New Early Cretaceous shrimp (Decapoda) from the Sidi Aïch Formation of the Northern Chotts
Range, southern Tunisia: taxonomy, biostratigraphy, and palaeoenvironmental
implications

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Abstract

The fossil dendrobranchiate shrimp *Macropenaeus* was originally described from the Upper
Cretaceous (Cenomanian) limestones of Hadjoula, northwest Lebanon. A new species, *M.*
sidiaichensis sp. nov., was recovered from the Sidi Aïch Formation in the Northern Chotts Range,
southern Tunisia. The Barremian occurrence of the genus in Tunisia suggests that *Macropenaeus*
most likely originated in northern Africa and then migrated to Arabia in the Cenomanian. The

association of the fossil shrimp with conchostracans, plant fragments, and fish indicates the interaction of freshwater and marine conditions that characterized the northern African margin as part of widespread coastal complex, paralic environments during the Barremian.

Key words: Fossil shrimp, palaeoenvironment, Lower Cretaceous, Sidi Aïch Formation, Northern Chotts range, Southern Tunisia

1. Introduction

Since the 1950s, the main faunal and floral palaeontological discoveries in Tunisia have been from the Upper Jurassic to Upper Cretaceous sedimentary successions of the Tataouine Basin, southern Tunisia (**Fig.1A**). The Tataouine Basin has yielded Early Cretaceous fish, turtles, crocodiles, and dinosaur remains (Pervinquière, 1912; Lapparent and Taquet, 1966; Lapparent, 1951, 1960, 2000, 2002; Tlig, 1987; Bouaziz et al., 1988; Benton et al., 2000; Srarfi et al., 2004; Srarfi, 2006; Anderson et al., 2007; Cuny et al., 2010; Le Loeuff et al., 2010; Contessi and Fanti, 2012a, b; Fanti et al., 2012, 2014, 2016a, b). The key evolutionary position of some of the fossils, including titanosauriforms, makes this area one of the most important Mesozoic fossil sites in northern Africa, rivaling the much better known Jehol Biota (China), Santana Formation (Brazil), Tlayúa Formation (Mexico), and Solnhofen Lithographic Limestone and Posidonia Shale (Germany).

Lower to middle Cretaceous shallow marine and nonmarine fossils document various habitats, the most common of which are continental aquatic vertebrates (crocodiles, fish (*Lepidotes*, *Ceratodus*), and turtles. Putative marine vertebrates, elasmobranchs (*Hybodus*), osteichthyes (*Onchopristis*), and coelacanths (*Mawsonia*), are predecessors of forms inhabiting fresh water habitats in modern large equatorial or tropical rivers. Thus, both marine and

nonmarine organisms appear to represent a “mixed” Aptian-Albian macro and microfossil vertebrate assemblage (Bouaziz et al., 1988; Ben Ismail, 1991; Benton et al., 2000; Ouaja et al., 2002, 2004; Anderson et al., 2007; Cuny et al., 2010; Le Loeuff et al., 2010; Contessi and Fanti, 2012a, b; Fanti et al., 2012, 2014).

The Chotts-Gafsa Basin in the Southern Chotts Range (**Fig. 1B**) lies north from the Tataouine Basin. There, Lower Cretaceous (Aptian) strata have yielded an angiosperm flora (Barale and Ouaja, 2001). A number of large excavations were made in the Lower Cretaceous strata from southern Tunisia (particularly in the Tataouine Basin), which produced a huge number of macro and microfossil remains, but no preserved fossil shrimp were found. The present paper provides palaeontological and biostratigraphical analyses of shrimp collected from a new fossil site in the Northern Chotts Range yielding well preserved fossil fish, clam shrimp, shrimp, plants, and other organisms recently discovered in Lower Cretaceous siliciclastic sediments (**Fig. 1B**). This diverse fauna will permit reconstitution and understanding of the Early Cretaceous paralic sedimentary sequence in the Early Cretaceous system. Interpretation of this sequence has sparked a longstanding debate (Abdeljaouad and Zargouni, 1981; Abbès and Zargouni, 1986; M’Rabet, 1987; Abbès and Tlig, 1991; Gallala et al., 2009; Ouaja et al., 2011; Aloui et al., 2012; Gharbi et al., 2013). These faunal investigations are aimed at better understanding and reconstructing the Early Cretaceous ecosystems of the Chotts-Gafsa Basin (**Fig.1A**) and the taphonomic fate of their organisms.

2. Geological setting

2.1. Stratigraphy and age

Lying within the Chotts-Gafsa Basin, the Zimlet El-Beidha Anticline Structure (ZBAS) (**Fig. 1C**) constitutes the easternmost part of the Northern Chotts Range (**Fig. 1B**). The geological

age of the ZBAS ranges from Cretaceous to Quaternary. The Cretaceous rocks in the ZBAS (**Fig. 1C**) have been studied by numerous authors (Abdeljaouad and Zargouni, 1981; Abbès and Zargouni, 1986; Ben Youssef and Peybernes, 1986; M'Rabet, 1987; Abbès and Tlig, 1991; Louhaïchi and Tlig, 1993; Chaâbani and Razgallah, 2006; Lazzez and Ben Youssef, 2008; Lazzez et al., 2008; Gallala, 2009; Ouaja et al., 2011; Aloui et al., 2012; Gharbi et al., 2013; Boukhalfa et al., 2015; Li et al., 2017). The Cretaceous stratigraphic chart (**Fig. 2A**), a product of previous work in the Chotts B Lower Cretaceous deposits, documents three Lower Cretaceous formations, the Bouhedma, Sidi Aïch, and Orbata formations in ascending order (**Fig. 2B and C**).

The Bouhedma Formation (Burolet, 1956) is a 600 m succession considered Hauterivian–Barremian in age based on ostracod assemblages (Damotte et al., 1987; Damotte 1990; Chakhma et al., 1990).

Burolet (1956) named the Sidi Aïch Formation for a 120 m thick sequence at Jebel Sidi Aïch in the central Atlas Mountains of Tunisia. It consists of medium- to coarse-grained sandstone interbedded with siltstone layers that are exposed throughout the Chotts-Gafsa Basin. The Sidi Aïch Formation has been assigned a late Barremian age in the study area based on presence of the conchostracan, *Cratostracus? tunisiaensis* Boukhalfa, Li, Ben Ali, and Soussi, 2015, described from the Northern Chotts Range at the Zimlet El-Beidha Anticline Structure. The age of *C.? tunisiaensis* was based on it being congeneric with forms in China (Boukhalfa et al., 2015)

The Orbata Formation was named by Burolet (1956). Stratigraphic work (Bismuth et al. 1981; Ben Youssef et al. 1985; Ben Youssef and Peybernes 1986; Abdallah, 1987; M'Rabet, 1987; Chaâbani et al., 1992; Chaâbani and Razgallah, 2006), on the 260 m thick carbonate sequence has resulted in subdivision of the formation into five lithological units (Chaâbani and

Razgallah, 2006). The formation is characterized by Aptian benthic foraminiferal faunal associations (Chaâbani and Razgallah, 2006). In the Chotts region, the Orbata Formation has undergone a marked reduction in thickness, where it consists of 20 m of fossiliferous massive dolomite and marl interbedded with thin dolostone layers. The fauna consists of orbitolinid and miliolid foraminifera, bivalves including rudists, gastropods, and echinoderms (Chaâbani and Razgallah, 2006). The ages based upon this fauna are late Barremian–Gargasian (Ben Youssef and Peybernes, 1986) and Aptian (Bedoulian-Gargasian) (M’Rabet, 1987; Abdallah et al., 1995; Chaâbani and Razgallah, 2006; Lazzez et al., 2008; Hfaiedh et al., 2013).

2.2. Fossil-bearing strata

The strata of the Khanguet Aïcha exposure (**Fig. 3A**) permit detailed bed by bed logging of the Sidi Aïch Formation sequence (**Fig. 3B**), which consists of 120 m of sandstone arrayed in thick, fining upward sequences. Each sequence is dominated by fine-grained sandstone with channelized basal lag deposits and intercalations of thin claystone and red palaeosol. The middle part of the Sidi Aich Formation in the Khanguet Aicha section (**Fig. 3B, C, and D**) exposes a 20 m, thick light to dark green laminated claystone interval that yields an important biota composed of shrimp, fish, clam shrimp, and plants (**Fig. 3D**) (Boukhalifa et al., 2015). This paper focuses on the taxonomy, biostratigraphy, and palaeoenvironmental significance of the shrimp fauna.

3. Materials and methods

The shrimp specimens are from the middle part of the Sidi Aïch Formation. Specimens are preserved as part and counterpart and were revealed when split in the field. The specimens are catalogued and housed in the collections of the Department of Geology, Faculty of Sciences of

115 Tunis as ECSHKATU 01 – 07. The acronym denotes Early Cretaceous Shrimp from Khanguet
116 Aïcha section, Tunisia.

117 Because of the fragile nature of the specimens, only limited preparation with microjacks
118 and dental needles was conducted. The specimens were photographed with a Nikon D3100
119 camera with a Nikkor AF-S Micro 60 mm lens. Images were processed using Adobe Photoshop®.

120

121 **4. Systematic paleontology**

122 Order Decapoda Latreille, 1802

123 Suborder Dendrobranchiata Spence Bate, 1888

124 Superfamily Penaeoidea Rafinesque-Schmaltz, 1815

125 *Included families.* Aciculopodidae Feldmann and Schweitzer, 2010 (extinct); Aegeridae
126 Burkenroad, 1963 (extinct); Aristeidae Wood-Mason and Alcock, 1891, Benthescymidae Wood-
127 Mason *in* Wood-Mason and Alcock, 1891, Carpopenaeidae Garassino, 1994 (extinct); Penaeidae
128 Rafinesque-Schmaltz, 1815; Sicyonidae Ortmann, 1898; Solenoceridae Wood-Mason *in* Wood-
129 Mason and Alcock, 1891.

130 *Diagnosis.* All five pairs of pereopods well developed; pereopods 1-3 chelate, none significantly
131 enlarged. At least 11 branchiae on each side of the cephalothorax. Pleon with posterior part of
132 pleura overlapping anterior part of succeeding one. (Modified from Pérez and Kensley, 1997).

133 *Remarks.* Identified Tunisian specimens display characteristics of Dendrobranchiata (pleura of
134 pleonite 2 overlapping that of pleonite 1; ECSHKATU 03 a) and Penaeoidea (first three
135 pereopods chelate; ECSHKATU 01). Additional features that support placement in Penaeoidea
136 include development of all five pereopods, best observed in ECSHKATU 01. This is in contrast
137 with the only other superfamily within Dendrobranchiata, Sergestoidea Dana, 1852, in which

pereiopods 4 and 5 are often reduced or absent (Pérez and Kensley, 1997). The rostrum of sergestoid shrimp is often of reduced length (shorter than eyestalks) or even absent, whereas the rostrum of one Tunisian specimen exceeds the length of the eyestalks (ECSHKATU 01), though on the rest of the specimens the rostrum is not preserved. Sergestoid shrimp are also typically characterized by having an elongate pleomere 6 (Pérez and Kensley, 1997, Tavares et al., 2009); the Tunisian specimens display a quadrate to subquadrate pleonite 6 (ECSHKATU 01, ECSHKATU 03 a, and ECSHKATU 05 a).

Family Penaeidae Rafinesque-Schmaltz, 1815

Diagnosis. Body and rostrum laterally compressed. Rostrum well developed, often bearing dorsal and occasionally ventral teeth. Carapace without orbital spine; hepatic and antennal spines usually present. Pereiopods 4 and 5 not reduced (modified from Pérez and Kensley, 1997).

Remarks. The phylogenetic relations within Dendrobranchiata have been studied to some extent, yet no study has found the members of Penaeidae to form a natural group (Tavares et al., 2009).

The family is the most speciose of the penaeoids and includes both fossil and extant species.

Historically, the family has included even more fossil species. Several fossil species have been reassigned to different families in more recent years, such as species of Sicyonidae,

Benthesicymidae (Glaessner, 1969; Schweitzer et al., 2010), Carpopenaeidae (Glaessner, 1929,

Schweitzer et al., 2010), and Aegeridae (Burkenroad, 1963). The features used as diagnostic

characters for Penaeidae by most authors are not exclusive for the family and the group is widely

considered to be what some refer to as a “wastebasket taxon” wherein all species with unknown

affinities within a group are placed (Tavares et al., 2009).

Garassino et al. (2013) named two species from the Cenomanian of Mexico, *Zoquepenaeus spinirostratus* and *Tzeltalpenaeus exilichelatus*, which they assigned to Penaeidae. Based upon their illustrations, the differences between the two species would seem to be largely a question of completeness of preservation; however, both species seem to exhibit characters consistent with placement in Penaeidae.

The placement of the Tunisian specimens within Penaeidae results from a process of elimination from the other penaeoid families. The specimens do not bear a postorbital spine (ECSHKATU 01 and ECSHKATU 05 a), so they do not belong to Solenoceridae. They do not present uniramous pleopods (ECSHKATU 03 a, and ECSHKATU 05 a), eliminating placement within Sicyoniidae. The new material bears more than 3 rostral teeth (ECSHKATU 01, ECSHKATU 05 a), so they cannot be placed within Aristeidae or Benthescymidae, they do not have elongate third maxillipeds (ECSHKATU 01, ECSHKATU 03 a and ECSHKATU 05 a), so they are eliminated from Aegeridae. Only a single specimen from the Devonian is placed in Aciculopodidae (Feldmann and Schweitzer, 2010). The remaining alternative is the placement of the Tunisian specimens within Penaeidae. Investigation of placement of fossil taxa within Penaeidae is ongoing.

Genus *Macropenaeus* Garassino, 1994

Type species. Penaeus incertus Roger, 1946, by original designation.

Other species. Macropenaeus sidiachensis new species, by original designation.

Diagnosis. Long, crested, downturned rostrum with five to seven suprarostal teeth, the proximal ones of which are large and strong, the distal ones of which are small and thin. Hepatic and cervical grooves may be present. Meri and carpi of pereopods elongate. Overall inflated pleon with subquadrate pleonite 6 (Modified from Garassino, 1994).

183 *Occurrence.* The genus was originally based upon specimens collected in the Hadjoula quarry in
184 Lebanon which is Cenomanian in age; the new material is Barremian.

185 *Discussion.* The specimens are placed in the genus *Macropenaeus* based upon their diagnostic
186 dendrobranch features mentioned above, their characteristically crested rostrum morphology
187 bearing dorsal spines, their long and thin pereopods with elongated meri and carpi, and the
188 overall inflated pleon that gives the genus its name. Additional features that coincide with the
189 description of *Macropenaeus* are a narrow and shallow ocular incision behind the rostrum,
190 subrectangular pleopod sympodites, and a slightly longer pleonite 6 than those anterior to it
191 (Garassino, 1994).

192 Specimens of *Macropenaeus incertus* Garassino, 1994, the type and only other species
193 currently recognized within the genus, are reported to lack ornamentation on the telson and
194 carapace (Garassino, 1994). Upon closer inspection of the holotype we observed that the carapace
195 region is generally devoid of cuticle and exposes the endophragm. It is our opinion that carapace
196 ornamentation existed on the organism, but may not have been preserved in the fossil. We were
197 unable to confirm the presence of an epigastric tooth on the holotype and therefore question its
198 use as a diagnostic. The morphological features observed on the carapace of the Tunisian
199 specimens (the hepatic spine and cervical groove displayed in ECSHKATU 01 and ECSHKATU
200 04 b) and the different number of dorsal rostral spines (bearing 7 rather than 5 in *M. incertus*)
201 may serve as characters to emend the diagnosis of the genus.

202 The genus *Macropenaeus* has a temporal distribution starting in the early Cretaceous
203 (Garassino, 1994); the geographic distribution of *Macropenaeus* prior to this work was reported
204 only from Lebanon sites. The Tunisian occurrence expands its geographic distribution westward
205 to Northern Africa as well as its temporal distribution back to the late Barremian.

206 *Macropenaeus sidiachensis* new species

207 **(Figs. 4 and 6)**

208 *Diagnosis.* Rostrum bearing 7 dorsal spines; carapace bearing prominent cervical groove and
209 small hepatic spine. Pleopods elongate, extending up to two times the height of their respective
210 pleonites.

211 *Etymology.* Referring to Sidi Aïch, the formation from which the specimens where collected.

212 *Description.* Medium to large shrimp exhibiting overall poor preservation. Cephalothorax
213 approximately equal to half the length of pleon and telson. Carapace subrectangular, narrowing
214 slightly anteriorly; width about half the length; bearing a poorly preserved, short, downturned,
215 curved rostrum with 7 dorsal rostral spines (ECSHKATU 01). Cephalothorax bearing small
216 hepatic spine and cervical groove, the latter extending from ventral margin and nearly reaching
217 dorsal margin (ECSHKATU 01). Scaphocerite flat, about one third carapace length
218 (ECSHKATU 01 and ECSHKATU 04 a and b); a mesial scaphocerite keel extends longitudinally
219 (ECSHKATU 01). Antennular peduncles possibly exceeding length of rostrum; dorsal surface
220 with slight concavity (ECSHKATU 01); antennules biflagellate (ECSHKATU 03 a). Antennae,
221 observed on a single specimen (ECSHKATU 01) to project anteriorly a full length of the
222 carapace, are interrupted by the edge of the sample. Antennal peduncle extends half the
223 scaphocerite length.

224 Pereiopods long, slender, smooth; arising from posteriormost section of carapace,
225 segments smooth. Pereiopods progressively longer from 1 through 3 and all terminate in small
226 chelae. Pereiopods 4 and 5 are terminal and long, though shorter than pereiopod 3. All pereiopods
227 have elongate carpi and meri (ECSHKATU 01 and ECSHKATU 05).

Pleon robust with greatest height at junction between pleomere 3 and 4 (ECSHKATU 05). Pleonites rectangular except for pleonite 6 which is subquadrate (ratio of length/height between 1 and 1.15 on specimens with complete pleonite preservation) and longer than those anterior to it; pleura rounded. Pleopod sympodites large and ovate; pleopods long, biflagellate, and multiarticulate. Uropods present without a diaeresis; telson long, unadorned and appears to terminate in a point (ECSHKATU 01).

Material. *Macropenaeus sidiaichensis* new species (Penaeidae) ECSHKATU 01 (holotype), ECSHKATU 02 a and b, ECSHKATU 03 a and b, ECSHKATU 04 a and b, ECSHKATU 05 and ECSHKATU 06. Comparative material includes *Macropenaeus incertus* (**Fig. 5**) from Lebanon: SMNS 65544 from the Museum of Natural History of Stuttgart; MNHN i12148 (holotype), i5912, and i24789 from the Museum of Natural History of Milan.

Measurements. Refer to Table 1.

Discussion. The morphologic distinction between *Macropenaeus sidiaichensis* and *Macropenaeus incertus* (**Fig. 5**) is partially based upon a difference in the number of dorsal rostral spines (7 in *M. sidiaichensis* and 5 in *M. incertus*) and on the presence of an hepatic spine as well as a cervical groove on *M. sidiaichensis* and the apparent lack of these carapace features in *M. incertus*. These differences in carapace morphology, though true morphologic distinctions, might arise due to differences in preservation. The carapace of shrimp in general is very thin and prone to taphonomic modification throughout fossilization in which carapace features can be lost or added. For instance, it is not uncommon to find specimens displaying apparent carapace grooves and/or spines which are more likely to result from the carapace being preserved over the endoskeleton morphology than actual carapace structure (personal observation). The specimens of *Macropenaeus incertus*, the type species of the genus, do not lack observable carapace features

(personal observation). These, however, must have been interpreted to be taphonomic in nature as the species is reported to have a completely unadorned carapace (Garassino, 1994). We, therefore, place little diagnostic value on fossil shrimp lateral carapace ornamentation as it is subject to numerous sources of potential modification.

An additional diagnostic feature observed in *Macropenaeus sidiachensis* but not in *M. incertus* is elongate pleopods measuring up to two times the height of their respective pleonites. Specimens of *M. incertus* lack preserved pleopods (Garassino, 1994), so this character might be shared between both species. The holotype of *M. sidiachensis* lacks preserved pleopods, but they are clearly observed in ECSHKATU 05. Some of the specimens, namely ECSHKATU 02 a and b, ECSHKATU 04 a and b, and ECSHKATU 06 lack some or all of the diagnostic features that allowed us to place the specimens within *Macropenaeus*. The characteristic curved rostrum cannot be observed in these specimens since the entire carapace is missing from ECSHKATU 02 a and b and the rostrum is missing from ECSHKATU 04 a and b and ECSHKATU 06. Another diagnostic feature that is not observed in these specimens is the subquadrate pleonite 6. In ECSHKATU 02 a and b and in ECSHKATU 04 a and b pleonite 6 appears to be much more elongate; in ECSHKATU 06 the entire telson as well as the posteriormost pleonites are lost at the edge of the sample.

Despite the lack of these diagnostic features, there are other characteristics displayed by these specimens that allow us to assert that they are indeed the same species as the ones we identified as belonging to *Macropenaeus sidiachensis*. ECSHKATU 02 a and b and ECSHKATU 04 a and b have an elongate pleon and display long pleopods measuring up to two times the height of their respective pleonites. Although the holotype has no preserved pleopods, these can be clearly observed in ECSHKATU 05.

The difference in the morphologies of pleonite 6 between the specimens identified as *Macropenaeus sidiachensis* and ECSHKATU 02 a and b and ECSHKATU 04 a and b is problematic. We believe, however, that this difference arises from the incomplete preservation of pleonite 6 in ECSHKATU 02 a and b and ECSHKATU 04 a and b as they display incomplete cuticle preservation throughout their morphology and even within single structures such as their pleonites.

The identification of ECSHKATU 06 is more problematic, as virtually no aspect of its morphology is complete with characteristic features. Its preservation style, however, is reminiscent of some samples of *Macropenaeus incertus* from Lebanon (personal observations of SS, RMF, and CES). Like the Lebanese samples, the preserved cuticle of the specimen is a dark brown color. The cuticle preservation is very poor, but it is displayed in a more three-dimensional aspect than the typical fossil shrimp fossils such as those from the Solnhofen Lagerstätte and most of those from Lebanon and Tunisia. We, therefore, identify ECSHKATU 06 as *Macropenaeus sidiachensis* due to the co-occurrence with the other specimens and its particular preservation style which has also been observed in the type species of its genus.

Penaeoidea indeterminate

(Fig. 7)

Material. ECSHKATU 07 a and b.

Description. Small shrimp ca. 3 cm total length and 0.5 cm maximum height. Carapace poorly preserved, with no ornamentation identifiable. Rostrum partially preserved, displaying at least 5 small dorsal spines. Only basal portions of the pereopods preserved, unadorned. Pleon poorly preserved; pleonites not differentiated in sample.

This specimen also exhibits what we interpret to be an extremely long pleonite 6 with a length/height ratio of 2 which accounts for around 30% of the total organism length.

Discussion. – The positive identification of ECSHKATU 07 is difficult as there are not enough displayed characters to do so. It is possible that the specimen represents a decapod shrimp larval stage, probably zoea or decapodid, due to its relatively small size compared to the other samples and its very elongated pleonite 6 which is observed in larvae of several extant dendrobranchs such as *Penaeus brasiliensis* (Latreille, 1817) and *Pleoticus muelleri* (Bate, 1888.), as well as caridean shrimp including *Nauticaris magellanica* (A. Milne-Edwards, 1891) and *Palaemonetes cummingi* Chace, 1954. It is even possible that the specimens represent a larval stage of *Macropenaeus sidiachensis* due to the presence of 5 suprarostal spines as is within the range for the genus. Carapace ornamentation, however, is known to change as larvae develop toward adulthood, in some cases losing spines throughout ontogeny (e.g. *Pleoticus muelleri* and *Palaemonetes cummingi*) (Anger, 2001; Tavares and Martin, 2010, Wicksten, 2010). Additionally, the rostrum does not appear to be curved as is that of *M. sidiachensis* which is not a character reported to change drastically throughout ontogeny.

5. Palaeoenvironmental significance

Shrimp are known to occur in the modern environment in a wide variety of marine and freshwater settings. The fossil shrimp genus *Macropenaeus*, previously recovered in the Late Cretaceous (Cenomanian) limestones of Hadjoula, northwest Lebanon, has been interpreted as having inhabited shallow marine setting in small shallow basins corresponding to intra-shelf palaeoenvironment (Audo and Charbonnier, 2013). However, in our study, fossil shrimp are preserved with fish, freshwater clam shrimp, and plants (Boukhalfa et al., 2015). The mixing of freshwater and marine fauna could be the result of fluctuating shorelines (Tasch and Zimmerman,

1961) or by the dispersal of clam shrimp eggs to coastal areas by the widespread sheet of water that drained toward the sea (Lana and Carvalho, 2002). Hence, during the Barremian, the study area could represent a complex paralic system in which both freshwater and marine paleoenvironments exist simultaneously.

6. Conclusion

The newly recovered shrimp assemblage from the Lower Cretaceous Sidi Aïch Formation is represented by a *Macropenaeus sidiachensis* sp. nov. fauna, which is the second species described in the genus *Macropenaeus*. Its occurrence in the Chotts area during the Barremian suggests that the genus originated in northern Africa and then spread across North Africa and Arabia by the Cenomanian at which time Lebanon and the whole Arabian Peninsula were part of the African platform in the northern part of the Gondwana continent.

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548 Table 1. Measurements of the morphology for the Tunisian samples. All in cm.

	Total length	Max height	Carapace length	Carapace height	Pleon length	Pleon height	Pleonite 6 length	Pleonite 6 height
ECSHKATU 01	4.5	1	2	1	2.5	?	0.75	0.65
ECSHKATU 02	?	1.5	?	?	4	1.5	1.25	0.75
ECSHKATU 03	7.5	1.5	3	?	4.5	1.5	1	1
ECSHKATU 04	2.25	0.5	1	0.5	1.25	0.4	0.4	0.25
ECSHKATU 05	4	1	1.5	0.5	2.5	1	0.75	0.75
ECSHKATU 06	?	1.25	2	1.1	?	1.25	?	?
ECSHKATU 07	1.75	0.25	0.75	0.25	1	0.25	0.5	0.25

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550

Figure and table captions

Fig.1. A. Map of Tunisia showing the position of Tataouine and Chotts-Gafsa Basins. The dashed-line box shows the study area. **B.** Geological map showing the Chotts Basin within northern and southern Chotts Ranges. The dashed-line circle indicates the study area which is located at the eastern end part of the northern Chotts Range, Southern Tunisia. **C.** Geological map (Abdeljaoued, 1983; Louhaïchi and Tlig, 1993; Gharbi et al., 2013) showing the main lithostratigraphic formations cropping out in the ZBAS and particularly the location of the Sidi Aïch Formation at the Khanguet Aïcha locality.

Fig.2. A. Schematic Lower Cretaceous stratigraphy showing main formation nomenclatures from the South (Landward) to the North (Seaward). **B.** Panoramic view of the Gafsa Group (Bouhedma, Sidi Aïch and Orbata formations) cropping out in the ZBAS area with reference to the location of the Khanguet Aïcha biota site. **C.** Synthetic lithostratigraphical column associated with the depositional environment interpretations of the Gafsa Group cropping out in the northern Chotts range.

Fig.3. A. Close-up of the well exposed Lower Cretaceous Sidi Aïch Formation in the Khanguet Aïcha locality showing at the base the red dolocrete marker bed of the top of the Bouhedma Formation, the claystone biota site in its middle part, and the overlaying Aptian Orbata Formation. **B.** Detailed lithostratigraphic column of the Sidi Aïch Formation (Upper Barremian) at the Khanguet Aïcha locality. **C** and **D.** Close-up of the claystone biota site showing the occurrence and abundance of the main faunal and floral assemblages and particularly the shrimp fauna.

574
575 **Fig. 4. A.** ECSHKATU01, holotype of *Macropenaeus sidiaichensis*. **B.** Enlargement of anterior
576 carapace, cervical groove (e) and hepatic (b1) spine indicated by arrows. **C.** Enlargement of
577 pereopods. Scale bars = 1cm.

578
579 **Fig. 5.** Holotype of *Macropenaeus incertus* (MNHN i12148). Scale bars = 1cm.

580
581 **Fig 6. A and B.** ECSHKATU02 specimens a and b respectively, *Macropenaeus sidiaichensis*. **C.**
582 ECSHKATU03 specimen, *Macropenaeus sidiaichensis*. **D.** and **E.** ECSHKATU04 specimens a
583 and b respectively, *Macropenaeus sidiaichensis*; **F.** ECSHKATU05 specimen, *Macropenaeus*
584 *sidiaichensis*; **G.** ECSHKATU06 specimen, *Macropenaeus sidiaichensis*; Scale bars = 1cm.

585
586 **Fig 7. A and B.** ECSHKATU07 specimens a and b respectively, indeterminate but suspected to
587 be *Macropenaeus sidiaichensis* larva; Scale bars = 1cm.

588
589 Table 1. Measurements of the morphology for the Tunisian samples. All in cm.

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