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Interacción planta-insecto sobre hojas de Bennettitales en la localidad Cerro el Matador del Jurásico Medio, Formación Otlaltepec (Puebla)

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Resumen

La Formación Otlaltepec aflora en la parte sur del estado de Puebla, y se caracteriza por contener improntas de gimnospermas con baja diversidad, donde predominan las Bennettitales. Dado el estado de conservación que presentan los fósiles, corresponderían a componentes autóctonos de la localidad Cerro el Matador. El objetivo de esta publicación es dar a conocer la evidencia de interacción planta-insecto más antigua para México. En esta localidad se registra la presencia de dos tipos de interacción; la alimentación en el margen de tipo discontinua se observa en los géneros *Otozamites* y *Zamites*, variando en tamaño entre ambos. La segunda interacción del tipo mina, que se encuentra en los mismos géneros, sin embargo el mayor número de minas temporales se localiza en *Otozamites hespera* y se propone que fue causada por un insecto monófago. Es importante comentar que estas interacciones son raras para el Jurásico y cuando existen se encuentran asociadas a las Cicadofitas; en este estudio se observa la presencia de dos tipos de daño diferentes sobre un mismo hospedero.

Palabras clave: alimentación en el margen, herbivoría, Jurásico Medio, México, *Otozamites*, *Zamites*.

Abstract

The Otlaltepec Formation outcropped in the south of the state of Puebla. It is characterized by the content of gymnospermae flora with low diversity, in which Bennettitales predominate. Given the state of preservation exhibited by fossils, they correspond to autochtonous components of the locality "Cerro el Matador". Two types of plant-insect interactions represent the oldest record in Mexico to this date. Discontinuous feeding at the leaf's margin is observed in both Otozamites and Zamites genera, the size being variable between the two of them. The second interaction is of the mining type and it is found in the same genera. However, the greatest number of temporal minings is located in Otozamites hespera and thus it is proposed that they were caused by a monophagous insect. It is important to emphasize that such interactions are rare in the Jurassic, but when they are observed, they are associated with Cycadophytes. In this study, the presence of two types of damage is observed on the same host.

Keywords: external leaf feeding, herbivory, Middle Jurassic, Mexico, Otozamites, Zamites.

1. Introducción

En México los estudios realizados sobre herbivoría son escasos, interacción que podría ser definida como la alimentación de tejido de plantas por los animales, siendo una relación que se ha incrementado desde su registro en el Paleozoico inferior hasta nuestros días debido a la aparición de nuevos registros de insectos y plantas *e.g*. angiospermas (Scott *et al*., 1992). Autores como Schoonhoven *et al*. (2005) calculan que en la actualidad se han descrito más de un millón de insectos herbívoros. El registro fósil provee las evidencias del desarrollo de esta interacción a lo largo del tiempo que involucra la evolución y adaptación de los actores y del medio ambiente.Labandeira *et al*. (2007) realizaron una guía donde ilustran varios tipos de interacciones principalmente en hojas de angiospermas. Hasta el momento en México Galdámez (2006) registró la presencia de minas y agallas sobre hojas de angiospermas en el Plioceno de Hidalgo. Para el Jurásico, Lozano-Carmona (2012) mencionó la existencia de galerías de descortezadores en la Formación Zorrillo-Taberna indiferenciadas.

La localidad estudiada pertenece a la Formación Otlaltepec, definida por Ortega-Guerrero (1989). Posteriormente, el estudio más detallado de Cruz-Cruz (2012) permite proponer la presencia de un miembro inferior de 197 m y uno superior de 629.5 m. El objetivo del presente trabajo es dar a conocer el registro de la interacción planta-insecto más antiguo realizado en México hasta el momento.

2. Materiales y métodos

Se recolectaron improntas en la localidad denominada Cerro el Matador que aflora en las cercanías a Santo Domingo Tianguistengo en el sur del estado de Puebla (Figura 1). La parte inferior del miembro superior de la Formación Otlaltepec está compuesta por arenisca de grano fino y conglomerado (Figura 2). Los ejemplares de estudio están depositados en la Colección Paleontológica de la Facultad de Estudios Superiores Zaragoza (UNAM) bajo las siglas CFZ Ot-01-252. Los fósiles fueron examinados y fotografiados con un microscopio estereoscópico Nikon SMZ. Las fotos digitales se tomaron con una cámara Sony HD. Para la determinación de los especímenes de plantas se emplearon fotos de los tipos y bibliografía especializada. Se determinó el tipo de interacción planta-insecto que se presenta, agrupándolo de acuerdo a la clasificación de Vialov (1975).

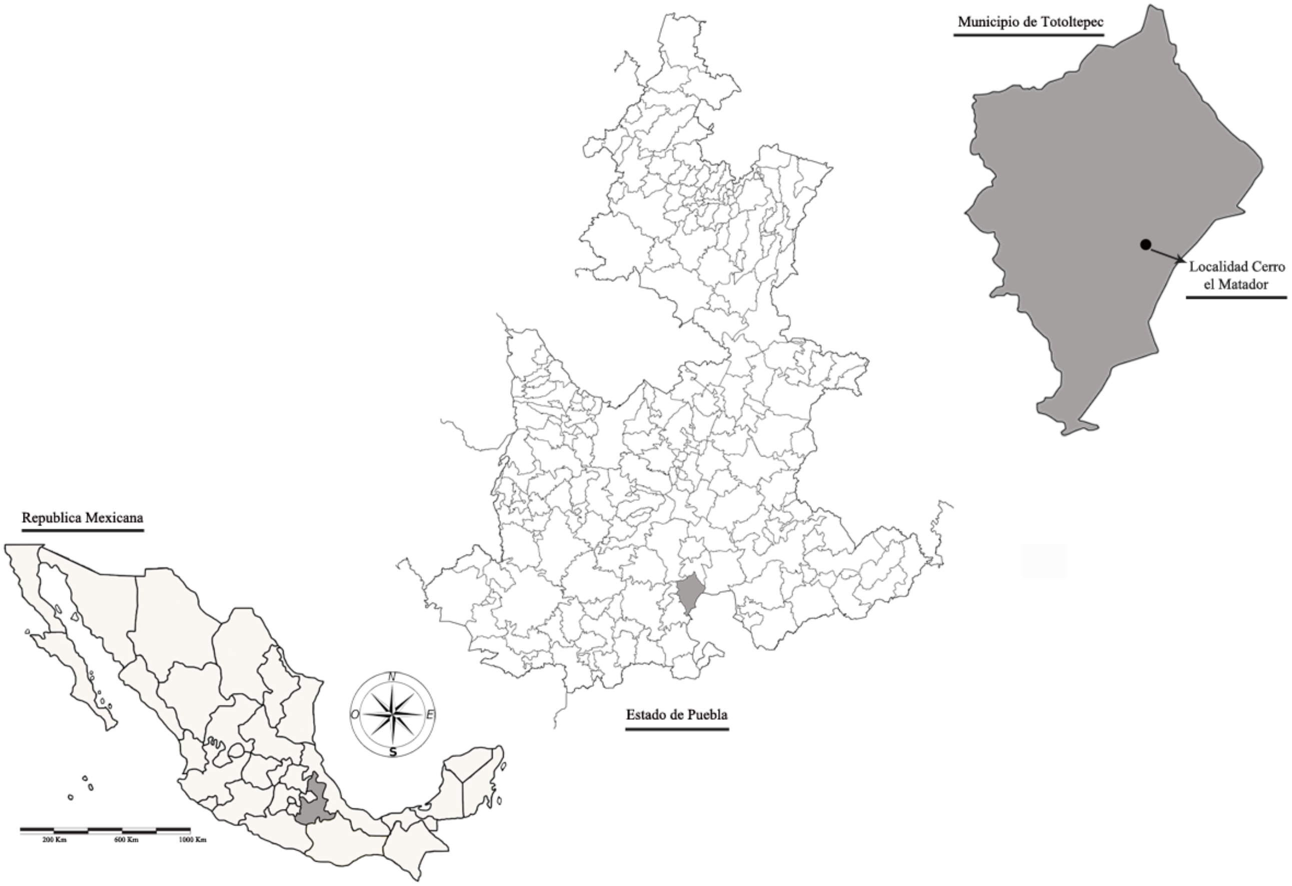

Figura 1. Mapa de ubicación de la localidad Cerro el Matador, estado de Puebla, al sur de la República Mexicana.

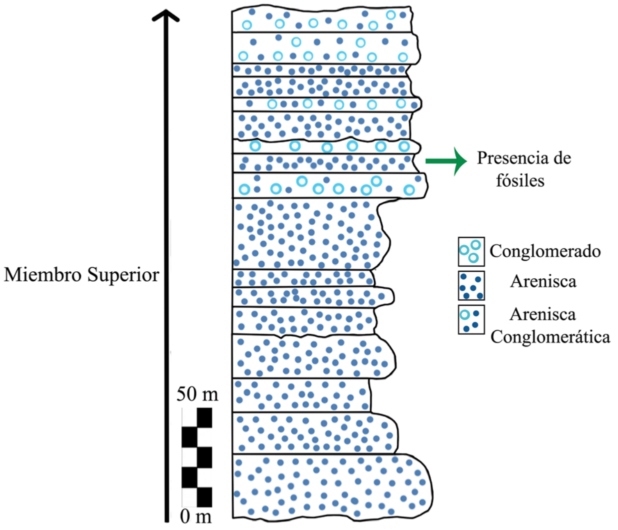

Figura 2. Fragmento del miembro superior de la columna estratigráfica de la Formación Otlaltepec donde se indica la zona de colecta (modificado de Cruz-Cruz, 2012).

3. Resultados

Se revisaron 252 fósiles, que presentaban un buen estado de conservación, interpretándose como flora autóctona; se identificaron diez géneros y 11 especies de gimnospermas (Velasco-de León y Flores-Barragán,2012) (Tabla 1). Las especies de plantas más abundantes son: *Zamites lucerenis* (Wieland) Person y Delevoryas, *Otozamites hespera* Wieland y el género *Brachyphyllum* Brongniart. Solamente 11 hojas muestran señales de actividad, identificándose dos tipos de interacciones diferentes (Tabla 1). De estas, cinco se localizaron sobre *Otozamites hespera*, decreciendo el número por especie. También se observa que la abundancia por tipo de actividades diferente, con una clara predominancia por *O. hespera*.

La interacción por alimentación en el margen (Phagophytichnidae) se da exclusivamente en los géneros *Otozamites* y *Zamites*, variando el tamaño en ambos; su rango comprende de 1 – 5 mm de longitud y de 1 – 8 mm de profundidad; se observa en la parte apical y lateral de las pinnas con un arreglo espaciado (Figura 3A-C). Algunos autores (Scott *et al*., 1992) han puntualizado que si se observa un oscurecimiento en la zona aprovechada significa que el insecto se alimentó cuando la hoja se localizaba aún sobre la planta, lo cual se aprecia en el ejemplar de Puebla.

Al igual que en la interacción anterior las minas (Paleominidae) se observan en *Otozamites* y *Zamites*, sin embargo el mayor número se encuentra en *O. hespera*. Las minas generalmente son solitarias, rectas, con una disposición semiparalela a las venas, con un largo máximo de 23 mm y un ancho de 1 mm (Figura 3D-F); en la Figura 3D se observa una marca donde después de un corto desarrollo la larva sale de la mina, por lo que correspondería a minas temporales en el sentido de Krassilov y Shuklina (2008).

Cabe resaltar que el tipo de interacciones no es excluyente, pues es posible encontrar los dos tipos de interacciones en un mismo ejemplar, lo cual puede ser visto en el espécimen CFZ Ot-44 (Figura 3F).

4. Discusión

En la Tabla 1 se observa que las Bennettitales son el grupo dominante para esta localidad y probablemente su abundancia influyó en ser el grupo seleccionado por los insectos. En el caso de alimentación en el margen (Figura 3 A-C) las zonas aprovechadas son muy similares entre sí, indicándonos que probablemente el mismo grupo de insectos fue el causante; el tipo de daño similar en hojas de diferentes géneros permite suponer que las provocó un organismo de alimentación generalista (Pérez-Contreras, 1999). En la localidad de Yorkshire, Scott *et al*. (1992) reportaron una interacción muy similar en cicadas, estos autores comentan que previo al Cretácico este tipo de daño es raro, sin embargo nuestra localidad corresponde al Jurásico Medio.

Con excepción del ejemplar CFZ Ot-56 las minas se localizan sobre *Otozamites hespera*, todas ellas son similares entre sí (minas temporales), se propone que fueron causadas por insectos monófagos, mostrando una preferencia a *O. hespera*. Krassilov y Shuklina (2008) concluyeron que la mayoría de insectos que construyen minas temporales son monófagos. Lo anterior concuerda con los patrones encontrados en herbivoría después del Triásico. Labandeira (2006) y Scott *et al*. (1992) sugieren que para este tiempo la interacción con el hospedero se hace más específica en la alimentación interna sobre la externa.

En la literatura está poco documentada la presencia de dos tipos de daños sobre el mismo hospedero, como es el caso de *Otozamites hespera* (CFZ Ot-44) donde se localiza alimentación en el margen y minas provocados por dos tipos de insectos; se podría tener dos propuestas para explicar lo anterior: 1) este fósil-taxón no había desarrollado ningún sistema de defensa, por ejemplo y a diferencia de *Anomozamites villousus* que apareció primero en el registro fósil y se supone que sus vellosidades pudieron servir como defensa (Pott *et al*., 2012) ó 2) que esta interacción ha llegado a un equilibrio, dada la abundancia de esta especie en la localidad y a que en ninguno de los casos donde se observa herbívora la lámina se encuentra completamente invadida (Figura 3F). Esto estaría en desacuerdo con la propuesta realizada por Ponomarenko (1998), quien comenta que los bajos niveles de herbivoría en el Mesozoico pueden ser probablemente atribuidos a la estructura xeromórfica de las plantas del Mesozoico con un bajo nivel nutricional y a un gran volumen de tejidos protectores.

Para el Jurásico, autores como Pott *et al*. (2008, 2012) y Popa y Zaharia (2011) consideran que falta por esclarecer los

Tabla 1. Número de géneros en la localidad Cerro el Matador y el total de ejemplares que presentan daño en la hoja y el tipo al que corresponde.

Género	**Especie**	**Número de ejemplares**	**Ejemplares con algún daño**	**Alimentación al margen**	**Minas**
Cycadolepis	*Cycadolepis mexicana*	1	0	-	-
Otozamites	*Otozamites hespera*	38	**5**	2	3
Otozamites	*Otozamites mandeloshni*	1	0	-	-
Otozamites	*Otozamites* sp.	1	0	-	-
Pterophyllum	*Pterophyllum* sp.	1	0	-	-
Ptilophyllum	*Ptilophyllum cutchense*	1	**1**	1	-
Ptilophyllum	*Ptilophyllum* sp.	3	0	-	-
Williamsonia	*Williamsonia huitzilopochtli*	4	0	-	-
Williamsonia	*Williamsonia netzahualcoyotli*	1	0	-	-
Williamsonia	*Williamsonia* sp.	1	0	-	-
Zamites	*Zamites fenionis*	2	**1**	1	-
Zamites	*Zamites lucerensis*	75	**3**	2	1
Zamites	*Zamites oaxacensis*	9	0	-	-
Zamites	*Zamites* sp.	13	**1**	-	1
Brachyphyllum	*Brachyphyllum* sp.	31	0	-	-
Pelourdea	*Pelourdea* sp.	1	0	-	-
Mexiglosa	*Mexiglosa varia*	3	0	-	-
Sphenopteris	*Sphenopteris* sp.	1	0	-	-
Total		**252**	**11**	-	-

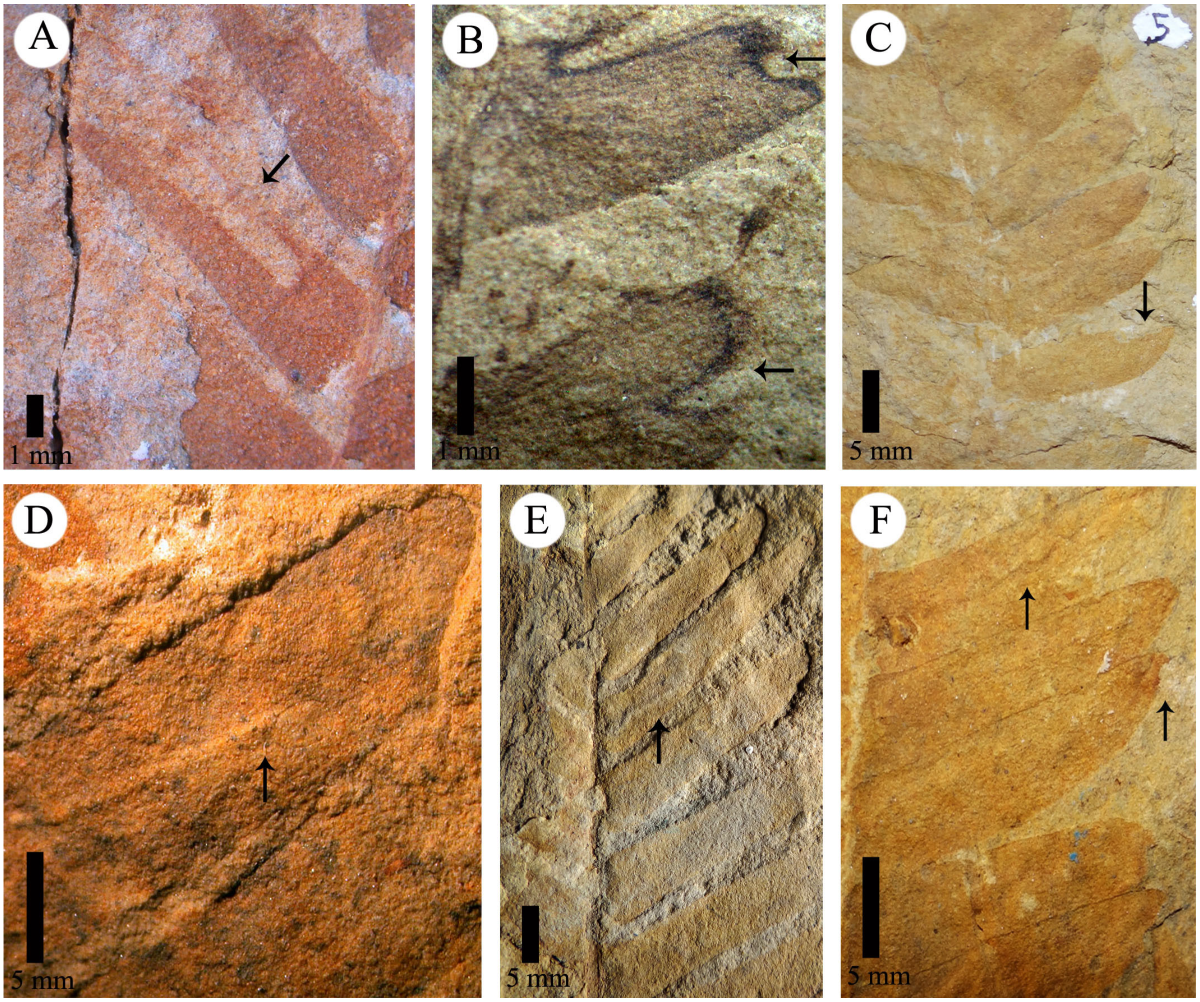

Figura 3. A, alimentación en el margen discontinua sobre hoja de *Zamites lucerensis* (CFZOt-57). B, daño por alimentación externa en el ápice de pina de *Otozamites* sp. (CFZ Ot-87), nótese la zona oscura donde ocurrió necrosis del tejido; el mismo tipo de deterioro se observa en C. C, *Otozamites hespera* (CFZ Ot-57). D – F, minas sobre hojas de *Otozamites hespera* y *Zamites* sp., el tamaño varía en ambos, su rango comprende de 1 – 5 mm de longitud y de 1 – 8 mm de profundidad. D, se observa al final de la mina (flecha) una marca circular, se interpreta como punto de salida del insecto. F, se indica (flechas) alimentación en el margen y presencia de mina sobre un mismo ejemplar (CFZ Ot-44).

patrones de herbivoría, pero las Bennettitales pudieron ser el grupo con más herbívoros de esta edad, lo que corresponde al patrón que se muestra también en esta localidad.

5. Conclusiones

La herbivoría para el Jurásico Medio se restringe hasta el momento a las Bennettitales para la localidad Cerro el Matador, Puebla. La alta herbivoría que se manifiesta en *Otozamites hespera*, probablemente fue causada en el caso de las minas por un insecto monófago. La presencia de un segundo daño por alimentación en el margen, permite proponer que en este fósil-taxón no se aprecia una adaptación, a diferencia de sus géneros afines que se encuentran en esta localidad. Se propone la presencia de por lo menos dos tipos de insectos causantes de los daños ya mencionados. Es necesario continuar el estudio con otras localidades en México para tener una mayor comprensión de este tipo de interacciones.

Referencias

Cruz-Cruz, M.A., 2012, Análisis estratigráfico de la secuencia Jurásica de la región de Santo Domingo Tianguistengo, Oaxaca, Santa Cruz Nuevo Puebla, México: México, Facultad de Geología, UNAM, Tesis de Licenciatura, 109 p.

Galdámez, E.I., 2006, Herviboría en angiospermas fósiles de la Formación Atotonilco El Grande, Hidalgo. México: México, Facultad de Estudios Superiores Zaragoza, UNAM, Tesis de licenciatura, 36 p.

Krassilov, V., Shuklina, S., 2008, Arthropod trace diversity on fossil leaves from the mid-Cretaceous of Negev, Israel: Alavesia, 2, 239–245.

Labandeira, C.C., 2006, Silurian to Triassic Plant and Insect Clades and their associations: New Data, a Review, and interpretations: Arthropod Systematics & Phylogeny, 64 (1), 53–94.

Labandeira, C.C., Wilf, P., Johnson, K.R., Marsh, F., 2007, Guide to Insect (and other) damage types on compressed plant fossils. Version 3.0. Smithsonian Institution, Washington, D.C., 25 p.

Lozano-Carmona, D.E., 2012, Paleoclima y flora fósil de rio Ñumí, Formación Zorrillo-Taberna Indiferenciada, Oaxaca: México, Facultad de Estudios Superiores Zaragoza, UNAM, Tesis de licenciatura, 170 p.

Ortega-Guerrero, B., 1989, Paleomagnetismo y Geología de las unidades clásticas mesozoicas del área de Totoltepec-Ixcaquixtla, Estados de Puebla y Oaxaca, México: Facultad de Ciencias, UNAM, Tesis de maestría, 155 p.

Pérez-Contreras, T., 1999, La especialización en los insectos fitófagos: una regla más que una excepción: Evolución y Filogenia de Arthropoda: Boletín de la Sociedad Entomológica Aragonesa, 26, 759–776.

Ponomarenko, A.G., 1998, Paleobiology of angiospermization: Palaeontological Journal (Russia), 32 (4), 325–331.

Popa, M.E., Zaharia, A., 2011, Early Jurassic ovipositories on bennettitalean leaves from Romania: Acta Palaeontologica Romaniae, 7, 285–290.

Pott, C., Labandeira, C.C., Krings, M., Kerp, H., 2008, Fossil insect eggs and ovipositional damage on bennettitalean leaf cuticles from the Carnian (Upper Triassic) of Austria: Journal of Paleontology, 82, 778–789.

Pott, C., McLoughlin, S., Wu, S.Q., Friss, E.M., 2012, Trichomes on the leaves of *Anomozamites villosus* sp. nov. (Bennettitales) from the Daohugou beds (Middle Jurassic), Inner Mongolia, China: mechanical defense against herbivorous arthropods: Review of Palaeobotany and Palynology, 169, 48–60.

Schoonhoven, L.N., van Loon, J.A., Dicke, M., 2005, Insect-plant Biology: United Kingdom, Oxford University Press, 2nd edition, 421 p.

Scott, A.C., Stephenson, J., Chaloner, W.G., 1992, Interaction and coevolution of plants and arthropods during the Palaeozoic and Mesozoic: Philosophical Transactions of the Royal Society of London, 335, 129–165.

Velasco-de León, M.P., Flores Barragán, M.A., 2012, Estudio taxonómico del registro fósil de gimnospermas, en la formación Otlaltepec. México (Resumen), *en* VI Jornadas Paleontológicas y I Simposio de Paleontología en el Sureste de México, 100 años de paleontología en Chiapas: Tuxtla Gutiérrez, Chiapas, 55 p.

Vialov, O.S., 1975, The fossil traces of nourishment of the insects: Paleontologichesky Sbornik, 1–2, 147–155.

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Un amonite con un traumatismo en la concha del Aptiano (Cretácico inferior) del estado de Durango, norte de México

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Resumen

Por vez primera se reporta en México un amonite del Cretácico inferior con un traumatismo en un flanco. Por medio de un análisis detallado de los trabajos más importantes sobre lesiones en amonites, se compara el traumatismo del ejemplar mexicano con las tipologías más similares. Esto nos permite identificar el tipo particular de lesión a la que corresponde y su posible origen. El ejemplar estudiado se asigna a la forma *verticata* Rippenscheitelung, la cual se asocia a lesiones en la concha que dañan el manto.

Palabras clave: lesión, amonite, *verticata*, Cretácico inferior, México.

Abstract

For the first time, a Lower Cretaceous ammonite with a trauma on the flank is reported in Mexico. We compare the trauma of the Mexican specimen with the most similar typologies through an accurate analysis of the most important papers about injuries in ammonites. This allows us to identify the particular type of injury and its possible origin. The studied sample is assigned to the forma verticata *Rippenscheitelung, which is related to injuries that damage the shell mantle.*

Keywords: injury, ammonite, verticata*, Lower Cretaceous, Mexico.*

1. Introducción

Los amonites con presencia de traumatismos han sido ampliamente estudiados, especialmente en los últimos 35 años (*e.g.* Hengsbach, 1979, 1996; Keupp e Ilg, 1992; Larson, 2007; Hammer y Bucher, 2005). Gracias a estos trabajos se ha generado una amplia terminología específica para los diferentes tipos de traumatismo con base al tipo de morfología, lesión y reparación. En muchos casos se conocen los procesos que ocasionaron las lesiones, tales como traumatismos e interacciones paleoecológicas (*e.g.* parasitismo). Para una adecuada interpretación de las causas que generan dichos traumatismos muchos autores las han comparado con procesos similares que ocurren en organismos actuales como por ejemplo en el caso de *Nautilus* (*e.g.* Arnold, 1985). En el presente trabajo se analiza un chelonicerátido que presenta una lesión en la concha colectado por el tercer autor (J.Q.-B.) procedente del Aptiano inferior terminal de la Formación La Peña de la Sierra del Rosario, estado de Durango, norte de México. Este ejemplar se halla depositado en el Museo Paleontológico de la Laguna (= MPL) en Torreón, estado de Coahuila. Dicho fósil se compara con otros amonites que presentan lesiones figurados en la literatura y se asigna a una tipología, para posteriormente discutir las posibles causas que la originaron. Hasta la presente contribución no existían trabajos que estudiaran traumatismos en amonites del Cretácico inferior de México, por lo que esta es la primera aportación.

2. Material

Un único ejemplar, MPL-104, preservado como un molde interno calizo; se trata de una macroconcha con un diámetro máximo de 30.5 cm. El ejemplar es un chelonicerátido. Sin embargo la denominación genérica es complicada pues podría pertenecer al género *Cheloniceras* Hyatt, 1903 (Aptiano inferior) o al género *Epicheloniceras* Casey, 1954 (Aptiano superior), pero la preservación y el estado ontogénetico del ejemplar estudiado impide su identificación genérica con una total certeza. El género *Epicheloniceras* se caracteriza por la presencia de dos filas de tubérculos ventrales y una depresión sifonal. En el género *Epicheloniceras* los tubérculos ventrales están únicamente sobre costillas primarias, que además son algo más anchas que las secundarias, hecho que permite diferenciar claramente ambos tipos de costillas en vista ventral. En cambio, *Cheloniceras* no posee ninguno de estos elementos ornamentales en la región ventral, siendo imposible diferenciar entre costillas primarias y secundarias. Los caracteres del género *Epicheloniceras* que permiten la diferenciación genérica desaparecen durante el desarrollo ontogenético, estando únicamente presentes en formas juveniles, adquiriendo posteriormente los caracteres plesiomórficos del género *Cheloniceras*. Sin embargo, el ejemplar objeto de estudio posiblemente corresponda al género *Cheloniceras* pues se registra conjuntamente con un nautílido, *Heminautilus* cf. *lallierianus* (d'Orbigny, 1841), forma que está restringida al Aptiano inferior.

3. Descripción de la lesión del ejemplar estudiado MPL-104

El ejemplar estudiado muestra en el flanco derecho (Figuras 1A, 2 y 3) un conspicuo traumatismo ubicado en el tercio superior del mismo, no estando alterada la ornamentación en las otras áreas de la concha (Figura 1B-D). El traumatismo es muy notorio en la última vuelta del ejemplar. Sin embargo, es poco visible en el cuarto terminal de la vuelta, la zona más próxima a la abertura de la concha, debido a que el fósil se halla bastante erosionado. La región umbilical se encuentra cubierta por matriz, con lo que no es posible saber donde se inicia el traumatismo. Este consiste en un marcado chevron de las costillas de uno de los flancos con un ángulo agudo de unos 40 grados en sentido adapical. En términos generales, las costillas se unen en el vértice del *chevron* salvo alguna excepción, donde parece no llegar a tocarse, existiendo un espacio entre ambas.

4. Antecedentes de traumatismos similares al ejemplar MPL-104

A continuación se presentan algunos de los ejemplos más destacables existentes en la literatura de traumatismos muy similares al aquí estudiado. Uno de los más antiguos sería el deshayesítido del Aptiano inferior figurado por Semenov (1899, lámina 3, figura 11) que muestra en medio del flanco una lesión caracterizada por costillas dispuestas en *chevron.* Casi sesenta años después, Hölder (1956, figuras 3, 4 y 6) ilustra varios amonites jurásicos con lesiones muy similares a la aquí estudiada, las cuales se hallan ubicadas en la mitad del flanco o en el tercio superior del mismo. En los tres ejemplos figurados por este autor las costillas no se unen en el vértice de los *chevron*. Esta tipología de lesión es nombrada como forma *verticata*. Keupp (1973) ilustra varias estructuras de costillas dispuestas en *chevron* (Keupp, 1973, figuras 6, 7 y 9) sumamente parecidas a las del ejemplar estudiado sin asignarlas a ninguna tipología. Posteriormente, el mismo autor (Keupp, 1976) ejemplifica varias formas con distintas lesiones, siendo nuevamente la forma verticata la más similar al ejemplar aquí estudiado. Las formas figuradas por este autor muestran su *chevron* característico mayoritariamente en la zona ventral (Keupp, 1976, figuras 1, 2 y 4). En este mismo trabajo, Keupp divide la forma *verticata* en dos tipologías. La primera Rippenscheitelung (= costillas con vértice), consiste en un *chevron* donde las costillas o líneas de crecimiento se unen en el vértice. En la segunda tipología, Rippenknickung (= costillas curvas), las costillas o líneas de crecimiento no se unen en el vértice, siendo interrumpidas por un canal central o cicatriz. En un trabajo posterior se figuran también amonites con la presencia del *chevron* característico asignándolos a la forma *verticata* (Keupp e Ilg, 1992, figuras 4, 5, 12, tabla 1). Los traumatismos figurados en dicho trabajo se localizan principalmente en el tercio superior del flanco, al igual que en el ejemplar estudiado. Ese mismo año, Thomel muestra un amonite cenomaniano con una lesión prácticamente idéntica (Thomel, 1992, lámina 49, figura 4), sin asignar la misma a ninguna tipología en particular. Es destacable que las costillas dispuestas en *chevron* del ejemplar de Thomel aparecen en torno a la mitad de la última vuelta, no estando presentes antes. Seltzer (2001, lámina 3, figura 3) figura una estructura de costillas dispuestas en *chevron* que no asigna a ninguna tipología en particular. Es remarcable mencionar que la misma se halla en el tercio inferior del flanco. Larson (2007, figura 16.14a-c) figura un amonite con desplazamiento de costillas en forma de *chevron* en el último tercio del flanco y otros dos ejemplares que presentan esta misma lesión en la zona ventral. Este autor atribuye estas lesiones, muy similares al amonite objeto de estudio, a la forma *syncosta*. Zatoń (2010) figura ampliamente la forma verticata constatando nuevamente que se trata de uno de los traumatismos más comunes entre los amonoideos. Slotta *et al*. (2011, figura 6), ilustra la presencia de un *chevron* en

Figura 1: Ejemplar MPL-104 vistas laterales, A y B, adoral, C, y ventral, D. La escala gráfica equivale a un centímetro.

las líneas de crecimiento de un amonoideo del Paleozoico atribuyéndolo a la forma verticata.

5. Asignación del ejemplar a una tipología y discusión

Los trabajos previos muestran que la lesión del amonite mexicano debe ser asignada a la forma *verticata*. No obstante, existen unas pocas excepciones que asignan tipologías similares a la forma *syncosta*. Este sería el caso del trabajo de Keupp (1973), donde se ilustran varias estructuras de costillas dispuestas en *chevron* (Keupp, 1973, figuras 6, 7 y 9) sin asignarles tipología alguna. Sin embargo, posteriormente Larson (2007) las atribuyó a la forma *syncosta*. Larson figura otros ejemplares en su trabajo (Larson, 2007, figura 16.14a, b y c) con una lesión muy similar a la del ejemplar mexicano asignándolas también a la forma *syncosta*. La forma *syncosta* es de difícil interpretación, siendo las fuentes más fiables el trabajo original donde se describió (Hengsbach, 1979) y un trabajo posterior del mismo autor (Hengsbach, 1996). Keupp e Ilg (1992) contribuyen a la dificultad de reconocer

Figura 2: Vista del flanco del ejemplar MPL-104 afectado por la lesión constituida por un marcado *chevron* en las costillas de la última vuelta de la concha. La escala gráfica equivale a un centímetro.

Figura 3: Dibujo de la vista del flanco del amonite MPL-104 donde se ilustra la lesión. La escala gráfica equivale a un centímetro.

la forma *syncosta* atribuyéndola a una variedad de la forma *substructa*. La forma *substructa*, de acuerdo a la descripción original de Hölder (1973), está asociada a una ruptura no letal de la concha, tras la cual se regenera pero muestra una pequeña distorsión en la disposición de la ornamentación. Hengsbach (1979) describió la forma *syncosta* sin figurarla refiriéndose a unos *Amaltheus* ilustrados por Heller (1964). La forma *syncosta* consiste en la unión anómala de dos costillas independientes en una carena ventrolateral nodulosa. Claramente, la tipología *syncosta* según la concepción original de Hengsbach (1979), es fácilmente discernible de la *verticata*, la cual no está asociada a un relieve positivo de la concha tipo carena nodulosa. En nuestra opinión los traumatismos similares al ejemplar mexicano ilustrados por Keupp (1973) y los mostrados por Larson (2007) se corresponden, en realidad, a la forma *verticata* tal como es el caso del ejemplar MPL-104. En el caso del ejemplar mexicano es además posible atribuirlo específicamente a la forma *verticata* Rippenscheitelung, pues en términos generales las costillas convergen en los vértices de los *chevron* (Figura 3).

6. Causas que originan la tipología *verticata*

Las patologías existentes en los amonites son sumamente diversas e incluyen diferentes morfologías; algunas de ellas consisten en deformaciones de la concha como en el caso de la forma *inflata*, caracterizada por la presencia de protuberancias; la forma *undaticarinata*, que implica un desplazamiento de una parte de la concha respecto al plano de simetría; y la forma *gigantea*, que consiste en un gigantismo mórbido. Sin embargo, Kröger (2002) plantea que no todas las lesiones producen deformaciones en la concha, ya que algunas sólo afectan los patrones de ornamentación como en el caso de la forma *cacoptycha*, que consiste en una reducción o desaparición de elementos ornamentales en una parte de la concha; o las formas *substructa* y *verticata*, que hacen referencia al desplazamiento de las costillas o líneas de crecimiento. La nomenclatura desarrollada para nombrar las distintas tipologías es descriptiva, pero en algunos casos también se conocen las diferentes causas que las originan, por ejemplo: Hengsbach (1996) relaciona las formas *inflata* y *undaticarinata* a la presencia de parásitos que causan las deformaciones de la concha. Keupp (2006) describe la forma *fenestra* como un caso de compensación ornamental donde se deforma la concha debido a la interacción con depredadores. Larson (2007) indica que la presencia de epibiontes también puede causar perforaciones en la concha dando origen a diferentes tipos de lesiones como fracturas, protuberancias, cicatrices y depresiones.

En el caso de la forma *verticata*, que es el traumatismo que nos ocupa, han sido varias las interpretaciones que ha recibido por lo que hace referencia a las causas que la originan. Uno de los primeros trabajos que interpreta el origen de la forma verticata es Hölder (1970) que propone que el manto es dañado y se regenera retrocediendo respecto a su posición original. Keupp (1979) incluye el parasitismo como una posible causa de la forma *verticata*, y posteriormente, Keupp e Ilg (1992), atribuyen la forma *verticata* a una lesión puntual causada probablemente por cangrejos, teniendo como referencia las lesiones en nautilos actuales. Ese mismo año Keupp (1992) indica que gasterópodos y pelecípodos también pueden lesionar el manto de nautílidos y amonites causando posteriormente un surco o cicatriz en la concha. Hengsbach (1996) interpreta la forma *verticata* como el resultado de una lesión externa y mecánica más o menos puntual, siendo una de las lesiones más comunes. Explica también que en la forma *verticata* tipo Rippenscheitelung el tejido del manto fue dañado superficialmente pero continuó funcionando con cierta normalidad. Por lo contrario, en la forma *verticata* tipo Rippenknickung el daño condujo a una disfunción local del manto que produjo la cicatriz ubicada en los vértices del *chevron*. Kröger (2002) señala que la tipología *verticata* no afecta la forma de la concha pero en cambio sí causa fuertes anomalías en la ornamentación mediante la presencia de compensación ornamental. En el caso de la forma *verticata*, esta compensación se produce mediante la presencia de costillas y/o líneas de crecimiento dispuestas en forma de *chevron* y relaciona la presencia de la forma *verticata* con lesiones producidas por ostras, braquiópodos y cirrípedos. Zatoń (2010) confirma que la forma *verticata* está relacionada a lesiones subletales, es decir, que el individuo puede seguir viviendo y alcanzar la madurez después de la lesión.

El amonite mexicano, atribuible a la forma *verticata* Rippenscheitelung, sufrió una lesión en la concha que dañó el manto, pero esa afectación no fue muy severa. Son diversos los grupos de organismos que pudieron originar la lesión del amonite aquí estudiado, tales como cangrejos, braquiópodos, cirrípedos, gasterópodos y pelecípodos. La Formación La Peña, en el área de donde procede el ejemplar estudiado, contiene de forma casi exclusiva fósiles de amonites y nautílidos. La falta de registro significativo de otros grupos fósiles impide inferir que organismos pudieron ocasionar la lesión en la concha del amonite.

7. Conclusiones

Por primera vez se estudia detalladamente una lesión en un amonite del Cretácico inferior de México asignándose a la forma *verticata* Rippenscheitelung. Este traumatismo se atribuye a lesiones en la concha que dañan el manto. Se estima que dicha afectación no fue muy severa en el caso que nos ocupa.

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Referencias

Arnold, J.M., 1985, Shell Growth, Trauma, and Repair as an Indicator of Life History for *Nautilus*: The Veliger, 27 (4), 386–396.

Casey, R., 1954, New genera and subgenera of Lower Cretaceous ammonites: Journal of the Washington Academy of Sciences, 44 (4), 106–115.

Hammer, Ø., Bucher, H., 2005, Models for the morphogenesis of the molluscan shell: Lethaia, 38 (2), 111–122.

Heller, F., 1964, Neue Fälle von Gehäuse-Mibildungen bei Amaltheiden: Paläontologische Zeitschrift, 38 (3/4), 136–141.

Hengsbach, R., 1979, Weitere Anomalien an Amaltheen-Gehäusen (Ammonoidea; Lias): Senckenbergiana Lethaes, 60 (1/3), 243–251.

Hengsbach, R., 1996, Ammonoid pathology, *en* Landman, N.H., Tanabe, K., Davis, R.A. (eds), Ammonoid paleobiology: New York, Plenum Press, 581–605.

Hölder, H., 1956, Über Anomalien an jurassischen Ammoniten: Paläontologische Zeitschrift, 30 (1/2), 95–107.

Hölder, H., 1970, Anomalien an Molluskenschalen, insbesondere Ammoniten und deren Ursachen: Paläontologische Zeitschrift, 44 (3/4), 182–195.

Hölder, H., 1973, Miscellanea cephalopodica: Münstersche Forschung zur Geologie und Paläontologie, 29, 39–76.

Hyatt, A., 1903, Pseudoceratites of the Cretaceous: Monographs of the United States Geological Survey, 44, 1–151.

Keupp, H., 1973, Der Wert anomaler Perisphincten (Ammonoidea) für die Deutung der Parabelgenese: Geologische Blätter für Nordost-Bayern und angrenzende Gebiete, 32 (1), 20–35.

Keupp, H., 1976, Neue Beispiele für den Regenerationsmechanismus bei verletzten und kranken Ammoniten: Paläontologische Zeitschrift, 50 (1/2), 70–77.

Keupp, H., 1979, Nabelkanten-Präferenz der forma *verticata* Hölder 1956 bei Dactylioceraten (Ammonoidea, Toarcien): Paläontologische Zeitschrift, 53 (3/4), 214–219.

Keupp, H., 1992, Rippenscheitel bei Ammoniten Gehäusen: Fossilien, 1992 (5), 283–290.

Keupp, H., 2006, Sublethal punctures in body chambers of Mesozoic ammonites (form *aegra fenestra* n.f.), a tool to interpret synecological relationships, particularly predator-prey interactions: Pälaontologische Zeitschrift, 80 (2), 112–123.

Keupp, H., Ilg, A., 1992, Paläopathologie der Ammonitenfauna aus dem Obercallovium der Normandie und ihre palökologische Interpretation: Berliner Geowissenschaftliche Abhandlungen (E), 3, 171–189.

Kröger, B., 2002, Antipredatory traits of the ammonoid shell – Indications from Jurassic ammonoids with sublethal injuries: Paläontologische Zeitschrift, 76 (2), 223–234.

Larson, N.L., 2007, Deformities in the Late Callovian (Late Middle Jurassic) ammonite fauna from Saratov, Russia, *en* Landman, N.H., Davis, R.A., Mapes, R.H.. (eds.), Cephalopods present and past: new insights and fresh perspectives: Dordrecht, Springer, 344–374.

Orbigny, A. D', 1841, Paléontologie française. Description zoologique et géologique de tous les animaux mollusqes et rayonnés fossiles de France. Terrains Crétacés. 1, Céphalopodes. Part II (1841): París, Cosson, 121–430.

Seltzer V.B., 2001, About anomal shells from the Callovian ammonites: Transactions of the Scientific Research Geological Institute of the N. G. Chernyshevskii Saratov State University, New Series, 8, 29–45. [en Ruso]

Semenov, V.P., 1899, The fauna of the Cretaceous deposits of Mangychlak and some other localities in the Transcaspian province: Trudy Imperatorskogo Sankt Petersburgskogo Obshchestva Estestvoispytatelei, 28 (5), 1–178. [en Ruso]

Slotta, F., Korn, D., Klug, C., Kröger, B., Keupp, H., 2011, Sublethal shell injuries in Late Devonian ammonoids (Cephalopoda) from Kattensiepen (Rhenish Mountains): Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen, 261 (3), 321–336.

Thomel, G., 1992, Ammonites du Cénomanien et du Turonien du Sud-Est de la France. Tome 2: Nice, Serre Editeur.

Zatoń, M., 2010, Sublethal injuries in Middle Jurassic ammonite shells from Poland: Geobios, 43 (3), 365–375.

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The Cretaceous corals from the Bisbee Group (Sonora; Late Barremian - Early Albian): Solenocoeniidae

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Abstract

The current work constitutes the third part of the systematic revision about the corals from the Bisbee Group (Late Barremian to Early Albian) and deals with the Solenocoeniidae. This family taxon is applied instead of the poorly defined Cyathophoridae. The family has three genera in the Cretaceous of Sonora: *Confusaforma*, *Cryptocoenia*, and *Cyathophoropsis*. To distinguish samples within the Sonoran fauna and species of this genus, systematic measurements of the corals were taken and statistically analysed. From the Bisbee Group, two *Confusaforma*, six *Cryptocoenia*, and one *Cyathophoropsis* species are here described and illustrated. Most are common Early Cretaceous species with a wide geographic and stratigraphic distribution.

Keywords: corals, Scleractinia, Early Cretaceous, Bisbee Group.

Resumen

El presente trabajo constituye la tercera parte de la revisión sistemática de los corales del Grupo Bisbee (Barremiano temprano a Aptiano tardío), la cual trata sobre la familia Solenocoeniidae, que se ha aplicado en lugar de la familia Cyathophoridae la cual se encuentra mal definida. La familia tiene tres géneros en el Cretácico de Sonora: Confusaforma, Cryptocoenia y Cyathophoropsis. Para distinguir las muestras dentro de la fauna y las especies del género se hicieron mediciones sistemáticas de los corales y se analizaron estadísticamente. Del Grupo Bisbee se describen e ilustran dos especies del género Confusaforma, seis especies del género Cryptocoenia, y una especie del género Cyathophoropsis. La mayoría de ellas son especies comunes en el Cretácico Temprano con una distribución geográfica y estratigráfica amplia.

Palabras clave: corales, Scleractinia, Cretácico Temprano, Grupo Bisbee.

1. Introduction

Building off the first part of the series (Löser, 2011), which introduced the Early Cretaceous (Late Barremian to Albian) coral fauna from the Bisbee Basin, this third part deals with material traditionally assigned to the very common coral family Cyathophoridae Vaughan and Wells, 1943. After re-examination of relevant material of the type from the type species of *Cyathophora*, *Cyathophora richardi* Michelin, 1843, it was concluded that the family Cyathophoridae, based on this genus, could no longer be used because the type material is poorly preserved and contradicts its ascribed characteristics. Instead of the Cyathophoridae, the family Solenocoeniidae Roniewicz, 2008 is applied here. The definition of the subfamily Cyathophorinae Vaughan and Wells, 1943 and its later elevation into the range of a family by Alloiteau (1952) was not accompanied by a diagnosis based on the correct type material.

Four genera belonging to this family occur in the study area: *Confusaforma* Löser, 1987, *Cryptocoenia* Orbigny, 1849, *Cyathophoropsis* Alloiteau, 1946, and *Holocystis* Lonsdale, 1849. The latter genus was revised in Löser (2006), and Sonoran material was included (*Holocystis* *dupini*, *Holocystis elegans*). Three of the four genera were reported in previous studies (Baron-Szabo and González-León, 1999, 2003), but newly collected material allows for an increase in the number of species. Details on the study area, lithology, stratigraphy, and outcrops are reported in Löser (2011). Details on the sample locations cited in the occurrence section in the systematic description are given in Löser (2011: tab. 1).

2. Material

The material varies in its state of preservation. Samples from marly layers are slightly better preserved than samples from carbonates. For the latter, it was more difficult to obtain good thin sections for the purpose of exact measurements and illustrations. Colony surfaces are rarely well preserved. Only thin sections were used for the determination. All specimens described here are kept at the Universidad Nacional Autónoma de México, Instituto de Geología, Estación Regional del Noroeste in Hermosillo, Sonora, México (ERNO). The material described by Baron-Szabo and González-León (1999, 2003) was available for study and, for many specimens, further thin sections were prepared to specify the morphology and taxonomy of species described by the two authors.

3. Methods

3.1. Sample preparation

Thin sections were prepared, all from well-preserved samples in both transversally and longitudinally oriented directions, where possible. The thin sections were scanned using a flatbed scanner with an optical resolution of 6400 dpi. The images were saved as 8-bit grey scale JPG files without compression. To increase the quality of the images, contrast stretching was applied. The images were used to prepare illustrations and to systematically record calicular dimensions.

3.2. Species separation

Traditionally, species separation in *Cryptocoenia* is based on the calicular diameter and the number of septal cycles that occur in a general hexameral symmetry. The number of septa within one specimen is relatively constant, and the (smaller) calicular diameter shows a low variation (the larger calicular diameter shows a slightly larger variation) in one colony. The differentiation of species is difficult. Statistical analyses yield groups that are not well separated. The definition of the morphologic range of a species depends much on subjective decisions. The number of existing taxa is, therefore, extremely high: the Mid-Jurassic to early Late Cretaceous coral genus *Cryptocoenia* and its synonyms equal, according to the literature, up to 150 species (Lathuilière, 1989; Löser, 2000). Here, species are separated by cluster analysis using the small calicular diameter and the number of septal cycles. About 400 specimens from the Late Jurassic to early Late Cretaceous were included; among them were 64 type specimens. The analysis resulted in 31 species. The definition of what constitutes a species or how large or small the groups are is highly subjective.

Cyathophoropsis is morphologically comparable to *Cryptocoenia* and differs only by a trimeral instead of hexameral symmetry. However, this genus is rarer and more restricted in its stratigraphical distribution. Only about 25 specimens were available, resulting in three species: the type species, *C. ramosa* Hackemesser, 1936, and a yet unnamed species. The same applies to *Confusaforma*; for this genus, 20 specimens were available resulting in three species: the type species and two yet unnamed species. The unnamed species are also represented by Sonoran material, but it does not allow for the establishment of a new species due to its poor state of preservation. *C. carpathica* Kolodziej, 1995 was not included because it shows the presence of a main septum, which is a characteristic unknown from the type species.

3.3. Distribution data

The distribution data (as reflected in the synonymy lists) are entirely based on well-examined material. Material only mentioned in the literature and material not available for study has not been taken into account. To obtain better insight into the distribution patterns of the corals from Sonora, additional unpublished material – indicated by a collection acronym and sample number in parenthesis – was included.

4. Systematic description

4.1. Abbreviations

Collection abbreviations are as follows:

- BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany;
- CGS, Ceská geologická sluzba, Praha, Czech Republic;
- ERNO, Universidad Nacional Autónoma de México, Instituto de Geología, Estación Regional de Noroeste, Hermosillo, Mexico;
- IGM, Instituto de Geología, Ciudad de México, Mexico.
- IRScNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;
- MGSB, Museo Geológico del Seminario de Barcelona, Spain;
- MNHN, Muséum National d'Histoire Naturelle,

Paris, France;

- MV, Vinseum, Vilafranca del Penedès, Spain;
- NHM, The Natural History Museum, London, England;
- NHMW, Naturhistorisches Museum, Wien, Austria;
- PU, Museo di Geologia e Paleontologia dell' Università di Torino, Italy;
- SAZU, Paleontoloski institut Ivana Rakovca, Ljubljana, Slovenia;
- SMF, Senckenbergmuseum, Frankfurt, Germany;
- TUM, The Tohoku University Museum, Sendai, Japan;
- UP, Université de Provence, Marseille, France.

The following abbreviations are used describing the dimensions of the corals:

- ccd, distance between calicular centres;
- cl max, large lumen;
- cl min, small lumen;
- s, number of radial elements in adult calices.

The following abbreviations are used describing the statistical data:

- n, number of measurements;
- min-max, absolute range (mm);
- µ, arithmetic mean (mm);
- s, standard deviation (mm);
- cv, coefficient of variation (%);
- µ±s, first interval (mm).

The abbreviations used in the synonymy lists follow Matthews (1973): *: earliest valid publication of the species name; p: the described material belongs only in part to the species concerned; v: the specimen was observed by the author.

4.2. Taxonomy

Order Scleractinia Bourne, 1900
Suborder ?Stylinina Alloiteau, 1952
Family Solenocoeniidae Roniewicz, 2008

Remarks. Here, it is proposed that the family Cyathophoridae should no longer be used, for the following reasons. The name-giving genus *Cyathophora* is based on *C. richardi* Michelin, 1843. The type material of the species was not available for long; observations on the genus were made on topotypical material (*e.g.*, Alloiteau, 1948). In 2009, the type and figured specimen of *C. richardi* was discovered (MNHN A32288). The specimen was later observed (Zaman and Lathuilière, 2014), but the new illustration is insufficient, and the description corresponds to the concept of the genus, not to the type specimen. Thin sections were not prepared from the type specimen, although it is large and would allow this type of preparation. A diagnosis of the type specimen MNHN A32288 based on the authors' observation would be as follows: Cerioid colony. Calicular outline circular, diameter 6 – 7 mm, centres depressed. Septa compact. Microstructure of septa unknown. Septal outline, thickness, and symmetry unknown. Number of septa *ca*. 30 – 40. Septal length not recognisable. Septa occasionally connected to each other. Septal distal margin, lateral face, and inner margin unknown. Pali or paliform lobes, Columella, and costae unknown. Synapticulae absent. Endotheca consists of regular tabulae and occasional dissepiments. Wall compact, but structure unknown. Coenosteum absent. Budding extracalicinal. Specimen MNHN A32288 corresponds in its septal patterns to the illustration in Alloiteau (1948) and contradicts the characteristics ascribed to the family, where the septa are never connected to each other. Because of this and the poor knowledge on the genus *Cyathophora*, the family Cyathophoridae can no longer be used.

The family taxon Pentacoeniidae with Duncan (1884) as author cannot be applied as proposed by Löser (2014) because Duncan (1884) introduced the name as an Alliance. In the nomenclatory rules, this term is not mentioned as a level of the family group and because Duncan has arranged it below the Tribus, Alliance rather denominates a generic group. This family taxon cannot be used for genera formerly assigned to the Cyathophoridae family.

For the moment, the genera currently belonging to the Cyathophoridae family are assigned to the Solenocoeniidae family. This family is based on the Late Jurassic Solenocoenia Roniewicz, 1976. The genus is closely related to *Cryptocoenia* and differs only by channel-like structures that connect neighboured calices. Lauxmann (1991) considers the genus an intraspecific morphologic variation of *Cryptocoenia* because the presence and abundance of the channels vary much within the colonies.

Systematic position. The family Cyathophoridae was traditionally assigned to the suborder Stylinina because of certain affinities to the family Stylinidae. Gill (1977) proposed to consider the family Stylinidae and suborder Stylinina in a more limited sense. Both are characterised by the presence of an ear-like ornamentation of their inner septal margin (auricula; plural auriculae). Auriculae are also present in the suborder Rhipidogyrina. Members of the Solenocoeniidae (Cyathophoridae) show auriculae only very rarely and can, therefore, not remain in this suborder. The family differs from the Stylinidae also due to the strict absence of a columella. The form of the septa, the poor ornamentation of the distal septal margins and lateral faces, and the well-developed endotheca makes the Solenocoeniidae comparable to the Eugyridae family where all genera are meandroid or hydnophoroid.

Genus *Confusaforma* Löser, 1987

Type species. *Confusaforma weyeri* Löser, 1987 by original designation.

Diagnosis. Cerioid colony. Calicular outline irregular. Septa compact. Microstructure of septa unknown. Septa in cross section thick close to the wall and of triangular outline. Symmetry of septa irregular. Number of septa low (less than 12). Septa very short, reduced to ridges, not connected to each other. No main septum. Septal lateral face smooth, inner margin smooth. Pali or paliform lobes, costae, synapticulae, columella absent. Endotheca consists of numerous and regular tabulae. Wall compact, probably septothecal. Budding extracalicinal, probably also septal.

Species. Formerly described are two species as mentioned above, but there exist more unnamed material. Löser *et al.* (2013a) described a species in open nomenclature from the Late Albian of southern Spain. This species – *C.* aff. *weyeri* – can be only compared to the type species but may represent a new taxon as well. The determination of species in the framework of this study is mainly based on the direct comparison of the calicular dimensions (smaller and larger diameter). Septal counts are not helpful because the formation of septa is irregular and septal numbers are always low.

Confusaforma weyeri Löser, 1987
Figs. 1A-C

v 1909 *Polytremacis glomerata* - Prever, p. 69, pl. 27: 2.

*v 1987 *Confusaforma weyeri* Löser, p. 234, pl. 1: 1-3.

v 1989 *Confusaforma weyeri* Löser 1987 - Löser, p. 104, text-fig. 10-13, pl. 22: 1-5.

v 2003 *Confusaforma weyeri* Löser, 1987 - Baron-Szabo and González León, p. 207, fig. 7B.

v 2014 *Confusaforma weyeri* Löser, 1987 - Löser, p. 46, fig. 7g.

Description. Cerioid coral colony with calices with an irregular outline. Septa almost not visible, without symmetry, in a low number. Endotheca well developed.

Material examined. ERNO 3216.

Dimensions.

(3216)	n	min–max	μ	s	cv	μ±s
cl min	20	0.67–1.06	0.87	0.10	12.4	0.76–0.98
cl max	20	0.93–1.32	1.12	0.10	9.4	1.01–1.22
ccd	20	0.97–1.63	1.27	0.18	14.7	1.08–1.46
s	3–7					

Occurrence in Sonora. Early Albian of Municipio Opodepe, Tuape, Cerro de la Espina.

Occurrence elsewhere. Early Aptian of Italy (Abruzzi, L'Aquila) Monti d'Ocre, Fossa Mezza Spada; Slovenia (West Slovenia) Banskja Planota, Osojnica (SAZU P-525). Early Cenomanian of Greece (Kozani) Kozani, Nea Nikopolis (BSPG 2003 XX 5827). Early Cenomanian (Mantelliceras dixoni Zone) of Spain (Cantabria, Santander) Cobreces,

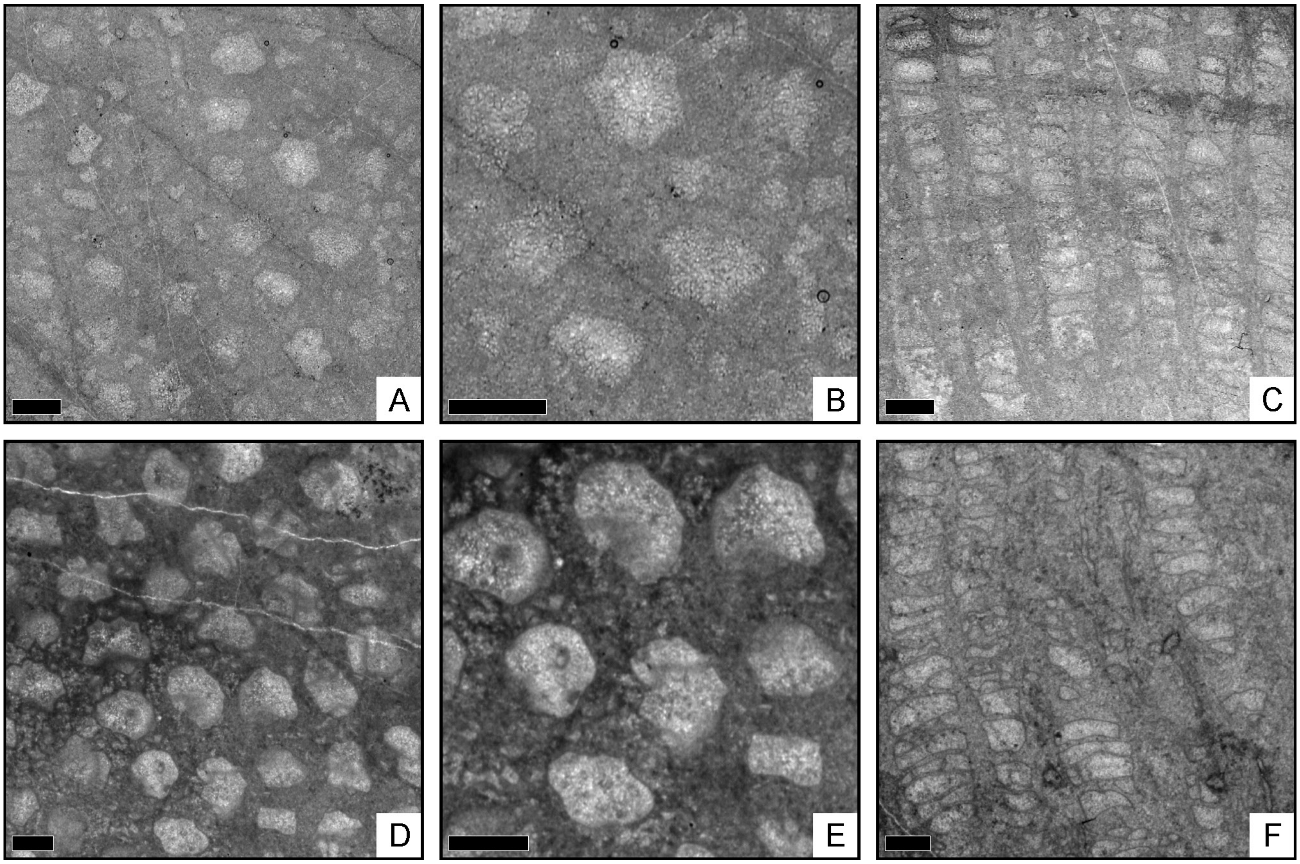

Figure 1. A-C, *Confusaforma weyeri* Löser, 1987, ERNO 3216. A, transversal thin section. B, transversal thin section, detail. C, longitudinal thin section. D-F, *Confusaforma* aff. *weyeri* Löser, 1987, ERNO 3214. D, transversal thin section. E, transversal thin section, detail. F, longitudinal thin section. Scale 1mm.

Luaña playa (BSPG 2007 V 230). Late Cenomanian of the Czech Republic (Central Bohemian region) Kolín, Planany (CGS HF 2476). Late Cenomanian (Actinocamax plenus Zone) of Germany (Sachsen) Dresden-Plauen, Ratssteinbruch.

Confusaforma aff. *weyeri* Löser, 1987
Figs. 1D-F

v 2003 *Confusaforma weyeri* Löser, 1987 - Baron-Szabo and González León, p. 207, fig. 7B.

v 2013a *Confusaforma* sp. - Löser *et al.*, p. 29, pl. 9: 10-12.

Description. Cerioid coral colony with calices with an irregular, circular to rectangular outline. Septa almost not visible, without symmetry, in a low number. Endotheca well developed.

Material examined. ERNO 3179, 3214, L-4251.

Dimensions.

(3214)	n	min–max	μ	s	cv	μ±s
cl min	40	0.81–1.34	1.08	0.13	12.3	0.94–1.21
cl max	40	1.28–1.69	1.45	0.12	8.3	1.33–1.58
ccd	40	1.46–1.99	1.68	0.15	9.1	1.53–1.84
s	3–7					

Remarks. The material differs from the type species by larger dimensions.

Occurrence in Sonora. Early Albian of Municipio Opodepe, Tuape, Cerro de la Espina.

Occurrence elsewhere. Early Valanginian of Spain (Andalucía, Jaén) Sierra de Cazorla, Cabañas, Puerto Llano section (ERNO L-1217079). Early Aptian of Italy (Abruzzi, L'Aquila) Monti d'Ocre, Sotto Colle Pagliare (PU 18162). Early Late Albian (Mortoniceras inflatum Zone) of Spain (Valencia, Alicante) Sierra de Llorença.

Genus *Cryptocoenia* Orbigny, 1849

Type species. *Confusaforma alveolata* Goldfuss, 1826 by monotype.

Diagnosis. Plocoid colony. Calicular outline circular. Septa compact. Microstructure of septa unknown. Symmetry of septa radial and regularly hexameral. Cycles of septa regular. Septal cycles differ in length. Septa short, not connected to each other. Septal lateral face and inner margin smooth. Pali or paliform lobes absent. Costae present, confluent or sub-confluent. Synapticulae and columella absent. Endotheca consists of regular tabulae and occasional dissepiments. Wall compact, probably parathecal. Coenosteum present, consists of costae and tabulae. Budding extracalicinal.

Species. *Cryptocoenia* is – with its synonyms – one of the species-rich coral genera in the Early to early Late Cretaceous. The determination of species in the framework of this study is mainly based on the direct comparison of the calicular dimensions and septal counts of type material and the studied material. This includes uncertainty because, for the majority of the type material, statistical values are not available. These values can only be obtained from a thin section, a peel or a large, well-preserved, polished section. Most type specimens do not have a polished section that would allow for the measuring of these values, and most institutions do not permit making large sections or obtaining thin sections that would result in any destruction of the type specimen. From Sonora, six species are distinguished.

Cryptocoenia almerai (d'Angelis d'Ossat, 1905)
Figs. 2A-C

*v 1905 *Convexastraea almerai* Angelis d'Ossat, p. 213, pl. 14: 11.

vp 2003 *Confusaforma weyeri* Löser, 1987 - Baron-Szabo and González León, p. 207, fig. 7B.

v 2013a *Cryptocoenia almerai* (d'Angelis d'Ossat 1905) - Löser *et al.*, p. 30, pl. 10: 6-7 [= here complete synonymy].

v 2014 *Cryptocoenia almerai* (Angelis d'Ossat, 1905) - Löser, p. 47, fig. 7h.

Description. Plocoid colony with circular calices. Septa very short. Septal cycles do almost not distinguish. Coenosteum narrow, with costae. Endotheca well developed.

Material examined. ERNO 2208, 3187, L-4298.

Dimensions.

(3187)	n	min–max	μ	s	cv	μ±s
cl min	30	1.06–1.52	1.31	0.12	9.7	1.18–1.44
cl max	30	1.29–1.69	1.46	0.11	7.9	1.34–1.58
ccd	30	1.40–1.87	1.59	0.12	8.0	1.47–1.72
s	6+6					

Occurrence in Sonora. Early Albian of Municipio Opodepe, Tuape, Cerro de la Espina.

Occurrence elsewhere. Cretaceous of Greece (Fokída) Kiona massif, Panourgias. Hauterivian to Barremian of Chile (Atacama) Copiapo, Chañareillo, Molle-Alto. Barremian to Early Aptian of France (Bouches-du-Rhône) La Fare, Canal EDF (UP 4758.5). Barremian (*Moutoniceras moutonianum*, *Toxancyloceras vandenheckii*, *Gerhardtia sartousiana* and *Imerites giraudi* zones) of France (Drôme) Serre de Bleyton. Late Barremian to Early Aptian of Poland (Malopolskie). Aptian of Mexico (Puebla) San Juan Raya (IGM 9256). Early Aptian of Greece (Viotía) Arachova; Italy (Abruzzi, L'Aquila) Monti d'Ocre, Fossa Cerasetti; Mexico (Michoacán) Turitzio, Loma de San Juan (ERNO L-4878); Mexico (Puebla) San Juan Raya, Barranca Grande (ERNO L-R11696); Serbia (East Serbia) Pirot, Bela Palanka. Late Aptian of Japan (Iwate-ken) Shimohei-gun, Iwaizumi-cho, Omoto (TUM 65984). Late Aptian (*Acanthohoplites nolani* Zone) of Spain (Cataluña, Barcelona) Comarca del Garraf, Municipi de Vilanova i la Geltrú, Les Mesquites. Albian of Madagascar (Mahajanga) Ampanihy. Earlymost Albian (*Leymeriella tardefurcata* Zone) of Spain (Cataluña, Tarragona) Comarca del Baix

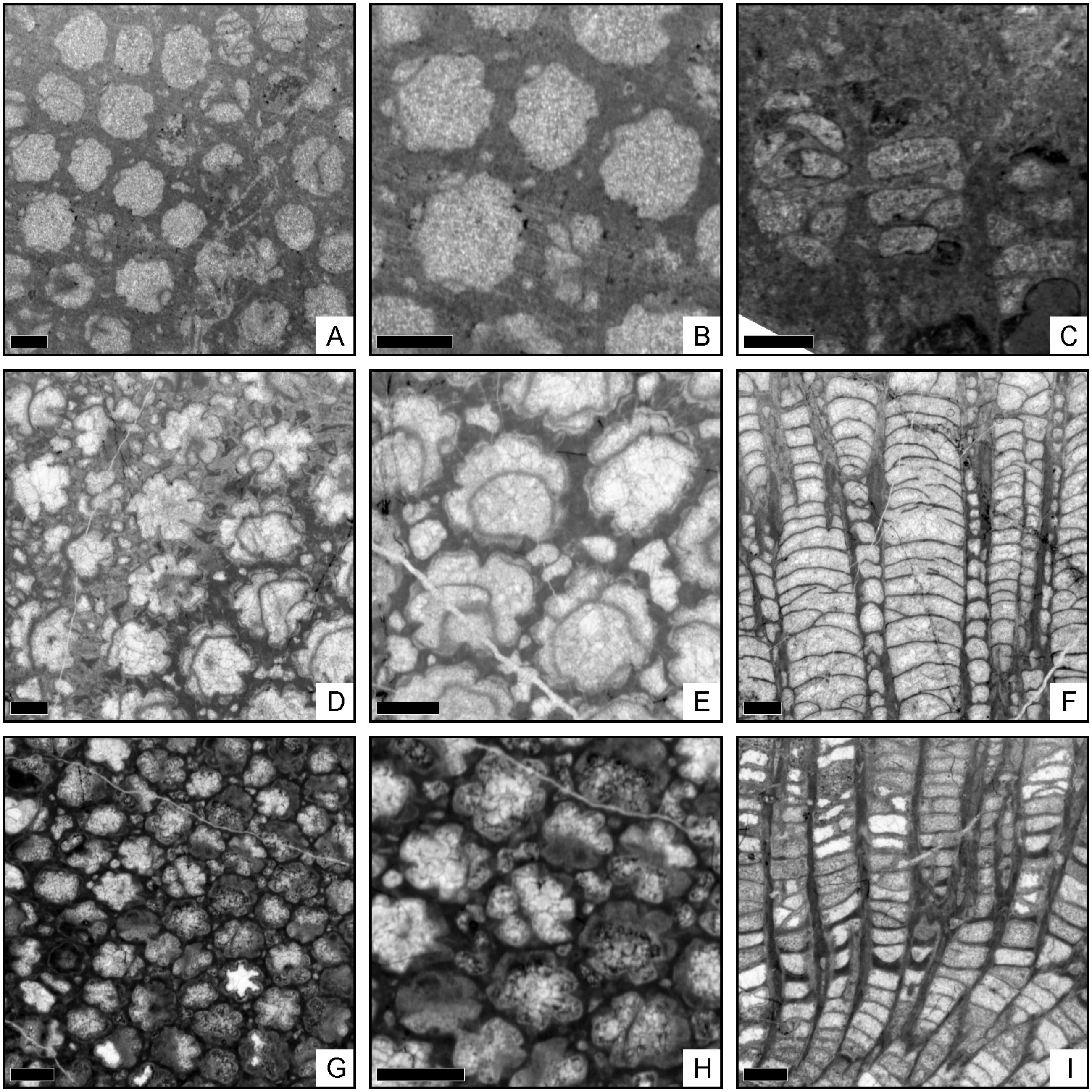

Figure 2. A-C, *Cryptocoenia almerai* (d'Angelis d'Ossat, 1905), ERNO 3187. A, transversal thin section. B, transversal thin section, detail. C, longitudinal thin section. D-F, *Cryptocoenia biedai* (Morycowa, 1964), ERNO L-4267. D, transversal thin section. E, transversal thin section, detail. F, longitudinal thin section. G-I, *Cryptocoenia dubia* (Koby, 1897), ERNO L-4305. G, transversal thin section. H, transversal thin section, detail. I, longitudinal thin section. Scale 1 mm.

Penedés, Municipi del Montmell, Marmellà, Can Xuec (BSPG 2003 XX 6221) and Municipi d'Olivella, Can Grau (MV 12751). Early Albian of Spain (Cantabria, Santander) Cabo de Ajo; Mexico (Baja California) Santo Tomás, Arroyo de la Cueva (ERNO L-1347137). Early to Middle Albian of Spain (Valencia, Alicante) Sierra de Seguili. Late Early Albian (*Douvilleiceras mammillatum* Zone) of Spain (Cantabria, Santander) Cala de Islares (ERNO L-133113). France (Aude) Padern, SE Le Crès, 1.45 km WWS Padern (SMF 75613). Early Late Albian (*Mantelliceras mantelli* Zone) of Spain (Valencia, Alicante) Sierra de Llorença. Late Albian of Spain (Murcia) Jumilla, Sierra del Carche (BSPG 2014 XV 34). Early Cenomanian (*Mantelliceras mantelli* Zone) of Germany (Nordrhein/Westfalen) Mülheim/Ruhr, Kassenberg. Early Cenomanian of France (Charente-Maritime) Fouras (BSPG 2003 XX 1710). France (Charente-Maritime) Ile d'Aix (MNHN). Middle Cenomanian (*Mantelliceras mantelli*, *Mantelliceras dixoni*, *Cunningtoniceras inerme* and *Acanthoceras rhotomagense* zones) of Belgium (Hainaut) Tournai (IRScNB I. G. 5496

/ L16). Early Cenomanian (*Mantelliceras dixoni* Zone) of Germany (Sachsen) Meißen-Zscheila, Trinitatis church. Late Cenomanian (*Cunningtoniceras guerangeri* Zone) of Czech Republic (Central Bohemian region) Korycany (NM O 1875) and Netreba (CGS HF 1502). Late Cenomanian (*Actinocamax plenus* Zone) of Germany (Sachsen) Dresden-Plauen, Ratssteinbruch.

Cryptocoenia biedai (Morycowa, 1964)

Figs. 2D-F

*v 1964 *Adelocoenia biedai* Morycowa, 1964, p. 26, pl. 4: 2, pl. 5: 5.

v 2004 *Adelocoenia desori* (Koby, 1897) - Löser and Mohanti, p. 580, fig. 2ab.

v 2010 *Cryptocoenia ramosa* Toula, 1889 - Löser, p. 595, fig. 3.9.

v 2013 *Cryptocoenia bulgarica* (Toula, 1884) - Löser, p. 33, fig. 11de.

Description. Plocoid colony with circular calices. Septa short. Septal cycles distinguish in septal length. Coenosteum narrow, with costae and exothecal dissepiments. Endotheca well developed.

Material examined. ERNO 2201, L-4267, L-4296, L-4829.

Dimensions.

(L-4267)	n	min–max	µ	s	cv	µ±s
cl min	30	1.54–1.92	1.72	0.12	7.3	1.60–1.85
cl max	30	1.62–2.29	1.97	0.18	9.2	1.79–2.15
ccd	30	1.74–2.35	2.05	0.16	8.0	1.88–2.21
s	6–12					

Occurrence in Sonora. Early Albian of Municipio Arizpe, Arizpe, Cerro La Ceja; Municipio Cucurpe, Cucurpe, La Mesa; Municipio Opodepe, Tuape, Cerro de la Espina.

Occurrence elsewhere. Barremian (*Moutoniceras moutonianum*, *Toxancyloceras vandenheckii*, *Gerhardtia sartousiana* and *Imerites giraudi* zones) of France (Drôme) Serre de Bleyton. Early Aptian of Greece (Viotía) Arachova (BSPG 2003 XX 5456); Mexico (Michoacán) Turitzio, Loma de San Juan (ERNO L-4879), Early Albian of Late Early Albian (*Douvilleiceras mammillatum* zone) of France (Aude) Padern, SE Le Crès, 1.45 km WWS Padern. Cenomanian of Greece (Fokída) Kiona massif, Panourgias (ERNO L-5904); India (Tamil Nadu) Kunnam. Early Cenomanian of Greece (Kozani) Kozani, Nea Nikopolis (BSPG 2003 XX 5848). Early Cenomanian (*Mantelliceras dixoni* Zone) of Germany (Sachsen) Meißen-Zscheila, Trinitatis church (ERNO L-6042). Late Cenomanian (*Cunningtoniceras guerangeri* Zone) of Czech Republic (Central Bohemian region) Korycany, Netreba (CGS HF 1474).

Cryptocoenia dubia (Koby, 1897)

Figs. 2G-I

*v 1897 *Convexastrea dubia* Koby, p. 31, pl. 4: 1-3

v 1932 *Astreopora* (?) *leightoni* Wells, p. 254, pl. 36: 6

v 1964 *Orbignycoenia pygmaea* (Volz, 1903) - Morycowa, p. 30, pl. 4: 1, pl. 7: 1.

v 1976 *Cyathophora pygmaea* Volz 1903 - Turnšek and Buser, p. 11, 38, pl. 1: 1, 2.

Description. Plocoid colony with circular calices. Septa short but well visible. Coenosteum very narrow, with costae and some exothecal dissepiments. Endotheca well developed.

Material examined. ERNO L-4238, L-4269, L-4305, L-4369, L-4428, L-4488.

Dimensions.

(L-4305)	n	min–max	µ	s	cv	µ±s
cl min	50	0.72–1.12	0.91	0.09	10.7	0.81–1.01
cl max	50	0.93–1.31	1.10	0.09	8.9	1.00–1.20
ccd	50	0.80–1.37	1.05	0.14	13.7	0.91–1.20
s	6					

Occurrence in Sonora. Early Albian of Municipio Agua Prieta, E San Bernardino Valley, Cordon Caloso; Municipio Arizpe, Arizpe, Cerro La Ceja; Municipio Opodepe, Tuape, Cerro de la Espina; Municipio Ures, Cerro de Oro.

Occurrence elsewhere. Cretaceous of Slovenia (West Slovenia) Banjska planota, Kanalski Lom. Barremian of France (Doubs) Morteau. Barremian (*Moutoniceras moutonianum*, *Toxancyloceras vandenheckii*, *Gerhardtia sartousiana* and *Imerites giraudi* zones) of France (Drôme) Serre de Bleyton. Early Aptian of Spain (Murcia) Jumilla, Solano del Sopalmo (MGSB 73673); Italy (Abruzzi, L'Aquila) Monti d'Ocre, Fossa Agnese (ERNO L-5306); Poland (Malopolskie, Wadowice) Lanckorona, Jastrzebia. Late Aptian of Spain (Valencia, Castellón) Benicasin, La Venta (MGSB 73722). Early Albian of USA (Texas) Comal County. Early Cenomanian (*Mantelliceras mantelli* Zone) of Germany (Nordrhein/Westfalen) Mülheim/Ruhr, Kassenberg (BSPG 2003 XX 1255).

Cryptocoenia cf. *kiliani* (Prever, 1909)

Figs. 3A-C

v 1964 *Cyathophora minima* Etallon 1862 - Morycowa, p. 22, pl. 3: 1, pl. 5: 4.

v 1981 *Cyathophora pygmaea* Volz 1903 - Turnšek and Mihajlovic, p. 18, pl. 13: 1, 2

vp 2003 *Confusaforma weyeri* Löser, 1987 - Baron-Szabo and González León, p. 207, fig. 7B.

v 2010 *Cryptocoenia miyakoensis* (Eguchi, 1936) - Löser, p. 593, fig. 3.7.

Description. Plocoid colony with circular calices. Septa short. Coenosteum very narrow. Endotheca developed.

Material examined. ERNO 2174, 3209, L-4431, L-4950.

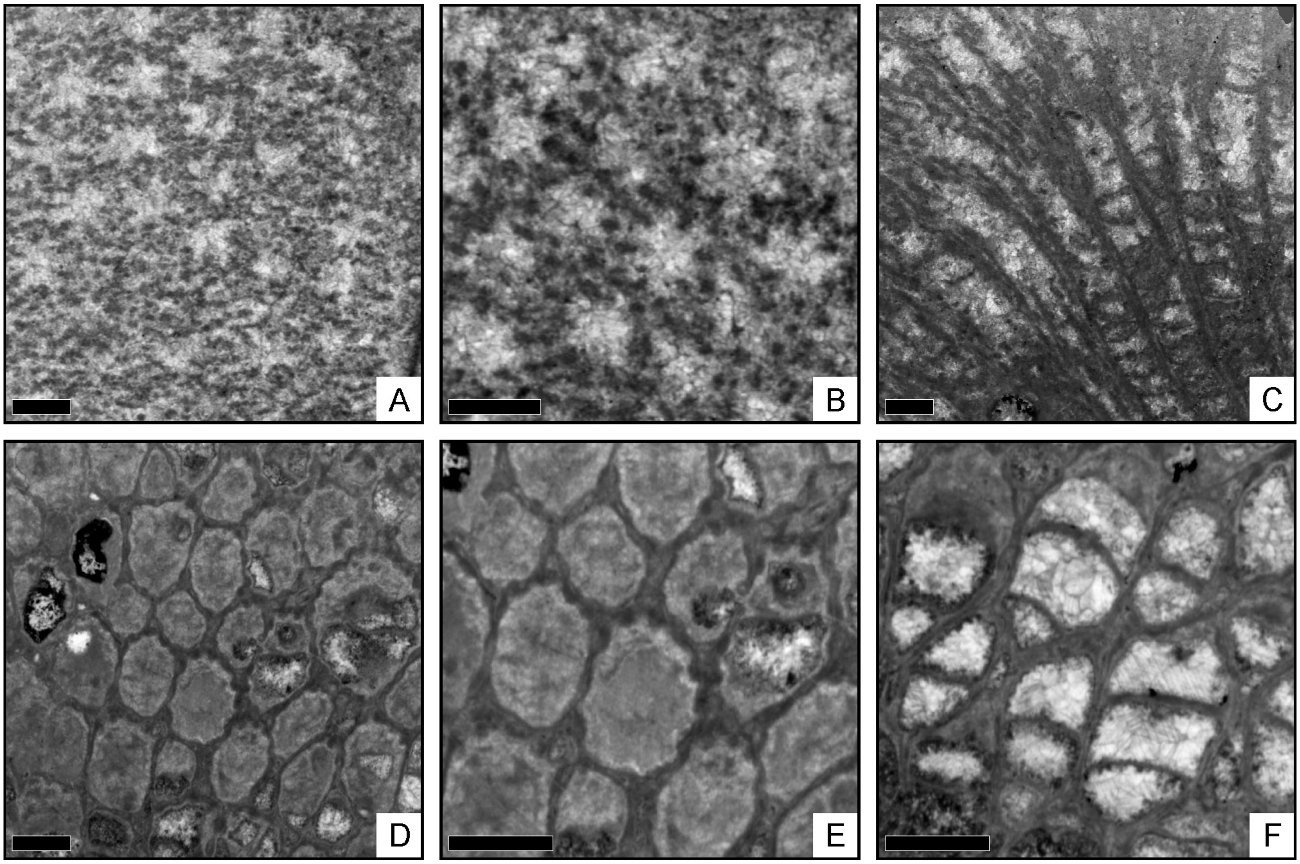

Figure 3. A-C, *Cryptocoenia kiliani* (Prever, 1909), ERNO L-4950. A, transversal thin section. B, transversal thin section, detail. C, longitudinal thin section. D-F, *Cryptocoenia reussiana* (Stoliczka, 1873), ERNO L-4299. D, transversal thin section. E, transversal thin section, detail. F, longitudinal thin section. Scale 1mm.

Dimensions.

(3209)	n	min–max	μ	s	cv	μ±s
ccd	15	0.93–1.38	1.17	0.11	9.6	1.06–1.28
cl min	15	0.78–1.23	1.00	0.11	11.5	0.88–1.11
cl max	15	0.97–1.69	1.31	0.16	12.8	1.14–1.48
s	6					

Remarks. The material differs from *C. kiliani* by larger calicular dimensions.

Occurrence in Sonora. Early Albian of Municipio Opodepe, Tuape, Cerro de la Espina; Municipio Santa Ana, Santa Ana; Municipio Ures, Cerro de Oro.

Occurrence elsewhere. Barremian (*Moutoniceras moutonianum*, *Toxancyloceras vandenheckii*, *Gerhardtia sartousiana* and *Imerites giraudi* zones) of France (Drôme) Serre de Bleyton. Early Aptian of Poland (Malopolskie, Wadowice) Lanckorona, Jastrzebia; Serbia (East Serbia) Sopot. Early Albian of Mexico (Baja California) Santo Tomás, Arroyo de la Cueva (ERNO L-1347115). Middle Albian of Mexico (Sonora) Municipio San Pedro de la Cueva, Tepache, Lampazos area, Espinazo de Diablo (ERNO L-134211).

Cryptocoenia cf. *miyakoensis* (Eguchi, 1936)

Figs. 4AB

Description. Plocoid colony with calices of an irregular outline. Septa short. Coenosteum narrow. Endotheca well developed.

Material examined. ERNO L-4260, L-4283.

Dimensions.

(L-4260)	n	min–max	μ	s	cv	μ±s
cl min	20	1.21–1.46	1.35	0.07	5.4	1.27–1.42
ccd	20	1.41–2.40	1.85	0.29	16.1	1.55–2.15
s	6					

Remarks. The material differs from *C. miyakoensis* by slightly larger dimensions. The material is poorly preserved.

Occurrence in Sonora. Early Albian of Municipio Cucurpe, Cucurpe, La Mesa; Municipio Opodepe, Tuape, Cerro de la Espina.

Occurrence elsewhere. Early Aptian of Greece (Viotía) Levadia, Perachorion (BSPG 2003 XX 5768). Aptian to Early Albian of Japan (Iwate-ken) Miyako-shi, Sakiyama, Hideshima (TUM L-NN-10). Late Aptian of Japan (Miyagi-ken) (TUM L-NN-9). Early Cenomanian of Greece (Kozani) Kozani, Nea Nikopolis (BSPG 2003 XX 5883).

Cryptocoenia reussiana (Stoliczka, 1873)

Figs. 3D-F

*v 1873 *Astrocoenia reussiana*, Stoliczka, p. 27, pl. 5: 3, 4.

v 1947 *Cyathophora fontserei* Bataller, p. 48, text-fig.

v 1971 *Cyathophora pygmaea* Volz, 1903 - Morycowa, p. 40, text-fig. 6 b, 6 c, pl. 5: 1.

v 1974 *Cyathophora pygmaea* Volz - Turnšek and Buser, p. 12, 33, pl. 4: 1.

v 1981 *Cyathophora pygmaea* Volz 1903 - Turnšek and Mihajlovic, p. 18, pl. 13: 1, 2.

v 1994 *Adelocoenia pygmaea* (Volz 1903) - Löser, p. 10, text-fig. 4, 5, pl. 12: 1, 2.

v 2013b *Cryptocoenia fontserei* (Bataller, 1947) - Löser et al., p. 66, pl. 9: 7-9.

Description. Plocoid colony with circular calices. Septa extremely short, almost not visible. Septal cycles do not distinguish. Coenosteum very narrow. Endotheca developed.

Material examined. ERNO L-4236, L-4299.

Dimensions.

(L-4299)	n	min–max	µ	s	cv	µ±s
cl min	30	0.75–1.00	0.88	0.07	9.0	0.80–0.96
cl max	15	0.99–1.40	1.22	0.14	11.7	1.07–1.36
ccd	30	0.85–1.40	1.06	0.14	13.9	0.91–1.21
s	6+6					

Occurrence in Sonora. Early Albian of Municipio Opodepe, Tuape, Cerro de la Espina.

Occurrence elsewhere. Late Barremian to Early Aptian of Bulgaria (Veliko Tarnovska oblast) Veliko Tarnovo (NHMW). Early Aptian of Spain (Vascongadas, Vizcaya) Bilbao, Mina Abandonada; Slovenia (West Slovenia) Banskja Planota, Osojnica; Serbia (East Serbia) Sopot. Early Aptian (*Palorbitolina lenticularis* Zone) of Romania (Suceava) Pojorîta area, Cîmpulung-Moldovenesc, Valea Izvorul Alb. Late Albian of United Kingdom (Devonshire) Exeter, Haldon Hill (NHM R54423); India (Tamil Nadu) Karai. Early Cenomanian (*Mantelliceras mantelli* Zone) of Germany (Nordrhein/Westfalen) Mülheim/Ruhr, Kassenberg. Early Cenomanian of France (Charente-Maritime) Fouras (ERNO L-5593). Middle Cenomanian (*Mantelliceras mantelli*, *Mantelliceras dixoni*, *Cunningtoniceras inerme* and *Acanthoceras rhotomagense* zones) of Belgium (Hainaut) Tournai (IRScNB I. G. 6852 / L 17). Early Cenomanian (*Mantelliceras dixoni* Zone) of Spain (Cantabria, Santander) Cobreces, Luaña playa (BSPG 2007 V 064). Middle Cenomanian of Germany (Bayern) Roßstein-Almen.

Genus *Cyathophoropsis* Alloiteau, 1946

Type species. *Cyathophoropsis hupei* Alloiteau, 1946 by original designation.

Diagnosis. Plocoid colony. Calicular outline circular, diameter generally less than two millimetres, pit depressed. Septa compact. Microstructure of septa unknown. Septa in cross section thick close to the wall, thinner toward the centre. Symmetry of septa radial and regularly trimeral. Cycles of septa regular. Septal cycles differ in length. Septa short, not connected to each other. Septal distal margin unknown, lateral face smooth, inner margin with auriculae in places. Pali or paliform lobes absent. Costae present, sub-confluent to non-confluent, surface unknown. Synapticulae and columella absent. Endotheca consists of regular tabulae and occasional dissepiments. Wall present, compact, probably parathecal. Coenosteum narrow, consists of costae and tabulae. Budding extracalicinal.

Species. Formerly described is only the type species; the here presented species was originally assigned to the genus *Heterocoenia*.

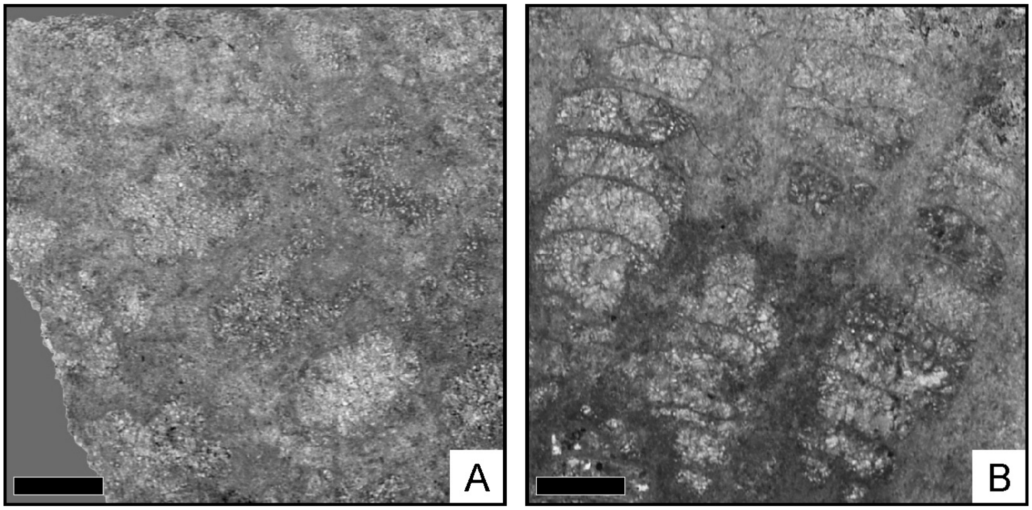

Figure 4. A-B, *Cryptocoenia* cf. *miyakoensis* (Eguchi, 1936), ERNO L-4260. A, transversal thin section. B, longitudinal thin section. Scale 1mm.

Cyathophoropsis ramosa Hackemesser, 1936
Fig. 5A-C

v* 1936 *Heterocoenia decipiens* Prv. var. *ramosa* n. var. Hackemesser 1936, p. 29, pl. 4: 3.

v 1999 *Cyathophora miyakoensis* (Eguchi, 1936) - Baron-Szabo and González-León, p. 478.

Description. Plocoid colony with irregularly formed calices. Septa short. Two septal cycles in a trimeral symmetry. Coenosteum and endotheca well developed.

Material examined. ERNO 2177.

Dimensions.

(2177)	n	min-max	µ	s	cv	µ±s
cl min	20	1.77-2.37	2.14	0.15	7.4	1.98-2.30
cl max	20	2.17-2.80	2.50	0.19	7.6	2.30-2.69
s	3+3					

Remarks. This specimen is the first indication of the genus in the Western Hemisphere, and also the oldest indication at all. All other known material is from the Late Aptian to Early Albian with a questionable indication in the Cenomanian.

Occurrence in Sonora. (? Late Barremian to) Early Aptian of Municipio Ures, Cerro de Oro.

Occurrence elsewhere. Cretaceous of Greece (Fokída) Kiona massif, Panourgias.

5. Discussion

The Sonoran species of the genera *Confusaforma* and *Cryptocoenia* show a long stratigraphical (Fig. 6) and wide palaeogeographical distribution. For the *Cyathophoropsis* species, ranges are not available because of the uncertainty of the type locality's stratigraphy. Most of the species occur from the Aptian and reach into the Cenomanian. Both genera have their last occurrence in the Late Cenomanian; therefore, no younger occurrence exists. Geographically, the

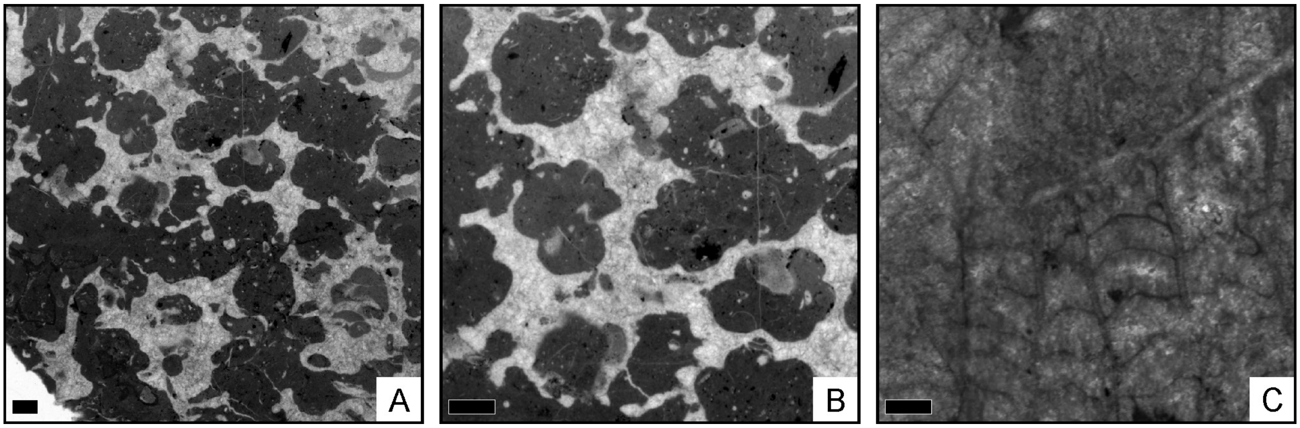

Figure 5. A-C, *Cyathophoropsis ramosa* Hackemesser, 1936, ERNO 2177. A, transversal thin section. B, transversal thin section, detail. C, longitudinal thin section. Scale 1mm.

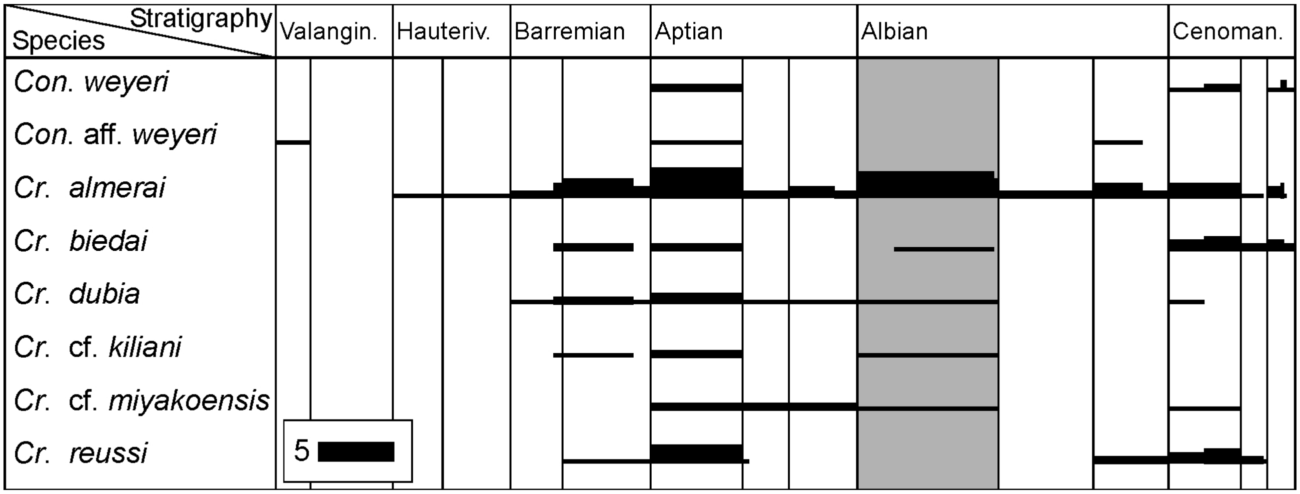

Figure 6. Stratigraphic distribution and commonness of species. The thickness of the bars indicates the number of localities in which the species concerned was found. Grey area marks the study area (Upper Mural Formation).

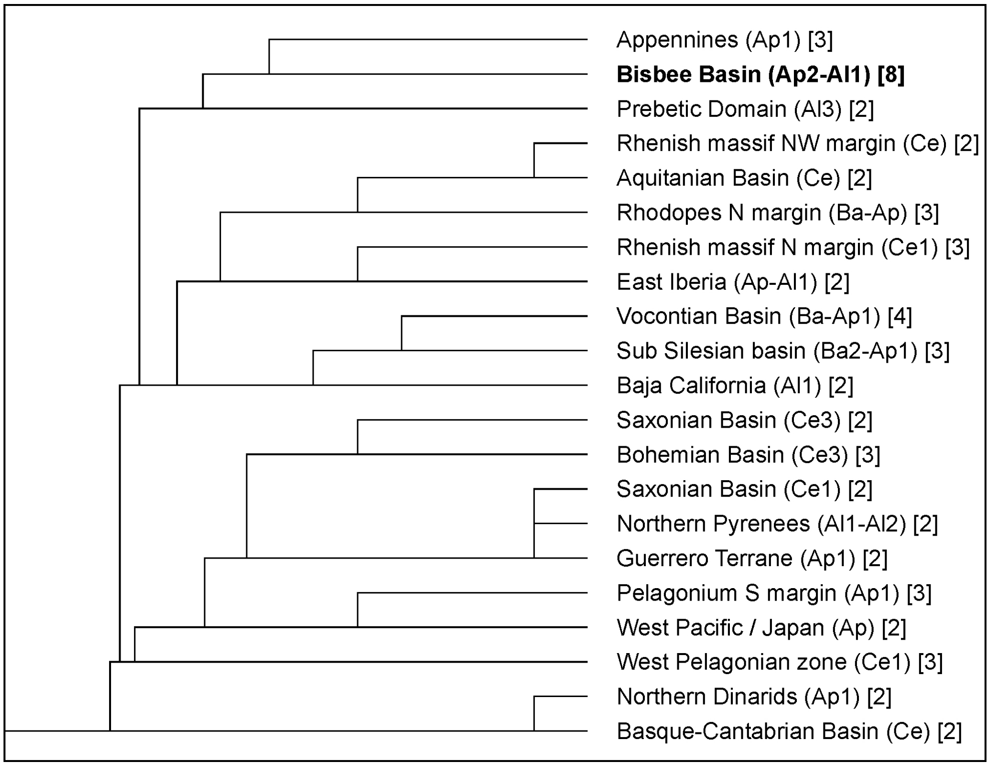

Figure 7. Correlation of provinces with joint species of the study area. Provinces with only one joint species are suppressed. The Correlation Ratio coefficient was applied. For details of calculation see Löser and Minor (2007).

Sonoran species of the Solenocoeniidae family only show a relationship to Western and Central Tethyan faunas (Fig. 7). The species almost do not co-occur in nearby localities, such as the Texas Platform, Baja California, or the Puebla Basin. *Confusaforma* and *Cryptocoenia* are unknown from the (Late Barremian? to) Early Aptian Cerro de Oro Formation in Sonora, and *Cyathophoropsis ramosa* is unknown to the Mural Formation.

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References

Alloiteau, J., 1948, Polypiers des couches albiennes à grandes trigonies de Padern (Aude): Bulletin de la Société géologique de France, 5, (18), 699–738.

Alloiteau, J., 1952, Embranchement des coelentérés, *in* Piveteau, J. (ed.), Traité de Paléontologie: Paris, Masson, 376–684.

Angelis d'Ossat, G. de, 1905, Coralli del Cretacico inferiore della Catalogna: Palaeontographia Italica, 9, 169–251.

Baron-Szabo, R.C., González-León, C. M., 1999, Lower Cretaceous corals and stratigraphy of the Bisbee Group (Cerro de Oro and Lampazos areas), Sonora, Mexico: Cretaceous Research, 20, 465–497.

Baron-Szabo, R.C., González-León, C.M., 2003, Late Aptian-Early Albian corals from the Mural Limestone of the Bisbee Group (Tuape and Cerro de Oro areas), Sonora, Mexico, *in* Scott, R.W. (ed.), Bob F. Perkins Memorial Volume: Special Publications in Geology, 187–225.

Bataller, J., 1947, Sinopsis de las especies nuevas del Cretácico de España: Memorias de la Real Academia de Ciencias y Artes de Barcelona, (3), 28 (12), 279–392.

Duncan, P.M., 1884, A revision of the families and genera of the sclerodermic Zoantharia Edwards et Haime, or Madreporaria (*M. rugosa* excepted) (1-4): Journal of the Linnean Society of London, Zoology, 18, (104/105), 1–204.

Gill, G.A., 1977, Essai de regroupement des Stylinides (hexacoralliaires) d'après la morphologie des bords internes de leurs septes, *in* Second International Symposium on Corals and Coral Reefs, 1975: Paris, France, Mémoires du Bureau de Recherches Géologiques et Minières, 89, 283–295.

Hackemesser, M., 1936, Eine kretazische Korallenfauna aus Mittel-Griechenland und ihre paläobiologischen Beziehungen: Palaeontographica, (A), 84, 1–97.

Koby, F., 1897, Monographie des polypiers crétacés de la Suisse (2): Abhandlungen der Schweizerischen Paläontologischen Gesellschaft, 23, 29–62.

Lathuilière, B., 1989, Répertoire objectif des coraux jurassiques: Nancy, Presses universitaires, 76 p.

Lauxmann, U., 1991, Revision der oberjurassischen Korallen von Württemberg (SW-Deutschland), exclusive Fungiina: Palaeontographica, (A), 219, 107–175.

Löser, H., 1987, Zwei neue Gattungen der Korallen aus der Sächsischen und Böhmischen Oberkreide: Vestnik Ustredního ústavu geologického, 62 (4), 233–237.

Löser, H., 1989, Die Korallen der sächsischen Oberkreide (1) Hexacorallia aus dem Cenoman: Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden, 36, 88–154.

Löser, H., 1994, La faune corallienne du mont Kassenberg à Mülheim-sur-la-Ruhr (Bassin crétacé de Westphalie, Nord Ouest de l'Allemagne): Coral Research Bulletin, 3, 1–93.

Löser, H., 2000, Repertoire of Species: Catalogue of Cretaceous Corals, 1, 1–137.

Löser, H., 2006, Taxonomy, stratigraphic distribution and palaeobiogeography of the Early Cretaceous coral genus *Holocystis*: Revista Mexicana de Ciencias Geológicas, 23 (3), 288–301.

Löser, H., 2010, The Barremian coral fauna of the Serre de Bleyton mountain range (Drôme, France): Annalen des Naturhistorischen Museums in Wien, 112, 575–612.

Löser, H., 2011, The Cretaceous corals from the Bisbee Group (Sonora; Late Barremian - Early Albian): introduction and family Aulastraeoporidae: Revista Mexicana de Ciencias Geológicas, 28 (2), 254–261.

Löser, H., 2013, An Early Albian shallow marine coral fauna from Southern France – insight into evolution and palaeobiogeography of Cretaceous corals: Palaeobiodiversity and Palaeoenvironments, 93, 1–43.

Löser, H., 2014, 3. Korallen / 3. Corals, *in* Niebuhr, B., Wilmsen, M. (eds.), Kreide-Fossilien in Sachsen, Teil 1: Geologica Saxonica, 60 (1), 17–56.

Löser, H., Castro, J.M., Nieto, L.M., 2013a, Late Albian Scleractinian corals from the Prebetic Zone (SE Spain): Palaeontographica, 301 (1/2), 1–62.

Löser, H., Minor, K., 2007, Palaeobiogeographic aspects of Late Barremian to Late Albian coral faunas from Northern Mexico (Sonora) and the southern USA (Arizona, Texas): Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 245, 193–218.

Löser, H., Mohanti, M., 2004, A Cenomanian coral assemblage from southern India: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 10, 577–594.

Löser, H., Werner, W., Darga, R., 2013b, A Middle Cenomanian coral fauna from the Northern Calcareous Alps (Bavaria, Southern Germany) – new insights into the evolution of Mid-Cretaceous corals: Zitteliana, A53, 37–76.

Matthews, S.C., 1973, Notes on open nomenclature and on synonymy lists: Palaeontology, 16 (4), 713–719.

Morycowa, E., 1964, Hexacoralla des couches de Grodziszcze (Néocomien Carpathes): Acta Palaeontologica Polonica, 9 (1), 1–114.

Morycowa, E., 1971, Hexacorallia et Octocorallia du Crétacé inférieur de Rarau (Carpathes orientales roumaines): Acta Palaeontologica Polonica, 16 (1/2), 1–149.

Prever, P.L., 1909, Anthozoa, in La fauna coralligena del Cretaceo dei Monti d'Ocre nell'Abruzzo Aquilano: Parona, Italy, Memorie descrittive della carta geologica d'Italia, 5 (1), 51–147.

Stoliczka, F., 1873, The corals or Anthozoa from the Cretaceous rocks of South India: Memoirs of the Geological Survey of India, Palaeontologia Indica, (4), 8 (4/5), 130–202.

Turnšek, D., Buser, S., 1974, Spodnjekredne korale, hidrozoji in hetetide z Banjske Planote in Trnovskega Gozda: Razprave Slovenska akademija znanosti in umetnosti, (4), 17 (2), 81–124.

Turnšek, D., Buser, S., 1976, Knidarijska favna iz senonijske brece na Banjski Planoti: Razprave Slovenska akademija znanosti in umetnosti, (4), 19 (3), 37–88.

Turnšek, D., Mihajlovic, M., 1981, Lower Cretaceous Cnidarians from eastern Serbia: Razprave Slovenska akademija znanosti in umetnosti, (4), 23, (1), 1–54.

Wells, J.W., 1932, Corals of the Trinity Group of the Commanchean of central Texas: Journal of Paleontology, 6 (3), 225–256.

Zaman, S., Lathuilière, B., 2014, A lectotype for *Cyathophora richardi* Michelin 1843: Zootaxa, 3795 (2), 198–200.

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A new homolid crab, *Peedeehomola deanbogani* n. gen., n. sp., from the Peedee Formation (late Maastrichtian), Rocky Point Member, North Carolina, USA

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Abstract

A new homolid crab *Peedeehomola* new genus, with *Peedeehomola deanbogani* n. gen., n. sp., is reported from the Late Cretaceous (late Maastrichtian) of the Rocky Point Member of the Peedee Formation (North Carolina). *Peedeehomola deanbogani* n. gen., n. sp. possesses peculiar characters, such as the pseudorostral spine as long as the rostrum, the two supraorbital spines directed forward and the prominent anterolateral spine directed outward, not shared with any known genus within the Homolidae.

Keywords: Brachyura, Homolidae, new genus, new species, Late Cretaceous, North Carolina, USA.

Resumen

Un nuevo cangrejo homólido, Peedeehomola nuevo género, con Peedeehomola deanbogani n. gen., n. sp., es reportado del Cretácico tardío (Maastrichtiano tardío) del Miembro Rocky Point de la Formación Peedee (Carolina del Norte). Peedeehomola deanbogani n. gen., n. sp. presenta características peculiares, tales como una espina pseudorostral tan larga como el rostro, las dos espinas supraorbitales dirigidas hacia el frente y la prominente espina anterolateral, dirigida externamente. Ninguno de estos caracteres se observa en algún género conocido de los Homolidae.

Palabras clave: Brachyura, Homolidae, nuevo género, nueva especie, Cretácico tardío, Carolina del Norte, EUA.

1. Introduction

The type locality of *Peedeehomola deanbogani* n. gen., n. sp. is located at N 34°24'54", W77°55'30" in Rocky Point, Pender County, North Carolina, USA (Figure 1). The location is within the active mining operation of the Mr. Kent Mitchell mine. The mine produces fill sand from the Rocky Point Member of the Peedee Formation for construction sites and road grading.

The Rocky Point Member has seen considerable attention since Swift and Heron (1969) informally described it. The term "Rocky Point Member" was later formalized by Wheeler and Curran (1974). It was subsequently renamed the Scotts Hill Member by Ward and Blackwelder (1978). Use of the original name was defended by Harris and others (1986). Sohl and Owens (1991) placed the Peedee in a sequence stratigraphic framework and noted the time transgressive nature of the Rocky Point Member. Blake and Sturgeon (1995) described an astropectinid asteroid, *Aldebarania arenitea*, from loose arenite in a local quarry approximately 4 kilometers from the *Peedeehomola deanbogani* type locality. Parris *et al.* (2004) describe a possible Azhdarchid Pterosaur femur from the Rocky Point Member at Maple Hill, North Carolina. Ciampaglio and Weaver (2007) report a new occurrence for the regular echinoid *Phymotaxis tourneri* in North Carolina extending

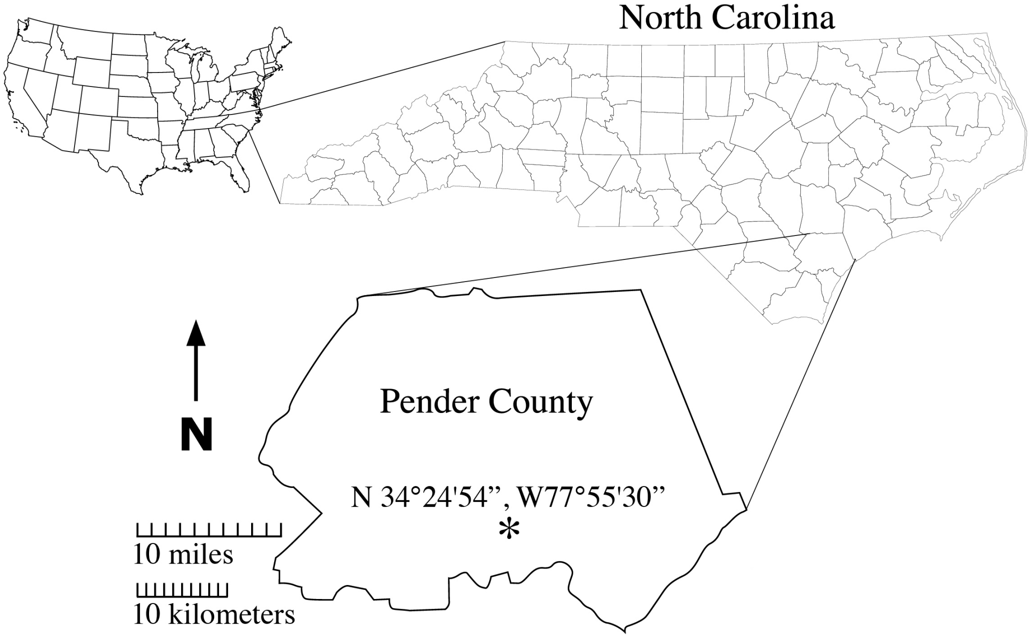

Figure 1. Geographic map with the fossiliferous locality in North Carolina, SE USA.

its known range from Europe through North Carolina to Texas. Their specimens were also from the loose arenite lithology of the Rocky Point Member.

2. Geological setting

Harris (1978) described the Rocky Point Member as being deposited in a shallow marine Cape Shoal complex. The sediments vary from a basal quartz sand arenite, to pelecypod biosparrudite, sandy pelecypod biosparite and sandy biosparudite. The studied specimen was collected from a block of indurated *Flemingostrea subspatulata* (Forbes, 1845) bioherm limestone within the basal quartz sand arenite of the Rocky Point Member (Figure 2). The structure of these oyster bioherms within the loose arenite can be easily observed in the mine due to the removal of adjacent product sand (Figure 3). Because the specimens of *F. subspatulata* are in life position within the indurated blocks we assume that the commensal fauna which includes *Peedeehomola deanbogani* n. gen., n. sp., the complete starfish *Aldebarania arenitea* Blake and Sturgeon, 1995 and the echinoids with spines attached *Hardouinia mortonis* (Michelin, 1850) and *Phymotaxis tournoueri* (Cotteau, 1866) both with spines attached are autochtonous (Figure 4). Longshore sediment drift was suggested by Harris (1978) and presumably a change in drift direction buried the oyster bioherm and its cohabitants. A major storm event may have been the cause of rapid burial resulting in the unusually complete preservation of the fossils. There is no indication of a presumption of conditions suitable for the formation of oyster bioherms in the approximately 10 meters of loose arenite above them.

3. Material

The three-dimensional studied specimen, assigned to *Peedeehomola* nov., with *P. deanbogani* n. sp. (Homolidae De Haan, 1839), is housed in North Carolina Museum of Natural History (NCMNH).

3.1. Abbreviations

lcxp: carapace length; P1-P5: pereiopods 1 to 5; wcxp: carapace width.

4. Systematic Palaeontology

Infraorder Brachyura Linnaeus, 1758
Section Homoloida Karasawa, Schweitzer and Feldmann, 2011
Superfamily Homoloidea De Haan, 1839
Family Homolidae De Haan, 1839

Genus *Peedeehomola* nov.

Type species. *Peedeehomola deanbogani* n. sp.

Diagnosis. Subquadrate carapace with well-marked linea homolica; one pseudorostral spine; two supraorbital spines; one prominent anterolateral spine with two supplementary basal spines; one small posterolateral spine; regions nearly smooth and slightly raised.

Figure 2. Block of oyster reef showing abundance and position of *Flemingostrea* sp. (bottom side up). Scale bar equals 30 cm.

Figure 4. A) *Aldebarania arenitea* and B) *Hardouinea mortonis* on indurated *Flemingostrea* sp. reef. Scale bar equals 20 mm.

Figure 3. Indurated *Flemingostrea* sp. reefs standing out in relief after removal of product sediment.

Etymology. The generic name refers to the Peedee Formation where the studied specimen was collected.

Discussion. Recognition of *Peedeehomola* as a new genus is based upon the pseudorostral spine as long as the rostrum, the two supraorbital spines directed forward and the prominent anterolateral spine directed outward. This combination of characters distinguishes the genus from all other known fossil forms (Bell, 1863; Beurlen, 1928; Bishop, 1983, 1988; Collins, 1997; Collins and Saward, 2006; Collins *et al*., 2005; De Angeli and Alberti, 2012; Feldmann and Schweitzer, 2009; Guinot and Richer de Forges, 1995 and Karasawa, 1992).

Peedeehomola deanbogani n. sp.

Figure 5A, 5B

Etymology. In honor of Dean Bogan, who discovered the holotype and sole specimen.

Holotype. NCMNH12009

Type locality. Rocky Point, Pender County, North Carolina (USA).

Geological age. Late Cretaceous (late Maastrichtian).

Material and measurements. one complete specimen in dorsal view [NCMNH 12009 – lcxp: 40 mm ; wcxp: 35 mm (including the anterolateral spine)].

Description. Carapace – Carapace subquadrate, slightly longer than wide, moderately vaulted transversely, less so longitudinally; lateral sides nearly subvertical; regions almost smooth well marked by grooves; short rostrum not sulcate axially; one pseudorostral spine, as long as the rostrum, directed slightly upward; two supraorbital spines, as long as the rostrum and pseudorostral spine, directed slightly upward; anterolateral margin with one prominent spine directed outward; anterolateral spine with a pair of supplementary small basal spines directed upward; posterolateral margin smooth, with one small spine proximally directed outward; posterior margin wide, slightly concave, with narrow, well-defined rim; cervical groove almost straight proximally and slightly downturned posterior to mesogastric lobe; branchiocardiac groove almost straight proximally downturned posterior to gastric lobe; epigastric lobe defined by a pair of tubercles positioned just posterior to pseudorostral spines; mesogastric lobe marked by smooth grooves laterally and well-defined cervical groove posteriorly; mesogastric lobe with pair of tubercles close to gastric pits; protogastric lobe with one tubercle positioned just posterior first suprarostral spine and one tubercle positioned just posterior first supplementary basal spine of the anterolateral spine; narrow mesobranchial lobe with one tubercle positioned just posterior second supplementary basal spine of the anterolateral spine; metabranchial lobe with four small tubercle aligned along *linea homolica* proximally and medially; metabranchial lobe with four small tubercles nearly aligned centrally; metabranchial lobe with one large tubercle positioned close

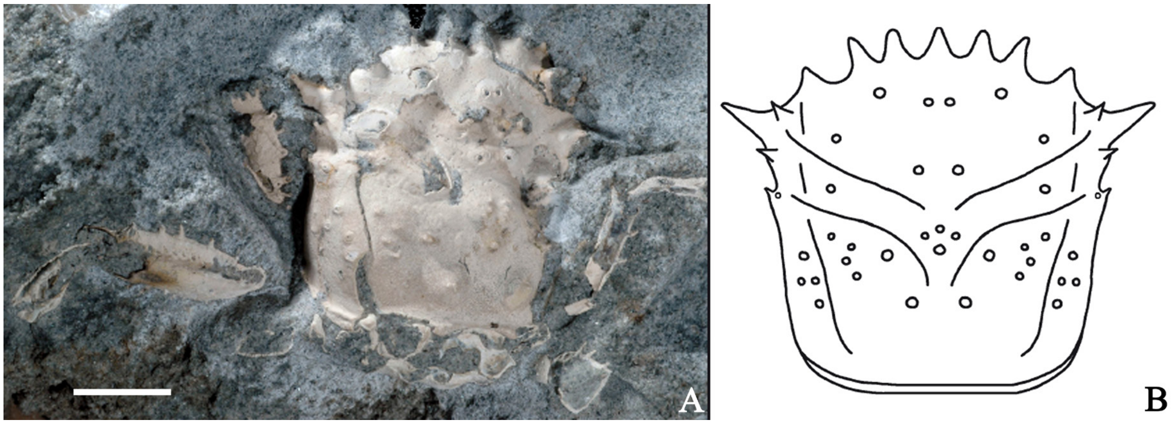

Figure 5. A) *Peedeehomola deanbogani* n. gen., n. sp., NCMNH 12009, holotype, dorsal view. B) Idealized reconstruction of dorsal carapace. Scale bar equals 10 mm.

to branchiocardiac groove distally and one large tubercle positioned close intestinal lobe distally; triangular cardiac lobe with one central tubercle surmounted by three smaller tubercles; intestinal lobe long, narrow, smooth, and slightly depressed. Thoracic appendages – Chelae unknown; P1 left merus partially preserved with spiny margins; P2 and P5 unknown; right P3 long and narrow; P3 merus with spiny lower margin; left P4 stouter than P3; P4 merus with spiny upper margin.

Discussion. Guinot and Richer de Forges (1995) reported three families within Homoloidea De Haan, 1839 as follows: Homolidae De Haan, 1839; Poupiniidae Guinot, 1991; Latreillidae Stimpson, 1858. According to Guinot and Richer de Forges (1995) the *linea homolica* distinguishes Homilidae from Poupiniidae and Latreillidae. Based upon this main diagnostic character, *Peedeehomola* n. gen. is assigned to Homolidae for the presence of a well-marked *linea homolica* not present in the other two families within Homoloidea. According to Schweitzer *et al*. (2010) and De Angeli and Alberti (2012) 14 genera are assigned to Homolidae, as follows: *Dagnadus* Guinot and Richer de Forges, 1995; *Doerflesia* Feldmann and Schweitzer, 2009; Homola Leach, 1816; *Homoliformis* Collins *et al*., 2005; *Homolopsis* Bell, 1863; *Hoplitocarcinus* Beurlen, 1928; *Latheticocarcinus* Bishop, 1988; *Lignihomola* Collins, 1997; *Londinimola* Collins and Saward, 2006; *Nogarhomola* De Angeli and Alberti, 2012; *Paramola* Wood-Mason in Wood-Mason and Alcock, 1891; *Paromolopsis* Wood-Mason in Wood-Mason and Alcock, 1891; *Prohomola* Karasawa, 1992 and *Zygastrocarcinus* Bishop, 1983.

We justify the description of *Peedeehomola* n. gen. for the pseudorostral spine as long as the rostrum, the two supraorbital spines directed forward and the prominent anterolateral spine directed outward. In *Dagnadus* and *Doerflesia* the pseudorostral spine is longer than the rostrum and the supraorbital spines are absent. In *Homola* the pseudorostral spine is shorter than the rostrum and two anterolateral spines. Even though *Homoliformis* lacks the front, the anterolateral margins are smooth. In *Homolopsis*, *Hoplitocarcinus*, *Latheticocarcinus*, *Lignihomola*, *Londinimola*, and *Zygastrocarcinus* the pseudorostral, supraorbital, and anterolateral spines are absent. In *Paromola* the pseudorostral spine is slightly longer than rostrum and the supraorbital spines are absent. In *Prohomola* the pseudorostral spine is shorter than rostrum and supraorbital spines are absent. Finally in *Nogarohomola* the pseudorostral spines are longer than rostrum and divergent.

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References

Bell, T., 1863, Some account of the Crustacea of the coasts of South America, with descriptions of new genera and species, founded principally on the collections obtained by Mr. Cuming and Mr. Miller. (Tribus 1, Oxyrhynchi): Proceedings of the Zoological Society of London, 3 (1835), 169–173.

Beurlen, K., 1928, Die fossilen Dromiaceen und ihre Stammesgeschichte: Paläontologische Zeitschrift, 10, 144–183.

Bishop, G.A., 1983, Two new species of crabs, *Notopocorystes* (*Eucorystes*) *eichhorni* and *Zygastrocarcinus griesi* (Decapoda: Brachyura) from the Bearpaw Shale (Campanian) of northcentral Montana: Journal of Paleontology, 57 (5), 900–910.

Bishop, G.A., 1988, New fossil crabs, *Plagiophthalmus izetti*, *Latheticocarcinus shapiroi*, and *Sagittiformosus carabus* (Crustacea, Decapoda) from the Western Interior Cretaceous, U.S.A.: Proceedings of the Biological Society of Washington, 101, 375–381.

Blake, D.B., Sturgeon, K., 1995, *Aldebarania arenitea*, a new genus and species of Astropectinidae (Asteroidea: Echinodermata) from the Maastrichtian (Upper Cretaceous) Peedee Formation of North Carolina: Journal of Paleontology, 69 (2), 376–380.

Ciampaglio, C.N., Weaver, P.G., 2007, Maastrichtian (Cretaceous) Regular Echinoids from the Rockey Point Member, Peedee Formation Southeastern North Carolina: Southeastern Geology, 45 (1), 43–49.

Collins, J.S.H., 1997, Fossil Homolidae (Crustacea; Decapoda): Bulletin of the Mizunami Fossil Museum, 24, 51–71.

Collins, J.S.H., Saward, J., 2006, Three new genera and species of crabs from the Lower Eocene of London Clay of Essex, England: Bulletin of the Mizunami Fossil Museum, 33, 67–76.

Collins, J.S.H., Schulz, B.P., Jakobsen, S.L., 2005, First record of brachyuran decapods (Crustacea, Decapoda) from Fur Formation (early Eocene) of Mors and Fur Island, Denmark: Bulletin of the Mizunami Fossil Museum, 32, 17–22.

Cotteau, G., 1866, Échinides nouveaux ou peu connus: Revue et Magasin de Zoologie, 2 (18), 201–209, 262–268.

De Angeli, A., Alberti, R., 2012, *Nogarhomola aurorae* n. gen., n. sp. (Decapoda, Brachyura, Homolidae) dell'Eocene medio dei Monti Lessini Orientali (Vicenza, Italia settentruonale): Studi Trentini di Scienze Naturali, 92, 63–70.

De Haan, W., 1833-1850, Crustacea, *in* Von Siebold, P.F. (ed.), Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit: i-xvii, i-xxxi, ix-xvi, 1-243, pls. A-J, L-Q, 1-55, circ. table 2. (J. Müller et Co., Lugduni Batavorum [=Leyden]).

Feldmann, R.M., Schweitzer, C.E., 2009, Revision of Jurassic Homoloidea De Haan, 1839, from the Ernstbrunn and Štramberk limestones, Austria and the Czech Republic: Annalen des Naturhistorischen Museums in Wien, (A) 111, 183–206.

Forbes, E., 1845, On the fossil shells collected by Mr. Lyell from the Cretaceous formations of New Jersey: Geological Society of London, Quarterly Journal, 1, 61–64.

Guinot, D., 1991, Établissement de la famille des Poupiniidae pour *Poupinia hirsuta* gen. nov, sp. nov. de Polynésie (Crustacea Decapoda Brachyura Homoloidea): Bulletin du Muséum national d'Histoire naturelle, section A, ser. 4, 12 (3/4), 577–605.

Guinot, D., Richer de Forges, B., 1995, Crustacea Decapoda Brachyura: révision de la famille des Homolidae De Haan, 1839, *in* Crosnier, A. (ed.), Résultats des Campagnes MUSORSTOM, 13: Mémoires du Muséum National d'Histoire Naturelle, Paris, 163, 283–517.

Harris, W.B., 1978, Stratigraphic and Structural Framework of the Rocky Point Member of the Cretaceous Peedee Formation, North Carolina: Southeastern Geology, 19 (4), 207–229.

Harris, W.B., Thayer, F.A., Curran, H.A., 1986, The Cretaceous Tertiary Boundary on the Cape Fear Arch, North Carolina, U.S.A.: Cretaceous Research 7, 1–17.

Karasawa, H., 1992, Fossil decapod crustaceans from the Manda Group (Middle Eocene), Kyushu, Japan: Transactions and Proceedings of the Palaeontological Society of Japan, (new series) 167, 1247–1258.

Karasawa, H., Schweitzer, C.E., Feldmann, R.M., 2011, Phylogenetic analysis and revised classification of podotrematous Brachyura (Decapoda) including extinct and extant families: Journal of Crustacean Biology, 31, 523–565.

Leach, W.E., 1816 [imprint 1815], A tabular view of the external characters of four classes of animal which Linne arranged under Insecta: with the distribution of the genera composing three of these classes into orders and c. and descriptions of several new genera and species. Transactions of the Linnean Society of London, 11(2), 306–400, and 'Errata'. [Dated 1815, but published 24 January 1816.].

Linnaeus, C. [VON], 1758, Systema Naturae per Regna tria Naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis (ed. 10), 1, 1–824. (Laurentii Salvii, Holmiae [=Stockholm]).

Michelin, H., 1850, Notice sur deux espèces d´échinides fossiles: Revue et Magasin de Zoologie, série 2 (2), 240–241.

Parris, D.C., Grandstaff, B.S., Clements, D., 2004, A Pterosaur Femur from the Upper Cretaceous of North Carolina: Southeastern Geology, 43 (1), 51–55.

Schweitzer, C.E., Feldmann, R.M., Garassino, A., Karasawa, H., Schweigert, G., 2010, Systematic list of fossil decapod crustacean species: Crustaceana Monographs, 10, 1–222.

Sohl, N.F., Owens, J.P., 1991, Cretaceous stratigraphy of the Carolina Coastal Plain, *in* Morton, J.W., Zullo, V.A. (eds.), The Geology of the Carolinas: Carolina Geological Society Fiftieth Society Anniversary Volume: 191–220.

Stimpson, W., 1858, Crustacea Anomura. Pars VII. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit W. Stimpson, Pars VII: Proceedings of the Academy of Natural Sciences of Philadelphia, 10, 225–252.

Swift, D.J.P, Heron, S.D., Jr., 1969, Stratigraphy of the Carolina Cretaceous: Southeastern Geology, 10, 201–245.

Ward, L.W., Blackwelder, B.W., 1978, Scotts Hill Member (New Name) of the Cretaceous Peedee Formation of Southeastern North Carolina and East-Central South Carolina, U.S.: Geological Survey Bulletin, 1482-A, A87-A88.

Wheeler, W.H., Curran, H.A., 1974, Relation of the Rocky Point Member (Peedee Formation) to the Cretaceous-Tertiary boundary in North Carolina: American Association of Petroleum Geologists Bulletin, 59, 1751–1757.

Wood-Mason, J., Alcock, A., 1891, A note on the result of the last season's deep-sea dredging: natural history notes from H.M. Indian Marine Survey Steamer "Investigator", Commander, R.F. Hoskyn, R.N. Commanding, no. 21: Annals and Magazine of Natural History, 6 (7), 258–272.

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Nuevos hallazgos de los moluscos *Nemrac carmenensis* Clark 1946 (Gastropoda, Turbinoidea, Turbinidae) y *Solena* (*Eosolen*) *bolivarensis* Clark 1946 (Bivalvia - Solenida - Solenidae): Precisiones estratigráficas y paleoambientales para las faunas del Eoceno tardío del Caribe colombiano

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Resumen

Se reporta el hallazgo de nuevos ejemplares del gasterópodo *Nemrac carmenensis* Clark 1946 y del bivalvo *Solena* (*Eosolen*) *bolivarensis* Clark 1946, en rocas del Paleógeno del Cinturón Plegado de San Jacinto, Caribe colombiano; complementando la información disponible de estas especies, de las cuales solo se habían colectado ejemplares únicos durante la primera mitad del siglo pasado. Este descubrimiento permite establecer la posición estratigráfica de estas y otras faunas halladas previamente en el Eoceno del Caribe colombiano en la parte alta de la Formación Arroyo Seco, asignándole una edad Bartoniense – Priaboniense (Eoceno tardío) y un paleoambiente de depósito de frente deltáico.

Palabras clave: Caribe, Cinturón Plegado de San Jacinto, Colombia, Eoceno tardío, Formación Arroyo Seco, moluscos.

Abstract

New specimens of the gastropod Nemrac carmenensis Clark 1946 and the bivalve Solena (Eosolen) bolivarensis Clark 1946, in Paleogene rocks of San Jacinto Fold Belt (SJFB), Colombian Caribbean region were found and reported to complement the information available for these species. These findings of unique specimens had only been collected during the first half of the last century. This discovery allows to define the stratigraphic position of these and other faunas previously found in the Eocene of the Colombian Caribbean region at the upper levels of Arroyo Seco Formation, allowing the assignment of a Late Eocene age (Bartonian – Priabonian) and a delta-front environment.

Palabras clave: Caribbean, San Jacinto Fold Belt, Colombia, late Eocene, Arroyo Seco Formation, mollusks.

1. Introducción

El gasterópodo *Nemrac carmenensis* Clark 1946 y el bivalvo *Solena* (*Eosolen*) *bolivarensis* Clark 1946, fueron descritos por el Dr. Bruce L. Clark (Clark y Durham, 1946) a partir de ejemplares únicos colectados en trabajos de campo de la Standard Oil Company y del paleontólogo estadounidense Dr. Frank Marion Anderson (Anderson, 1928), en la región de Carmen de Bolívar, Colombia, durante la primera mitad del siglo XX. Los fósiles aquí estudiados forman parte de una serie de moluscos paleógenos, poco conocidos (la mayoría endémicos), que incluyen numerosas especies de bivalvos y gasterópodos, así como algunos registros de nautiloideos, corales y crustáceos, de los cuales no existían nuevos reportes desde hace ya casi 70 años.

Los trabajos originales de Anderson (1928) y Clark y Durham (1946) no presentaban una localización geográfica ni estratigráfica precisa, por lo que la posición exacta de estos hallazgos era prácticamente desconocida, lo que desafortunadamente restó valor a la importancia de sus estudios, claves para la paleontología del Caribe colombiano y del norte de Sur América. Teniendo en cuenta esto, se realizó una búsqueda de las localidades fosilíferas reportadas de manera aproximada por ellos y tras su hallazgo, se realizó la descripción estratigráfica y la colecta de abundantes ejemplares de moluscos, cuyo estudio aún se encuentra en desarrollo, pero arroja ya sus primeros resultados.

El presente trabajo reporta el descubrimiento de nuevos ejemplares de moluscos en el área de los hallazgos originales, lo que ha permitido ubicar de forma precisa, estratigráfica y geográficamente, estos horizontes fosilíferos y en particular, colectar nuevos ejemplares de especies de los que solo existía el holotipo; así como describirlos e ilustrarlos sin las limitaciones editoriales de mediados del siglo pasado. La descripción detallada de las secuencias sedimentarias aflorantes, ha permitido además conocer la litología, facies y paleoambientes sedimentarios de estos horizontes. Determinaciones micropaleontológicas recientes aportan la edad precisa de estos depósitos.

La fauna de moluscos del Eoceno reportada en los trabajos del siglo pasado guarda información valiosa acerca de la evolución, paleoambientes y paleogeografía del norte de Sur América durante el Paleógeno. El re-descubrimiento de estos fósiles y su integración dentro del escenario estratigráfico y evolutivo del Caribe colombiano, permite tener un marco de referencia para los nuevos hallazgos que se están realizando en el área y brindan una mejor comprensión de la importancia de los estudios paleontológicos de Anderson (1928) y Clark y Durham (1946), pioneros en el estudio de los moluscos paleógenos de Colombia; así como de los nuevos datos por descubrir, permitiendo además, por primera vez, tener ejemplares de esta malacofauna en las colecciones paleontológicas de Colombia para su estudio por parte de los investigadores nacionales.

El material estudiado está depositado en la Colección Paleontológica del Departamento de Geociencias de la Universidad Nacional de Colombia, sede Bogotá, con el acrónimo UN-DG. El criterio de clasificación que se sigue en los gasterópodos es el de Bouchet *et al*., 2005 y en los bivalvos el del *Treatise on Invertebrate Paleontology* (Moore y Teichert, 1969) y su terminología revisada recientemente (Carter *et al*., 2012).

2. Localización y marco geológico

El horizonte fosilífero que contiene los ejemplares aquí descritos se localiza sobre el arroyo Mancomoján (75°16´12´´W; 9°37´28´´N), a unos 2.3 km al NW del municipio de Pijiguay, departamento de Bolívar, Colombia (Figura 1). Geológicamente el nivel muestreado se ubica en el flanco oeste de anticlinal El Cedro, sobre la parte alta de la Formación Arroyo Seco y corresponde a una litoarenita fosilífera de grano fino, de color gris verdoso, con cemento calcáreo y abundantes restos de moluscos, fragmentos leñosos y de carbón (Figura 2).

De acuerdo a los datos suministrados por Clark y Durham (1946), este nivel correspondería aproximadamente o estaría muy cerca de los niveles fosilíferos descritos en su localidad S-60, así como dentro de la misma estructura y unidad litoestratigráfica de otras localidades, que ellos ubicaron en la denominada Zona C (ver Figura 1).

Los moluscos aquí descritos, a pesar de haber sido encontrados en un mismo horizonte fosilífero, habían sido reportados originalmente por Clark y Durham (1946) en zonas diferentes y exclusivas; *Nemrac carmenensis* fue reportado en la localidad CAS 31694 (Zona B), mientras que *Solena* (*Eosolen*) *bolivarensis* fue reportado en la localidad S-60 (Zona C), lo que pone en duda la utilidad de dichas zonas, lo cual debe revisarse en el futuro.

3. Estratigrafía

La Formación Arroyo Seco (Paleoceno tardío – Eoceno tardío), constituye la base del Paleógeno del Cinturón Plegado de San Jacinto (CPSJ) y está constituida por proporciones variables de conglomerados polimícticos (particularmente importantes hacia la base de la unidad), arenitas líticas y lodolitas. La unidad reposa discordantemente sobre la Formación Cansona (Coniaciano – Maastrichtiano) y es a su vez suprayacida por las calizas de la Formación Toluviejo o las areniscas fosilíferas de la Formación San Jacinto (Eoceno tardío – Oligoceno), las cuales representan facies heterópicas isócronas que se interdigitan en esta región del CPSJ (Bermúdez *et al*., 2009).

La edad de la Formación Arroyo Seco ha sido determinada con foraminíferos, palinología y nanofósiles calcáreos, como Paleoceno medio – Eoceno tardío (Herrera *et al*., 2009; Universidad de Caldas – ANH, 2009; Bermúdez *et al*., 2009) e incluye además diversos horizontes fosilíferos con moluscos marinos y de agua salobre-dulce (Bermúdez *et al*., 2013). Los foraminíferos planctónicos ilustran la presencia de las zonas P3 a P16 de Berggren y Pearson (2005); a partir de nanoplancton calcáreo se identifican las zonas NP5 a NP20 de Martini (1971), mientras que los palinomorfos muestran la presencia de las zonas T02-T07 de Jaramillo *et al*., (2009).

Las determinaciones bioestratigráficas disponibles para la parte alta de la unidad (en donde se encuentran los niveles fosilíferos de moluscos de afinidad marina aquí descritos), obtenidas de estudios de pozos y secciones aledañas (ATG-ANH, 2009; Universidad de Caldas – ANH, 2009), restringen la edad de depósito del techo de la Formación Arroyo Seco al Bartoniense – Priaboniense (Eoceno tardío ~ 40.4 – 33.9 m.a), especialmente con base en la presencia de foraminíferos como *Acarinina collactea*, *A. bullbrooki*, *A. medizzai*, *A. primitiva*, *A. rohri*, *A. topilensis*, *Clavigerinella colombiana*, *C. eocanica*, *Globigerina officinalis*, *G. linaperta*, *Igorina broedermanni*, *Morozovella spinulosa*, *Paragloborotalia griffinoides*, *P. nana*, *Planorotalites pseudoscitula*, *Subbotina eocaena*,

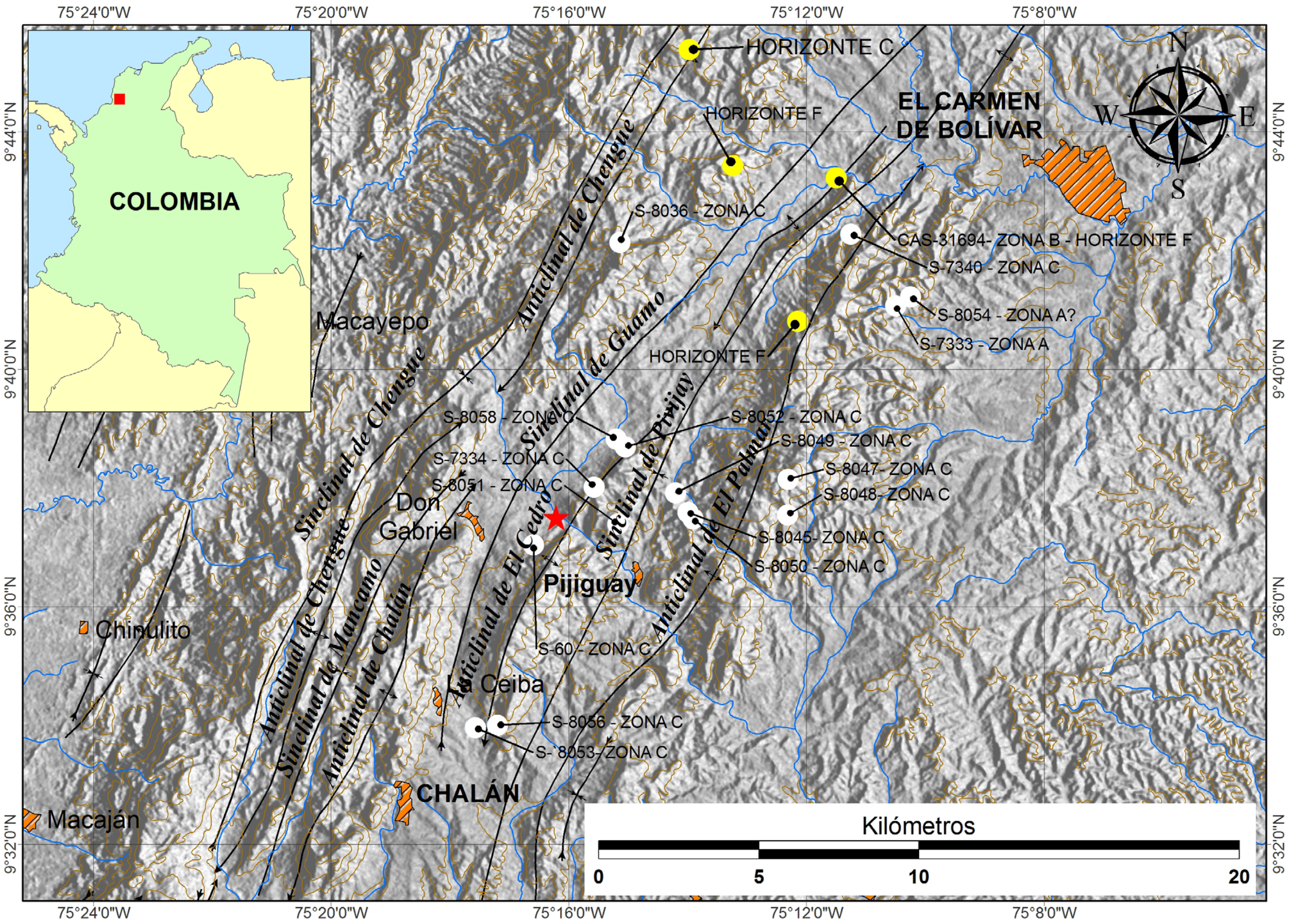

Figura 1. Mapa de localización del horizonte fosilífero descrito en este trabajo (estrella roja), al NW del municipio de Pijiguay, Departamento de Bolívar, Colombia, ilustrando además la posición aproximada de las localidades de Clark y Durham (1946) —puntos blancos— y de Anderson (1928) —puntos amarillos—.

S. linaperta, *Turborotalia pomeroli*, *T. cerroazulensis* y *T. posagnoensis* y los nanofósiles calcáreos *Chiasmolithus solitus*, *C. nitidus*, *Helicosphaera lophota*, *H. seminulum*, *Nannotetrina cristata*, *Reticulofenestra bisecta*, *R. reticulata* y *Sphenolithus radians*.

4. Paleontología sistemática

Clase Gastropoda Cuvier, 1797
Superfamilia Turbinoidea Rafinesque, 1815
Familia Turbinidae Rafinesque, 1815
Género *Nemrac* Clark, 1946

Tipo. *Nemrac carmenensis* Clark, 1946, Eoceno, región Caribe de Colombia.

Nemrac carmenensis Clark, 1946
(Figura 3)

Nemrac carmenensis Clark, 1946, p. 14, lám. 19, fig. 8, 14, 15.

Descripción. Los tres hipotipos descritos presentan una concha pequeña turbinada, relativamente alta (casi ¾ del ancho máximo) con 5½ vueltas, de las cuales 1½ a 2 corresponden a la protoconcha, la cual es baja, casi planispiral y ligeramente inclinada y luce como una continuación del resto de la concha. Las vueltas de la teleoconcha son lisas, suavemente convexas y presentan en su parte interna una banda sutural crenulada estrecha, definida por un surco granulado, que desaparece en la protoconcha, lo que la diferencia de la teleoconcha (Figura 3 D); la base de la concha, muy bien definida en el hipotipo UN-DG-GT-005a (Figura 3 B), presenta abertura circular y ombligo abierto del que irradian costillas irregulares separadas por un surco.

Material examinado. Tres especímenes (en excelente condición), identificados con los números de catálogo UN-DG-GT-005a, UN-DG-GT-005b, y UN-DG-GT-005c.

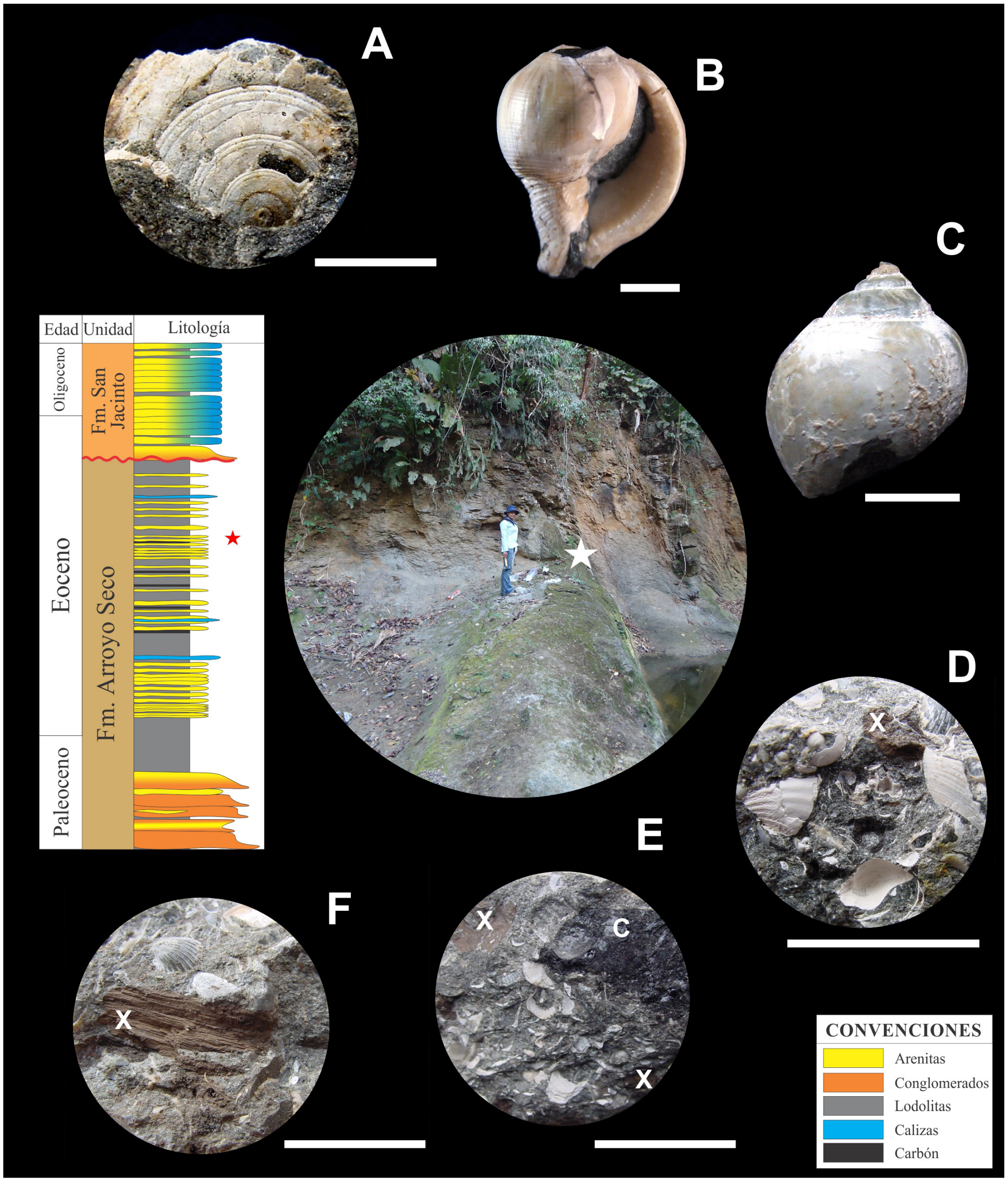

Figura 2. Columna estratigráfica, aspecto del afloramiento, detalle de las facies y alguna de la fauna asociada de moluscos. A) *Architectonica* sp. B) *Peruficus* sp. C) *Crommium* sp. D-F) Aspecto de la facies de litoarenitas fosilíferas con fragmentos de carbón (c) y restos leñosos (x) donde se encontraron los moluscos aquí descritos. La barra equivale a 1 cm.

El holotipo (a la vez genotipo) de *Nemrac carmenensis*, está depositado en el Departamento de Paleontología de la Academia de Ciencias de California, CAS, por sus siglas en inglés, (Localidad CAS 31694, espécimen No. 7936) y no pudo ser consultado.

Dimensiones.

Holotipo CAS 31694, No. 7936: Altura= 4.1 mm; ancho máximo= 5.7 mm.

Hipotipo UN-DG-GT-005a: Altura= 4.3 mm; ancho máximo= 6.5 mm.

Hipotipo UN-DG-GT-005b: Altura= 4.2 mm; ancho máximo= 6.1 mm.

Hipotipo UN-DG-GT-005c: Altura= 5.0 mm; ancho máximo= 6.6 mm.

Ocurrencia. Pijiguay, Carmen de Bolívar. Región Caribe colombiana.

Discusión. Los tres ejemplares encontrados corresponden inequívocamente a la descripción original del holotipo de Clark (1946), quien de acuerdo a sus características únicas erigió una nueva especie (así como un nuevo género), que hasta la fecha solo se ha reportado en el Eoceno del Caribe colombiano. Originalmente el género *Nemrac* fue asignado a la familia Turbinidae aunque posteriormente Sepkoski (2002) lo asignó a la orden Archaeogastropoda. Sin tener

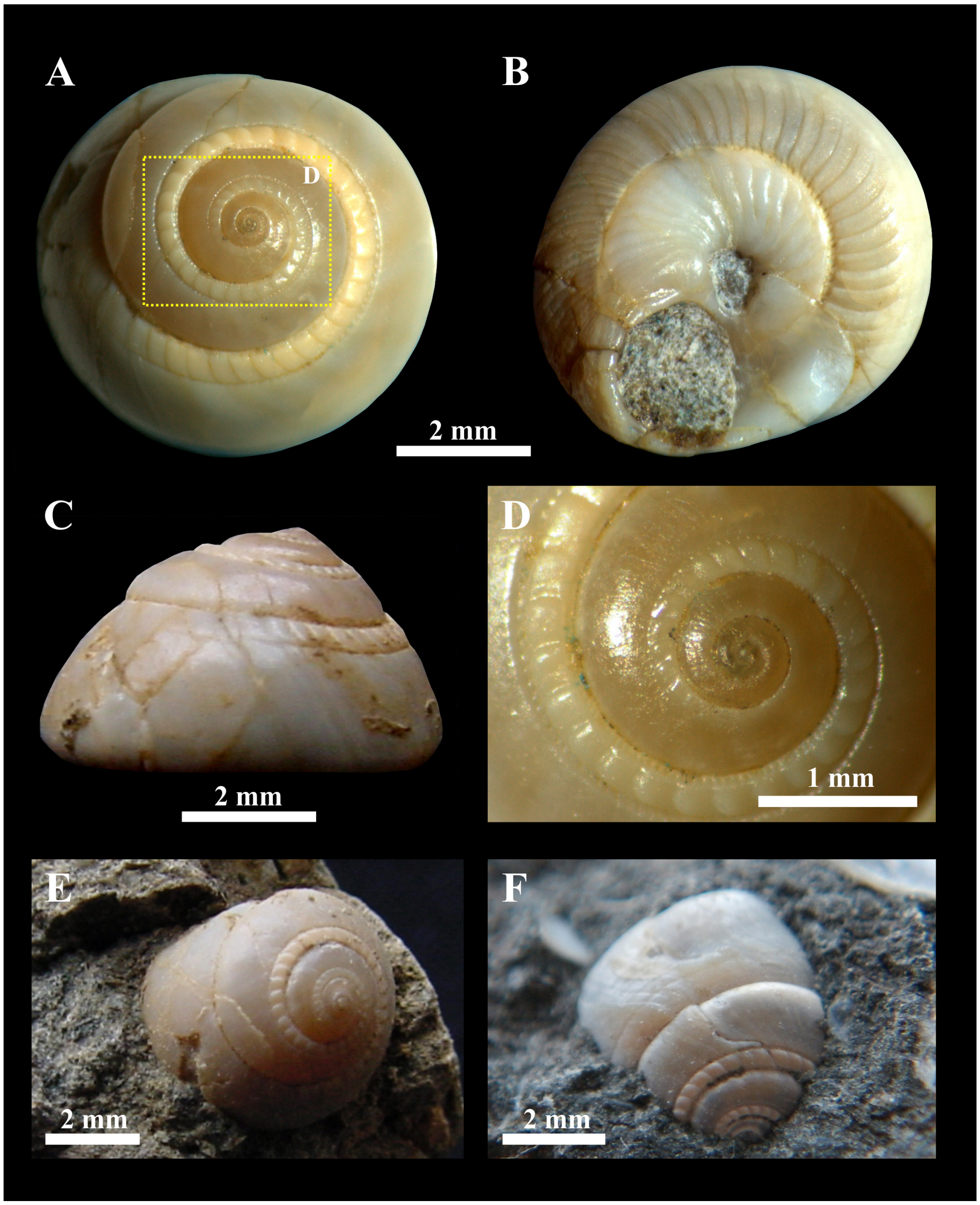

Figura 3. *Nemrac carmenensis* Clark 1946. Formación Arroyo Seco, Colombia. A-D) Hipotipo UN-DG-GT-005a. A) Vista superior B) Vista basal. C) Vista lateral. D) Detalle de la protoconcha. E) Hipotipo UN-DG-GT-005b. F) Hipotipo UN-DG-GT-005c.

acceso al holotipo y solo con la descripción de los tres ejemplares hallados en este trabajo, se prefiere mantener la asignación original de Clark (1946).

Las dimensiones de los ejemplares colectados en este trabajo son muy similares entre sí, aunque ligeramente más grandes a las del holotipo, lo que permite suponer que la especie tiene un tamaño cercano a los 6 mm.

Clase: Bivalvia Linnaei, 1758
Subclase: Autobranchia Groblen, 1894
Infraclase: Heteroconchia Cox, 1960
Orden: Solenida Dall, 1889
Superfamilia: Solenoidea Lamarck, 1809
Familia: Solenidae Lamarck, 1809

Género: *Solena* Mörch, 1853
Tipo. *Solen obliquus* Spengler. Reciente. Caribe.

Subgénero: *Eosolen* Stewart, 1930
Tipo. *Solen plagiaulax* Cossmann. Eoceno. Cuenca de París.

Solena (*Eosolen*) *bolivarensis* Clark, 1946
(Figura 4)

Solena (*Eosolen*) *bolivarensis* Clark, 1946, p. 73, lám. 13, fig. 17, 18.

Descripción. Concha alargada, relativamente gruesa, con bordes dorsal y ventral paralelos y aproximadamente rectos; extremo anterior redondeado (solo se preserva éste en el hipotipo UN-DG-BV-010, Figura 4 A); superficie lisa con notorias líneas de crecimiento.

Material examinado. Un espécimen con buena preservación (solamente se conservó la valva derecha), identificado con el número de catálogo UN-DG-BV-010.

El holotipo de *Solena* (*Eosolen*) *bolivarensis*, está depositado en el Museo de Paleontología de la Universidad de California, Berkeley, UC por sus siglas en inglés (Localidad UC S60, espécimen No. 34915) y no pudo ser consultado.

Dimensiones.

Holotipo UC S60 No. 34915: Altura= 21.5 mm; ancho máximo del ejemplar roto = 46 mm.

Hipotipo UN-DG-BV-010: Altura= 20 mm; ancho máximo del ejemplar roto = 61 mm.

Ocurrencia. Pijiguay, departamento de Bolívar. Región Caribe colombiana.

Discusión. A pesar de contar con un solo ejemplar, las características morfológicas coinciden claramente con la descripción original de *Solena* (*Eosolen*) *bolivarensis* de Clark, 1946, la cual constituye una forma endémica solo descrita en el Eoceno de Colombia. Al igual que en la descripción original, donde la especie fue referida con reservas al subgénero *Eosolen*, debido a la ausencia del surco umbonal tan común en la mayoría de especies de *Eosolen*, la preservación del nuevo ejemplar (solo una valva) no permite una asignación exenta de dudas. De cualquier manera se coincide con el autor original en que las líneas irradiantes en el borde anterior dorsal sugieren una posible relación con *Eosolen*.

A partir de las proporciones observadas en los dos ejemplares existentes, se calcula un ancho máximo aproximado de 85 mm.

5. Precisiones estratigráficas y paleoambientales

El hallazgo de estos dos ejemplares (de distintas zonas) en un mismo horizonte fosilífero, sugiere que las tres zonas definidas por Clark y Durham (1946) no necesariamente corresponden a niveles con faunas exclusivas y que la posición estratigráfica relativa de estos dos moluscos es incierta. La presencia del gasterópodo *Faunus* (*Pseudofaunus*) cf. *chiraensis* en la “Zona A” de dichos autores, refuerza esta idea, ya que *Faunus* es un gasterópodo de aguas salobres y dulces, que actualmente vive en la desembocadura de los ríos en el Pacífico occidental (Woodring, 1973), y es muy similar a los gasterópodos encontrados en la Formación

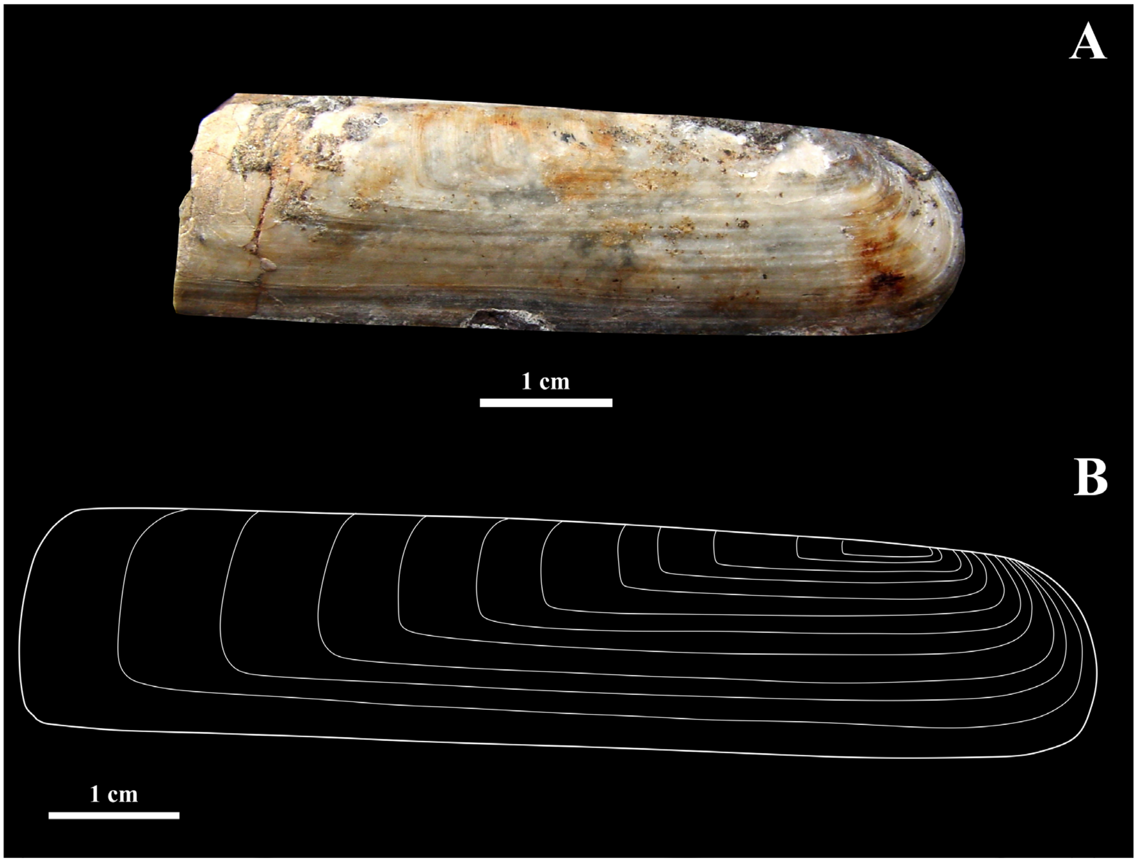

Figura 4. *Solena* (*Eosolen*) *bolivarensis* Clark 1946. A) Aspecto del hipotipo UN-DG-BV-010. B) Reconstrucción esquemática a partir de la información suministrada por el holotipo y el hipotipo hallado en este trabajo.

Arroyo Seco en el área de Chalán (unos 10 km al sureste de la localidad aquí estudiada), que incluyeron además de *Faunus* sp., *Pachychilus canoasensis*, *Hannatoma gesteri* y *H. emendorferi* (Bermúdez *et al*., 2013), en niveles carbonosos de clara afinidad paleoambiental con zonas pantanosas; lo que sugiere que proviene de un horizonte diferente, quizás más inferior. Esta situación es clara en el área de Chalán, donde los horizontes con fósiles marinos solo se desarrollan en la parte alta de la unidad; mientras que los horizontes carbonosos con fósiles se localizan sobre la parte media de la Formación Arroyo Seco, tal como también se pudo apreciar en el arroyo Mancomojan, hacia el núcleo del anticlinal El Cedro, unos 100 m estratigráficos por debajo del horizonte aquí descrito.

De cualquier manera el conjunto de la mayoría de hallazgos fósiles del CPSJ conforman una serie de asociaciones faunísticas muy bien definidas, que reflejan condiciones de depósito muy someras y clima tropical, que se asocia a depósitos marinos de litoral, sometidos al influjo de las olas y las tormentas y de frente deltaico (Anderson, 1928; Clark y Durham, 1946; ATG-ANH, 2008; Universidad de Caldas – ANH, 2009; Bermúdez *et al*., 2009), que no sustentan la idea de que el Paleógeno del CPSJ se acumuló en paleoambientes marinos profundos, incluyendo turbiditas y depósitos de zonas de talud, batiales y abisales, tal como plantean muchos estudios (Duque-Caro, 1972, Duque-Caro *et al*.,1996; Caro, 2003; Guzmán *et al*., 2004, entre otros).

El abundante registro fósil del Eoceno del Caribe colombiano, es afín al encontrado en las asociaciones del Eoceno y Oligoceno del Perú (Olsson, 1929, 1930, 1931; Woods, 1922), Centro América e incluso las Antillas y EEUU (Maury, 1912; Aldrich, 1921; Clark y Durham, 1946; Woodring, 1973), aunque muchas de las formas descritas parecen ser endémicas (Clark y Durham, 1946).

Estudios en desarrollo están empezando a redescubrir la paleontología de moluscos del Caribe colombiano, con la colecta y estudio de nuevo material, lo que unido a la descripción estratigráfica detallada, la micropaleontología y la cartografía regional será clave en el entendimiento de las relaciones faunísticas de Norte y Sur América

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References

Aldrich, T.H., 1921, New Eocene species from Alabama: Bulletins of American Paleontology, 9 (37), 1–32.

Anderson, F.M., 1928, Notes on Lower Tertiary deposits of Colombia and their molluscan and foraminiferal fauna: Proceedings of the California Academy of Sciences, Fourth Series, 17 (1), 1–29.

Asesorías Técnicas Geológicas - Agencia Nacional de Hidrocarburos (ATG-ANH), 2009, Cartografía geológica, levantamiento de columnas estratigráficas, toma de muestras y análisis bioestratigráficos. Sector de Chalán (Cuenca Sinú–San Jacinto): Reporte interno a la ANH con 12 anexos, *disponible en* <http://www.anh.gov.co/es/index.php?id=133>, *consultado*: 20 de junio de 2011.

Berggren, W.A., Pearson, P.N., 2005, A revised tropical and subtropical Paleogene planktonic foraminiferal zonation: Journal of Foraminiferal Research, 35 (4), 279–298.

Bermúdez, H.D., Alvarán, M., Grajales, J.A., Restrepo, L.C., Rosero, J.S., Guzmán, C., Ruiz, E.C., Navarrete, R.E., Jaramillo, C., Osorno, J.F., 2009, Estratigrafía y evolución geológica de la secuencia sedimentaria del Cinturón Plegado de San Jacinto, *en* Memorias XII, congreso colombiano de Geología: Paipa, 100–123.

Bermúdez, H.D., Vega, F.J., Corredor, V.E., Numpaque, A., 2013, Los moluscos del Paleógeno del CPSJ y su relevancia en las interpretaciones paleoambientales del Caribe colombiano (resumen), *en* Memorias XIV Congreso Colombiano de Geología: Paipa, 333.

Bouchet, P., Rocroi, J.P., Fryda, J., Hausdorf, B., Ponder, W., Valdés, Á., Warén, A., 2005, Classification and Nomenclator of Gastropod Families: Malacologia, 47 (1/2), 1–397.

Caro, M., 2003, Structural evolution of the San Jacinto fold belt, NW Colombia: Calgary, Alberta, Canada, University of Calgary, thesis of Master of Science, 82 p.

Carter, J.G., Harries, P.J., Malchus, N., Sartori, A.F., Anderson, L.C., Bieler, R., Bogan, A.E., Coan, E.V., Cope, J.C.W., Cragg, S., Garcia-March, J., Hylleberg, J., Kelley, P., Kleemann, K., Kriz, J., McRoberts, C., Mikkelsen, P.M., Pojeta, J., Skelton, P.W., Tëmkin, I., Yancey, T., Zieritz A., 2012, Part N, Revised, Volume 1, Chapter 31: Illustrated Glossary of the Bivalvia. Treatise Online, 48, 1–209.

Clark, B.L., Durham, J.W., 1946, Eocene Faunas from the Department of Bolívar, Colombia: Geological Society of America, Memoir 16, New York, 126 p.

Cox, L.R., 1960, Thoughts on the classification of the Bivalvia: Proceedings of the Malacological Society of London, 34, 60–88.

Cuvier, G., 1797, Tableau élémentaire de l'histoirenaturelle des animaux: Paris, Baudouin, 710 p.

Dall, W.H., 1889, On the hinge of pelecypods and its development with an attempt toward a better subdivision of the group: American Journal of Science, series 3, 38, 445–462.

Duque-Caro, H., 1972, Ciclos tectónicos y sedimentarios en el Norte de Colombia y sus relaciones con la Paleoecología: Boletín Geológico Instituto Nacional de Investigaciones Geológico Mineras, Bogotá, 19 (3), 1–23.

Duque-Caro, H., Guzmán, G., Hernández, R., 1996, Mapa geológico de la plancha 38, Carmen de Bolívar, escala 1:100000: Bogotá, Colombia, Ingeominas, 1 mapa con texto.

Groblen, C., 1894, Zur Kenntnis der Morphologie, der Verwandtschaftsverhältnisse und des Systems der Mollusken: Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften, 103 (1), 61–86.

Guzmán, G., Gómez, E., Serrano, B., 2004, Geología de los Cinturones del Sinú, San Jacinto y borde occidental del Valle Inferior del Magdalena, Caribe Colombiano, escala 1:300000: Memoria técnica Ingeominas. Bogotá, 134 p.

Herrera, J., Bermúdez, H., Alfonso, M., Calderón, J., Pardo, A., Lozano, A., 2009, Cartografía Geológica de un área del Cinturón Plegado de San Jacinto, en Memorias 10th Simposio Bolivariano Exploración Petrolera en Cuencas Subandinas, Cartagena, Colombia, 1–10.

Jaramillo, C., Rueda,M., Bayona, G., Santos, C., Flórez, P., Parra, F., 2009, Biostratigraphy breaking paradigms: Dating the Mirador Formation in the Llanos Basin of Colombia, *en* Demchuck, T. (ed), Geologic problems solving with microfossils: A volume in honor of Gary D. Jones, Society for Sedimentary geology, Special Publication 93, Tulsa, 29-40.

Lamarck, J.B.P. de, 1809, Philosophie zoologique: Dentu, Paris, 1, 428 p.

Linnaei, C., 1758, Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, species, cum Characteribus, Differentiis, Synonymis, locis: Tomus I, EditioDecima, Reformata, Holmiae, 824 p.

Martini, E., 1971, Standard Tertiary and Quaternary Calcareous Nannoplankton Zonation, *en* Farinaci, A. (ed), Proceeding of the 2nd Planktonic Conference, Roma, Edizioni Tectonscienzas, 2, 739–785.

Maury, C.J., 1912, A contribution to the paleontology of Trinidad: Journal of the Academy of Natural Sciences of Philadelphia, 15, 1–112.

Moore, R.C., Teichert, C., (eds.), 1969, Treatise on Invertebrate Paleontology: Lawrence, Kansas, University of Kansas Press, Part N, Mollusca 6: Bivalvia, 1-2, xxxvii + 952 p.

Mörch, O.A.L., 1853, Catalogus Conchyliorumquae Reliquit D. Alphonso d´Aguirra & Gadea, comes de Yoldi. Fasc. Sec.: Acephala. Hafniae, 74 p.

Olsson, A.A., 1929, Contributions to the Tertiary paleontology of northern Peru: Part 2. Upper Eocene Mollusca and Brachiopoda: Bulletins of American Paleontology, 15 (57), 1–96.

Olsson, A.A., 1930, Contributions to the Tertiary Paleontology of Northern Peru: Part 3. Eocene Mollusca: Bulletins of American Paleontology, 17 (62), 1–96.

Olsson, A.A., 1931, Contributions to the Tertiary Paleontology of Northern Peru: Part 4. The Peruvian Oligocene: Bulletins of American Paleontology, 17 (63), 97–264.

Rafinesque, C.S., 1815, Analyse de la nature, ou Tableau de l'univers et des corps organisées: Palermo, 224 p.

Sepkoski, J.J., 2002, A compendium of fossil marine animal genera: Bulletins of American Paleontology, 363, 1–560.

Stewart, R.B., 1930, Gabb's California Cretaceous and Tertiary Type Lamellibranchs: The Academy of Natural Sciences of Philadelphia, Special Publication, 3, 1–314.

Universidad de Caldas - Agencia Nacional de Hidrocarburos (ANH), 2009, Estudio integrado de los núcleos y registros obtenidos de los pozos someros tipo "slim holes" en la Cuenca Sinú: Reporte interno a la ANH con 2 tomos y 6 anexos, *disponible en* <http://www.anh.gov.co/es/index.php?id=133> *consultado* 20 de junio de 2011.

Woodring, W.P., 1973, Geology and Paleontology of Canal Zone and Adjoining Parts of Panama, Description of Tertiary Mollusks (Additions to gastropods, scaphopods, pelecypods: Nuculidae to Malleidae): Geological Survey, Professional paper, 306-E, 124 p.

Woods, M.A., 1922, Mollusca from the Eocene and Miocene deposits of Peru, *en* Bosworth, T.O. (ed), Geology of the Tertiay and Quaternary periods in the North-West part of Peru: MacMillan and Co. Ltd, London. 51–111.

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Scleractinia Corals of the Jandaíra Formation (Turonian- Campanian), Rio Grande do Norte state, Brazil

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Abstract

This work deals with the systematic study of the corals collected in the Jandaíra Formation, Turonian-Campanian of the Rio Grande do Norte state, Brazil. The specimens were recognized as *Actinastrea decaturensis* (Vaughan, 1919), *A. guadalupae* (Roemer, 1849), *Stephanocoenia guadalupae* Wells, 1932, *Madracis johnwellsi* Frost and Langenheim, 1974, *Isastrea whitneyi* Wells, 1932, *Paracycloseris effrenatus* Filkorn and Pantoja-Alor, 2009 and *Orbicella travisensis* Wells, 1932, as well as *Isastrea* sp. and two doubtful species, *Turbinolia* (*Turbinolia*)? *insignifica* Vaughan, 1900 and *Placotrochus*? *texanus* (Vaughan, 1903). The majority of these species occurs in the Aptian-Albian of USA and Mexico, as well as the Lower Tertiary of Central America and north of South America. This fauna is the westernmost hermatypic assemblage of the Turonian scleractinian and has affinities with others shallow marine Cretaceous units within USA and Mexico.

Keywords: Brazil, corals, Jandaíra Formation, Scleractinia, Turonian.

Resumen

Varias especies de corales colectadas en estratos del Cretácico Superior (Turoniano-Campaniano), correspondientes a la Formación Jandaíra en el estado de Rio Grande do Norte, Brasil fueron identificadas y descritas en este trabajo. Esta fauna está representada por Actinastrea decaturensis (Vaughan, 1919), A. guadalupae (Roemer, 1849), Stephanocoenia guadalupae Wells, 1932, Madracis johnwellsi Frost y Langenheim, 1974, Isastrea whitneyi Wells, 1932, Paracycloseris effrenatus Filkorn y Pantoja-Alor, 2009 y Orbicella travisensis Wells, 1932, así como Isastrea sp. y dos especies dudosas: Turbinolia (Turbinolia)? insignifica Vaughan, 1900 y Placotrochus? texanus (Vaughan, 1903). La mayoría de las especies se registran en el Aptiano-Albiano de Estados Unidos y México, así como con el Terciario Inferior de América Central y norte de Sudamérica. Esta fauna es la asociación más occidental del conjunto hermatípico de escleractineos Turonianos y tiene afinidades con otras unidades marinas poco profundas del Cretácico de Estados Unidos y México.

Palabras clave: Brasil, corales, Formación Jandaíra, Scleractinia, Turoniano.

1. Introduction

The records of the corals of the Jandaíra Formation were collected in informal manuscripts without descriptions or illustrations, located in the Museu de Paleontologia at the old Escola Superior de Agricultura de Mossoró (ESAM). According to these notes, specimens are found in the cities of Ipanguaçu (5º 29' 56" S, 36º 51' 10" W), Upanema (5º 38' 32" S, 37º 15' 27" W) and Governador Dix Sept Rosado (5º 27' 34" S, 37º 31' 16" W) (Figure 1). The first and only systematic study was done by Fernandes and Wanderley (2000) whose three specimens were collected on an outcrop in Igaraçu (5º 34' 18" S, 36º 54' 36" W), individualizing two distinct taxa.

This paper deals the systematic studies on 10 specimens housed in the Professor Vingt-Un Rosado Maia collection at Museu Câmara Cascudo - Universidade Federal do Rio Grande do Norte (MCC/UFRN), and other 3 specimens of the paleoinvertebrates collection at Museu Nacional/ Universidade Federal Rio de Janeiro (MN/UFRJ), from the cities of Ipanguaçu (5º 29' 56" S, 36º 51' 10" W), Pendências (5º 15' 28"S, 36º 43' 26" W) and Alto do Rodrigues (5º 17' 21" S, 36º 45' 29" W), chief fossiliferous localities of the Jandaíra Formation (Figure 1). The majority of these corals were reef- building species, lived in symbiotic relationship with zooxanthellae algae, and limited their ecologic distribution to substrates in shallow, well-lit, warm marine waters.

This research expands the current knowledge about corals of the Brazilian Cretaceous, helping to define detailed

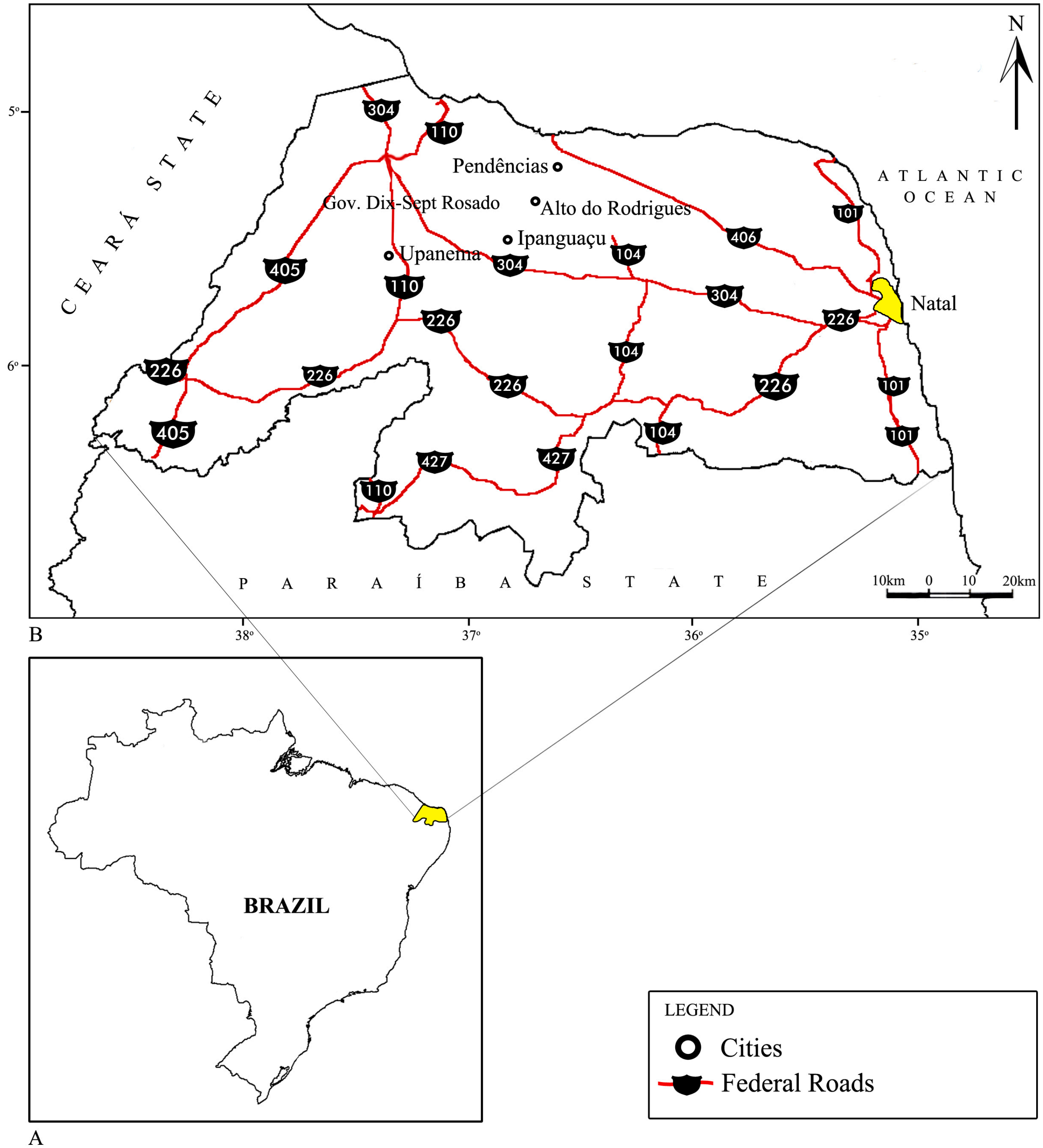

Figure 1: A. Map with special reference to the Rio Grande do Norte state, Brazil. B. Map showing the location of the study area in the Rio Grande do Norte state and the cities where the fossil corals were collected.

future biogeographic patterns in the Caribbean and South American regions of the Tethyan Sea.

2. Location and stratigraphy

The Potiguar Basin (Figure 2) is located in northeastern Brazil, between 4º 10’ and 5º 50’ latitude S and 35º 00’ and 38º 20’’ longitude W, encompassing parts of the Rio Grande do Norte and Ceará states, covering an area of 21500 km^2 onshore and 26500 km^2 offshore. The sediments of this basin were deposited from the Early Cretaceous to present times, and are traditionally divided in the Rift (Early Cretaceous), Post-rift (Alagoas Age) and Drift (Albian to the Holocene) Supersequences (Santos Filho *et al*., 2015).

The Jandaíra Formation belongs to the Drift Supersequence. It consists of calcarenites with bioclasts of mollusks, green algae, bryozoans and echinoids, bioclastic lime mudstones and calcilutites with bird’s-eye structures. Its basal portion is intercalated with sandstones and shales deposited from tidal flats, lagoons, platform and open sea environments. The litostratigraphic unit represents the great expansion of the carbonate domain, which encompassed the whole emerged area of the basin. Its upper contact is limited by a regional erosive unconformity that crops out in several places on the onshore section of the basin, which is the richest in fossils in the Potiguar Basin, including paleoinvertebrates, represented here by mollusks, echinoids, conchotraceans, bryozoans, corals and polychaetes (Cassab, 2003; Santos Filho *et al*., 2015). The age of deposition of the Jandaíra Formation was considered to be Turonian, Coniacian, Santonian and Turonian-Maastrichtian. However, studies based on calcareous nannofossils and ostracods suggest a Turonian-Campanian age, also supported by mollusks (Cassab, 2003; Santos Filho *et al*., 2015).

3. Material and methods

The collection analyzed comprises 13 specimens, all isolated corals, where colonial corals dominate. The cnidarians are filled or replaced with a fine, crystallized calcite and the surface structures and fine ornamentation of the septal borders are well preserved to a degree, while

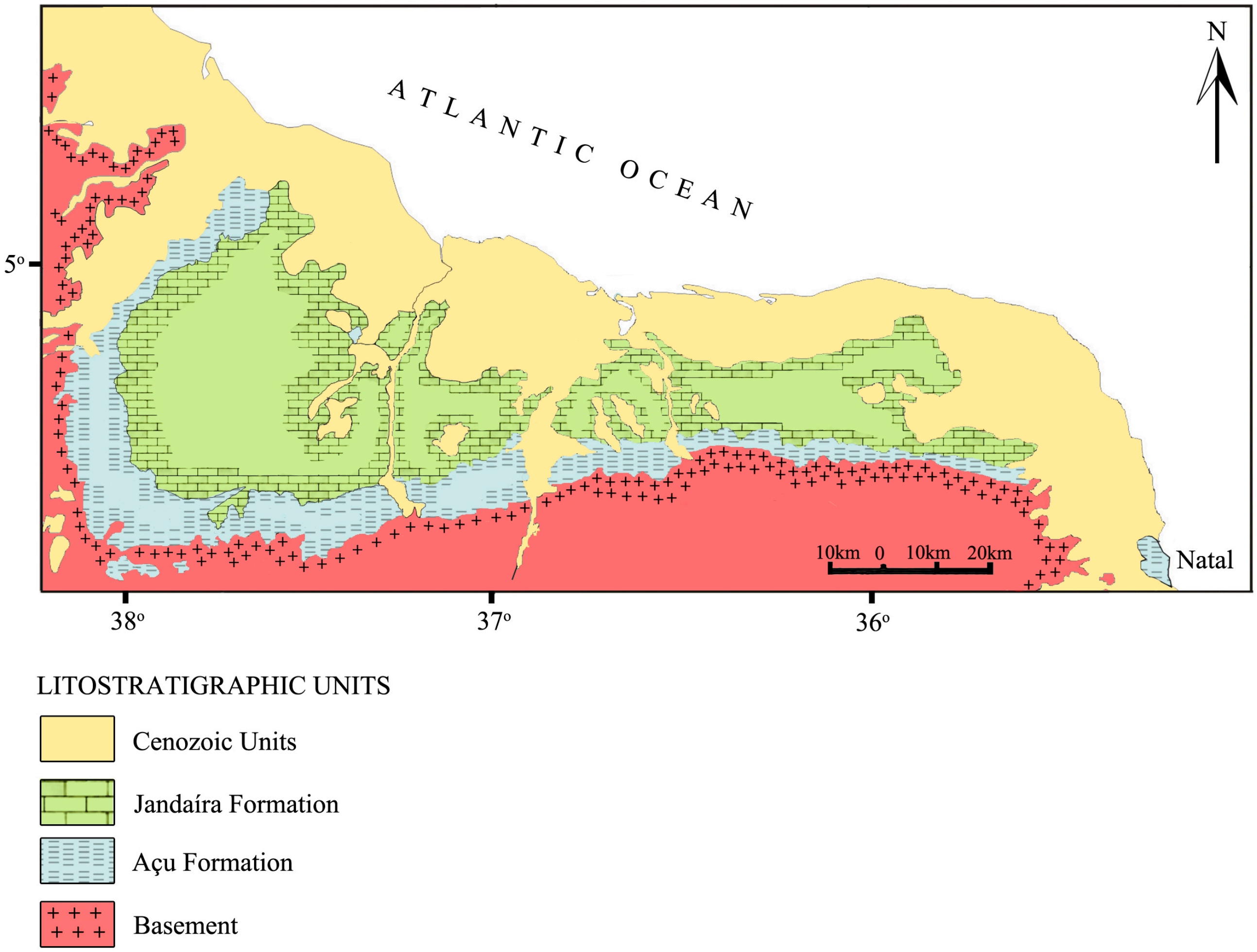

Figure 2. Geologic map of the Potiguar Basin (modified from Cassab, 2003).

the inner structures are partially destroyed due their more delicate nature. The examination of these corals was carried out using a binocular microscope, a precision caliper for obtaining measurements, and photographs taken by a Sony DSC-HX1 digital camera.

The corals at the Jandaíra Formation are very rare, and the specimens illustrated here are the best preserved. Detailed descriptions are provided depending on the degree of preservation of the material, especially in regards to the diagnostic morphological structures, such as the septa, pali and columella. These features were described with the help of a stereomicroscope, thus eliminating the need to make polished or thin sections.

4. Systematic descriptions

The systematic classification used in this paper as well as the essential terminology are mainly based on Wells (1956). The terms and nomenclature in the descriptions follow the proposals of Baron-Szabo *et al*. (2006), Baron-Szabo (2006, 2014), Filkorn *et al*. (2005), Filkorn and Pantoja-Alor (2009), Roniewicz and Stolarski (1999), Von der Osten (1957), and Wells (1932, 1933, 1934, 1941, 1945, 1946). In addition, complementary references such as Vaughan (1919), Geyer (1954), Budd *et al*. (1992), Löser (2013), and Fernandes and Wanderley (2000) were used.

The following abbreviations are used to indicate dimensions in the descriptions of the corals: h: height; l: length; w: width; cd: calicular diameter; s: septa; and cdp: calice depth. In the case of *Madracis johnwellsi*, measurements of the branch diameter (bd) and branch length (bl) are also included. The wt (wall thickness) is another dimension added to the descriptions of the cerioid and plocoid scleractinian taxa.

Order Scleractinia Bourne, 1900
Suborder Archaeocoeniina Alloiteau, 1952
Family Actinastraeidae Alloiteau, 1952
Genus *Actinastrea* d'Orbigny, 1849

Type species. *Actinastrea goldfussi* d'Orbigny, 1850.

Diagnosis. Corallum colonial, massive, ramose or incrusting, cerioid to subcerioid or subplocoid. Corallites small, prismatic, directly united by septothecal walls, smooth or porous. Septa compact, radials, non-confluent and granulated laterally. Columella styliform well developed. Paliform lobes and endothecal dissepiments sparse and thin. Synapticulae situated laterally. Based on Wells (1956) and Baron-Szabo (2014).

Distribution. Jurassic - Recent (Geyer, 1954; Wells, 1956; Baron-Szabo, 2014).

Actinastrea decaturensis (Vaughan, 1919)
Figure 3A

Description. Corallum colonial, massive, incrusting, cerioid to subplocoid, subeliptic in outline, transversally cut. Corallites numerous, small and subcircular, separated by slightly thick walls, smooth and narrowly merged. Calices polygonal and monocentric, hexagonal or pentagonal in outline, arched and moderately shallow. Septa straight, equal to subequal, laminar, equidistant, octamerally arranged in two incomplete to complete cycles, ranging from 14 to 16 units. Septal margins elevated until the surface of the calice, smooth to subcrenulated. The septa from the first cycle extends to the columella and its terminations are prominent in the separation walls between the corallites. The septa from the second cycle are about a quarter of the calicular diameter and, apparently, do not merge to the columella, which is well developed, cylindrical and styliform. Holotheca, pali, synapticulae, trabecular structures, endothecal and exothecal dissepiments absent, as well as internal morphological details of the calices, septa and separation walls between the corallites.

Occurrence. Panama: Gatuncillo Formation, Middle Eocene; Antigua: Antigua Formation, Late Oligocene; Cuba: Mogote Peak, Late Oligocene; United States of America: Flint River, Early Miocene (Vaughan, 1919; Budd *et al*., 1992). Brazil: Jandaíra Formation, Turonian-Campanian (present sudy).

Material. a fragment of a colony (MN 5566-I) found on the RN-118 road, 20 km from the crossroad with BR-304, Ipanguaçu city, Rio Grande do Norte state, Brazil. Deposited on the paleoinvertabrates collection at Museu Nacional/ UFRJ.

Dimensions. h: 11 mm; l: 32 mm; w: 12 mm; cd: 1.6 – 2.2 mm; s: 14 – 16; wt: 0.1 – 0.3 mm; cdp: 0.2 – 0.3 mm.

Discussion. The taxonomic relationship between *Actinastrea* d'Orbigny, 1849 and *Astrocoenia* Milne Edwards and Haime, 1848 has been discussed for the past 60 years. Initially, Milne Edwards and Haime (1848) individualized the genus *Astrocoenia*, and d'Orbigny (1849) proposed *Actinastrea* based on morphologically identical copies, characterized by its colonial cerioids with small calicular diameter. Alloiteau (1954) corroborated the existence of two genus, based on the differences of the calicular extremities, septal walls, endothecal dissepiments and columella. Ever since, the characterization of the species assigned to the *Astrocoenia* - *Actinastrea* clade was confused and insufficiently enlightening (Baron-Szabo, 2014).

Geyer (1954) considered *Astrocoenia* restricted to the Triassic, and attributed all of the Jurassic appearances of this clade to *Actinastrea*. Thus, all species of Central and South America considered as *Astrocoenia*, such as *A. barranquinensis* Wells, 1944, *A. dickersoni* Wells, 1941, *A. guadalupae* Roemer, 1848, *A. hexamera* Fritzsche, 1923, and *A. peruviana* Wells, 1941 must to be attributed in *Actinastrea*.

Although the internal structure of the calice, septa and separation walls between the corallites is usually destroyed by the recrystallization, the shape and diameter of the

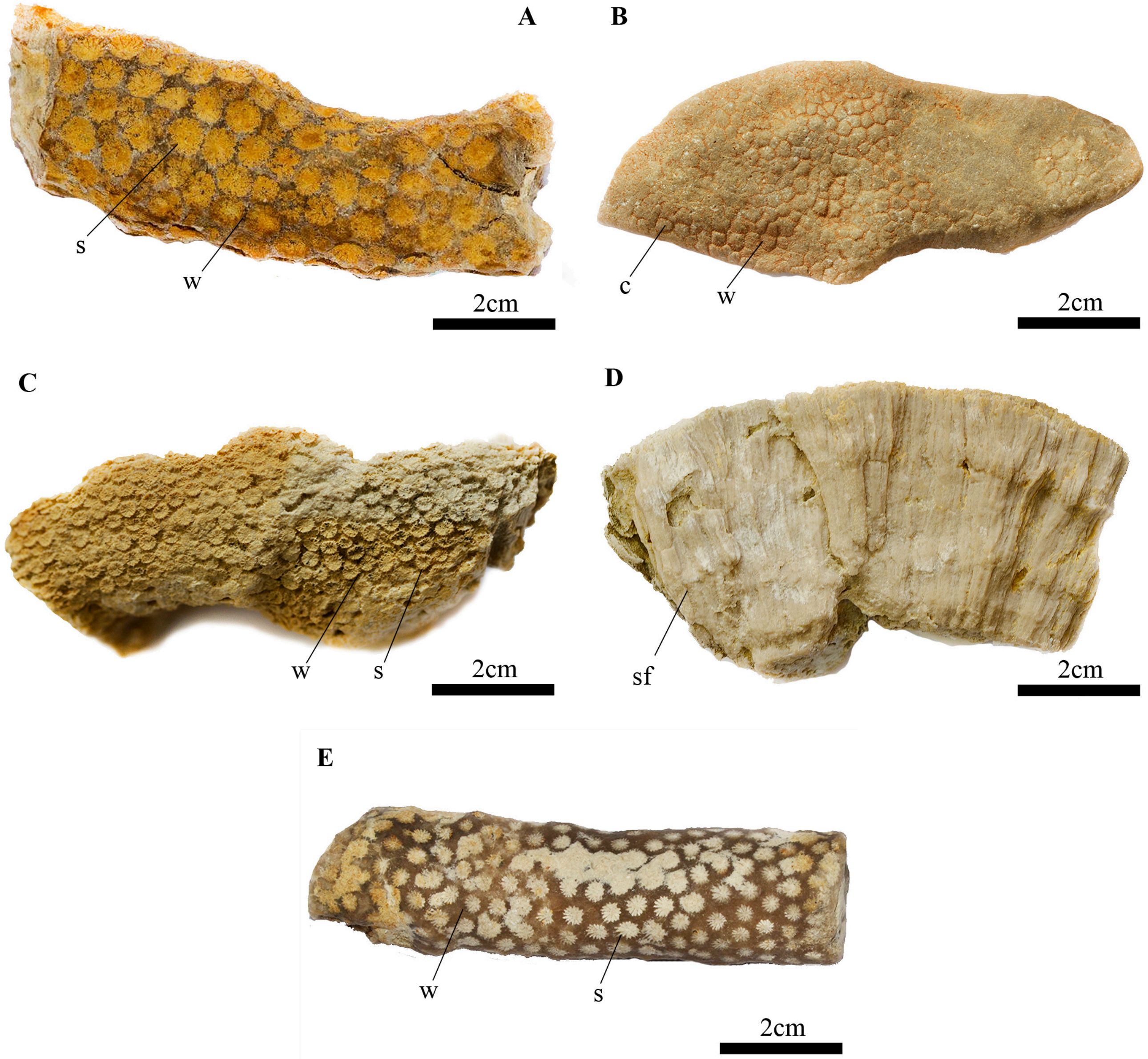

Figure 3. A. *Actinastrea decaturensis* (Vaughan, 1919) (MN 5566-I): corallum cerioid to subplocoid and subcircular corallites; B. *A. guadalupae* (Roemer, 1849) (MCC.C.2-363): corallum cerioid to subcerioid, prismatic corallites and shallow calices; C. *Stephanocoenia guadalupae* Wells, 1932 (MCC.C.2-108): corallum plocoid to subplocoid and small and circular corallites, closely separated; D. *Stephanocoenia guadalupae* Wells, 1932 (MCC.C.2-108): side view of holotheca showing the septal furrows; E. *Madracis johnwellsi* Frost and Langenheim, 1974 (MCC.C.2-350): corallum branch with numerous and spherical corallites, separated by thick walls (c: calice; s: septa; sf: septal furrows; w: walls).

corallites, the number, arrangement and septal disposition, and the thickness of the walls allow framing this specimen as *Actinastrea decaturensis* (Vaughan, 1919). Thus, this is the first occurrence of this species on the Cretaceous of South America, previously restricted to the Cenozoic of North and Central America.

The identifiable morphological features in *A. decaturensis* (Vaughan, 1919) differ from the previously described *A. guadalupae* (Roemer, 1849), because in *A. decaturensis* the corallites have subcircular shape, thicker separation walls and less numerous and octamerally arranged septa. Furthermore, Vaughan species present similarities with *A. incrustans* (Duncan, 1873) and *A. jukesbrownei* (Wells, 1945), differentiated by the bigger diameter of the corallites and thicker separation walls.

Remarks. Fernandes and Wanderley (2000) marked this specimen as representative of the genus *Astrocoenia* Milne Edwards and Haime, 1848.

Actinastrea guadalupae (Roemer, 1849)
Figure 3B

Description. Corallum colonial, massive, incrusting, cerioid to subcerioid and subeliptical. Corallites numerous, small and prismatic, separated by slightly thick walls, narrowly merged, smooth or ornamented by granules. Calices shallow, equivalent to the surface of the corallum, polygonal, monocentric, ranging among hexagonal, pentagonal, quadrangular and triangular in drawing. Septa equal or subequal, straight, laminar to thick, equidistant and hexamerally arranged in three cycles, incomplete to complete, ranging between 14 and 24 units. Septal margins smooth to subcrenulated. The first and second cycle septa are subequal, moderately thick and merge to the columella. The septa form the third cycle are less thick, less than one third of the calicular diameter and apparently do not merge to the columella. Columella little visible, small, cylindrical and styliform. Holotheca, pali, synapticulae, trabecular structures, endothecal and exothecal dissepiments are absent, as well as the internal morphological details from the calice, septa and corallum.

Occurrence. United States: Edwards Limestone Formation, Middle Albian; Devils River Limestone, Late Albian; Mexico: Mal Paso Formation, Late Albian (Wells, 1933; Filkorn and Pantoja-Alor, 2009); Brazil: Jandaíra Formation, Turonian-Campanian (present study).

Material. a colony fragment (MCC.C.2-363) from the Mulungu locality, Pendências city, Rio Grande do Norte state, Brazil.

Dimensions. h: 24 mm; l: 103 mm; w: 43 mm; cd: 1.8 – 3.0 mm; s: 14 – 24; wt: 0.1 – 0.2 mm.

Discussion. *Actinastrea guadalupae* (Roemer, 1849) has morphological similarities with *Actinastrea barranquinensis* (Wells, 1944) in the shape and diameter of the corallites, as well as in the thickness of the wall that separates them. However, *A. barranquinensis* presents more septa, less thick and disposed in nonamers arrangement. Besides, the endothecal dissepiments are moderately developed in *A. barranquinensis*. On the other hand, the dissepiments in the *A. guadalupae* type were not individualized.

Affinities between *A. guadalupae* and *A. hexamera*, *A. dickersoni* and *A. peruviana* were also recognized. However the characters related to the septa (number and arrangement) and corallites (shape, disposition and diameter) are particularly distinct.

Remarks. We must highlight that the variation in the calice shapes regarding the calicular extremity and the corallites accretion pattern varies with the convexity of the substratum, and may interfere in the taxonomic characterization of the *Astrocoenia* - *Actinastrea* clade.

Suborder Astrocoeniina Vaughan and Wells, 1943
Family Astrocoeniidae Koby, 1890
Subfamily Astrocoeniinae Koby, 1890
Genus *Stephanocoenia* Milne Edwards and Haime, 1848

Type species. *Astrea intersepta* Lamarck, 1816

Diagnosis. Corallum colonial massive, plocoid to subcerioid. Corallites small to medium size, separated by septothecal to parathecal walls. Septa disposed in three cycles with denticulate outlines and composed by a 12 paliform lobes system in the first two cycles. Columella styliform. Endothecal and exothecal dissepiments, evenly spaced. Based on Wells (1956) and Budd (1987).

Distribution. Cretaceous - Recent (Wells, 1956; Budd, 1987).

Stephanocoenia guadalupae Wells, 1932
Figures 3C, 3D

Description. Corallum colonial massive, incrusting, plocoid to subplocoid and irregularly flat-convex. Corallites numerous, small and cylindrical, separated by thin, smooth or granule-ribs ornamented septothecal walls. Calices shallow, monocentric, circular projected above the surface of the corallum and elevated in its superior edges. Septa equal to subequal, straight, equidistant, laterally beaded and hexamerally arranged in three incomplete to complete cycles, ranging from 22 to 24 units. Septal margins arched upwards, denticulate and smooth. The septa from the first and second cycle are even, elongated, thick and merged internally in a ring-shaped system of 12 pali, surrounding the columella, with its thickness measuring less than two thirds based on the thickness of the first septa. The septa from the third cycle are short, laminated, less than half of the size of the first two types and does not merge to the paliform system. Columella well developed, thick and irregularly styliform. Tabular exothecal dissepiments well developed and distributed through the side segments of the corallum. Delicate, continuous and closely spaced external septal furrows. Endothecal dissepiments absent.

Occurrence. United States: Cuchillo Formation, Early Cretaceous; Glen Rose Formation, Early Cretaceous; Venezuela: Barranquín Formation, Early Cretaceous (Wells, 1932, 1946; Von der Osten, 1957); Brazil: Jandaíra Formation, Turonian - Campanian (present study).

Material. a colony fragment (MCC.C.2-108) from São José locality, Alto do Rodrigues city, Rio Grande do Norte state, Brazil.

Dimensions. h: 41 mm; l: 73 mm; w: 25 mm; cd: 1.5 – 2.0 mm; s: 22 – 24; wt: 0.3 – 0.8 mm; cdp: 0.1 – 0.2 mm.

Discussion. *Stephanocoenia guadalupae* Wells, 1932 is similar to *S. intersepta* (Lamarck, 1816) in the general shape of the corallum, corallites, columella, septa number, arrangement of the paliform elements and calicular diameter. However, the calices in *S. intersepta* are shallower and there is no occurrence of the *S. guadalupae* diagnostic ornamentations. Another comparable species is *S. peruviana* Vaughan, 1922, but the number, shape and septa arrangement are dissimilar. There were also some recognized similarities with *S. formosa* Milne Edwards and Haime, 1849 and *S. storrsi* Wells, 1941, regarding the number and depth of the calice, the shape, number and arrangement of septa and corallites, as well as the paliform structures.

Family Pocilloporidae Gray, 1842
Genus *Madracis* Milne Edwards and Haime, 1849

Type species. *Madracis asperula* Milne Edwards and Haime, 1850.

Diagnosis. Corallum colonial plocoid, submassive to branchy. Septa few disposed in two octameral cycles, incomplete to complete. Septa from the first cycle merge to the collumela or with the paliform lobe system. Septa from the second cycle rudimental to absent. Columella styliform proeminent. Based on Wells (1956) and Neves and Johnsson (2009).

Distribution. Late Cretaceous - Recent (Wells, 1956; Baron-Szabo, 2006).

Madracis johnwellsi Frost and Langenheim, 1974
Figure 3E

Description. Corallum colonial thick, branching, cylindrical, dendroid and plocoid with oval extremity. Corallites massive, numerous, small and spherical, separated by thick granulated walls, smooth or beaded. Calices shallow equivalent to the surface of the corallum, monocentric, circular with slightly arched margins, corresponding to the septal elements. Septa equal to subequal, laminate to thick, equidistant and octamerally arranged in two incomplete to complete cycles, ranging from 14 to 16 units. Septal margins arched, subcrenulated and beaded by granules. The septa from the first cycle are equal, elongated, thick and internally merged in an eight pali ring-shaped system surrounding the columella, with its thickness equivalent to that of the first septa. The septa from the second cycle are rudimental, laminated, not merged to the paliform system. Columella well developed, thick, styliform, with a central tubercle inside. Holotheca, synapticula, trabecular structures, endothecal and exothecal dissepiments absent.

Occurrence. China: Gamba County Houshan, Campanian-Maastrichtian; Mexico: Cerralvo, Early Maastrichtian; Jamaica: Maldon Formation, Late Maastrichtian; Mexico: Ixtaclum Shale Formation, Late Eocene (Frost and Langenheim, 1974; Baron-Szabo, 2006). Brazil: Jandaíra Formation, Turonian - Campanian (present study).

Material. A colony fragment (MCC.C.2-350) from Arapuá locality, Ipanguaçu city, Rio Grande do Norte state, Brazil.

Dimensions. bl: 42 mm; bd: 10 mm; cd: 1.1 – 1.5 mm; s: 14 – 16; wt: 0.6 – 1.5 mm; cdp: 0.1 – 0.2 mm.

Discussion. *Madracis johnwellsi* Frost and Langenheim, 1947 presents some morphological similarities with *M. vaughani* Wells, 1941 and *M. densa* Budd, 1992, particularly in the shape of the corallum, corallites, calices and columella. However, in Wells' species, the branches of the corallum are thinner, the corallites are bigger, the separation walls are thicker and the septa appear in larger quantities, arranged in a decameral arrangement. Whereas Budd's species shows thinner separation walls between the corallites, deeper calices and septa disposed in a different arrangement, and displayed in different numbers.

Suborder Fungiina Verril, 1865
Family Montlivaltiidae Löser, 1994
Genus *Isastrea* Milne Edwards and Haime, 1851

Type species. *Astrea helianthoïdes* Goldfuss 1826

Diagnosis. Corallum colonial, massive and cerioid. Corallites monocentric or dicentric, polygonal over the calicular outline, separated by zig zag-shaped septothecal to parathecal walls. Costae rudimentary or absent. Septa delicate, compact, confluent, anastomosing in the axial zone, continuous, arched to recurved, rarely winding and uneven when it comes to length and width. Endothecal dissepiments numerous, small and vesicular. Synapticulae rarely present. Columella absent, but trabecular in depths of axial zone. Based on Wells (1956).

Distribution. Middle Jurassic - Cretaceous (Wells, 1956).

Isastrea whitneyi Wells, 1932
Figure 4A

Description. Corallum colonial, massive, incrusting, cerioid to subplocoid and irregularly convex. Corallites small and prismatic, separated by thick, continuous or zig-zag oriented synapticulathecal walls. Calices subshallow, broad, monocentric, polygonal ranging from pentagonal to quadrangular in outline. Septa equal to subequal, straight, laminate, equidistant, continuous, compact and hexamerally arranged in four incomplete cycles, ranging from 28 to 44 units. Septal margins subcrenulated, slightly arched and beaded by granules. The septa from the first and second cycle are subequal, extended to the central area where it merges to the columella. Conversely, the septas from the third and fourth cycles are less thick than the first two types, apparently not merging to the columella. Columella poorly preserved subtrabecular to trabecular, continuous and elongated. Holotheca, pali, trabecular structures, endothecal and exothecal dissepiments absent, as well as the internal morphological details of the septa in the corallum.

Occurrence. United States: Cuchillo Formation, Early Cretaceous; Glen Rose Formation, Early Cretaceous; Venezuela: Barranquín Formation, Early Cretaceous (Wells, 1932, 1946; Von der Osten, 1957); Brazil: Jandaíra Formation, Turonian - Campanian (present study).

Material. a colony fragment (MCC.C.2-025) from São José locality, Alto do Rodrigues city, Rio Grande do Norte state, Brazil.

Dimensions. h: 26 mm; l: 36 mm; w: 30 mm; cd: 3 – 4.5 mm; s: 28 – 44; wt: 0.3 – 0.5 mm; cdp: 0.5 – 0.8 mm.

Discussion. The morphological features of *Isastrea whitneyi* Wells, 1932 are very similar to the ones recognized

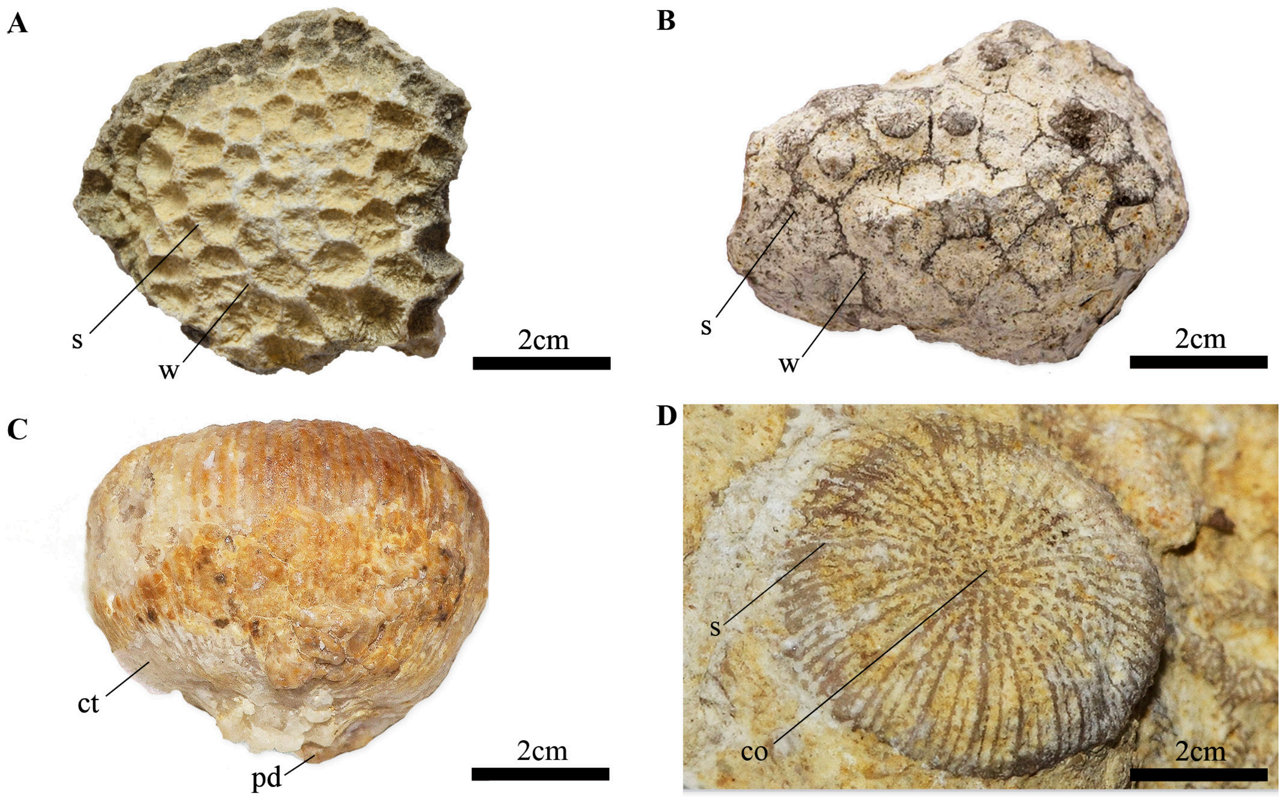

Figure 4. A. *Isastrea whitneyi* Wells, 1932 (MCC.C.2-025): upper surface view of prismatic corallites and polygonal calices; B. *Isastrea* sp. (MN 5565-I-A): corallum cerioid to subplocoid and big and prismatic corallites; C. *Paracycloseris effrenatus* Filkorn and Pantoja-Alor, 2009 (MCC.C.2-312): corallum tympanoid and cupuliform, with a small and delicate pedicel; D. *Paracycloseris effrenatus* Filkorn and Pantoja-Alor, 2009 (MCC.C.2-303): upper surface view of discoid calice and circular to subcircular calicular extremity (co: columella; ct: costae; s: septa; pd: pedicel; w: walls).

in some species of *Actinastrea* d'Orbigny, 1849, especially *A. kellumi* (Wells, 1946), *A. barranquinensis* (Wells, 1944) and *A. guadalupae* (Roemer, 1849) regarding the shapes of corallum, corallites and calices. However, *A. kellumi*, *A. barranquinensis* and *A. guadalupae* differentiate themselves by presenting smaller corallites in diameter, shallower calices, less numerous septa, styliform columella and abundant endothecal dissepiments.

Isastrea sp.
Figure 4B

Description. Corallum colonial massive, incrusting, cerioid to subplocoid and irregularly convex. Corallites big and prismatic, separated by thin, continuous and straight synapticulathecal walls. Calices shallow, broad, monocentric, polygonal ranging between pentagonal and hexagonal. Septa equal to subequal, straight, laminate, equidistant, continuous, compact and inferred from 20 to 24 units with no arrangement definition or cycle order. Columella, holotheca, pali, trabecular structures, endothecal and exothecal dissepiments absent, as well as diagnostic morphological details concerning the insides of the calices and septa.

Occurrence. Brazil- Jandaíra Formation, Turonian-Campanian (present study).

Material. two colony fragment (MN 5565-I-A and MN 5565-I-B) from the RN-118 road, 20 km from the crossroad with BR-304, Ipanguaçu city, Rio Grande do Norte state, Brazil, housed on the paleoinvertebrates collection at Museu Nacional/UFRJ.

Dimensions. (MN 5565-I-A) h: 14 mm; l: 31 mm; w: 23 mm; cd: 1.6 – 2 mm; s: 20 – 24; wt: 0.4 – 1.2 mm. (MN 5565-I-B) h: 17 mm; l: 30 mm; w: 24 mm; cd: 4.8 – 6.8 mm; wt: 0.2 – 0.3 mm; cdp: 0.5 – 0.8 mm.

Discussion. The cerioid shape of the corallum, polygonal corallites, septothecal walls and absent columella are enough to consider these specimens as *Isastrea*. The effects of the diagenetic processes destroyed or erased the morphological features of corallites, calice and septa, which impeded its identification at specific level.

Remarks. These specimens were identified only up to order level by Fernandes and Wanderley (2000).

Suborder Microsolenina Morycowa and Roniewicz, 1995
Family Felixaraeidae Beauvais, 1982
Genus *Paracycloseris* Wells, 1934

Type species. *Paracycloseris elizabethae* Wells, 1934

Diagnosis. Corallum solitary and depressed, cupolate, patellate, conical to convex and flat in shape. Epitheca thick, wrinkled and concentric, with indistinct walls. Calice circular, with oval to elongated fosseta, superficial on the juvenile and shallow on the adult specimens. Septa numerous, compressed, trabecular-fenestrated, united as in *Cycloseris*, with pores filled with lacerated teeth, and covered with granules. Columella thick, well developed, papillose. Irregular synpaticulae on the corallum, around the border of the calice. Dissepiments absent. Diagnosis based on Wells (1934, 1956).

The morphological features of this taxon are very similar to the ones seen on *Podoseris* Duncan, 1869, especially regarding the size and shape of the corallum, the pattern and outline of the calice, and the number and disposition of the septa. However, this taxon is primarily distinguished by its septal trabecular microstructures around the central septa area, the ornamentation pattern of its epitheca, its styliform columella and the big number of endothecal dissepiments. (Löser, 2012).

Distribution. Early to Late Cretaceous (Wells, 1956; Filkorn and Pantoja-Alor, 2009).

Paracycloseris effrenatus Filkorn and Pantoja-Alor, 2009
Figures 4C, 4D

Description. Corallum small, solitary, free, tympanoid with a subconvex base on the juvenile specimen and flat cupuliform with a subconcave to convex base on the adult specimen. Calice monocentric, discoid, slightly depressed with circular to subcircular calicular extremity, fixed by a small and delicate pedicel with subdeltaic outline and rounded extremity. Epitheca ornamented by regularly spaced wrinkles, concentric transversal ripples and granules. Septa hexamerally arranged in five complete cycles and an incomplete one with about 104 units on the adult sample and five incomplete cycles with about 81 on the younger sample. Septa numerous, straight, equal to subequal, equidistant arched upwards, laminar, closely spaced and laterally granulated. The first two cycles are equal, thicker than the others, extended to the columella, its top edges are provided with well developed teeth. The septa from the third cycle are smaller than the ones from the first and second cycle, yet get attached to the columella with top edges with smaller teeth. The fourth cycle septa are fused to the fifth cycle septa, with its teeth being smaller than the first three cycles, but they do not merge to the columella. The few septal pairs on the sixth cycle are provided with smaller teeth compared to the bigger cycles and they do not merge to the columella. Fosseta elliptical and shallow. Columella well developed, subtrabecular, with its superior surface being papillose to spongy, vertically continuous and narrow. Synapticulae poorly preserved and present in medium-upper segments on the peripheral region next to the calice. Costae, endotheca, dissepiments and palliform lobes not visible, as well as the morphological details concerning the wall of the corallum.

Occurrence. Mexico: Mal Paso Formation, Late Albian (Filkorn and Pantoja-Alor, 2009); Brazil: Jandaíra Formation, Turonian - Campanian (present study).

Material. A young specimen (MCC.C.2-303) and an adult specimen (MCC.C.2-312) from São José locality, Alto do Rodrigues city, Rio Grande do Norte state, Brazil.

Dimensions. (MCC.C.2-303) l: 9 mm; w: 8 mm; cd: 9 mm. (MCC.C.2-312) h: 13 mm; l: 16 mm; w: 15 mm; cd: 16 mm.

Discussion. Similarities between this species and *Paracycloseris elizabethae* Wells, 1934 were noticed regarding the general shape of the corallum, pattern and outline of the calice, shape and depth of the fosseta, ornamentation of the epitheca, presence of synapticulae on the peripheral portions of the corallum, and absence of dissepiments and columella shape. However, these species differ in the dimensions of the corallum, septa number and width of the collumela. *P. elizabethae* displays a bigger callicular diameter and about 200 septa disposed in seven incomplete cycles. Moreover, the columella is well developed with its upper surface being papillose to spongy, trabecular and narrower in *P. effrenatus* and trabecular and thicker in *P. elizabethae*.

Family Merulinidae Verrill, 1866
Genus *Orbicella* Dana, 1846

Type species. *Madrepora annularis* Ellis and Solander, 1786

Diagnosis. Corallum colonial, equal to subequal corallites, with septothecal and parathecal separation walls. Calice circular, small in diameter (< 4 mm) and depth (< 3 mm). Septa laterally granulated arranged in three cycles, ranging between 24 and 36 units. Columella trabecular, discontinuous, either bigger or equal to a quarter of the calice diameter. Epitheca moderately to well developed. Paliform lobes absent. Diagnosis based on Wells (1932, 1956).

The diagnostic features of these taxa are similar to the features of *Polyphylloseris* Fromentel, 1857, especially the shapes of corallum, corallites and columella. However, Fromentel's genus is distinguished by the presence of bigger corallites, an elevated calice and abundant synapticulae and endothecal dissepiments. It is also possible to recognize affinities with *Montastraea* Blainville, 1830 regarding the shape of the corallum, corallites, calice and columella (Wells, 1941, 1956).

Distribution. Cretaceous - Recent (Wells, 1932).

Orbicella travisensis Wells, 1932
Figure 5A

Description. Corallum colonial massive, incrusting, subplocoid to plocoid, subeliptical outline, convex. Corallites numerous, small and cylindrical, separated by septothecal thick walls, beaded by granules and ribs corresponding to the septa. Calices shallow, monocentric, circular and elevated in its superior edges. Septa equal to subequal, straight to recurved, laminated, equidistant, laterally granulated and hexamerally arranged in three incomplete to complete cycles, ranging between 20 and 24 units. Septal margins denticulate, smooth and arched to upper segments to the calice. The septa from the first and second cycles are subequal, thick and extended to the center where they merge to the columella. The septa from the third cycle are less thick, rarely extended to more than a third of the length of the first ones. Columella trabecular, well developed, continuous and elongated. Exothecal dissepiments sparse, present on the separation walls between the corallites. Holotheca, pali, synapticulae, trabecular structures and endothecal dissepiments absent.

Occurrence. United States: Travis Peak Formation, Early Cretaceous (Wells, 1932); Brazil: Jandaíra Formation, Turonian - Campanian (present study).

Material. Two colony fragments (MCC.C.2-105 e MCC.C.2-111) from São José locality, Alto do Rodrigues city, Rio Grande do Norte state, Brazil.

Dimensions. (MCC.C.2-105) h: 15 mm; l: 72 mm; w: 30 mm; cd: 1.7 – 2.1 mm; s: 20 – 24; wt: 0.5 – 1.1 mm. (MCC.C.2-111) h: 21 mm; l: 65 mm; w: 20 mm; cd: 1.6 – 2 mm; s: 20 – 24; wt: 0.4 – 1.2 mm.

Discussion. *Orbicella travisensis* Wells, 1932 has some similarities with *O. whitneyi* (Wells, 1932) and *O. roemeriana* Wells, 1933 related to the general shape of corallum and corallites, calice depth, and number, shape and disposition of calices. However, the corallites in *O. whitneyi* are smaller, the separation walls between them are less thick, columella is spongy and exothecal dissepiments are more abundant. On *O. roemeriana* the corallites are bigger, the separation walls between them are thicker and the columella is spongy to styliform.

Suborder Caryophylliina Vaughan and Wells, 1943
Family Turbinoliidae
Subfamily Turbinollinae Milne Edwards and Haime, 1848
Genus *Turbinolia* Lamarck, 1816

Type species. *Turbinolia sulcata* Lamarck, 1816 emend. Milne Edwards and Haime, 1850.

Diagnosis. Corallum solitary trochoid, ceratoid, conical and circular on the calicular outline. Walls smooth or externally perforated, separated by deep furrows. Septa disposed from two to four cycles, duplicated in number around the calicular border. Columella styliform or laterally compressed, formed by the fusion of primary septa. Pali absent. Diagnosis based on Wells (1956, p. F425).

Distribution: Eocene - Oligocene (Wells, 1956; Cairns, 1989).

Subgenus *Turbinolia* (*Turbinolia*) Lamarck, 1816

Type species. same as the genus.

Diagnosis. Walls and septa smooth and not ornamented. Diagnosis based on Wells (1956).

Distribution. same as genus (Wells, 1956).

Turbinolia (*Turbinolia*) *insignifica*? Vaughan, 1900
Figure 5B

Description. Corallum solitary, small, free, conical to turbinated and laterally compressed. Calice subcircular, monocentric, shallow, with slightly convex edges, smooth and continuous in extremity and oval to subeliptical outline. Pedicel small, cylindrical and well developed with rounded and oblate base. Costae smooth and well defined on the calicular margin, regularly spaced and bounded by dense ribs corresponding to the first septal cycle, separated by shallow and planed furrows. Septa arranged in a heptamerally complete cycle with seven units, well developed, straight, equal to subequal, dense, smooth, equidistant and regularly spaced. Septa joined by the base to the pedicel, radially arched above the calice surface, shaped by pronounced denticulations that merge itselves to form the columella. Pit subcircular and shallow. Columella styliform and papillose. Synapticulae, trabecular structures, paliform lobes, endothecal and exothecal dissepiments absent.

Occurrence. United States: Red Bluff Formation, Oligocene (Vaughan, 1900); Brazil: Jandaíra Formation, Turonian - Campanian (present study).

Material. a juvenile specimen (MCC.C.2-359) from São José locality, Alto do Rodrigues city, Rio Grande do Norte state, Brazil.

Dimensions. h: 14 mm; l: 11 mm; w: 10 mm; cd: 9 mm.

Discussion. *Turbinolia* (*Turbinolia*) *insignifica* Vaughan, 1900 is recorded on the Oligocene of North America. However, its morphological affinities with the specimen here described may represent the first occurrence of this taxon, so as *Turbinolia* Lamarck, 1816 in the Cretaceous. The reported specimen presents similarities with *T.* (*T.*) *insignifica* in the shape and size of corallum, calice, pedicel and columella, as well as in costae and septa arrangement. But the internal diagnostic morphological features of the calice, and the morphology and septal organization of the epitheca, are little visible due to the preservation process, preventing the undoubted positioning as *T.* (*T.*) *insignifica*.

There were also some recognized affinities with *T. sulcata* Lamarck, 1816 and *T. pharetra* Lea, 1833, both Cenozoic species. In Lamarck's species, besides the general shape of calice, pedicel and columella, and the costae arrangement being similar, the corallum is more flattened and septa are present in bigger number and divergent arrangements. In relation to *T. pharetra*, the general shape of the calice and columella are similar, where in Lea's specie, the corallum is more elongated, the septa are more numerous and ornamented and the pedicel is more tapered.

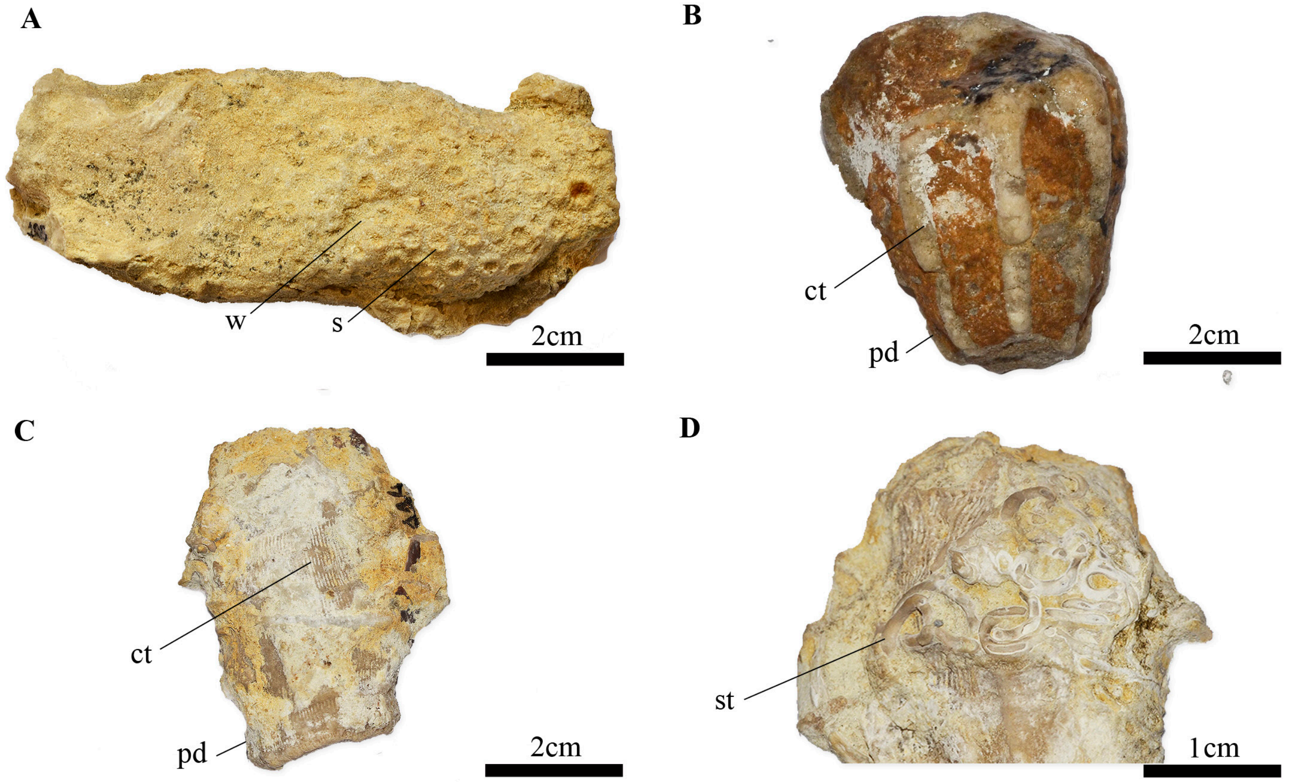

Figure 5: A. *Orbicella travisensis* Wells, 1932 (MCC.C.2-105): corallum subplocoid to plocoid with small and cylindrical coralites, separated by thick walls; B. *Turbinolia* (*Turbinolia*)? *insignifica* Vaughan, 1900 (MCC.C.2-359): lateral view of corallum conical and turbinated and a cylindrical and well developed pedicel; C. *Placotrochus*? *texanus* (Vaughan, 1903) (MCC.C.2-114): lateral view of corallum tympanoid to turbinated, moderately recurved and a well developed pedicel; D. *Placotrochus*? *texanus* (Vaughan, 1903) (MCC.C.2-114): lateral view of the corallum and thick stereome deposits. (ct: costae; pd: pedicel; s: septa; st: stereome; w: walls).

Family Flabellidae Bourne, 1905
Genus *Placotrochus* Milne Edwards and Haime, 1848

Type species. *Placotrochus laevis* Milne Edwards and Haime, 1848

Diagnosis. Corallum solitary cuneiform, turbinated and laterally compressed. Epitheca well developed and tecal extremity ornamented by thorns. Septa numerous, disposed in four to seven cycles. Columella rudimentary and irregularly lamellar. Pali absent. Diagnosis based on Wells (1956).

Distribution. Late Cretaceous - Recent (Wells, 1933; 1956).

Placotrochus texanus? (Vaughan, 1903)
Figures 5C, 5D

Description. Corallum solitary, cuneiform, moderately recurved, tympanoid to turbinated, laterally compressed, elliptical when transversally cut and subconvex base. Calice monocentric, elliptical on the upper edge and fixed by a well developed pedicel endowed with subcircular outline and irregularly rounded extremity. Costae equivalent to the septal walls, ornamented by granules and thorns. Epitheca well developed, discontinuous due to thick stereome deposits in medium-superior segments of the corallum. Septa hexamerally arranged in six incomplete cycles with about 110 units, numerous, straight, equal to subequal, laminated and laterally granulated. Fosseta subcircular. Columella rudimentary, elongated and irregularly lamellar. Synapticulae, paliform lobes and dissepiments not visible, as well as the morphological details of the septa in the calice and corallum.

Occurrence. United States: Buda Formation, Late Cretaceous (Wells, 1933); Brazil: Jandaíra Formation, Turonian - Campanian (present study).

Material. an adult specimen (MCC.C.2-114) from São José locality, Alto do Rodrigues city, Rio Grande do Norte state, Brazil.

Dimensions. h: 33 mm; l: 25 mm; w: 14 mm; cd: 17 mm.

Discussion. The North American species *Placotrochus texanus* (Vaughan, 1903) was the first one belonging to *Placotrochus* Milne Edwards and Haime, 1848 to be recognized in the Cretaceous. The sample here described presents similarities with this species in the general shape of corallum and calice, costae arrangement, septal number and disposition, shape of the columella, presence of tereome, and absence of dissepiments. Moreover, the dimensions of the North American species are smaller and proportional to the specimen here studied. However, the internal diagnostic morphological features of the calice and septa are poorly visible, preventing the undoubted framing as *P. texanus*.

There were also recognized similarities with *P. fuscus* Vaughan, 1907 and *P. laevis* Milne Edwards and Haime, 1848, both Cenozoic species. In Vaughan's species, the shape of corallum and columella, epithecal development and septal ornamentations are similar, but the shape of calice and pedicel, costae disposition and number of septa are really distinct. *P. laevis* shares a similar shape of calice and columella, epithecal development and septal number and arrangement. However, the calice from the individual that belongs to the Jandaíra formation is compressed laterally to a bigger extent, the septa are present in bigger number and the pedicel is more pronounced.

5. Age and palaeobiogeographic distribution

The high diversity in the coral associations studied in this work suggests proximity to center-of-diversity and high ocean surface temperature. This scenario reveals that the species are transported on surface currents into high-diversity regions from surrounding, isolated peripheral areas and subsequently dispersed from these high-diversity centers. The Cretaceous corals of southwestern Mexico are very important due to southern continental Mexico being centrally positioned in the tropical western Tethyan region during the Early and Middle Cretaceous (Filkorn and Pantoja-Alor, 2009).

The faunal similarity among the early Aptian coral species of Mexico and the coral fauna of the European region with adjacent areas of southeastern Mexico, northern South America, northwestern Mexico-southwestern USA and northern Mexico-Texas, indicates that the species were dispersed to North America and Mexico from localities in the European region, first by a westward flowing surface current, then by a southern route through the western Tethys Sea, typifying a very low endemism (Filkorn and Pantoja-Alor, 2009). The temporal-spatial distribution of the species in the late Albian-early Cenomanian indicates a much higher endemism, as well as the development of a south to southwest flowing surface current from Texas to southern Mexico and the Caribbean region (Filkorn and Pantoja-Alor, 2009), probably spreading continuously to northeastern Brazil during the Turonian-Campanian. This distribution attests to the existence of a southward flowing surface current streaming from the northeastern Mexico-Texas region to southwestern Mexico during the middle to late Albian. The occurrence of the genus *Paracycloseris* Wells, 1934, for example, in the Albian of Egypt, the late Albian-early Cenomanian of Mexico, and Upper Cretaceous of Jamaica, Cuba, Mexico and Brazil may help to establish a dispersal pathway along the more southern route. Also, the corals of the Jandaíra Formation show affinities to Lower Tertiary faunas of Central America (Panama, Jamaica, Cuba, Antigua) and Venezuela in South America. Future studies will allow to define other possible intermediate biogeographic connecting points existing in the Caribbean and South America regions (Filkorn and Pantoja-Alor, 2009), as suggested by the occurrence of the *Stephanocoenia guadalupae*, *Isastrea whitneyi*, *Actinastrea guadalupae*, *Paracycloseris effrenatus* and *Orbicella travisensis* species, typical of the Lower Cretaceous. The recognition of *Actinastrea decaturensis* and *Turbinolia* (*T.*) *insignifica* is seen to be related to the scleractinian high diversity that occurs in the Cretaceous (Budd, 2000) and which lasted until the Neogene.

The record of the Agaricidae Gray, 1847, Caryophyllidae Gray, 1847 and Flabellidae Bourne, 1905 families and the Fungiicae Dana, 1846 and Faviicae Gregory, 1900 superfamilies in the Jandaíra Formation (Turonian of northeastern Brazil) and the Pirabas Formation (Lower Miocene of northern Brazil) confirms that a dispersal pathway along to southern route was very important to scleractinian establishment and biogeographical spreading in the South Atlantic during the Tertiary and Quaternary.

6. Conclusions

This work presents the first detailed taxonomic study of the Turonian - Campanian coral fauna from the Jandaíra Formation of Rio Grande do Norte state, Brazil. This fauna is composed of 10 species, including 7 colonial, reef-building species and 3 solitary species. This is the first time that 9 of these 10 species have been reported from Brazil. The majority of these species are restricted to the United States and Mexico. Moreover the coralinofaune shows close affinities to Lower Tertiary faunas of Central America (Panama, Jamaica, Cuba, and Antigua) as well as Venezuela in South America.

This similarity supports the correlation of the Jandaíra Formation with other shallow marine Cretaceous units within the United States and Mexico. The studied association represents the westernmost hermatypic assemblage of the scleractinian coral occurrence of the Turonian, characterized by massive and branching growth types and plocoid, cerioid and dendroid polyp integration types. Tympanoid, cuneiform and conical solitary taxa were also found.

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References

AAlloiteau, J., 1954, Le genre *Actinastrea* d'Orbigny, 1849 dans le Crétacé supérieur français: Annales Hébert et Haug, 8, 9–104.

Baron-Szabo, R.C., 2006, Corals of the K/T - Boundary: Scleractinian Corals of the Suborders Astrocoeniina, Faviina, Rhipidogyrina and Amphiastraeina: Journal of Systematic Paleontology, 4 (1), 1–108.

Baron-Szabo, R.C., 2014, Scleractinian Corals from the Cretaceous of the Alps and N Dinarides: Abhandlungen der Geologi schen Bunde sans talt, 68, 1–296.

Baron-Szabo, R.C., Schafhauser, A., Götz, S., Stinnesbeck, W., 2006, Scleractinian corals from the Cardenas Formation (Maastrichtian), San Luis Potosí, Mexico: Journal of Paleontology, 80 (6), 1033–1046.

Budd, A.F., 1987, Neogene Paleontology in the northern Dominican Republic: Bulletins of American Paleontology, 93 (328), 5–43.

Budd, A.F., 2000, Diversity and extinction in the Cenozoic history of Caribbean reefs: Coral Reefs, 19, 25–35.

Budd, A.F., Stemann, T.A., Stewart, R. H., 1992, Eocene Caribbean Reef Corals: a Unique Fauna from the Gatuncillo Formation of Panama: Journal of Paleontology, 66 (4), 570–594.

Cairns, S. D., 1989, A Revision of the Ahermatypic Scleractinia of the Philippine Islands and Adjacent Waters, part I: Fungiacyathidae, Micrabaciidae, Turbinoliidae, Guyiidae and Flabellidae: Smithsonian Contributions to Zoology, 486, 1–136.

Cassab, R.C.T., 2003, Paleontologia da Formação Jandaíra, Cretáceo Superior da Bacia Potiguar, com ênfase na Paleobiologia dos Gastrópodes: Rio de Janeiro, Brasil, Universidade Federal do Rio de Janeiro, Ph.D. thesis, 184 p.

Fernandes, A.C.S., Wanderley, M.D., 2000, Corais (Cnidaria – Anthozoa – Scleractinia) da Formação Jandaíra, Cretáceo Superior do Rio Grande do Norte: Boletim do Museu Nacional, 55, 1–7.

Filkorn, H.F., Avendaño-Gil, J., Coutiño-Jose, M.A., Vega-Vera, F. J., 2005, Corals from the Upper Cretaceous (Maastrichtian). Ocozocoautla Formation, Chiapas Mexico: Revista Mexicana de Ciências Geológicas, 22 (1), 115–128.

Filkorn, H.F., Pantoja-Alor, J., 2009, Cretaceous corals from the Huetamo region, Michoacán and Guerrero, southwestern Mexico: Boletín Universidad Nacional Autónoma de México Instituto de Geologia, 116, 168 p.

Frost, S.H., Langenheim, R.L., 1974, Cenozoic Reef Biofacies: Northern Illinois Press: Dekalb, 388 p.

Geyer, O.F., 1954, Die oberjurassische Korallenfauna von Württemberg: Palaeontolographica, Abteilung A, Paläozoologie-Stratigraphie, 104, 4–6.

Löser, H., 2012, *Podoseris*- a poorly known solitary coral from the Albian of England (Scleractinia): Paleodiversity, 5, 7–11.

Löser, H., 2013, Revision of the family Felixaraeidae (Scleractinia; Cretaceous): Geodiversitas 35 (4), 747–765.

Milne Edwards, H., Haime J., 1848, Recherches sur les polypiers; quatrième mémoire: monographie des Astréides: Annales des Sciences Naturelles, Troisième Série, Zoologie, (10), 209–320.

Neves, E., Johnsson, R., 2009, Taxonomic revision of the southwestern Atlantic Madracis and the description of *Madracis fragilis* n. sp. (Scleractinia: Pocilloporidae), a new coral species from Brazil: Scientia Marina, 73 (4), 739–746.

Orbigny, A.d', 1849, Note sur des polypiers fossils: Paris, Victor Masson, 12 p.

Roniewicz, E., Stolarski, J., 1999, Evolutionary trends in the epithecate scleractinian corals: Acta Palaeontologica Polonica, 44 (2), 131–166.

Santos Filho, M.A.B., Piovesan, E.K., Fauth, G., Srivastava, N.K., 2015, Paleoenvironmental interpretation through the analysis of ostracodes and carbonate microfacies: study of the Jandaíra Formation, Upper Cretaceous, Potiguar Basin: Brazilian Journal of Geology, 45 (1), 23–34.

Vaughan, T.W., 1900, The Eocene and Lower Oligocene Coral Faunas of the United States with descriptions of a few doubtfully Cretaceous Species: U.S. Government Printing Office, 263 p.

Vaughan, T.W., 1919, Fossil corals from Central America, Cuba, and Porto Rico, with an account of the American Tertiary, Pleistocene, and Recent coral reefs: Smithsonian Institution Bulletin, 103, 189–524.

Von der Osten, E., 1957, A Fauna from the Lower Cretaceous Barranquín Formation of Venezuela: Journal of Paleontology, 31 (3), 571–590.

Wells, J.W., 1932, Corals of the Trinity Group of the Comanchean of Central Texas: Journal of Paleontology, 6 (3), 225–256.

Wells, J.W., 1933, Corals of the Cretaceous of the Atlantic and Gulf Coastal Plains and Western Interior of the United States: Bulletins of American Paleontology, 18 (67), 85–288.

Wells, J.W., 1934, Some fossil corals from the West Indies: Proceedings of the United States National Museum, 83 (2975), 71–110.

Wells, J.W., 1941, Upper Cretaceous Corals from Cuba: Bulletins of American Paleontology, 26 (97), 286–300.

Wells, J.W., 1944, Cretaceous, Tertiary, and Recent Corals, a Sponge and an Alga from Venezuela: Journal of Paleontology, 18 (5), 429–447.

Wells, J.W., 1945, West Indian Eocene and Miocene corals: Geological Society of America Memoir, 9 (2), 25 p.

Wells, J.W., 1946, Some Jurassic and Cretaceous Corals from Northern Mexico: Journal of Paleontology, 20 (1), 1–7.

Wells, J.W., 1956, Scleractinia, *in* Moore, R.C. (ed.), Treatise on Invertebrate Paleontology, Coelenterata, Part F, Lawrence, The University of Kansas Press, F328–F444.

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