Archaeochiapasidae n. fam., a new early Cenomanian brachyuran family from Chiapas, Mexico, new hypothesis on Lecythocaridae Schweitzer & Feldmann, 2009, and phylogenetic implications (Crustacea, Decapoda, Brachyura, Eubrachyura)

Danièle Guinot, Gerardo Carbot-Chanona, Francisco J Vega

To cite this version:

Danièle Guinot, Gerardo Carbot-Chanona, Francisco J Vega. Archaeochiapasidae n. fam., a new early Cenomanian brachyuran family from Chiapas, Mexico, new hypothesis on Lecythocaridae Schweitzer & Feldmann, 2009, and phylogenetic implications (Crustacea, Decapoda, Brachyura, Eubrachyura). Geodiversitas, 2019, 41 (1), pp.285. 10.5252/geodiversitas2019v41a7 . hal-02323037

HAL Id: hal-02323037

https://hal.sorbonne-universite.fr/hal-02323037v1

Submitted on 21 Oct 2019

Archaeochiapasidae n. fam., a new early Cenomanian brachyuran family from Chiapas, Mexico, new hypothesis on Lecythocaridae Schweitzer & Feldmann, 2009, and phylogenetic implications (Crustacea, Decapoda, Brachyura, Eubrachyura)

Danièle GUINOT
Institut de Systématique, Evolution, Biodiversité (ISYEB),
Muséum national d'Histoire naturelle, CNRS, EPHE, Sorbonne Universités,
case postale 53, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
guinot@mnhn.fr (corresponding author)
Gerardo CARBOT-CHANONA
Museo de Paleontología "Eliseo Palacios Aguilera", Secretaría de Medio Ambiente
e Historia Natural, Tuxtla Gutiérrez, Chiapas, Mexico
Francisco J. VEGA
Instituto de Geología, Universidad Nacional Autónoma de México,
Ciudad Universitaria, Coyoacán, CDMX 04510, Mexico

"*Rien n'est plus imminent que l'impossible*." [*Nothing is more imminent than the impossible."]* Victor Hugo, Les misérables

KEY WORDS Cretaceous, lower Cenomanian, Jurassic, El Chango quarry, Dorippoidea, Majoidea, Oregoniidae, Inachoididae, Inachidae, Hymenosomatoidea, exceptional preservation, new family, new genus, new species

Guinot D., Carbot-Chanona G. & Vega F. J. — Archaeochiapasidae n. fam., a new early Cenomanian brachyuran family from Chiapas, Mexico, new hypothesis on Lecythocaridae Schweitzer & Feldmann, 2009, and phylogenetic implications (Crustacea, Decapoda, Brachyura, Eubrachyura). *Geodiversitas*

ABSTRACT

A small brachyuran crab, *Archaeochiapasa mardoqueoi* n. gen., n. sp., is reported from the lower Cenomanian (Upper Cretaceous) of the Sierra Madre Formation at El Chango Lagerstätte, Chiapas State, southeastern Mexico. Although it is decorticated and only the counterpart keeps a large part of the cuticle, the single male specimen exhibits an exceptional three-dimensional preservation that allows its description to be based not only on the dorsal carapace, both chelipeds and most walking legs, but also on remarkably conserved ventral structures: mxp3, thoracic sternum, and pleon. *Archaeochiapasa mardoqueoi* n. gen., n. sp. provides a morphological combination that does not conform to any previously known fossil brachyuran and furthermore to any extant family. The high number of major differences suggest that *Archaeochiapasa* n. gen. must be included in the Eubrachyura Saint Laurent, 1980. A series of apomorphies supports the erection of a new family for which we introduce the new name Archaeochiapasidae n. fam. This fortunate discovery allows us to identify one of the earliest eubrachyurans with unique features, namely a very wide thoracic sternum displaying an unexpected structure for a lower Cenomanian representative, and a depressed, rimmed area ('flange') along the carapace postero- and postero-lateral margin. The new family is compared to the other fossil Eubrachyura known from the Early and mid-Cretaceous, which are very scarce and often incomplete, and to the more basal heterotreme clades that are presently recognised on the basis of morphological, larval, spermatozoal and genetic data, e.g. the Dorippoidea MacLeay, 1838, and to the basal families of Majoidea Samouelle, 1819 (Oregoniidae Garth, 1958, Inachoididae Dana, 1851, and Inachidae MacLeay, 1838). A challenging hypothesis based on new interpretations is that the Late Jurassic Lecythocaridae Schweitzer & Feldmann, 2009 (in Glaessneropsoidea Patrulius, 1959), only known by dorsal carapaces and formerly included in the Dromiacea De Haan, 1833, could belong with still obscure relationships, or at least be related, to the same lineage as the Archaeochiapasidae n. fam. The two families actually show striking similarities, such as the overall morphology of carapace, a depressed area along the carapace posterior margin, and a bifurcate short rostrum. Therefore, we assume that, despite their Jurassic age, Lecythocaridae may well also be Eubrachyura, which brings the first "true crabs" or eubrachyurans (i.e. non-podotreme crabs) back to the Jurassic, contrary to the current opinions of paleontologists. The discovery of Archaeochiapasidae n. fam. raises a crucial question: the development of a very wide thoracic sternum in this old eubrachyuran. Is it the expression of an ancestral dispostion (plesiomorphy) or the result of an already existing evolutionary process of carcinisation (apomorphy)? And what is its phylogenetic significance?

Abridged Title: New early Cenomanian eubrachyuran family from Chiapas, Mexico

RÉSUMÉ

Un petit crabe brachyoure, *Archaeochiapasa mardoqueoi* n. gen., n. sp., est signalé du Cénomanien inférieur (Crétacé) de la Sierra Madre Formation dans la carrière El Chango, dans l'Etat de Chiapas, sud-est Mexico. Bien qu'il soit decortiqué et que seul le contre-moule ait conservé la plus grande partie de la cuticule, le seul spécimen mâle montre une exceptionelle préservation en trois dimensions, qui permet une description basée non seulement sur la face dorsale de la carapace, les deux chélipèdes et la plupart des pattes ambulatoires, mais aussi sur les structures de la face ventrale remarquablement conservées: les mxp3, le sternum thoracique, et le pléon. *Archaeochiapasa mardoqueoi* n. gen., n. sp. montre une combinaison de caractères morphologiques qui n'est conforme à aucun groupe eubrachyoure fossile connu et, de plus, à aucune famille actuelle. Le nombre élevé d’importantes différences montre qu’*Archaeochiapasa* n. gen. doit être inclus dans les Eubrachyura Saint Laurent, 1980. Une série d’apomorphies justifient l’établissement d’une famille nouvelle, pour laquelle nous introduisons le nom nouveau Archaeochiapasidae n. fam. Cette heureuse découverte permet d’identifier l’un des premiers eubrachyoures, avec des traits uniques, à savoir un très large sternum thoracique, révélant une structure inattendue chez un représentant du Cénomanien inférieur, et une zone déprimée et garnie d'un bord épais (‘rebord’) tout le long du bord postérieur et postéro-latéral de la carapace. La nouvelle famille est comparée aux autres Eubrachyura fossiles connus du Crétacé inférieur et moyen, lesquels sont très rares et souvent incomplets, ainsi qu’aux clades hétérotrème reconnus à ce jour comme les plus basaux, sur la base de données morphologiques, larvaires, spermatologiques et génétiques, e.g. les Dorippoidea MacLeay, 1838, et les familles basales de Majoidea Samouelle, 1819 (Oregoniidae Garth, 1958, Inachoididae Dana, 1851 et Inachidae MacLeay, 1838). Une hypothèse audacieuse basée sur de nouvelles interprétations est que la famille Lecythocaridae Schweitzer & Feldmann, 2009 (dans les Glaessneropsoidea Patrulius, 1959), du Jurassique tardif, seulement connue par des carapaces dorsales et précédemment incluse dans les Dromiacea De Haan, 1833, donc considérée comme une famille podotrème, pourrait appartenir, avec des relations encore obscures, ou tout au moins être apparentée à la même lignée que les Archaeochiapasidae n. fam. Les deux familles montrent en effet de surprenantes similitudes, comme la morphologie d’ensemble de la carapace, une zone déprimée le long du bord postérieur de la carapace, et un rostre court, bifurqué. C'est pourquoi nous émettons l’hypothèse que, malgré leur âge Jurassique, les Lecythocaridae pourraient aussi être des Eubrachyura, ce qui ferait remonter au Jurassique les premiers “vrais Crabes” ou eubrachyouriens (à savoir non podotrèmes), ce qui est en contradiction avec les opinions en cours des paléontlogistes. La découverte de la famille Archaeochiapasidae n. fam. soulève une question cruciale : le développement d’un très large sternum thoracique chez l’un des tout anciens eubrachyoures connus. Est-ce l’expression d’une dispostion ancestrale (plésiomophie) ou le résultat d’un processus évolutif de carcinisation déjà existant (apomorphie)? Et quelle signification phylogénétique?

MOTS CLÉS Crétacé, Cenomanien, Jurassique, carrière El Chango, Dorippoidea, Majoidea, Oregoniidae, Inachoididae, Inachidae, Hymenosomatoidea, préservation exceptionelle, famille nouvelle, genre nouveau, espèce nouvelle.

INTRODUCTION

A small male brachyuran crab was recently found at El Chango Lagerstätte, Chiapas, southeastern Mexico, in the lower Cenomanian (Upper Cretaceous) of the Sierra Madre Formation, in an environment that has already yielded a rich faunal and floral assemblage, with several new taxa (Figs 1-4). The specimen (Figs 5-12) is decorticated, with the counterpart keeping most of the cuticle (Fig. 6B-D), which makes the description of the exfoliated dorsal surface difficult (in particular for the anterior part of the carapace), and may result in misinterpretations (Klompmaker *et al.* 2015a; Robins *et al*. 2016). The crab, however, has an exceptional three-dimensional preservation, with near-complete dorsal carapace, articulated chelipeds and pereiopods, external maxillipeds, thoracic sternum, and pleonal somites (Figs 7, 9-12). To know the location of the cuticular ornamention on the carapace dorsal surface, we provide a composite picture with the superposition of the cuticle and the exfoliated carapace (Fig. 8). Our fossil displays a combination of morphological features that has not been recognised previously in the fossil records, as well as in the extant Brachyura Latreille, 1802. The search for its identity and affinities made it clear that it was a truly unique taxon. As even the carapace itself does not conform to any previously known fossil or extant brachyuran, the conclusion is that it represents a new crab genus, *Archaeochiapasa* n. gen., and a new species, *A. mardoqueoi* n. sp., in an ancient family-level lineage.

The Cretaceous is a period where brachyurans flourished and diversified, with the first known appearances of eubrachyuran crabs, all heterotremes. Although the majority of modern brachyuran families have a fossil record with at least one species reported, only a few families are not represented by a species found also or exclusively in the fossil record (De Grave *et al.* 2009). While fossil eubrachyurans are relatively well represented in Upper Cretaceous deposits (Jagt *et al.* 2015), in contrast there is a small number of heterotreme families currently reported from the early mid-Cretaceous and Early Late Cretaceous, and nothing is known about the early Cretaceous history (Luque 2015b; Prado *et al*. 2018).

Our investigations showed a real disparity between the oldest heterotreme representatives, e.g. Componocancridae Feldmann, Schweitzer & Green, 2008, Dorippoidea MacLeay, 1838, Priscinachidae Breton, 2009, Marocarcinidae Guinot, De Angeli & Garassino 2008, Telamonocarcinidae Larghi, 2004, Tepexicarcinidae Luque, 2015, and Eogeryonidae Ossó, 2016. The possible relationships of *Archaeochiapasa* n. gen. with these families, including their first known occurrences, are examined and discussed below, leading to the introduction of a new family, Archaeochiapasidae n. fam.

Archaeochiapasa mardoqueoi n. gen., n. sp. represents a fortunate, informative discovery: it documents the development of a very wide thoracic sternum in one of the earliest known eubrachyurans. This raises a crucial question: is this crab a heterotreme, similar to those of the same period or later, e.g. from the Campanian or Maastrichtian, all with a less broadened, differently configured thoracic sternum? Another question needs to be asked concerning the apparent coexistence of two coeval eubrachyuran stocks of crabs during the Cretaceous. It is required to discuss whether the archaeochiapasid configuration corresponds to an ancestral heterotreme dispostion (plesiomorphy) or can be interpreted, at this early stage, as it has already been the result of the evolutionary process of carcinisation (apomorphy).

The unusual shape of the carapace, with a flange bordered by a strong rim (Figs 6, 7, 8, 9B, 12C) and the broad thoracic sternum (Fig. 11) are, despite significant differences, vaguely reminiscent of that encountered in the controversial family Hymenosomatidae MacLeay, 1838, in which a basal position in Brachyura is supported by a wide range of data, including larval and adult morphology, spermatozoal and molecular data coexisting, however, with sternal male gonopores. The tentative idea of a relative proximity between Archaeochiapasidae n. fam. and Hymenosomatoidea, the latter unknown in the fossil record, is considered. We also investigate whether some recognised podotreme taxa from the same time period or even earlier or later exhibit similar traits. The enigmatic family Lecythocaridae from the Upper Jurasssic of Europe, has proven to have comparable characteristics, which are dicussed.

STRATIGRAPHY AND PALAEOENVIRONMENT

The El Chango locality is located approximately 17 km in a straight line southwest of Tuxtla Gutiérrez, Chiapas, southeastern Mexico (Fig. 1A, B). This locality belongs to the lower Cenomanian Cintalapa Member of the Sierra Madre Formation (Alvarado-Ortega & Than-Marchese 2013; Díaz-Cruz *et al*. 2016, 2019) (Fig. 4). The Sierra Madre Formation includes 2,590 m of Aptian-Santonian limestones and dolomites, deposited under shallow marine tropical conditions (Michaud & Fourcade 1989; Rosales-Domínguez *et al*. 1997). The depositional environment for the laminar dolomites and limestones of the El Chango Quarry is interpreted as an estuarine or salty lagoon with ephemeral freshwater influx (Vega *et al*. 2006, 2007a). Marine crabs could have been transported by tidal influence; occasional occurrence of ammonites actually indicates periodic influence of marine water. The record of ammonites in the El Chango section provides the most precise age calibration available for this stratigraphic interval (Moreno-Bedmar *et al.* 2014). The tiny crab here described could had been transported to the shallow estuarine environment of El Chango by means of storms or tides, but, once deposited there, the environment should have been extremely quiet, as suggested by the preseved articulated, long, slender pereopods and pleon. In fact, the paleoenvironment may have been so quiet that a corpse of a fish has been preserved with the scales still surrounding the body (Fig. 2F). The abundance and good preservation of gymnosperms and angyosperms (Fig. 2C-E) suggest a close presence to the continent (Guerrero-Márquez *et al*., 2013; González-Ramírez *et al*., 2013) and a low-energy environment.

An exceptional richness and state of preservation of faunal and floral fossil assemblages occur in the Sierra

Madre Formation, a promising region in relation to the presence of fossil decapod crustaceans from the Cretaceous. Well-preserved plants, fishes, and decapods are found in the white to cream-colour laminar limestones (Figs 2, 3), with, however, scarce and not so well-preserved mollusks (Ovalles-Damián *et al*. 2006; Vega *et al*. 2006, 2007a; Alvarado-Ortega & Ovalles-Damián 2008; Alvarado-Ortega *et al*. 2009; Garassino *et al*. 2013; González-Ramírez *et al*. 2013; Guerrero-Márquez *et al*. 2013). Previously, Garassino *et al*. (2013) reported from the El Chango quarry four new genera of shrimps, considered to represent the richest known fossil shrimp community from the Mesozoic of the Americas, and also palinurids and two brachyurans.

The palaeobiodiversity of El Chango assemblage is today increased by the discovery of *Archaeochiapasa mardoqueoi* n. gen., n. sp. The exceptional preservation of all these crustaceans, thanks to a quiet environment, recalls that seen in other Lagerstätte localities, such as the Upper Jurassic Solnhofen in Germany (Oppel 1862; Förster 1966; Schweigert 2001, 2011; Schweigert & Garassino 2004; Garassino & Schweigert 2006; Charbonnier & Garassino 2012; Winkler 2012, among others). Vega *et al*. (2007a) suggested a shallow lagoon or estuary, with periodic influence of freshwater for the El Chango limestones. Another example of near-perfect fossilisation is the Santana Group, the Araripe Group in the Araripe Basin of northeastern Brazil, dated to the Aptian to Albian stages of the Early Cretaceous, where the formations were deposited in a lacustrine to subtidal shallow marine environment. Among its worldwide famous palaeontological heritage are the podotreme crabs *Araripecarcinus ferreirai* Martins-Neto, 1987 from the Albian (Guinot & Breton 2006; Luque 2015a) and the orithopsid *Exucarcinus gonzagai* Prado & Luque, 2018 from the upper Aptian-lower Albian (Prado *et al.* 2018).

Archaeochiapasa mardoqueoi n. gen., n. sp. here reported is preserved in three dimensions, with dorsal surface, mxp3, both articulated chelipeds, most of the pereiopods, thoracic sternum, and pleonal somites. The specimen (part and counterpart into a medium-sized slab) was preserved in laminated dolomitic limestones (Steinkern) (Figs 5, 6, 8).

MATERIAL AND METHODS

The reported specimen was photographed with a Zeiss Tessovar, with an adapted Canon Eos 5D Mark II. Close ups were taken with a Zeiss Axio Zoom V16, with an objective Plan-NEOFLUAR Z 1.0x/0.25 FWD 56mm and a Zeiss digital camera. Images edited and modified using Adobe Photoshop Elements 2.0. The specimen was prepared with a Paleo Tools Micro Jack # 1 and 3, under an American Optical stereomicroscope, which enabled the thoracic sternum and pleon to be cleared with minimum damage.

The holotype is deposited at the Museo de Paleontología “Eliseo Palacios Aguilera”, Tuxtla Gutiérrez, Chiapas, Mexico (IHNFG).

Measurements are provided in millimetres and reported as carapace length (cl) x carapace width (cw) respectively, taken at its maximum (including rostrum). The following abbreviations are used in the text: mxp3, third maxillipeds; P1-P5, first to fifth pereopods (P1 as chelipeds; P2-P5 corresponding to walking legs 2-5); 1-6: pleonal somites 1 to 6. The thoracic somites are numbered from 1 to 8. The thoracic sternal sutures are referred to by the number of the two thoracic sternites that they involve, and thus are numbered from 1/2 to 7/8.

ABBREVIATIONS

GPIT, Institut für Geowissenschaften der Universität, Tübingen, Germany;
IHNFG, Secretaría de Medio Ambiente e Historia Natural, Tuxtla Gutiérrez, Chiapas, Mexico;
MNHN, Muséum national d'Histoire naturelle, Paris, France;
SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

SYSTEMATIC PALAEONTOLOGY

Order DECAPODA Latreille, 1802

Infraorder BRACHYURA Latreille, 1802

Section EUBRACHYURA Saint Laurent, 1980

Subsection HETEROTREMATA Guinot, 1977

Superfamily *Incertae sedis*
Family ARCHAEOCHIAPASIDAE n. fam.

TYPE GENUS. — *Archaeochiapasa* n. gen. by present designation. Gender feminine.
DIAGNOSIS. — Cuticle very thin. Carapace with lateroposterior and posterior regions expanded, forming all around a narrow, sunken, continuous area ("flange") bordered by a strongly rimmed, thickened, raised margin. Carapace posterior margin deeply concave. Dorsal surface with a few, small, regularly distributed tubercles; some regions strongly inflated and separated by distinct grooves. Hepatic region conspicuous, delimitated by margin forming right angle; subbhepatic and branchial regions expanded laterally; cardiac region large, extending nearly to posterior border. Cervical and postcervical grooves marked; gastrocardiac groove deep. Rostrum short, sulcate, bifurcate. Chelipeds stout, equal, homomorph, with massive merus, carpus and propodus. P2, P3 very long and slender. Only one last pereiopod (P4 or P5) preserved, straight, and only reduced approximately by about half compared to P3. Thoracic sternum extremely wide compared to the carapace width;

sutures 5/6-7/8 reaching margins of pleon, complete on exposed portion of sternum, sutures underneath the folded pleon being not visible. Pleon triangular, of six free somites, plus telson; first three somites dorsal; somite 6 with two lateral prominences, probably at location of sockets for pleonal-locking mechanism; no pleotelson.

REMARKS. — In Brachyura the ventral part provides a reliable complex of characters, in particular the thoracic sternum. The organisation of the thoracic sternum and pleon, remarkably well preserved in *Archaeochiapasa mardoqueoi* n. gen., n. sp. (Fig. 11), is indicative of a non-podotreme crab, in contradiction with what the carapace suggested, and provide evidence of a eubrachyuran affiliation. The new fossil from the lower Cenomanian of Mexico is therefore quite distinct from the podotreme crabs found preserved in Albian-Cenomanian deposits from southern England and France (Wright & Collins 1972; Breton & Collins 2011; Valentin *et al.* 2014), from Navarra, northern Spain (Fraaije *et al.* 2008; Klompmaker *et al.* 2011, 2013; Artal *et al.* 2012), from Tarragona, southern Spain (Ossó *et al*. 2018), from Sicilia (Checchia Rispoli 1917), from Mexico and Colombia (Vega *et al*. 2007a, 2010), from Texas (Vega *et al*. 2014), and from a wide range of regions (Karasawa *et al*. 2011; Van Bakel *et al.* 2012).

Genus *Archaeochiapasa* n. gen.

TYPE SPECIES. — *Archaeochiapasa mardoqueoi* n. sp., by present designation.

ETYMOLOGY. — After the Chiapas State, a worldwide famous place for its historic and natural beauties, and from the Ancient Greek "*arkhaios*" that means "archaic", "ancient".

DESCRIPTION. — As for the species.

Archaeochiapasa mardoqueoi n. gen, n. sp.

(Figs 5-12)

MATERIAL. — Holotype and single specimen, male, collected by Gerardo Carbot-Chanona March 14, 2018 (IHNFG-5616 part and counterpart); carapace length: 10.3 mm; width: 11.1 mm; carapace + chelipeds length: 16.2 mm; P2 length: 22.5 mm; P3 length: 26.5 mm; P4 or P5 length: 13.5 mm.

ETYMOLOGY. — In honour of Don Mardoqueo Carbot-Trujillo, father of Gerardo Carbot-Chanona and well-known natural sciences enthusiast from Chiapas, Mexico.

TYPE LOCALITY. — El Chango, 17 km southwest of Tuxtla Gutiérrez, Chiapas, southeastern Mexico.

HORIZON AND AGE. — El Chango quarry, Cintalapa Member, Sierra Madre Formation, early Cenomanian (Fig. 4) near the top of the section, along with diagnostic ammonites.

DESCRIPTION

Counterpart

Cuticle very thin, not heavily calcified. A depression well marked along carapace postero- and posterolateral border; posterior margin deeply concave. A few small, regularly distributed spiniform teeth, only visible on the counterpart. Rostrum produced, bifurcate.

Carapace (internal cast)

Carapace nearly devoid of cuticle, small, nearly as long as wide, semiquadrate to subpentagonal, with moderate anterior narrowing. Anteriorly, an area enclosing the whole lateroanterior region, including front. A strong tooth at level of each mesobranchial region at the junction of both antero- and posterolateral margins. Lateral margin with globose swellings. Dorsal surface marked by bosses. Mesogastric region prolonging into elongate process, on each part of protogastric regions; hepatic regions large, as two lateral conspicuous areas, externally delimitated by deep groove forming right angle; subhepatic region represented by markedly swollen area on each side; gastric region developed; cardiac region inflated. Branchial regions expanded laterally, forming swellings. Several grooves well defined, deep, mainly cervical, postcervical and branchiocardiac; deep branchio-cardiac grooves forming two marked median depressions. Rostrum bifurcate, medially depressed, arising well below carapace margin, seemingly integrated into carapace outline. Antero-lateral carapace margins rounded, unarmed, except for a strong tooth at level of each mesobranchial region about at the junction of both antero- and posterolateral margins. Posterior margin long, deeply concave. Carapace posterolateral and posterior margins strongly thickened and raised, expanded to form all around a narrow, markedly depressed area, continuous and undivided (here called ‘flange’). Eyes, cephalic appendages not preserved.

Thoracopods

Mxp3 complete, broad, almost entirely covering buccal cavern; exopodite stout, reaching about distal margin of merus. Chelipeds extended forwards, elongated, not longer than twice carapace width, stout, equal, homomorph, probably unarmed; merus, carpus robust; propodus thicker; fingers rather long, not bent at an angle to palm. P2, P3 extended, very long, much longer than P1 (P3: 26.5 mm, the longest), very slender, cylindrical throughout length, unarmed. Only one last leg (P4 or P5) preserved, shorter than P2, P3, straight, only reduced by about half compared to P3, the only one clearly recognisabe measuring 13.5 mm.

Thoracic sternum

Thoracic sternum preserved in greater part, extremely wide and extended laterally, mainly sternite 5; sternite 4 proportionally narrower; sternite 1 seemingly small, triangular; no apparent suture between sternites 2-3; sternites 5-8 laterally extended; sternites 6 to 8 gradually diminishing backwards; sternite 8 small, obliquely oriented. Sutures 5/6-7/8 reaching margins of pleon, complete on exposed portion of sternum, sutures underneath the folded pleon being not visible.

Male pleon

Pleon preserved in most part, triangular, of six three somites; first three somites not folded ventrally, in continuity with carapace, dorsally exposed; last somite (somite 6) enlarged, with two lateral prominences, probably at location of sockets for pleonal-locking system, seemingly corresponding to an effective mechanism; telson triangular, moderately long, reaching the level of suture 4/5.

Male gonopores

Not visible (see Discussion).

REMARKS

The most characteristic character of the carapace of the new family is the depressed, undivided area, delimitated by a strongly rimmed and raised margin, here called ‘flange’, which is all along the concave posterior margin of the carapace and extends along most part of posterolateral margin (Figs 7, 9B). The flange is well visible in the counterpart (Fig. 6).

ASSOCIATED BRACHYURANS

There are two other brachyurans from the Cenomanian Sierra Madre Formation of El Chango quarry. The crab (IHNFG-4720) (Fig. 3F) is a podotreme, with preserved articulated chelipeds and pereiopods, noticeably long P2-P4 and “slightly reduced” P5. It corresponds to the species previously reported by Garassino *et al.* (2013: 269, fig. 4H-I) without being assigned to a genus and family; at first glimpse it might have a vague resemblance to crabs in the family Cenomanocarcinidae Guinot, Vega & Van Bakel, 2008, especially with regard to the slightly flattened P4, but it does not seem conspecific with *Cenomanocarcinus renfroae* Stenzel, 1945 (see Vega *et al*. 2010: fig. 8.7-8.9) and is regarded as “undetermined cenomanocarcinid”.

Another specimen recently found (IHNFG-5617), part and counterpart (Fig. 3G, H), with a relatively poor preservation, is a eubrachyuran with characters as follows: carapace trapezoidal, with inverted shape; dorsal surface with pustulose ornamentation; front wide; rostrum projected, bifid; orbits wide, with two fissures; pleon triangular; chelae strong; P2, P3 long and slender, with sharp, acute dactyli. Possible affinities with the Tepexicarcinidae Luque, 2015 (Luque 2015b) need to be evaluated.

PHYLOGENETIC RELATIONSHIPS

Is Archaeochiapasidae n. fam. a podotreme or an eubrachyuran?

Archaeochiapasidae n. fam. from the early Cenomanian (about 100 my ago) is not a basal podotreme family since an extremely wide thoracic sternum (Fig. 11) is interposed between the pleon and the appendages (see Guinot & Tavares 2001, 2003). Furthermore, it does not belong to the less basal podotreme clades that retain a pair of spermathecae at the extremity of sternal sutures 7/8 together with a portion of thoracic sternum exposed at each side of the pleon (Guinot 1993; Guinot & Quenette 2005). That is the case of Dakoticancroidea Rathbun, 1917, in which the exposed portion of the sternum is either wide (Dakoticancridae Rathbun, 1917) or narrow (Ibericancridae Artal, Guinot, Van Bakel & Castillo, 2008) and where P4 and P5 (Ibericancridae) or only P5 (Dakoticancridae) are conspicuously reduced and subdorsal. Despite the lack of a female specimen, in Archaeochiapasidae n. fam. there is no evidence of dakoticancroid characters (Bishop 1981; Guinot 1993; Bishop *et al.* 1998; Artal *et al.* 2008; Feldmann *et al.* 2013; Bishop 2016). On the other hand, Archaeochiapasidae n. fam. does not share the features of Cyclodorippoidea Ortmann, 1892 and Gymnopleura Bourne, 1922, both podotremes and with an oxystome condition (Van Bakel *et al.* 2012: 13, 171, fig. 50; Guinot *et al*. 2013: fig. 41), corresponding to the Archaeobrachyura *sensu* Guinot & Tavares 2003.

It is easy to confuse podotreme crabs and dorippoids (Eubrachyura) because of a similar carapace structure, with dorsal grooves outlining a human 'face' and a similar dorsal location and reduction of last pereiopod(s). The distinction between cyclodorippids and dorippids, and more generally between crabs with female coxal gonopores versus female sternal gonopores (vulvae) has been clarified only in the recent past (Guinot 1977). This is the case of the Albian crab *Hillius youngi* Bishop, 1983, first considered as a possible eubrachyuran with dorippoid affinities (Bishop 1983a: fig. 8C, pl. 1, figs 8-11; De Grave *et al*. 2009; Schweitzer *et al.* 2010), but finally recognised as a podotreme, possibly related to either Cyclodorippidae Ortmann, 1892 (Karasawa *et al.* 2011; Schweitzer & Feldmann 2011) or tentatively to Gymnopleura (Van Bakel *et al*. 2012; Guinot *et al*. 2013; Jagt *et al.* 2015). Hence, the difficulty of identifying the fossils, and especially the early forms without the possibility of examining gonopores and thoracic sternum, and to differentiate the earliest representatives of Eubrachyura from the abundant and diversified Cretaceous podotremes.

The overall morphology of *Archaeochiapasa mardoqueoi* n. gen., n. sp. and, mainly, its very wide thoracic sternum (Fig. 11) are indicative of a true eubrachyuran; moreover, the conspicuous prominences on the pleonal somite preceding the telson (somite 6) (Fig. 12B) are interpreted as part of a typical heterotreme press-button mechanism that tightly locks the pleon (Guinot & Bouchard 1998). Although we have not examined a female, we can confidently asumme a location of the vulvae (female gonopores) on sternite 6, as in all eubrachyurans. The male gonopores are generally very difficult to discern on fossils, we are only assuming they are located on the P5 coxae (see Discussion).

At first sight, the body (mostly the counterpart, see Fig. 6) and the rostrum (Figs 7, 8, 9A) of *Archaeochiapasa mardoqueoi* n. gen., n. sp. look like an inachoidid or an inachid, but many characters seem not consistent with such an affiliation. Neither inachoidids nor inachids show the concave posterior carapace margin and the flange of Archaeochiapasidae n. fam. (Figs 7, 8, 9B, 12C). In addition, the pleotelson (i.e., somite 6 fused to telson), which bears at its base the locking buttons, typical of both Inachidae MacLeay, 1838 and Inachoididae Dana, 1851 (Guinot *et al*. 2013: figs 49C, D, 50A-D, F), does not exist in Archaeochiapasidae n. fam., where the male pleon consists of six free somites (1-3 being dorsally positioned) plus the telson (Figs 9B, 11, 12). Additionally, the last two legs of majoids may be modified but they are generally not markedly reduced, only P5 being sometimes slightly reduced or modified (Griffin & Tranter 1986), versus at least one of the two pairs (P4 or P5) reduced, only approximately half as much as P3, in the new family (Figs 9B, 12C). An exception is the oregoniid genus *Chionoecetes* Krøyer, 1838 (Rathbun 1925: 232, figs 88, 89, pls 84-91, 234), in which the P5 is significantly reduced (but not carried dorsally), with in addition a quadrate carapace and broad branchial regions in all species. In fact, the affinities of Archaeochiapasidae n. fam. could be researched near the Oregoniidae Garth, 1958 (Garth 1958) that is the more basal majoid family (see below under this name). The laterally dilated hepatic and the postorbital regions forming an alate expansion in the extant *Hyas coarctatus* Leach, 1814 (Rathbun 1925: 252, fig. 93, pls 94, 95: pl. 13), are reminiscent of the carapace shape found in *A. mardoqueoi.* But, to our knowledge, a flange is never present in Majoidea, and we consider for the moment the Archaeochiapasidae n. fam. a eubrachyuran extinct family *incertae sedis*.

Comparison with Lecythocaridae Schweitzer & Feldmann, 2009

The most diagnostic and unusual feature of Archaeochiapasidae n. fam. is the carapace postero- and postero-lateral margin expanded into a flange corresponding to a depressed, undivided area, hollowed as a channel, and delimitated by a strongly rimmed, raised margin. This flange, also visible on the counterpart (Figs 6, 7, 9B), and clearly a part of the carapace, is unique to Eubrachyura. Such a characteristic feature is not shared by the majoid Inachoididae (Fig. 16A) and Inachidae, and by the Dorippoidea MacLeay, 1838, see below. Although Archaeochiapasidae n. fam. appears not to be a podotreme, it was nevertheless useful to explore whether some recognised podotreme taxa could exhibit a so strange and rare trait.

We found surprising resemblances with the family Lecythocaridae from the Upper Jurasssic of Europe, known only by several tiny and poorly sclerotised carapaces and which is therefore a carapace-based taxon, such as practically all the Jurassic brachyuran taxa. Actually, the Lecythocaridae seems not to exhibit a particularly thickened and raised border as in the Archaeochiapasidae n. fam.; however, the concave carapace posterior region is remarkably depressed in all lecythocarid species: this depressed area, called ‘rim’ by the authors, is somewhat reminiscent of the ‘flange’ of Archaeochiapasidae n. fam.

It seems premature to recognise as homologous all the rims or flanges found in various Jurassic and Cretacous families assigned either to Homolodromioidea Alcock, 1900 or Glaessneropsoidea Patrulius, 1959: for example, a concave rimmed margin occurs in podotremes such as the Longodromitidae Schweitzer & Feldmann, 2008 or the Goniodromitinae Beurlen, 1932 (see Hyžný *et al*. 2015). This condition, perhaps corresponding to a plesiomorphic character state, is not well documented (Guinot in press).

The occurrence of the small crab in the Cenomanian of the Chiapas is a fortunate finding since what it teaches us allows better understanding the morphology of the tiny and similar-looking lecythocarid crabs of the Upper Jurassic of Europe.

The genus *Lecythocaris* von Meyer, 1860, initially considered a “precursor” of the Majoidea (Patrulius (1959: 253) but assigned to the Prosopidae von Meyer, 1860 (Patrulius 1966: 508, pl. 30, fig. 9) and included in Homolodromioidea (Van Straelen 1925: 163; Müller *et al*. 2000: figs 1, 7, 17J; see also Krobicki & Zatoń 2008: fig. 1) until Schweitzer & Feldmann (2009: 62, 94, tables 1, 6) establish the Lecythocaridae, with two species: *L. paradoxa* (von Meyer, 1858) (von Meyer 1860: 215, pl. 23, fig. 31, as *Prosopon paradoxum*) and another one, *L. obesa* Schweitzer & Feldmann, 2009 (Schweitzer & Feldmann 2009: 99, figs 1.7, 6.6-6.8), with a conspicuous flange. The family was included in the Dromiacea De Haan, 1833, within the Glaessneropsoidea Patrulius, 1959 (besides the superfamily Homolodromioidea), therefore considered a podotreme.

Lecythocaridae was initially diagnosed by the globular swellings of the carapace and a large cardiac region extending to the posterior margin, both features “not seen in any other brachyurans” (Schweitzer & Feldmann 2009: 94). The particular shape of the carapace posterior margin was described “with a broad, smooth, marginal furrow” (von Meyer 1860: 216), later not especially noticed (see Schweitzer & Feldmann 2009: 94; Schweitzer *et al.* 2012: fig. 15.1a-c). According to Schweitzer & Feldmann (2009), the strong pustular ornamentation of lecythocarid crabs, as well as the inflated areas, deep grooves could have served as camouflage for a semi-cryptic lifestyle in hard substrates. All the known species are remarkably tiny (Schweitzer *et al.* 2009: table. 6), often measuring less than 5.0 mm in width and never exceeding 10 mm; larger specimens, of double size, exist (B. van Bakel, pers. comm.).

Lecythocaris paradoxa, the type species, has a “broad, smooth, marginal furrow”, bordered by the “incised” [i.e., concave] rimmed posterior margin of carapace (von Meyer 1860: 216, translation by Schweitzer

& Feldmann 2009: 96, 97, 98, fig. 6.1- 6.5, 6.8). *L. paradoxa*, represented by the neotype fixed by Wehner (1988) and measuring 5.5 x 5.2 mm (see Wehner 1988: 65) (Fig. 13A) and now known by several specimens, has been recorded from the latest Kimmeridgian and Tithonian of several countries of Europe, e.g. Austria, Germany, Poland, Romania (see Quenstedt 1867: pl. 26, fig. 11, as *Prosopon*; Moericke 1899 [also quoted from 1889 and 1897]: 58, pl. 6, fig. 12, as *Prosopon*; Van Straelen 1925: 357, fig. 163; Patrulius 1966: 509, pl. 30, fig. 9, as *L. paradoxa strambergensis*; Glaessner 1969: R484, fig. 294.4; Wehner 1988: 64, fig. 18, pl. 4, figs 8, 9; Müller *et al.* 2000: 52, figs 1, 7, 17J; Schweitzer & Feldmann 2009: 94, fig. 6.1-6.5, table 1; Schweigert & Robins 2016: fig. 2C, D; Schweigert 2019; Schweitzer *et al*. 2018: fig. 17.11).

The carapace shape of *Lecythocaris paradoxa* figured by Schweigert & Robins (2016: fig. 2C) (Fig. 13A) differs from that of *A. mardoqueoi* n. gen., n. sp. (Fig. 6) by the ornamentation and grooves. In *Lecythocaris stoicai* Franţescu, 2011, from the late Oxfordian to early Kimmeridgian of Romania, the posterior rim is very conspicuously defined along the whole posterior margin (Franţescu 2011: 20, fig. 14).

A “posterior rim” is found in *Prolecythocaris hauckei* Schweigert & Robins, 2016, from the lower Kimmeridgian of Franconia, Germany (Schweigert & Robins 2016: 327, fig. 2A, B), with “the holotype in cuticle preservation and the paratype preserved as steinkern” (Fig. 13B). It is a very small species: the pentagonal carapace of the holotype mesures 3.6 x 4.0 mm, whereas the paratype mesures 5.9 x 6.4 mm. The mode of fossil preservation and the palaeoecology in a pelmicritic limestone are similar to those of *Archaeochiapasa mardoqueoi* n. gen., n. sp. *P. rieberi* Schweigert, 2019 from the Late Jurassic, late Kimmeridgian, measuring 3.6 x 4.0 mm and preserved with its calcified cuticle, is characterised by a smooth posterior rim in contrast with the coarsely pustulose dorsal surface, the inflated, coarsely tuberculated subhepatic region, the blunt trapezoidal rostrum, and the well developed cervical groove (Fig. 13C) (Schweigert 2019: fig. 2A-D).

According to Schweigert (2019: 38) the co-occurrence in a coeval bed of the same area of *Lecythocaris paradoxa* and the stratigraphically younger *Prolecythocaris rieberi* supports the origin of Lecythocaridae at the northern Tethyan margin and a sister-group relationship between the two genera, i.e., sharing a common ancestor, as previously suggested by Schweigert & Robins (2016). Both *Lecythocaris* and *Prolecythocaris* Schweigert & Robins, 2016 inhabited relatively deep environments within sponge-microbial mound; representatives *of Lecythocaris* were considered a typical component of coral reef communities (Schweitzer *et al.* 2018). In conclusion, the southern Germany with the record of both *Prolecythocaris* and the oldest specimen of *Lecythocaris paradoxa* led to the assumption (Schweigert 2019) that it could have been the originating area for Lecythocaridae.

One of the most differentiating characters between Lecythocaridae and Archaeochiapasidae n. fam. is the flange. In Lecythocaridae it is restricted to the carapace posterior border, with a slightly variable length depending on the carapace shape (Fig. 13A-C). In Archaeochiapasidae n. fam., the flange is longer, extending up along the postero-lateral margins (Figs 7, 12C), and the narrow deeply depressed area is bordered by a raised, thicker rim. In *A. mardoqueoi* n. gen., n. sp. the first pleonal somites have been preserved extended dorsally, which corresponds to an unfolded pleon (Figs 7, 9B, 12A, C). In known Lecythocaridae the pleon has not been preserved: naturally folded pleon or only the result of taphonomy? Other differences are related to the huge rostrum in the lecythocarid specimens, so the protogastric process is preserved (versus a narrow rostrum in *Archaeochiapasa* n. gen., the protogastric process not extending beyond a pair of small tubercles, which are not seen in lecythocarid specimens). Shared characters by both lecythocarid genera (*Lecythocaris* and *Prolecythocaris*) and *Archaeochiapasa* n. gen. are the distinct grooves on the carapace dorsal surface.

According to all previous authors who were unable to examine the ventral traits, the Upper Jurassic Lecythocaridae was until now thought to belong to the Dromiacea (see for example Karasawa *et al.* 2011: tables 1, 2). What overall morphology of Archaeochiapasidae n. fam. teaches us leads usus to assume that, despite their Jurassic age, Lecythocaridae could, just as well, be eubrachyurans. Nevertheless, the two families Archaeochiapasidae n. fam. and Lecythocaridae are quite distinct. Their grouping in a same superfamily is problematic and in any case premature. The only existing superfamily that could nonetheless be an eligible candidate to accommodate Archaeochiapasidae n. fam. and Lecythocaridae is the Majoidea, a crown group that, with its almost 1,000 species, poses some of the most interesting problems for studies on brachyuran phylogeny. We share the opinion of Patrulius (1959: 253) who assumed that *Lecythocaris* could be a precursor of the majoid lineage, a hypothesis rejected by Schweitzer & Feldmann (2009: 95) arguing that the rostrum and the construction of the orbits were different. The orbital configuration is extremely diversified among Majoidea, varying from more or less incomplete to complete depending on the families/subfamilies. Schweitzer & Feldmann (2009) regarded the analogous shape of lecythocarids and majoids as, perhaps, an adaptation to a semi-cryptic, benthic lifestyle “in which concealment in vegetation or niches was facilitated by a compact body form and irregular outline”. In contrast, the preserved ventral parts and pereiopods of *A. mardoqueoi* n. gen,. n. sp. allow a comparison of both Archaeochiapasidae n. fam. and Lecythocaridae with the Majoidea, especially with the Oregoniidae Garth, 1958 (Garth 1958), see below under this name and Guinot (in press: fig. 14).

As we have to believe that other glaessneropsoids, as in the case of lecythocarids, could be by any chance eubrachyurans, the first precautionary step is to check whether the type genus and type species of Glaessneropsoidea, i.e., *Glaessneropsis heraldica* (Moericke, 1889) [quoted from 1897 by Schweitzer &

Feldmann (2009), but from 1889 by Jagt *et al.* (2015)], from the Upper Jurassic (Tithonian of Czech Republic) and exclusively known from carapace material (Schweitzer & Feldmann 2009, 2010a), would not be an eubrachyuran.

With regard to the extinct family Viaiidae Artal, Van Bakel, Fraaije, Jagt & Klompmaker, 2012, from the Albian-Cenomanian (with *Viaia* Artal, Van Bakel, Fraaije, Jagt & Klompmaker, 2012 and *Heeia* Wright & Collins, 1972), tentatively assigned to the Glaessneropsoidea, Artal *et al.* (2012: 405) rejected the hypothesis of a majoid relationship due to many distinctive characters that were discussed at length. A reappraisal of this family and many other glaessneropsoid representatives, Jurassic as well as Cretaceous, would be, however, not in vain.

A comparison with the eubrachyuran families, including some extinct taxa from the Cretaceous, is fully justified, even more when they are among the oldest representaives of Eubrachyura. The oldest eubrachyuran groups are briefly outlined below, arranged by higher categories, and listed alphabetically.

COMPONOCANCROIDEA FELDMANN, SCHWEITZER & GREEN, 2008

Componocancridae Feldmann, Schweitzer & Green, 2008

Componocancridae, from the Albian (~110–100 Ma) of North America (Shell Creek Shale of Montana), is the oldest confirmed heterotreme eubrachyuran. The female of the type genus and species *Componocancer roberti* Feldmann, Schweitzer & Green, 2008 has a well preserved thoracic sternum with large vulvae, whereas it shows a low preservation in a male (Feldmann *et al*. 2008: fig. 2D, G). This is seemingly the oldest occurrence of a vulva known to date in Brachyura. The suprafamilial diagnosis, based on a poorly informative carapace but on exceptionally well preserved ventral parts (Feldmann *et al*. 2008: 505), indicated that all sutures were interrupted except for suture 6/7, therefore with sternites 3-6 “fused axially and free laterally”, “sternites 7 and 8 free axially and laterally”, the condition of suture 7/8 (complete or not) being uncertain. The thoracic sternum is rather well developed but not very wide, and all sutures 4/5-7/8 are obliquely directed forwards. These features are combined with: elongate, narrow, triangular anterior shield (sternites 1-3) deeply inserted between the mxp3; posterior sternites proportionally widened in both sexes; absence of median line; reduced P4 and smaller dorsal P5, supposedly “carried dorsally”, by inference to the reduced and dorsally directed sternites 7 and 8 (Feldmann *et al*. 2008: fig. 2A-G).

Componocancridae, which displays an enigmatic combination of characters (Luque 2015b: 260), does not share sternal traits with Dorippidae and Ethusidae. The different general shape of the thoracic sternum of *C. roberti* (sternites 1-3 narrow, with triangular sternite 1; sternites 2+3 seemingly fused; suture 3/4 marked but not deep; suture 6/7 complete) does not support a dorippoid affiliation (sutures 4/5-7/8 all interrupted, with a different orientation in dorippoids). The set of characters of Componocancridae, which is clearly apart from other early-branching eubrachyuran clades (see Discussion), is distinct from the archaeochiapasid condition.

DORIPPOIDEA MACLEAY, 1838

Dorippidae MacLeay, 1838 and Ethusidae Guinot, 1977

A family that could show some similarities with Archaeochiapasidae n. fam. is the Dorippidae. Both share an incomplete folding of the first three pleonal somites, a wide thoracic sternum (leading to a coxo-sternal condition of the penis in Dorippoidea, see Guinot & Bouchard 1998: fig. 16; Guinot *et al*. 2013: figs 15-19), and a strong reduction of P4 and P5 in contrast to the long P2 and P3. In Dorippidae, pleurites 5–7 have their latero-external portions slightly exposed at the P2, P3, and P4 levels (Guinot *et al*. 2013: figs 46A, B, 47B), in a way somewhat similar to that of Inachoididae and Inachidae (see below), but this partial, hardly discernible exposure of certain pleurites is entirely different from the archaeochiapasid pattern, consisting of a depressed posterolateral and posterior area bordered by a strong rim. In addition, the strongly thickened posterior margin of the dorippid carapace is straight, instead of concave as in Archaeochiapasidae n. fam. The configuration of the branchiostegite cannot be inferred from the fossil *Archaeochiapasa mardoqueoi* n. gen, n. sp., so we do not know if it is reduced, weakly expanded ventrally as in Dorippidae, and how the carapace is exactly positioned (in Dorippidae the carapace simply rests close to the bases of P1–P3, which are laterally inserted).

Similar differences separate Archaeochiapasidae n. fam. from the Ethusidae, in which the branchiostegite is more developed that in Dorippidae, so the carapace better envelops the cephalothorax, as in other Eubrachyura. We assume that the formation of the Milne Edwards openings as pterygostomial slits, separated from the chelipeds due to the fusion of the sternite 3 with the pterygostome (thoracic sternum/pterygostome junction) (Van Bakel *et al.* 2012: fig. 47D; Guinot *et al*. 2013: fig. 42C), and which are unique structures of Dorippidae (not in present in Ethusidae where the condition is similar to that of other Brachyura), is correlated to the weak development of the branchiostegite.

The thoracic sternum of Dorippidae (Fig. 14) is wide, with sutures 4/5-7/8 all interrupted, the suture 5/6 having a marked curve that receives the press-button, and the suture 3/4 being strongly marked, ending in a boutonniere, the perforation of the cuticle corresponding to an invagination. The pleon is posteriorly positioned, with the first somites dorsally exposed.

It is surprising that Dorippidae and Ethusidae have their oldest representatives only very late, in the

Eocene: for instance, *Bartethusa hepatica* Quayle & Collins, 1981 and *Medorippe ampla* Garassino, de Angeli, Gallo & Pasini, 2004 (Dorippidae), and *Ethusa evae* Müller & Collins, 1991 (Ethusidae) (Garassino *et al*. 2004; De Angeli *et al.* 2009; Jagt *et al*. 2015). For most, unfortunately thoracic sternum and pleon are not known. To our knowledge, the only fossil dorippid with well preserved ventral parts is *Heikeopsis tuberculata* (Morris & Collins, 1991, as *Heikea*) from the Miocene Lower Miri Formation, Sarawak (Morris & Collins 1991: fig. 1a, 1b seemingly representing an inverted ventral view carapace), and redescribed with new material by Collins *et al*. (2003: 200, pl. 1, fig. 5a-d, as *Heikea*): the Milne Edwards openings are clearly recognisable and the curvature of the suture 5/6 is discernible (see Guinot & Bouchard 1998: fig. 16A, B; Guinot *et al.* 2013: fig. 42C), all typical characters for the family Dorippidae.

Telamonocarcinidae Larghi, 2004

Dorippoidea is represented in the fossil record since the early Albian by the family Telamonocarcinidae Larghi, 2004 (family status in Guinot *et al.* 2013: 268, 306) (see Larghi 2004; Schweitzer & Feldmann 2011; Luque 2015b; Ossó 2016; Charbonnier *et al*. 2017), with *Telamonocarcinus* Larghi, 2004 and *Eodorippe* Glaessner, 1980.

Telamonocarcinus antiquus Luque, 2015 (Luque 2015b: fig. 2A), from the upper Aptian–lower Albian of Colombia, only known by dorsal carapace with a concave posterior border (as in basal podotremes and *Archaeochiapasa* n. gen.) and a rough dorippoid aspect, may well represent the oldest known eubrachyuran (Luque *et al*. 2017). *T. gambalatus* Larghi, 2004, type species of the genus, from the Cenomanian of Lebanon (Fig. 15) (Larghi 2004: 539, figs 5, 6, 7.2-7.8; see also Garassino *et al.* 2008: 61; Guinot *et al.* 2013: 188, 306; Luque 2015b: fig. 2B; Charbonnier *et al*. 2017: 207, figs 451-469), shares with *Archaeochiapasa mardoqueoi* n. gen., n. sp. several features: P2 and P3 long; at least one of the last two pereiopods reduced; thoracic sternum very wide; pleon small, posteriorly positioned, with subdorsal first somites; but the carapace shape is distinctive. *Telamonocarcinus* sp., from the Cenomanian of Japan (Luque 2015b: fig. 2C, D), and *Telamonocarcinus* cf. *gambalatus* Garassino *et al.* (2008), from the Cenomanian-Turonian of southern Morocco (Garassino *et al.* 2008), which are only known by carapaces that do not allow a complete comparison, yet they seem different enough from Archaeochiapasidae n. fam.

Eodorippe spedeni Glaessner, 1980, from the Campanian-Maastrichtian of New Zealand (Glaessner 1980: fig. 13, 13A) and type species of the genus, missing ventral characters, has a well preserved, typically dorippoid carapace, with, however, a concave posterior margin that is not found in extant members but plausibly in earliest members; the "long and narrow, spatulate, pointing forward rostrum" in the sktech of Glaessner (1980: 185, fig.

13A), could simply correspond to the endostomial gutter that projects anteriorly in the median incision of the front and visible dorsally to a lesser extent in extant dorippoids (see Guinot *et al.* 2013: 188, 189). The new figure and redescription of the holotype (seemingly without an extremely long "rostrum") by Luque (2015b: 256, fig. 2E) support the hypothesis of true dorippoid affinities. *Eodorippe binodosa* Collins, Kane & Karasawa, 1993, from the Cenomanian of Japan (Collins *et al.* 1993: 203, fig. 2.6), tentatively assigned to Telamonocarcinidae by Larghi (2004) and Guinot *et al*. (2013: 188, as *Telamonocarcinus binodosus*), and again studied by Luque (2015b: 256, fig. 2F) who gave an excellent figure of the holotype, is likely a dorippoid. Schweitzer (2001) reported unpublished occurrence of *Eodorippe* from the Cretaceous of Oregon.

According to Guinot *et al.* (2013) and Luque (2015b) *Telamonocarcinus* and *Eodorippe*, with both Old and New World worlds occurrences and which have not survived the K/Pg extinction (Schweitzer 2001; Schweitzer & Feldmann 2005), are true dorippoids, distinct from both Dorippidae and Ethusidae, and also from Archaeochiapasidae n. fam.

Goniochelidae Schweitzer & Feldmann, 2011

The dorippoid affinities of *Goniochele* Bell, 1858, from the Eocene, suggested by Glaessner (1969) and Guinot *et al.* (2008: 709), have been recognised by the establishment of a separate family within Dorippoidea, Goniochelidae (see Schweitzer & Feldmann 2011), a widely accepted status (Jagt *et al.* 2015; Luque 2015b: fig. 4; Luque *et al.* 2017). The dorsal position of P4 and P5, evident from the disposition of their coxae, and the concave posterior margin of the carapace are plesiomorphic traits that are shared with Archaeochiapasidae n. fam. (however, in the latter only one of the last two pereiopds, P4 or P5, is preserved, being only about half as much as P3) but the carapace and the thoracic sternum (Collins & Jakobsen 2004: pl. 2, figs 1-4) are quite distinct (see discussion in Guinot *et al.* 2013: 201). The posterior margin is thickened but the presence of a flange or 'rim' should be verified. Beschin et al.

GONEPLACOIDEA MACLEAY, 1838

Mathildellidae Karasawa & Kato, 2003

The Mathildellidae, with *Mathildella* Guinot and Richer de Forges, 1981 as type genus and including a large number of fossil taxa such as *Branchioplax* Rathbun, 1918, *Tehuacana* Stenzel, 1944, and *Prebranchiopax* Vega & Ahyong, 2018, and recently evaluated by Vega *et al.* (2018), is distinct from Archaeochiapasidae n. fam. (see Karasawa & Kato 2003; Beschin *et al*. 2018).

HYMENOSOMATOIDEA MacLeay, 1838

See Discussion.

MAJOIDEA SAMOUELLE, 1819

Inachidae MacLeay, 1838

The taxonomy of the Inachidae was recently significantly modified (Marco-Herrero *et al.* 2013), notably with the removal of several genera for a placement within the Oregoniidae (see below under this name) and the exclusion of *Macrocheira* De Haan, 1839 (Guinot *et al.* 2013: 231) according to the results of Clark & Webber (1991) and Marques & Pohle (1998). The skeletal configuration of Inachidae is different from that of Inachoididae. The pleurites 5–8 (in particular 5, 8) are much less exposed and remain detached from the carapace edge, only showing as pointed, minute sclerites, so the carapace is not inserted into a setting gutter (Guinot 2012; Guinot *et al.* 2013: fig. 49A). It is likely that this character cannot be distinctly visible in fossil inachids, which are only known since the Cenozoic (Jagt *et al.* 2015), with e.g. *Planobranchia palmuelleri* Artal, Van Bakel & Onetti, 2014, from the middle Eocene of Catalonia, Spain (Artal *et al.* 2014). Carapace of *P. palmuelleri* shows inflated branchial regions, an extended posteriorly cardiac region, a convex, notably rimmed posterior margin merging with the posterolateral margin, the both nearly occupying the maximum carapace width. *Planobranchia laevis* (Lőrenthey, 1909) and *P. simplex* (Remy in Gorodiski & Remy, 1959) from the Eocene, referred to the Majidae in Majinae Samouelle, 1819 rather than in Micromaiinae Beurlen, 1930 by Schweitzer & Feldmann (2010b: 407, fig. 2A, B), has a narrower carapace, with similar characters. A comparison with *Lecythocaris paradoxa* would be interesting. See also Beschin *et al.* 2018.

Inachoididae Dana, 1851

Inachoididae shows an exposure of the latero-external portions of pleurites 5–8 that extend beyond each side of carapace, by being calcified and ornamented like the dorsal surface (Fig. 16A). All of this results in the formation of a strip divided in several portions (each exposed portion corresponding to each pleurite 5 to 8) and in the insertion of the carapace into a setting gutter (marking the separation between the covered internal portion of the pleurites and their uncovered latero-external portion). The arthrodial cavities of pereopods become placed in the same plane as the carapace, in relation with the weakly developed or even suppressed branchiostegite beyond the P1. The ‘incorporation’ of lateral parts of the pleurites (and also of the first male pleonal somite) into the cephalothorax is only a false, misleading appearance (and many authors, such as Rathbun 1925; Garth 1958, have been invariably mistaken). In Inachoididae the exposed areas beyond the sides of the carapace are a part of the axial skeleton (Drach & Guinot 1982, 1983; Guinot 1984; Guinot & Richer de Forges 1997; Santana 2008; Guinot 2011b, 2012; Guinot *et al.* 2013; Colavite *et al*. 2019). Conversely, in Archaeochiapasidae n. fam. the depressed and rimmed strip unambiguously is a part of the carapace itself.

The inachoidid thoracic sternum (Fig. 16B) is wide or very wide, with a conspicuous anterior shield inserted between the mxp3 and with a developed, medially inflated sternite 3; suture 3/4 is laterally visible, medially prolonging in deep depression; sutures 4/5–7/8 are all interrupted, with distant interruption points; a median line extends along sternites 7 and 8. There is in some species a sternum/pterygostome junction thanks to a curved extension of sternite 4 (Fig. 16C). The rather long male pleon has all somites free, except for somite 6 fused to telson (pleotelson).

Fossils assigned to Inachoididae are reported only since the early Eocene (Schweitzer *et al*. 2010; Jagt *et al.* 2015). *Pyromaia inflata* Collins & Morris, 1978, from the early Eocene of Pakistan (Collins & Morris 1978: pl. 116, figs 7-9), in which is preserved the thoracic sternum, and *Eoinachoides senni* Van Straelen, 1933, from the Upper Eocene of Venezuela (Van Straelen 1933: fig. 3; see Artal *et al.* 2014), do not show the special configuration of the carapace margins, even if this is a feature difficult to discern on the photographs. Fortunately, the lower Miocene *Eoinachoides* sp. reported from Venezuela by Aguileira *et al.* (2014: fig. 6.3.5, 6.3.6) clearly exhibits the carapace border flanked by the typically exposed pleurites. The rather wide thoracic sternum can be compared to that of the extant *Anasimus latus* Rathbun, 1894 figured by Guinot & Richer de Forges (1997: fig. 12D) and Santana (2008: fig. 6C), which confirms that *Eoinachoides* sp. is a true inachoidid. *Vicetiulita granulata* De Angeli & Ceccon, 2015, from the early Eocene (Ypresian) of Monte Magrè, northern Italy (De Angeli & Ceccon 2015: fig. 2:1, 2), does not seem to have the typical inachoidid carapace border but actually reminds *Paradasygyius depressus* (Bell, 1835) and *Paulita tuberculata* (Lemos de Castro, 1949) (Fig. 16A) (see Guinot 2012) with which it has been related.

Oregoniidae Garth, 1958

All datasets, morphological (Rathbun 1925; Garth 1958; Griffin & Tranter 1986), larval (Rice 1981, 1983, 1988; Clark & Webber 1991; Pohle 1991; Marques & Pohle 1998; Marco-Herrero *et al.* 2013), spermatozoal (Tudge *et al.* 2014) and genetic (Hultgren *et al.* 2009; Chen *et al.* 2019: fig. 3; Marco-Herrero *et al.* 2013: fig. 7; Ma *et al.* in press: fig. 1), support the Oregoniidae as the most basally branching majoid family. The family Oregoniidae is the only majoid group unambiguously resolved as monophyletic (Hultgren *et al*. 2008: 447). Actually, most majoid families are paraphyletic, the Oregoniidae and the Inachidae + Inachoididae groups forming a clade in unconstrained analyses (Marques & Pohle 2003; see Guinot *et al.* 2013; Davie *et al.* 2015). Oregoniids were considered primarily limited to boreal regions (unlike the majority of majoid families whose species are worldwide distributed), until several new Indo-West Pacific genera were transferred to the family, in their own subfamily, the Pleistacanthinae Števčić, 2005: *Bothromaia* Williams & Moffitt, 1991, *Ergasticus* A. Milne-Edwards, 1882, *Parapleisticantha* Yokoya, 1933, *Pleistacantha* Miers, 1879, and *Pleisticanthoides* Yokoya, 1933 (Marco-Herrero *et al.* 2013; Ng *et al*. 2017). The Oregoniinae Garth, 1958 accommodates the two boreal genera *Hyas* Leach, 1814 and *Chionoecetes*.

The carapace shape of extant species as *Hyas coarctatus*, with laterally dilated hepatic and postorbital regions forming an alate expansion, displays real similarities with that of *A. mardoqueoi.* Another extant oregoniid *Chionoecetes tanneri* Rathbun, 1893, possesses significantly reduced P5 and moderately long P4 compared to the very long P2-P3, a quadrate carapace with broad, swollen branchial regions and deeply depressed interbranchial space (Rathbun 1925: 232, figs 88, 89, pls 84-91, 234; Breton 2009: fig. 9). The genus *Chionoecetes*, in which all species have reduced, although not carried dorsally, P5, shows evident relationships between the Archaeochiapasidae n. fam. and the Oregoniidae. The genus *Pleistacantha* and allies (Pleistacanthinae Števčić, 2005), despite a quite different carapace ornamentation, show some similar characteres, e. g. a prominently swollen branchial regions with the inner margins almost touching along the carapace midline, a carapace posterior margin that is gently concave in some species and the first pleonal somites not folded ventrally in some species (Marco-Herrero *et al.* 2013; Ng *et al.* 2017).

The thoracic sternum, not very often documented in Majoidea, is rather wide in *Hyas coarctatus* (Rathbun 1925: pl. 95) *Chionoecetes* spp. (Rathbun 1925: pls 85, 87, 89, 91), *Cyrtomaia* Miers, 1886 (Guinot & Richer de Forges 1982: fig. 2A; see Marco-Herrero *et al.* 2013) and in *Pleistacantha* species (Ng *et al*. 2017: figs 9A, C, E, 11C) but however not so wide as in *A. mardoqueoi* (Fig. 11), and the pleon is quite distinctive.

All the fossil oregoniid members are relatively recent, the earliest fossil record of the genus *Hyas*, *H. meridionalis* Glaessner, 1928 from the early Middle Miocene (Glaessner 1928: pl. 3 fig. 15), *Hyas oranensis* Van Straelen, 1936 (Van Straelen 1936: pl. 33, fig. 2) and *Hyas tsuchidai* Imaizumi, 1952 (Imaizumi 1952: figs 1-5; Kato *et al*. 2013: pl. 1, figs. 1, 2) are not well informative while the early Pliocene *Hyas tentokujiensis* Kato & Nakashima (Kato *et al.* 2013: pl. 3, figs. 1-4) shows the same characteristics as the extant *Hyas*. Fossil *Chionoecetes* are known from the late Pleistocene (Miller & McGovern 1997). The family includes *Oregonia spinifera* Schweitzer, Feldmann, Gonzáles-Barba & Vega, 2002 from the Oligocene El Cien Formation of Baja California Sur (Schweitzer *et al*. 2002).

There is conclusive evidence to advocate for an eubrachyuran affilliation of the family Lecythocaridae and for an extinct representative of the Majoidea; it can be reliably associated with the extant family Oregoniidae (see Guinot in press).

Priscinachidae Breton, 2009

The earliest known majoid family is the Priscinachidae, represented by two monotypic genera reported from the upper Albian of northern Spain in reef carbonates: *Cretamaja* Klompmaker, 2013 (with C. *granulata* Klompmaker, 2013) and *Koskobilius* Klompmaker, 2013 (with *K. postangustus* Klompmaker, 2013) (see Klompmaker 2013; Klompmaker *et al.* 2013). The type genus of the family, *Priscinachus* Breton, 2009 (with *P. elongatus* Breton, 2009), was based on four incomplete specimens collected from two lower Cenomanian exposures in the western Paris Basin (Breton 2009: figs 3-8). Priscinachidae is an extinct family that is among the oldest record not only for the Majoidea but also for the Eubrachyura. All priscinachids have a narrow, much longer than wide carapace, may be pyriform, a bifid rostrum, and an areolated, ornamented, pustulose dorsal surface (with large, subcircular orbits directed forward and upward in *C. granulata*). Unfortunately, only the dorsal carapace of these spider crabs is preserved, which considerably limits the comparison with *Archaeochiapasa mardoqueioi* n. gen., n. sp. Nevertheles, the differences (the carapace is wider than long in *A. mardoqueioi*, whereas it is much longer than wide in the Priscinachidae: two times as long as wide in *P. elongatus*, one third longer than wide in C. *granulata*) are so evident that close affinities are not suspected.

Other fossil Majoidea Samouelle, 1819

The fossil record of the Majoidea is rather scarce, with its first appearance in the Early Cretaceous (see above), with other first occurrences common since the Miocene and with most reports from the Eocene to the Pleistocene of Europe (for an overview, see Klompmaker *et al.* 2015b). In several extant majoid families there is a weak exposure of pleurites 6 and 7 beyond the carapace shown as triangular sclerites at the P3, P4 coxae levels; therefore, the carapace does not lie inside a gutter (Guinot *et al.* 2013: 232).

The status of Micromaiinae Beurlen, 1930 (type species: *M. tuberculata* Bittner, 1875) (see Schweitzer & Feldmann 2010b; Feldmann *et al.* 2011; Artal *et al.* 2014) should be reviewed.

Stenocionops primus Rathbun, 1935, from the lower Campanian or Santonian of the USA, based on the proximal portion of the right palm (Rathbun 1935: 58, pl. 13, figs 9-12) and assigned to the Majidae with respect to its strong resemblance to that of extant species of *Stenocionops* Desmarest, 1823, represents a doubtful occurrence (Bishop 1986; Breton 2009). If its status is confirmed, it would be ascribed to the

Mithracidae MacLeay, 1838 (Klompmaker *et al.* 2015b: fig. 1, table 1). *Chondromaia antiqua* Feldmann, Schweitzer, Baltzly, Bennett, Jones, Mathias, Weaver & Yost, 2013, based on an incomplete carapace from the lower Maastrichtian of the Mount Laurel Formation of New Jersey, USA (Feldmann *et al.* 2013: fig. 15), is considered the oldest representative of Majidae. The unnamed crab from the Maastrichtian Cárdenas Formation, Mexico, which lacks frontal and anterolateral regions and tentatively assigned to the Majidae by Vega *et al*. (1995: fig. 5), was considered doubtful (Breton 2009). The members of the extinct subfamily Micromaiinae Beurlen, 1930 and all other fossil majoids are common in the Paleogene and later (Schweitzer *et al.* 2010; Jagt *et al.* 2015). Archaeochiapasidae n. fam. is quite different from all these majoids.

MAROCARCINIDAE GUINOT, DE ANGELI & GARASSINO, 2008, superfamily *incertae sedis*

Marocarcinidae, from the Upper Cretaceous (Cenomanian-Turonian) of Gara Sbaa (Kem Kem) Lagerstätte (Martill *et al*. 2011), shows apparent similarities with the Componocancridae, e.g. an ovoid thoracic sternum, with a narrow triangular shield, a developed sternite 4, interrupted sternal sutures 4/5, 5/6 and 7/8 and seemingly complete suture 6/7 (Guinot *et al.* 2008: figs 1B, 2); but the elongate, strong, not dorsal P4 and P5 and the presence of a median line extending along sternites 7 and 8 are distinctive, whereas the precise condition of sutures 6/7 and 7/8 needs to be verified in males of the two families.

Marocarcinus pasinii Guinot, De Angeli & Garassino, 2008 shares with *Romualdocarcinus salesi* Prado & Luque, 2018 (?Eogeryonidae Ossó, 2016, see below) three anterolateral teeth on the carapace margin and a bifid rostrum with secondary lateral spines, but it has smaller orbits, lacks orbital fissures, and shows different cervical and branchiocardial grooves (see Prado *et al*. 2018). There is no affinities between Marocarcinidae and Archaeochiapasidae n. fam.

PALICOIDEA BOUVIER, 1898

Palicidae Bouvier, 1898

In the rare fossil Palicidae, which are rare in the fossil record and known only from the Eocene to Oligocene (Beschin *et al*. 1996; De Angeli & Beschin 2000; Beschin & De Angeli 2003; Müller 2006; De Angeli & Ceccon 2014; Jagt *et al.* 2015; Beschin *et al.* 2018), the thoracic sternum, the pleon, and the fragile, reduced P5, carried dorsally for camouflage (Guinot & Wicksten 2015), are not preserved. The family is likely basal such as Archaeochiapasidae n. fam. but relationships between these two lineages are not supported. Most evidence places the family close to the Dorippidae (Guinot *et al.* 2013).

?PORTUNOIDEA RAFINESQUE, 1815

Eogeryonidae Ossó, 2016

Based on *Eogeryon elegius* Ossó, 2016, from the late Cenomanian of Condemios de Arriba, Guadalajara, Spain, the family Eogeryonidae, with a relatively narrow thoracic sternum, a short, four-tipped rostrum, proportionally long P2-P4, massive chelae, and P5 not preserved but seemingly smaller and subdorsal, was assigned to Portunoidea. The recently established taxon *Romualdocarcinus salesi*, from the upper Aptian–lower Albian Romualdo Formation of the Santana Group, Araripe Basin, Brazil, only represented by plural carapaces, considered to fit within Eubrachyura and tentatively assigned to Eogeryonidae, shares with *Eogeryon* a sub-hexagonal to sub-square carapace, anterolateral margins with three spines, wide orbits, and an elongated, bifid rostrum with secondary lateral spines (Prado & Luque 2018: fig. 4). No main characters are shared with Archaeochiapasidae n. fam., except for the concave posterior margin of the carapace in the puzzling *R. salesi.*

Lithophylacidae Van Straelen, 1936

The comparison between Lithophylacidae, from the Upper Cretaceous (Cenomanian) of France (Breton & Collins 2007), and Archaeochiapasidae n. fam. is superfluous in view of all the differences, both on the dorsal and ventral carapace, and also the pereiopods. The main shared trait is the wide thoracic sternum, however proportionally less wide in *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879, which fortunately reveals the condition of all the sutures, a median line on sternite 7, and subdorsal, reduced sternite 8 leading to a reduced, dorsal P5 (Guinot & Breton 2006). A specialised stridulatory apparatus is present. The basal position of Lithophylacidae within the Portunoidea Rafinesque, 1815, suggested by several autors (Karasawa *et al.* 2008; Ossó 2016), precludes any relationships with Archaeochiapasidae n. fam.

Icriocarcinidae Števčić, 2005

Icriocarcinidae, an extinct family whose representatives occurred in the Upper Cretaceous (late Campanian-Maastrichtian) and showing a wide geographic distribution during the Cretaceous, with *Icriocarcinus xestos* Bishop, 1988, from the late Campanian, and *Branchiocarcinus* Feldmann & Vega, 2005, from the Campanian-Maastrichtian, is considered to occupy a basal position within the Portunoidea (Karasawa *et al*. 2008; Teodori *et al.* 2013; Phillips *et al.* 2014; Nyborg *et al.* 2014; Jagt *et al.* 2015; Ossó 2016). Among others, the inverted subtrapezoidal carapace, the very wide orbits all along the carapace anterior margin, the long pseudorostrum, and the modified P5 dactyli are all characters that differentiate it from Archaeochiapasidae n. fam.

Longusorbiidae Karasawa, Schweitzer & Feldmann, 2008 and Carcineretidae Beurlen, 1930

Members of Longusorbiidae such as *Longusorbis* Richards, 1975, from the Coniacian-Campanian of the Pacific Coast of Northern and Central America, *Binkhorstia* Noetling, 1881, from the Maastrichtian of Europe, and members of Carcineretidae Beurlen, 1930 (as *Carcineretes* Beurlen, 1930, from the Maastrichtian, and *Woodbinax* Stenzel, 1952 from the Cenomanian), included among Portunoidea (see comparisons in Ossó 2016), are clearly distinguishable from Archaeochiapasidae n. fam.

Other fossil Portunoidea

Ophthalmoplax Rathbun, 1935, from the Upper Cretaceous of North and South America (Vega *et al.* 2013), also known from the Upper Cretaceous (Campanian) of Morocco (Ossó-Morales *et al*. 2010) and recently found from the Campanian of Brasil (Pralon *et al.* 2017), was assigned to the Macropipidae Stephenson & Campbell, 1960. No relationships with the Archaeochiapasidae n. fam. can be detected.

RETROPLUMOIDEA GILL, 1894

Archaeopidae Karasawa, Kishimoto, Ohara & Ando, 2019

The family Archaeopidae, recently established to accommodate the genus *Archaeopus* Rathbun, 1908 (type species by monotypy: *A. antennatus* Rathbun, 1908) previously included in Retroplumidae Gill, 1894, was distinguished on the basis of carapace, sternal and pleonal characters (Karasawa *et al*. 2019).

Retroplumidae Gill, 1894

Retroplumidae, represented by a reduced number of extant representatives (only two genera and ten species; see Ng *et al.* 2008: 181), but known from many fossils, was an old flourishing group since the Cretaceous from soft bottoms similar to that of extant members; it survived the K/Pg extiction, reaching its greatest diversity in the Eocene (Saint Laurent 1989; Vega & Feldmann 1992: fig. 7; Artal *et al.* 2006; Jagt *et al.* 2015; Hyžný *et al.* 2016). The clearly coxal gonopores (no coxo-sternal condition) determined its inclusion in the Heterotremata (Guinot 1978: 25) instead of the previous assignation to thoracotremes (or catometope crabs); its apomorphic features set the clade apart from other Eubrachyura, hence its elevatation to suprafamilial rank, Retroplumoidea by Saint Laurent (1989). *Cristipluma* Bishop, 1983 is known from the upper Campanian of the Mississippi Embayment (Bishop 1983b: 428, figs 3K, 8A-C). Guinot *et al*. (2013: fig. 34) examined its morphology, in particular its genital region; the thoracic sternum is wide, with parallel and interrupted sutures 4/5-7/8 in extant members as in fossil genera such as *Costacopluma* Collins & Morris, 1975 (Fig. 17) (Fraaije *et al.* 2006; Nyborg *et al*. 2009: fig. 4; Vega *et al*. 2018: fig. 6.12) or fossil *Retropluma* Gill, 1894 (Hyžný *et al*. 2015: fig. 5D, E; Gašparič & Križnar 2017: fig. 3B; Gašparič *et al*. 2019: fig. 5.3-6), and compared it with close eubrachyuran lineages, e. g., the Palicoidea and Hexapodoidea Miers, 1886. The reduced, dorsal and re-entrant P5, preserved in the smallest fossil représentative described to date, *R. minuta* Gašparič, Hyžný, Jovanović, Ćorić & Vrabac, 2019 from the Middle Miocene, lower Badenian (Gašparič *et al.* 2019: figs 4.5, 5.2, 6.6) is an apomorphic trait, unique in Brachyura.

TEPEXICARCINOIDEA LUQUE, 2015

Tepexicarcinidae Luque, 2015

Tepexicarcinus Feldmann, Vega, Applegate & Bishop, 1998, with *T. tlayuaensis* Feldmann, Vega, Applegate & Bishop, 1998, from the Early Cretaceous, late Albian of Mexico (~110), type and sole species of the genus, first tentatively assigned to the Homolidae H. Milne Edwards, 1837 (Feldmann *et al.* 1998), then to Dorippoidea Telamonocarcininae (Larghi 2004: 534, 535, 536; Vega *et al*. 2006a: 28, fig. 4, pl. 2, figs 2-12) and to Telamonocarcinidae (Guinot *et al.* 2013), was assigned to the new family Tepexicarcinidae by Luque (2015b: 258). The characters, dorsal (e.g. carapace longer than wide; rostrum square, anteriorly bifid; three anterolateral teeth; P5 short, carried subdorsally) as well as ventral (thoracic sternum subpentagonal, with large sternites 5 and 6; pleon with four free somites and two fused), are so distinctive from those of Dorippidae, Ethusidae and Telamonocarcinidae that Luque (2015b) hypothetised that Tepexicarcinidae may represent a separate evolutionary lineage of early eubrachyuran or stem-eubrachyuran crabs, probably in its own superfamily, Tepexicarcinoidea, which cannot accommodate our new family. See Fig. 3G, H.

DISCUSSION

Although the Eubrachyura has a comparatively robust fossil record in sedimentary rocks of Late Cretaceous and Paleogene-Neogene (Cenozoic) age, its still poorly known origin frustrates our understanding of the early evolutionary development of crabs, in being one of the most challenging issues. A poor preservation or the lack of key characters often occurs in early fossils, but this is not the case of our specimen of *Archaeochiapasa mardoqueoi* n. gen., n. sp. that, despite a very thin cuticle, is practically complete. Although represented by a single specimen, it satisfies to the highest degree the criteria for its own description, its elevation to the family rank, and furthermore for the evaluation of the other oldest known taxa. This unique occurrence could result from collection biases due to the extremely small size and weakly sclerotised cuticle of the species.

There is a very wide thoracic sternum in *Archaeochiapasa mardoqueoi* n. gen., n. sp. (Fig. 11), a structure that proves to represent an optimal support for the brachyuran systematics and phylogeny, based on morphology (Guinot 1979; Guinot *et al.* 2013, 2018). We hypothesise that the Late Jurassic Lecythocaridae (Fig.13), which lacks ventral parts, may have possessed a similar condition to that of Archaeochiapasidae n. fam., or at least close. It requires great attention because it is challenging what scientists have long believed and leads us to some new insights that somewhat risk to negate certain positions or received ideas. It can be assumed that the male gonopores are coxal, but can we be sure of that?

The above review of the earliest known heterotremes highligthed some important issues.

All data, morphological, larval, spermatozoal as well as genetic (Ahyong *et al.* 2007; see also Tsang *et al.* 2014: fig. 2; Chu *et al*. 2015: fig. 71-13.2) support the Dorippoidea as the more deeply rooted branch in the eubrachyuran phylogenetic tree. The palaeontological data are consistent, since the earliest dorippoid, *Telamonocarcinus* (Fig. 15), displays a wide sternal plate together with reduced, dorsal P4 and P5. These specialised P4 and P5, present in all dorippoid members, are related to a carrying behaviour, considered a relict behaviour (Guinot & Wicksten 2015). Recent remarkable studies of the female reproductive system in several dorippids led to surprising but consistent results. Hayer *et al.* (2016) discovered in *Dorippe sinica* Chen, 1980 a separate, ectodermic, sperm-storage chamber, not corresponding to a split between the plates of the intersegmental phragma 7/8 as in all podotreme crabs, but being nevertheless an independent structure (a cuticular invagination of sternite 6), leading to an external fertilisation as in podotremes. In other dorippids, *Dorippe quadridens* (Fabricius, 1793), *Medorippe lanata* (Linnaeus, 1767) and *Paradorippe granulata* (De Haan, 1841) the female reproductive system also shows unique characters, leading to an external fertilisation (Vehof *et al*. 2017, 2018). This dorippid condition, which is reminiscent of the podotreme spermatheca and could be an evolutionary step or transition, challenges our common concept of reproduction in the Eubrachyura, in which the fertilisation has traditionally been considered internal.

Like with all species of Dorippoidea (Fig. 14), a wide thoracic sternum occurs in several other extant eubrachyuran clades that are considered the most basal. In Retroplumoidea, the extant members, all with only P5 being dorsal (Guinot 1979: fig. 30C-E; Saint Laurent 1989: figs 5, 22), and the fossil representatives, like *Costacopluma* (Fig. 17), display a wide sternal plate. Majoidea, a very large group with a rich diversification and obscure relationships, which has its first known members from the late Albian lacking ventral parts (Priscinachidae), should be also a deeply rooted clade, with extant oregoniids, inachoidids and inachids displaying a rather similar organisation.

Interestingly, the thoracic sternum of these basal heterotremes (Dorippoidea, Retroplumoidea) is wider than in crabs considered the most derived, the thoracotremes (see Guinot *et al.* 2018: figs 5, 8, 9), with, however, some exceptions, as e.g. the macrophthalmid Ilyograpsinae Števčić, 2005, see Komai & Fujita 2018: fig. 2K; or in Aphanodactylidae Ahyong & Ng, 2009, all species displaying a wide thoracic sternum (see Ahyong & Ng 2009: fig. 1F).

Some other eubrachyuran taxa from the Early–Late Cretaceous (Albian, Cenomanian, Campanian), thus almost contemporaneous or even older, display a quite distinct organisation than Archaeochiapasidae n. fam., in particular of the thoracic sternum: the Componocancroidea, the oldest of them, has a much narrower thoracic sternum, with differently oriented sutures 4/5-7/8.

We submit the following proposals or, rather, directions for future research

The Archaeochiapasidae n. fam. belongs to a basal stock of Eubrachyura that includes the Dorippoidea, especially the Telamonocarcinidae from the early Albian with unequivocal dorippoid features, and the Majoidea, which first appeared in the Early Cretaceous. Porter *et al.* (2005: fig. 2) and Crandall *et al.* (2009: fig. 2), based on a molecular estimation of decapod phylogeny, pointed out a divergence of Majoidea from the rest of Brachyura approximately 254 million years (i.e., late Permian) – however, their both figures 2 show this to be in the middle Triassic - and recovered the Majoidea as the oldest brachyuran lineage. All data, spermatozological (Jamieson & Tudge 2000; Tudge *et al.* 2014), larval (Rice 1981, 1983) as well as genetic (Ahyong *et al.* 2007), are congruent to corroborate Majoidea as a basal, deeply rooted lineage. According to the molecular tree of Ahyong *et al.* (2007: 583, figs 3, 4) both majoids and dorippids occupy a "low" position, and a "majoid–hymenosomatid–dorippoid clade" is supported, whereas thoracotreme genera form an advanced group within the heterotreme assemblage. The phylogenetic molecular trees of Tsang *et al.* (2014: fig. 2) and Chu *et al.* (2015: fig. 71-13.2) support dorippoids and majoids as among the most basal eubrachyurans, although with obscure phylogenetic positions (see also Ma *et al.* in press).

Previously, Guinot *et al.* (2013: 212, 217, 266) recognised an ancestral stock of basal heterotremes distinct from a more modern stock, both present in the Early Cretaceous, all with a wide sternal plate crossed by horizontal and equidistant sutures corresponding to a transversal compartmentalisation of the axial skeleton (plesiomorphy). Two assemblages could be recognised in this ancestral stock. The first assemblage included the Dorippoidea (with reduced and dorsal P4 and P5) and the Majoidea like Inachoididae and Inachidae (with normal P5, may be only slightly smaller than P4), to which was added the Hymenosomatoidea. Archaeochiapasidae n. fam. appears to belong to this ancestral group. The second assemblage of basal heterotremes included the Palicoidea, Retroplumoidea (both with reduced, dorsal P5), and Hexapodoidea (with vestigial P5, only a coxa), all with modified sternite 8 and pleurite 8 (Guinot *et al.* 2013: 215). It was premature at that time to introduce high-ranked names to eventually accommodate these superfamilies in a new monophyletic group, and all the more so since the *International Code of Zoological Nomenclature* (1999) regulates only the nomina of taxa from the superfamily group to the subspecies group, and not taxa above the superfamilies. The wide or very wide thoracic sternum of the ancestral stock of extant crown groups (Dorippoidea, Majoidea, Retroplumoidea) is similar to that found in their known Cretaceous members (the disposition of sutures 4/5-7/8, interrupted or complete, is unknown). Thus, results obtained from the phylogeny of extant Brachyura are corroborated by the palaeontological data placing many of them among the most basal eubrachyurans.

Other heterotreme taxa, also present in the Early Cretaceous, seem to pertain to another stock of eubrachyurans, more ‘modern’, with a narrower thoracic sternum crossed by oblique sutures corresponding to a distinct skeletal organisation (that chiefly attests to a different location of the centre of gravity of the crab), in comparison with that of the ‘ancestral’ stock. The high-ranked lineages that should belong to this more ‘modern’ stock are: the Componocancroidea (supposedly with reduced, dorsal P4, P5), Marocarcinidae (P4 and P5 normal), Eogeryonidae (P5 probably smaller, subdorsal) and other basal Portunoidea (P5 variously modified), and maybe also the Tepexicarcinoidea (P5 short, carried subdorsally). This is in line with the remarks of Prado *et al.* (2018: 747) who hypothetised that the supposed eogeryonid genus *Romualdocarcinus* was more reminiscent of “modern looking eubrachyurans” in comparison to the more basal eubrachyuran branches Dorippoidea and Majoidea.

We will address an issue, the controversial placement within the Brachyura of Hymenosomatoidea MacLeay, 1838, probably the most ecologically diverse extant family of brachyuran crabs that, despite a worldwide and multiple ecological occurrences, is not known in the fossil record. Is the thin cuticle and the small size, thus with a low preservation potential, of hymenosomatids sufficient to explain their lack in the fossil record? Can the absence of hymenosomatoids in the fossil record also be biased by sampling and collection? Or should we consider that these crabs could not successfully establish a long-term lineage, or that it is a very recent clade? The family has been considered either heterotreme, close to or within the Majoidea (Guinot & Richer de Forges 1997; Ng *et al.* 2008), hence the name of “false spider crabs”, or thoracotreme with respect to the sternal emergence of the male ejaculatory duct and gonopore (Guinot *et al*. 2013: fig. 58A, B, E). Hymenosomatoidea actually displays contradictory features: plesiomorphic (retention of free uropods in Odiomarinae Guinot, 2011; weak cephalic condensation, with absence of orbits and proepistome in basal representatives or incomplete orbits in more derived taxa), and apomorphic (sternal male gonopores). The very wide thoracic sternum, appearing extremely expanded laterally in the first young crab (Fig. 18B, C), is actually the widest known in Eubrachyura, with sutures 4/5-7/8 extremely short, only lateral, confined to the sides of the sternal plate in both males and females. The arrangement of the carapace (Fig. 18A) with a rim all around (not around the frontal region in some genera) is unique to Brachyura. Tavares & Santana (2015: fig. 2A, C) have noted a part of the thoracic pleurite 8 visible between the carapace, pleonal somites 1-2, and P5 coxa, a plesiomorphic trait (see above, Dorippoidea, Inachoididae).

On the basis of the spermatozoal ultrastructure (Richer de Forges *et al.* 1997; Jamieson & Tudge 2000), Hymenosomatidae has been found to be unique among the Brachyura, apart from the three brachyuran sections Podotremata Guinot, 1977, Heterotremata Guinot, 1977 and Thoracotremata Guinot, 1977. The larval sequence of hymenosomatids seems to be the result from the retention of the ancestral early larval stages and the loss of the later ones (including the megalopa), with, in the final analysis, the assumption of advanced features in the larval development (Rice 1980, 1981, 1983). Molecular data are scarce, but the molecular phylogenetic tree of Windsor & Felder (2014: fig. 1) for Mithracidae MacLeay, 1838 seems to include the three analysed hymenosomatid species (in three genera) within Majoidea. Unique characters of the family appear as autapomorphies that corroborate its monophyly: despite an extreme diversification, the groundplan is homogene in all members, hence its elevation to suprafamilial rank by Guinot (1978).

Recent study of the female reproductive system of an hymenosomatid species has showed a thoracotreme affiliation (Kienbaum *et al.* 2018). We refute the assertion of these authors that parallel trends in the evolutionary transformation have been used as “proper characters” by Guinot *et al*. (2013). We maintain our hypothesis of an ancestral eubrachyuran clade is maintained for the moment. The comparison of the carapaces of Archaeochiapasidae n. fam. and Hymenosomatidae (Fig. 18A) is interesting, since both share a wide thoracic sternum, a rim on the carapace margin, which is however very distinct, but not other family relationships can be recognised for the moment.

At this point in the discussion, a question arises: how to explain the presence of a very wide thoracic sternum in the eubrachyuran stock considered the most basal and the oldest, all the more that genetic and larval data provide a similar unequivocal inference? Furthermore, is it possible that *Archaeochiapasa* n. gen. could be a thoracotreme? And are the male gonopores located on the P5 coxae (as in podotremes and heterotremes) or on the sternite 8 (as in thoracotremes)?

Recent evidence from the fossil record indicates an explosive evolution of Brachyura in the Jurassic, in which approximately more than 30 podotreme families and subfamilies were already represented (Jagt *et al*. 2015). Based on Schweitzer & Feldmann (2010), Ma *et al*. (in press:: xx) recently allocated to Brachyura “a relatively ancient radiation”, and an “origin dated back to early to mid-Jurassic”. We suggest that the evolutionary history of Brachyura started much earlier, and in this we share the view of geneticians.

Preliminary results of a multilocus molecular phylogeny of Brachyura by Ahyong *et al.* (2010) suggested a Carboniferous origin, with a Permian origin for the heterotremes. According to Klaus *et al*. (2011) molecular calibration on marine brachyuran fossils dates their last common ancestor before the fragmentation of Gondwana. Analyses based on new genomic and transcriptomic sequences (Wolfe *et al.* in press: fig. 3) support podotremes as the deepest split in the late Triassic and the divergence of each of the two eubrachyuran sections (heterotremes and thoracotremes) in the Early Cretaceous (Schweitzer & Feldmann 2005; Robin *et al*. 2017) (note that thoracotremes are only known from the Palaeogene onwards, during which they underwent rapid diversification into numerous families).

The early evolutionary history of crabs is obscure. We ignore how the major and interrelated events that occurred in the evolution of Brachyura convergently led to a crab-like morphotype (not in sequence: reduction and folding of pleon, loss of locomotory pleopods, flattening of body and carapace lateral margins, exclusion of internal organs from pleon, thoracic sternites more or less fused to form sternal plate, reorganisation of sexual organs, arching of posterior thoracic somites, development of holding- or locking-pleonal mechanism, changes in the axial skeleton and in the internal anatomy), implying the broadening of the cephalothorax, in particular that of the thoracic sternum. Carcinisation, e.g. "one of the many attempts of Nature to evolve a crab", a term introduced by Borradaile (1916), ~~to describe~~ the process of the evolutionary transformation the evolution of the crab-like habitus in Brachyura (but also in Anomura MacLeay, 1838, in which several evolutionary lineages show forms resembling 'true' crabs), i.e., the evolution from a long-bodied ancestor to a crab-like body (Guinot *et al*. 2013). Although the mechanisms underlying the origin of evolutionary novelties remains poorly understood, according to Tsang *et al.* (2011) the modern view of carcinisation must be restricted to clades outside of the Brachyura, so that brachyurans are considered "by definition fully-carcinized decapods" (Anker & Paulay 2013: 10; see also Hiller *et al*. 2010). This is true in the sense that all Brachyura (with very few exceptions) have a reduced, completely folded and firmy held male pleon resulting in the exclusion of main internal organs (except in Pinnotheroideaa De Haan, 1833, Cryptochiroidea Paul'son, 1875, and few other taxa, in which the gonads extend into anterior pleonal somites in various degrees, see Becker *et al*. 2011; Vehof *et al*. 2016), have lost the biramous pleopods 3-6 in males and the caudal furca in both sexes, therefore lost the locomotory function of pleopods, and show an excavation between the pereiopods (sterno-pleonal depression or cavity) receiving the pleon. This is neither the time nor the place to discuss about such an important issue, for example whether carcinisation occurred at least twice within the Brachyura, both within podotremes, whether crab-like characters can be lost in a process of 'decarcinization' (Scholtz 2014), whether a regressive evolution occurred, for example in Gymnopleura (Raninoidea) (Števčić 1973) or even a reversal (see Guinot 2011; Van Bakel *et al.* 2012).

We agree with Keiler *et al*. (2017) that carcinisation is an evolutionary process as a whole, but the actual objects of transformation are individual characters (sensu Hennig 1966). It remains however logical to consider the widening of the thoracic sternum is a part of the process during which the gonopores, first the female one and then the male ones, abandoned their appendicular location (likewise in other decapods and podotremes) as a consequence a brachyuran carcinisation. Thus, the thoracic sternum is one of the most reliable structures to evaluate the degree of carcinisation within the Brachyura, although Scholtz (2014: 101) wrote “a wide sternum seems not so crucial”.

The debate is open: if a crab has a wide thoracic sternum does this mean it retains the basal condition, is the condition actually derived in that its ancestors had narrow sternum? Is a narrow thoracic sternum derived relative to the wide sternum ancestral condition but basal to the secondary wide condition ? Within an evolutionary context, the direction of character state transformations is fundamental to identify the synapomorphies that diagnose clades. Is the polarity from a wide thoracic sternum to a narrower one? Which are the character polarity and the character state phylogeny in Eubrachyura? Is a very broad thoracic sternum an ancestral disposition or the result of a widening related to a developed carcinisation, i.e. the evolution towards the crab-like morphotype? It is problematic to suppose that this disposition appeared suddenly, thus the origin has to be investigated in earlier times. If outgroup comparison and, to a lesser extent, ontogeny are considered the primary evidence for polarity and rooting, the reliance to palaeontological method, despite its limitations, is accepted as appropriate for the polarity determination (e.g. Simpson 1961; Wiley 1981). In any event, the family Archaeochiapasidae n. fam. is the oldest known fossil that can be assigned to the Eubrachyura with such a widened thoracic sternum.

Acknowledgements

Our sincere gratitude to the following persons for assistance during fieldwork: Jesús Alvarado, A. Bruno, Than Marchese, Maria Fernandez Duarte and Marco A. Coutiño. This research was supported under the project "Prospección y reguardo del patrimonio paleontológico de Chiapas”, and by the Project PAPIIT, IN107617, Dirección General de Apoyo al Personal Académico, Universidad Nacional Autónoma de México.

We want to thank Àlex Ossó (Tarragona, Catalonia) for his kind help to D.G. for the interpretation of the carapace and for the photographs of two rare fossil crabs of his private collection, Barry van Bakel (Oertijdmuseum De Groene Poort, WB Boxtel and Naturalis Biodiversity Center Leiden, the Netherlands) for the photograph of *Medorippe lanata*, and William Santana (Museu de Oceanografia, Recife, Pernambuco, Brazil) for his advice about the identity of our fossil crab. We are very grateful to the two reviewers J. Luque and B. W. M.

van Bakel for their careful reading, constructive comments and recommendations. We address special thanks to Emmanuel Côtez, Assistant editor of *Geodiversitas*, for his professional and kind assistance for the iconography.

REFERENCES

Aguilera O., de Aguilera D. R., Vega F. J. & Sanchez-Villagra M. R. 2010. — Mesozoic and Cenozoic Decapod Crustaceans from Venezuela and Related Trace-Fossil Assemblages, *in* Sanchez-Villagra M. R., Aguilera O. & Carlini A. A. (eds), *Urumaco and Venezuelan paleontology. The fossil record of the northern Neotropics*: 103-128. Indiana University Press, Bloomington.

Ahyong S. T. & Ng P. K. L. 2009. — Aphanodactylidae, a new family of thoracotreme crabs (Crustacea: Brachyura) symbiotic with polychaete worms. *Zootaxa* 2289: 33-47.

Ahyong S. T., Lai J. C. Y., Sharkey D., Colgan D. J. & Ng P. K. L. 2007. — Phylogenetics of the brachyuran crabs (Crustacea: Decapoda): the status of Podotremata based on small subunit nuclear ribosomal RNA. *Molecular Phylogenetics and Evolution* 45 (2): 576-586.

Ahyong S. T., Tsang L. M., Lai J. C. Y., Chan T. Y., Ng P. K. L. & Chu K. H. 2010. — Molecular phylogeny of the Brachyura: origin of the freshwater crabs, *in Seventh International Crustacean Congres, Qingdao, China, June 20–25, 2010*. Program & Abstracts: p. 2.

Alvarado-Ortega J. & Ovalles-Damián E. 2008. — *Triplomystus applegatei*, sp. nov. (Teleostei: Ellimmichthyiformes), a rare "triple armored herring" from El Espinal Quarry (Early Cretaceous), Chiapas, southeastern Mexico. *Journal of Vertebrate Paleontology* 28 (1): 53-60.

Alvarado-Ortega J. & Than-Marchese B. A. 2012. — A Cenomanian aipichthyoid fish (Teleostei, Acanthomorpha) from America, *Zoqueichthys carolinae* gen. and sp. nov. from El Chango quarry (Cintalapa Member, Sierra Madre Formation), Chiapas, Mexico. *Revista Mexicana de Ciencias Geológicas* 29 (3): 735-748.

Alvarado-Ortega J., Ovalles-Damián E. & Blanco-Piñó A. 2009. — The fossil fishes from the Sierra Madre Formation, Ocozocoautla, Chiapas, Southern Mexico. *Palaeontología Electrónica* 12 (2. 4A): 1-22.

Anker A. & Paulay G. 2013. — A remarkable new crab-like hermit crab (Crustacea, Decapoda, Paguridae) from French Polynesia, with comments on carcinization in the Anomura. *Zootaxa* 3722: 283-300.

Artal P., van Bakel B. W. M. & Castillo J. 2006. — *Retropluma* Gill, 1894 (Crustacea, Decapoda) from the Eocene of the eastern Pyrenees (Spain, France). *Cainozoic Research* 5 (1-2): 65-71.

Artal P., van Bakel B. W. M. & Onetti A. 2014. — A new inachid crab (Brachyura, Majoidea) from the Middle Eocene of the provinces of Barcelona and Girona (Catalonia, Spain), *in* Fraaije R. H. B., Hyžný

M., JAGT J. W. M., KROBICKI M. & VAN BAKEL B. W. M. (eds), Proceedings of the 5th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Krakow, Poland, 2013: a tribute to Pál Mihály Müller. *Scripta Geologica* 147: 153-161.

ARTAL P., GUINOT D., VAN BAKEL B. & CASTILLO J. 2008. — Ibericancridae, a new dakoticancroid family (Decapoda, Brachyura, Podotremata) from the upper Campanian (Upper Cretaceous) of Spain. *Zootaxa* 1907: 1-27.

ARTAL P., VAN BAKEL B. W. M., FRAAIJE R. H. B., JAGT J. W. M. & KLOMPMAKER A. A. 2012. — New Albian–Cenomanian crabs (Crustacea, Decapoda, Podotremata) from Monte Orobe, Navarra, northern Spain. *Revista Mexicana de Ciencias Geológicas* 29: 398-410.

BECKER C., BRANDIS D. & STORCH V. 2011. — Morphology of the female reproductive system of European pea crabs (Crustacea, Decapoda, Brachyura, Pinnotheridae). *Journal of Morphology* 272: 12-26.

BESCHIN C. & DE ANGELI A. 2003. — *Spinipalicus italicus*, nuovo genere e specie di Palicidae (Crustacea, Decapoda) dell'Eocene del Vicentino (Italia settentrionale). *Associazone Amici del Museo Civico* "*G. Zannato*", *Montecchio Maggiore*: 7-12.

BESCHIN C., BUSULINI A., DE ANGELI A. & TESSIER G. 1996. — *Eopalicus* nuovo genere di brachiuro (Decapoda) del Terziario Veneto (Italia settentrionale). *Lavori Società Veneziana di Scienze Naturali* 21: 75-82.

BESCHIN C., BUSULINI A., FORNACIARI E., PAPAZZONI C. A. & TESSIER G. 2018. — La fauna di crostacei associati a coralli dell'Eocene superiore di Campolongo di Val Liona (Monti Berici, Vicenza, Italia nordorientale). *Bollettino del Museo di Storia Naturale di Venezia* 69: 129-215.

BISHOP G. A. 1981. — Occurrence and fossilization of the *Dakoticancer* Assemblage, Upper Cretaceous Pierre Shale, South Dakota, *in* GRAY J., BOUCOT A. J. & BERRY W. B. N. (eds), *Communities of the past*, 13, 383-413. Hutchinson Ross Publishing Company, Stroudsburg, PA.

BISHOP G. A. 1983a. — Fossil decapod crustaceans from the Lower Cretaceous, Glen Rose Limestone of central Texas. *Transactions of the San Diego Society of Natural History* 20: 27-55.

BISHOP G. A. 1983b. — Fossil decapod Crustacea from the Late Cretaceous Coon Creek Formation, Union Country, Mississippi. *Journal of Crustacean Biology* 3 (3): 417-430.

BISHOP G. A. 1986. — Occurrence, preservation, and biogeography of the Cretaceous crabs of North America, *in* GORE R. H. & HECK K. L. (eds), *Crustacean Biogeography*. A. A. Balkema, Rotterdam, The Netherlands: 111-142.

BISHOP G. A. 2016. — The Coon Creek decapod assemblages; Cretaceous marine paleocommunities of northern Mississippi and Tennessee. *Bulletin Alabama Museum of Natural History* 33: 7-20.

BISHOP G. A., FELDMANN R. M. & VEGA F. 1998. — The Dakoticancridae (Decapoda, Brachyura) from the Late Cretaceous of North America and Mexico. *Contributions to Zoology* 67: 237-255.

BORRADAILE L. A. 1916. — Crustacea. Part II. P*orcellanopagurus*: an instance of carcinization. British Antarctic ('Terra Nova') Expedition, 1910. *Natural History Reports*, Zoology 3: 111-126.

BRETON G. 2009. — Description of *Priscinachus elongatus* n. gen., n. sp., and Priscinachidae n. fam. for the earliest spider crab (Crustacea, Decapoda, Majoidea), from the French Cretaceous (Cenomanian). *Geodiversitas* 31: 509-523.

BRETON G. & COLLINS J. S. H. 2007. — Decapod fauna from the Cenomanian stratotype. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 35 (2): 17-20.

BRETON G. & COLLINS J. S. H. 2011. — New and rare Cenomanian crabs (Crustacea, Decapoda, Brachyura) from the Paris Basin (France), and a comparison with necrocarcinids, etyids and dynomenids from Devon (England). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 260: 141-156.

CHARBONNIER S., AUDO D., GARASSINO A. & HYŽNÝ M. 2017. — Fossil Crustacea of Lebanon. *Mémoires du Muséum national d'Histoire narturelle* 210: 1-252

CHARBONNIER S. & GARASSINO A. 2012. — The marine arthropods from the Solnhofen Lithographic Limestones (Late Jurassic, Germany) in the collections of the Muséum national d'Histoire naturelle, Paris. *Geodiversitas* 34 (4): 857-871.

CHECCHIA-RISPOLI G. 1917. — *Distefania*, nuovo genere di Brachiuri del Cenomaniano della Sicilia. *Bollettino della Società Zoologica Italiana, serie 3* 3 (12): 173-186.

CHEN J., XING Y., YAO W., XU X., ZHANG C., ZHANG Z. & LIU Q. 2019. — Phylomitogenomics reconfirm the phylogenetic position of the genus *Metaplax* inferred from the two grapsid crabs (Decapoda: Brachyura: Grapsoidea). *PLoS ONE* 14 (1): e0210763. https://doi.org/10.1371/journal. pone.0210763

CHU K. H. C., SCHUBART C. D., SHIH H.-T. & TSANG L. M. 2015. — Genetic diversity and evolution of Brachyura (Chapter 71-13), *in* CASTRO P., DAVIE P. J. F., GUINOT D., SCHRAM F. R. & VON VAUPEL KLEIN J. C. (eds), *Decapoda: Brachyura, Treatise on Zoology – Anatomy, Taxonomy, Biology*. Vol. 9C-2, Crustacea. Brill, Leiden and Boston: 775-820.

CLARK P. F. & WEBBER W. R. 1991. — A redescription of *Macrocheira kaempferi* (Temminck, 1836) zoeas with a discussion of the classification of the Majoidea Samouelle, 1819 (Crustacea, Brachyura). *Journal of Natural History* 25: 1259-1279.

COLAVITE J., WINDSOR A. & SANTANA W. 2019. Three new species and a new genus of majoid crabs from the eastern Pacific (Decapoda, Brachyura*)*. *ZooKeys* 825: 1-24. https://doi.org/10.3897/zookeys.825.32271

COLLINS J. S. H. & JAKOBSEN S. L. 2004. — New crabs (Crustacea Decapoda) from the Eocene (Ypresian/Lutetian), Lillebaelt Clay Formation of Jutland, Denmark. *Bulletin of the Mizunami Fossil Museum* 30[2003]: 57-60.

COLLINS J. S. H. & MORRIS F. 1978. — New Lower Tertiary crabs from Pakistan. *Palaeontology* 21 (4): 957-981.

COLLINS J. S. H., LEE C. & NOAD J. 2003. — Miocene and Pleistocene crabs (Crustacea, Decapoda) from Sabah and Sarawak. *Journal of Systematic Palaeontology* 1 (3): 187-22. DOl: 10.1017/S1477201903001o68

CRANDALL K. A., PORTER M. L. & PEREZ-LOSADA M. 2009. — Crabs, shrimps, and lobsters (Decapoda), *in* HEDGES S. B. & KUMAR S. (eds.), *The Timetree of Life*. Oxford University Press, Oxford: 293-297.

DAVIE P. J. F., GUINOT D. & NG P. K. L. 2015. — Phylogeny of Brachyura (Chapter 71-16), *in* CASTRO P., DAVIE P. J. F., GUINOT D., SCHRAM F. R. & VON VAUPEL KLEIN J. C. (eds), Decapoda: Brachyura, *Treatise on Zoology – Anatomy, Taxonomy, Biology*. Vol. 9C-2, Crustacea. Brill, Leiden and Boston: 921-979.

DE ANGELI A. & BESCHIN C. 2000. — Due nuove specie di *Eopalicus* (Decapoda, Palicidae) nel Terziario del Veneto (Italia settentrionale). *Studi e Ricerche, Associazone Amici del Museo Civico* "*G. Zannato*", *Montecchio Maggiore* (Vicenza): 7-12.

DE ANGELI A. & CECCON L. 2014. — Nuovi crostacei brachiuri (Decapoda) dell'Eocene inferiore di Monte Magrè (Vicenza, Italia settentrionale). *Lavori Società Veneziana di Scienze Naturali* 39: 77-92.

DE ANGELI A. & CECCON L. 2015. — New brachyuran crustaceans from the Eocene of Monte Magrè (Vicenza, northern Italy). *Lavori Società Veneziana di Scienze Naturali* 40: 119-138.

DE ANGELI A., GARASSINO A. & PASINI G. 2009. — New reports of anomurans and brachyurans from the Cenozoic of Tuscany (Italy). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano* 150 (2): 163-196.

DE GRAVE S., PONTCHEFF N. D., AHYONG S. T., CHAN T.-Y., CRANDALL K. A., DWORSCHAK P. C., FELDER D. L., FELDMANN R. M., FRANSEN C. H. J. M., GOULDING L. Y. D., LEMAITRE R., LOW M. E. Y., MARTIN J. W., NG P. K. L., SCHWEITZER C. E., TAN S. H., TSHUDY D. & WETZER R. 2009. — A classification of living and fossil genera of decapod crustaceans. *Raffles Bulletin of Zoology* Supplement 21: 1-109.

DÍAZ-CRUZ J. A., ALVARADO-ORTEGA J. & CARBOT-CHANONA G. 2016. — The Cenomanian short snout enchodontid fishes (Aulopifomes, Enchodontidae) from Sierra Madre Formation, Chiapas, southeastern Mexico. *Cretaceous Research* 61: 136-150.

DÍAZ-CRUZ J. A., ALVARADO-ORTEGA J. & CARBOT-CHANONA G. 2019. — *Dagon avendanoi* gen. and sp. nov., an Early Cenomanian Enchodontidae (Aulopiformes) fish from the El Chango quarry, Chiapas, southeastern Mexico. *Journal of South American Earth Sciences* 91: 272-284.

DRACH P. & GUINOT D. 1982. — Connexions morphologiques et fonctionnelles d'un type nouveau dans le squelette des Brachyoures du genre *Paradasygius* [*sic*] Garth (carapace, pleurites, sternites, pléon). *Comptes rendus de l'Académie des Sciences sér. 3* 295: 715-720.

DRACH P. & GUINOT D. 1983. — Les Inachoididae Dana, famille de Majoidea caractérisée par des connexions morphologiques d'un type nouveau entre carapace, pleurites, sternites et pléon (Crustacea Decapoda). *Comptes rendus de l'Académie des Sciences sér. 3*, 297: 37-42.

FELDMANN R. M., SCHWEITZER C. E. & GREEN R. M. 2003. — Unusual Albian (Early Cretaceous) Brachyura (Homoloidea: Componocancroidea New Superfamily) from Montana and Wyoming, U.S.A. *Journal of Crustacean Biology* 28 (3): 502-509

FELDMANN R. M., VEGA F. J., APPLEGATE S. P. & BISHOP G. A. 1998. — Early Cretaceous Arthropods from the Tlayúa Formation at Tepexi de Rodríguez, Puebla, México. *Journal of Paleontology* 72 (1): 79-90.

FELDMANN R. M., SCHWEITZER C. E., BENNETT O., FRANTESCU O. D., RESAR N. & TRUDEAU A. 2011. — New Eocene Brachyura (Crustacea: Decapoda) from Egypt. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 262: 323-353. DOI: 10.1127/0077-7749/2011/0202

FELDMANN R. M., SCHWEITZER C. E., BALTZLY L. M., BENNETT O. A., JONES A. M., MATHIAS F. F., WEAVER K. L. & YOST S. L. 2013. — New and previously known decapod crustaceans from the Late Cretaceous of New Jersey and Delaware, USA. *Bulletin of the Mizunami Fossil Museum* 39: 7-37.

FÖRSTER R. 1966. — Über die Erymiden, eine alte konservative Familie der mesozoischen Dekapoden. *Palaeontographica* 125 (4-6): 61-175.

FRAAIJE R. H. B., VAN BAKEL B. W. M., JAGT J. W. M. & ARTAL P. 2008. — New decapod crustaceans (Anomura, Brachyura) from mid-Cretaceous reefal deposits at Monte Orobe (Navarra, northern Spain), and comments on related type-Maastrichtian material. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 78: 193-208.

FRAAIJE R. H. B., VEGA F. J., VAN BAKEL B. W. M. & GARIBAY-ROMERO L. M. 2006. — Late Cretaceous dwarf decapods from Guerrero, southern Mexico and their migration pattern. *Contributions to Zoology* 75 (3/4): 121-132.

FRANȚESCU O. D. 2011. — Brachyuran decapods (including five new species and one new genus) from Jurassic (Oxfordian-Kimmeridgian) coral reef limestones from Dobrogea, Romania. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 259: 271–297.

FUKUDA Y. 1981. — Larval development of *Trigonoplax unguiformis* (De Haan) (Crustacea, Brachyura) reared in the laboratory. *Zoological Magazine* 90: 164-173.

GARASSINO A. & SCHWEIGERT G. 2006. — The Upper Jurassic Solnhofen decapod crustacean fauna: review of the types from old descriptions. Part I. Infraorders Astacidea, Thalassinidea, and Palinura. *Memorie della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano* 34 (1): 1-64.

GARASSINO A., DE ANGELI A., GALLO L. M. & PASINI G. 2004. — Brachyuran and anomuran fauna from the Cenozoic of Piedmont (NW Italy). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 145 (2): 251-281.

GARASSINO A., DE ANGELI A. & PASINI G. 2008. — New decapod assemblage from the Upper Cretaceous (Cenomanian-Turonian) of Gara Sbaa, southeastern Morocco. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano* 149 (1): 37-67.

GARASSINO A., VEGA F. J., CALVILLO-CANADELL L., CEVALLOS-FERRIZ S. R. S. & COUTIÑO M. A. 2013. — New decapod crustacean assemblage from the Upper Cretaceous (Cenomanian) of Chiapas, Mexico. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 269 (3): 261-270.

GARTH J. S. 1958. — Brachyura of the Pacific coast of America, Oxyrhyncha. *Allan Hancock Pacific Expeditions* 21 (1): xxii + 499; (2), 501-854, pls. A-Z4, 1-55.

GAŠPARIČ R. & KRIŽNAR M. 2017. — Early Miocene decapod *Retropluma slovenica* Gašparič & Hyžný, 2014 from Govce beds of Tunjice Hills (Central Slovenia). *Geologija* 60 (1): 77-85.

GAŠPARIČ R., HYŽNÝ M., JOVANOVIĆ G., ĆORIĆ S. & SEJFUDIN V. 2019. — Middle Miocene decapod crustacean assemblage from the Tuzla Basin (Tušanj, Bosnia and Herzegovina), with a description of two new species and comparison with coeval faunas from Slovenia. *Palaeontologia Electronica* 22.1.9A 1-21. https://doi.org/10.26879/894 palaeo-electronica.org/content/2019/2430-decapods-from-the-tuzla-basin

GLAESSNER M. F. 1928. — Die Dekapodenfauna des österreichischen Jungtertiärs. *Jahrbuch der Geologischen Bundesanstalt Wien* 78 (12): 161-219.

GLAESSNER M. F. 1969. — Decapoda, *in* MOORE R. C. (ed.), *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4(2*). University of Kansas Press, Lawrence and Geological Society of America, Boulder, Colorado, Part R, Arthropoda, 4: R399-R533, R626-R628.

GLAESSNER M. F. 1980. — New Cretaceous and Tertiary crabs (Crustacea: Brachyura) from Australia and New Zeland. *Transactions of the Royal Society of South Australia* 104 (6): 171-192.

GONZÁLEZ-RAMÍREZ I., CALVILLO-CANADELL L. & CEVALLOS-FERRIZ S. R. S. 2013. — Coníferas Cupresáceas fósiles de "El Chango", Chiapas (Aptiano). *Paleontología Mexicana* 63: 24-31.

GRIFFIN D. J. G. & TRANTER H. A. 1986. — The Decapoda Brachyura of the Siboga Expedition. Part VIII. Majidae. *Siboga Expeditie*, 39C4, livr. 148: 1-335.

GUERRERO-MÁRQUEZ G., CALVILLO-CANADELL L., CEVALLOS-FERRIZ S. R. S. & AVENDAÑO-GIL M. J. 2013. — Angiospermas cretácicas de la localidad "El Chango", Chiapas, México. *Paleontología Mexicana* 63: 32-39.

GUINOT D. 1977. — Proposition pour une nouvelle classification des Crustacés Décapodes Brachyoures. *Comptes Rendus hebdomadaires des séances de l'Académie des Sciences (Paris), sér. D* 285: 1049-1052.

GUINOT D. 1978. — Principes d'une classification évolutive des Crustacés Décapodes Brachyoures. *Bulletin biologique de la France et de la Belgique n.s.* 112 (3): 211-292.

GUINOT D. 1979. — Données nouvelles sur la morphologie, la phylogenèse et la taxonomie des Crustacés Décapodes Brachyoures. *Mémoires du Muséum national d'Histoire naturelle sér. A* Zoologie, 112: 1-354.

GUINOT D. 1993. — Données nouvelles sur les crabes primitifs (Crustacea Decapoda Brachyura). *Comptes rendus de l'Académie des Sciences sér. 3*, 316 (10): 1225-1232.

GUINOt D. 1984. — Le genre *Leurocyclus* Rathbun, 1897 (Crustacea Decapoda Brachyura). *Bulletin du Muséum national d'Histoire naturelle sér. 4* 6, sect. A (2): 377-395.

GUINOt D. 2011a. — Odiomarinae nov. subfam., a new subfamily for two primitive genera of the Hymenosomatidae MacLeay, 1838 (Crustacea, Decapoda, Brachyura). *Zootaxa* 2732: 20-32.

GUINOt D. 2011b. — The position of the Hymenosomatidae MacLeay, 1838, within the Brachyura (Crustacea, Decapoda). *Zootaxa* 2890: 40-52.

GUINOt D. 2012. — Remarks on Inachoididae Dana, 1851, with the description of a new genus and the resurrection of Stenorhynchinae Dana, 1851, and recognition of the inachid subfamily Podochelinae Neumann, 1878 (Crustacea, Decapoda, Brachyura, Majoidea). *Zootaxa* 3416: 22-40.

GUINOt D. 2019. — New hypotheses on the earliest brachyurans (Crustacea, Decapoda, Brachyura). *Geodiversitas* (accepted).

GUINOT D. & BOUCHARD J.-M. 1998. — Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura). *Zoosystema* 20 (4): 613-694.

GUINOT D. & BRETON G. 2006. — *Lithophylax trigeri* A. Milne-Edwards & Brocchi, 1879 from the French Cretaceous (Cenomanian) and status of the family Lithophylacidae Van Straelen, 1936 (Crustacea Decapoda Brachyura). *Geodiversitas* 28 (4): 591-633.

GUINOT D. & QUENETTE G. 2005. — The spermatheca in podotreme crabs (Crustacea, Decapoda, Brachyura, Podotremata) and its phylogenetic implications. *Zoosystema* 2 (2): 267-342.

GUINOT D. & RICHER DE FORGES B. 1982. — Révision du genre indo-pacifique *Cyrtomaia* Miers, 1886: campagnes océanographiques du "Challenger", de l' "Albatross", du "Siboga" et du "Vauban" (Crustacea, Decapoda, Brachyura). *Annales de l'Institut océanographique de Monaco* 58 (1): 5-87.

GUINOT D. & RICHER DE FORGES B. 1997. — Affinités entre les Hymenosomatidae MacLeay, 1838 et les Inachoididae Dana, 1851 (Crustacea Decapoda Brachyura). *Zoosystema* 19 (2, 3): 453-502.

GUINOT D. & TAVARES M. 2001. — Une nouvelle famille de crabes du Crétacé, et la notion de Podotremata Guinot, 1977 (Crustacea, Decapoda, Brachyura). *Zoosystema* 23 (3): 507-546.

GUINOT D. & TAVARES M. 2003. — A new subfamilial arrangement for the Dromiidae de Haan, 1833, with diagnoses and description of new genera and species (Crustacea, Decapoda, Brachyura). *Zoosystema* 25 (1): 43-129.

GUINOT D. & WICKSTEN M. K. 2015. — Phylogeny of Brachyura (Chapter 71-11), *in* CASTRO P., DAVIE P. J. F., GUINOT D., SCHRAM F. R. & VON VAUPEL KLEIN J. C. (eds), Decapoda: Brachyura, *Treatise on Zoology – Anatomy, Taxonomy, Biology*. Vol. 9C-2, Crustacea. Brill, Leiden and Boston: 583-638.

GUINOT D., DE ANGELI A. & GARASSINO A. 2008. — Marocarcinidae, a new eubrachyuran family, and *Marocarcinus pasinii* n. gen., n. sp. from the Upper Cretaceous (Cenomanian-Turonian) of Gara Sbaa, southeastern Morocco (Crustacea, Decapoda, Brachyura). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano* 149 (1): 25-36.

GUINOT D., TAVARES M. & CASTRO P. 2013. — Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa. *Zootaxa* 3665: 1-414. DOI 10.11646/zootaxa.3665.1.1.

GUINOT D., NG N. K. & RODRÍGUEZ-MORENO P. 2018. — Review of grapsoid families for the establishment of a new family for *Leptograpsodes* Montgomery, 1931, and a new genus of Gecarcinidae H. Milne Edwards, 1837 (Crustacea, Decapoda, Brachyura, Grapsoidea MacLeay, 1838). *Zoosystema* 40 (26): 547-604.

HAYER S., KÖHNK S., BORETIUS S. & BRANDIS D. 2016. — Ever more complex: a new type of organization of the reproductive organs in female *Dorippe sinica* Chen, 1980 (Decapoda: Brachyura: Dorippidae). *Zoology* 119 (5): 455-483.

HENNIG W. 1966. — *Phylogenenetics Systematics*. University of Illinois Press, Urbana, 263 pp.

HILLER A., VIVIANI C. A. & WERDING B. 2010. — Hypercarcinisation: an evolutionary novelty in thecommensal porcellanid Allopetrolisthes spinifrons (Crustacea: Decapoda: Porcellanidae). *Nauplius* 18 (1): 95-102.

HULTGREN K.M., GUERAO G., MARQUES F. P. L. & PALERO F. P. 2009. — Assessing the contribution of molecular and larval morphological characters in a combined phylogenetic analysis of the superfamily Majoidea, *in* MARTIN J. W., CRANDALL K. A. & FELDER D. L. (eds), *Decapod Crustacean Phylogenetics*. *Crustacean Issues* 18: 437-455.

HYŽNÝ M., STARZYK N., ROBINS C. M. & KOČOVA VESELSKÁ M. 2015. — Taxonomy and palaeoecology of a decapod crustacean assemblage Oxfordian of Stránska skála (Southern Moravia, Czech Republic). *Bulletin of Geosciences* 90 (3): 633-650.

HYŽNÝ M., PERRIER V., ROBIN N., MARTIN J. E. & SARR R. 2016. — *Costacopluma* (Decapoda: Brachyura: Retroplumidae) from the Maastrichtian and Paleocene of Senegal: a survivor of K/Pg events. *Cretaceous Research* 57: 142-156.

ICZN (International Commission of Zoological Nomenclature) 1999. — *International Code of Zoological Nomenclature. Fourth edition*. Fourth edition. The International Trust for Zoological Nomenclature, The Natural History Museum, London: xxx + 306 p.

IMAIZUMI R. 1952. — A Miocene crab, *Hyas tsuchidai* n. sp., from the Wakkanai Formation of Teshio Province, Hokkaido. *Transactions and Proceedings of the Palaeontological Society of Japan, new series* 5: 179-183.

JAGT J. W. M., VAN BAKEL B. W. M., GUINOT D., FRAAIJE R. H. & ARTAL P. 2015. — Fossil Brachyura. p. 847-920, *in* CASTRO P., DAVIE P. J. F., GUINOT D., SCHRAM F. R. & VON VAUPEL KLEIN J. C. (eds), *Treatise on Zoology - Anatomy, Taxonomy, Biology*. The Crustacea, Vol. 9 Part C-II. Leiden and Boston, Brill.

JAMIESON B. G. M. & TUDGE C. C. 2000. — Crustacea-Decapoda, *in* ADIYODI K. G. & ADIYODI R. G. (series eds), JAMIESON B. G. M. (volume ed.), *Reproductive Biology of Invertebrates*. *Progress in Male Gamete Ultrastructure and Phylogeny.* Volume 9, part C. John Wiley and Sons, Chichester: 1-95.

KARASAWA H. & KATO H. 2003. — The family Goneplacidae MacLeay, 1838 (Crustacea: Decapoda: Brachyura): systematics, phylogeny, and fossil records. *Paleontological Research* 7 (2): 129-151.

KARASAWA H., SCHWEITZER C. E. & FELDMANN R. M. 2008. — Revision of Portunoidea Rafinesque, 1815 (Decapoda: Brachyura) with emphasis on the fossil genera and families. *Journal of Crustacean Biology* 28 (1): 82-127.

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.

KARASAWA H., KISHIMOTO S., OHARA M. & ANDO Y. 2019. — Late Cretaceous Decapoda from the Izumi Group of Japan, with descriptions of two new genera and one new species of Axiidea and one new family of Brachyura. *Bulletin of the Mizunami Fossil Museum* 45: 43-85, 1 appendix.

KATO H., NAKASHIMA R. & YANAGISAWA Y. 2014. — Two new Early Pliocene species of the crab genus *Hyas* Leach, 1814 (Majoidea, Oregoniidae) from northeast Japan, *in* FRAAIJE R. H. B., HYŽNÝ M., JAGT J. W. M., KROBICKI M. & VAN BAKEL B. W. M. (eds), *Proceedings of the 5th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Krakow, Poland, 2013: A tribute to Pál Mihály Müller*. *Scripta Geologica* 147:

269-287.

KEILER J., WIRKNER C. S & RICHTER S. 2017. — One hundred years of carcinization – the evolution of the crab-like habitus in Anomura (Arthropoda: Crustacea). *Biological Journal of the Linnean Society* 20: 1-23.

KIENBAUM K., VEHOF J., BECKER C. & SCHOLTZ G. 2018. — The reproductive system of *Limnopilos naiyanetri* indicates a thoracotreme affiliation of Hymenosomatidae (Decapoda, Eubrachyura). *Arthropod Structure & Development* 47 (5): 513-520. doi: 10.1016/j.asd.2018.06.008

KLAUS S.**,** YEO D. C. J. & AHYONG S. T. 2011. — Freshwater crab origins — Laying Gondwana to rest. *Zoologischer Anzeiger* 250: 449-456

KLOMPMAKER A. A. 2013. — Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: implications for Cretaceous decapod paleoecology. *Cretaceous Research* 41: 150-185.

KLOMPMAKER A. A., ORTIZ J. D. & WELLS N. A. 2013. — How to explain a decapod crustacean diversity hotspot in a mid-Cretaceous coral reef. *Palaeogeography, Palaeoclimatology, Palaeoecology* 374: 256-273.

KLOMPMAKER A. A., HYŽNÝ M. & JAKOBSEN S. L. 2015a. — Taphonomy of decapod crustacean cuticle and its effect on the appearance as exemplified by new and known taxa from the Cretaceous-Danian crab *Caloxanthus*. *Cretaceous Research* 55: 1-151.

KLOMPMAKER A. A., PORTELL R. W., KLIER A. T., PRUETER V. & TUCKER A. L. 2015b. — Spider crabs of the Western Atlantic with special reference to fossil and some modern Mithracidae. *Cretaceous Research* 41: 150-185. doi: 10.7717/peerj.1301

KOMAI T. & FUJITA Y. 2018. — A new genus and new species assigned to Macrophthalmidae (Decapoda: Brachyura: Thoracotremata) from the Ryukyu Islands, Japan. *Zootaxa* 4531 (1): 109-116.

KROBICKI M. & ZATOń M. 2008. — Middle and Late Jurassic roots of brachyuran crabs: palaeoenvironmental distribution. *Palaeogeography, Palaeoclimatology, Palaeoecology* 263: 30-43.

LARGHI C. 2004. — Brachyuran decapod Crustacea from the Upper Cretaceous of Lebanon. *Journal of Paleontology* 78 (3): 528-541.

LUCAS J. S. 1980. — Spider crabs of the family Hymenosomatidae (Crustacea: Brachyura) with particular reference to Australian species: systematics and biology. *Records of the Australian Museum* 33 (4); 148-247.

LUQUE J. 2015a. — A puzzling frog crab (Crustacea: Decapoda: Brachyura) from the Early Cretaceous Santana Group of Brazil: frog first or crab first? *Journal of Systematic Palaeontology* 13 (2): 153-166. DOI: 10.1080/14772019.2013.871586

Luque J. 2015b. — The oldest higher true crabs (Crustacea: Decapoda: Brachyura): insights from the Early Cretaceous of the Americas. *Palaeontology* 58 (2): 251-263.

Luque J., Schweitzer C. E., Santana W., Portell R. W., Vega F. J. & Klompmaker A. A. 2017. — Checklist of fossil decapod crustaceans from tropical America. Part I: Anomura and Brachyura. *Nauplius* 25: e2017025

Ma□ K. Y, Qin□ J., Lin□ C.-W., Chan □T.-Y., Ng□ P. K. L., Chu□ K. H. & Tsang L. M. in pess. — Phylogenomic analyses of brachyuran crabs support early divergence of primary freshwater crabs. *Molecular Phylogenetics and Evolution* xxx: xxx-xxx. DOI: *10.1016/j.ympev.2019.02.001*

Marco-Herrero A., Torres P., Cuesta J. A., Guerao G., Palero F. & Abelló P. 2013. — The systematic position of *Ergasticus* (Decapoda, Brachyura) and allied genera, a molecular and morphological approach. *Zoologica Scripta* 42 (4): 427-439.

Marques F. & Pohle G. 1998. —The use of structuralreduction in phylogenetic reconstruction of decapods and a phylogenetic hypothesis for 15 genera of Majidae: testing previous larval hypotheses and assumptions. *InvertebrateReproduction & Development* 33 (2-3): 241-262. DOI: 10.1080/07924259.1998.9652636

Marques F. & Pohle G. 2003. — Searching for larval support for majoid families (Crustacea: Brachyura) with particular reference to Inachoididae Dana, 1851. *Invertebrate Reproduction and Development*, 43: 71-82.

Martill D. M., Ibrahim N., Brito P. M., Baider L., Zhoun S., Loveridge R., Naish D. & Hing R. 2011. — A new Plattenkalk Konservat Lagerstätte in the Upper Cretaceous of Gara Sbaa, south-eastern Morocco. *Cretaceous Research* 32 (4): 433-446.

Melrose M. J. 1975. — The marine fauna of New Zealand: family Hymenosomatidae (Crustacea, Decapoda, Brachyura). *Memoirs of the New Zealand Oceanographic Institute* 34: 1-123.

Meyer H. von 1860. — Die Prosoponiden oder die Familie der Maskenkrebse. *Palaeontographica* 7: 183-222, pl. 23.

Marco-Herrero E., Torres A. P., Cuesta J. A., Guerao G., Palero F. & Abelló P. 2013. — The systematic position of *Ergasticus* (Decapoda, Brachyura) and allied genera, a molecular and morphological approach. *Zoologica Scripta* 42 (4): 427-439. https://doi.org/10.1111/zsc.12012

Michaud F. & Fourcade E. 1989. — Stratigraphie et paléogéographie du Jurassique et du Crétacé du Chiapas (Sud-Est du Mexique). *Bulletin de la Société géologique de France* 5 (3): 639-650. 1997

Miller R. F. & McGovern J. H. 1997. — Late-glacial marine invertebrate macrofossils from Point Lepreau, New Brunswick. *Atlantic Geology* 33: 217-221.

Moericke W. 1899. — Die Crustaceen der Stramberger Schichten. *Palaeontographica* (1897) Supplement 2, 6:

43-72, pl. 6.

MORENO-BEDMAR J. A., LATIL J. L., VILLANUEVA-AMADOZ U., CALVILLO-CANADELL L. & CEVALLOS-FERRIZ S. R. S. 2014. — Ammonite age-calibration of the El Chango Fossil-Lagerstätte, Chiapas state (SE Mexico). *Journal of South American Earth Sciences* 56: 447-453.

MORRIS S. F. & COLLINS J. S. H. 1991. — Neogene crabs from Brunei, Sabah and Sarawak. *Bulletin of the British Museum Natural History* (*Geology*) 47: 1-33.

MÜLLER P. M. 2006. — New decapods from the Miocene of Hungary - with remarks about their environment. *Földtani Közlöny* 136: 37-49.

MÜLLER P. M., KROBICKI M. & WEHNER G. 2000. — Jurassic and Cretaceous primitive crabs of the family Prosopidae (Decapoda: Brachyura) - Their taxonomy, ecology and biogeography. *Annales Societatis Geologorum Poloniae* 70: 49-79

NG P. K. L., GUINOT D. & DAVIE P. J. F. 2008. — Systema Brachyurorum: Part 1. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology* Supplement 17: 1-286. [updates at http://rmbr.nus.edu.sg/research/cotw/ supplement17.php]

NG P. K. L, RAVINESH R. & RAVICHANDRAN S. 2017. — A new large oregoniid spider crab of the genus *Pleistacantha* Miers, 1879, from the Bay of Bengal, India (Crustacea, Brachyura, Majoidea). *ZooKeys* 716: 127-146. https://doi. org/10.3897/zookeys.716.21349

NYBORG T., OSSÓ À. & VEGA F. J. 2014. — A new species of icriocarcinid crab (Crustacea, Portunoidea) fom the uppermost Cretaceous of California, USA: palaeobiogeographic implications, *in* FRAAIJE R. H. B., HYŽNÝ M., JAGT J. W. M., KROBICKI M. & VAN BAKEL B. W. M. (eds), Proceedings of the 5th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Krakow, Poland, 2013: A tribute to Pál Mihály Müller. *Scripta Geologica* 147: 83-93.

NYBORG T. G., VEGA F. J. & FILKORN H. F. 2009. — First described species of *Costacopluma* (Crustacea: Brachyura: Retroplumidae) from the Pacific slope, Paleocene of California, USA. *Boletín de la Sociedad Geológica Mexicana* 61 (2): 203-209.

OPPEL A. 1862. — Über jurassische Crustaceen (Decapoda macrura). *Palaeontologische Mittheilungen aus dem Museum des koeniglich Bayerischen Staates* 1: 1-120.

OSSÓ À. 2016. — *Eogeryon elegius* n. gen. and n. sp. (Decapoda: Eubrachyura: Portunoidea), one of the oldest modern crabs from late Cenomanian of the Iberian Peninsula. *Bolletín de la Sociedad Geólogica Mexicana* 68 (2): 231-246.

OSSÓ-MORALES À., ARTAL P. & VEGA F. J. 2010. — New crabs (Crustacea, Decapoda) from the Upper

Cretaceous (Campanian) of the Moyenne Moulouya, northeast Morocco. *Revista Mexicana de Ciencias Geológicas* 27: 213-224.

OSSÓ À., VAN BAKEL B. M. W., FERRATGES-KWEKEL F. A. & MORENO-BEDMAR J. A. 2018. — A new decapod crustacean assemblage from the lower Aptian of La Cova del Vidre (Baix Ebre, province of Tarragona, Catalonia). *Cretaceous Research* 92: 94-107.

OVALLES-DAMIÁN E., ALVARADO-ORTEGA J. & BLANCO-PIÑÓN A. 2006. — Los peces fósiles del Cretácico Inferior de Ocozocoautla, Chiapas, *in Memoria X Congreso Nacional de Paleontología y libreto guía de la excursión a Tepexi de Rodríguez, Puebla*. Publicación especial 5. Instituto de Geología, 61 pp.

PATRULIUS D. 1959. — Contributions à la systématique des décapodes néojurassiques. *Revue de Géologie et Géographie* 3 (2): 249-257.

PATRULIUS D. 1966. — Les Décapodes du Tithonique inférieur de Woźniki (Carpates Polonaises Occidentales). *Annales de la Société Géologique de Pologne* 36: 495-517.

PHILLIPS G. E., NYBORG T. & VEGA F. J. 2014. — Icriocarcinidae: a family of portunoid crabs from the Upper Cretaceous of North America. *Paläontologische Zeitschrift* 88: 139-158.

POHLE G. W. 1991. — Larval development of Canadian Atlantic oregoniid crabs (Brachyura: Majidae), with emphasis on *Hyas coarctatus alutaceus* Brandt, 185 1, and a comparison with Atlantic and Pacific conspecifics. *Canadian Journal of Zoology* 69: 2717-2737.

PORTER M. L., PÉREZ-LOSADA M. & CRANDALL K. A. 2005. — Model-based multi-locus estimation of decapod phylogeny and divergence times. *Molecular Phylogenetics and Evolution* 37: 355-369.

PRADO L. A. C., LUQUE J., BARRETO A. M. F. & PALMER A. R. — New brachyuran crabs from the Aptian–Albian Romualdo Formation, Santana Group of Brazil: evidence for a Tethyan connection to the Araripe Basin. *Acta Palaeontologica Polonica* 63 (4): 737-750. DOI: 10.4202/app.00480.2018

PRALON B. G. N., SARAIVA A. Á., BEZERRA L. E. A, MONTEIRO F. A. C. & GREGATI R. A. 2017. — First record of *Ophthalmoplax brasiliana* (Maury, 1930) (Crustacea, Decapoda, Brachyura) from the Upper Cretaceous (Campanian) of the Potiguar Basin, Northeast of Brazil. *Revista Brasileira de Paleontologia* 20: 269-274.

QUAYLE W. J. & COLLINS J. S. H. 1981. — New Eocene crabs from the Hampshire Basin. *Palaeontology* 24: 733-758.

QUENSTEDT F. A. 1867. — *Handbuch der Petrefaktenkunde.* 2nd edition. H. Laupp, Tübingen: 982 p., Atlas with 86 pls.

RATHBUN M. J. 1925. — The spider crabs of America. *Bulletin of the United States National Museum* 129: 1-xx, 1-613.

RATHBUN M. J. 1935. — Fossil Crustacea of the Atlantic and Gulf Coastal Plain. *Geological Society of America* Special Paper 2: viii + 160 p.

RICE A. L. 1980. — Crab zoeal morphology and its bearing on the classification of the Brachyura. *Transactions of the Zoological Society of London* 35: 271-424. http://dx.doi.org/10.1111/j.1096-3642.1980.tb00060.x

RICE A. L. 1981. — Crab zoeae and brachyuran classification: a re-appraisal. *Bulletin of the British Museum of Natural History* 40 (5): 287-296.

RICE A. L. 1983. — Zoeal evidence for brachyuran phylogeny, *in* SCHRAM F. R. (ed.), *Crustacean Phylogeny. Crustacean Issues* 1: 313-329.

RICE A. L. 1988. — The megalopa stage in majid crabs, with a review of spider crabs relationships based on larval characters, *in* FINCHAM A. A. & RAINBOW P. S. (eds), *Aspects of Decapod Crustacean Biology*. Proceedings of a Symposium, Zoological Society of London. Clarendon Press, Oxford, pp. 27-46.

RICHER DE FORGES B., JAMIESON B. G. M., GUINOT D. & TUDGE C. C. 1997. — Ultrastructure of the spermatozoa of Hymenosomatidae (Crustacea: Brachyura) and the relationships of the family. *Marine Biology* 130: 233-242.

ROBIN N., VAN BAKEL B. W. M., PACAUD J.-M. & CHARBONNIER S. 2017. — Decapod crustaceans from the Paleocene (Danian) of the Paris Basin (Vigny stratotype and allied localities) and a limpet palaeoassociation. *Journal of Systematic Palaeontology* 15: (4): 257-273. DOI: 10.1080/14772019.2016.1182950

ROBINS C. M., FELDMANN R. M., SCHWEITZER C. E. & BONDE A. 2016. — New families Paragalatheidae and Catillogala-theidae (Decapoda: Anomura: Galatheoidea) from the Mesozoic, restriction of the genus Paragalathea, and establishment of 6 new genera and 20 new species. *Annalen des Naturhistorischen Museums in Wien* (A) 118: 65-131.

ROSALES-DOMÍNGUEZ M. C., BERMÚDEZ-SANTANA J. C. & AGUILAR-PIÑA M. 1997. — Mid and Upper Cretaceous foraminiferal assemblages from the Sierra de Chiapas, southeastern Mexico. *Cretaceous Research* 18: 697-712.

SAINT LAURENT M. DE 1989. — La nouvelle superfamille des Retroplumoidea Gill, 1894 (Decapoda, Brachyura): systématique, affinités et évolution, *in* FOREST J. (ed.), Résultats des Campagnes MUSORSTOM, vol. 5. *Mémoires du Muséum national d'Histoire naturelle sér. A* Zoologie 144: 103-179.

SANTANA W. R. A. 2008. — *Revisão taxonômica e relações filogenéticas em Inachoididae Dana, 1851 (Crustacea, Brachyura, Majoidea).* Unpublished tesis Doctoral, Instituto de Biociências, Universidad de São Paulo, São Paulo. 10.11606/T.41.2008.tde-29012009-100852

SCHOLTZ G. 2010. — Deconstructing morphology. *Acta Zoologica* 91: 44-63.

SCHOLTZ G. 2014. — Evolution of crabs - history and deconstruction of a prime example of convergence. *Contributions to zoology Bijdragen tot de dierkunde* 83 (2): 87-105.

SCHWEIGERT G. 2001. — The late Jurassic decapod species *Aeger tipularius* (Schlotheim, 1822) (Crustacea: Decapoda: Aegeridae*). Stuttgarter Beiträge zur Naturkunde Serie B* 309: 1-10.

SCHWEIGERT G. 2011. — The decapod crustaceans of the Upper Jurassic Solnhofen Limestones: a historical review and some recent discoveries. *Neues Jahrbuch für Geologie und Palaontologie, Abhanlungen* 260 (2): 131-140.

SCHWEIGERT G. 2019. — An additional representative of Lecythocaridae (Decapoda: Brachyura: Dromiacea) from the Upper Jurassic of southern Germany. *Journal of Crustacean Biology* 39 (1): 36-39. https://doi.org/10.1093/jcbiol/ruy092

SCHWEIGERT G. & GARASSINO A. 2004. — New genera and species of shrimps (Crustacea: Decapoda: Dendrobranchiata, Caridea) from the Upper Jurassic lithographic limestones of S Germany. *Stuttgarter Beiträge zur Naturkunde* B, 350: 1-33.

SCHWEIGERT G. & ROBINS C. M. 2016. — Earliest representatives of Lecythocaridae (Crustacea: Brachyura) from the Upper Jurassic of southern Germany. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 280 (3): 325-330. DOI: 10.1127/njgpa/2016/0583

SCHWEITZER C. E. 2001. — Paleobiogeography of Cretaceous and Tertiary Decapod Crustaceans of the North Pacific Ocean. *Journal of Paleontology* 75 (4): 808-826.

SCHWEITZER C. E. & FELDMANN R. M. 2010. — The oldest Brachyura (Decapoda: Homolodromioidea: Glaessneropsoidea) known to date (Jurassic). *Journal of Crustacean Biology* 30: 251-256.

SCHWEITZER C. E. & FELDMANN R. M. 2011a. — New fossil Brachyura (Decapoda: Homoloidea, Dorippoidea, Carpilioidea) from the United Kingdom. *Bulletin of the Mizunami Fossil Museum* 37: 1-11.

SCHWEITZER C. E. & FELDMANN R. M. 2001b. — New Cretaceous and Tertiary decapod crustaceans from western North America. *Bulletin of the Mizunami Fossil Museum* 28: 173-210.

SCHWEITZER C. E. & FELDMANN R. M. 2005. — Decapod crustaceans, the K/P event, and Palaeocene recovery, *in* KOENEMAN S. & JENNER R. A. (eds), *Crustacea and Arthropod Relationships*, pp. 17–53.

SCHWEITZER C. E. & FELDMANN R. M. 2009. — Revision of the Prosopinae sensu Glaessner, 1969 (Crustacea:

Decapoda: Brachyura) including four new families, four new genera, and five new species. *Annalen des Naturhistorischen Museums in Wien* 110 A: 55-121.

SCHWEITZER C. E. & FELDMANN R. M. 2010a. —The oldest Brachyura (Decapoda: Homolodromioidea: Glaessneropsoidea) known to date (Jurassic). *Journal of Crustacean Biology* 30: 251-256.

SCHWEITZER C. E. & FELDMANN R. M. 2010b. — New fossil decapod crustaceans from the Remy Collection, Muséum national d'Histoire naturelle, Paris. *Geodiversitas* 32 (3): 399-415.

SCHWEITZER C. E., FELDMANN R. M. & KARASAWA H. 2012. — *Treatise Online, Number 51. Part R, Revised, Volume 1, Chapter 8M: Systematic descriptions: Infraorder Brachyura, Section Dromiacea*: 1-43.

SCHWEITZER C. E., FELDMANN R. M., GONZÁLES-BARBA G. & VEGA F. J. 2002. — New crabs from the Eocene and Oligocene of Baja California Sur, Mexico and an assessment of the evolutionary and paleobiogeographic implications of Mexican fossil decapods. *Paleontological Society, Memoir 59* (Supplement to No. 76): 1-43.

SCHWEITZER C. E., FELDMANN R. M., A. GARASSINO A., KARASAWA H. & SCHWEIGERT G. 2010. — Systematic list of fossil decapod crustacean species. *Crustaceana Monographs* 10: 1-221.

SCHWEITZER C. E., FELDMANN R. M., LAZăR I., SCHWEIGERT G. & FRANţESCU O. D. 2018. — Decapoda (Anomura; Brachyura) from the Late Jurassic of the Carpathians, Romania. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 288: 307-341.

SCHWEITZER C. E., FELDMANN R. M., FAM J., HESSIN W. A., HETRICK S. W., NYBORG T. G. & ROSS R. L. M. 2003. — *Cretaceous and Eocene Decapod Crustaceans from Southern Vancouver Island, British Columbia, Canada*. NRC Research Press Canada, Ottawa, Ontario: 66 p.

SIMPSON G. G. 1961. — *Principles of Animal Taxonomy*, Columbia University Press, New York, xii + 247 p.

ŠTEVCIć Z. 1973. — The systematic position of the family Raninidae. *Systematic Zoology* 22: 625-632.

TAVARES. M. & SANTANA W. 2015. — A new genus and two new species of hymenosomatid crabs (Crustacea: Brachyura: Hymenosomatidae) from the southwestern Atlantic and eastern Australia. *Zootaxa* 3905 (1): 91-106.

TEODORI D., OSSO À., NYBORG T. & VEGA F. 2013. — The Icriocarcinidae (Brachyura, Portunoidea), a widely distributed family during the latest Cretaceous times, *in* KROBICKI M. (ed.), *5th Symposium on Mesozoic and Cenozoic Decapod Crustaceans*, Kraków, Poland. Abstract Book. Polish Geological Institute, National Research Institute, Warszawa: p. 72.

TSANG L. M., CHAN T. Y., AHYONG S. & CHU K. H. 2011. — Hermit to king, or hermit to all: multiple transitions to crab-like forms from hermit crab ancestors. *Systematic Biology* 60 (6): 616-629.

TSANG L. M., SCHUBART C. D., AHYONG S. T., LAI J., AU E., NG P. K. L, CHAN T. Y. & CHU K. H. 2014. — Evolutionary history of the true crabs (Crustacea, Decapoda, Brachyura), including the origin of the freshwater crabs. *Molecular Phylogenetics and Evolution* 31: 1173-1187.

TUDGE C. C., SCHELTINGA D. M., JAMIESON B. G. M., GUINOT D. & RICHER DE FORGES B. 2014. — Comparative ultrastructure of the spermatozoa of the Majoidea (Crustacea, Decapoda, Brachyura) with new data on six species in five genera. *Acta Zoologica* 95: 1-20.

VALENTIN X., GOMEZ B., DAVIERO-GOMEZ V., CHARBONNIER S., FERCHAUD P., KIREJTSHUK A. G., LICHT A., NERAUDEAU D., VULLO R. & GARCIA G. 2014. — Plant-dominated assemblage and invertebrates from the lower Cenomanian of Jaunay-Clan, western France. *Comptes Rendus Palevol* 13 (5): 443-454.

VAN BAKEL B. W. M., GUINOT D., ARTAL P., FRAAIJE R. H. B. & JAGT J. W. M. 2012. — A revision of the Palaeocorystoidea and the phylogeny of raninoidian crabs (Crustacea, Decapoda, Brachyura, Podotremata). *Zootaxa* 3215: 1-216.

VAN STRAELEN V. 1925. — Contribution à l'étude des Crustacés décapodes de la période jurassique. *Mémoires de l'Académie Royale de Belgique, Cl. Sci. series 2*, 7: 1-462, pls 1-10.

VAN STRAELEN V. 1933. — Sur des Crustacés Décapodes Cénozoïques du Venezuela. *Bulletin du Musée royal d'Histoire naturelle de Belgique* 9 (10): 1-14.

VAN STRAELEN V. 1936. — Sur quelques crabes du Sahélien moyen des environs d'Oran (Algérie). *Bulletin de la Société géologique de France* (5) 6: 473-480.

VEGA F. J. & FELDMANN R. M. 1992. — Occurrence of *Costacopluma* (Decapoda: Brachyura: Retroplumidae) in the Maastrichtian of southern Mexico and its paleobiogeographic implications. *Annals of Carnegie Museum* 61: 133-152.

VEGA F. J., FELDMANN R. M. & SOUR-TOVAR F. 1995. — Fossil crabs (Crustacea: Decapoda) from the Late Cretaceous Cárdenas Formation, East-Central Mexico. *Journal of Paleontology* 69 (2): 340-350.

VEGA F. J., ÁLVAREZ F. & CARBOT-CHANONA G. 2007a. — Albian penaeoidea [*sic*] (Decapoda: Dendrobranchiata) from Chiapas, Southern Mexico. *Memorie della Societá Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 35 (2): 6-8.

VEGA F. J., JACKSON J. & OSSÓ À. 2014. — Exceptional preservation of a late Cenomanian (Late Cretaceous) crab from Texas, U.S.A. *Boletín de la Sociedad Geológica Mexicana* 66 (1): 1-7.

VEGA F. J., BRUCE N. L., SERRANO L., BISHOP G. A. & PERRILLIAT M. D. C. 2005. — A review of the Lower Cretaceous (Tlayúa Formation: Albian) Crustacea from Tepexi de Rodríguez, Puebla, Central Mexico. *Bulletin of the Mizunami Fossil Museum* 32: 25-30.

VEGA F. J., GARCÍA-BARRERA P., PERRILLIAT M. DEL, C., COUTIÑO M. A. & MARIÑO-PÉREZ R. 2006b. — El Espinal, a new plattenkalk facies locality from the Lower Cretaceous Sierra Madre Formation, Chiapas, southeastern Mexico. *Revista Mexicana de Ciencias Geológicas* 23 (3): 323-333.

VEGA F. J., AHYONG S. T., ESPINOSA B., FLORES-VENTURA J., LUNA L. & GONZÁLEZ-GONZÁLEZ A. H. 2018. — Oldest record of Mathildellidae (Crustacea: Decapoda: Goneplacoidea) associated with Retroplumidae from the Upper Cretaceous of NE Mexico. *Journal of South American Earth Sciences* 82: 62-75.

VEGA F. J., NYBORG T., ROJAS-BRICEÑO A., PATARROYO P., LUQUE J., PORRAS-MUZQUIZ H. & STINNESBECK W. 2007b. — Upper Cretaceous Crustacea from Mexico and Colombia: similar faunas and environments during Turonian times. *Revista Mexicana de Ciencias Geológicas* 24: 403-422.

VEGA F. J., PHILLIPS G. E., NYBORG T., FLORES-VENTURA J., CLEMENTS D., ESPINOSA B. & SOLIS-PICHARDO G. 2013. — Morphology and size variation of a portunoid crab from the Maastrichtian of the Americas. *Journal of South American Earth Sciences* 47: 116-135.

VEGA F. J., NYBORG T., KOVALCHUK G., LUQUE J., ROJAS-BRICEÑO A., PATARROYO P., PORRAS-MUZQUIZ H., ARMSTRONG A., BERMUDEZ H. & GARIBAY L. 2010. — On some Panamerican Cretaceous crabs (Decapoda: Raninoida). *Boletín de la Sociedad Geológica Mexicana* 62 (2): 263-279.

VEHOF J., VAN DER MEIJ S. E. T., TÜRKAY M. & BECKER C. 2016. — Female reproductive morphology of coral-inhabiting gall crabs (Crustacea: Decapoda: Brachyura: Cryptochiridae). *Acta Zoologica* 97: 117-126.

VEHOF J., SCHOLTZ G. & BECKER C. 2017. — Morphology of the female reproductive system of three dorippid crabs (Crustacea: Decapoda; Brachyura: Dorippidae) and the role of accessory cuticle structures associated with seminal receptacles. *Invertebrate Biology* 136 (3): 271-289. DOI: 10.1111/ivb.12181

VEHOF J., SCHOLTZ G. & BECKER C. 2018. — *Paradorippe granulata* — a crab with external fertilization and a novel type of sperm storage organ challenges prévalent ideas on the evolution of reproduction in Eubrachyura (Crustacea: Brachyura: Dorippidae*). Athropod Structure & Development* 47: 82-90.

WEHNER G. 1988. — *Über die Prosoponiden (Crustacea, Decapoda) des Jura*. Inaugural-Dissertation zur Erlangung des Doktorgrades der Fakultät für Geowissenschaften der Ludwig-Maximilians-Universität zu München: 154 pp., 8 pls.

WILEY E. O. 198. — *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. John Wiley and Sons, New York: xv + 439 p.

WINDSOR A. M. & FELDER D. L. 2014. — Molecular phylogenetics and taxonomic reanalysis of the family Mithracidae MacLeay (Decapoda : Brachyua : Majoidea). *Invertebrate Systematics* 28: 73-145. DOI 10.1071/IS13011.

WINKLER N. 2012. —*Libanocaris annettae* nov. sp. (Crustacea: Dendrobranchiata: Penaeidae) from the Upper Jurassic Solnhofen Lithographic Limestones of Eichstätt. *Zitteliana* A 52: 59-65.

WOLFE J. M., BREINHOLT J. W., CRANDALL K. A., LEMMON A. R., MORIARTY LEMMON E., TIMM L. E., SIDDALL M. E. & BRACKEN-GRISSOM H. D. in press. — A phylogenomic framework, evolutionary timeline, and genomic resources for comparative studies of decapod crustaceans. DOI: 10.1101/466540

WRIGHT C. W. & COLLINS J. S. H. 1972. — British Cretaceous crabs. *Monograph of the Palaeontographical Society* London 126: 1-113, pls1-22.

FIGURE CAPTIONS

Fig. 1. — **A**, Location map of study area in Chiapas, southeastern Mexico (modified from The North America Tapestry of Time and Terrain, by Kate E. Barton, David G. Howell, José F. Vigil, at https://pubs.usgs.gov/imap/i2781/); **B**, Detailed map with location of El Chango Quarry, southwest of Tuxtla Gutiérrez, Chiapas State (from Google Earth Pro).

Fig. 2. — **A**, **B**, Outcrops of the Cintalapa Member of the Sierra Madre Formation at El Chango locality. **C**, **D**, Cupressaceae conifers. **E**, Angiosperm fruit. **F**, Unidentified bony fish. **G**, Bony fish, *Saurorhamphus* sp.; **H**, Bony fish, *Zoqueichthys carolinae* Alvarado-Ortega & Than-Marchese, 2012 (Teleostei, Acanthomorpha, Aipichthyoidea); **I**, Bony fish, *Unicachichthys multidentata* Díaz-Cruz, Alvarado-Ortega & Carbot-Chanona, 2016 (Teleostei, Euteleosteomorpha, Enchodontodei). Scale bars: C, D, G, H, 1 cm.

Fig. 3. — Crustaceans from El Chango Quarry, Cenomanian (A-D, shrimps; F-H, crabs). **A**, *Zoquepenaeus spinirostratus* Garassino, Vega, Calvillo-Canadell, Cevallos-Ferriz and Coutiño, 2013. **B**, *Tzeltalpenaeus exilichelatus* Garassino, Vega, Calvillo-Canadell, Cevallos-Ferriz & Coutiño, 2013. **C**, *Mexicania grijalvaensis* Garassino, Vega, Calvillo-Canadell, Cevallos-Ferriz & Coutiño, 2013. **D**, *Mokaya changoensis* Garassino, Vega, Calvillo-Canadell, Cevallos-Ferriz & Coutiño, 2013. **E**, undetermined Palinuridae Latreille, 1802. **F**, undetermined cenomanocarcinid (podotreme crab, Cenomanocarcinidae Guinot, Vega & Van Bakel, 2008); **G**, **H**, undetermined ?Tepexicarcinidae Luque, 2015 (Eubrachyura): dorsal (F, G) and ventral (H) views. Scale bars: A-D, F-H: 1 cm.

Fig. 4. — Stratigraphic section of the Sierra Madre Formation, showing relative position of deposits that crop out at El Chango, sedimentological structures and fossil distribution.

Fig. 5. — *Archaeochiapasa mardoqueoi* n. gen., n. sp., holotype, male Chiapas, El Chango Quarry, lower Cenomanian Cintalapa Member of the Sierra Madre Formation (IHNFG-5616). **A**, specimen whitened with ammonium chloride; **B**, specimen submerged in water. See first three dorsally positioned pleonal somites, extremely long P2, P3, and a reduced last pereiopod, P4 or P5. Scale bar: A, B, 0.5 cm.

Fig. 6. — *Archaeochiapasa mardoqueoi* n. gen., n. sp. holotype, male (IHNFG-5616). **A**, specimen photographed *in situ* at El Chango Quarry; **B-D**, steinkern (counterpart): B, illuminated with oblique yellow light; C, illuminated with incident light and coated with ammonium chloride; D, illuminated with oblique, blue light and submerged in water. Scale bars. A, 1 cm; B-D, 5 mm.

Fig. 7. — *Archaeochiapasa mardoqueoi* n. gen., n. sp., Chiapas, El Chango Quarry, lower Cenomanian Cintalapa Member of Sierra Madre Formation, G. Carbot-Chanona coll., holotype, male, 10.3 x 11.1 mm (IHNFG-5616): dorsal view, with proximal part of pleon (actually a1-a3) dorsally visible. **a1**, pleonal somite 1; **fl**, flange; **p.c.**, concave posterior border of carapace; **r**, thickened carapace border. Scale bar: 5 mm.

Fig. 8. — *Archaeochiapasa mardoqueoi* n. gen., n. sp., male 10.3 x 11.1 m, holotype (IHNFG-5616): superposition of the decorticated crab carapace and the counterpart with cuticle to show ornamentation of dorsal surface. **fl**, flange. Scale bar: 5 mm.

Fig. 9. — *Archaeochiapasa mardoqueoi* n. gen., n. sp., male 10.3 x 11.1 m, holotype (IHNFG-5616. **A**, close-up of front and rostrum; **B**, close-up of posterior portion of carapace. **p.c.**, concave posterior border of carapace; **P**, reduced P4 or P5; **a1-a3**, pleonal somites 1-3; **ro**, rostrum. Scale bars: A, 2 mm; B, 2,5 mm.

Fig. 10. — *Archaeochiapasa mardoqueoi* n. gen., n. sp., male 10.3 x 11.1 m, holotype (IHNFG-5616). **A**, close-up of mxp3, with developed exopodite; **B**, **C**, left and right chelipeds. **ex**, exopodit; **i**, endopodite ischion; **m**, endopodite merus; **t.s.**, thoracic sternum. Scale bars: A, 1 mm; B, C: 2 mm.

Fig. 11. — *Archaeochiapasa mardoqueoi* n. gen., n. sp., male 10.3 x 11.1 m, holotype (IHNFG-5616): thoracic sternum and pleon. **a4-a6**, pleonal somites 4-6; **t**, telson; **3-8**, thoracic sternites 3-8; **4/5, 5/6/, 7/8**, sternal sutures 4/5, 5/6/, 7/8. Scale bar: 3 mm.

Fig. 12. — *Archaeochiapasa mardoqueoi* n. gen., n. sp., male 10.3 x 11.1 m, holotype (IHNFG-5616): close-up of pleon. **A**, first three somites (a1-a3) in dorsal position; **B**, last somites plus telson; **C**, close-up of posterior portion of carapace, with first three pleonal somites and reduced P4 or P5. **a1-a3**, pleonal somites a1-a3 in dorsal position; **a4-a6**, pleonal somites 4-6, ventrally folded; **b.p.**, location of pleonal socket covering sternal press-button; **fl**, flange; **r**, thickened carapace border; **t**, telson. Scale bars: A, 2 mm; B, 1 mm; C, 3 mm.

Fig. 13. — Lecythocaridae Schweitzer & Feldmann, 2009 (Glaessneropsoidea Patrulius, 1959). **A**, *Lecythocaris paradoxa* (von Meyer, 1858), Oberjura-Massenkalke Formation, late Jurassic, latest Kimmeridgian, Beckeri Zone, Oerlinger Tal near Ulm, Germany: cast of neotype, 5.5 x 5.2 mm (GPIT/58/26/11). **B**, *Prolecythocaris hauckei* Schweigert & Robins, 2016, early Kimmeridgian, Arzbzeg Formation, Hypselocyclum Zone, Titting, Bavaria, Germany: holotype 3.6 x 4.0 mm, in cuticle preservation (SMNS 70326/1) (see Schweigert & Robins 2016: fig. 2C, A, respectively); **C**, *Prolecythocaris rieberi* Schweigert, 2019, Upper Jurassic, Oberjura-Massenkalk Formation, late Kimmeridgian, Acanthicum Zone, Donzdorf, southwestern Germany: holotype, 3.6 x 4.0 mm (SMNS 70451) (Schweigert 2019: fig. 2A): see the inflated subhepatic regions. **p.c.**, concave posterior border of carapace; **fl**, flange. Scale bars: A-C, 2 mm. All photographs by Günter Schweigert and courtesy of G. Schweigert.

Fig. 14. —Dorippidae MacLeay, 1838 (Dorippoidea MacLeay, 1838). *Medorippe lanata* (Linnaeus, 1767), male, Mediterranean Sea (MNHN, skeleton prepared by S. Secretan): thoracic sternum, without pleon. **b.p**., press-button located in curved sternal suture 4/5; **cx1**, **cx5**, P1, P5 coxae; **G1, G1**, first and second gonopods; **j**, sternum/pterygostome junction; **m.o**., Milne Edwards opening as pterygostomial slit; **p**, perforation at the ends of sternal suture 3/4; **3-8**, thoracic sternites 3-8; **3/4-6/7**, sternal sutures 3/4-6/7. Scale bar: 1 cm. Photography by Barry van Bakel and courtesy of B. van Bakel.

Fig. 15. — Telamonocarcinidae Larghi, 2004 (Dorippoidea MacLeay, 1838): thoracic sternum of *Telamonocarcinus gamabalatus* Larghi, 2004, Sannine Formation, Cenomanian, Hadjoula, Lebanon (AO467, Private Collection Àlex Ossó). Photography by Àlex Ossó and courtesy of À. Ossó.

Fig. 16. — Inachoididae Dana, 1851 (Majoidea Samouelle, 1819). **A**, *Paulita tuberculata* (Lemos de Castro, 1949) (Inachoididae), male 19.1 x 19.7 mm, French Guiana, Durand coll. 1958, IU-2017-8286 (= MNHN-B19506): carapace (modified, after Guinot 2012: fig. 2A). **B**, *Paradasygyius depressus* (Bell, 1835), male,

México, Bahía Santa Inés, M. E. Hendrickx det. and leg. 1988, IU-2017-8270 (= MNHN-B20818): thoracic sternum (after Guinot 2012: fig. 3C); **C,** *Paulita tuberculata* (Lemos de Castro, 1949), male 21.0 x 21.8 mm, French Guiana (MNHN-B19509): carapace, ventral anterior view (after Guinot 2012: fig. 2B). **a1**, first pleonal somite; **cx1**, **cx5**, P1, P5 coxae; **p**., exposed pleurites; **e5–e8**, exposed pleurites 5–8; **j**, thoracic sternum/pterygostome junction; **M.o.,** Milne Edwards openings; **pt**, pleotelson (somite 6 fused to telson); **3-8**, thoracic sternites 3-8; **3/4-7/8**, sternal sutures 3/4-7/8.

Fig. 17. — Retroplumidae Gill, 1894 (Retroplumoidea Gill, 1894). *Costacopluma maroccana* Ossó-Morales, Artal & Vega, 2010, Calcaires à slumps de Taghit Formation, late Campanian, Merija**,** Morocco: thoracic sternum and pleon. **4-7**, thoracic sternites 4-7; **3/4-6/7**, sternal sutures 3/4-6/7 (AO39, Private Collection Àlex Ossó). Scale bar: 10 mm. Photography by Àlex Ossó and courtesy of À. Ossó.

Fig. 18. — Hymenosomatidae MacLeay, 1838 (Hymenosomatoidea MacLeay, 1838). **A**, generalised hymenosomatid based on *Halicarcinus cookii* (Filhol, 1885) (modified, after Melrose 1975: fig. 1); **B**, *Trigonoplax unguiformis* (De Haan, 1839), Japan: thoracic sternum (much widened) of 3rd young stage crab (modified, after Fukuda 1981: fig. 3D): **C,** *Halicarcinus planatus* (Fabricius, 1775), IU-2014-11916 (= MNHN-B25960): thoracic sternum (modified, after Guinot 1979: fig. 30A). **c.ca.cx1**, arthrodial cavity of P1 coxa; **cx5**, P5 coxa; **r.**, hymenosomian rim; **mxp3**, external maxillipeds; **b.p.**, location of press-button for pleonal locking; **r**, hymenosomian rim, all around carapace margin; **1-8**, thoracic sternites 4-7; **3/4-7/8**, sternal sutures 3/4-7/8.