Re-evaluation of *Procraspedites* SPATH, 1930 (Ammonitina) from the Upper Kimmeridgian of Mexico

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Key words. - Ammonitina, Upper Jurasssic, Mexico.

Abstract. - Procraspedites from the Mexican Altiplano, studied with precise stratigraphic control, are coeval with the horizons rich in Glochiceras (Coryceras) carinatum [Del Castillo and Aguilera, 1895]. The interval with Procraspedites is dated as Eudoxus Chron (p.p.) of the Submediterranean late Kimmeridgian. The presence of parabolic structures on the inner whorls, followed by double furcations in *Procraspedites*, indicates Ataxioceratinae. The type species *Procraspedites praecursor* [Burckhardt, 1906] is interpreted to be the only valid species of this genus in the Americas.

Réinterprétation du genre Procraspedites SPATH, 1930 (Ammonitina) dans le Kimméridgien supérieur du Mexique

Mots clés. - Ammonitina, Jurassique supérieur, Mexique.

Résumé. - L'analyse stratigraphique détaillée dans l'Altiplano mexicain, montre que la répartition biostratigraphique du genre Procraspedites coïncide avec les niveaux riches en *Glochiceras (Coryceras) carinatum* [Del Castillo and Aguilera, 1895]. Cet intervalle est daté de la zone à Eudoxus (p.p.) du Kimméridgien supérieur subméditerranéen. La présence de structures paraboliques sur les tours internes et la différenciation ultérieure de côtes subpolyplocoïdes, indiquent que le genre *Procraspedites* appartient à la sous-famille des Ataxioceratinae. L'espèce-type *Procraspedites praecursor* [Burckhardt, 1906] reste la seule espèce valide de ce genre en Amérique.

VERSION FRANÇAISE ABRÉGÉE

Le genre Procraspedites est un taxon peu fréquent, et assez connu au Mexique. Sur les vingt citations présentes en Amérique [Burckhardt, 1906, 1930; Imlay, 1939; Cantú-Chapa, 1970; Imlay et Herman, 1984; Araujo et Casar, 1987; Schumann, 1988; Villaseñor et González-Arreola, 1988; Villaseñor, 1991; Michalzik et Schumann, 1994], seuls huit individus sont illustrés; l'un d'entre-eux provenant du Sud de Texas (USA). Selon Verma et Westermann [1984], ce genre se trouve également dans le Tithonien inférieur de Mombassa (Kenya).

Le genre Procraspedites est créé par Spath [1930] qui le place dans la famille des Idoceratidae, mais sa définition originelle brève laissait la possibilité pour des attributions aux involuticeratidés [Salfeld, 1917; Imlay, 1939, 1943], aux ataxioceratidés [Arkell et al., 1957; Imlay et Hermann, 1984; Villaseñor et González-Arreola, 1988; Villaseñor, 1991], aux aulacostéphanidés [Verma et Westermann, 1984], comme aux «pseudoraseniidés» [Callomon, 1992]. Bien que les deux espèces, praecursor et mazapilensis (espèce la plus fréquente) récoltées par Burckhardt [1906] dans ses « Couches à Haploceras Fialar», aient été classées originellement dans le genre Craspedites, elles sont inclues traditionnellement dans le genre Procraspedites. Pour les différents auteurs [Burckhardt, 1906, 1930; Imlay, 1939; Cantú-Chapa, 1970; Imlay et Hermann, 1984] les niveaux stratigraphiques à Procraspedites sont attribués au Kimméridgien inférieur, moyen ou supérieur. Le genre Procraspedites est également cité en association stratigraphique avec les genres Idoceras et Hybonoticeras dans le secteur d'Iturbide à Nuevo León au Mexique [Schumann, 1988]. De par les citations, seules Involuticeras picachosense IMLAY, 1943, et Procraspedites cf. P. africanus (ZWIERZICKY) in Verma et Westermann [1984] pourraient constituer les témoins tithoniens du genre Procraspedites, qui perdrait, alors, le caractère de taxon endémique dans le Kimméridgien sur la marge sud de la plaque nord-américaine (Mexique et sud des USA).

Le présent travail est basé sur une récolte abondante de quelques 5 785 ammonites sur des coupes levées banc par banc et dont certaines font l'objet de première découverte dans l'Altiplano mexicain (Sierra de Catorce, Sierra de Symón, Sierra de Palotes, Sierra de Santa Rosa, Sierra de Mazapil, Sierra de La Muralla). Dans le même cadre de travail, nous avons : (1) révisé le matériel type de la collection de Burckhardt, et (2) examiné les illustrations bibliographiques aussi bien des espèces mexicaines que de toutes celles pouvant avoir une relation avec le genre en question. Les types figurés des collections de Imlay [1939] et de Verma et Westermann [1984] sont également analysés.

La totalité du matériel récolté par les auteurs provient des niveaux carbonatés riches en Glochiceras (Coryceras) carinatum de l'Altiplano mexicain, où les autres ammonites présentes sont Haploceras transatlanticum BURCKHARDT, Glochiceras (Lingulaticeras) semicostatum BERCKHEMER, Taramelliceras (Metahaploceras) costatum (BURCKHARDT non QUENSTEDT). ainsi que de rares perisphinctidés similaires à Pachysphinctes (en cours d'étude). Sur le plan biostratigraphique, plusieurs faits permettent de cadrer l'intervalle à Procraspedites dans la zone à Eudoxus (p.p.) du Kimméridgien élevé [Hantzpergue et al., 1991] : (1) les horizons riches en Glochiceras (Coryceras) carinatum sont situés clairement au dessus de l'intervalle à Idoceras dans l'Altiplano mexicain; (2) dans le secteur d'El Cañon de San Matias (Zacatecas) ces horizons apparaissent directement sur un niveau à Taramelliceras sp. gr. pseudoflexuosum (FAVRE) et Aulacostephanus sp.; et (3) le niveau étudié est situé nettement sous le premier niveau d'apparition du genre Hybonoticeras.

Les données nouvelles permettent d'exclure l'existence du genre Procraspedites dans le Tithonien basal, fait corroboré par la non association de ce genre avec les ammonites bien connues dans le Tithonien mexicain. Ainsi, Involuticeras picachosense IMLAY, récolté par Imlay [1943] dans un niveau du «Portlandien» du Placer de Guadalupe (Chihuahua), ne peut-être attribuée à *Procraspedites*. Elle s'en distingue, en fait, par sa taille plus grande, par le type d'ornementation incluant des constrictions dans le tour externe, par la ligne de suture avec le lobe latéral plus large et la première selle

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latérale plus étroite; elle s'en écarte également par le fait que des périsphinctidés lui sont associés. Par ailleurs, l'analyse de *Procraspedites* cf. *P. africanus* (ZWIERZICKY) qui fut attribuée soit au Tithonien basal de Mombassa (Kenya) par Verma et Westermann [1984], soit au Kimméridgien terminal par Schweigert *et al.* [1996], révèle des différences ontogéniques notables par rapport aux *Procraspedites* mexicains : (1) allure plus globuleuse de la coquille; (2) le type de section (jamais en «flèche»); (3) l'ombilic très ouvert aux stades adultes; (4) la costulation toujours plus grossière; (5) la suture plus complexe avec selle latérale plus large, second lobe latéral nettement plus réduit, ainsi que le développement plus grand du lobe suspensif.

L'analyse réalisée sur des spécimens démontés jusqu'au diamètre de 10-16 mm, fournit pour la première fois des informations précises sur le mode de développement ontogénique du genre Procraspedites auparavant inconnus, et permet de procéder à une comparaison plus adéquate avec les espèces africaines qui lui sont attribuées. Deux critères fondamentaux permettent d'inclure le genre Procraspedites dans la sous-famille des Ataxioceratinae : (1) la présence de structures paraboliques dans les tours internes (< 20 mm), et (2) le développement postérieur des doubles bifurcations (côtes subpolyplocoïdes). Dans le matériel récolté la distribution ontogénique des caractères analysés révèle une diversité en mosaïque notable, mais qui devrait être intraspécifique compte-tenu de l'absence d'une séparation géographique et stratigraphique entre les individus étudiés. Dans ce contexte, les espèces décrites par Burckhardt [1906] pourraient représenter des phénotypes proches des limites de la variabilité des peuplements des Procraspedites, et ce sur le bord sud de la plaque nord-américaine. S'agissant des deux espèces originellement décrites par Burckhardt [1906] et inclues classiquement dans le genre Procraspedites, « Craspedites » praecursor et « Craspedites » mazapilensis, ces dernières apparaissent comme deux morphotypes appartenant à une seule bioespèce mais pour laquelle l'expression du dimorphisme sexuel reste à préciser. Seule la désignation subséquente due à Arkell *et al.* [1957] implique l'usage de *Procraspedites praecursor* comme unique espèce valide de ce genre, et ce en dépit : (1) du fait que le type originel de Burckhardt [1906] est incomplet par rapport à celui de l'autre «espèce», mazapilensis (qui reste le seul exemplaire connu conservant le péristome), (2) du fait que mazapilensis est reconnue par Burckhardt comme l'espèce la plus fréquente, et de répartition stratigraphique mieux connue et (3) du fait que la dénomination de mazapilensis réfère mieux à la localité-type, alors que par *praecursor* l'auteur voulait suggérer une relation évolutive avec le *Craspedites* boréal. Actuellement, il n'est pas encore possible de préciser quelle pourrait-être l'origine du genre *Procraspedites*.

INTRODUCTION

Procraspedites SPATH, 1930 is a rare genus, cited a few times from Mexico [Burckhardt, 1906, 1930; Imlay, 1939; Cantú-Chapa, 1970; Araujo and Casar, 1987; Schumann, 1988; Villaseñor and González-Arreola, 1988; Villaseñor, 1991; Michalzik and Schumann, 1994], southern United States [Imlay and Herman, 1984] and Kenya [Verma and Westermann, 1984]. Among the 20 references in the Americas (fig. 1), only eight specimens have so far been illustrated. The reference from outside the Americas reports two specimens from the interpreted Lower Tithonian of Mombassa, Kenya.

Spath created *Procraspedites* for the "group of Idoceratids... of which Burckhardt's *Craspedites praecursor* may be considered to be typical" [Spath, 1930, p. 56]. With such a terse original diagnosis and without precise data on the ontogeny, *Procraspedites* has been related to idoceratids [Spath, 1930]; involuticeratids [Salfeld, 1917; Imlay, 1939, 1943]; ataxioceratids [Arkell *et al.*, 1957; Imlay and Herman, 1984; Villaseñor and González-Arreola, 1988; Villaseñor, 1991]; aulacostephanids [Verma and Westermann, 1984]; and "pseudo-rasenids" [Callomon, 1992].

Traditionally, species included in *Procraspedites* are *P. praecursor* (BURCKHARDT) and *P. mazapilensis* (BURCKHARDT), both from the "couches à *Haploceras Fialar*" in the Upper Kimmeridgian of Zacatecas, northcentral Mexico [Burckhardt, 1906, 1930]. *P. praecursor* has been recorded also from southern Texas, USA [Imlay and Herman, 1984]. Burckhardt [1906, p. 100] was apparently uncertain about the stratigraphic level of his single specimen of *P. praecursor*, but in the caption to plate 18 indicates the "couches à *Haploceras*". According to him, *P. mazapilensis* is the most frequent species associated with *P. praecursor* at Vereda del Quemado in Zacatecas. Burckhardt assumed specific differences based on the tighter coiling of the inner whorls and the stronger and earlier reduction of ornamentation in *P. mazapilensis;* stated differences affecting the external saddle in the adult suture are difficult to recognize in the illustrations [Burckhardt, 1906; Pl. 17, fig. 3 and Pl. 18, fig. 3]. Only two specimens from Burckhardt's collection (IGM 197; IGM 213) survived in the Museum of Palaeontology of the Institute of Geology of the UNAM [Burckhardt, 1906, pl. 17, fig. 4, and pl. 18, fig. 2].

Burckhardt [1930] cited Craspedites sp. and Craspedites? from the Sierra de Catorce (San Luis Potosí) and Nuevo León, respectively. Imlay [1939] cited Involuticeras aff. I. mazapilensis associated with Glochiceras fialar (BURCKHARDT non OPPEL) from the upper part of his Middle Kimmeridgian "*Idoceras beds*" of Coahuila. Cantú-Chapa [1970] illustrated a fragment of *Procraspedites* aff. P. mazapilensis from an imprecise supposedly Lower Kimmeridgian horizon in Samalayuca, Chihuahua. Imlay and Herman [1984, Pl. 1, fig. 22], registering *Procraspedites* praecursor from the Texaco-White well N° 1 in southern Texas, concluded : "An early to late Kimmeridgian age... is shown by the presence of *Glochiceras* and *Procraspedites* in association with early forms of Haploceras and Metahaploceras and with late forms of Taramelliceras". Araujo and Casar [1987] cited Procraspedites from Samalayuca (Chihuahua). Two well preserved specimens of P. mazapilensis, associated with Glochiceras (C.) carinatum (DEL CASTILLO and AGUILERA) in a black limestone (La Casita Formation, Cuencamé, Durango), were illustrated by Villaseñor and González-Arreola [1988, Figs. 6a, 6b]. In Nuevo León, Schumann [1988] found Procraspedites in ' ...a horizon, with shells of Haploceras, Glochiceras, Idoceras, Hybonoticeras, Aspidoceras,... and others", and Michalzik and Schumann [1994] cited Procraspedites from Iturbide, in association with Haploceras, Metahaploceras, Subplanitoides, Virgataxioceras and Glochiceras. These citations from northern Mexico include references to the association of Procraspedites with Idoceras and/or other ammonites, but without palaeontological analyses or precise stratigraphy. Our research in the Iturbide area (Nuevo León), failed to recognize the association of Procraspedites, Idoceras and Hybonoticeras.

Thus, *Procraspedites* is chiefly a rare genus in the Kimmeridgian of the Americas, with only two species known



FIG. 1. – Index map to *Procraspedites* localities from Mexico and southern USA, and schematic lithostratigraphic columns of the Upper Kimmeridgian in studied sections of the Mexican Altiplano with first and/or last appearances datum planes (FAD/LAD) of *Idoceras* and *Hybonoticeras*, and the record of *Procraspedites* and "*Procraspedites*-like" ammonites. Cuencamé, Sierra de Palotes, Durango (CU); El Pastor, Sierra de Catorce, San Luis Potosí (EP); Iturbide, Sierra La Muralla, Nuevo León (IT); Escondida-Soledad, Sierra Madre Oriental, Nuevo León (ES); Limestone County, Texas, (LC); Melchor Ocampo, Sierra de Zuloaga, Zacatecas,(MO); Puerto Blanco and Cañada de las Bocas, Sierra de Santa Rosa, Mazapil, Zacatecas, (PB-CB); Rancho La Victoria, Sierra de Parras, Coahuila (RV); undetermined outcrop in Sierra de Catorce, San Luis Potosí (SC); San Lázaro, Nuevo León (SL); Cañón de San Matías, Sierra de Santa Rosa, Mazapil, Zacatecas (SM); Sierra de Samalayuca, Chihuahua (SMY); Cañón del Toboso, Sierra de Symón, Durango (TO); Vereda del Quemado, Sierra de La Caja, Mazapil, Zacatecas (VQ).

FIG. 1. – Carte des sites ayant livré les Procraspedites du Mexique et du sud des USA, et colonnes lithostratigraphiques synthétiques du Kimméridgien supérieur dans les coupes étudiées de l'Altiplano mexicain, montrant les niveaux d'apparition (FAD) et/ou de disparition (LAD) des genres Idoceras et Hybonoticeras, ainsi que les niveaux à Procraspedites et ammonites « de type Procraspedites ». Cuencamé, Sierra de Palotes, Durango (CU); El Pastor, Sierra de Catorce, San Luis Potosí (EP); Iturbide, Sierra La Muralla, Nuevo León (IT); Escondida-Soledad, Sierra Madre Oriental, Nuevo León (ES); Limestone County, Texas (LC); Melchor Ocampo, Sierra de Zuloaga, Zacatecas (MO); Puerto Blanco et Cañada de las Bocas, Sierra de Santa Rosa, Mazapil, Zacatecas (PB-CB); Rancho La Victoria, Sierra de Parras, Coahuila (RV); affleurement indéterminé dans la Sierra de Samalayuca, Chihuahua (SMY); Cañón del Toboso, Sierra de Symón, Durango (TO); Vereda del Quemado, Sierra de La Caja, Mazapil, Zacatecas (VQ). without precise stratigraphy [Burckhardt, 1906]. In addition, two species have been directly or indirectly referred to *Procraspedites* : *Involuticeras picachosense* IMLAY, 1943 and *Procraspedites* cf. *P. africanus* (ZWIERZICKY) in Verma and Westermann [1984], which have been interpreted as "Portlandian" and early Tithonian in age, respectively.

REVISED MATERIAL

Among 5785 ammonites collected, only seven *Procraspedites* were obtained in classical [Burckhardt, 1906, 1919-21; Verma and Westermann, 1973] and new Upper Jurassic sections of Mexico, located at El Pastor (Sierra de Catorce, San Luis Potosí; IGM 5092), Cañón del Toboso (Sierra de Symón, Durango; IGM 5088), Cuencamé (Sierra de Palotes, Durango; IGM 3371, 3372), Cañada de las Bocas (Sierra de Santa Rosa, Zacatecas; IGM 5091), Vereda del Quemado (Sierra de Mazapil, Zacatecas) and Iturbide (Sierra La Muralla, Nuevo León; IT-NL, IGM 5089, 5090) (fig. 1).

Thus, we analysed five well-preserved specimens and two fragments (the only records in their sections) with precise stratigraphy, as well as a well preserved phragmocone (*ex situ*, at Iturbide, Nuevo León; IT-NL), and the surviving specimens from Burckhardt's collection. We also studied the plaster cast of the *Involuticeras* sp. ind. juv. of Imlay [1939; UM 19528], and the more complete specimen of *Procraspedites* cf. *P. africanus* described by Verma and Westermann [1984]. Moreover, we revised previous illustrations of *Procraspedites* and equivalents. The specimens IGM 3371 and IGM 5088, as well as *P. cf. P. africanus* of Verma and Westermann (ROM 34604) were taken apart to analyse their ontogeny.

Specimens collected with precise stratigraphy

The material was collected in the horizons with *Glochiceras* (C.) carinatum. Incomplete imprints of *Procraspedites*-like ammonites from the overlying horizons below the first record of *Hybonoticeras* (fig. 1) were excluded because of difficult identification (bad preservation). The following observations are based on disassembled specimens (IGM 3371 and IGM 5088), and on specimens of variable shell size (IGM 3372, 5089, 5090, 5091, 5092, and IT-NL). In general, the nucleus is often poorly preserved and the body-chamber begins at between 85 and 110 mm.

At 10-16 mm, deep interrib spaces may be constrictions; one arched, oblique constriction has been noted at 15 mm (IGM 5088). Irregularities affecting the external ribs may represent vestiges of more or less preserved parabolae (pl. I, figs. 1, 3, 4). Ribbing is mainly bifurcate at mid-flanks, simple ribs are scarce, and rare incomplete ataxioceratoid rib, or double furcation [polyplok Rippen of Geyer, 1961; "côte subpolyplocoïde incomplète" in Atrops, 1982] appears. Some bifurcation may be near the umbilical edge (limited observation). There are no reinforced primaries, and the external ribs are thick, blunt, and projected on the venter. The whorl section is ovate with slightly convex flanks; the maximum width is in the lower flank, and the umbilical wall is vertical (pl. I, figs. 1, 2). From 20 mm, the primaries are prominent on the umbilical edge where some furcations appear, although bifurcations generally occur higher below the mid-flank; residual ribs connect with bifurcates resulting in incomplete and rigid ataxioceratoid divisions (pl. I, figs. 5,6). One oblique, simple, costule that does not reach the venter could mark a new growth phase at around of 30 mm, without significant changes in the whorl section. At 30-45 mm begins the periumbilical reinforcing of primaries and a clearly incomplete ataxioceratoid ribbing, in which the second furcation is at the mid-flank. This is preceded

by development of simple, bifurcate and intercalatory ribs. Constrictions are absent. The whorl section becomes acuteovate, with flattened flanks, narrow venter, and maximum width at the umbilical edge (pl. I, fig. 7, 8, 11).

At 45-55 mm, weakened sculpture is variable at the midflank and ataxioceratoid ribs can become smooth undulations; occasionally there is no change in rib strength. Thick external ribs occur and intercalatories are related to defective furcations. Constrictions are absent. Above from 55 mm only low, broad undulations (vestiges of ataxioceratoid ribs) connect simple, or forked, and prominent external ribs with short and weak primaries which become more or less obsolete around 70 mm (pl. I, fig. 7; pl. II, figs. 3, 4). The whorl section remains acute-ovate with maximum width slightly above the umbilical edge, moving occasionally to the mid-flank (pl. I, fig. 10; pl. II, fig. 3); the umbilical wall is vertical and well developed. At 90-100 mm the shell is nearly smooth at the mid-flank, and the whorl section is typically acute-ovate, "en flèche". The umbilicus is small, deep, with vertical walls. Maturity can be related to progressive uncoiling from 100 mm (pl. I, figs. 9, 13). The maintenance, density, and strength of external ribs varies in the outer whorl, as do the vestiges of reinforced primaries.

Burckhardt's collection

Burckhardt [1906, p. 98; Pl. 18, figs. 1-3] created Craspedites praecursor (IGM 213; tabl. I), highlighting the small and deep umbilicus with vertical walls, showing periumbilical ribs of inner whorls. He outlined the acute whorl section (arrow-like, "en flèche"). The extreme fading of ribs casts doubt on the detailed analysis of divisions made by Burckhardt around the end of the phragmocone. But ataxioceratoid ribs, with short primaries and a high costal index, indicate a late ontogenetic phase --- "toutes les côtes principales (celles qui restaient simples et celles qui se subdivisaient) se divisent dans deux à trois côtes externes et en outre l'on observe des côtes externes intercalées" [Burckhardt, 1906, p. 99]. Highly significant in C. praecursor (IGM 213) are the prominent primaries on the phragmocone, which are visible within the umbilicus. According to Burckhardt [1906, p. 100], C. praecursor is less frequent than C. mazapilensis and its stratigraphic level is undetermined -- "Il est douteux si cette espèce provient de la zone à Haploceras Fialar ou des couches un peu plus anciennes à Idoceras". The specimens illustrated by Burckhardt came from his "Couches à Haploceras Fialar".

Burckhardt [1906, p. 100-102] mentioned several specimens of *C. mazapilensis* and figured two; that in Pl. 17, fig. 1 is lost [Perrilliat-Montoya, 1981], while the other (IGM 197 : *ibid.*, Pl. 17, fig. 4) survived. Burckhardt stressed the small and deep umbilicus in his larger (lost) specimen, which is essentially complete with pre-peristomal constriction and uncoiling reducing the final overlap at half the whorl height. The whorl section is acute ("en flèche") as in *Craspedites praecursor*. Smoothing affects the inner flanks and expands the outer two-thirds in the adult, which has shorter external ribs in the outer whorl. Burckhardt's statements on rib divisions are excessive and his illustrations indicate an earlier blunting of ribs in *C. mazapilensis* than in *C. praecursor*. Thus, *C. mazapilensis* had precocious ataxioceratoid-fasciculate ribbing, but no periumbilical reinforcements of ribs.

Imlay's collection

Imlay [1939, p. 41-42, Pl. 6, figs. 6, 7] collected *Involuticeras* sp. ind. juv. (UM 19528; tabl. I) from the "*Glochiceras fialar* beds" at Melchor Ocampo (Zacatecas) interpreting this to be immature, much coarser ribbed than



PLATE I. – FIGS. 1-13. – Procraspedites praecursor (BURCKHARDT, 1906). 1-8, 9: IGM 5088. 1-2 at 18.5 mm (arrows for parabolic nodes); 3-4 oblique views showing parabolic nodes, × 2; 5-6 at 29.6 mm; 7, 8 at 44 mm; 9 at 99 mm. Cañón del Toboso (Sierra de Symón, Durango, La Caja Formation); 10-13: IGM 3371. 10, 12 at 69 mm; 11 at 46.7 mm; 13 at 134 mm. Cuencame-1 section (Sierra de Palotes, Durango, La Casita Formation). All from the Carbonate horizon rich in *Glochiceras (C.) carinatum*, Upper Kimmeridgian, Eudoxus Zone, × 1 unless otherwise designated.
PLANCHE I. – FIGS. 1-13. – Procraspedites praecursor (BURCKHARDT, 1906). 1-8, 9: IGM 5088. 1-2: à 18,5 mm (flèches sur l'ornementation parabolique); 3-4: vue oblique montrant l'ornementation parabolique, × 2; 5-6 à 29.6 mm; 7-8 à 44 mm; 9 à 99 mm. Cañón del Toboso (Sierra de Symón, Durango, formation de La Caja); 10-13: IGM 3371. 10, 12 à 69 mm; 11 à 46.7 mm; 13 à 134 mm. Coupe de Cuencame-1 (Sierra de Palotes, Durango, formation de La Casita). Tous les échantillons proviennent de l'horizon carbonaté riche en Glochiceras (C.) carinatum, Kimméridgien supérieur, zone à Eudoxus, × 1 sauf indication contraire.



TABLE I. – Measurements (in mm) and other characteristics. * Estimated. Underlined the reproduced measurements by Burckhardt [1906] which do not correspond with the illustrated *Craspedites praecursor* (PI. 18, figs. 1, 2). (+) Lost specimen of *Craspedites mazapilensis* [Burckhardt, 1906, PI. 17, fig. 1]. Abbreviations : DM, shell diameter; U, width of the umbilicus; W, whorl width; H, whorl height; UR, number of umbilical or primary ribs; ER, number of external or secondary ribs; ER2, number of ER per half whorl; ER4, number of ER at last quarter whorl at given diameter; and CI, costal index (ER/10 UR).

TABLE I. – Mesures (en mm) et autres charactéristiques de la coquille. * Estimé. Sont soulignées les mesures fournies par Burckhardt [1906] mais qui ne correspondent pas avec illustrations de Craspedites praecursor (Pl. 18, figs. 1, 2). (+) Spécimen perdu de Craspedites mazapilensis [Burckhardt, 1906, Pl. 17, fig. 1]. Abréviations : DM, diamètre de la coquille; U, largeur de l'ombilic; W, largeur de tour; H, hauteur de tour; UR, nombre des côtes primaires; ER, nombre des côtes externes; ER2, nombre des ER par demi-tour; ER4, nombre des ER dans le dernier quart de tour pour un diamètre donné; et CI, index costal (ER/10UR).

SPECIMEN	DM	Ű	Ŵ	н	U/D	W/D	H/D	W/H	ÜR	ER	ER/2	ER/4	CI
IGM 3371	134	19.1	45.9	66.0	0.14	0.34	0.49	0.69					
	123*	15.4	29.5	62,5	0.12	0.23	0.50	0.47			••••		
	98*	13.2	29.3	50 0	0.13	0.29	0 5 1	0.58				33	
	94.5	12	29	48.9	0.12	D 30	0.51	0.59	12	81.	59*	33	3.0
	69.0	11.5	23.4	35 5	0.15	0.33	0.51	0.65	23	71*	44.	23	4.3
	46.3	9.7	14 4	23.1	0.20	0.31	0.49	0.62	28*	61.	38	23	26
	18.0	3.2	6,4*	8.3	0.17	0.35	0.46	0 77					
IGM 3372	113.6	18.5	30.5	49.0	0.16	0.26	0.43	0.62					
	88.3	13.9	27.3	45.8	0.15	0.30	0.51	0 59			68	37	
	85.5	13 5	27 2	44.3	0.15	0.31	0 51	0.61			67	*****	
IGM 5088	122,5*	19.2	32,2	61,01	015	0.26	0.49	0.52					
	96.7	15.5	30.6	47.0	0.16	0.31	0.48	0.65	15	96		33.	8.6
	68.9	11.5	22.4	35.0	0.16	0.32	0.50	0.64	17	81		25	5.7
	44.0	8.0	15.5	23.0	0.18	0.35	0.52	0.67	19	66		21	4.4
	28.5	5.5	9.0	155	0 19	0.31	0 54	0.58	24-25	58-59	****	17	2,7-2,8
	18,1	3-3,5'	70	9.3	0,16-0.19	0.38	0.52	0.75	25*	47.50*		15	1,5-1,7*
IGM 5090	70.0	14.2	23.0	34 1	0.20	0.32	0.48	0.67	15	97-98		30	7,1-7,2
	52.0	10.5	21 0	26 0	0.20	0.40	0.50	0.80	15			23	>5,0
IT-NL	139.0											66	
	122.0	23.0		65.0	0.18		0.53						
	107.0	18.0		50.0	0.16		0.46						
	102.0	17 0		49.0	0.16		0.45					•	
(+)	118.5	26.5	34.0	51.0	0.22	0.28	0.43	0.66					
	70.0	11.0		34.0	0.15		0.48					38	
IGM 197	63.3	10.1	23,0*	32,5*	0.16	0 36	0,51*	0.70			57	33	
	52.0	9.1	18,8*	27,0*	0.16	0 36	0.52*	0.70	••••		50	25	
IGM 213	86.0	19.0	26.0	42.5	0.22	0.30	0 49	0.61					
	108.2	22.2	30.6	50.8	0.20	0.28	0 46	0.60	6	70*			
	94.1	21.0	28.1	47 0	0.22	0.30	0.50	0.59				33	
	83.8	17.2	26.4	40.6	0.20	0.31	0.48	0.65					
UM 19528	37.5	7.5		19.6	0 20		0.53		22	71	46	25	4.3
	27.7	5.9	11.5	14 4	0 21	0 41	0.51	0.79	13	•	42	24	2.9
USNM 103352	175.0	45.0	50 0	75.0	0.25	0 28	0.42	0.66					
ROM 34604	167.0	58.0	53 2	68.3	0 34	0.31	0.40	1.28			••••		
	107.7	18 5	39.3	52.8	0 17	0 36	0 49	1 34				18	
	75.5	15 1	311	37 9	0.20	0.41	0.5	1 21				21	
	58.1	13.3	28.5	30 5	0 22	0 49	0.52	1.07				22	
KNMI-MA47	148.0	35 0	34.0	58 0	0.23	0 22	0.39	0 58					

Mazapil' species [Burckhardt, 1906], and close to "Involuticeras" praecursor (BURCKHARDT), but made no comments on suture lines. At 22 mm, the whorl section is ovate with slightly convex flanks, maximum width near the small, deep umbilicus with vertical umbilical wall. Ribs are fine, sinuous, mainly bifurcating slightly below mid-flank, but some singles and intercalatories exist. Double furcations are typical at 22-37.5 mm, with divisions at variable height, wider interrib spaces, and bifurcate intercalatories. At 40 mm weakening of sculpture is clear. This individual has whorls slightly more inflated than in Burckhardt' specimens. Ribbing is similar to IGM 5088, but ribs are thinner (contrasting with Imlay's observation) and there are no constrictions. IGM 3371 has stiffer ribs with narrower interrib spaces at 36-45 mm. Imlay [1939] assigned UM 19528 to Involuticeras following Salfeld [1917, p. 73-74] who included Craspedites praecursor and C. mazapilensis in that genus.

Verma and Westermann's collection

Verma and Westermann [1984, p. 58-59, Pl. 11, figs. 1, 2] illustrated two specimens (ROM 34604, KNMI-MA47) from Kenya, which were interpreted as *Procraspedites* cf. *P. africanus*. The only specimen described by these authors (ROM 34604) has been disassembled at 167, 108, and 76 mm (pl. II, figs. 5-9).

At 45-58 mm, the external ribs are thin and markedly prosiradiate, low undulations at mid-flank correspond to smoothed ataxioceratoid ribs with periumbilical divisions and reinforcement of primaries. Intercalatories and some subfasciculate ribs occur (five to six secondaries per umbilical rib). One or two, shallow constrictions are present. At 60 mm flanks are smooth with only peripheral ribs. At 65-107 mm, coarse and prorsiradiate ribs exist on the outer third of the flanks, and, due to ribbing shortness and parallelism, no divisions appear. At 75 mm, the whorl section is ovate with wide venter and maximum width slightly above the inconspicuous umbilical edge; the umbilical wall is oblique. Sculpture consists of thick and slightly prorsiradiate external ribs. At 79-80 mm a large and shallow constriction, inconspicuous on venter, indicates a transient peristome. Uncoiling and reducing umbilical wall and edge beyond 100 mm result in a large and shallow umbilicus. Ornamentation disappears between 107 and 127 mm (unpreserved shell). The last suture is recognized at 127 mm, and half the outer whorl belongs to body-chamber, with no traces of the peristome. The larger preserved whorl is 167 mm in size, and there is no change in the wide ovate whorl section (never acute as in Mexican Procraspedites).

PLATE II. – FIGS. 1-4. – *Procraspedites praecursor* (BURCKHARDT, 1906). 1, 2: IGM 5091, fragments of the last preserved whorl with local preservation of epigenized shell (note fine external ribs and wide umbilicus showing vestiges of reinforced primaries). Cañada de las Bocas section (Sierra de Santa Rosa, Mazapil, Zacatecas, La Caja Formation). 3-4: IGM 5090, *ex situ* at 70 mm, from a slop near Iturbide (Sierra La Muralla, Nuevo León, La Caja Formation). All from the Carbonate horizon rich in *Glochiceras (C.) carinatum*, Upper Kimmeridgian, Eudoxus Zone, × 1. FIGS. 5-9. – "*Procraspedites*" cf. "P". africanus (ZWIERZICKY). ROM 34604, with partial preservation of epigenized shell. 5-7 at 76 mm; 8 at 107.5 mm; 9 at 167 mm. About 600 m southwest of the New Mto Panga Shale Tithonian, × 1.

PLANCHE II. – FIGS. 1-4. – Procraspedites praecursor (BURCKHARDT, 1906). 1, 2 IGM 5091. fragments préservés du dernier tour avec préservation locale de la coquille épigénisée (notez la finesse des côtes externes et la largeur de l'ombilic conservant les vestiges des côtes primaires renforcées). Coupe de Cañada de las Bocas (Sierra de Santa Rosa, Mazapil, Zacatecas, formation de La Caja). 3-4 IGM 5090, ex situ à 70 mm, sur une pente près d'Iturbide (Sierra de La Muralla, Nuevo León, formation de La Caja). Tous les échantillons proviennent de l'horizon carbonaté riche en Glochiceras (C.) carinatum, Kimméridgien supérieur, zone à Eudoxus, × 1.

FIGS. 5-9. – «Procraspedites» cf. « P » africanus (ZWIERZICKI). ROM 34604, avec la préservation partielle de la coquille épigénisée. 5-7 à 76 mm; 8 à 107,5 mm; 9 à 167 mm. 600 m environ au sud-ouest de New Mto Argiles de Panga, Tithonien, × 1.

Significant differences between *Procraspedites* cf. *P. africanus* (ROM 34604, pl. II, figs. 1-5; figs. 2-3; tabl. I) and the Mexican *Procraspedites* are : (1) the greater and more inflated shell; (2) the ovate, never acute, whorl section; (3) the U/D ratio similar below 107 mm, but higher at greater size (0.36, see tabl. I); (4) the coarser ribbing; and (5) the suture line (similarly preserved in Mexican *Procraspedites* and Kenyan ROM 30604) is more complex, with a wider first lateral saddle, an extremely reduced second lateral lobe, and a greatly extended suspensive lobe (fig. 2E).

The stated differences as well as the assumed younger age of *P. cf. P. africanus*, recorded together with *Hybonoticeras* (lowermost Tithonian or uppermost Kimmeridgian according to Verma and Westermann [1984] and Schweigert *et al.* [1996], respectively) from the Freretown section at Mombassa, suggest that Mexican *Procraspedites* are not cogeneric with the Kenyan form.

Specimens reviewed from the literature

Procraspedites aff. *P. mazapilensis* (BURCKHARDT) in Cantú-Chapa [1970, pl. 1, fig. 9] is a fragment (Ac-166) from Sierra de Samalayuca (Chihuahua, Mexico), and is difficult to interpret even at the genus level. Precise stratigraphy is also unknown.

From Texaco Well White N° 1, County Texas, Imlay and Herman [1984, pl. 1, fig. 22] identified USMM 340046 as *Procraspedites praecursor*. The fragment belongs to a shell ca. 60 mm with rib prominence and density close to *P. praecursor*, but its stratigraphy is uncertain.

Involuticeras picachosense IMLAY (USNM 103352) came from an undetermined "Portlandian" horizon [Imlay, 1943, p. 529, pl. 87, figs. 4-5; locality 17258] near Placer de Guadalupe (Chihuahua). Imlay [1943, p. 532] separated this species from *P. praecursor* through its greater size, finer and more persistent ventral ribs, coarser primaries, and the wider first lateral lobe. In addition to Imlay's observations of faint constrictions on the outer whorl, we noted the narrowing of the first lateral saddle. The latter is an unusual trait in Burckhardt's *Procraspedites*, but known from *Ringsteadia tenuiplexa* (QUENSTEDT), a rare species of the lower Kimmeridgian of southern Germany alluded to by Imlay. Diameter (175 mm), coiling (25 percent), whorl width (28 percent) and whorl height (42 percent) in Involuticeras picachosense, as well as its constrictions on the outer whorl, and stratigraphy, cast doubt on any relationship with the smaller Kimmeridgian Procraspedites of Mexico. According to Imlay, Craspedites limitis BURCKHARDT [1930 = Perisphinctes aff. P. erinus D'ORBIGNY of Burckhardt, 1903, Pl. 9, figs. 1, 2] has similar sculpture, less acute whorl section, and wider sutural lobes. Leanza [1980, p. 33] included Craspedites limitis in Choicensisphinctes, a genus of the Argentine lower Tithonian, which is more in accordance with the Tithonian affinity of "Subplanites' fresnosensis IMLAY, the only ammonite associated with Involuticeras picachosense according to Imlay [1943, p. 529-530]. Moreover, Verma and Westermann [1984] placed Craspedites limitis in Pseudoinvoluticeras, close to their Phanerostephanus (Nothostephanus) digoi from the interpreted basal Tithonian of Mombassa (Kenya).

DISCUSSION

Burckhardt [1906] did not make detailed comparisons between "*Craspedites*" praecursor and mazapilensis, but identified the latter through tightly coiled inner whorls in more smoothed shells. Thus, without significant differences in suture lines, *Procraspedites praecursor* would differ in retaining the umbilical ribs over practically the entire phragmocone.

In the stratigraphically collected material of *Procraspedites*, the species differentiation established by Burckhardt [1906] is not supported by morphology. Rather, the types of *praecursor* and *mazapilensis* appear to be morphs, perhaps the extremes, of a single intergrading species, although more material is required for a complete analysis.

Figure 3A-E display data for coiling, whorl width, whorl height, and ribbing of our new specimens together with those illustrated by Burckhardt [1906], UM 19528, USNM 103352 from Zacatecas and Chihuahua [Imlay, 1939, 1943], and ROM 34604 and KNMI-MA47 from Kenya [Verma and Westermann, 1984]. Burckhardt' specimens are comparatively more evolute than those collected by us. The convergence of the coiling-curves of *mazapilensis* (Burckhardt' specimens) and IGM 3371, IGM 5088, IGM 5090, and UM 19528 at diameters smaller than 75 mm (fig. 3A) is signi-



FIG. 2. – A-E, : Diagrammatic representation of septal sutures of *Procraspedites praecursor* (BURCKHARDT, 1906). A : *Craspedites praecursor* reproduced from Burckhardt [1906, Pl. 18, fig. 3]; B : *Craspedites mazapilensis* reproduced from Burckhardt [1906, Pl. 17, fig. 3]; C : IGM 5090 right flank at 69 mm; D : IGM 3372 left flank at 75 mm approximately; E : ROM 34604 on the right flank at 88.5 mm.

FIG. 2. – A-E, : Représentation des sutures septales de Procraspedites praecursor (BURCKHARDT, 1906). A : Craspedites praecursor, reproduite d'après Burckhardt [1906, Pl. 18, fig. 3]; B : Craspedites mazapilensis, reproduite d'après Burckhardt [1906, Pl. 17, fig. 3]; C : IGM 5090, flanc droit à D = 69 mm; D : IGM 3372, flanc gauche à D = 75 mm environ; E : ROM 34604, sur le flanc droit à D = 88,5 mm.

ficant. Specimen IT-NL (fig. 3A) is closest to mazapilensis and its umbilicus is even smaller. In the Mexican Procras*pedites* studied, the coiling values diverge above 100 mm, which is especially accentuated in the Tithonian specimens from Chihuahua and Kenya (fig. 3A). Whorl-height values show strong homogeneity, with minimums for mazapilensis, whereas width values are more variable (fig. 3B-C), indicating palaeobiological features of Procraspedites populations; the Kenyan ROM 34604 is clearly separated by higher width values throughout its ontogeny. Rib weakening in all new specimens of Mexican Procraspedites is closer to Burckhardt's praecursor (IGM 213), except for specimen IT-NL, which is closer to mazapilensis. In general, the persistence of primaries on the phragmocone in the new material resembles praecursor, but both their density and strength vary; thus, specimens IGM 3371 and 3372 (fig. 3) show more widely spaced and weaker primaries, and consequently approach *mazapilensis*, whereas in the middle and external parts of the flanks, the ornamentation is as in praecursor; the external ribs in IGM 5091 resemble mazapilensis and the primaries are spaced but reinforced as in praecursor (pl. II, figs. 1, 2, respectively). Specimen UM 19528 (Imlay's collection) shows mean values for small sizes, except denser external ribs (fig. 3D-E). Specimen ROM 34604 from Kenya shows decreasing values from 50 mm onwards.

Thus, the combination of ribbing and coiling in the new material of Mexican *Procraspedites* display phenotypic traits in "mosaic" (fig. 3A-E). IGM 3371 (Pl. I, fig. 13) and IGM 3372 are even more involute than *mazapilensis* and their primaries persist, but differ from the typical appearance of primaries in *praecursor*; by contrast, the weakening of the flank sculpture is as in *praecursor*, but the higher density of the external ribs resembles to *mazapilensis*. IGM 5091 also reveal a combination of characters, with coiling and persistent primaries as in *praecursor*, but atypically more spaced, and density of external ribs as in *mazapilensis*. IGM 5088 shows ribbing typical of *praecursor*, but coiling is tighter than in *mazapilensis*. Ion the contrary, IT-NL represents an extreme *mazapilensis*-like coiling.

The combination of traits in "mosaic", the coexistence in the carbonate intercalation rich in *Glochiceras (C.) carinatum*, and the absence of geographic segregation, all indicate that *Procraspedites* studied from the southern North American plate belong to the same biospecies. The phenotypic diversity in this biospecies suggests a rather complex combination of characters between a *mazapilensis* morph and a *praecursor* morph. Although conclusive evidence is lacking that those morphs represent sexual dimorphism, the absence of a sexual antimorph in the same stratigraphic interval could nevertheless suggest the possibility that, as in *Nautilus* and some ammonites (Aspidoceratidae), these morphs could be the weak expression of sexual dimorphism in *Procraspedites*. To resolve this question would require the analysis of complete specimens.

As interpreted above, "Craspedites" praecursor and mazapilensis Burchhardt [1906] belong to a single biospecies. The subsequent designation made by Arkell et al. [1957] validated praecursor as the type species of the genus Procraspedites, invalidating three arguments in favour of using mazapilensis as the type species : (1) reference to the typearea of Procraspedites (Mazapil, Zacatecas); (2) preclusion to presumed evolutionary relationships between Procraspedites and Boreal Craspedites as suggested by the name praecursor given by Burckhardt; and (3) the larger mazapilensis illustrated by Burckhardt [1906, Pl. 17, figs. 1, 2] is the most complete among known Procraspedites, showing a partly preserved peristome. In addition, Burckhardt considered praecursor to be comparatively scarce and did not know its precise age as previously quoted [see p. 9 and Burckhardt, 1906, p. 100].

The classification of Procraspedites has been rather unclear because of the scarce material. Burckhardt did not discuss affinities and compiled references only to the previous interpretations by other authors [e. g. Salfeld, 1917 in Burckhardt, 1930, p. 110]. Creating this genus, Spath [1930] related it to idoceratids. Arkell et al. [1957] included Procraspedites in Perisphinctidae, subfamily Ataxioceratinae, together with *Idoceras* and its supposed synonym Subnebrodites. These authors did not regard double bifurcations as virgatotomic ribs. The polyphyletic subfamily Ataxioceratinae was reinterpreted by Zeiss [1968] to embrace mainly the Kimmeridgian perisphinctids, a proposal followed by Olóriz [1978], Atrops [1982], Meléndez [1989] and Atrops and Meléndez [1993]. Recently, Procraspedites has been interpreted as ataxioceratid, being referred to both at the subfamily [Villaseñor, 1991] and the family level [Imlay and Herman, 1984; Villaseñor and González-Arreola, 1988]. Its relationship with aulacostephanids, claimed by Salfeld [1917], was supported by Imlay [1939], who reinterpreted Burckhardt's "Craspedites" as Involuticeras within the Perisphinctidae. Ziegler [1962] clearly differentiated raseniids from aulacostephanids and did not place Procraspedites in the aulacostephanids. Verma and Westermann [1984] also included Procraspedites in Aulacostephaninae, but without discussion, and Callomon [1992] considered it informally as "pseudo-rasenid".

The ontogeny of specimens IGM 3371 and IGM 5088 permits additional conclusions on the suprageneric classification of *Procraspedites*. In the Kimmeridgian, the style of ribbing [ataxioceroid skulptur in Geyer, 1961] with parabolic structures in the inner whorls, at least, followed by double furcations, frequently incomplete ["côtes subpolyplocoïdes incomplètes" in Atrops, 1982], and perhaps fasciculate ribs, typifies Ataxioceratinae. The absence of ventral discontinuity, the type of reinforcement of umbilical ribs and traits of the septal suture, such as the large size of saddles and the low suspensive lobe, distinguish *Procraspedites* from the Aulacostephanidae as understood by Callomon [1981]. According to the systematic proposal by Zeiss [1968], *Procraspedites* should be placed in the Ataxioceratinae, although precise biostratigraphic data are lacking to identify the immediate ancestor.

In conclusion, the genus *Procraspedites* SPATH 1930, type species *Craspedites praecursor* BURCKHARDT 1906 by subsequent designation [Arkell *et al.*, 1957], is included in the subfamily Ataxioceratinae BUCKMAN 1921. *Craspedites mazapilensis* BURCKHARDT [1906, p. 98, Pl. 18, figs. 1-3] is a junior synonym.

BIO-CHRONOSTRATIGRAPHIC REMARKS

Burckhardt [1930] assumed a clear stratigraphic difference between his "C." praecursor and mazapilensis, and others only mentioned but never described by him, i.e., from his "Couches à Haploceras Fialar", Upper Kimmeridgian, and the "Couches à Idoceras" of the Mazapil region, respectively. He compared undescribed forms with Craspedites subditus and C. fragilis, TRAUTSCHOLD spp., but not with "C". praecursor and "C". mazapilensis. On the whole, Boreal Craspedites mentioned by Burckhardt [1930] have more evolute shells with less compressed whorls than do Mexican Procraspedites. On stratigraphic ground, "Couches à Idoceras", the "Mexican Craspedites" mentioned but never described by Burckhardt [1930, p. 110] could be Raseniidae or even macroconchs of Idoceras.



FIG. 3. – A-E, : Bivariate plots of shell dimensions (in mm) and ribbing curves against diameter. A : umbilical amplitude; B : whorl width; C : whorl height; D and E for ER4 and CI values, respectively (see table I). FIG. 3. – A-E : représentation bivariée des dimensions de la coauille (en mm) et courbes de costulation par rapport au diamètre. A : amplitude

FIG. 3. – A-E, : représentation bivariée des dimensions de la coquille (en mm) et courbes de costulation par rapport au diamètre. A : amplitude ombilicale; B : largeur de tour; C : hauteur de tour; D et E : correspondant respectivement aux valeurs des ER4 et CI (voir table 1).

Between the first appearances of *Idoceras* and *Hybonoticeras*, we collected 2096 entire or fragmented ammonites bedby-bed. The stratigraphic data do not support the occurrence of *Procraspedites* in the *Idoceras* interval, and indicate no differences in the ranges of *P. praecursor* and *P. mazapilensis*; both come from the carbonate intercalations rich in *Glochiceras* (*C.*) carinatum. The records by Imlay [1939] of *Invo*- luticeras aff. I. mazapilensis in the "Idoceras beds" is due to his inclusion of the horizons of "Glochiceras gr. of fialar (OPPEL)" in the "Idoceras beds". However, this "Glochiceras horizon" is a younger and highly characteristic interval in the Mexican Altiplano, as later recognized by Imlay [1980, 1982]. Procraspedites aff. P. mazapilensis [Cantú-Chapa, 1970, p. 40, Pl. 1, fig. 9] is a fragment of difficult interpretation, has no precise stratigraphy and, thus, its association with *Idoceras* cannot be confirmed.

The record of Procraspedites from below the horizons with Glochiceras (C.) carinatum have not been confirmed by our intense sampling in the Mexican Altiplano, where horizons of extreme condensation containing Idoceras together with Hybonoticeras [Schumann, 1988] have not been found. In the Mexican Altiplano, ammonites associated with P. praecursor are Glochiceras (C.) carinatum (DEL CASTILLO and AGUILERA), Haploceras transatlanticum BURCKHARDT, G. (Lingulaticeras) semicostatum BERCKHEMER, Taramelliceras (Metahaploceras) costatum (BURCKHARDT non QUENSTEDT), and rare coarse-ribbed perisphinctids similar to Pachysphinctes (under study). This ammonite assemblage appears well above the last record of *Idoceras* and directly overlies the horizon with Taramelliceras sp. gr. pseudoflexuosum (FA-VRE) and rare Aulacostephanus sp. Villaseñor [1991, p. 121] included her unit MZ-K6 ("Taxon range Zone of Glochi-ceras. (C.) carinatum") as "an interval in the Upper Kimmeridgian Eudoxus Zone between the one assigned to the assemblage Zone of Taramelliceras sp. gr. pseudoflexuosum and Aulacostephanus sp. and the later one recognized un-derlying the Beckeri Zone" (free translation). This interpreta-tion coincides basically with that of Burckhardt [1930, Tabl. 5], who correlated his "Couches à Haploceras Fialar" with the Pseudomutabilis Zone [= Eudoxus Zone in Hantzpergue et al., 1991], and with that of Callomon [1992] for his M8 unit ("Beds/Zone with Haploceras ex gp. fialar (OPPEL) of Burckhardt, Imlay and Cantú-Chapa").

The associated Aulacosphinctoides? (Subdichotomoceras?) sp. [Villaseñor and González-Arreola, 1988] are morphologically close to Pachysphinctes. Olóriz [1978] indicated that epioceanic records of Pachysphinctes below Hybonoticeras began during the Compsum Chron (= Mutabilis + early Eudoxus Chrons), while in epicontinental platforms occurred during the Eudoxus Chron, or equivalent, in agreement with Krishna and Pathak [1993] and Krishna et al. [1994]. This is compatible with the scanty records in the Mexican platforms and consistent with the age we assigned to Procraspedites.

In Zacatecas, Durango and Nuevo León, we recognized *Procraspedites*-like forms between the *P. praecursor – Glochiceras (C.) carinatum* horizons and the first record of *Hybonoticeras*, but they are preserved as very incomplete imprints [see Villaseñor, 1991]. The association of *Procraspedites* with *Hybonoticeras* has not been recognized in the

Mexican Altiplano. Therefore, the interval with *Procraspedites*, below the range of *Hybonoticeras*, represents a diagnostic interval which can be correlated regionally on the southern margin of the North American plate [Olóriz *et al.*, 1992]. Thus, the younger *Involuticeras picachosense* and *Procraspedites* cf. *P. africanus* are doubtful references.

CONCLUSIONS

The new material collected from the Mexican Altiplano provides a precise stratigraphy for the genus *Procraspedites*, as well as information on the ontogeny and morphological variability. All this favours the revision of previous interpretations at the species and family levels.

The stratigraphic range of *Procraspedites* coincides with horizons rich in *Glochiceras* (*C.*) carinatum in the Mexican Altiplano. Younger records of *Procraspedites* below the first record of *Hybonoticeras* are doubtful due to limited preservation. The stratigraphic interval with *Procraspedites* is correlated with the Eudoxus Zone of the Submediterranean Upper Kimmeridgian, except for its lower part. There is no evidence for the presence of *Procraspedites* in the Tithonian.

The appearance of parabolic structures and rare constrictions in the juvenile shell (< 20 mm), the reinforcement of primary ribs beyond 30 mm, the fading of the ribbing above 40 mm, and the presence of double bifurcations in large sizes, indicate an ontogenetic development compatible with the inclusion of *Procraspedites* in the subfamily Ataxioceratinae.

The morphological variability in a mosaic pattern in specimens from a single horizon, indicates that the two originally described Mexican species belong to the single species *Procraspedites praecursor* (BURCKHARDT).

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