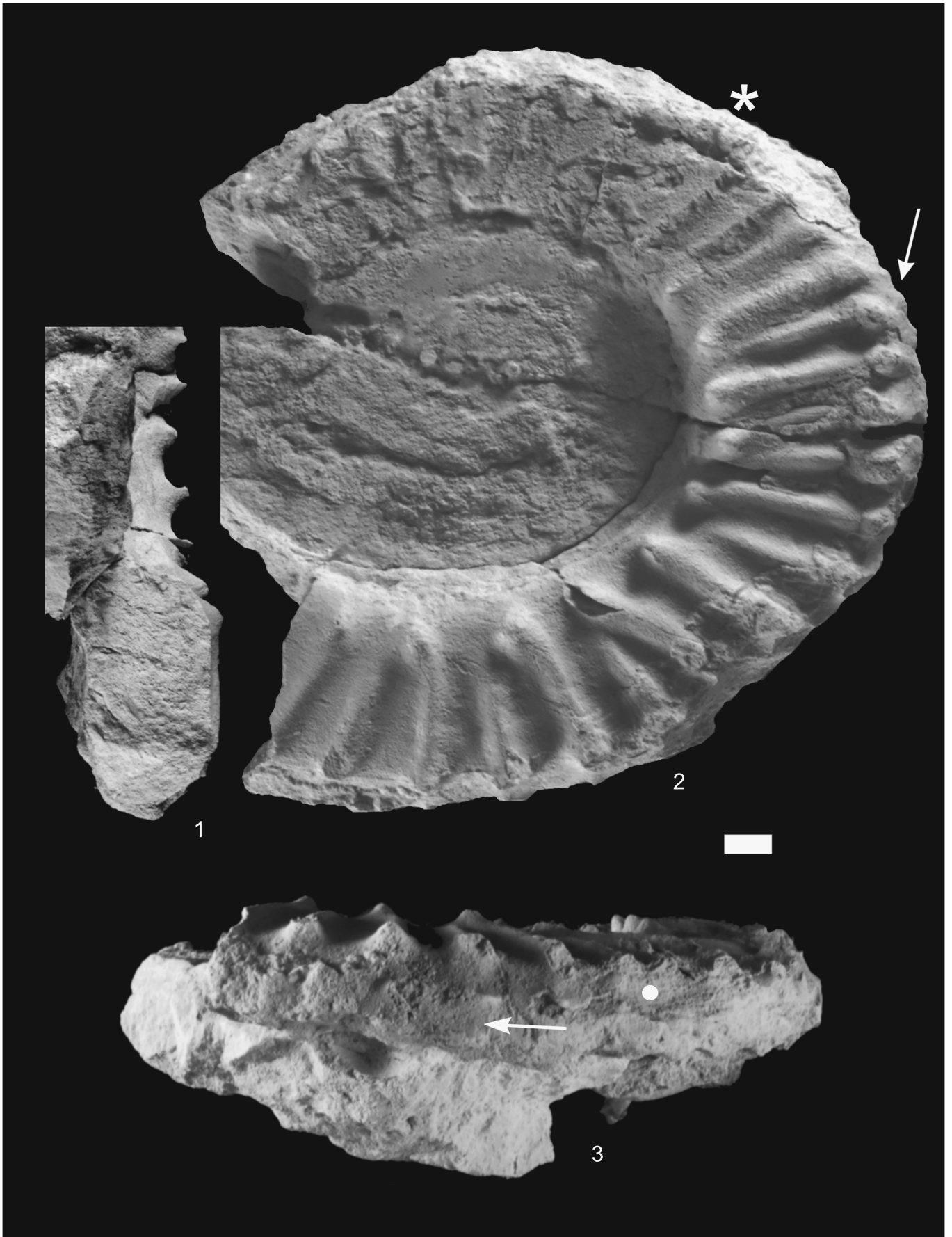
Type species.—*Ammonites hybonotus* Oppel, 1863 from the Lithographischer Schiefer, Solnhofen (Bavaria), Germany.

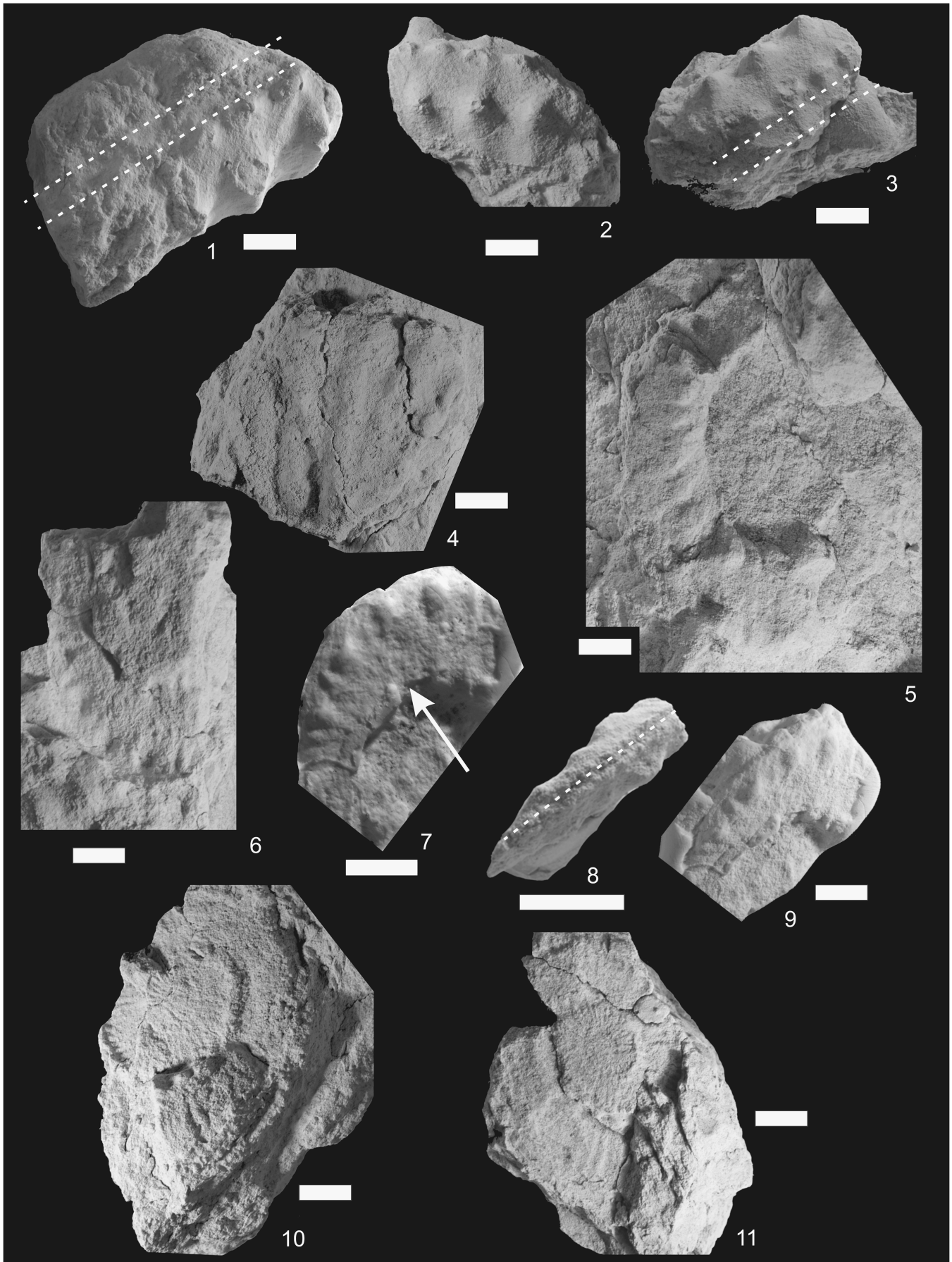
Hybonoticeratas authariformis new species

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Figures 3.1–3.3, 4.1–4.4, 5.1, 5.6, 5.9; Table 2

Figure 3. *Hybonoticeratas authariformis* n. sp. [M], holotype, IGM 4698, bed AL-5.4t in section Alamos 5 (AL-5), specimen AL-5.4t.1, La Caja Formation, lower Tithonian: (1) adapertural view; (2) left-lateral view showing crushed, eroded inner whorls and preserved outer whorl, which largely belongs to the body chamber (asterisk marks end of the phragmocone), with stiff, simple ribs, two rows of well-developed tubercles, local preservation of ventral tubercles (arrow), and accentuated difference in rib crowding due to slight, postmortem deformation; (3) ventral view, showing a shallow and wide venter (arrow), elongate ventral tubercles, and a wide left-lateral shoulder; note missing preservation of the ventral region to the right (dot). Scale bar = 1 cm.





Holotype.—IGM 4698, corresponding to specimen AL-5.4t.1, Upper Jurassic, lower Tithonian, from bed 4t in the section Alamitos 5 (AL-5) close to the village of Alamitos de los Diaz, San Luis Potosí, Mexico.

Diagnosis.—Shell large, evolute. Whorl section rectangular. Two rows of well-developed tubercles on the outer whorl. Coarse ribs on the outer whorl. Wide, shallow ventral groove outlined by nodate keels. Peristome and suture line unknown.

Occurrence.—Lower Tithonian, El Pastor Member La Caja Formation, Sierra de Catorce, San Luis Potosí, Mexico. Its association with *Hybonoticeras pseudohybonotum* Vigh, 1984 allows interpretation of its provenance from lowermost Tithonian horizons.

Description.—The most complete specimen (holotype, IGM 4698; Fig. 3.1–3.3) shows the left flank favorable for sculpture description (see measurements in Table 2). The shell is large (Dm = 180 mm), evolute (U/Dm = 0.5–0.52), and planulate. The whorl section is rectangular (H/W = 1.4–2) with a high, abrupt umbilical wall and flat flanks (Fig. 3.1). The sculpture preserved on the outer whorl is of coarse but acute tubercles that have spiny extremes on both the umbilical edge and just below the shoulders. The number of periumbilical tubercles is constant (12; see Table 2) between 150 and 180 mm in diameter, whereas the external, ventrolateral tubercles are more numerous (20–21). Sturdy, rigid, more or less radial to rursiradiate ribs link the tubercles of the two lateral rows developed on the flanks. Intercalatory ribs with similar trajectories occur, extending over the flank to the inner third, even closer to the position of the periumbilical row of tubercles. Real ‘V’-connections of ribs (i.e., the rib connections close to the periumbilical edge) are not observed, but some cases of a ‘quasi-V’ pattern exist, in which the influence of some degree of taphonomic distortion could be present. No looped, geminate ribs were observed. The ventral region is preserved at the adapertural part of the outer whorl, showing wide and slightly raised ventrolateral areas (shoulders) without identifiable remains of riblets connecting external tubercles to the keels. Hence, the latter appear as beaded, nodated reliefs in which tubercles seem to be clavate and clearly elongated longitudinally (Fig. 3.1–3.3). The groove that occupies the midline of the venter is shallow and as wide as one-third of the venter amplitude (Fig. 3.3). At least a half whorl belongs to the body chamber. There is no preserved trace of the adapertural structure. No suture lines are preserved.

Ammonite fragments IGM 4699, 4700, 4701, and 10189 are preliminarily included in *Hybonoticeras authariformis* n. sp. [M]. They show coarse, rigid ribs connected to the ventrolateral tubercles, with wide, excavated inter-rib spaces, and wide,

shallow ventral grooves. There is no preservation of the inner flanks. Specimen IGM 4699 (Fig. 4.1) is a fragment showing a presumed body chamber smaller than that of the holotype. It shows a wide whorl section, well-developed shoulders and prominent dentate keels, but the preservation is limited. Of particular interest is the occurrence of a potential, prorsiradiate riblet connecting a coarse ventrolateral tubercle with a crescentic, adaperturally placed relief of the keel (see below). Specimen IGM 4700 (Fig. 4.2, 4.3) is an even smaller fragment that shows the typically strong sculpture with prominent, spiny ventrolateral tubercles connected to coarse, rigid ribs, and a keel of more rounded tubercles (corresponding to the smaller shell?). Specimen IGM 4701 (Fig. 4.4) is a poorly preserved fragment showing 3 or 4 coarse, rigid ribs with eroded ventrolateral tubercles and its interpretation is tentative. Specimen IGM 10189 is an inner cast showing ~9 cm long left lateral view of a fragment belonging to a shell that could be 150 mm in diameter. The umbilicus is wide. Shell crushing is slight and the restored section shows an H/W of ~2. The flank sculpture is well preserved, but the venter is eroded. External tubercles have wide bases and are more numerous than the periumbilical ones. All tubercles are connected to stiff, coarse ribs, some of which are shorter intercalatories extending to the flank and producing ‘quasi-V’ connections with the internal range of tubercles.

Etymology.—From morphological similarity with *Hybonoticeras autharis* (Oppel in Berckhemer and Hölder, 1959).

Materials.—One specimen with well-preserved outer whorls (IGM 4698, holotype), and four fragments (IGM 4699–4701 and 10189, paratypes).

Preservation.—Evaluation of potential reworking is crucial before interpreting the biostratigraphic meaning of ammonite records. Hence, special relevance is given to the taphonomic analysis of the best-preserved specimen, the designed holotype.

Holotype IGM 4698 is preserved in volume as an inner cast showing a silty-to-fine sandy, grayish, and more-or-less calcareous matrix including very fine, scattered medium sand grains, and rare coarse sand grains, the latter two grain-size classes being commonly phosphatized (see below). The four fragments—paratypes IGM 4699 (AL-5.4t.2), IGM 4700 (AL-5.4t.3), IGM 4701 (AL-5.4t.4), and IGM 10189 (AL-5.5.1)—are inner casts tentatively included in the new species and likewise preserved.

Crushing was not relevant for paleontological identification. A case of multiphased taphonomic history has been identified and can be interpreted for holotype IGM 4698, and its paleontological identification is supported by careful analysis of the left and ventral views (Fig. 3.2, 3.3).

Figure 4. *Hybonoticeras* from beds AL-5.4t and AL-5.6 in section Alamitos 5 (AL-5), San Luis Potosí, La Caja Formation, lower Tithonian. *Hybonoticeras authariformis* n. sp. [M]: (1) paratype, IGM 4699, specimen AL-5.4t.2, oblique-ventral view showing coarse external and ventral tubercles; (2, 3) paratype, IGM 4700, bed AL-5.4t, specimen AL-5.4t.3, lateral (2) and ventral (3) views, showing coarse external and ventral tuberculation; (4) paratype, IGM 4701, specimen AL-5.4t.4, fragment of external whorls showing stiff primary and intercalatory ribs. *Hybonoticeras* cf. *H. pseudohybonotum*, bed AL-5.4t in section Alamitos 5 (AL-5): (5–9) IGM 4707, specimen AL-5.4t.5, partially preserved as an imprint and inner cast in volume, and a fragment preserved in volume; (5) right-lateral view; (6) imprint; (7–9) plaster cast of Figure 4.6; (7) left lateral view, showing smoothed ‘quasi-V’ pattern of rib connection (arrow); (8) ventral view; (9) oblique view, showing dense crenulation of the keel; (10, 11) IGM 4711, specimen AL-5.4t.9, sample separation in two halves resulting in preservation as inner cast and imprint. Dotted white lines indicate ventral furrows. Scale bar = 1 cm (note different bar for Figs. 4.7, 4.8).

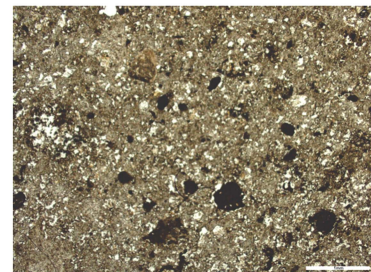
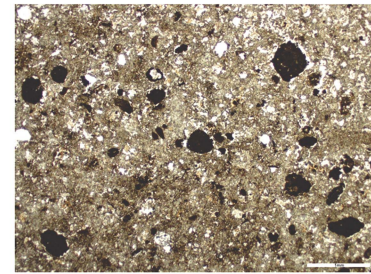
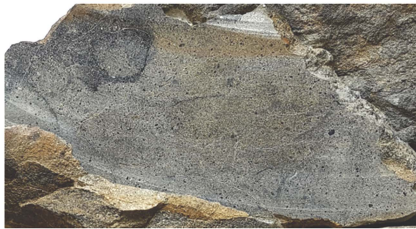
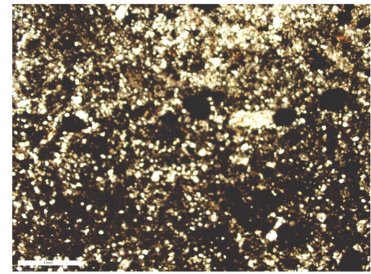
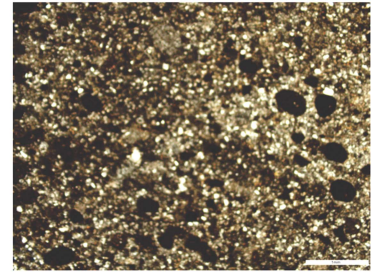
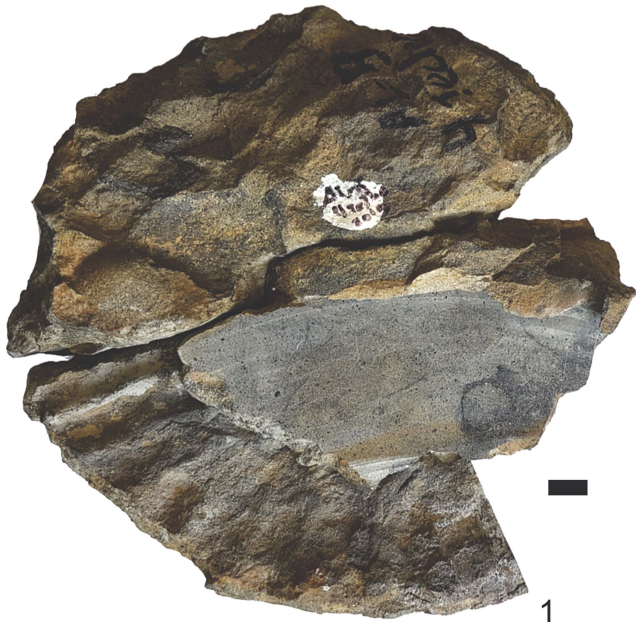


Table 2. Measurements of *Hybonoticeras authariformis* n. sp. [M], holotype, IGM 4698, AL-5.4t.1, at five different diameters.

Dm	U	H	W	U/Dm	H/Dm	H/W	UR/2	IT/2	ET/2
180	92.5	50.3	28	0.51	0.54	1.80	20	12	21*
165	83.4	50	24.8	0.51	0.60	2.02	22*	12*	21
133*	69.2*	39*	22*	0.52	0.56	1.77	21*	-	20
111.9	56	30.5	21.8	0.50	0.54	1.40	-	-	-
86.1	39.2	27.2	-	0.46	0.69	-	-	-	-

CI = costal or ribbing index indicating the number of external, peripheral, secondary ribs per 10 primary ribs; Dm = shell diameter; ET/2 = number of external tubercles per half whorl; H = whorl height; H/Dm = whorl height to shell diameter ratio; H/W = whorl height to whorl width ratio; IT/2 = number of internal tubercles per half whorl; U = umbilicus; U/Dm = umbilicus to shell diameter ratio; UR/2 = number of umbilical ribs per half whorl; W = whorl width; * = approximated value; - = not available. All figures in millimeters except when expressing ratios.

Taphonomic observations conducted on holotype IGM 4698 show differential preservation, more or less affecting half of the preserved outer whorl. The adapertural half whorl is preserved in volume whereas the aboral one is comparatively crushed. Moreover, the inner whorls in left lateral view were slightly displaced from the plane of shell coiling and symmetry (Fig. 5.6). Analysis of the right side shows rather severe crushing of the adapertural half outer whorl, which forced a corresponding reduction in shell thickness (Fig. 5.1, 5.9). Thus, flattening of the right side of the outer whorl impedes any direct evaluation of shell thickness for this part of the inner cast, which belongs to the body chamber.

The taphonomic features just described can be interpreted according to a taphonomic course that includes common reworking of an incompletely infilled shell, and can be summarized as follows: (1) horizontal to slightly subhorizontal settling of the shell with the right side upward; (2) partial sedimentary infilling affecting the body chamber and, most probably, a large part of the phragmocone; no observations were available for evaluating the precise degree of sedimentary infilling within the chambered part of the shell, but incomplete infilling of the phragmocone would determine low internal support for the right side of the shell (settled as the roof of the carcass) against the sedimentary load and related dissolution; (3) rapid burial hampering shell colonization by epibionts during background depositional conditions; (4) an early burial phase close to the sea bottom, increasing unfavorable conditions for colonization by macroepibionts while the shell underwent progressive dissolution; in a short time and within a benthos-rich substrate, the combination of dissolution and increased sedimentary load forced limited plastic deformation of the upper (right) side (the relative roof of the settled shell), therefore, the body chamber and presumably the most prominent parts of the phragmocone were affected on their right side; (5) sedimentary overburden determined limited crushing of the upper (right) side of the shell in both the body chamber and the phragmocone; most probably, more severe crushing affected the phragmocone

(limited observation); (6) early lithification progressed, resulting in formation of the inner cast (steinkern), which reproduced a partially modified shell morphology on the right side; (7) common reworking, i.e., reworking below biostratigraphic resolution, exhumed and redeposited the steinkern, with no significant difference between the silty-to-fine sandy and the more or less calcareous matrix that previously infilled the interior of the empty shell and the sediment outside the steinkern (Fig. 5, note the coarse-silty-to-fine-sandy and more or less calcareous matrix outside the inner cast, including fine sand with a variable abundance of medium and less common coarse sand grains [Fig. 5.2–5.5], whereas the equivalent matrix in the body chamber infilling includes very fine and more scattered medium sand grains, and rare coarse sand grains [Fig. 5.6–5.8, 5.10]); brownish grains are made of colophane showing moderate thermal alteration; a diluted hydrochloric acid reaction is similar for the matrix of the encasing rock and the infilling of the body chamber; (8) final settling after reworking, now with the left side upward and under background depositional conditions, i.e., no special, relevant difference in matrix composition between the steinkern and enclosing sediments (see details in point 7); (9) burial related to reworking rapid enough to impede macroscopic colonization of the steinkern by epibionts, e.g., epizoa such as common serpulids recorded from the same horizon, an endorather than epibenthos-rich seabed; (10) final settlement of the steinkern with the left side upward, hence, the left side is better preserved than the overturned right side, which inherited crushing from the pre-reworking burial phase; and (11) sedimentary overburden forcing increased pressure selectively on the umbilical and slightly concretionary plug, thus resulting in limited downward, oblique displacement of the inner cast corresponding to the phragmocone exposed in the umbilicus.

In addition, the dominant-to-nearly-exclusive preservation of other ammonites in the section is as fragments of inner casts of haploceratines and perisphinctines that are difficult to identify at the genus level (IGM 4702–4706, 10190–10224), fragments of *Hybonoticeras* (IGM 4699, 4707, 4709, 4711, 4770, 4701, 4708, 4710, 10189), and more complete *Mazapilites* (IGM 4713–4715), all showing variable degrees of erosion but no differences with respect to the silty-to-fine sandy, grayish ochre, and more or less calcareous encasing rock.

Remarks.—*Hybonoticeras authariformis* n. sp. [M] is similar to *H. autharis* as illustrated by Berckhemer and Hölder (1959, pl. 5, fig. 18). Both are large, evolute hybonoticeratines, showing rather radial to prorsiradiate ribs, strong ventrolateral tubercles, and shallow, wide ventral grooves. No other hybonoticeratines are comparable in these terms. *Hybonoticeras authariformis* n. sp. [M] differs from *H. autharis* in developing coarser, less crowded sculpture, in which periumbilical tubercles are much more prominent, and are clavate on the keels of the holotype. The ‘V’-connection of ribs might seem to be more

Figure 5. Preservation state of *Hybonoticeras authariformis* n. sp. (M) and matrix of the encasing rock from bed AL-5.4t in section Alamitos 5 (AL-5), Sierra de Catorce, San Luis Potosí, La Caja Formation, lower Tithonian, holotype, IGM 4698, specimen AL-5.4t.1: (1, 4) right-lateral view of hand sample including the described specimen and showing the sliced area in the enclosing rock (detail in Fig. 5.4); (2, 3) photomicrographs of encasing deposits showing coarse-silt to fine-sand matrix with scattered grains of colophane (darker grains) of fine and medium-sized sand grains; (5) thin-section appearance to compare with that corresponding to the infilling of the body chamber (Fig. 5.10); (6) opposite view of the same hand sample showing the left side of the described specimen with limited displacement (arrow) of the inner whorls; (7, 8) photomicrographs showing finer silty matrix with very fine, scattered medium, and rare, coarse, sand-sized grains of colophane (darker grains) in the infilling of the body chamber; (9, 10) sliced area (9) and thin-section appearance to compare with that corresponding to the encasing sediment (Fig. 5.5). Scale bars = 1 cm. See text for taphonomic features and interpretation.

common in *H. autharis* according to the specimen illustrated by Berckhemer and Hölder (1959, pl. 5, fig. 18), but neither this illustration nor that of the lectotype proposed by Berckhemer and Hölder (1959, p. 32) and illustrated by Quenstedt (1888, pl. 124, fig. 14 = *Ammonites perarmatus* Quenstedt, 1888) allow for a conclusive interpretation. In contrast, careful analysis of a plaster cast of the specimen illustrated by Berckhemer and Hölder (1959, fig. 18) confirms that no real 'V'-connections occur, that two consecutive intercalatories could be developed showing external, lateroventral tubercles, that there are periumbical tubercles unconnected to ribs, and that the keels show spiny tubercles. In addition, prosiradiate ribblets, or incipient reliefs, on the shoulders commonly connect ventrolateral tubercles to those of the keels in large, mature specimens of *H. autharis*, a feature that cannot be conclusively determined in *H. authariformis* n. sp. [M] due to limited preservation of the ventral region in the holotype (other fragments are too incomplete). The interpretation by Spath (1931, p. 646) of the specimen of *H. ammonites autharis* illustrated by Oppel (1863, pl. 71, fig. 4) as being "typical of [*H.*] *autharis*," and later proposed as a lectotype by Zeiss (2001, p. 63), as well as that by Malinowska (1989, pl. 5, figs. 3, 4) of an assumed juvenile of the species *H. autharis*, reinterpreted as *H. knopi* (Neumayr, 1873) by Schweigert et al. (1996), do not help to clarify the range of variation in the sculpture of *H. autharis*. On the preserved body chamber, the ventral tuberculation in *H. authariformis* n. sp. [M] appears to be more elongated, less oblique, and spiner than those shown in the adapertural quarter of the preserved outer whorl in the specimen illustrated by Berckhemer and Hölder (1959, fig. 19).

Hybonoticerias hybonotum has been interpreted in a broad sense, including closely related and inconclusively known forms (see paleobiogeographic range in Fig. 2.1). Such an interpretation can be recognized in the illustrations and/or synonymy lists by Oppel (1863), Benecke (1866), Favre (1877), Di Stefano (1883), Valduga (1954), Barthel (1959), Berckhemer and Hölder (1959), Collignon (1959, at least for *H. laevigatum* Collignon, 1959), Stephanov (1959), Enay et al. (1971, 2005), Olóriz (1978), Sapunov (1979), Mariotti et al. (1979), Rossi (1984), Sarti (1984, 1985), Verma and Westermann (1984), Geyssant in De Wever et al. (1986), Howarth (1992, 1998), Pathak (1993), Wierzbowski (1994), Benzagaggh and Atrops (1997), Caracuel and Olóriz (1999), Cecca (1999), Benzagaggh (2000), Zeiss (2001), Enay (2009), Fözy et al. (2011), Grigore (2011), and Schweigert et al. (2012), among others. Revision based on well-preserved material collected bed-by-bed is needed to propose a precise interpretation (e.g., Zeiss, 2001), which must be based on population-level data to reach a conclusive evaluation of phenotype variability in the Oppel species. As usually interpreted, *H. hybonotum* did not develop such coarse, stiff, crowded ribbing, and its keels could be made of more rounded tubercles. The latter are well expressed in the ventral region illustrated by Oppel (1863, pl. 71, fig. 1) in the specimen proposed as lectotype by Zeiss (2001), and are nicely shown in a color photo of this specimen kindly provided by G. Schweigert (Staatliches Museum für Naturkunde Stuttgart).

Hybonoticerias pseudohybonotum is another inconclusively known species commonly occurring with hybonoticeratines. No well-preserved inner whorls are known either from recently collected material or from specimens interpreted as closely related forms (e.g., Zeiss, 2001). On the basis of the phenotypic variability envisaged by the accepted conspecific relationships among *Ammonites hybonotum* Benecke (1866, pl. 11, fig. 1a–c), *H. pseudohybonotum* (see Vigh, 1984, pl. 2, fig. 1), *H. hybonotum beneckeii* Geyssant (in De Wever et al., 1896, p. 160, pl. 1, figs. 2, 3), and *H. aff. H. pseudohybonotum* (see Haberl et al., 1999, p. 15, pl. 1, fig. 1a–d), no comparable ribbing is seen with respect to *H. authariformis* n. sp. [M].

Lower Tithonian *Hybonoticerias* species reported from the Betic Cordillera, southern Spain (Olóriz, 1978), and included in the *H. hybonotum* group, commonly show somewhat more involute shells and no comparable crowded, coarse, rigid ribbing (except in *H. hybonotum autharis*)—their interpretation at the species or subspecies levels accords with the preference of given authors in any case. Specimens representing *H. autharis* in southern Spain developed less common intercalatory ribs, and less massive whorl sections than those of *H. authariformis* n. sp. [M]. Other lower Tithonian hybonoticeratin species reported from southern Spain by Olóriz (1978) have different keels, whorl sections, and sculpture.

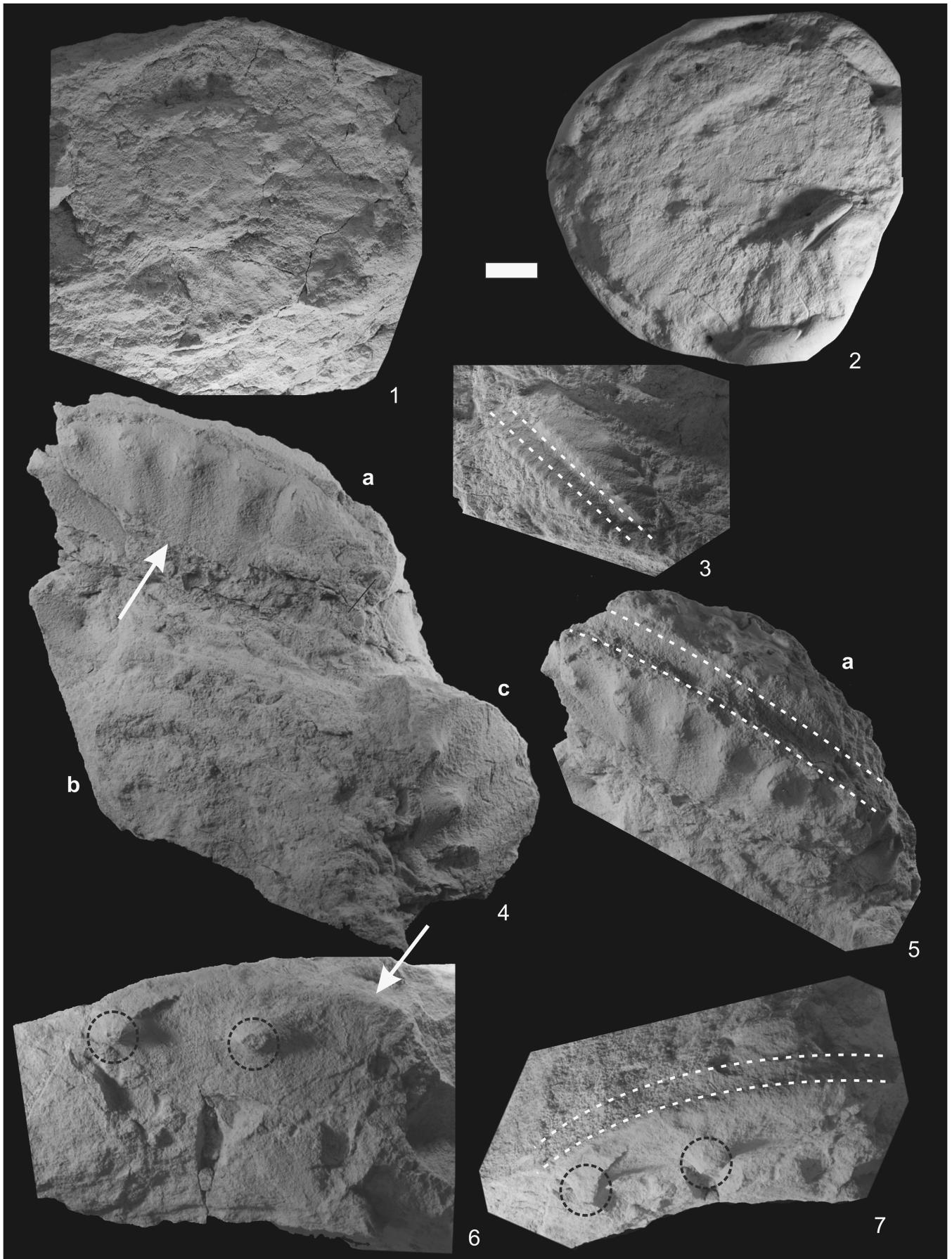
Hybonoticerias species from the uppermost Kimmeridgian *Hybonoticerias beckeri* Biozone, do not develop comparable sculpture, and the ventral groove is narrower and more excavated.

Hybonoticerias authariformis n. sp. [M] was collected with fragmented material morphologically close to *H. pseudohybonotum* from beds 4 and 5 in the AL-5 section, 110 cm and 20 cm below *H. sp. gr. H. hybonotum* and *Mazapilites mexicanus*, which were retrieved from bed 6 at the AL-5 section. The suggested biostratigraphic horizon for *H. authariformis* n. sp. [M] is basal Tithonian, which lends precision to the age interpretation of the single illustrated co-occurrence of *Hybonoticerias* and *Mazapilites* in Mexico (this paper) as occurring very early during the Tithonian but not during the earliest Tithonian.

As for determining the association between the highest sea levels during the Jurassic and colonization of epicontinental shelves by *Hybonoticerias* (Olóriz et al., 1993, 2000; Schweigert et al., 1996; Enay, 2009), more complete material is necessary to the reliable evaluation of the paleobiogeographic meaning of the Mexican records (Fig. 2.1). Because no other record of *H. authariformis* n. sp. [M] is known, the new species is considered endemic of Mexico. The recognition of a case of endemism in macroconchiate *Hybonoticerias* from Mexico adds new information to the previous identification of phenotype deviations and endemism among microconchiate *Hybonoticerias* (Olóriz et al., 1999, 2000), and opens new perspectives to revise records of *Hybonoticerias* in epicontinental shelves adjacent to water masses related to the Tethyan Ocean.

Hybonoticerias cf. *H. pseudohybonotum* Vigh, 1984
Figures 4.5–4.11, 6.1–6.5

Figure 6. *Hybonoticerias* cf. *H. pseudohybonotum*, bed AL-5.4t in section Alamitos 5 (AL-5), San Luis Potosí, La Caja Formation, lower Tithonian: (1, 2) IGM 4709, specimen AL-5.4t.7; (1) lateral view of the imprint; (2) plaster cast of Figure 6.1; (3) IGM 4708, specimen AL-5.4t.6, ventral view showing crenulate keels; (4, 5) IGM 4710, specimen AL-5.4t.8, lateral (4) and ventral (5) views (see text for explanation of lettering). *Hybonoticerias* sp. gr. *H. hybonotum*, IGM 4712, specimen AL-5.6.1, bed AL-5.6 in section Alamitos 5 (AL-5): (6) lateral, and (7) ventral views showing smoothed but dense crenulation of the keel (white arrow) and coarse external tubercles (dotted circles). Dotted white lines indicate ventral furrows. Scale bar = 1 cm.



- cf. 1886 *Ammonites hybonotum* Benecke, p. 187, pl. 11, fig. 1a–c.
- cf. 1984 *Hybonoticerias pseudohybonotum* Vigh, p. 73, 179, pl. 2, fig. 1.
- cf. 1986 *Hybonoticerias hybonotum beneckeii*; De Wever et al., p. 160, pl. 1, figs. 2, 3.
- cf. 2001 *Hybonoticerias* cf. *H. pseudohybonotum*; Zeiss, p. 64, text-figs. 76, 7.

Holotype.—MÁFI J.9762, *Ammonites hybonotum* (Benecke, 1886, p. 187, pl. 11, fig. 1a–c), Diphyakalk, lower Tithonian, from Volano, Roveredo, southern Alps, southern Tirol, Italy.

Diagnosis.—Medium-sized to large shell. Moderately evolute. Rectangular whorl section. Two rows of lateral, well-developed tubercles. Rather coarse, rigid ribs on the outer whorls. Riblets connecting ventrolateral tubercles with the keels. Inner whorls inconclusively known. Peristome preceded by a large constriction and assumed to be simple.

Occurrence.—*Hybonoticerias pseudohybonotum* characterizes lowermost Tithonian horizons in sub-Mediterranean Europe. The studied material is suggested to belong to equivalent lowermost horizons of the Tithonian in Sierra de Catorce, San Luis Potosí, Mexico.

Description.—The material collected is incomplete or fragmented, and its preservation barely allows identification of morphological features that point to the species proposed by Vigh (1984). The inner cast IGM 4707 (Fig. 4.5–4.9) is partly deformed by crushing. It is ~90 mm in diameter, and corresponds to a relatively complete outer whorl of an evolute shell. The inner whorls cannot be identified. The preserved outer whorl shows flattened flanks with well-developed periumbilical tubercles and more numerous ventrolateral tubercles (Fig. 4.7). The keel is crenulate and riblets connect the ventrolateral tubercles to the small, ventral crenulations (Fig. 4.8, 4.9). Ribs are not well preserved but they exist, even showing a probable case of looping (Fig. 4.9).

Specimen IGM 4711 (Fig. 4.10, 4.11) of ~65 mm diameter and coiling degree of 40% was partially preserved as an inner cast and imprint after sample separation into two halves. It shows rigid ribbing on the inner whorls, coarse but taphonomically smoothed ribbing on the outer whorl, and fine tuberculation on the keels. Due to the limitations of preservation, the interpretation of this specimen is only tentative.

The inner cast IGM 4709 (Fig. 6.1, 6.2) is severely flattened and its preservation barely allows for identification of fine crowded ribs that connect two rows of lateral tubercles. A case of rib looping could exist. Fine prorsiradiate and concave forward ribs occur in intertubercular spaces on the shoulder. No information could be obtained about the inner whorls.

Fragment IGM 4708 (Fig. 6.3) belongs to a ventral region in which a midventral groove, as wide as one-third the width of the venter, is outlined by two crenulate keels connected by prorsiradiate riblets to well-developed ventrolateral tubercles.

Specimen IGM 4710 (Fig. 6.4, 6.5) shows three adjacent fragments (Fig. 6.4a–c) potentially belonging to the same

evolute shell with a broken outer whorl (note preservation of the inner whorls in the lowermost fragment of Fig. 6.4c). In the larger one (upper fragment of the preserved outer whorl in Fig. 6.4a), an incomplete, flat flank can be observed, with two well-developed periumbilical tubercles connected to rigid, simple ribs, as well as a possible case of ‘quasi-V’ connection (Fig. 6.4a, arrow); a third periumbilical tubercle was damaged during sampling; the ventral region has a very wide midventral groove outlined by two poorly preserved keels and shoulders (Fig. 6.5a). This fragment looks similar to *Hybonoticerias* aff. *H. pseudohybonotum* illustrated by Haberl et al. (1999, pl. 1, fig. 1). The second, slightly smaller fragment (Fig. 6.4c, lower right fragment) shows an incomplete, flat right flank with three periumbilical tubercles. The third fragment (Fig. 6.4b, lowermost fragment) is severely eroded (smoothed?) and barely allows identification of middle to inner whorls with two potential ventrolateral tubercles.

Materials.—Four incomplete specimens and fragments: IGM 4707 (AL-5.4t.5), 4708 (AL-5.4t.6), 4709 (AL-5.4t.7), and 4710 (AL-5.4t.8), preserved as inner casts. In addition, IGM 4711 (AL-5.4t.9) is preserved as an inner cast and imprint.

Remarks.—*Hybonoticerias pseudohybonotum* is an inconclusively known species which is usually interpreted on the basis of the illustrations provided by Benecke (1866), Vigh (1984), and De Wever et al. (1986). All of these illustrations show inner whorls either idealized (Benecke, 1866) or not well preserved (Vigh, 1984; De Wever et al., 1986). Subsequent interpretations of closely affiliated forms (e.g., Haberl et al., 1999; Zeiss, 2001) did not improve this situation, because no inner whorls were preserved. According to Zeiss (2001, p. 63), this species of the *H. hybonotum* group developed subtle but typical connections among ventrolateral tubercles and the keels; the author held that this feature serves to identify *H. pseudohybonotum* compared to other members of the *H. hybonotum* group. As is usual with hybonoticeratines, precise knowledge at the species level is inconclusive at present.

Insofar as the incomplete specimens collected in Mexico allow for morphological comparison, the crushed specimen of *Hybonoticerias* cf. *H. pseudohybonotum* illustrated by Zeiss (2001, fig. 7) would appear to be the closest relative. This interpretation is reinforced by the occurrence of well-developed ventrolateral tubercles from which riblets connect with the keels. In addition, the wide ventral groove serves to relate the lowermost Tithonian European species of reference with the Mexican specimens.

In addition to lateral sculpture in the European specimens included in *Hybonoticerias pseudohybonotum*, the occurrence of a wide ventral groove, the type of keels, and the ventrolateral tuberculation shown by Vigh’s species and the Mexican specimens relate them to lower Tithonian hybonoticeratines. *Hybonoticerias pseudohybonotum* has been interpreted as representing a basal Tithonian horizon (Zeiss, 2001, p. 69). According to present information, a closely equivalent biostratigraphic horizon is envisaged for the fragmentary material collected in Mexico, but more precise biostratigraphy is

needed both in Europe and Mexico to arrive at a conclusive interpretation.

Hybonoticer *pseudohybonotum* and close forms have been interpreted as characterizing the lowermost horizons of the lower Tithonian in Tethyan, Mediterranean, and sub-Mediterranean areas. Lacking more complete specimens, the scarce and fragmentary material obtained in the Mexican AL-5 section impedes any reliable paleobiogeographic interpretation, and a mere mention of morphological similarity with the species erected by Vigh would apply. Among lower Tithonian *Hybonoticer* of the *H. hybonotum* group in southern Spain showing ‘quasi-V’ connections of ribs, *H. robustum* Olóriz, 1978 clearly differs in showing a more equidimensional section; coarser, stiffer and more regular sculpture; and coarser tubercles on the keels (Olóriz, 1978, p. 342–344, pl. 33, fig. 1).

As previously stated, the combination of favorable, high sea level, and widespread colonizations of epicontinental shelves by *Hybonoticer* (Olóriz et al., 1993, 2000; Schweigert et al., 1996; Enay, 2009) do not allow determination of precise paleobiogeographic dynamics and the meaning of the Mexican records described. More complete information on population data and composition of the ammonite assemblage is needed.

Hybonoticer sp. gr. *H. hybonotum* (Opper, 1863)
Figure 6.6, 6.7

- gr. 1863 *Ammonites hybonotus* Opper, p. 254, pl. 71, figs. 1, 2.
gr. 1877 *Ammonites (Aspidoceras) hybonotus* Benecke; Favre, p. 58, pl. 8, fig. 1.
gr. 1954 *Waagenia* sp. cf. *hybonota*; Valduga, p. 26, pl. 6, fig. 1.
gr. 1959 *Hybonoticer* *hybonotum*; Barthel, p. 63, text-fig. 7a–c.
pars. gr. 1959 *Hybonoticer* *hybonotum* sensu lato; Berckhemer and Hölder, p. 30.
gr. 1959 *Hybonoticer* *hybonotum*; Stephanov, pl. 1, fig. 3, pl. 2, figs. 3, 4.
gr. 1979 *Hybonoticer* *hybonotum*; Sapunov, p. 161, pl. 51, fig. 1.
gr. 1984 *Hybonoticer* *hybonotum hybonotum*; Sarti, p. 508, pl. 3, fig. 2a, b.
pars. gr. 1978 *Hybonoticer* (*Hybonoticer*) *hybonotum*; Olóriz, p. 336, pl. 33, fig. 2.
gr. 1993 *Hybonoticer* *hybonotum*; Pathak, p. 127, pl. 1.
gr. 1994 *Hybonoticer* *hybonotum*; Wierzbowski, p. 231, pl. 4, fig. 6a, b.
gr. 1997 *Hybonoticer* (*Hybonoticer*) *hybonotum*; Benzagaggh and Atrops, pl. 4, fig. 4.
pars. gr. 1999 *Hybonoticer* sp. gr. *hybonotum*; Caracuel and Olóriz, p. 588, pl. 6, fig. 10.
gr. 2001 *Hybonoticer* *hybonotum*; Zeiss, p. 63.
gr. 2011 *Hybonoticer* *hybonotum*; Fözy et al., pl. 6, figs. 10, 11.

Lectotype.—SNSB-BSPG AS I 567 (Opper, 1863, pl. 71, fig. 1), Lithographischer Schiefer, lower Tithonian, Solnhofen, Bavaria, Germany, designated by Zeiss (2001).

Diagnosis.—Shell large, evolute, with two rows of well-developed, lateral tubercles. Ribbing of variable strength, inconclusively known. Wide and shallow ventral groove. Peristome unknown but assumed to be simple.

Occurrence.—*Hybonoticer* of the *Hybonoticer* *hybonotum* group characterize the lower Tithonian elsewhere. Here, the analyzed *Hybonoticer* sp. gr. *H. hybonotum* is suggested to represent lower but nonbasal horizons of the lower Tithonian at the investigated section AL-5.

Description.—Fragment IGM 4712 (Fig. 6.6, 6.7) belongs to an outer whorl (body chamber?) of a large shell and is preserved as inner cast. The only preserved parts are the external portion of a flat flank, two coarse ventrolateral tubercles, and a wide, shallow groove on the midventer. The keels are crenulated but taphonomically smoothed.

Materials.—One fragment of an inner cast, IGM 4712, specimen AL-5.6.1 from bed 6 in the section Alamitos 5 (AL-5).

Remarks.—*Hybonoticer* *hybonotum* is an imperfectly known species due to the extremely incomplete illustration provided by Opper (1863), and subsequent interpretations (see above). However, the sculpture and type of ventral groove make it possible to refer the described fragment to the group of *H. hybonotum*. No *hybonoticer* of the uppermost Kimmeridgian *beckeri* Zone developed a comparable type of shell and ventral region.

Specimen IGM 4712 was collected with two specimens interpreted as belonging to the morphological group of *Mazapilites mexicanus*. Thus, the co-occurrence of *Hybonoticer* and *Mazapilites* in Mexico is demonstrated for the first time by specimens retrieved from the same bed and section (bed 6 in section AL-5.6).

Forms belonging to the group of *Hybonoticer* *hybonotum* characterize the lower Tithonian elsewhere in Tethyan areas, and in those epicontinental areas under the influence of waters connected to the Tethyan Ocean. More complete material is necessary to determine the precise paleobiogeographic dynamics and meaning of the Mexican records within the context of the accepted relationships among the highest sea levels during Late Jurassic times and the colonization of epicontinental shelves by *Hybonoticer* (e.g., Olóriz et al., 1993, 2000; Schweigert et al., 1996; Enay, 2009).

Notes for an updated evaluation of the genus *Mazapilites*

Analysis of the typical Mexico-Caribbean, endemic genus *Mazapilites* is of special interest because of its inconclusive stratigraphic relationship with the worldwide genus *Hybonoticer*.

Burckhardt (1919 in 1919–1921) erected the genus *Mazapilites* for coarse-ribbed oppeliids found at the Cañón del Toboso, Durango. Burckhardt identified four new species and included a fifth one previously described as *Eurynoticer* *zitteli* Burckhardt, 1906 from several locations across the Sierras de Mazapil and Santa Rosa (Burckhardt, 1906).

Present knowledge of Mexican *Mazapilites* is limited to material housed at IGM (18 specimens and fragments), and at ERNO (one specimen). These specimens belong to the collections of Burckhardt (1906, four specimens and three fragments; 1919–1921, five specimens and two fragments, here reillustrated in Fig. 7), Peña-Muñoz (1964, two specimens), Verma and Westermann (1973, one specimen), Olóriz et al. (1999, one specimen), and Villaseñor et al. (2005, one specimen) (Fig. 8). The loose, and lost, syntype illustrated by Del Castillo and Aguilera (1895, two specimens illustrated) was available in the form of a plaster cast provided by USNM PAL (Fig. 8.2). Two more specimens, plus one dubious fragment, were recently collected by the authors from bed 6 at the AL-5 section (Fig. 8.5–8.8). Hence, a total of 23 specimens and fragments were available for this revision.

Careful revision of Burckhardt's collection (1906, 1919–1921) was undertaken to approach a preliminary, updated evaluation of genus *Mazapilites* at the species level. Burckhardt's descriptions and illustrations reveal interesting traits in his collection of *Mazapilites*, which is the largest reported to date, comprising specimens preserved in volume (Fig. 7):

(1) Phragmocone preservation overwhelmingly dominates (Burckhardt, 1906, p. 110; 1919–1921, p. 4–11), and only four cases of partial and crushed body-chamber preservation are known (Burckhardt, 1919–1921, p. 4, pl. 1, fig. 9, p. 7, pl. 2, figs. 1, 6; note that the partial body chamber shown by Burckhardt, 1919–1921, pl. 1, fig. 2, is lost). A fourth case of body-chamber preservation was reported by Peña-Muñoz (1964, pl. 1, fig. 1; Fig. 8.9) and is found in the Peña-Muñoz collection, showing a left-lateral view of a somewhat crushed specimen preserved in siltstone.

(2) Sculpture smoothing was recognized in the adult body chamber of *Mazapilites symonensis* Burckhardt, 1919 (Burckhardt, 1919–1921, p. 3–5, pl. 1, fig. 9; Fig. 7.10). Another smoothed body chamber was illustrated by Burckhardt from a specimen collected from the Cañón del Toboso (Burckhardt, 1921, pl. 1, figs. 1–5, especially figs. 1–3 for the type), but the body chamber of this specimen is lost and only the phragmocone is preserved in the Burckhardt collection (Fig. 7.9). The specimen of *M. symonensis* illustrated by Peña-Muñoz (1964, pl. 1, fig. 1; Fig. 8.10) shows the same appearance, with sculpture smoothing of the body chamber. However, sculpture smoothing cannot be considered typical of the genus *Mazapilites* because coarsely sculptured body chambers are known for *M. crassicosatus* Burckhardt, 1919 (Burckhardt, 1919–1921, p. 8, pl. 2, figs. 1, 6; Fig. 7.11, 7.12).

(3) Ribbing composed of simple ribs and unstable, defectively realized 'bifurcations' was identified (Fig. 7.1–7.12), resulting in the occurrence of more or less clear intercalatory ribs (Burckhardt, 1906, p. 108, 109; 1919–1921, p. 3, 5, 7–10). Variable rib coarseness was identified within a given species (Burckhardt, 1906, p. 6, *Eurynoticerias* = *Mazapilites zitteli*; Burckhardt, 1919, p. 8, *M. zitteli*, p. 9, 10, *M. tobosensis* Burckhardt, 1919). Although sculpture (i.e., ribbing) was considered

similar among the species described (Burckhardt, 1919–1921, p. 3), a slight difference in sculpture was used for species identification (Burckhardt, 1919–1921, p. 8 for *M. crassicosatus* vs. coarse-ribbed *M. zitteli*; p. 9 for *M. crassicosatus* vs. *Mazapilites* sp. indet. illustrated on pl. 2, figs. 5, 8, 9; and p. 10 for *M. carinatus* Burckhardt, 1919 vs. *M. tobosensis*). Rib crowding was considered variable (Burckhardt, 1906, 1919–1921).

(4) Whorl sections change from more or less oval to acute during ontogeny, but ovate whorl sections can persist throughout ontogeny, and some cases of acute whorl sections ("forme d'une fleche") were identified in the preserved outer whorls (Burckhardt, 1906, p. 108; 1919–1921, p. 3).

(5) Suture line analysis was detailed, revealing some degree of suture variability in Burckhardt's descriptions (Burckhardt, 1906, p. 109, 110; 1919–1921, p. 3, 5, 6, 8, 10, 11), the systematic significance of which, at the species level, was correctly subordinated to shell morphology and sculpture (Burckhardt, 1906, p. 110, but see Burckhardt, 1919–1921, p. 6). In addition, shell morphology and sculpture were recognized as resulting in polymorphic combinations, especially for his species *M. zitteli* ("bastante polimorfa," Burckhardt, 1919–1921, p. 2, 6).

(6) Venter 'tricarination' with variable development occurs during an ephemeral ontogenetic phase in some of the species erected based on material collected from the "capas superiores con *Mazapilites*" at the Cañón del Toboso, Sierra de Symón, Durango (Burckhardt, 1919–1921, p. 2, 3, and p. 4, 5 for *M. symonensis*, p. 7 for *M. crassicosatus*, p. 9 for *M. tobosensis*, and p. 10 for *M. carinatus*; Burckhardt referred this section or 'locality' as belonging to the Zacatecas state).

Observations on the type material available from old collections and the recently collected material additionally show that:

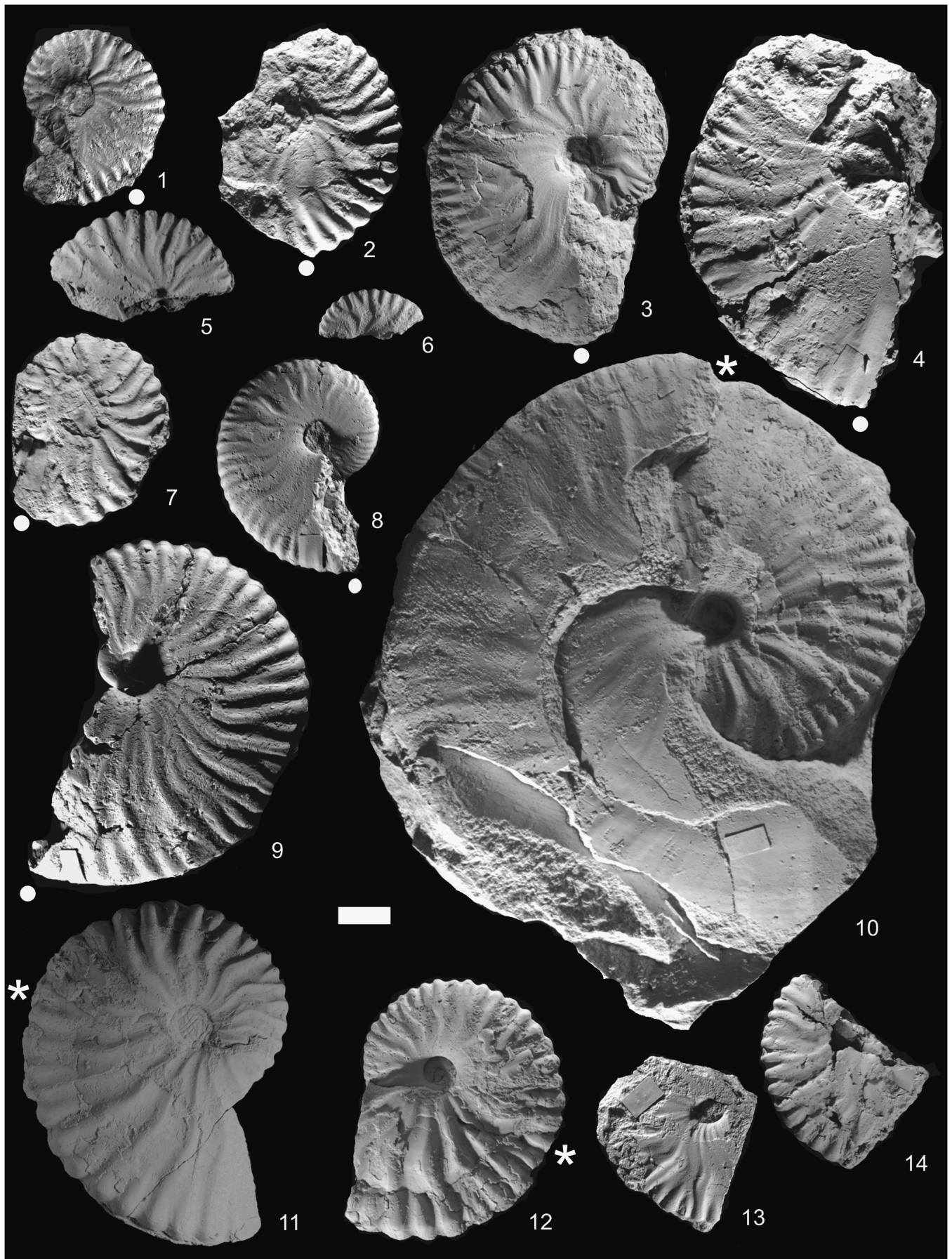
(7) No complete specimens exist, because crushing affected the four existing cases of incomplete body-chamber preservation (a fifth one is an isolated, recently collected fragment of dubious interpretation) and, therefore, very limited information is available about the body chamber's sculptural variability.

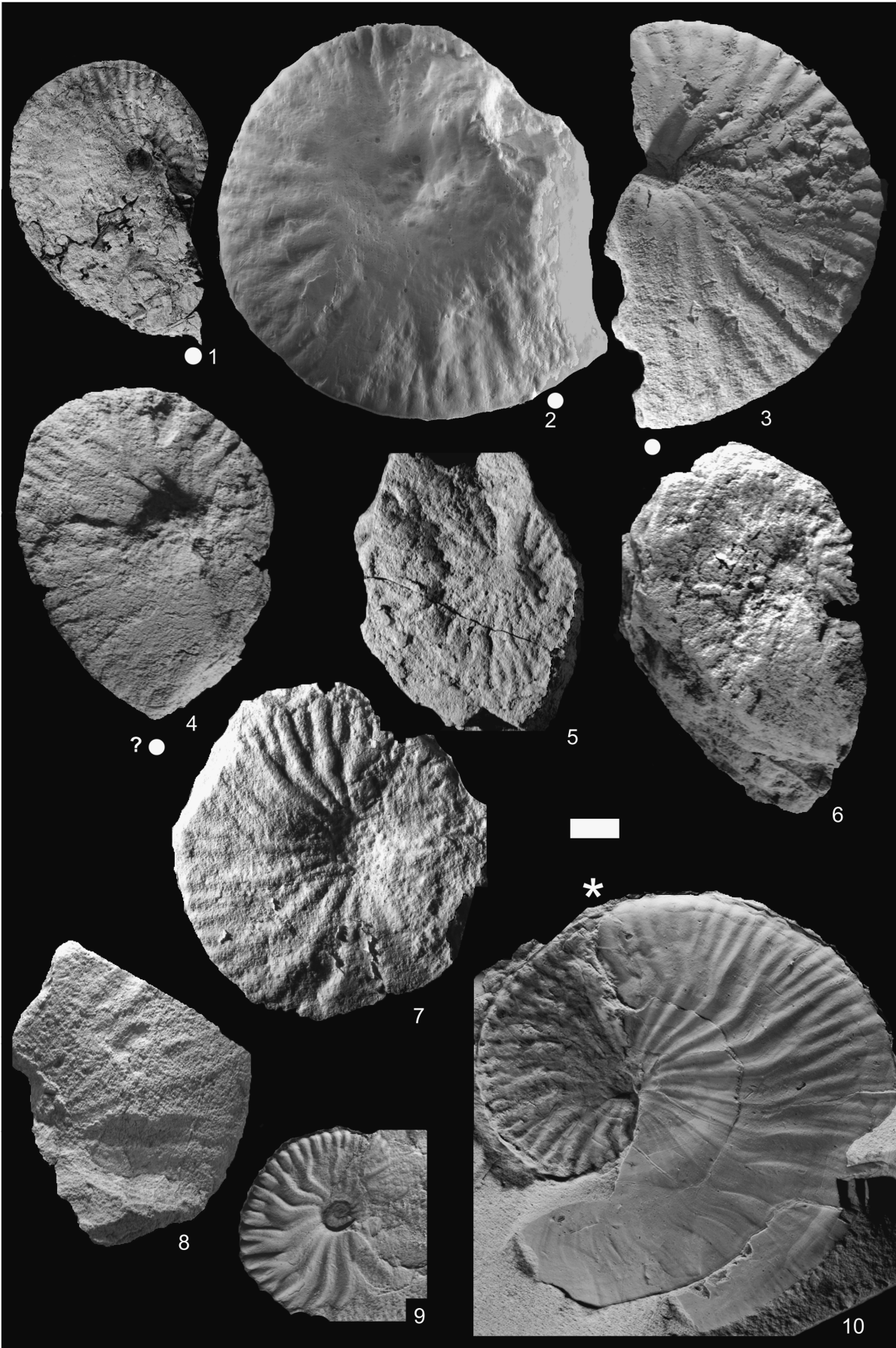
(8) Smoothed and sculptured body chambers developed in *Mazapilites* (e.g., *M. symonensis* and *M. crassicosatus*, respectively), but one doubt is evident: was sculpture smoothing in the body chamber exclusive of *M. symonensis* or was it a typical feature of final growth? Hence, the well-sculptured body chamber known in *M. crassicosatus* could indicate incomplete growth or serve to identify a smaller, separate species.

(9) Ribbing consists mainly of simple and intercalatory ribs, which sometimes connect to umbilical or primary ribs at the midflank inflexion ('knickung' or 'codo' of Burckhardt, 1919–1921, p. 5, 7, 8). The more accentuated the rib inflexion, the clearer these connections are, the connections being realized in aboral or apertural position with respect to the umbilical or primary ribs; very common, even dominant, is the occurrence of obscure or incomplete rib connections.

(10) Burckhardt's species *Mazapilites crassicosatus* shows a difference in rib coarseness on the inner whorls, whereas specimens with coarser ribs at the same shell size and

Figure 7. *Mazapilites* spp. from the Burckhardt collection (1906, from the Sierras de Mazapil and Santa Rosa, northern Zacatecas State, and 1919–1921 from Cañón del Toboso, eastern Durango State), lower Tithonian. *Mazapilites zitteli*: (1) IGM 246; (2) IGM 245a = 7166; (3) IGM 245; (4) IGM 246c = 7170; (5) IGM 246B = 7169; (6) IGM 245; (7) IGM 246a = 7168. *Mazapilites tobosensis*: (8) IGM 1567. *Mazapilites symonensis*: (9) IGM 1562; (10) IGM 1563. *Mazapilites crassicosatus*: (11) IGM 2684; (12) IGM 1564. *Mazapilites* sp.: (13) IGM 1566; (14) IGM 1565, from Burckhardt (1919–1921). White dots indicate last preserved suture lines; asterisks mark beginnings of the preserved body chambers. Scale bar = 1 cm. See text for interpretations.





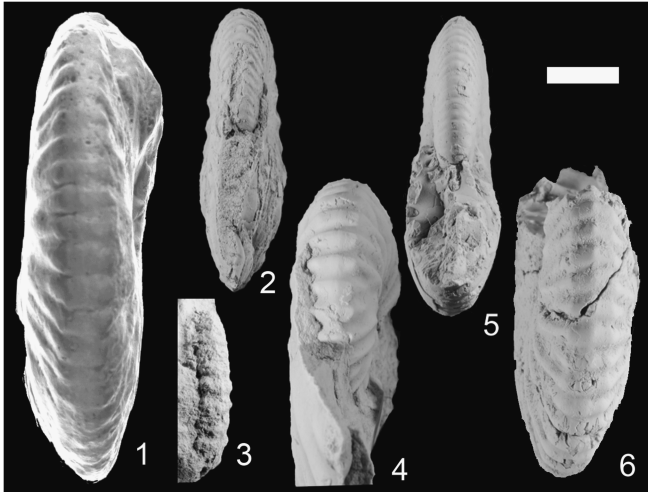


Figure 9. Ventral views of specimens of *Mazapilites* showing variable development of the ventral tubercles and ventrolateral reliefs (prominences) presumably related to shell inflation: (1) *M. mexicanus*, USNM PAL 103295, plaster cast, San Luis Potosí State, Sierra de Catorce, lower Tithonian (see Del Castillo and Aguilera, 1895, pl. 6, fig. 8); (2) *M. crassicosatus*, IGM 1564, eastern Durango State, Cañón del Toboso, lower Tithonian; (3) *Mazapilites?* sp., IGM 4715, San Luis Potosí State, Sierra de Catorce, lower Tithonian; (4) *M. crassicosatus*, IGM 2684, eastern Durango State, Cañón del Toboso, lower Tithonian; (5) *M. tobosensis*, IGM 1567, eastern Durango State, Cañón del Toboso, lower Tithonian; (6) *M. symonensis*, IGM 1562, eastern Durango State, Cañón del Toboso, lower Tithonian. Scale bar = 1 cm. See text for explanation.

collected from the same ‘locality’ (Cañón del Toboso) were interpreted as a potential new species of *Mazapilites* (e.g., Burckhardt, 1919–1921, p. 9, pl. 2, figs. 5, 8, 9). Updated reinterpretation cannot deny the possibility of intraspecific diversity, as was suggested for *M. zitteli* by Burckhardt (1919–1921, p. 2).

(11) The general, ontogenetic trend for higher and narrower whorl sections is less accentuated in *Mazapilites crassicosatus* (e.g., Burckhardt, 1919–1921, p. 7).

(12) The thorough analysis of suture lines made by Burckhardt was correctly interpreted in general (but see Burckhardt, 1919–1921, p. 6), although without paying particular attention to the potential bias forced by preservation in silty-limy to fine sandy, phosphoritic deposits.

(13) Venter ‘tricarination’ seems to be a constructional effect rather than one related to real tuberculation; it is affected by preservation and the convexity of flanks, and can disappear early or late in ontogeny (see also Burckhardt, 1919–1921, p. 2, 3, 5, 7, 9–11). There are cases of real, subtle, subrounded to elongated tubercles only at the midventral line (Fig. 9.4?, 9.5?, 9.6); the ventrolateral swellings mentioned by Burckhardt (e.g., Burckhardt, 1919–1921, ‘hinchamientos’ on p. 2, 3, 9 and ‘ensanchamientos’ on p. 5, 7, 11) are not real tubercles, yet show longitudinal elongation, and seem to be related to the

differentiation of relatively well-developed, distinct shoulders—i.e., the more accentuated the angular transition between the flanks and the ventral region, the more enhanced the ventrolateral reliefs (Fig. 9.4, 9.6 vs. 9.1, 9.2, 9.5) identified between 30 and 40 mm in the revised material. An exception is a case at 60 mm diameter in the plaster cast USNM PAL 103295 corresponding to the type of *Mazapilites mexicanus* illustrated by Del Castillo and Aguilera (1895, pl. 6, fig. 8).

(14) Isolated, incomplete, large inner casts affected by variable crushing and erosion, collected by Verma and Westermann (1973, pl. 26, fig. 7; Fig. 8.3), Olóriz et al. (1999, pl. 7, figs. f, g; Fig. 8.4), and Villaseñor et al. (2005, pl. 4, fig. d; Fig. 8.1) from silty-sandy and phosphoritic deposits, are large phragmocones between 60 and 90 mm shell diameter. These specimens show comparatively little sinuous ribbing with low intercalatories typical of the morphological group represented by *Mazapilites mexicanus*, but the absence of body chamber preservation impedes their conclusive interpretation at the species level. Small (~30 mm) phragmocones preserved in siltstone are difficult to interpret (e.g., Peña-Muñoz, 1964, pl. 1, fig. 2; Fig. 8.9).

(15) Measurements of shell diameter, coiling degree, and ribbing conducted on the type material available from old collections and the recently collected material are represented in Table 3 and Figures 10 and 11. The obtained information indicates that:

(15.1) The range of shell size in specimens belonging to the nominal species of *Mazapilites* are 32 mm for *M. carinatus* (a single, lost phragmocone), close to 40 mm for *M. tobosensis* (the single known phragmocone), 33–65 mm for *M. zitteli* (seven existing phragmocones), 47–72 mm for *M. crassicosatus* (two existing specimens with preserved body chambers), 61–86 mm for *M. mexicanus* (five existing phragmocones, a plaster cast, and a fragment of dubious interpretation), and 38?–68–119 mm for *M. symonensis* (two existing phragmocones and two specimens, including body-chamber preservation; interpretation of the smallest phragmocone is dubious). Of six nominal species, four are represented by small to medium-sized phragmocones (up to 65 mm), but one species (*M. crassicosatus*) includes two specimens with body chambers of <70 mm; one species (*M. mexicanus*) is represented by medium-sized to large phragmocones; and a single species (*M. symonensis*) includes adult body-chamber preservation. The interpretation of small phragmocones is inconclusive (e.g., Peña-Muñoz, 1964, pl. 1, fig. 2; Fig. 8.9).

(15.2) Coiling degrees expressed by the U/Dm ratio (Fig. 10.1) are uniform among the nominal species of *Mazapilites*, and show a clear trend for wider umbilici at larger shell diameters (~60 mm and larger), as well as some cases of <60 mm in *M. mexicanus* and *M. symonensis* (Fig. 10.1, 10.2). The use of the U/Dm ratio vs. Dm (Fig. 10.2) reveals a general, decreasing trend during growth, except for some phragmocones between 40 and 86 mm interpreted as *M. mexicanus*, and in some cases interpreted as *M. symonensis* (Fig. 10.2).

Figure 8. *Mazapilites mexicanus*, Sierra de Catorce, San Luis Potosí State and Rancho la Colgada, Sonora State, lower Tithonian: (1) ERNO 8031, right-lateral view, Rancho La Colgada, Sonora State, Cucurpe Formation, lower Tithonian (see Villaseñor et al., 2005); (2) USNM PAL 103295, right-lateral view, plaster cast (see Del Castillo and Aguilera, 1895, pl. 6, fig. 8); (3) McM-J1506/380 = IGM 2746, left-lateral view (see Verma and Westermann, 1973); (4) IGM 6292, right-lateral view (see Olóriz et al., 1999); (5, 6) from bed AL-5.6 in section Alamitos 5 (AL-5), San Luis Potosí, La Caja Formation, lower Tithonian; (5) IGM 4714, right-lateral, and (6) imprint views; (7) IGM 4713, right-lateral view. *Mazapilites?* sp., bed 6 in the section Alamitos 5 (AL-5), San Luis Potosí, La Caja Formation, lower Tithonian; (8) IGM 4715, fragment of body chamber. *Mazapilites symonensis*, Durango State (Peña-Muñoz, 1964), lower Tithonian; (9) IGM 7335, right-lateral view; (10) IGM 1216-1, left-lateral view of the nearly complete specimen. White dots mark last preserved suture lines; asterisks mark beginnings of the preserved body chambers. Scale bar = 1 cm. See text for interpretations.

Table 3. Measurements (in mm, rounded decimal figures) of *Mazapilites* spp. from various authors, as indicated, in chronological order for each species. Measurements of the new material obtained (two specimens) are added at the end of the table.

SPECIMEN	Dm	U	H	W	U/Dm	H/Dm	UR/2	ER/2	CI
<i>M. mexicanus</i>	85	9*	45	-	0.10	0.53	12	26	2.6
Del Castillo and Aguilera, 1895 pl. 7, fig. 1	55	6*	33	-	0.20	0.60	11	24	2.2
<i>M. mexicanus</i>	81.93	8.1*	45.64	19.65	0.99	0.56	11*	31	2.8
Del Castillo and Aguilera, 1895 plastotype, USNM PAL 103295	72.46	7.63*	36.57	17.94	0.10	0.50	7*	23*	-
<i>M. mexicanus</i>	85	9	50	-	0.10	0.59	12	27	2.4
Burckhardt, 1919–1921 pl. 3, fig. 2	62	7	35	-	0.11	0.56	12	23	2
<i>M. mexicanus</i>	81.5+	9.2	48.9	20.9*	0.11	0.60	11	27	2.5
Verma and Westermann, 1973 McM-J 1506/380 = IGM 2746	67.1	8.1	46.9	16.2	0.12	0.70	-	-	-
<i>M. mexicanus</i>	63.5+	6.8	34	17.2	0.11	0.53	8	28	2.7
Olóriz et al., 1999 IGM 6292	49.7	4.7	3.6	11.5	0.09	0.07	8	23	-
<i>M. mexicanus</i>	86+	8.8	53.5	-	0.10	0.62	12	25	-
Villaseñor et al., 2005 ERNO 8031	63.8	6	35	-	0.09	0.55	11	-	2.8
<i>M. zitteli</i>	63.5+	7.7	35.4	18.1	0.12	0.56	10	28	2.8
Burckhardt, 1906 IGM 245	49.2	7.5	21.7	-	0.15	0.44	10	25	2.5
<i>M. zitteli</i>	33.3/30+	6	17.8	10.5	0.18	0.53	10	22	2.2
Burckhardt, 1906 IGM 246	26.1	5.4	14.2	9.3	0.20	0.54	10	21	2.1*
<i>M. zitteli</i>	37.4+	5.7	20.4	12.8	0.15	0.54	9	16	1.7
Burckhardt, 1906 IGM 246a = 7168	30.5	5.3	19.1	12.7	0.17	0.63	9	14	1.6
<i>M. symonensis</i>	119.1	8.8	63.3	-	0.07	0.53	8	24	3.1
Burckhardt, 1919–1921 IGM 1563	94.7	8	50	-	0.08	0.53	10	33	3.3
<i>M. symonensis</i>	72.3+	7.2	39.6	-	0.01	0.55	10	25	2.5
Burckhardt, 1919–1921 IGM 1562	68.6+	8	39.3	20.5	0.12	0.57	11	28	2.6
<i>M. symonensis</i>	60.3	8	35	18.7	0.13	0.58	10	24	2.4
Burckhardt, 1919–1921 IGM 1562	38.8	4.5	-	-	0.12	-	-	-	-
<i>M. symonensis</i>	95	6.3	53.2	-	0.07	0.56	9	19	2.9
Peña-Muñoz, 1964 IGM 1216-1	83.9	5.9	53.3	-	0.07	0.63	12	31	2.5
<i>M. symonensis</i>	64.4+	5.5	40.1	-	0.08	0.62	12	28*	2.5
Burckhardt, 1919–1921 IGM 7335	38	5.8	18.4	-	0.15	0.48	8	19*	2.3
<i>M. symonensis</i>	31.5	5.6	15.7	-	0.18	0.50	9*	23*	2.3
Burckhardt, 1919–1921 IGM 7335	25.3	5.3	13.3	-	0.21	0.52	9	22	-
<i>M. crassicosatus</i>	72.5	9.1	41.2	-	0.12	0.57	10	19	1.9
Burckhardt, 1919–1921 IGM 2684	50.9+	8.9	26.7	16.7	0.17	0.52	10	17	1.7
<i>M. crassicosatus</i>	41.6	8.3	20.8	16	0.20	0.50	10	16	1.6
Burckhardt, 1919–1921 IGM 1564	49.8	7.5	29.1	-	0.15	0.58	9	21	2.2
<i>M. tobosensis</i>	40+	6.4	22.1	-	0.16	0.55	9	21	2.4
Burckhardt, 1919–1921 IGM 1564	32.8	6.1	12.2	-	0.19	0.37	10	22	2.2
<i>M. tobosensis</i>	42.2+	5.6	22.6	12.1	0.13	0.53	10	26	2.6
Burckhardt, 1919–1921 IGM 1567	31	5.2	18.1	9.8	0.17	0.58	10	24	2.4
<i>M. mexicanus</i>	25.1	4.5	14.6	8.5	0.18	0.58	13	24	1.8
Burckhardt, 1919–1921 IGM 4713 (AL-5.6.1M)	67	10	34.5	-	0.15	0.51	10	25*	2.5
<i>M. mexicanus</i>	54.8	7.2	30.4	-	0.13	0.55	9	19*	-
Burckhardt, 1919–1921 IGM 4714 (AL-5.6.2M)	61.8	6.9	35.2	-	0.11	0.57	8	22	2.6
<i>M. mexicanus</i>	39.5	6.6	20.4	-	0.17	0.51	8	22*	-

Abbreviations as in Table 1; + = phragmocone diameter.

(15.3) Ribbing was investigated in terms of the number of periumbilical or primary ribs per half whorl (UR/2), the number of external ribs per half whorl (ER/2), and the costal or ribbing index represented as the number of external ribs per 10 primary ribs (CI) (Fig. 11).

CI behavior (Fig. 11.1) is congruent with that shown by ER/2 (Fig. 11.2), even featuring deviations in the same two small phragmocones mentioned as exceptions for ER/2 curves.

ER/2 (Fig. 11.2) displays a general trend for increasing numbers of external ribs up to ~90 mm diameter, at which point sculpture smoothing is observed together with wider rib interspaces and a proliferation of lirae affecting body chambers in large shells (*M. symonensis*). Three exceptions are the small phragmocone (<40 mm) interpreted as *M. symonensis* by Peña-Muñoz (1964, pl. 1, fig. 2), the most probably the immature specimen of *M. crassicosatus* with crushed body chamber illustrated by Burckhardt (1919–1921, pl. 2, fig. 1), and an incomplete specimen

(<60 mm) interpreted as *M. mexicanus* collected by the authors from the AI-5 section (IGM 4714; Fig. 8.5, 8.6).

UR/2 (Fig. 11.3) illustrates the incidence of shell size in the number of primaries, which are especially strong in some nominal species and can show dense crowding of fine striations early during ontogeny (<30 mm). A rather constant number of primary ribs occurs in phragmocones between 30 and 60 mm (with only two rib fluctuations). A slight increase in variation in primary rib crowding is recorded between 60 and 90 mm (four rib fluctuations). There is a clear decrease in the number of primary ribs in larger shells, related to sculpture smoothing of adult body chambers (at present only known from *M. symonensis*). The overall intranomial species variability in the number of primary ribs is higher for *M. mexicanus* and *M. symonensis*, which are the two large-shelled *Mazapilites* species.

Based on a revision of available material interpreted as nominal species of the genus *Mazapilites* by various authors,

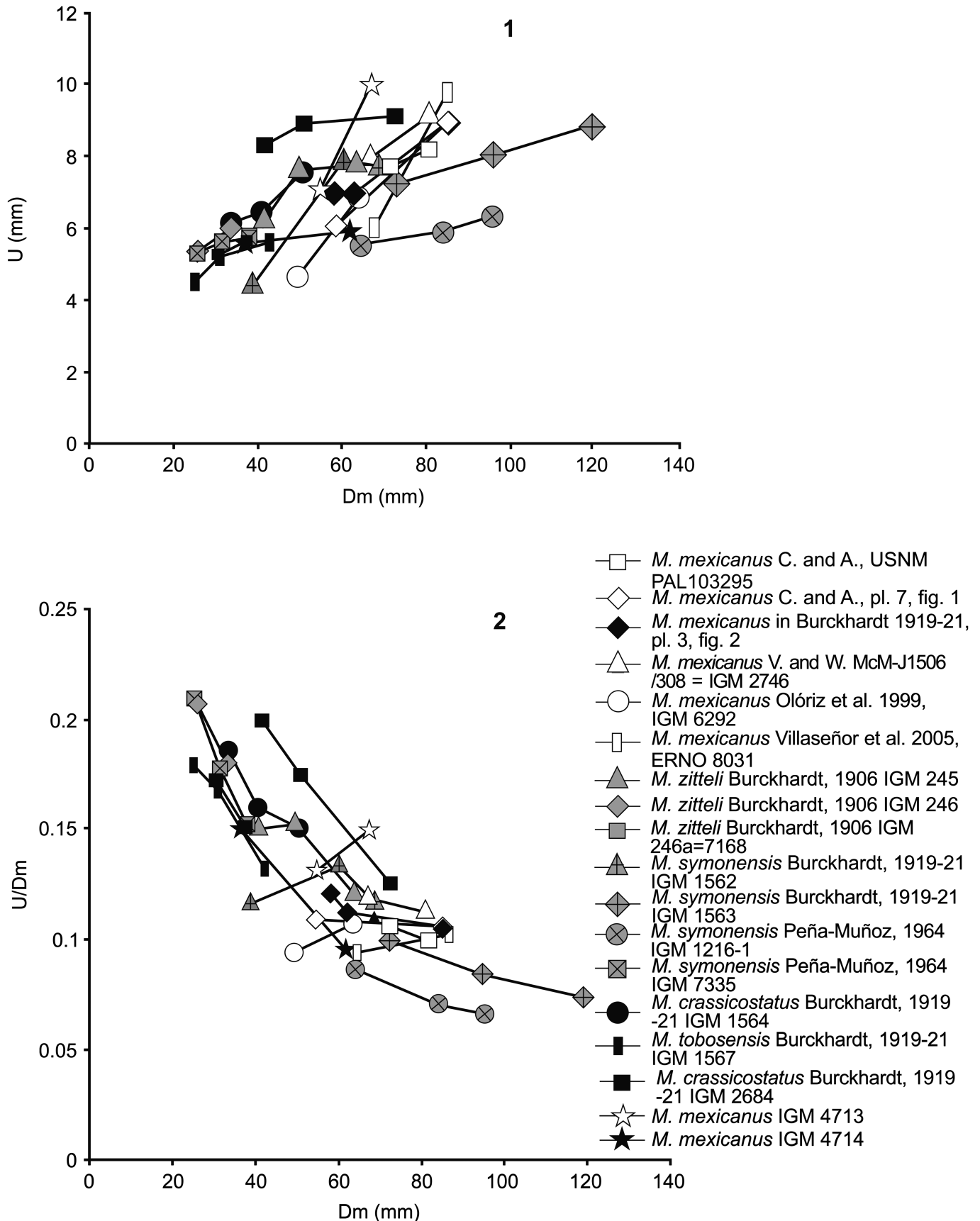


Figure 10. Bivariate plots of studied *Mazapilites*: (1) umbilicus (U) vs. shell diameter (Dm); (2) U/Dm ratio vs. shell diameter (Dm). C and A = Del Castillo and Aguilera, 1895; V and W = Verma and Westermann, 1973, from San Luis Potosí State, Sierra de Catorce, lower Tithonian. See text for explanation.

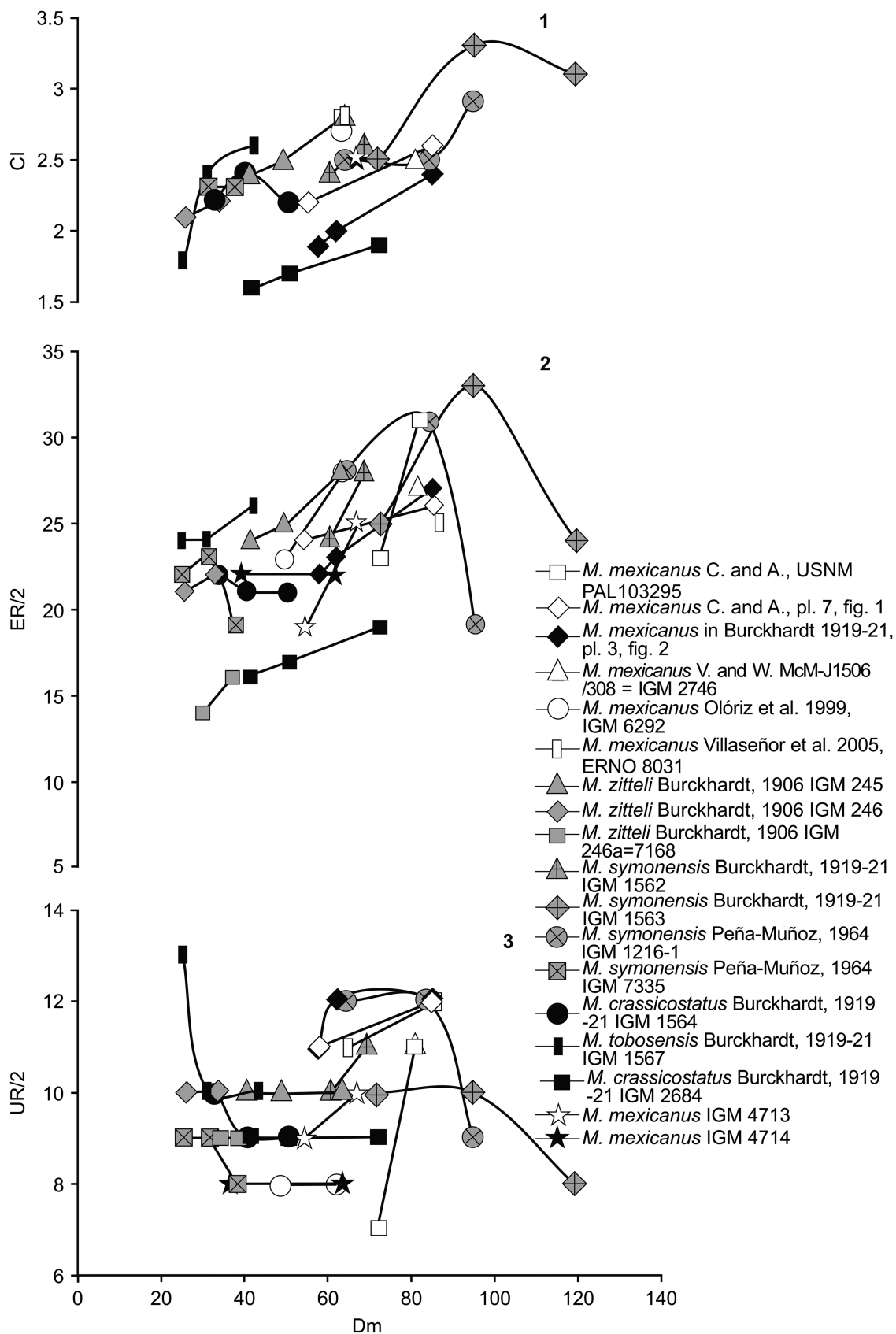


Figure 11. Ribbing curves and costal index of studied *Mazapilites*: (1) CI vs. Dm; (2) ER/2 vs. Dm; (3) UR/2 vs. Dm. Shell diameter (Dm) in millimeters. Abbreviations as in Figure 10. See text for explanation.

some traits can be outlined for an updated yet preliminary interpretation: (1) shell type, in terms of coiling and whorl section, is well established in *Mazapilites*; shell type variability and sculpture coarseness could be combined and interpreted at the intraspecies level with a reduction of nominal species; (2) the whorl section covaries with ribbing coarseness, showing coarser sculpture in wider shells (at the ventral area), resulting in a relatively high phenotype variability (e.g., Burckhardt, 1906, p. 2, 6); *M. mexicanus* could represent an intermediate case; (3) ventral ‘tricarination’ is essentially a constructional effect because no real ventrolateral tuberculation occurs (Fig. 9); (4) the sculptural pattern in *Mazapilites* is fairly constant in terms of rib crowding in phragmocones, however, variable inflexion of primary ribs at the midflank forcing connections with external ribs occurs and, therefore, the number of intercalatories has a rather unstable pattern (Figs. 7, 8); in fact, variation in ribbing within and among the nominal species is incompletely known; (5) a relatively large intraspecies variability was originally suggested for *M. zitteli*, the sole nominal species “trouvé dans les conches phosphoritiques rouges de la Sierra de Mazapil en grande abondance” (Burckhardt, 1906, p. 108, with 10 specimens illustrated on pl. 29 and 30 if pl. 29, fig. 15 is considered as a separate specimen from those shown in his figs. 16, 17); (6) a majority of nominal species of *Mazapilites* are known from phragmocones, and the interpretation of smaller ones is inconclusive; the lack of body chamber in larger specimens impedes evaluation of the potential relationship with specimens (adults) having preserved body chambers; (7) body-chamber preservation is rare, therefore, knowledge about ontogeny is inconclusive, with the exception of one of the existing nominal species; (8) specimens with body-chamber preservation are only known for Burckhardt’s species *M. crassicostatus* and *M. symonensis*, the former probably pertaining to immature specimens whereas the latter shows adult, mature specimens (Figs. 7.10, 8.10); (9) no precise stratigraphy is available for most of the records of *Mazapilites*; this suggests incomplete knowledge about the biostratigraphic ranges of the nominal species, and makes difficult any attempt to interpret potential evolutionary lineages; and (10) measurements of coiling and ribbing conducted on the available material of the Mexico-Caribbean endemic genus *Mazapilites* indicate that reinterpretation at the species level calls for a thorough revision based on new material collected bed-by-bed.

Discussion (with a chronological revision of previous reports of *Hybonoticeras* and *Mazapilites* from Mexico and Cuba, and updated interpretation of their co-occurrence)

On the whole, a major difficulty identified during this revision concerns the level of stratigraphic accuracy characterizing pioneer and relevant works in the area. The reference section at the Cañón del Toboso (Burckhardt, 1919–1921), which provided the original material on which the genus *Mazapilites* was erected, is a good example. Relevant information provided by Burckhardt (1919–1921) in his introductory chapter indicated the provenance of the studied material and the timing of publication. Later, revealing data were provided by Böse (1923), who showed interesting information on: (1) the provenance of Upper Jurassic

fossils from the Sierrita de Symón, and the publication context (Böse, 1923, p. 5, 6); (2) the use and meaning of stratigraphic terms such as ‘capa,’ ‘banco,’ and ‘horizonte,’ used in his field surveys and most probably revealing standard procedures among good field geologists and paleontologists (Böse, 1923, p. 19–26); and (3) the respective accuracy of the collection of Upper Jurassic fossils and field stratigraphy, to derive their potential influence in Burckhardt’s work (Böse, 1923, p. 63, 64). Finally, Burckhardt (1930, p. 55, 56, fig. 17) provided precise information on the origin of the first stratigraphic section known from the Cañón del Toboso at the Sierra de Symón (see earlier comments by Böse, 1923). As expected, differences in sampling strategies, the influences of the assumed scientific authority at the time, and other factors, determined interpretations until the last decade of the past century, and made precise biostratigraphic control and correlation difficult tasks. In the following text, we will attempt clarification.

The following revision of publications focused on the genera *Hybonoticeras* and *Mazapilites* collected by various authors in the Mexico-Caribbean area is presented chronologically according to their original interpretations. The corresponding reviews will follow the original interpretations in each of the contributions considered.

Unfortunately, reports of the genus *Hybonoticeras* from Cuba are comparatively recent (Myczyński, 1998; Pszczółkowski and Myczyński, 2010, p. 232), scarce, poorly preserved, and, therefore, barely illustrated (Myczyński, 1999, figs. 5.1, 5.2, 6; Pszczółkowski and Myczyński, 2010, fig. 17.1). Such a situation impedes a conclusive revision. The co-occurrence of *Hybonoticeras* with *Mazapilites* in Cuba has been not illustrated, although an *Hybonoticeras-Mazapilites* Biozone was first proposed by Myczyński (1999, fig. 3) for Sierra de los Órganos in western Cuba. These topics will be considered in the last two subsections.

The occurrence of Hybonoticeras in Mexico.—As early as 1906, Burckhardt (1906, p. 103–105) identified “*Waagenia* sp. ind. (plusieurs espèces),” the taxon name erected by Neumayr (1878) for the group of ‘hybonoten’ that he separated from the genus *Aspidoceras* Zittel, 1868, and which was subsequently replaced by the new taxon name *Hybonoticeras* proposed by Breistroffer (1947).

Concerning *Waagenia*, Burckhardt (1906, p. 103) noted “assez nombreux ... exemplaires ne permettent pas une détermination certaine, car on n’en peut pas apprécier les dimensions ni observer les cloisons.” Among the five specimens illustrated by Burckhardt (1906, pl. 27, figs. 1–5) as *Waagenia* sp. indet. from Mazapil, Zacatecas, a single specimen was considered identical to *W. harpephora* Neumayr in Fontannes, 1879 (Burckhardt, 1906, pl. 27, fig. 1). Numerous specimens were interpreted as close to *W. harpephora*, but only two were illustrated (Burckhardt, 1906, pl. 27, figs. 2, 3). A single specimen was interpreted as probably conspecific with *W. knopi* (see Burckhardt, 1906, pl. 27, fig. 5), and one as related to *W. beckeri* (see Burckhardt, 1906, pl. 27, fig. 4). All of the illustrated specimens were incomplete and/or small, and were preserved in siltstone. Burckhardt (1906, p. 178) correlated his “argiles à *Waagenia*” with the “calcaires à *Waagenia beckeri*” that he correctly identified with the “somet du Kimmeridgien” in southeastern France.

Revision of the types illustrated by Burckhardt (1906, p. 104, 105, pl. 27, figs. 1–5) indicates that on the basis of the illustrated material, the interpretation of *Waagenia* (= *Hybonoticerias*) was basically correct in reference to forms morphologically close to, or belonging to, the groups of *H. beckeri* (see Burckhardt, 1906, pl. 27, fig. 4; Fig. 12.4) and *H. harpephorum* (Neumayr, 1873) (sensu Neumayr, 1873 and Fontannes, 1879; Burckhardt, 1906, pl. 27, figs. 1–3; Fig. 12.1, 12.2, 12.5). More debatable is Burckhardt's interpretation of the specimen that he related to *H. knopi* (see Burckhardt, 1906, pl. 27, fig. 5; Fig. 12.3). Even assuming general correctness in Burckhardt's interpretations, morphological traits in the ammonites that he illustrated point to a more or less evident separation from the European types mentioned (local to regional effects?). Thus, Mexican specimens related to the group of *H. harpephorum*, rather than to Neumayr's type, show a greater frequency of bifurcations on the umbilical edge and of intercalatory ribs (including the specimen he envisaged as close to the *H. knopi* group), along with coarser and less rigid ribbing (Fig. 12.1–12.3, 12.5). The specimen that Burckhardt related to the group of *H. beckeri* shows a more evolute shell with more stiff, simple ribs on the inner whorls than in Neumayr's type, and on slightly later whorls, regular, coarse geminate (looped) ribs suggesting morphological relationships with *H. beckeri ornatum* (Spath, 1931) (or simply *H. ornatum*, depending on the preference of given authors), but lacking its typical, fine, irregular, geminate ribbing on the inner whorls. Therefore, the occurrence of a local variant of the group of *H. beckeri* sensu stricto is probable (Fig. 12.4). The age of the species cited is late to latest Kimmeridgian elsewhere in the world, but a conclusive interpretation of phenotypic differences with respect to the aforementioned European species will depend on new material collected bed-by-bed.

Burckhardt (1919–1921, p. 14, pl. 4, fig. 11; Fig. 12.6) described a single ammonite imprint from the Cañón del Toboso, Durango, as *Waagenia* sp., and suggested its close similarity with *Ammonites autharis*, the only one of the two species of hybonoticeratines erected by Oppel (1863) with a known lateral view. Burckhardt (1919–1921, p. 14, 15) emphasized the pattern of ribbing and tuberculation, as well as the rather irregular, sinuous, fine ribs preserved on the outer whorl. Burckhardt (1919–1921, p. 15, 61, 64, 65) furthermore indicated its provenance from the “capas inferiores con *Mazapilites*,” which he correlated with the base of his Portlandian, interpreted as equivalent to the “capas superiores de Crussol,” the “zona de la *Oppelia lithographica*,” and the “capas de Solnhofen” containing *A. autharis*. Because the Mexican specimen is lost, only the illustration can be analyzed.

A second isolated imprint collected at the Pico de Teyra, Zacatecas, was briefly commented on and illustrated by

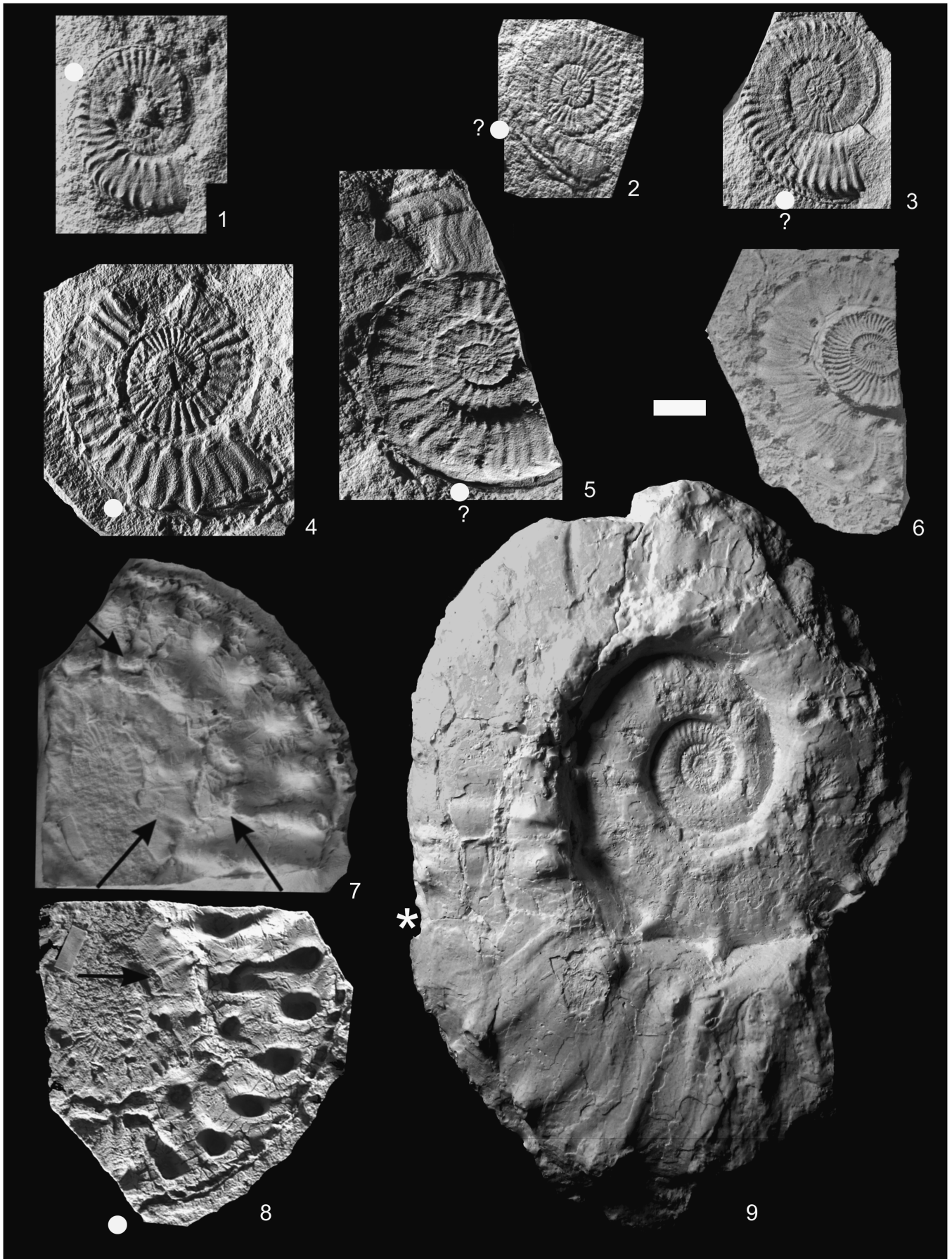
Burckhardt (1919–1921, footnote on p. 15, and pl. 4, fig. 12; Fig. 12.7, 12.8), yet he did not provide stratigraphic data or the precise section, and interpreted this record as “*Waagenia* cfr. *hybonota* Oppel sp.” Burckhardt (1919–1921) emphasized observations on the outer whorl, especially the occurrence of two rows of prominent tubercles linked by prominent ribs, which he interpreted as closely resembling forms illustrated by Oppel (1863, pl. 71, figs. 1–3), Benecke (1866, pl. 11, fig. 1), and Favre (1877, pl., 8, fig. 1). Subsequently, Burckhardt (1930, p. 69) simply referred to this record from the Pico de Teyra as gathered from the “couches a *Mazapilites*” without offering more precise comments about its provenance from a particular section.

Callomon (1992, p. 267) assumed Burckhardt's (1919–1921, p. 14, 15, pl. 4, fig. 11; Fig. 12.6) interpretation of one specimen as close to *Waagenia autharis*. Revision of Burckhardt's illustration shows that the sculpture on the inner whorls might be compatible with that seen in a young specimen of *Hybonoticerias autharis* illustrated by Oppel (1863, pl. 71, fig. 5), however, ribs in the Mexican type are subtly rursiradial (preservation effects?), whereas they are radial to slightly prorsiradial in the German specimen shown by Berckhemer and Hölder (1959; see also Zeiss, 2001). Moreover, the irregular, fine ribbing preserved on the outer whorl of the Mexican specimen is very different from that of *H. autharis* by Oppel (1863) and resembles *Hybonoticerias* of the *H. beckeri* group, especially if the looping of the ribs is real (e.g., just at the beginning, the middle, and the last part of the outer whorl in what appears entirely to be a phragmocone; Fig. 12.6). In such a case, updated age interpretation points to latest Kimmeridgian rather than Tithonian horizons.

Burckhardt (1919–1921, p. 64, 65) interpreted the “capas inferiores con *Mazapilites*” as the stratigraphic interval that provided his *Waagenia* sp. indet. (“cfr. *W. autharis* Oppel sp.”), but he did not provide the precise thickness of this interval or the relative location of this specimen. An early Tithonian age was assumed by Burckhardt (1919–1921, p. 65) for his *Waagenia*. The interpretation of this incomplete specimen is not conclusive at present and a latest Kimmeridgian age is rather favored.

The interpretation of *Waagenia* cf. *W. hybonota* by Burckhardt (1919–1921, p. 15, pl. 4, fig. 12; Fig. 12.7, 12.8) of the isolated imprint gathered at the Pico de Teyra casts doubts. Burckhardt (1919–1921) alluded to types illustrated by Oppel (1863), Benecke (1866), and Favre (1877). However, Oppel's illustrations of *Ammonites hybonotus* are not appropriate for comparison because they are exclusively ventral views; the Benecke type shows very different inner whorls; and the Favre type has no preserved inner whorls or suture lines. Revision of the imprint interpreted as “*Waagenia* cfr. *hybonota*

Figure 12. Macroconchiate *Hybonoticerias* from Burckhardt (1906, from Sierras de Mazapil and Santa Rosa, northern Zacatecas State, uppermost Kimmeridgian), Burckhardt (1919–1921, from Cañón del Toboso, eastern Durango State, most probably from horizons close to the Kimmeridgian-Tithonian boundary), and Imlay (1939, from the northern side of the Cañón del Toboso, Sierra del Chivo, eastern Durango State, most probably from the uppermost Kimmeridgian): (1) *Waagenia* sp., IGM 242, from Burckhardt (1906, pl. 27, fig. 2); (2) *W.* sp., IGM 281, from Burckhardt (1906, pl. 27, fig. 1); (3) *W.* sp., IGM 241, from Burckhardt (1906, pl. 27, fig. 5); (4) *W.* sp., IGM 240, from Burckhardt (1906, pl. 27, fig. 4); (5) *W.* sp., IGM 196, from Burckhardt (1906, pl. 27, fig. 3); (6) *W.* sp. indet. (lost specimen; reproduced from Burckhardt, 1919–1921, pl. 4, fig. 11); (7, 8) *W.* cf. *W. hybonota*, IGM 1707, from Burckhardt (1919–1921, pl. 4, fig. 12), plaster cast of the original imprint (7) and original imprint (8), black arrows indicate lumped ribs and the beginning of intertubercular ribs that could result in potential ‘quasi-V’ rib connections due to the higher number of outer tubercles; (9) *W. parrasensis*, plaster cast of UM 17623, from Imlay (1939, pl. 3, fig. 12). White dots indicate last preserved suture lines; asterisks mark beginnings of the preserved body chambers. Scale bar = 1 cm. See text for updated reinterpretation.



Oppel sp.” housed at the IGM (Fig. 12.7, 12.8) shows that: (1) it belongs entirely to the imprint of a phragmocone; (2) the first three whorls had simple, straight ribs; (3) small outer protuberances or tubercles could occur at < 10 mm, whereas small outer tubercles at 10 mm preceded the occurrence of inner tubercles on the umbilical edge; (4) there were looped ribs on the penultimate whorl of the specimen, and a structure compatible with the potential development of ‘quasi-V’ rib connections at the end of the outer whorl is preserved on the imprint, given the first occurrence of intertubercular ribs and the higher number of outer tubercles; (5) the keels were made of two rows of crowded, small, spiny, and rather oblique tubercles; and (6) no observations can be made about the ventral groove. If the comparisons made by Burckhardt (1919–1921) are suggestive of what today is interpreted as *Hybonoticeras pseudohybonotum* or other close forms, the features enumerated above discard this possibility, given the clear difference in the inner whorls of Burckhardt’s type with respect to Benecke’s and Vigh’s types. Furthermore, the near absence of well-preserved inner whorls in specimens recently interpreted as related to *H. pseudohybonotum* (e.g., Haberl et al., 1999; Zeiss, 2001) deserves attention when interpreting Vigh’s species. The combination of the early occurrence of looped ribs and later coarse tuberculation could support a relationship between the imprint described by Burckhardt (1919–1921) and the group of *H. beckeri extraspinum* Berckhemer and Hölder, 1959 (or simply *H. extraspinum*, according to some authors). However, crushing of the inner cast and the difficulty of precise observation of the preserved penultimate whorl and of the inner whorls, which are partially recovered or not preserved, limits interpretation of the actual separation of the umbilical tubercles from the line of whorl overlap. A reasonable interpretation within the present state of knowledge seems to be a form close to *H. sp. gr. H. beckeri extraspinum*. *Hybonoticeras interlaevigatum* Berckhemer, 1922 could be another close form, but this species is not well known from the illustrations of juveniles by Berckhemer (1922, pl. 1, fig. 15) and Berckhemer and Hölder (1959, fig. 16), the lectotype proposed by Zeiss (2001, p. 65; Berckhemer and Hölder, 1959, pl. 3, fig. 12), and the larger specimens illustrated by Schweigert et al. (1996, fig. 5d) and Schweigert (2000, pl. 2, fig. 4). Hence, a latest *H. beckeri* Chron age is favored against the earliest *H. hybonotum* Chron, and its provenance from horizons very close to the Kimmeridgian-Tithonian boundary could apply.

Burckhardt (1930) merely reproduced his previous interpretations about Mexican *Waagenia* (= *Hybonoticeras*), and no complementary revision applies.

Imlay (1937, p. 600–604) described four sections and mentioned six fossiliferous localities from La Casita Formation throughout the middle part of Sierra de Parras, Coahuila. No *Waagenia* species were cited in his fossiliferous localities (Imlay, 1937, p. 602, 603) nor in his *Waagenia* beds (Imlay, 1937, p. 604, table 3). Only his report of separate stratigraphic intervals for *Waagenia* and *Mazapilites* is relevant here.

Imlay (1939, p. 12) reported *Waagenia* sp. from Puerto Blanco, Sierra de Santa Rosa, associated with involute aspidoceratids that he identified as *Physodoceras* Hyatt, 1900. He suggested a youngest middle Kimmeridgian age, at the very top of the *Streblites tenuilobatus* Biozone, just below the *Aulacostephanus eudoxus-Neochetoceras sterspispis* Biozone (sensu Spath, 1933 in 1927–1933) that he used for correlation

(Imlay, 1939, p. 21, tables 1, 2). Moreover, Imlay (1939, p. 31, 32) erected *W. parrasensis* (Fig. 12.9) among the ammonites collected from concretions in the La Casita Formation at Sierra de Parras, Coahuila, without providing precise stratigraphic data about the section studied. He interpreted his single specimen as being close to *W. hybonota*, and referred to Oppel’s illustrations (Oppel, 1863, pl. 71, figs. 1–3). However, these illustrations only show ventral regions that have been the subjects of variable interpretations since Oppel’s times, including the most recent one by Zeiss (2001). Imlay (1939, p. 32) considered *W. beckeri* to be less closely related morphologically to the new Mexican species. Imlay (1939, table 10) placed his *W. parrasensis* at the top of his middle Kimmeridgian, just below the stratigraphic interval characterized by *Torquatisphinctes* Spath, 1924 and *Mazapilites*.

Examination of a cast of the type of *Waagenia parrasensis* (UM 17623; Fig. 12.9) is congruent with the original description, but also shows smoothed looping of the ribs on the adoral part of the preserved incomplete body chamber. This feature, plus those following, are relevant in an updated interpretation of a secondary, subordinate meaning of the Imlay type: (1) the differential development of tuberculation on the penultimate whorl, which shows spiny and well-developed external tubercles; (2) the fading of subtle ribs before reaching the shoulders; and (3) the wide umbilical wall severely affected by crushing in the preserved outer whorl. On this basis, and with the limits imposed by the unpreserved inner whorls of the holotype of *Hybonoticeras beckeri extraspinum* (see Berckhemer and Hölder, 1959, p. 30, pl. 4, fig. 17), the type of the subspecies erected by Berckhemer and Hölder (1959) is the morphologically closest macroconchiate *Hybonoticeras*, most probably revealing a lineage relationship. In contrast, a clear difference in sculpture exists between the inner whorls of Imlay’s type and those in the *H. extraspinum-interlaevigatum* group. Therefore, assuming age correlation for phenotype similarity among *Hybonoticeras* species from different areas, the envisaged morphological relationships among the types described by Imlay, Berckhemer and Hölder, and Berckhemer point to a late *beckeri* Chron age for *H. parrasensis* according to data retrieved from European sections (e.g., Berckhemer and Hölder, 1959; Olóriz, 1978; De Wever et al., 1986; Schweigert et al., 1996; Schweigert, 1998).

According to Imlay (1939, p. 22, 35), ammonites associated with his *Waagenia parrasensis* were *Torquatisphinctes?* aff. *T. diversecostatus* (Burckhardt, 1919) and *Subdichotomoceras?* sp. (Imlay, 1939, p. 22), or *Aulacosphinctoides?* (*Subdichotomoceras?*) sp. (Imlay, 1939, p. 35). The last was interpreted as an immature specimen of the large perisphinctids that Burckhardt (1919–1921) identified as *Perisphinctes* Waagen, 1869 and *P. (Aulacosphinctes)*, such as *P. alexii* Burckhardt, 1919 and *P. diversecostatus* (see Imlay, 1939, p. 22, 35), together with *Glochiceras* sp., *Aulacosphinctoides?* (*Subdichotomoceras?*) sp. and *Aulacosphinctoides* aff. *A. diversecostatus* (see Imlay, 1939, table 10). These identifications point to rather incomplete ammonites showing a more or less loosely coiled, ‘colubrinoïd’ shell and sculpture on the inner whorls, and simple, *Torquatisphinctes*-like ribbing in comparatively more globose, incomplete shells, thus being of no help in determining precise biostratigraphy.

Imlay (1943, p. 531, 532) provided a chart of “faunal divisions of northern Mexico,” including a *Waagenia* interval,

and reported many small specimens of *Waagenia* spp. collected from shales and sandstones in Placer de Guadalupe, eastern Chihuahua. He interpreted these records as identical to those illustrated by Burckhardt (1906, p. 103–105) as *Wagenia* sp., highlighting similarities with *W. harpephora*, *W. knopi*, and *W. beckeri*. Although Imlay (1943) maintained his previous biostratigraphic interpretations (Imlay, 1939), he noticed a significant increase in thickness between his beds with *Waagenia* and those containing ammonites that he identified as *Subplanites* Spath, 1925, *Virgatosphinctes* Uhlig, 1910, and *Kossmatia* Uhlig, 1910. Imlay (1943) did not provide illustrations of the *Waagenia* spp. collected in Placer de Guadalupe or data about other accompanying ammonites at locality 17254 sampled by the Texas Bureau of Economic Geology staff. Reinterpretation of the *Waagenia* spp. that Imlay (1943) reported without illustration from his locality 17254 in the Placer de Guadalupe district would be difficult. His report does not allow for precise age interpretations, and any attempt would be inconclusive because no information exists about associated ammonites. The information provided by Imlay (1943) can only be considered as occurrence data.

Imlay (1953, p. 50) reported *Waagenia* as the only ammonite genus collected from brownish shales including a limestone bed intercalated at the Vereda del Quemado section, Sierra de La Caja, north of Mazapil, Zacatecas. He considered the stratigraphic interval to be 30 m thick, and to represent his middle Kimmeridgian. Because Imlay (1953) did not mention species-level identifications or precise biostratigraphy, no precise, updated interpretation is available, and the information that he provided can only be considered as occurrence data. The same applies to that provided by Imlay (1965) who merely mentioned a biostratigraphic unit with *Hybonoticeras*.

Erben (1957: pl. 2) interpreted a correlation chart with a “faunal sequence in Mexico,” partially following previous stratigraphic correlations (Imlay, 1953, reported as 1952) and showing a *Waagenia* interval below a *Mazapilites* interval. These stratigraphic intervals were correlated with the biozone of *Gravesia gravesiana* (d’Orbigny, 1850) and *G. gigas* (Zieten, 1830) for the former, and with the stratigraphic interval defined by the total range of *Subplanites* sp.-*S. wheatleyensis*-*Pectinatites pectinatus*-*Pavlovia rotunda*-*Pavlovia pallasioides* for the latter. Updated interpretation indicates that the former stratigraphic interval basically corresponds to the lowermost Tithonian *hybonotum* Zone, whereas the latter embraces lower levels of the lower Tithonian up to the lowermost upper Tithonian and the lower middle Volgian according to authors (e.g., Verma and Westermann, 1973; Gerasimov et al., 1975; Zeiss, 2003; Rogov and Zakharov, 2009). Thus, the former stratigraphic interval refers to that typical for lower Tithonian hybonoticeratines, but in absence of paleontological descriptions, no interpretation at the species level, which is relevant for precise biostratigraphy, is possible. The information provided by Erben (1957) can only be considered as occurrence data.

Enay (1962) approached a general context for correlation of Mexican and European fauna based on a revision of the literature available at the time. Enay (1962, p. 364, table 4) used data compiled by Arkell (1956) to interpret a lower stratigraphic interval with *Hybonoticeras* in Mexico, for which he suggested a latest Kimmeridgian age corresponding to the *beckeri* Zone.

This interpretation was basically correct based on the information available at the time, and agrees, on the whole, with the results of the present revision.

Imlay (1980) mentioned *Hybonoticeras*, without illustration, from subsurface records of eastern and northeastern Tamaulipas, these probably being the most northeastern records reported from Mexico. They were indirectly interpreted as lowermost Tithonian (Imlay, 1980, p. 33), which agrees with his correlation charts (Imlay, 1980, figs. 16, 21) assuming the co-occurrence of the youngest *Hybonoticeras* and the oldest *Mazapilites* (with doubts for the Gulf of Mexico region and nearby areas; Imlay, 1980, fig. 21). As for the cases above, no biostratigraphic or species-level interpretations are available, and the information provided by Imlay (1980) can be considered only as occurrence data.

Imlay (1984, p. 10, fig. 6) interpreted the record of *Hybonoticeras* in northern and eastern Mexico as latest Kimmeridgian to earliest Tithonian in age, and placed below *Mazapilites*. In the absence of paleontological descriptions, this information can only be considered as occurrence data with basic mention of the relative stratigraphic, topological, position between these two genera.

Contreras et al. (1991) illustrated two macroconchiate specimens of *Hybonoticeras* within a compilation of Mexican ammonites sponsored by the Instituto Mexicano del Petróleo. These specimens, gathered from Aramberri, southeastern Nuevo León, and Los Alamitos, Sierra de Catorce, Zacatecas, were respectively interpreted as *H. (Hybonoticeras) beckeri* aff. *H. beckeri* and *H. (Hybonoticeras) beckeri* aff. *H. beckeri harpephorum*. In the absence of data about precise sections and stratigraphic horizons, they were interpreted to indicate the upper Kimmeridgian.

Examination of the illustrations by Contreras et al. (1991: RF-15 and Mc-5) shows two specimens interpreted as belonging to the *Hybonoticeras beckeri* group, indicating the upper Kimmeridgian. Without data about the precise section, stratigraphy, or potential body-chamber preservation, *H. (Hybonoticeras) beckeri* aff. *H. beckeri*, with provenance from Nuevo León, shows well-developed looping of rather strong ribs, and a narrow ventral groove. It is therefore better related to *H. (Hybonoticeras) beckeri ornatum*, or *H. (H.) ornatum* according to some authors, most probably as a local and coarsely ribbed variant. Lacking stratigraphic information as for the first specimen, *H. (Hybonoticeras) aff. H. beckeri harpephorum*, from Sierra de Catorce, Zacatecas, shows flattened flanks, rather rigid, rursiradiate ribs with strong, prorsiradiate inflexion on the shoulders, fine tuberculation on both the umbilical edge and the mentioned inflexion points, and a wide ventral groove delimited by two keels resulting from a small, oblique, acute serration. This fragmentary specimen, which in lateral view resembles some of Burckhardt’s *Waagenia* revised above (Fig. 12.1–12.3), most probably represents a new morphospecies related to the lineage of *H. harpephorum*, from which the most outstanding difference is the wide, shallow ventral groove (also see previous comments on *Waagenia* sp. illustrated by Burckhardt, 1906; Fig. 12.1–12.3). On the assumption of a phenotype-age correlation with European records of *Hybonoticeras*, a latest Kimmeridgian (uppermost *beckeri* Zone) is envisaged for the first specimen from Nuevo

León, and a latest Kimmeridgian to earliest Tithonian age could probably apply for the second recovered from Zacatecas, considering recent findings by the authors in Sierra de Catorce, Zacatecas (this paper and research in progress).

Callomon (1992) provided a new attempt at approaching a general context of correlation between Mexican and European faunas based on revisions of the available literature. Callomon (1992, p. 267, table 12.3) interpreted his M9 faunal horizon to represent the “beds with *Waagenia* of Mazapil and Symón” to be correlated with the *beckeri* Zone, but he recognized uncertainty in a more precise correlation due to the scarcity of data about associated ammonites.

The interpretation by Callomon (1992) of his M9 faunal horizon was basically correct, and he was especially right in highlighting doubts concerning reaching a precise biostratigraphic interpretation. Of particular interest is restricting the correlation potential of the “beds with *Waagenia* of Mazapil and Symón” to *beckeri* Zone horizons, because fossils indicating the lower part of the *beckeri* Zone have been not documented to date (Villaseñor et al., 2000, p. 251, fig. 2; 2012, p. 257, fig. 2). Callomon (1992, p. 267) interpreted that all the *Hybonoticer* figured from Symón (i.e., the Cañón del Toboso section, but restricted to illustrations by Burckhardt, 1906) seem to indicate the *beckeri* Zone. However, he (Callomon, 1992, p. 267) accepted the real occurrence in Mexico of *Hybonoticer* cf. *H. autharis* in his M11 faunal horizon “beds with *Waagenia* and *Mazapilites*” at Toboso based on data by Burckhardt (1919–1921, pl. 4, fig. 11). In this case, Callomon referred to *Hybonoticer* from the Cañón del Toboso section to propose correlation with an upper part of the *hybonotum* Zone in his table 12.3 (potential protraction of the top of M11 within the lowermost horizon of the *Semiformiceras darwini* Biozone would result from a drawing artifact?). He interpreted the microconch of *H. hybonotum* as *H. cf. H. autharis* (but see above for updated reinterpretation). Based on the envisaged occurrence of a single specimen of the assumed *H. cf. H. autharis*, a precise correlation of the M11 faunal horizon proposed by Callomon (1992, table 12.3) within the *hybonotum* Zone would be difficult.

Based on field surveys across north-central Mexico, Olóriz (1992, p. 104–105) interpreted a paleoenvironmental context of shallow to moderate water depths, 30–80 m, and fluctuating barrier effects related to bottom topography, marine currents, and water types to be common during the Late Jurassic in north-central and northeastern Mexico. He related the typical record of unbalanced ammonite assemblages dominated by one or two taxa as revealing moderate-to-strong Platform Effect conditions (Olóriz, 1986, 1988, 1990), which also resulted in variable degrees of endemism during *Hybonoticer* and *Mazapilites* times. Subsequent data based on bed-by-bed sampling support the paleoenvironmental and eco-evolutive scenario that Olóriz (1992) interpreted, even for *hybonoticer* ammonites (Olóriz and Villaseñor, 1999; Olóriz et al., 2000; Villaseñor et al., 2012).

Olóriz et al. (1993) reported and illustrated the first records of *Hybonoticer* registered bed-by-bed from Mexico. *Hybonoticer* (*Hybonoticer*) *beckeri harpephorum*, *Hybonoticer* (*Hybonoticer*) *beckeri extraspinum*, *Hybonoticer* sp. gr. *H. beckeri*, and *Hybonoticer* (*Hybonotella*) sp. were retrieved from transitional deposits between the La Caja and La

Casita formations at the Barranquito del Alacrán section, in the surroundings of Cuencamé, Durango. The *hybonoticer* collected were interpreted as latest Kimmeridgian to earliest Tithonian in age.

Revision of previous works indicates that this was the first attempt to approach a precise identification of the Kimmeridgian-Tithonian boundary based on bed-by-bed sampling of ammonites in Mexico. Olóriz et al. (1993) first reported uppermost Kimmeridgian *beckeri* Zone *Hybonoticer* collected bed-by-bed in Mexico, and used a single specimen of *Subplanitoides siliceum* (Quenstedt, 1857) recorded slightly above *Hybonoticer* sp. gr. *H. harpephorum* (= *Hybonoticer* sp. of Olóriz et al., 1993, pl. 2, fig. 1) to interpret the Kimmeridgian-Tithonian boundary. Lacking new contributions refining the Kimmeridgian-Tithonian boundary during the two previous decades (Cecca and Zeiss, 1994), Olóriz et al. (1993) interpreted this boundary following the available information and usual stratigraphic interpretations at the time (e.g., Hölder and Ziegler, 1959; Zeiss, 1968; Ohmert and Zeiss, 1980). The preliminary knowledge about phenotype characterization and precise ranges of *Hybonoticer* in Mexico, plus the limited information provided by associated perisphinctids and haploceratids, determined the use of the single specimen of *Subplanitoides siliceum* to correlate with the *Lithacoceras ulmense* Biozone and to interpret the base of the Tithonian (see citations above and compare the revised biozonation scales proposed by Hantzpergue et al., 1991, and Geysant and Enay, 1991). Existing information from Mexico at that time gave no records of *H. hybonotum* or *hybonoticer* belonging unequivocally to the *hybonotum* Zone from the section studied at the Barranquito del Alacrán, or elsewhere in the Mexican Altiplano. At the same time, and working on material gathered from southern Germany, Schweigert (1993) lent support to an older proposal of a *Subplanitoides siliceum* Subbiozone at the top of the *beckeri* Zone (e.g., Roll, 1931), although interpretations of *S. siliceum* as a lower Tithonian species persisted afterward (e.g., Schlegelmilch, 1994). Subsequently, Schweigert et al. (1996) maintained the proposal by Schweigert (1993), despite some doubts about the occurrence of *S. siliceum* homeomorphs or related forms in the uppermost Kimmeridgian (e.g., Geysant, 1997; Hantzpergue et al., 1997). More recently, German authors reinforced the proposal of the real occurrence of the *siliceum* Subzone at the top of the Kimmeridgian (Schweigert, 1998; Zeiss, 2001). In the event of confirmation of an uppermost subzone based on *S. siliceum*-like forms at the top of the Kimmeridgian, and in absence of new data from the same section, the Kimmeridgian-Tithonian boundary interpreted by Olóriz et al. (1993) at the Barranquito del Alacrán section could move up. Although data collected from this section thus far do not offer precision in this sense, a new horizon for the Kimmeridgian-Tithonian boundary placed above in this section is feasible according to new information regarding *Hybonoticer* collected bed-by-bed in other sections of the Mexican Altiplano (research in progress). Such an interpretation would reinforce the overwhelming dominance of records of uppermost Kimmeridgian *hybonoticer* in the Mexican Altiplano.

Olóriz and Villaseñor (1999) identified five new species of microconchiate *Hybonoticer* from sections investigated

bed-by-bed in the Mexican Altiplano. As is usual in Mexican sections, limitations related to preservation in siltstones, impoverished ammonite assemblages composed of incomplete specimens, and the lack of records of macroconchiate *H. hybonotum* and associated hybonoticeratines, impeded the precise interpretation of the Kimmeridgian-Tithonian boundary in the absence of other diagnostic ammonites. Hence, the biostratigraphic ranges of these new species were interpreted to embrace the uppermost Kimmeridgian and the lowermost Tithonian. New data recently obtained from these and other sections in the Mexican Altiplano confirm that at least two of the new species described, *H. aff. H. striatulum* Berckhemer and Hölder, 1959 [m] and *H. geminatum* Olóriz and Villaseñor, 1999 [m], seem to be restricted to the uppermost Kimmeridgian, upper *beckeri* Zone.

Olóriz et al. (2000) reported the first population-level study of microconchiate hybonoticeratines to compare European populations of *Hybonoticeras mundulum* (Opperl, 1865) [m] with Mexican ones retrieved from sections sampled bed-by-bed in the Durango and Zacatecas states. The collected material provided valuable information about local-regional intraspecific diversity and the possibility of relating differential phenotype trends to differences in paleoenvironmental contexts, as well as a means to approach the paleobiogeographic dynamics underlying those colonization events. At present, no new data have been obtained to reach a more accurate biostratigraphy for these ammonites in Mexico.

Zell et al. (2014) gave the last reported record of macroconchiate *Hybonoticeras* from Mexico since those illustrated by Olóriz et al. (1993). The specimens registered in a complex ‘coquinite’ (shell bed) containing marine invertebrates and vertebrates along with wood at the Sierra del Jabalí, Coahuila, were interpreted as *H. sp. gr. H. beckeri* of a latest Kimmeridgian age.

Examination of data presented by Zell et al. (2014) and plaster casts of their types indicates unfavorable preservation (see below), as could be expected from interpreted processes forcing the taphonomic condensation noticed by Zell et al. (2014, p. 102). Their interpretation as *Hybonoticeras sp. gr. H. beckeri* of a latest Kimmeridgian age is supported by the occurrence of looped ribs and chordate keels. Limited knowledge about complete perisphinctids of the same age in Mexico complicate the use of the ammonites illustrated by Zell et al. (2014) to assist in age interpretation of their *Hybonoticeras* specimens. Plaster casts of specimens CPC 1132, 1133, and 1134, illustrated by Zell et al. (2014, fig. 5.1–5.3), show severe crushing and dominance of very limited preservation, making their precise interpretation difficult. CPC 1132 has inner, distorted whorls with strong ribs and tubercles, some of which have spiny projections, and a ventral region with crowded, slightly oblique undulations bounding a narrow, deep groove (enhanced by severe crushing perpendicular to the plane of coiling?); unfortunately, only the left side of the shell is available for sculptural analysis, and the preserved outer whorl is eroded, showing a possible geminate rib at its adoral extreme. All of the traits recognized show a combination of features known in forms belonging mainly to the species group of *H. beckeri*, and secondarily to that of *H. knopi*. CPC 1133 looks similar to the specimen illustrated in situ by Zell et al. (2014, fig. 3.4), showing the opposite left-lateral view. It is poorly

preserved and partially covered by sediment but allows one to identify irregular, very strong ribbing and tuberculation, possible evidence of geminate ribs, zigzag connections, and forward projection of ribs on the shoulders with obscure connections to a chordate, barely preserved keel. This specimen could be related to the group of *H. ornatum* (or *H. beckeri ornatum*, according to some authors). CPC 1134 is the smallest and best-preserved incomplete specimen. Its exposed left side shows strong sculpture with geminate ribs, and a local adoral projection of ribs on the shoulders connecting to minute, oblique nodations, or crenulations, of a chordate and relatively prominent keel. All of these traits point to the group of *H. beckeri*. On the whole, analysis of these plaster casts opens the possibility for occurrence of new local, coarsely sculptured forms related to the group of *H. beckeri*, but better-preserved material is needed to be conclusive. Whatever the case, there is no evidence of lower Tithonian forms among the *Hybonoticeras* reported by Zell et al. (2014).

The occurrence of Mazapilites in Mexico.—According to the revision presented in the Systematic paleontology chapter, the following considerations especially focus on reports of geographic occurrences and stratigraphic interpretations according to authors.

Mazapilites is widely distributed from northwestern Mexico (Cucurpe, northern Sonora) to north-central Mexico (Sierra de Parras, Coahuila; Sierra del Chivo and Cañón del Toboso, eastern Durango; Sierras de Mazapil and Santa Rosa, northern Zacatecas; Sierra de Catorce, San Luis Potosí), northeastern Mexico (eastern Sierra Madre, westward from Ciudad Victoria, Tamaulipas, and east-northeastern Tamaulipas), central Mexico (Cuesta de Huasmazontla, Querétaro), eastern Mexico (Tamanzunchale, southeastern San Luis Potosí; eastern Puebla; Poza Rica, northern Veracruz); and southeastern Mexico (southern Veracruz; Campeche Shelf) (citations below).

Of the six ‘species’ included in *Mazapilites*, five erected by Burckhardt (1906, 1919–1921) and one other originally described as *Pulchellia mexicana* by Aguilera in Del Castillo and Aguilera (1895), *M. tobosensis* appears to be the one most frequently identified in Mexican sites. *Mazapilites tobosensis* has been reported from eastern Durango, southeastern San Luis Potosí and eastern Puebla (Burckhardt, 1919–1921; Imlay, 1939; Peña-Muñoz, 1964; Cantú-Chapa, 1971, 1984), followed by *M. symonensis* from eastern Durango and northern Zacatecas (Burckhardt, 1919–1921; Imlay, 1939; Peña-Muñoz, 1964; Villaseñor, 1991) and *M. mexicanus* from northern San Luis Potosí and northern Sonora (Del Castillo and Aguilera, 1895; Verma and Westermann, 1973; Olóriz et al., 1999; Villaseñor et al., 2005; this paper). *Mazapilites zitteli* (see Burckhardt, 1906, 1930; Imlay, 1937, 1953) is geographically restricted to separate areas, in a moderately large one in northern Zacatecas, Sierra de Parras, Coahuila (Imlay, 1937), and in western Tamaulipas. Burckhardt’s ‘species’ *M. carinatus* and *M. crassicosatus* are known only from a small sector in eastern Durango (Burckhardt, 1919–1921). *Mazapilites sp.* has been reported from across the entire geographic range of the genus in Mexico, including the submerged areas of the Campeche Shelf in southeastern Mexico (Cantú-Chapa and Ortuño-Maldonado, 2003).

Mazapilites was originally interpreted as representing the base of the Portlandian, in which Burckhardt (1919–1921, correlation chart between p. 71 and 72) included his “arcillas con *Waagenia*” recorded at the Mazapil region. Burckhardt (1930, table 10) interpreted the “couches à *Waagenia*” to be below the “couches à *Mazapilites*,” but included *Waagenia* in the lower part of the latter.

Imlay (1937, p. 603) cited *Mazapilites* sp. and *M.* cf. *M. zitteli*, together with *Katrolicerias* sp., *Idoceras?* sp., and *Belemnopsis* sp. from his fossiliferous locality 46 in La Casita deposits at Cañón del Órgano, Sierra de Parras, Coahuila, but no section was provided. This ammonite assemblage characterized his *Mazapilites* beds (Imlay, 1937, p. 604, table 3). Imlay (1943, p. 531) interpreted his “faunal divisions of northern Mexico” including a *Mazapilites* interval characterizing the upper Kimmeridgian sensu Spath (1933); he used *Mazapilites* just above an interval with *Waagenia* (= *Hybonoticerias*), but he did not describe *Mazapilites* from Placer de Guadalupe, Chihuahua. Imlay (1953, p. 49) reported *Mazapilites* from finely bedded sandstones, calcareous marls, and brownish sands belonging to the La Casita Formation, 4 km west of Huizachal, southwestern Tamaulipas. From the same 15 m thick stratigraphic interval, Imlay (1953, p. 49) mentioned ammonites that today would be interpreted to be late Tithonian, even early Berriasian in age—“*Kossmatia*, *Berriasella*, *Corongoceras*, *Micracanthoceras*, *Mazapilites* y *Aulacosphinctes*.” Imlay (1953, p. 50) identified *Mazapilites* and *Aspidoceras* from reddish phosphoritic limestones, 1.5 m thick, which were interpreted to represent his upper Kimmeridgian. Imlay (1953, p. 57) identified *Mazapilites* among other Kimmeridgian ammonites from the middle part of the Taman Formation, recorded as 500 m thick at the Valle del Río Moctezuma, southwestward from Tamazunchale, southeastern San Luis Potosí. In these three cases, no species-level interpretations or precise biostratigraphy were provided by Imlay (1953). Imlay (1965) interpreted *Mazapilites* as an endemic representative of the Pacific Realm (Imlay, 1965, p. 1024, fig. 1) and most probably endemic to the Gulf of Mexico region, although the latter was not clearly stated (Imlay, 1965, p. 1030–1032). Imlay (1965) assumed a middle to late Kimmeridgian age (sensu Arkell, 1956) for *Mazapilites* based on his previous interpretations.

Subsequent attempts to interpret the range of *Mazapilites* offer variable degrees of accuracy, and were rarely based on bed-by-bed sampling. More often, *Mazapilites* has been reported from horizons above those containing *Hybonoticerias*, but Olóriz et al. (1999) envisaged the lower boundary of the *Mazapilites* Biozone to be within the *hybonotum* Zone (see also Imlay and Jones, 1970; Imlay, 1980). Based on bed-by-bed sampling in Sierra de Catorce, San Luis Potosí, these authors recorded *Mazapilites* from stratigraphic horizons that Olóriz et al. (1999) considered to have equivalents within the *Virgatosisomoceras albertinum-Semiformiceras darwini* Biozone. Villaseñor et al. (2005) suggested equivalent horizons for its record in Sonora. Villaseñor et al. (2012) suggested a biostratigraphically undetermined, imprecise boundary between the biostratigraphic units characterized by *Hybonoticerias* and *Mazapilites* in Mexico.

The upper range of *Mazapilites* has been interpreted at several more or less precise levels within the lower Tithonian. Enay (1962, table 4) assumed the last occurrence of *Mazapilites*

to be clearly above of that of *Hybonoticerias*, at least within *Semiformiceras semiforme-Haploceras verruciferum* Biozone horizons, without eliminating uncertainty because elucidating the precise range of *Mazapilites* was out of focus. Subsequently, based on Burckhardt and Imlay’s works, Enay (1973) interpreted the youngest *Mazapilites* to be of late *albertinum-darwini* Chron, if correlation of the sub-Mediterranean *Franconites vimineus* Biozone with the Mediterranean standard of Zeiss (2003) is accepted. Cantú-Chapa (1971) and Verma and Westermann (1973) interpreted the uppermost *Mazapilites* to be upper lower Tithonian (three-fold division). Imlay (1980, fig. 16) added a question mark to the top of his unit with *Mazapilites*, which could be correlated with a major part of the *albertinum-darwini* Zone of the Mediterranean Tethys, except for its lowermost horizons and an indeterminate part of its younger levels.

Callomon (1992: 267) proposed his M12 faunal horizon with *Mazapilites* (“beds with *Mazapilites*”) above the last occurrence of *Hybonoticerias* in Mexico. He did not suggest stratigraphic continuity between these two biostratigraphic horizons, as was depicted in his table 12.3 without precise comments in text (Callomon, 1992, p. 267). Hence, the lower M12a faunal horizon of *M. symonenis* proposed by Callomon (1992) was correlated with a stratigraphic interval embracing the *albertinum-darwini* Zone except for a lower-middle part (thus, roughly equivalent to the epicontinental *vimineus* and *Danubisphinctes palatinus* biozones of the Secondary Standard Biochronostratigraphic Scale for the Mediterranean Province in the Tethyan Realm of Geysant, 1997, table 13, and to the *vimineus* Zone of Zeiss, 2003, fig. 5). The M12b faunal horizon with *M. zitteli* was correlated with the *semiforme-verruciferum* Zone except, perhaps, its lowermost and uppermost parts (thus, roughly equivalent to a lower, corresponding part of the epicontinental *Sublithacoceras penicillatum-Virgatosisomoceras rothpletzi* Biozone of Geysant, 1997, p. 100, table 13, and equivalent levels of Zeiss, 2003, p. 92, fig. 5). Highlighting limitations for precise biostratigraphic interpretations, Callomon (1992, p. 267) expressed uncertainty about the real stratigraphic order of his faunal horizons M12a and M12b. Given that the older M11 faunal horizon “beds with *Waagenia* and *Mazapilites*” of Callomon (1992, p. 267 = *H. autharis* M11 in table 12.3) was correlated with the upper-to-uppermost *hybonotum* Zone, this implies a stratigraphic range for *Mazapilites* beginning in lower Tithonian horizons below the top of the *hybonotum* Zone to the top of the *semiforme-verruciferum* Zone—i.e., levels within the lower-to-mid-lower Tithonian (two-fold division; Olóriz, 1978; Enay, 2009) or within the lower and lower-middle Tithonian (three-fold division; Geysant, 1997; Zeiss, 2003; Villaseñor et al., 2000, 2012).

Cantú-Chapa (2001, p. 9) suggested a *Mazapilites* event in Mexico that characterized the top of the lower Tithonian (two-fold division), thus indicating the youngest age assumed for the last *Mazapilites* species and, therefore, levels younger than previously considered by Cantú-Chapa (1971). Recent data obtained by the authors at Cañón de San Matias indicate the occurrence of *Mazapilites* in horizons equivalents to the M10 faunal horizon of Callomon (1992, p. 267, table 12.3), which ranges from stratigraphic horizons close to the Kimmeridgian-Tithonian boundary to a large part of the *hybonotum* Zone, according to the correlation proposed by Callomon (1992).

At present, it can be established that there are no conclusive data to interpret the precise biostratigraphic range of *Mazapilites* in Mexico. On the whole, *Mazapilites* biostratigraphy is poorly known due to information derived from very scarce, imprecise data provided by bed-by-bed sampling, together with geographically separate records without associated ammonites of interest for high-resolution biostratigraphy. Hence, new data collected bed-by-bed are needed to establish the precise stratigraphic range of *Mazapilites* in Mexico. Of special interest is the reinterpreted biostratigraphy that resulted from the previous revision of Burckhardt's *Waagenia* (= *Hybonoticeras*), because it opens the possibility of a latest Kimmeridgian age for the oldest *Mazapilites* in Mexico.

The co-occurrence of Hybonoticeras and Mazapilites in Mexico.—The analyses just presented for reinterpreting the reported and existing material of Mexican *Hybonoticeras* and *Mazapilites* have shown how distinct, and limited, the present knowledge is in terms of precise biostratigraphy and correlation potential, as well as the differential degree of uncertainty that applies to their taxonomic interpretation at the species level. According to the revision facilitated above, the co-occurrence of *Waagenia* (= *Hybonoticeras*) and *Mazapilites* in Mexico was based on a single imprint of *Waagenia* sp., interpreted by Burckhardt (1919–1921) as an indication of the base of his Portlandian (= lowermost Tithonian), without giving precise stratigraphy supporting his interpretation. Hence, the real co-occurrence of *Waagenia* and *Mazapilites*—i.e., collected from the same horizon—is doubtful if strictly based on the information provided by Burckhardt (1919–1921). Supporting this evaluation is the fact that all new species of *Mazapilites* erected by Burckhardt (1919 in 1919–1921, p. 4–11) were collected from his “capas superiores con *Mazapilites*,” and no single *Mazapilites* identified at the species level was reported from the “capas inferiores con *Mazapilites*,” in which *Waagenia* sp. was collected as a single imprint without additional stratigraphic detail. Thus, reference to material gathered from the “capas inferiores con *Mazapilites*” could indicate poor preservation, poor stratigraphy, loose specimens, or a combination of all factors.

In contrast to the inconclusive information provided by Burckhardt (1919–1921) about the co-occurrence of *Waagenia* and *Mazapilites*, Burckhardt (1930) gave comprehensive data both about records of *Waagenia* without *Mazapilites*, and vice versa. The alluded information agrees with: (1) his scheme of stratigraphic correlation for the Upper Jurassic in Mexico and southeastern France (Burckhardt, 1930, p. 64, table 5), in which he correlated the interval with *Waagenia* with the “Zone à *beckeri*,” and that corresponding to *Mazapilites* with the “Zone à *Oppelia lithographica* (couches de Solhofen)”; (2) the biostratigraphic synthesis for the Upper Jurassic in central and northern Mexico (Burckhardt, 1930, table 6); and (3) key fauna in his “faciès à Céphalopodes preponderant” in the synthesis about the main facies of the Mexican Jurassic (Burckhardt, 1930, table 9). On this basis, a reasonable assumption is that Burckhardt (1919–1921, 1930) envisaged, rather than demonstrated, the co-occurrence of *Waagenia* (= *Hybonoticeras*) and *Mazapilites*, which he supported with very limited and at present questionable data (see above comments about the data of Burckhardt, 1919–1921).

Imlay (1937, p. 604, table 3) clearly interpreted the record of *Waagenia* (*Waagenia* beds) below that of *Mazapilites* (*Mazapilites* beds) in Sierra de Parras, Coahuila, northeastern Mexico, but later (Imlay, 1939) added unclear information in evaluating the co-occurrence of *Waagenia* (= *Hybonoticeras*) and *Mazapilites* in Mexico. In fact, the difference between his text and the corresponding stratigraphic column and chart with the distribution of ammonites (Imlay, 1939, p. 10, 22, fig. 4, table 2) is clearly identifiable and, therefore, his contribution could include uncertainty. The relevance of this report of the co-occurrence of *Waagenia* (= *Hybonoticeras*) and *Mazapilites* in Mexico is that the stratigraphic interpretation made by Imlay (1939) for records considered below the *eudoxus-steraspis* Zone (see above) refers rather to the present upper Kimmeridgian *beckeri* Zone, which could indicate the occurrence of *Mazapilites* in the uppermost Kimmeridgian, thus dating its co-occurrence with *Hybonoticeras* of latest Kimmeridgian age.

Comparison of three correlation charts provided by Imlay (1965, fig. 6a; 1980, p. 32, fig. 21; 1984, p. 10, fig. 6) shows inconclusive information and changing interpretation on the co-occurrence of *Waagenia* (= *Hybonoticeras*) and *Mazapilites* in Mexico—in the first case, showing co-occurrence (Imlay, 1965, fig. 6a); then showing separate horizons (Imlay, 1980, p. 32) to support co-occurrence, based on data without illustrations by Imlay (1939, p. 10, 11), while showing co-occurrence with doubts (Imlay, 1980, fig. 21); and finally showing *Hybonoticeras* below *Mazapilites* with an allusion to different ages (early Tithonian and late early Tithonian, respectively), and without any mention of co-occurrence (Imlay, 1984, p. 10, fig. 6).

Attempts by other authors interpreting a potential co-occurrence of *Hybonoticeras* and *Mazapilites* in Mexico, without analyzing new data collected bed-by-bed, merely assumed Burckhardt's and/or Imlay's interpretations, which did not provide supporting illustrations. Thus, based on data by Arkell (1956), Enay (1962, p. 364, 365, table 4) interpreted the upper and wider stratigraphic interval of *Hybonoticeras* in Mexico to include a combined record of *Hybonoticeras* and *Mazapilites*, characterizing the older early Tithonian. Enay (1962, p. 365, table 4) assumed that “l'apparition du genre particulier *Mazapilites* (couches à *Hybonoticeras* et *Mazapilites*) marquerait, au Mexique, le début du Tithonique,” and gave precise indication of the European fauna used for correlation (Enay, 1962, table 4). Cantú-Chapa (1963, p. 16) assumed that “*Mazapilites* (Oppedidae caractéristique du Mexique) est très remarquable dans cette partie du Kimméridgien supérieur (ou Portlandien inférieur?) comprise entre la Zone à *beckeri* (limite inf.) et le Tithonique (limite sup.).” Enay (1963, p. 4) promoted his previous hypothesis of “au Mexique, l'assemblage *Hybonoticeras-Mazapilites* caractériserait la base du Tithonique.” Callomon (1992, p. 265, 267, table 12.3) approached the interpretation of ammonite horizons in Mexico as a discontinuous succession that he tentatively correlated with the European standard biostratigraphic scales; unfortunately, Callomon did not provide precise biostratigraphic comments for all of the ‘faunal horizons’ to support their correlation depicted in his table 12.3. His M11 faunal horizon, labeled *H. autharis* in a table (see Callomon, 1992, table 12.3), and “beds with *Waagenia* and *Mazapilites*” at Toboso, Sierra de Symón in text (Callomon, 1992, p. 267), assumed the

co-occurrence of *Waagenia* (= *Hybonotoceras*) and *Mazapilites*. Accordingly, a middle *hybonotum* Chron age would correspond to the oldest record of *Mazapilites* in Mexico (Callomon, 1992, table 12.3).

In contrast to the inconclusiveness of previous information, and the absence of the corresponding illustrations, a real case of co-occurrence of *Hybonotoceras* and *Mazapilites* in Mexico has been shown for the first time by recent bed-by-bed sampling in Sierra de Catorce, San Luis Potosí (AL-5 section; this paper). This co-occurrence is illustrated with ammonite records from horizons that can be correlated with a much lower, but not the lowermost, part of the *hybonotum* Zone in the secondary biostratigraphic scale for the Tithonian in Mediterranean and sub-Mediterranean Europe (e.g., Geysant, 1997). At present, the new information provided in this paper is limited and must be complemented with data from other sections investigated bed-by-bed in Mexico.

The occurrence of Mazapilites in Cuba.—*Mazapilites* has long been considered endemic to Mexico (e.g., Burckhardt, 1919–1921, p. 2, 65; 1930, p. 109; Cantú-Chapa, 1963, p. 16, 1979, p. 21; Enay, 1973, p. 300), typical among Upper Jurassic ammonite genera from the Gulf of Mexico region, and representative of the Pacific Realm (Imlay, 1965, p. 1030). *Mazapilites* was even considered to be a South American taxon by Berckhemer and Hölder (1959, p. 73), although Cantú-Chapa (2001, p. 9) cited Berckhemer and Hölder (1959) in envisaging the occurrence of *Mazapilites* in Germany as the single one identified outside from Mexico.

Houša and De la Nuez (1972, 1973) first proposed a *Mazapilites* Zone for western Cuba, and Houša and De la Nuez (1975, p. 57) characterized the oldest Tithonian horizon with “*Mazapilites*, *Protancyloceras*, *Pseudolissoceras*, *Physodoceras* etc.,” interpreting its correlation “approximately at the level of the Mexican upper Kimmeridgian.” Records of *Mazapilites* were subsequently reported and illustrated from Sierra de los Órganos in western Cuba by Myczyński (1989, p. 53, 92), who interpreted the occurrence of *M. zitteli* (see Myczyński, 1989, pl. 2, figs. 1–3, 5). This author reported *Mazapilites* sp., *Protancyloceras* aff. *P. gracile* (Oppel, 1865), *Neochetoceras* sp., and *Lithacoceras* (?), among other ammonites with minor relevance for biostratigraphy, from an interval 2.5–3 m thick in the lower part of the El Americano Member. This ammonite assemblage would most likely indicate lowermost horizons within the Tithonian. Myczyński (1989, p. 93) reported *M. zitteli* and *M. sp.* from the lower part of the El Americano Member in sections B and C of the Hacienda el Americano. Unfavorable preservation complicates the interpretation of *M. sp.* (Myczyński, 1989, pl. 2, fig. 4, pl. 5, fig. 7) recovered from the lower part of the El Americano Member. Myczyński (1989, p. 56) reported *M. zitteli* with *Pseudolissoceras zitteli* (Burckhardt, 1903), among other ammonites, from a 6 m thick stratigraphic interval in section C at Hacienda el Americano, mentioning the possibility of their provenance from slightly different horizons (Myczyński, 1989, fig. 6). The latter can be confirmed by the record of *P. zitteli* as being identified “slightly above the *Mazapilites* Zone” (Myczyński, 1989, p. 85). Limited preservation impedes analysis of the illustrations of *P. zitteli* provided by Myczyński, except for the specimen

collected at the Loma Ferretero section, LF, in Sierra del Rosario (Myczyński, 1989, pl. 10, fig. 4b). Myczyński (1989, p. 67, footnote 2) indicated that “the genus *Mazapilites* in Cuba seems to represent a zone younger than the Mexican *Hybonotoceras* Biozone, as it is concurrent in Cuba not with *Hybonotoceras*, but with *Protancyloceras*, whence *Pseudolissoceras* is present too.” Pszczołkowski and Myczyński (2003, and references therein) reported, without illustration, *Mazapilites* spp. from Guaniguanico sections in western Cuba, and *M. symonensis* “?” from the Camajuani Belt in central Cuba.

Despite being of indubitable value, Cuban data for *Mazapilites* cannot support precise biostratigraphic interpretation and correlation, as shown below.

Summary remarks on the co-occurrence of Hybonotoceras and Mazapilites in the Mexico-Caribbean area.—Co-occurrence of *Hybonotoceras* and *Mazapilites* has been proposed for both Mexico and Cuba, and their confirmation would be of interest for interpreting the underlying paleobiogeographic dynamics if precise biostratigraphy were available.

Burckhardt (1919–1921) reported the co-occurrence of *Waagenia* (= *Hybonotoceras*) and *Mazapilites* within the lower range of the latter (“*capas inferiores con Mazapilites*”) in the Mexican Altiplano. However, the absence of detailed sections with reference to particular beds and the precise thickness at which these genera were recorded makes any approach for obtaining biostratigraphic details inconclusive according to the demands of present-day biostratigraphy. Burckhardt (1919–1921, p. 64) considered a 20 m thick section for the complete stratigraphic interval with *Mazapilites*: 17 m were poor in fossils, and the remaining 3 m would contain the “*capas inferiores con Mazapilites*” at the bottom, and the “*capas superiores con Mazapilites*” at the top, but without specifying the respective thicknesses of these ‘beds.’

Burckhardt (1930, p. 45–165) provided summarized data and conclusions from his 25 years of research on the Upper Jurassic in Mexico. This author clearly placed his “*argiles à Waagenia*” below the “*couches à Mazapilites*,” but supported co-occurrence of these genera in the Sierra de Santa Rosa, Mazapil, Zacatecas (Burckhardt, 1930, p. 68, table 6), and in the Sierras de Symón and Ramirez, Zacatecas-Durango (Burckhardt, 1930, p. 56, fig. 17, table 6). The former case refers to the “*couches à Mazapilites ... probablement représentées par la partie supérieur des ‘argiles à Waagenia’*” (Burckhardt, 1930, p. 68). The second evokes two imprints obtained in 1919—that of *W. sp. indet.* (“*cfr. W. autharis* Oppel sp.”) collected from the mentioned “*capas inferiores con Mazapilites*” at the Cañón del Toboso (Burckhardt, 1919–1921, p. 64; see above), and reported as “*Waagenia cfr. autharis*” by Burckhardt (1930, p. 69), and another isolated record found at the Pico de Teyra (Burckhardt, 1930, p. 69) and interpreted to come from the same “*capas inferiores con Mazapilites*” without reference to precise section and biostratigraphy.

Imlay (1937, table 3; 1939, table 2) clearly identified two consecutive stratigraphic intervals, a lower one with *Waagenia* (= *Hybonotoceras*) and an upper one with *Mazapilites*. Imlay (1939) referred to the latter as a common stratigraphic interval in the upper Kimmeridgian that he correlated with the lower part of

the *eudoxus-steraspis* Zone of Spath (1933, as cited by Imlay, 1939, table 1). From the northern side of the Cañón del Toboso, Sierra del Chivo, Imlay (1939, p. 10, 22, table 6) reported the co-occurrence of *W. sp.* (then *Waagenia*, and finally *W. cf. W. autharis*), *Mazapilites sp.*, and *Torquatisphinctes sp.* from gray shales (coll. 18 of Imlay, 1939), although he indicated a separate lower horizon for *W. sp.* in the corresponding stratigraphic column (Imlay, 1939, fig. 4). As was the case for previous reports of co-occurring *Waagenia* (= *Hybonotoceras*) and *Mazapilites* in Mexico, this author did not provide illustrations of the specimens of *Waagenia* and *Mazapilites* recorded at the Cañón del Toboso section.

Imlay (1943, p. 531) interpreted his “faunal divisions of northern Mexico” with a *Waagenia* interval below the *Mazapilites* interval (see above).

Imlay (1965, table 6a) assumed a limited overlap of *Hybonotoceras* and *Mazapilites* with no additional comments, because his text was focused on faunal differentiation and potential forcing factors. *Mazapilites* and other Upper Jurassic genera from Mexico and Cuba were suggested as representatives of the Pacific Realm that he accepted following Arkell (1956) and not related to latitude (Imlay, 1965, p. 1024).

Imlay and Jones (1970, fig. 2) used a correlation chart showing a small stratigraphic interval with *Hybonotoceras* and *Mazapilites*, but they did not comment on these genera.

Enay (1973, table 1) envisaged a limited overlap of the ranges of *Mazapilites* and *Hybonotoceras* based on the contributions by Burckhardt and Imlay, without specification (Enay, 1973, p. 306, noting the omission of publications cited by Arkell, 1956), but he did not consider the occurrence of *Mazapilites* outside of Mexico.

Imlay (1980, p. 32) alluded to his previous data (Imlay, 1939, p. 10, 22) on the co-occurrence of *Waagenia* (= *Hybonotoceras*) and *Mazapilites* in the Cañón del Toboso, Sierra del Chivo, Durango. Imlay (1980, figs. 16, 21) assumed the possibility of the youngest records of *Hybonotoceras* overlapping the earliest ones of *Mazapilites* and the so-called *Virgatosphinctes* and *Subdichotomoceras* Spath, 1925 in Mexico, as well as the earliest record of *Mazapilites* with *V. aguilari* (Burckhardt, 1906) in the Gulf of Mexico region and surrounding areas. Imlay (1984, p. 10, fig. 6) interpreted the record of *Hybonotoceras* in northern and eastern Mexico to be of latest Kimmeridgian to earliest Tithonian in age, and to occur below *Mazapilites* of late-early Tithonian age, without mention of the potential co-occurrence that he had previously assumed.

Houša and De la Nuez (1972, 1973) first characterized a stratigraphic interval with *Mazapilites* in Cuba (the oldest Tithonian ammonite horizon of Houša and De la Nuez, 1975). Subsequently, Myczyński (1989, p. 67, footnote 2), without records of *Hybonotoceras* in Cuba, envisaged the records of Cuban *Mazapilites* to be younger than those of *Hybonotoceras* in Mexico. Pszczółkowski and Myczyński (2010, fig. 18) reported the co-occurrence of *H. spp.* and *M. zitteli* throughout the lower part of the range of the latter in Cuba. Crucial information came from earlier research: Myczyński (1998; also mentioned by Pszczółkowski and Myczyński, 2010, p. 232) first reported *Hybonotoceras* from Cuba. Myczyński (1998, p. 114) mentioned two specimens of *H. (Hybonotoceras) sp. gr. H. beckeri* ~1.60 m above *Mazapilites* from the El Americano Member of the Guasasa Formation at the lowermost Hacienda El

Americano section in Sierra de los Órganos, as well as one specimen of *H. sp.* ~120 cm in diameter, and several specimens of *H. (Hybonotella) cf. H. mundulum striatulum*, from the La Zarza Member of the Artemisa Formation at the La Catalina section in western Sierra del Rosario. Myczyński (1999, p. 103–106) described and illustrated macro- and microconchiate *Hybonotoceras* from Cuba (most probably those reported by Myczyński, 1998), and proposed a lowermost Tithonian *Hybonotoceras-Mazapilites* Zone for Sierra de los Órganos, whereas the lower boundary of the *Hybonotoceras (Hybonotella)* Biozone in Sierra del Rosario was considered uncertain. Myczyński (1999, fig. 5.1, 5.2) described and illustrated *H. (Hybonotoceras) sp. gr. H. beckeri* from El Americano section at Sierra de los Órganos, and *H. (Hybonotella) cf. H. mundulum striatulum* from La Catalina section in Sierra del Rosario. Poor preservation limited their interpretation at the species and subspecies level, respectively (Myczyński, 1999, p. 103, 105). The specimen of *H. (Hybonotoceras) sp. gr. H. beckeri* reported from the El Americano section is difficult to interpret from its illustration. According to the description provided by Myczyński (1999, p. 103, 105), showing dominant simple ribs at ~80 mm shell diameter, this specimen corresponds to *Hybonotoceras harpephorum* or to a local related form, the age of which could be latest Kimmeridgian rather than earliest Tithonian, but preservation impedes a conclusive interpretation. In the absence of clear records of upper Kimmeridgian or lower Tithonian macroconchiate hybonoceratines (see below), age uncertainty could be unsolvable in this case. Given that this specimen was collected 1.6 m above *Mazapilites* (Myczyński, 1999, p. 96), confirmation of a sound age reinterpretation is relevant for reinterpreting the older biostratigraphic range of *Mazapilites* in the area, and the lowermost Tithonian horizon recorded in Cuba. In fact, Myczyński (1999) correctly used age interpretations accepted at the time to reveal uncertainty about discrimination of an upper Kimmeridgian from a lowermost Tithonian interval based exclusively on the *Hybonotoceras* specimens that he described. Therefore, he used the occurrence of *Mazapilites* to interpret a lower Tithonian age (e.g., Myczyński, 1989) for his *H. (Hybonotoceras) sp. gr. H. beckeri* from El Americano section, while correctly interpreting a Late Kimmeridgian to earliest Tithonian age for the known record of *H. (Hybonotella) cf. H. mundulum striatulum* from La Catalina section (Myczyński, 1999, p. 96, 105). Hence, lowermost *hybonotum* Zone horizons were envisaged but not demonstrated by the record of clear *hybonotum* Zone hybonotoceratines and/or other ammonites with potential, reliable biostratigraphic correlation outside Cuba.

Pszczółkowski and Myczyński (2010, p. 232) reported macro- and microconchiate *Hybonotoceras* from the southern Rosario succession: *H. (Hybonotoceras) sp.* and *H. (Hybonotella) cf. H. mundulum striatulum* from the La Catalina section, without illustration (probably referring to the specimen described and illustrated by Myczyński, 1999, figs. 5.2, 6). Pszczółkowski and Myczyński (2010, p. 232) also mentioned *H. (Hybonotella) gr. mundulum striatulum*, and *H. gr. mundula striatula* (Pszczółkowski and Myczyński, 2010, p. 241, fig. 17), which was identified from partly recrystallized remains, 5–6 mm in size, in microfacies from the Loma Redonda section (Pszczółkowski and Myczyński, 2010, fig. 17.1). Pszczółkowski and Myczyński (2010, p. 238, 239, fig. 2) confirmed the *Hybonotoceras-Mazapilites* Zone for

western Cuba, the bottom of which coincided with the drowning of carbonate shelves and could be correlated with a relevant occurrence of mazapilitines on inner shelves (Pszczółkowski and Myczyński, 2010, fig. 21).

Unfortunately, illustrations of Cuban *Hybonotoceras* and *Mazapilites* are too limited for an in-depth evaluation of their precise biostratigraphic significance.

In the context of this revision, the oldest records of *Mazapilites* could belong to the uppermost Kimmeridgian in the Mexico-Caribbean area according to revised data by Burckhardt (1919–1921), Imlay (1939), and Myczyński (1999), and, therefore, the stratigraphic range of its co-occurrence with *Hybonotoceras* would embrace, at least, stratigraphic horizons from the uppermost Kimmeridgian, upper *beckeri* Zone (e.g., Imlay, 1939, without illustration) to the lower Tithonian, lower *hybonotum* Zone (this paper, with illustration). New data collected bed-by-bed are needed to establish the precise stratigraphic location of the upper range of *Mazapilites*.

Conclusions

A thorough bibliographic revision has revealed how present-day biohorizon biostratigraphy clashes with the stratigraphic accuracy that characterizes relevant pioneer works. Differences in sampling strategy, scientific authority, and other factors have conditioned interpretations over time, making precise biostratigraphic control, interpretation, and correlation difficult tasks today. New data obtained from sampling bed-by-bed have led to revision of some keystones of Upper Jurassic biostratigraphy in the Mexico-Caribbean area, in this case paying special attention to improving the approach to the Kimmeridgian-Tithonian boundary.

The *hybonotum* Zone pro parte is clearly identified in Mexico for the first time based on hybonoticeratin ammonites, with illustration of macroconchiate *Hybonotoceras* collected bed-by-bed from Sierra de Catorce, San Luis Potosí.

Hybonotoceras authariformis n. sp. [M] designates the oldest Tithonian horizon identified in Mexico. Macroconchiate *Hybonotoceras* species interpreted as indicating the basal Tithonian in epicontinental Europe are recorded from the same horizon containing *H. authariformis* n. sp. [M] in the section investigated, in the surroundings of Alamitos de los Díaz, San Luis Potosí, México, and below horizons with forms closer to *H. hybonotum*.

Reported records of *Hybonotoceras* from Mexico are revised, with special attention paid to macroconchiate specimens. Upper *beckeri* Zone hybonoticeratines are well itemized, whereas the record of unequivocal *hybonotum* Zone hybonoticeratines has remains elusive.

Phenotype deviation and cases of endemism identified among Mexican hybonoticeratines open new ways to interpret *Hybonotoceras* as a well-known colonizer of epicontinental shelves during the highest sea levels in Jurassic times. The paleoenvironmental reconstruction proposed will assist future research, which must be focused on population levels and the meaning of endemism, and which must be based on data recovered bed-by-bed elsewhere, before proposing a conclusive interpretation about the records of hybonoticeratines from distant areas.

This revision of the existing material of *Mazapilites* reveals limitations for an updated interpretation of the nominal species included in this genus. Uncertainty persists about intraspecific diversity and the potential relationships among the existing nominal species described from Mexico, and no precise stratigraphy is available at this level. New material collected bed-by-bed, featuring the preservation of adult body chambers, is necessary to put forth a more conclusive interpretation of this genus.

In contrast to common interpretations, the first occurrence of *Mazapilites* in the Mexico-Caribbean area could belong to the uppermost Kimmeridgian, upper *beckeri* Zone horizons, but new material based on bed-by-bed sampling is needed to be conclusive. At present, no conclusive data exist on the last occurrence of *Mazapilites*.

The co-occurrence of *Hybonotoceras* and *Mazapilites* in Mexico is illustrated for the first time by material gathered from horizons belonging to the lower Tithonian, lower but not lowermost *hybonotum* Zone, slightly above the oldest Tithonian horizon identified by the record of macroconchiate *Hybonotoceras*. Previous interpretations of this co-occurrence were not demonstrated but rather envisaged from records reported without precise stratigraphy nor illustration, except for a single report without illustration gathered from interpreted late Kimmeridgian deposits in Mexico (Imlay, 1939). On this basis, the co-occurrence of *Hybonotoceras* and *Mazapilites* in Mexico would embrace, at least, uppermost Kimmeridgian (upper *beckeri* Zone) and lower Tithonian (lower *hybonotum* Zone) horizons.

Existing information about hybonoticeratines and mazapilitines from Cuba is limited and cannot be conclusively interpreted, and their co-occurrence cannot be demonstrated. However, the revision of Myczyński (1999) suggests the potential occurrence of *Mazapilites* in upper Kimmeridgian horizons in Cuba, paralleling that reported from Mexico, and reinforces the possibility of combined occurrence with *Hybonotoceras* in the future.

At present, evaluation of the oldest co-occurrence of *Hybonotoceras* and *Mazapilites* in Mexico-Caribbean areas remains an open question in terms of precise biohorizon biostratigraphy. The results obtained here improve upon previous knowledge on the records of *Hybonotoceras* and *Mazapilites* in Mexico-Caribbean areas, providing biostratigraphic precision in the interpreted range of macroconchiate *Hybonotoceras*, and favoring precision in long-distance correlations.

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