The first *Microcharon* (Crustacea, Isopoda, Microparasellidae) from the Moroccan North Saharan Platform. Phylogeny, origin and palaeobiogeography

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Abstract

The interstitial stygobites of the genus *Microcharon* (Crustacea, Isopoda, Microparasellidae) are highly diversified in Morocco, especially in the High Atlas. A new species from the North Saharan platform is described. *Microcharon oubrahimae* n. sp. is characterized by the original morphology of the first male pleopod which exhibits a concave inner margin of the distal part and a subdistal position of the armature. From a phylogenetic point of view, *M. oubrahimae* does not belong to the lineage which includes the Moroccan Atlasian species. In contrast, it belongs to the eastern-Mediterranean group of species. It is related to the species of the group *M. orghidani-M. bureschi-M. phlegetonis* from Romania and Bulgaria. The two-step model of colonization and evolution provides an understanding of the origin and evolutionary history of this stygobiont. *M. oubrahimae* derived from marine ancestors that lived in the littoral interstitial waters of the marine gulfs which covered the Errachidia-Boudnib-Erfoud basin within the pre-African trench during the Turonian or more likely Early Senonian. These marine ancestors might have settled in fresh groundwater during the regressive phases of the Turonian embayment or more likely of the brief Coniacian-Santonian gulf.

Contents

Introduction

The interstitial crustacean isopods of the genus *Microcharon* (Microparasellidae) are widely diversified in Morocco. Species are regularly sampled in river groundwater and wells located in several regions both north of the High Atlas and within the High Atlas. *Microcharon marinus* was first recorded from the Mediterranean sandy beaches (Coineau, 1971, 1986). Later, Pesce *et al.* (1981) discovered one species in western Morocco, and Messouli (1984) collected the genus in springs of the Haouz. Then, Boutin and Boulanouar (1984), Boulanouar (1986, 1995) and Boutin (1993) reported an unnamed species from Marrakesh groundwaters. Later, Yacoubi-Khebiza discovered several endemic species from different valleys of the High Atlas (Yacoubi-Khebiza, 1990, 1996; Boulanouar *et al.,* 1995; Yacoubi-Khebiza, 1996; Yacoubi-Khebiza *et al.,* 1997, 1999). Each species resulted endemic to only one hydrographic system. These species can be considered rhoendemics, i.e. vicariant taxa (Myers and De Grave, 2000; Fattorini, 2006). Another species, *M. alamiae*, has been described from the northern south-Rifian region of Morocco (Boulanouar *et al.,* 1997; Coineau *et al.,* 2001).

Recently, and for the first time, investigations in groundwater from the south eastern region of the Kingdom has provided a new species from the Errachidia-Boudnib-Erfoud basin, south of the High Atlas. This species is described hereafter. Its evolutionary relationships, and its origin are described and interpreted under a palaeogeographic perspective.

Systematics

Microcharon oubrahimae n. sp.
(Figs. 1-3)

Material.– One male, one female, one young male from the Mosque well, Tazouguert, October 6, 2004; nine females, three males, one young female and one young male from the Mosque
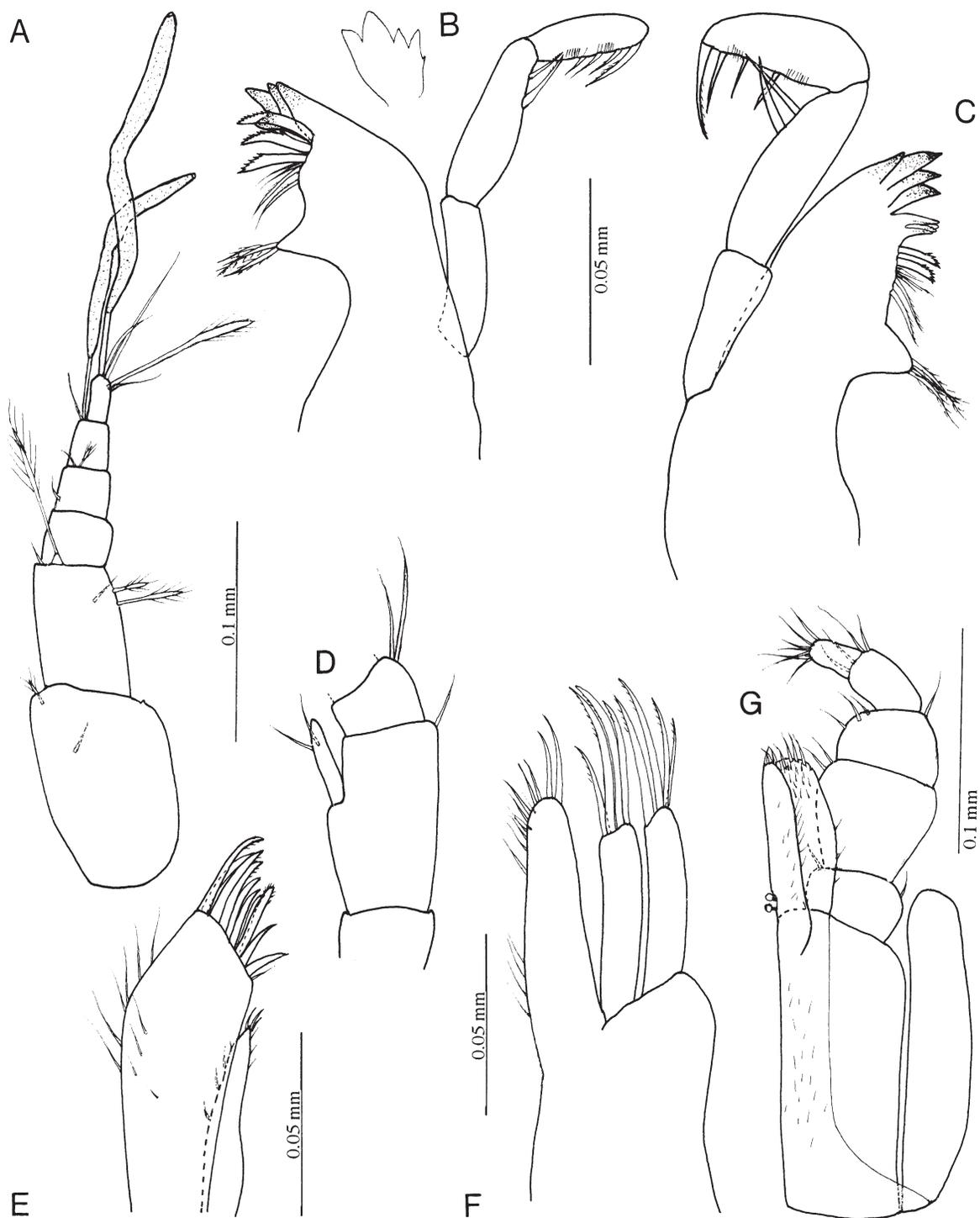
Fig. 1. Microcharon oubrahimae n. sp. A, Antenna 1; B, right mandible and pars incisiva; C, left mandible; D, Antenna 2; E, Maxilla 1; F, Maxilla 2; G, Maxilliped.

well and the Oumidin well, Zouala, October 7, 2004, March 18, 2005. Isopods collected with the Cvetkov net (Cvetkov, 1968). Syntype series: 14 individuals dissected or observed. Three specimens of the syntype series are deposited in the Muséum d'Histoire Naturelle de Marrakech, Morocco (one male, one male witout pleopod 1, and one female): registration number: MHNM 06 ZT 1.

Derivatio nominis: in memory of my mother Oubrahima (Ali Aït Boughrous).

Description.– Body length from 1.80 to 2.00 mm (males) and from 2.00 to 2.36 mm (females).

Anterior margin of the cephalon with a very short rounded rostrum.

Antenna 1. Six-segmented as in most freshwater species. Chetotaxy similar to the classical scheme of other species: first article clearly longer than wide with two plumose and bare setae; second article longer than wide exhibiting three subdistal setae (two plumose and one normal) and two distal setae; the long characteristic plumose seta reaches the distal part of the article 5; length of the four last articles together as long as the first one; only one aesthetasc on articles 5 and 6 in both sexes (Fig. 1A).

Antenna 2. All collected individuals have lost this appendage which is broken at segment 4. Exopod as a long scale armed with two subdistal setae (Fig. 1D).

Mandible (Fig. 1 B, C). Right mandible: pars incisiva composed of four teeth plus one very small one; three denticulate spines, two naked and two pectinate setae between pars incisiva and pars molaris; conical pars molaris armed with three pectinate setae. Left mandible differing from the right one by the lacinia mobilis composed of four conical pectinate teeth, only two denticulated spines and two pectinate setae between pars incisiva and pars molaris.
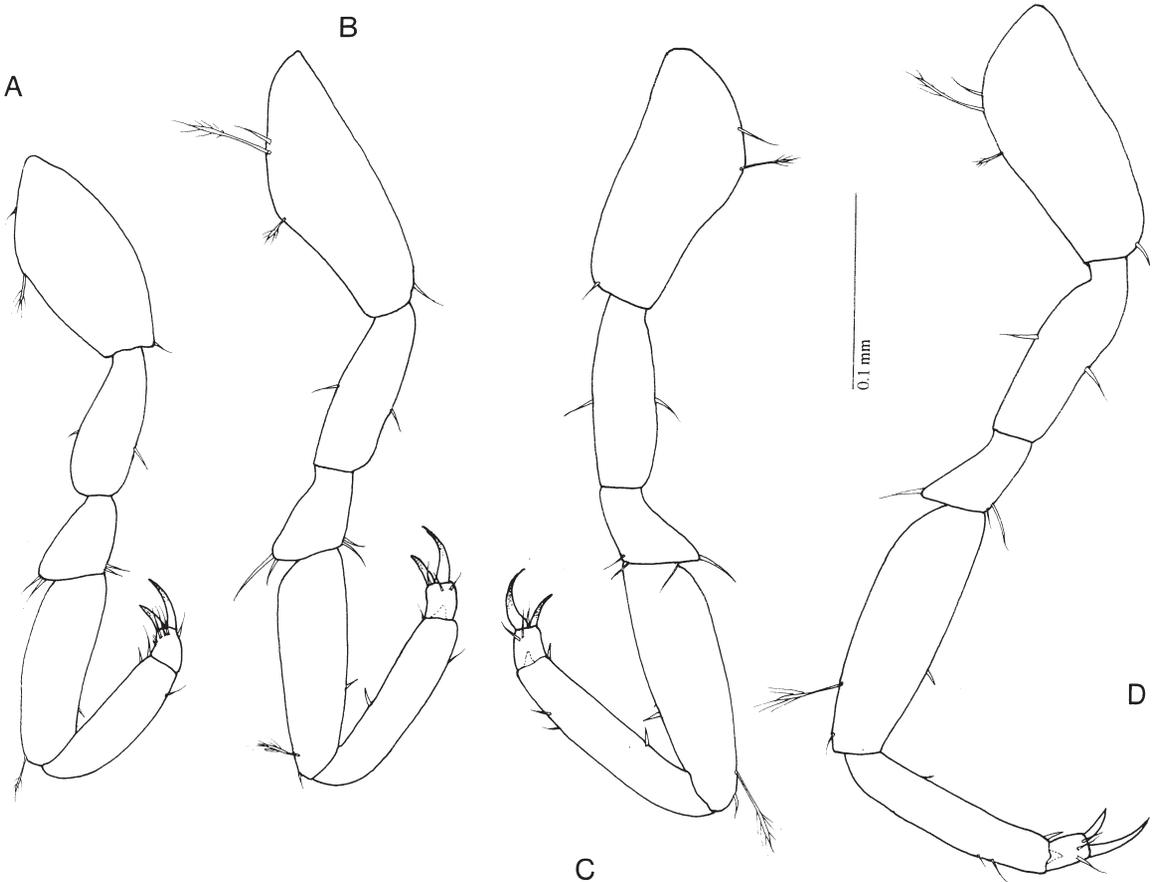
Fig. 2. Microcharon oubrahimae n. sp. Pereiopods. A, P1; B, P3; C, P6; D, P7.
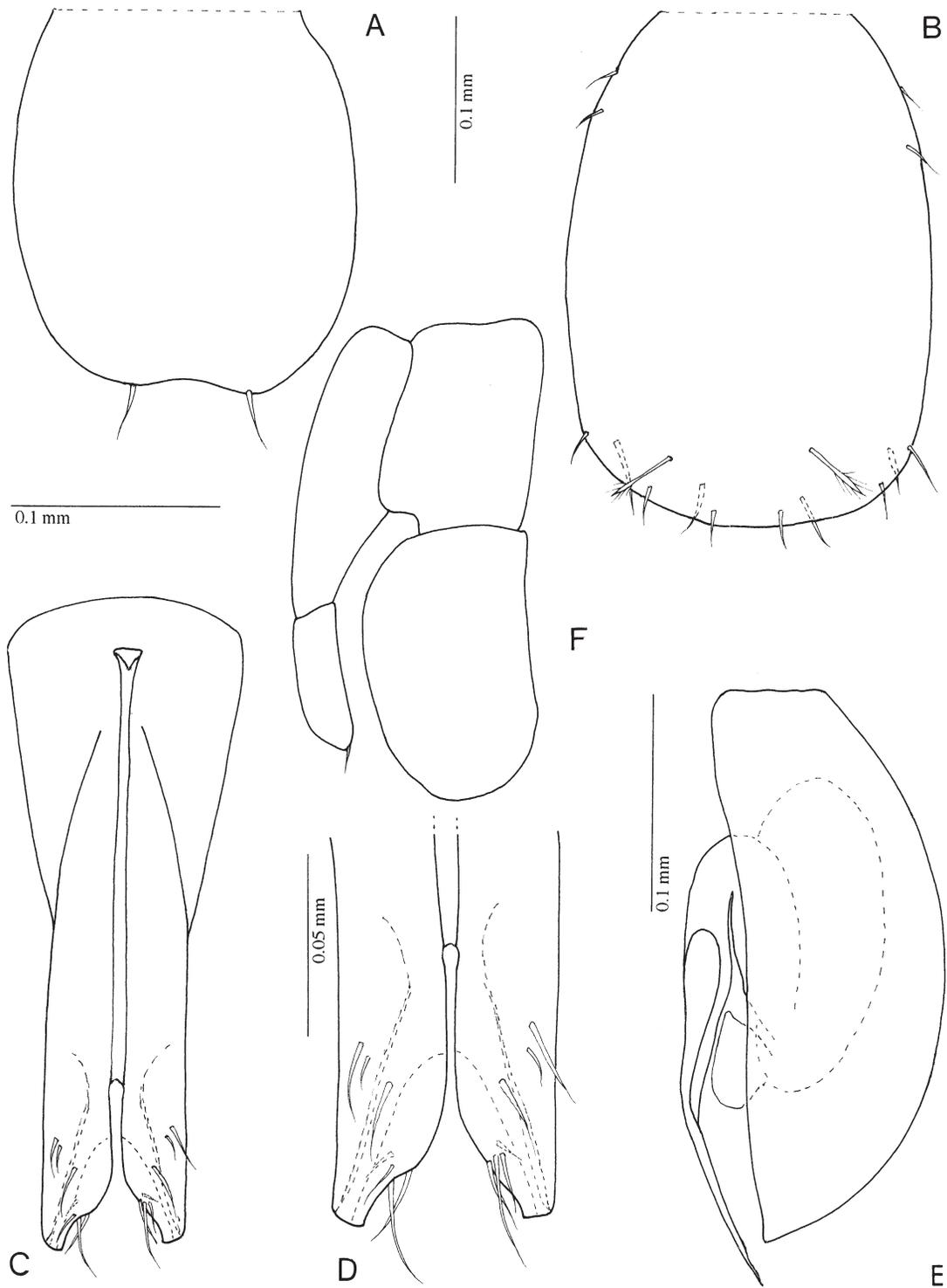
Fig. 3. Microcharon oubrahimae n. sp. A, Female pleopod 2; B, pleotelson; C, Male pleopod 1; D, Distal part of male pleopod 1; E, Male pleopod 2; F, Pleopod 3.

Maxilla 1 (Fig. 1E). Inner ramus narrow with three distal setae and several small subdistal setae; outer ramus with 10-11 pectinate, ciliate and naked teeth; six long and fine setae on outer margin.

Maxilla 2 (Fig. 1F). Inner endite clearly longer and wider than the remaining two; it bears five naked apical setae and two series of short and fine marginal setae; median and outer endites with four long and pectinate setae.

Maxilliped (Fig. 1G). Epipod apex reaching the distal limit of palp segment 1; Endite short and armed with six distal setae; a lot of setules both on margin and blade; two retinacula. Palp of five segments: first one short and wide with two setae; segment 2 the widest and the longest with two setae; segment 3 very short and wide, with three + one setae; two last segments relatively short with four and seven setae.

Pereiopods (Fig. 2A, B, C, D). Long and narrow basis, moderately enlarged with one (P7), two (P1) and three (P2 to P6) setae on the tergal part; meropod long; chetotaxy similar to that of other species; the two distal claws long and unequal.

Pleotelson (Fig. 3B). Width/length ratio = 3/4; distal margin regularly rounded. Chetotaxy similar to that of other species.

Male pleopod 1 (Fig. 3C, D). Basal region coalescent and enlarged; exopod separated only at the 1/4 of total length; inner lobes rounded, extended beyond the four very long subdistal setae and with a concave subdistal inner margin ending in a pointed angle at the apex; fold and hyaline edge extended and slightly diverging toward outer part of exopod far from the four subdistal setae;

the latter part very long, three setae in the medial zone of the fold.

Male pleopod 2 (Fig 3E). Sympodite long and narrow, exhibiting an inner distal lobe pointed; appendix masculina long and narrow with needle-like apex.

Female pleopod 2 (Fig. 3A). Nearly as wide as long; with a concave margin ornated with two long setae.

Pleopods 3 (Fig 3F). Globular and smooth endopod, exopod short, the second article does not reach endopodal apex.

All collected specimens have lost their uropods because of the sampling method (Cvetkov, 1968). No dimorphism has been detected on antenna 1.

Remarks.– *Microcharon oubrahimae* n. sp. is quite different from all the Moroccan species as well as from congeners by the original morphology of the first male pleopod. The concave inner margin of the exopod, the position of the four subdistal setae far from the apex, the fold and the lobe extended in their distal part, markedly overreaching seta insertion and diverging toward the outer corner are unique features of the new species.

Phylogenetic relationships

The cladistic analysis was performed using the software programs PAUP 3.1.1 (Swoford, 1993), PAUP 4.0 (Swofford, 2002) and MacClade 3.0 (Maddison and Maddison, 1993). Three outgroups were selected to root the cladogramms: the Janiridae *Jaera italica* Kesselyak,

Table I. List of characters

1. rostrum present (0), absent (1)
2. Cephalon wider than long (0), longer than wide (1)
3. Eyes present (0), absent (1)
1. Pereionite wider than long (0), longer than wide (1)
5. Antenna 1: number of articles: 6 (0), 5 (1)
6. Scale on third antenna 2 article (0), no scale (1)
7. Mandible molar process truncated (0), long and pointed (1), short, conical (2)
8. Mandible palp with > 4 spines (0), 3 spines (1)
9. Maxilliped with > 2 hooks (0), 2 hooks (1)
10. Number of pereiopod claws: 3 (0), 2 (1)
11. Claws short (0), inequal (1), long (2)
12. Male pleopod 1: inner lobe long (0), short (1), reduced (2)
13. Male pleopod 1: fold subdistal (0), medial (1), distal (2)
14. Coupling process present (0), absent (1)
15. Male pleopod 1: hyaline edge diverging at apex (0), medial (1), ending medially at apex (2)

16. Male pleopod 1: inner lobe with a regular apical margin (0), margin concave or oblique (1)
17. Male pleopod 1: inner lobe setae numerous at apex (0), few (1)
18. Male pleopod 1: inner lobe setae: distal (0), subdistal (1)
19. Male pleopod 1: outer distal part: short (0), extended (1)
20. Female pleopod 2 long, apically triangular (0), bilobed (1), rounded (2)
21. Female pleopod 2: with numerous setae (0), two setae (1), without seta (2)
22. Male pleopod 2 sympod: apical part elongated (0), moderately elongated with a lobe (1), rounded (2)
23. Male pleopod 2: appendix masculina short (0), as long as sympod (1), longer than sympod (2)
24. Pleopod 3 endopod with setae (0), witout seta (1)
25. Uropod reduced (0), only sympod reduced (1), no reduction (2)
26. Uropod sympod: shorter than endopod (0), longer than endopod (1)

Table II. Character data for the outgroups *Jaera italica*, *Iais aquilei* and *Jaeropsis dollfusi*, and nine selected species of the genus *Microcharon*. ? in the matrix refers to unknown character state.

characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Jaera italica	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	2	2	0	0	1
Iais aquilei	0	0	0	0	1	1	0	2	1	0	0	0	0	0	0	0	0	0	1	1	2	2	0	1	0	0
Jaeropsis dollfusie	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	?	0	2	0	0	0	1
Microcharon bureschi	1	1	1	1	0	0	2	2	1	1	0	2	2	0	0	0	1	1	1	0	2	2	1	1	2	0
M. karamani	1	1	1	1	0	0	2	1	1	1	1	0	1	1	1	0	1	0	0	0	1	1	0	1	2	0
M. nuragicae	1	1	1	1	0	0	2	2	1	1	1	1	2	1	2	0	1	0	0	2	2	2	2	1	2	0
M. orghidani	1	1	1	1	0	0	2	1	1	1	1	2	2	1	0	1	1	1	1	2	1	0	2	1	2	0
M. oubrahimae	1	1	1	1	0	0	2	1	1	1	1	2	2	1	0	1	1	1	1	0	1	1	2	1	2	?
M. ourikensis	1	1	1	1	0	0	2	1	1	1	1	0	1	1	1	0	1	0	0	0	1	0	0	1	2	0
M. phlegetonis	1	1	1	1	0	0	2	?	1	1	1	2	2	0	0	0	1	0	0	0	1	0	2	1	2	0
M. rouchi	1	1	1	1	0	0	2	2	1	1	1	1	2	1	1	0	1	0	0	2	2	0	0	1	2	0
M. teissieri	1	1	1	1	1	0	2	1	1	1	0	1	2	0	0	0	1	0	0	0	?	0	2	0	2	1

1938, *Iais aquilei* Coineau, 1977 and *Jaeropsis doll-fusi* Norman, 1899. In his phylogenetic study of the Janiridae, Wilson (1994) regarded the Microparasellidae as one of the outgroups. The operational taxonomic units within the ingroup *Microcharon* included nine species as representatives of different clades resulting from a preliminary cladistic analysis (Coineau, 1994), and on the basis of the evolutionary groups established by Cvetkov (1968) and Galassi *et al.* (1995). Concerning the characters, incomplete species descriptions in the literature limited the selection of informative characters. The list is given in table 1. The coding was inferred from the outgroup species, since they are all epigean Janiridae (Table II). Therefore, they exhibit numerous characters in the plesiomorphic state compared to interstitial isopods that have modifications, reduction and loss of morphological structures as an adaptation to life within granular substrates. The matrix was processed using the branch and bound Search option. After several runs with ordered and unweighted data, characters were ordered. The consensus trees (Strict, semi Strict, Majority rule and Adams) were calculated.

The genus *Microcharon* is monophyletic in all trees. *Microcharon oubrahimae* does not belong to the *ourikensis-karamani* group of species as do other species of the Atlas. In contrast, the southerm Moroccan new species appears to be a member of the phylogenetic "Eastern Mediterranean group" of species composed of *M. bureschi*, *M. orghidani* and *M. phlegetonis*. *M. orghidani* is the sister species of *M. oubrahimae*. Both are characterised by the oblique or concave inner margin of the inner lobe of the male pleopod 1 (16) and the subdistal position of the armature (18). The eastern Mediterranean group of species, defined by a reduced inner lobe of the male pleopod 1 (12), is the sister group of "the western Mediterranean" species *M. rouchi* and

M. nuragicae together with the Moroccan-Algerian species *M. ourikensis* and *M. karamani*. *M. teissieri* is a fully marine species and appears as the sister species of all other species of *Microcharon* (Fig. 4).

In *M. oubrahimae*, both the distal part of the fold and the outer part of the inner lobe are elongated, as in *M. orghidani* (Serban, 1964; Cvetkov, 1968), but this elongation is more important, so that the subterminal setae are far from the distal margin. In *M. phlegetonis*, only the distal part of the fold is elongated and the hyaline edge sticks out of the apex (Galassi *et al.,* 1995a, b; Cvetkov, 1968) , while in *M. bureschi* both the hyaline edge and the outer distal part of the fold are protruding (Cvetkov, 1976).

Historical biogeography, origin and age

Microcharon oubrahimae n. sp. occurs in the interstitial groundwater of the Guir River at Tazouguert, ca 40 km east from Errachidia. The species inhabits also groundwater of the Ziz River at Zouala, ca 20 km south of Errachidia (Fig. 4). Therefore, it is distributed in the Errachidia-Boudnib-Erfoud basin (EBE) within the pre-African trench between the High Atlas and the eastern part of the Anti Atlas (Choubert and Faure-Muret, 1962; Combe, 1977; Chamayou and Ruhard, 1977; Rhalmi, 2000). *M. oubrahimae* exhibits the most south eastern distribution in Morocco, compared to all other known species which occur north of and within the western High Atlas. It is the first time that the genus *Microcharon* is discovered south of the High Atlas.

The freshwater species of *Microcharon* originated from marine ancestors (Delamare Deboutteville, 1960; Stock, 1977; Coineau, 1971, 1986, 1992, 1994; Dole and Coineau, 1987; Wägele, 1990; Coineau *et al.,* 1994; Coineau *et al.,* 2001; Boulanouar *et al.,* 1995, 1997;
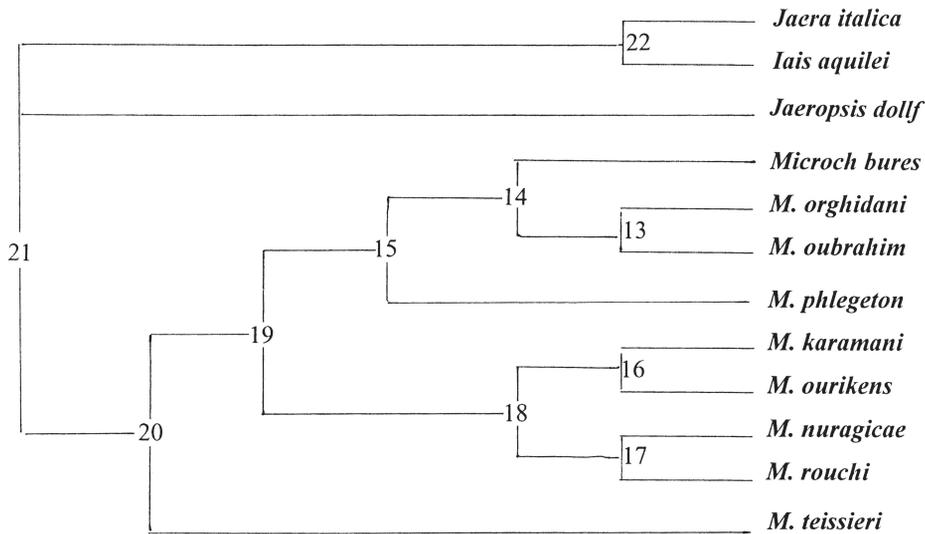
Fig. 4. One of the shortest trees of the genus *Microcharon* including the three outgroups of the Janiridae family *Jaera italica*, *Iais aquilei* and *Jaeropsis dollfusi*. Ingroup taxa: see table II in the matrix. CI = 0.590; RI = 0.709; RC = 0.419.

Galassi, 1991; Galassi *et al.,* 1995a, b; Stoch and Galassi, 2002; Yacoubi *et al.,* 1997).

The so-called two-step model of colonization and evolution provides an understanding of the settlement of the marine ancestors within interstitial fresh groundwaters (Boutin and Coineau, 1990; Notenboom, 1991; Coineau and Boutin, 1992; Holsinger, 1994 who exposed a more complete scenario called the «three-step model»). During the first step, which represents an active dispersion, the marine ancestor colonized interstitial sandy and shallow bottoms in the littoral areas of the Tethys. At the same time, the large surface ancestor evolved into a dwarfish organism due to progenetic evolutionary processes during the penetration into the interstitial habitats. During the second step, the interstitial marine isopod settled progressively in brackish and then fresh groudwaters during a regression of the Tethys. Vicariance processes occurred as soon as the genetic flux between populations remaining in fresh groundwaters and population staying in the littoral seashore was interrupted. Stock (1980) called the second step the "Regression Model Evolution».

Fully marine species of *Microcharon,* as well as species living in the brackish groundwaters of sandy beaches, are still known. The latter species may be considered as putative ancestors for future freshwater species after further marine regressions. In Morocco, all the species are distributed in areas formerly covered by marine gulfs (Boulanouar *et al.,* 1995, 1997; Yacoubi *et al.,* 1997; Coineau *et al.,* 2001).

The Errachidia-Boudenib-Erfoud basin (EBB), as well as the Ouarzazate basin and the Atlas domain were successively invaded by late Cenomanian (96-91 MA) and early Turonian (91-88 MA) marine transgressions (Fig. 5; Choubert and Faure-Muret, 1962; Michard, 1976). In the late Cenomanian, at the maximum of the transgressive phase, the sea was opened to the north and the east in the Errachidia-Boudnib basin, and there was, furthermore, a connection between the South Atlantic and the Tethys, i.e. the shallow epicontinental trans-Saharan corridor (Boudouresque *et al.,* 1982; Dufaure *et al.,* 1984; Reyment, 1986, 2004; Reyment and Dingle, 1987; Courville *et al.,* 1991; Néraudeau, 2000).

During the Turonian, the Ouarzazate basin exhibited an Atlantic marine facies, while the Errachidia-Boudnib basin displayed a Tethyan pertinence (Ferrandini *et al.,* 1985; Courville, 1991; Rhalmi, 2000; Meister and Rhalmi, 2002; Ettachfini and Andreu, 2004). There was already a shallow, the so-called Tinejdad "seuil", between the two southern basins in the early Turonian (Rhalmi, 2000). At the same time, in the Errachidia-Boudenib basin, the sea was deeper, arriving from both east and north-east, and several transgressive pulses occurred.

Later on, in the Senonian (Late Cretaceous, 88-65 MA), a new transgressive gulf invaded the Ouarzazate basin (Gauthier, 1952; Choubert and Salvan, 1950; Choubert and Faure-Muret, 1962; Algouti 1999; Algouti and Algouti, 1999; Marzogi and Pascal, 2000). In contrast, according to Choubert and Faure-Muret (1962), the eastern Errachidia-Boudnib basin only underwent marine influences from the eastern north up to the Errachidia region during the Coniacian (88-87 MA) at the base of the continental Senonian (Fig. 6). After
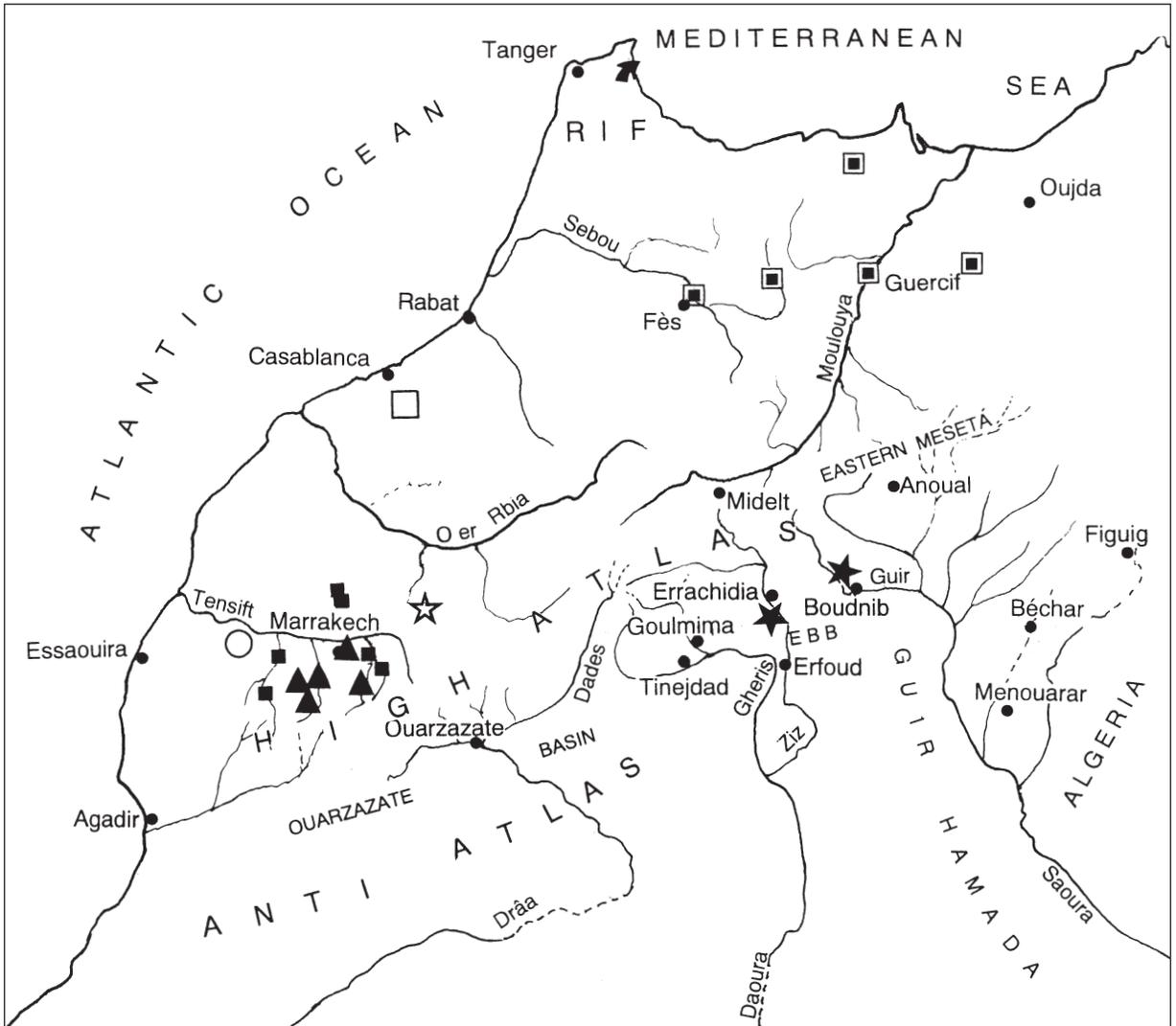
Fig. 5. Distribution of the different species of *Microcharon* from Morocco. Filled star, *Microcharon oubrahimae* n. sp.; filled squares, *M. boutini*; filled triangles, *M. ourikensis* and species of the *messoulii* group; double square, *M. alamiae*; open star, *M.* sp 1.; open circle, *M.* sp. 2; arrow, *M. marinus*.

these events, the marine Senonian within the Erra-chidia-Boudnib basin has not been documented up to now and has yet to be investigated. Nevertheless, pal-aeogeographic data (choubert and Faure-Muret, 1962) show that the sea reached the region of Tadighoust in the Senonian, about 50 km west from Zouala and the Ziz valley in the Tafilalt. At Tadighoust (Ettachfini and Andreu, 2004), the stratigraphic column and the dis-tribution of benthic foraminifera and ostracods ex-hibit a marine Santonian association (Andreu, 1998, 2001). Furthermore, several palaeogeographic maps of the Early Coniacian (Reyment, 1980, 1986; Reyment and Dingle, 1987) display a western marine gulf

briefly covering the most north-eastern part of the Er-rachidia-Boudnib basin and linked to the brief epicon-tinental marine and trans-Saharan connection between the Southern Atlantic and the Tethys. By the end of the Coniacian, there was a regressive phase. No further transgressions reached the Errachidia-Boudnib-Erfoud Basin.

In the groundwaters of the Ziz River *Microcharon oubrahimae* n. sp. is located in areas covered succes-sively by the Cenomanian and the Turonian embayments lying only at 50 km from Tadighoust as well as within the former Coniacian gulfs shown by Choubert and Faure-Muret (1962). Therefore, the ancestors of *M.*
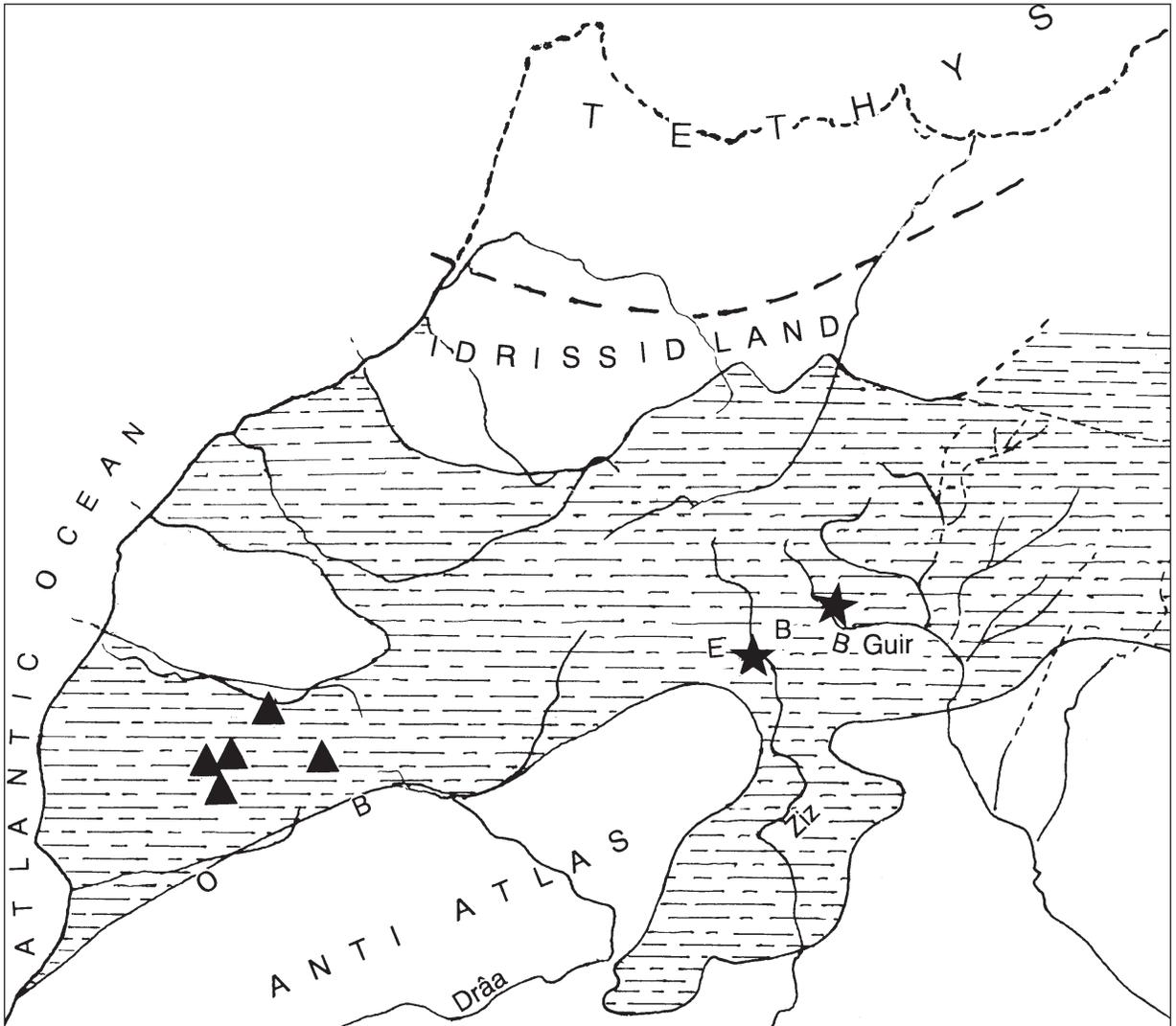
Fig. 6. Extension of the main marine embayments in Morocco during the Cenomanian-Turonian periods and distribution of the species of *Microcharon* in the High Atlas and in the Errachidia-Boudnib-Erfoud basin (EBB). Triangles: species of the *messoulii* group; stars: *M. oubrahimae* n. sp.; OB: Ouarzazate basin. Shorelines after Choubert and Faure-Muret (1962) modified, and Rhalmi (2000).

oubrahimae probably lived in the shallow littoral bottoms of the sea during the Turonian, or more likely during the Coniacian-Santonian since this species exhibits derived characters. They might have settled in fresh groundwaters at the end of the last Turonian regression, or more likely at the end of the Coniacian regression.

Microcharon orghidani lives in Romania. The common ancestor of *M. oubrahimae* and *M. orghidani* might have occupied the two sides of the Tethys in the late Cretaceous. After the regressive phases which left the common ancestor in fresh groundwater of Morocco, this ancestor continued to evolve in the Tethys littoral,

and later on, in the Parathethys, since the evolutionary history of *M. orghidani* and other related species *M. phlegetonis* and M. *bureschi* from Bulgaria, is associated with the evolution of the Parathethys sea (Coineau, 1994; Galassi *et al.,* 1995).

Discussion

The findings in this study raise the question as to whether *Microcharon oubrahimae* has a Turonian or a Coniacian origin.

Based on both morphological affinities of *M. oubra-*
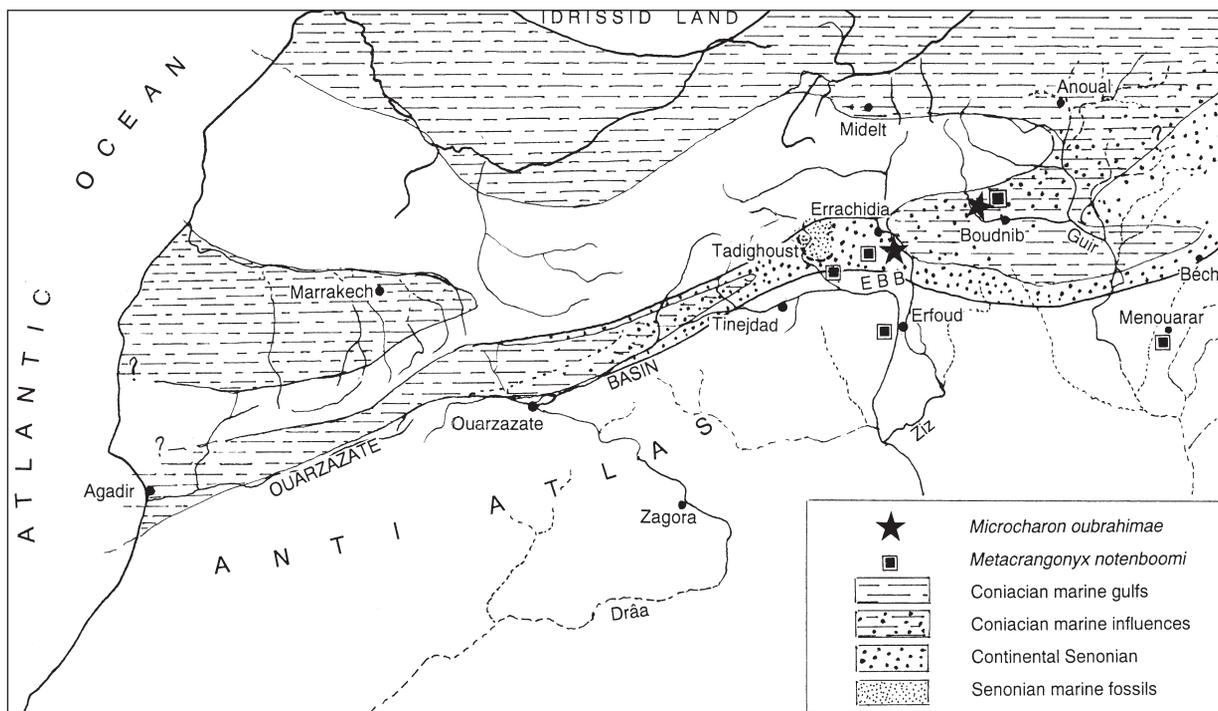
Fig. 7. Middle and southern Morocco during the Senonian period and distribution of *Microcharon oubrahimae* (stars) and the amphipod *Metacrangonyx notenboomi* (squares) within the Errachidia-Boudnib-Erfoud basin (EBB). Marine Coniacian embayments and influences, and continental Senonian (after Choubert and Faure-Muret (1962), modified); location of Coniacian-Santonian marine fossils at Tadighoust (after Ettachfini and Andreu, 2004).

himae with Romanian species, and palaeogeographic data, a Senonian marine origin is more probable than a Turonian one. As a matter of fact, the derived characters of the species suggest a relatively recent settlement in continental groundwaters after a longer period of evolution in unstable marine littoral habitats. Moreover, *M. oubrahimae* has no strong phylogenetic relationships with the Moroccan Atlasian species. It clearly belongs to another phylogenetic lineage, the *orghidani-phlegetonis-bureschi*-group which occurs in Bulgaria and Romania. Moreover, up to now, no species of the genus have been discovered in the Ouarzazate basin in spite of numerous long term sampling compaigns in this region. If the basic vicariant event resulted from a Turonian regression, it (or closely related species) would have occurred also in the Ouarzazate basin, since the Turonian transgression covered both the latter basin and the Errachidia-Boudnib-Erfoud basin (Fig. 6), and there was a connection between the two basin gulfs (Rhalmi, 2000; Ettachfini and Andreu, 2004). In the Ouarzazate basin, other subterranean crustaceans such as the amphipods Metacrangonyctidae, and the isopods Microcerberidae, have been regularly collected. These groups have closely related species of Turonian origin in both

basins, and of Coniacian origin for the Metacrangonyctidae of the *panousei*-group (Boutin *et al.,* 1992). In contrast to Turonian embayments, the Senonian gulfs (Fig. 7) were separated: the "Atlantic" transgression hardly reached Tinrhir in the Ouarzazate basin (Algouti *et al.,* 1999) and there was an exposed high land in the region of Tinjedad between the two basins. In the eastern basin, information on the marine Senonian is poorly available. Often, authors depicted continental senonian deposits (Dresch *et al.,* 1952; Joly, 1952; Combe, 1977; Chamayou and Ruhard, 1977; Cartes géologiques du Maroc, 1986, 1997; Boudab, Haddoudmi, Rhalmi pers. comm.). Others reported marine Senonian sediments (Choubert and Faure-Muret, 1962; Michard, 1976), or Senonian without specification of the origin. Nevertheless, *Microcharon oubrahimae* inhabits phreatic groundwater harbouring other crustaceans of clear marine origin, such as several species of the amphipod *Metacrangonyx*, the isopod *Typhlocirolana* and Thermobaenaceans (Boutin and Cals, 1985; Boutin *et al.,* 1992; Boutin, 1993, 1994; Messouli, 1994). Some of them, such as the amphipods *Metacrangonyx notenboomi* Boutin *et al.,* 1992 and *M. goulmimensis* Boutin *et al.,* 1992 of the *panousei*-group entered

fresh groundwater of the Errachidia-Boudnib-Erfoud basin, especially at Goulmima and in the Tafilalt *s. stricto*, during the regression of the Senonian sea as other species of the same phylogenetic group (Boutin *et al.,* 1992; Messouli, 1994). Furthermore, *M. notenboomi* is the species exhibiting the most apomorphic character states of the phylogenetic group it belongs to (Messouli, pers. comm.). Other closely related species are distributed in the Ouarzazate basin and in the High Atlas. The same authors recognized a Senonian establishment of these species in fresh groundwater during the regression of the Atlantic western Senonian gulf. The Senonian formation from Tadighoust, in the western part of the Errachidia-Boudnib-Erfoud basin, is unquestionably of marine origin (Ettachfini and Andreu, 2004). Organisms within this formation such as the benthic foraminifera Buliminidae and the ostracods *Reticulocosta* gr. *tarfayensis* and *Nigeroloxoconcha* aff. *tagregraensis*, are fully marine species. The latter ostracods are circalittoral species (Andreu pers. comm.). Moreover, the association of the two species defines the marine Santonian facies (Andreu *et al.,* 1998, 2002; Ettachfini and Andreu, 2004). The ostracod *Nigeroloxoconcha* aff *tagregraensis* is known from the marine Coniacian-Santonian of the Ouarzazate Basin, and from Algeria. Other species are distributed in the Cenomanian up to the Eocene formations from Algeria, Niger, Nigeria and The Ivory Coast. As a matter of fact, several authors described the trans-Saharan seaway which connected the South Atlantic to the Tethys (Reyment, 1980, 1986; Reyment and Dingle, 1987; Néraudeau, 2000). Did this epicontinental Coniacian corridor reach the Guir region up to Tazouguert, and the Ziz region as suggested on the maps of Reyment (1986) and Reyment and Dingle (1987)? What may reinforce this hypothesis is the occurrence of the amphipods *Metacrangonyx notenboomi* and *M. longicaudus* (Messouli, 1994) both in Algeria at Menouarar (Saoura basin), and in Morocco at Tazouguert, and within the Tafilalt (Fig. 7). It can be seen that the Coniacian northwestern seaway extended up to at least the Saoura basin in Algeria, and probably up to a more western region. So that Choubert and Faure-Muret (1962) wrote "marine influences" in these latter regions.

Another reason for marine influences in the Errachidia-Boudnib basin would be due to the large depth of the Turonian gulf. A regression process did not work only once: there were always several successive regressive phases. Therefore, during the Coniacian, just after the Turonian, the marine regression was not completed and temporary marine influences might have persisted in the area of the eastern basin.

An alternative possibility could be that the marine influences arrived from the north, since the Tethys covered the Eastern Meseta and the southern plateaus in the Coniacian (Médioni, 1960; Choubert and Faure-Muret, 1962; Medioni, 1968, 1969; du Dresnay, 1976; Haddoumi pers. comm.). The marine Coniacian-Santonian formation from Tadighoust favors a marine connection with this northern embayment. More eastward in the region of Anoual, the Senonian facies was fully marine and far from the coasts which might extend markedly southward (H. Haddoumi pers. comm.), therefore not far away from Tazouguert. According to Rhalmi (pers. comm), most of the High Atlas domain was already an exposed land in the Senonian. Since the orogenesis started in the Lutetian, this exposed land displayed probably only hills and some narrow seaways might arrive from the north in the Errachidia basin through valleys between islands of the future High Atlas.

The marine Senonian layers have probably been eroded by the high erosion processes which affected all the Errachidia-Boudnib-Erfoud basin during the Atlas orogenesis which began during the Lutetian. Therefore the marine Coniacian and Santonian formations, which were very thin since the marine incursions between regressive pulses were very brief (the Coniacian is known as mostly regressive), are not detectable at the top of the stratigraphic columns except in the western part of the basin in the area of Goulmima (Ettachfini and Andreu, 2004). In Algeria, the erosion activity was not so important. According to Dubar (1952), thin marine Senonian sediment can be observed at Meski (at only 6 km north of Zouala) as well as between Meski and Boudnib.

Alternatively, *M. oubrahimae* might have passively drifted along the Guir and the Ziz Rivers and along their tributaries from upstream to dowstream during heavy rains and floods. Such phenomenon might have occurred during the Atlas orogenesis or in the Present. The upstream sections of these streams are located not far from Anoual in the Eastern Meseta, which was covered by the Coniacian marine gulfs. Such passive drift of other crustaceans has already often been observed in several species of the amphipods *Metacrangonyx* and isopods *Typhlocirolana* (Boutin *et al.,* 1992) or in meiobenthic organisms when currents and erosive flow are rapid after heavy rains. Both animals and sediments are tranported downstream (Palmer 1984, 1988, 1992; Palmer and Molley, 1986; Bouck and Thistle, 2006).

Both the northern part of the eastern High Atlas and the eastern Moroccan Meseta, as well as the southeastern part of Morocco are to be investigated since en-

demic species closely related to *Microcharon oubrahi-mae* will be probably discovered: Coniacian-Santonian formations which were thicker than in the EBB still occur in these regions. Such further discoveries together with other groundwater crustaceans of Senonian marine origin will be additional proof that *M. oubrahi-mae* was more likely left during the Coniacian marine regression rather than by the Turonian recession.

Acknowledgements

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