

New crabs (Crustacea, Decapoda) from the Upper Cretaceous (Campanian) of the Moyenne Moulouya, northeast Morocco

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ABSTRACT

The presence of the genera Costacopluma and Ophthalmoplax in Upper Cretaceous (Campanian) Moroccan strata is documented on the basis of specimens collected from the Calcaires à slumps de Taghit Formation, Moyenne Moulouya (Morocco). Two new species are described, Ophthalmoplax minimus and Costacopluma maroccana. The first record for Ophthalmoplax in the west Tethyan realm is reported, and systematic affinities of this genus and its species are discussed. An absolute age of the late Campanian was obtained for this assemblage from ⁸⁷Sr/⁸⁶Sr analysis applied to well preserved cuticle calcitic remains of Ophthalmoplax minimus. Costacopluma maroccana represents the 14th species for this genus and the fourth Cretaceous species. Its morphology reinforces hypothesis of two main phyletic groups for this genus.

Key words: Crustacea, Decapoda, Ophthalmoplax, Costacopluma, Campanian, Morocco.

RESUMEN

Se documenta la presencia de los géneros Ophthalmoplax y Costacopluma con base en especímenes recolectados en sedimentos del Cretácico Superior (Campaniano) de la Moyenne Moulouya (Marruecos). Se describen dos nuevas especies: Ophthalmoplax minimus y Costacopluma maroccana. Se identifica y localiza (por primera vez en la parte occidental del dominio del Tethys) el género Ophthalmoplax, discutiéndose las afinidades sistemáticas de este género y sus especies. A partir de análisis del ⁸⁷Sr/⁸⁶Sr; practicados en restos calcíticos de cutícula bien preservada del Ophthalmoplax minimus, se ha obtenido la edad absoluta, datándose los restos como pertenecientes al Campaniano tardío. Costapluma maroccana representa la especie número 14 de este género y la cuarta para el Cretácico. Sus características morfológicas refuerzan la hipótesis de la existencia de dos grupos filéticos para este género.

Palabras clave: Crustacea, Decapoda, Ophthalmoplax, Costacopluma, Campaniano, Marruecos.

INTRODUCTION

Formal reports on fossil decapod crustaceans from Africa are very scarce, in particular those from Morocco (Secretan, 1961; Garassino *et al.*, 2007). The present study is a contribution to the systematic, paleobiogeographic and evolutionary knowledge of Late Cretaceous decapod crustaceans from the Tethyan realm, and documents the presence of *Ophthalmoplax* Rathbun, 1935, previously considered as an exclusively Pan-American genus. Our knowledge on the distribution patterns, endemism and origins of crustacean decapod taxa is expanding rapidly, and drastic changes are being experienced in the way we understand the evolution of this interesting group. The Ibericancridae Artal, Guinot, Van Bakel and Castillo, 2008, a new brachyuran family closely related with what was once considered an exclusively American group (Dakoticancridae Rathbun, 1917, see Bishop *et al.*, 1998), was recently reported for the upper Campanian of Spain (Artal *et al.*, 2008).

The crustaceans herein described were collected from the Calcaires à slumps de Taghit Formation that crops out near to the village of Merija, between the cities of Missour

and Talsint in northeast Morocco, within the Plis Marginaux at the Moyenne Moulouya region (Figures 1 and 2). The Calcaires à slumps de Taghit Formation was established for the zone situated between Tizi Zaoumit and Ras Rcheg, with a range of Coniacian-Campanian; it overlies the Calcaires de Tizi Zaoumit Formation, which comprises the Cenomanian-Turonian interval (Charroud, 2002) (Figure 3). The fossiliferous outcrops consist of yellow calcareous marls with scarce macrofauna (Figure 4). Complete absence of index fossils (microfossils, ammonoids, rudists, etc.) makes it difficult to define a biostratigraphic age. However, studies on the stratigraphy and general geology from nearby areas (Enßlin, 1993; Charroud, 2002; Haddoumi *et al.*, 2008) indicate an Upper Cretaceous sedimentary sequence for the regional lithostratigraphic units. With the aim to resolve the chronological uncertainty of the strata where the fossil crustaceans were found, we obtained $^{87}\text{Sr}/^{86}\text{Sr}$ isotopic analyses on carapace fragments of *Ophthalmoplax minimus* new species. The carapace fragments were extracted by handpicking and its chemical composition was analyzed by X-ray diffraction at the Laboratorio de Difracción de Rayos X, Instituto de Geología, UNAM,

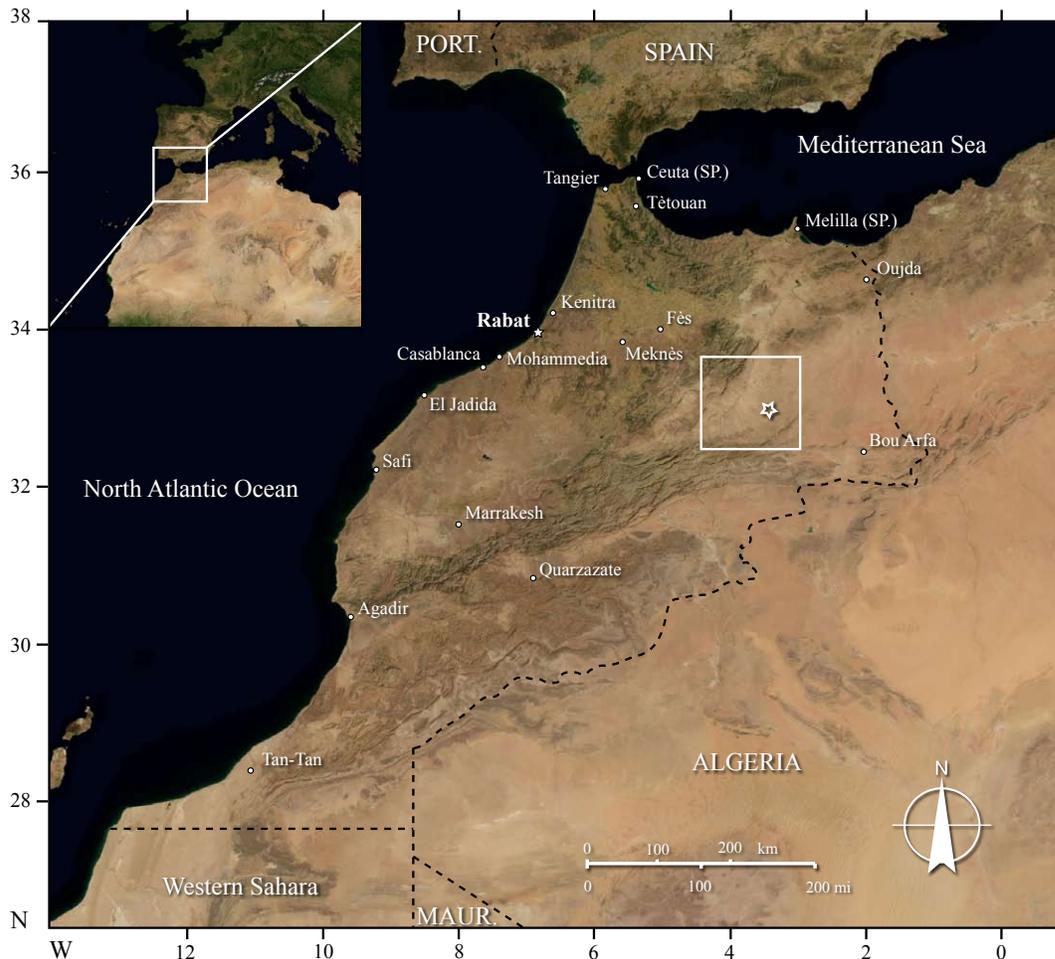


Figure 1. Location map on northwest Africa, Morocco. Rectangle area with star correspond to Figure 2.

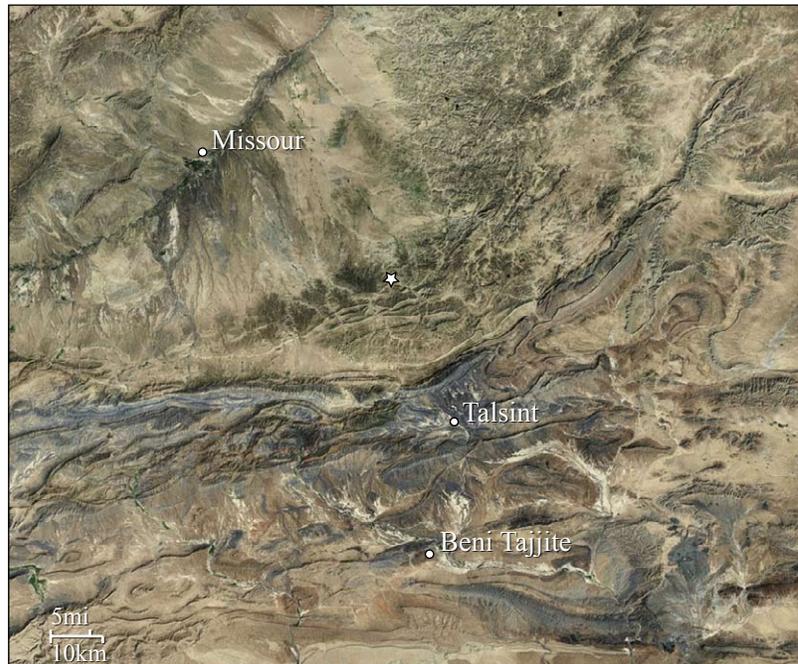


Figure 2. Location map of fossil locality (star) at Plis Marginaux at the Moyenne Moulouya area, northeast Morocco.

with a result of 100% calcite. The calcite is considered to be of primary origin based upon its mineralogy and textural preservation. The measurement of the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio was made by mass spectrometry with a thermal ionisation mass spectrometer Finnigan MAT 262, after acid digestion and cation exchange separation, all processed at the Laboratorio Universitario de Geoquímica Isotópica, Instituto de Geología, UNAM. We obtained a value of $^{87}\text{Sr}/^{86}\text{Sr} = 0.707595 \pm 0.000028$ (one standard deviation) for a run of 58 measurements. By comparison with the $^{87}\text{Sr}/^{86}\text{Sr}$ seawater curve for the Late Cretaceous–Paleogene (McArthur and Howarth, 2004), the obtained isotopic ratio corresponds to an age of the late Campanian (approximately 76 Ma; Figure 5).

The associated fauna includes small oysters and echinoids, mainly *Goniopygus* sp. and *Mecaster fourneli* Deshayes, in Agassiz and Desor, 1847. *Goniopygus* has been usually assigned to *Goniopygus durandi* in Cotteau, Peron and Gauthier, 1881 (Petitot, 1959), but the current attribution of this species has been questioned (Gallemí, pers. comm.). The presence of oysters and echinoids, together with the eustatic conditions for the Upper Cretaceous deposits, suggests a shallow marine environment from the Coniacian to the Campanian in the study area. Previous studies suggest a markedly regressive cycle, and the connection to an Atlantic realm more than a Tethyan influence (Charroud, pers. comm.).

Specimens are deposited in the paleontological collection of the Museo Geológico del Seminario de Barcelona, under acronym MGSB, and in the Museo Civico di Storia Naturale di Milano, under acronym MSNM.

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1802
 Infraorder Brachyura Latreille, 1802
 Superfamily Portunoidea Rafinesque, 1815
 Family Macropipidae Stephenson and Campbell, 1960
 Genus *Ophthalmoplax* Rathbun, 1935

Type species. *Ophthalmoplax stephensoni*, Rathbun, 1935, by original designation.

Ophthalmoplax minimus new species

Figure 6

Diagnosis. Carapace small, transversely subtrapezoidal in outline, orbito-frontal margin large, with triangular supramarginal spines fairly directed upwards; dorsal surface longitudinally convex, somewhat less in transverse section; orbits large; front relatively narrow, strongly deflexed, with robust, salient orbital nodes and bifid tip; lateral margins of carapace arched, with stout spines; dorsal surface bearing acute transverse ridges on gastric, branchial and cardiac regions; stenum large, subcircular, with sternite 3 extending laterally; male abdomen not totally covering sternites 7 and 8; eyestalks long, chelipeds large, with short spines on ventral and dorsal margins of palm; palm ridged on lateral surface.

Etymology. From the latin *minimus*, in reference to the reduced size of carapaces, compared with the large size in other species.

Description. Carapace small to medium in size, transversely

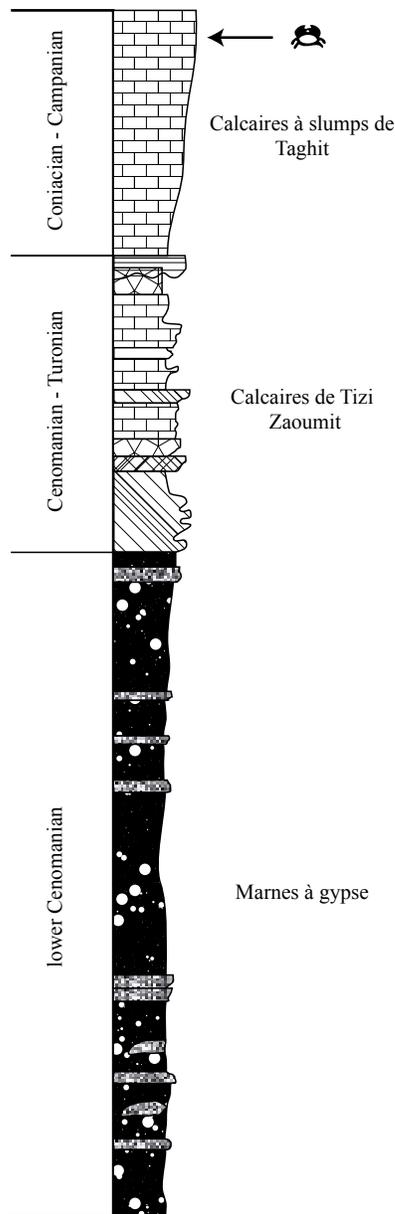


Figure 3. Stratigraphic units that crop out in the study area, including the position of level with crustaceans. No vertical scale. Modified after Charroud, 2002.

subtrapezoidal in outline, somewhat broader than long, maximum width at the level of epibranchial region; dorsal surface fairly convex in longitudinal section. Orbito-frontal margin notably large, bearing a reduced fissure with angular marginal corners and a subtriangular tooth markedly directed upwards, close to the outer orbital spines which are stout, robust, with triangular base. Front relatively narrow, deflexed, with salient orbital nodes and bifid termination. Anterolateral margins short, slightly concave, with cervical notch. Posterolateral margins longer, arched, bearing four large spines or tubercular nodes, and two additional smaller ones between first and second spines. Posterior margin noticeably shorter than orbito-frontal margin, straight, weakly

rimmed. Swellings and furrows define dorsal regions of carapace. Mesogastric region large, subpentagonal, with anterior process narrow, long bounded by weak furrows; ridge at medial portion. Protogastric lobes large, inflated, with transverse ridge. Epigastric lobes small, defined by two small swellings. Anterior epibranchial lobes slightly inflated, leading to a robust marginal spine, posterior lobes inflated, oblique, axially bounded by branchiocardiac furrow. Mesobranchial regions large, with two marginal nodes and short transverse ridges. Metabranchial regions small, with short transverse crest. Cardiac region large, inverted subpentagonal in shape; medial ridge, protuberance present at lower corner. Intestinal region depressed. Pterygostomial regions small, subtriangular, rimmed. Buccal frame large. Sternum large, subcircular. Sternites 1-2 subtriangular, small. Sternite 3 salient, extending laterally, axially depressed. Small notch separating sternites 3 from 4. Sternite 4 with raised oblique margins. Sternites 5 to 7 decreasing in size posteriorly, with long episternites directed backwards. Abdomen sexually differentiated. Narrow in males, subtriangular, not totally covering sternites 7-8; telson triangular; pleomere 6 subtrapezoidal; pleomere 5 subsquare, as wide and long as pleomere 6; pleomere 4 subrectangular elongated, slightly shorter and narrower than pleomere 5, with median ridge; pleomere 3 broader, extending laterally. Broad, suboval abdomen in females; telson broad, subtriangular; pleomere 6 subtrapezoidal, one-third wider but one-fourth shorter than telson; pleomere 5 rectangular, one third the length and nearly as wide as pleomere 6, with median transverse ridge; pleomere 4 very similar to pleomere 5; pleomere 3 nearly as wide but slightly shorter than pleomere 4, concave on median portion of anterior margin, with median transverse ridge; pleomere 2 one-third narrower than pleomere 3, with median transverse ridge. Chelipeds robust, basis-ischium fused, merus robust and long with tubercles on inner surface; carpus with denticled surface, palm long, robust, outer surface medially ridged, margins profusely spinose; dactily spinose, with robust inner denticles; first tooth of mobile finger stout and extremely long on right cheliped. Pereiopods 2 to 5 long, flattened. Lateral surface covered by large, spaced granules.

Material. Holotype MSGB74546; paratypes MGSB74547a, MGSB74547b and MGSB74547c.

Measurements (in mm). Holotype MSGB74546, carapace length = 23, width = 26, orbito-frontal width = 25; paratypes MGSB74547a, carapace length = 21, width = 23, orbito-frontal width = 21; paratype MGSB74547b, carapace length = 31, carapace width = 33, orbito-frontal width = 30; MGSB74547c, carapace length = about 50.

Genus discussion. *Ophthalmoplax* has been reported from the Upper Cretaceous Atlantic and Gulf Coast of the SE of North America (South Carolina, Alabama, Mississippi, Texas, Coahuila, Nuevo León) (Rathbun, 1935; Stenzel, 1952; Vega and Feldmann, 1991, as *Mascaranada*; Schweitzer et al., 2007; Vega et al., 2007) and also from the Upper Cretaceous of South America (Colombia, Venezuela,

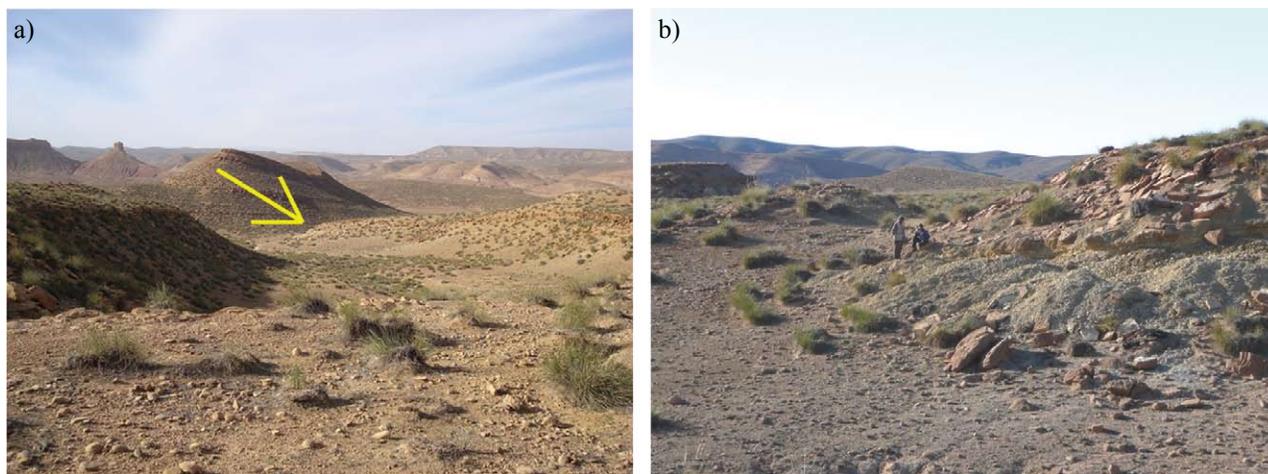


Figure 4. Fossiliferous beds of the Calcaires à slumps de Taghit Formation. a: Landscape of Moyenne Moulouya area. Arrow points at outcrop of next photograph. b: Outcrop from which crabs were collected.

Brazil) (Maury, 1930, as *Zanthopsis*; Beurlen, 1958; 1965 as *Archaeopus*; Feldmann and Villamil, 2002; Souza-Lima *et al.*, 2003; Aguilera *et al.*, 2010). Feldmann *et al.* (1999) described *Ophthalmoplax spinosus* from the Turonian of Colombia; however, Guinot *et al.* (2008) considered it to be *Cenomanocarcinus vanstraeleni* Stenzel, 1945. All of the stratigraphic occurrences for *Ophthalmoplax* in America correspond to Maastrichtian lithostratigraphic units, except for *O. triambonatus* Feldmann and Villamil, 2002 assigned to upper Turonian sediments of the Puerto Romero Formation in the north-central part of the Middle Magdalena River Valley, Colombia; in their report, Feldmann and Villamil (2002, p. 718) commented: “Baculitid ammonites encountered in association with the crab specimens are possibly of Maastrichtian age (Etayo, pers. comm.); however, baculites are poorly known for this region of South America and the age is not reliable”. Their interpretation for a Turonian age is then based on bivalves and foraminifera that suggest an age not younger than Coniacian; however, other foraminifera from the study section indicated a Campanian age (Feldmann and Villamil, 2002, p. 720). Nevertheless, other stratigraphic studies suggest a late Maastrichtian age for the Puerto Romero Formation (Vásquez *et al.*, 2000). A summary of current status of species described as *Ophthalmoplax* is presented in Table 1.

Schweitzer *et al.* (2007) considered the following species of *Ophthalmoplax*: *O. stephensoni* Rathbun, 1935; *O. brasiliensis* (Maury, 1930); *O. comancheensis* Rathbun, 1935; *O. triambonatus* Feldmann and Villamil, 2002; and questionably *O. spinosus* Feldmann *et al.* (1999). Similarities between *O. brasiliensis* and *O. triambonatus* were noticed by Feldmann and Villamil (2002, p. 273), and used differences in shape of carapace and degree of development of dorsal regions of carapace to define a new species. However, the sole type specimen of *O. triambonatus* is deformed, and thus differences observed may be result of such deformation. Large specimens of *O. stephensoni* from Maastrichtian

deposits of NE Mexico are under study, but show that such large forms of *Ophthalmoplax* were present in the Tethyan realm during Maastrichtian times. *Ophthalmoplax comancheensis* was described on the basis of small movable and fixed fingers that according to Rathbun (1935, p. 54) “...resemble those of *O. stephensoni* more than any other Cretaceous species”. Based on the stratigraphic occurrence of *O. comancheensis* in Albian deposits of Texas, Feldmann and Schweitzer (2006) considered an origin of this genus during the Early Cretaceous. Similarity with *Archaeopus rathbunae* Beurlen, 1965 from the Albian of Brazil and members of the Carcineretidae has been suggested (Vega and Feldmann, 1992). The inverted subtrapezoidal shape of the

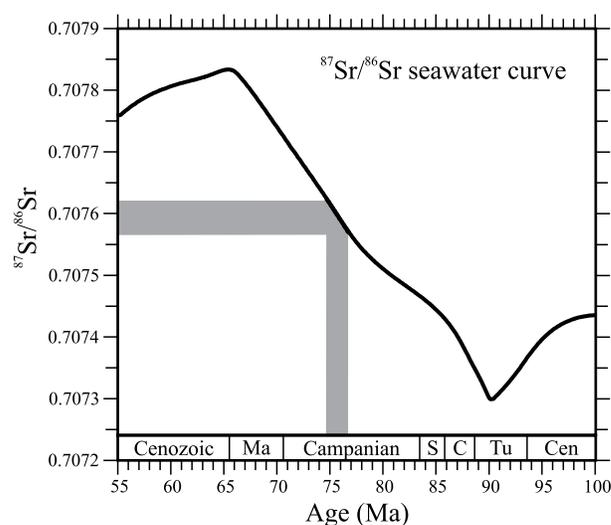


Figure 5. Curve of seawater strontium isotopic composition for the Late Cretaceous and Paleogene (after McArthur and Howarth, 2004). The grey bars indicate the $^{86}\text{Sr}/^{87}\text{Sr}$ ratio obtained for carapace fragments of *Ophthalmoplax minimus* new species and the corresponding late Campanian age. Sr isotopic ratios were measured by the method described in the text.

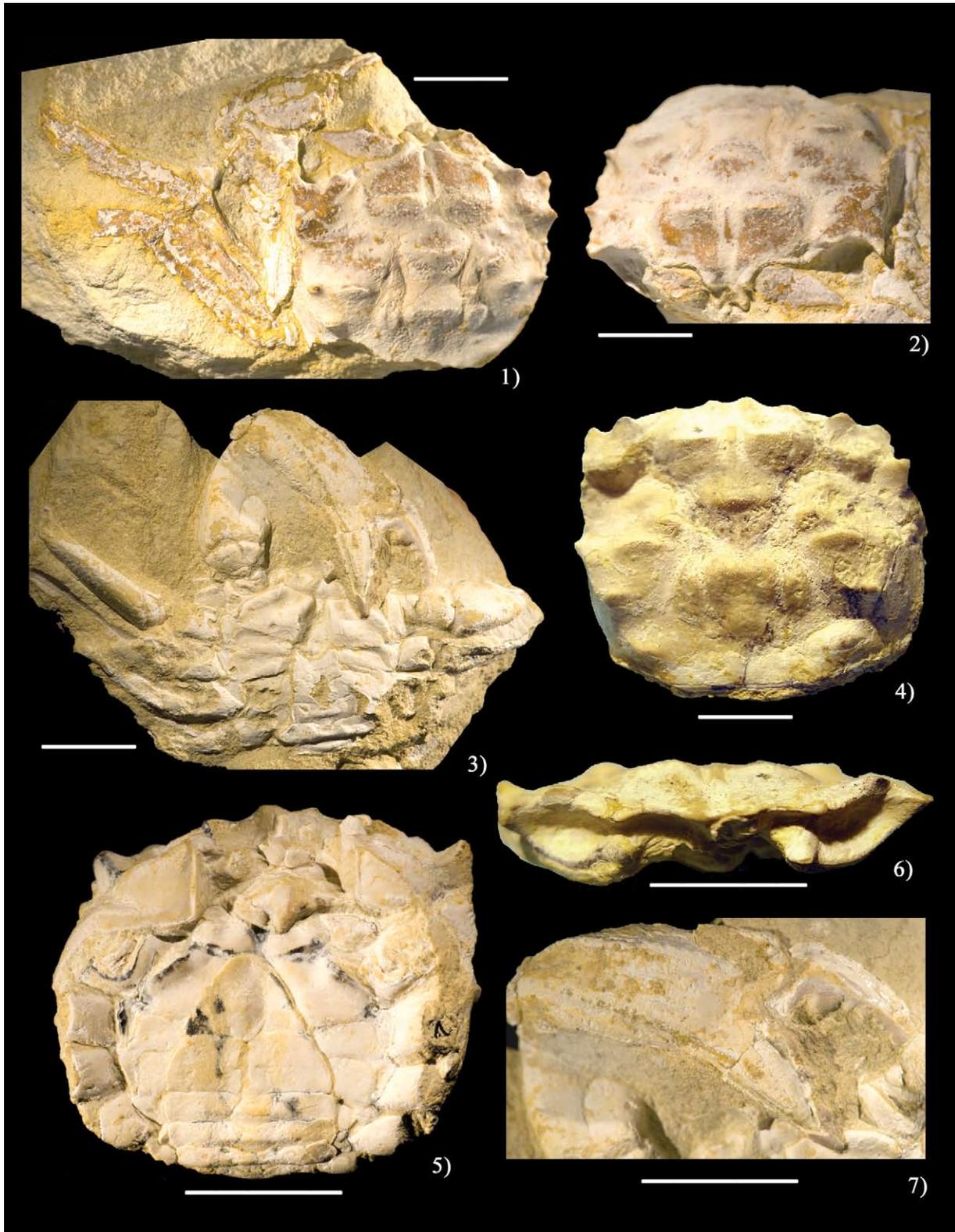


Figure 6. *Ophthalmoplax minimus* new species, Calcaires à slumps de Taghit Formation, upper Campanian, Morocco. 1: Holotype MGSB74546, dorsal view of carapace with left cheliped and pereopods; 2: Frontal view of carapace, same specimen; 3: Paratype MGSB74547c, ventral view of male carapace; 4: Paratype MGSB74547b, dorsal view of female carapace; 5: Ventral view of female carapace, same specimen; 6: Frontal view of female carapace, same specimen; 7: Paratype MGSB74547c, right chela of male specimen. Scale bar = 1 cm.

Table 1. Stratigraphic and geographic distribution of species of *Ophthalmoplax*, including current and suggested systematic status for each species.

Species	Age	Locality	Current/Suggested status
<i>Ophthalmoplax stephensoni</i>	Maastrichtian	SE USA	<i>Ophthalmoplax stephensoni</i>
<i>O. brasiliانا</i>	Maastrichtian	Brazil, Venezuela	<i>O. stephensoni</i>
<i>O. triambonatus</i>	Maastrichtian	Colombia	<i>O. stephensoni</i>
<i>O. spinosus</i>	Turonian	Colombia	<i>Cenomanocarcinus vanstraeleni</i>
<i>O. minimus</i>	Campanian	NW Africa	<i>Ophthalmoplax minimus</i>
<i>Mascaranada difuntaensis</i>	Maastrichtian	NE Mexico	<i>O. stephensoni</i>

carapace and the bifid rostrum resembles *Ophthalmoplax*, but the small size (18×15 mm) and the inclined epi- and mesobranchial ridges makes it different. The sharp, inclined ridges recall those of *Branchiocarcinus* Vega, Feldmann and Sour-Tovar, 1995, from the Maastrichtian of NE Mexico, but the epibranchial ridges are inclined in a different direction. A direct observation of the holotype is needed in order to define if “*Archaeopus*” *rathbunae* is the oldest representative of this carcineretid/portunid group.

Based on morphological similarities between *Ophthalmoplax* and *Bathynectes* Stimpson, 1871 and *Raymaninnus* Ng, 2000, genera of the Subfamily Polybiinae Ortmann, 1893, Schweitzer *et al.* (2007) removed *Ophthalmoplax* from the Carcineretidae Beurlen, 1930, to include it into the Portunidae. Later, Karasawa *et al.* (2008) included *Ophthalmoplax* into the Macropipidae. Although we agree in this systematic placement, there are some features to be discussed for a future review of the familiar affinity of *Ophthalmoplax*. Carapace morphology of the extant genera referred to the Macropipidae is not so similar to *Ophthalmoplax*, whose flattened fifth pereopods are most similar to members of the Portunidae Rafinesque, 1815. Also, *Bathynectes* and *Raymaninnus* have transverse dorsal ridges relatively similar to *Ophthalmoplax*, but their anterolateral margins bear two to four sharp spines, the orbits are smaller, rostrum with two sharp spines, female telson is smaller and triangular and the male abdomen wider at its base, among other differences. In commenting the systematic affinity of *Ophthalmoplax* to the Macropipidae, Karasawa *et al.* (2008, p. 102) stated: “The extinct members of the family form a remarkably homogenous group in terms of dorsal carapace morphology with the exception of *Ophthalmoplax*, the only Cretaceous form. However, the features of the male sternum and abdomen of *Ophthalmoplax* are remarkably congruent with those of the other members of the family.” In our opinion, the combination of a subtrapezoidal, flattened carapace, sharp transverse ridges on dorsal carapace, bifid rostrum, sharp, inclined outer orbital spine, male abdominal segments keeled, female abdominal segments smooth and spinose dorsal and ventral chelipeds margins may justify to keep *Ophthalmoplax* into a different subfamily. At this moment, we follow Karasawa *et al.* (2008), confirmed by a more recent classification (De Grave *et al.*, 2009) that place *Ophthalmoplax* as part of the Macropipidae.

Species discussion. *Ophthalmoplax minimus* new species differs from other species of the genus by the following combination of characters: smaller size of the carapace; outer orbital and anterolateral spines proportionally smaller; protogastric process stronger, dividing protogastric transverse ridge; cardiac ridge not so sharp; intestinal region clearly defined; male abdomen proportionally wider; and dorsal and ventral margins of chelae with not so developed sharp spines.

The late Campanian record of *O. minimus* new species may represent the oldest record for the genus, and suggest a possible African origin, with a westward migration across the proto-Atlantic, to rapidly spread along the northeast coast of South America and the southeast coast of North America. The absence of *Ophthalmoplax* in Maastrichtian sediments of southern Mexico and the Caribbean region may have been due to competition, habitat preference (most Maastrichtian deposits with decapod crustaceans in southern Mexico and the Caribbean are reefal, in contrast with the terrigenous deposits of SE North America and NE South America), preference for more temperate waters, or a combination of those elements.

Superfamily Retroplumoidea Gill, 1894
 Family Retroplumidae Gill, 1894
 Genus *Costacopluma* Collins and Morris, 1975

Type species. *Costacopluma concava* Collins and Morris, 1975, by original designation.

***Costacopluma maroccana* new species**
Figure 7

Diagnosis. Carapace of moderate size, transversely suboval to rounded subhexagonal in outline; wider at posterior half of the carapace; orbito-frontal margin long; front narrow, bifid, slightly to fairly downturned; orbit large; anterolateral margins very short; posterolateral margins longer, broadly arched; posterior margin wider than orbito-frontal margin; lateral flanks nearly at right angles from dorsal surface; dorsal surface bearing a set of transverse crests, with top of ridges from sharp to slightly rounded; dorsal regions swollen, ornamented with ridges; cervical furrow well-defined

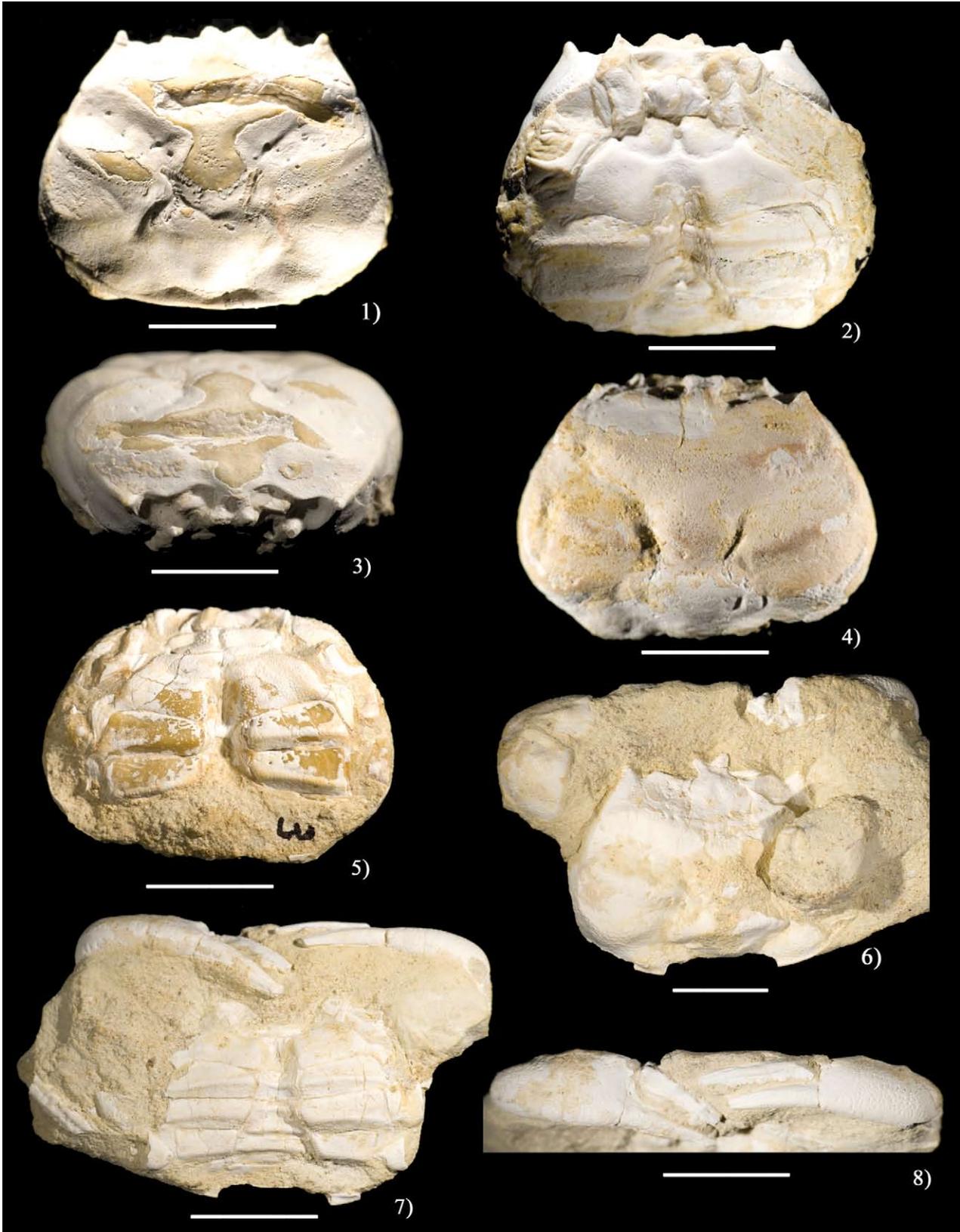


Figura 7. *Costacopluma maroccana* new species, Calcaires à slumps de Taghit Formation, upper Campanian, Morocco. 1: Holotype MGSB74544, dorsal view of carapace; 2: Ventral view of carapace, same specimen; 3: Frontal view of carapace, same specimen; 4: Paratype MGSB74545b, dorsal view of carapace; 5: Ventral view of carapace, same specimen; 6: Paratype MSNMi27216, dorsal view of carapace with right and left chelipeds; 7: Ventral view of carapace, same specimen; 8: View of right and left chelipeds, same specimen. Scale bar = 1 cm.

Table 2. Stratigraphic and geographic distribution of the two groups of species of *Costacopluma*. Group A is represented by species of small to medium size, with an ovate carapace shape, wider than long. Group B includes small species, with an inverted subtrapezoidal carapace.

Species	CRETACEOUS			PALEOGENE	
	Coniacian-Santonian	Campanian	Maastrichtian	Paleocene	Eocene
GROUP A	<i>Costacopluma bishopi</i>	Mexico			
	<i>C. concava</i>		Nigeria - India		
	<i>C. maroccana</i> n. sp.		Morocco		
	<i>C. mexicana</i>			Mexico	
	<i>C. grayi</i>				Alabama
	<i>C. senegalensis</i>				Senegal
GROUP B	<i>C. binodosa</i>		Greenland		
	<i>C. bifida</i>			Venezuela	
	<i>C. nordestiana</i>			Brazil	
	<i>C. australis</i>			Argentina	
	<i>C. salamanca</i>			Argentina	
	<i>C. texana</i>			Texas	
	<i>C. squiresi</i>			California	

at lateral margins; mesogastric region large, subrhomboidal in shape; protogastric lobes fairly swollen; cardiac region extremely large, subpentagonal inverted in shape; sternum broad, anterior portion (sternites 3-4) subtrapezoidal, posterior portion (sternites 5-7) transversely subrectangular, strongly ridged; oblique deep depressions separating sternite 3 from sternite 4; eyestalks long.

Etymology. Named after Maroc (Morocco), country of collection.

Description. Carapace of medium size for the genus, transversely suboval in outline, broader than long; dorsal surface convex in both directions, maximum width at the posterior half of the carapace, at level of postbranchial regions. Orbito-frontal margin long, with robust outer orbital spines directed forward; dorsal border sinuous, infraorbital margin terminating in long and conical spine. Eyestalk very long, slender, subcylindrical. Front relatively narrow, with bifid tip, downturned, lateral margins fairly concave, broadening distally to a two divergent rounded lobes. Anterolateral margins short, nearly straight. Cervical notch well-marked at lateral margins and sides of carapace. Posterolateral margins longer than anterolateral margins, broadly arched. Lateral sides (flanks of carapace) from extraorbital spine to posterior margin, situated at about right angles from dorsal surface. Posterior margin convex, with axial portion nearly straight, noticeably longer than orbito-frontal margin. Dorsal regions well defined by swellings and depressions, crossed by a set of three transverse crests. Anterior crest markedly sinuous, with convex lateral portions directed forwards and axial portion forwardly concave. Two median crests nearly straight, obliquely directed from lateral margins to branchiocardiac furrow, being fairly interrupted by mesogastric lobe. Posterior crest relatively well-defined by lateral branchial swellings and a transverse ridge in cardiac region. Mesogastric region large, subrhomboidal in shape, weakly separated from protogastric regions, bounded by

posterolateral deep furrows. Protogastric regions large, swollen, crossed by anterior crest. Small epigastric swellings present at base of front. Branchial regions fairly swollen. Cardiac region well-defined, large, subpentagonal inverted in shape, bounded by shallow but evident branchiocardiac furrow; median portion of cardiac lobe crossed by a strong transverse crest that may be more or less rounded or ridged by preservation/deformation, inferior portion bearing a small protuberance. Intestinal region depressed. Dorsal surface with numerous granules mainly at top of inflations of regions and densely pitted at depressions. Sternum large, anterior portion (sternites 3-4) subtrapezoidal, posterior portion (sternites 4-7) transversely subrectangular. Sternite 3 swollen, axially depressed, separated from sternite 4 by a weak notch and oblique depressions. Sternite 4 large with oblique margins, gynglyme for the first pereopod fairly re-entrant. Sternites 5 to 7 transversely disposed, strongly ridged, with spaced granules. Sternoabdominal cavity relatively deep, fairly narrow in males. Abdomen narrow in males, subtriangular in shape. All pleomeres free, with medial transverse ridges. Pleomere 6 with salient posterior portion for abdominal holding system. Telson slightly elongated, rounded distally. Buccal frame large; third maxiliped large. Chelipeds robust, palm relatively large, somewhat flattened dorsoventrally; dactyli long and slender, inner teeth robust. Merus short; carpus long, globular. Pereiopods 2 to 4 fairly long, flattened. Pereiopod 5 not seen.

Material. Holotype MGSB74544; paratypes MSGB74545a, MSGB74545b, MSNMi27216.

Measurements (in mm). Holotype MGSB74544, carapace length = 19, width = 23, orbito-frontal width = 14; paratypes MGSB74545a, carapace length = 15, width = 19, orbito-frontal width = 11; MGSB74545b, carapace length = 19, width = 25, orbito-frontal width = 15; MSNMi27216, carapace length = 19, width = 25, orbito-frontal width = 16.

Discussion. To the moment, 13 species of *Costacopluma*

have been reported from Upper Cretaceous and Paleogene sediments of America, Greenland, West Africa, India and Europe (Table 2). Most species are known from Paleogene deposits of Venezuela (*C. bifida* Collins, Higgs and Cortitula, 1994), Brazil (*C. nordestiana* Feldmann and Martins-Neto, 1995), Argentina (*C. australis* Feldmann, Casadio Chirino-Gálvez, and Aguirre-Urreta, 1995; *C. salamanca* Feldmann, Rodríguez, Marínez and Aguirre-Urreta, 1997), Senegal (*C. senegalensis* [Rémy in Gorodiski and Rémy, 1959]), Alabama (*C. grayi* Feldmann and Portell, 2007), Texas (*C. texana* Armstrong, Nyborg, Bishop, Ossó-Morales and Vega, 2009), California (*C. squiresi* Nyborg, Vega and Filkorn, 2009) and Hungary (*Costacopluma* sp. [Müller and Collins, 1991]). The first report for a Paleocene species from the Pacific slope has recently been published from California (Nyborg et al., 2009). It is interesting to note that all Paleocene species are of small size (about 1 cm in width), while Cretaceous species tend to be larger, with the exception of the Coniacian *C. bishopi* Vega and Feldmann, 1992, with a mean width of 4 mm and *C. binodosa* Collins and Rasmussen, 1992 from the Campanian of Greenland. Small size has been interpreted as a response to environmental stress (Fraaije et al., 2006; Armstrong et al., 2009). The origin and paleobiogeographic distribution patterns of *Costacopluma* are still a matter of debate. McLay (2006) suggested that only four species of *Costacopluma* should be considered true retroplumids. A discussion on interpretations of this author are given by other authors (Armstrong et al., 2009; Nyborg et al., 2009). It is important to note existence of two main morphologic groups that embrace all of the described species of *Costacopluma*. The first group (Group A, Table 2) includes species with an ovate carapace, comprising species from the Cretaceous to the Eocene of Africa and America, while second group (Group B, Table 2) includes species with a subhexagonal to inverted subtrapezoidal carapace, comprising only Paleocene species from America. A closer morphological study of all of the species within this genus is needed in order to define if it is pertinent to formally subdivide in these two groups all the species of *Costacopluma*. Presence of this genus in Campanian sediments of NW Africa is expected, on the basis of the occurrence of *C. concava* Collins and Morris, 1975 in the Maastrichtian of North India (Gaetani et al., 1983) and Coniacian to ?Maastrichtian (mostly Campanian) sediments of Nigeria (Collins and Morris, 1975, although no lithostratigraphic unit is mentioned by these authors, and recent regional stratigraphic reports must be reviewed in order to define the stratigraphic range for this species), and the presence of *C. senegalensis* in Paleocene strata of Senegal (Rémy in Gorodiski and Rémy, 1959). *Costacopluma maroccana* new species is most similar to *C. concava*, but the new species can be clearly distinguished by the following main features: a more inflated-globose general appearance; swollen and rounded ridges and regions (even the lateral margins); a broader posterior half of carapace, being more subhexagonal in *C. concava*; a

different orbito-frontal/width ratio, about 0.6 (about 0.5 in *C. concava*). *Costacopluma senegalensis* is smaller and ridges of the dorsal carapace are more slender, with coarser tubercles on crests. *Costacopluma bishopi* is much smaller and has an ovate shape of carapace, widest at midlength of the carapace. *Costacopluma mexicana* Vega and Perrilliat, 1989 has a similar shape of the carapace; however, crests of transverse ridges are typically flat, with strong tubercles, and the protogastric ridge is much more sinuous in the Mexican species. *Costacopluma grayi* is smaller, has narrow ridges on dorsal carapace with tubercles on crests. Remainder Paleocene species are the smaller, inverted subtrapezoidal carapace and ridges of the dorsal carapace are slender and have tubercles on crests.

CONCLUSIONS

The presence of *Ophthalmoplax minimus* new species in sediments of the Calcaires à slumps de Taghit Formation, Morocco, represents the oldest and the first record for the genus outside the Americas. $^{87}\text{Sr}/^{86}\text{Sr}$ analysis based on cuticle remains of *O. minimus* indicate a Campanian age for this lithostratigraphic unit. A second species, *Costacopluma maroccana* new species, is found associated with *O. minimus* and represents the second Cretaceous species for the genus in Africa, and confirm that *Costacopluma* was one of the most diverse brachyuran genus during the Late Cretaceous.

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