

Groundwater crustaceans as useful geological tools

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Abstract

Many stygobiont crustaceans presently living in continental subterranean waters are derived from ancestral coastal marine species which stay in sediments when shorelines receded far away during the geological periods of marine regression. The dispersal ability of stygobionts in continental groundwaters is especially low. Thus the present distribution of thalassoid stygobionts fits well with that of areas formerly covered by the sea; such stygobionts may provide information about the place of paleoshores, even when marine sediments were removed by erosion. The place of paleoshores of South-West Morocco are partly known from the survey and the analysis of the present regional stygofauna. The species groups resulting from the phylogenetic analysis of genera or families of thalassoid stygobionts and the analysis of their distribution, allow to date the colonization of groundwater by their marine ancestors. Thus the emersion of a Canarian island was dated by this way, as is datable the emergence of lands in Israel and Palestine.

Introduction and general background

Some extant aquatic subterranean species may be used by geologists to locate the shoreline of a former transgressive sea or to date the definitive emersion of a continental sedimentary basin or of an oceanic island (STOCK, 1986; COINEAU, 1990; BOUTIN, 1993a, 1993b). Among metazoans, the crustacean group is the most diversified within groundwaters, both in plain and valley aquifers and in cave rivers or lakes. Such *stygobiontic* crustaceans (*i.e.* aquatic and subterranean) are *troglobites*, in karstic open water, or tiny interstitial *phreatobites*, in saturated porous sediments. *Thalassostygobionts* live in littoral marine cave or sediments and *limnostygobionts* occur in cave and aquifer freshwaters. Only the latter are considered hereafter.

Some limnostygobionts belong to groups living also in surface freshwaters. They are derived from freshwater surface ancestors and are termed *limnicoid*. A well known example is that of the species of the amphipod *Gammarus* (CULVER et al., 1995). This kind of limnicoid stygobionts provides very few information about the period or the geological events related to the colonization of groundwaters by their ancestors, as this colonization may have occurred repeatedly at the same place and at different periods of the past, up to now. Therefore they are generally considered as uninformative for geologists.

Other limnostygobionts belong to marine groups not known in freshwaters. Due to their direct marine origin they are called *thalassoid* limnostygobionts (COINEAU & BOUTIN, 1992; BOUTIN, 1993a, 1993b). The marine origin of such crustaceans has been proposed for a long time (JEANNEL, 1943; DELAMARE DEBOUTTEVILLE, 1957, 1960; VANDEL, 1964, GINET & DECOU, 1977 etc...). For example, out of 350 cirolanid species (isopods), some 85% are epigean, marine or littoral, whereas the other 15% are freshwater stygobites more or less resembling their marine littoral ancestors (BOTOSANEANU, 1986). These stygobionts evolved from marine ancestral populations which first colonized littoral sediments (or sometimes littoral caves) in the Mesozoic or Cenozoic periods; thereafter they adapted to brackish water, then to freshwater and settled during a marine regression when the shoreline receded. This "Regression model evolution" (STOCK, 1977, 1980) was analysed and viewed as the second stage of a "Two step model of colonization and evolution" (BOUTIN & COINEAU, 1990; NOTENBOOM, 1991; COINEAU & BOUTIN, 1992; HOLSINGER, 1994).

Thalassoid limnostygobionts consequently occur in sedimentary basins of continents formerly covered by the sea during a transgression, before the shoreline recede during the following regression. It is well known and generally accepted that interstitial crustaceans have very poor dispersal abilities (see for example HOLSINGER, 1986) and that stygobiontic populations stay in place and remain alive up today as "Living fossils" (DELAMARE DEBOUTTEVILLE & BOTOSANEANU, 1970; TERMIER, 1983), so that the most internal part of the present distribution area of a thalassoid stygobiont provides a good information about the place of the paleoshore during the maximum of the transgression (which occurred before the marine regression which will allow the colonization of groundwaters). Finally these living fossils are present markers of paleoshores. Geologists used to consider the limits of occurrence of sedimentary rocks deposited during a period of embayment as the location of the paleo-shorelines at the same period, except when there is a clear evidence of erosion of the considered layer. However in some cases these sedimentary rocks may have been completely removed by an important continental erosion. Consequently the groundwater primitively contained in these marine sedimentary formations have moved down and lasted in more ancient sediments or in the basal altered plutonic rocks, thus

allowing the survival and permanence of thalassoid stygobiontic populations which remain the sole evidence of the marine transgression. Therefore the location of paleo-shorelines may be inferred only from the limits of the present distribution area of these stygobionts.

On the other hand the colonization of continental groundwaters by some thalassostygobiontic populations may have occurred during the marine regression which resulted in the definitive emersion of a sedimentary basin (or an oceanic island when thalassoid limnostygobionts occur in groundwaters of an island). If it is possible to date this colonization - i.e. the ecological change of crustacean biotopes, from coastal marine environment to continental groundwaters - then it is possible to date the simultaneous marine regression. Now it is well known by paleontologists as well as by stygobiologists (DUCASSE *et al.*, 1983; BOUTIN & COINEAU, 1991, 2000) that the evolutionary rate is faster in a changing and unstable environment, such as coastal biotopes, than in a more stable biotope like bathyal or phreatic and continental biotopes. Continental groundwater appears as a conservative environment housing a lot of "living fossils". Recent colonizers of groundwater - which evolved for a longer time in littoral milieus than older colonizers - exhibit therefore a more important morphological evolution than the more ancient colonizers, which evolved in littoral biotopes for a shorter period. It is why the phylogenetic analysis of the stygobitic species forming a genus or a family, generally shows that the most primitive lineages (monophyletic groups of species) include the species with a distribution indicating a freshwater entrance during the oldest geologic periods. In contrast, the most derived lineage comprises species, the origin of which is correlated with the latest marine regression in the study area. Therefore when the divergences of a cladogram are dated, based on biogeographic and geological data from a well known region, then it is possible to infer the date of a marine regression in another region if a new stygobiontic species of the group occurs in this new region.

Moroccan stygobiontic models used in the Mediterranean Basin

The geological history of Morocco is relatively well known, and two groups of stygobiontic crustaceans occur in numerous regions of this country. They are both sufficiently diversified in many species presently well known; their phylogenetic and biogeographic study provides the possibility of dating the origin of different lineages within each group.

The family Metacrangonyctidae include to date more than 40 stygobiontic species of amphipods, about 36 of which occur in Morocco (MESSOULI, 1994). The cladistic analysis of the family clearly shows four lineages; three of them belong to the genus *Metacrangonyx* and the fourth and most derived one forms the genus *Longipodacrangonyx* (MESSOULI, 1988, 1994; BOUTIN, 1994b). The two more primitive lineages, morphologically well characterized, arise from a trifurcation dated from the Turonian regression (some 90 My BP), the third lineage appears later and in relation with the Senonian marine regression (70 My BP), and the last one, originating the genus *Longipodacrangonyx*, is related with the Lutetian regression (some 40 Ma) as the species of this genus occur only within the limits of eocene gulfs.

The cirolanid isopods of the "*Typhlocirolana* group" include to date four genera and more than 25 stygobiontic species of which about 12 belong to two genera occurring in Morocco (BOUTIN, 1993a, 1993b). The cladogram of Moroccan species exhibit exactly the same topology as that of the metacrangonyctid amphipods, showing four clearly distinguishable lineages. The two more primitive lineages (having retained a number of characteristics of extant marine cirolanids) occur in regions flooded during the Cenomano-Turonian times, the third lineage includes the most derived species of the genus *Typhlocirolana* which occurs in regions flooded during the Senonian, and the fourth lineage is formed by the genus *Marocolana*, whose distribution is included within the paleoshores of the Lutetian gulfs.

The striking similarity of the two phylogenetic cladograms and that of the two area cladograms was pointed out by BOUTIN (1993a) and suggests the same historical biogeography of the two stygobiont groups, and the same sequence of geological events in the regions where representatives of the groups occur.

Results

The age of some islands could be reconsidered from the stygobiological evidence, in Canary archipelago and in Mediterranean islands. The limits of past Tethyan transgressions on the African continent were reevaluated in the Souss and the Anti Atlas regions of Atlantic Morocco. The age of Israel-Palestinian lands could also be reevaluated.

Fuerteventura (Canary Island) is mainly formed by volcanic rocks but in its western region the "Basal complex" is a series of metamorphic sedimentary rocks including mesozoic marine fossils. The island age was generally considered by geologists as ranging from 21 to 34 Ma (mid-Miocene to Oligocene), based on K/Ar datings of the most ancient volcanic rocks. A stygobiontic amphipod, *Metacrangonyx repens*, presently occurs in groundwaters of the "Basal complex" and is lacking in all other parts of Fuerteventura and in any other Canary islands completely formed of volcanic rocks. As *M. repens* belongs to the third lineage of Metacrangonyctidae, the colonization of emerged land by its ancestral marine populations occurred necessarily during the Senonian as in the other Moroccan regions (BOUTIN, 1993b). The age of the sampled volcanic rocks and the age of the emergence of the Basal complex appear quite different, as evidenced by its present stygofauna. The most ancient parts of the island can date back to the Senonian (70 Ma).

The occurrence of *Metacrangonyx longipes* and *Typhlocirolana moraguesi* in Balearic Islands, as these two species belong to the first - and more ancient - lineage of their group means that some part of the archipelago certainly emerged during the Turonian regression (90 Ma BP), even if most parts are formed of cenozoic marine sediments are more recent.

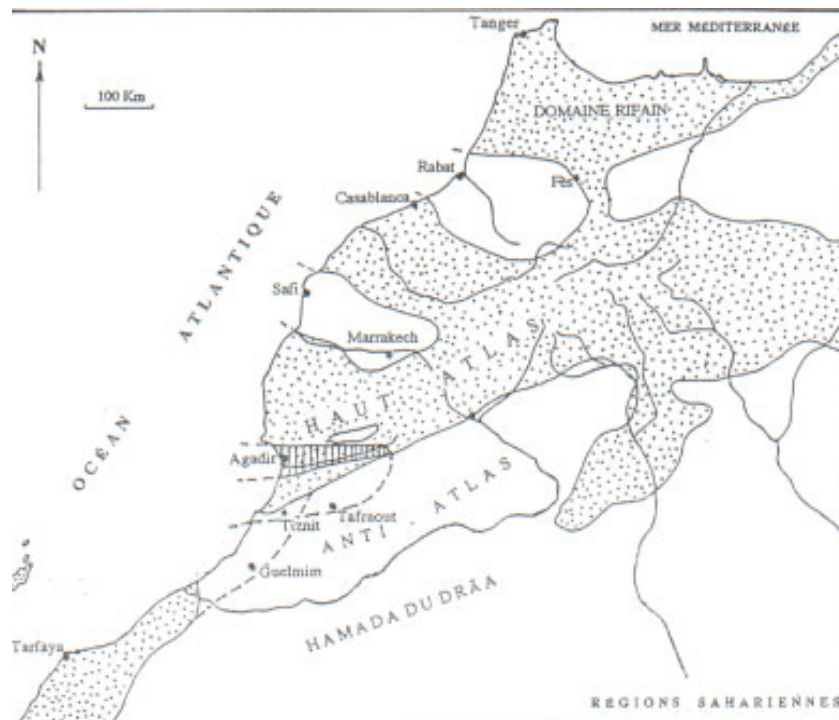


Figure 1 - Synthetic paleogeographic sketch map of Morocco. Dotted areas are regions covered by the Cenomano-Turonian seas; vertically hatched area shows the known limits of the Eocene Soussian gulf, from the authors. Dotted line 1 shows the minimal western shoreline of Atlantic Morocco during the Turonian and dotted line 2 the minimal southern limit of the Soussian gulf, from Boutin (1997) modified.

Similarly a part of the Elba Island, between Corsica and Italy, where *Metacrangonyx ilvanus* was recently discovered (STOCH, 1999) likely emerged during the Senonian, as *M. ilvanus* belongs to the third lineage of the family.

The closure of the Eastern Mediterranean, where the lands of Israel and Palestine partly - and step by step - have emerged, resulting in a present geologically heterogeneous area, is generally considered as relatively recent (Cenozoic). However in the Dead Sea region and in the Egyptian Sinai, two different species of *Metacrangonyx*, *M. ortalii* and *M. sinaicus*, occur and belong to the third lineage, suggesting, in these areas, a Senonian emersion (some 70 Ma). Moreover, in the same Dead Sea region, several cirolanid isopods also occur, belonging to the "*Typhlocirolana* group". BOTOSANEANU & NOTENBOOM (1989) consider that all *Typhlocirolana* species from Israel can be assigned to the genus *Turcolana*, the most derived lineage of the group, located in regions where the marine embayment remained a long time after the Eocene. However BOUTIN (1993a) considers that the species *Typhlocirolana reichi* and *T. detecta* have rightfully to remain included in the genus *Typhlocirolana*. These two species, belonging to the third lineage of the Mediterranean stygobiontic cirolanids are thus another evidence of a Senonian emersion, some 70 Ma ago. Finally the Palestino-Israelian and Sinai lands are in some parts more ancient as generally considered (BOUTIN, 1997).

The limits of the Souss Eocene gulf (East of Agadir in Morocco) are known from Eocene sediments still exposed by places on the north and south margins of the Souss Basin. Thus geologists, following CHOUBERT & FAURE-MURET (1962), used to represent a narrow Eocene gulf, extending eastwards from Agadir, and covering only the present Souss valley (Fig. 1). In this region occurs the genus *Longipodacrangonyx*, forming the fourth and most derived lineage of the Metacrangonyctidae. However a site of *Longipodacrangonyx* was recently discovered just East of Tafraout, some 50 Km south of the supposed limits of the Souss Eocene gulf. Near Tafraout there is no more mesozoic sediments because when the Anti Atlas was repeatedly uplifted and especially during the last Atlasic orogenic periods, an important correlative erosion probably removed completely the superficial sedimentary formations. Finally, groundwaters, previously contained in sedimentary rocks, had to descend to the now superficial decomposed granites. *Longipodacrangonyx* which could not have arrived in its present location by active or passive dispersal, strongly suggests that in reality the Eocene "Souss" gulf extended at least 50 Km more southward, near the latitude of Tiznit and Tafraout (BOUTIN, 1998). When the continental erosion is so important, the thalassoid stygobionts may be the sole evidence of a past marine presence.

Similarly the total gap of mesozoic sediments in the plains of Tiznit and Guelmim (western Anti Atlas domain, between the High Atlas in the North and the Tarfaya Basin in the South, where Cretaceous marine sediments abound) was enough enigmatic and Tarfaya and the High Atlas were generally considered as two separated marine cretaceous gulfs. The presence of a *Metacrangonyx* species belonging to the first lineage in the Tiznit and the Guelmim regions, 30 and 40 Km West of the present coast, means that the Cenomanian-Turonian transgression connected the two regions and that the shoreline was at least 40 Km East of the present coast. During the different stages of the Cenozoic and recent orogenesis, the cretaceous sediments were removed by continental erosion before the deposit of quaternary limestones now exposed.

Conclusion

In a number of particular situations, the distribution of extant thalassoid stygobionts can provide useful evidences of past geological events. The knowledge of their specific diversity and up to date phylogeny may thus be useful out of the field of stygobiology and organisms biology.

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References

- BOTOSANEANU, L. (Ed) 1986. *Stygofauna mundi*. A faunistic, distributional and ecological synthesis of the world fauna inhabiting subterranean waters (including the marine interstitial). E.J. Brill/W. Blackhuys Publ. Leiden, 740 p.
- BOTOSANEANU, L. & J. NOTENBOOM. 1989. Eastern Mediterranean freshwater stygobiont cirolanids (Isopoda, Cirolanidae). With description of three new species. Zool. Jahrb. Abt. f. Syst. 116: 1-19.
- BOUTIN, C. 1993a. Biogéographie historique des Crustacés Malacostracés stygobies du Maroc. Thèse de Doctorat, Université Claude Bernard Lyon 1, 263 p.
- BOUTIN, C. 1993b. Biogéographie historique des Isopodes Cirolanidae stygobies du groupe *Typhlocirolana* dans le Bassin Méditerranéen. C. R. Acad. Sc. Paris 316 (12): 1505-1510.
- BOUTIN, C. 1994a. Phylogeny and biogeography of metacrangonyctid amphipods in North Africa. Hydrobiologia 287: 49-64.
- BOUTIN, C. 1994b. Stygobiology and historical geology: the age of Fuerteventura (Canary Island), as inferred from its present stygofauna. Bull. Soc. géol. France 165(3): 273-285.
- BOUTIN, C. 1997. Stygobiologie et Géologie Historique: l'émersion des terres de Méditerranée orientale datée à partir des Amphipodes Metacrangonyctidae actuels (Micro-crustacés souterrains). Geobios 21: 67-74.
- BOUTIN, C. 1998. Stygobiologie et paléorivages téthysiens entre les bassins crétacés/éocènes du Souss et de Tarfaya (Maroc occidental). Comm. Symposium "Les marges téthysiennes d'Afrique du Nord", Soc. Géol. France, Paris, 16-17 déc. 1997. Abstracts: 68-69.
- BOUTIN, C. & N. COINEAU, 1990. "Regression Model", "Modèle Biphase d'évolution" et origine des micro-organismes interstitiels continentaux. Revue Micropal. 33 (3-4): 303-322.
- BOUTIN, C. & N. COINEAU, 1991. Instabilité des conditions environnementales et vitesse de l'évolution. L'exemple des micro-crustacés souterrains d'origine marine dans les pays méditerranéens. Bull. Inst. Géol. Bassin d'Aquitaine, Bordeaux 50: 63-69.
- BOUTIN, C. & N. COINEAU, 2000. Evolutionary rates and phylogenetic age in some stygobiontic species. In: (H. Wilkens, D.C. Culver & W.F. Humphreys eds.): "Subterranean Ecosystems", Ecosystems of the World, Elsevier, Amsterdam-New York, 30: 433-451.
- CHUBERT, G. & A. FAURE-MURET, 1962. Évolution du domaine atlasique marocain depuis les temps paléozoïques. In "Livre à la mémoire du Professeur Paul Fallot", Mém. H.S. Soc. Géol. France 1: 447-544.
- COINEAU N., 1990. Marqueurs tectoniques, volcaniques, paléoclimatiques, transgressifs et régressifs marins permettant de dater l'ancienneté des espèces, les divergences et les périodes de colonisation du milieu souterrain. Comm. Congr. Intern. Biospéol., Reims, 10-15 sept. 1990.
- COINEAU, N. & C. BOUTIN. 1992. Biological processes in space and time: colonization, evolution and speciation in interstitial stygobionts. In (Camacho A.I., ed.): The Natural History of Biospeleology. Monografias 7, Mus Nac Cie Nat & C.S.I.C. (Madrid): 423-451.
- CULVER, D.C., T.C. KANE & D.W. FONG. 1995. Adaptation and Natural Selection in Caves. The Evolution of *Gammarus minus*. Harvard Univ. Press, Cambridge, 223 p.
- DELAMARE DEBOUTTEVILLE, C. 1957. Lignées marines ayant pénétré dans les eaux souterraines continentales. Un problème de biogéographie actuelle. C.R. somm. Soc. Biogéogr. Paris, 296/297: 53-67.
- DELAMARE DEBOUTTEVILLE, C. 1960. Biologie des eaux souterraines littorales et continentales. Vie Milieu, suppl. 9, 740 p.
- DELAMARE DEBOUTTEVILLE, C. & L. BOTOSANEANU. 1970. Formes primitives vivantes. Hermann, Paris, 232 p.
- DUCASSE, O., L. ROUSSELLE & J.P. PEPOUQUET. 1983. Processes of evolution in marginal-coastal and bathyal ostracods in Paleogene of Aquitaine, France. In: (R.F. Maddocks, ed.): Applications of Ostracoda. Univ. Houston Geosc.: 605-611.
- GINET, R. & V. DECOU. 1977. Initiation à la biologie et à l'écologie souterraines. J.P. Delarge, Paris, 345 p.

- HOLSINGER, J.R. 1986. Zoogeographic patterns of North American subterranean amphipod crustaceans. In: (R.H. Gore & K.L. Heck eds): Crustacean Biogeography. Balkema, Rotterdam: 85-106.
- HOLSINGER, J.R. 1994. Pattern and process in the biogeography of subterranean amphipods. In: Biogeography of subterranean crustaceans: the effect of different scales. Hydrobiologia 287(1): 131-145.
- JEANNEL, R. 1943. Les fossiles vivants des cavernes. In "L'avenir de la science" N.S.(1), Gallimard, Paris, 321 p.
- MESSOULI, M., 1988. Les Crustacés Amphipodes du groupe *Metacrangonyx*: répartition, systématique et phylogénie. Thèse 3^e cycle, Univ. Marrakech, 234 p.
- MESSOULI, M., 1994. Evolution, phylogénie et biogéographie historique des Metacrangonyctidae, Crustacés stygobies du Nord de l'Afrique et des régions voisines. Thèse doctorat d'Etat, Univ. Marrakech (Maroc), 309 p.
- STOCH, F. 1997. *Metacrangonyx ilvanus* n. sp., the first Italian representative of the family Metacrangonyctidae (Crustacea: Amphipoda). Annls Limnol. 33 (4): 255-262.
- STOCK, J.H. 1977. The taxonomy and zoogeography of the Hadziid Amphipoda, with emphasis of West Indian taxa. Studies Fauna Curaçao 177: 1-81.
- STOCK, J.H. 1980. Regression model evolution as exemplified by the genus *Pseudoniphargus* (Amphipoda). Bijdr. Dierk. 50 (1): 105-144.
- STOCK, J.H. 1986. Caribbean biogeography and a biological calendar for geological events. In: (R.H. Gore & K.L. Heck eds): Crustacean Biogeography. Balkema, Rotterdam: 195-203.
- TERMIER, H. & G. 1983. Formes panchroniques ou fossiles vivants ? Bull. Soc. Zool. Fr. 108(4): 534-557.
- VANDEL, A. 1964. Biospéologie. La Biologie des Animaux Cavernicoles. Coll. Intern. Géobiologie, Ecologie, Aménagement, C. Delamare Deboutteville Dir., Gauthier-Villars, Paris, 619 p.